Universidade de São Paulo

Sistemática de *Eugenia* (Myrtaceae, Myrteae): evolução da flor e da inflorescência e implicações taxonômicas

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Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para obtenção de Título de Doutor em Ciências, na Área de Botânica.

Orientador: Prof. Dr. Paulo Takeo Sano

Co-orientadora: Profa. Dra. Evelyn Lucas

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Prof. Dr. Paulo Takeo Sano

Orientador

Dedico à Lena (*in memoriam*), minha querida mãe, que demonstrou vigor espiritual em situações que exigiam debilidade

Quem me dera
um mapa de tesouro
que me leve a um velho baú
cheio de mapas de tesouro

Paulo Leminski

Trecho original: Quarenta clics em
Curitiba, retirado de Toda Poesia

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Índice geral

Resumo

Myrtaceae possui cerca de 4.600-5.800 espécies, distribuídas em áreas tropicais e subtropicais. Myrteae é uma das tribos mais ricas da família, com ca. de 2.500 espécies. Estudos sobre desenvolvimento e evolução de flor em Myrteae têm mostrado a condição homoplástica de caracteres anteriormente considerados diagnósticos, culminando em um melhor entendimento taxonômico. O hiper-diverso gênero *Eugenia*, com ca. de 1.050 espécies, está incluído nessa tribo e tem se mostrado morfologicamente homogêneo. Contudo, gêneros previamente segregados de *Eugenia* pelo grau de fusão do cálice são fontes de controvérsia taxonômica. A filogenia molecular baseada em cinco regiões de DNA reconstruiu que o cálice fundido evoluiu independentemente diversas vezes em *Eugenia*. A investigação morfológica da fusão do cálice revelou cinco padrões de desenvolvimento, além da condição dos lobos livres. Embora os padrões de desenvolvimento sejam homoplásticos, o sinal filogenético indicou que eles podem ser utilizados para complementar caracteres e sustentar clados. O padrão *membranissépalo* é uma exceção, sendo exclusivo e diagnóstico de um clado Amazônico. Espécies tradicionalmente reconhecidas com seis pétalas são interpretadas como padrão *petaloide*, isto é, quatro pétalas são precedidas por duas sépalas internas e petaloides, e duas sépalas externas e fundidas entre si. Padrão *longohipanto* é reconhecido como uma condição extremamente rara em *Eugenia*, em que o hipanto se alonga estende, bem como os verticilos estaminais, resultando em estames curvos no botão em vez de eretos. Mudanças nomenclaturais e uma recircunscrição e revisão taxonômica de *Eugenia* sect. *Schizocalomyrtus* derivam destes resultados. Dez espécies são descritas e comentadas em suas distribuições, sua conservação e taxonomia. A inflorescência de *Eugenia* também é analisada sob uma abordagem integrativa, que revela arranjos previamente ignorados como relevantes para a sistemática e taxonomia. Sete padrões foram descritos, e cinco deles são considerados para uma análise evolutiva. O padrão *auxotélico* foi recuperado em linhagens que primeiro divergiram. Isso sugere que o seu ancestral hipotético é similar ao padrão *auxotélico*. O padrão *fasciculiforme* é amplamente distribuído na seção de maior riqueza, *Eugenia* sect. *Umbellatae*, indicando que altas taxas de diversificação podem estar relacionadas com a aquisição desse padrão. Este estudo também fornece novas hipóteses para a evolução dos arranjos da inflorescência, indicando que flexibilidade no padrão racemoso de ramificação é, provavelmente, a inovação chave que promoveu a diversificação de *Eugenia*.

Abstract

Myrtaceae has about 4600-5800 species distributed in tropical and subtropical areas. Myrteae is one of the most species rich tribe in Myrtaceae with ca. 2500 species. Studies on Myrteae flower development and evolution have shown the homoplastic nature of characters previously considered diagnostic that are now culminating in much-improved taxonomic understanding. The hyper-diverse *Eugenia* with ca. 1050 species is nested in this tribe, and have been shown as morphologically homogeneous. However, genera previously segregated from *Eugenia* by the degree of calyx fusion are source of controversy. Molecular phylogeny based on five DNA regions reconstructed fused calyx as evolved several times independently in *Eugenia*. Morphological assessment of the calyx fusion revealed five development patterns besides the standard condition of the free lobes. Although the development patterns are homoplastic, phylogenetic signal indicates that they can be used in combination to complementary characters to support clades. *Membranisepalous* pattern is an exception, recovered as exclusive allowing to be used to diagnose an Amazonian clade. Traditionally six-petal species are newly interpreted as *petaloid* pattern, i.e. four petals are followed by two internal petal-like sepals, and two external fused sepals. *Longohypanthium* pattern is recognized as an extremely rare condition in *Eugenia* which hypanthium extends as the stamens whorl resulting in a display of curved stamens in the bud instead the standard straight. Nomenclatural changings and a taxonomic revision of *Eugenia* sect. *Schizocalomyrtus* newly circumscribed follow these results. Ten species are detailed described and commented under distribution, conservation, and taxonomy. The inflorescence of *Eugenia* was also analysed under an integrative approach that revealed arrangements previously ignored as relevant for systematic and taxonomy. Seven patterns were described but five are regarded to an evolutionary assessment. *Auxotelic* pattern was recovered in the early lineages. It suggests that a hypothetical ancestral is similar to the *auxotelic* pattern. *Fasciculiform* pattern is widely found in the most speciose *Eugenia* sect. *Umbellatae*, indicating that high rates of diversification may be related to the acquisition of this pattern. This study also provides insights in the evolution of inflorescence arrangement by indicating that flexibility in the racemose branching pattern is likely the innovative key that promoted the diversification of *Eugenia* in the Neotropics.

Introdução Geral

Myrtaceae é uma das maiores famílias de angiospermas, com 132 gêneros e cerca de 5.500 espécies (WCSP 2017), ocupando a terceira posição como a família arbórea com maior riqueza de espécies (Beech *et al.* 2017). Myrtaceae é distribuída principalmente nas regiões tropicais e subtropicais, com centros de diversidade na Austrália, sudeste da Ásia e América tropical (Wilson *et al.* 2001). Myrtaceae pode ser reconhecida pelas folhas aromáticas, bem como demais estruturas vegetativas e reprodutivas, com numerosas glândulas de óleos essenciais; flores polistêmones com ovário epígeno, geralmente actinomorfas, e tronco com ritidoma esfoliante (Wilson 2011).

Myrtaceae era tradicionalmente dividida em duas subfamílias, segundo características do fruto. Espécies principalmente paleotropicais com frutos secos e deiscentes pertenciam à Leptospermoideae, dividida em três tribos; enquanto espécies principalmente distribuídas em regiões tropicais, com frutos carnosos e indeiscentes, compreendiam Myrtoideae, com apenas uma tribo, Myrteae (Niedenzu 1893). O primeiro indício de inconsistência dessa classificação surgiu por meio de uma análise cladística construída com dados morfológicos (Briggs & Johnson 1979). Análises filogenéticas baseadas em dados moleculares reforçaram a necessidade de uma nova circunscrição infrafamiliar. Uma nova classificação foi amplamente adotada, dividindo Myrtaceae nas subfamílias Psiloxyloideae, com apenas duas tribos, e Myrtoideae com 15 tribos, dentre elas, Myrteae (Wilson *et al.* 2001, 2005).

A tribo Myrteae

Myrteae é a maior tribo de Myrtaceae em riqueza, com cerca de 2.500 espécies, bem como em número de gêneros (51 gêneros), o que representa aproximadamente metade da diversidade de Myrtaceae (Vasconcelos *et al.* 2017b; Wilson 2011). Myrteae é majoritariamente tropical, com cerca de 80% de sua diversidade na região Neotropical (WCSP 2017). Tradicionalmente, Myrteae era dividida em três subtribos (Eugeniinae O.Berg, Myrciinae O.Berg e Myrtinae O.Berg) segundo aspectos do embrião (Berg 1856, 1857). Reconstruções filogenéticas com base em dados moleculares sugeriram o abandono dessa classificação, considerando a condição homoplástica relativa ao tipo dos embriões (Lucas *et al.* 2005, 2007). Incluindo 46 de um total de 51 gêneros, a mais representativa filogenia molecular de Myrteae recuperou 10 grupos informais (Vasconcelos *et al.* 2017b) que serão formalizados em breve dentro de uma nova classificação para a tribo (Vasconcelos *et al.* em prep.). A filogenia de Myrteae trouxe um grande avanço para o entendimento das relações supragenéricas. Contudo, a datação da filogenia foi um dos maiores desafios enfrentados, devido à escassez de fósseis confiáveis. Nesse contexto, microfósseis (principalmente pólen) foram avaliados como mais parcimoniosos para datar a filogenia de Myrteae em relação aos macrofósseis. Com isso, a linhagem que originou Myrteae possivelmente surgiu há cerca de 60 Ma. e começou a diversificar por volta de 40 Ma. (Vasconcelos *et al.* 2017b).

Diversidade e aspectos morfológicos

Eugenia P.Micheli ex Linnaeus foi recuperado pela filogenia da tribo Myrteae (Vasconcelos *et al.* 2017b), bem como por outras filogenias (Bünger *et al.* 2016; Faria 2014; Mazine *et al.* 2014), com alto suporte estatístico. *Eugenia* tem distribuição pantropical e compreende cerca de 1.050 espécies, principalmente encontradas na região Neotropical (Mazine *et al.* 2014; Wilson 2011), o que compreende metade da diversidade da tribo Myrteae. *Eugenia* também figura dentre os gêneros arbóreos do mundo de maior riqueza, ocupando a segunda colocação, atrás apenas de outra Myrtaceae, *Syzigium* Yehns (Beech *et al.* 2017). Além disso, *Eugenia* é o gênero mais rico no Brasil, com cerca de 390 espécies, e um dos maiores em número de espécies endêmicas (BGF 2015). As espécies estão principalmente distribuídas na costa leste Atlântica (Flora do Brasil 2020), o que permite afirmar que seu centro de diversidade encontra-se na Floresta Atlântica, onde *Eugenia* é ecologicamente importante, sendo frequentemente o gênero arbóreo dominante (Oliveira-Filho & Fontes 2000). Tais características fazem de *Eugenia* um excelente modelo tanto para avaliação do estado de conservação da Floresta Atlântica (Rigueira *et al.* 2013), como para estudos evolutivos na região Neotropical (Lucas & Bünger 2015).

Por um lado, a elevada diversidade de *Eugenia* é marcante; por outro, a relativa homogeneidade morfológica de flores e frutos é uma dificuldade recorrente para o reconhecimento das espécies. Isso se reflete na tradicional classificação de *Eugenia*: nela, caracteres marcantes da inflorescência e da flor foram utilizados para embasar classificações infragenéricas e, até mesmo, servir de justificativa para segregação de gêneros (Berg 1857; Kiaerskou 1893; Niedenzu 1893). *Calycorectes* O.Berg e *Schizocalyx* O.Berg foram reconhecidos por Berg (1856) basicamente pelo botão com lobos do cálice fundidos, que se rasgam durante a antese. Outras características morfológicas que sugeriam relação com *Eugenia* foram ignoradas e *Calycorectes* foi reconhecido como um gênero à parte por mais de um século, embora a ampla variação no grau de fusão dos lobos do cálice tornasse sua delimitação taxonômica inconsistente, motivando o recorrente questionamento de sua circunscrição (Landrum & Kawasaki 1997; McVaugh 1969; Sobral 2003). A tal panorama, foram somadas evidências moleculares (Bünger *et al.* 2016; Faria 2014; Mazine *et al.* 2014) cujas hipóteses filogenéticas também sugeriram a inclusão de *Calycorectes* em *Eugenia.* Duas espécies de *Calycorectes* (atualmente *Eugenia brevistyla* D.Legrand e *E. subterminalis* DC.) foram amostradas em uma filogenia molecular ainda com dados preliminares (Mazine *et al.* 2014), que demonstrou que o evento de fusão do cálice surgiu apenas uma vez em *Eugenia*. Este clado, com alto suporte estatístico, foi mais tarde reconhecido como *Eugenia* sect. *Calycorectes* (Mazine *et al.* 2016). Contudo, nenhuma das análises incluiu a espécie-tipo, *Calycorectes grandifolius* O.Berg, procedente do Escudo das Guianas (Amshoff 1951). Além disso, a documentação de eventos de paralelismo no desenvolvimento de flores de *Myrcia s.l.* (Vasconcelos *et al.* 2017a) tem levantado dúvidas quanto a um cenário evolutivo de que o cálice fundido em *Eugenia* tenha surgido apenas uma vez.

Inflorescência de Eugenia

Aspectos arquiteturais da inflorescência foram tradicionalmente utilizados para classificação infragenérica de *Eugenia* (Berg 1856), bem como para segregar gêneros como *Stenocalyx* O.Berg. Nenhum estudo sobre arquitetura de inflorescência em Myrtaceae excedia a esfera taxonômica, exceto por uma análise com base no arranjo final da inflorescência de Myrtaceae sob uma ótica evolutiva realizada por Briggs & Johnson (1979). Se, por um lado, tal trabalho resultou na análise de uma gama de arranjos e foi um marco para os estudos de inflorescência em Myrtaceae; por outro lado, a especificidade e a complexidade da terminologia utilizada, bem como suas frequentes exceções, desfavoreceram sua adoção por parte dos estudiosos da família. Desde então, nenhum estudo tratando de inflorescência em Myrtaceae sob uma ótica evolutiva foi realizado. É neste cenário que se desenvolve o trabalho desta tese de doutorado.

Bibliografia

Amshoff, G.J.H. (1951) Myrtaceae. In: A. Pulle (Ed), *Flora of Suriname*. The Royal Institute for the Indies, Utrecht, pp. 56–158.

Beech, E., Rivers, M., Oldfield, S. & Smith, P.P. (2017) GlobalTreeSearch: The first complete global database of tree species and country distributions. *Journal of Sustainable Forestry* 36(5): 454–489.

Berg, O. (1856) Revisio Myrtacearum Americae D. F. L. Von Schlenchtendal (Ed). *Linnaea* 27: 1–799.

Berg, O.C. (1857) Myrtaceae I C. F. P. de Martius (Ed). *Flora Brasiliensis* 14(1): 1–468.

BGF (2015) Growing knowledge: An overview of Seed Plant diversity in Brazil. *Rodriguésia* 66(4): 1085–1113.

Briggs, B.G. & Johnson, L.A.S. (1979) Evolution in the Myrtaceae - Evidence from inflorescence structure. *Proceedings of The Linnean Society of New South Wales* 102: 157–256.

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. *Annals of Botany* 118: 1209–1223.

Faria, J.E.Q. (2014) Revisão taxonômica e filogenia de *Eugenia* sect. *Pilothecium* (Kiaersk.) D.Legrand (Myrtaceae). Tese de Doutorado. Universidade de Brasília

Flora do Brasil 2020 (em andamento). *Projeto Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil*. Disponível em: http://floradobrasil.jbrj.gov.br (acesso em 24 julho 2017).

Kiaerskou, H. (1893) Enumeratio Myrtacearum Brasiliensium. In: E. Warming (Ed), *Symbolarum ad floram Brasiliae Centralis cognoscendam*, pp. 200.

Landrum, L.R. & Kawasaki, M.L. (1997) The Genera of Myrtaceae in Brazil: An Illustrated Synoptic Treatment and Identification Keys. *Brittonia* 49(4): 508.

Lucas, E.J., Belsham, S.R., Nic Lughadha, E.M., Orlovich, D. a., Sakuragui, C.M., Chase, M.W. & Wilson, P.G. (2005) Phylogenetic patterns in the fleshy-fruited Myrtaceae - Preliminary molecular evidence. *Plant Systematics and Evolution* 251(1): 35–51.

Lucas, E.J. & Bünger, M.O. (2015) Myrtaceae in the Atlantic forest: their role as a ‘model’ group. *Biodiversity and Conservation* 24(9): 2165–2180.

Lucas, E.J., Harris, S.A., Mazine, F.F., Belsham, S.R., Nic Lughadha, E.M., Telford, A., Gasson, P.E. & Chase, M.W. (2007) Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* 56(4): 1105–1128.

Mazine, F.F., Bünger, M.O., Faria, J.E.Q., Lucas, E. & Souza, V.C. (2016) Sections in *Eugenia* (Myrteae, Myrtaceae): nomenclatural notes and a key. *Phytotaxa* 289(3):

225–236.

Mazine, F.F., Souza, V.C., Sobral, M., Forest, F. & Lucas, E. (2014) A preliminary phylogenetic analysis of *Eugenia* (Myrtaceae: Myrteae), with a focus on Neotropical species. *Kew Bulletin* 69(2): 1–14.

McVaugh, R. (1969) The Botany of the Guyana Highland - Part VIII: Myrtaceae. *Memoirs of the New York Botanical Garden* 18(2): 55–286.

Niedenzu, F. (1893) Myrtaceae. In: A. Engler and K. Prantl (Eds), *Die Natürlichen Pflanzenfamilien*, pp. 57–105.

Oliveira-Filho, A. & Fontes, M. (2000) Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate. *Biotropica* 32(March 1999): 793–810.

Rigueira, D.M.G., da Rocha, P.L.B. & Mariano-Neto, E. (2013) Forest cover, extinction thresholds and time lags in woody plants (Myrtaceae) in the Brazilian Atlantic Forest: Resources for conservation. *Biodiversity and Conservation* 22(147): 3141–3163.

Sobral, M. (2003) *A família Myrtaceae no Rio Grande do Sul*. Editora Unisinos, São Leopoldo.

Vasconcelos, T.N.C., Prenner, G., Santos, M.F., Wingler, A. & Lucas, E.J. (2017a) Links between parallel evolution and systematic complexity in angiosperms — A case study of floral development in *Myrcia* s. l. (Myrtaceae). *Perspectives in Plant Ecology, Evolution and Systematics* 24: 11–24.

Vasconcelos, T.N.C., Proença, C.E.B., Ahmad, B., Aguilar, D.S., Aguilar, R., Amorim, B.S., Campbell, K., Costa, I.R., De-carvalho, P.S., Faria, J.E.Q., Giaretta, A., Kooij, P.W., Lima, D.F., Mazine, F.F., Peguero, B., Prenner, G., Santos, M.F., Soewarto, J., Wingler, A. & Lucas, E.J. (2017b) Myrteae phylogeny, calibration, biogeography and diversification patterns: Increased understanding in the most species rich tribe of Myrtaceae. *Molecular Phylogenetics and Evolution* 109: 113–137.

WCSP (2017) World Checklist of Selected Plant Families. *Facilitated by the Royal Botanic Gardens, Kew*. Disponível em: apps.kew.org/wcsp/myrtaceae (acesso em 26 Julho 2017).

Wilson, P.G. (2011) Myrtaceae. In: K. Kubitzki (Ed), *The families and genera of vascular plants. Flowering plants, eudicots: Sapindales, Cucurbitales, Myrtaceae*. Springer-Verlag, Berlin, pp. 436.

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 Systematics and Evolution* 251(1): 3–19.

Wilson, P.G., O´Brien, M.M., Gadek, P.A. & Quinn, C.J. (2001) Myrtaceae Revisited : a Reassessment of infrafamilial groups. *American journal of botany* 88(11): 2013–2025.

Capítulo 1

Chapter 1

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PHYLOGENETIC PLACEMENT OF NEW SPECIES WITH FUSED CALYX REVEALS HOMOPLASTIC CHARACTER IN *EUGENIA* (MYRTACEAE)

Abstract—*Eugenia petaloidea*, a new species of calyx fused is here described, illustrated, a distribution map is provided, assessed according to IUCN criteria, and phylogenetically positioned into the genus. The phylogeny provided first evidence for the homoplasy of the fused calyx in Eugenia. Eugenia petaloidea can be distinguished from other Eugenia species by the closed calyx in the bud that splits into two external lobes in the bud, with two internal petaloid calyx lobes differentiated by the relative position of the petal between sepals, glabrous hypanthium outside, and fruits with two persistent external sepal lobes.

Keywords— Atlantic forest, homoplasy, Myrteae, northeastern Brazil, parallelism.

Myrtaceae has about 4600-5800 species (Nic Lughadha and Snow 2000; WCSP 2017) widespread on all continents except Antarctica but is most commonly distributed in tropical and subtropical areas (Wilson 2011). Myrteae is one of the most species rich tribe in Myrtaceae with c. 2500 species where the hyper-diverse *Eugenia* P.Micheli ex L. is nested. The high diversity of *Eugenia* with c. 1050 species (Mazine et al. 2016), i.e. almost half of the all Myrteae species and its ubiquity in most tropical biomes, makes it an appropriate model for evolutionary studies in the Neotropics (Biffin et al. 2010; Lucas and Bünger 2015).

The forests of the Eastern coast of Brazil support c. 250 *Eugenia* species of which more than 200 are endemic (Flora do Brasil 2020); the assumption is that these Atlantic forests are a center of *Eugenia* species diversity where it is ecologically important and often dominant tree genus (Oliveira-Filho and Fontes 2000). High species diversity contrasts however, with the relative morphological homogeneity of flowers and fruits. As a result, suites of character are commonly used by taxonomists to accurately recognize genera rather than relying on single diagnostic characters (see Landrum and Kawasaki 1997; Vasconcelos et al. 2017).

Studies on Myrteae flower development and evolution have shown the homoplastic nature of characters previously considered diagnostic (Vasconcelos et al. 2015; Vasconcelos et al. 2017). As consequence, systematics is now culminating in much-improved taxonomic understanding (e.g. Lucas and Sobral 2011, A.R.L Lourenço pers. com.). These trends are also consonant with current phylogenetic *versus* morphological assessment that indicate that *Eugenia* taxonomy is even more variable than previously assumed (Giaretta et al. Chapter 2). Indeed, current understanding of

Eugenia is focused on reassessment of morphological boundaries resulting in the merging of groups traditionally segregated by one or few characters (see Mazine et al. 2016).

Calycorectes O.Berg, traditionally segregated from but currently treated under *Eugenia* (Flora do Brasil 2020), fits the morphological delimitation of the latter except in its calyx lobes that are fused in the bud and tear at anthesis (Berg 1856). Phylogenetic reconstruction (Mazine et al. 2014) demonstrated a single evolutionary event of calyx fusion in *Eugenia* in the well-supported 'clade 7'. An alternative pattern of calyx fusion in *Eugenia* is here reported and is included in a molecular phylogenetic framework to assess the consistency of the fused calyx in the evolution of *Eugenia*. A new species demonstrating this calyx fusion is here described, illustrated including line drawing, photographs of habitat as well as a distribution map.

MATERIAL AND METHODS

Taxonomy—Material was processed according to Fidalgo and Bononi (1984), incorporated to the UFP collection and duplicates sent to JPB, K, NY, RB, SPF (acronyms follow Thiers 2017). The description was based on dried and hydrated material and illustrations were based on dried material as well as photographs of fresh material. The distribution map was produced using QGIS (2017).

Molecular survey**—**A *Eugenia* sample was selected according to DNA sequence data that was both available and appropriate. The ETS and the ITS of the ribosomal DNA (rDNA) and plastid spacer *psbA-trnH*, used to phylogenetic reconstruction, were extracted from the GenBank (Benson et al. 2013). The total sample of 60 terminals includes species from all known *Eugenia* clades (sensu Mazine et al. 2014) that correspond to taxonomic sections within *Eugenia* (Mazine et al. 2016), and an outgroup. The outgroup includes species of the Australasian, *Eugenia*, *Myrcia*, and *Pimenta* groups within (Lucas et al. in prep.). This phylogenetic framework was designed to ensure maximally reliable placement of the species here described.

Extraction and sequencing**—**Approximately 0.2 mg of leaf tissue dried in silica-gel was used for extraction from five samples of the focused species. DNA extractions followed the CTAB protocol (Doyle and Doyle 1987). Amplification and purification of target DNA regions was performed following the protocol of Lucas et al. (2007) and Bünger et al. (2016). Amplified products were sent for sequencing at LABCEN/CCB at the Universidade Federal de Pernambuco, Brazil. Each locus was aligned separately using Muscle (Edgar 2004) implemented in Geneious version 7.1.9. (Kearse et al. 2012).

Phylogenetic analysis—The two nuclear regions were combined in a nuclear dataset (ncDNA). Thus, the phylogenetic analysis is based on two partitions: ncDNA and chloroplast. The evolutionary models that best fit each partition were chosen using JModelTest 2 (Darriba et al. 2012). The best model for both the ncDNA and chloroplast partition was GTR+G+I. These models were used in conjunction with the respective datasets to run two independent Bayesian Inference (BI) analysis using MrBayes (Ronquist et al. 2012) on XSEDE version 3.2.6 executed at the CIPRES gateway (Miller et al. 2010). Each analysis consists of two independent runs of 12.000.000 generations sampling every 1000 trees with a burn-in of 10%. Output was examined using Tracer version 1.6 (Drummond and Rambaut 2007) to confirm all chains had converged. Visual comparison of resulting topologies revealed no significant incongruence in the phylogenies, supporting combination of the ncDNA and chloroplast partition. This combined partition was subject to independent Maximum Likelihood (ML) and BI analysis to compare topology and nodes support (bootstrap vs. posterior probabilities). ML was run in RAxML-HPC2 (Stamatakis 2006), also implemented in CIPRES.

RESULTS

The ETS alignment data set included 59 taxa and was 451 bp long, the ITS alignment data set included 57 taxa and was 797 bp long, and the *psb*A-*trn*H included 58 taxa and was 621 bp long. The combined (ETS + ITS + *psbA-trnH*) aligned data matrix resulted in 1869 characters (Tab. 1). Trees obtained from ML and BI analyses were highly congruent, therefore only the topology of BI is discussed here (Fig. 1). Branch support values obtained from ML and posterior probabilities on BI analyses are indicated in Fig. 1.

TAB. 1. Summary of the molecular partitions used to run Bayesian inference.

	ETS	**ITS**	***psb*A-*trn*H**	**Nuclear datasets**	**All data combined**
No. of taxa	59	57	58	60	60
Aligned length (bp)	451	797	621	1.248	1.869
Conserved characters	201 (44.5%)	445 (55.8%)	326 (52.4%)	646 (51.7%)	972 (52.0%)
Variable characters	240 (53.2%)	328 (41.1%)	211 (33.9%)	568 (45.5%)	779 (41.6%)
Substitution model	GTR+I+G	GTR+I+G	GTR+I+G		

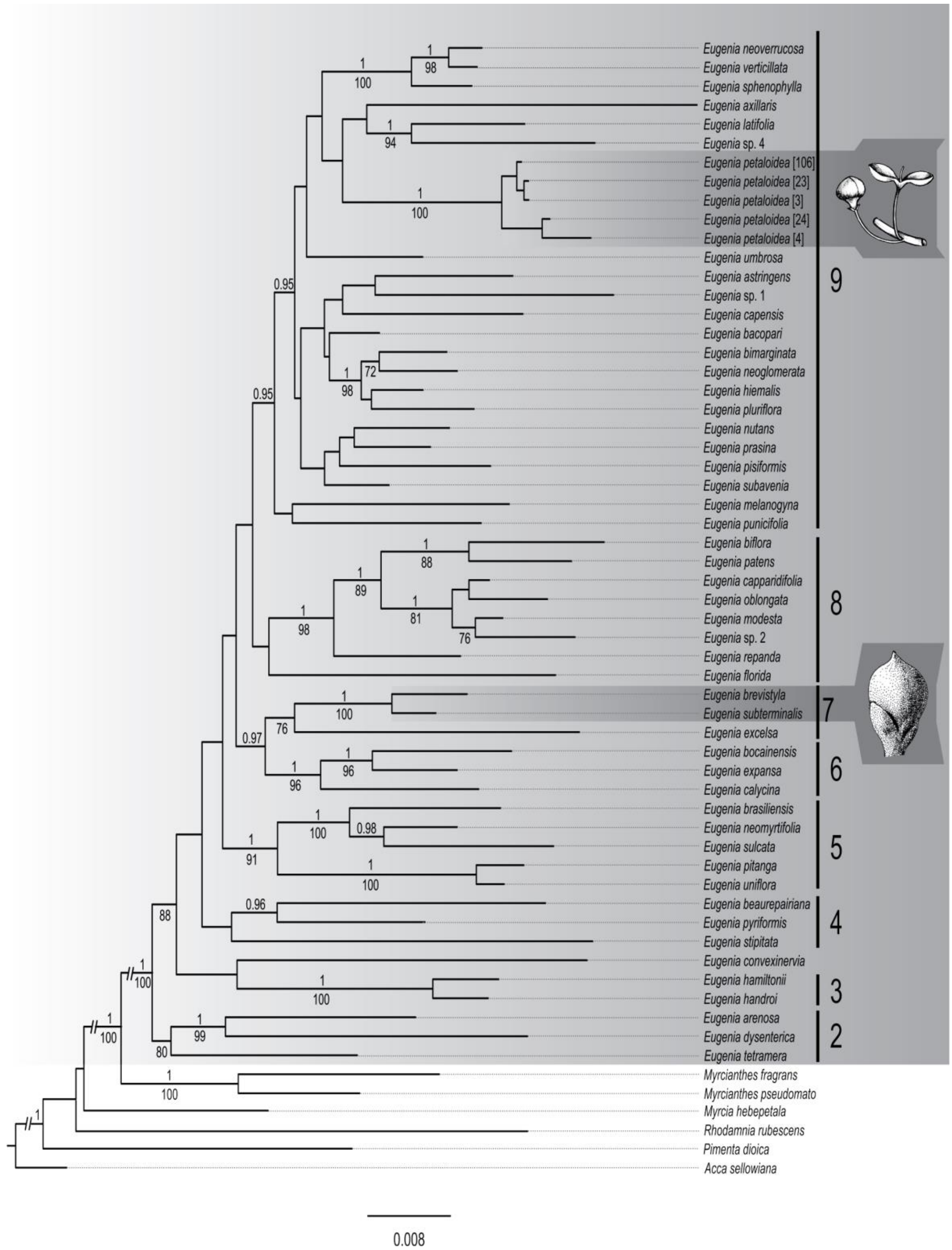

FIG. 1. Majority rule consensus tree resulting from Bayesian inference analysis of the ETS, ITS and *psb*A-*trn*H regions. Clades from Mazine et al. (2014) are indicated by the numbers 2–8. Clades with calyx lobes fused in bud are highlighted. Values above branches are posterior probabilities (PP) and values below the branches are bootstrap percentages (BS).

Eugenia was recovered as monophyletic with high support (bootstrap\BS 100; posterior probabilities\PP 1) and sister to *Myrcianthes* O.Berg (BS 100; PP 1). Within *Eugenia*, all eight clades proposed by Mazine et al. (2014) were recovered. *Myrcianthes*, sister group of *Eugenia*, has free calyx lobes, therefore, it is assumed that this character state is the ancestral condition in *Eugenia*. Currently, most clades of *Eugenia* are recognized as having free calyx lobes except for 'clade 7' that has species with calyx lobes fused in the bud (Mazine et al. 2014). *Eugenia* sect. *Calycorectes* (O.Berg) Mattos was assigned to 'clade 7' by Mazine et al. (2016) as its calyx is totally or partially closed, tearing open at anthesis. However, *Eugenia petaloidea* has fused calyx lobes in the bud and emerges within *Eugenia* sect. *Umbellatae* O.Berg (clade 9 sensu Mazine et al. 2014). The phylogenetic relationship presented here provides first evidence for the homoplasy of the fused calyx in *Eugenia* as it appears at least twice over the evolution of the genus. Furthermore, *Eugenia petaloidea* and species from 'clade 7' (*E. brevistyla* D.Legrand and *E. subterminalis* DC.) share fused calyces that tear at anthesis but differ in the consistently four calyx lobes, fused in the latter pair of species. It seems that there are at least two types of calyx fusion in *Eugenia*. Future studies should be focused on calyx fusion in *Eugenia* to carefully investigate and reassess its systematic relevance.

TAXONOMIC TREATMENT

EUGENIA PETALOIDEA Giaretta & B.S. Amorim, sp. nov.—TYPE: BRAZIL. Pernambuco: Municipality of Jaqueira, Reserva Particular do Patrimônio Natural Frei Caneca, Mata do Quengo, 650–750 m elev., 08º42'41"S, 35º50'31"W, 30 Jan 2013 (fl.), *B.S. Amorim 1765, J.L. Costa-Lima, D. A. Araújo, S.N. Moreira & M.A. Chagas* (holotype: UFP!; isotypes: JPB!, K!, NY!, RB!, SPF!).

Eugenia petaloidea is morphologically similar to *Calycorectes batavorum* McVaugh (1969) but can be segregated by the leaves with a cuneate base (vs. obtuse), 6–8 pairs of lateral veins (vs. 10 pairs), glabrous hypanthium (vs. dense-pubescent), and glabrous staminal ring (vs. pubescent).

Shrub to treelet to 4 m; young stems glabrous or covered by scattered simple white trichomes. **Leaves** arrangement decussate; petiole 5–7 mm long, sulcate adaxially, glabrous; leaves blade elliptic or lanceolate, 9.5–16×3–6.5 cm, membranaceous with appressed simple hairs abaxially (more evident when young) and scattered simple hairs adaxially; gland dots less than 0.2 mm in diameter, 3-6 per square millimeter, darker abaxially; base cuneate; apex acute; midvein flat and glabrous on the upper surface, raised with scattered hairs on the lower surface; lateral veins prominent abaxially, 6–8 pairs; marginal vein 4–5 mm from the margin, intra-marginal vein c. 1 mm from the margin. **Inflorescences** fasciculiform, axillary, the main-axis 2 mm long, with 1–3 pairs of flowers; bracts lanceolate, scattered trichomes adaxially, 1 × 2 mm, deciduous in fruit; pedicels 8–15 mm long, appressed simple trichomes; bracteoles lanceolate, 1 × 1 mm, glabrous, persistent after anthesis but deciduous in fruit. **Flowers** hypanthium glabrous; bud completely closed, opening by regular splitting of the two external sepal lobes, 3–4 × 5–6 mm, rounded, concave, persistent, appressed scattered trichomes on the external surface, green but reddish when dried, two internal lobes free, 7–8 × 6–7 mm, ovate, petaloide, white, slightly concave, deciduous after anthesis, glabrous; petals-4, 7–8 × 5–6 mm, ovate, white, convex, glabrous; stamens c. 200, filaments 3–4 mm long, glabrous, anthers c. 2 mm long, ellipsoid; staminal ring 2–3 mm diameter, circular, glabrous; ovary bilocular, internally glabrous; style to 11 mm long, glabrous, stigma punctiform. **Fruits** 16–23 × 12–13 mm, ellipsoid, greenish when immature, crowned by the two persistent external calyx lobes, surface glandular; 1 seed per fruit, 14–21 × 1–11 mm, ellipsoid; cotyledons fused, hypocotyl not evident. Figures 2–4.

Geographic Distribution and Ecology**—***Eugenia petaloidea* is restricted to submontane forest (up to 700 m high) of Pernambuco state in the northern portion of the Atlantic Forest (Fig. 2). This area is known for its high species richness (Pessoa and Alves 2015a; Melo et al. 2016) and several endemic species recently described (Sothers 2003; Amorim and Alves 2012; Costa-Lima and Alves 2013; Amorim and Alves 2015; Pessoa and Alves 2015b; Zelenski et al. 2016). *Eugenia petaloidea* is part of the sub-canopy community and has often been collected growing in the same vicinity as *Eugenia culicina* Sobral, *E. submontana* B.S.Amorim, *Myrcia amplexicaulis* (Vell.) Hook. f. (Myrtaceae), *Chusquea bahiana* L.G.Clark. (Poaceae), *Quiina cruegeriana* Griseb. (Quiinaceae), *Daphnopsis racemose* Griseb. (Thymelaeaceae) and *Paypayrola blanchetiana* Tul. (Violaceae).

Etymology**—**The epithet "*petaloidea*" refers to the two internal petaloid calyx lobes that are a diagnostic character for this species.

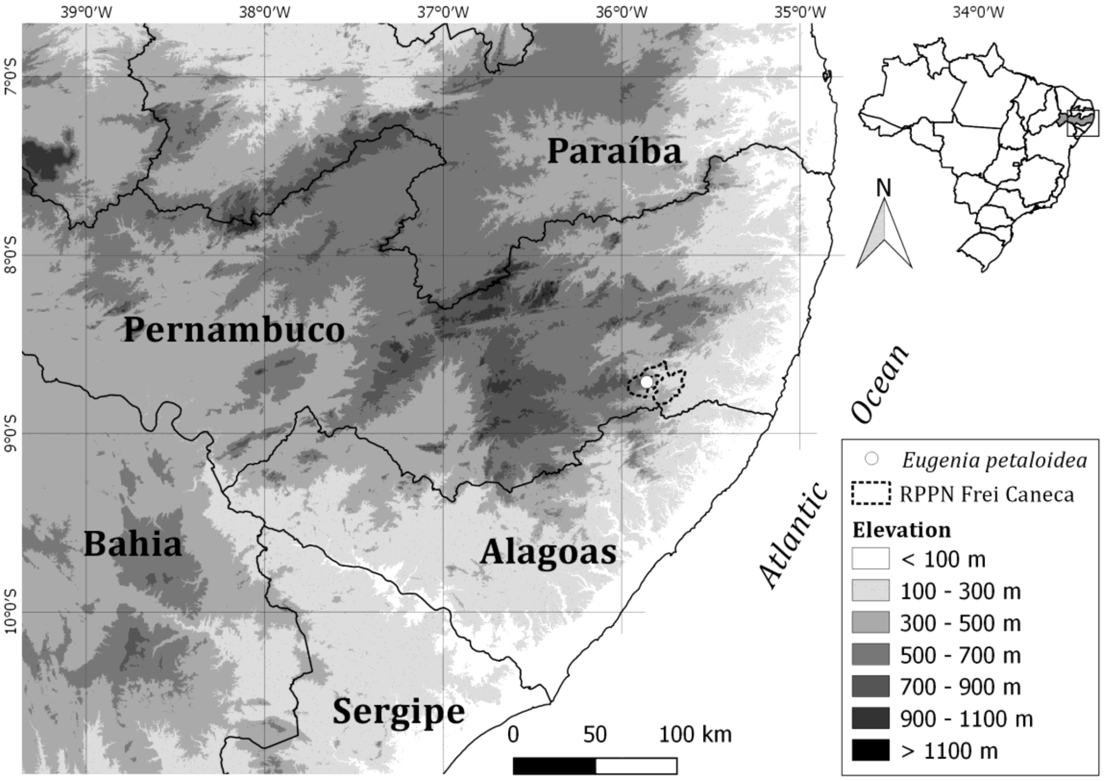

FIG. 2. Geographic distribution of *Eugenia petaloidea* Giaretta *&* B.S. Amorim in the state of Pernambuco. (RPPN – Reserva Particular do Patrimônio Natural).

Phenology*—*Eugenia petaloidea has been collected flowering from January to April and fruiting from April to May.

***Conservation Status*—**The species is currently known from remnants of submontane Atlantic Forest with the known population occurring in forest fragments of ca. 360 ha. The species meets the criteria of Vulnerable (VU) due to its restricted population D2 (IUCN 2001; IUCN 2016). There may be other populations in areas of submontane forests close to the type locality, but they are not presently known.

***Taxonomic notes*—**Flower of *Eugenia petaloidea* appear to have only two sepals and six petals in contrast to the normal *Eugenia* arrangement of four-sepals and four-petals. However, Myrtaceae flower development studies have highlighted the consistent position of a petal located between each pair of sepals, in tribe Myrteae (Belsham and Orlovich 2002; Belsham and Orlovich 2003). Perianth position is a good diagnostic character for *Eugenia petaloidea*, supported by thicker internal sepals (S2; Fig. 4C, D). This calyx type may be found in other 'six-petaled' *Eugenia* species. This latter condition is rare in *Eugenia*, first described for the type species of *Calycorectes* (*C. grandifolius* O.Berg, currently *Eugenia neograndifolia* Mattos). Although other species share this rare condition (e.g. *Calycorectes batavorum* McVaugh and *C. enormis* McVaugh, respectively currently under *Eugenia batavora* (McVaugh) Mattos and *E. enormis* (McVaugh) Mattos), there is no evidence that they are closely related. *Eugenia petaloidea* can be distinguished from other *Eugenia* species by the closed calyx in the bud that splits into two external lobes in the bud, with two internal petaloid calyx lobes differentiated by the relative position of the petal between sepals and their thicker texture relative to the sepals, glabrous hypanthium outside, and fruits with two persistent external sepal lobes instead four persistent lobes as the standard condition found in *Eugenia* (Figs. 3, 4).

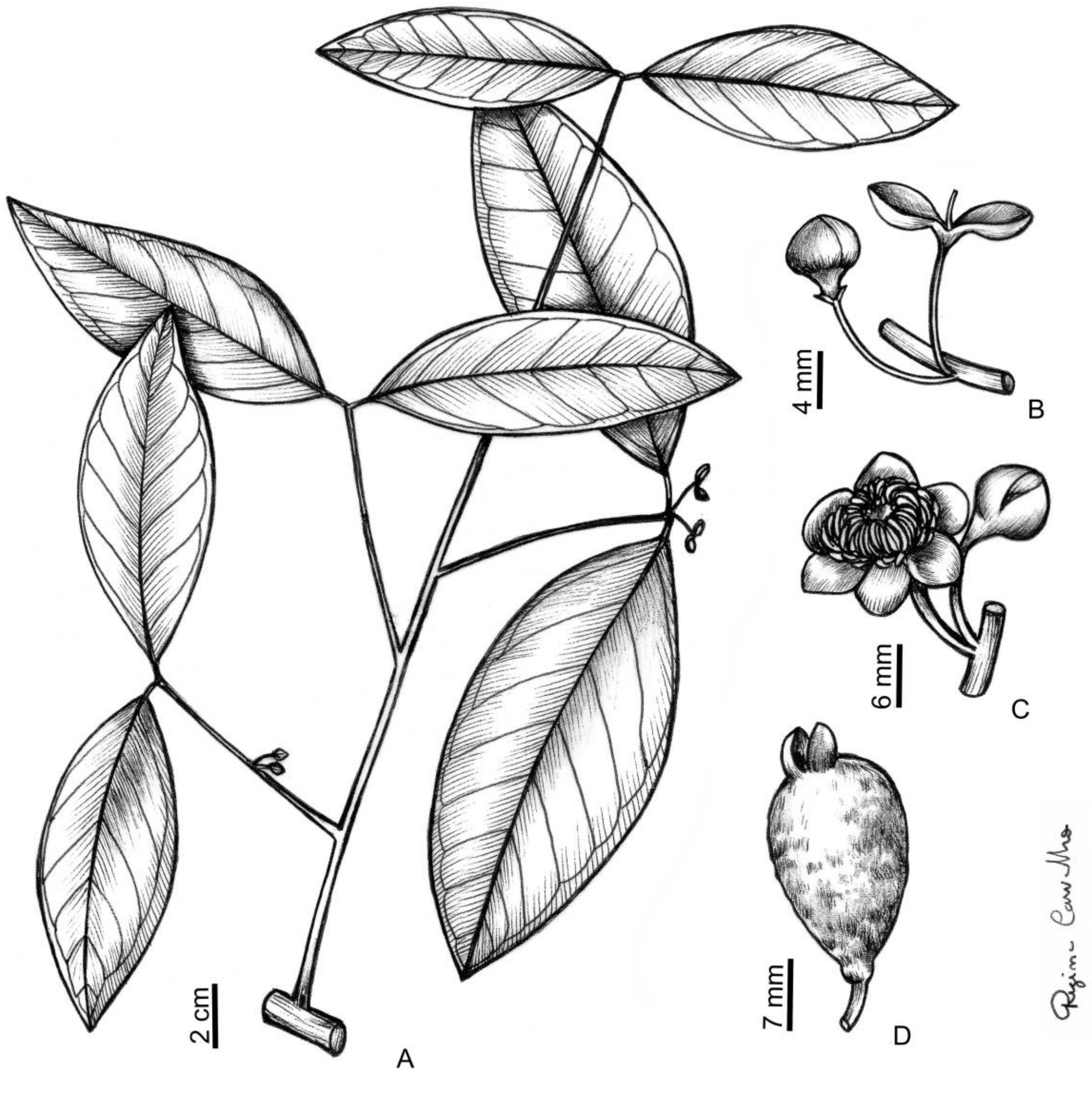

FIG. 3. *Eugenia petaloidea* Giaretta & B.S.Amorim. A. Flowering branch. B. Detail of flower bud and external sepals. C. Detail of flower. D. Detail of fruit crowned by the two persistent external calyx lobes. (A, B and C from the holotype *B.S. Amorim 1765 et al.*, D from *B.S. Amorim 1836 et al.*).

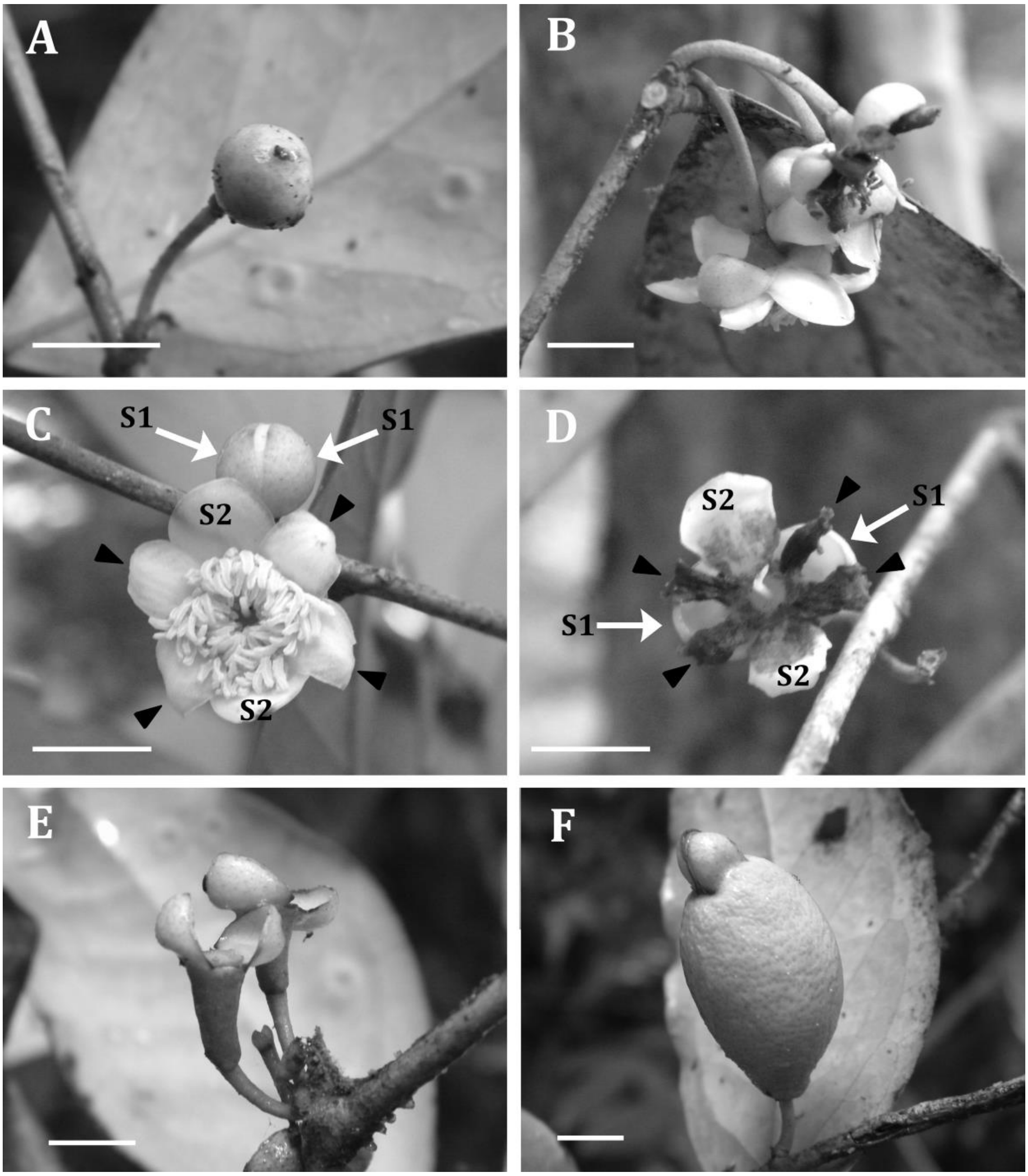

FIG. 4. *Eugenia petaloidea* Giaretta & B.S.Amorim. A. Flower bud. B. Flowers at anthesis. C. Flower at anthesis and a pre-anthetic flower bud. D. Flower with senescent petals. E. Young fruit. F. Immature fruit crowned by the calyx (A–E from the holotype *B.S. Amorim 1765 et al.*; F from the *B.S. Amorim 1836 et al.* – photos by B.S. Amorim). S1. External sepal. S2. Internal sepal. Black triangles indicate the petals. Scale bars 5 mm.

Additional Specimens Examined—BRAZIL. Pernambuco: Municipality of Jaqueira, Reserva do Patrimônio Natural Frei Caneca, Mata do Quengo, 08º42'41"S, 35º50'310"W, 650–750 m alt., 30 Apr. 2013 (fr.), *B.S. Amorim, A. Melo & M.A. Chagas 1835* (UFP); *Ibid.*, 30 Apr. 2013 (fr.), *B.S. Amorim, A. Melo & M.A. Chagas 1836* (UFP); *Ibid.*, 28 Apr. 2014 (fr.), *B.S. Amorim 1987, J.R. Maciel, D. Cavalcanti & A. Melo* (UFP).

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LITERATURE CITED

Amorim, B.S. and M. Alves. 2012. A New Species of *Eugenia* (Myrteae, Myrtaceae) from the Brazilian Atlantic Forest. *Systematic Botany* 37:694–698. doi: 10.1600/036364412X648661

Amorim, B.S. and M. Alves. 2015. *Eugenia submontana* (Myrteae, Myrtaceae), a new species from the Atlantic Forest of northeastern Brazil and notes on *Eugenia culicina*. *Phytotaxa* 208:209–216. doi: 10.11646/phytotaxa.208.3.3

Belsham, S.R. and D.A. Orlovich. 2002. Development of the hypanthium and androecium in New Zealand Myrtoideae (Myrtaceae). *New Zealand Journal of Botany* 40:687–695. doi: 10.1080/0028825X.2003.9512836

Belsham, S.R. and D.A. Orlovich. 2003. Development of the hypanthium and androecium in *Acmena smithii* and *Syzygium australe* (*Acmena* alliance, Myrtaceae). *Australian Systematic Botany* 16:621–628. doi: 10.1071/SB02036

Benson, D.A., M. Cavanaugh, K. Clark, I. Karsch-Mizrachi, D.J. Lipman, J. Ostell, and E.W. Sayers. 2013. GenBank. *Nucleic Acids Research* 41:36–42. doi: 10.1093/nar/gks1195

Berg, O.C. 1856. Revisio Myrtacearum huc usque cognitarum s. Klotzschii “Flora Americae aequinoctialis” exhibens Myrtaceas. *Linnaea* 27:129–384.

Biffin, E., E.J. Lucas, L.A. Craven, I.R.da Costa, M.G. Harrington, and M.D. Crisp. 2010. Evolution of exceptional species richness among lineages of fleshy-fruited Myrtaceae. *Annals of Botany* 106:79–93. doi: 10.1093/aob/mcq088

Bünger, M.O., F.F. Mazine, F. Forest, M.L. Bueno, R. Stehmann, and E.J. Lucas.2016.

The evolutionary history of *Eugenia* sect. *Phyllocalyx* (Myrtaceae) corroborates historically stable areas in the southern Atlantic forests. Annals of Botany 118:1209–1223. doi: 10.1093/aob/mcw209

Costa-Lima, J.L. and M. Alves. 2013. A new species of *Erythroxylum* (Erythroxylaceae) from the Brazilian Atlantic Forest. *Phytotaxa* 141:55–60.

Darriba, D, G.L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9:772–772. doi: 10.1038/nmeth.2109

Doyle, J.J. and J.L. Doyle.1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19:11–15.

Drummond, A. and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7:214. doi: 10.1186/1471-2148-7-214

Edgar, R.C. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics* 5:113. doi: 10.1186/1471-2105-5-113

Fidalgo, O. and V.L.R. Bononi. 1984. *Técnicas de coleta, preservação e herborização de material botânico*, Manual nº4. Instituto de Botânica, São Paulo.

Flora do Brasil 2020. [continuously updated] *Flora do Brasil 2020*. in Projeto Flora do Brasil 2020. Jard. Botânico do Rio Janeiro, Rio Janeiro, Brazil. http://floradobrasil.jbrj.gov.br (accessed 24 Jul 2017).

IUCN. 2001. IUCN Red List Categories and Criteria: Version 3.1. Gland, Switzerland and Cambridge, UK: IUCN.

IUCN. 2016. Guidelines for Using the IUCN Red List - Categories and Criteria. Version 12. Gland, Switzerland and Cambridge, UK: IUCN.

Kearse, M., R. Moir, A. Wilson, S. Stones-Havas, M. Cheung, S. Sturrock, S. Buxton, A. Cooper, S. Markowitz, C. Duran, T. Thierer, B. Ashton, P. Meintjes, and A. Drummond. 2012. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28:1647–1649. doi: 10.1093/bioinformatics/bts199

Landrum, L.R. and M.L. Kawasaki. 1997. The Genera of Myrtaceae in Brazil: An Illustrated Synoptic Treatment and Identification Keys. *Brittonia* 49:508. doi: 10.2307/2807742

Lucas, E.J. and M.O. Bünger. 2015. Myrtaceae in the Atlantic forest: their role as a “model” group. Biodiversity and Conservation 24:2165–2180. doi: 10.1007/s10531-015-0992-7

Lucas E.J., S.A. Harris, F.F. Mazine, S.R. Belsham, E.M. Nic Lughadha, A. Telford, P.E. Gasson, and M.W. Chase.2007. Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* 56:1105–1128. doi: 10.2307/25065906

Lucas E.J. and M. Sobral. 2011. Proposal to conserve the name *Myrcia* against *Calyptranthes* (Myrtaceae). *Taxon* 60:605.

Mazine, F.F., M.O. Bünger, J.E.Q. Faria, E.J. Lucas, and V.C Souza. 2016. Sections in *Eugenia* (Myrteae, Myrtaceae): nomenclatural notes and a key. *Phytotaxa* 289:225–236.

Mazine, F.F., V.C. Souza, M. Sobral, F. Forest, and E.J. Lucas.2014. A preliminary phylogenetic analysis of *Eugenia* (Myrtaceae: Myrteae), with a focus on Neotropical species. *Kew Bulletin* 69:1–14. doi: 10.1007/s12225-014-9497-x

McVaugh, R. 1969. The Botany of the Guyana Highland - Part VIII: Myrtaceae. *Memoirs of the New York Botanical Garden* 18:55–286.

Melo, A., B.S. Amorim, E. Pessoa, J.R. Maciel, and M. Alves. 2016. Serra do Urubu, a biodiversity hot-spot for angiosperms in the northern Atlantic Forest (Pernambuco, Brazil). *Check List* 12:1–25.

Miller, M.A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp 1-8 in *Proceedings of the Gateway Computing Environments Workshop*, GCE. New Orleans, LA.

Nic Lughadha, E.M. and N. Snow. 2000. Biology and Evolution of the Myrtaceae: A Symposium. *Kew Bulletin* 55:591–592.

Oliveira-Filho, A. and M. Fontes. 2000. Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate. *Biotropica* 32:793–810. doi: 10.1111/j.1744-7429.2000.tb00619.x

Pessoa, E and M. Alves. 2015a. Orchidaceae from Serra do Urubu: an area of montane forest, state of Pernambuco, Brazil. *Hoehnea* 42:109–133.

Pessoa, E. and M. Alves. 2015b. A new *Campylocentrum* (Vandeae; Epidendroideae; Orchidaceae) from submontane Atlantic Forest of northeastern Brazil. *Phytotaxa* 197:54–58.

QGIS. 2017. *QGIS Development Team*. in Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project http://qgis.osgeo.org.

Ronquist, F., M. Teslenko, P. van der Mark, D.L. Ayres, A. Darling, S. Hohna, B. Larget, L. Liu, M.A. Suchard, and J.P. Huelsenbeck. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61:539–542. doi: 10.1093/sysbio/sys029

Sothers, C.A. 2003. New species of *Diospyros* (Ebenaceae) from Brazil. *Kew Bulletin* 58:473–477.

Stamatakis, A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22:2688–2690. doi: 10.1093/bioinformatics/btl446

Thiers, B. 2017. [continuously updated] *Index Herbariorum: A global directory of public herbaria and associated staff.* in New York Botanical Garden's Virtual Herbarium http://sweetgum.nybg.org/ih/ (accessed 26 Jul 2017).

Vasconcelos, T.N.C., G. Prenner, M.O. Bünger, P.S. de-Carvalho, A. Wingler, and E.J. Lucas. 2015. Systematic and evolutionary implications of stamen position in Myrteae (Myrtaceae). *Botanical Journal of the Linnean Society* 179:388–402.

Vasconcelos, T.N.C., G. Prenner, M.F. Santos, A. Wingler, and E.J. Lucas. 2017. Links between parallel evolution and systematic complexity in angiosperms — A case study of floral development in *Myrcia* s. l. (Myrtaceae). *Perspectives in Plant Ecology, Evolution and Systamtics* 24:11–24. doi: 10.1016/j.ppees.2016.11.001

WCSP. 2017. *World Checklist of Selected Plant Families*. in Facilitated by the Royal Botanic Gardens, Kew. apps.kew.org/wcsp/myrtaceae (accessed 26 Jul 2017).

Wilson, P.G. 2011. Myrtaceae. P. 436 in *The families and genera of vascular plants. Flowering plants, eudicots: Sapindales, Cucurbitales, Myrtaceae*, ed. K. Kubitzki. Springer-Verlag, Berlin.

Zelenski, A., L. Rocha, R.B. Louzada. 2016. Rediscovery of *Turnera pernambucensis* (Passifloraceae s.l.) in the northern Atlantic Forest and an uptade for its description. *Phytotaxa* 286:177–185.

APPENDIX 1. Voucher information and Genbank accessions numbers for sampled taxa. Taxon name and authority are followed by provenance, collector and voucher no.; Herbarium; Genbank accession numbers of ETS, ITS and *psbA-trnH*. New sequences generated in this work are indicated by an asterisk (*). Missing data are indicated by a n-dash (–).

Ingroup: *Eugenia arenosa* Mattos, Mazine 1021; ESA, K; KJ187658, KJ187605, KJ469654. *Eugenia astringens* Cambess. Brazil, Mazine 782; ESA, K; KJ187659, KJ187606, KJ469655. *Eugenia axillaris* (Sw.) Willd. Turks and Caicos, Hamilton 553; FTG, K; KJ187660, KJ187607, KJ469656. *Eugenia bacopari* D. Legrand. Brazil, Mazine 967; ESA, K; KJ187661, KJ187608, KJ469657. *Eugenia beaurepaireana* (Kiaersk.) D. Legrand. Brazil, Mazine 1008; ESA, K; KJ187662, KJ187609, KJ469658. *Eugenia biflora* (L.) DC. Brazil, Mazine 1075; ESA, K; KJ187663, KJ187610, KJ469659. *Eugenia bimarginata* DC. Brazil, Mazine 469; ESA, K; KJ187664, KJ187611, KJ469660. *Eugenia bocainensis* Mattos. Brazil, Duarte s.n. ESA 85677; ESA, K; KJ187665, KJ187612, KJ469661. *Eugenia brasiliensis* Lam. Brazil, Lucas 126; ESA, K; KJ187666, KJ187613, KJ469662. *Eugenia brevistyla* D. Legrand. Brazil, Mazine 993; ESA, K; KJ187667, KJ187614, KJ469663. *Eugenia calycina* Cambess. Brazil, Mazine 1018; ESA, K; KJ187669, KJ187616, KJ469665. *Eugenia capensis* subsp. *natalitia* (Sond.) F. White. South Africa, Reeves 68; NBG; AY454141, AY463135, –. *Eugenia capparidifolia* DC. Brazil, Mazine 845; ESA; –, KJ187617, KJ469666. *Eugenia convexinervia* D. Legrand. Brazil, Mazine 994; ESA, K; KJ187670, KJ187618, KJ469667. *Eugenia expansa* Spring ex Mart. Brazil, Mazine 950; ESA, K; KJ187671, KJ187619, KJ469668. *Eugenia dysenterica* DC. Brazil, Mazine 466; ESA, K; KJ187672, KJ187620, KJ469669. *Eugenia excelsa* O. Berg. Brazil, Lucas 125; K; KJ187673, KJ187621, KJ469670. *Eugenia florida* DC. Brazil, Mazine 965; ESA, K; KJ187674, KJ187622, KJ469671. *Eugenia hamiltonii* (Mattos) Mattos. Brazil, Mazine 1033; ESA, K; KJ187706, KJ187653, KJ469703. *Eugenia handroi* (Mattos) Mattos. Brazil, Mazine 951; ESA, K; KJ187707, KJ187654, KJ469704. *Eugenia hiemalis* Cambess. Brazil, Mazine 970; ESA, K; KJ187675, KJ187623, KJ469672. *Eugenia latifolia* Aubl. French Guiana, Prévost 4707; CAY, K; AM489913, AM234091, AM489831. *Eugenia melanogyna* (D. Legrand) Sobral. Brazil, Mazine 969; ESA, K; KJ187676, KJ187624, KJ469673. *Eugenia modesta* DC. Brazil, Mazine 854; ESA, K; KJ187677, KJ187625, –. *Eugenia neoglomerata* Sobral. Brazil, Mazine 461; ESA, K; KJ187678, KJ187626, KJ469674. *Eugenia neomyrtifolia* Sobral. Brazil, Mazine 953; ESA, K; KJ187679, KJ187627, KJ469675. *Eugenia neoverrucosa* Sobral. Brazil, Lucas 118; K, MBM; KJ187680, KJ187628, KJ469676. *Eugenia nutans* O. Berg. Brazil, Lucas 281; ESA, K; KJ187681, KJ187629, KJ469677. *Eugenia oblongata* O. Berg. Brazil, Mazine 804; ESA, K; KJ187682, KJ187630, KJ469678. *Eugenia patens* Poir. French Guiana, Lucas 104; ESA, K; KJ187685, KJ187633, KJ469681. *Eugenia petaloidea* Giaretta & B.S. Amorim. Brazil, B.S. Amorim 1765 [3]; UFP, K; GenNumbETS*, GenNumbITS*, GenNumbPSBA*. *Eugenia petaloidea* Giaretta &

B.S. Amorim. Brazil, B.S. Amorim 1765 [4]; UFP, K; GenNumbETS*, GenNumbITS*, GenNumbPSBA*. *Eugenia petaloidea* Giaretta & B.S. Amorim. Brazil, B.S. Amorim 1765 [23]; UFP, K; GenNumbETS*, GenNumbITS*, GenNumbPSBA*. *Eugenia petaloidea* Giaretta & B.S. Amorim. Brazil, B.S. Amorim 1765 [24]; UFP, K; GenNumbETS*, –, GenNumbPSBA*. *Eugenia petaloidea* Giaretta & B.S. Amorim. Brazil, B.S. Amorim 1765 [106]; UFP, K; GenNumbETS*, GenNumbITS*, GenNumbPSBA*. *Eugenia pisiformis* Cambess. Brazil, Lucas 232; K; KJ187686, KJ187634, KJ469682. *Eugenia pitanga* (O. Berg) Kiaersk. Brazil, Mazine 1044; ESA, K; KJ187687, KJ187635, KJ469683. *Eugenia pluriflora* DC. Brazil, Mazine 961; ESA, K; KJ187688, KJ187636, KJ469684. *Eugenia prasina* O. Berg. Brazil, Mazine 959; ESA; KJ187689, KJ187637, KJ469685. *Eugenia punicifolia* (Kunth) DC. Brazil, Mazine 1065; ESA, K; KJ187690, KJ187638, KJ469686. *Eugenia pyriformis* Cambess. Brazil, Mazine 1028; ESA, K; KJ187691, KJ187639, KJ469687. *Eugenia repanda* O. Berg. Brazil, Lucas 273; K, RB; KJ187692, KJ187640, KJ469688. *Eugenia sphenophylla* O. Berg. Brazil, Lucas 257; BHCB. K, RB; KJ187697, KJ187644, KJ469693. *Eugenia stipitata* McVaugh. Cultivated, Holst 8872; SEL; KJ187698, KJ187645, KJ469694. *Eugenia subavenia* O. Berg. Brazil, Mazine 805; ESA, K; KJ187699, KJ187646, KJ469695. *Eugenia subterminalis* DC.Brazil, Mazine 974; ESA, K; KJ187700, –, KJ469696. *Eugenia sulcata* Spring ex Mart. Brazil, Mazine 787; ESA, K; KJ187701, KJ187647, KJ469697. *Eugenia tetramera* (McVaugh) M. L. Kawasaki & B. K. Holst. French Guiana, Holst 9422; SEL; KJ187702, KJ187648, KJ469698. *Eugenia umbrosa* O. Berg. Brazil, Mazine 1085; ESA, K; KJ187703, KJ187649, KJ469699. *Eugenia uniflora* L. Cultivated RBG Kew, Lucas 207; K; AM489910, AM234088, AM489828. *Eugenia* sp, 1. Brazil. Mazine 1077; ESA, K; KJ187693, KJ187641, KJ469689. *Eugenia* sp, 2. Brazil. Mazine 1090; ESA, K; KJ187694, –, KJ469690. *Eugenia* sp, 4. French Guiana. Holst 9435; SEL; KJ187696, KJ187643, KJ469692.

Outgroup: *Acca sellowiana* (O. Berg) Burret. Cultivated RBG Kew, Lucas 205; K; AM489888, AM234067, AM489807. *Myrcia hebepetala* DC. Brazil, Lucas 64; K; AM489916, AM234111, AM48934. *Myrcianthes fragrans* (Sw.) McVaugh Cultivated, unknown origin, Holst 8862; SEL; KJ187708, KJ187655, KJ469705. *Myrcianthes pseudomato* (D. Legrand) McVaugh. Brazil, Beck 9667; K; AM489951, AM234100, AM489868. *Pimenta dioica* (L.) Merr. Cultivated RBG Kew, Lucas 212; K;

AM489958, AM234081, AM489874. *Rhodamnia rubescens* (Benth.) Miq. Cultivated RBG Melbourne. Belsham M83; OTA; AM489963, AM234127, AM489879.

Capítulo 2

Chapter 2

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CALYX (CON)FUSION IN THE HYPER-DIVERSE GENUS *EUGENIA* (MYRTACEAE): HOMOPLASTIC EVOLUTION OF UNUSUAL FLOWER PATTERNS

Abstract

Eugenia comprises ca. 1000 species, found mostly in the Neotropics. High levels of morphological homogeneity make species identification notoriously difficult. However, genera have been segregated from *Eugenia* on the basis of differences in degree of fusion and dehiscence of the calyx. Morphological homoplasy that historically misleads systematists and taxonomists still hampers the organization of diversity. The approach used here integrates molecular phylogeny and a careful investigation of flower morphology of *Eugenia* to clarify systematic relationships among fused calyx species. Five DNA regions of 24 fused calices *Eugenia* further 62 taxa were sequenced and recovered a robust phylogeny used as framework for evolutionary analysis. Ancestral character reconstruction indicated that fused calyx had ten independent origins within *Eugenia*. Fused calyx was previously scored as a unique character, however, five development patterns were recognized using SEM. The *heterosepalous* and *homosepalous* development patterns are polyphyletic, each recovered independently at least four times as well as *petaloid* pattern. The only exception is *membranisepaly* that is exclusive to an Amazonian clade supported by the high phylogenetic signal. The *longohypanthium* pattern is an exceptional extreme in flower morphology of *Eugenia*. These results have major impact on the current systematics of *Eugenia* and further exemplify how detailed morphological survey using a phylogenetic framework reveals complexity rather than simplification. Ultimately, it has implications for better interpreting patterns of floral evolution and systematics in angiosperms.

Keywords: homoplasy, systematics, Myrteae, morphology, character reconstruction, phylogeny

1. Introduction

Classical authors recognized two tribes of Myrtaceae, circumscribed according to the presence of dry-capsular or fleshy-berry fruits (Candolle, 1828). Cladistic insight (Briggs and Johnson, 1979) and phylogenetic inference (Gadek et al., 1996; Wilson et al., 2001, 2005) demonstrated that many characters presumed diagnostic in previous classifications were in fact more homoplastic than previously appreciated. Myrtaceae is classified into 17 tribes; the most up to date classification groups fleshy-fruited Neotropical species into tribe Myrteae while extra-neotropical fleshy-fruited genera are included in other tribes (Wilson et al., 2005; Wilson, 2011). Myrteae comprises half of the species diversity of the family, with 51 genera and ca. 2500 species (Wilson, 2011; WCSP, 2017) and includes the hyper-diverse genus *Eugenia*.

Eugenia has a pantropical distribution and comprises ca. 1000 species, found mostly in the Neotropics (Wilson, 2011; Mazine et al., 2014; Mazine et al., 2016). *Eugenia* has high ecological importance because is the dominant tree genus in some regions of the Atlantic coastal forest (Oliveira-Filho and Fontes, 2000), however, high levels of homogeneity of taxonomically important characters such as flowers and fruits makes species identification notoriously difficult (Lucas and Bünger, 2015). Nevertheless, it is here shown that *Eugenia* morphology is not as homogeneous as previously thought. Although morphologically similar, genera have been segregated from *Eugenia* on the basis of differences in degree of fusion and dehiscence of the calyx (Amshoff, 1951; McVaugh, 1969; Legrand and Klein, 1972). As a consequence, genera such as *Calycorectes*, including species that resemble *Eugenia* in all but possession of a fused calyx are taxonomically controversial. Some authors segregate *Calycorectes* from *Eugenia* based on calyx morphology whereas an 'unified *Eugenia*' is supported by most contemporary authors (e.g. Mazine et al., 2014; Flora do Brasil, 2020).

A seminal molecular phylogenetic framework focused on infra-generic classification in *Eugenia* confirmed that the genus can only be monophyletic if fused calyx species (Mazine et al., 2014) were included. In contrast, at the infra-generic level, molecular data cannot diagnose and recognize sub-clades with high statistical support. The character of the fused calyx conveniently diagnosed *Eugenia* sect. *Calycorectes* Mattos (Mazine et al., 2014) but variable degree and pattern of calyx fusion suggest that closer scrutiny of developmental aspects of this character might allow more accurate use. In addition, it is desirable to assess this character over a more representative sample than the two species previously used (Mazine et al., 2014). It is estimated that 35 species of *Eugenia* have some degree of calyx fusion.

Phylogenetic relationships based on molecular data have been investigated at various ranks in Myrteae, resulting in current, increasingly accurate, phylogenetic based classifications (Lucas et al., 2007; Lucas et al., 2011; Mazine et al., 2014; Bünger et al., 2016b; Vasconcelos et al., 2017c). However, recurring morphological homoplasy that historically misleads systematists and taxonomists still hampers the organization of diversity (e.g. Vasconcelos et al., 2017a). Insufficiently investigated morphological characters produce classifications that lack predictability and the necessary insight can be gleaned by morphological assessment. The approach used here integrates molecular phylogeny and a survey of calyx development patterns to 1) clarify systematic relationships among fused calyx species in the hyper-diverse genus *Eugenia*; 2) re-evaluate the fused calyx in *Eugenia* through careful investigation of flower morphology and; 3) diagnose new and relevant clades in *Eugenia*. Survey of the fused calyx is necessary for accurate understanding of phenotypic response to environmental pressure so identifying underlying evolutionary processes that drive Neotropical diversity.

2. Material and methods

2.1. Molecular and morphological sampling

Material of 24 Myrtaceae taxa were extracted and sequenced from 30 samples. The survey prioritized species that fit to the current delimitation of *Eugenia* (see Mazine et al., 2016) with some level of calyx fusion in the bud, including as much morphological and geographical variation as possible. This survey corresponds to ca. 70% of *Eugenia* subg. *Calycorectes* sensu Berg (1856b). A further 48 species of *Eugenia* s.l. more two *Myrcianthes* were included to recover internal relationships among recognised clades. Six additional Myrteae genera were used as the outgroup. Taxonomy used is in accordance to the Flora do Brasil (2020) with complementary information from Mattos (2005). The internal transcriber spacer (ITS) of the ribosomal nucleus and the plastid regions *psb*A-*trn*H, *rpl*16, *trn*L-*rpl*32 and *trn*Q5’-*rps*16 were used. In total, 149 new sequences were provided with the remaining obtained from existing published (Lucas et al., 2007; Mazine et al., 2014; Bünger et al., 2016a) and unpublished work (J.E. Faria, UB, Brasília, Brazil, unpubl. res.). The molecular sampling of 86 accessions is available on Appendix A.

Development patterns were assessed from floral buds collected and conserved in 70% ethanol at all development stages as possible from East-West Brazil and French Guiana. A complementary survey was based on buds from recent herbarium collection available at K; material was rehydrated in boiling water for 10 min, left cool overnight and then conserved in 70% ethanol. A total of 25 samples representing 18 taxa of *Eugenia* with fused calices were surveyed for comparative development pattern analysis. A list of analysed material using the scanning electron microscopy (SEM) is provided in Appendix B.

2.2. DNA sequencing

Total DNA was extracted using QIAGEN® DNeasy® Plant Maxi Kits from until 0.2 g of silica-gel dried leaf material generating 1.5 ml of total DNA. Amplification and purification of DNA regions were performed according to protocols outlined in Lucas et al. (2007, 2011) and (Shaw et al., 2007) for *rpl*32-*trn*L and *trn*Q5'-*rps*16. PCR conditions were executed according to Bünger et al. (2016). Nucleotide sequencing follow the protocols outlined by (Lucas et al., 2007). Sequences were assembled and aligned using MUSCLE (Edgar, 2004) and edited when necessary using Geneious v7.9 (Kearse et al., 2012). DNA samples are stored in the DNA Bank and Tissue Collections of Royal Botanic Gardens, Kew.

2.3. Phylogenetic analysis

Search and analysis for the best scoring Maximum Likelihood (ML) tree under default parameters were performed to each DNA region using RAxML v7.6.3 (Stamatakis, 2006). Lack of statistically supported incongruence was established by eye and the four chloroplast-DNA regions (cpDNA) were combined resulting in a matrix of 3,226 base pairs; the nuclear ITS partition comprised 671 base pairs. Independent ML and Bayesian Inference (BI) were performed on both the cpDNA and nuclear ITS regions. The best nucleotide substitution models were selected with jModeltest2 v2.2 (Darriba et al., 2012); GTR+I+G was implemented for both ITS and cpDNA datasets. The models were implemented in MrBayes v3.2.1 (Ronquist et al., 2012) on XSEDE v.3.2.6. Two independent runs with four Monte Carlo Markov Chains (MCMC) each were performed with 5 million generations, sampling every 1000 trees and using a burn-in of 15% (750000 trees). Output was examined using Tracer v1.6 (Drummond and Rambaut, 2007) to confirm chain convergence. Visual inspection of ML and BI topologies detected no statistically supported incongruence and concatenation of cpDNA and nuclear datasets resulted in a matrix of 3,874 base pairs, then subjected to independent ML and BI analysis implemented in CIPRES (Miller et al., 2010). *Myrtus communis* was used to root the phylogeny. The resulting BI phylogeny was selected as a final framework on which the following ancestral character reconstruction and phylogenetic signal analysis was based. Phylogenetic reconstructions not shown are provided in the Appendix C (S2 to S10).

2.4. Development pattern analysis

Flowers bud were dehydrated in alcohol series and left overnight in 100% ethanol. Material was then brought to dehydration in a critical-point dryer using an Autosamdri-815B (Tousimis Research, Rockville, Maryland, USA). Dried material was mounted onto aluminum stubs, coated with platinum using a Quorum Q-150-T sputter coater (Quorum Technologies, East Grinsted, UK) and examined in detail using Hitachi cold field emission Scanning Electron Microscopy S-4700-II (Hitachi High Technologies, Tokyo, Japan). Different stages of development of the same species were examined from different collections when necessary. Relative orientation among bracteoles and structural whorls was used as reference for developing structures. A total of 306 images were analysed.

2.5. Ancestral character reconstruction analysis

Character reconstruction was performed to recognize if development patterns arose independently (homoplasy) or by descendent. The function *ace (ancestral character estimation)* available in the package *ape* (Paradis et al., 2004) implemented in R was used to recover ancestral character state probabilities of the nodes. The parameter “type=discrete” was used since development patterns were coded as discrete. Analysis was performed using one accession per taxon, where necessary selecting the sample that better matched the type specimen. The function “drop.tip” from the package *ape* (Paradis et al., 2004) was used to remove a polytomy in the outgroup (*Myrceugenia alpigena)* as required to run the analysis and more than one accession per taxon.

2.6. Phylogenetic signal

Phylogenetical signal was measured for different development patterns resulting in calyx fusion, to interpret statistical dependence between patterns in relation to their phylogenetic relatedness (Revell et al., 2008). Fused patterns were also contrasted with the development pattern resulting in free calyx lobes. Five independent analyses were performed, and are here coded as discrete character states. Phylogenetic signal of these patterns was measured using the "fitDiscrete" function available in the package *geiger* (Harmon et al., 2008) implemented in R. This function uses likelihood models of discrete character evolution in a continuous-time Markov model. The parameter "transform=lambda" was selected, this assumes equal rates (ER) of transition since no estimate of evolutionary rate is provided (Pagel, 2004), it also takes into account branch length scaled by nucleotide substitution rates. This analysis generates a log-likelihood value (*lnl*) and lambda index (λ) to rank the phylogenetic signal. Values of lambda fluctuate from 0 to 1, i.e. values close to 0 suggest phylogenetic independence while a value of 1 indicates phylogenetic non-independence compared to that expected under Brownian motion. Different properties of data unrelated to phylogenetic history can impact phylogenetic signal (Revell et al., 2008; Münkemüller et al., 2012) such as more than one accession per taxon. Phylogenetic signal analysis was performed using one accession per taxon. Again, the function "drop.tip" was used to remove polytomies, extra terminals and the outgroups.

3. Results

3.1. Systematics relationships among fused calyx Eugenia

Bayesian inference (BI) and Maximum likelihood (ML) topologies recover *Eugenia* as a well-defined group in the combined (1 posterior probability/PP and 100% bootstrap/BS), nuclear (99 PP; 75 BS) and cpDNA datasets (96 PP; 97 BS). The combined Bayesian inference tree is presented (Fig. 1) with the equivalent ML topology available in the Supplementary Data (S4). The topology of BI and ML are congruent with *Eugenia* phylogenies produced until now (Mazine et al., 2014; Faria et al., in prep., Bünger et al., 2016) except in a single case. In this study, *Eugenia* sect. *Eugenia* is represented by *E. uniflora* and *E. brasiliensis* that emerge with low support (0.55 PP; 49 BS) as successive sister groups to *Eugenia* sect. *Pilothecium.*

Species with a fused calyx have ten independent origins within *Eugenia* (marked in red on Fig. 1); the following results and discussion focus on relationships between and within these species. Most species with a fully or partially fused calyx emerge in *Eugenia* sect. *Umbellatae*; they are found in continental American and Caribbean clades but not outside of the Neotropics. Caribbean endemic genera *Calyptrogenia* and *Hottea* with fused calices are included within *Eugenia*, supporting the results of Vasconcelos et al. (2017b). The following other novel relationships are noted for the first time: a well-supported clade (1 PP; 100 BS) emerges within *Eugenia* sect. *Umbellatae* (node A) that is here informally called the "*Eugenia moschata* group". A further informal group with high support (0.99 PP; 74 BS), the "*Calycorectes* group" (node C) includes *Calycorectes grandifolius,* the type species of *Calycorectes,* and *Calycorectes bergii*. Newly sampled *Eugenia vattimoana, E. acutata, E. cambucae, E. guanabarina, E. zuccarinii* and *E. paradisiaca* ined. emerge in *Eugenia* sect. *Schizocalomyrtus* (Giaretta et al., Chapter 4) with high support (1 PP; 100 BS). Other newly sampled, fused calyx species *Eugenia fissurata*, *E. lagoensis, E. rara, E. caloneura, E.* sp 2, *E.* sp 3 and *E. petaloidea* ined. also emerge in *Eugenia* sect. *Umbellatae*, sister to species with free calyx lobes. *Eugenia* sect. *Schizocalomyrtus* (published as *Eugenia* sect. *Calycorectes* sensu Mazine et al., 2016) contains a majority of fused calices species previously included in *Calycorectes* and emerges in the same position as in previous analyses. *Eugenia* sect. *Schizocalomyrtus* was recovered as sister to *Eugenia* sect. *Phyllocalyx* in the BI with low support (0.63 PP) but in the ML as sister to *Eugenia* sect. *Excelsae* ined. (52 BS), and subsequently sister to *Eugenia* sect. *Phyllocalyx* (48 BS).

3.2. Development patterns of calyx fusion

Scanning electron microscopy analysis revealed all *Eugenia* flowers examined to be tetramerous with external sepals decussate relative to the bracteoles; the petals are positioned between sepals, as consistently found in tribe Myrteae (see Belsham and Orlovich, 2002, 2003) (Fig. 2); the fusion of the calyx is post-genital, i.e. the fusion follows the calyx lobes emergence. *Eugenia* with free sepals (Fig. 3A) are here assumed to have followed the *aposepalous* calyx pathway of Vasconcelos et al. (2017a). Five distinct patterns of closed bud are a derived condition of calyx fusion observed in *Eugenia* that are here considered in conjunction with the other known Myrteae (*Myrcia* s.l.) development pathways presented by Vasconcelos et al. (2017a). These patterns are described as follows:

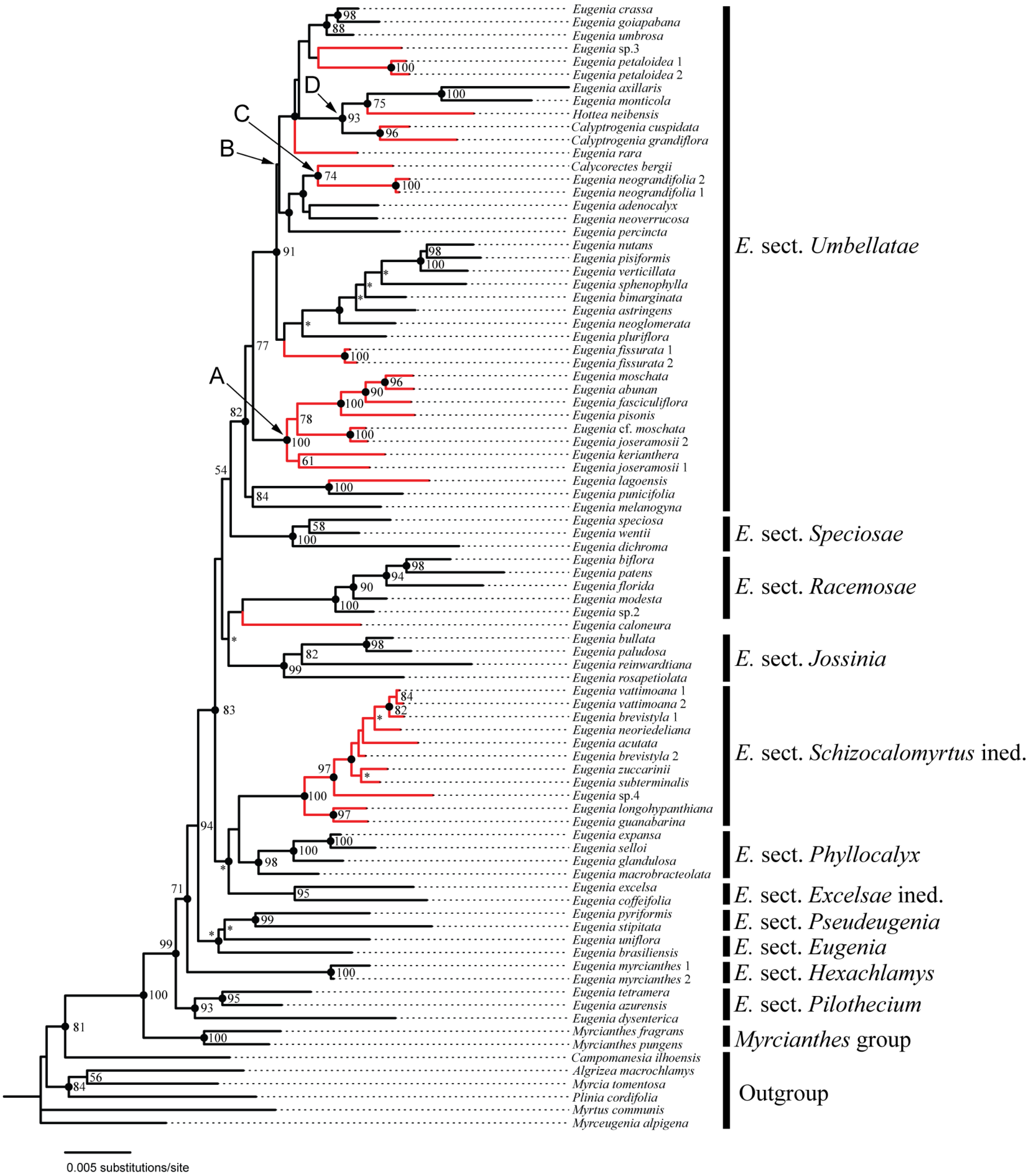

Figure 1. Bayesian Inference tree of *Eugenia* resulting from the combined dataset. Nodes receiving posterior probabilities greater than 0.95 are indicated by black dots; bootstrap percentages recovered by the Maximum Likelihood (ML) equal or greater than 50 are shown above branches. * indicates nodes not recovered in the ML. Red branches indicate taxon with calyx fused.

3.3. *Heterosepalous pattern*

Flowers that follow this pattern have four calyx lobes fused to a varying degree at the base. Lobes are most commonly fused along two thirds of the length of the bud leaving an opening of ca. 1 mm diameter. Buds in which fusion is as little as one third of bud length or as much as near complete closure are also found. In this arrangement, the line of fusion is along the edge of each calyx lobe and results in heterogeneous thickness of the calyx that tapers into a fragile tissue between each sepal. The different degrees of fusion observed suggest that the timing of calyx fusion varies from early to late during the developmental process although it is most frequently early. At anthesis the fragile calyx tissue splits into four regular lobes. There are four free petals, each positioned between the bases of the sepals. The stamens are straight in bud, attached to the tissue between the corolla and style (Fig. 3B-F).

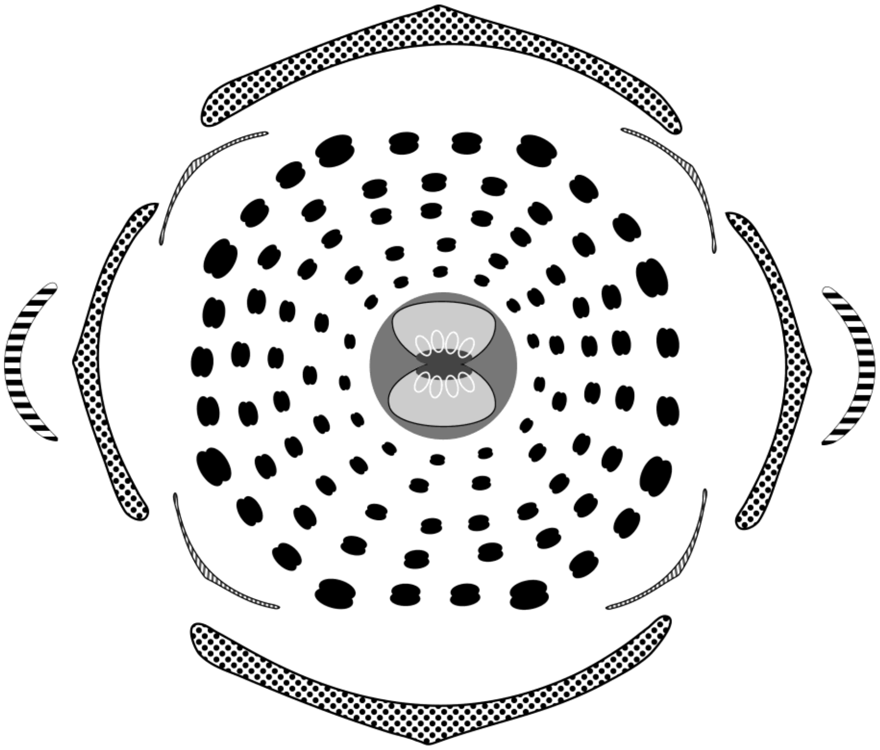

Figure 2. Floral diagram of the standard flower of *Eugenia* showing the most recurrent ground-plan. Pattern coding: horizontal dash, bracteole; dot, sepal; vertical dash, petal; black ellipsoid, stamens; grey circle, gynoecium.

3.4. Homosepalous pattern

Buds that follow this pattern are nearly closed except at the apex where the remains of four vestigial lobes are free. Again, the presence of vestigial lobes indicates early fusion of calyx lobes. In this arrangement, the line of fusion is along the edge of each calyx lobe resulting in a homogeneous tissue without evidence of sepalar seams. Anthesis follows two possible opening patterns that can vary between accessions of observed species: the fused calyx 1) tears resulting in two to four irregular lobes; 2) opens transversely via a tear at the calyx base resulting in a structure that resembles a calyptra. The four petals are free, each positioned between the bases of the sepals; the corolla is occasionally reduced to one petal. The stamens are straight in bud, attached to the tissue between the corolla and style (Fig. 3G-M).

3.5. Membranisepalous pattern

Flowers that follow this pattern have four calyx lobes visible in the bud that are partially fused in the lower third of the bud. The fully developed lobes suggest later fusion during the developmental process. The line of fusion between the external and internal sepals occurs along the boundary of the external sepals but well within the edge on the dorsal face of the internal sepals leaving free, membranous tissue beneath the seam. At anthesis tearing occurs in this lower third of the calyx and is evident in open flowers. In some cases, e.g. *Eugenia fasciculiflora*, the fusion can appear complete to the apex of the bud. However, the membranous parts of the free lobes are so fragile that rather than opening freely, internal pressures cause these membranous regions to split unevenly. This latter condition and the degree (length) of splitting, varies within an individual accession. In the *membranisepalous* pattern, the four petals are free and each petal is positioned between the bases of the sepals. The stamens are straight in bud and are attached to the tissue between the corolla and style (Fig. 4A-D).

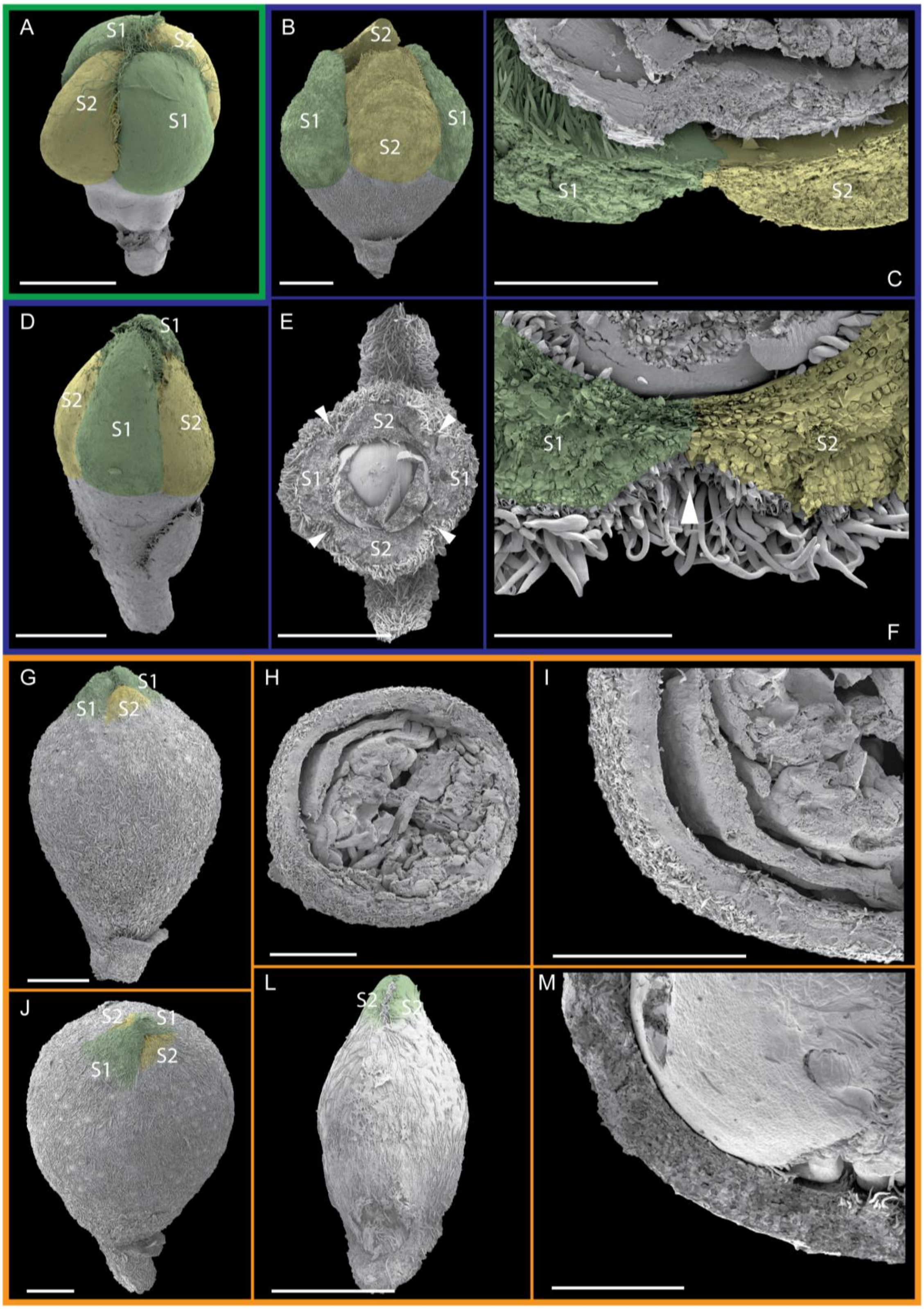

Figure 3. Comparative development patterns of the calyx in *Eugenia*. A (green box). Standard condition of free calyx lobes in *Eugenia uniflora*. B-F (blue boxes). *Heterosepalous* pattern. Calyx lobes partially fused and free at the apex of *E. brevistyla* (B) and *E. subterminalis* (D). Transversal section in a fused portion of the bud showing the heterogeneous thickness of the calyx tissue caused by the tapering between each sepal lobes indicated by the arrows in *E. acutata* (E). Detail of the transversal section of *E. brevistyla* (C) and *E. acutata* (F). G-M (orange boxes). *Homosepalous* pattern. Calyx

lobes nearly closed except at the apex where the remains of the four vestigial lobes are free in *E. neoriedeliana* (G) and *E. vattimoana* (J) but only the two external lobes can be seen at this stage in *E. guanabarina* (L). Transversal section in a fused portion of the bud showing the homogeneous thickness of the calyx tissue of *E. neoriedeliana* (H). Detail of the transversal section of *E. neoriedeliana* (I) and *E. guanabarina* (M). Scales bars = 1 mm. Colour coding: external sepals (S1), green; internal sepals (S2), yellow; petal (P).

3.6. Petaloid pattern

Flowers that develop according to this pattern have buds that are nearly closed except at the apex where the remains of two vestigial lobes persist. These vestigial lobes suggest early fusion of the two external sepals during development. In this arrangement, the line of fusion is along the edge of the external pair of calyx lobes and results in a homogeneous or heterogeneous thickening of the calyx. Anthesis follows three possible opening patterns, rarely varying between accessions of observed species: the fused calyx 1) tears irregularly in two to six lobes; 2) splits into two regular lobes; 3) opens transversely via a tear at the calyx base resulting in a structure that resembles a calyptra. Two internal sepals remain free and always in the same orientation as the bracteoles. Internal sepals are white and petal-like but differ from the petals in their greater size and thickness. The number of petals is always the same as the sepals; the four petals are free, each positioned between the bases of the sepals. Stamens are straight in the bud, attached to the tissue between the corolla and style (‘hypanthium’ *sensu* (Vasconcelos et al., in press). At anthesis the floral display commonly gives the impression that the flower has six petals, i.e. four petals and two petaloid-sepals, all presumably playing a role in the attraction of pollinators (Fig. 4E-I).

3.7. Longohypanthium pattern

Observed in only one species, flowers that follow this unusual pattern have nearly closed buds with the remains of four, thick vestigial lobes surrounding an apical pore. Extremely rarely in *Eugenia*, the tissue between the corolla and style lengthens into a tubular hypanthium that extends up to two thirds of the bud, internally covered in staminal whorls. The line of fusion of the calyx lobes is along their edges resulting in a homogeneous tube of tissue in which the calyx lobes are indistinguishable. At anthesis the fused calyx and staminal whorls tear into three or four irregular lobes. Four petals,

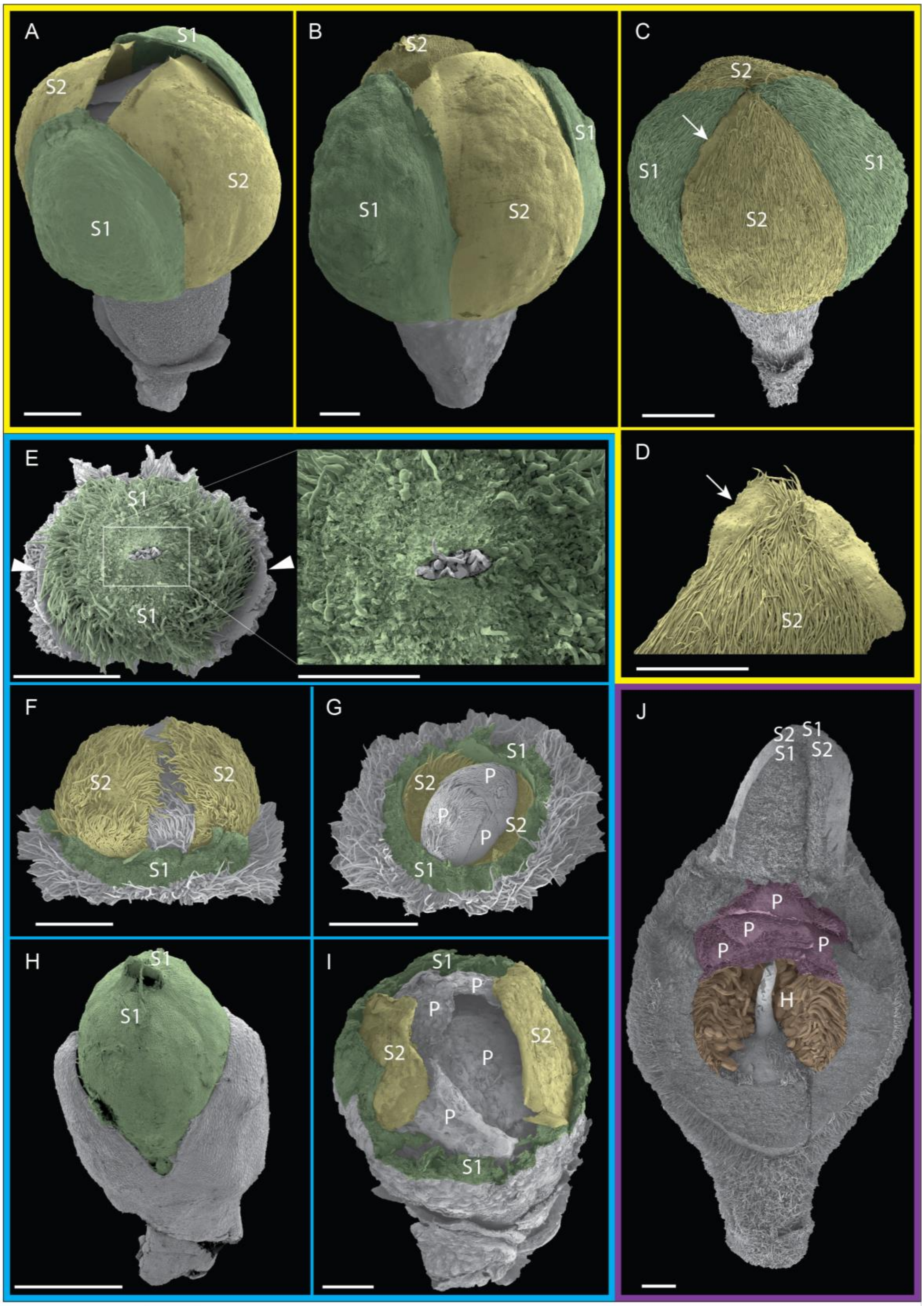

Figure 4. Comparative development patterns of the calyx in *Eugenia*. A-D (yellow box). *Membranisepalous* pattern. Calyx lobes partially fused in the lower third of the bud showing that the line of fusion between the S2 and S1 occurs along the boundary of the S2 but well within the edge on the dorsal face of the S1 leaving free, membranous tissue beneath the seam in *Eugenia joseramosii* (A), *E. pisonis* (B) and *E. fasciculiflora* (C). Detail of the membranous tissue of a calyx lobe indicated by an arrow in *E.*

fasciculiflora (D). E-I (ligh-blue boxes). *Petaloid* pattern. Bud nearly closed except at the apex where the remains of the two vestigial lobes persist in *Eugenia neograndifolia* (E); head arrows indicate the bracteoles position. Successively, the both fused S1 were removed revealing two free and petal-like S2 (F); and both S2 were removed showing the three of the four petals underneath (G). Bud nearly closed except by the remain of the two lobes of S1 at the apex of *Hottea neibensis* (H). Fused S1 removed revealing two free, petal-like S2 and four petals of *Calyptrogenia cuspidata* (I). J (purple box). *Longohypanthium* pattern. Longitudinal section of a bud showing the extending hypanthium covered in staminal whorls, which supports strongly incurved stamens (J). Scales bars = 1 mm. Colour coding: external sepals (S1), green; internal sepals (S2), yellow; petal (P), purple; hypanthium (H), orange.

each positioned between the bases of the sepals are attached at the hypanthium summit. Again, rare in *Eugenia* (Vasconcelos et al., in press), the stamens are strongly incurved in the bud. From outside, two thirds of the bud is the visible hypanthium; at anthesis the irregular lobes reflex, exhibiting the attached stamens. The exhibition of the stamens, the showiest part of the *Eugenia* display, is particularly striking in this arrangement; the petals further increase the diameter of the flower, presumably increasing attraction to pollinators (Fig. 4J).

3.8. Ancestral character reconstruction of development patterns

Ancestral reconstruction shows that the ancestral state of all extant *Eugenia* is free calyx lobes (Fig. 5). The only apparent instance of reversal to free lobes within *Eugenia* sect. *Schizocalomyrtus* was observed in *Eugenia zuccarinii*, however, it is here scored as *heterosepalous* due to a small degree of fusion (ca. 1 mm of length) at the base of the lobes. The fused calyx condition is homoplastic and evolved independently, several times in *Eugenia,* as did the different development patterns. The only exception is *membranisepaly* that is exclusive to the '*Eugenia moschata group*' (Fig. 1 node A). *Heterosepaly* has evolved at least five times and is the most common arrangement in *Eugenia* sect. *Schizocalomyrtus*. *Homosepaly* appears five times and is the most common pattern by which fusion is achieved. The *Petaloid* pattern arose four independent times and is exclusive to node B (Fig. 1) of *Eugenia* sect. *Umbellatae*.

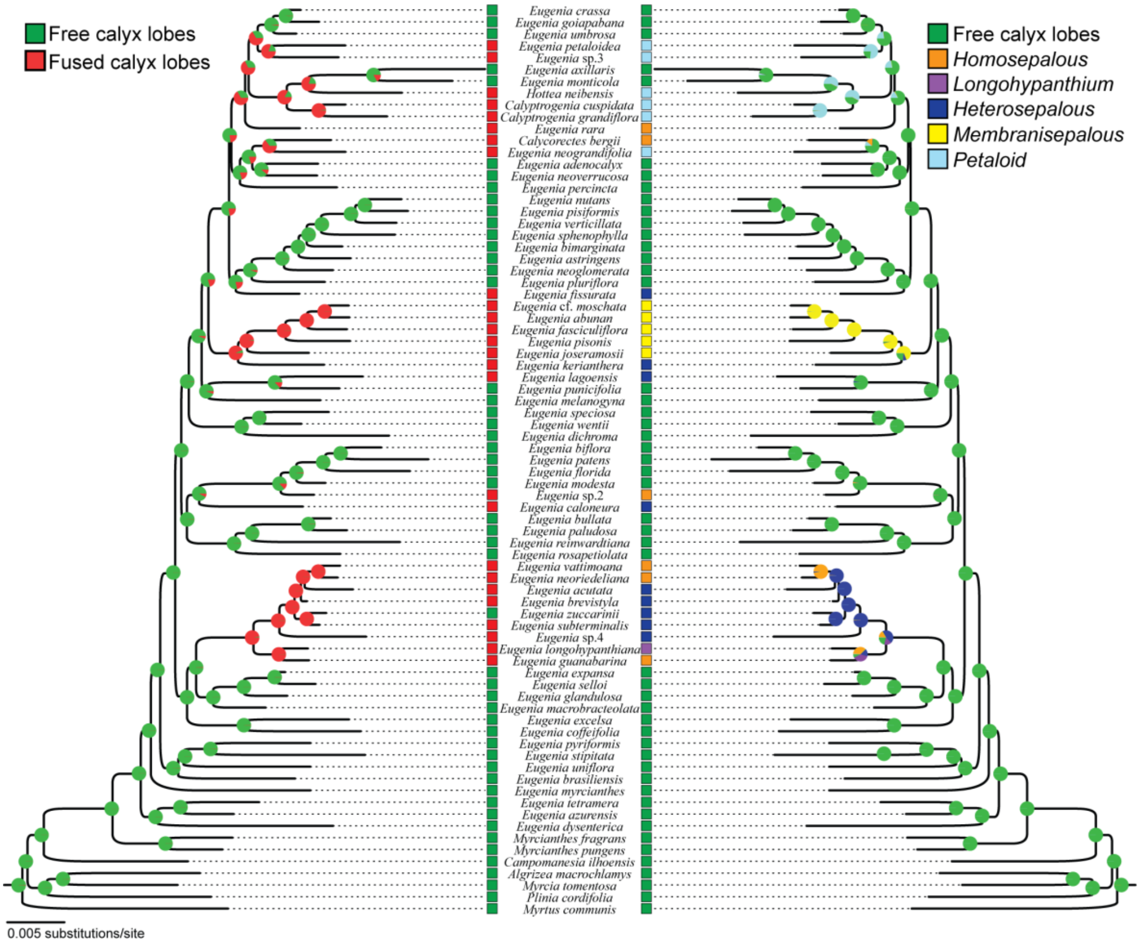

Figure 5. Reconstruction of the comparative development patterns of calyx fusion in *Eugenia*. Left shows the previous scenario of fused calyx scored as a single character state. Right shows the current scenario of development pattern herein described. Colours correspond to the coloured boxes of the Figures 2 and 3.

3.9. Phylogenetic signal of Eugenia *fused calyx*

Results presented here clearly show the *Eugenia* fused calyx to be a homoplastic character. Although fused calyx scores a high value of lambda (λ = 1.0), the log-likelihood is the very low (*lnl* = -34.735) inferring low correlation with the phylogenetic hypothesis. Phylogenetic relatedness of different development patterns to the phylogeny are presented in Table 1, showing that these values were lower for *heterosepaly* (λ = 0.89; *lnl* = -22.769) and *homosepaly* (λ = 0; *lnl* = -21.036). *Membranisepaly* returns high phylogenetic signal (λ = 1.0; *lnl* = -7.404). The *Petaloid* pattern returns a high lambda (λ = 1.0; *lnl* = -17.514), indicating phylogenetic non-independence, and low log-likelihood. The *longohypanthium* pattern is an exceptional extreme in *Eugenia* represented by a single species, preventing analysis of phylogenetic signal.

Table 1. Comparison of phylogenetic signal among developmental patterns ordered according to the higher log-likelihood.

Previous scenario	***lnl***	**λ**
Fused calyx	-34,735	1
Development patterns		
Membranisepalous	-7,404	1.0
Petaloid	-17,514	1.0
Homosepalous	-21,036	0.0
Heterosepalous	-22,769	0.89

4. Discussion

4.1. Systematic relationships of fused calyx Eugenia

Although *Eugenia* with fused calices have traditionally been treated as *Calycorectes*, results presented here clearly show that characters of the calyx alone are insufficient for generic delimitation. This character has arisen on at least ten instances according to character reconstruction and provides no support for segregation of such species from *Eugenia.* Morphological argument for this inclusive arrangement has been made (McVaugh, 1969; Landrum and Kawasaki, 1997; Sobral, 2003) and as a consequence, many traditional *Calycorectes* species have been transferred to *Eugenia* (see Mattos, 2005) although some species still require nomenclatural adjustment (see Giaretta et al., Chapter 2).

It is not surprising that calyx fusion has misled *Eugenia* taxonomy. The strong phylogenetic signal (λ) exhibited by the character of the fused calyx indicates phylogenetic relatedness and an inherited condition. However, low log-likelihood suggests recurrent independent evolutions of this character, reinforcing its inefficiency for *Eugenia* systematics, especially when used alone. Variable bud closure mechanisms have misled taxonomy in other Myrtaceae genera such as *Angophora* and *Eucalyptus* (Drinnan and Ladiges, 1988; Ladiges et al., 1995; Bayly, 2016) that also show independent development pathway origins. Closed buds in Neotropical genera such as *Myrcia* s.l. (Lucas et al., 2011, Wilson et al., 2016) have also been shown to be morphologically and developmentally homoplastic, with low systematic value, apparently the result of parallel evolution in closely related species (Vasconcelos et al., 2017b). Adding to this confusion, what may be thought to be a “closed bud” or “fused calyx” in Myrtaceae could have calycine or corolline origins, or even synchrony between them (Drinnan and Ladiges, 1988; Drinnan and Ladiges, 1989).

Results of the character reconstruction indicate that species with fused calyx lobes are derived from flowers with free lobes, where two or four lobes are fused in different ways and degrees. Calyx lobes are free in *Myrcianthes* (sister to *Eugenia*) and in some lineages emerging from the oldest nodes of *Eugenia* (Vasconcelos et al., 2017c). All calyx lobe fusion in *Eugenia* are post-genital, i.e. the fusion is followed by the emergence of distinctive lobes; this is reinforced by the presence of vestigial free lobes at the apex of the bud (free lobes are evident in *membranisepaly*). *Eugenia* sect. *Umbellatae* is the section that contains most species (ca. 800 spp; Mazine et al., in press). All but three of the ten occurrences of calyx fusion identified in *Eugenia* are found in *E.* sect. *Umbellatae* where all development patterns described here except *longohypanthium* can be found. The high levels of heterogeneity of calyx fusion reported here in *Eugenia* may be linked to rapid and recent speciation reported in *Eugenia* sect. *Umbellatae* (Vasconcelos et al., 2017b).

4.2. Systematic relevance of calyx fusion

Five morphological development patterns leading to calyx fusion are reported here including the ancestral condition with free lobes. The *heterosepalous* and *homosepalous* development patterns are polyphyletic, each recovered independently at least four times. The phylogenetic signal of *heterosepaly* returns high lambda because it is almost exclusively found in *Eugenia* sect. *Schizocalomyrtus*, except for *Eugenia lagoensis* (in *Eugenia* sect. *Umbellatae*). Low internal resolution in *Eugenia* sect. *Schizocalomyrtus* increases phylogenetic uncertainty and is likely responsible for the low value of log-likelihood recovered. The low phylogenetic signal recovered for *homosepaly* indicates a highly homoplastic character with low systematic relevance. In contrast, the *membranisepalous* pattern is more systematically relevant, evolving just once in the evolution of the genus and returning high phylogenetic signal. *Membranisepaly* is exclusive to the “*Eugenia moschata group*” (Fig.1 node A) mainly distributed in the Amazon forest.

The tetra-merous flower is the basic arrangement found in most *Eugenia* species, however, *Eugenia neograndifolia* (the type species of *Calycorectes* under *C. grandifolius*) is unusual in having a hexamerous corolla (Amshoff, 1951; Lemée, 1953;

McVaugh, 1969). Results presented here newly interpret this condition as the *petaloid* pattern, where the two external fused calyx lobes cover the bud while the two internal calyx lobes are free and petaloid, giving the impression of six petals. A similar condition is found in *Eugenia petaloidea* ined. (Fig. 6) in which the effective display of the corolla is significantly intensified with an apparent increase to six petals at anthesis. The 'hexamerous' corolla was also described in at least two other species, *Calycorectes batavorum* and *C. enormis* (McVaugh, 1969), currently under *Eugenia batavorum* (McVaugh) Mattos and *E. enormis* (McVaugh) Mattos, respectively. The low phylogenetic signal of the *petaloid* pattern contrasts with a high value of lambda. This indicates that the distribution of this character over the phylogeny is non-independent and homoplastic. The *petaloid* pattern is exclusive to node B (Fig. 1) within *Eugenia* sect. *Umbellatae* and arose at least four times within it; two of these fusion events occurred in lineages corresponding to the genera *Calyptrogenia* and *Hottea,* both nested in the Caribbean clade (Fig. 1 node D). The bud of *Calyptrogenia cuspidata* opens via a calyptra-like structure. However, this structure is not homologous to the calyptra found in *Calyptranthes* (*Myrcia* s.l) that results from complete fusion of five calyx lobes (Vasconcelos et al., 2017b). The calyptra-like structure of *Calyptrogenia* results from fusion of two calyx lobes whilst the two internal petaloid lobes remain free (Fig. 4I). A similar condition is likely to be found in *Hottea,* where two vestigial lobes at the apex of the bud indicate fusion of the two external calyx lobes. *Hottea* buds open by irregular tearing (Fig. 4H).

Stamen position in the bud has systematic implication in *Myrteae* (Vasconcelos et al., 2015) and taxonomic relevance for *Eugenia*. This is a useful character when only flowering material is available, allowing distinction of e.g. fused calyx *Eugenia* from *Plinia* by straight stamens in the bud in the former and strongly curved in the latter. The character of straight stamens in the bud is almost ubiquitous in *Eugenia* and sister clade *Myrcianthes* making it likely the ancestral condition in *Eugenia*. However, in an extreme exception to the rule, flowers of the *longohypanthium* pattern have strongly curved stamens as found in *Eugenia longohypanthiana* ined. (Fig. 4J). Elongation of the hypanthium and the extended tissue bearing whorls of stamens results in a condition similar to the *hyper-hypanthium* pathway found in *Myrcia* s.l. (Vasconcelos et al., 2017b).

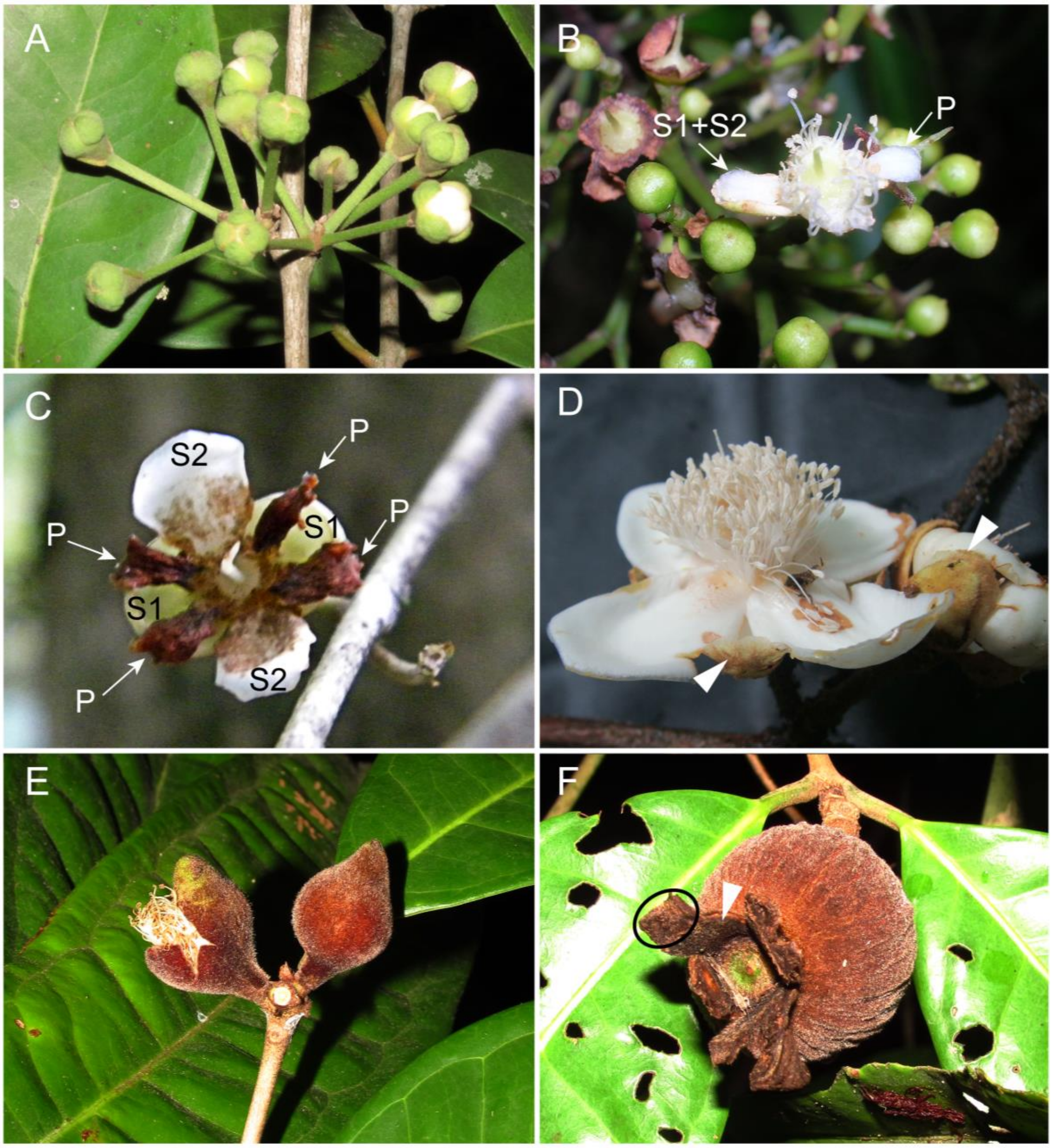

Figure 6. Field pictures of flowers showing the different patterns of calyx fusion in *Eugenia*. A. *Heterosepalous* pattern. B. *Homosepalous* pattern in *E. guanabarina* opening transversely resulting in a structure calyptra-like. C. *Petaloid* pattern in *E. petaloidea* ined. D. *Membranisepalous* pattern in *E.* abunan; head arrows indicates the membranous tissue. E-F. *Longohypanthium* pattern. E. flower buds of *E. longohypanthiana*. F. Remnant of the calyx (circled) and hypanthium (head arrow) in the fruit of *E. longohypanthiana*. External sepals (S1); internal sepal (S2); petal (P).

4.3. Geographical relevance of calyx fusion

In several cases, lineages with fused calices have narrow distributions in specific biogeographic regions. For example, the *Eugenia* sect. *Schizocalomyrtus* species are mostly restricted to the Atlantic forest except for widely distributed species such as *Eugenia acutata* and *E. subterminalis* and species of the "*Eugenia moschata* group" are associated with Amazonian forest. The "*Calycorectes* group" is endemic to Guiana Shield, an area noted for its long-term climatic stability (Hoorn et al., 2010). The calyx of *Eugenia* has apparently fused on at least six occasions in clades comprising mostly Atlantic forest species, once in an Amazonian forest clade, once on the Guiana Shield and twice in Central America. It appears that calyx fusion in *Eugenia* is associated with shaded or highly humid habitats. Even widely distributed species that occur in the Cerrado domain (Brazilian *savanna*) are restricted to forest along rivers. Common responses to adaptive selection can result in similar phenotypes (Wake et al., 2011) that are here apparently expressed independently as a fused calyx.

4.4. Functional role of the fused calyx

Similar floral displays were recovered by different opening patterns of the calyx. For instance, species that tear into irregular lobes can result from three patterns (*petaloid*, *longohypanthium* and *homosepalous*) whereas species that open via a calyptra-like structure can result from two patterns (*petaloid* and *homosepalous*). The opening patterns evolved independently in different lineages as did the fused calyx patterns (*homosepalous*, *heterosepalous* and *petaloid*). However, the standard flower display of white petals and many stamens with anthers attached to long filaments retaining pollen as reward (Proença and Gibbs, 1994) shared by all *Eugenia*, including fused calyx species, is likely the strategy conserved along lineages for pollinator attraction.

It is remarkable that species of *Eugenia* as well as phylogenetically distant genera such as *Angophora*, *Syzygium*, *Pleurocalyptus* and *Corymbia* also have species with flower modifications that close the bud. These more distantly related groups have developed independent mechanisms to close the bud, e.g. by means of opercular structure resulting from coralline whorl attachments in *Angophora* and bloodwood eucalypts (Drinnan and Ladiges, 1988), or by simultaneous attachment of coralline and calycine whorls in 'Eudesmieae B' eucalypts (Drinnan and Ladiges, 1989). These related groups have independently developed mechanisms for bud closure. In the context of Neotropical Myrtaceae, one development pathway of *Myrcia* s.l., by which buds close by means of hypanthium extension ('hyper-hypanthium' of Vasconcelos et al., 2017a), shares similarities with the *longohypanthium* development pattern here described in *Eugenia*. There is no single pathway of floral modification resulting in bud closure in Myrtaceae; the trait has evolved independently several times. Parallelism in closely related groups is more common than previously appreciated; it appears that its role driving diversification in the Neotropics may have been underestimated (Giussani et al., 2001; Bess et al., 2005; Goldenberg et al., 2008; Simon et al., 2009).

Hypotheses for the functional role of closed buds in Myrtaceae can appear paradoxical, for instance the character may relate to protection of the flower from dehydration but also from excess moisture favouring fungal proliferation (pers. obs.). In groups with lignified reproductive structures (Wilson, 2011) such as *Angophora*, *Eucalyptus* and *Corymbia*, the closed calyx may provide fire-resistance (Macphail and Thornhill, 2016). The inference that the evolution of the closed bud in Myrtaceae is a response to different environmental pressures, further emphasises that the trait evolved several times. Similarly, in the Neotropical genera *Campomanesia* and *Psidium,* species with closed buds have evolved independently in both humid and dry environment. The functional role of the closed bud is uncertain in some cases. Fusion of different structures attached to floral whorls may be in response to particular conditions (Belsham and Orlovich 2002, 2003) that require further investigation before their contribution to diversification in the Neotropics is fully understood.

4.5. Systematic implications of morphology and diagnosis of clades

As demonstrated here, the fused calyx, associated with several mechanisms floral development can be found throughout *Eugenia.* However, the calyx is commonly fused to some degree in three strongly supported clades. One of these is *Eugenia* sect. *Schizocalomyrtus* (Giaretta et al., Chapter 4), the two others fall within *Eugenia* sect. *Umbellatae*.

Eugenia sect. *Schizocalomyrtus* has calyx lobes fused from two thirds of the bud to completely closed, usually leaving a 1–3 mm diameter pore surrounded by four vestigial lobes. Calyx fusion is mostly *heterosepalous* but *homosepaly* and the unusual *longohypanthium* pattern are also found in this clade. *Eugenia* sect. *Schizocalomyrtus* occurs principally in the Atlantic Forest of eastern Brazil.

The *"Calycorectes group"* includes the type species *Calycorectes grandifolius* (currently under *E. neograndifolia*); it has calyx lobes that are nearly closed leaving two or four vestigial lobes. Calyx fusion in this group follows the *homosepalous* and *petaloid* patterns. The *"Calycorectes group"* mostly occurs in the lowland forests of the Guiana Shield.

The *"Eugenia moschata group"* consistently follows the *membranisepalous* development pattern, with *Eugenia kerianthera*, sister to the rest, exhibiting *heterosepaly*. The *"Eugenia moschata group"* is mainly found in Amazon lowland forest extending to the Guiana shield and gallery forests of the Brazilian *savanna* in the case of the widespread *Eugenia moschata* complex (as *Eugenia feijoi* complex in McVaugh, 1969).

5. Conclusions

Results presented here further exemplify how detailed morphological survey of fused calyx in *Eugenia* using a phylogenetic framework reveals complexity rather than simplification. This complexity should be incorporate into future classifications as part of more integrative taxonomy that incorporates evidence from multiple sources. The homoplastic nature of the calyx fusion provides more evidence that sets of characters can be used to diagnose taxa instead of the pursuit of single innovative synapomorphies. Due to high species diversity in *Eugenia*, this study is not an exhaustive survey of fused calyx species. Homoplasy may further increase as the number of taxa studied increases. However, results presented here have major implications for better interpreting patterns of floral evolution and systematics in angiosperms. Future directions include investigate functional and ecological factors driving flower morphology and diversifications rates, particularly in the mega-diverse *Eugenia* sect. *Umbellatae*. Evaluate the mechanisms that shape diversity in *Eugenia* may have major impact to the understanding of the Neotropical diversification.

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References

Amshoff, G.J.H., 1951. Myrtaceae. In: Pulle, A. (Ed.), Flora of Suriname, 2nd edn. The Royal Institute for the Indies, Utrecht, pp. 56-158.

Bayly, M.J., 2016. Phylogenetic studies of eucalypts: Fossils, morphology and genomes. Proc. R. Soc. Victoria 128,12–24. doi: 10.1071/RS16002.

Belsham, S.R., Orlovich, D.A., 2002. Development of the hypanthium and androecium in New Zealand Myrtoideae (Myrtaceae). New Zeal. J. Bot. 40, 687–695. doi: 10.1080/0028825X.2003.9512836.

Belsham, S.R., Orlovich, D.A., 2003. Development of the hypanthium and androecium in *Acmena smithii* and *Syzygium australe* (*Acmena* alliance, Myrtaceae). Aust. Syst. Bot. 16, 621–628. doi: 10.1071/SB02036.

Berg, O.C., 1856. 129-384 Revisio Myrtacearum huc usque cognitarum s. Klotzschii “Flora Americae aequinoctialis” exhibens Myrtaceas. Linnaea 27,129–384.

Bess, E.C., Doust, A.N., Kellogg, E.A., 2005. A naked grass in the "bristle clade’’: A phylogenetic and developmental study of Panicum section Bulbosa (Paniceae : Poaceae). Int. J. Plant. Sci. 166, 371–381. doi: 10.1086/428701.

Briggs, B.G., Johnson, L.A.S., 1979. Evolution in the Myrtaceae - Evidence from inflorescence structure. Proc. Linn. Soc. New South Wales 102, 157–256.

Bünger, M.O., Mazine, F.F., Forest, F., Bueno, M.L., Stehmann, R., Lucas, E.J., 2016a. The evolutionary history of *Eugenia* sect. *Phyllocalyx* (Myrtaceae) corroborates historically stable areas in the southern Atlantic forests. Ann. Bot. 118, 1209–1223. doi: 10.1093/aob/mcw209

Bünger, M.O., Mazine, F.F., Lucas, E.J., Stehmann, J.R., 2016b. Circumscription and synopsis of *Eugenia* section *Speciosae* Bünger & Mazine (Myrtaceae). PhytoKeys 61, 73–80. doi: 10.3897/phytokeys.61.7904

Candolle, A.P. de, 1828. Myrtaceae. In: Candolle, A.P. de (Ed.), Prodromus systematis naturalis regni vegetabilis. Treuttel et Würtz, Paris, pp. 207–296.

Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. Nat. Methods 9, 772–772. doi: 10.1038/nmeth.2109.

Drinnan, A.N., Ladiges, P.Y., 1988. Perianth development in Angophora and the bloodwood Eucalypts (Myrtaceae). Plant Syst. Evol. 160, 219–239. doi: 10.1007/BF00936049.

Drinnan, A.N., Ladiges, P.Y., 1989. Corolla and androeeium development in some *Eudesmia eucalypts* (Myrtaceae). Plant Syst. Evol. 165, 239–254.

Drummond, A., Rambaut, A., 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7, 214. doi: 10.1186/1471-2148-7-214.

Edgar, R.C., 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. BMC Bioinformatics 5, 113. doi: 10.1186/1471-2105-5-113.

Flora do Brasil 2020 (ongoing). Jardim Botânico do Rio Janeiro, Rio Janeiro, Brazil. http://floradobrasil.jbrj.gov.br. Accessed. 24 Jul 2017.

Gadek, P., Wilson, P., Quinn, C., 1996. Phylogenetic reconstruction in Myrtaceae using matK, with particular reference to the position of Psiloxylon and Heteropyxis. Aust. Syst. Bot. 9, 283–290. doi: http://dx.doi.org/10.1071/SB9960283.

Giussani, L.M., Cota-Sánchez, J.H., Zuloaga, F.O., Kelloggm E., 2001a. A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C4 photosynthesis. Am. J. Bot. 88, 1993–2012. doi: 10.2307/3558427.

Goldenberg, R., Penneys, D.S., Almeda, F., Judd, W.S., Michelangeli, F.A., 2008. Phylogeny of *Miconia* (Melastomataceae): Patterns of Stamen Diversification in a Megadiverse Neotropical Genus. Int. J. Plant Sci. 169, 963–979. doi: 10.1086/589697.

Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E., Challenger, W., 2008. GEIGER: Investigating evolutionary radiations. Bioinformatics 24, 129–131. doi: 10.1093/bioinformatics/btm538.

Hoorn, C., Wesselingh, F.P., Steege, H. ter, Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T., Antonelli, A., 2010. Amazonia Through Time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity. Science 330(12), 927–931. doi: 10.1126/science.1194585.

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., Meintjes, 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. doi: 10.1093/bioinformatics/bts199.

Ladiges, P.Y., Udovicic, F., Drinnan, A.N., 1995. Eucalypt phylogeny - Molecules and Morphology. Aust. Syst. Bot. 8, 483–497. doi: 10.1071/SB9950483.

Landrum, L.R., Kawasaki, M.L., 1997. The Genera of Myrtaceae in Brazil: An Illustrated Synoptic Treatment and Identification Keys. Brittonia 49, 508. doi: 10.2307/2807742.

Legrand, C.D., Klein, R.M., 1972. Mirtáceas: Calycorectes. In: Reitz, P.R. (Ed), Flora Ilustrada Catarinense. Itajaí, pp. 555–569.

Lemée, A., 1953. Flore de la Guyane Française. In: Lechevalier, P. (Ed), Flore de la Guyane Française, Tome III. Paris, pp. 138–167.

Lucas, E.J., Bünger, M.O., 2015. Myrtaceae in the Atlantic forest: their role as a “model” group. Biodivers. Conserv. 24, 2165–2180. doi: 10.1007/s10531-015-0992-7.

Lucas, E.J., Harris, S.A., Mazine, F.F., Belsham, S.R., Nic Lughadha, 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. doi: 10.2307/25065906.

Lucas, E.J., 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. Plant Sci. 172, 915–934. doi: 10.1086/660913.

Macphail, M., Thornhill, A.H., 2016. How old are the eucalypts? A review of the microfossil and phylogenetic evidence. Aust. J. Bot. 64, 579–599. doi: 10.1071/BT16124.

Mattos, J.R., 2005. Considerações sobre *Calycorectes* O.Berg. Loefgrenia 120, 1–24.

Mazine, F.F., Bünger, M.O., Faria, J.E.Q., Lucas, E., Souza, V.C., 2016. Sections in *Eugenia* (Myrteae, Myrtaceae): nomenclatural notes and a key. Phytotaxa 289, 225–236.

Mazine, F.F., Souza, V.C., Sobral, M.M., Forest, F., Lucas, E., 2014. A preliminary phylogenetic analysis of *Eugenia* (Myrtaceae: Myrteae), with a focus on Neotropical species. Kew Bull. 69, 1–14. doi: 10.1007/s12225-014-9497-x.

McVaugh, R., 1969. The Botany of the Guyana Highland - Part VIII: Myrtaceae. Mem. N. Y. Bot. Gard.18, 55–286.

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. New Orleans, LA, pp. 1–8.

Münkemüller, T., Lavergne, S., Bzeznik, B., Dray, S., Jombart, T., Schiffers, K., Thuiller, W., 2012. How to measure and test phylogenetic signal. Methods Ecol. Evol. 3, 743–756. doi: 10.1111/j.2041-210X.2012.00196.x.

Oliveira-Filho, A., Fontes, M., 2000. Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate. Biotropica 32, 793–810. doi: 10.1111/j.1744-7429.2000.tb00619.x.

Pagel, M., 2004. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proc. R. Soc. Lond. B. 255, 37–45.

Paradis, E., Claude, J., Strimmer, K., 2004. APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20, 289–290. doi: 10.1093/bioinformatics/btg412.

Proença, C.E.B., Gibbs, P.E., 1994. Reproductive biology of eight sympatric Myrtaceae from Central Brazil. New Phytol. 126, 343–354.

Revell, L., Harmon, L., Collar, D., 2008. Phylogenetic Signal, Evolutionary Process, and Rate. Syst. Biol. 57, 591–601. doi: 10.1080/10635150802302427.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61, 539–542. doi: 10.1093/sysbio/sys029.

Sanderson, M.J., Hufford, L., 1996. Homoplasy and the evolutionary process: an afterword. In: Sanderson, M.J., Hufford, L. (Eds), Homoplasy: the recurrence of similarity in evolution. Academic Press, San Diego, California, pp. 327–330.

Shaw, J., Lickey, E.B., Schilling, E.E., Small, R.L., 2007. Comparison of whole chloroplast genome sequences to choose noncoding regions for phylogenetic studies in angiosperms: the tortoise and the hare III. Am. J. Bot. 94, 275–288.

Simon, M.F., Grether, R., de 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. Natl. Acad. Sci. 106, 20359–20364. doi: 10.1073/pnas.0903410106.

Sobral, M., 2003. A família Myrtaceae no Rio Grande do Sul. Editora Unisinos, São Leopoldo.

Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688–2690. doi: 10.1093/bioinformatics/btl446.

Vasconcelos, T.N.C., Lucas, E.J., Faria, J.E.Q., Prenner, G., 2017a. Floral heterochrony promotes flexibility of reproductive strategies in the morphologically homogeneous genus Eugenia (Myrtaceae). Ann. Bot. 1–14. doi: 10.1093/aob/mcx142.

Vasconcelos, T.N.C., Prenner, G., Bünger, 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., 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. Evol. Syst. 24, 11–24. doi: 10.1016/j.ppees.2016.11.001.

Vasconcelos TNC, Proença CEB, Ahmad B, Aguilar, D.S., Aguilar, R., Amorim, B.S., Campbell, K., Costa, I.R., De-carvalho, P.S., Faria, J.E.Q., Giaretta, A., Kooij, P.W., Lima, D.F., Mazine, F.F., Peguero, B., Prenner, G., Santos, M.F., Soewarto, J., Wingler, A., Lucas, E.J., 2017c. Myrteae phylogeny, calibration, biogeography and diversification patterns: Increased understanding in the most species rich tribe of Myrtaceae. Mol. Phylogenet. Evol. 109:113–137. doi: 10.1016/j.ympev.2017.01.002.

Wake, D.B., Wake, M.H., Specht, C.D., 2011. Homoplasy: from detecting pattern to determining process and mechanism of evolution. Science 33, 1032–1035.

WCSP., 2017. World Checklist of Selected Plant Families. In: Facil. by R. Bot. Gard. Kew. apps.kew.org/wcsp/myrtaceae. Accessed. 26 Jul 2017.

Wilson, C.E., Forest, F., Devey, D.S., Lucas, E.J., 2016. Phylogenetic Relationships in Calyptranthes (Myrtaceae) with Particular Emphasis on Its Monophyly Relative to Myrcia s.l. Sist. Bot. 41, 378–386. doi: 10.5061/dryad.8p800.

Wilson, P.G., 2011. Myrtaceae. In: Kubitzki, K. (Ed), The families and genera of vascular plants. Flowering plants, eudicots: Sapindales, Cucurbitales, Myrtaceae, 10th edn. Springer-Verlag, Berlin, p. 436.

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. doi: 10.1007/s00606-004-0162-y.

Wilson, P.G., O´Brien, M.M., Gadek, P.A., Quinn, C.J., 2001. Myrtaceae Revisited : a

Reassessment of infrafamilial groups. Am. J. Bot. 88, 2013–2025. doi: 10.2307/3558428.

Appendix

Appendix A. Molecular sampling list, collection locality and DNA bank number for the species used in the phylogenetic analysis. Blank space indicates missing data. Accessions with en-dash (–) indicate that DNA aliquots are not available on DNA bank.

Species	**Collector**	**Number**	**Herbarium**	**ITS**	**psbA-trnH**	**rpl16**	**rpl32-trnL**	**trnQ-rps16**
Algrizea macrochlamys (DC.) Proença & Nic Lugh.	A. Giulietti	1648	BHCB	KEW16833	KEW16833	KEW16833	KEW16833	KEW16833
Calycorectes bergii Sandwith	A. Giaretta	1587	K, SPF	KEW46506	KEW46506	KEW46506	KEW46506	KEW46506
Calyptrogenia cuspidata Alain	T. Vasconcelos	593	K	MF954023	MF954280	MF954321	MF954207	MF954087
Calyptrogenia grandiflora Burret	T. Vasconcelos	588	K	MF954024	MF954281	MF954322	MF954208	MF954088
Campomanesia ilhoensis Mattos	M. Ibrahim	122	K	KEW34650	KEW34650	KEW34650	KEW34650	KEW34650
Eugenia abunan Sobral	G. Pereira-Silva	16487	CEN	KEW46519	KEW46519	KEW46519	KEW46519	KEW46519
Eugenia acutata Miq.	T. Vasconcelos	506	K	MF954031	MF954288	MF954331	MF954216	MF954095
Eugenia adenocalyx DC.	A. Giaretta	1441	K	MF954042	MF954299	MF954342	MF954219	MF954105
Eugenia astringens Cambess.	F. Mazine	782	ESA, K	KJ187606	KJ469655	KEW20843	KEW20843	KEW20843
Eugenia axillaris (Sw.) Willd.	M. Hamilton	553	K	KJ187607	KJ469656	KEW30702	KEW30702	KEW30702
Eugenia azuruensis O.Berg	J. Faria	4186	UB	MF954033	MF954290	MF954333	MF954423	
Eugenia biflora (L.) DC.	F. Mazine	1075	ESA	KJ187610	KJ469659	KEW20687	KEW20687	KEW20687
Eugenia bimarginata DC.	F. Mazine	469	ESA, K	KJ187611	KJ469660	KEW20830	KEW20830	KEW20830
Eugenia brasiliensis Lam.	E. Lucas	126	K	KEW20949	KEW20949	KEW20949	KEW20949	KEW20949
Eugenia brevistyla D.Legrand 1	A. Giaretta	1493	K, SPF	–	–	–	–	–
Eugenia brevistyla D.Legrand 2	F. Mazine	993	ESA, K	KJ187614	KJ469663	KEW20683	KEW20683	KEW20683
Eugenia bullata Pancher ex Guillaumin	T. Vasconcelos	608	K	MF954034	MF954291	MF954334	MF954424	MF954097
Eugenia caloneura Sobral & Rigueira	E. Lucas	1160	K	KEW46494	KEW46494	KEW46494	KEW46494	KEW46494
Eugenia coffeifolia DC.	B. Holst	9516	SEL	KEW36243	KEW36243	KEW36243	KEW36243	KEW36243
Eugenia crassa Sobral	L. Giacomin	1860	BHCB	KX789269	KX789296	KX789321	KX789350	KX910671

Species	Collector	Number	Herbarium	ITS	psbA-trnH	rpl16	rpl32-trnL	trnQ-rps16
Eugenia dodonaeifolia Cambess.	E. Lucas	257	ESA, K	KJ187644	KJ469693	KEW45793	KEW45793	KEW45793
Eugenia dysenterica DC.	F. Mazine	466	ESA, K	KJ187620	KEW20844	KJ469669	KEW20844	KEW20844
Eugenia excelsa O.Berg	E. Lucas	125	ESA, K	KJ187621	KJ469670	KEW20950	KEW20950	KEW20950
Eugenia expansa (O.Berg) Nied.	M. Bünger	634	BHCB, K	KX789279	KX789297	KX789322	KX789351	KX910672
Eugenia fasciculiflora O.Berg	M. Simon	2032	CEN	KEW46515	KEW46515	KEW46515	KEW46515	KEW46515
Eugenia fissurata Mattos 1	A. Giaretta	1639	K	KEW46510	KEW46510	KEW46510	KEW46510	KEW46510
Eugenia fissurata Mattos 2	A. Giaretta	1640	K	KEW46511	KEW46511	KEW46511	KEW46511	KEW46511
Eugenia florida DC.	F. Mazine	965	ESA, K	KJ187622	KJ469671	KEW20841	KEW20841	KEW20841
Eugenia glandulosa Cambess.	J. Faria	37	BHCB	KX789277	KX789299	KX789324	KX789353	KX910674
Eugenia goiapabana Sobral & Mazine	M. Bünger	s/n	BHCB	KX789270	KX789300	KX789325	KX789354	KX910675
Eugenia guanabarina ined.	A. Giaretta	1629	K, SPF	KEW46509	KEW46509	KEW46509	KEW46509	KEW46509
Eugenia joseramosii M.A.D. Souza & Scudeller 1	A. Giaretta	1651	SPF, K	KEW46513	KEW46513	KEW46513	KEW46513	KEW46513
Eugenia joseramosii M.A.D. Souza & Scudeller 2	A. Giaretta	1655	SPF, K	KEW46514	KEW46514	KEW46514	KEW46514	KEW46514
Eugenia kerianthera M.A.D.Souza	A. Giaretta	1517	SPF	KEW46504	KEW46504	KEW46504	KEW46504	KEW46504
Eugenia lagoensis Kiaersk.	C. Fraga	2436	K	–	–	–	–	–
Eugenia longohypanthiana ined.	A. Giaretta	1500	SPF, K	–	–	–	–	–
Eugenia macrobracteolata Mattos	J. Faria	3050	UB	KX789283	KX789303	KX789328	KX789357	KX910678
Eugenia melanogyna (D.Legrand) Sobral	F. Mazine	969	ESA, K	KJ187624	KJ469673	KEW20694	KEW20694	KEW20694
Eugenia modesta DC.	F. Mazine	854	ESA, K	KJ187625	KEW20832	KEW20832	KEW20832	KEW20832
Eugenia monticola (Sw.) DC.	T. Vasconcelos	566	K	MF954037	MF954294	MF954337	MF954427	MF954100
Eugenia moschata (Aubl.) Nied. ex T.Durand & B.D.Jacks	M. Simon	971	CEN	KEW46492	KEW46492	KEW46492	KEW46492	KEW46492
Eugenia cf. moschata (Aubl.) Nied. ex T.Durand & B.D.Jacks	A. Giaretta	1514	SPF	KEW46503	KEW46503	KEW46503	KEW46503	KEW46503
Eugenia myrcianthes Nied. 1	J. Faria	2850	UB	KEW44019	KEW44019	KEW44019	KEW44019	KEW44019
Eugenia myrcianthes Nied. 2	A. Giaretta	s/n	K	–	–	–	–	–

Species	Collector	Number	Herbarium	ITS	psbA-trnH	rpl16	rpl32-trnL	trnQ-rps16
Eugenia neograndifolia Mattos 1	A. Giaretta	1615	SPF	KEW46507	KEW46507	KEW46507	KEW46507	KEW46507
Eugenia neograndifolia Mattos 2	A. Giaretta	1616	SPF	KEW46508	KEW46508	KEW46508	KEW46508	KEW46508
Eugenia neoriedeliana ined.	A. Giaretta	1489	SPF, K	KEW46500	KEW46500	KEW46500	KEW46500	KEW46500
Eugenia neoverrucosa Sobral	E. Lucas	118	ESA, K	KJ187628	KJ469676	KEW20951	KEW20951	KEW20951
Eugenia nutans O.Berg	E. Lucas	281	ESA, K	KJ187629	KJ469677	KEW20829	KEW20829	KEW20829
Eugenia paludosa Pancher ex Brongn. & Gris	T. Vasconcelos	646	K	MF954038	MF954295	MF954338	MF954428	MF954101
Eugenia patens Poir.	E. Lucas	104	ESA, K	KJ187633	K20947	KJ469681	KX789361	KX910681
Eugenia percincta McVaugh	M. Simon	1158	CEN	KEW46493	KEW46493	KEW46493	KEW46493	KEW46493
Eugenia petaloidea 1 ined.	B. Amorim	1765[4]	UFP	–	–	–	–	–
Eugenia petaloidea 2 ined.	B. Amorim	1765[23]	UFP	–	–	–	–	–
Eugenia pisiformis Cambess.	E. Lucas	232	ESA, K	KJ187634	KJ469682	KEW20948	KEW20948	KEW20948
Eugenia pisonis O.Berg	A. Giaretta	1419	SPF	KEW46495	KEW46495	KEW46495	KEW46495	KEW46495
Eugenia pluriflora DC.	F. Mazine	961	ESA, K	KJ187636	KJ469684	KEW20831	KEW20831	KEW20831
Eugenia punicifolia Kunth (DC.)	F. Mazine	1065	ESA, K	KJ187638	KJ469686	KEW20691	KEW20691	KEW20691
Eugenia pyriformis Cambess.	F. Mazine	1028	ESA, K	KJ187639	KJ469687	KEW20944	KEW20944	KEW20944
Eugenia rara Rigueira & Sobral	A. Giaretta	1646	SPF, K	KEW46512	KEW46512	KEW46512	KEW46512	KEW46512
Eugenia reinwardtiana (Blume) DC.	E. Biffin	9245	Cultivated QRS	AY487301		AY463131		
Eugenia roseopetiolata N.Snow & Cable	T. Vasconcelos	s/n	Cultivated Kew	MF954040	MF954297	MF954340	MF954430	MF954103
Eugenia selloi B.D.Jacks	M. Bünger	566	BHCB, RB	KX789278	KX789308	KX789334	KX789363	KX910684
Eugenia sp.2	A. Brandão	283	RBR	KEW46488	KEW46488	KEW46488	KEW46488	KEW46488
Eugenia sp.3	A. Brandão	305	RBR	KEW46489	KEW46489	KEW46489	KEW46489	KEW46489
Eugenia sp.4	P. Fiaschi	3141	SPF	KEW46518	KEW46518	KEW46518	KEW46518	KEW46518
Eugenia speciosa Cambess.	M. Bünger	585	BHCB	KX789274	KX789310	KX789336	KX789365	KX910686
Eugenia stipitata McVaugh	T. Vasconcelos	677	K	MF954043	MF954300	MF954343	MF954220	
Eugenia subterminalis DC.	F. Mazine	s/n	K	KEW35910	KEW35910	KEW35910	KEW35910	KEW35910

Species	**Collector**	**Number**	**Herbarium**	**ITS**	**psbA-trnH**	**rpl16**	**rpl32-trnL**	**trnQ-rps16**
Eugenia umbrosa O.Berg	A. Giaretta	1498	SPF, K	KEW46502	KEW46502	KEW46502	KEW46502	KEW46502
Eugenia uniflora L.	E. Lucas	207	Cultivated K	AM234088	AM489828	AF215627*		KP722202
Eugenia vattimoana Mattos 1	A. Giaretta	1465	K, SPF	KEW46496	KEW46496	KEW46496	KEW46496	KEW46496
Eugenia vattimoana Mattos 2	A. Giaretta	1487	K, SPF	KEW46499	KEW46499	KEW46499	KEW46499	KEW46499
Eugenia verticillata (Vell.) Angely	Duarte	s/n (ESA85678)	ESA, K	KJ187650	KJ469700	KEW45805	KEW45805	KEW45805
Eugenia wentii Amshoff	B. Holst	9421	K	KJ187651	K35646	KJ469701	KX789368	KX910689
Eugenia zuccarini O.Berg	A. Brandão	159	RBR	KEW46487	KEW46487	KEW46487	KEW46487	KEW46487
Hotea neibensis Alain	T. Vasconcelos	590	K	MF954046	MF954303	MF954347	MF954224	MF954109
Myrceugenia alpigena (DC.) L.R. Landrum	E. Lucas	167	K	KX789289	KX789313	KEW19066	KX789370	KEW19066
Myrcia tomentosa (Aubl.) DC.	Savassi	s/n (ESA85681)	ESA	KEW20697	KEW20697	KEW20697	KEW20697	KEW20697
Myrcianthes fragrans (Sw.) McVaugh	M. Hamilton	552	K	KEW30701	KEW30701	KEW30701	KEW30701	KEW30701
Myrcianthes pungens (O.Berg) D.Legrand	J.E.Q. Faria	2759	UB	KEW43970	KEW43970	KEW43970	KEW43970	KEW43970
Myrtus communis L.	E. Lucas	211	Cultivated K	AM234149	AM489872	KEW10347	KEW10347	KEW10347
Plinia cordifolia (D.Legrand) Sobral	F. Mazine	957	ESA	KX789291	KX789315	KEW20679	KX789372	KEW20679

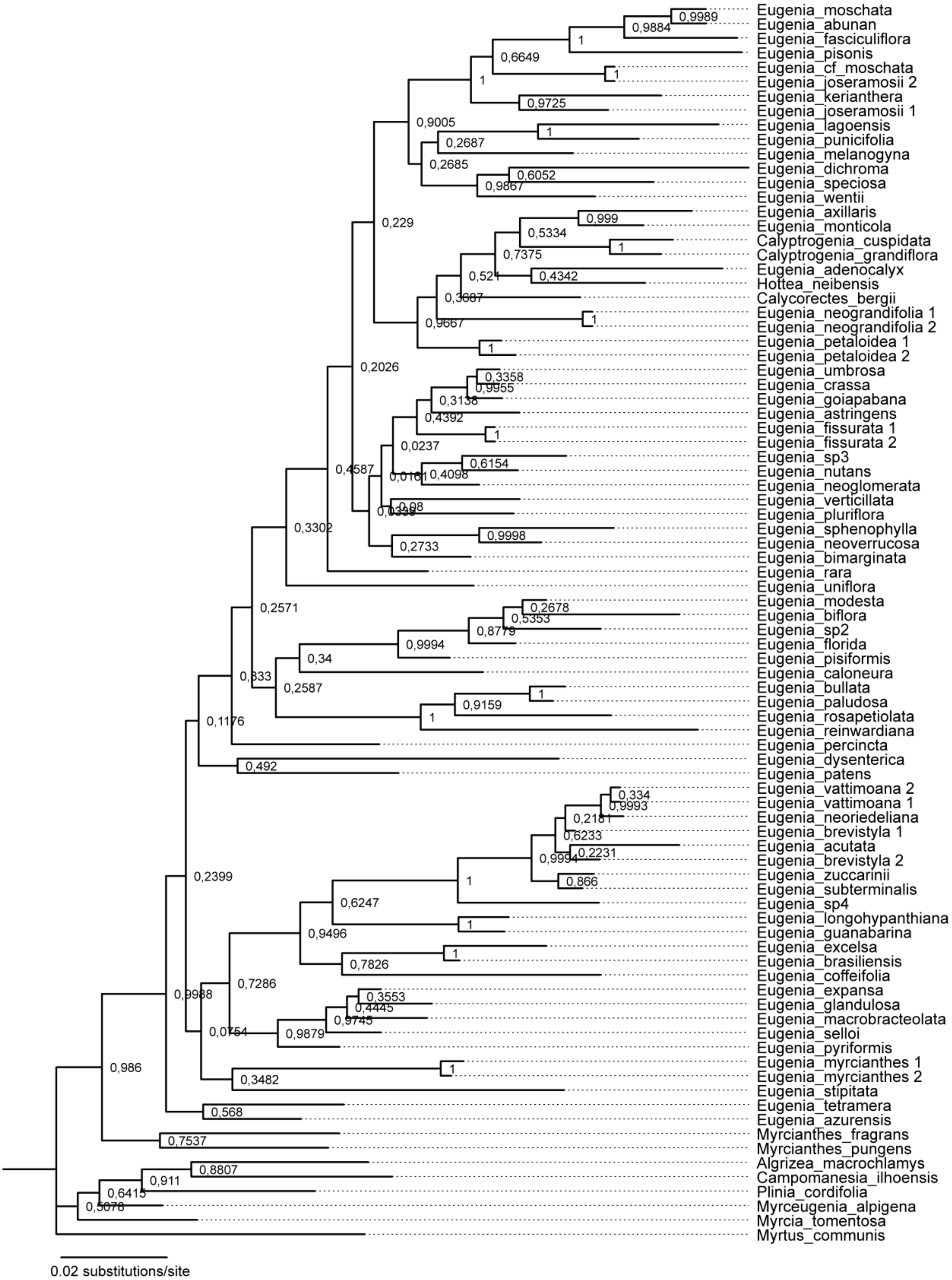
Appendix B. S1. Species analysed using the scanning electron microscopy (SEM).

Collector	**Number**	**Herbarium**	**Species**	**Section/group**	**Collection locality**	**Survey**	**Patterns**
E. Lucas	1125	K	*Calyptrogenia cuspidata* Alain	*Umbellatae*	Dominican Republic	Herbarium specimen	*Petaloid*
T.N. Vasconcelos	593	K	*Calyptrogenia cuspidata* Alain	*Umbellatae*	Dominican Republic	Herbarium specimen	*Petaloid*
T.N. Vasconcelos	506	K	*Eugenia acutata* Miq.	*Schizocalomyrtus*	Brazil	Spirit collection	*Heterosepalous*
F.F. Mazine	1009	K	*Eugenia brevistyla* D.Legrand	*Schizocalomyrtus*	Brazil	Herbarium specimen	*Heterosepalous*
F.F. Mazine	993	K	*Eugenia brevistyla* D.Legrand	*Schizocalomyrtus*	Brazil	Herbarium specimen	*Heterosepalous*
E. Lucas	1160	K	*Eugenia caloneura* Sobral & Rigueira	*uncertain*	Brazil	Herbarium specimen	*Homosepalous*
Oldman	B3581	K	*Eugenia fasciculiflora* O.Berg	*Umbellatae*	French Guiana	Herbarium specimen	*Membranisepalous*
A. Giaretta	1629	K	*Eugenia guanabarina* ined.	*Schizocalomyrtus*	Brazil	Spirit collection	*Homosepalous*
A. Giaretta	1630	K	*Eugenia guanabarina* ined.	*Schizocalomyrtus*	Brazil	Spirit collection	*Homosepalous*
J.E.L.S. Ribeiro	1767	INPA	*Eugenia joseramosii* M.A.D. Souza & Scudell.	*Umbellatae*	Brazil	Spirit collection	*Membranisepalous*
s.c.	s.n.	INPA	*Eugenia kerianthera* M.A.D.Souza	*Umbellatae*	Brazil	Spirit collection	*Membranisepalous*
A. Giaretta	1500	K	*Eugenia longohypanthiana* ined.	*Schizocalomyrtus*	Brazil	Spirit collection	*Longohypanthium*
A. Giaretta	1616	K	*Eugenia neograndifolia* (O.Berg) Mattos	*Umbellatae*	French Guiana	Spirit collection	*Petaloid*
H.C. Lima	2244	K	*Eugenia neoriedeliana* ined.	*Schizocalomyrtus*	Brazil	Herbarium specimen	*Homosepalous*
A. Giaretta	1419	K	*Eugenia pisonis* O.Berg	*Umbellatae*	Brazil	Spirit collection	*Membranisepalous*
Zardini	3616	K	*Eugenia subterminalis* DC.	*Schizocalomyrtus*	Paraguay	Herbarium specimen	*Heterosepalous*
T.N. Vasconcelos	s.n.	K	*Eugenia uniflora* L.	*Eugenia*	RBG Kew	Spirit collection	Free lobes

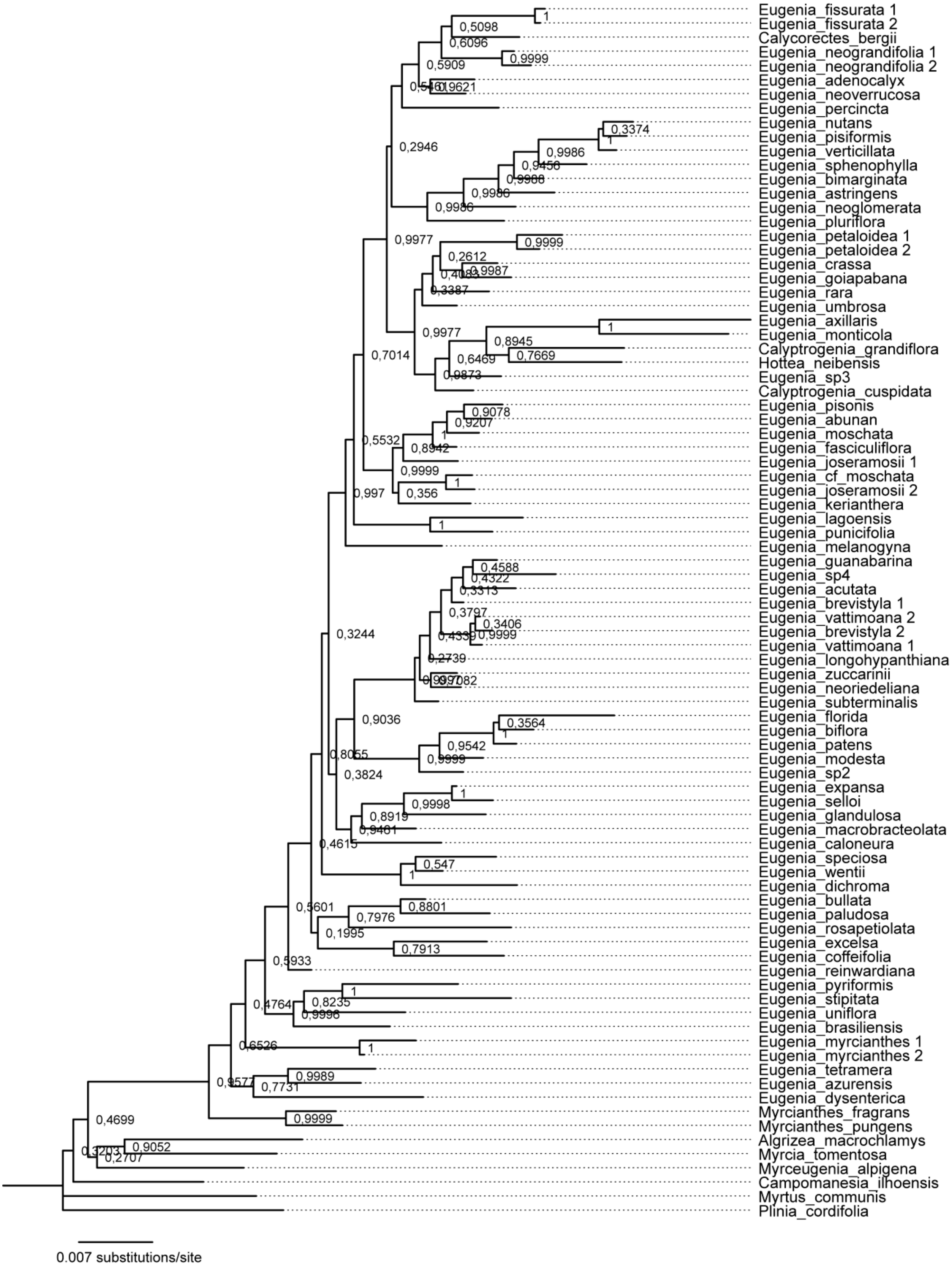
Collector	Number	Herbarium	Species	Section/group	Collection locality	Survey	Patterns
J.E.Q. Faria	6294	K	*Eugenia uniflora* L.	*Eugenia*	Brazil	Spirit collection	Free lobes
Angeli	597	K	*Eugenia vattimoana* Mattos	*Schizocalomyrtus*	Brazil	Herbarium specimen	*Homosepalous*
Angeli	191	K	*Eugenia vattimoana* Mattos	*Schizocalomyrtus*	Brazil	Herbarium specimen	*Homosepalous*
T.N. Vasconcelos	590	K	*Hottea neibensis* Alain	*Umbellatae*	Dominican Republic	Spirit collection	*Petaloid*
J.E.Q. Faria	4277	K	*Myrcianthes fragrans* (Sw.) McVaugh	*Umbellatae*	Brazil	Spirit collection	Free lobes
T.N. Vasconcelos	7	K	*Myrcianthes pungens* (O.Berg) D.Legrand	*Myrcianthes*	Costa Rica	Spirit collection	Free lobes
T.N. Vasconcelos	s.n.	K	*Myrtus communi*s L.	*Myrtus*	RBG Kew	Spirit collection	Free lobes
A. Giaretta	s.n.	K	*Myrtus communis* L.	*Myrtus*	RBG Kew	Spirit collection	Free lobes

Appendix C. Supplementary material of S2 to S10.

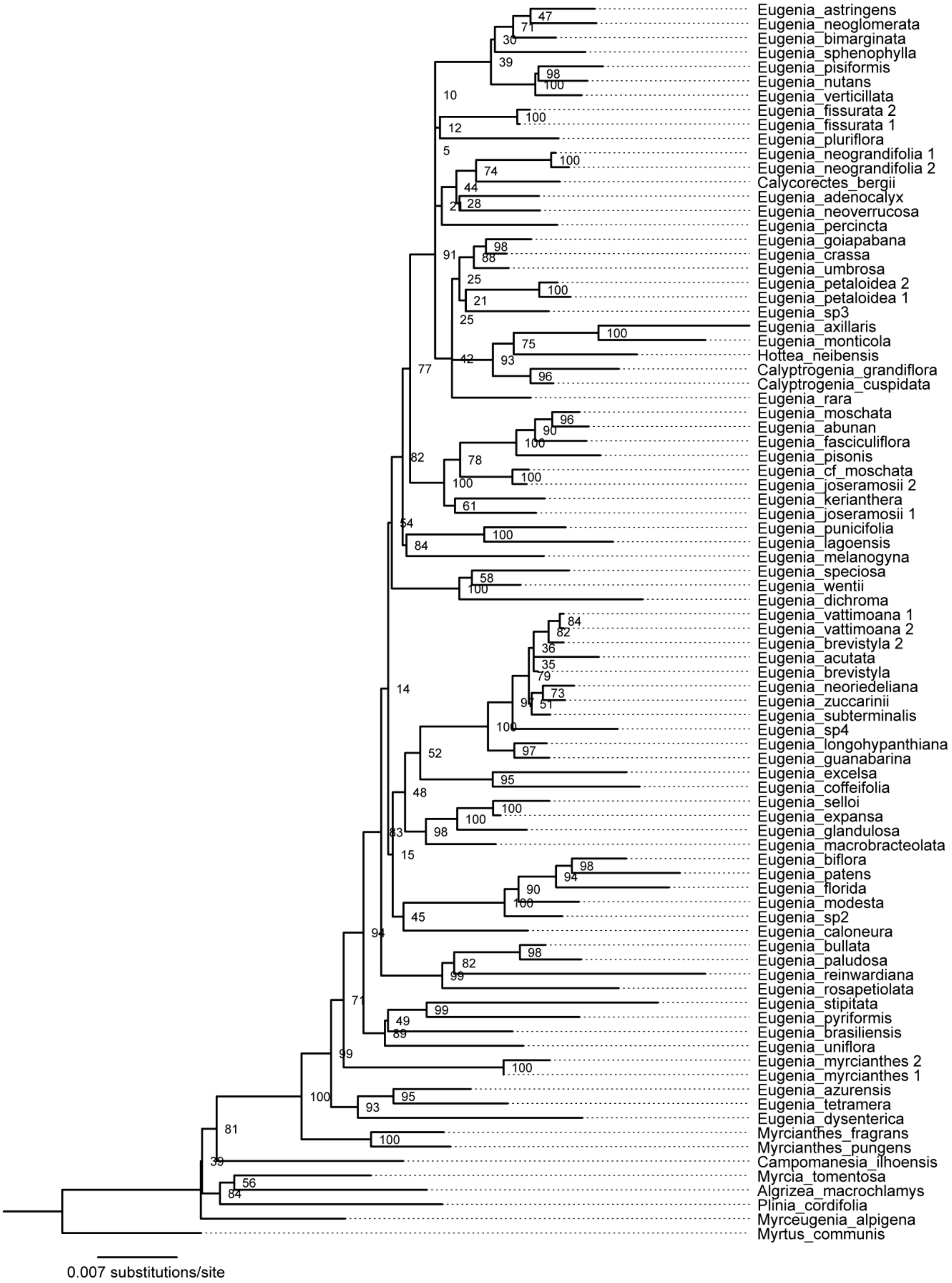
S2. Bayesian Inference tree of *Eugenia* resulting from the nuclear dataset. Posterior probabilities are shown above branches.



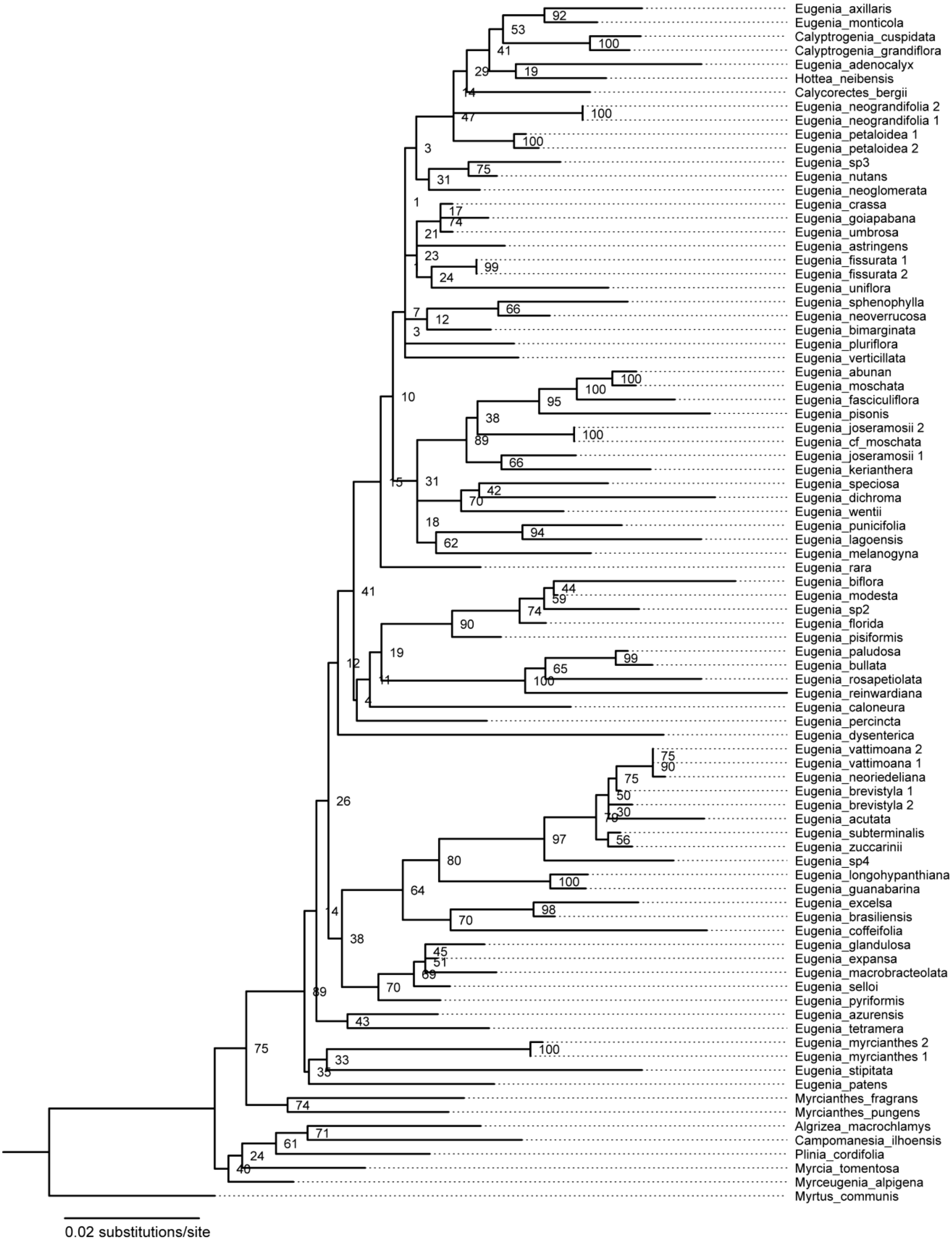
S3. Bayesian Inference tree of *Eugenia* resulting from the plastid dataset. Posterior probabilities are shown above branches.



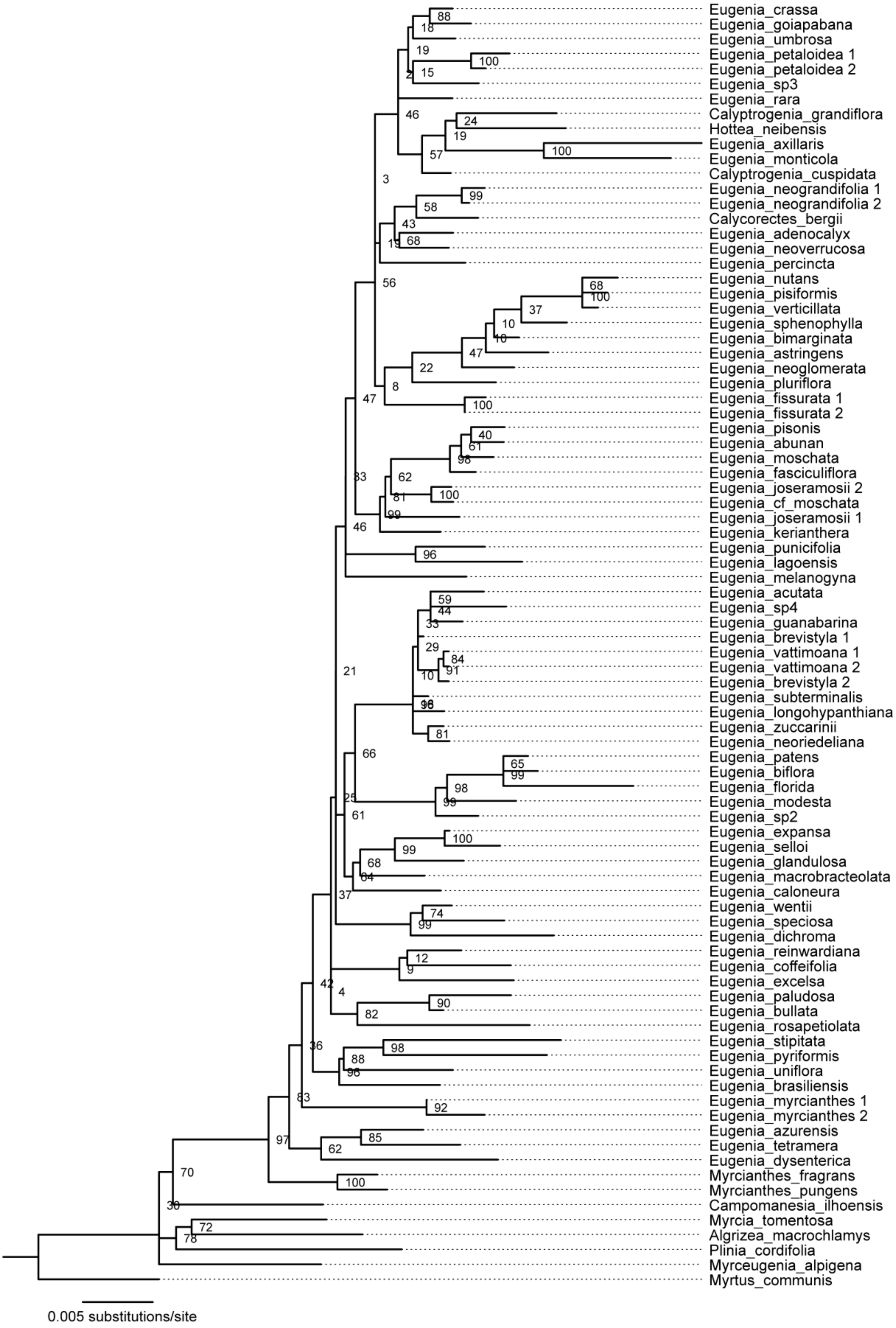
S4. Maximum likelihood tree of *Eugenia* resulting from the combined datasets. Bootstrap percentages are shown above branches.



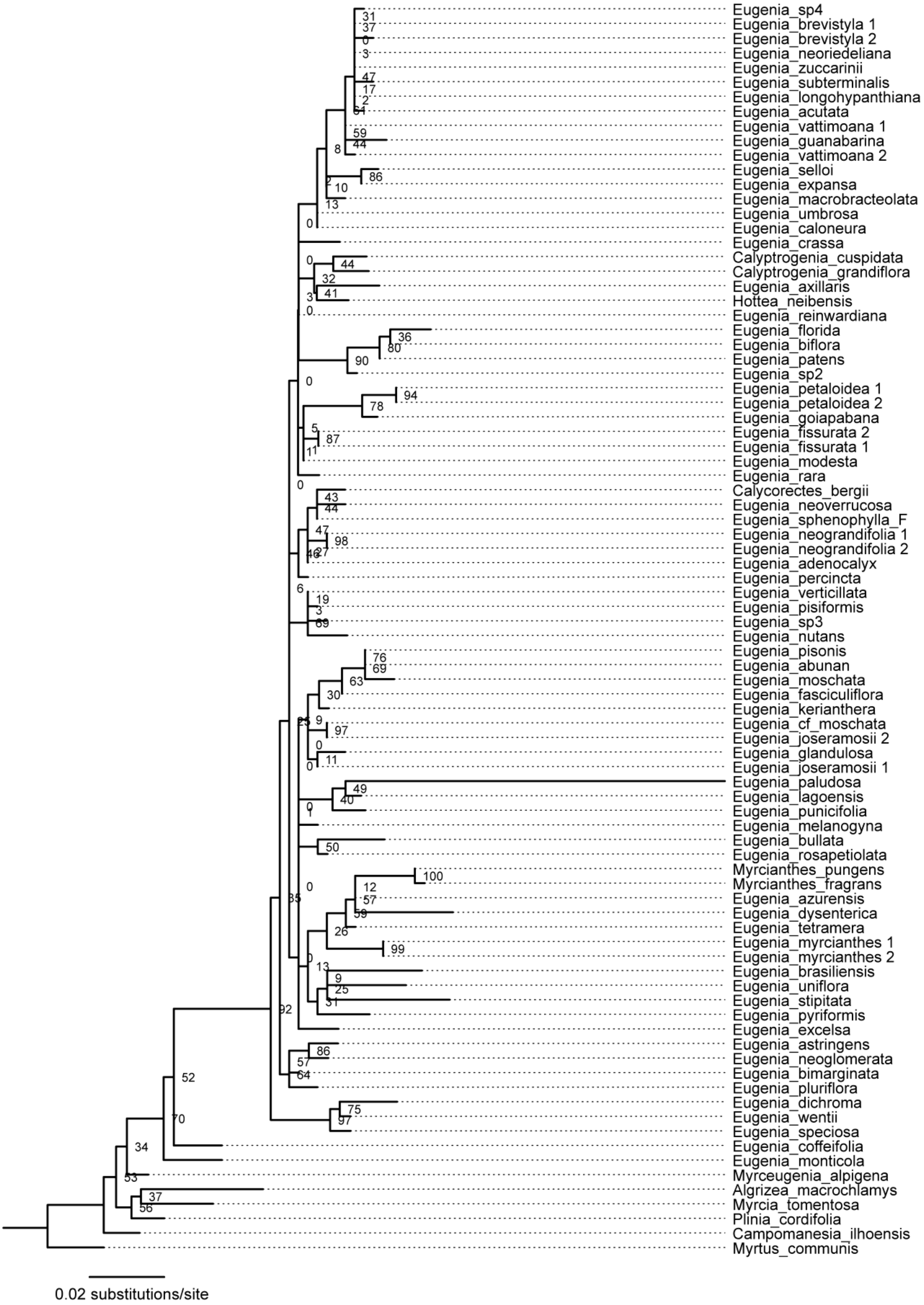
S5. Maximum likelihood tree of *Eugenia* resulting from the nuclear dataset. Bootstrap percentages are shown above branches.



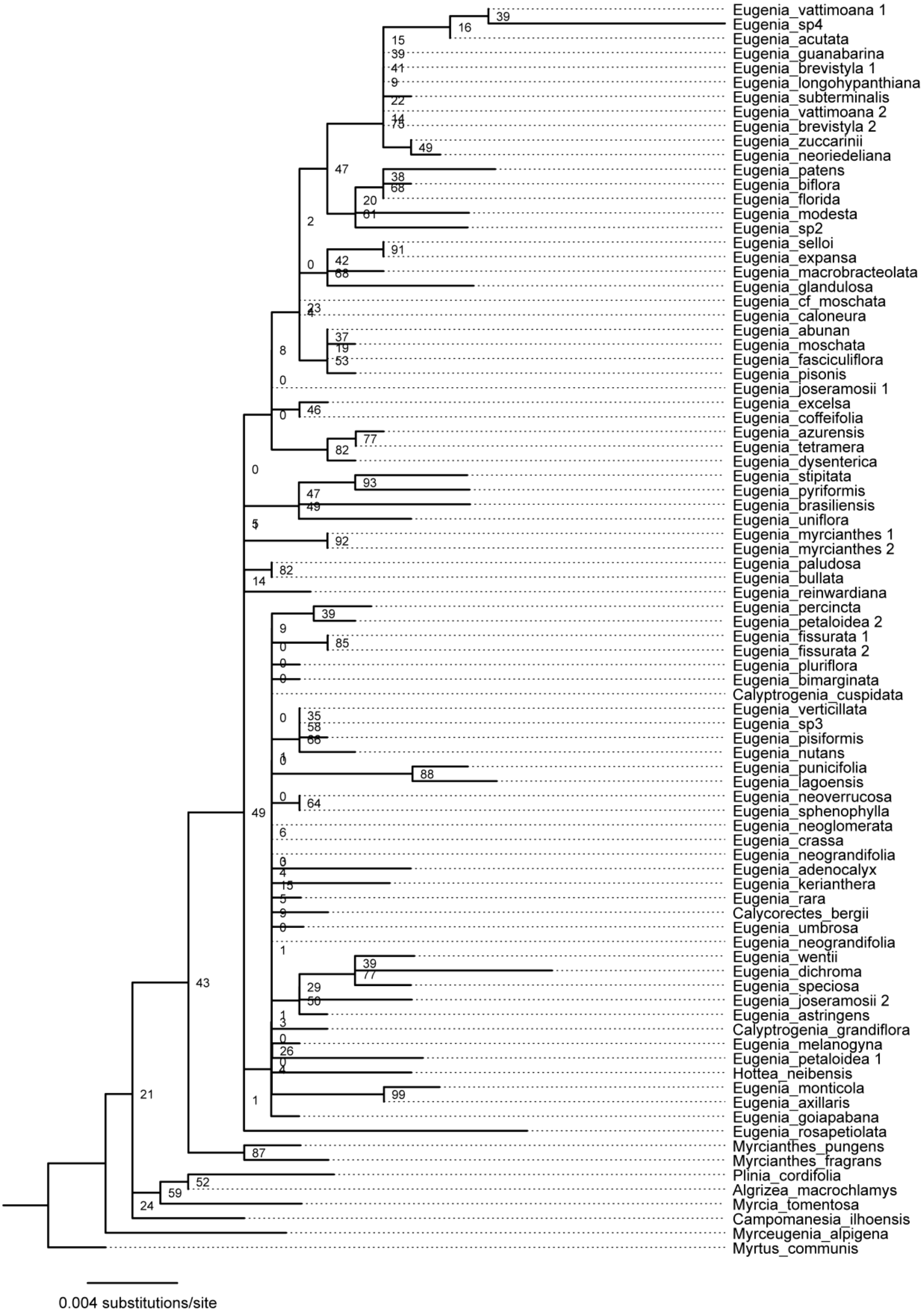
S6. Maximum likelihood tree of *Eugenia* resulting from the plastid dataset. Bootstrap percentages are shown above branches.



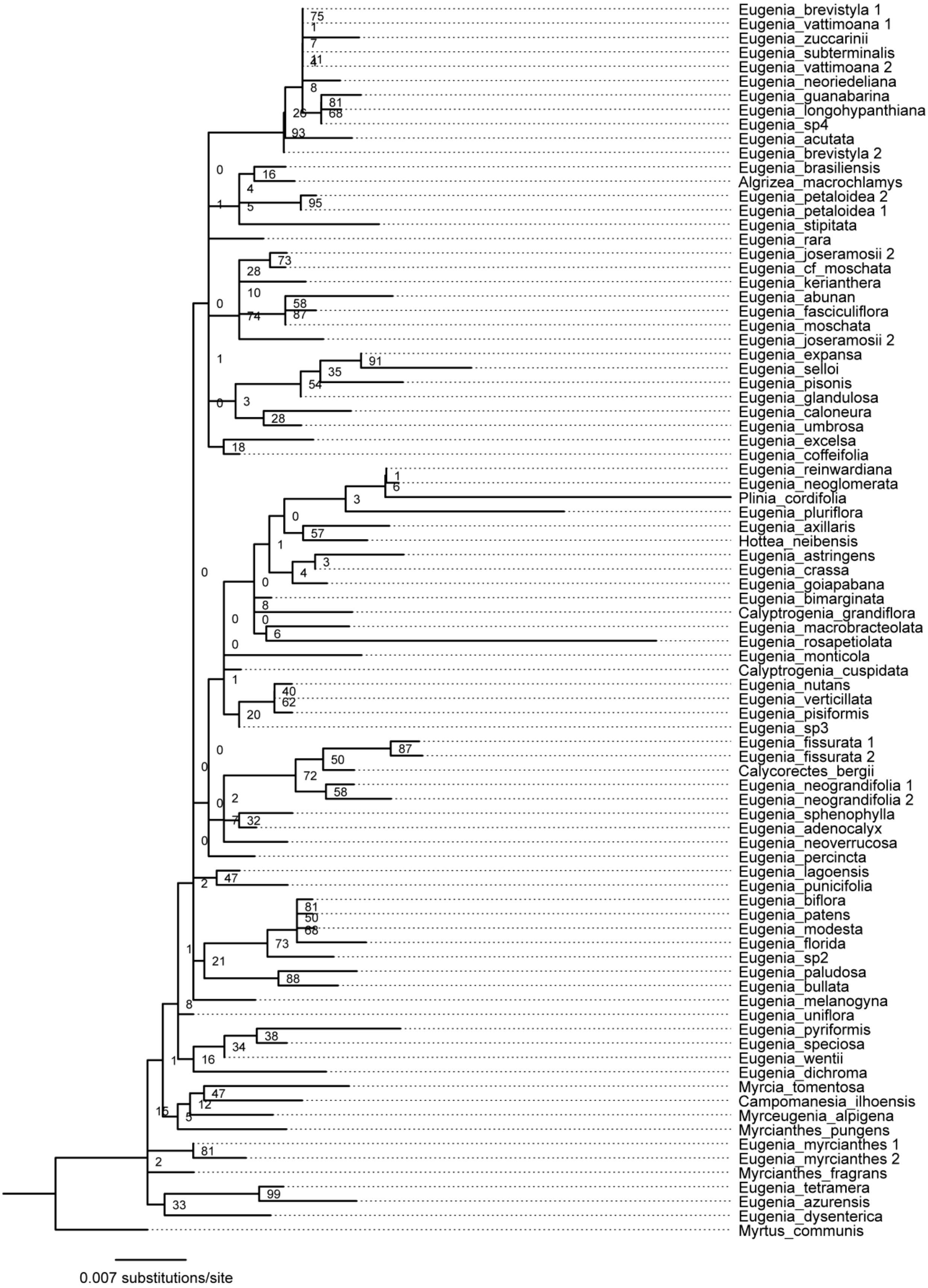
S7. Maximum likelihood tree of *Eugenia* resulting from the *psb*A-*trn*H plastid region. Bootstrap percentages are shown above branches.



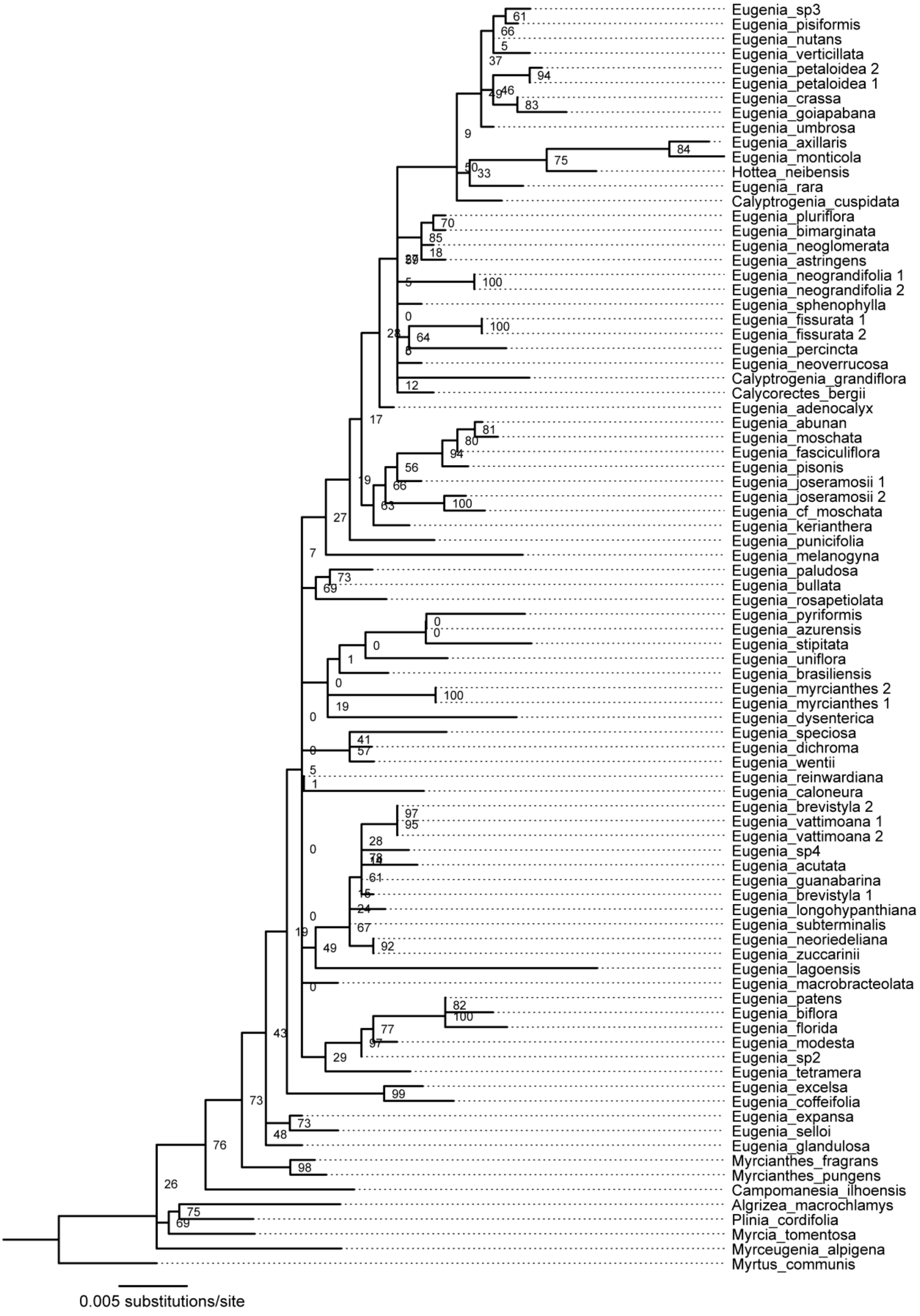
S8. Maximum likelihood tree of *Eugenia* resulting from the *rpl*16 plastid region. Bootstrap percentages are shown above branches.



S9. Maximum likelihood tree of *Eugenia* resulting from the *trn*L-*rpl*32 plastid region. Bootstrap percentages are shown above branches.



S10. Maximum likelihood tree of *Eugenia* resulting from the *trn*Q5’-*rps*16 plastid region. Bootstrap percentages are shown above branches.



Capítulo 3

Chapter 3

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NOMENCLATURAL NOTES ON *EUGENIA* WITH CLOSED CALYCES: *CALYCORECTES* O.BERG AND *MITRANTHES* O.BERG (MYRTACEAE)

Abstract

This study incorporates results of the latest phylogenetic framework to support nomenclatural adjustment in *Eugenia*, including to its circumscription with regard to the genera *Calycorectes* and *Mitranthes*. Five synonyms, two new names and one new combination in *Eugenia* are provided; a pre-existing name for a *Eugenia* section is re-established.

Keywords: taxonomy, *Schizocalyx*, *Schizocalomyrtus*, *Neomitranthes*

Introduction

The hyper-diverse *Eugenia* P.Micheli ex Linnaeus (1753: 470) comprises c. 1000 species and has a pantropical distribution with most species found in South and Central America (c. 800 spp; Mazine *et al.* 2014; Wilson 2011). *Eugenia* is considered morphologically homogeneous and difficult to identify at the species level. As a result, over-emphasis has been placed on more remarkable morphological characters, often overlooking dissimilarities in favour of similarities (e.g. extended sepals, Bünger *et al.* 2016b; fused calyx, Giaretta *et al.* in prep.) and ignoring others (andro- and gynoecium, Vasconcelos *et al.* in press.). *Calycorectes* O.Berg (1856: 317) and *Schizocalomyrtus* Kausel (1966: 367) were described and defined based mostly on the degree of calyx fusion, despite other shared characters that suggested a relationship to *Eugenia* (Landrum & Kawasaki 1997; Sobral 2003). Both genera have been considered as synonyms of *Eugenia* (WCSP 2017), currently supported by recent phylogenetic reconstructions that recovered *Eugenia* as a monophyletic group including these and other traditionally related genera (Bünger *et al.* 2016a; Mazine *et al.* 2014; Faria *et al.* in prep.; Giaretta *et al.* in prep.). A recent nomenclatural adjustment incorporates the current phylogenetic framework into a new infrageneric classification of *Eugenia* (Mazine *et al.* 2016) and includes the following nine sections: *Eugenia* sect. *Calycorectes* (O.Berg) Mattos (2005: 3), *E.* sect. *Eugenia*, *E.* sect. *Hexachlamys* (O.Berg) Mazine (2016: 228), *E.* sect. *Phyllocalyx* Niedenzu (1893: 82), *E.* sect. *Pilothecium* (Kiaersk.) D.Legrand (1975: 37), *E.* sect. *Pseudeugenia* Mazine & Faria in Mazine *et al.* (2016: 227), *E.* sect. *Racemosae* O.Berg (1856: 278), *E.* sect. *Speciosae*

Bünger & Mazine in Bünger *et al.* (2016b: 75) and *E.* sect. *Umbellatae* O.Berg (1856: 204), the latter including an old world clade.

Two species corresponding to the traditional circumscription of *Calycorectes* surveyed in the phylogeny by Mazine *et al.* (2014) (*Eugenia brevistyla* D.Legrand in Legrand & Klein (1977: 18) and *E. subterminalis* DC. (1828: 263)) emerged in 'clade 7' (sensu Mazine *et al.* 2014). Testing the consistency of 'clade 7' by including more accessions, a phylogenetic reconstruction (Giaretta *et al.* in prep.) based on five DNA regions (one nuclear; four plastids) recovered a well-supported phylogeny on which the changing proposed in this paper are founded. In addition to these manoeuvres, two species of *Neomitranthes* D.Legrand (1977: 671) are in fact *Eugenia* with fused calyx lobes (Souza 2009), here brought into synonymy of the latter genus.

Material & Methods

Baseline taxonomy used here follows the World Checklist of Selected Plant Species (WCSP 2017) with modifications according to the Flora do Brasil (2020). The following herbaria collections were consulted: ALCB, BM, CAY, CEN, CHOCO, COAH, COL, CVRD, ESA, G, GUA, HSTM, HUSC, IAN, IBGE, INPA, JBB, K, LE, MFS, MG, P, R, RB, RFA, SP, SPF, SPSF, UB, UEC and W. High resolution pictures of specimens available online were examined to support taxonomic decisions, these are indicated "photo!". Synonyms are listed exhaustively for *Eugenia* section *Schizocalomyrtus* but are cited only when they are involved in a nomenclatural act or typification for species from other sections (complete statements are available in Mazine *et al.* 2016). Lectotypes are designated following the ICBN (McNeill *et al.* 2012) and are made even when an apparent holotype appears obvious due to doubt regarding exactly which specimen was examined by the author (McNeill 2014). Selected lectotypes are the most likely 'top set' specimens used by the species author, from the most representative gathering available in the maximum number of herbarium collections. Where multiple syntypes are listed by the author, the lectotype is the collection judged to best match the protologue description. Known isolectotypes and remaining syntypes are also listed. The two-stage lectotypification process narrowing a designation to a single specimen follows the process described in the ICBN Art 9.7 (McNeill *et al.* 2012).

Nomenclatural changes

1. ***Eugenia* section *Umbellatae*** O.Berg (1856: 204). Type species: *Eugenia umbellata* De Candolle (1828: 273). Type:—BRAZIL. Goiás, "Vao do Paranau", s.d., *Martius s.n.* (M 0171149 [photo]!).

Calycorectes O.Berg (1856: 317), **syn. nov.** *Eugenia* section *Calycorectes* (O.Berg) Mattos (2005: 3). *Eugenia* subgenus *Calycorectes* (O.Berg) Mattos (2005: 3). Type species: *Calycorectes grandifolius* O.Berg (1856: 317). Type:—SURINAME. 'Guiana Batava, in sylvis reg. inter. ad fl. Surinam. pr. stationem Victoriam', December 1843, *Kappler 1365* (lectotype P!, first-step lectotype designated by McVaugh 1969: 224, **second-step lectotype designated here** P! [00780939]; isolectotypes G!, LE! [2 sheets], M! [0171259-photo], MO! [2527970-photo], P! [00780937, 00780938], U, W! [2 sheets]).

Calycorectes section *Tetrapetalae* Mattos (1990: 3), **syn. nov.** *Eugenia* (subgenus *Calycorectes* section *Calycorectes*) subsection *Tetrapetalae* (Mattos) Mattos (2005: 3). Type species: *Calycorectes mexicanus* O.Berg (1856: 318). Type:—MEXICO. 'Habitat in montibus Cordilleras ad Oaxaca', April 1840, *Galeotti 2867* (**lectotype designated here** W [0075416-photo!]; isolectotypes BR [000000523056-photo!] (*pro parte*; two branchlets at sheet top), G! [00227496], K! [000565056 (*pro parte*; left-hand branchlet at sheet bottom), 000277093 (*pro parte*; left-hand branchlet)], LE! [00004069, 00004070], P! [05229271]).

Calycorectes (subgenus *Brevitubia*) section *Eucalycorectes* Niedenzu (1893: 82), *nom. inval.*

Notes: *Calycorectes grandifolius* (currently *Eugenia neograndifolia* Mattos (2005: 10) emerged within *Eugenia* sect. *Umbelaltae* according to the phylogeny of Giaretta *et al.* (chapter 2) and *Calycorectes* is here synonymized. Although McVaugh (1969) have designed a lectotype in P for the type species *Calycorectes grandifolius*, two specimens under different herbarium codes causing ambiguity motivated the second-step of lectotypification here designated. The lectotype was arbitrarily chosen as the most representative of the species since no clear reference was made in his original publication. Although the type species *Calycorectes mexicanus* is not sampled in the molecular phylogeny of Giaretta *et al.* (chapter 2), *Calycorectes* section *Tetrapetalae* is here synonymized motivated by a consistent Caribbean clade nested in *Eugenia* section *Umbellatae* (see Vasconcelos *et al.* 2017). Careful examination revealed a branchlet bearing two leaves on the bottom left-hand of the BR sheet and a loose leaf, not to belong to the type specimen of *Calycorectes* subsection *Tetrapetalae*. Two labels (*Galeotti 2867* and *Galeotti 593*) are attached to the K sheet (K000565056). It is assumed that the labels *Galeotti 2867* placed close to the respective branchlets correspond to the respective collection. Also, branchlets corresponding to two different collections are attached to the K sheet (K000277093); it is assumed that left-hand branchlet corresponds to the *Galeotti 2867*.

2. ***Eugenia* section *Schizocalomyrtus*** (Kausel) Mattos (2005: 3). *Schizocalomyrtus* Kausel (1967: 367). *Schizocalyx* O.Berg (1856: 319), *nom. illeg.*, non *Schizocalyx* Scheele (1843: 575), non *Schizocalyx* Hochstetter (1844: 1), non *Schizocalyx* Weddell (1854: 73, *nom cons.*). *Calycorectes* subgenus *Schizocalyx* Kiaerskou (1893: 117). *Calycorectes* section *Schizocalyx* Niedenzu (1893: 82). *Calycorectes* subgenus *Schizocalomyrtus* (Kausel) Mattos (1990: 3). Type species: *Schizocalyx pohliana* O.Berg (1856: 319).

Calycorectes (subgenus *Calycorectes* section *Tetrapetalae*) subsection *Subpaniculatae* Mattos (1990: 4), **syn nov.** Type species: *Calycorectes cucullatus* Mattos (1989: 10). Type:—BRAZIL. São Paulo, Serra do Mar, na descida Jequitiba-Miracatu, [20] September 1969, *M. Kuhlmann s.n.* (holotype HAS [87502-photo!]; isotypes FLOR, SP! [006200, 114160-herbarium number]).

Calycorectes subgenus *Eucalycorectes* Kiaerskou (1893: 116), *nom. inval.*

Notes: *Eugenia* section *Schizocalomyrtus* is here assigned to 'clade 7' (sensu Mazine *et al.* 2014) replacing the previous name *Eugenia* section *Calycorectes* (O.Berg) Mattos assigned by Mazine *et al.* (2016). Infrageneric classification of Kiaerskou (1893) and Niedenzu (1893) are indirect references to the respective replacement names; therefore, both are treated as *nomen novum* according to the Art. 41.3 of the Code (also see Art. 58.1). *Schizocalomyrtus* is a legitimate replacement name to *Schizocalyx* O.Berg, however, *Schizocalomyrtus pohliana* (O.Berg) Kausel is not in accordance with the Art. 6.10 since it is based in an illegitimate basionym. Mattos (2005) proposed the new sectional rank *Eugenia* section *Schizocalomyrtus* (Kausel) Mattos based on the legitimate *Schizocalomyrtus*, thus, the later available name to be used. *Calycorectes* subsection *Subpaniculatae* is synonymized here since the holotype of *Calycorectes* *cucullatus* fits within the morphological recircumscription of *Eugenia* section *Schizocalomyrtus* (Giaretta *et al.*, Chapter 5) as does its Atlantic forest range.

3. ***Eugenia longohypanthiana*** Giaretta, **nom. nov.** *Calycorectes pohlianus* Kiaerskou (1893: 117) [non *Calycorectes pohlianus* Bentham ex Niedenzu (1893: 82)]. *Schizocalyx pohliana* O.Berg (1856: 319), *nom. illeg*. *Schizocalomyrtus pohliana* Kausel (1967: 367), *nom. illeg*. *Eugenia cambucae* Mattos (2005: 11), *nom. illeg.* Type:—BRAZIL. Rio de Janeiro, 'Habitat in Brasiliae prov. Rio de Janeiro', s.d., *Pohl 5844* (**lectotype designated here** W! [0071556]; isolectotypes G [not found], GH [00068863-photo!], OXF! [00067686], W! [0071557]).

Notes: The replacement name *Calycorectes pohlianus* was simultaneously published by Kiaerskou (1893) and Niedenzu (1893) originally as combinations based on *Schizocalyx*, a later illegitimate homonym. *Calycorectes pohlianus* Kiaerskou and Niedenzu are treated as indirect references to a replacement name to the illegitimate *Schizocalyx pohliana* according to the Art. 41.3 of the Code. In the circumstance that priority cannot be fulfilled, *Calycorectes pohlianus* Kiaerskou is chosen as the later available name to be transferred to *Eugenia*. The pre-existence of *Eugenia pohliana* De Candolle (1828: 264) requires a replacement name. *Eugenia cambucae*, an tentavively replacement name to *Schizocalyx pohliana* is not in accordance with the Art. 38.1 due to the type reference not concerning its original place of the valid publication. Thus, *Eugenia longohypanthiana* is here proposed. The epithet alludes to the extending flower hypanthium of the species that contrasts to the standard flat hypanthium found in *Eugenia*, an extreme exception in the genus (see Giaretta *et al.*, chapter 2).

4. ***Eugenia guanabarina*** (Mattos & D.Legrand) Giaretta & M.C.Souza, **comb. nov.** *Marlierea guanabarina* Mattos & D.Legrand (in Legrand & Mattos 1975: 6)**.** Type:—BRAZIL. Rio de Janeiro, Recreio do Bandeirantes, Pedra de Itaúna, 22 [July] 1965, *N. Santos 5967* (holotype MVM '18113 herbarium number' [photo!]; isotype R).

Chytraculia bergiana Kuntze (1891: 238). *Mitranthes langsdorffii* O.Berg (1859: 595). *Neomitranthes langsdorffii* (O.Berg) Mattos (1981: 2), **syn. nov.** Type:—BRAZIL. Bahia, s.d., *Blanchet 2309* (**lectotype designated here** LE!; isolectotypes F [69177 negative number-photo!], G! [00222536-2 sheets, 00222537-2 sheets], K! [000018787], NY [00405346-photo!], P! [00162722, 05232287], W! [0118258-herbarium number]). Remaining syntypes: BRAZIL. Bahia, 'in silvis ad flumen Itahype prope Castel novo', s.d., *Riedel s.n.* (G! [00222538, 00222539-2 sheets], K! [000331517], LE! [6 sheets], M [0146829-photo!], MEL [666925-photo!], P! [05232220, 05232222], W! [0070788, 0100484-herbarium number]).

Calycorectes teixeireanus Mattos (1996: 1). *Eugenia teixeireana* (Mattos) Mattos (2005: 9), **syn. nov.** Type:—BRAZIL. Rio de Janeiro, Barra da Tijuca, 13 July 1964, *W. Hoehne 5759* (holotype SP! [001302]; isotypes FLOR, MBM! [69215-herbarium number], NY [00886386-photo!], UB!, UEC).

Notes: Taxonomy of this species has been historically confused due to the combination of the closed calyx in the bud tearing via a calyptra-like structure and thyrsoid inflorescence, features commonly associated with *Myrcia s.l.*, and the embryo with fused cotyledons that suggests a relation to the '*Plinia* group' (sensu Lucas *et al.* 2007) and *Eugenia*. Its relationship to *Eugenia* was previously suggested (Souza 2009) and is here transferred by its highly supported emergence in *Eugenia* sect. *Schizocalomyrtus* according to the phylogenetic reconstruction of Giaretta *et al.* (chapter 2). *Chytraculia bergiana* is a replacement name to *Mitranthes langsdorffii*; therefore, the later available basionym. However, the new combination is unavailable in *Eugenia* due to pre-existence of *Eugenia bergiana* Grisebach (1860: 182). Thus, *Marlierea guanabarina* is the later name available to be combined. Although the epithet has an improper Latin termination, the original spelling must be retained since it does not fit to any conditional rule of the Code (see Art. 60 in McNeill *et al.* 2012).

5. ***Eugenia neoriedeliana*** M.C.Souza & Giaretta, **nom. nov.** *Mitranthes riedeliana* O.Berg (1859: 595). *Chytraculia riedeliana* (O.Berg) Kuntze (1891: 238). *Calyptrogenia riedeliana* (O.Berg) Burret (1941: 546). *Neomitranthes riedeliana* (O.Berg) Mattos (1990: 6), **syn. nov.** Type:—BRAZIL. Rio de Janeiro, 'Habitat in silvis prope Madiocca', s.d., *Riedel & Langsdorff s.n.* (**lectotype designated here** K! [000331528]; isolectotypes F [72823-negative number-photo!], LE! [6 sheets], M [0146828-photo!], NY [00405349-photo!], P! [00723175, 00723176, 00723177], S [photo!], OXF! [00071623, 00071645]).

Notes: Although the floral morphology of *Mitranthes riedeliana* is in accordance with the current circumscription of *Eugenia*, the opening of the bud at anthesis via a calyptra-like structure mislead for Berg (1859), as did the absence of available fruits at the time. However, straight stamens in the bud in *Eugenia* (*vs.* strongly curved in *Myrcia s.l.* and the '*Plinia* group'; see Vasconcelos *et al.* 2015) suggest its correct placement in *Eugenia* sect. *Schizocalomyrtus*, confirmed by the molecular phylogeny of Giaretta *et* *al.* (chapter 2). A replacement name is here assigned since *Mitranthes riedeliana* is unavailable in *Eugenia* due to the pre-existence of *Eugenia riedeliana* (Berg 1857: 261).

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References

Berg, O.C. (1856) Revisio Myrtacearum huc usque cognitarum s. Klotzschii "Flora Americae aequinoctialis" exhibens Myrtaceas. *Linnaea* 27: 129–384.

Berg, O.C. (1857) Myrtaceae I C. F. P. de Martius (Ed). *Flora Brasiliensis* 14(1): 1–468.

Berg, O.C. (1859) Myrtographiae Brasiliensis Supplementum C.P.F. Martius (Ed). *Flora Brasiliensis* 14(1): 530–636.

Bünger, M.O., Mazine, F.F., Forest, F., Bueno, M.L., Stehmann, R. & Lucas, E.J. (2016a) The evolutionary history of *Eugenia* sect. *Phyllocalyx* (Myrtaceae) corroborates historically stable areas in the southern Atlantic forests. *Annals of Botany* 118: 1209–1223. https://10.1093/aob/mcw209

Bünger, M.O., Mazine, F.F., Lucas, E.J. & Stehmann, J.R. (2016b) Circumscription and synopsis of *Eugenia* section *Speciosae* Bünger & Mazine (Myrtaceae). *PhytoKeys* 61: 73–80. doi: 10.3897/phytokeys.61.7904

Burret, M. (1941) Myrtaceen-Studien. *Notizblatt des Botanischen Gartens und Museums zu Berlin* 15: 479–550.

De Candolle, A.P. (1828) Myrtaceae. In: A.P. de Candolle (Ed). In: *Prodromus systematis naturalis regni vegetabilis* 3. Treuttel et Würtz, Paris, pp. 1–494.

Flora do Brasil 2020 (on going). *Projeto Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil.* Available from: http://floradobrasil.jbrj.gov.br

(July 24, 2017).

Grisebach, A.H.R. (1860). Myrtaceae. *Plantae Wrightianae Cubenses* 1: 154-536.

Hochstetter, C.F. (1844) Nova genera plantarum Africae, proponit et describit. *Flora* 27(1, Bes. Beil.): 1–8.

Kausel, E. (1967) Lista de las Mirtáceas e Leptospermáceas Argentinas. *Lilloa* 32: 323–368.

Kiaerskou, H. (1893) Enumeratio Myrtacearum Brasiliensium. *In:* Warming, E. (Ed), *Symbolarum ad floram Brasiliae Centralis cognoscendam*. pp. 1–200.

Kuntze, O. (1891) Revisio Generum Plantarum. *Myrtaceae* 1: 1–374.

Landrum, L.R. & Kawasaki, M.L. (1997) The Genera of Myrtaceae in Brazil: An Illustrated Synoptic Treatment and Identification Keys. *Brittonia* 49(4): 508. doi: 10.2307/2807742

Legrand, C.D. & Klein, R.M. (1977) Mirtáceas - Suplemento I P. *In:* Reitz, R. (Ed). *Flora Ilustrada Catarinense*. pp. 1–34.

Legrand, D. (1975) Sobre Pilothecium (Kiaersk.) Kausel. *Bradea* 2(8): 33–40.

Legrand, D. & Mattos, J.R. (1975) Novidades taxonômicas em Myrtaceae. *Loefgrenia* 67: 1–32.

Linnaeus, C. (1753) *Species Plantarum*. Impensis Laurentii Salvii, Stockholm.

Lucas, E.J., Harris, S.A., Mazine, F.F., Belsham, S.R., Nic Lughadha, E.M., Telford, A., Gasson, P.E. & Chase, M.W. (2007) Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* 56(4): 1105–1128. doi: 10.2307/25065906

Mattos, J.R. (1981) Novidades taxonômicas em plantas do Brasil. *Loefgrenia* 76: 1–3.

Mattos, J.R. (1989) Novidades taxonômicas em Myrtaceae - V. *Loefgrenia* 94: 1–12.

Mattos, J.R. (1990) Novidades taxonômicas em Myrtaceae - VI. *Loefgrenia* 99: 1–6.

Mattos, J.R. (1996) Novidades taxonômicas em Myrtaceae - XIII. *Loefgrenia* 109: 1–3.

Mattos, J.R. (2005) Considerações sobre *Calycorectes* O.Berg. *Loefgrenia* 120: 1–24.

Mazine, F.F., Bünger, M.O., Faria, J.E.Q., Lucas, E. & Souza, V.C. (2016) Sections in *Eugenia* (Myrteae, Myrtaceae): nomenclatural notes and a key. *Phytotaxa* 289(3):

225–236.

Mazine, F.F., Souza, V.C., Sobral, M., Forest, F. & Lucas, E. (2014) A preliminary phylogenetic analysis of *Eugenia* (Myrtaceae: Myrteae), with a focus on Neotropical species. *Kew Bulletin* 69(2): 1–14. doi: 10.1007/s12225-014-9497-x

McNeill, J. (2014) Holotype specimens and type citations: general issues. *Taxon* 63(5): 1112–1113. doi: 10.12705/635.7

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Prado, J., Prud'Homme Van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). *Regnum Vegetabile*: 1–140.

McVaugh, R. (1969) The Botany of the Guyana Highland - Part VIII: Myrtaceae. *Memoirs of the New York Botanical Garden* 18(2): 55–286.

Niedenzu, F. (1893) Myrtaceae. *In:* Engler, A. & Prantl, K. (Eds) *Die Natürlichen Pflanzenfamilien*. pp. 57–105.

Scheele, A. (1843) Beiträge zur deutschen und schweizerischen Flora. *Flora* 35: 573–588.

Sobral, M. (2003) *A família Myrtaceae no Rio Grande do Sul*. Editora Unisinos, São Leopoldo.

Souza, M.C. (2009) *Estudos taxonômicos em Myrtaceae no Brasil: Revisão de Neomitranthes Kausel ex D.Legrand e contribuição ao conhecimento da diversidade e conservação de Plinia L. no Domínio Atlântico.* PhD thesis. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, pp. 1–133.

Vasconcelos, T.N.C., Prenner, G., Bünger, M.O., De-Carvalho, P.S., Wingler, A. & Lucas, E.J. (2015) Systematic and evolutionary implications of stamen position in Myrteae (Myrtaceae). *Botanical Journal of the Linnean Society* 179(3): 388–402.

Vasconcelos, T.N.C., Proença, C.E.B., Ahmad, B., Aguilar, D.S., Aguilar, R., Amorim, B.S., Campbell, K., Costa, I.R., De-carvalho, P.S., Faria, J.E.Q., Giaretta, A., Kooij, P.W., Lima, D.F., Mazine, F.F., Peguero, B., Prenner, G., Santos, M.F., Soewarto, J., Wingler, A. & Lucas, E.J. (2017) Myrteae phylogeny, calibration, biogeography and diversification patterns: Increased understanding in the most species rich tribe of Myrtaceae. *Molecular Phylogenetics and Evolution* 109: 113–

137. doi: 10.1016/j.ympev.2017.01.002

WCSP (2017) World Checklist of Selected Plant Families. *Facilitated by the Royal Botanic Gardens, Kew* Available from: apps.kew.org/wcsp/myrtaceae (July 26, 2017).

Weddell, H.A. (1854) Quelques Rubiacées de l'Amérique Tropicale. *Annales des Sciences Naturelles* sér. 4(1): 65–80.

Wilson, P.G. (2011) Myrtaceae. *In:* Kubitzki, K. (Ed) *The families and genera of vascular plants. Flowering plants, eudicots: Sapindales, Cucurbitales, Myrtaceae*. Springer-Verlag, Berlin, pp. 1–436.

Capítulo 4

Chapter 4

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EVOLUTIONARY ASSESSMENT OF MYRTACEAE INFLORESCENCE WITH EMPHASIS ON THE LARGE, TAXONOMICALLY COMPLEX GENUS *EUGENIA* (MYRTACEAE)

INTRODUCTION

An enhanced understanding of phylogenetic relationships among flowering plant taxa has increased interest in comparative morphological and developmental analysis of the inflorescence (Giribet, 2015; Lee and Palci, 2015; Wanninger, 2015). This interest has encouraged consideration and inference regarding the functional and evolutionary significance of inflorescence architecture (Benlloch *et al.*, 2007; Castel *et al.*, 2010; Claßen-Bockhoff and Bull-Hereñu, 2013; Prenner *et al.*, 2009). Flexibility of inflorescence arrangement and diversity is high in many angiosperm groups (Harder and Prusinkiewicz, 2013; Tooke *et al.*, 2005). This has produced a dizzying number of possible inflorescence permutations, preventing development of terminologies applicable to all groups and a constant need for exceptions in definitions. Typological definitions of inflorescences are many and broadly disseminated; most are based on mature inflorescences (e.g. Weberling, 1988; Troll and Weberling, 1989; Rickett, 1944). There has been relatively little consideration of the environmental and genetic constraints that influence ultimate architectures (Prusinkiewicz *et al.*, 2007; Kirchoff and Claßen-Bockhoff, 2013) or how widely variable and flexible mature arrangements may reflect external stimuli rather than evolutionary relationship.

Briggs and Johnson (1979) provide a broad and detailed study of Myrtaceae, focusing on evolutionary relationships based on mature inflorescence architecture. Those authors considered all Myrtaceae genera and produced a seminal work that set a bench-mark for integration of inflorescence and phylogeny (Lucas *et al.*, 2007). However, this focus on final inflorescence arrangements resulted in a multitude of exceptions that and produced a highly complex and daunting terminology. A comprehensive analysis of character reconstruction is now needed to address the link between inflorescence architecture and evolutionary relationships in Myrtaceae and to encourage similar studies in this and other groups.

Recent studies show that terminological inflation is due, in part, to different terms being applied to structures repeating in different ways and resulting in variable levels of hierarchy (i.e. first, second order branching) (Prusinkiewicz *et al.*, 2007; Endress, 2010; Harder and Prusinkiewicz, 2013). Focus on the development of reproductive structures reduces the phenotypic diversity possible from a limited number of processes, disentangling terminological confusion. As a result, the work presented here harmonises terminology and updates assessment of homologues. This study considers inflorescence evolution, terminology and homology in the species-rich genus *Eugenia* in the context of tribe Myrteae (Myrtaceae). Limitations of these questions at the level of family include that a clear understanding of directional character transformations is required to define homologues at a broad scale. This problem is particularly acute in Myrtaceae where parallel character evolution is documented (Vasconcelos *et al.*, 2015, 2017a) and risk of misinterpretation as a consequence of homoplasy (Wake *et al.*, 2011) is high. However, assessment of homologues at the level of genus or tribe as performed here, is assumed to be more accurate and less susceptible to homoplasy.

This work focuses on inflorescence development patterns in *Eugenia*, a genus with more than 1,000 species mainly found in South and Central America. Phylogenetic frameworks of *Eugenia* are consistent and well-resolved (Mazine *et al.*, 2014; Bünger *et al.*, 2016). High levels of inflorescence architecture diversity in *Eugenia* make it an appropriate model for evolutionary studies. The central hypothesis of this work is that all variation in *Eugenia* inflorescences results from a homologous development pattern in which successive orders of branching lead to more elaborate arrangements. This is addressed as three specific aims: 1) identify the main inflorescence developmental patterns in Myrteae with a focus on *Eugenia*, 2) test seemingly homologous structures in light of current evolutionary understanding, 3) assess traditional terminology of inflorescences in those groups and update where appropriate.

MATERIAL AND METHODS

Phylogenetic inference

The phylogenetic reconstruction of *Eugenia* used in this study was recovered using DNA sequences of the internal transcribed spacer (ITS: ITS1, 5.8S Gene and ITS2) of the nuclear region and four chloroplast regions (*psb*A-*trn*H, *rp*L*16, rp*L*32-trn*L, *trn*Q-*5'rps16*). These sequences were acquired from recent molecular studies (Bünger *et al.* 2016; Vasconcelos *et al.* 2017b; Mazine *et al.* in prep.; Giaretta *et al.* Chapter 2). This sample of 65 species (Tab. 1) is representative of all *Eugenia* clades including *Myrcianthes*, the sister group of *Eugenia* and maximizes morphological and geographical diversity. Three taxa of tribe Myrteae were used as outgroup including the *Myrtus* and Australasian groups (sensu Lucas *et al.* 2007). The nuclear and combined chloroplast datasets were concatenated to performed Bayesian Inference (BI) using

Tab. 1. Molecular sampling, vouchers, DNA regions, GenBank and RBG-Kew accession numbers, and country. Accession deposited in the Royal Botanic Gardens-Kew (RBG) are indicated by KEW.

Species	**Collector**	**Number**	**Herbarium**	**ITS**	**psbA-trnH**	**rpl16**	**rpl32-trnL**	**trnQ-rps16**	**Country**
Calycorectes bergii Sandwith	A. Giaretta	1587	K, SPF	KEW46506	KEW46506	KEW46506	KEW46506	KEW46506	French Guiana
Eugenia acutata Miq.	T. Vasconcelos	506	K	MF954031	MF954288	MF954331	MF954216	MF954095	Brazil
Eugenia adenocalyx DC.	A. Giaretta	1441	K	MF954042	MF954299	MF954342	MF954219	MF954105	Brazil
Eugenia astringens Cambess.	F. Mazine	782	ESA, K	KJ187606	KJ469655	KEW20843	KEW20843	KEW20843	Brazil
Eugenia aurata O.Berg	V. Staggemeier	315	K	KEW46457	KEW46457	KEW46457	KEW46457	KEW46457	Brazil
Eugenia axillaris (Sw.) Willd.	M. Hamilton	553	K	KJ187607	KJ469656	KEW30702	KEW30702	KEW30702	Turks & Caicos
Eugenia azuruensis O.Berg	J.E.Q. Faria	4186	UB	MF954033	MF954290	MF954333	MF954423	-	Brazil
Eugenia biflora (L.) DC.	F. Mazine	1075	ESA	KJ187610	KJ469659	KEW20687	KEW20687	KEW20687	Brazil
Eugenia bimarginata DC.	F. Mazine	469	ESA, K	KJ187611	KJ469660	KEW20830	KEW20830	KEW20830	Brazil
Eugenia brasiliensis Lam.	E. Lucas	126	K	KEW20949	KEW20949	KEW20949	KEW20949	KEW20949	Brazil
Eugenia brevistyla D.Legrand	A. Giaretta	1493	K, SPF	-	-	-	-	-	Brazil
Eugenia bullata Pancher ex Guillaumin	T. Vasconcelos	608	K	MF954034	MF954291	MF954334	MF954424	MF954097	New Caledon
Eugenia cerasiflora Miq.	T. Vasconcelos	419	K, UB	KEW45793	KEW45793	KEW45793	KEW45793	KEW45793	Brazil
Eugenia coffeifolia DC.	B. Holst	9516	SEL	KEW36243	KEW36243	KEW36243	KEW36243	KEW36243	Brazil
Eugenia convexinervia D.Legrand	F. Mazine	994	ESA, K	KJ187618	KJ469667	KEW20686	KEW20686	KEW20686	Brazil
Eugenia dichroma O.Berg	T. Vasconcelos	466	K	MF954041	MF954298	MF954341	MF954218	MF954104	Brazil
Eugenia dodonaeifolia Cambess.	E. Lucas	257	ESA, K	KJ187644	KJ469693	KEW45793	KEW45793	KEW45793	Brazil
Eugenia dysenterica DC.	F. Mazine	466	ESA, K	KJ187620	KEW20844	KJ469669	KEW20844	KEW20844	Brazil
Eugenia egensis DC.	T. Vasconcelos	319	K	KEW45800	KEW45800	KEW45800	KEW45800	KEW45800	Brazil
Eugenia excelsa O.Berg	E. Lucas	125	ESA, K	KJ187621	KJ469670	KEW20950	KEW20950	KEW20950	Brazil
Eugenia expansa (O.Berg) Nied.	M. Bünger	634	BHCB, K	KX789279	KX789297	KX789322	KX789351	KX910672	Brazil
Eugenia feijoi O.Berg	M. Simon	2032	CEN	KEW46515	KEW46515	KEW46515	KEW46515	KEW46515	Brazil
Eugenia flavescens DC.	D. Zappi	415	K	KEW10110	KEW10110	KEW10110	KEW10110	KEW10110	Brazil
Eugenia florida DC.	F. Mazine	965	ESA, K	KJ187622	KJ469671	KEW20841	KEW20841	KEW20841	Brazil
Eugenia foetida Pers.	B. Holst	8865	Cultivated MSBG	KEW36426	KEW36426	KEW36426	KEW36426	KEW36426	unkown

Eugenia goiapabana Sobral & Mazine	M. Bünger	s/n	BHCB	KX789270	KX789300	KX789325	KX789354	KX910675	Brazil
Eugenia guanabarina ined.	A. Giaretta	1629	K, SPF	KEW46509	KEW46509	KEW46509	KEW46509	KEW46509	Brazil
Eugenia handroi Mattos	F. Mazine	951	ESA, K	KJ187654	KJ469704	KEW20698	KEW20698	KEW20698	Brazil
Eugenia involucrata DC.	M. Bünger	551	BHCB	KX789281	KX789294	KX789319	KX789348	KX910669	Brazil
Eugenia joseramosii M.A.D. Souza & Scudeller	A. Giaretta	1655	SPF, K	KEW46514	KEW46514	KEW46514	KEW46514	KEW46514	Brazil
Eugenia lagoensis Kiaersk.	C. Fraga	2436	K	-	-	-	-	-	Brazil
Eugenia melanogyna (D.Legrand) Sobral	F. Mazine	969	ESA, K	KJ187624	KJ469673	KEW20694	KEW20694	KEW20694	Brazil
Eugenia modesta DC.	F. Mazine	854	ESA, K	KJ187625	KEW20832	KEW20832	KEW20832	KEW20832	Brazil
Eugenia monticola (Sw.) DC.	T. Vasconcelos	566	K	MF954037	MF954294	MF954337	MF954427	MF954100	Dominican Republic
Eugenia myrcianthes Nied.	J.E.Q. Faria	2850	UB	KEW44019	KEW44019	KEW44019	KEW44019	KEW44019	Brazil
Eugenia neoglomerata Sobral	F. Mazine	461	ESA, K	KJ187626	KJ469674	KEW20939	KEW20939	KEW20939	Brazil
Eugenia neograndifolia Mattos	A. Giaretta	1616	SPF	KEW46508	KEW46508	KEW46508	KEW46508	KEW46508	French Guiana
Eugenia neoverrucosa Sobral	E. Lucas	118	ESA, K	KJ187628	KJ469676	KEW20951	KEW20951	KEW20951	Brazil
Eugenia nutans O.Berg	E. Lucas	281	ESA, K	KJ187629	KJ469677	KEW20829	KEW20829	KEW20829	Brazil
Eugenia paludosa Pancher ex Brongn. & Gris	T. Vasconcelos	646	K	MF954038	MF954295	MF954338	MF954428	MF954101	New Caledon
Eugenia patens Poir.	E. Lucas	104	ESA, K	KJ187633	K20947	KJ469681	KX789361	KX910681	French Guiana
Eugenia pisiformis Cambess.	E. Lucas	232	ESA, K	KJ187634	KJ469682	KEW20948	KEW20948	KEW20948	Brazil
Eugenia pistaciifolia DC.	J.E.Q. Faria	1782	UB	KEW43963	KEW43963	KEW43963	KEW43963	KEW43963	Brazil
Eugenia pitanga (O.Berg) Nied.	F. Mazine	1044	ESA, K	KJ187635	KJ469683	-	-	-	Brazil
Eugenia pluriflora DC.	F. Mazine	961	ESA, K	KJ187636	KJ469684	KEW20831	KEW20831	KEW20831	Brazil
Eugenia protenta DC.	T. Vasconcelos	350	K	KEW45803	KEW45803	KEW45803	KEW45803	KEW45803	Brazil
Eugenia punicifolia Kunth (DC.)	F. Mazine	1065	ESA, K	KJ187638	KJ469686	KEW20691	KEW20691	KEW20691	Brazil
Eugenia pyrifera Faria & Proença	J.E.Q. Faria	3870	UB	KEW34960	KEW34960	KEW34960	KEW34960	KEW34960	Brazil
Eugenia pyriformis Cambess.	F. Mazine	1028	ESA, K	KJ187639	KJ469687	KEW20944	KEW20944	KEW20944	Brazil

Eugenia reinwardtiana (Blume) DC.	E. Biffin	9245	Cultivated QRS	AY487301	-	AY463131	-	-	Queensland
Eugenia selloi B.D.Jacks	M. Bünger	566	BHCB, RB	KX789278	KX789308	KX789334	KX789363	KX910684	Brazil
Eugenia sonderiana O.Berg	T. Vasconcelos	735	K	KEW46413	KEW46413	KEW46413	KEW46413	KEW46413	Brazil
Eugenia speciosa Cambess.	M. Bünger	585	BHCB	KX789274	KX789310	KX789336	KX789365	KX910686	Brazil
Eugenia stipitata McVaugh	T. Vasconcelos	677	K	MF954043	MF954300	MF954343	MF954220	-	Brazil
Eugenia subterminalis DC.	F. Mazine	s/n	K	KEW35910	KEW35910	KEW35910	KEW35910	KEW35910	Brazil
Eugenia umbrosa O.Berg	A. Giaretta	1498	SPF, K	KEW46502	KEW46502	KEW46502	KEW46502	KEW46502	Brazil
Eugenia uniflora L.	E. Lucas	207	Cultivated K	AM234088	AM489828	AF215627*	-	KP722202	Brazil
Eugenia vattimoana Mattos	A. Giaretta	1487	K, SPF	KEW46499	KEW46499	KEW46499	KEW46499	KEW46499	Brazil
Eugenia verticillata (Vell.) Angely	Duarte	s/n (ESA85678)	ESA, K	KJ187650	KJ469700	KEW45805	KEW45805	KEW45805	Brazil
Eugenia wentii Amshoff	B. Holst	9421	K	KJ187651	K35646	KJ469701	KX789368	KX910689	French Guiana
Eugenia zuccarini O.Berg	A. Brandão	159	RBR	KEW46487	KEW46487	KEW46487	KEW46487	KEW46487	Brazil
Myrcianthes fragrans (Sw.) McVaugh	M. Hamilton	552	K	KEW30701	KEW30701	KEW30701	KEW30701	KEW30701	Turks & Caicos
Myrcianthes pungens (O.Berg) D.Legrand	J.E.Q. Faria	2759	UB	KEW43970	KEW43970	KEW43970	KEW43970	KEW43970	Brazil
Myrtus communis L.	E. Lucas	211	Cultivated K	AM234149	AM489872	KEW10347	KEW10347	KEW10347	unkown
Rhodamnia rubescens (Benth.) Miq.	S. Belsham	83	Cultivated OTA	AM234127	AM489879	-	-	-	Melbourne

MrBayes (Ronquist *et al.* 2012) implemented in CIPRES (Miller *et al.* 2010). The best nucleotide models were chosen using jModeltest 2 v.2.2 (Darriba *et al.* 2012); these were GTR gamma + inv for both ITS and cpDNA datasets. Two independent runs with four chains (MCMC) were performed with 5 million generations and burn-in of 15%. Output was examined using Tracer v1.6 (Drummond and Rambaut 2007) to assess chain convergence. The topology of majority consensus trees and posterior probabilities (pp) were generated sampling every 1,000 trees.

Survey of morphological development patterns

The survey encompasses two development stages of the reproductive phase. Initial and mature stages were analysed in conjunction to incorporate flexible arrangement and provide evolutionary and comparative perspective. Descriptions of initial and mature phases run from base to apex.

Comparative ontogenetic analysis — A general survey of inflorescence development was carried out to recognize common patterns and those specific to the sections of *Eugenia*. Inflorescence material collected in different development stages from tropical America and Asia was examined in the spirit collection (70% alcohol) at the Royal Botanic Gardens, Kew. In total, 37 samples of 28 taxa were prepared for comparative ontogenetic analysis using scanning electron microscopy (SEM) (Tab. 2). Preliminary hypotheses of developmental patterns were defined when a pattern was found to be fixed in more than two species (where available) for each section of *Eugenia* (sensu Mazine *et al.* 2014; Giaretta *et al.*, Chapter 2). All developmental pattern stages are imaged and presented from a single species. For comparative purposes, the following relevant traits are recorded: position (e.g. axillary or apical), structural development sequence (e.g. flower follows prophyll emergence), degree of extension (e.g. relative length of successive internodes in an axis), origin of second-order branches (e.g. meristem apical or lateral), apical growth (e.g. continued or latent) and accessory flowering axes (e.g. development stage equivalent or delayed to the main axis).

To place a study of *Eugenia* inflorescences in context, it is necessary to understand inflorescence variation in sister groups. A literature review of tribe Myrteae inflorescence accounts with emphasis on the work of Briggs and Johnson (1979) was undertaken. In addition, developmental patterns of species from clades emerging from the deepest nodes in the most recent phylogenetic reconstruction of Myrteae (one

Tab. 2. Ontogenetic sampling deposited in the spirit collection from Royal Botanic Gardens-Kew.

Species	**Collector**	**Number**	**Collection**
Decaspermum humile (Sweet ex G.Don) A.J.Scott	T.N. Vasconcelos	728	K
Eugenia acutata Miq.	T.N. Vasconcelos	506	K
Eugenia angustissima O.Berg	T.N. Vasconcelos	405	K
Eugenia angustissima O.Berg	T.N. Vasconcelos	278	K
Eugenia biflora (Lam.) L.	T.N. Vasconcelos	589	K
Eugenia biflora (Lam.) L.	A. Giaretta	1531	K
Eugenia candolleana DC.	T.N. Vasconcelos	s.n.	K
Eugenia adenocalyx DC.	A. Giaretta	1441	K
Eugenia paludosa Pancher ex Brongn. & Gris	T.N. Vasconcelos	646	K
Eugenia coffeifolia DC.	A. Giaretta	1592	K
*Eugenia dichroma*O.Berg	T.N. Vasconcelos	466	K
Eugenia dysenterica DC.	J.E.Q. Faria	6364	K
Eugenia dysenterica DC.	J.E.Q. Faria	6480	K
Eugenia involucrata DC.	J.E.Q. Faria	4047	K
Eugenia ligustrina (Sw.) Willd.	T.N. Vasconcelos	570	K
Eugenia modesta DC.	T.N. Vasconcelos	476	K
Eugenia myrcianthes Nied.	J.E.Q. Faria	6547	K
Eugenia neograndifolia Mattos	A. Giaretta	1616	K
Eugenia pohliana DC.	J.E.Q. Faria	4184	K
Eugenia protenta McVaugh	A. Giaretta	1433	K
Eugenia protenta McVaugh	T.N. Vasconcelos	350	K
Eugenia sp.1	J.E.Q. Faria	4218	K
Eugenia sonderiana O.Berg	T.N. Vasconcelos	735	K
Eugenia sonderiana O.Berg	T.N. Vasconcelos	740	K
Eugenia splendens O.Berg	J.E.Q. Faria	4196	K
Eugenia stipitata McVaugh	T.N. Vasconcelos	677	K
Eugenia guanabarina (D.Legrand & Mattos) Giaretta & M.C.Souza	A. Giaretta	1629	K
Eugenia guanabarina (D.Legrand & Mattos) Giaretta & M.C.Souza	A. Giaretta	1630	K
Eugenia uniflora L.	T.N. Vasconcelos	s.n.	K
Eugenia uniflora L.	J.E.Q. Faria	6294	K
Myrcianthes fragrans (Sw.) McVaugh	J.E.Q. Faria	4277	K
Myrcianthes fragrans (Sw.) McVaugh	J.E.Q. Faria	4777	K
Myrcianthes pungens (O.Berg) D.Legrand	T.N. Vasconcelos	7	K
Myrtus communis L.	T.N. Vasconcelos	s.n.	K
Myrtus communis L.	A. Giaretta	s.n.	K
Rhodamnia cinerea Jack	T.N. Vasconcelos	672	K
Rhodomyrtus tomentosa (Aiton) Hassk.	T.N. Vasconcelos	678	K

Myrtus group; two Australasian group) were studied to identify directional trends of inflorescence trait evolution and potential correlations among traits.

Comparative analysis of mature patterns — A total of 65 species were surveyed, corresponding to all taxa included in the phylogenetic reconstruction and one more from the Australasian group (*Rhodamnia rubescens*). A minimum of five specimens of each species was sampled using light microscopy of the mature inflorescence (Supplementary Data S1). Specimens from the Kew herbarium (K), with complementary material from the MBM, RB, SPF and CAY were examined and scored for hypothesized development patterns (acronyms according to Thiers 2018). As mature inflorescences often show flexibility of development, the most common arrangement is recorded. Brief descriptions linking ultimate architectures to their respective development patterns are provided to allow recognition of patterns from mature material. To account for the unquantifiable influence of environment on architectural flexibility, ultimate inflorescence architectures are recorded as the most consistently recurring arrangements.

Terminology

A traditional classification of the Myrtaceae inflorescence is provided by Briggs and Johnson (1979) where a detailed and highly specific terminology is used and evolutionary trends in the family are considered. That work was followed by others such as Landrum and Kawasaki (1997) who introduced a more general and more intuitive terminology to support a taxonomic overview. Subsequently, independent studies have used a wide and non-standardised suite of terms, often for the same structures. To avoid redundant use of terms in the present study and to maximally simplify terminology, no single scheme is embraced. Instead, a descriptive approach is adopted based on three growth processes commonly found in flowering plants: branching, elongation and reiteration. The former relates to two regular branching patterns: 1) racemose, with a first-order axis and a variable number of lateral, second-order branches and 2) cymose, with no more than two second-order lateral branches (see Endress, 2010). The second corresponds to extended length allowing exploitation of spatial resources and for floral and fruiting display. The later refers to the repetition of the total or partial architectural unit (Barthélémy 1991).

A seasonal shoot system (SSS) is here used to refer to the seasonal growth unit of woody plants supporting vegetative meristems at terminal and axillary positions (Claßen-Bockhoff and Bull-Hereñu 2013). Flowering shoot system (FSS) is adopted when an SSS arrives at a reproductive stage, i.e. flanked by flowers. Some vegetative meristems become reproductive whereas others continue vegetative growth or stop at a vegetative bud. These terms are helpful to refer to assemblage of units in a flexible system and are different from the 'seasonal growth unit' of Briggs and Johnson (1979) that is a shoot or network of shoots (vegetative or flowering) grown in a single season.

Development pattern analysis

Reproductive and vegetative material was dehydrated in alcohol series and left overnight in 100% ethanol. Samples were taken to the last step of dehydration in an Autosamdri-815B critical-point dryer (Tousimis Research, Rockville, Maryland, USA). Dried material was mounted onto alumininum stubs, coated with platinum using a Quorum Q-150-T sputter coater (Quorum Technologies, East Grinstead, UK) and detailed examined using Hitachi cold field emission Scanning Electron Microscopy S-4700-II (Hitachi High Technologies, Tokyo, Japan). Different stages of development of the same species available from different collections were surveyed when necessary. A total of 1092 images were analysed.

Ancestral character reconstruction

The resulting BI phylogeny was used to perform character reconstruction. Character reconstruction was performed to recover ancestral states allowing comparative analysis. The function *ace (ancestral character estimation)* available in the package *ape* (Paradis *et al.* 2004) implemented in R was used to recover ancestral character state probabilities of the nodes. The parameter "type=discrete" was used since the development patterns were coded as discrete states.

Phylogenetic signal of development patterns

The phylogenetic signal of the inflorescence development patterns was measured to interpret the statistical dependence of these traits on their phylogenetic relatedness (Revell *et al.* 2008). Phylogenetic signal was measured using the "fitDiscrete" function available in package *geiger* (Harmon *et al.* 2008) implemented in R. This function uses likelihood models of discrete character evolution in a continuous-time Markov model. The parameter "transform=lambda" was selected, assuming an equal rates (ER) of transition since no estimation of evolutionary rate was provided (Pagel 2004). The phylogenetic signal also considers branch length scaled by the nucleotide substitution rates. This analysis generated a log-likelihood value (*lnl*) and lambda index (λ) to rank the phylogenetic signal. Values of lambda fluctuate from 0 to 1, i.e. values close to 0 reflect phylogenetic independence while a value of 1 indicates phylogenetic non-independence over that expected under Brownian motion. *Auxotelic* and *auxotelic cataphylls* patterns were also analysed in conjunction to provide an alternative perspective (see discussion) as well as for *fasciculiform* and *glomeruliform* development patterns.

RESULTS

Architectural model of Myrteae

Myrteae has an array of plant architectural arrangements (see examples in Wilson, 2011) though a model that fits most Neotropical species can be reliably provided through qualitative analysis, following the terminology of Chomicki *et al.* (2017). Neotropical Myrteae have dichotomous sympodial branching and a determinate pattern of body enlargement though modular units that retain the apical meristem and its growth potential. Branching orders increase rapidly from successive axillary meristems from where stems subtended by leaves arise. The stem grows and branches seasonally, in a rhythmic activity that regulates rate of total vegetative production. A seasonal shoot system (SSS) results that can easily be identified by a new shoot, evident on a branch segment of the previous season. Protective organs such as involucres of cataphylls, i.e. bracteose leaves disposed in condensed internodes, are associated to growth units in some species (see *auxotelic cataphylls*). The orientation of growth of a stem is orthotropic, i.e. vertical growth resulting in a radial symmetry. Leaves are opposite, disposed alternately and successively in a decussate fashion.

Main inflorescence developmental patterns in Eugenia group

Seven inflorescence development patterns were observed. The three-flowered dichasium is treated as a secondary development (see discussion) and is here included under the *Thyrsoid* development pattern. The wide variety of arrangements in *Eugenia* rely on the flexibility of a few structures, i.e. 1) the extension and number of flowering shoot systems (FSS) arising from the same axil and their ultimate appearance; 2) the branching potential of the prophyll axil; and 3) the potential to recover vegetative bud activity at the FSS apex. A brief guide to the terminology used to describe inflorescence patterns is provided (Fig. 1). Phyllome: the axil of a leaf from where a branch or flower can emerge. Pherophyll: subtending leaf of a flower or a branch, i.e. its position rather than the appearance (bractose or foliage leaf) must be regarded as pertinent. Pherophylls are often referred to as bracts in the literature. Prophyll: pairs of bracteose leaves subtending the hypanthium, often termed bracteoles in the literature. Pedicel: (if present) these are the internodes between subtending pherophylls and the immediate succeeding pair of prophylls. Internode: the stem portion between two successive nodes. Main axis: first-order axis subtended by a pherophyll and bearing lateral flowers or flower-branches.

Auxotelic pattern

Development pattern — The main axis (first-order) including pherophylls subtending flowers correspond to a FSS; this is subtended by a bracteose or foliose pherophyll, and the main axis undergoes homogeneous extension of the internodes (Fig. 1). The FSS arises from the lateral meristem of the SSS whereas all subsequent lateral flowers (second-order) arise acropetally from lateral meristem of the FSS, i.e. from base to apex. While the main axis elongates leaving a primordium on the apical meristem, decussate pairs of lateral flowers emerge acropetally from successive phyllomes; the pedicel extends early in the flower development at a similar rate of growth as the bud. A vegetative primordium remains active at the apex of the main axis giving origin to vegetative tissues; internodes of main axes still extend after the bud achieves full size. No delayed accessory flowering axis was observed. (Fig. 2A–D).

Mature inflorescence — A foliose pherophyll subtends the main axis which can vary in length in the same specimen. The inflorescence arises from a previous season’s branch and typically appears as vegetative shoot with bracteose or foliose pherophylls each subtending a flower. Conversely, in the same specimen, the main axis might be expressed as a shoot with discrete elongation that gives the appearance of a raceme with bracteose pherophylls bearing flowers; usually the bracteose pherophylls are deciduous.

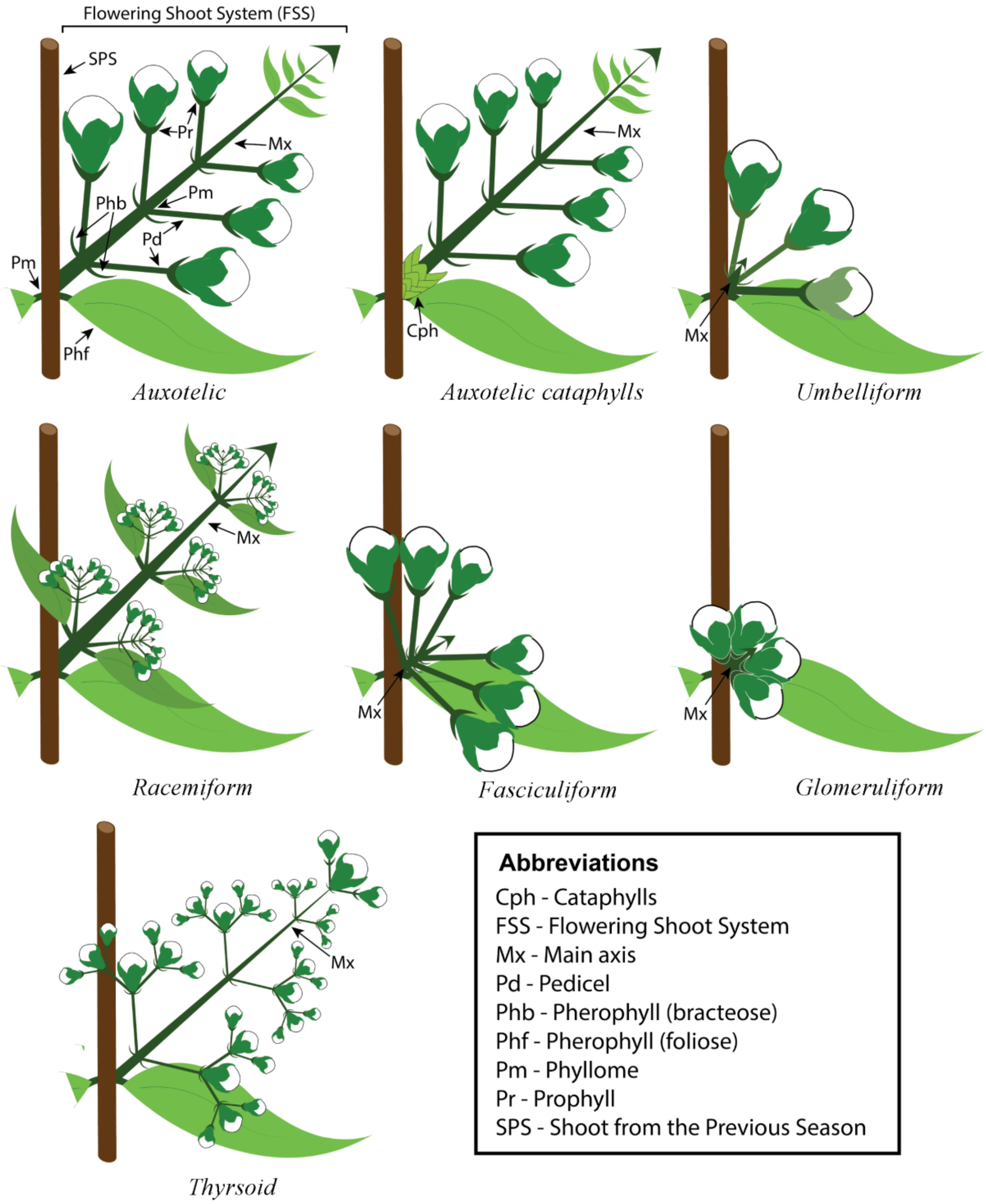

Fig. 1. Comparative flowering shoot system (FSS) of the described patterns showing the mature stage.

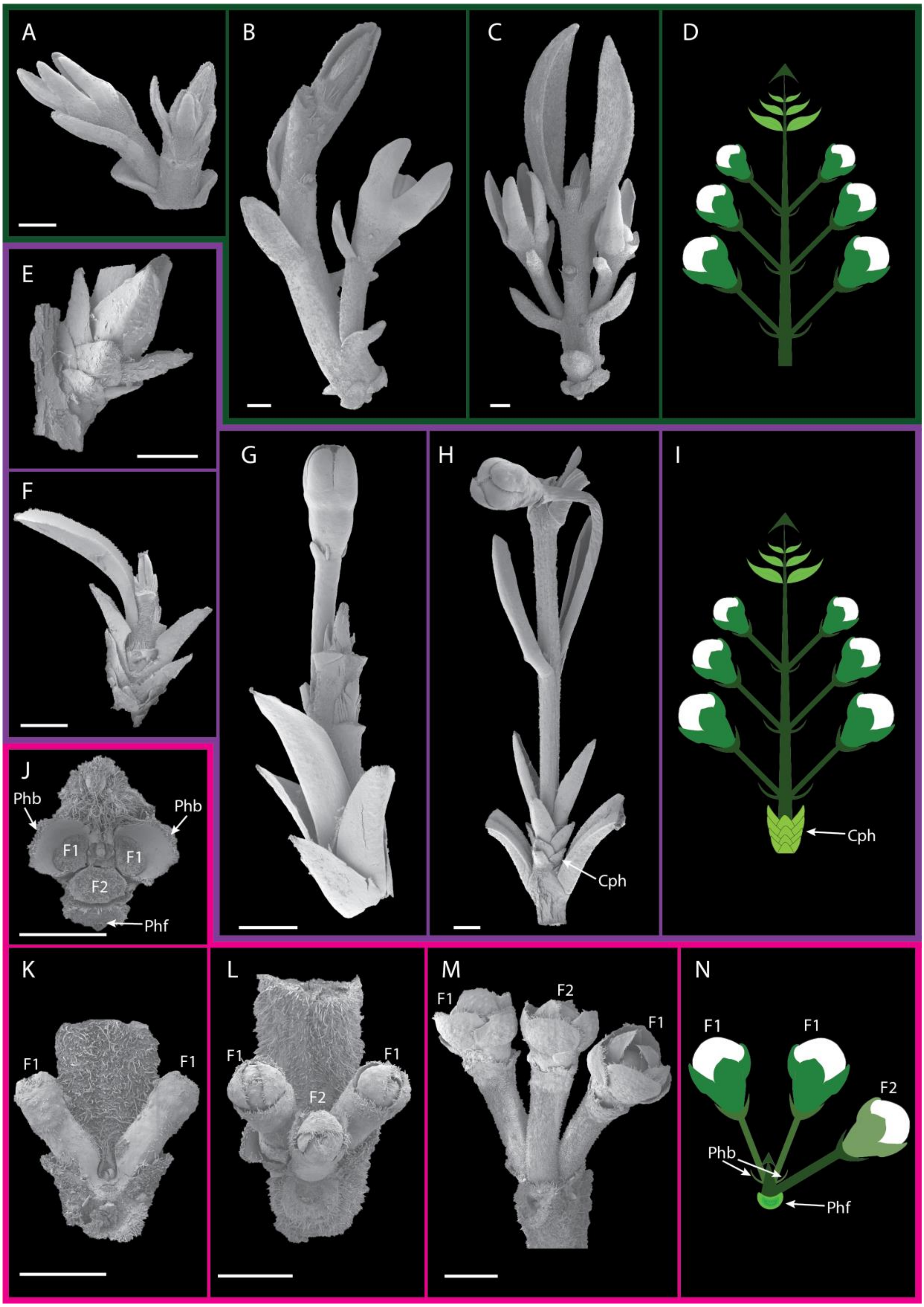

Fig. 2. Comparative development analysis of the inflorescence patterns in *Eugenia*. A-D (green box). *Auxotelic* pattern. (A-C) Flowering axis development of *Eugenia dichroma*. (D) Scheme representing the *auxotelic* pattern. E-I (purple box) *Auxotelic cataphylls*. (E) Initiation covered by bracteose pherophylls (cataphylls) of *E. ligustrina*. (F) Bracteose

pherophylls were removed revealing the primordia. (G-H) Flowering axis development. (I) Scheme of the *auxotelic cataphylls* pattern. J-N (pink box). *Umbelliform* pattern. (J). Upper view of the flowering axis of *E. sonderiana*; three flowers were removed. (K-M) Flowering axis development; F2 was removed in L. (N) Scheme representing the *umbelliform* pattern. Cph: cataphylls; F1: flower pair that first emerged according to the developmental sequence; F2: flower that later emerged according to the developmental sequence; Phb: bracteose pherophyll; Phf: foliose pherophyll. Scale bars = 1 mm.

Internodes of the main axis are similar in length. Flower pedicel is variable in length, less often absent. The apex of the FSS bears an active vegetative bud that often continues to develop vegetative tissue beyond the flower region. The relative position of the flower/fruit become basal in the branch as much as the internodes elongate and vegetative tissue is newly produced. In the same specimen, some FSS might cease growth early and not develop vegetative tissue. No delayed accessory flowering axis were observed. Instead, more than one FSS rarely share a phyllome – these are at the same development stage.

Auxotelic cataphylls pattern

Development pattern — The main axis (first-order), including pherophylls subtending flowers and densely arranged bracteose pherophylls, correspond to an FSS (Fig. 1). The FSS is subtended by a foliose pherophyll and the main axis undergoes heterogeneous extension of the internodes. Preceding the arisen of the apical meristem, successive pairs of bracteose, decussate pherophylls densely cover the primordia along tiny internodes (cataphylls). The ultimate internode is followed by a further short-extension that accommodates the axillary flowers. Successive internodes then elongate acropetally and fully until each axil is subtended by a bracteose pherophyll that gradually becomes foliage. The FSS arises from the lateral meristem of the SSS whereas all subsequent lateral flowers (second-order), arise acropetally from lateral meristems of the FSS. While the main axis elongates leaving a primordium on the apical meristem, decussate pairs of lateral branches emerge acropetally from successive phyllomes and pedicels extend early in the flower development at a similar rate of growth as the bud. A vegetative primordium remains active at the apical meristem giving rise to vegetative tissue. Internodes of the main axis continue to extend after the bud achieves full development size. No delayed accessory flowering axis was observed. (Fig. 2E–I).

Mature inflorescence — A foliose pherophyll subtends the main axis that varies in length in the same specimen. The pherophyll arises from a previous season’s branch, typically as a vegetative shoot with former FSS internodes bearing bracteose pherophylls densely arranged (cataphylls). These are short and decussate; subsequent internodes with foliage pherophylls are elongated, cataphylls are usually persistent in flowering leaving scars along the base of the main axis in the mature branchlet. Conversely, in the same specimen, the main axis might be expressed as a shoot with discrete elongation that gives the appearance of a raceme with bracteose pherophylls subtending basal flowers. Distal flowers are usually subtended by foliose pherophylls; usually bracteose pherophylls are deciduous. Internodes of the main axis bearing cataphylls are very short and more elongated internodes bearing leaves (foliose pherophylls) are similar in length. Flower pedicel is variable in length. The apex of the FSS bears an active vegetative bud that often continues to develop vegetative tissue beyond the flower region; the relative position of the flower/fruit become basal in the branch as much as the internodes elongate and vegetative tissue is newly produced. In the same specimen, some FSS might cease growth early and not develop vegetative tissue. No delayed accessory flowering axes were observed.

Umbeliform

Development pattern — The main axis (first-order) bears bracteose pherophylls subtending flowers and more foliose pherophylls that simultaneously subtend a flower and the main axis; this arrangement corresponds to a FSS (Fig. 1). The main axis has homogeneous growth extending sufficiently to accommodate at least three flowers. Flower faced to the vegetative stem often not arises. FSS arise from lateral meristems of the SSS whereas all subsequent lateral flowers (second-order) arise acropetally from lateral meristems of the FSS. The main axis elongates very slowly leaving a primordium on the apical meristem. Meanwhile, decussate pairs of lateral flowers emerge acropetally from successive phyllomes and pedicels extend at a similar rate of growth as the bud. A vegetative primordium remains inactive at the apex of the main axis. No accessory flowering axes were observed. (Fig. 2J–N).

Mature inflorescence — A foliose pherophyll simultaneously subtends a flower and the main axis; the other flowers are subtended by bracteose pherophylls. The flowers are arranged in tiny internodes giving the appearance of a cluster of up to 4-flowers (but usually 2-3 flowers). The internodes of the main axis are always similar in length; these are of relatively constant in length in the same specimen. Pedicels at least are four times longer than axis internodes. Main axes end in vegetative buds, never developing vegetative tissue beyond the flowering region. Only one main axis occurs at each phyllome.

Racemiform pattern

Development pattern — The main axis (first-order) including bracteose pherophylls subtending flowers corresponds to a FSS; this is subtended by a foliose pherophyll, and the first internode of the main axis undergoes before subsequent ones, i.e. the main axis exhibits heterogeneous growth (Fig. 1). The FSS arises from the lateral meristem of the SSS whereas all subsequent flower bearing lateral branches (second-order) arise acropetally from the lateral meristem of the FSS. This early elongated first internode supports a tight group of second-order flowers. Towards the end of the extension of the main axis, subsequent internodes elongate with further decussate pairs of flowers emerging acropetally from successive phyllomes; pedicel extends late in the flower development as the bud achieves almost full grow. A vegetative primordium remains inactive at the apex of the main axis. An accessory flowering axis commonly occur aligned between the pherophyll and the main axis (Fig. 3D); this is delayed but total or partial reiterated FSS. (Fig. 3A–F).

Mature inflorescence — A foliose pherophyll subtends the main axis which has a relatively constant length at the same specimen. The first internode of the main axis is markedly more elongated than the others and each flower is subtended by a bracteose pherophyll. Flower pedicel usually twice as long as axis internodes. Main axis ends in a vegetative bud, rare in a flower; a flowering axis might be expressed in the terminal SSS. An accessory flowering axis is eventually positioned between the leaf (pherophyll) petiole and the main axis – some species have up to two accessory flowering axes per axil aligned in a development sequence; the accessory flowering axis is delayed in development in contrast to the main axis, however, it is not obvious when advanced in development stage (e.g. fruiting).

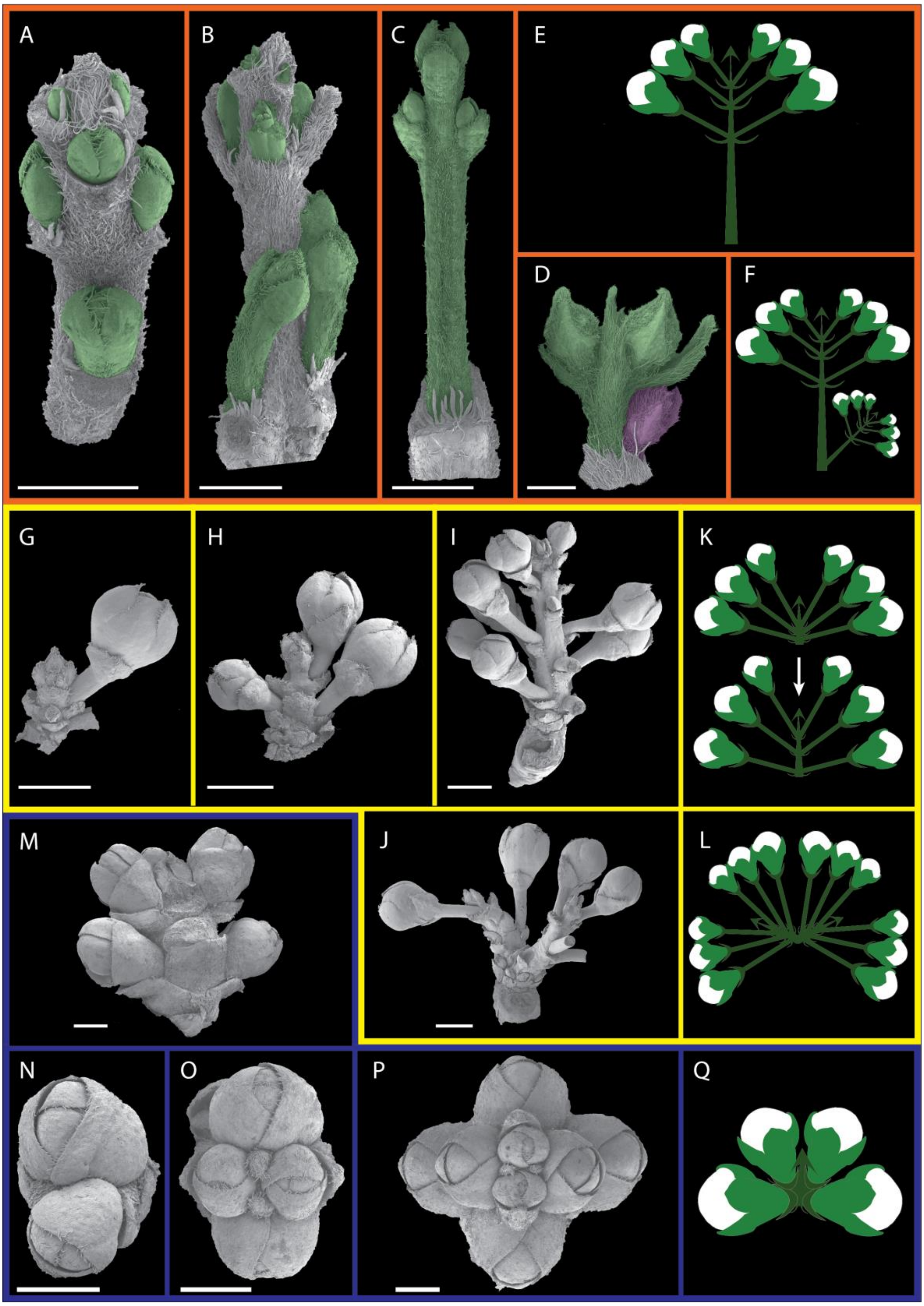

Fig. 3. Comparative development analysis of the inflorescence patterns in *Eugenia*. A-F (orange box). *Racemiform* pattern. (A-C) Flowering axes (green structures) development until before the elongation of the flower pedicels of *Eugenia modesta*. (D) Delayed accessory flowering axis (purple) of *E. biflora*. (E) Scheme of the *racemiform* pattern. (F) Scheme representing delayed accessory flowering axis. G-L (yellow box). *Fasciculiform* pattern. (G-I) Flowering axis development of *E. protenta*. (J) Two

flowering axes at the same development stage sharing a phyllome. (K) Scheme representing the flexibility of the main axis length. (L) Scheme showing two flowering axes at the same development stage sharing a phyllome. M-Q (dark-blue box). *Glomeruliform* pattern. (M) Lateral view of a flowering axis of *E. adenocalyx*; two flowers were removed. (N-P) Upper view of the flowering axis development. (Q) Scheme showing the *glomeruliform* pattern. Scale bars = 1 mm.

Fasciculiform pattern

Development pattern — The main axis (first-order), including bracteose pherophylls subtending flowers corresponds to an FSS. The FSS itself is subtended by an often early deciduous, foliose pherophyll (Fig. 1). The main axis undergoes homogeneous extension of the internodes, i.e. internodes of the main axis grow at a similar rate. The FSS arises from the lateral meristem of the SSS whereas all subsequent lateral flowers (second-order) arise acropetally from lateral meristems of the FSS. The main axis elongates leaving a primordium on the apical meristem while decussate pairs of lateral flowers emerge acropetally from successive phyllomes; the pedicel extends early in the flower development at a similar rate of growth as the bud. A vegetative primordium remains inactive at the apex of the main axis. No delayed accessory flowering axes were observed. Instead, two flowering axes at the same development stage might share a phyllome (Fig. 3J) in an arbitrary position. (Fig. 3G–L).

Mature inflorescence — An often deciduous foliose pherophyll, subtends the main axis that can vary in length in the same specimen. This length variation leads to the possibility of the short, cluster-flowered condition or a looser arrangement of flowers. The internodes of the main axis are always similar in length and each flower is subtended by a bracteose pherophyll. Pedicels are at least twice as long as axis internodes. Main axes end in a vegetative bud, rarely in a flower, and never develop vegetative tissue beyond the flowering region. More than one main axis often shares a phyllome – these are equivalent in development; the FSS often emerges from a deciduous leaf phyllome from the previous seasonal growth period.

Glomeruliform pattern

Development pattern — The main axis (first-order), including bracteose pherophylls subtending flowers corresponds to an FSS (Fig. 1). The FSS itself is subtended by an often early deciduous, foliose pherophyll. The main axis undergoes homogeneous growth, extending sufficiently to accommodate the flowers. The FSS arises from the lateral meristem of the SSS whereas all subsequent lateral flowers (second-order) arise acropetally from lateral meristems of the FSS. The main axis elongates very slowly leaving a primordium on the apical meristem while decussate pairs of lateral flowers emerge acropetally from successive phyllomes. The pedicel does not extend and remains inconspicuous. A vegetative primordium remains inactive at the apex of the main axis. No delayed accessory flowering axes were observed. Instead, two flowering axes at the same development stage might share a phyllome in an arbitrary position. (Fig. 3M–Q).

Mature inflorescence — An often deciduous foliose pherophyll subtends the main axis, main axes are of relatively constant length in a single specimen. The internodes of the main axis are always similar in length and each flower is subtended by a bracteose pherophyll. Pedicels are indistinct and can appear absent. The main axis ends in a vegetative bud. More than one main axis can share a phyllome of equivalent development; the FSS often emerges from a deciduous leafy phyllome from the previous seasonal growth period.

Thyrsoid

Development pattern — The main axis (first-order) including bracteose pherophylls subtending branching or flowers, corresponds to an FSS (Fig. 1). The FSS is subtended by a foliose pherophyll and undergoes homogeneous internode extension. The FSS arises from the lateral meristem of the SSS whereas all subsequent lateral branching and/or flowers (second-order) arise acropetally from the lateral meristem of the FSS. The apical meristem of the FSS retains its activity resulting in further elongation of the main axis that is later replaced by a central-flower (Fig. 4A) or, rarely, a ceased vegetative bud remains. Alternatively, the apical meristem of the FSS is early replaced by a central-flower that results in absent or discrete branching elongation (Fig. 4B). Lateral branchings or flowers (second-order) are subtended by bracteose pherophylls. Each flower is subtended by a pair of prophylls that retain branching potential at its axil (phyllome) from where a flower (third-order) can emerge with potential to generate successive and repeating further branching orders. The three-flowered partial dichasium develops basipetally, i.e. the middle flower develops before the lateral ones. The pedicel of the central flower does not extend whereas those of the lateral flowers extend at a similar rate of growth as the bud. The vegetative primordium is usually replaced by a flower. No accessory flowering axis was observed. (Fig. 4A–F).

Mature inflorescence — A foliose pherophyll subtends the main axis that can vary in length in the same specimen. The FSS has a flexible arrangement, i.e. it might be short with lateral branches bearing three-flowered partial dichasia. Alternatively, the main axis extends, usually undergoing elongated lateral branching with four or more orders at the lowermost portion and successively decreasing in branching orders towards the uppermost portion. The latter arrangement gives rise to a pyramidal appearance. Internodes of the main axis usually shorten towards apex. Each branch is subtended by a bracteose pherophyll while each flower is subtended by pair of bracteose prophylls that become pherophylls of the next order in case of branching. The main axis ends in a sessile premature flower but eventually remains a ceased vegetative bud. Although no accessory flowering axis was observed, lateral branching from the very base of the main axis can be misleading.

Phylogenetic relationship and ancestral reconstruction

The backbone of *Eugenia* has good support in the combined dataset with ca. 60% of the lineages with >0.95 posterior probability while internal relationship is stronger with c. 65% with this >0.95 PP or higher. All previously reported infrageneric groupings of *Eugenia* were recovered (Mazine *et al.* 2014; Bünger *et al.* 2016; Faria *et al.* in prep.) providing a coherent framework for the reconstruction of the seven inflorescence development patterns here described.

Character reconstructions recovered the expression of the cymose branching pattern associated with earlier diverging lineages whilst later diverging lineages recovered exclusively the racemose pattern (Fig. 5). The *Auxotelic* pattern is returned as the condition at the ancestral node of *Eugenia* and *Myrcianthes*, and is the most probable ancestral condition until the diversification of *Eugenia* sect. *Umbellatae*. Development patterns always arise from *auxotelic* pattern irrespective of their phylogenetic position. *Auxotelic cataphylls* appear in earlier diverging lineages of *Eugenia* and have evolved as least five times independently.

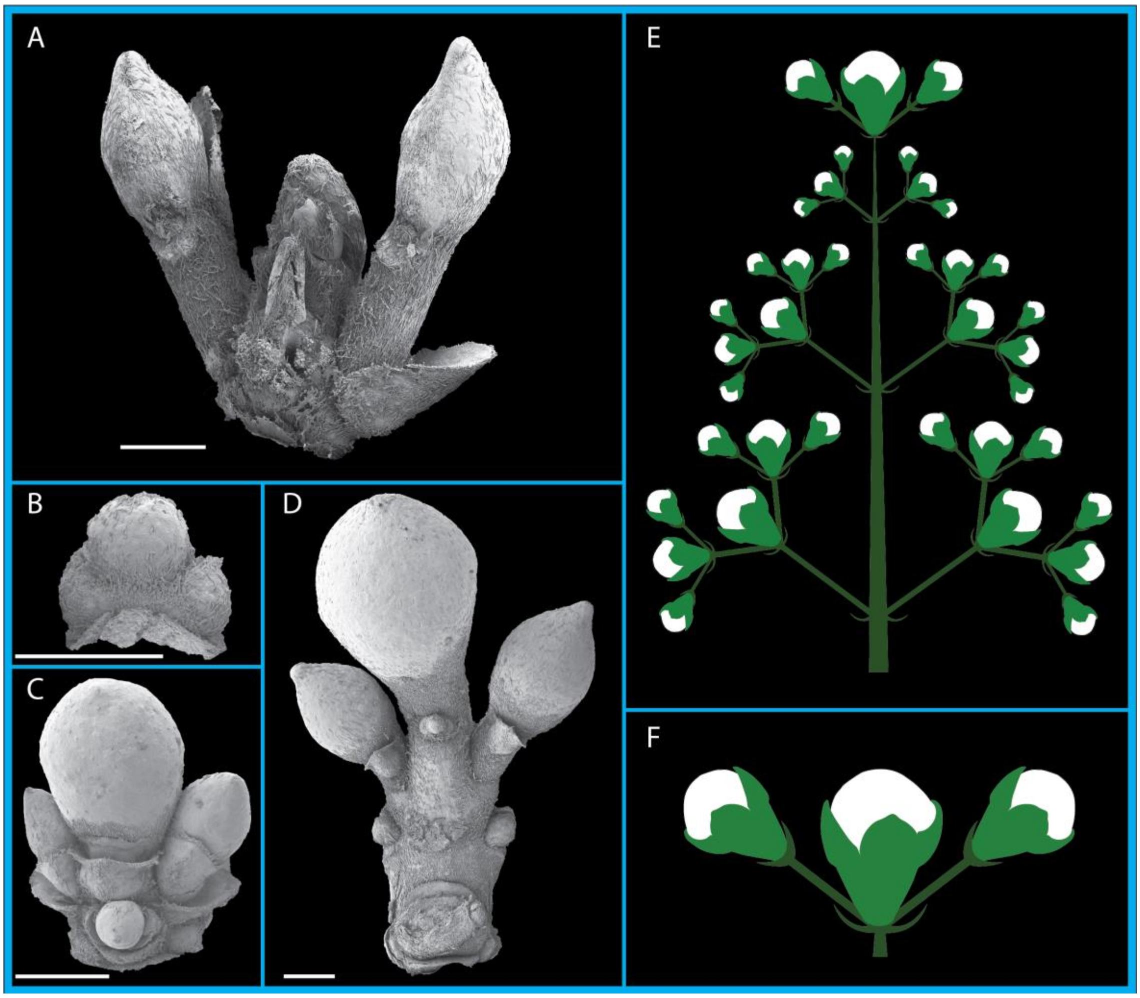

Fig. 4. Comparative development analysis of the inflorescence patterns in *Eugenia*. A-E (light-blue). *Thyrsoid* pattern. (A) The apical meristem retained its activity resulting in early elongation of the lateral branching. (B-D) The apical meristem is early replaced by a central-flower resulting in absent or discrete branching elongation. (E) Scheme representing *thyrsoid* pattern. (F) Scheme representing a dichasial arrangement. Scale bars = 1 mm.

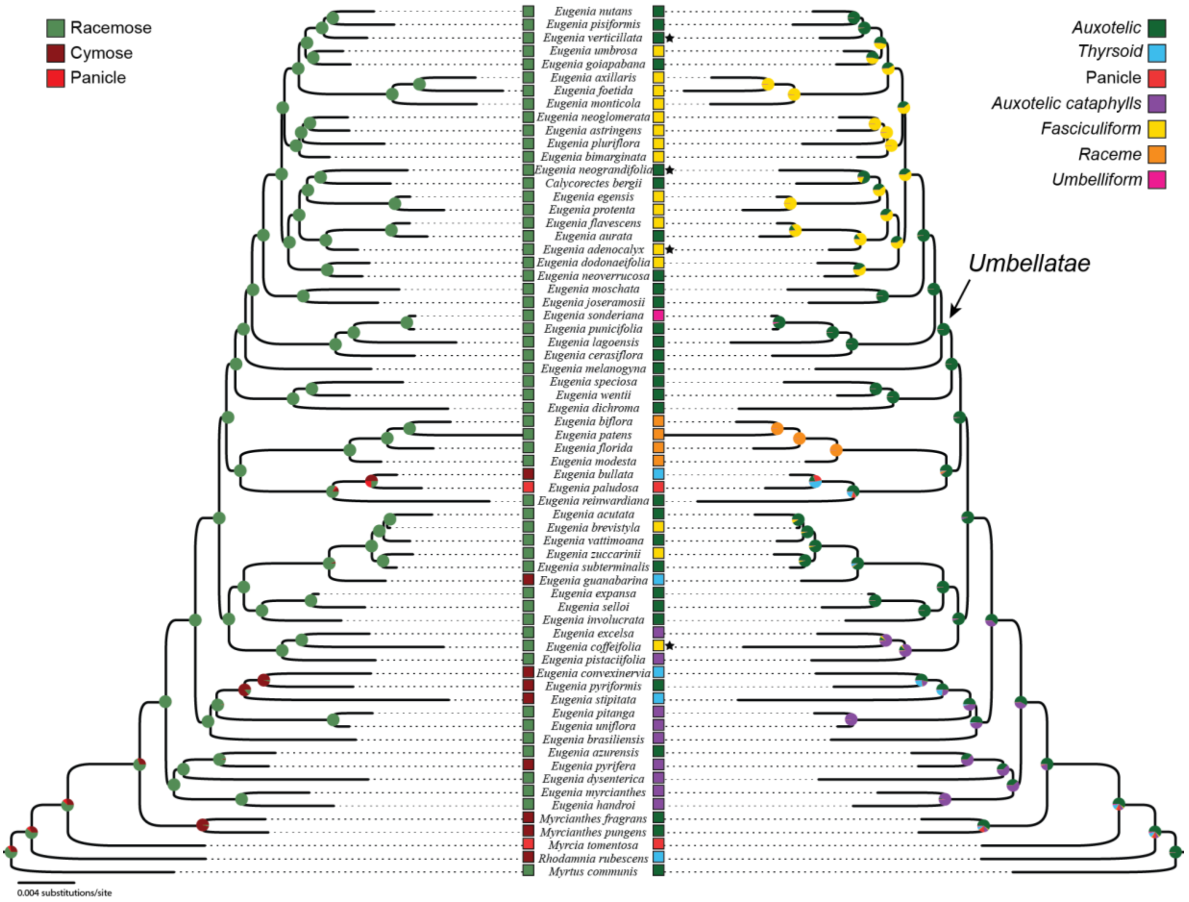

Fig. 5. Character reconstruction of the inflorescence development patterns of *Eugenia*. Racemose and cymose branching pattern are shown on the left; when present, cymose was scored as a secondary development. Reconstruction of the inflorescence development patterns here described are demonstrated on right.

The *Umbelliform* pattern is found at earlier diverging nodes of *Eugenia* sect. *Umbellatae*, represented here only by *Eugenia sonderiana*. *Fasciculiform* and *glomeruliform* patterns were scored in found at earlier diverging nodes of *Eugenia* sect. *Umbellatae*, represented here only by *Eugenia sonderiana*. *Fasciculiform* and *glomeruliform* patterns were scored in conjunction (see discussion) and arose later in the evolutionary history of *Eugenia*. Those latter patterns are exclusive to *Eugenia* sect. *Umbellatae*, except for *E. coffeifolia* (assigned as *glomerulifom*) that emerges in *Eugenia* sect. *Excelsae* ined. (Mazine *et al.*, in prep.). The *Racemiform* pattern appears to have evolved only once and is exclusive to *Eugenia* sect. *Racemosae*. *Thyrsoid* apparently evolved independently at least four times within *Eugenia*. The reconstructed ancestral node of the extra-Neotropical lineage retains *auxotelic* as the highest probability.

Phylogenetic signal

The cymose branching pattern appears to be a secondary development expressed in earlier diverging lineages whilst later diverging lineages tend to express a strictly racemose pattern demonstrated by high phylogenetic signal (*lnl* -23.373, λ = 0.96). *Auxotelic* was the most recurrent pattern in *Eugenia* with very low scores of log-likelihood and lambda (*lnl* -45.494, λ = 0.0) according to comparative estimates (Tab. 3). In contrast, *Racemiform* retains the higher value of log-likelihood and lambda as indicative of high phylogenetic congruence (*lnl* -5.078, λ = 1.0). *Auxotelic cataphylls* returned high lambda (λ = 1.0) showing that there is a strong trend that this pattern is associated with early diverging lineages but a low score of log-likelihood (*lnl* -21.118) indicates this is not exclusive. *Auxotelic* and *auxotelic cataphylls* patterns analysed in conjunction scored very low log-likelihood (*lnl* -44.039) and moderate lambda (λ = 0.77). *Fasciculiform* and *glomeruliform* were also evaluated in conjunction returning low score of log-likelihood (*lnl* -33.195) and moderate (λ = 0.71) that indicates a trend for expression of these patterns in later diverging lineages. Phylogenetic signal decreases distinguishing *glomeruliform* from *fasciculiform* (*lnl* -31.475, λ = 0.49). *Thyrsoid* appears more common in early diverging lineages of *Eugenia* with a high phylogenetic signal (*lnl* -11.825, λ = 0.93), suggesting trait dependence on phylogeny.

Traits associated with clades within *Eugenia* sect. *Umbellatae* were assessed using phylogenetic signal in order to reveal relevant character to support subgroups. The recurrence of flowering axes sharing a phyllome at the same developing stage recovered moderate lambda (λ = 0.72) and low log-likelihood (*lnl* -34.150). The *fasciculiform* within this section recovered moderate log-likelihood and high lambda (*lnl* -26.656, λ = 0.89). *Auxotelic* showed high lambda (λ = 0.81) and low log-likelihood (*lnl* -32.500).

DISCUSSION

The inflorescence in tribe Myrteae

Opposite and decussate phyllotaxy with highly flexible arrangements is considered the primitive inflorescence of Myrtaceae (Briggs and Johnson 1979). The remarkable diversity of Myrteae, representing half of the family's species richness is also reflected in highly flexible inflorescence morphology. The most common arrangement patterns in Myrteae are presented in this section, following the works of previous authors.

Tab. 3. Comparative phylogenetic signal of the inflorescence development patterns.

Patterns	***lnl***	**λ**
Cymose branching	-23,373	0,96
Racemose branching	-23.634	1.0
Auxotelic	-45,494	0.00
Auxotelic cataphylls	-21,118	1.0
Auxotelic + Auxotelic cataphylls	-44.039	0.77
Fasciculiform + Glomeruliform	-33.195	0.71
Fasciculiform without Glomeruliform	-31.475	0.49
Glomeruliform	-14.936	0.0
Thyrsoid	-11,825	0.93
Racemiform	-5,078	1.0
Eugenia sect. *Umbellatae*		
Axes sharing a phyllome	-34.150	0.72
Auxotelic	-32.500	0.81
Fasciculiform	-26.656	0.89

Auxotelic shoot — An axillary branch that may be described as auxotelic raceme (Briggs and Johnson 1979) if the main axis is prolifically extended and maintains late vegetative growth potential in the apex from an active bud (Prenner *et al.* 2009). Lateral flowers are subtended by frondose (foliose) bracts providing a system equivalent to a flowering shoot system (Kirchoff and Claßen-Bockhoff 2013), sometimes producing a 'late proliferation' shoot (Prenner *et al.* 2009). Solitary flowers can be also interpreted as auxotelic shoots as can aggregations of monads in a lateral leaf shoots terminated by an active vegetative bud (see Briggs and Johnson 1979). Depending on the degree of main axis reduction, the appearance may be of a raceme with foliose pherophylls. A related arrangement is 'stenocalyx raceme' (Barroso *et al.* 1991) in allusion to a genus currently treated within *Eugenia*.

Bracteate shoot — A flowering axis with bracteose pherophylls subtending flowers and axes terminated by a flower or vegetative bud that can recover vegetative growth (Landrum and Kawasaki 1997). The terms racemiform (e.g. Giaretta and Fraga 2014) or raceme (e.g. Lourenço *et al.* 2013) have been used as equivalents. When solitary flowers express foliage pherophylls, this can also be termed a bracteate shoot (e.g. Faria *et al.* 2015). The degree of morphological extremity of bracteose or foliose forms of the pherophyll determines the most appropriate terminology.

Fascicle — A flowering axis with short internodes bearing pedicellate flowers subtended by bracteose pherophylls. Fascicles have been related to bracteate shoots with reduced main axes (Landrum and Kawasaki 1997). Such arrangements are also termed fasciculiform (Sobral *et al.* 2012). When the main axis is even more reduced, it is often called an umbel, umbelliform (e.g. McVaugh 1963) or umbel-like (Landrum 1991). Eventually, the main axis of a fascicle recovers vegetative growth by expressing an auxotelic shoot. The length of the main axis is relevant to the use of the term 'fascicle'.

Glomerule — A flowering axis with short internodes bearing sessile flowers subtended by bracteose pherophylls. However, flower with very short pedicels (subsessile) are also termed glomerules (e.g. Souza *et al.* 2016). Although flexible, the pedicel length influences the use of the term 'glomerule'.

Dichasium — A solitary flower subtended by a pair of prophylls (bracteoles) from where a flower emerges from each axil and results in a three-flowered arrangement (McVaugh 1963b); the middle flower is premature in development relative to the lateral ones. Successive repetition of the branching pattern to unspecified degrees, can result in compound-dichasia as found in *Blepharocalyx* (see Souza and Morim 2008).

Thyrsoid — This is formed when branching from the axes of flowering prophylls is expressed as a raceme, i.e. a racemose branching pattern followed by a cymose pattern (Endress 2010) at branch apices. The main axis (first-order) exhibits branching (second-order) usually in the lowermost portion and supports compound-cymes (third-order or higher). Branching is gradually reduced to second-order towards apex, giving a pyramidal appearance. This arrangement is terminated by a flower, then termed thyrsoid (Briggs and Johnson 1979). The term metabotryoid was introduced by Briggs and Johnson (1979) due to its uncertain derivation of a lateral branches reduction from a thyrsoid or a panicle.

Panicle — Two conditions must be filled, i.e. the main axis (first-order) should end in a flower and should subtend a series of lateral (second to further orders) axes also terminated by flowers (Prusinkiewicz *et al.* 2007). This arrangement is unpredictable, and consequently typological definitions are often inaccurate and do not incorporate all variation. The panicle can also be compared to a thyrsoid with depauperate branching termination that prevents an obvious cymose pattern, thus it cannot be consistently assigned as derivation of racemose neither cymose because it lacks the limitation of these branching patterns (Endress 2010).

In summary, Myrteae inflorescences can be divided into racemose or cymose branching patterns (Endress, 2010), except panicles. Whether the inflorescence is determinate or indeterminate is not relevant to assign branching pattern (Endress, 2010). Instead, classification relies on hierarchical branching number, i.e. number of branching orders. The number of branching orders is limited to two in the racemose branching pattern, i.e. the main axis (first-order) is fixed whereas number of branching axes (second-order) corresponding to flowers is variable and unlimited. This arrangement is common in Myrteae where repetition of basic flowering units results in partially compound arrangements, e.g. a diplobotryum when determinate, or diplobotryoid when determinate (terminated by a flower). In a cymose branching pattern, the number of branching orders is unlimited, i.e. the number of lateral branches is limited to two but the number of orders is variable; the basic arrangement can repeat successively (Endress 2010).

Plant architectural traits relative to inflorescence interpretation

Architecture is a consequence of traits, how these traits are arranged and their relative position and successive repetition. As result, plants are modular organisms of multidimensional processes driven by endogenous growth and exogenous constraints that define their form and resulting architecture (Barthélémy and Caraglio 2007; Chomicki *et al.* 2017). Plant architectural traits must be understood before considering general inflorescence development.

Repetition of partial or whole architectural units from otherwise dormant meristems is termed delayed reiteration (Chomicki *et al.* 2017) and is clearly implicated in the architectural expression of Neotropical Myrteae. The *auxotelic* pattern is here treated as a reiterated SSS with bracteose or foliose leaves but when subtended by axillary flowers it is called FSS. *Auxotelic* reiteration produce more phyllomes that give rise to axillary reproductive units, increase branching order in the plant architecture, and ultimately contribute to vegetative production and space exploitation. Apical meristems can also differentiate into reproductive units and express inflorescences arrangements that reflect architectural units of the body plant. Dormant meristematic buds are maintained in the apex of branches or inflorescence units, termed indeterminate (Troll and Weberling 1989; Weberling 1988) or blastotelic (Briggs and Johnson 1979). Two types of indeterminate behaviours are seen in the tribe, i.e. 1) a pattern that cease growth at some stage, often early in the development, and 2) a vegetative bud that cease growth but latter recovery the extending capacity given rise to a vegetative shoot. These conditions are presumably related to the meristematic vigour in produce vegetative tissue (Claßen-Bockhoff and Bull-Hereñu 2013).

Phylogenetic implications of branching patterns

Racemose and cymose branching patterns are recognized as fundamental inflorescence architectures (Endress 2010); both are found in *Eugenia*. The cymose pattern appears secondary in *Eugenia,* derived from an *auxotelic,* primary racemose pattern. Vigour in branching potential from phyllomes subtended by prophylls modulates a cymose arrangement. Therefore, cymose branching pattern is always partial in *Eugenia* as a derivation from a racemose primarily architecture.

The racemose branching pattern in Myrteae apparently first thrive in the *Myrtus* group, sister to the neotropical lineage, and is here assumed to be the ancestral condition of *Eugenia* (Fig. 5). Cymose is the standard inflorescence pattern of Eugenia's sister genus, *Myrcianthes* (Grifo 1992), which is associated with the early diverging lineages of the Neotropical lineage. *Eugenia* sect. *Pilothecium* and *Eugenia* sect. *Pseudeugenia* have conserved ancestral arrangements as highlighted by the array of distinct cymose inflorescence types (see Faria 2014). This trend may be linked to the branching potential of subtending prophylls conserved in those lineages. It has major implications to inflorescence architecture, flower display, and ultimately impacts pollinator behaviour (Harder *et al.* 2004; Ishii *et al.* 2008).

Homologous arrangements in light of current evolutionary understanding

Auxotelic pattern was recovery in the early lineages and in the backbone with highest probabilities (Fig. 5). Thus, it is hypothesised here that the ancestral inflorescence arrangement of *Eugenia* is similar to the *auxotelic* pattern hereafter called Hypothetical Auxotelic Ancestral (HAA) (Fig. 6). This view is supported by means of

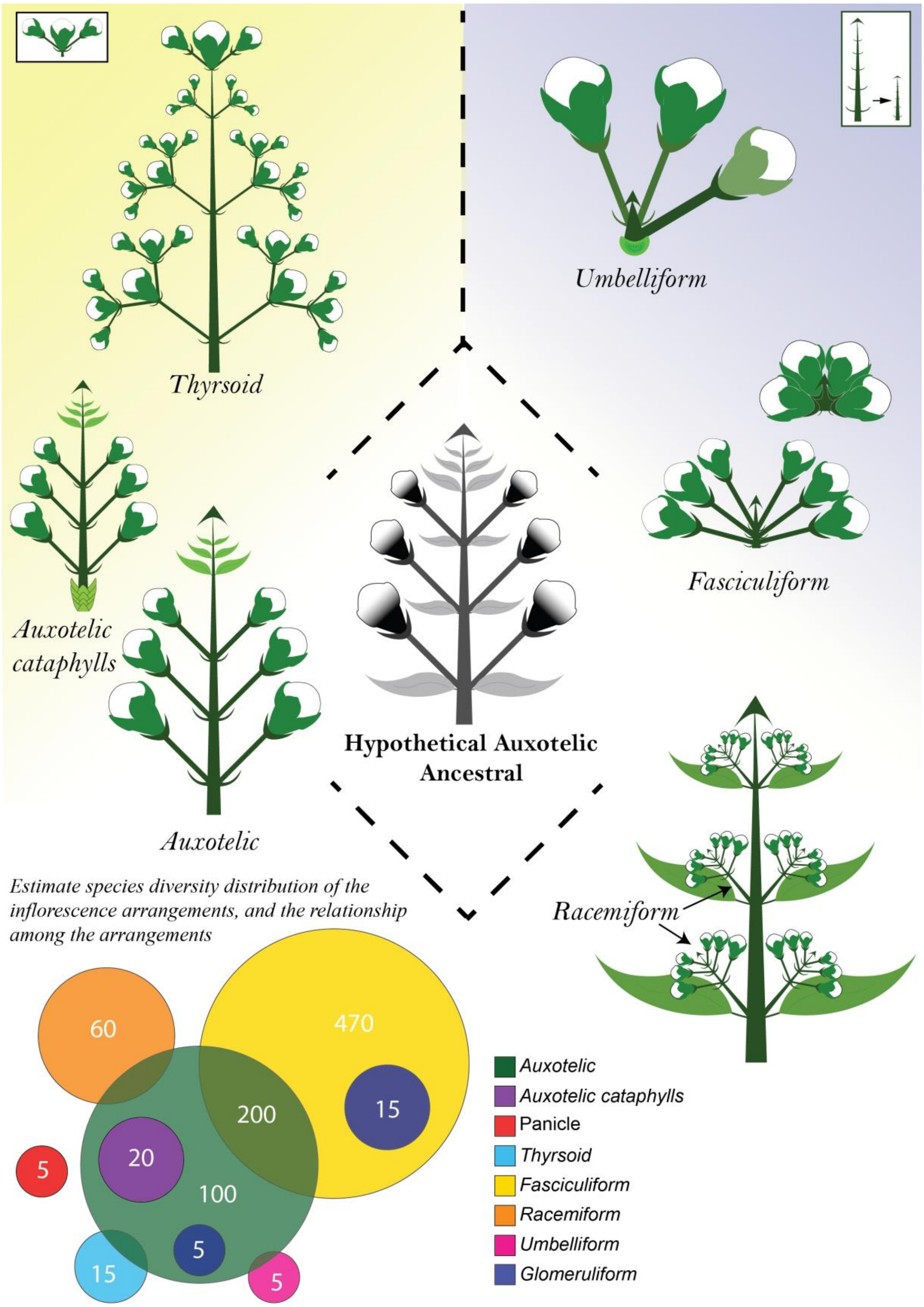

Fig. 6. Homology hypothesis of the inflorescence pattern in *Eugenia*. The hypothetical auxotelic ancestral (HAA) is shown in the middle. Representing schemes of the development pattern are hypothesised to be homologue to the HAA. Two

morphological trends are represented by the colour gradient, i.e. towards yellow increases the vigour of the branching potential from phyllomes subtended by prophylls (bracteoles) whereas towards blue decreases the length of the main axis of a flowering axis. The names follow the described development. The diagram on the left-bottom represents the relationship among the development patterns; numbers indicates the species diversity.

the *Myrtus* and *Myrcianthes* groups express the *auxotelic* pattern. As consequence, flexible arrangements found in *Eugenia* are result of plastic phenotypes of the basic HAA arrangement. Evolutionary changes among development pattern are regarded as belonging to a spectrum of continuities rather than homoplastic conditions that evolved independently.

The conservation of the *auxotelic* condition through multiple lineages may be related to the efficiency of this architecture that saves energy supporting both photosynthetic leaves and reproductive units. The genetic machinery behind inflorescence development of eudicots is still far from understood (Irish and Litt 2005; Prenner *et al.* 2009). However, studies demonstrate that small shifts in meristematic activity (Bull-Hereñu and Claßen-Bockhoff 2011) have a major impact on final architecture (Benlloch *et al.* 2007). The development sequence of *auxotelic cataphylls* is essentially *auxotelic* except for a basal zone of condensed bracteose pherophylls that cover the primordia. The protected bud is an adaptation to tolerance of fire-prone environments (Charles-Dominique *et al.* 2015) such as the Brazilian savanna (Simon *et al.* 2009), where most species occur. This pattern is also found in *Eugenia excelsa* and *E. pistaciifolia* that occur in warm and drought-prone environments and may be related to protection against dehydration. As a consequence, *auxotelic* and *auxotelic cataphylls* should be investigated in conjunction in order to focus on evolutionary traits rather than presumed ecological responses.

Developmental flexibility plays an important role in inflorescence arrangement *Eugenia* through shifts to more specialised arrangements. Reversions from *fasciculiform* to *auxotelic* were clearly recorded in *Eugenia* sect. *Umbellatae*. Flowering axis length reduced is commonly found in this section though the apical meristem eventually recovers its activity in some species and develops to a shoot. This condition is recurrent in some species, consistent with their clades (Fig. 7, nodes A, B, C and G) and is scored as *auxotelic* rather than *fasciculiform*. Combinations of characters described in the mature material allow more practical use and recognition of the patterns. Short

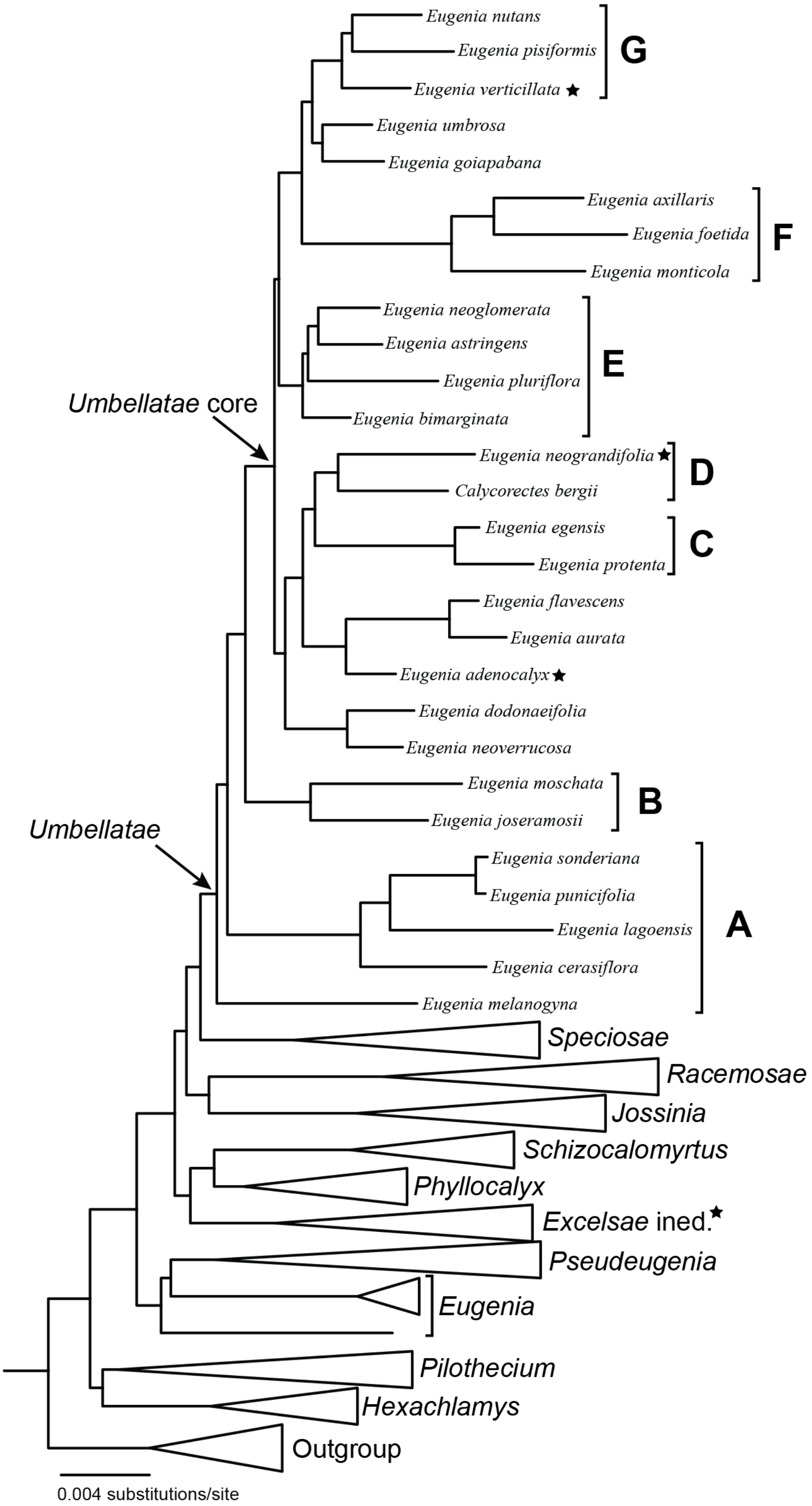

Fig. 7. Phylogenetic tree supporting this research summarizing *Eugenia* with focus on *Eugenia* sect. *Umbellatae*. Morphological relevance of the highlighted clades is discussed. ★Species scored as *glomeruliform* pattern.

flowering axes can resemble umbel or main axes might extend and express a raceme appearance. Shifts in main axis length and expression of the *auxotelic* pattern may provide enhanced adaptability to environmental constraints and pollinator availability. Dimensional arrangement of flowers was demonstrated to influence the pollinator behaviour (Harder *et al.* 2004).

The *umbelliform* pattern is apparently rare in *Eugenia*, recorded only once in this analysis. The arrangement of the subtending pherophyll simultaneously shared with the flowering axis and a flower is unique in *Eugenia* and has not been noticed before. Although this arrangement makes this pattern easily distinguishable, suppression of structures in developmental sequence decreases the accuracy of the inference (Prenner *et al.* 2009). The flowering axis of the *umbelliform* pattern is treated as homologue to a flower in the HAA, therefore the foliose pherophyll subtends the flowering axis rather than the F2 (Fig. 2J). This is inferred by the slightly advanced developmental stage of the F1 flower pair in contrast to F2, reinforced by the consistent decussate developmental arrangement observed in *Eugenia*. Availability of space has an important role in the development of *Eugenia* (Vasconcelos *et al.* 2018) and is highlighted as the main driver of the recurrent three-flowered arrangement observed in the *umbelliform* pattern. This hypothesis is supported by the four-flowered arrangement expressed at the terminal node in response to greater available spatial resource. Suppression of the F2 subtending pherophyll is seemingly a consequence of the spatial constraint resulting from the very short main axis. Thus, the flowering axis subtended by foliose pherophylls in the *umbelliform* pattern is equivalent to the FSS of the HAA.

Developmental sequence and final arrangement provide a consistent framework to distinguish the *racemiform* pattern. The flower of the HAA is interpreted as homologous to the flowering axis in the *racemiform*. As a consequence, the FSS of the *racemiform* achieves third-order branching, i.e. it encompasses the subtended shoot, the axillary flowering axis subtended by foliose pherophylls, and the axillary flowers subtended by bracteose pherophylls. The flowering axis of the *racemiform* pattern is a compound arrangement where the second-order axis is subtended by third-order flowers. This view is supported by the apex of the FSS that recovers its potential for growth whereas the main axis of the *racemiform* pattern never further develops. The delayed accessory flowering axis of the racemiform pattern, exclusive in *Eugenia*, is curiously also found in *Myrtus communis*. Instead of a flowering axis, a delayed accessory flower positioned between the foliose pherophyll and the main flower is often expressed in *Mytus communis*. This reiteration is treated as a plesiomorphic mechanism to increases flower availability and is presumably related to the superimposed arrangement of *Myrceugenia* that can express a sequential row of accessory units in a axil leaf (Landrum and Kawasaki 1997).

Fasciculiform and *glomeruliform* have identical development patterns (except for the pedicel absence in the former) and are treated in conjunction. The FSS of the HAA is interpreted as homologous to the flowering axis of the *fasciculiform* pattern. This is supported by the position of subtending foliose pherophyll and retains a vegetative meristem at the apex that has ceased growth. The capacity for two or more flowering axes at the same development stage, sharing a node, is treated as reiteration of the FSS rather than an accessory flowering axis. Although functionally equivalent, they are analogous strategies that appear independently in *Eugenia*, increasing the number of available flowers in the inflorescence arrangements.

The first-order branching of the *thyrsoid* pattern is treated as homologue to the subtended shoot of the HAA. Thus, branching of the *thyrsoid* (second order) is equivalent to a flower of the HAA, and further orders are result of vigorous branching potential expressed from the successive subtending prophylls. This hypothesis of homology is supported by the consistent primary racemose arrangement of the *thyrsoid.* Although the main axis is terminated by a flower, the determinacy of the apex have is not relevant to assign branching pattern (Endress 2010). This is reinforced by the enormous numbers of parallel origins of the terminal flower among angiosperms (Bull-Hereñu and Claßen-Bockhoff 2011). Apical dominance presumably moderates inflorescence branching (Harder and Prusinkiewicz 2013) and may be involved in the ultimate pyramidal architecture of the *thyrsoid*.

Diagram of the estimate species diversity distribution of the inflorescence arrangements (Fig. 6) graphically demonstrates the relationship among the patterns here described. The ellipse overlay indicates homologue hypothesis here proposed and the numbers an estimative of the species diversity that express each pattern. *Auxotelic* totally comprises the *auxotelic cataphylls* but differs by a presumably ecological adaptation. *Glomeruliform* is simultaneously encompassed by *auxotelic* and *fasciculiform*. It indicates that *glomeruliform* is related to two patterns, i.e. the capacity to recover the vegetative growth also shared by the others species in its clade (Fig. 7, clade G★) supports relation to *auxotelic* whilst the others species that fit to the *glomeruliform* but are terminated by a ceased vegetative bud (Fig. 7, ★ except from the clade G) are seemly related to the *fasciculiform*. An estimation of 200 species that fit to the *fasciculiform* except by often recovers the vegetative growth are in the edge between *fasciculiform* and *auxotelic* (scored in the current analysis following the prevalent *auxotelic* pattern). Panicle remains without recognized relationship.

Systematic implication of the inflorescence patterns

Auxotelic is assigned to morphological circumscription of infrageneric groups such as *Eugenia* sect. *Phyllocalyx* and *Eugenia* sect. *Speciosae* (Fig. 7). However, this pattern is recurrent in the genus demonstrated by the low phylogenetic signal. Combination of additional morphological characters should be used to consistently diagnose these sections (Bünger *et al.* 2016a; Bünger *et al.* 2016b).

The *Auxotelic cataphylls* pattern is recovered with strong phylogenetic signal of lambda supporting its relevance for recognition of earlier diverging lineages such as *Eugenia* sect. *Hexachlamys*, *E.* sect. *Pilothecium*, *E.* sect. *Eugenia* and *E.* sect. *Pseudeugenia*. However, the *auxotelic cataphylls* pattern may be related to ecological or environmental responses (Charles-Dominique *et al.* 2015) rather than to inheritance. It appears that *Eugenia* sect. *Excelsae* species may have adaptations to drought-prone environments.

The *Racemiform* pattern is consistently associated with *Eugenia* sect. *Racemosae,* supported by high phylogenetic signal. Accessory flowering axis with delayed development (in contrast to the main axis) is exclusive to this section and can be consistently used for species diagnoses. The extra-Neotropical *Eugenia* sect. *Jossinia* was recovered with low support as sister to *Eugenia* sect. *Racemosae*. *Eugenia* sect. *Jossinia* has remarkable distinct inflorescence arrangements, in contrast to neotropical species. Inflorescence development studies focusing on the extra-neotropical species may reveal evolutive traits that have influenced migration events to other regions.

Fasciculiform assessed in conjunction to *glomeruliform* are not exclusive to, but are often expressed in the *Eugenia* sect. *Umbellatae* core (Fig. 7). This acquisition seems important for *Eugenia* diversification, especially *Eugenia* sect. *Umbellatae,* the most species-rich section that encompass ca. 680 species of all *Eugenia* (Mazine *et al.* 2016). The relative number of main axes that arise from a phyllome are shown to be systematically relevant within this section. Species with two or more independent axes at equivalent development stage sharing a phyllome (Fig. 7) were recovered at clades C, E and F with low log-likelihood but moderate lambda (*lnl* -34.150, λ = 0.72). Although recurrent in the phylogeny, this trait is consistent with some clades and can be used in combination with other characters.

The *auxotelic* pattern never shares a phyllome with two or more flowering axes as found in *fasciculiform* (see Mature inflorescence in the *auxotelic* pattern). Additionally, *auxotelic* is usually associated with the earlier diverging lineages of *Eugenia* sect. *Umbellatae* supported by high lambda in the phylogenetic signal (*lnl* -32.500, λ = 0.81) but low log-likelihood indicating that it is not exclusive, also expressing in later diverging lineages such as clades A, D and G (Fig. 7). The only exception with *fasciculiform* that develops further to a shoot and simultaneously share a phyllome with two or more flowering axes was recorded in the clade B (Fig. 7) suggesting that this trait combination may be related to the informal "*Eugenia moschata* group".

Assessment of traditional terminology

This is the first attempt to integrate to current knowledge of the evolution of different inflorescence architectural types of Myrteae, within a single circumscription. This approach incorporates initial development sequences and flexible arrangements of the mature architecture, towards a unified terminology. This approach does not follow the long-standing, traditional basis on mature morphology that are known to be inaccurate due to imperfect understanding of homologies (Castel *et al.* 2010; Prenner *et al.* 2009). Terminology relies on definition of the most common arrangements based on the mature material, eventually assuming flexibly arrangements as distinctive (see Briggs and Johnson 1979). This increases the phenotype possibilities and hampers the accuracy of the terminology application. Rather than seek better definitions of arrangements or newly introduce more terms, the focus is how to apply existing terminology.

The definition of auxotelic conflorescence by Briggs and Johnson (1979) relies on the capacity of the apex to recover vegetative growth while axillary flowers (or flowering axes) emerge. *Auxotelic* and *auxotelic cataphylls* patterns are described in detail here expanding the circumscription of the term auxotelic which is suggested to be adopted referring to an inflorescence arrangement when flowering (Tab. 4). It is

Tab. 4. Comparative traits of the inflorescence development pattern and terminology here proposed.

Development patterns	***Auxotelic***	***Auxotelic cataphylls***	***Umbelliform***	***Racemiform***	***Fasciculiform***	***Glomeruliform***	***Thyrsoid***
Proposed terminology	Auxotelic	Auxotelic	Umbelliform	Raceme	Fasciculiform	Fasciculiform	Thyrsoid
Branching pattern	racemose	racemose	racemose	racemose	racemose	racemose	racemose and cymose
Subtending pherophyll of the main-axis	foliose	foliose	foliose	foliose	foliose	foliose	foliose
Subtending pherophyll of the flower	foliose	foliose	one foliose (shared with the main-axis) and others bracteose	bracteose	bracteose	bracteose	bracteose
Bracteose pherophylls densely arranged (cataphylls)	absent	present	absent	absent	absent	absent	absent
Persistence of the main-axis pherophyll	persistent	persistent	persistent	persistent	usually deciduos	usually deciduos	persistent
Main-axis relative length	long	long	very short	moderate	short or moderate	short	long
Frequency of dichasial arrangement expression	low	moderate	not observed	very low	low	not observed	high

Main-axis internodes extension	homogeneous	heterogeneous	homogeneous	heterogeneous	homogeneous	homogeneous	homogeneous
Pedicel extension in the flower development	early	early	early	late	early	inconspicuous	early
Capacity to recover vegetative growth	present	present	ceased by vegetative a bud	ceased by vegetative a bud	ceased by vegetative a bud	ceased by vegetative a bud	ceased by a flower
Number of main-axes sharing a phyllome and relative position	one	one	one	two (rarely three) aligned	up to three in arbitraty position	up to three in arbitraty position	one
Reiterated flowering axis	not observed	not observed	not observed	delayed	at the same development stage	at the same development stage	not observed

equivalent to the solitary flower (Landrum and Kawasaki 1997), late proliferation (Prenner *et al.* 2009), proliferating synflorescence (Weberling 1988) or stenocalyx raceme (Barroso *et al.* 1991). Although the focus of the terminological assessment is in the hyper diverse genus *Eugenia*, the expanded terminological reference of auxotelic can be applied to others Neotropical genera.

The *racemiform* pattern is here associated to the term raceme in order to best circumscribe its use. Raceme is suggested to be adopted in reference to *Eugenia* sect. *Racemosae* (sensu Mazine *et al.* 2016). This term have been used to described inflorescence arrangements of species from this section (Mazine and Souza 2010; Souza and Morim 2008a).

Fascicles have been inconsistently used in specialised taxonomic literature, commonly referring to an axillary flowering axis with short main-axis (e.g. Barrie *et al.* 2016; Lourenço *et al.* 2013). The relative length fluctuation of the main-axis motivated the use of the terms raceme, short-raceme (Souza *et al.* 2015), fasciculiform (Sobral *et al.* 2012) or fasciculate (Barrie *et al.* 2016) adding more chaos to the plethora of terminologies. Thus, fasciculiform term is re-circumscription here and suggested to be adopted in allusion to the *fasciculiform* pattern. Fasciculiform rather than fascicle should be used due the flexible length of the main-axis of the former, contrasting with the typological definition of the fascicle (Weberling 1988) as a raceme with a very short main-axis that does not entirely fit into the *Eugenia*. The *glomeruliform* pattern is included under fasciculiform as re-circumscribed here. Although absence of flower pedicel impacts the ultimate arrangement display, results presented indicate this is related to stochastic factors affecting populations rather than inheritance. This view is reinforced by the fasciculiform arrangement seen in nature, simultaneously expressed both as absence and presence of pedicellate flowers (see *E. neoglomerata* in Lima *et al.* 2015). Second inconsistence in using the term glomerule relies on *Eugenia adenocalyx* that has sessile flowers and fits the *fasciculiform* pattern. In contrast, *Eugenia verticillata* has sessile flowers and fits the *auxotelic* pattern. This also supports that absence or presence of pedicel should not be regarded to recognize racemose inflorescence arrangements in *Eugenia*.

Umbelliform and umbel are recurrent in the taxonomic literature (Sobral *et al.* 2012) and are mostly related to the *fasciculiform* pattern expressing a very short main-axis. The typological definition of umbel refers to a raceme with compressed main-axis (Weberling 1988), however, this is a generalist definition that cannot be accurately applied to *Eugenia*. Umbelliform term is recurrently used and is appropriate because alludes only to the ultimate appearance. Thus, it is here suggested that the term umbelliform should be adopted for the *umbelliform* pattern. This pattern is apparently rare in *Eugenia*.

Thyrsoid, firstly employed by Briggs and Johnson (1979) has been used in the taxonomic literature in a conservative sense. Although the thyrsoid arrangement is flexible, its recognition is facilitated by the unique combination of the racemose branching pattern expressed in the first-order and cymose branching pattern in further orders (Endress 2010). Thus, the term thyrsoid should be adopted incorporating the *thyrsoid* pattern. Metabotryoid (sensu Briggs and Johnson 1979) is treated as flexibility in the thyrsoid arrangment by cessation of the braching potential of the phyllome subtended by the prophyll, and is incorporated under the term thyrsoid in the Neotropical *Eugenia*.

The dichasium is often refered to as an inflorescence arrangement in the Myrtaceae literature (Faria *et al.* 2015; McVaugh 1969), however, dichasial arrangments are always secondary in development. The ramecose branching pattern is primary in development and must be used to recognize the inflorescence arrangement rather than the cymose. Dichasial arrangement is associated with the braching pontetial of the flower rather than to the FSS. Thus, the recurrent dichasium refered to as inflorescence in the Myrtaceae literature is often an auxotelic inflorescence with a dichasial arrangement.

CONCLUSION

This work integrates inflorescence development and ultimate architecture in light of current evolutionary understanding in Myrtaceae. Previously overlooked inflorescence arrangements are revealed as relevant for systematic and taxonomy for the first time. Insights to the ancestral condition allow hypotheses of homology to be proposed and contribute to current understanding of recurring, highly flexible arrangements found in nature. It appears that this flexibility is the convention rather than the exception of a rigid inflorescence model. Typological definition should incorporate inflorescence ontogeny in association with evolutionary understanding to provide more accurate terminology while remaining descriptive and practical. Systematists and taxonomists should be comfortable to use terminology that describes the basic homologous arrangement as proposed here, in conjunction with complementary descriptions of morphological particularities. This study provides insights into the evolution of inflorescence arrangement in a hyper-diverse genus, suggesting that the flexibility of the racemose branching pattern may be the key innovation that promoted *Eugenia* species in the Neotropics. Future studies that disentangle the processes that allow such flexibility to adapt to environmental constraints will further contribute to a fuller understanding of Neotropical species diversification.

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LITERATURE CITED

Barrie FR, Ramos C, Ortiz OO, Vergara-Pérez I, McPherson G. 2016. Five New Species of Eugenia (Myrtaceae) from Panama. *Novon* **24(4)**: 333–342. https://10.3417/2015040

Barroso GM, Peixoto AL, Ichaso CLF, Costa CG, Guimarães EF, Lima HC. 1991. Myrtaceae. In: *Sistemática de Angiospermas do Brasil*. Universidade Federal de Viçosa, Viçosa, pp. 377.

Barthélémy D. 1991. Levels of organization and repetition phenomena in seed plants. *Acta Biotheoretica* **39**: 309–323.

Barthélémy D, Caraglio Y. 2007. Plant architecture: A dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany* **99(3)**: 375–407. https://10.1093/aob/mcl260

Benlloch R, Berbel A, Serrano-Mislata A, Madueño F. 2007. Floral initiation and inflorescence architecture: A comparative view. *Annals of Botany* **100(3)**: 659–

676. https://10.1093/aob/mcm146

Briggs BG, Johnson LAS. 1979. Evolution in the Myrtaceae - Evidence from inflorescence structure. *Proceedings of The Linnean Society of New South Wales* **102**: 157–256.

Bull-Hereñu K, Claßen-Bockhoff R. 2011. Ontogenetic course and spatial constraints in the appearance and disappearance of the terminal flower in inflorescences. *International Journal of Plant Sciences* **172(4)**: 471–498. https://10.1086/658922

Bünger MO, Mazine FF, Forest F, Bueno ML, Stehmann JR, Lucas EJ. 2016a. The evolutionary history of *Eugenia* sect. *Phyllocalyx* (Myrtaceae) corroborates historically stable areas in the southern Atlantic forests. *Annals of Botany* **118**: 1209–1223. https://10.1093/aob/mcw209

Bünger MO, Mazine FF, Lucas EJ, Stehmann JR. 2016b. Circumscription and synopsis of *Eugenia* section *Speciosae* Bünger & Mazine (Myrtaceae). *PhytoKeys* **61**: 73–80. https://10.3897/phytokeys.61.7904

Castel R, Kusters E, Koes R. 2010. Inflorescence development in petunia: Through the maze of botanical terminology. *Journal of Experimental Botany* **61(9)**: 2235–2246. https://10.1093/jxb/erq061

Charles-Dominique T, Beckett H, Midgley GF, Bond WJ. 2015. Bud protection: A key trait for species sorting in a forest-savanna mosaic. *New Phytologist* **207(4)**: 1052–1060. https://10.1111/nph.13406

Chomicki G, Coiro M, Renner SS. 2017. Evolution and ecology of plant architecture: integrating insights from the fossil record, extant morphology, developmental genetics and phylogenies. *Annals of Botany* **120:** 855–891. https://10.1093/aob/mcx113

Claßen-Bockhoff R, Bull-Hereñu K. 2013. Towards an ontogenetic understanding of inflorescence diversity. *Annals of Botany* **112(8)**: 1523–1542. https://10.1093/aob/mct009

Darriba D, Taboada GL, Doallo R, Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9(8)**: 772–772. https://10.1038/nmeth.2109

Drummond A, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* **7(1)**: 214. https://10.1186/1471-2148-7-214

Endress PK. 2010. Disentangling confusions in inflorescence morphology: Patterns and diversity of reproductive shoot ramification in angiosperms. *Journal of Systematics and Evolution* **48(4)**: 225–239. https://10.1111/j.1759-6831.2010.00087.x

Faria JEQ. 2014. *Revisão taxonômica e filogenia de Eugenia sect. Pilothecium (Kiaersk.) D.Legrand (Myrtaceae)*. PhD thesis. Universidade de Brasília. Brasília, Brazil.

Faria JEQ, Mazine FF, Proença C. 2015. Two new species of *Eugenia* (Myrtaceae) from the Cabo Frio Center of Plant Diversity, Rio de Janeiro, Brazil. *Phytotaxa* **208(3)**: 201–208.

Giaretta A, Fraga CN. 2014. Two new *Eugenia* species (Myrtaceae) from the Brazilian Atlantic forest. *Phytotaxa* **163(2)**: 113–120. https://10.11646/phytotaxa.163.2.5

Giribet G. 2015. Morphology should not be forgotten in the era of genomics-a phylogenetic perspective. *Zoologischer Anzeiger* **256**(June): 96–103. https://10.1016/j.jcz.2015.01.003

Grifo FT. 1992. *A revision of Myrcianthes Berg (Myrtaceae)*. Cornell University, Michigan, USA.

Harder LD, Jordan CY, Gross WE, Routley MB. 2004. Beyond floricentrism: The pollination function of inflorescences. *Plant Species Biology* **19(3)**: 137–148. https://10.1111/j.1442-1984.2004.00110.x

Harder LD, Prusinkiewicz P. 2013. The interplay between inflorescence development and function as the crucible of architectural diversity. *Annals of Botany* **112(8)**: 1477–1493. https://10.1093/aob/mcs252

Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008. GEIGER: Investigating evolutionary radiations. *Bioinformatics* **24(1)**: 129–131. https://10.1093/bioinformatics/btm538

Irish VF, Litt A. 2005. Flower development and evolution: Gene duplication, diversification and redeployment. *Current Opinion in Genetics and Development* **15(4)**: 454–460. https://10.1016/j.gde.2005.06.001

Ishii HS, Hirabayashi Y, Kudo G. 2008. Combined effects of inflorescence architecture, display size, plant density and empty flowers on bumble bee behaviour: Experimental study with artificial inflorescences. *Oecologia* **156(2)**: 341–350. https://10.1007/s00442-008-0991-4

Kirchoff BK, Claßen-Bockhoff R. 2013. Inflorescences: Concepts, function, development and evolution. *Annals of Botany* **112(8)**: 1471–1476. https://10.1093/aob/mct267

Landrum LR. 1991. A new genus of Myrtaceae (Myrtinae) from Mesoamerica. *Systematic Botany* **16(1)**: 21–29. https://10.2307/2418970

Landrum LR, Kawasaki ML. 1997. The Genera of Myrtaceae in Brazil: An Illustrated Synoptic Treatment and Identification Keys. *Brittonia* **49(4)**: 508. https://10.2307/2807742

Lee MSY, Palci A. 2015. Morphological phylogenetics in the genomic age. *Current Biology* **25(19)**: 922–929. https://10.1016/j.cub.2015.07.009

Lima DF, Caddah MK, Goldenberg R, Lucas E. 2015. A família Myrtaceae na Ilha do Mel, Paranaguá, Estado do Paraná, Brasil. *Hoehnea* **42(3)**: 497–519. https://10.1590/2236-8906-68/2014

Lourenço ARL, Amorim BS, Alves M. 2013. *Eugenia pipensis*, a new species of *Eugenia* sect. *Umbellatae* (Myrtaceae) from northeastern Brazil. *Phytotaxa* **104(1)**: 30–34. https://10.11646/phytotaxa.104.1.4

Lucas EJ, Harris SA, Mazine FF, Belsham SR, Nic Lughadha EM, Telford A, Gasson PE, Chase MW. 2007. Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* **56(4)**: 1105–1128. https://10.2307/25065906

Mazine FF, Bünger MO, Faria JEQ, Lucas E, Souza VC. 2016. Sections in *Eugenia* (Myrteae, Myrtaceae): nomenclatural notes and a key. *Phytotaxa* **289(3)**: 225–236.

Mazine FF, Souza VC. 2010. Three new species of *Eugenia* sect. *Racemosae* (Myrtaceae) from the cerrados of the state of Mato Grosso, Brazil. *Revista Brasileira de Botânica* **33(2)**: 285–290. https://10.1590/S0100-84042010000200009

Mazine FF, Souza VC, Sobral M, Forest F, Lucas E. 2014. A preliminary phylogenetic analysis of *Eugenia* (Myrtaceae: Myrteae), with a focus on Neotropical species. *Kew Bulletin* **69(2)**: 1–14. https://10.1007/s12225-014-9497-x

McVaugh R. 1963a. Flora of Guatemala - Part VII. *Fieldiana: Botany* **24(3)**: 1689–1699. https://10.1017/CBO9781107415324.004

McVaugh R. 1963b. Tropical American Myrtaceae II. *Fieldiana: Botany* **29(8)**: 395–532.

McVaugh R. 1969. The Botany of the Guayana Highland - Part VIII: Myrtaceae. *Memoirs of the New York Botanical Garden* **18(2)**: 55–286.

Miller MA, 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*. New Orleans, LA, pp. 1–8.

Pagel M. 2004. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society B: Biological Sciences* **255(1342)**: 37–45.

Paradis E, Claude J, Strimmer K. 2004. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* **20(2)**: 289–290. https://10.1093/bioinformatics/btg412

Prenner G, Vergara-Silva F, Rudall PJ. 2009. The key role of morphology in modelling inflorescence architecture. *Trends in Plant Science* **14(6)**: 302–309. https://10.1016/j.tplants.2009.03.004

Prusinkiewicz P, Erasmus Y, Lane B, Harder LD, Coen E. 2007. Evolution and development of inflorescence architectures. *Science* **316(5830)**: 1452–1456. https://10.1126/science.1140429

Revell L, Harmon L, Collar D. 2008. Phylogenetic Signal, Evolutionary Process, and Rate. *Systematic Biology* **57(4)**: 591–601. https://10.1080/10635150802302427

Rickett HW. 1944. The Classification of Inflorescences. *Botanical Review* **10(3)**: 187–231.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61(3)**: 539–542. https://10.1093/sysbio/sys029

Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT, Hughes CE. 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences* **106(48)**: 20359–20364. https://10.1073/pnas.0903410106

Sobral M, Grippa CR, Souza MC, Aguiar OT, Bertoncello R, Guimarães TB. 2012. Fourteen new species and two taxonomic notes on Brazilian Myrtaceae. *Phytotaxa* **50**: 19–50.

Souza MAD, Scudeller VV, Mendonça MSDE. 2015. Three new species of *Eugenia* (Myrtaceae) from Brazilian Amazonia. *Phytotaxa* **212(1)**: 87–94.

Souza MADDE, Scudeller VV, Mendonça MSDE. 2016. Two new species of *Eugenia* (Myrtaceae) from Central Amazonia, Brazil. *Phytotaxa* **289(2)**: 167–174.

Souza MC, Morim MP. 2008a. A new species of *Eugenia* (Myrtaceae) from southeastern Brazil. *Botanical Journal of the Linnean Society* **158(2)**: 306–308. https://10.1111/j.1095-8339.2008.00923.x

Souza MC, Morim MP. 2008b. Subtribos Eugeniinae O. Berg e Myrtinae O. Berg (Myrtaceae) na Restinga da Marambaia, RJ, Brasil. *Acta Botanica Brasilica* **22(3)**: 652–683. https://10.1590/S0102-33062008000300006

Thiers B. 2017. Index Herbariorum: A global directory of public herbaria and associated staff. *New York Botanical Garden's Virtual Herbarium* Available from: http://sweetgum.nybg.org/ih/ (July 26, 2017).

Tooke F, Ordidge M, Chiurugwi T, Battey N. 2005. Mechanisms and function of flower and inflorescence reversion. *Journal of Experimental Botany* **56(420)**: 2587–2599. https://10.1093/jxb/eri254

Troll W, Weberling F. 1989. *Infloreszenzuntersuchungen an monotelen Familien. Materialien zur Infloreszenzmorphologi*. Fischer, Stuttgart.

Vasconcelos TNC, Lucas EJ, Faria JEQ, Prenner G. 2018. Floral heterochrony promotes flexibility of reproductive strategies in the morphologically homogeneous genus *Eugenia* (Myrtaceae). *Annals of Botany* **121(1)**: 161–174. https://10.1093/aob/mcx142

Vasconcelos TNC, Prenner G, Bünger MO, De-Carvalho PS, Wingler A, Lucas EJ. 2015. Systematic and evolutionary implications of stamen position in Myrteae (Myrtaceae). *Botanical Journal of the Linnean Society* **179(3)**: 388–402.

Vasconcelos TNC, Prenner G, Santos MF, Wingler A, Lucas EJ. 2017a. Links between parallel evolution and systematic complexity in angiosperms — A case study of floral development in *Myrcia* s. l. (Myrtaceae). *Perspectives in Plant Ecology, Evolution and Systematics* **24**: 11–24. https://10.1016/j.ppees.2016.11.001

Vasconcelos TNC, Proença CEB, Ahmad B, Aguilar DS, Aguilar R, Amorim BS, Campbell K, Costa IR, De-carvalho PS, Faria JEQ, Giaretta A, Kooij PW, Lima DF, Mazine FF, Peguero B, Prenner G, Santos MF, Soewarto J, Wingler A, Lucas EJ. 2017b. Myrteae phylogeny, calibration, biogeography and diversification patterns: Increased understanding in the most species rich tribe of Myrtaceae. *Molecular Phylogenetics and Evolution* **109**: 113–137. https://10.1016/j.ympev.2017.01.002

Wake DB, Wake MH, Specht CD. 2011. Homoplasy: from detecting pattern to determining process and mechanism of evolution. *Science* **33**: 1032–1035.

Wanninger A. 2015. Morphology is dead - long live morphology! Integrating MorphoEvoDevo into molecular EvoDevo and phylogenomics. *Frontiers in Ecology and Evolution* **3**(May): 1–9. https://10.3389/fevo.2015.00054

Weberling F. 1988. *Morphology of flowers and inflorescence*. Cambridge University Press, Cambridge.

Wilson PG. 2011. Myrtaceae. In: Kubitzki K.ed. *The families and genera of vascular plants. Flowering plants, eudicots: Sapindales, Cucurbitales, Myrtaceae*. Springer-Verlag, Berlin, pp. 436.

SUPPLEMENTARY DATA

S1. Herbarium sampling and voucher of the mature material consulted.

Species	Collector	Number	Barcode	Collection
Calycorectes bergii Sandwith	Forest Department	2412		K
Calycorectes bergii Sandwith	N.Y. Sandwith	558		K
Calycorectes bergii Sandwith	H.F. Talbot	s.n.		K
Calycorectes bergii Sandwith	D.B. Fanshawe	22925		K
Calycorectes bergii Sandwith	M. Hoff	6022		K
Calycorectes bergii Sandwith	D. Toriola	1009		CAY
Eugenia acutata Miq.	F. Barros	2357		K
Eugenia acutata Miq.	J. Mattos	16387		K
Eugenia acutata Miq.	M. Verdi	6538		K
Eugenia acutata Miq.	A. Giaretta	1460		K
Eugenia acutata Miq.	P.L.R. Moraes	2494		RB
Eugenia adenocalyx DC.	U.N. Maciel	181		K
Eugenia adenocalyx DC.	A. Giaretta	1441		K
Eugenia adenocalyx DC.	T.N. Vasconcelos	xxx		K
Eugenia astringens Cambess.	Sellow	s.n.	000276545	K
Eugenia astringens Cambess.	C. Farney	2342		K
Eugenia astringens Cambess.	C. Farney	4641		K
Eugenia astringens Cambess.	H.M. Dias	141		K
Eugenia astringens Cambess.	D. Sucre	2618		K
Eugenia aurata O.Berg	V.G. Staggemeier	500		K
Eugenia aurata O.Berg	V.G. Staggemeier	410		K
Eugenia aurata O.Berg	C.A.C. Ferreira	6376		K
Eugenia aurata O.Berg	Sellow	5637		K
Eugenia aurata O.Berg	J.A. Ratter	7982		K
Eugenia axillaris (Sw.) Willd.	E. Cabrera	8884		K
Eugenia axillaris (Sw.) Willd.	E. Matuda	16508		K
Eugenia axillaris (Sw.) Willd.	W.A. Schipp	825		K
Eugenia axillaris (Sw.) Willd.	P.C. Standley	56628		K
Eugenia axillaris (Sw.) Willd.	J.A. Ratter	6598		K
Eugenia azuruensis O.Berg	J.E.Q. Faria	2642		RB
Eugenia azuruensis O.Berg	J.E.Q. Faria	4186		RB
Eugenia azuruensis O.Berg	F.S. Araujo	1014		RB
Eugenia biflora (L.) DC.	M.A.D. Souza	76		K
Eugenia biflora (L.) DC.	C.N.Fraga	2918		K
Eugenia biflora (L.) DC.	D.J. Atkinson	53		K
Eugenia biflora (L.) DC.	G.S. Jenman	200		K
Eugenia biflora (L.) DC.	D.C. Daly	286		K
Eugenia bimarginata DC.	W.J. Burchell	5029		K
Eugenia bimarginata DC.	W.J. Burchell	4664		K
Eugenia bimarginata DC.	L. Kawasaki	1633		K
Eugenia bimarginata DC.	D.R. Hunt	5925		K
Eugenia bimarginata DC.	W. Ganev	1107		K

Eugenia brasiliensis Lam.			001018524	K
Eugenia brasiliensis Lam.			001018525	K
Eugenia brasiliensis Lam.	R.C. Forzza	4717		K
Eugenia brasiliensis Lam.	M. Peron	257		K
Eugenia brasiliensis Lam.	A.F. Vaz	698		K
Eugenia brevistyla D.Legrand	F. Barros	1759		K
Eugenia brevistyla D.Legrand	Reitz	9070		K
Eugenia brevistyla D.Legrand	J.M. Silva	1769		K
Eugenia brevistyla D.Legrand	F.F. Mazine	1010		K
Eugenia brevistyla D.Legrand	N.M. Ivanauskas	246		RB
Eugenia bullata Pancher ex Guillaumin	Guillaumin	7700		K
Eugenia bullata Pancher ex Guillaumin	H.S. Mackee	46038		P
Eugenia bullata Pancher ex Guillaumin	Vieillard	480	00543900	P
Eugenia bullata Pancher ex Guillaumin	J.P. Blanchon	196		P
Eugenia bullata Pancher ex Guillaumin	M. Balansa	87		P
Eugenia cerasiflora Miq.			001021737	K
Eugenia cerasiflora Miq.	G. Hatschbach	52165		K
Eugenia cerasiflora Miq.	R.M. Harley	22656		K
Eugenia cerasiflora Miq.	W. Ganev	2870		K
Eugenia cerasiflora Miq.	W. Ganev	3236		K
Eugenia coffeifolia DC.			000275728	K
Eugenia coffeifolia DC.	R.A.A. Oldeman	2562		K
Eugenia coffeifolia DC.	R.A.A. Oldeman	1671		K
Eugenia coffeifolia DC.			001018809	K
Eugenia coffeifolia DC.	L. Barrabe	236		K
Eugenia convexinervia D.Legrand	Reitz	4156		K
Eugenia convexinervia D.Legrand	Reitz	6323		K
Eugenia convexinervia D.Legrand	Reitz	6332		K
Eugenia convexinervia D.Legrand	F.F. Mazine	994		K
Eugenia convexinervia D.Legrand	J.M Silva	3890		K
Eugenia dichroma O.Berg	A.P. Duarte	6055		RB
Eugenia dichroma O.Berg	A. Giaretta	1021		RB
Eugenia dichroma O.Berg	A. Giaretta	1312		RB
Eugenia dichroma O.Berg	D. Folli	31		RB
Eugenia dichroma O.Berg	J.G. Jardim	4332		RB
Eugenia dodonaeifolia Cambess.	Y. Mexia	4688		K
Eugenia dodonaeifolia Cambess.	E.B. Foresto	129		K
Eugenia dodonaeifolia Cambess.	S.V.A. Pessoa	807		K
Eugenia dodonaeifolia Cambess.	R. Marquete	4122		K
Eugenia dodonaeifolia Cambess.	Riedel	355		K
Eugenia dysenterica DC.	H.S. Irwin	5860		K
Eugenia dysenterica DC.	M.A. Silva	4455		K
Eugenia dysenterica DC.	J.A. Ratter	4410		K
Eugenia dysenterica DC.	E.P. Heringer	5289		K
Eugenia dysenterica DC.	A. Glaziou	21198		K
Eugenia dysenterica DC.	F.F. Mazine	466		K

Eugenia egensis DC.	C.R.D. Vieira	4895	00969783	RB
Eugenia egensis DC.	J.E.Q. Faria	4859		RB
Eugenia egensis DC.	L. Cayola	1413		RB
Eugenia egensis DC.	M. Lewis	40582		RB
Eugenia egensis DC.	M.G. Bovini	3074		RB
Eugenia excelsa O.Berg	B.A. Krukoff	1125		K
Eugenia excelsa O.Berg	R.S. Pinheiro	283		K
Eugenia excelsa O.Berg	A.F. Regnell	562		K
Eugenia excelsa O.Berg	D.S.D. Araujo	405		K
Eugenia excelsa O.Berg	J.G. Rando	152		RB
Eugenia excelsa O.Berg	E.J. Lucas	125		K
Eugenia expansa (O.Berg) Nied.	M.F. Santos	713		K
Eugenia expansa (O.Berg) Nied.	S.V.A. Pessoa	476		K
Eugenia expansa (O.Berg) Nied.	H.C. Lima	2265		K
Eugenia expansa (O.Berg) Nied.	G. Martinelli	10037		K
Eugenia expansa (O.Berg) Nied.	R. Guedes	2167		K
Eugenia flavescens DC.			000579518	K
Eugenia flavescens DC.	J.A. Ratter	4073		K
Eugenia flavescens DC.	G. Eiten	9109		K
Eugenia flavescens DC.	J.R. Grifford	G31	001021634	K
Eugenia flavescens DC.	N.T. Silva	1461		K
Eugenia florida DC.	K.M. Redden	4935		K
Eugenia florida DC.	R.T. Pennington	342		K
Eugenia florida DC.	R. Schnell	11754		K
Eugenia florida DC.	J.A. Ratter	1337		K
Eugenia florida DC.	G.C.G. Argent	6722		K
Eugenia florida DC.	E.P. Heringer	5463		K
Eugenia foetida Pers.	E. Cabrera	8768		K
Eugenia foetida Pers.	G.F. Gaumer	24123		K
Eugenia foetida Pers.	P.H. Gentle	1202		K
Eugenia foetida Pers.	W.A. Schipp	427		K
Eugenia foetida Pers.	F. Gaumer	s.n.	000276275	K
Eugenia goiapabana Sobral & Mazine	J.E.Q. Faria	2481		K
Eugenia goiapabana Sobral & Mazine	A.P. Fontana	5419		K
Eugenia goiapabana Sobral & Mazine	R.C. Forzza	4999		RB
Eugenia guanabarina ined.	L.A. Mattos	614		K
Eugenia guanabarina ined.	P. Duarte	6058		K
Eugenia guanabarina ined.	K. Matsumoto	818		K
Eugenia guanabarina ined.	L.A.M. Silva	2515		K
Eugenia guanabarina ined.	A. Giaretta	1360		K
Eugenia handroi Mattos	G. Hatschbach	19555		RB
Eugenia handroi Mattos	P.C. Porto	743		RB
Eugenia handroi Mattos	J.E.Q. Faria	3100		RB
Eugenia handroi Mattos	N.M. Ivanauskas	6175		RB
Eugenia handroi Mattos	P.R.C. Farág	215		RB
Eugenia handroi Mattos	C. Farney	3924		RB

Eugenia involucrata DC.	L.O. Williams	7409		K
Eugenia involucrata DC.	E.M.N. Lughadha	222		K
Eugenia involucrata DC.	W.J. Burchell	5832		K
Eugenia involucrata DC.	C. Angeli	277		K
Eugenia involucrata DC.	M.F. Santos	732		K
Eugenia joseramosii M.A.D. Souza & Scudeller	J.E.L.S.	1767		K
Eugenia joseramosii M.A.D. Souza & Scudeller	M.A.D. Souza	155		K
Eugenia joseramosii M.A.D. Souza & Scudeller	M.A.D. Souza	248		K
Eugenia joseramosii M.A.D. Souza & Scudeller	Vicentini	1141		K
Eugenia joseramosii M.A.D. Souza & Scudeller	J.R. Nascimento	588		RB
Eugenia lagoensis Kiaersk.	C.N.Fraga	2436		K
Eugenia lagoensis Kiaersk.	D.C. Zappi	1843		RB
Eugenia lagoensis Kiaersk.	V.C. Souza	32896		RB
Eugenia lagoensis Kiaersk.	P.M. Andrade	644		RB
Eugenia melanogyna (D.Legrand) Sobral	F.F. Mazine	969		K
Eugenia melanogyna (D.Legrand) Sobral	J.M. Silva	3831		K
Eugenia melanogyna (D.Legrand) Sobral	G. hastschbach	44462		RB
Eugenia melanogyna (D.Legrand) Sobral	M.L. Brotto	1703		RB
Eugenia melanogyna (D.Legrand) Sobral	Reitz	4321		K
Eugenia modesta DC.	R.M. Harley	22975		K
Eugenia modesta DC.	M.L. Guedes	5658		K
Eugenia modesta DC.	M. Peron	594		K
Eugenia modesta DC.	T.N. Vasconcelos	476		K
Eugenia modesta DC.	Riedel	2589		K
Eugenia monticola (Sw.) DC.	R. Liesner	13243		MBM
Eugenia monticola (Sw.) DC.	C.L. Jones	129		MBM
Eugenia monticola (Sw.) DC.	R. Espinoza	824		K
Eugenia monticola (Sw.) DC.	Q. Jiménez	862		K
Eugenia monticola (Sw.) DC.	G. Rivera	1200		K
Eugenia monticola (Sw.) DC.	P. Sánchez	1299		K
Eugenia monticola (Sw.) DC.	W.C. Holmes	6630		MBM
Eugenia monticola (Sw.) DC.	C.L. Jones	129		MBM
Eugenia monticola (Sw.) DC.	R. Liesner	13243		MBM
Eugenia moschata O.Berg	Spruce	1063		K
Eugenia moschata O.Berg	Spruce	991		K
Eugenia moschata O.Berg	C.A.C. Ferreira	7612		K
Eugenia moschata O.Berg	Oldeman	3581		K
Eugenia moschata O.Berg	A. Silva	227		K
Eugenia myrcianthes Nied.	F.C. Silva	s.n.	001178048	K
Eugenia myrcianthes Nied.	K. Fiebrig	34		K
Eugenia myrcianthes Nied.	B. Balansa	1322		K
Eugenia myrcianthes Nied.	J.R.I. Wood	26859		K

Eugenia myrcianthes Nied.	J.R.I. Wood	26896		K
Eugenia myrcianthes Nied.	H.A. Keller	5756		K
Eugenia neoglomerata Sobral	Pohl	1041		K
Eugenia neoglomerata Sobral	M. Glaziou	11999		K
Eugenia neoglomerata Sobral	A. Glaziou	7640		K
Eugenia neoglomerata Sobral	W.H. Stubbebine	13200		K
Eugenia neoglomerata Sobral	J.M.A. Braga	3089		K
Eugenia neograndifolia Mattos	G. Wachenheim	480		K
Eugenia neograndifolia Mattos	J.J. Granville	11207		K
Eugenia neograndifolia Mattos	J.J. Granville	4585		CAY
Eugenia neograndifolia Mattos	A. Giaretta	1616		K
Eugenia neograndifolia Mattos	T.R. van Andel	4676		K
Eugenia neograndifolia Mattos	B. Maguirre	23834		K
Eugenia neoverrucosa Sobral	E.J. Lucas	118		K
Eugenia neoverrucosa Sobral	F. Chagas	1411		K
Eugenia neoverrucosa Sobral	E. Lucas	132		K
Eugenia neoverrucosa Sobral	J.C. Lindeman	5837		K
Eugenia neoverrucosa Sobral	Reitz	3850		K
Eugenia nutans O.Berg	J.E.Q. Faria	2422		K
Eugenia nutans O.Berg	M.F. Santos	531		K
Eugenia nutans O.Berg	H.S. Irwin	19864		K
Eugenia nutans O.Berg	E. Lucas	260		K
Eugenia nutans O.Berg	J.E.Q. Faria	2464		K
Eugenia paludosa Pancher ex Brongn. & Gris	J.M. Veillon	8033		P
Eugenia paludosa Pancher ex Brongn. & Gris	H.S. Mackee	29306		P
Eugenia paludosa Pancher ex Brongn. & Gris	H.S. Mackee	29248		P
Eugenia paludosa Pancher ex Brongn. & Gris	H.S. Mackee	38796		P
Eugenia paludosa Pancher ex Brongn. & Gris	H.S. Mackee	5480		K
Eugenia patens Poir.	R.A.A. Oldeman	284		K
Eugenia patens Poir.	R.A.A. Oldeman	1888		K
Eugenia patens Poir.	Spruce	2261		K
Eugenia patens Poir.	W. Balée	2684		K
Eugenia patens Poir.	B.V. Rabelo	2403		K
Eugenia patens Poir.	I.L. Amaral	240		K
Eugenia pisiformis Cambess.	A. Glaziou	19364		K
Eugenia pisiformis Cambess.			001021558	K
Eugenia pisiformis Cambess.	S.J. Silva-Neto	457		K
Eugenia pisiformis Cambess.	A.C.S. Cavalcanti	265		k
Eugenia pisiformis Cambess.	R.O. Perdiz	911		RB
Eugenia pisiformis Cambess.	M.O. Bünger	562		RB
Eugenia pistaciifolia DC.	L.P. Queiroz	3839		K
Eugenia pistaciifolia DC.	L. Passos	5546		K

Eugenia pistaciifolia DC.	W. Ganev	1420		K
Eugenia pistaciifolia DC.	W. Ganev	1400		K
Eugenia pistaciifolia DC.	M.O.O. Pellegrini	359		RB
Eugenia pitanga (O.Berg) Nied.	F.F. Mazine	1020		K
Eugenia pitanga (O.Berg) Nied.	F.F. Mazine	1030		K
Eugenia pitanga (O.Berg) Nied.	C. Giraldi	s.n.	001018480	K
Eugenia pitanga (O.Berg) Nied.	T.M. Pedersen	6560		K
Eugenia pitanga (O.Berg) Nied.	E. Hassler	3218		K
Eugenia pluriflora DC.	W.J. Burchell	4930		K
Eugenia pluriflora DC.	J.C. Lindeman	1137		K
Eugenia pluriflora DC.	W.J. Burchell	4724		K
Eugenia pluriflora DC.	M. Glaziou	10806		K
Eugenia pluriflora DC.	Riedel	2186		K
Eugenia protenta DC.	R. Spruce	3816		K
Eugenia protenta DC.	M.A.D. Souza	97		K
Eugenia protenta DC.	M.A.D. Souza	99		K
Eugenia protenta DC.			000276652	K
Eugenia protenta DC.	A. Vicentini	1022		K
Eugenia punicifolia Kunth (DC.)	A.C. Smith	3352		K
Eugenia punicifolia Kunth (DC.)	B.A. Whitton	222		K
Eugenia punicifolia Kunth (DC.)	Gardner	4164		K
Eugenia punicifolia Kunth (DC.)	V. Staggemeier	302		K
Eugenia punicifolia Kunth (DC.)	F.F. Mazine	1065		K
Eugenia pyrifera Faria & Proença	J.E.Q. Faria	897		RB
Eugenia pyrifera Faria & Proença	J.E.Q. Faria	4122		RB
Eugenia pyrifera Faria & Proença	J.E.Q. Faria	2120		RB
Eugenia pyrifera Faria & Proença	J.E.Q. Faria	899		RB
Eugenia pyrifera Faria & Proença	J.E.Q. Faria	5178		RB
Eugenia pyriformis Cambess.	G. Eiten	6582		K
Eugenia pyriformis Cambess.	O. Handro	2093		K
Eugenia pyriformis Cambess.	G.F.J. Pabst	9185		K
Eugenia pyriformis Cambess.	G.Y. Saiki	s.n.	001018052	K
Eugenia pyriformis Cambess.	E. Hassler	5058		K
Eugenia pyriformis Cambess.	F.F. Mazine	1028		K
Eugenia reinwardtiana (Blume) DC.	Rahman	6759		K
Eugenia reinwardtiana (Blume) DC.	Backer	29415		K
Eugenia reinwardtiana (Blume) DC.	A. Mail	3910		K
Eugenia reinwardtiana (Blume) DC.	D.I. Nicholson	s.n.	001000274	K
Eugenia reinwardtiana (Blume) DC.	P. Orolfo	3793		K
Eugenia selloi B.D.Jacks	A.Q. Lobão	358		K
Eugenia selloi B.D.Jacks	D. Sucre	6054		K
Eugenia selloi B.D.Jacks	M.O. Bünger	566		K
Eugenia selloi B.D.Jacks	M.C. Souza	638		K
Eugenia selloi B.D.Jacks	D. Sucre	9548		K
Eugenia sonderiana O.Berg	P.T. Sano	CFCR 14863	96432	SPF
Eugenia sonderiana O.Berg	M.A. Pena	802		SPF

Eugenia sonderiana O.Berg	F.F. Mazine	674		SPF
Eugenia sonderiana O.Berg	G. Hatschbach	41770		SPF
Eugenia sonderiana O.Berg	J.R. Stehmann	2316		SPF
Eugenia speciosa Cambess.	R.C. Forzza	4826		K
Eugenia speciosa Cambess.	P. Claussen	s.n.	001018490	K
Eugenia speciosa Cambess.			001018492	K
Eugenia speciosa Cambess.	E. Hassler	6259		K
Eugenia speciosa Cambess.	L.B. Smith	7256		K
Eugenia stipitata McVaugh	C.R. Sperling	6361		K
Eugenia stipitata McVaugh	B.A. Krukoff	6591		K
Eugenia stipitata McVaugh	G.T. Prance	5601		K
Eugenia stipitata McVaugh	C.N.Fraga	3188		RB
Eugenia stipitata McVaugh	V.G. Staggemeier	835		K
Eugenia subterminalis DC.	F.F. Mazine	974		K
Eugenia subterminalis DC.	A.A. Arantes	689		K
Eugenia subterminalis DC.	F.F. Mazine	1086		K
Eugenia subterminalis DC.	G. Hatschbach	61319		K
Eugenia subterminalis DC.	K. Fiebrig	100		K
Eugenia umbrosa O.Berg	M.F. Santos	792		K
Eugenia umbrosa O.Berg	M. Glaziou	8387		K
Eugenia umbrosa O.Berg	A. Glaziou	3008		K
Eugenia umbrosa O.Berg	A. Giaretta	1498		K
Eugenia umbrosa O.Berg	G. Martinelli	8488		K
Eugenia uniflora L.	F.C. Silva	1742		K
Eugenia uniflora L.	J.C. Lindeman	2076		K
Eugenia uniflora L.			001021251	K
Eugenia uniflora L.			001021242	K
Eugenia uniflora L.			001021240	K
Eugenia vattimoana Mattos	J. Miers	3802		K
Eugenia vattimoana Mattos	C. Angeli	191		K
Eugenia vattimoana Mattos	Gardner	5462		K
Eugenia vattimoana Mattos	R.N. Damasceno	1161		RB
Eugenia vattimoana Mattos	H.N. Braga	641		RB
Eugenia verticillata (Vell.) Angely	Reitz	6634		K
Eugenia verticillata (Vell.) Angely	G. hastschbach	14104		K
Eugenia verticillata (Vell.) Angely	J. Mattos	10825		K
Eugenia verticillata (Vell.) Angely	P. Claussen	107		K
Eugenia verticillata (Vell.) Angely	M. Glaziou	10790		K
Eugenia verticillata (Vell.) Angely	W.J. Burchell	3116		K
Eugenia wentii Amshoff	A. Prelle	351	001019880	K
Eugenia wentii Amshoff	B. Maguirre	24665		K
Eugenia wentii Amshoff	BW	6178	001019882	K
Eugenia wentii Amshoff	R. Evans	2712		K
Eugenia wentii Amshoff	M.F. Prévost	4705		K
Eugenia wentii Amshoff	S. Mori	22970		K
Eugenia wentii Amshoff	C.A.C. Ferreira	9286		K

Eugenia wentii Amshoff	L.O.A. Teixeira	604		K
Eugenia zuccarini O.Berg	S.A. Mori	12996		K
Eugenia zuccarini O.Berg	D.Sucre	7283		K
Eugenia zuccarini O.Berg	D. Sucre	5935		K
Eugenia zuccarini O.Berg	A.F. Vaz	952		RB
Eugenia zuccarini O.Berg	L.B. Pimentel		00837793	RB
Myrcianthes fragrans (Sw.) McVaugh	P.P. Moreno	22662		K
Myrcianthes fragrans (Sw.) McVaugh	G.B. Hinton	404		K
Myrcianthes fragrans (Sw.) McVaugh			000277416	K
Myrcianthes fragrans (Sw.) McVaugh			000261864	K
Myrcianthes fragrans (Sw.) McVaugh	G.P. DeWolf	160		
Myrcianthes pungens (O.Berg) D.Legrand	M. Lewis	40768		K
Myrcianthes pungens (O.Berg) D.Legrand	J.R.I. Wood	10521		K
Myrcianthes pungens (O.Berg) D.Legrand	J.C. Solomon	11080		K
Myrcianthes pungens (O.Berg) D.Legrand	J.M. Silva	6019		RB
Myrcianthes pungens (O.Berg) D.Legrand	V. Santos	77		RB
Myrtus communis L.	R.D. Kelly	29		K
Myrtus communis L.	G. Nicholson	s.n.		K
Myrtus communis L.	G. Nicholson	s.n.		K
Myrtus communis L.	N.D. Simpson	5332		K
Myrtus communis L.	Rein	54		K
Rhodamnia rubescens (Benth.) Miq.			00931	K
Rhodamnia rubescens (Benth.) Miq.	J. Garden	17246		K
Rhodamnia rubescens (Benth.) Miq.	A. Cunningham	s.n.		K
Rhodamnia rubescens (Benth.) Miq.	L.G. Adams	1632		K
Rhodamnia rubescens (Benth.) Miq.	A. Morrison	5599		K

Capítulo 5

Chapter 5

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RECIRCUMSCRIPTION AND TAXONOMIC REVISION OF *EUGENIA* SECT. *SCHIZOCALOMYRTUS* (KAUSEL) MATTOS (MYRTACEAE: MYRTEAE), A GROUP OF UNUSUAL FLOWER PATTERN ON THE HYPER-DIVERSE GENUS *EUGENIA*

Abstract—Taxonomic revision of the Eugenia sect. Schizocalomyrtus supported by molecular and morphological evidence is here presented. The unusual fused calyces species of this section contrasts with the standard free calyx lobes of Eugenia. However, the fused calyx is recurrent in Myrtaceae and historically mislead by taxonomists. Thus, a key for Neotropical genera with fused calyx is presented. Additionally, a description of the Eugenia sect. Schizocalomyrtus, a key for the ten species included in this section (two newly described), detailed species descriptions, notes of distribution and habitat, phenology, conservation status, nomenclatural and taxonomic comments, list of specimens examined, collector list, illustrations, and maps of distribution are provided.

Keywords—fused calyx, homoplasy, monograph, nomenclature, Atlantic forest

Myrtaceae occur on all continents except Antarctica but are most commonly distributed in tropical and subtropical areas (Wilson 2011). Myrtoideae is the richest subfamily and includes tribe Myrteae DC. that comprises 49 genera and ca. 2500 species mainly from Neotropics (Lucas et al. 2007). The hyper-diverse *Eugenia* P.Micheli ex Linnaeus comprises ca.1000 species and has pantropical distribution but it is mostly distributed in South and Central America (ca. 800 spp; Mazine et al. 2014; Wilson 2011). *Eugenia* is considered morphologically homogeneous and taxonomically difficult (see a discussion in Lucas and Bünger 2015). As a result, over-emphasis has been placed on some more remarkable morphological characters, so overlooking dissimilarities in favor of similarities (e.g. extended sepals, Bünger et al. (2016b); fused calyx, Giaretta et al. Chapter 2) and not enough on others (andro- and gynoecium, Vasconcelos et al. 2018). *Calycorectes* O.Berg and *Schizocalyx* O.Berg were described based mostly on the degree of calyx fusion, despite other shared characters that suggested a relationship to *Eugenia* (Landrum and Kawasaki 1997; Sobral 2003).

Taxonomic History of Calycorectes and Schizocalyx—Traditionally, Berg (1857) circumscribed *Calycorectes* and *Schizocalyx* according to the flower morphology, i.e. the former has calyx complete closed on bud which tears into four to six longitudinal lobes whereas the last has closed calyx on the bud, except for a pore in the apex, that tears irregularly; the last represented by only *Schizocalyx pohliana* O.Berg. Presumed fragile segregation encouraged a rearrangement of the infrageneric classifications as follow. Niedenzu (1893) combined *Schizocalyx* into a new status under *Calycorectes* section *Schizocalyx* (O.Berg) Nied.; also, he proposed *Calycorectes* section *Brevitubia* Nied. to nest the rest of the species. At the same year, Kiaerskou (1893) created *Calycorectes* subgenus *Schizocalyx* (O.Berg) Kiaersk. and *Calycorectes* subgenus *Eucalycorectes* Kiaersk.

Kausel (1967) noticed that *Schizocalyx* O.Berg was a later homonym and replaced it for *Schizocalomyrtus* Kausel. Later, Mattos (1990) reassessed *Calycorectes* and established a new classification creating *Calycorectes* subgenus *Schizocalomyrtus* (Kausel) Mattos to accommodate *Schizocalomyrtus pohliana* Kausel. Mattos (1990) also added two ranks bellow *Calycorectes* subgenus *Calycorectes*: *Calycorectes* section *Tetrapetalae* subsection *Tetrapetalae* to accommodate *Calycorectes mexicanus* O.Berg; and *Calycorectes* (section *Tetrapetalae*) subsection *Subpaniculatae* to accommodate *Calycorectes cucullatus* Mattos.

A large variation on the degree of calyx fusion among newly recognized species resulted in an unworkable classification as documented by McVaugh (1969). His study was the first to attempt to sort a great number of newly recognized species assigned to *Calycorectes*. However, intra and interspecific variation of the diagnostic characters, i.e. degree of fusion of the calyx lobes as well as the lobing pattern made *Calycorectes* species delimitation unreliable and arduous to be applied. Inconsistent diagnostic character and morphological evidence encouraged a widely *Eugenia* integrating related genera previously segregated (Landrum and Kawasaki 1997; Sobral 2003). Mattos (2005) transferred *Schizocalyx* and a great part of *Calycorectes* species to *Eugenia* subgenus *Calycorectes* following this trend.

Insights on the systematics of Eugenia—Current understanding of phylogenetic relationship supports *Eugenia* as a consistent group including *Calycorectes* and other traditionally related genera (Mazine et al. 2014; Bünger et al. 2016; Faria et al. in prep.). A recent nomenclatural adjustment incorporated a phylogenetic framework into a new infrageneric arrangement of *Eugenia* (Mazine et al. 2016). Two species corresponding to the *Eugenia* sect. *Calycorectes* (O.Berg) Mattos were surveyed in that phylogeny (*Eugenia brevistyla* D.Legrand and *E. subterminalis* DC.) demonstrating a single evolutionary event of calyx fusion in *Eugenia* within the well-supported ‘clade 7’ (sensu Mazine et al. 2014). Alternatively, calyx fusion as consistent character to support a clade within *Eugenia* has been questioned (Giaretta et al. Chapter 1). A phylogenetic reconstruction based on five DNA regions (one nuclear; four plastids) confirm homoplastic nature of calyx fusion in *Eugenia* and recover well-supported *Eugenia* section *Umbellatae*, including the type species of *Calycorectes grandifolius* O.Berg (Giaretta et al. Chapter 2). Thus, *Schizocalomyrtus* Kausel provided a convenient name for the 'clade 7', i.e. *Eugenia* sect. *Schizocalomyrtus* (Kausel) Mattos (Giaretta et al. Chapter 3).

A molecular phylogenetic framework shows *Eugenia* sect. *Schizocalomyrtus* as well-supported and sister to *Eugenia* sect. *Phyllocalyx* (Mazine et al. 2014; Lucas and Bünger 2015; Giaretta et al. Chapter 2). These sections share extended sepals in the early flower development (Vasconcelos et al. 2018). However, in *Eugenia* sect. *Schizocalomyrtus* it is expressed in several degrees of calyx fusion recognized mainly on two development patterns, i.e. *homosepalous* and *heterosepalous* (detailed descriptions in Giaretta et al. Chapter 2). The *homosepalous* pattern is recognized by flower bud nearly closed except at the apex where four vestigial lobes are free; it tears in irregular lobes or transversely via a structure that resembles a calyptra. *Heterosepalous* pattern has four calyx lobes most commonly fused along two-thirds of the length of the bud leaving an opening of 1–2 mm diameter; the line of fusion is along the edge of each calyx lobe and results in a heterogeneous thickness of the calyx that tapers into a fragile tissue between each sepal. Although these patterns are relevant to recognize *Eugenia* sect. *Schizocalomyrtus*, they have been shown homoplastic appearing in other clades and should be used with others characters. The *longohypanthium* pattern is also found in this section but it is an extreme exception in *Eugenia*. It is recognized by flower bud nearly closed and extended tissue between the corolla and style into a tubular hypanthium that prolongs up to two thirds of the bud length, covered by staminal whorls where stamens are strongly incurved; at anthesis the fused calyx and the staminal whorls deeply tear into three or four irregular lobes (detailed description in Giaretta et al. Chapter 2).

Insights on the current phylogenetic relationship and morphological assessment of fused calyces species of *Eugenia* (Giaretta et al. Chapter 2) allow revaluate the previous classification and support a consistent taxonomic treatment. Thus, a taxonomic revision of ten species included in *Eugenia* section *Schizocalomyrtus* (Kausel) Mattos, a lineage with fused calyx species is here presented (Fig. 1). The current work includes a key for Neotropical closed calyx genera, a description of the section, key for species included in the section (two newly described), detailed species descriptions, notes of distribution and habitat, phenology, conservation status, taxonomic comments, list of specimens examined, collector list, illustrations and maps of distribution.

MATERIAL AND METHODS

Fieldwork in East-West Brazil and France Guiana were conducted between 2014 and 2016. The specimens were deposited in SPF and duplicates were sent to K, RB and VIES when available. The following herbarium collections were consulted: ALCB, BM, CAY, CEN, CEPEC, CHOCO, COAH, COL, CVRD, ESA, G, G-DC, GUA, HRB, HSTM, HUSC, IAN, IBGE, INPA, JBB, K, LE, LINN, MBM, MBML, MFS, MG, OXF, P, R, RB, RFA, SAMES, SP, SPF, SPSF, UB, UEC, VIES and W (acronyms follow Thiers 2017). Recognizing genera of closed calyx species is not always obvious. Thus, a key for Neotropical genera of calyptrate, closed, or partially fused calyx flowers is presented. A detailed synopsis of the *Eugenia* section *Schizocalomyrtus* and a key are provided to identify the species based on morphology. This arrangement is also in congruence to the current phylogenetic framework (Giaretta et al. Chapter 2). Specimens examined represent all material analysed and photographed which identification was reassessed in different moments. Thus, here is presented the conclusion of the ultimate species circumscription. The adopted species delimitation is based on morphology discontinuities, i.e. species correspond to the smallest units that can be recognized by fixed character states.

Leaf description as well as structures shape follow Hickey (1973) and indumentum type follows Payne (1978). The high plasticity of inflorescence makes its typological delimitation sometimes inconsistent. Insights on inflorescence development of *Eugenia* in an evolutionary overview showed distinct structures have been intuitively considered in conjunction unrespect to homology (Giaretta et al. Chapter 4). As a consequence, distorted concept hampers the understanding of arrangement flexibility of *Eugenia*. Thus, for inflorescence arrangements of *Eugenia* was adopted a reassessed inflorescence terminology (Giaretta et al. Chapter 4). Landrum and Kawasaki (1997) was adopted for the inflorescence terminology for the key of genera. Geographic distribution, habitat and phenology were taken from herbarium label and personal observation. References from municipalities were assumed when geographic coordinates were not provided. When available and reliable, records location were

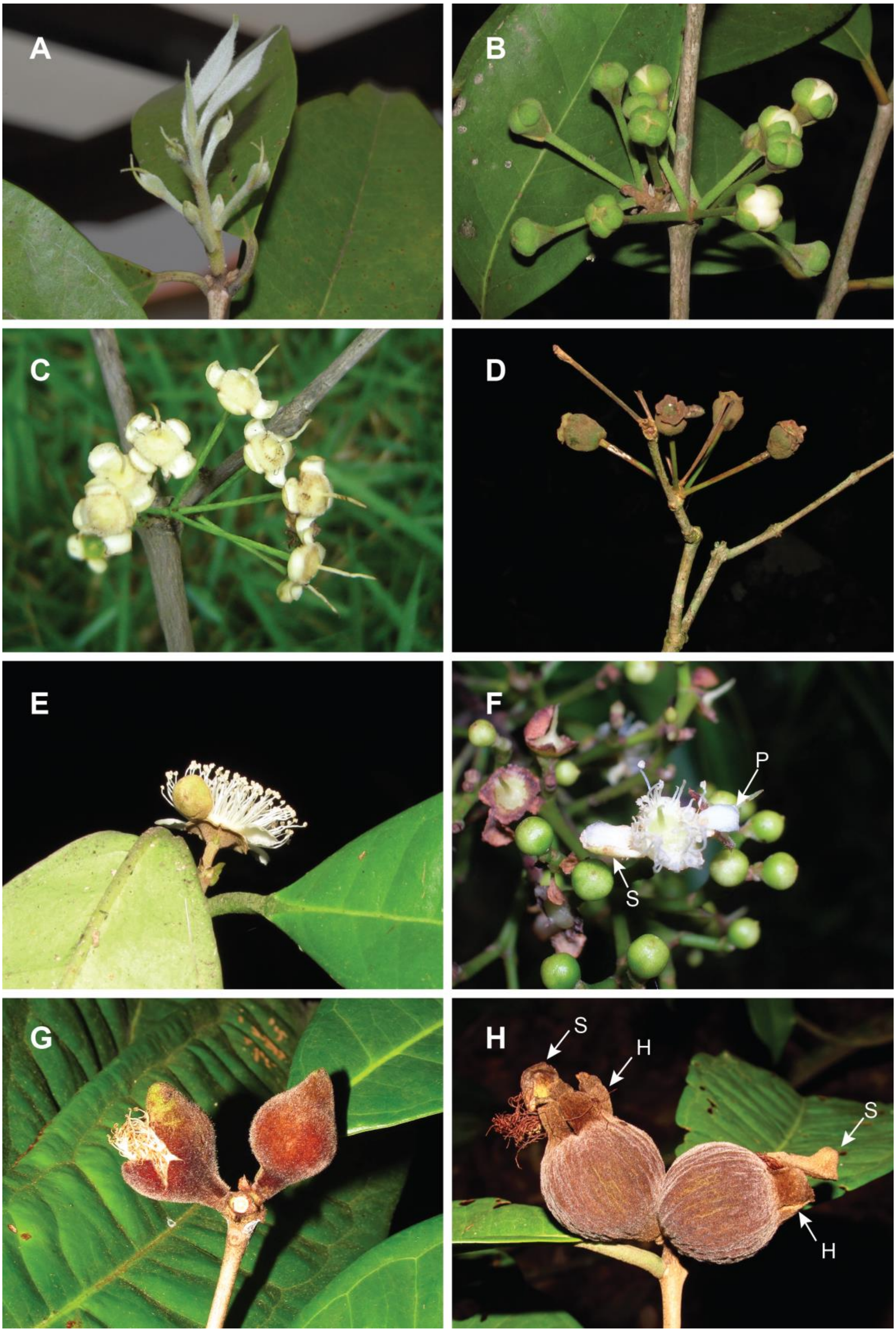


FIG. 1. Diversity of *Eugenia* sect. *Schizocalomyrtus*. A–B. *E. acutata*. A. Auxotelic inflorescence recovering the vegetative growth. B. Flowers at anthesis. C–D. *E. brevistyla*. C. Flowers. D. Immature fruits. E. *E. neoriedeliana*. Flower opening via transversal tearing at the calyx base resulting in a structure calyptra-like. F. *E. guanabarina*. Flowers opening via transversal tearing at the calyx base resulting in a structure calyptra-like (S) placed in opposition

to a petal (P). G–H. *E. longohypanthiana*. G. Flower bud tearing irregularly at anthesis. H. Immature fruits crowned by the remnant of the calyx lobes (S) and the remaining hypanthium (H). (A–B: *A. Giaretta 1460*; C: *J.E.Q. Faria 1000*; D: *A. Giaretta 1493*; E: *A. Giaretta 1489*; F: *A. Giaretta 1035*; G: *A. Giaretta 1500*; H: *A. Giaretta 1502).*

improved according to sheets label. The conservation status was assessed on the bases of the guidelines provided by IUCN (2016); GeoCAT (Bachman et al. 2011) was used to infer Area of Occupancy (AOO) and Extend of Occurrence (EEO) based on the current known species distribution. Distribution maps were based on examined specimens, except cultivated and built using QGis (2017). Extra-Brazilian occurrences were extracted and reviewed from GBIF. This monograph was partially built using the package *monographaR* (Reginato 2016) implemented in R. The following functions used were 'tableToDescription', 'examinedSpecimens', 'collectorList', and 'phenoHist'.

RESULTS

Eugenia incorporating previous segregated genera such as *Calycorectes* and *Hexachlamys* is recognized among Neotropical genera by the tetra-merous flowers, rarely penta or hexa-merous (see *petaloid* development pattern in Giaretta et al. (Chapter 2) for an apparent hexamerous flower), stamens straight on bud (Vasconcelos et al. 2015), hypanthium widely flat and not extended, ovary 2(3)-locular with few to many ovules per locule, and embryo with indistinct cotyledons fused into a solid mass (Landrum and Kawasaki 1997; Sobral 2003; Wilson 2011). Although the combination of characters consistently support *Eugenia*, unusual character of calyx fused on Neotropical Myrtaceae can mislead taxonomist mainly when the collection is not simultaneously representative of flower and fruit. Thus, the identification key is an attempt to fill this gap as well as illustration of the diagnostic characters (Fig. 2). This key was tentatively built to be workable with flower or fruits separately or together. Characters such as 'hypanthium prolonged', type of stigma or inflorescence architecture are presumably persistent in the early fruiting period at least in most specimens observed.

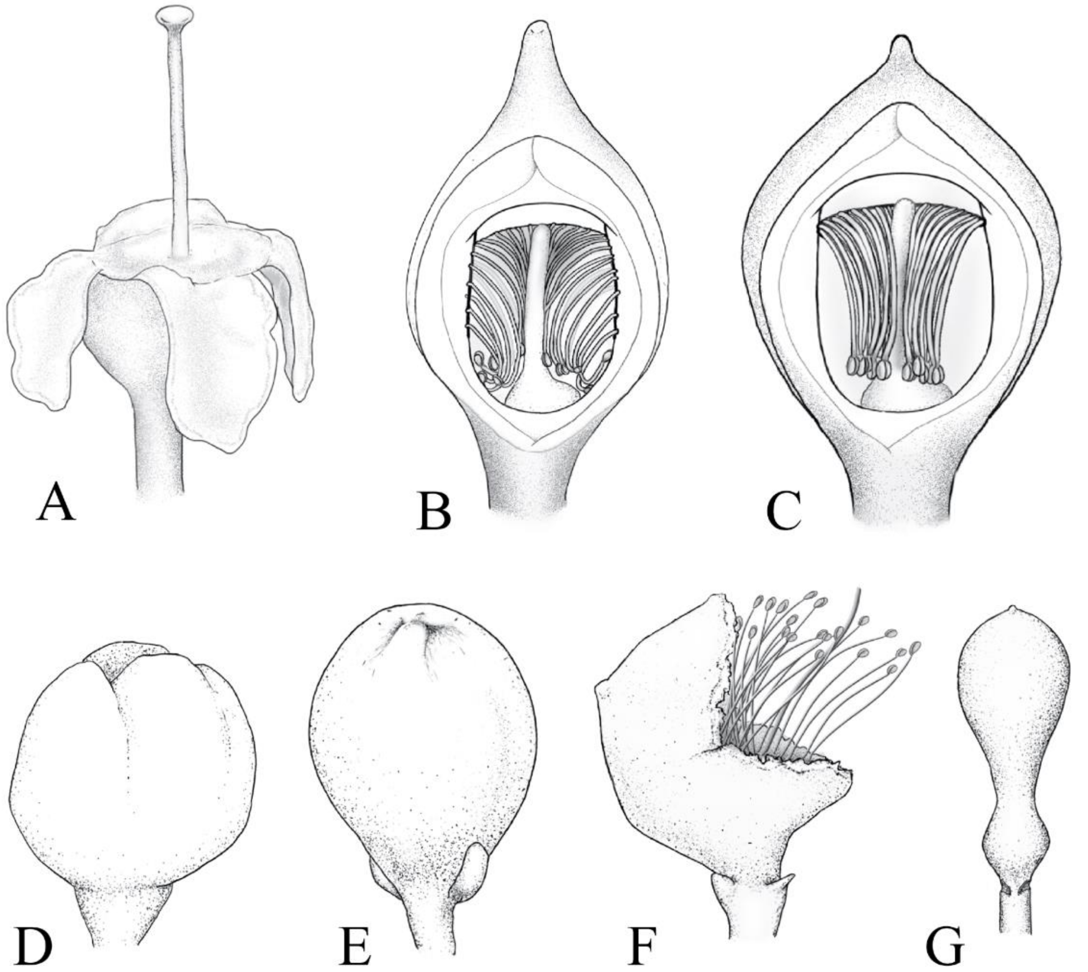


FIG. 2. Diagnostic characters of Neotropical genera with calyptrate, closed or partially fused calyx flower. A. Stigma wider than the style (*Psidium cattleyanum*). B. Longitudinal section of a bud showing stamens semi-curved as result of staminal whorl extension (*Eugenia longohypanthiana*). C. Longitudinal section of a bud showing stamens strongly curved attached to the hypanthium summit (*Calyptranthes brasiliensis*). D. Bud with calyx lobes partially fused by the first third (*Eugenia pisonis*). E. Bud with calyx lobes fused except by the four vestiginal lobes at the apex (*Eugenia vattimoana*). F. Bud tearing tranversaly resulting in a structure calyptra-like (*Eugenia neoriedeliana*). G. Hipanthium tube contracted at the ovary summit (*Siphoneugena widgreniana*). Drawns by Monique Rached.

KEY TO THE GENERA OF CALYPTRATE, CLOSED, OR PARTIALLY FUSED CALYX FLOWERS OF NEOTROPICAL MYRTACEAE

1. Stigma wider than the style 2
   2. Ovary 5–18 locules; fruits with strongly glandular locule wall working as a false seed coat .... *Campomanesia*
   2. Ovary 2–5 locules; fruits with bony seed coat .... *Psidium*
1. Stigma equal or narrower than the style 3
   3. Stamens straight in the bud in longitudinal section; hypanthium not prolonged above the ovary summit 4
      4. Ovary 2 locules; fruits with 1–3 seeds, embryo solid .... *Eugenia*
      4. Ovary 4 locules; fruits with ca. 40 seeds, embryo curved (C-shaped) .... *Accara elegans*
   3. Stamens semi-curved or strongly curved in the bud in longitudinal section; hypanthium prolonged above the ovary summit 5
      5. Inflorescence panicle or compound-dichasium 6
         6. Calyx lobes tearing regularly in triangular lobes at anthesis, deciduous at anthesis; fruit with squared scar, embryo curved (C-shaped), whitish .... *Blepharocalyx eggersii*
         6. Calyx lobes tearing irregularly or opening via calyptra at anthesis, persistent or deciduous after anthesis; fruit with the remnant of the irregular lobes or with a rounded scar, embryo with two foliaceous cotyledons, folded, and greenish .... *Myrcia* s.l.
      5. Inflorescence glomerule, fascicle, botryo, botryoid, spike, simple-dichasium, superimposed peduncles or less often bracteate shoot 7
         7. Flowers with staminal whorl extending up to two-thirds of the bud length, tearing deeply at anthesis; fruits crowned by the remnant of the calyx lobes where scars left by stamens insertion are evident, embryo solid with indistinguishable cotyledons .... *Eugenia longohypanthiana*

7. Flowers with staminal whorl flat or at summit of the prolonged hypanthium, not tearing at anthesis; fruits crowned by remnant of the calyx lobes, stamens scars are restricted to the staminal whorl, embryo foliaceous or with two separated plano-convex cotyledons 8

8. Stamens semi-curved in the bud in longitudinal section; fruits with 1–5 seeds, embryo with two foliaceous cotyledons, folded, greenish ....*Myrceugenia*

8. Stamens strongly curved in the bud in longitudinal section; fruits usually with 1–2 seeds, embryo with two separated plano-convex cotyledons, whitish 9

9. Hypanthium tube contracted at the ovary summit ....

.... *Siphoneugena*

9. Hypanthium tube not contracted at the ovary summit 10

10. Flower opens via calyptra; fruit with circular scar ....

.... *Neomitranthes*

10. Flower opens by calyx tearing in regular or irregular lobes; fruit crowned by reminiscence of calyx lobes ......

.... *Plinia*

TAXONOMIC TREATMENT

EUGENIA sect. SCHIZOCALOMYRTUS (Kausel) Mattos, Loefgrenia 120: 3. 2005. *Schizocalomyrtus* Kausel, Lilloa 32: 367. 1967. *Schizocalyx* O.Berg, Linnaea 27: 319. 1856, nom. illeg., non Scheele, 1843 (Lamiaceae), non Hochst., 1844 (Salvadoraceae), non Wedd., 1854 (Rubiaceae, nom. cons.). *Calycorectes* subgenus *Schizocalyx* Kiaersk., Enum. Myrt. Bras.: 117. 1893. *Calycorectes* section *Schizocalyx* Nied., Nat. Pflanzenfam. 3(6): 82. 1893. *Calycorectes* subgenus *Schizocalomyrtus* (Kausel) Mattos, Loefgrenia 99: 3. 1990.—TYPE: *Schizocalyx pohlianus* O.Berg.

Calycorectes (subgenus *Calycorectes* section *Tetrapetalae*) subsection *Subpaniculatae* Mattos, Loefgrenia 99: 4. 1990.—TYPE: *Calycorectes cucullatus* Mattos.

Calycorectes subgenus *Eucalycorectes* Kiaersk., Enum. Myrt. Bras.: 116. 1893, nom. inval.—TYPE: *Calycorectes sellowianus* O.Berg.

Shrub or tree 1 to 20 m tall. Young leaves glabrous or usually glabrescent. Leaves opposite, decussate, petiolate; petiole adaxially canaliculate or sulcate; blades oblanceolate to wide-elliptic, chartaceous, usually glabrous; base acute to obtuse; apex acuminate; midvein elevate abaxially; venation brochidodromus, secondary veins usually evident. Inflorescence undetermined, terminal, subterminal or axillary; main-axis with pairs of opposite flowers or branches; flowers pedicellate; bracteoles lanceolate to ovate, free. Flower buds usually obovate, closed by the calyx lobes fused in several degrees, tearing at anthesis regularly or irregularly, less often in a structure calyptra-like; petals (1)4, white, concave, suborbicular to spatulate; stamens straight, rarely curved; filaments flattened and erect at anthesis, glabrous; anthers yellowish, aperture rimose; staminal whorls usually not extended above the ovary summit, rarely extending, puberulent, less often pubescent; style usually glabrous, stigma equal or narrower than the style; ovary 2-3 locules, internally glabrous, 3-19 ovules per locule. Fruit crowned by the remnant of the calyx; seeds 1-2; embryo with cotyledons fused and indistinguishable. Ten species.

Comments:—*Eugenia* sect. *Schizocalomyrtus* comprises ten species and can be recognized by leaves with veins usually well-marked and innermost intramarginal vein far from the margin (from 2 to 8 mm), margin not undulate neither hyaline; inflorescences are often fasciculiform with short (0.5 mm long) to elongated (up to 30 mm long) main-axis, up to 3 axes sharing a node, but can be auxotelic, sometimes with 3-flowered dichasial arrangement, or thyrsoid; flower bud with several degrees of calyx fusion fitting to *homosepalous* and *heterosepalous* development patterns but rarely to *longohypanthium* (see above); fruit globose crowned by lobes teared at anthesis.

Eugenia sect. *Schizocalomyrtus* is exclusively distributed in the Atlantic forest except by *Eugenia acutata* and *E. subterminalis,* widely distributed species in the Cerrado (Brazilian *savanna*) restrict to humid forest along river in gallery forest. *Eugenia subterminalis* also occurs in highland forest in the East of Paraguay, North of Argentina, Bolivia, Peru, south Colombia and Ecuador (Fig. 3). The combination of the morphological circumscription and the geographic distribution provides a reliable diagnose of the *Eugenia* sect. *Schizocalomyrtus*.

Flowers of *Eugenia* sect. *Schizocalomyrtus* have been mainly collected from September to November while fruiting from October to January (Fig. 4). Phenological fluctuations seems to be related to the environment conditions. *E. zuccarinii* from Atlantic province was collected flowering mainly from August to November whereas flowers were collected from January to April in the Caatinga province. *Eugenia guanabarina* and *E. zuccarinii* (Atlantic) are from coastal *Restinga* vegetation and have similar phenological diagrams; also, *E. acutata*, E. *brevistyla* and *E. subterminalis* which have great range of distribution in the Ombrophyllous Dense Forest share similar phenological patterns. *E. majepensis*, *E. neoriedeliana*, *E. paradisiaca* and *E. vattimoana* occur in the costal forest and have similar phenological pattern. In constrat, flowers of *E. longohypanthiana* from trasition between Semideciduous to Ombrophyllous Dense Forests were atypically collected mainly in March and April and fruits from May to August.

KEY TO THE SPECIES OF *EUGENIA* SECT. *SCHIZOCALOMYRTUS*

1. Stamens curved in the bud in longitudinal section; staminal whorls extend up to two-thirds of the bud length and deeply tearing at anthesis; fruits densely puberulent, and crowned by the reminiscence of the hypanthium with scars left by stamens insertion .... 4. *Eugenia longohypanthiana*

1. Stamens straight in the bud in longitudinal section; staminal whorls flat and not tearing at anthesis or less often tearing slightly; fruits glabrous or less often densely puberulent, and crowned by the reminiscence of the calyx lobes 2

    2. Calyx lobes apparently free but fused at the base by ca. 1 mm long; fruit crowned by the calyx that tears discreetly in a longitudinal manner .... 10. *Eugenia zuccarinii*

    2. Calyx lobes partially fused by at least 2 mm long to closed; fruits crowned by the calyx that tears evidently in a longitudinal or transversal manner 3

        3. Calyx lobes tearing transversely resulting in a structure calyptra-like; fruits usually crowned by the calyx opened via calyptra-like structure 4

4. Inflorescence thyrsoid, terminal or subterminal; bud closed at the tip leaving an apiculum; bracteole deciduous after anthesis; ovary 3–5 ovules per locule .... 3. *Eugenia guanabarina*

4. Inflorescence fasciculiform, terminal or axillary; bud partially fused and nearly closed leaving four vestigial free lobes at the tip; bracteole persistent after anthesis; ovary 9–15 ovules per locule .... 6. *Eugenia neoriedeliana*

3. Calyx lobes tearing longitudinally resulting in 3–4 lobes; fruits crowned by 3–4 calyx lobes 5

5. Leaves dense puberulent abaxially, persistent; the innermost intramarginal vein 4.5–10 mm from the margin; bud tears irregularly at anthesis in 3–4 lobes; fruits 30–45 mm diam. and crowned by the remnant of the irregular calyx lobes .... 9. *Eugenia vattimoana*

5. Leaves glabrous, pubescent or tomentose abaxially, glabrescent; the innermost intramarginal vein 1.5–5 mm from the margin; bud tears regularly at anthesis in 4 lobes; fruits 7–20 mm diam. and crowned by the remnant of the regular calyx lobes 6

6. Leaves with 5–7 secondary veins, petioles 1.5–5 mm long; bracteoles persistent in the fruit; fruit red when ripe .... 8. *Eugenia subterminalis*

6. Leaves with 9–22 secondary veins, petioles 5–18 mm long; bracteoles deciduous before or after anthesis; fruit artropurpureum or yellowish when ripe 7

7. Bud glabrous outside, calyx lobes equal in size 8

8. Young leaves glabrous; buds 5–7 × 4–6.5 mm, calyx lobes 2.5–4 × 2.5–3 mm; staminal whorl 4–5 mm diam., rounded .... 5. *Eugenia majepensis*

8. Young leaves with trichomes 0.2–0.4 mm long, appressed, glabrescent; buds 9–11 × 8–9 mm, calyx

lobes 4–8 × 4–9 mm; staminal whorl 9–10 mm diam., squared .... 7. *Eugenia paradisiaca*

7. Bud puberulent outside, pubescent or tomentose, calyx lobes two unequal pairs in size 9

    9. Leaves with secondary veins 11–22 per side; inflorescence rachis 3–30 mm, pubescent, up to one rachis per axil; buds 6–8 × 4.5–7 mm, staminal whorl 4.5 mm diam.; fruits ellipsoid, yellowish when ripe .... 1. *Eugenia acutata*

    9. Leaves with secondary veins 9–12 per side; inflorescence rachis 0.5–5 mm, puberulent or tomentose, up to two rachises sharing the same axil; buds 3–5 × 2.5–5 mm, staminal whorl 3 mm diam.; fruits globose, artropurpureo when ripe .... 2. *Eugenia brevistyla*

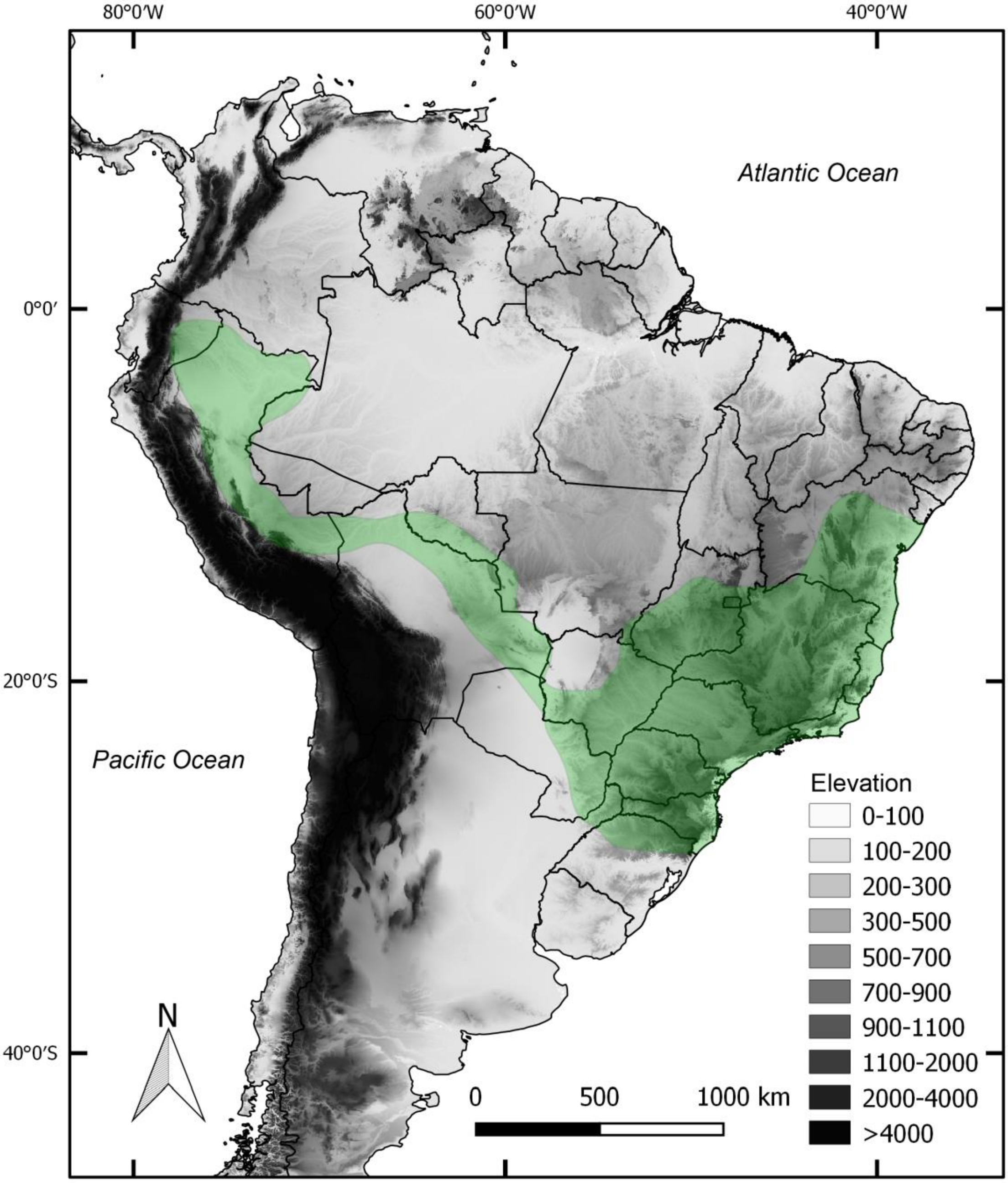


FIG. 3. Estimate distribution of the *Eugenia* sect. *Schizocalomyrtus* based on herbarium specimens.

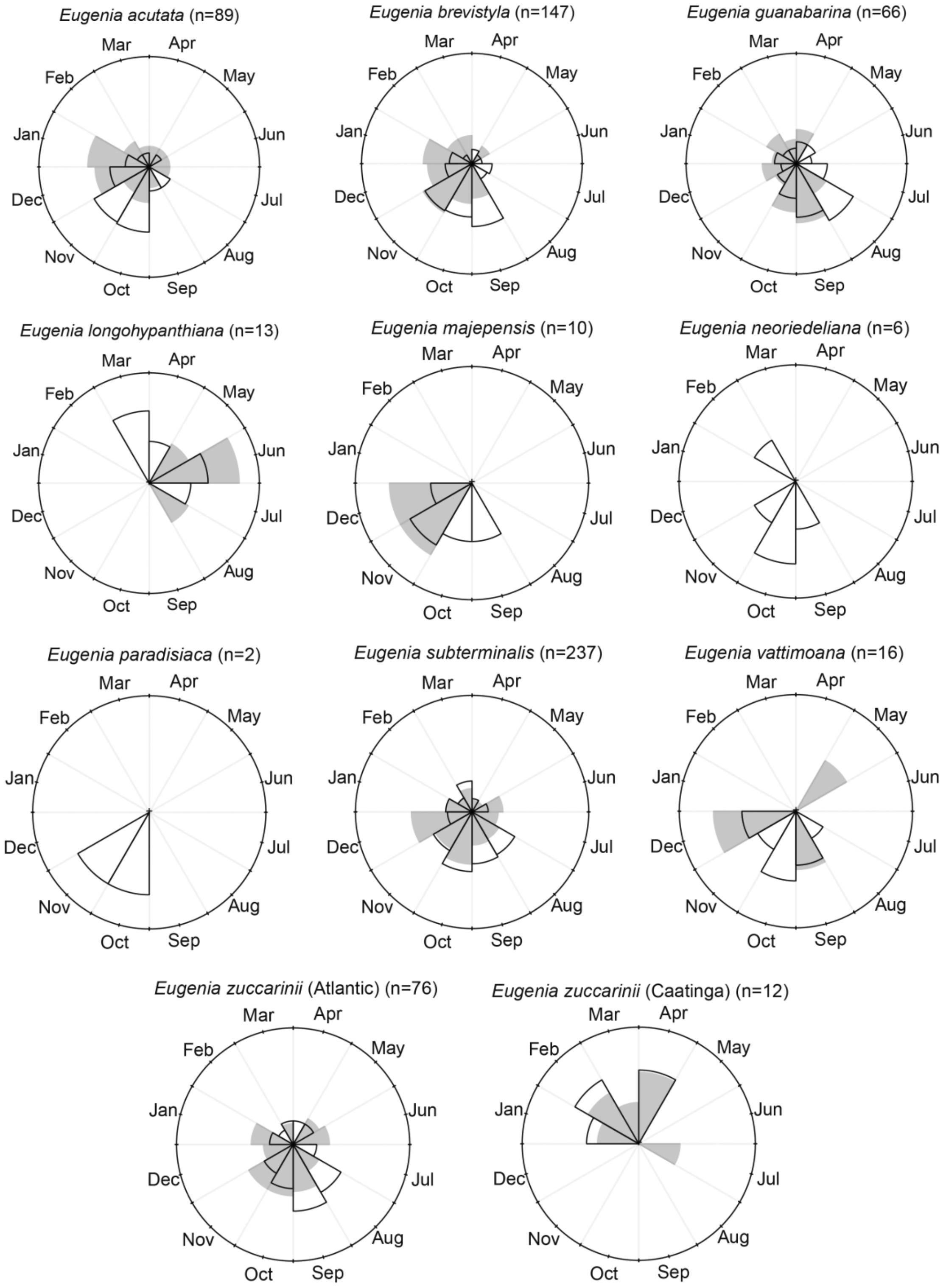


FIG. 4. Frequency distribution (n) of flowering (black-line triangle) and fruiting (grey-filled triangle) stages based on herbarium material of *Eugenia* sect. *Schizocalomyrtus* species.

1. EUGENIA ACUTATA Miq., Linnaea 22: 535. 1849. *Calycorectes acutatus* (Miq.) Toledo, Relat. Anual Inst. Bot.: 40. 1945.—TYPE: BRAZIL. Minas Gerais, ad Caldas, fl., s.d., *Regnell 2-115* (**lectotype designated here:** P! [05156360]; isolectotypes: MEL [1540501-photo!], SP! [010821]).

Calycorectes martianus O.Berg, Fl. Bras. 14(1): 596. 1859. *Eugenia martiana* (O.Berg) Mattos, Loefgrenia 120: 6. 2005.—TYPE: BRAZIL. Rio de Janeiro, habitat prope Mandioca, fl., s.d., *L. Riedel and Langsdorff s.n.* (**lectotype designated here:** LE! [00004071]; isolectotype: P! [05229272]).

Eugenia ademireana Mattos, Loefgrenia 120: 6. 2005. *Calycorectes cucullatus* Mattos, Loefgrenia 94: 10. 1989.—TYPE: BRAZIL. São Paulo, Serra do Mar, na descida Jequitiba-Miracatu, fl., 20 September 1969, *M. Kuhlmann s.n.* (holotype: HAS; isotypes: FLOR, SP! [006200, 114160-herbarium number]). **syn. nov.**

Eugenia ezechiasii Mattos, Loefgrenia 120: 6. 2005. *Calycorectes heringerianus* Mattos, Loefgrenia 101: 1. 1992.—TYPE: BRAZIL. Minas Gerais, Lagoa Preta, margem do rio Paraopeba, fl., 30 October 1957, *E.P. Heringer s.n.* (holotype: ICN; isotypes: IAC, NY [00906791-photo!], SP! [028149]). **syn. nov.**

Eugenia fontellae Mattos, Loefgrenia 120: 5. 2005. *Calycorectes fluminensis* Mattos, Loefgrenia 62: 1. 1974.—TYPE: BRAZIL. [Rio de Janeiro], Itatiaia, lote 70, fl., 20 November 1918, *C. Pôrto 840* (holotype: RB! [00265662]; isotypes: HBR, M, SPF!). **syn. nov.**

Eugenia plicata Nied., Nat. Pflanzenfam. 3(7): 91. 1893. *Stenocalyx riedelianus* O.Berg, Fl. Bras. 14(1): 349. 1857. non *Eugenia riedeliana* O.Berg, Fl. Bras. 14(1): 261. 1857.—TYPE: BRAZIL. Rio de Janeiro, habitat prope praedium Mandiocca, fl., February [1823], *Riedel s.n.* (lectotype designated here: P [00602809-photo!]; isolectotypes: BR [000000526056-photo!, 0000005260560-photo!], G, LE). **syn. nov.**

Eugenia springiana O.Berg, Linnaea 27: 229. 1856. *Eugenia laurifolia* Spring ex Mart., Flora 20(2 Beibl.): 82. 1837, nom. illeg., non (DC.) Roxb., Fl. Ind. ed. 1832, 2: 489. 1832., non Cambess., Fl. Bras. Merid. 2: 357 1829[1833], nom. illeg.—TYPE: BRAZIL. São Paulo, in sylvis humilioribus (Caapoens) ad fluvium Capivary, fl., 1836, *Padre da Silva Manso 283* (**lectotype designated here:** BR [000000526064-photo!]).

Shrub or tree 1.5 to 30 m tall. Young leaves with brownish trichomes up to 1 mm, matted, appressed, dense or sparse, glabrescent. Young twigs flattened or compressed, pubescent, glabrescent; bark longitudinally striate exfoliating on membranaceous sheets, glabrous. Leaves with petioles 5–10 × 1–1.5 mm, canaliculate adaxially, glabrous or puberulent, often darkish when dry; blades 5–12 × 2–4.5 cm, elliptic or narrow–elliptic, chartaceous, discolourous, sometimes concolourous when dry, glabrous but sometimes sparse–puberulent abaxially; base acute or cuneate; apex acuminate, 0.5–2 cm long, often attenuate; midvein canaliculate adaxially; secondary veins 11–22 per side, slightly prominent on both surfaces, often indistinct; marginal veins two, the innermost 2–3 mm from the margin, the outermost 0.5–1 mm from the margin, often indistinct, margin slightly revolute; glandular dots indistinct adaxially, slightly prominent abaxially, concolourous or discolourous. Inflorescence axillary or terminal, auxotelic, often recovering the vegetative growth; bracts 1.5–2.5 × 1.5–2 mm, wide-ovate, puberulent or pubescent; rachis 3–30 mm long, flattened, pubescent; 1–4 pairs of flowers, rarely expressing 3–flowered dichasial arrangement, pedicels 10–30 × 1 mm, pubescent; up to one rachis per axil; bracteoles 3–6 × 0.5 mm, lanceolate, puberulent or pubescent, deciduous before anthesis. Flower buds 6–8 × 4.5–7 mm, obovate, marked by 6–10 glandular dots per mm², calyx lobes partially fused but free at the tip leaving an aperture of 1–4 mm diameter, tearing regularly at anthesis in 4 lobes, two unequal pairs, the outermost 4–6 × 3–5 mm, wide–ovate, the innermost 3–5 × 2.5–4.5 mm, wide–ovate, puberulent, dense on hypanthium, or pubescent outside, puberulent or pubescent inside; petals 4–7 × 4–7 mm, obovate or suborbiculate, glabrous; stamens straight in the bud, filaments up to 9 mm long, anthers 0.8–1 mm long, oblong; staminal whorls flat, 4.5 mm diameter, squared, slightly tearing at anthesis, puberulent; style 6–8 mm long, glabrous; ovary (1)2–locules, 5–17 ovules per locule. Fruits 12–20 × 10–15 mm, ellipsoid, yellowish when ripe, glabrous or sparsely puberulent, crowned by the remnant of the regular calyx lobes; seeds 1–2. Figure 5.

Etymology:—The specific epithet likely refers to the shape of the leaf apex.

Distribution and habitat:—*Eugenia acutata* is wide distributed occurring in Southeastern (Minas Gerais and São Paulo), Central-western (Goiás) and Northeastern Brazil (Bahia), known from several vegetation types in the Serra do Mar, Serra da

FIG 5. *Eugenia acutata*. A. Leaf twig with opened flowers. B. Inflorescence with flowers bud. C. Fruits. (A: *A.C. Leonello s.n.*; B: *M. Verdi 6538*; C: *N.M. Ivanauskas 5020*).

Matiqueira, and Planalto Central, at elevations between 0 to 1100 m a.s.l. (Fig. 6). It is usually tree distributed along the coastal lowland and slope forests, sometimes reaching the coast in the shrub vegetation on well-drained sandy soil, within Ombrophyllous Dense Forest, and towards inland in the dry forest on calcarean soil within Semideciduous Forest, and more often in the savanna gallery forest on basaltic soil, both in the Cerrado province. It also rarely occurs in the Mixed Ombrophyllous Forest (with *Araucaria*).

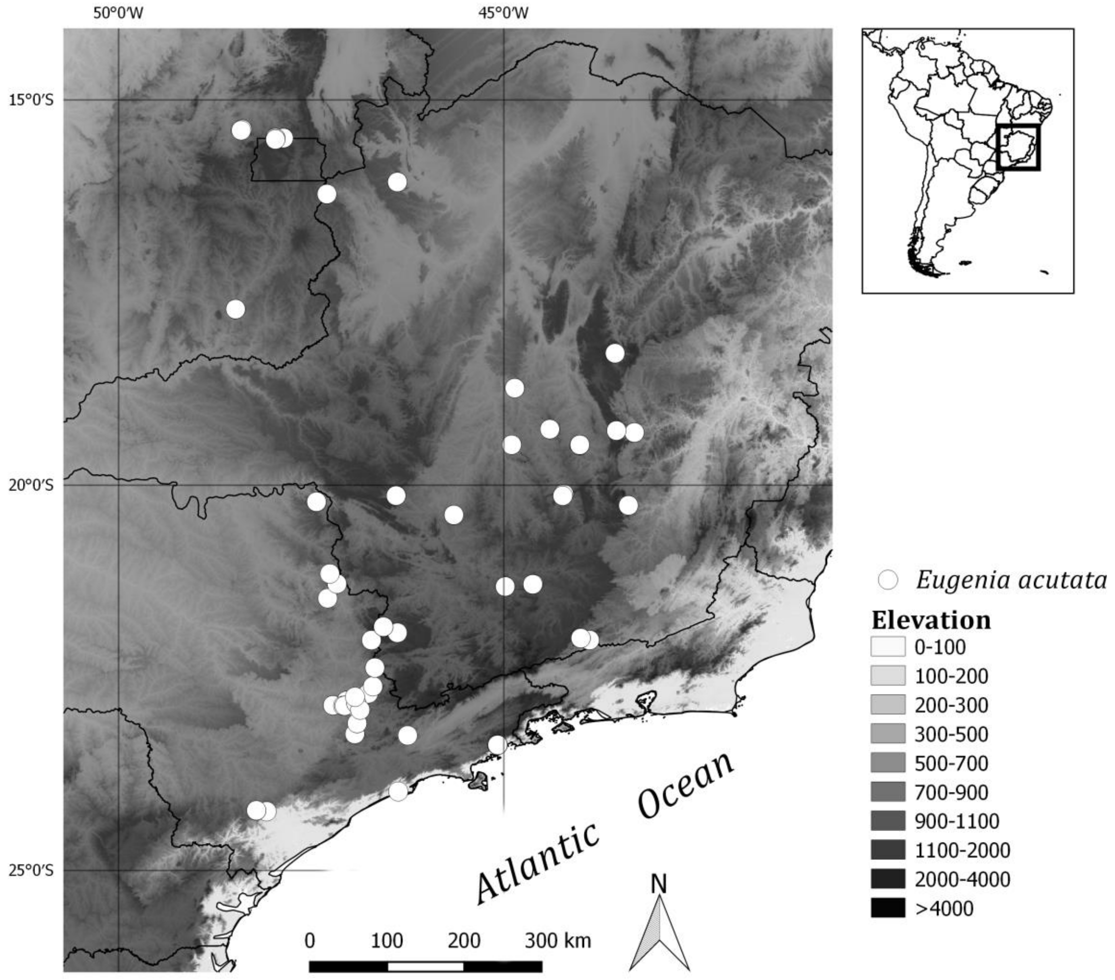


FIG. 6. Geographic distribution distribution of *Eugenia acutata*.

Phenology:—Flowers have been collected from August to March and fruiting from September to July (Fig. 4).

Conservation status:—Least Concern (LC). *Eugenia acutata* occurs in protected and non-protected areas in primary and secondary sites with EOO of 589,873 km². Although not threatened regarding its entire distribution, populations in the northeast range are vulnerable to local extinction due to the recurrent suppression of the coastal environments to urbanization whereas populations on extreme south range occur in isolated remnants of Montane Mixed Forest.

Comments:—Five taxa are newly treated as synonym under examination of the respective type collection as well as four lectotypification are designated. *Eugenia acutata* can be distinguished from other species of *Eugenia* sect. *Schizocalomyrtus* by the combination of the inflorescence auxotelic with one rachis per axil, highly variable in length, and often recovering the vegetative growth seen by young leaves formed at the apex of the rachis, bracteoles lanceolate, and flower partially fused tearing regularly in four lobes (*heterosepalous* pattern). *E. acutata* expressing flowers arranged in dichasium can be confused to *E. guanabariana* but differs form this species by the combination of the 11-22 secondary veins (*vs.* 8-12) and calyx lobes tearing regularly in four lobes (*vs.* calyptra-like).

Specimens examined:**—Brazil. Bahia:** Porto Seguro, 12 July 1988, fr., *G.L. Farias 206* (CEN); próximo Subauma, 10 February 1980, fl. and fr., *A.P. Araújo 236* (HRB, RB). **Espírito Santo:** Santa Leopoldina, 29 November 2007, fr., *V. Demuner 4612* (MBML). **Goiás:** Anápolis, Reserva do campus da Universidade Estadual de Goiás, 24 November 2007, fl., *J.E.Q. Faria 245* (UB). Caldas Novas, Parque Estadual Serra de Caldas Novas, 26 October 2009, fr., *D.I. Junqueira 565* (CEN, UB). Distrito Federal, 1 km após a entrada para a Colônia agrícola Ribeirão, Córrego do Ouro, 10 October 2001, fl., *M. Carvalho-Silva 78* (CEN, SPF). Ipameri, margem esquerda do rio Corumba, 300m a jusante da ponte São Bento, 19 March 1996, fl., *G. Pereira-Silva 3530* (CEN, RB, UB). Padre Bernardo, margem da BR 414, 17 March 2014, fr., *J.E.Q. Faria 3949* (UB). Pirenópolis, 27 January 2011, fr., *J.E.Q. Faria 1030* (UB). **Minas Gerais:** 1838, fl., *M. Claussen 740* (P); 1839, fl., *M. Claussen s.n.* (G); Brumadinho, Inhotim, 22 January 2008, *fr., J.G. Oliveira 92* (RB). Cabeceira Grande, mata próxima ao túnel de fuga, 26 November 2012, fr., *A.A. Santos 1653* (CEN). Felixlândia, Córrego Bagre, BR 040, 8 September 2013, fr., *R.G. Chacon 1243* (JBB). Lagoa Santa, APA de Lagoa Santa, 16 October 1995, fl., *A.E. Brina s.n.* (MBM, SP). Lavras, defronte a entrada do Parque do Rio Bonito, estrada de Lavras-Luminárias km 8,5, 26 December 2002, fl., *J. Chaddad-Jr. 152* (ESA); estrada para São João Del Rey, estrada para Serrinha, 3 km de asfalto, 25 December 2002, fr., *J. Chaddad-Jr. 148* (ESA). Matozinhos, 3 December 2006, fr., *G.C.T. Ceccantini 3039* (SPF); Lapa do Santo, fazenda Cauaia, 23 October 2006, fl., *J.C.F. Melo Jr. 560* (SPF). Muriaé, fazenda Barra Alegre, 23 October 1989, fl., *R. Simão-Bianchini 209* (SPF). Nazareno, 11 December 2011, fl., *M. Sobral 14454* (RB, SP). Pains, 28 October 2003, fr., *P.H.A. Melo 920* (SPF). Palmital, área de encontro Ribeirão Jabuticaba e Rio Preto, 31 August 2001, fl., *A.E. Ramos 1593* (JBB). Paraopeba, Estação Florestal, 5 February 1975, fr., *E.P. Heringer 14377* (UB). Poços de Caldas, 7 December 1971, fl., *J. Mattos 16387* (SP); estrada de Minas Gerais, 30 October 1981, fl., *J.Y. Tamashiro 1647* (ESA, UEC); ibid., fazenda Chiqueirão, 3 December 1981, fl., *F.R. Martins 1611* (ESA, UEC). Santana do Riacho, 25 February 1985, fr., *P.M. Andrade 8730* (MBM); APA Morro da Pedreira, Pedra do Elefante, 14 October 2013, fl., *M. Verdi 6538* (RB). São Roque de Minas, RPPN Cachoeira do Cerradão, 7 January 2008, fr., *C. Proença 3476* (ESA, MBM, UB). Unaí, Garapuava, 26 November 2000, fl., *L.C. Milhomens 22* (UB). **Paraná:** Dois Vizinhos, foz do rio Chopim, 9 October 1974, fl., *G. Hatschbach 35107* (MBM). **Rio de Janeiro:** Rio de Janeiro, 26 January 2015, fl. and fr., *A. Giaretta 1460* (SP, SPF); cultivada no arboreto do Jardim Botânico do Rio de Janeiro, canteiro 8B. Indiv: 1979, 7 April 1999, es., *Coleta do Arboreto s.n.* (RB). **São Paulo:** estrada Valinhos-Itatiba, 30 August 1997, fl., *A.C. Siani s.n.* (RB, SPF). Águas da Prata, 9 November 1966, fl., *J. Mattos 14211* (SP); Floresta Estadual, 9 November 1966, fl., *J. Mattos 14182* (SP). Amparo, Monte Alegre, fazenda Nossa Senhora da Encarnação, 8 May 1942, fl. and fr., *E. Kuehn 1189* (SP, UEC). Campinas, 13 October 1977, fl., *L.A.F. Mathes 275* (RB); 13 October 1977, fl., *L.A.F. Mathes 293* (RB); 13 October 1977, fl., *L.A.F. Mathes 295* (RB); 13 October 1977, fl., *L.A.F. Mathes 468* (RB); 13 October 1977, fl., *L.A.F. Mathes 654* (RB); 20 October 1977, fl., *L.A.F. Mathes 19* (RB); 28 December 1977, fl., *L.A.F. Mathes 21* (RB); 29 September 1977, fl., *L.A.F. Mathes 7736* (MBM); 5 August 1977, es., *L.A.F. Mathes 300* (RB); 7 November 1977, fl., *L.A.F. Mathes 124* (RB); s.d., fl., *C. Novaes 1144* (SP); Bosque dos Jequitibás, 1965, fr., *H.M. Souza s.n.* (SP); ibid., 20 November 1969, fl., *H.M. Souza s.n.* (MBM); Bosque São José, 22 October 1993, fl., *D.A. Santin 33602* (ESA); Chácara Valinhos, 17 December, fl., *A.C. Leonello s.n.* (RB); mata da Fazenda (Fragmento G2), 13 September 2001, es., *K. Santos 4109* (ESA); Sousas, 22 October 1996, fl. and fr., *K. Santos 106* (SP). Cássia dos Coqueiros, sítio Nossa Senhora do Carmo, 9 November 1994, fl., *A.M.G.A. Tozzi s.n.* (SP, SPF, UEC). Funil, s.d., fl., *C. Novaes 1321* (SP). Helvetia, 10 November 1943, fl., *D. Ildefonso s.n.* (SPSF); 18 January 1945, fr., *D.B.J. Pickel s.n.* (SPSF); 4 November 1943, fl., *D.B.J. Pickel s.n.* (SPSF); 4 November 1946, fl., *D.B.J. Pickel s.n.* (SPSF). Iguape, 13

December 1990, fr., *M.P. Costa 10* (SP), 27 October 1993, fl., *L. Rossi 1346* (SP, SPSF); Estação Ecológica Juréia-Itatins, 14 December 1992, fl., *L. Rossi 1222* (SP, SPSF); ibid., 12 December 1990, fl., *I. Cordeiro 793* (SP); ibid., 14 December 1990, fr., *M.P. Costa 28* (SP). Itapira, fazenda Malheiros, 12 January 1994, fr., K.D. *Barreto 1778* (ESA, SP). Jundiaí, Estação Experimental do IAC, 5 April 1995, fr., *S.L.J. Mendaçolli 1416* (SP). Lindóia, estrada de ferro velho, 3 September 1994, fl., *G.F. Arbocz 749* (RB, SP). Martinho Prado, fazenda Campininha, 21 June 1988, fr., *S. Romaniuc-Neto 1114* (SP). Mogi Guaçu, 28 December 1961, fr., *J. Mattos 9633* (SP). Mogi Guaçu, Estação Experimental, 26 November 1976, fl., *P.E. Gibbs 3554* (MBM, UB, UEC); Reserva Florestal, 14 October 1973, fl., *J. Mattos 16322* (SP). Pedregulho, Parque Estadual Furna do Bom Jesus, 16 November 1997, fl., *E.E. Macedo 276* (SPSF). Piracicaba, Estação Experimental de Tupi, 10 November 1998, fl., *E. Giannotti s.n.* (SPSF). Piracicaba, Estação Experimental Tupi, 10 November 1998, fl., *E. Giannotti s.n.* (ESA). Santo Antônio da Alegria, bairro do Baú, 10 November 1994, fl., *A.M.G.A. Tozzi s.n.* (SP, UEC). São João da Boa Vista, estrada para Andradas, 12 October 2001, fl., *P.L.R. Moraes 2494* (ESA). São Paulo, 3 January 1992, fr., *B. Lopes s.n.* (SPSF); área administrativa, Arboreto Bassoti, 27 October 2005, fl., *M.N. Sakita s.n.* (ESA, SPSF); Horto Florestal, 14 December 1942, fr., *D.B.J. Pickel s.n.* (SP). São Vicente, Parque Estadual Xixová-Japuí, trilha da pedreira, primeiro acesso após o mirante, 17 August 2001, fl., *J.A. Pastore 1073* (ESA). Serra Negra, alto da serra, 22 November 1991, fl., *F. Barros 2357* (MBM, MBML, SP, SPF); ibid., 22 November 1991, fl., *F. Barros 2363* (MBM, SP, SPSF, UEC). Sete Barras, fazenda Intervales, 10 November 1994, fr., *V.B. Zipparro 818* (SP); Parque Estadual Intervales, 12 January 1999, fl., *D. Sampaio 157* (SP, UEC); ibid., 14 November 2000, fl., *V.B. Zipparro 2024* (SP); ibid., 15 November 2000, fl., *V.B. Zipparro 2029* (SP); ibid., 15 November 2000, fl., *V.B. Zipparro 2031* (SP); ibid., 15 November 2000, fl., *V.B. Zipparro 2032* (SP), 15 November 2000, fl., *V.B. Zipparro 2034* (SP); ibid., 16 January 2001, fr., *V.B. Zipparro 2059* (SP); ibid., 16 November 2000, fl., *V.B. Zipparro 2036* (SP); Rio Preto, sítio do Manuel Português, 16 January 2004, fr., *N.M. Ivanauskas 5020* (RB). Socorro, estrada das guabirobas, 8 October 1994, fl., *G.F. Arbocz 891* (ESA, SP). Ubatuba, Estação Experimental do Instituto Agronômico de Campinas, 18 December 1978, fr., *A.F. Silva 9222* (IBGE). Valinhos, Estação Ecológica, 18 November 2002, fl., *J.R. Guillaumon s.n.* (MBM, SPSF); ibid., 2 November 2003, fl., *J.R. Guillaumon s.n.* (SPSF); ibid., 6 October 2002, fl., *J.R. Guillaumon s.n.* (MBM, SPSF); ibid., estrada dos fundos, borda da mata natural, 6 October 2002, fl., *J.R. Guillaumon s.n.* (ESA, SPSF); Estação Experimental Valinhos (IF), 6 October 1983, fl., *S. Gandolfi 15618* (IBGE, INPA). Vinhedo, 2 November 2002, fl., *J.R. Guillaumon s.n.* (SPSF); Condomínio Estância Marambaia, 15 September 2002, fl., *J.R. Guillaumon s.n.* (SPSF); ibid., 23 November 2003, fl., *J.R. Guillaumon s.n.* (MBM); rodovia Anhanguera, km 74, borda da mata, 13 January 2003, fl., *J.R. Guillaumon s.n.* (ESA).

2. EUGENIA BREVISTYLA D.Legrand, Fl. Ilustr. Catarin. 1(Mirt. Suppl.): 18. 1977.—TYPE: BRAZIL. Santa Catarina, Florianópolis, Ilha de S[anta] Catarina, Tapera, Ribeirão, 300 m a.s.l., fl., 18 November 1969, *Klein and Bresolin 8426* (holotype: MVM; isotypes: ICN, FLOR, MBM! [139774], MO, PACA).

Calycorectes pirataquinensis Mattos, Loefgrenia 107: 1. 1995. *Eugenia pirataquinensis* (Mattos) Mattos, Loefgrenia 120: 8. 2005.—TYPE: BRAZIL. Bahia, Ilhéus, Pirataquiné, fl., 3 September 1944, *H. Velloso [1006]* (holotype: R! [41[9]82 herbarium number]). **syn. nov.**

Eugenia falkenbergiana Mattos, Loefgrenia 120: 4. 2005. *Calycorectes duarteanus* D.Legrand, Comun. Bot. Mus. Hist. Nat. Montevideo 4(51): 2. 1970.—TYPE: BRAZIL. Santa Catarina, Lui[z] Alves, [Braço Joaquim], 300 m a.s.l., fl., 21 June 1956, *R.M. Reitz and Klein 3337* (holotype: MVM; isotypes: B [100244672-photo!], HUEFS, MBM! [51522], US [00118236-photo!], MO).

Eugenia imaruiensis D.Legrand, Fl. Ilustr. Catarin. 1(Mirt. Suppl.): 22. 1977.—TYPE: BRAZIL. Santa Catarina, Imaruí, Alto rio D’una, 450 m a.s.l., fl., 15 January 1974, *A. Bresolin 1098* (holotype: MVM; isotypes ICN [photo!], FLOR, MO). **syn. nov.**

Eugenia neoaustralis Sobral, Fam. Myrtac. Rio Grande do Sul: 68. 2003. *Calycorectes australis* D.Legrand, Sellowia 13: 333. 1961.—TYPE: BRAZIL. Santa Catarina, Brusque, [Mata S. Pedro], fl., 3 November 1949, *Reitz 3173* (holotype: MVM; isotypes: H [1386639-photo!, 1386640-photo!, 1386641-photo!], MO, PACA, S [05-3092 herbarium number-photo!], SI [002720-photo!], US [00048257-photo!]).

Calycorectes australis var. *impressovenosus* D.Legrand, Sellowia 13: 334. 1961. *Eugenia neoaustralis* var. *impressovenosa* (D.Legrand) Mattos, Loefgrenia 120: 11. 2005.—TYPE: BRAZIL. Santa Catarina, Horto Florestal I.N.P., Ibirama, 400 m a.s.l., fl., 28 September 1957, *Klein 2214* (holotype: MVM; isotypes: H {1386638-photo!], MO, NY [00561481-photo!], SI [002721-photo!], US [00048256-photo!]).

Tree 5 to 20 m tall. Young leaves with brownish trichomes up to 1 mm long, matted, dense on both sides, glabrescent, or whitish trichomes up to 0.2 mm long, appressed, dense on both sides, glabrescent. Young twigs compressed, tomentose, pubescent or puberulent, glabrescent; bark longitudinally striate exfoliating on chartaceous irregular sheets, glabrous. Leaves with petioles 5–13 × 0.5–1 mm, canaliculate adaxially, pubescent or glabrous; blades 4–15 × 1.2–5 cm, elliptic, narrow–obovate or less often narrow–oblong, chartaceous, concolourous or discolourous when dry, glabrous but sometimes pubescent abaxially; base acute or cuneate; apex acuminate, 0.5–2 cm long, sometimes attenuate; midvein canaliculate adaxially; secondary veins 9–12 per side, slightly prominent adaxially, often indistinct, prominent abaxially; marginal veins two, the innermost 2–5 mm from the margin, the outermost 0.5–1 mm from the margin, slightly revolute; glandular dots depressed adaxially, slightly prominent abaxially, often indistinct, concolourous. Inflorescence axillar or terminal, fasciculiform, rarely auxotelic and recovering the vegetative growth; bracts 0.5–1.2 × 1–1.5 mm, wide–ovate, puberulent; fasciculiform rachis 0.5–5 mm long, flattened, puberulent, or sometimes tomentose; 1–4 pairs of flowers, pedicels 5–30 × 0.7–1 mm, glabrous, sometimes puberulent or tomentose; up to two rachises sharing an axil; bracteoles 0.5–4 × 0.5–1 mm, ovate or less often lanceolate, puberulent or pubescent, deciduous before or after anthesis. Flower buds 3–5 × 2.5–5 mm, obovate, marked by 5–14 glandular dots per mm^2, calyx lobes partially fused but free at the tip leaving an aperture of 1–2 mm diameter, or rare calyx lobes apparently free but fused at the base by 2 mm, tearing regularly at anthesis in 4 lobes, two unequal pairs, the outermost 2–5 × 2–4 mm, wide–ovate, the innermost 2–5 × 2–2.5 mm, ovate or narrow–ovate, puberulent, dense on hypanthium or tomentose outside, puberulent or pubescent inside; petals 3–6 × 2.5–3 mm, obovate, glabrous or sparsely pubescent; stamens straight in the bud, filaments up to 6 mm long, anthers 0.5–0.7 mm long, oblong or orbiculate; staminal whorls flat, 3 mm diameter, squared, not tearing at anthesis, puberulent or pubescent; style 4–6 mm long, glabrous or sometimes pubescent at the base; ovary 2–locules, 8–13 ovules per locule. Fruits 10–15 × 10–20 mm, globose, atropurpureo when ripe, glabrous or sparsely puberulent, crowned by the remnant of the regular calyx lobes; seeds 1–2. Figure 7.

FIG. 7. *Eugenia brevistyla*. A. Leaf twig with opened flowers. B. Inflorescence with flowers bud. C. Fruits. (A: *N.M. Ivanauskas 892*; B: *J.M. Silva 1757*; C: *G. Hatschbach 54927*).

***Etymology*:—**The specific epithet refers to the short style in the flower.

Distribution and habitat*:—Eugenia brevistyla* occurs in Southern (Paraná, Rio Grande do Sul and Santa Catarina), Southeastern (Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo) and Northeastern Brazil (Bahia), known from the coastal forest in the Serra do Mar and in the forest on quartzitic soil in the countryside, at elevations between 0 to 1300 m a.s.l. (Fig. 8). Although the species has a wide range, it is frequent southward region growing in well-drained soil forest in the coast from lowland to slope forest, within Ombrophyllous Dense Forest, in the Atlantic province, and occurs in the transitional zone to the Cerrado province, in the outcrop forest on quartzitic soil, within the Semideciduous Forest.

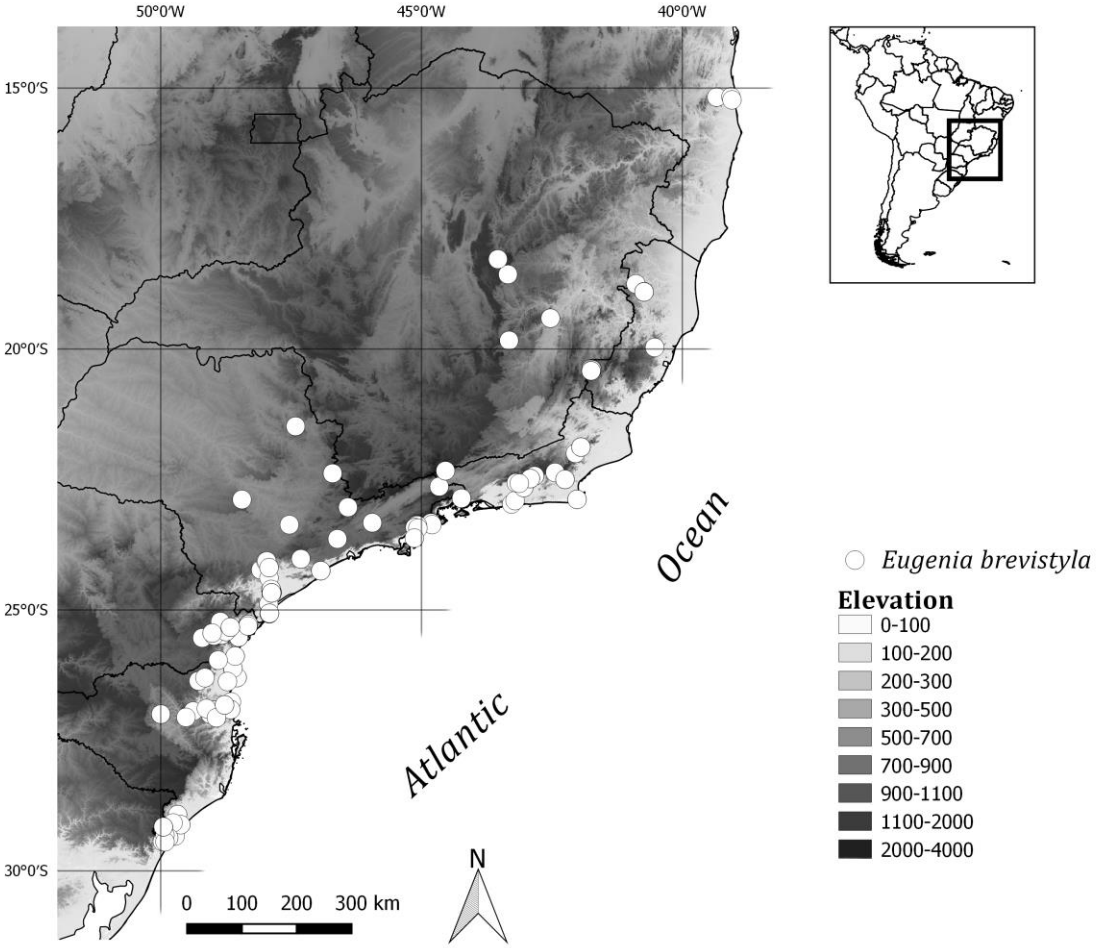


FIG. 8. Geographic distribution of *Eugenia brevistyla*.

***Phenology*:—**Flowers have been collected from August to February and fruiting from September to March (Fig. 4).

Conservation status:—Least Concern (LC). *Eugenia brevistyla* occurs in protected and non-protected areas in primary and secondary sites with EOO of 596,924 km². Populations northeastward tend to be naturally scarce, intensified due to the suppression of coastal environments to urbanization, increasing the risk of local extinction. Populations in the transitional zone between Atlantic forest and Cerrado provinces are rare, therefore, more vulnerable to local extinction in case of environmental disturbs.

Comments:—The highly variable degree of calyx fusion of the *Eugenia brevistyla* mislead Legrand and Klein (1977) whom also admitted that only this character might be not consistent to diagnose species. Calyx fusion degree in the bud varies from by 2 mm length at the base to nearly closed except by the free lobes at the apex. Fusion of the calyx is homoplastic in *Eugenia* and must be used in combination with additional morphological characters (Giaretta *et al.*, Chapter 2). *Calycorectes pirataquinensis* is synonymized under type examination, and synonymization of *Eugenia imaruiensis* is endorsed by the examination of the photo of the type in combination to the protologue description. *Eugenia brevistyla* can be confused to *E. acutata* but differs by the well-marked leaf venation with 9-12 pairs of secondary veins (*vs.* slightly marked with 11-22 pairs), inflorescence often fasciculiform mostly emerging from leafless nodes (*vs.* auxotelic axes highly variable in length), up two rachises sharing an axil (*vs.* one rachis per axil), and bud 3–5 mm long (*vs.* 6–8 mm long).

Specimens examined:**—Brazil. Bahia:** Arataca, Serra do Peito-de-Moça, 24 September 2006, fl., *A.M. Amorim 6406* (CEPEC). Ilhéus, s.d., fl., *Blanchet s.n.* (G); Pirataquissé, 3 September 1944, fl., *H. Velloso 1006* (R). Una, Fazenda Presente, plantação de cacau, cabruca, 24 September 2004, fl., *R. Sambuichi 549* (RB); Reserva Biológica de Una, trilha do rio Maruim, 28 September 2001, fl. and fr., *L.A. Passos Jr. 851* (ALCB). **Espírito Santo:** Águia Branca, Assentamento 16 de Abril, 3 July 2007, fl., *R.R. Vervloet 2717* (MBML); ibid., 4 October 2007, fl., *H.Q. Boudet 3512* (MBML). Conceição da Barra, estrada de Riacho Doce para Pedro Canário, 28 August 2012, fl., *T.B. Flores 1226* (MBML, RB, VIES, UEC). Ibitirama, Pedra Roxa, estrada para o alojamento do ICMBio, 25 October 2012, fl., *T.B. Flores 1528* (ESA, MBML, RB, UEC); Santa Marta, ao lado do alojamento do ICMBio, 28 October 2012, fl., *T.B. Flores 1643* (ESA, MBML, RB, VIES). Sooretama, Mata de Tabuleiro situada ao lado norte da sede de Sooretama, 14 July 1969, fl., *D. Sucre 5543* (GUA, RB, SPF). **Minas Gerais:** Caratinga, Estação Biológica Caratinga, E.B.C. Matão, caminho Rafael, 25 September 1985, fl., *P.M. Andrade 716* (RB, SP). Descoberto, Reserva Biológica da Represa do Grama, 23 September 2002, fl., *R.C. Forzza 2234* (RB). Itambacurí, 24 September 1956, fl., *M. Magalhães s.n.* (IAN). Jequeri, Usina de Providência, 20 November 1997, fl., *A. Salino 3772* (SP). Marliérea, Parque Estadual do Rio Doce, 28 November 1999, fl., *T.C. Sposito s.n.* (MBM). Santana do Paraíso, 23 December 2011, fr., *M. Sobral 14571* (RB, SP). São Gonçalo do Rio Abaixo, 3 December 2012, fl., *J.E.Q. Faria 3129* (UB); margem da BR - 381, entre João Monlevade e São Gonçalo do Rio Abaixo, 14 November 2010, fl., *J.E.Q. Faria 1000* (CEN, UB). **Paraná:** Antonina, along to road Guaraquecaba, 10 December 1981, fr., *L. Landrum 4009* (MBM, RB). Antonina, rio Itaqui, 11 January 1991, fr., *G. Hatschbach 54927* (MBM). Carvalho, 18 November 1909, fl., *P. Dusén 8957* (K, P). Guaraqueçaba, Paruquara, 7 December 1972, fl., *G. Hatschbach 30938* (MBM, UEC); rio do Cedro, 21 May 1968, fl., *G. Hatschbach 19234* (INPA, MBM, P, UEC); Serra Negra, 8 November 1994, fl., *S.R. Ziller 575* (MBM). Guaratuba, APA de Guaratuba, 5 November 2013, fl., G. Felitto 743 (MBM); Descampado, 14 October 1989, fl., *G. Hatschbach 53526* (ESA, G, MBM, SP, SPF, W); Guaruva, 15 November 1958, fl., *G. Hatschbach 5214* (MBM); Morro do Morrete, 26 October 1963, fl., *G. Hatschbach 10759* (MBM); rio Arraial, Fazendo Bamerindus, 1 November 1996, fr., *J.M. Silva 1769* (K, MBM); rio Saí, 5 September 1968, fl., *G. Hatschbach 19674* (MBM, UEC); Guaruva, Palmital, 30 September 1983, fl., *R. Kummrow 2320* (INPA, MBM). Itajaí, Morro da Ressoada, 15 September 1955, fl., *R. Klein 1585* (MBM, UB). Morretes, 12 June 1979, fl., *L.T. Dombrowki 10728* (MBM); 29 November 1964, fl., *G. Hatschbach 11913* (MBM, UEC); 3 October 1968, fr., *G. Hatschbach 19897* (MBM); América de Baixo, 16 October 2007, fl., *J.M. Silva 6129* (MBM, RB); América de Cima, 17 October 2006, fl., *J.M. Silva 5137* (MBM); ca. 20 km of municipio of Morretes, 25 January 1985, fr., *A. Gentry 49837* (RB); Col. Floreta, 4 October 1968, fl., *G. Hatschbach 19907* (BM, HRB, INPA, JBB, MBM, RB); Estação Marumbi, 23 November 1984, fl., *R. Kummrow 2537* (INPA, MBM, SPSF, W); Grota Funda, 20 January 1987, fr., *J.M. Silva 285* (MBM); Limeira, 8 November 2007, fr., *J.M. Silva 6138* (MBM); Pilão de Pedra, 5 November 1961, fl., *G. Hatschbach 8440* (MBM); Rio Nunes, N of Morretes, forest remnant along river and adjacent swampy roadside, 24 January 1985, fr., *A. Gentry 49815* (RB); rio Sagrado de Cima, 17 September 1968, fl., *G. Hatschbach 19734* (MBM, RFA, SPF); Serra Marumbi, 1

December 1966, fl., *G. Hatschbach 15324* (MBM, P). Paranaguá, Guarany, 2 November 1965, fl. and fr., *G. Hatschbach 13073* (G, MBM); Ilha do Mel, 26 September 1987, fl., *R.M. Britez 1781* (UB, UEC); Limeira, 14 February 1968, fl., *G. Hatschbach 19500* (MBM, P, SPSF); rio Cambará, 24 April 1968, fl., *G. Hatschbach 20134* (MBM, W); Serra da Prata, beira da estrada, 9 November 2003, fl., *F.F. Mazine 1009* (ESA, K, MBM, SPF); ibid., próximo à colônia Limeira, 9 November 2003, fl., *F.F. Mazine 1010* (ESA, K); Sítio do Meio, 24 November 1962, fl., *G. Hatschbach 10175* (MBM); Tinguçú, 27 November 2014, fr., *R.A. Bonaldi 991* (MBM). Piraquara, Recreio da Serra, 24 October 2013, fl., *M.L. Brotto 1377* (MBM); Serra do Emboque, 3 February 1992, fr., *G. Hatschbach 56770* (MBM). Quatro Barras, Morro Sete, 7 November 2013, fl., *F.F. Mazine 992* (MBM); ibid., trilha para o alto do morro, 7 November 2003, fl., *F.F. Mazine 993* (K); trilha para o Pico do Paraná, 7 November 2003, fr., *F.F. Mazine 996* (ESA). São José dos Pinhais, Castelhanos, 30 October 1996, fl., *J.M. Silva 1754* (G, MBM); ibid., rio São João, 31 October 1996, fl., *J.M. Silva 1757* (ESA, INPA, MBM, RB, SPSF). Tijucas do Sul, Matulão, 22 October 1958, fl., *G. Hatschbach 5174* (MBM). **Pernambuco:** Rio Formoso, Horto Florestal de Saltinho, 9 September 1954, fl., *J.I.A. Falcão 986* (RB, SPF, UB). **Rio de Janeiro:** Angra dos Reis, Ilha Grande, caminho para o Bico do Papagaio, 24 September 1996, fl., *D. Flores s.n.* (GUA). Cachoeiras de Macacu, Estação Ecológica Estadual do Paraíso, acima da represa da CEDAE, 9 June 1992, es., *B.C. Kurtz s.n.* (RB). Guapimirim, Parque Estadual Três Picos, 9 February 2015, fr., *A. Giaretta 1493* (SP, SPF). Magé, Distrito de Piabetá, 3 December 2000, fl., *A. Quinet 13/55* (RFA); Paraíso, Centro de Pimatologia do RJ, caminho para o focinho do porco, 24 October 1984, fl., *H.C. de Lima 2302* (RB); ibid., 10 October 1984, fl., *G. Martinelli 9986* (K, MBM); ibid., 17 October 1984, fl., *H.C. de Lima 2222* (K); ibid., 4 October 1984, fl., *G. Martinelli 9971* (K, MBML); Paraíso, Serra dos Porcos, 13 November 1984, fl., *H.C. de Lima 2396* (RB). Mangaratiba, Reserva Ecológica do Rio das Pedras, 30 November 1996, fl., *M.G. Bovini 1107* (RB); ibid., trilha do cambucá, 19 October 1996, fl., *J.A. Lira Neto 463* (GUA, RB); ibid., 22 December 1996, fl. and fr., *M.G. Bovini 1131* (GUA, RB, SPF, UB); ibid., margem do rio Grande, 20 January 2000, fl., *C. Mynssen 316* (RB). Nova Friburgo, Sítio Cedro, margem do rio Macaé, 30 January 2015, fr., *A. Giaretta 1478* (SPF). Nova Iguaçu, Boa Esperança, 21 September 1994, fl., *S.J. Silva-Neto 456* (RB). Paraty, a ca. de 23km do trevo de Paraty, entrada a direita na Rio/Santos, após a entrada de Laranjeiras, no sítio do Sr. Paulo, 28 September 1993, fr., *R. Marquete 891* (RB);

estrada próxima ao rio dos Meros, 10 May 1994, fr., *R. Marquete 1768* (RB). Resende, Visconde de Mauá, estrada Mauá-Resende, 7 December 2006, fl., *V.F. Mansano 6-352* (K, RB). Rio Claro, Distrito de Lídice, 15 January 2002, fl., *F. Britto 36/141* (RFA, SPF). Rio das Ostras, Reserva Biológica União, 13 August 1997, fl., *P.P. Oliveira 1006* (SP); ibid., 19 November 1999, fr., *P.P. Oliveira 4167* (MBM). Rio de Janeiro, Floresta da Tijuca, 1857, fl., *Casaretto 1871* (G). Santa Maria Madalena, subida para a Pedra do Desengano, 2 March 2004, fr., *E.J. Lucas 226* (GUA, K, RB). São Pedro da Aldeia, 26 September 2013, fl., *L.B. Pimentel s.n.* (RB). Silva Jardim, Rebio Poço das Antas, mata do rio Pau Preto, 6 July 1995, fl., *S.V.A. Pessoa 790* (GUA, RB). **Rio Grande do Sul:** Torres, Lageadinho, 15 November 1979, fr., *Wechter 1465* (RB). Torres, Morro Azul, 18 October 1990, fl., *J.A. Jarenkow 1740* (MBM). **Santa Catarina:** Araranguá, Sombrio, na orla do capão, 27 September 1944, fl. and fr., *P.R. Reitz 704* (RB); Turvo, 20 October 1943, fl., *P.R. Reitz 69* (RB). Blumenau, September 1888, fl., E. *Ule 919* (P). Florianópolis, Alto Ribeirão, 11 December 1972, fr., *A. Bresolin 648* (MBM); Morro Costa da Lagoa, 10 September 1968, fl., *R. Klein 7902* (MBM); ibid., 10 September 1968, fl., *R. Klein 7906* (MBM); Morro do Rio Vermelho, 11 September 1968, fl., *R. Klein 7914* (MBM); rio Tavares, 13 November 1972, fl., *A. Bresolin 628* (MBM); Tapera, 18 November 1969, fl., *R. Klein 8424* (MBM). Guarámirim, 29 September 1947, fl., *D. Hans 181* (R). Guaruva, Monte Cristo, 11 October 2004, fr., *F.C.S. Vieira 511* (MBM); São Francisco do Sul, 21 December 1957, fl., *R. Reitz 5813* (MBM). Inferninho, Araquarí, 6 October 1957, fl., R. *Reitz 4059* (HRB, K). Itajaí, Cunhas, 29 September 1955, fl., *R. Klein 1617* (MBM); Morro da Fazenda, 9 September 1955, fl., *R. Klein 1552* (G, RFA). Itapoá, Reserva Volta Velha, 27 September 1992, fl., *R. Negrelle A-394* (UB). Joinville, 21 December 2000, fr., *L. Sevegnani 2988* (MBM); Sambaqui do Cubatão, 20 October 2006, fl., *F.C.S. Vieira 1856* (MBM). Jordão, Governador Celso Ramos, 21 September 1971, fl., *R. Klein 9696* (ALCB, HRB, MBM). Laguna, Cabeçuda, 1 October 1988, fl., *G. Hatschbach 52330* (HRB, INPA, MBM, SP). Navegantes, Florística Fito IFFSC 753, entorno do fragmento, 14 September 2009, fl., *A. Stival-Santos 825* (JBB, MFS). Pirão Frio, Sombrio, 31 October 1959, fr., *R.R. Reitz 9307* (G). Praia Grande, Fito IFFSC 4/N/68, 22 September 2009, fl., *M. Verdi 2625* (JBB, MFS). São Francisco do Sul, Ilhas da Babitonga, s.d., fl., *E. Spitzner 163* (MBM). São Pedro, Brusque, 27 October 1949, fl., *R.R. Reitz 86* (G). Sombrio, Pirão Frio, 5 September 1959, fl., *R.R. Reitz 9070* (G, K). **São Paulo:** Parque Estadual Carlos Botelho, 8 November 1984, fl., *A.C. Dias s.n.* (SPSF). Serra da Mantiqueira, Fazenda

Cruzeiro, 3 January 1884, fl., *s.c., s.n.* (R). Águas da Prata, Floresta Estadual, 9 November 1966, fl. and fr., *J. Mattos 14178* (RB); ibid., 9 November 1966, fl., *J. Mattos 14178* (SP); ibid., 9 November 1966, fr., *J. Mattos 14184* (SP); Reserva Estadual de Águas da Prata, 21 March 1994, fr., *A.B. Martins 31411* (SP, UEC). Campinas, Pariquera-Açu, Estação Experimental do IAC, 20 July 1995, fl., *N.M. Ivanauskas 246* (ESA); ibid., 21 September 1996, fl., *N.M. Ivanauskas 892* (ESA, GUA, RB, SP, SPSF, UEC); ibid., Beira da rodovia Regis Bittencourt, área com fragmentos de Mata Atlântica, 5 September 1994, fl., *E.B. Bastos 14* (ESA, MBM, RB, SP, SPF). Cananéia, Ilha do Cardoso, 27 September 1989, fl., *F. Barros 1753* (SP); ibid., 8 September 1988, fl., *F. Barros 1583* (SP); Morro Três Irmãos, 27 October 1989, fl., *F. Barros 1759* (K, SP); Parque Estadual da Ilha do Cardoso, November 2007, fl., *V.G. Staggemeier 111* (MBM, RB, UB). Caratinguetá, Reserva Florestal da Escola de Especialistas de Aeronáutica, 7 October 1996, fr., *D.C. Cavalcanti 166* (SP). Cubatão, vale do rio Pilões, 4 October 1988, fl., *H.F. Leitão-Filho 20816* (UB). Iguape, Estação Ecológica Juréia-Itatins, 21 September 1990, fl., *S.J.G. Silva 68* (SP, SPSF); Reserva Ecológica da Juréia, 20 September 1990, fl., *M.C.H. Mamede 334* (SP, SPSF). Itanhém, Parque Estadual da Serra do Mar, Núcleo Curucutu, 2005, fl., *R. Cielo-Filho 389* (SPSF). Itapira, Fazenda Bom Retiro, 22 January 1994, fr., *K.D. Barreto 1840* (ESA, SP). Jacapiranga, 9 September 1976, fl., *P.H. Davis 60821* (SP, UEC). Peruíbe, Estação Ecológica de Peruíbe, October 1992, fl., *M. Sobral 7489a* (MBM). Picinguaba, Casa da Farinha, seguindo a trilha para o Corrisco, no caminho da rasa, próximo à divisa com RJ, APA Cairuçu, 13 November 1990, fl., *R. Marquete 285* (HRB, IBGE, RB, SPF). Porto Ferreira, Parque Estadual, 8 August 1997, fl., *J.E.A. Bertoni 504* (ESA, SPSF). Santa Rita do Passa Quatro, Parque Estadual de Vassununga, 16 October 1978, fl., *F.R. Martins 10053* (MBM). São Miguel Arcanjo, beira da estrada de serviço, 6-8 September 1994, fl., *P.L.R. Moraes 1060* (ESA, SP); Parque Estadual Carlos Botelho, 17 November 1992, fl., *P.L.R. Moraes 738* (ESA, RB, SP); ibid., 17 November 1992, fl., *P.L.R. Moraes 752* (ESA, SP); ibid., 17 November 1992, fl., *P.L.R. Moraes 752* (ESA); ibid., 20 January 1993, fl., *P.L.R. Moraes 782* (ESA, SP, UB); ibid., 20 April 2002, fl., *A.P. Savassi 238* (SPF); ibid., borda da estrada de serviço, 6-8 September 1994, fl., *P.L.R. Moraes 1060* (ESA); ibid., beira do rio Taquaral 37, baixada, 12 January 1991, fl., *P.L.R. Moraes 366* (RB); ibid., beira da estrada, 17 November 1992, fl., *P.L.R. Moraes 737* (ESA, SP); ibid., 4 October 1996, fl., *P.L.R. Moraes 1288* (ESA). Sete Barras, Parque Estadual Carlos Botelho, 26 October 1984, fl., *A.C. Dias 8* (SPSF), s.d., es., *F.F. Mazine 460* (ESA); ibid., parcela permanente, s.d., fl., *V.C. Souza 30126* (ESA); Parque Estadual de Intervales, 14 September 1999, fl., *V.B. Zipparro 1789* (SP). Ubatuba, 16 September 1970, fl., *H.F. Leitão-Filho 1050* (MBM); Picinguaba, 29 November 1994, fl., *A. Takahasi 57* (SP); ibid., 29 November 1994, fl., *A. Takahasi 65* (SP, SPF, SPSF, UEC).

3. EUGENIA GUANABARINA (Mattos and D.Legrand) Giaretta and M.C.Souza, Phytotaxa in press (Giaretta et al. Chapter 3). *Marlierea guanabarina* Mattos and D.Legrand, Loefgrenia 67: 6. 1975.—TYPE: BRAZIL. Rio de Janeiro, Recreio do Bandeirantes, Pedra de Itaúna, fl., 22 [July] 1965, *N. Santos 5967* (holotype: MVM [18113 herbarium number-photo!]; isotype: R).

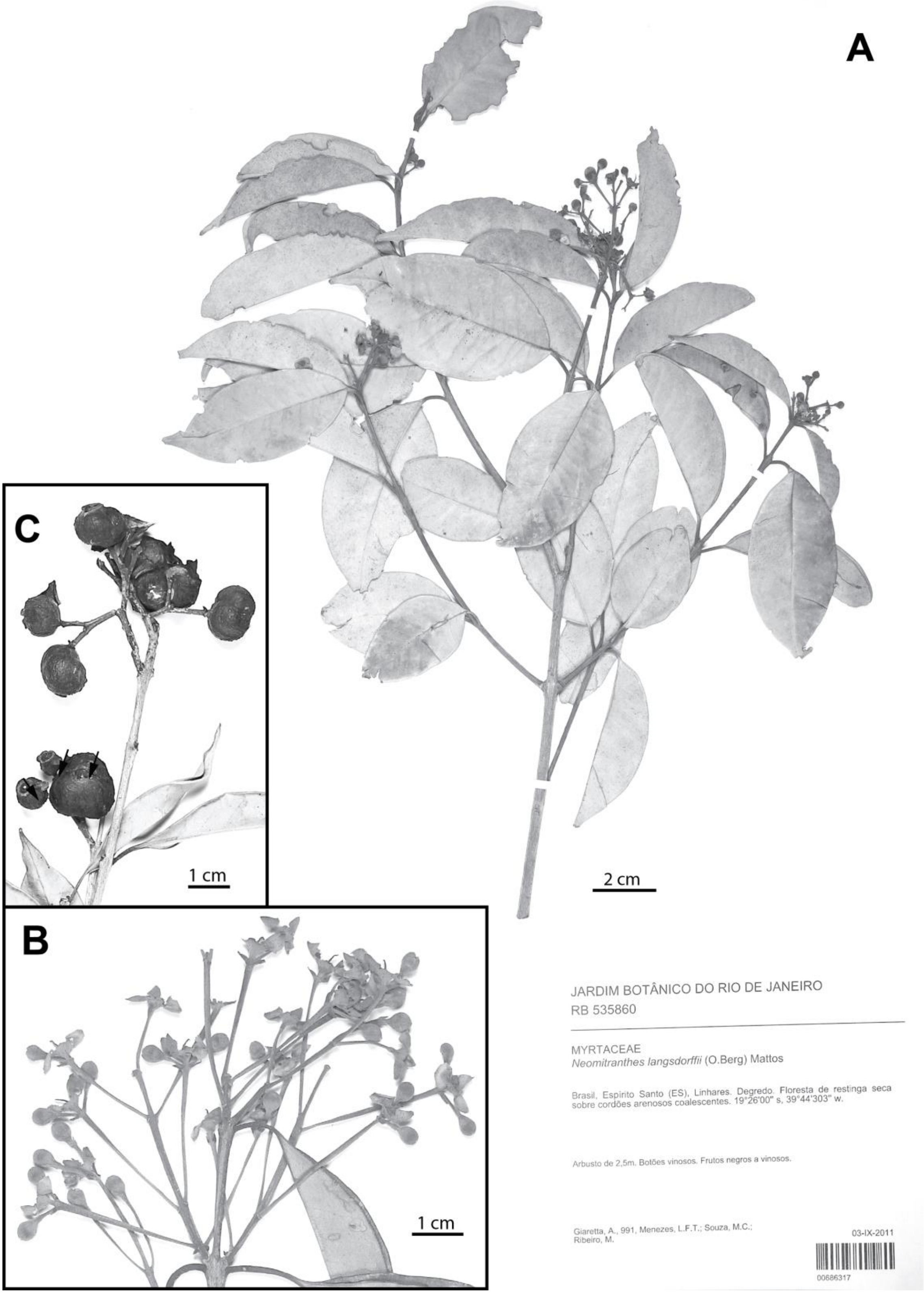
Chytraculia bergiana Kuntze, Revis. Gen. Pl. 1: 238. 1891. *Mitranthes langsdorffii* O.Berg, Fl. Bras. 14(1): 595. 1859. *Neomitranthes langsdorffii* (O.Berg) Mattos, Loefgrenia 76: 2. 1981.—TYPE: BRAZIL. Bahia, fl., s.d., *Blanchet 2309* (lectotype designated in Giaretta et al. (Chapter 3): LE!; isolectotypes: F [69177 negative number-photo!], G! [00222536-2 sheets, 00222537-2 sheets], K! [000018787], NY [00405346-photo!], P! [00162722, 05232287], W!).—REMAINING SYNTYPE: BRAZIL. Bahia, 'in silvis ad flumen Itahype prope Castel novo', s.d., *Riedel s.n.* (G! [00222538, 00222539-2 sheets], K! [000331517], LE! [6 sheets], M [0146829-photo!], MEL [666925-photo!], P! [05232220, 05232222, 05232223], W! [2 sheets]).

Calycorectes teixeireanus Mattos, Loefgrenia 109: 1. 1996. *Eugenia teixeireana* (Mattos) Mattos, Loefgrenia 120: 9. 2005.—TYPE: BRAZIL. Rio de Janeiro, Barra da Tijuca, fl., 13 July 1964, *W. Hoehne 5759* (holotype: SP! [001302]; isotypes: FLOR, MBM! [herbarium number 69215], NY [00886386-photo!], UEC).

Shrub or tree 2 to 13 m tall. Young leaves with light-brownish trichomes 0.5–1 mm long, appressed, moderately sparse abaxially, glabrate adaxially, glabrescent. Young twigs flattened; bark longitudinally striate exfoliating on horizontal fissures, puberulous, glabrescent. Leaves with petioles 7–12 × 1.5–2 mm, canaliculate adaxially, glabrous; blades 5–18 × 2.5–7 cm, elliptic or narrow–elliptic, chartaceous, concolourous or discolourous when dry, glabrous; base acute, cuneate or obtuse; apex acuminate, 0.5–3.5 cm long, or narrowly acute, rare obtuse; midvein canaliculate adaxially; secondary veins 8–12 per side, slightly prominent on both surfaces; marginal veins two, the innermost 1.5–3.5 mm from the margin, the outermost 0.5–1 mm from the margin, sometimes indistinct due to slight revolute margin; glandular dots inconspicuous or slightly prominent on both surfaces, concolourous. Inflorescence subterminal or terminal, thyrsoid; bracts 1.5–2.5 × 1–1.2 mm, wide–ovate, puberulent; rachis 5–80 mm long; 1–4 pairs of lateral axes emerging from the rachis, lateral axes becoming shorter towards the apex, 5–40 mm long, flattened, puberulent; each lateral axis with a 3 to 7-flowered dichasial arrangement, middle flower sessile, lateral flowers with pedicels 3–10 × 0.5 mm; one rachis per axil; bracteoles 1–2 × 1–1.5 mm, ovate or wide–ovate, puberulent, deciduous after anthesis. Flower buds 3–6 × 2.5–4 mm, obovate, marked by 3 glandular dots per mm², calyx lobes fused and closed at the tip leaving an apiculum 0.3–1.5 mm long, tearing transversely at the calyx base resulting in a structure calyptra-like, 3–5 mm diameter, rare tearing irregularly in 3–4 lobes, puberulent, usually dense on hypanthium outside, puberulent becoming puberulous towards the top inside; petals (1)4, 2.5–3.5 × 3–4.5 mm, obovate, sometimes irregular, glabrous; stamens straight in the bud, filaments up to 6 mm long, anthers 0.5–1 mm long, oblong or elliptic; staminal whorls flat, 3.5–5 mm diameter, rounded, not tearing at anthesis, puberulent; style 3–5 mm long, glabrous; ovary 2–locules, 3–5 ovules per locule. Fruits 12–14 × 14–16 mm, globose, atropurpureo when ripe, glabrous, often crowned by the remnant of the calyx calyptra–like; seeds 1–2. Figure 9.

Etymology:—The specific epithet likely refers the type location of the Guanabara state, a previous name for the Rio de Janeiro state used between 1960 and 1975.

Distribution and habitat:—*Eugenia guanabarina* is distributed along Southeastern (Espírito Santo and Rio de Janeiro) and Northeastern (Bahia) Brazil, often known from lowland coastal vegetation at elevations between 0 to 120 m (Fig. 10). It is usually a small tree occurring in the shrub vegetation on marine sandy soil called *Restinga*, and also occurs as a tall tree in the forest vegetation on non-marine sandy soil locally called *Muçununga* (Peixoto et al. 2008), both within the Ombrophyllous Dense Forest in the Atlantic province.



JARDIM BOTÂNICO DO RIO DE JANEIRO
RB 535860

MYRTACEAE
Neomitranthes langsdorffii (O.Berg) Mattos

Brasil, Espirito Santo (ES), Linhares. Degredo. Floresta de restinga seca sobre cordões arenosos coalescentes. 19°26'00" s, 39°44'303" w.

Arbusto de 2,5m. Botões vinosos. Frutos negros a vinosos.

Giaretta, A., 991, Menezes, L.F.T.; Souza, M.C.; Ribeiro, M.
03-IX-2011

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FIG. 9. *Eugenia guanabarina*. A. Leaf twig with flowers. B. Inflorescence with flowers in dichasial arrangement. C. Fruits; arrows showing the remnant of the calyx calyptra-like. (A: *A. Giaretta 991*; B: *C. Farney 4036*; C: *A.Q. Lobão 151*).

Phenology:—Flowers have been mainly collected from July to November and less often from March to May, and fruiting from August to April (Fig. 4).

Conservation status:—Least Concern (LC). *Eugenia guanabarina* is known to protected and non-protected areas with broad EOO (173,938.3 km²). Although it is not threatened, anthropization of coastal environments and sand exploitation have a negative impact on natural populations. The species has not been collected in most part of the localities in Bahia for up to 50 years.

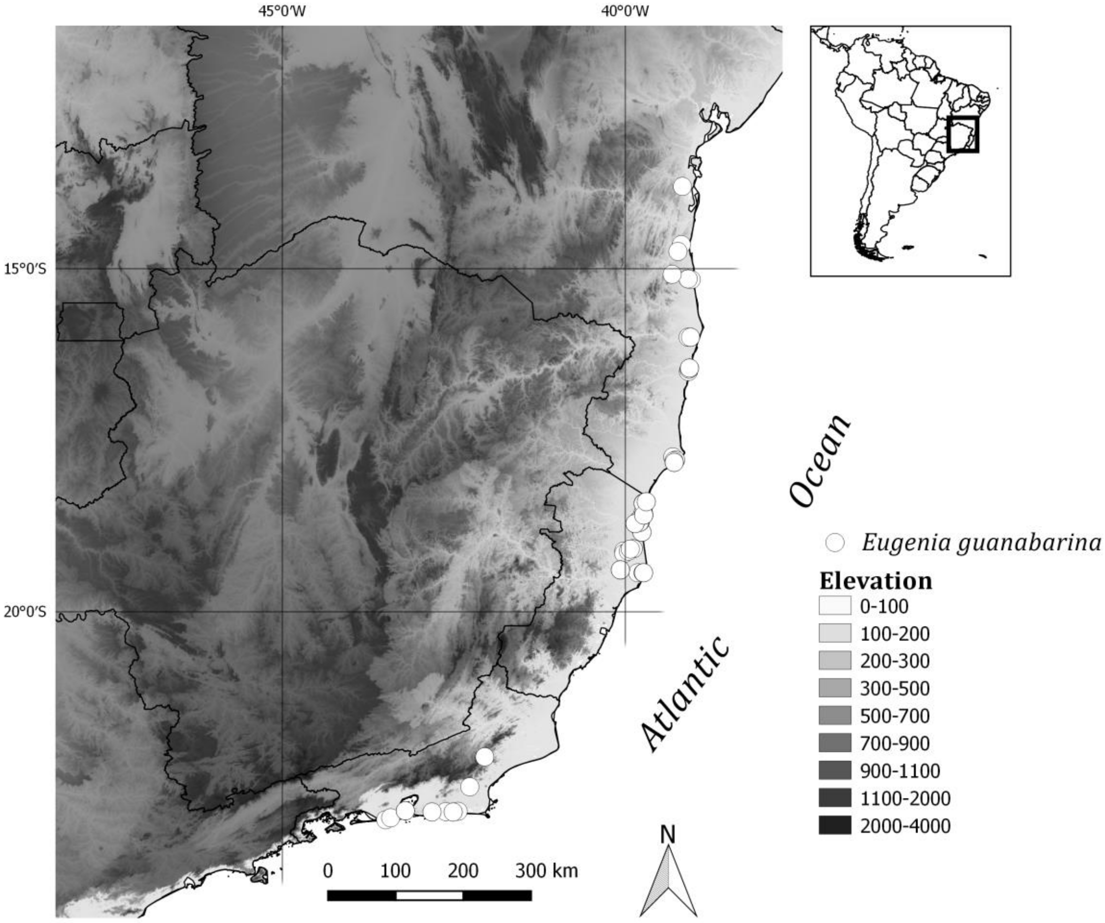


FIG. 10. Geographic distribution of *Eugenia guanabarina*.

Comments:—Taxonomic misleading surrounding *Eugenia guanabarina* was motivated by the combination of fused calyx in the bud usually opening via a structure calyptra-like, thyrsoid inflorescence, features commonly associated with *Myrcia* s.l., and the embryo with fused cotyledons that suggests a relation to the '*Plinia* group' (sensu Lucas *et al.* 2007) and *Eugenia* (Souza 2009). *Eugenia guanabarina* was previously accepted under *Neomitranthes* (Mattos 1981), however, a phylogenetic reconstruction consistently recovered *E. guanabarina* within *Eugenia* (Giaretta et al., Chapter 2) reinforced by the straight stamens on bud, in opposition to the strongly curved stamens in *Myrcia* s.l. and ‘*Plinia* group’ (Vasconcelos et al. 2015). The combination of the thyrsoid inflorescence and bud tearing via structure calyptra-like is convenient to recognize *E. guanabarina*. However, examination of the thyrsoid should consider expression of eventual depauperated architecture. At this case, *E. guanabarina* can be confused to *E. acutata* but differs by the 8-12 secondary veins (*vs.* 11-22), bracteoles ovate or wide-ovate (*vs.* lanceolate), flower with staminal whorl rounded (*vs.* squared) and not tearing at anthesis (*vs.* slightly tearing), and fruit atropurpureo when ripe (*vs.* yellowish). *Chytraculia bergiana* is a replacement name to *Mitranthes langsdorffii* therefore, the earlier available basionym. However, the new combination is unavailable in *Eugenia* due to pre-existence of *Eugenia bergiana* Griseb. Thus, *Marlierea guanabarina* is the earlier name available to be combined (Giaretta *et al.*, Chapter 3). Although the epithet has an improper Latin termination, the original spelling must be retained since it does not fit any conditional rule of the Code (see Art. 60). This combination is not intended to be validly published here.

Specimens examined:**—Brazil.** s.d., fl., *R.J. Shuttleworth s.n.* (BM). **Bahia:** s.d., fl., *M. Blanchet 69* (P); s.d., fl., *Riedel 305* (K). Arraial D'Ajuda, entre Ajuda e Porto Seguro, 29 August 1961, fl., *A.P. Duarte 6058* (K, RB, SPF). Belmonte, ramal para o rio Ubu, 27 September 1979, fl., *L.A. Mattos Silva 614* (CEPEC); ibid., com entrada no km 30 da rodovia Belmonte-Itapebi, 4-8 km adentro, 27 September 1979, fl., *L.A. Mattos-Silva 614* (K, RB). Buerarema, estrada São José da Vitória-Buerarema, 15 October 2003, fl. and fr., *P. Fiaschi 1685* (CEPEC). Canavieiras, rodovia Santa Luzia, 3 November 1971, fl., *R.S. Pinheiro 1692* (CEPEC). Caravelas, ilha do Curussubá, região conhecida como "Telhas", próximo à região de Barra Velha, distrito de Nova Viçosa, 9 October 2007, fl., *H.M. Dias 297* (RB, SPF, VIES); rio Caribé de Areia, 9 November 2007, fl., *L.F.T. Menezes 1778* (SAMES, VIES). Eunápolis, rodovia BR5, 28 September 1966, fl., R.P. *Belém 2684* (CEPEC). Ibirapitanga, s.d., fl., *T.S. Santos 1050* (CEPEC). Ilhéus, CEPLAC, 18 October 2007, fr., *M.M.M. Lopes 1531* (CEPEC). Mucuri, vale do Mucuri, s.d., fl., *T.S. Santos 942* (CEPEC). Porto Seguro, entre Porto Seguro e Ajuda, 29 August 1961, fl., *A.P. Duarte 6066* (RB); Parque Nacional Pau-Brasil, 26 September 2012, fl., H.A. *Ogasawara 241* (SPF); ramal para povoados de N.S. D'Ajuda e Trancoso, 25 August 1988, fl., *L.A. Mattos-Silva 2515* (CEPEC, K, SP). Una, Reserva

Biológica de Una, entrada no km 46 da rodovia BA-001/Una, estrada principal para a sede, trilha piedade, 10 September 2006, es., *M.C. Souza 385* (RB); rodovia São José/Una, 28 February 1986, fl., *T.H. Brito 4066* (CEPEC). **Espírito Santo:** Conceição da Barra, APA de Conceição da Barra, 16 October 2012, fr., *A. Giaretta 1330* (RB, SAMES, VIES); área 157 da Aracruz Celulose, 12 August 1993, fl., *O.J. Pereira 4835* (VIES); ibid., 14 December 1993, fl., *O.J. Pereira 5212* (VIES); ibid., 23 August 1993, fl., *O.J. Pereira 4721* (RB, VIES); ibid., 25 July 1992, fl., *O.J. Pereira 3764* (RB, VIES); ibid., 27 September 1992, fr., *O.J. Pereira 3879* (RB, VIES); ibid., 28 October 1993, fl., *O.J. Pereira 5138* (RB, VIES); ibid., 29 July 1993, fl., *O.J. Pereira 4826* (VIES); ibid., 9 September 1992, fl., *O.J. Pereira 3837* (RB, VIES); ibid., 9 September 1992, fr., *O.J. Pereira 3829* (RB, VIES); floresta de restinga seca próximo à foz natural do rio Itaúnas, 24 October 2012, fr., *A. Giaretta 1360* (RB, SAMES, VIES); Itaúnas, área atrás da fazendo Jequitaia, 22 August 2009, fl. and fr., *A.G. Oliveira 572* (RB, SAMES, VIES); ibid., 26 September 2009, fr., *A. Giaretta s.n.* (VIES); Lajinha, 5 September 2011, fl., *A. Giaretta 1026* (RB, SAMES, SPF, VIES); ibid., próximo ao rio São Mateus seguindo a estrada de terra atrás do campus do CEUNES, próximo ao bairro litorâneo, 1 August 2007, fl., *R.F.A. Martins 161* (RB, SAMES, VIES); Parque Estadual de Itaúnas, 7 July 2012, fl., *L.F.T. Menezes 2042* (VIES); ibid., área atrás da fazendo Jequitaia, 7 September 2011, fl., *A. Giaretta 1035* (RB, SAMES, SPF, VIES); ibid., matinha de Itaúnas, 9 December 2011, fr., *A.G. Oliveira 1135* (SAMES, VIES); Quadrado, atrás do CEUNES, 30 November 2011, fr., *A. Giaretta 1099* (SAMES, VIES). Linhares, 12 August 2009, fl., *A.L.S.S. Peres 372* (VIES); Degredo, 3 September 2011, fl., *A. Giaretta 991* (RB, SAMES, SPF, VIES); Reserva Natural Vale, 7 July 1983, fl., *D.A. Folli 449* (CEPEC); ibid., 8 August 1992, fl., *G.L. Webster 29677* (MBM); ibid., aceiro com Aracruz, 15 October 2012, fl., *K. Matsumoto 818* (K, UEC); ibid., estrada Jacarandá, ant. 232, km 2,925, lado esquerdo, 10 August 1978, fl., *I.A. Silva 16* (RB); ibid., estrada Jacarandá, km 2,925, 10 August 1978, fl., *I.A. Silva 16* (RB); ibid., estrada Jataipeba, km 0.185, lado direito, 7 July 1983, fl., *D.A. Folli 449* (RB); ibid., estrada Municipal, próximo ao nativo João Pedro, lado direito, 19 August 1988, fl., *D.A. Folli 780* (RB); ibid., estrada Orelha de Onça, km 1, 8 August 2006, fl., *M.C. Souza 351* (RB, SPF); ibid., final da estrada Bomba D'água, ant. 213, 27 August 1991, fl., *D.A. Folli 1394* (RB); final da estrada Paraju, ant. 211, lado esquerdo, 29 August 1991, fl., *D.A. Folli 1399* (RB, UEC). São Mateus, 1 September 1996, fl., Canal, M. 142 (VIES); bairro Litorâneo, 1 August 2007, fl., *R.F.A. Martins 31*

(SAMES); bairro Quadrado, 31 January 2016, fl. and fr., *A. Giaretta 1629* (SPF); ibid., 31 January 2016, fl., *A. Giaretta 1630* (SPF); ibid., atrás do CEUNES, 28 August 2009, fr., *R. Coelho 45* (SAMES, VIES); ibid., fragmento de restinga pleistocênica, seguindo uma estrada de terra, ca. de 10 km do campus CEUNES, 28 August 2009, fl., *M. Ribeiro 9* (RB, SAMES, VIES); Guriri, às margens da estrada para Barra Nova, próximo a Samauma, 2 February 2012, fr., *A. Giaretta 1226* (RB, SAMES, VIES); bairro Liberdade, 22 September 2010, fr., *A.G. Oliveira 876* (SAMES, VIES). **Rio de Janeiro:** Barra da Tijuca, Guanabara, Pedra de Itaúna, a uns 50m da base da Pedra, 10 September 1970, fr., *P.J. Fontella 424* (MBM, RB). Maricá, terminal Ponta Negra, 11 May 2012, fl., *I.E. Santos 809* (HB, RB). Recreio dos Bandeirantes, estrada da Guanabara, Pedra de Itaúna, 17 May 1964, fl., *N. Santos 5131* (R); ibid., 9 August 1964, fl., *N. Santos 5201* (R). Rio de Janeiro, praia Marapendi, 8 June 1973, fl., *E.A. Montalvo 100* (RB); restinga de Jacarepagua, situada do lado sul da Pedra de Itauna, 2 September 1969, fl. and fr., *D. Sucre 5903* (RB, SP); ibid., 2 September 1969, fl., *D. Sucre 5905* (RB, SPF). Saquarema, Jaconé, proximidades do Sambaqui de Jaconé, 29 March 2000, fl. and fr., *C. Farney 4036* (RB, SPF); Reserva Ecológica Estadual de Jacarepiá, 12 December 1990, es., *C. Farney 3212* (RB); ibid., 22 April 1994, fl., *C. Farney 3324* (RB, SPF); ibid., 27 April 1996, fr., *A.Q. Lobão 151* (RB, SPF); ibid., nas trilhas da vegetação em regeneração, 12 February 1992, fr., *D*.S.D. *Araujo 9581* (GUA, RB); ibid., restinga de Ipitangas, 25 April 1992, fl. and fr., *C. Farney 3140* (RB, SPF). Silva Jardim, Reserva Biológica de Poço das Antas, 20 December 1994, fr., *D.S. Farias 353* (CEPEC).

4. EUGENIA LONGOHYPANTHIANA Giaretta, Phytotaxa in press (Giaretta et al. Chapter 3). *Calycorectes pohlianus* Kiaersk., Enum. Myrt. Bras.: 117. 1893, non Benth. ex Nied., Nat. Pflanzenfam 3(6): 82. 1893. *Schizocalyx pohlianus* O.Berg, Linnaea 27: 320. 1856, nom. illeg. *Eugenia cambucae* Mattos, Loefgrenia 120: 11. 2005, nom. illeg. *Schizocalomyrtus pohliana* (O.Berg) Kausel, Lilloa 32: 367. 1967, nom. illeg.—TYPE: BRAZIL. Rio de Janeiro, Habitat in Brasiliae, prov. Rio de Janeiro, s.d., *Pohl 5844* (lectotype designated in Giaretta et al. (Chapter 3): W! [0071556]; isolectotypes: G [not found], GH [00068863-photo!], OXF! [00067686], W! [0071557]).

Schizocalyx pohliana var. *panicularis* O.Berg, Fl. Bras. 14(1): 358. 1857, nom. illeg.—TYPE: BRAZIL. Rio de Janeiro, fl. s.d., [*Pohl s.n.*] (**lectotype designated here:** M [0171258-photo!]).

Schizocalyx pohliana var. *triflorus* O.Berg, Fl. Bras. 14(1): 358. 1857, nom. illeg.—TYPE: BRAZIL. Rio de Janeiro, fl., s.d., [*Pohl s.n.*] (**lectotype designated here:** BR [000000523121-photo!]).

Tree 3 to 12 m tall. Young leaves with brownish to reddish trichomes 0.1–0.5 mm long, appressed, moderately sparse abaxially and on the midvein, glabrous adaxially, glabrescent. Young twigs terete or compressed close to the nodes; bark slightly striate, puberulous, glabrescent. Leaves with petioles 7–20 × 1.5–2.5 mm, canaliculate adaxially, pubescent; blades 8–33 × 3.5–7.5 cm, narrow elliptic to elliptic, chartaceous, concolourous or dark brown above and light brown below when dry, surrounding midvein sparsely puberulent abaxially; base acute or cuneate, decurrent along the petiole; apex acuminate, 1–3 cm long, narrowly acute or less often obtuse; midvein canaliculate adaxially; secondary veins 14–25 per side, sulcate of slightly prominent adaxially, prominent abaxially; marginal veins two, the innermost 3–8 mm from the margin, the outermost 0.5–3 mm from the margin, sometimes indistinct due to slight revolute margin; glandular dots inconspicuous adaxially, slightly prominent abaxially, concolourous. Inflorescence terminal, less often axillary, auxotelic, sometimes with a terminal flower; bracts 0.7–1 × 1.2–1.5 mm, wide-ovate, pubescent; rachis 5–45 mm long, terete or flattened at the third portion, puberulent; 1–5 pairs of flowers, sessile or with pedicels 10–30 × 1.5 mm; up to one rachis per axil; bracteoles 1.5–4 × 1.5–3 mm, ovate, pubescent, deciduous before anthesis. Flower buds 12–16.5 × 9–11 mm, obovate or piriform, marked by 3 glandular dots per mm², calyx lobes partially fused but free at the tip leaving an aperture of 1–5 mm diameter, tearing irregularly at anthesis in 3–5 lobes, 6–13 × 5–9 mm, pubescent to puberulent outside, puberulent inside; petals 6–8.5 × 6–8.5 mm, orbiculate or obovate, puberulent at the base; stamens curved in the bud, filaments up to 10 mm long, anthers 0.7–1.5 mm long, oblong; staminal whorls extending up to two thirds of the bud length, 16–18 mm diameter, deeply tearing at anthesis, puberulent; style 10–11 mm long, glabrous; ovary 2–locules, 5–10 ovules per locule. Fruits 25–32 × 15–40 mm, globose and longitudinally striate, densely covered by reddish or brownish puberulent indumentum, crowned by the remnant of the calyx and hypanthium with scars left by stamens insertion; seeds 1–2. Figure 11.

Etymology:—The specific epithet alludes to the extending flower hypanthium that contrasts to the standard flat hypanthium found in *Eugenia*, an extreme exception in the genus (see Giaretta *et al.*, Chapter 2).

Distribution and habitat:—*Eugenia longohypanthiana* occurs in Southeastern Brazil (Espírito Santo and Rio de Janeiro), known from rock outcrop forest near to the coast and lowland forest further in the countryside, at elevation between 0 to 650 m a.s.l. (Fig. 12). Usually shrubs or small trees occurring in populations in the Ombrophyllous Dense Forest to the transition to the Semideciduous Forest, both in the Atlantic province.

Phenology:—Flowers have been collected from March to July and fruiting from May to August (Fig. 4).

Conservation status:—Endangered (EN) B1ab(iii). Although *Eugenia longohypanthiana* is known from three localities, tentatives to collect this species around Rio de Janeiro city was unsuccessful and is here considered locally extinct in the Monumento Natural dos Morros do Pão de Açúcar e da Urca, suggesting loss of habitat quality and consequent population reduction. On the other hand, Conservation Unit in Espírito Santo (APA Mestre Álvaro) better ensures protection to natural populations. The three population are isolated each other by ca. 200 km of a fragmented landscape. It is estimated that *Eugenia longohypanthiana* produces a small number of large fruits with poor dispersal ability which increase isolation of the populations. Thus, this species fulfil criterion B1 with EOO (2,524.4 km^2) smaller than 5,000 km^2, with less than five known locations (a), and decline of habitat quality (b iii).

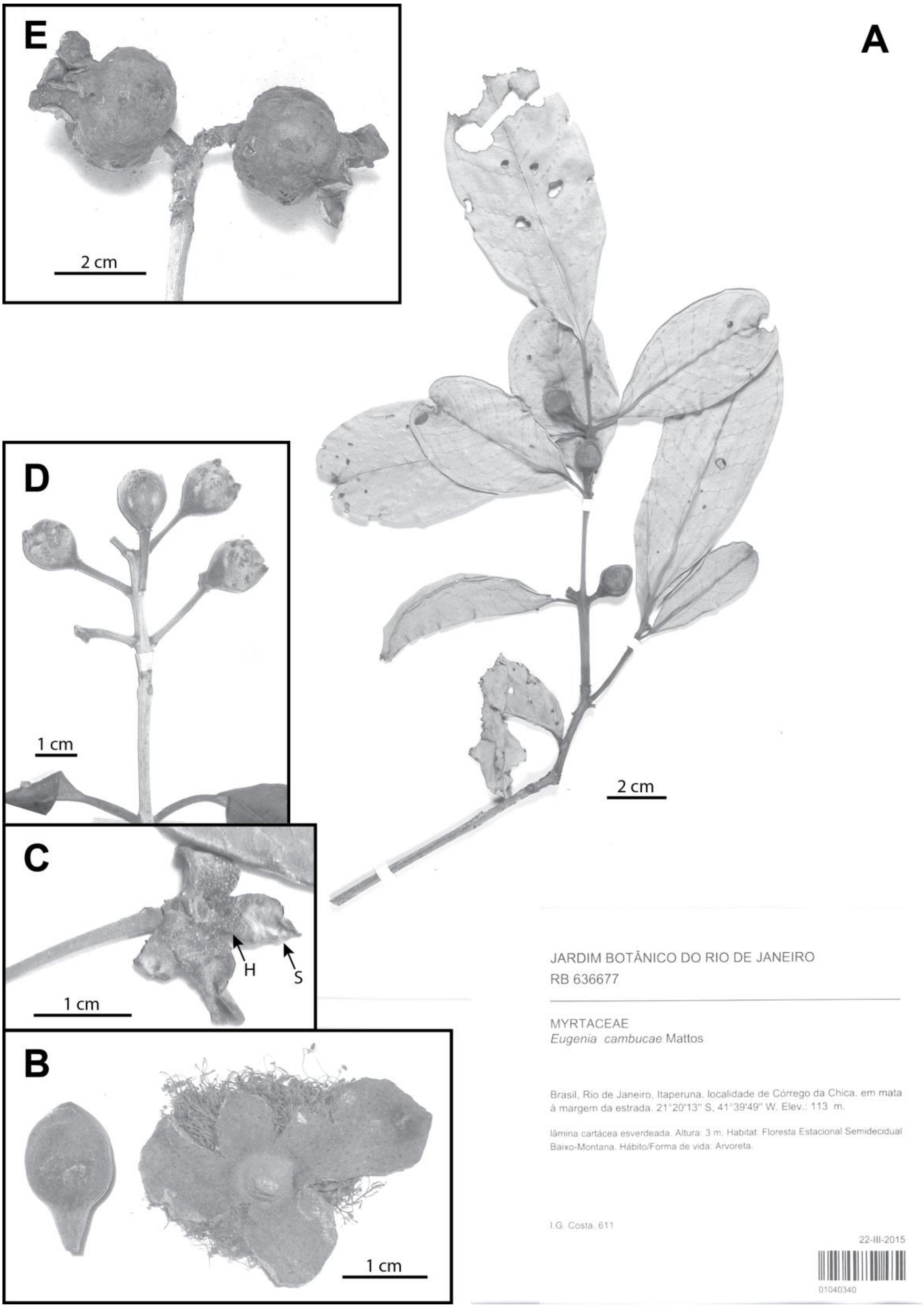


FIG. 11. *Eugenia longohypanthiana*. A. Leaf twig with flower buds. B. Flower bud (left) and lower view of an opened flower showing the irregular lobes (right). C. Upper view of an opened flower showing a sepal lobe (S) and the hypanthium (H) with scars left by the stamens insertion. D. Inflorescence. E. Fruits showing the remnant of the calyx and hypanthium. (A: *I.G. Costa 611*; B: *D.A. Folli* 6594; C: *J. Miers s.n.* (BM000043151); D: *I.A. Rodrigues 88*; E: *A. L. Mautone 243*).

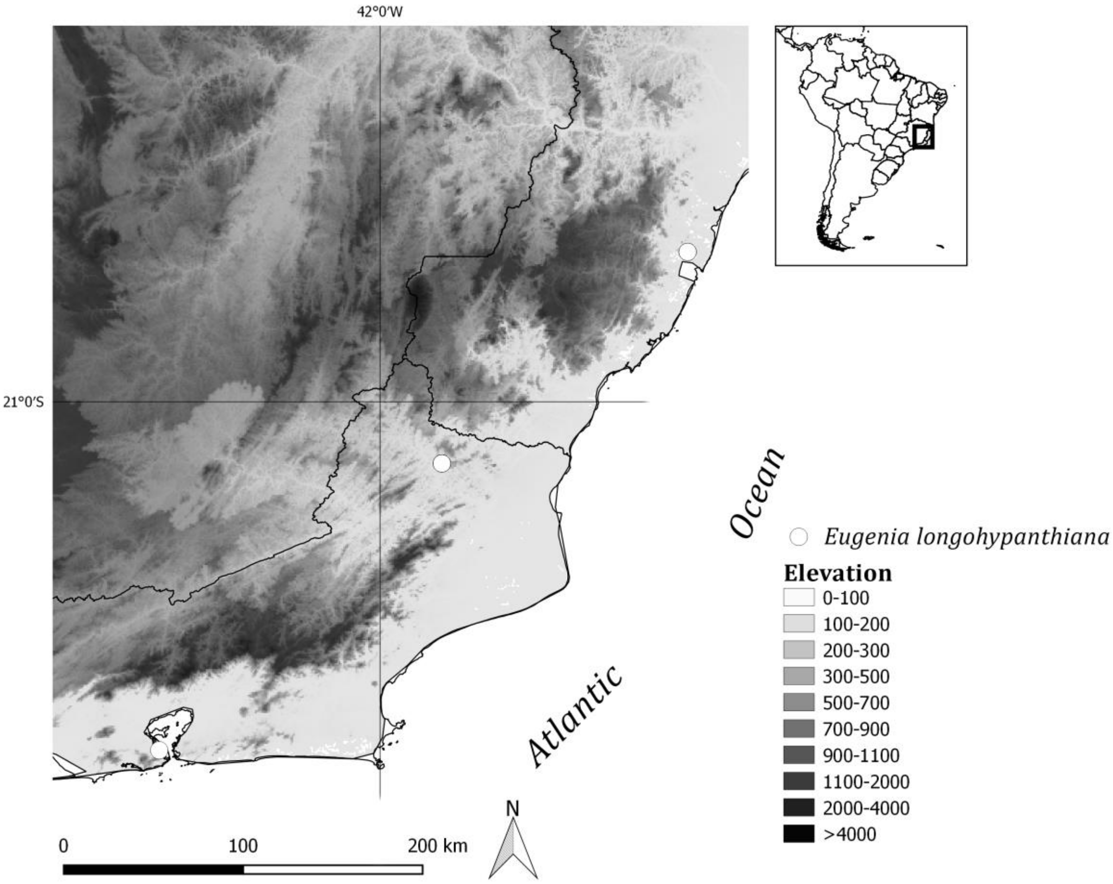


FIG. 12. Geographic distribution of *Eugenia longohypanthiana*.

Comments:—*Eugenia longohypanthiana* has fused calyx and stamens curved rather than straight in the bud, an extreme exception in the genus. This combination of characters was likely the main reason for such taxonomic instability surrounding this species. The replacement name *Calycorectes pohlianus* was simultaneously published by Kiaerskou (1893) and Niedenzu (1893) originally as combinations based on *Schizocalyx* O.Berg, a later illegitimate homonym. *Calycorectes pohlianus* Kiaersk. and *C. pohlianus* Nied. are treated as indirect references to a replacement name to the illegitimate *Schizocalyx pohlianus* O.Berg according to the Art. 41.3 of the Code (McNeill et al. 2012). In the circumstance that priority cannot be fulfilled, *Calycorectes pohlianus* Kiaersk. was chosen as the available name to be transferred to *Eugenia*. The pre-existence of *Eugenia pohliana* DC. requires a replacement name. *Eugenia cambucae* Mattos, an expected replacement name to *Schizocalyx pohliana* O.Berg is not in accordance with the Art. 38.1 due to the type reference not concerning its original place of the valid publication. Thus, *Eugenia longohypanthiana* was proposed (Giaretta et al. Chapter 3). This species is easily recognized by staminal whorls extending up to two-thirds of the bud length which tears deeply in the anthesis resembling development of the closed bud of *Marlierea* (Vasconcelos et al. 2017), and flower and fruit densely covered by reddish or brownish pubescence. The fruit is crowned by the irregular lobes from the remaining calyx where scars left by stamens insertion are evident. This replacement name is not intended to be validly published here.

***Specimens examined:*—Brazil:** s.d., fl., *J. Pohl 5849* (W). **Espírito Santo:** Serra, Morro Mestre Álvaro, 17 March 2010, fl., *D.A. Folli 6594* (CVRD, RB, SPF, UB**). Rio de Janeiro:** Itaperuna, 26 June 2015, fr., *A. Giaretta 1501* (K, SPF); 26 June 2015, fr., *A. Giaretta 1502* (K, SPF); Córrego da Chica, 22 March 2015, fl., *I.G. Costa 611* (RB); ibid., 26 June 2015, fl., *A. Giaretta 1500* (K, SPF); ibid., 9 June 2015, fr., *I.G. Costa 651* (RB). Magé, 1879, fl., *J. Miers s.n.* (BM). Rio de Janeiro, 1876, fl., *Glaziou 8898* (LE); APA Praia Vermelha, Encosta do morro Pão de Açúcar, 13 April 1977, fl., *I.A. Rodrigues 88* (K, RB); Corcovado à lagoinha, 29 June 1878, fl., *Glaziou 9435* (K, P, R); mata do Teixeira Borges, perto da sede do Horto Florestal Rio, 16 May 1927, fr., *J.G. Kuhlmman s.n.* (GUA, RB); Urca, Guanabara, 20 July 1966, fl., *P. Occhioni 2263* (RFA); ibid., Morro do Pão de Açúcar, 17 August 1977, fr., *L. Mautone 243* (RB).

5. EUGENIA MAJEPENSIS Giaretta, sp. nov.—TYPE: BRAZIL. Rio de Janeiro, Magé, estrada da Parada Modelo para Cachoeiras de Macacu, ramal de acesso ao Centro de Primatologia da FEEMA, 22º 29’ 44.1’’ S, 42º 54’ 42.8’’ W, ca. 50 m a.s.l., 2 September 2006, fl., *P. Fiaschi and A.Q. Lobão 3141* (holotype: SPF 176157!; isotypes: BHCB, K!, RB!).

Eugenia majepensis is morphologically similar to *Eugenia acutata* but differs by flower glabrous (*vs.* puberulent or pubescent) with equal lobes in size (*vs.* two unequal pairs), and staminal whorl rounded and not tearing at anthesis (*vs.* squared and slightly tearing at anthesis).

Tree 3 to 16 m tall. Young leaves glabrous. Young twigs compressed, darkish when dry, with brownish trichome up to 0.1 mm, appressed, sparse, glabrescent; bark longitudinally striate exfoliating on membranaceous sheets, glabrous. Leaves with petioles 5–18 × 1.5–2 mm, canaliculate or sulcate adaxially, glabrous, darkish when dry; blades 8–18 × 2–6 cm, oblanceolate or elliptic, chartaceous, concolourous or slightly discolourous when dry, glabrous; base acute or cuneate; apex acuminate or abruptly acuminate, 1–2 cm long, or acute; midvein canaliculate adaxially; secondary veins 15–22 per side, slightly prominent on both surfaces; marginal veins two, the innermost 1.5–3 mm from the margin, the outermost 0.5 mm from the margin, sometimes indistinct due to slight revolute margin; glandular dots indistinct adaxially, slightly prominent abaxially, discolourous. Inflorescence axillar or terminal, fasciculiform; bracts 1 × 1.5 mm, wide–ovate, puberulent; rachis 1–20 mm long, terete, puberulent; 1–4 pairs of lateral flowers emerging from the rachis, pedicels 15–55 mm long, flattened, glabrous; flowers often expressing 3–flowered dichasial arrangement, middle flower sessile or with a pedicel up to 1 mm long, lateral flowers with pedicels 5–10 × 0.2–0.4 mm, glabrous; up to two rachises sharing an axil; bracteoles 2–3 × 0.5 mm (seen from young flower), lanceolate, glabrous, deciduous before anthesis. Flower buds 5–7 × 4–6.5 mm, obovate, marked by 7–9 glandular dots per mm², calyx lobes partially fused but free at the tip leaving an aperture of 1–4 mm diameter which borders are often abaxially revolute, tearing regularly at anthesis in 4 lobes, 2.5–4 × 2.5–3 mm, ovate, glabrous outside, puberulent inside; petals 5–6 × 4.5–5 mm, wide–ovate, glabrous; stamens straight in the bud, filaments up to 6 mm long, anthers 0.9–1.2 mm long, oblong; staminal whorls flat, 4–5 mm diameter, rounded, not tearing at anthesis, puberulent; style 4–6 mm long, glabrous; ovary 2–locules, 14–17 ovules per locule. Fruits 10–12 × 9–11 mm, ellipsoid, colour when ripe unknown, glabrous, crowned by the remnant of the regular calyx lobes; seeds 1. Figure 13.

Etymology:—The specific epithet is derivative from the indigenous language Tupi '*Majepe-mirim*' that means short (*mirim*) wizard (*pajé*). As general, *pajé* is a position in the indigenous community assigned to a man who presumably has healing powers. *Majepe-mirim* was the first reference name to a settlement that originates the current municipality of the type location Magé, Rio de Janeiro.

Distribution and habitat:—*Eugenia majepensis* is distributed in Southeastern (Espírito Santo, Rio de Janeiro and São Paulo) and Northeastern Brazil (Bahia), known from the coastal forest in the Serra do Mar, at elevations between 30 and 200 m a.s.l (Fig. 14). It is shrub or tree known from coastal vegetation on slope and lowland forests, within Ombrophyllous Dense Forest in the Atlantic province.

Phenology:—Flowers have been collected from September to December and fruiting in December (Fig. 4). Fruiting period is unknown.

Conservation status:—Near Threatened (NT). *Eugenia majepensis* is known from protected and non-protected areas in primary and secondary sites with EOO of 108,847.2 km². Although it is not threatened regarding its entire range, there is a significant risk of local extinction due to intense suppression of vegetation to urbanization in all States of its range distribution that left less than 20% of natural vegetation (SOS Mata Atlântica 2017). Fragmented landscape intensified by loss of habitat quality increases its risk of extinction, therefore regional assessment is encouraged to identify the main threating factors.

Comments:—*Eugenia majepensis* has flower with fused calyx fitting to the *heterosepaly* and fasciculiform inflorescence often expressing 3-flowered dichasial arrangement in accordance with the *Eugenia* sect. *Schizocalomyrtus*. This placement is also supported by the molecular phylogeny (Giaretta et al. Chapter 2). Inflorescence with dichasial arrangement is assumed as the standard condition, however, few specimens may not express dichasia (see *Almeida 68*, *Pirani 3390* and *Hatschbach 68366*). Except for the dichasial arrangement, these specimens lack morphological differences. Purely cymose branching pattern in *Eugenia* was demonstrated secondary in development (Giaretta et al. Chapter 4) and is evaluated as irrelevant to support segregation into two species. When expressing fasciculiform inflorescence without dichasial arrangement, *Eugenia majepensis* can be confused to *E. acutata* but differs by the inflorescence with up to two rachises sharing an axil (*vs.* up to one rachis per axil), leaves with darkish petioles when dry (*vs.* not darkish), and glabrous flowers (*vs.* pubescent or puberulent). This species is not intended to be validly published here.

FIG. 13. *Eugenia majepensis*. A. Leaf twig with young flower buds. B. Inflorescence and young flowers in dichasial arrangement. (A–B: *P. Fiaschi 3141*).

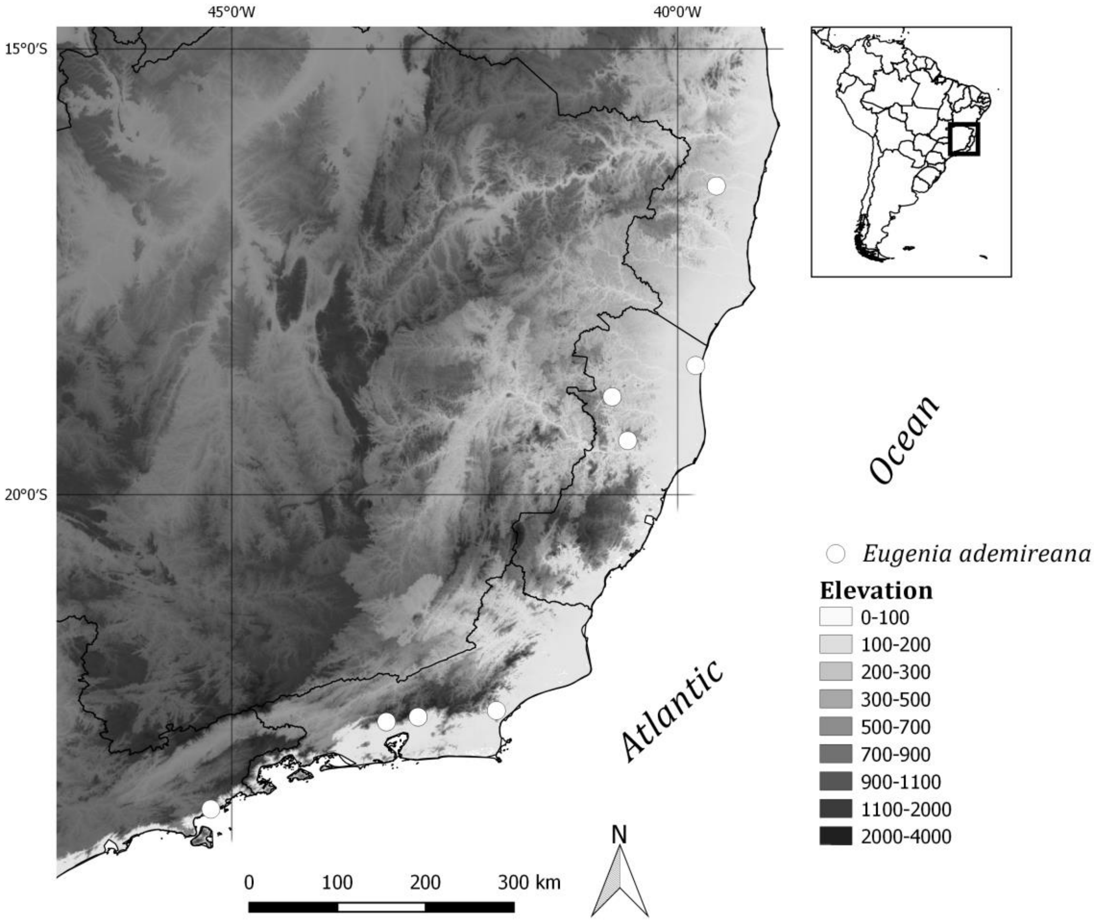


FIG. 14. Geographic distribution of *Eugenia majepensis*.

Paratypes:**—Brazil. Bahia:** Itabela, saída de Itabela ao queimado de Porto Seguro, 17 September 1968, fl., *J. Almeida 68* (CEPEC, RB). **Espírito Santo:** Conceição da Barra, 10 October 1998, fl., *G. Hatschbach 68366* (G, MBM, MBML, SP). Marilândia, propriedade do sr. Euclides Canal e família, 5 December 1994, fl., *J.R. Pirani 3390* (SP, SPF). **Rio de Janeiro:** Caxias, reserva da Petrobrás, trilha ao redor da barragem, lado direito, interior de mata, 17 November 1999, fl., *S.J. Silva-Neto 1331* (K, RB, UB). Magé, estrada de Parada Modelo para Cachoeiras de Macacu, ramal de acesso ao Centro de Primatologia FEEMA, 2 September 2006, fl., *P. Fiaschi 3141* (K, RB, SPF). Rio das Ostras, Reserva Biológica da União, trilha 4, 18 November 1997, fl., *P.P. Oliveira 82A* (SP); ibid., trilha 5, 10 December 1997, fr., *P.P. Oliveira 82B* (SP). **São Paulo:** Ubatuba, praia de Maranduba, 16 November 1993, fl., *P.C. Lobo 29370* (SP, UEC).

6. EUGENIA NEORIEDELIANA M.C.Souza and Giaretta, Phytotaxa in press (Giaretta et al. Chapter 3). *Mitranthes riedeliana* O.Berg, Fl. Bras. 14(1): 595. 1859. *Chytraculia riedeliana* (O.Berg) Kuntze, Revis. Gen. Pl. 1: 238. 1891. *Calyptrogenia riedeliana* (O.Berg) Burret, Notizbl. Bot. Gart. Berlin-Dahlem 15: 546. 1941. *Neomitranthes riedeliana* (O.Berg) Mattos, Loefgrenia 99: 6. 1990. syn. nov.—TYPE: BRAZIL. Rio de Janeiro, Habitat in silvis prope Madiocca, s.d., *Riedel and Langsdorff s.n.* (lectotype designated in Giaretta *et al.* (Chapter 3): K! [000331528]; isolectotypes: F [72823 negative number-photo!], LE! [6 sheets], M [0146828-photo!], NY [00405349-photo!], P! [00723175, 00723176, 00723177], S [herbarium number S-R-9472-photo!], OXF! [00071623, 00071645]).

Tree 3 to 12 m tall. Young leaves with whitish trichomes up to 0.1 mm long, appressed, sparse abaxially, glabrous adaxially, glabrescent. Young twigs flattened; bark longitudinally striate exfoliating on membranaceous sheets, puberulent, glabrescent. Leaves with petioles 7–10 × 1–1.5 mm, canaliculate adaxially, puberulent, glabrescent; blades 6.5–14 × 2.5–4.5 cm, obovate, elliptic or narrow elliptic, chartaceous, concolourous or slightly discolourous when dry, sparsely puberulent abaxially; base acute; apex abruptly acuminate, 1–2 cm long, or less often narrowly acute; midvein canaliculate adaxially; secondary veins 7–10 per side, sulcate of slightly prominent adaxially, prominent abaxially; marginal veins two, the innermost 3–6 mm from the margin, the outermost 1–1.5 mm from the margin, indistinct due to slight revolute margin; glandular dots slightly prominent on both surfaces, discolourous. Inflorescence axillary or terminal, fasciculiform; bracts 0.5–1 × 0.5–1.2 mm, wide-ovate, puberulent; rachis 1–5 mm long, puberulent, terete, brownish; 1–4 pairs of flowers, pedicels 5–18 × 0.5–1 mm; up to three rachises sharing an axil; bracteoles 1–2 × 1 mm, ovate or wide-ovate, puberulent, persistent after anthesis. Flower buds 4–6 × 3.5–4.5 mm, obovate or elliptic, apiculate, marked by 9–12 glandular dots per mm^2, calyx lobes partially fused and nearly closed leaving four vestigial free lobes at the tip, tearing transversely at the calyx base resulting in a structure calyptra-like, 4–5 mm diameter, puberulent, dense on hypanthium, brownish outside, puberulent inside; petals 2–3 × 1.5–3 mm, wide–ovate or oblong, occasionally two petals fused at the base, sparsely puberulent internally; stamens straight in the bud, filaments up to 6 mm long, anthers 0.4–0.6 mm long, oblong; staminal whorls flat, 5–6 mm diameter, rounded, not tearing at anthesis, puberulent; style 5–6.5 mm long, glabrous; ovary 2–locules, 9–15 ovules per locule. Fruit not seen. Figure 15.

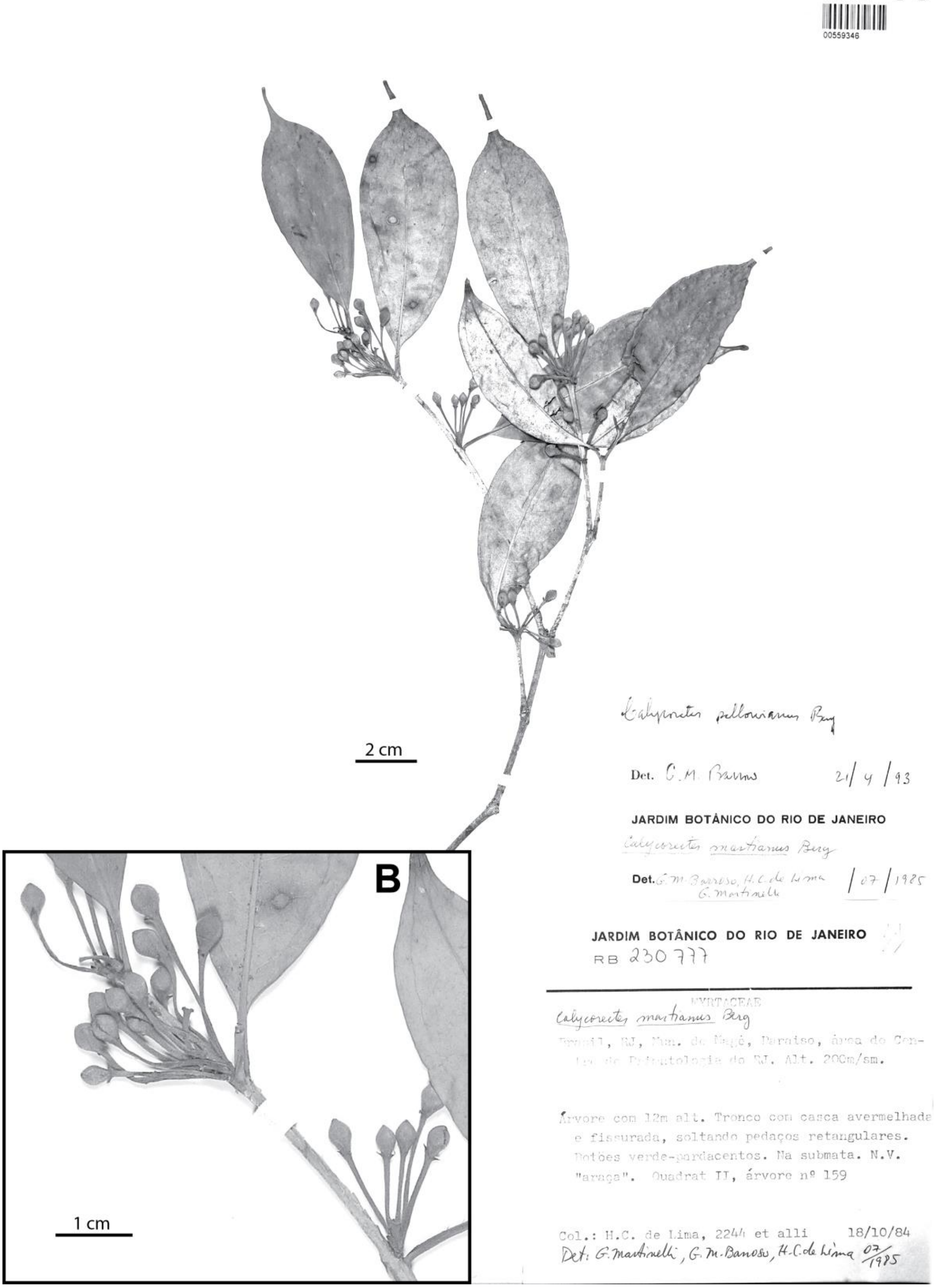
Etymology:—The *neo* preceding the specific epithet means “new” from Greek in reference to the replacement name assigned to the species.

Distribution and habitat:—*Eugenia neoriedeliana* occurs in Southeastern Brazil (Rio de Janeiro), known from the Serra do Mar at elevations between 20-600 m a.s.l. (Fig. 16). It is usually a shrub in populations with frequent individuals but can be a tall tree both mainly distributed on slope forest and less often on lowland coastal forest, within Ombrophyllous Dense Forest in the Atlantic province.

Phenology:—Flowers have been collected from September to November (Fig. 4). Fruiting period is unknown.

Conservation status:—Endangered (EN) B1ab(iii). *Eugenia neoriedeliana* is endemic from Rio de Janeiro, known to primary protected areas (Parque Nacional da Serra do Mar and Reserva Biológica do Tinguá) and to the secondary nature reserve of Monumento Natural dos Morros do Pão de Açúcar e da Urca with restricting EOO (1,570.7 km^2). Although populations are protected in a primary area, fragmented population in the understory persist in the secondary site under historical and present anthropogenic pressure leading to the habitat suppression and decrease of habitat quality; regional extinction is potentialized by the invasion of exotic species, fire and improper human occupancy. A revaluation of the extinction risk must be done in a short-term to update the threat status. Thus, this species fulfil criterion B1 with EOO smaller than 5,000 km^2, with less than five known locations (a), and decline of habitat quality (b iii).

Comments:—Uncertainty surrounding the circumscription of *Eugenia neoriedeliana* was likely motivated by the bud dehiscence misleading Berg (1859) who assigned it to *Mitranthes riedeliana*, later combined with *Neomitranthes riedeliana*. The



Calyptrantes pellowianus Berg

Det. C.M. Barros 21/4/93

JARDIM BOTÂNICO DO RIO DE JANEIRO

Calycorectes martianus Berg

Det. G. M. Barroso, H. C. de Lima G. Martinelli /07/1985

JARDIM BOTÂNICO DO RIO DE JANEIRO
RB 230777

MYRTACEAE

Calycorectes martianus Berg

Brasil, RJ, Mun. de Magé, Paraíso, área do Centro de Primatologia do RJ. Alt. 200m/sm.

Árvore com 12m alt. Tronco com casca avermelhada e fissurada, soltando pedaços retangulares. Botões verde-pardacentos. Na submata. N.V. "araça". Quadrat II, árvore nº 159

Col.: H.C. de Lima, 2244 et alli 18/10/84
Det: G. Martinelli, G. M. Barroso, H. C. de Lima 07/1985

FIG. 15. *Eugenia neoriedeliana*. A. Leaf twig with flower buds. B. Inflorescence and flowers buds. (A–B: *H.C. de Lima 2244*).

current circumscription within *Eugenia* is supported by straight stamens in the bud (*vs.* strongly curved in *Myrcia s.l.* and '*Plinia* group') and confirmed its placement in *Eugenia* sect. *Schizocalomyrtus* by the molecular phylogeny (Giaretta et al., Chapter 2). A replacement name is here assigned since *Mitranthes riedeliana* is unavailable in *Eugenia* due to the pre-existence of *Eugenia riedeliana* (Berg 1857: 261). *Eugenia neoriedeliana* is often confused to *E. brevistyla* and *E. vattimoana* but is easily distinguished by the bud tearing transversely at the calyx base resulting in a structure calyptra-like (*vs.* flower tearing in regular and irregular lobes, respectively). This replacement name is not intended to be validly published here.

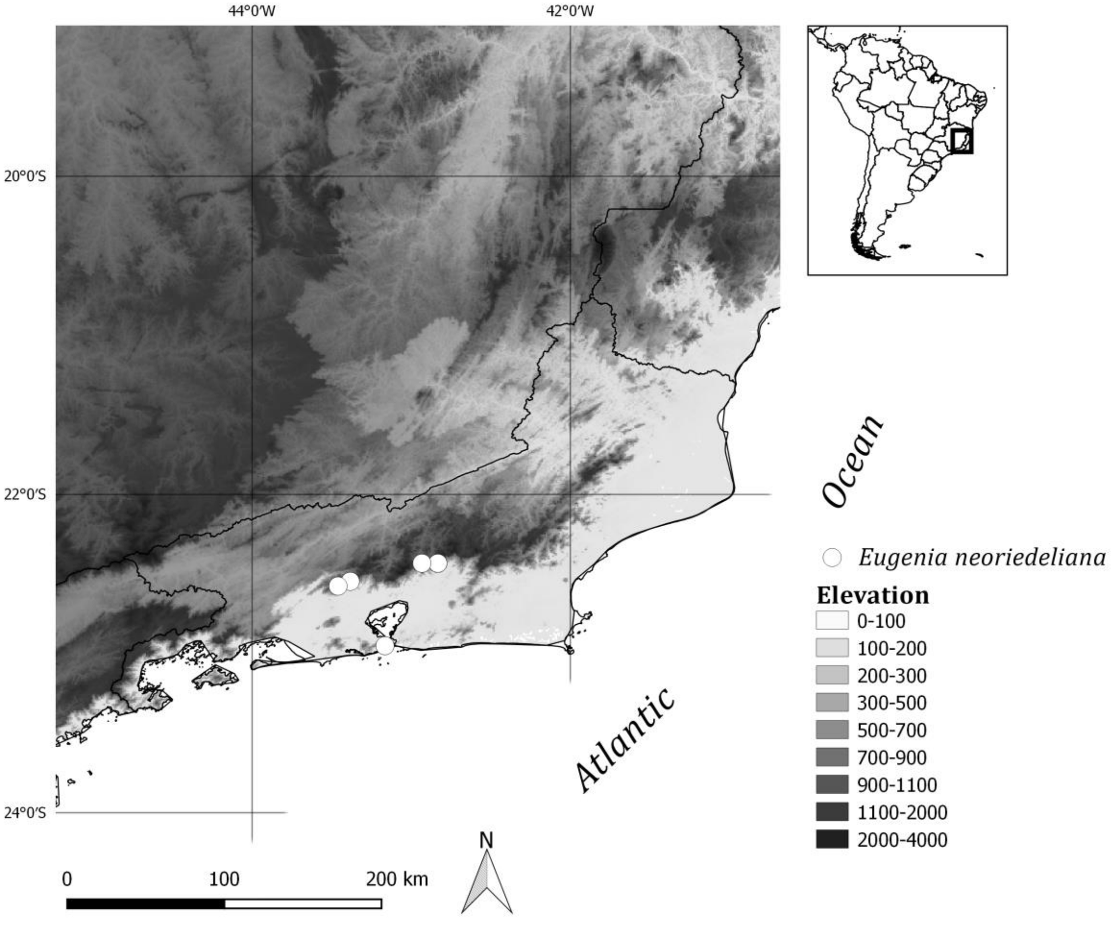


FIG. 16. Geographic distribution of *Eugenia neoriedeliana*.

***Specimens examined:*—Brazil. Rio de Janeiro:** Magé, Núcleo Paraíso, Centro de Primatologia do RJ-FEEMA, 18 October 1984, fl., *H.C. de Lima 2244* (GUA, INPA, K, RB); ibid., 2 October 1984, fl., *G. Martinelli 9905* (CEPEC, R, RB); ibid., caminho para o Focinho do Porco, 24 October 1984, fl., *H.C. de Lima 2302* (GUA, K, RB); ibid., 3 October 1984, es., *G. Martinelli 9926* (K, RB). Nova Iguaçu, Reserva Biológica do Tinguá, 16 September 2006, fl., *L.M. Versieux 292* (SPF). Rio de Janeiro, Morro da Urca, margem da trilha para o bondinho, 3 February 2015, fl., *A. Giaretta 1489* (K, SPF); Serra dos Órgãos, Pico do Garrafão, 30 November 1976, fl., *P. Occhioni 7981* (RFA).

7. EUGENIA PARADISIACA Giaretta, sp. nov.—TYPE: BRAZIL. Rio de Janeiro, Guapimirim, Estação Ecológica Estadual de Paraíso, Serra Queimada, Água Comprida, 22º26'/22º32' S, 42º50'/42º56' W, 21 November 1991, fl., *H.C. de Lima et al. 4347* (holotype: RB! [00558771-2 sheets]; isotypes: CEPEC!, MBM, SPF!).

Eugenia paradisiaca is morphologically related to *Eugenia longohypanthiana* (for alternative description see Berg (1856: 320) under *Schizocalyx pohliana* O.Berg) but differs by leaves glabrous (vs. surrounding midvein sparsely puberulent abaxially), bud 9-11 × 8-9 mm (*vs.* 12-16.5 × 9-11 mm) with straight stamens (*vs.* curved), and staminal whorl not splitting at anthesis (*vs.* deeply splitting at anthesis).

Tree ca. 12 m tall. Young leaves with brownish trichomes 0.2–0.4 mm long, appressed, moderately sparse abaxially and on the midvein, glabrous adaxially, glabrescent. Young twigs compressed; bark darkish becoming greyish when maturing, glabrous. Leaves with petioles 11–17 × 1.5 mm, canaliculate adaxially, glabrous, darkish when dry; blades 6.5–13 × 3–5.5 cm, elliptic or sometimes obovate, chartaceous, slightly discolourous when dry, glabrous; base cuneate or decurrent along the petiole; apex acuminate, 1–1.5 cm long, less often acute or obtuse; midvein sulcate adaxially; secondary veins 10–17 per side, slightly prominent on both sides; marginal veins two, the innermost 1.5–5 mm from the margin, the outermost 0.5–1 mm from the margin, often indistinct due to slight revolute margin; glandular dots indistinct adaxially, slightly prominent abaxially, concolourous. Inflorescence terminal, auxotelic, vegetative growth recovering not observed; bracts 2 × 1.5 mm, oblong, puberulent; rachis 3–21 mm long; 1–3 pairs of lateral axes emerging from the rachis, each lateral axis with a 3-flowered dichasial arrangement, middle flower sessile or with pedicel up to 30 mm long, lateral flowers with pedicels 5–25 × 0.5–0.8 mm, glabrous; lateral axes 18–42 mm long (to the first pair of bracteoles scar), flattened, glabrous; up to one rachis per axil; bracteoles not seen, deciduous before anthesis. Flower buds 9–11 × 8–9 mm, obovate, marked by 6–11 glandular dots per mm², calyx lobes partially fused but free at the tip leaving an aperture of ca. 1 mm diameter, tearing regularly at anthesis in 4 lobes, 4–8 × 4–9 mm, ovate, glabrous outside, puberulent becoming puberulous towards the top inside; petals 7–12 × 7–10 mm, orbicular or spatulate, sparsely puberulous inside; stamens straight in the bud, filaments up to 14 mm long, anthers 0.8–1.2 mm long, oblong; staminal whorls flat, 9–10 mm diameter, squared, not tearing at anthesis, puberulent; style 6.5 mm long, glabrous; ovary 2–locules, 14–19 ovules per locule. Fruit not seen. Figure 17.

Etymology:—The specific epithet is derivative from Latin '*paradisiacus*' that means 'from paradise'. It alludes to the type location, a protected area in the district of Paraíso, Rio de Janeiro, Brazil.

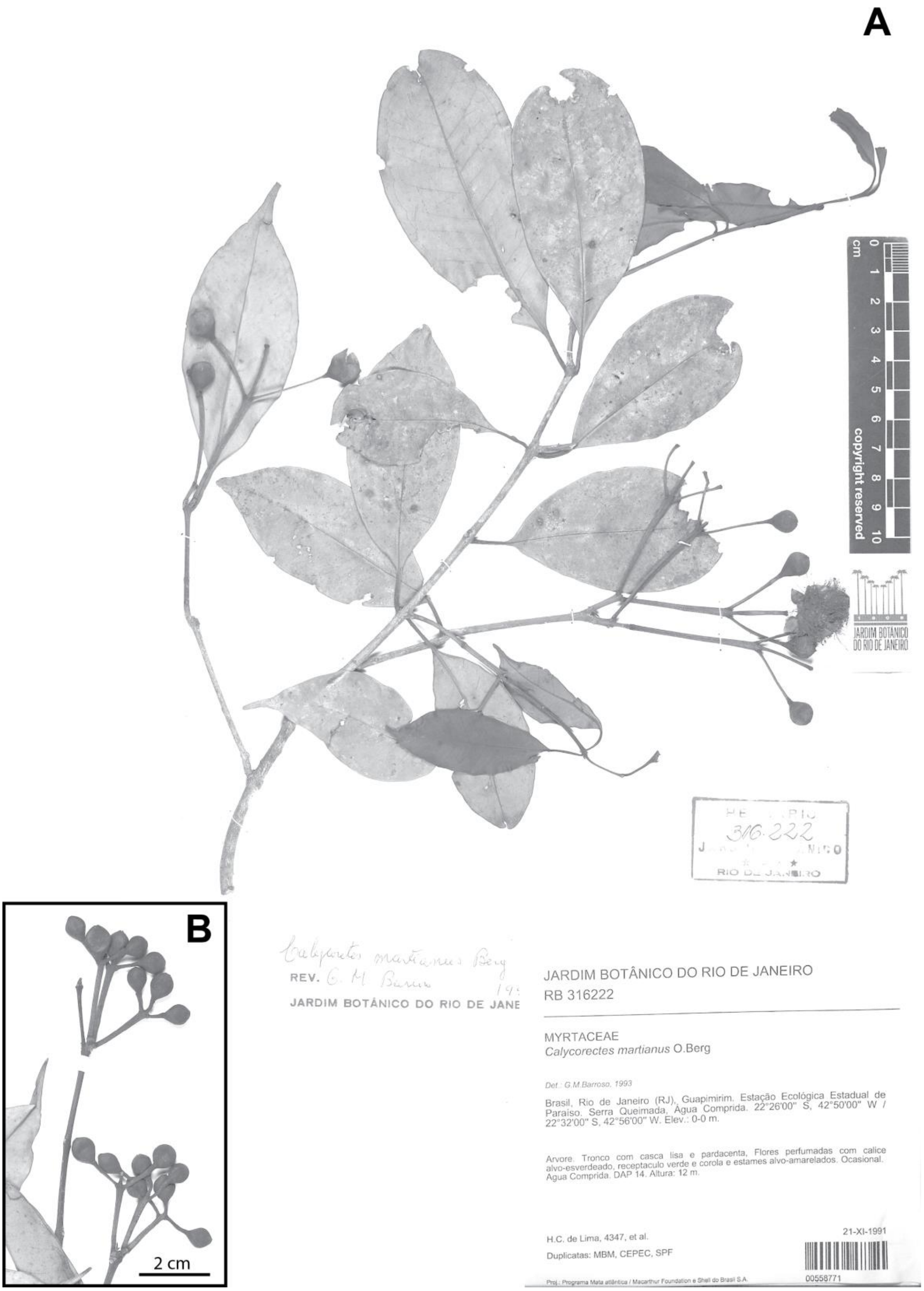
Distribution and habitat:—*Eugenia paradisiaca* is distributed in Southeastern Brazil (Rio de Janeiro), known from the Serra do Mar at elevation between 50 to 450 m a.s.l. (Fig. 18). It is known from forest on slope faced to the coast, occurring within the Ombrophyllous Dense Forest in the Atlantic province.

Phenology:—Flowers were collected in October and November (Fig. 4). Fruiting period is unknown.

Conservation status:**—**Critically Endangered (CR) B2ab(iii). *Eugenia paradisiaca* is endemic to Rio de Janeiro known from a primary protected area of Estação Ecológica de Paraíso, with restricting AOO of 8 km². Although population occur in a protected area, its range is very restricted, and Rio de Janeiro have lost ca. 80% of its original vegetation (SOS Mata Atlântica 2017) that indicates loss of habitat. The last collection was made 26 years ago and tentatively re-collection was unsuccessful suggesting its rarity. Therefore, this species fits the criterion B2 with AOO smaller than 10 km², known from one location (a), and loss of habitat (b iii).

Comments:**—**Although *Eugenia paradisiaca* was not sampled in the molecular phylogeny, fused calyx that fits the *homosepalous* development pattern (Giaretta et al. Chapter 2) and inflorescence with 3-flowered dichasial arrangement are in accordance to the current morphological circumscription of *Eugenia* sect. *Schizocalomyrtus*. *Eugenia paradisiaca* had been identified as *Calycorectes martianus*, however, examination of the type allows assign it to the current *E. acutata*. Further scrutiny concluded that *E. paradisiaca* does not fit to any current species and is here newly described. This species is morphologically similar to the *E. longohypanthiana* but distinguish by the flower glabrous (*vs.* densely pubescent), inflorescence with 3-flowered dichasial arrangement (*vs.* dichasial arrangement not recorded), and squared staminal whorl not splitting at anthesis (*vs.* extended staminal whorl up to two thirds of bud length and deeply splitting). This species is not intended to be validly published here.

Paratype:—**Brazil. Rio de Janeiro:** Magé, Estação Ecológica de Paraíso, área do Centro de Primatologia do Rio de Janeiro, alt. 200 m a.s.l., 22 October 1984, fl., *H.C. de Lima et al. 2273* (BHCB, CEPEC!, K!, NY, RB!).



JARDIM BOTÂNICO DO RIO DE JANEIRO
RB 316222

MYRTACEAE
Calycorectes martianus O.Berg

Det.: G.M.Barroso, 1993

Brasil, Rio de Janeiro (RJ), Guapimirim. Estação Ecológica Estadual de Paraiso. Serra Queimada, Água Comprida. 22°26'00" S, 42°50'00" W / 22°32'00" S, 42°56'00" W. Elev.: 0-0 m.

Arvore. Tronco com casca lisa e pardacenta, Flores perfumadas com calice alvo-esverdeado, receptaculo verde e corola e estames alvo-amarelados. Ocasional. Agua Comprida. DAP 14. Altura: 12 m.

H.C. de Lima, 4347, et al.
21-XI-1991
Duplicatas: MBM, CEPEC, SPF
Proj.: Programa Mata atlântica / Macarthur Foundation e Shell do Brasil S.A.
00558771

FIG. 17. *Eugenia paradisiaca*. A. Leaf twig with flowers. B. Inflorescence and flowers buds. (A: *H.C. de Lima 4347*; B: *H.C. de Lima 2273*).

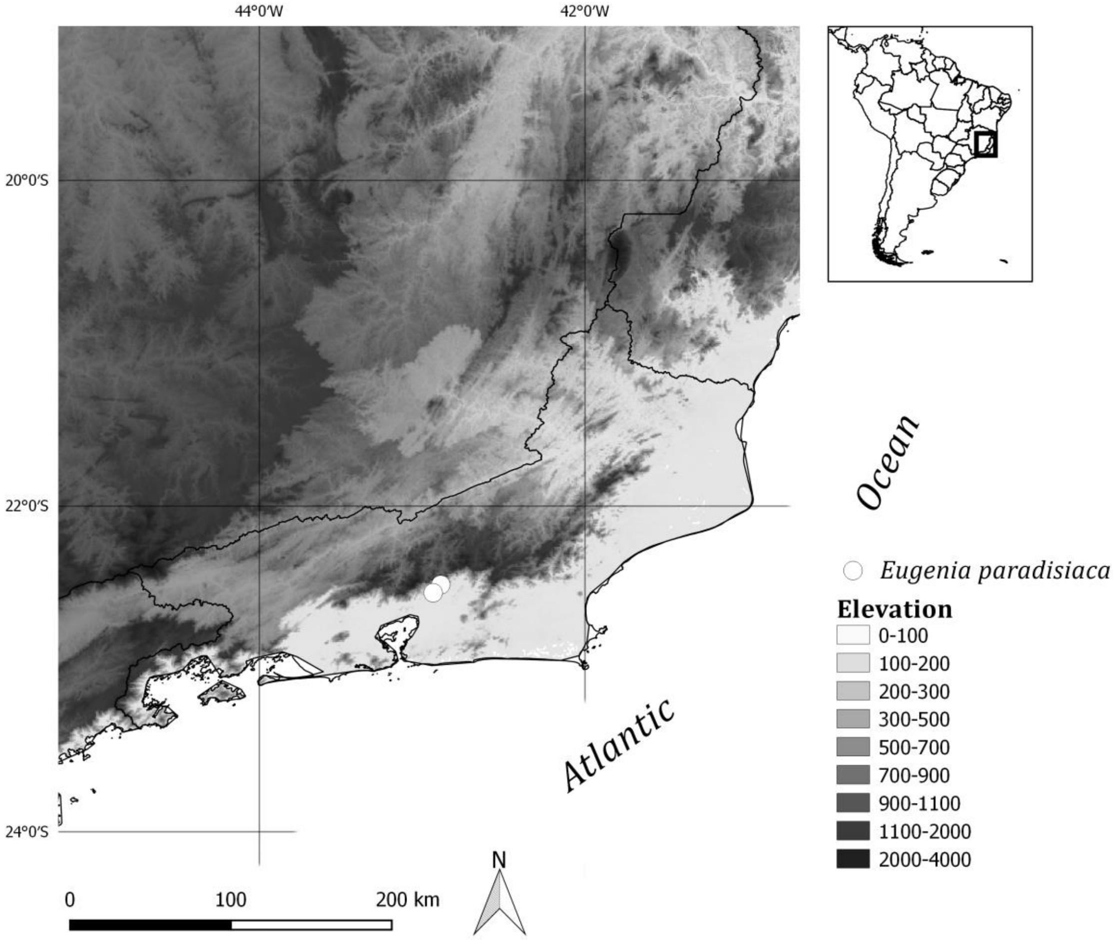


FIG. 18. Geographic distribution of *Eugenia paradisiaca*.

8. EUGENIA SUBTERMINALIS DC., Prodr. 3: 263. 1828.—TYPE: BRAZIL. [Bahia], ad flum. Ilheos, fr., s.d., *Martius s.n.* (**lectotype designated here:** G-DC! [00658292]; isolectotype: M [0171129-photo!]).

Calycorectes belemii Mattos, Loefgrenia 106: 1. 1995. *Eugenia belemii* (Mattos) Mattos, Loefgrenia 120: 4. 2005.—TYPE: BRAZIL. Bahia, Itabuna, margem do rio Cachoeira, fl., 23 September 1965, *R.P. Belém 1793* (holotype: UB [not found]; isotype: CEPEC! [717 herbarium number]). **syn. nov.**

Calycorectes legrandii Mattos, Loefgrenia 62: 1. 1974. *Calycorectes psidiiflorus* var. *legrandii* (Mattos) Mattos, Loefgrenia 102: 3. 1993.—TYPE: BRAZIL. São Paulo, Atibaia, Pedra Grande, 1100 a.s.l., fl., 29 November 1961, *J. Mattos 9528-A* (holotype: SP! [001299]; isotypes: HAS, P! [02436220]).

Calycorectes paraguayensis Mattos, Loefgrenia 62: 2. 1974.—TYPE: PARAGUAY: Juan Ximenes, fl., s.d., *Bertoni I-100* (holotype: AS; isotype: HAS). **syn. nov.**

Calycorectes psidiiflorus var. *triflorus* Mattos, Loefgrenia 102: 3. 1993. *Eugenia psidiiflora* var. *triflora* (Mattos) Mattos, Loefgrenia 120: 8. 2005.—TYPE: BRAZIL. Paraná, Guaira, Sete Quedas, fl., 18 August 1982, *G. Hatschbach 45214* (holotype: ICN; isotypes: MBM! [herbarium number 76497], MO).

Calycorectes schultzianus Mattos, Loefgrenia 101: 2. 1992. *Calycorectes psidiiflorus* var. *schultzianus* (Mattos) Mattos, Loefgrenia 108: 2. 1992. *Eugenia psidiiflora* var. *schultziana* (Mattos) Mattos, Loefgrenia 120: 8. 2005.—TYPE: BRAZIL. Rio Grande do Sul, Veranópolis, próximo ao rio das Antas, na mata, fl., 2 November 1984, *N. Silveira 1694* (holotype: FLOR; isotypes: HAS, RB! [00265680], R! [165543 herbarium number]).

Calycorectes striatulus Mattos, Loefgrenia 94: 9. 1989.—TYPE: BRAZIL. Rio Grande do Sul, São Francisco de Paula, perto da encruzilhada, na rodovia para Canela, 13 December 1978, fl., *J. Mattos et al. 19818* (holotype: HAS [90382 herbarium number-photo!]; isotype: MO).

Eugenia psidiiflora O.Berg, Fl. Bras. 14(1): 223. 1857. non *Eugenia mansoi* O.Berg, Fl. Bras. 14(1): 223. 1857. *Calycorectes psidiiflorus* (O.Berg) Sobral, Candollea 40: 636. 1985.—TYPE: BRAZIL. [São Paulo], habitat ad. S[ão] Carlos, fr., s.d., *Manso [36]* (lectotype designated here: W! [0075532]; probable isolectotype: F [fragment-photo!]). **syn. nov.**

Psidium pirayuense Barb.Rodr., Bull. Herb. Boissier, sér. 2, 7: 798. 1907. nom. nud.—SYNTYPES: PARAGUAY. in dumentis Villa Hayes, July, *E. Hassler 544* (G! [00166280, 00166281]); in dumentis pr. Pirayu, July, *E. Hassler 590* (G! [00166282, 00166283]); ad ripas fluminis Juqueri, December, *E. Hassler 1679* [unknown collection].

Psidium tobatyense Barb.Rodr., Bull. Herb. Boissier, sér. 2, 7: 798. 1907. nom. nud.—SYNTYPES: PARAGUAY. Tobaty, fl., September, *E. Hassler 6164* (BM! [000511334], G! [00072629], NY [01288092-photo!]); in silvis pr. Tucangua, fl., July, *E. Hassler 612* (K! [000565048], G! [00072623, 00072624, 00072625, 00072626]); ad ripam lacus Ypacaray, fl., August, *E. Hassler 861* (K! [000565049], G! [00072627, 00072628], P! [00780940]).

Stenocalyx rufescens Kausel, Lilloa 32: 368. 1967. *Calycorectes riedelianus* O.Berg, Fl. Bras. 14(1): 596. 1859. *Eugenia psidiiflora* var. *riedeliana* (O.Berg) Mattos, Loefgrenia 120: 8. 2005.—TYPE: BRAZIL. Bahia, ad ripam fluvii Itahype prope Almada, fl., August to September 1822, *Riedel s.n.* (**lectotype designated here:** LE! [00004119, *pro parte*: two bottom branchlets]; isolectotypes: F [fragment, 971423 herbarium number-photo!], G! [00227493, 00227494], GH [00068864-photo!], K! [000001393], LE! [3 sheets], M [0171257-photo!], NY [00386741-photo!], P! [05229259, 05229263, 05229265], S [05-3105 herbarium number-photo!], U [0116085-photo!], UB! [fragment, 4803-8 herbarium number], W! [100508 herbarium number, 0070611 herbarium number]).—REMAINING SYNTYPE: BRAZIL. Bahia, fl., s.d., *J.S. Blanchet 2340* (F [0064798-photo!], G! [3 sheets], K! [000565052], LE! [00004119, *pro parte*: top branchlet], MICH [1109800-photo!], NY [00386739-photo!, 00386740-photo!], OXF! [00067682], P! [00798905, 05229261], W! [121036 herbarium number, 121040 herbarium number]).

Shrub or tree 1 to 13 m tall. Young leaves glabrous or sometimes with whitish trichomes up to 0.2 mm long, appressed, glabrescent. Young twigs compressed, with whitish trichome up to 0.2 mm, erect, sparse, glabrescent; bark longitudinally striate exfoliating on membranaceous irregular and small sheets, greyish, puberulent, glabrescent. Leaves with petioles 1.5–5 × 0.6–0.8 mm, canaliculate or sulcate adaxially, puberulent; blades 1.5–7 × 0.5–2.5 cm, narrow-elliptic, elliptic or wide-elliptic, chartaceous, discolourous when dry, glabrous; base cuneate or acute, rare obtuse; apex attenuate, acute or acuminate, 0.2–2 cm long, rare obtuse; midvein canaliculate adaxially; secondary veins 5–7 per side, slightly prominent or plane on both surfaces, often inconspicuous; marginal veins two, the innermost 1–2.5 mm from the margin, the outermost 0.5 mm from the margin, often indistinct, slightly revolute; glandular dots slightly depressed adaxially, slightly prominent abaxially, discolourous. Inflorescence subterminal or terminal, less often axillary, auxotelic, often recovering vegetative growth; bracts 1–3 × 0.5–1 mm, ovate, glabrous; rachis 1–5 mm long, terete, puberulent; 1–3 pairs of flowers, pedicels 2–30 × 0.5–0.7 mm, glabrous or sparsely puberulent; up to one rachis per axil; bracteoles 0.5–1.5 × 0.5–1 mm, narrow-ovate, lanceolate or ovate, glabrous, persistent in the fruit. Flower buds 4.5–6 × 3–5 mm, obovate, marked by 10–15 glandular dots per mm², calyx lobes partially fused but free at the tip leaving an aperture of 1–2 mm diameter, tearing regularly at anthesis in 4 lobes, 2.5–3.5 × 2.5–4 mm, ovate, glabrous or dense on hypanthium outside, puberulent inside; petals 4–6.5 × 2.5–5 mm, obovate or elliptic, glabrous; stamens straight in the bud, filaments up to 8 mm long, anthers 0.5–1 mm long, oblong or elliptic; staminal whorls flat, 3.5–6 mm diameter, squared, not tearing at anthesis, puberulent; style 5–7 mm long, glabrous; ovary 2(3)–locules, 8–13 ovules per locule. Fruits 7–12 × 8–22 mm, globose, red when ripe, glabrous, crowned by the remnant of the regular calyx lobes; seeds 1–2. Figure 19.

Etymology:—The specific epithet likely refers to the flower often emerging from the terminal and sub-terminal axils.

Distribution and habitat:—*Eugenia subterminalis* is widely distributed and occurs in Southern (Rio Grande do Sul, Santa Catarina and Paraná), Southeastern (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo) and Central-West Brazil (Goiás and Mato Grosso do Sul), known from several vegetation types in the Planalto Meridional, Planalto Central, Serra Geral, Serra do Mar, Serra da Mantiqueira, Serra de Maracaju and Serra da Bodoquena, also with extra-Brazilian distribution occurring Northeastern Argentina (Corrientes and Misiones), Southern (Cordillera, Itapúa, Paraguarí and San Pedro), Eastern (Amambay, Canindeyú) and Northeastern Paraguay (Alto Paraguay), Northern Peru (San Martín and Maynas), Southern Colombia (Leticia), and from Eastern (Orellana) to Central Ecuador (Napo), at elevations between 0 to 900 m a.s.l. (Fig. 20). It is usually shrub or small tree frequent in the understorey mostly occurring along coast on slope forest and less often in lowland forest within the Ombrophyllous Dense Forest or Semideciduous Forest and sometimes reaching the shore in shrub vegetation on well-drained sandy soil (*Restinga*) in the Atlantic province, towards inland in savanna forest on sandy soil, basaltic or in gallery forest with calcarean outcrop within the Semideciduous Forest in the Cerrado province, and in the Mixed Ombrophyllous Forest (with *Araucaria*) in the Atlantic province.

Phenology:—Flowers have been collected mainly from August to December and fruiting from August to April (Fig. 4).

Conservation status:—Least Concern (LC). *Eugenia subterminalis* is known from protected and non-protected areas in primary and secondary sites over a broad EOO of ca. 6,760,000 km². Populations in the Central-West range Brazil are mostly restricted to the gallery forest and tend to be scarcer, a significant risk to be locally extinct due to the decrease of habitat quality caused by climate change and the deforestation not only locally but also upper riverside impacting the river flows.

FIG. 19. *Eugenia subterminalis*. A. Leaf twig with flowers. B. Inflorescence and flowers. C. Fruits. (A: *M. Peron 875*; B: *G. Hatschbach 45214*; C: *A. Quinet 2303*).

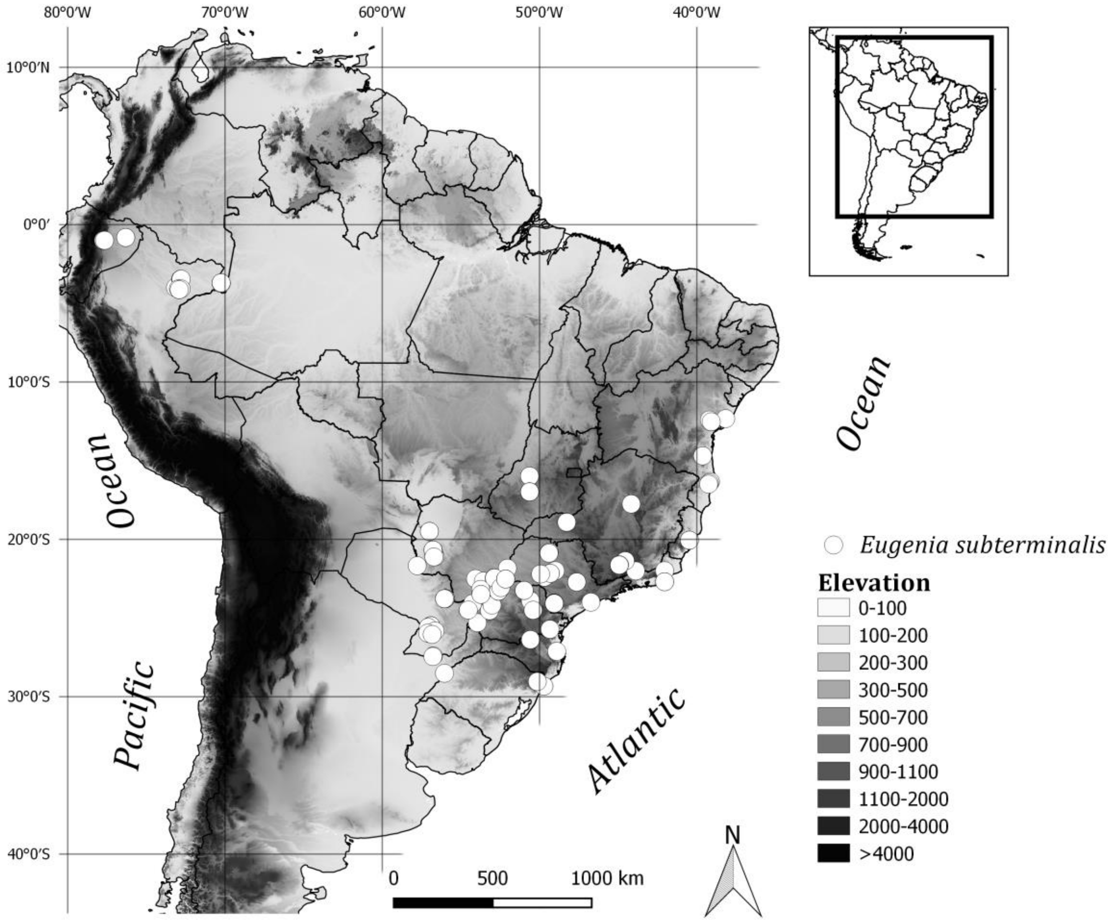


FIG. 20. Geographic distribution of *Eugenia subterminalis*.

Comments:—Although *Eugenia subterminalis* is a distinctive species, it is sometimes confused with *E. acutata* but can be easily distinguished by the auxotelic inflorescence with flowers emerging from the terminal and sub-terminal axils (*vs.* fasciculiform inflorescence with axes length highly variable) and persistent bracteoles (*vs.* deciduous before anthesis). *Eugenia subterminalis* can be confused to *E. lagoensis* that emerged in *Eugenia* sect. *Umbellatae* according to the molecular phylogeny (Giaretta et al. Chapter 2) but can be easily distinguished by the leaves with midvein canaliculate adaxially (*vs.* raised adaxially). It was thought that *E. subterminalis* would have populations with disjunction in Campinara sand soil forest in the Amazonian province, however, it is a distinctive species best circumscribed as *E. berlynensis*

O.Berg (1856c: 468) (M. Sobral, pers. comm.) by the flower with free lobes and leaf venation well-marked. A lectotypification and three synonyms were based on examination of type material, except *Calycorectes paraguayensis* which holotype neither isotypes were seen. However, protologue description and the saw paratype (*J.R. Mattos 14085*) provided basis to the synonymization here assigned. Berg (1857) notice that *Eugenia psidiiflora* and *E. mansoi* are under the collection *Manso 36*. He assigned no number to the type of *E. psidiiflora* likely to avoid further confusion and wrote '*Eugenia* ? *psidiiflora*' to manifest a possible mixture of specimens. Examination of the material deposited in W (0075532) released any doubt that it is the matter taxon.

Specimens examined:—Argentina. Corrientes: Santo Tomé, 16 January 1947, fl., *A.M.R. Huidobro 4371* (W); 20 January 1947, fl., *A.M.R. Huidobro 4291* (W); 20 January 1947, fl., *A.M.R. Huidobro s.n.* (P). **Misiones:** Candelaria, costa del rio Paraná, 15 January 1946, fl., *Bertoni 2641* (BM). Eldorado, Km 30, 10 December 1943, fr., *Barkart 14679* (K). San Javier, 18 February 1947, fr., *G.J. Schurarz 4123* (P); Alba Posse, 1 November 1947, fl., *G.J. Schurarz 4033* (W); ibid., 5 February 1947, fl., *G.J. Schurarz 4068* (IAN); Arroyo Chafariz, 17 March 1947, fr., *G.J. Schurarz 4346* (W); Durañana, 8 March 1947, fr., *G.J. Schurarz 4284* (P). San Miguel, Caballero Cué, 13 February 1908, fl., *K. Fiebrig 4926* (P, W). **Brazil.** s.d., fl., *R.J. Shuttleworth s.n.* (BM). **Bahia:** s.d., fl., *M. Blachet 2340* (P); s.d., fl., *M. Blanchet 103* (P). Cachoeira, vale dos rios Paraguaçu e Jacuípe, June 1980, fl., *C.P. Cavalo 219* (CEPEC); ibid., November 1980, fl., *C.P. Cavalo 912* (CEPEC); ibid., mata a NE de B. Bananeiras, November 1980, fr., *Grupo Pedra do Cabalo 912* (ALCB). Itabuna, barragem margem do rio Cachoeira, 23 September 1965, fl., *R.P. Belém 1793* (IAN). Itamaraju, rodovia Itamaraju-Teixeira de Freitas, 3 November 1983, fl., *C. Ricardo 1625* (CEPEC). Jacobina, s.d., fl., *J.S. Blanchet 103* (BM). Porto Seguro, aceiro com posseiro, lado esquerdo, 11 July 1989, fr., *G.L. Farias 295* (CEN, IBGE, RB); estrada Casa de Tábua, km 0,535, lado direito, 12 July 1988, fr., *G.L. Farias 208* (RB); RPPN Estação Veracel, 10 March 2010, fl., *L. Daneu 275* (CEPEC); ibid., 7 March 2010, fl., *G.M. Carvalho 279* (CEPEC). Salvador, Pojuquinha, 15 July 1993, fr., *s.c., H204* (P). Santa Cruz da Cabrália, arredores da Estação Ecológica do Pau-Brasil, 2 July 1978, fr., *S.A. Mori 10212* (CEPEC); Estação Ecológica do Pau-Brasil e arredores, cerca de 16 km a oeste de Porto Seguro, 22 March 1978, fl., *S.A. Mori 9839* (K, RB). **Espírito Santo:** Santa Leopoldina, fazenda Caioaba, 24 October 2007, fl., *V. Demuner 4365* (MBML). **Goiás:**

Paraúna, Parque Estadual de Paraúna, 1 June 2013, fr., *J.E.Q. Faria 3742* (UB); ibid., Ponte de Pedra, 1 June 2013, fr., *J.E.Q. Faria 3755* (CEN, RB, SP, UB). **Mato Grosso do Sul:** Amambai, rio Amambai, 15 October 1984, fl., *G. Hatschbach 48490* (G, INPA, MBM). Corumbá, fazenda Santa Verônica, 31 October 1999, fl. and fr., *A. Pott 8208* (UB). Jateí, rio Ivinhema, 26 August 1988, fr., *A. Teixeira s.n.* (MBM); ibid., 30 October 1988, fl., *M.A. Assis s.n.* (MBM). Naviraí, Porto Caiuá, 12km antes, 21 October 1986, fr., *U. Pastore 104* (HRB, RB). Porto Murtinho, Parque Municipal Cachoeirão do Apa, 15 March 2004, fl., *G. Hatschbach 77221* (G, MBM, UB). **Minas Gerais:** Braúnas, 27 September 1997, fl., *E. Temeirão-Neto 2558* (SP); UHE Porto Estrela, 9 October 1993, fl., *E. Tameirão-Neto 969* (MBM). Joaquim Felício, Serra do Cabral, 17 August 2007, fl., *J.M. Silva 6010* (ALCB, MBM, RB). Monjolinho de Minas, Q. Bananeira, L.B., P.22 (junto à Roupada), Monjolinho, CEC, 16 September 1986, fl., *s.c., s.n.* (RB, SPF). Nova Ponte, August 1987, fr., *J.R. Stehmann s.n.* (RB); Q. Bomba, última linha lado Albertia, Monjolinho, CEC, 22 September 1986, fl., *s.c., s.n.* (RB). São Tome das Letras, Pico do Gavião, contrafortes Sudoeste, 22 February 1999, fr., *E.M. Nic Lughadha 214* (ESA, K, RB, SP, SPF). Uberlândia, Estação Ecológica do Panga, 13 March 1996, fr., *A.A. Arantes 590* (SP); ibid., 22 August 1996, fl., *A.A. Arantes 689* (K); ibid., 26 June 1992, fr., *FEEP 239* (UB); reservatório de Miranda, ca. de 20 km do centro de Uberlândia, 21 November 2003, fr., *A.P.M. Santos 191* (ESA); ibid., 22 August 2003, fl. and fr., *A.P. Milla 121* (ESA, SPF); ibid., 26 September 2003, fl. and fr., *A.P. Milla 131* (ESA). **Paraná:** 4 March 1949, fl., *G.R. Prata 47* (RB); fazenda Lagoa, 6 April 1966, fr., *J.C. Lindeman 962* (MBM, UB); ibid., W of river Ivaí, 15km E of S.S. Tomé, forest on brown sand near second lagoa, 6 April 1966, es., *J.C. Lindeman 946* (RB); Parque Nacional do Igaçu, forest with abundance of Myrtaceae in line P4 near Aranha, 26 November 1966, fr., *J.C. Lindeman 3430* (MBM, RB). Amaporã, 22 October 1987, fr., *S. Goetzke 162* (MBM); ibid., 26 August 1987, fl., *S. Goetzke 100* (MBM). Campina Grande do Sul, 18 October 1959, fl., *G. Hatschbach 6362* (MBM). Capitão Leônidas Marques, rio Iguaçu, 7 May 2004, fr., *O.S. Ribas 6264* (MBM). Cianorte, fazenda Lagoa, 24 August 1967, fl., *G. Hatschbach 16954* (MBM). Goioerê, Parque Municipal Antônio Sestak, 18 September 2007, fl., *E.M. Silva s.n.* (MBM). Guaíra, 29 September 1986, fl., *J. Augusto s.n.* (R); 18 October 1962, fl., *G. Hatschbach 9312* (MBM); Parque Nacional das Sete Quedas, 17 March 1982, fl., *M. Kirizawa 689* (SP); ibid., a 6,5km do centro da cidade de Guaíra na pequena ilha, 15 September 1980, fl., *J. Fontella 1213* (RB, SPF); ibid., 19 September 1975, fl., *G.*

Hashimoto 16760 (SP); ibid., 25 September 1955, fl., *G. Hashimoto 16680* (SP); ibid., 30 September 1980, fl. and fr., *G. Hatschbach 43195* (G, MBM); ibid., 4 September 1979, fl., *E. Buttura 241* (MBM, SP); Taturi, 11 August 1960, fl., *G. Hashimoto 16747* (SP). Guarapuava, Serra da Esperança, 18 October 1960, fl., *G. Hatschbach 7383* (MBM). Ibiporã, fazenda Doralice, 18 November 1991, fr., *F. Chagas 1449* (UB). Icaraíma, Paredões das Araras, 28 August 1967, fl., *G. Hatschbach 17046* (G, MBM, P); Porto Camargo, 27 August 1967, fl., *G. Hatschbach 17034* (MBM); ibid., 28 August 1967, fl., *G. Hatschbach 17058* (MBM, UB). Jataizinho, 12 December 1996, fr., *F. Chagas 2199* (UB); ibid., 14 December 1995, fr., *F. Chagas 1898* (UB); ibid., 14 December 1995, fr., *L.H. Soares-Silva 1898* (SPF); arredores de Jataizinho, 4 October 1996, fl. and fr., *L.H. Soares-Silva 647* (ESA, RB, UB). Jundiaí do Sul, rio Noite Preta, 7 November 2002, fl. and fr., *J. Carneiro 1382* (MBM). Laranjeiras, Salto Osório, rio Iguaçu, 18 April 1970, fl., *G. Hatschbach 24168* (K, MBM). Leópolis, 29 August 1996, fr., *F. Chagas 1957* (MBM, UB). Londrina, Maravilha, 15 November 1995, fl. and fr., *L.H. Soares 512* (UB). Lupionópolis, RPPN Mata São Pedro, 27 October 2005, fl., *J.S. Carneiro 541* (MBM). Nova Cantu, 2014, fr., *G. Felitto 905* (MBM). Palotina, Parque Estadual de São Camilo, 4 November 2010, fl., *C. Kozera 3666* (MBM). Paraíso do Norte, próximo de Paraíso do Norte, 27 January 1982, fr., *P.P. Furtado 129* (HRB, RB); ibid., 27 January 1982, fr., *P.P. Furtado 130* (HRB, INPA, RB). Paranavaí, Bosque da Cidade, 17 August 1999, fl., *G. Hatschbach 69267* (ESA, G, MBM, UB). Pérola d'Oeste, rio Feliciano, 15 January 1983, fl. and fr., *J.R. Pirani 444* (SP, SPF). Querência do Norte, RPPN Fazenda da Mata, 16 September 2008, fl. and fr., *A.M. Amancio 161* (MBM), 27 August 2008, fl. and fr., *K.C. Almeida 128* (MBM); ibid., 30 September 2008, fr., *A.M. Amancio 197* (MBM). Santa Helena, São Clemente, 9 December 1977, fl., *G. Hatschbach 40564* (ESA, HRB, MBM). São Pedro do Iguaçu, Parque Estadual Cabeça do Cachorro, 26 September 2009, fr., *O.S. Ribas 8301* (MBM). Sapopema, 22 August 1996, fr., *F. Chagas 1946* (UB), 8 December 1995, fl., *L.H. Soares-Silva 568* (UB); fazenda Bom Sucesso, 17 December 1990, fr., *F. Chagas s.n.* (UB); ibid., 7 November 1991, fl., *F. Chagas 1581* (UB); ibid., 9 March 2007, fl., *F.C. Silva 1581* (SPSF); fazenda Guaporé, 9 December 1995, fr., *L.H. Soares 574* (UB); Salto das Orquídeas, margem do rio Lageado, 8 December 1995, fr., *F. Chagas 568* (ESA, R). Serranópolis do Iguaçu, estrada do Colono, 2 August 2004, fr., *E. Barbosa 957* (G, MBM). Sete Barras, 17 March 1982, fl., *M.M.R.F. Melo 321* (SP). Tapejara, 26 August 1967, fl., *G. Hatschbach 16996* (MBM). Tibagi, cânion do rio Iapó, Guartelá, 21 October 1993, fl., *G. Hatschbach 59690* (G, INPA, UB); Canyon Guartelá, 13 December 1996, fr., *J.M. Silva 1846* (MBM); ibid., 13 September 1996, fl., *C. Giraldi s.n.* (G, UB); ibid., 21 October 1993, fl., *G. Hatschbach 59690* (MBM); fazenda Batavo, 1991, fl., *S.M. Silva 1* (CEN); ibid., 1991, fr., *S.M. Silva s.n.* (ESA, UB); ibid., rio Lapo, 29 April 1990, fl., *E. Bianchini s.n.* (ESA); Guartelá, 13 September 1996, fl., *C. Giraldi s.n.* (MBM, SP); ibid., 21 October 1993, fl., *G. Hatschbach 59689* (MBM); Parque Estadual Guartela, 15 January 2004, fr., *M.R.B. Carmo 635* (UB); ibid., 2 November 2012, fl., *J. Cordeiro 4693* (MBM); ibid., 27 August 2011, fl., *E. Barbosa 3111* (MBM); ibid., estrada de acesso ao Canyon, 3 November 2003, fl., *F.F. Mazine 974* (K, SPF); ibid., 3 November 2003, fl., *F.F. Mazine 980* (ESA, K, MBM). Umuarama, Serra Dourada, 19 January 1967, fl., *G. Hatschbach 15741* (MBM). Uraí, 4 October 1996, fl., *L.H. Soares-Silva 640* (MBM, UB). Vila Alta, APA da Ilha Grande, 15 December 1995, fr., *S.R. Ziller 1124* (MBM); ibid., 15 December 1995, fr., *S.R. Ziller 1143* (MBM); APA da Ilha Grande, coletada na ilha dos Bandeirantes, rio Paraná, December 1995, fr., *S.R. Ziller 1077* (ESA, MBM); fazenda Santa Mônica, 5 December 1995, fr., *J. Caneiro 90* (MBM). **Rio de Janeiro:** Magé, IIIº Distrito, Paraíso, Centro de Primatologia do RJ, 7 November 1984, fl., *G. Martinelli 10202* (RB). Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, sítio Sophronites, 18 August 1989, fl., *M. Peron 875* (GUA, K, RB). Teresópolis, Parque Nacional da Serra dos Órgãos, matas do rio Paquequer próximo ao km 2 da estrada para a barragem, 11 March 2005, fl., *C.S. Prado 410* (RB, SPF); ibid., 3 November 2005, fr., *C.S. Prado 1811* (RB, SPF). **Rio Grande do Sul:** Cambará do Sul, Fortaleza, 24 November 1994, fl., *G. Hatschbach 61319* (K, MBM); ibid., 24 November 1994, fl., *G. Hatschbach 61325* (ESA, MBM, SP, SPSF); ibid., 27 December 1977, fl., *A. Sehnem 15643* (MBM); Itaimbezinho, 28 November 1982, fl., *M. Sobral 1268* (MBM, SPF). Taquara, Mundo Novo, 15 October 1985, fl., *R. Wasum 1580* (BM). Tenente Portela, Parque Estadual do Turvo, 11 October 1981, fl., *P. Brack s.n.* (MBM). Torres, Perdida, 17 November 1992, fl., *J.A. Jarenkow 2197* (ESA, MBM). Veranópolis, próximo do rio das Antas, 2 November 1984, fl., *N. Silveira 1694* (R, RB). **Santa Catarina:** Canoinhas, Serra da Morte, 8 November 2007, fr., *A.L Gasper 917* (MBM). Itapoá, Reserva Volta Velha, 11 January 1992, fr., *R. Negrelle A-14* (MBM). Paulo Lopes, Bom Retiro, 21 November 1973, fl., *A. Bresolin 981* (MBM). Tangará, 6 October 2005, fl., *G. Amaral 4A* (MBM). **São Paulo:** s.d., fr., *C. Geol s.n.* (R); Reserva Estadual da Cantareira, Pedra Grande, 11 October 1984, fl., *S. Romaniuc-Neto 191* (RB, SP, SPF, SPSF). Americana, bairro Parque Nova Carioba, 28 December

1951, fr., *M. Kuhlmann 2799* (SP, SPF). Atibaia, Pedra Grande, 29 November 1961, fl., *J.R. Mattos 9528-a* (SP). Avaí, aldeia Guarani, 1 October 1998, fr., *A.P. Bertoncini 917* (ESA); ibid., 29 September 1999, fr., *A.P. Bertoncini 1066* (SP). Caiuá, fazenda Caaporanga, 4 km de Caiuá, em direção a Presidente Epitácio, 14 November 1996, fr., *J.P. Souza 397* (ESA). Capão Bonito, 8km ao nordeste de Capão Bonito, rodovia Capão Bonito-São Miguel Arcanjo, 21 October 1966, fl., *J.R. Mattos 14085* (SP); Gália, Estação Ecológica de Caetetus, s.d., es., *M.T.Z. Toniato 78* (ESA). Gália, Estação Ecológica de Caetetus, parcela EEC, 3 August 2004, fl., *G. Durigan s.n.* (ESA); ibid., 31 August 2004, fl., *G. Durigan s.n.* (ESA). Itanhaém, Parque Estadual da Serra do Mar, Núcleo Curucutu, 2005, fr., *R. Cielo-Filho 408* (SPSF). Itapeva, Estação Ecológica, 25 November 2008, fr., *R.S. Almeida 31* (SPSF); ibid., trilha do rio Pirituba, 25 November 2008, fr., *C.R. Lima 215* (ESA, SPSF); Estação Experimental, 24 September 2009, fl., *B. Baitello 2399* (SPSF); ibid., 28 August 2008, fl., *C.R. Lima 219* (SPSF); ibid., trilha do Poço da Peroba, 22 September 2009, fl., *O.T. Aguiar 1282* (SPSF); ibid., 25 August 2009, fl., *C.R. Lima 246* (SPSF). Lutécia, fazenda Santa Maria do Monjolinho, margem da represa da sede, 10 September 1990, fl. and fr., *S.M. Salis 258* (IBGE). Marília, Estação Experimental de Marília, 10 September 1992, fl., *Durigan s.n.* (RB); ibid., 11 August 1992, fl., *Durigan s.n.* (RB); ibid., 13 October 1992, fr., *Durigan s.n.* (RB); ibid., 8 October 1987, fr., *Patricia 49-M* (ESA). Paraguaçu Paulista, Estação Experimental Água da Cachoeira, 25 October 1994, fl., *G.A.D.C. Franco 1281* (SPSF, UEC); ibid., 26 October 1994, fr., *J.B. Baitello 710* (SPSF). Piracicaba, B. Godinhos, área 2, 14 October 1993, fl., *N.M. Ivanauskas s.n.* (ESA, SP); em direção ao Anhembi, 7 September 2010, fl. and fr., *O. Campos s.n.* (ESA); mata de Godinhos, 13 November 2008, fl., *F.F. Mazine 1086* (K); ibid., 13 November 2008, fl., *F.F. Mazine 1088* (K); mata de pedreira, 17 September 1986, fl., *D.L. Pereira 15* (ESA); ibid., 7 October 1986, fl., *D.L. Pereira 16* (ESA); ibid., 17 September 1986, fl., *D.L. Pereira 19* (ESA); ibid., 7 October 1986, fl., *D.L. Pereira 17* (ESA). Rosana, Porto Maria, 17 October 1998, fr., *L.R.H. Bicudo 248* (SP). São Paulo, October 1947, fl., *D.B.J. Pickel s.n.* (SP); Parque Estadual Alberto Löfgren, Horto florestal, November 1943, fr., *D.B.J. Pickel s.n.* (SPSF); ibid., 12 November 1943, fl., *D.B.J. Pickel s.n.* (SPSF); ibid., 6 October 1947, fl., *J.P. Coelho 3081* (SPSF); Vila Amália, 5 December 1939, fr., *A. Rodrigues 651* (SPSF); ibid., 5 December 1939, fr., *A. Rodrigues s.n.* (SPF); ibid., 5 October 1939, fl., *L. Gonzaga s.n.* (MBM, SP, SPSF). Teodoro Sampaio, Parque Estadual do Morro do Diabo, October 1989, fr., *G. Durigan s.n.* (SPSF); ibid., 17

September 1984, fl., *O.T. Aguiar s.n.* (SPF, SPSF); ibid., 2 December 1986, fr., *J.A. Pastore 203* (SPSF); ibid., 2 December 1986, fr., *J.Y. Tamashiro 18803* (ESA, SPSF); ibid., 21 June 1994, fl., *R. Esteves 76* (SP); ibid., 21 October 1980, fl., *A.C. Dias s.n.* (SPSF); ibid., 22 June 1994, fl. and fr., *J.A. Pastore 498* (SP, SPSF, UEC); ibid., 22 November 1984, fr., *O.T. Aguiar s.n.* (SPF, SPSF); ibid., 29 October 1986, fr., *O.T. Aguiar 194* (SPSF); ibid., 4 December 1986, fr., *J.Y. Tamashiro 18855* (ESA, SP, SPSF); ibid., 4 December 1986, fr., *O.T. Aguiar 206* (SP); ibid., 6 December 1994, fr., *O.T. Aguiar 530* (SP, SPSF, UEC); ibid., estrada do 7000, na margem do caminho, 7 December 1994, fr., *J.B. Baitello 730* (SP, SPSF, UEC); ibid., Horto florestal, 17 October 1984, fl. and fr., *O.T. Aguiar s.n.* (SPF, SPSF); ibid., região da Mina da Serra, 22 June 1994, fr., *O.T. Aguiar 466* (SP, SPSF). **Paraguay.** March 1942, fr., A. Schinini 4360 (G); 12 October 1979, fl., *G. Schmeda 406* (G); 13 February 1908, fl., *K. Fiebrig 4926* (G); 1888, fr., *B. Balansa 3047* (G, P); 1914, fl., *R. Chodat s.n.* (G); 25 October 1874, fl. and fr., *B. Balansa 1289* (G, K, P); 7 October 1875, fl., *B. Balansa 1313* (G, P); s.d., fl., *K. Fiebrig 5869* (G); s.d., fl., *S.G. Tressens 3379* (G); s.d., fl., *K. Fiebrig 5463* (G); Alto Paraná, October 1909, fl., *K. Fiebrig 5422* (G, K, P); Parque Nacional Ybycui, 5 February 1984, fl., *W. Hahn 1961* (G). **Canindeyú:** Cordillera de Mbaraca, 30 October 1978, fl. and fr., *L. Bernardi s.n.* (BM); ibid., 30 October 1978, fr., *L. Bernardi 18276* (G); crica Guadalupe, 27 October 1978, fr., *L. Bernardi 18228* (G); Reserva Natural del Bosque Mbaracayú, borde de camino, 20 November 1996, fr., *B. Jiménez 1728* (BM); ibid., entrada a Arroyo Moroti, Lagunita, 11 September 1996, fl., *B. Jiménez 1506* (BM); ibid., sendero princical, 4 December 1996, fr., *B. Jiménez 1746* (BM, G); ibid., 6 September 1996, fl., *B. Jiménez 1483* (BM, G); ibid., km 53/4, 11 September 1996, fl., *B. Jiménez 1500* (BM). Guazui, road to Puerto Adela, 16 December 1982, fr., *J.F. Casas 957* (G). Jejui-mi, 6 September 1996, fl., *B. Jiménez 1486* (G). **Central:** Aregua, 6 December 1986, fl. and fr., *G. Schmeda 784* (G). **Cordillera:** Altos, September 1902, fl., *K. Fiebrig 176* (G, P); 9 October 1902, fl., *K. Fiebrig 100* (G, K, P); Cerro Tobatí, 23 October 1987, fl., *E. Zardini 3616* (K); ibid., 23 October 1987, fl., *E. Zardini 3632* (MBM); ibid., 23 October 1987, fl., *E. Zardini 3643* (G); ibid., 4 December 1987, fr., *R. Degen 587* (G). Colonia Rosado, cerca de Tobaty, 26 October 1986, fr., *A. Schinini 24875* (G). Salto Piraretá, 18 October 1994, fl. and fr., *A. Krapovickas 45691* (K). San Bernardino, 2 March 1946, fl., *G.W. Teague 669* (BM). Tobatí, Cerro Hytú, 23 October 1987, fr., *R. Degen 376* (G). **Itapúa:** Isla Yacyretá, 25 October 2003, fl., *M. Peña-Chocarro 1591* (BM). **Misiones:** Isla Yacyretá, 21 January

1997, fl., *E.M. Zardini 46306* (ESA). **Paraguarí:** 7 September 1916, fl., *O. Rojas 8936* (G); Cerro Acahay, 24 September 1985, fl., *R. Spichiger 1566* (G); Cerro Mbatori, 21 June 1988, fr., *N. Soria 2298* (G); Cerro Santo Tomas, 13 October 1991, fl., *R. Spichiger 5011* (G). Salto Cristal, 25 September 1985, fl., *R. Spichiger 1591* (G). Salto Piraretá, 13 December 1993, fr., *S. Tressens 4805* (G); 14 October 1993, fl., *A. Krapovickas 44582* (G); viam de Ybycuí ad La Colmena, 18 October 1978, fr., *L. Bernardi 18109* (BM, G, LE, P). Ybycuí, Parque Nacional Ybycuí, 12 September 1980, fl., *J.F. Casas 3527* (COL, G, MBM). **San Bernardino:** 2 March 1946, fl., *T. Rojas 13290* (W). **San Pedro:** Yaguareté forest (Sustainable Forest Systems Site), 29 July 1996, fr., *E.M. Zardini 45220* (ESA, P); ibid., north boundary, 23 August 1995, fl., E.M. Zardini 43487 (ESA); ibid., northern boundary, 23 August 1995, fl., *E.M. Zardini 43454* (ESA); ibid., 23 August 1995, fl., *E.M. Zardini 43466* (ESA, P); ibid., trail to rio Araguaya, 20 June 1995, fr., *E.M. Zardini 42908* (ESA); ibid., 23 August 1995, fl., *E.M. Zardini 43330* (RB); ibid., 23 August 1995, fl., *E.M. Zardini 43396* (ESA); ibid., 23 August 1995, fl., *E.M. Zardini 43402* (ESA); ibid., 23 August 1995, fl., *E.M. Zardini 43413* (ESA, RB); ibid., 23 August 1995, fl., *E.M. Zardini 43425* (ESA). **San Tomas:** 17 October 1882, fl., *B. Balansa 4496* (G); 7 September 1916, fl., *O. Rojas 8941* (G). **Tobatí:** Cerro de Tobatí, 10 January 1951, fl., *T. Rojas 14354* (W).

9. EUGENIA VATTIMOANA Mattos, Loefgrenia 120: 9. 2005. *Calycorectes sellowianus* O.Berg, Fl. Bras. 14(1): 356. 1857.—TYPE: BRAZIL. Rio de Janeiro, s.d., *F. Sellow s.n.* (**lectotype designated here:** K! [000565054]; isolectotypes: B [probably destroyed], BM! [000043153], LE!, P! [05229296]).

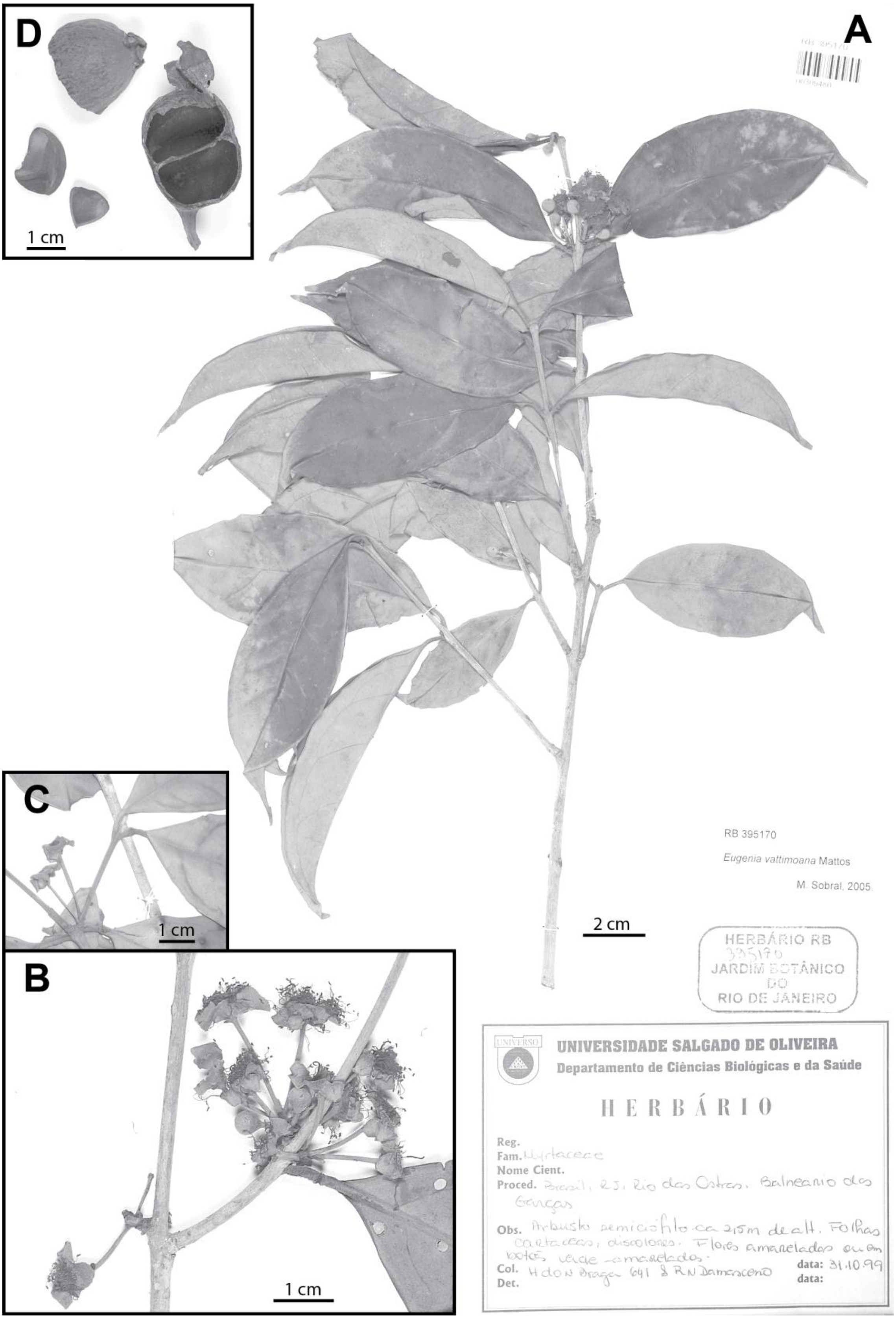
Tree 2 to 15 m tall. Young leaves with brownish trichomes up to 0.7 mm long, appressed, dense on both sides, glabrescent but often persistent abaxially. Young twigs flattened, puberulent, glabrescent; bark longitudinally striate exfoliating on membranaceous irregular sheets, greyish, pubescent, glabrescent. Leaves with petioles 6–11 × 1.5–2 mm, sulcate adaxially, glabrous or puberulent, darkish when dry; blades 7–16 × 3.5–7 cm, elliptic or sometimes obovate, chartaceous, concolourous when dry, puberulent abaxially; base acute or cuneate; apex acuminate, 0.7–1.5 cm long; midvein canaliculate adaxially; secondary veins 7–12 per side, slightly sulcate or prominent adaxially, prominent abaxially; marginal veins two, the innermost 4.5–10 mm from the margin, the outermost 1–3 mm from the margin, slightly revolute; glandular dots inconspicuous adaxially, slightly prominent abaxially, discolourous. Inflorescence axillary or terminal, auxotelic, sometimes recovering vegetative growth; bracts 1–1.5 × 1–1.5 mm, wide-ovate, puberulent; rachis 1–20 mm long, flattened, puberulent; 1–4 pairs of flowers, pedicels 13–35 × 1 mm; up to one rachis per axil; bracteoles 1–2 × 1 mm, ovate, puberulent, persistent in the fruit. Flower buds 5.5–7 × 4–5.5 mm, obovate, marked by 8–11 glandular dots per mm², calyx lobes partially fused and nearly closed except by four vestigial free lobes at the tip, sometimes leaving an aperture of ca. 0.5 mm diameter, tearing irregularly at anthesis in 3–4 lobes, 2–5 × 2.5–6 mm, puberulent outside, puberulent inside; petals 2–4 × 2.5–3.5 mm, ovate or wide–ovate, puberulent on both sides, sparsely inside; stamens straight in the bud, filaments up to 6 mm long, anthers 0.6–1 mm long, oblong or elliptic; staminal whorls flat, 5–7 mm diameter, rounded, slightly tearing at anthesis, puberulent; style 5–7 mm long, glabrous; ovary 2–locules, (3)11–12 ovules per locule. Fruits 30 × 45 mm, globose, densely covered by brownish puberulent indumentum, crowned by the remnant of the irregular calyx lobes; seeds 1–2. Figure 21.

Etymology:—The specific epithet honours Ida de Vattimo-Gil, a researcher from Instituto Jardim Botânico do Rio de Janeiro (Brazil) and expert in Lauraceae.

Distribution and habitat:—*Eugenia vattimoana* occurs in Southeastern Brazil (Espírito Santo and Rio de Janeiro), known from the Serra do Mar and coastal plain, at elevations between 0 to 530 m a.s.l. (Fig. 22). It can be a tree in populations with sparse individuals in the coastal slope and lowland forests, or shrub reaching the shore in scrub vegetation on well-drained sandy soil (*Restinga*) in the Ombrophyllous Dense Forest, both in the Atlantic forest province.

Phenology:—Flowers have been collected from August to December and fruiting from September to May (Fig. 4).

Conservation status:—Vulnerable (VU) B1ab(iii). *Eugenia vattimoana* is known from a secondary protected reserve (Parque Nacional da Tijuca) and non-protected areas with EOO of 14,670 km². Populations in protected secondary site are vulnerable to local extinction due to invasion of exotic species (e.g. *Artocarpus heterophyllus* Lam.) and eventual intervention caused by surrounding human communities. Fragmented populations occur mostly in non-protected areas in the *Restinga* vegetation that are under historical and present suppression to urbanization leading to loss of habitat, isolation of populations, and a decrease of habitat quality. Regional extinction is also potentialized by fire, shade caused by high edifices and invasion of exotic species. *Eugenia vattimoana* can be evaluated according to criterion



RB 395170
Eugenia vattimoana Mattos
M. Sobral, 2005

HERBÁRIO RB
395170
JARDIM BOTÂNICO
DO
RIO DE JANEIRO

UNIVERSIDADE SALGADO DE OLIVEIRA
Departamento de Ciências Biológicas e da Saúde
HERBÁRIO
Reg.
Fam. Myrtaceae
Nome Cient.
Proced. Brasil, RJ, Rio das Ostras, Balneario das Garças
Obs. Arbusto semicaófilo ca 2,5m de alt. Folhas cartaceas, discolores. Flores amareladas ou em botões verde-amarelados.
Col. H don Braga 641 & R N Damasceno data: 31.10.99
Det. data:

FIG. 21. *Eugenia vattimoana*. A. Leaf twig with flowers. B. Flowers. C. Auxotelic inflorescence with vegetative growth recovered. D. Fruit. (A: *H.N. Braga 641*; B: *A. Lobão 163*; C: *G.S.Z. Rezende 52*; D: *O.J. Pereira 1032*).

B1 with EOO smaller than 20,000 km², occurring in severely fragmented habitat (a), and continuing decline of habitat quality (b iii).

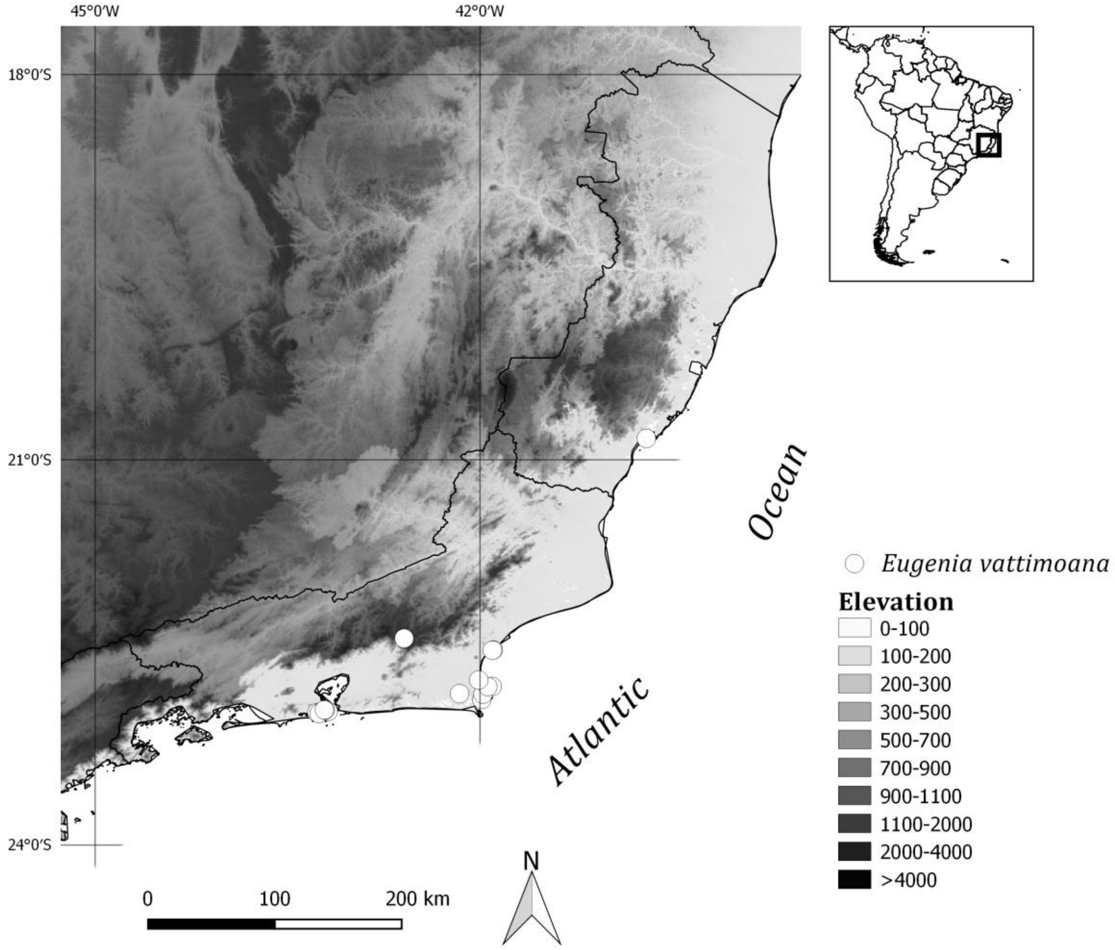


FIG. 22. Geographic distribution of *Eugenia vattimoana*.

Comments:—*Eugenia vattimoana* was previously synonym of *E. brevistyla* (WCSP 2017), however, it is proposed here to be elevated as accepted species. It is supported by the consistent *homosepaly* development pattern of the bud in *E. vattimoana* whereas *E. brevistyla* has *heterosepalous* pattern as described in Giaretta *et al.* (Chapter 2). As a consequence, the bud opens irregularly at anthesis in *E. vattimoana* while *E. brevistyla* opens regularly. Their distinction is also supported by the inflorescence auxotelic with up to one rachis per axil in *E. vattimoana* (*vs.* fasciculiform with up two rachises per axil) and persistent bracteoles (*vs.* deciduous before or after anthesis). *Eugenia vattimoana* is also confused with *E. neoriedeliana* but differs by the brownish indumentum often persistent as leaf puberulent abaxially (*vs.* whitish indumentum and glabrescent abaxially), inflorescence with one flattened rachis per axil (*vs.* up to three terete rachises per axil) and flower bud tearing irregularly in 3-4 lobes (*vs.* tearing transversely at the calyx base resulting in a structure calyptra-like).

***Specimens examined:*—Brazil.** 1841, fl., *Gardner 5462* (K, OXF); 1879, fl., *J. Miers s.n.* (BM); s.d., fl., *J. Miers s.n.* (P). **Espírito Santo:** Anchieta, praia de Iriri, 10 September 1987, fr., *O.J. Pereira 1032* (RB, VIES). **Rio de Janeiro:** 1878, fl., *J. Miers s.n.* (P). Armação de Búzios, Manguinhos, 4 August 1999, fl., *D. Fernandes 238* (RB). Cabo Frio, Armação de Búzios, mata de José Gonsalves, vizinha à fazenda Rancho 10, 8 August 1997, es., *P.R. Farág 602* (RB); distrito de Tamoios, condomínio Florestinha, 6 December 2001, fl. and fr., *G.S.Z. Rezende 52* (RB, SPF); praia das Conchas, 21 September 1987, fl., D.S.D. *Araujo 8150* (GUA, RB); praia do Peró, borda da mata com trilha, 18 September 1996, fl., *A. Lobão 163* (RB). Cachoeiras de Macacu, vale do rio Paraíso, 9 November 1984, fl., *R.R. Oliveira 624* (GUA). Rio das Ostras, Balneário das Garças, 1 May 1999, fr., *H.N. Braga 272* (RB); ibid., 31 October 1999, fl., *H.N. Braga 641* (RB, SPF); ibid., 31 October 1999, fl., *R.N. Damasceno 1161* (RB, SPF). Rio de Janeiro, alto da Boa Vista, Vista Chinesa, estrada da Vista Chinesa, próximo ao km 2, 7 October 1960, fl., *C. Angeli 191* (GUA, K, SP); ibid., 20 December 2001, fl., *C.A.L. de Oliveira 1940* (GUA, RB); estação Vista Chinesa, perto da sede do DECAM, 5 October 1976, fl., *D.S.D. Araujo 1241* (GUA); estrada da vista Chinesa, próximo ao DECAM, 25 October 1983, fl., *D. Martins 91* (GUA, HRB); Corcovado, 1841, fl., *Jaramir 5462* (BM); ibid., 1879, fl., *J. Miers s.n.* (BM); ibid., s.d., fl., *J. Miers 3802* (K); matas das obras públicas, próximo ao horto florestal, September 1927, fl., *Pessoal do Horto Florestal s.n.* (RB); morro do Sacopan, entre o do Salgueirinho e dos Cabritos, 26 November 1940, fl., *J.G. Kuhlmman 6141* (K, RB). São Pedro da Aldeia, Serra de Sapiatiba, 3 December 2001, fl. and fr., *C. Farney 4441* (RB, SPF).

10. EUGENIA ZUCCARINII O.Berg, Fl. Bras. 14(1): 257. 1857.—TYPE: BRAZIL. Rio de Janeiro, s.d., *Sellow s.n.* (**lectotype designated here:** K! [000276669]; isolectotypes B [probably destroyed], P! [01902285]).

Eugenia rostrata O.Berg, Fl. Bras. 14(1): 282. 1859.—TYPE: BRAZIL. s.d., *Sellow s.n.* (syntype B [probably destroyed]). **syn. nov.**

Shrub or tree 2 to 15 m tall. Young leaves glabrous or with brownish trichome up to 0.1 mm, appressed, sparse, glabrescent. Young twigs terete, puberulent, glabrescent; bark longitudinally striate exfoliating on membranaceous irregular sheets, glabrous. Leaves with petioles 5–10 × 1 mm, canaliculate adaxially, glabrous, darkish when dry; blades 2–12 × 1–4 cm, elliptic or narrow-elliptic, chartaceous or coriaceous, discolourous when dry, glabrous; base cuneate or acute, rare obtuse; apex abruptly acuminate or acuminate, 0.5–2 cm long, falcate, less often acute; midvein canaliculate adaxially; secondary veins 6–16 per side, slightly prominent adaxially, often inconspicuous abaxially; innermost marginal veins 1–3 mm from the margin, the outermost indistinct, slightly revolute; glandular dots slightly prominent abaxially but often inconspicuous on both surfaces, often concolourous. Inflorescence axillar or terminal, fasciculiform, rare auxotelic and recovering the vegetative growth; bracts 1–1.5 × 1–1.5 mm, wide-ovate, glabrous; rachis 1–10 mm long, terete, puberulent; 1–4 pairs of flowers, pedicels 5–15 × 0.5 mm; up to three rachises sharing an axil; bracteoles 0.5–1 × 0.5–0.8 mm, ovate, glabrous, usually persistent but eventually deciduous when fruiting. Flower buds 3–5 × 3–4 mm, obovate, marked by 9–13 glandular dots per mm^2, calyx lobes apparently free but fused by ca. 1 mm long at the base, tearing discreetly in the base at anthesis, two unequal pairs, the outermost 1–1.5 × 1.5–2 mm, wide-ovate, the innermost 2–2.5 × 2 mm, hemispherical, glabrous outside, puberulent inside; petals 3–4 × 4–5 mm, wide-ovate, glabrous; stamens straight in the bud, filaments up to 4 mm long, anthers 0.5–1 mm long, oblong or elliptic; staminal whorls flat, 2.5–3.5 mm diameter, squared, not tearing at anthesis, puberulent; style 4.5–5 mm long, glabrous; ovary 2–locules, 6–8 ovules per locule. Fruits 5–15 × 5–15 mm, globose or oblong, atropurpureo or reddish when ripe, glabrous, crowned by the remnant of the regular calyx lobes; seeds 1–3. Figure 23.

Etymology:—The specific epithet likely honour botanist and professor Joseph Gerhard Zuccarini from the University of Munich.

Distribution and habitat:**—*****Eugenia zuccarinii*** occurs in Southeastern (Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo) and Northeastern Brazil (Bahia), known from coastal forest in the Serra do Mar and sand plains, towards inland in the Chapada Diamantina in the gallery forest, at elevations between 0 and 900 m a.s.l. (Fig. 24). It is shrub or tree known from coastal vegetation on slope and lowland forests, reaching the coastal scrub vegetation on well-drained sand soil called *Restinga*, within Ombrophyllous Dense Forest in the Atlantic province, and in dense population in the

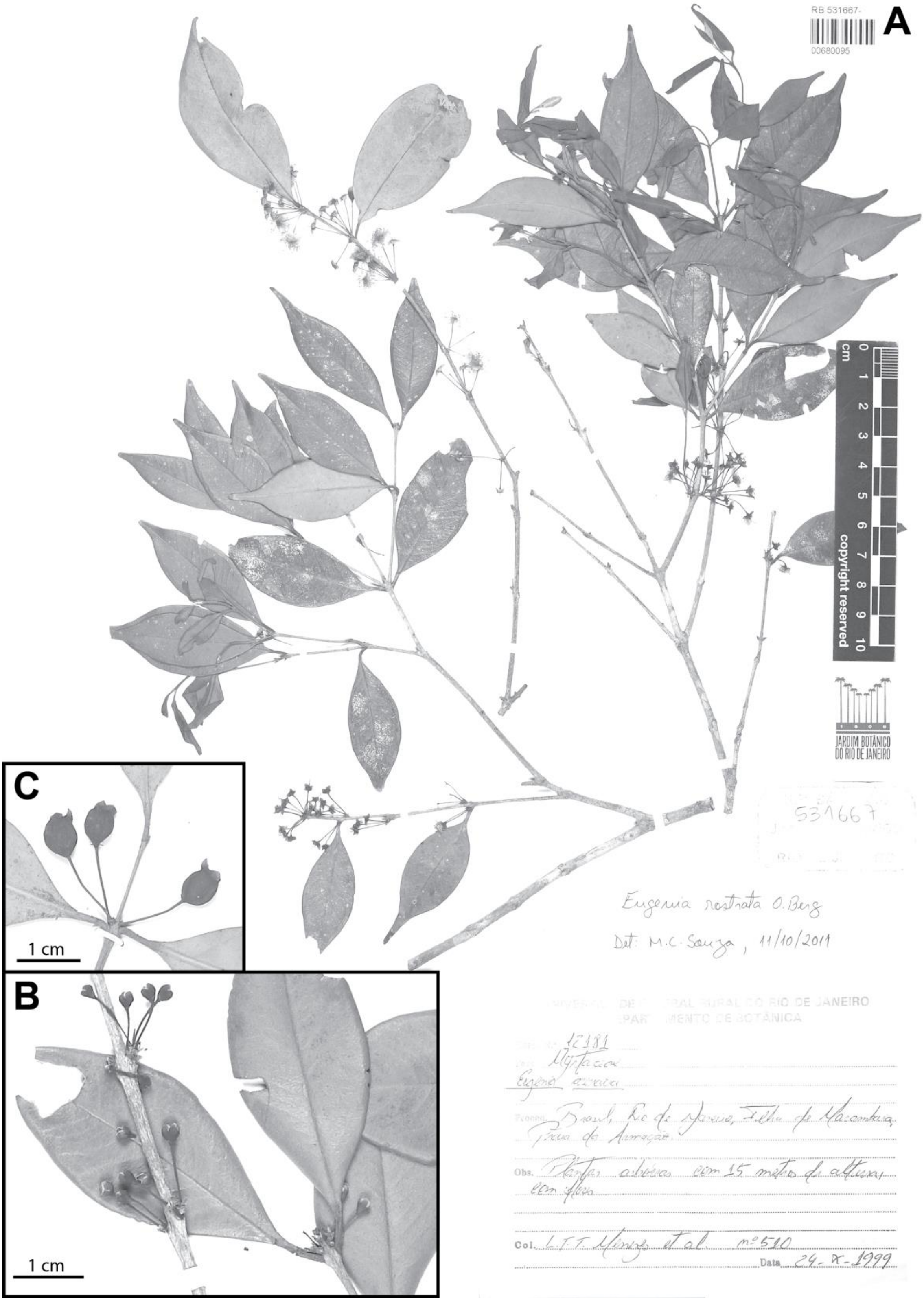


FIG. 23. *Eugenia zuccarinii*. A. Leaf twig with flowers. B. Flower buds. C. Fruit. (A: *L.F.T. Menezes 510*; B: *M.C. Souza 126*; C: *H.G. Dantas 355*).

well-drained litholic soil on stream-along humid forest or in erosive rift valley, within the Semideciduous Forest in the transition between Atlantic and Caatinga provinces.

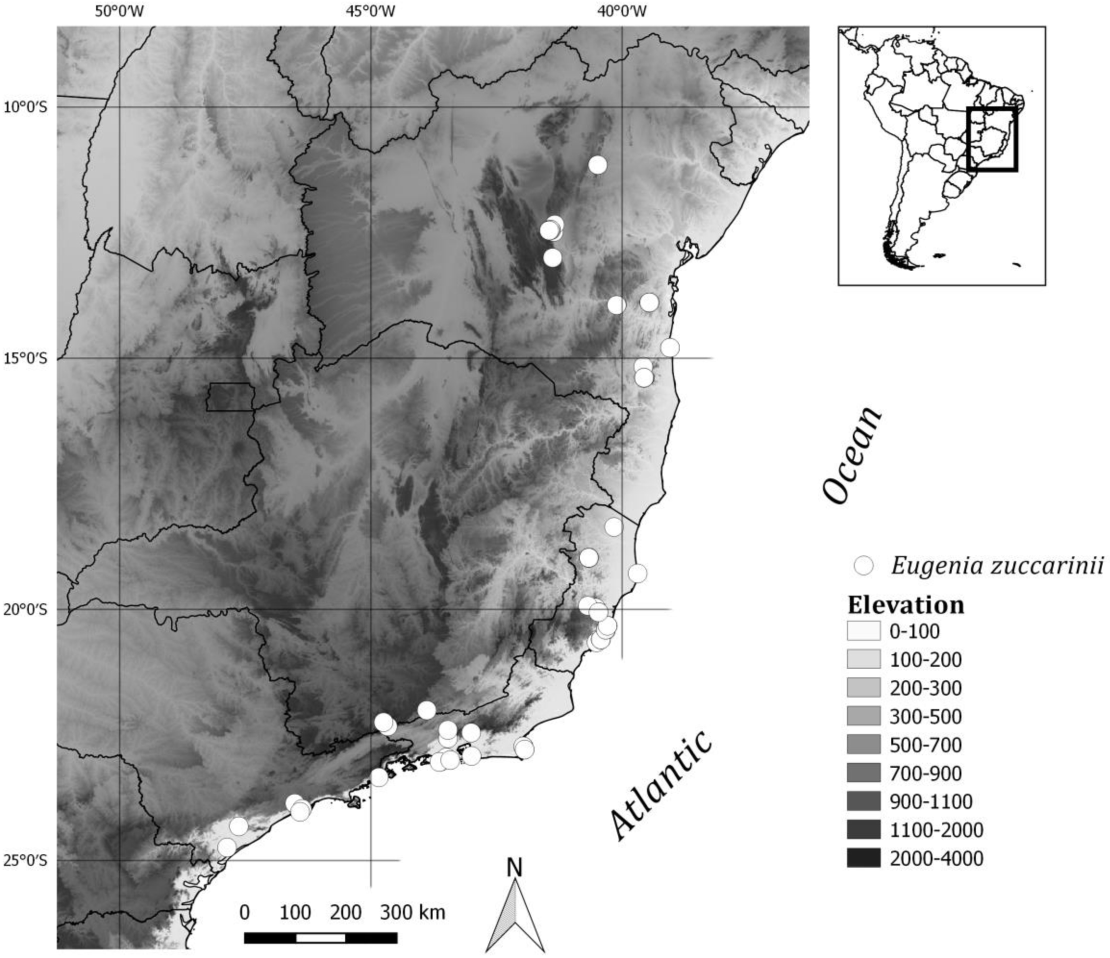


FIG. 24. Geographic distribution of *Eugenia zuccarinii*.

Phenology:—Flowers of specimens from Atlantic province, including *Restinga* vegetation, have been mainly collected from August to November and fruits from September to January (Fig. 4 - Atlantic). Flowers and fruits of specimens from Caatinga province were collected from January to April (Fig. 4 - Caatinga).

Conservation status:—Least Concern (LC). *Eugenia zuccarinii* is known from protected and non-protected areas in primary and secondary sites with EOO of 580,664.6 km². Although it is not threatened, there is a significant risk of local extinction due to suppression of coastal environments to urbanization mainly in the northeastern range where the morphological variability is wider. Although surrounded by a drier environment in the transitional zones in the Caatinga province, populations are restricted to humid forest stream-along or in the rift valley presumably caused by water flowing. It increases its vulnerability to climate change as well as to deforestation not only locally but also upper riverside hampering the stream flows.

Comments:—Although *Eugenia zuccarinii* apparently has a flower with free lobes, a discreet calyx fusion on the base of the lobes is in accordance to the circumscription of the *Eugenia* sect. *Schizocalomyrtus* also supported by the molecular phylogeny (Giaretta et al. Chapter 2). Type of the *Eugenia rostrata* was not found and presumably the only specimen was destroyed in the Second World War. Examination of the protologue descriptions of *E. rostrata* and *E. zuccarinii* and available type specimens of the latter support the taxonomic decision here provided. *Eugenia zuccarinii* have been identified as *E. rostrata* when occuring in the *Restinga* vegetation, however, carefully examination sustains no morphological characters to support the segregation into two species. Despite leaves dimensions overlap, populations from Caatinga province in the countryside Bahia tend to have narrow-elliptic leaves while elliptic or wide-elliptic leaves are frequent in the coast populations. The phenological period also varies between population of different vegetational provinces (Fig. 4). Phenological fluctuation among populations seems to be related to the environment but studies on genetic population might reveal insights on their historical segregation or even reveal cryptic species.

Specimens examined:**—Brazil.** 16 December 1926, fr., *W.J. Burchell 3672-2* (K). **Bahia:** Camacan, RPPN Serra Bonita, 15 January 2009, fl., *A.M. Amorim 7747* (CEPEC); ibid., 16 January 2009, fr., *A.M. Amorim 7771* (CEPEC, SPF); ibid., 6 June 2006, fr., *M.M.M. Lopes 810* (CEPEC). Ibirapitanga, Reserva Municipal Cachoeira do Pau, 19 March 2003, fr., *W.W. Thomas 13450* (CEPEC, SPF, UB). Ilhéus, área do CEPEC, 25 August 1981, fl., *J.L. Hage 1221* (SPF); CEPLAC, 31 October 1967, fr., *R.S. Pinheiro 342* (CEPEC). Jacobina, mata dos Bandeirantes, 8 April 2001, fr., *N.G. Jesus 1345* (CEPEC). Jequié, estrada para Serra dos Brejos, 5 February 2004, fl., *W.W. Thomas 13828* (CEPEC). Lençóis, Chapadinha, entrada da mata do Grotão, fenda na Serra do Brejão, 25 April 1995, fl., *M.C. Ferreira 1810* (ALCB, CEPEC, HRB, SPF); Parque Nacional da Chapada Diamantina, 23 February 2003, fr., *P. Fiaschi 1345* (CEPEC); ibid., rio Mandassaia, Barro Branco, 22 January 2000, fl., *A.A. Ribeiro-Filho 6* (ALCB); Serra da Chapadinha, 25 April 1995, fl., *M.C. Ferreira 1810* (K); ibid., 5 February 1995, fr., *A.M. Giulietti 1572* (RB) ibid., 8 July 1996, fr., *H.P. Bautista 3482*

(CEPEC, K, SPF). Palmeiras, Chapadinha, próximo ao rio Mucugezinho, rodovia Lençóis-Seabra, ca. 21 km NW de Lençóis, 17 February 1994, fl., *R.M. Harley CFCR (14176)* (ESA, SPF); ibid., 17 February 1994, fl., *R.M. Harley CFCR (14179)* (ESA, SPF); rio Capivara, trilha Lençóis-Fumaça, 5 April 1997, fl. and fr., *A.A. Conceição 491* (SPF); Palmeiras, Serra da Chapadinha, 28 April 1995, fr., *A. Pereira 1901* (CEPEC, K). Rio de Contas, mata da base do pico de Itobira, 29 January 1999, fr., *F.H.F. Nascimento 105* (CEPEC). Salvador, Jardim Botânico de Salvador, 12 May 2005, fl., *E.P. Queiroz 1301* (CEPEC); ibid., 25 November 2005, fl., *E.P. Queiroz 1255* (CEPEC). **Espírito Santo:** Águia Branca, Santa Luzia, 18 May 2007, fl., *V. Demuner 3992* (MBML); ibid., 18 October 2006, fl., *V. Demuner 2852* (MBML); ibid., 3 October 2007, fl., *H.Q. Boudet 3479* (MBML). Aracruz, Comboios, 28 September 1993, fl., *O.J. Pereira 4996* (RB, VIES); Reserva Biológica de Comboios, 27 September 1993, fl., *O.J. Pereira 4967* (RB, VIES); Vila do Riacho, 8 November 2010, fr., *J.M.L. Gomes 3955* (VIES). Guarapari, 7 August 1992, fl., *L.V. Rosa 255* (RB); afloramento rochoso entre Peracanga e Bacutia, 7 June 2015, fr., *A.C.S. Dal Col 376* (VIES); Parque Estadual de Setiba, 12 August 1992, fl., *L.V. Rosa 265* (RB, VIES); ibid., 8 July 1992, fl., *L.C. Fabris s.n.* (RB); Parque Estadual Paulo César Vinha, 10 October 2015, fr., *D.T. Wandekoken 94* (VIES); ibid., 14 October 1996, fr., *J.M.L. Gomes 2225* (VIES); ibid., 14 October 1999, fl., *A.M. Assis 738* (VIES); ibid., 16 September 1999, fr., *A.M. Assis 726* (VIES); ibid., 28 August 1996, fl., *J.M.L. Gomes 2205* (VIES); ibid., 28 August 1996, fl., *J.M.L. Gomes 2219* (VIES), 31 August 1998, fl., *A.M. Assis 535* (VIES), 5 September 1998, fl., *A.M. Assis 619* (VIES); Setiba, 12 August 1992, fl. and fr., *L.V. Rosa 267* (VIES); ibid., 12 August 1992, fl., *L.V. Rosa 275* (VIES); ibid., 12 August 1992, fl., *L.V. Rosa 277* (VIES); ibid., 15 May 1992, fr., *L.C. Fabris 823* (VIES); ibid., 7 August 1992, fl., *L.V. Rosa 255* (VIES). Santa Leopoldina, fazenda Caioaba, 9 August 2006, fl., *L.F.S. Magnago 1250* (MBML). Santa Maria de Jetibá, Belém, 19 November 2002, fr., *L. Kollmann 5752* (MBML). Santa Teresa, Estação Biológica Santa Lúcia, 13 May 1993, fr., *L.D. Thomaz 1463* (MBML). Vila Velha, 18 September 1983, fl., *B. Weinberg 437* (MBML); Interlagos, 11 October 1996, fr., *O. Zambom 303* (VIES); ibid., 18 September 1983, fl. and fr., *B. Weinberg s.n.* (MBML); ibid., 18 September 1997, fl., *O. Zambom 329* (VIES); ibid., 27 June 1996, fr., *O. Zambom 311* (VIES); ibid., 3 March 1997, fr., *O. Zambom 314* (VIES); Reserva Ecológica de Jacarenema, 23 October 1996, fr., J.M.L. *Gomes 2229* (VIES); ibid., 3 September 1989, fl., *L.D. Thomaz 583* (GUA, RB, VIES); ibid., 3 September 1989, fl., *L.D. Thomaz 592* (RB, VIES); ibid., 3 September 1989, fl., *L.D. Thomaz 593* (RB, VIES); ibid., 3 September 1989, fl., *L.D. Thomaz 595* (VIES); ibid., 3 September 1989, fl., *L.D. Thomaz 597* (RB, VIES); ibid., 8 October 1997, fl., *R.L. Dutra 275* (VIES); ibid., September 1989, fr., *L.D. Thomaz 600* (RB, VIES); restinga da Barra do Jucu, próximo a morada do Sol, em frente ao camping Club, 28 September 1999, fl., *C.N. Fraga 496* (ESA, MBML, UB). **Minas Gerais:** Rio Preto, Povoado do Funil, 28 November 2012, fr., *J.E.Q. Faria 3102* (UB). **Rio de Janeiro:** Armação de Búzios, morro das Emerências, 22 August 2008, fr., *J.C. Lopes 10* (SPF). Cabo Frio, distrito de Tamoios, condomínio Florestinha, 6 December 2001, fr., *G.S.Z. Rezende 37* (RB). Itatiaia, Parque Nacional de Itaiaia, trilha do Hotel Simon para os Três Picos, 9 November 1993, fl. and fr., *M.P.M. Lima 234* (K, MBM); ibid., 9 November 1993, fl., *M.P.M. Lima 234* (CEPEC). Mangaratiba, Ilha da Marambaia, 2 July 1999, fl., *M.C. Souza 126* (RB); ibid., 3 January 2002, fl. and fr., *L.F.T. Menezes 884* (RB); ibid., Praia da Armação, 24 October 1999, fl., *L.F.T. Menezes 510* (RB); ibid., 24 October 1999, fl., *L.F.T. Menezes s.n.* (RB); ibid., praia voltada para Baía de Sepetiba, 30 September 2001, fl., *A.L. Melo s.n.* (RB). Niterói, Parque Estadual da Serra da Tiririca, 21 August 2002, fl., *A.A.M. Barros 1668* (RB). Nova Iguaçu, Tinguá, 14 November 2001, fr., *H.C. de Lima 5940* (RB). Paraty, Praia Negra, 13 March 1992, fl., *C.* Farney 3094 (RB). Rio de Janeiro, bosque da Barra, 23 January 2002, fr., *s.c., s.n.* (RB); Jacarepaguá, 15 September 1969, fr., *D. Sucre 5935* (CEPEC); ibid., 23 September 1969, fr., *D. Sucre 5959* (CEPEC); ibid., lado sul-oeste da pedra de Itaúna, 15 September 1969, fr., *D. Sucre 5935* (K, SP); ibid., lado sul da pedra de Itaúna, 2 September 1969, fl., *D. Sucre 5896* (K); ibid., 23 September 1969, fr., *D. Sucre 5959* (K, SP); ibid., lado leste da pedra de Itaúna, 8 October 1970, fl., *D. Sucre 7283* (K). São Pedro da Aldeia, Serra de Sapiatiba, vertente norte, 22 September 2000, fl., *C. Farney 4214* (RB). Saquarema, Reserva Jacarepiá, 22 November 1996, fr., *C. Farney 3556* (RB). Teresópolis, Parque Nacional da Serra dos Órgãos, 20 November 2006, fl., *E.J. Lucas 589* (UB). Tijuca, 6 March 1972, fl., *D. Sucre 8204* (RB). **São Paulo:** Juquiá, 4 April 1961, fl., *J. Mattos 8873* (CEPEC); ibid., 4 April 1961, fl. and fr., *J. Mattos 8872* (SP); ibid., 4 April 1961, fl., *J. Mattos 8872* (SP). Pariquera-Açu, Estação Experimental do IAC, 10 January 1995, fr., *L.C. Bernacci 964* (SP, SPF). São Bernardo do Campo, Parque Caminhos do Mar, 31 October 1990, fr., *S. Ferreira s.n.* (SP). São Vicente, Parque Estadual Xixová-Japuí, 5 September 2003, fl., *J.A. Pastore 1255* (SPSF).

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LITERATURE CITED

Bachman, S., J. Moat, A.W. Hill, J. Torre and B. Scott. 2011. Supporting red list threat assessments with GeoCAT: Geospatial conservation assessment tool. *ZooKeys* 150: 117–126. doi: 10.3897/zookeys.150.2109

Berg, O.C. 1856a. Revisio Myrtacearum huc usque cognitarum s. Klotzschii “Flora Americae aequinoctialis” exhibens Myrtaceas. *Linnaea* 27: 129–384.

Berg, O.C. 1856b. Revisio Myrtacearum huc usque cognitarum s. Klotzschii “Flora Americae aequinoctialis” exhibens Myrtaceas. *Linnaea* 27: 385–472.

Berg, O.C. 1857. Myrtaceae in C. F. P. de Martius (Ed). *Flora Brasiliensis* 14(1): 1–468.

Berg, O.C. 1859. Myrtographiae Brasiliensis Supplementum in C.P.F. Martius (Ed). *Flora Brasiliensis* 14(1): 530–636.

Bünger, M.O., F.F. Mazine, F. Forest, M.L. Bueno, J.R. Stehmann and E.J. Lucas. 2016a. The evolutionary history of *Eugenia* sect. *Phyllocalyx* (Myrtaceae) corroborates historically stable areas in the southern Atlantic forests. *Annals of Botany* 118: 1209–1223. doi: 10.1093/aob/mcw209

Bünger, M.O., F.F. Mazine, E.J. Lucas and J.R. Stehmann. 2016b. Circumscription and synopsis of *Eugenia* section *Speciosae* Bünger and Mazine (Myrtaceae). *PhytoKeys* 61: 73–80. doi: 10.3897/phytokeys.61.7904

Hickey, L.J. 1973. Classification of the architecture of dicotyledonous leaves. *American Journal of Botany* 60(1): 17–33. doi: 10.2307/2441319

IUCN. 2016. Standards and Petitions Subcommittee of the IUCN Species Survival Commission *Guidelines for Using the IUCN Red List - Categories and Criteria. Version 12*. Available from: http://www.iucnredlist.org/documents/RedListGuidelines.pdf. (accessed 26 Jul 2016).

Kausel, E. 1967. Lista de las Mirtáceas e Leptospermáceas Argentinas. *Lilloa* 32: 323–368.

Kiaerskou, H. 1893. Enumeratio Myrtacearum Brasiliensium in E. Warming (Ed). *Symbolarum ad floram Brasiliae Centralis cognoscendam*: 1–200.

Landrum, L.R. and M.L. Kawasaki. 1997. The Genera of Myrtaceae in Brazil: an Illustrated Synoptic Treatment and Identification Keys. *Brittonia* 49(4): 508. doi: 10.2307/2807742

Lucas, E.J. and M.O. Bünger. 2015. Myrtaceae in the Atlantic forest: their role as a ‘model’ group. *Biodiversity and Conservation* 24(9): 2165–2180. doi: 10.1007/s10531-015-0992-7

Lucas, E.J., S.A. Harris, F.F. Mazine, S.R. Belsham, E.M. Nic Lughadha, A. Telford, P.E. Gasson and M.W. Chase. 2007. Suprageneric phylogenetics of Myrteae, the generically richest tribe in Myrtaceae (Myrtales). *Taxon* 56(4): 1105–1128. doi: 10.2307/25065906

Mattos, J.R. 1981. Novidades taxonômicas em plantas do Brasil. *Loefgrenia* 76: 1–3.

Mattos, J.R. 1990. Novidades taxonômicas em Myrtaceae - VI. *Loefgrenia* 99: 1–6.

Mattos, J.R. 2005. Considerações sobre *Calycorectes* O.Berg. *Loefgrenia* 120: 1–24.

Mazine, F.F., M.O. Bünger, J.E.Q. Faria, E. Lucas and V.C. Souza. 2016. Sections in *Eugenia* (Myrteae, Myrtaceae): nomenclatural notes and a key. *Phytotaxa* 289(3): 225–236.

Mazine, F.F., V.C. Souza, M. Sobral, F. Forest and E. Lucas. 2014. A preliminary phylogenetic analysis of *Eugenia* (Myrtaceae: Myrteae), with a focus on Neotropical species. *Kew Bulletin* 69(2): 1–14. doi: 10.1007/s12225-014-9497-x

McNeill, J., F.R. Barrie, W.R. Buck, V. Demoulin, W. Greuter, D.L. Hawksworth, P.S. Herendeen, S. Knapp, J. Prado, W.F. Prud'Homme Van Reine, G.F. Smith, J.H. Wiersema and N.J. Turland. 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). *Regnum Vegetabile*: 1–140.

McVaugh, R. 1969. The Botany of the Guyana Highland - Part VIII: Myrtaceae. *Memoirs of the New York Botanical Garden* 18(2): 55–286.

Niedenzu, F. 1893. Myrtaceae in A. Engler and K. Prantl (Eds). *Die Natürlichen Pflanzenfamilien*: 57–105.

Payne, W.W. 1978. A Glossary of Plant Hair Terminology. *Brittonia* 30(2): 239–255.

Peixoto, A.L., I.M. Silva, O. José, M. Simonelli and R.M. Jesus. 2008. Tabuleiro Forests North of the Rio Doce: Their Representation in the Vale do Rio Doce Natural Reserve, Espírito Santo, Brazil. *Memoirs of the New York Botanical Garden* 100: 319–350.

QGIS Development Team. 2017. *Quantum GIS Geographic Information System, Open Source Geospatial Foundation Project*. Available from: http://qgis.osgeo.org.

Reginato, M. 2016. monographaR: An R package to facilitate the production of plant taxonomic monographs. *Brittonia* 68(2): 212–216. doi: 10.1007/s12228-015-9407-z

Sobral, M. 2003. *A família Myrtaceae no Rio Grande do Sul*. Editora Unisinos, São Leopoldo.

SOS Mata Atlântica. 2017. *Atlas dos remanescentes florestais da Mata Atlântica, período de 2015 a 2016*. São Paulo.

Souza, M.C. 2009. *Estudos taxonômicos em Myrtaceae no Brasil: Revisão de Neomitranthes Kausel ex D.Legrand e contribuição ao conhecimento da diversidade e conservação de Plinia L. no Domínio Atlântico*. PhD thesis. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro.

Thiers, B. 2017. Index Herbariorum: A global directory of public herbaria and associated staff. *New York Botanical Garden's Virtual Herbarium*. Available from: http://sweetgum.nybg.org/ih/ (accessed 26 Jul 2017).

Vasconcelos, T.N.C., E.J. Lucas, J.E.Q. Faria and Prenner, G. 2018. Floral heterochrony promotes flexibility of reproductive strategies in the morphologically homogeneous genus *Eugenia* (Myrtaceae). *Annals of Botany* 121(1): 161–174. doi: 10.1093/aob/mcx142

Vasconcelos, T.N.C., G. Prenner, M.O. Bünger, P.S. De-Carvalho, A. Wingler and E.J. Lucas. 2015. Systematic and evolutionary implications of stamen position in Myrteae (Myrtaceae). *Botanical Journal of the Linnean Society* 179(3): 388–402.

Vasconcelos, T.N.C., G. Prenner, M.F. Santos, A. Wingler and E.J. Lucas. 2017. Links between parallel evolution and systematic complexity in angiosperms — A case study of floral development in *Myrcia* s. l. (Myrtaceae). *Perspectives in Plant Ecology, Evolution and Systematics* 24: 11–24. doi: 10.1016/j.ppees.2016.11.001

WCSP (2017) World Checklist of Selected Plant Families. *Facilitated by the Royal Botanic Gardens, Kew*. Available from: apps.kew.org/wcsp/myrtaceae (accessed 12 Aug 2017).

Wilson, P.G. 2011. Myrtaceae in K. Kubitzki (Ed). *The families and genera of vascular plants. Flowering plants, eudicots: Sapindales, Cucurbitales, Myrtaceae*. Springer-Verlag, Berlin.

APPENDIX 1.

I.i. List of accepted taxa ordered alphabetically

1. *Eugenia acutata*
2. *Eugenia brevistyla*
3. *Eugenia guanabarina*
4. *Eugenia longohypanthiana*
5. *Eugenia majepensis*
6. *Eugenia neoriedeliana*
7. *Eugenia paradisiaca*
8. *Eugenia subterminalis*
9. *Eugenia vattimoana*
10. *Eugenia zuccarinii*

I.ii. Examined specimens are arranged by collector (surname, initials), followed by collector's number (s.n. = without collector), and by the numerical list of taxa (I.i).

Aguiar, O.T. 194 (8); 206 (8); 466 (8); 530 (8); 1282 (8); s.n. SPSF8671 (8); s.n. SPSF8789 (8)

Almeida, J. 68 (5)

Almeida, K.C. 128 (8)

Almeida, R.S. 31 (8)

Amancio, A.M. 161 (8); 197 (8)

Amaral, G. 4A (8)

Amorim, A.M. 6406 (2); 7747 (10); 7771 (10)

Andrade, P.M. 716 (2); 8730 (1)

Angeli, C. 191 (9)

Arantes, A.A. 590 (8); 689 (8)

Araujo, D.S.D. 1241 (9); 8150 (9); 9581 (3)

Arbocz, G.F. 749 (1); 891 (1)

Assis, A.M. 535 (10); 619 (10); 726 (10); 738 (10)

Assis, M.A. s.n. MBM194256 (8)

Augusto, J. s.n. R (8)

Baitello, B. 2399 (8)

Baitello, J.B. 710 (8); 730 (8)

Balansa, B. 1289 (8); 1313 (8); 3047 (8); 4496 (8)

Barbosa, E. 957 (8); 3111 (8)

Barkart 14679 (8)

Barreto, K.D. 1778 (1); 1840 (2)

Barros, A.A.M. 1668 (10)

Barros, F. 1583 (2); 1753 (2); 1759 (2); 2357 (1); 2363 (1)

Bastos, E.B. 14 (2)

Bautista, H.P. 3482 (10)

Belém, R.P. 1793 (8); 2684 (3)

Bernacci, L.C. 964 (10)

Bernardi, L. 18109 (8); 18228 (8); 18276 (8); s.n. BM000591163 (8)

Bertoncini, A.P. 917 (8); 1066 (8)

Bertoni 2641 (8)

Bertoni, J.E.A. 504 (2)

Bianchini, E. s.n. ESA113076 (8)

Bicudo, L.R.H. 248 (8)

Blanchet s.n. G (2)

Blanchet, J.S. 103 (8)

Blanchet, M. 69 (3); 103 (8); 2340 (8)

Bonaldi, R.A. 991 (2)

Boudet, H.Q. 3479 (10); 3496 (5); 3512 (2)

Bovini, M.G. 1107 (2); 1131 (2)

Brack, P. s.n. MBM73968 (8)

Braga, H.N. 272 (9); 641 (9)

Bresolin, A. 628 (2); 648 (2); 981 (8)

Brina, A.E. s.n. SP330670 (1)

Britez, R.M. 1781 (2)

Brito, T.H. 4066 (3)

Britto, F. 36/141 (2)

Brotto, M.L. 1377 (2)

Burchell, W.J. 3672-2 (10)

Buttura, E. 241 (8)

Campos, O. s.n. ESA111966 (8)

Canal, M. 142 (3)

Carmo, M.R.B. 635 (8)

Carneiro, J. 90 (8); 1382 (8)

Carneiro, J.S. 541 (8)

Carvalho-Silva, M. 78 (1)

Carvalho, G.M. 279 (8)

Casaretto 1871 (2)

Casas, J.F. 957 (8); 3527 (8)

Cavalcanti, D.C. 166 (2)

Cavalo, C.P. 219 (8); 912 (8)

Ceccantini, G.C.T. 3039 (1)

Chacon, R.G. 1243 (1)

Chaddad-Jr., J. 148 (1); 152 (1)

Chagas, F. 568 (8); 1449 (8); 1581 (8); 1898 (8); 1946 (8); 1957 (8); 2199 (8); s.n. UB (8)

Chodat, R. s.n. G (8)

Cielo-Filho, R. 268 (1); 389 (2); 408 (8)

Claussen, M. 740 (1); s.n. G (1)

Coelho, J.P. 3081 (8)

Coelho, R. 45 (3)

Coleta do Arboreto s.n. RB343649 (1)

Conceição, A.A. 491 (10)

Cordeiro, I. 793 (1)

Cordeiro, J. 4693 (8)

Costa, I.G. 611 (4); 651 (4)

Costa, I.R. 595 (3)

Costa, M.P. 10 (1); 28 (1)

Dal-Col, A.C.S. 376 (10)

Damasceno, R.N. 1161 (9)

Daneu, L. 275 (8)

Davis, P.H. 60821 (2)

Degen, R. 376 (8); 587 (8)

Demuner, V. 2852 (10); 3992 (10); 4365 (8); 4612 (5)

Dias, A.C. 8 (2); s.n. SPSF8828 (2); s.n. SPSF6139 (8)

Dias, H.M. 297 (3)

Dombrowki, L.T. 10728 (2)

Duarte, A.P. 6058 (3); 6066 (3)

Durigan s.n. RB397924 (8); s.n. RB397897 (8); s.n. RB397896 (8)

Durigan, G. s.n. SPSF13226 (8); s.n. ESA110099 (8)

Dusén, P. 8957 (2)

Dutra, R.L. 275 (10)

Esteves, R. 76 (8)

Fabris, L.C. 823 (10); s.n. RB422411 (10)

Falcão, J.I.A. 986 (2)

Faria, J.E.Q. 245 (1); 1000 (2); 1030 (1); 3102 (10); 3129 (2); 3742 (8); 3755 (8); 3949 (1)

Farias, D.S. 353 (3)

Farias, G.L. 206 (1); 208 (8); 295 (8)

Farney, C. 3094 (10); 3140 (3); 3212 (3); 3324 (3); 3556 (10); 4036 (3); 4214 (10); 4441 (9)

FEEP 239 (8)

Felitto, G. 743 (2); 905 (8)

Fernandes, D. 238 (9)

Ferreira, M.C. 1810 (10)

Ferreira, S. s.n. SP270398 (10)

Fiaschi, P. 1345 (10); 1685 (3); 3141 (5)

Fiebrig, K. 100 (8); 176 (8); 4926 (8); 5422 (8); 5463 (8); 5869 (8)

Flores, D. s.n. GUA45027 (2)

Flores, T.B. 1226 (2); 1528 (2); 1643 (2)

Folli, D.A. 449 (3); 780 (3); 1394 (3); 1399 (3); 6594 (4)

Fontella, J. 1213 (8)

Fontella, P.J. 424 (3)

Forzza, R.C. 2234 (2)

Fraga, C.N. 496 (10)

Franco, G.A.D.C. 1281 (8)

Furtado, P.P. 129 (8); 130 (8)

Gandolfi, S. 15618 (1)

Gardner 5462 (9)

Gasper, A.L 917 (8)

Gentry, A. 49815 (2); 49837 (2)

Geol, C. s.n. R (8)

Giannotti, E. s.n. ESA118278 (1)

Giaretta, A. 991 (3); 1026 (3); 1035 (3); 1099 (3); 1226 (3); 1330 (3); 1360 (3); 1460 (1); 1478 (2); 1489 (6); 1493 (2); 1500 (4); 1501 (4); 1502 (4); 1629 (3); 1630 (3); s.n. VIES23688 (3)

Gibbs, P.E. 3554 (1)

Giraldi, C. s.n. SP332938 (8)

Giulietti, A.M. 1572 (10)

Glaziou 8898 (4); 9435 (4)

Goetzke, S. 100 (8); 162 (8)

Gomes, J.M.L. 2205 (10); 2219 (10); 2225 (10); 2229 (10); 3955 (10)

Gonzaga, L. s.n. SP338755 (8)

Grupo Pedra do Cavalo 912 (8)

Guillaumon, J.R. s.n. SPSF31156 (1); s.n. SPSF30367 (1); s.n. MBM277940 (1); s.n. ESA118673 (1); s.n. ESA118284 (1)

Hage, J.L. 1221 (10)

Hahn, W. 1961 (8)

Hans, D. 181 (2)

Harley, R.M. CFCR(14176) (10); CFCR(14179) (10)

Hashimoto, G. 16680 (8); 16747 (8); 16760 (8)

Hatschbach, G. 5174 (2); 5214 (2); 6362 (8); 7383 (8); 8440 (2); 9312 (8); 10175 (2); 10759 (2); 11913 (2); 13073 (2); 15324 (2); 15741 (8); 16954 (8); 16996 (8); 17034 (8); 17046 (8); 17058 (8); 19234 (2); 19500 (2); 19674 (2); 19734 (2); 19897 (2); 19907 (2); 20134 (2); 24168

(8); 30938 (2); 35107 (1); 40564 (8); 43195 (8); 48490 (8); 52330 (2); 53526 (2); 54927 (2); 56770 (2); 59689 (8); 59690 (8); 61319 (8); 61325 (8); 68366 (5); 69267 (8); 77221 (8)

Heringer, E.P. 14377-A (1)

Huidobro, A.M.R. 4291 (8); 4371 (8); s.n. P05229237 (8)

Ildefonso, D. s.n. SPSF1014 (1)

Ivanauskas, N.M. 246 (2); 892 (2); 5020 (1); s.n. SP292772 (8)

Jaramir 5462 (9)

Jarenkow, J.A. 1740 (2); 2197 (8)

Jesus, N.G. 1345 (10)

Jiménez, B. 1483 (8); 1486 (8); 1500 (8); 1506 (8); 1728 (8); 1746 (8)

Junqueira, D.I. 565 (1)

Kinoshita, L.S. 95-57 (1)

Kirizawa, M. 689 (8)

Klein, R. 1552 (2); 1585 (2); 1617 (2); 7902 (2); 7906 (2); 7914 (2); 8424 (2); 9696 (2)

Kolb, R.M. s.n. UEC (8)

Kollmann, L. 5752 (10)

Kozera, C. 3666 (8)

Krapovickas, A. 44582 (8); 45691 (8)

Kuehn, E. 1189 (1)

Kuhlmann, M. 2799 (8)

Kuhlmman, J.G. 6141 (9); s.n. RB111586 (4)

Kummrow, R. 2320 (2); 2537 (2)

Kurtz, B.C. s.n. RB332180 (2)

Landrum, L. 4009 (2)

Leitão-Filho, H.F. 1050 (2); 11792 (1); 20816 (2); 32298 (1)

Leite, E.C. 29253 (2)

Leonello, A.C. s.n. RB453384 (1)

Lima, C.R. 215 (8); 219 (8); 246 (8)

Lima, H.C. 2222 (2); 2244 (6); 2273 (7); 2302 (6); 2396 (2); 4347 (7); 5940 (10)

Lima, M.P.M. 234 (10)

Lindeman, J.C. 946 (8); 962 (8); 3430 (8)

Lira-Neto, J.A. 463 (2)

Lobão, A. 163 (9)

Lobão, A.Q. 151 (3)

Lobo, P.C. 29370 (5)

Lopes, B. s.n. SPSF14827 (1)

Lopes, J.C. 10 (10)

Lopes, M.M.M. 810 (10); 1531 (3)

Lucas, E.J. 226 (2); 589 (10)

Macedo, E.E. 276 (1)

Magalhães, M. s.n. IAN108115 (2)

Magnago, L.F.S. 1250 (10)

Mamede, M.C.H. 334 (2)

Mansano, V.F. 6-352 (2)

Manso, A.L.P.S. 36 (8)

Marquete, R. 285 (2); 891 (2); 1768 (2)

Martinelli, G. 9905 (6); 9926 (6); 9971 (2); 9986 (2); 10202 (8)

Martins, A.B. 31411 (2)

Martins, D. 91 (9)

Martins, F.R. 1611 (1); 10053 (2)

Martins, R.F.A. 31 (3); 161 (3)

Mathes, L.A.F. 19E (1); 21B (1); 124A (1); 275D (1); 293D (1); 295D (1); 300D (1); 468D (1); 654D (1); 7736 (1)

Matsumoto, K. 818 (3); 819 (3)

Mattos-Silva, L.A. 614 (3); 2515 (3)

Mattos, J. 8872 (10); 8873 (10); 9633 (1); 14178 (2); 14182 (1); 14184 (2); 14211 (1); 16322 (1); 16387 (1); 19818 (8)

Mattos, J.R. 9528-a (8); 14085 (8)

Mautone, L. 243 (4)

Mazine, F.F. 460 (2); 974 (8); 980 (8); 992 (2); 993 (2); 996 (2); 1009 (2); 1010 (2); 1086 (8); 1088 (8)

Melo-Jr., J.C.F. 560 (1)

Melo, A.L. s.n. RB531678 (10)

Melo, M.M.R.F. 321 (8)

Melo, P.H.A. 920 (1)

Mendaçolli, S.L.J. 1416 (1)

Menezes, L.F.T. 510 (10); 884 (10); 1778 (3); 2042 (3); s.n. RB531674 (10)

Miers, J. 3802 (9); s.n. P05234716 (9); s.n. BM000043151 (4); s.n. P05234715 (9)

Milhomens, L.C. 22 (1)

Milla, A.P. 121 (8); 131 (8)

Montalvo, E.A. 100 (3)

Moraes, P.L.R. 366 (2); 737 (2); 738 (2); 752 (2); 782 (2); 1060 (2); 1288 (2); 2494 (1)

Mori, S.A. 9839 (8); 10212 (8)

Mynssen, C. 316 (2)

Nascimento, F.H.F. 105 (10)

Negrelle, R. A-14 (8); A-394 (2)

Nic-Lughadha, E.M. 214 (8)

Novaes, C. 1144 (1); 1321 (1)

Occhioni, P. 2263 (4); 7981 (6)

Ogasawara, H.A. 241 (3)

Oliveira, A.G. 572 (3); 876 (3); 1135 (3)

Oliveira, C.A.L. 1940 (9)

Oliveira, J.G. 92 (1)

Oliveira, P.P. 82A (5); 82B (5); 1006 (2); 4167 (2)

Oliveira, R.R. 624 (9)

Passos-Júnior, L.A. 851 (2)

Pastore, J.A. 203 (8); 498 (8); 1073 (1); 1255 (10)

Pastore, U. 104 (8)

Patricia 49-M (8)

Pedroni, F. 31318 (2); 31319 (2)

Peña-Chocarro, M. 1591 (8)

Penha, A.S. 24 (1)

Pereira-Silva, G. 3530 (1)

Pereira, A. 1901 (10)

Pereira, D.L. 15 (8); 16 (8); 17 (8); 19 (8)

Pereira, O.J. 1032 (9); 3764 (3); 3829 (3); 3837 (3); 3879 (3); 4721 (3); 4826 (3); 4835 (3); 4967 (10); 4996 (10); 5138 (3); 5212 (3)

Peres, A.L.S.S. 372 (3)

Peron, M. 875 (8)

Pessoa, S.V.A. 790 (2)

Pessoal do Horto Florestal s.n. RB139506 (9)

Pickel, D.B.J. s.n. SPSF739 (8); s.n. SPSF731 (8); s.n. SP47538 (1); s.n. SPSF2843 (1); s.n. SP1300 (8)

Pimentel, L.B. s.n. RB593367 (2)

Pinheiro, R.S. 342 (10); 1692 (3)

Pirani, J.R. 444 (8); 3390 (5)

Pohl, J. 5849 (4)

Pott, A. 8208 (8)

Prado, C.S. 410 (8); 1811 (8)

Prata, G.R. 47 (8)

Proença, C. 3476 (1)

Silveira, N. 1694 (8)

Simão-Bianchini, R. 209 (1)

Simões, A.O. 350 (1)

Soares-Silva, L.H. 512 (8); 568 (8); 574 (8); 640 (8); 647 (8); 1898 (8)

Sobral, M. 1268 (8); 7489a (2); 14454 (1); 14571 (2)

Soria, N. 2298 (8)

Souza, H.M. s.n. SP84736 (1); s.n. MBM314458 (1)

Souza, J.P. 397 (8)

Souza, M.C. 126 (10); 351 (3); 385 (3)

Souza, V.C. 30126 (2)

Spichiger, R. 1566 (8); 1591 (8); 5011 (8)

Spitzner, E. 163 (2)

Sposito, T.C. s.n. MBM251945 (2)

Staggemeier, V.G. 111 (2)

Stehmann, J.R. s.n. RB388968 (8)

Stival-Santos, A. 825 (2)

Sucre, D. 5543 (2); 5896 (10); 5903 (3); 5905 (3); 5935 (10); 5959 (10); 7283 (10); 8204 (10)

Takahasi, A. 57 (2); 65 (2)

Tamashiro, J.Y. 1628 (1); 1647 (1); 18803 (8); 18855 (8)

Teague, G.W. 669 (8)

Teixeira, A. s.n. MBM194255 (8)

Temeirão-Neto, E. 969 (8); 2558 (8)

Thomas, W.W. 13450 (10); 13828 (10)

Thomaz, L.D. 583 (10); 592 (10); 593 (10); 595 (10); 597 (10); 600 (10); 1463 (10)

Toniato, M.T.Z. 78 (8)

Tozzi, A.M.G.A. s.n. SPF114924 (1)

Tressens, S. 4805 (8)

Tressens, S.G. 3379 (8)

Ule, E. 919 (2)

Urbanetz, C. 209 (2); s.n. UEC (1)

Velloso, H. 1006 (2)

Verdi, M. 2625 (2); 6538 (1)

Versieux, L.M. 292 (6)

Vervloet, R.R. 2717 (2)

Vieira, F.C.S. 511 (2); 1856 (2)

Wandekoken, D.T. 94 (10)

Wasum, R. 1580 (8)

Webster, G.L. 29677 (3)

Wechter 1465 (2)

Weinberg, B. 437 (10); s.n. MBML5145 (10)

Zambom, O. 303 (10); 311 (10); 314 (10); 329 (10)

Zardini, E. 3616 (8); 3632 (8); 3643 (8)

Zardini, E.M. 42908 (8); 43330 (8); 43396 (8); 43402 (8); 43413 (8); 43425 (8); 43454 (8); 43466 (8); 43487 (8); 45220 (8); 46306 (8)

Ziller, S.R. 575 (2); 1077 (8); 1124 (8); 1143 (8)

Zipparro, V.B. 818 (1); 1789 (2); 2024 (1); 2029 (1); 2031 (1); 2032 (1); 2034 (1); 2036 (1); 2059 (1)

I.iii. Unknown collector and collector number

P00047455 (8); SPF00309553 (8); RB273824 (8); RB262121 (8); RB262106 (8); R164359 (2); RB682694 (10)

Conclusão geral

Os resultados apresentados nestes trabalhos trouxeram uma nova perspectiva para a sistemática de *Eugenia*, sobretudo, criando um novo paradigma para intepretação da evolução da flor e da inflorescência no gênero. O cálice fundido em *Eugenia* foi revelado como um carácter homoplástico, embora seja diagnóstico para alguns clados como mostrado pelo sinal filogenético. Como consequência, hipóteses de homologia sobre os verticilos do perianto trouxeram uma reinterpretação das flores não usuais de *Eugenia*. A sinonimização de gêneros atualmente segregados, mas que emergiram incluídos na filogenia de *Eugenia*, possuem sustentação morfológica por meio desta nova interpretação. Além disso, espécies com circunscrição incerta, dado o elevado nível de mudanças em suas flores, também foram confirmadas como fazendo parte de *Eugenia*. Isso implica que processos de diversificação em *Eugenia*, embora tenham sido conservativos quanto à morfologia da flor para a maior parte das espécies, também foram importantes para que o cálice fundido pudesse se fixar em algumas linhagens, evoluindo diversas vezes. Nesse contexto, a diversificação de *Eugenia* é um processo complexo que culminou em flores não tão homogêneas como se pensava. Esse novo paradigma também foi incorporado ao âmbito taxonômico. Uma seção foi restabelecida, recircunscrita e revisada, sustentada por dados morfológicos e moleculares.

A inflorescência de *Eugenia* também foi foco desta tese, sendo analisada sob um ponto de vista evolutivo por meio de uma abordagem integrativa. A combinação da ontogenia com a morfologia madura da inflorescência, forneceu arcabouço suficiente para distinguir arranjos fundamentais daqueles que são resposta da influência exógena. Essa abordagem é sugerida para estudos futuros, pois, permitiu o reconhecimento do padrão racemoso de ramificação como ancestral e o padrão cimoso de ramificação como secundário na evolução de *Eugenia*. Além disso, o padrão de crescimento auxotélico está intimamente relacionado ao surgimento da fase reprodutiva. Assim, a reconstrução filogenética dos padrões descritos auxiliou a elaboração de hipóteses de homologia polarizadas. Isso resultou em uma nova proposta de terminologia de inflorescência de *Eugenia*, construída para harmonizar aspectos tipológicos sob uma óptica evolutiva, sem perder a perspectiva de aplicação prática. Aspectos particulares da inflorescência também foram revelados como recorrentes em clados altamente diversos, sugerindo que mudanças nos arranjos podem desempenhar um papel importante para os processos de diversificação de *Eugenia* na região Neotropical. A flexibilidade e permuta entre os padrões básicos também parece ser um fator que influenciou sua adaptabilidade.