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Estudo Sistemático de *Myrcia* sect. *Aulomyrcia* (Myrtaceae): O Grupo das Verticiladas

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“It is good to have an end to journey toward, but it is the journey that matters, in the end” (Ernest Hemingway).

RESUMO

Myrtaceae é uma família de angiospermas com distribuição pantropical, representada pela tribo Myrteae na região neotropical. Suas espécies são componentes fundamentais para a biodiversidade das florestas da região, seus frutos fazem parte da sustentação da fauna. Myrtaceae aparece nos primeiros lugares na lista das famílias mais ricas em espécies nas florestas neotropicais. Myrcia é um dos gêneros desta tribo, constituído por c. 780 espécies arbustivas e arbóreas distribuídas em nove seções. Uma destas seções é Myrcia sect. Aulomyrcia, cujas espécies são caracterizadas pelo hipanto prolongado acima do ápice do ovário. O “Grupo das Verticiladas” constitui-se de um clado emergente em análise filogenética da seção Aulomyrcia, composto por 22 espécies caracterizadas por suas folhas grandes, verticiladas, e inflorescências terminais assimétricas e espiraladas. A variação morfológica críptica no “Grupo das Verticiladas”, de espécies muito similares tanto nas características vegetativas como nas reprodutivas, apresenta um desafio às taxonomistas. Esse padrão de variação dificulta a identificação e circunscrição das espécies do clado. O principal objetivo deste trabalho foi desvendar a sistemática do Grupo das Verticiladas a partir de uma perspectiva filogenética e morfológica. O Grupo das Verticiladas emergiu monofilético das análises com um bom suporte e foi caracterizado devidamente quanto à sua morfologia foliar, da inflorescência espiralada e assimétricas com raquis tomentosa, das brácteas persistentes e do indumento branco ou avermelhado no hipanto e abaxialmente nos lobos. Testamos a monofilia de Myrcia amazonica que emergiu não monofilética, com um padrão de agrupamento de espécimes que reflete distribuição geográfica. Myrcia neoestrellensis emergiu fora do Grupo das Verticiladas, e sim no grupo E da seção Aulomyrcia. Myrcia neodimorpha foi considerada mais próxima do clado F devido às folhas grandes, opostas decussadas e inflorescências com brácteas permanente e pubescência branca. O conjunto de características morfológicas e anatômicas foliares de 13 espécie do Grupo das Verticiladas foi descrito com o objetivo de providenciar dados para delimitação das espécies, quando combinados aos estudos filogenéticos e taxonômicos. Foi desenvolvido estudo taxonômico das espécies do grupo com descrições, ocorrência, fenologia, imagens e comentários. O Grupo das Verticiladas de Myrcia sect. Aulomyrcia é um grupo coeso filogeneticamente.
Palavras-chave: Myrteae; morfologia; filogenia; Myrtales; neotropicos; anatomia foliar.

ABSTRACT

Myrtaceae is an Angiosperm family with pantropical distribution, represented by tribe Myrteae in the neotropical region. The species of the tribe are fundamental components for the biodiversity of forests in the region, fruit from its species sustain the fauna. Myrtaceae appears in the top in lists of species richness in neotropical forests. *Myrcia* is one of the genera of tribe Myrteae, composed of c. 780 species of shrubs or trees, distributed in nine sections. One of these sections is *Myrcia* sect. *Aulomyrcia*, of which species are characterized by hypanthium prolonged beyond the ovary apex. The Verticillate Group is an emergent clade from the phylogenetic analyses of section *Aulomyrcia*, composed of 22 species, characterized by large, verticillate leaves, and terminal and asymmetric inflorescences. Morphological variation among the species of the Verticillate Group can be somewhat cryptic, because these species are very similar either in vegetative or sexual characters. These types of variation make it difficult to identify and circumscribe the species in the clade. The main goal of this study was to unravel the systematics of the Verticillate Group from a phylogenetic and morphological perspective. The Verticillate Group emerged monophyletic from our analyses with good support and it was characterized accordingly regarding leaf morphology, spiral asymmetric inflorescences with tomentose rachis, persistent bracts, and white or red pubescence in the hypanthium and abaxially in the lobes. We tested the monophyly of *Myrcia amazonica* that emerged not monophyletic with a grouping pattern that reflects geographic distribution. *Myrcia neoestrellensis* emerged outside of the Verticillate Group, in group E of section *Aulomyrcia*. Myrcia neodimorpha was considered closer to clade F species due to the large opposite decussate inflorescences with permanent bracts and white pubescence. The set of leaf morphological and anatomical characteristics of 13 species of the Verticillate was described with the goal of providing data for species delimitation when combined with phylogenetic and taxonomic studies. It was developed a taxonomic study of the of the species in the group, with descriptions, occurrence, phenology, images, and commentaries. The Verticillate Group of *Myrcia* sect. *Aulomyrcia* is a cohesive group phylogenetically.

Keywords: Myrteae; morphology; phylogeny; Myrtales; neotropics; leaf anatomy.

SUMÁRIO

1. INTRODUÇÃO

Myrtaceae é uma família de plantas arbóreas e arbustivas composta por 137 gêneros e perto de 6500 espécies (POWO 2023). Apresenta distribuição pantropical com extensões para zonas subtropicais e temperadas. Ocorre predominantemente no hemisfério sul nos continentes que formaram Gondwana (THORNHILL et al. 2015). Myrtaceae tem importante representatividade na biodiversidade da região neotropical. No Brasil Myrtaceae é representado por aproximadamente 29 gêneros e 1203 espécies segundo a Flora e Funga do Brasil (2024). A exemplo disso, na Mata Atlântica, a família é fundamental na sustentação das espécies frugívoras (STAGGEMEIER et al. 2017) e suas espécies podem ser usadas como taxa modelo para estudos de evolução, ecologia e estratégias de conservação (MURRAY-SMITH et al. 2008, LUCAS & BÜNGER 2015). Na Amazônia, Myrtaceae aparece em sexto lugar na lista das famílias mais ricas em espécies (STEEGE et al., 2013; CARDOSO et al., 2017). As espécies neotropicais de Myrtaceae pertencem em sua maioria à tribo Myrteae, constituída exclusivamente por representantes de Myrtaceae com frutos carnosos (MCVAUGH 1968; LUCAS et al. 2005; VASCONCELOS et al. 2017). Nas Américas, no Chile existe a espécie *Metrosideros stipularis* (Hook. & Arn.) Hook. f., pertencente à tribo Metrosidereae (PILLON et al. 2015).

1.1 *MYRCIA* DC.

Myrcia DC. é um grupo monofilético, configurando entre os maiores gêneros de angiospermas com espécies exclusivamente neotropicais (POWO 2023 É o quarto maior gênero de Myrtaceae, depois de *Eucalyptus* L'Hér, *Eugenia* L. e *Syzygium* P. Browne ex Gaertn. (Lucas et al. 2018). É também um dos grandes gêneros da tribo Myrteae Juss., constituído por ca. 780 espécies arbustivas e arbóreas (POWO 2023). O gênero Myrcia apresenta alta diversidade principalmente na Mata Atlântica e no Cerrado bem como na Amazônia e no Caribe (GBIF 2023).

Primeiramente publicado por Candolle (1827), *Myrcia*, como é entendido atualmente, corresponde à subtribo Myrciinae O.Berg (quando se exclui *Myrceugenia* O. Berg (BERG, 1855, MCVAUGH, 1968).

Pois como é reconhecida nos tempos atuais, *Myrcia* inclui os gêneros considerados aceitos no passado como *Gomidesia* O. Berg, *Marlierea* Cambess., *Calyptranthes* Sw. Estes quatro gêneros foram hoje sinonimizados com *Myrcia* baseando-se em estudos filogenéticos (LUCAS et al., 2011; WILSON et al., 2016). Lucas & Sobral (2011), justificaram porque conservar Myrcia ao invés de Calyptranthes, mesmo este último sendo mais antigo, para combinar os quatro gêneros tradicionais em um gênero Myrcia mais inclusivo. Seu argumento para a conservação é justificado pelo maior número de sinonimizações e mudanças necessárias case Calytranthes fosse usado.

As relações filogenéticas dentro de *Myrcia* s.l. foram reconstruídas por inferência Bayesiana e parcimônia, de quatro regiões plastidiais (psbA-trnH, trnL, trnL-F and matK), e uma região do núcleo: ITS, por Lucas et al. (2011). Os autores avaliaram a hipótese filogenética em conjunto com caracteres morfológicos e fatores abióticos e justificaram a subdivisão de *Myrcia* s.l. em nove clados coesos. Outras análises filogenéticas (STAGGEMEIER et al. 2015, SANTOS et al. 2017) inferindo sobre as relações dentro de *Myrcia* confirmam os nove clados posteriormente formalizados em nove seções por Lucas et al. (2018). São eles: 1. *Myrcia* sect. *Calyptranthes* (Sw.) A.R. Lourenço & E. Lucas, 2. *Myrcia* sect. *Eugeniopsis* (O.Berg) M.F. Santos & E. Lucas, 3. *Myrcia* sect. *Gomidesia* (O.Berg) B.S. Amorim & E. Lucas, 4. *Myrcia* sect. *Aguava* (Raf.) D.F. Lima & E.Lucas, 5. *Myrcia* sect. *Myrcia* DC., 6. *Myrcia* sect. *Reticulosae* D.F. Lima & E. Lucas, 7. *Myrcia* sect. *Sympodiomyrcia* M.F. Santos & E. Lucas, 8. *Myrcia* sect. *Tomentosae* E. Lucas & D.F. Lima, e 9. *Myrcia* sect. *Aulomyrcia* (O.Berg) Griseb.

1.2 *MYRCIA* SECT. *AULOMYRCIA* (O.BERG) GRISEB.

O clado nove do estudo filogenético proposto por Lucas et al. (2011) corresponde à *Myrcia* sect. *Aulomyrcia* (O. Berg) Griseb. Esta seção foi inicialmente publicada como um gênero por Berg (1855), posteriormente reconhecida como uma seção de *Myrcia* por Grisebach (1864), Kiaerskou (1893), McVaugh (1968) e como subgênero por Niedenzu (1893) e Legrand (1961).

Segundo Lucas et al (2018), as espécies da seção *Aulomyrcia* apresentam o diferencial do hipanto no botão se prolongar acima do ápice do ovário e terminar em lobos do cálice fusionados ou parcialmente livres que se rasgam durante a antese, e discos estaminais glabrescentes. Estas características contrastam com outras seções de *Myrcia* que apresentam hipanto terminando com o ápice do ovário e discos estaminais tomentosos.

Staggemeier et al. (2015) revisitaram as relações filogenéticas dentro da seção *Aulomyrcia*, amostrando 53 táxons desta seção e 40 grupos externos, através de análises de Máxima Verossimilhança e Bayesiana. Destas análises emergiram sete clados chamados informalmente de A até G. O primeiro grupo de Aulomyrcia inclui os clados A, B e C, constituídos por espécies da Bacia Amazônica e da porção Norte da Mata Atlântica. O segundo grupo inclui os clados D a G, composto por espécies principalmente da Mata Atlântica, com algumas espécies amazônicas, e corresponde ao gênero *Marlierea* Cambess. reconhecido no passado, hoje sinonimizado com *Myrcia*.

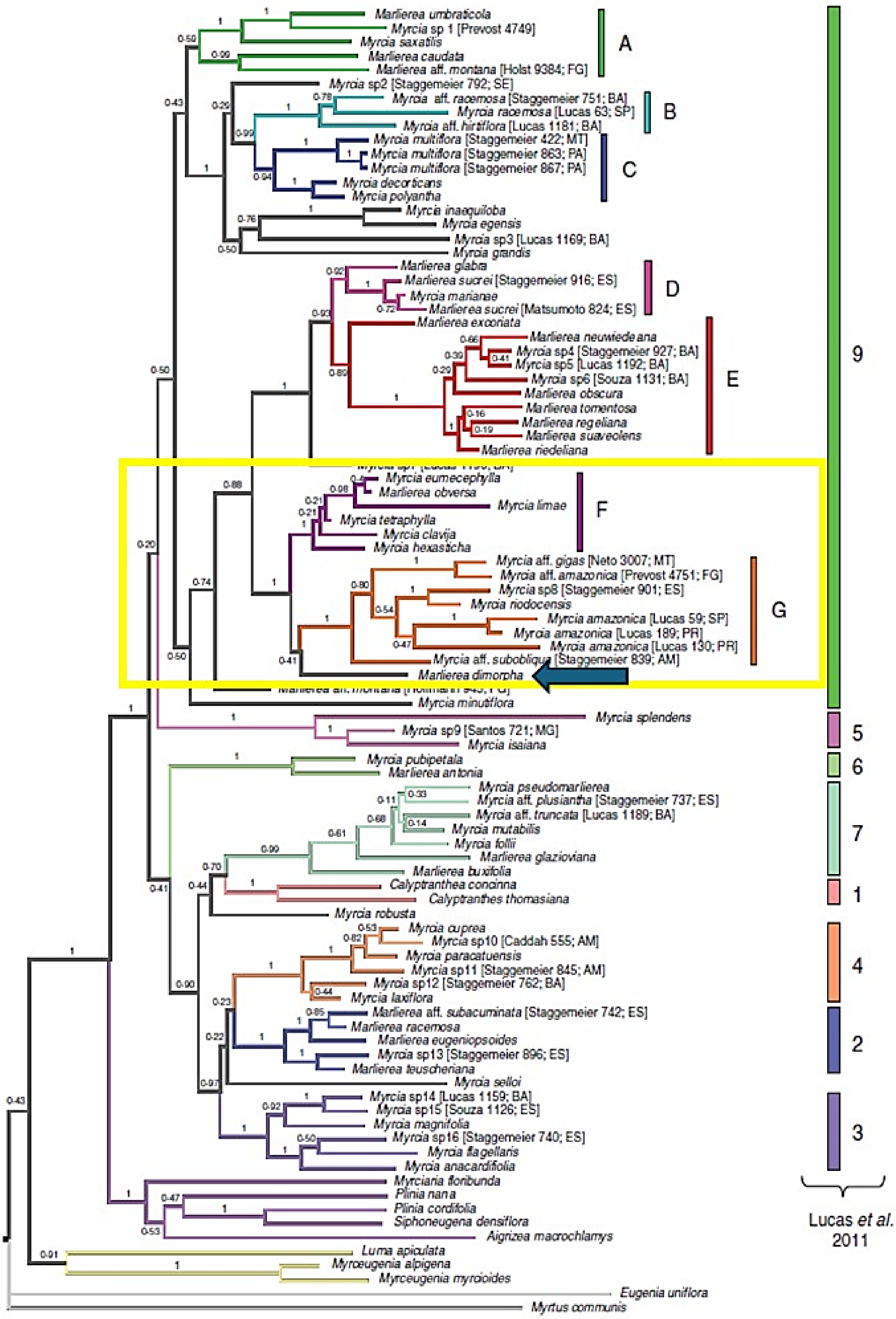
Myrcia sect. *Aulomyrcia* atualmente engloba ca. 140 espécies de acordo com Lucas et al. (2018), das quais 124 foram tratadas em um conspecto das espécies da seção (LUCAS et al., 2016). Segundo Santos et al. (2017), e Lima et al. (2017) *Myrcia* sect. *Myrcia* é filogeneticamente a seção mais próxima de *Myrcia* sect. *Aulomyrcia*. As espécies da seção *Aulomyrcia* se distinguem das da seção *Myrcia* por apresentarem folhas verticiladas, decussadas, ou opostas (contra folhas opostas somente em *Myrcia* sect. *Myrcia*); brácteas subflorais persistentes (contra caducas em *Myrcia* sect. *Myrcia*); inflorescências terminais frequentemente assimétricas (contra simétricas em *Myrcia* sect. *Myrcia*), lobos do cálice adaxialmente glabrescentes (contra pubescentes em *Myrcia* sect. *Myrcia*), hipanto levemente estendido além do ápice do ovário podendo rasgar-se na antese (contra hipantos curtos em *Myrcia* sect. *Myrcia*), disco estaminal levemente convexo, com um fino anel de estames (contra disco estaminal largo em *Myrcia* sect. *Myrcia*).

1.3 O GRUPO DAS VERTICILADAS

O Grupo das Verticiladas consiste em um grupo de 23 espécies da seção *Aulomyrcia*. A decisão de considerar estas espécies como um grupo monofilético vem embasada pela filogenia de Staggemeier et al. (2015) e pelo conspecto da seção *Aulomyrcia* por Lucas et al. (2016) demonstrado na Figura 1 abaixo. O Grupo das Verticiladas corresponde aos clados F e G de Staggemeier et al. (2015). A espécie *Myrcia neodimorpha* E. Lucas & C.E. Wilson (anteriormente *Marlierea* *dimorpha* O.Berg) dependendo da análise aparece horas como grupo irmão do clado F (Análise com o BEAST calibrada com fóssil), horas como grupo irmão do clado G (análise bayesiana). *Myrcia neodimorpha* apresenta características similares às do subclado F como folhas longas de até 27 cm, pecíolo com casca, e inflorescências surgindo na gema terminal dos ramos e não nas gemas axilares das folhas, com pubescência branca na raquis e em brácteas e lobos do cálice. Diante disso, o presente trabalho considera o conjunto dos clados F, G e *Myrcia neodimorpha* como o Grupo das Verticiladas.

As espécies do Grupo das Verticiladas apresentam características morfológicas semelhantes e apresentou suporte para sua monofilia em Staggemeier et al. (2015). No entanto ainda há dúvidas sobre o posicionamento de *Myrcia neodimorpha*, que apresenta características similares a um desses clados.

FIGURA 1. Hipótese filogenética de *Myrcia* de Staggemeier et al. (2015) baseada em inferência bayesiana de dados combinados de DNA nuclear e plastidial. O quadro amarelo evidencia o Grupo das Verticiladas, e a seta azul indica *Myrcia neodimorpha*.



modificado a partir de Staggemeier et al. (2015).

Ainda, segundo a filogenia de Staggemeier et al. (2015), o clado F corresponde às espécies: *M. eumecephylla* (O.Berg) Nied., *M. obversa* (D. Legrand) E.Lucas & C.E. Wilson, *M. clavija* Sobral, *M. hexasticha* Kiaersk., caracterizadas por folhas verticiladas e decussadas, nervura central proeminente, inflorescências assimétricas espiraladas. E o clado G corresponde à *M. amazonica* DC., uma espécie de ampla distribuição geográfica e *M. riodocensis* G.M. Barroso & Peixoto, do Domínio da Mata Atlântica (DMA). Os caracteres diagnósticos do clado G são o indumento avermelhado turvo, folhas opostas (em contraste às verticiladas e decussadas, observadas no clado F), com nervura central plana ou sulcada e inflorescências piramidais assimétricas.

Das espécies do Grupo das Verticiadas, *Myrcia amazonica* foi descrita há mais tempo e apresenta a distribuição mais ampla, estendendo por toda a região neotropical. Ao Sul, o limite de ocorrência de *Myrcia amazonica* é Santa Catarina. A partir daí sua distribuição se dá por todas as regiões do Brasil até a América Central e o Caribe (GBIF, 2023). *Myrcia amazonica* tem três sinônimos homotípicos e 27 sinônimos heterotípicos (FLORA DO BRASIL 2023), e apresenta variação no tamanho foliar (3-9 x 1.5-4 cm), e no indumento, podendo apresentar espécimes com inflorescências tomentosas a glabrescentes.

O trabalho de Staggemeier et al. (2015) citado anteriormente, foi seguido pela publicação do conspecto de Lucas et al. (2016), compilando taxonomia, morfologia, distribuição e estado de conservação de 124 espécies pertencentes à seção. Partindo deste conspecto, cinco subgrupos informais dentro de *Aulomyrcia* são considerados. Um destes corresponde ao grupo F da filogenia de Staggemeier et al. (2015) com adição de outras espécies morfologicamente próximas àquelas incluídas na filogenia, como *M. areolata* (McVaugh) E. Lucas & C.E. Wilson, *M. badia* (O.Berg) N. Silveira, *M. colpodes* Kiaersk., *M. gigantea* (O.Berg) Nied., *M. insularis* Gardner, *M. liesneri* B. Holst, *M. magna* D.Legrand, *M. neoestrellensis* E. Lucas & C.E. Wilson *M. tetraphylla* Sobral e *M. zetekiana* (Standl.) B.Holst. Um segundo grupo corresponde ao clado G da filogenia de Staggemeier et al. (2015), que contém *M. amazonica*, com a adição de *M. pyrifolia* (Desv. Ex Ham.) Nied., *M. rubiginosa* Cambess., *M. salticola* (Styerm.) McVaugh e *M. santateresana* Sobral ao grupo de espécies. Ou seja, no presente estudo consideramos tanto as espécies inclusas na filogenia de Staggemeier et al. (2015) quanto aquelas sugeridas pelo conspecto de Lucas et al. (2016) em grupos correspondentes. Nós incluimos a espécie *Myrcia* *neoverticillaris* E. Lucas & C.E. Wilson, que é muito similar às espécies do clado F, principalmente à *Myrcia tetraphylla*. A lista das espécies que correspondem ao Grupo das Verticiladas dentro dessa estrutura sugerida aqui está indicada na Tabela 1.

TABELA 1: Espécies pertencentes ao Grupo das Verticiladas e seus respectivos subclados segundo a combinação de informações dos trabalhos de Staggemeier et al. (2015) e Lucas et al. (2016).

Espécies	Subclados
Myrcia amazonica DC.	G
Myrcia areolata (McVaugh) E. Lucas & C.E.Wilson	F
Myrcia badia (O.Berg) N.Silveira	F
Myrcia clavija Sobral	F
Myrcia colpodes Kiaersk.	F
Myrcia eumecephylla (O.Berg) Nied.	F
Myrcia gigantea (O.Berg) Nied.	F
Myrcia hexasticha Kiaersk.	F
Myrcia insularis Gardner	F
Myrcia liesneri B. Holst	F
Myrcia magna D. Legrand	F
Myrcia neodimorpha E. Lucas & C.E. Wilson	
Myrcia neoestrellensis E. Lucas & C.E. Wilson	F
Myrcia neoverticillaris E. Lucas & C.E. Wilson	F
Myrcia obversa (D.Legrand) E. Lucas & C.E. Wilson	F
Myrcia pyrifolia (Desv. ex Ham.) Nied.	G
Myrcia riodocensis G.M. Barroso & Peixoto	G
Myrcia rubiginosa Cambess.	G
Myrcia salticola (Steyerm.) McVaugh	G
Myrcia santateresana Sobral	G
Myrcia speciosa (Amshoff) McVaugh	F
Myrcia tetraphylla Sobral	F
Myrcia zetekiana (Standl.) B. Holst	F

1.4 MORFOLOGIA E ANATOMIA FOLIAR

O conjunto de características morfológicas e anatômicas foliares podem auxiliar na circunscrição das espécies em Myrtaceae. Klucking (1988) descreveu os padrões de nervação foliar na família Myrtaceae, demonstrando que existe substancial correlação entre morfologia foliar e habitat em Myrtaceae, com espécies de florestas ombrófilas apresentando folhas largas e com muito mesofilo (Wilson 2011). Jonhson & Briggs (1984) sugerem a variação em características dos tricomas e da nervura intramarginal refletem os padrões filogenéticos de Myrtaceae.

As principais características foliares de Myrtaceae são folhas simples, com margem inteira (raramente crenulada), venação geralmente pinada e broquidródoma (raramente camptódroma), com venação intramarginal bem definida. A filotaxia mais comum é oposta, porém há folhas alternas e verticiladas. Quanto às características anatômicas: os tricomas são geralmente simples, ou braquiados (em forma de T com os lados de mesmo tamanho, ou de tamanhos diferentes), sem célula basal, com paredes espessas e unicelulares; as paredes epiteliais anticlinais podem ser retas, curvadas ou sinuosas; as lâminas foliares são de mesofilo dorsiventral ou isobilateral, hipoestomáticas, com cavidades secretoras esquizógenas adjacentes à epiderme em ambos os lados (WILSON 2011, AL-EDANY et al. 2012). O feixe vascular da nervura central é geralmente bicolateral com o floema incluso, e no pecíolo, o feixe tem o formato de arco, podendo apresentar os lados do arco dobrados para dentro ou ser um cilindro fechado e achatado transversalmente (WILSON 2011). As cavidades secretoras esquizógenas foliares, ou pontuações translúcidas, como também são chamadas, são das características mais marcantes conhecidas em Myrtaceae. Estas cavidades secretam metabólitos secundários na forma de monoterpenos ou sesquiterpenos, cíclicos ou de cadeia aberta, amido, glicídios, taninos, lipídios e alcaloides (DONATO & MORRETES 2011; PADOVAN et al. 2013; COSTA et al. 2020).

É possível explorar os dados morfológicos e anatômicos de várias maneiras diferentes, de acordo com os objetivos dos estudos e as características variáveis significativas em cada grupo. Em *Myrcia* Gomes e Neves (1997) descreveram em grande riqueza de detalhes a morfologia e anatomia foliar de duas espécies da atual *Myrcia* sect. *Gomidesia*: *Myrcia spectabilis* DC. and *Myrcia subsericea* A.Gray. No mencionado trabalho (Gomes & Neves 1997) estas duas espécies ainda eram consideradas como pertencentes ao gênero *Gomidesia* (O.Berg). O objetivo deste trabalho foi usar a anatomia como forma de circunscrever as duas espécies.

Gomes et al. (2009) compararam as características anatômicas foliares entre *Campomanesia adamantium* (Camb.) O.Berg, *Myrcia cordiifolia* DC., *M. guianensis* (Aubl.) DC, destacando o formato das células epidérmicas, a existência de camadas subepidérmicas, a disposição do feixe vascular da nervura mediana e a presença de tricomas braquiados como atributos taxonomicamente importantes para diferenciar estas espécies. Variação nos padrões de venação foram usados para distinguir espécies de *Myrcia* da restinga paraense (ALVAREZ & POTIGUARA 2002). A morfo-anatomia foliar de *Myrcia multiflora* (DC.) foi descrita por Donato e Morretes (2011).

Para Eugenia L. podemos citar aqui os estudos de Plessis & Wyk (1982), Fontenelle et al. (1994), e Armstrong et al. 2012. Já em *Campomanesia* Ruiz & Pavón, Oliveira et al. (2011) investigaram padrões de nervação foliar e o arranjo do feixe vascular no pecíolo a serem utilizados na taxonomia do gênero. Oliveira et al. (2018) usaram características morfológicas e anatômicas para circunscrever espécies dentro do complexo de *Campomanesia xanthocarpa* (Mart.) O.Berg. como o formato da base e da margem da lâmina foliar, presença de domácias, presença de ornamentações cuticulares, presença de fibras perivasculares e formato do feixe vascular.

Variações no conjunto de caracteres morfológicos e anatômicos foliares podem auxiliar na delimitação das espécies do Grupo das Verticiladas. Como exemplo de que são características importantes de serem consideradas: algumas espécies do clado F (*M. eumecephylla, M. hexasticha* e *M. obversa*) são muito próximas na morfologia foliar externa e caracteres anatômicos podem auxiliar na delimitação dessas espécies. Em vários estudos de florística no Brasil observa-se a presença de espécies de Myrtaceae designadas como morfotipos sem determinação de espécies (ex. MARTINI et al. 2007). Uma vez que as espécies da família apresentam variações sutis nos caracteres difíceis de serem percebidos até que se tenha maior experiência. Por este motivo, caracteres que possam ser práticos para identificação são muito bem-vindos. Como há variação de caracteres morfológicos e anatômicos foliares dentro do Grupo das Verticiladas, acreditamos que este estudo pode ser útil para corroborar na determinação de espécies.

1.4 JUSTIFICATIVA

Myrcia é um dos gêneros mais diversos e sistematicamente complexos da tribo Myrteae, composto por nove seções. Algumas destas seções já foram investigadas a fundo sistematicamente como *Myrcia* sect. C*alyptranthes* (Wilson et al. 2016), *Myrcia* sect. *Gomidesia* (Amorim et al. 2019), *Myrcia* sect. *Aguava* (Lima et al. 2021), *Myrcia* sect.. *Myrcia* (Lima et al. 2021), e *Myrcia* sect. *Sympodiomyrcia* (Santos et al. 2016). *Myrcia* sect. *Aulomyrcia* foi investigada anteriormente a partir de dados moleculares (Staggemeier et al., 2015) e dados taxonômicos e morfológicos no conspecto da seção por Lucas et al. (2016). Porém os diferentes clados emergentes dentro da seção *Aulomyrcia* representados no trabalho filogenético necessitam de aprofundamento. Um destes clados é o Grupo das Verticiladas, o qual até aqui não foi estudado quanto às relações filogenéticas de suas espécies e subgrupos, bem como as características morfológicas e anatômicas mais evidentes e com potencial de diagnose. Estudos de grupos de categorias inferiores à seção são desejáveis em *Myrcia* tanto para especialistas quanto para a conservação da biodiversidade, auxiliando na identificação de espécies em estudos de florística.

Estudos filogenéticos que incluam espécies ainda não amostradas ou revisadas podem elucidar a real composição destas linhagens e as relações entre elas.

O aprofundamento nas características morfológicas e anatômicas foliares das espécies do grupo busca encontrar características deste órgão que possam ajudar na determinação e circunscrição das espécies do Grupo das Verticiladas. Muitas vezes o material fértil destas espécies não está disponível em estudos de florística e de ecologia, quando as características morfológicas foliares podem ser utilizadas para a identificação juntamente com outros dados de localização geográfica, características da casca e comparações com espécimes de herbário. Uma chave dicotômica a partir das características foliares visa auxiliar no processo de determinação destas espécies. As características anatômicas foliares podem não ser práticas para a identificação das espécies quando em campo, porém em um laboratório, munidos de lâminas com cortes simples feitos à mão livre analisados em um microscópio ótico, pode auxiliar na diferenciação de espécies muito próximas, contribuindo para sua circunscrição e determinação.

O estudo taxonômico visa descrever em detalhe as características gerais das espécies do Grupo das Verticiladas como as dos ramos, as foliares, das inflorescências e flores e providenciar uma chave dicotômica para sua identificação. O estudo taxonômico visa também detalhar a ocorrência do Grupo como um todo e de cada espécie em particular, bem como providenciar mapas de ocorrência das espécies. Este visa também a inclusão de comentários das particularidades de cada espécie, com comparações com outras similares.

1.5 OBJETIVOS

Os objetivos do primeiro capítulo são os seguintes: realizar uma análise filogenética do Grupo das Verticiladas para então proceder com a caracterização do grupo como um todo, bem como a caracterização dos táxons internos; encontrar caracteres morfológicos que corroborem os clados encontrados; e testar a monofilia de Myrcia amazonica.

Quanto ao segundo capítulo, os objetivos foram: prover dados da morfologia e anatomia foliar de espécies muito similares de *Myrcia* sect. *Aulomyrcia*; caracterizar os clados de *Myrcia* sect. *Aulomyrcia* quanto a morfologia e anatomia foliar, como os clados F e G, e *Myrcia neodimorpha;* usando *Myrcia micropetala* do clado B para comparação.

O objetivo do terceiro capítulo é providenciar um estudo taxonômico das 23 espécies do Grupo das Verticiladas, providenciando informação nos tipos nomenclaturais, descrições morfológicas, distribuição geográfica e o estado de conservação de cada espécie. Bem como providenciar informações sobre fenologia; uma chave dicotômica e imagens de espécimes representativos.

2. CHAPTER 1 - A PHYLOGENETIC STUDY OF *MYRCIA* SECT. *AULOMYRCIA* (MYRTACEAE): THE VERTICILLATE GROUP

Manuscrito a ser submetido ao periódico Systematic Botany no futuro.

A phylogenetic study of *Myrcia* sect. *Aulomyrcia* (Myrtaceae): The Verticillate Group

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Abstract— *Myrcia* is the second largest genus of the tribe Myrteae (Myrtaceae), comprising *c.* 780 neotropical species of trees and shrubs. Nine sections are recognized within *Myrcia* and most have been the subject of recent systematic study, while others require more investigation, such as *Myrcia* sect. *Aulomyrcia*. The present study focused on a group of 23 species of *Myrcia* sect. *Aulomyrcia* that are hypothesized to belong to an informally named Verticillate Group, that present conspicuous verticillate leaves and spiral terminal inflorescences. These species occur in the Atlantic and Amazon Forests and in the Cerrado Domains, all the way to the Central American Isthmian & Colombian Coastal Forests. We aimed to develop phylogenetic analyses of the Verticillate Group and to examine relationships within and among other lineages of section *Aulomyrcia*; to characterize the Verticillate Group morphologically; and lastly to test the monophyly of the widespread species *Myrcia amazonica.* Five molecular markers (the nuclear ITS, and the plastidial *ndhF*, *psbA-trnH*, *trnQ-rps16*, and *trnL-trnF*) were used to infer relationships of 45 terminals of Myrtaceae (42 of *Myrcia* and the outgroups *Eugenia uniflora*, *Myrceugenia alpigena* and *Myrtus communis*) with Bayesian Inference and Maximum Likelihood analysis. The Verticillate Group is recovered as monophyletic with high support. *Myrcia amazonica* is not recovered as monophyletic in our analyses. *Myrcia* section *Aulomyrcia* presents two highly supported subclades. Our study provides a phylogenetic hypothesis of the Verticillate Group of *Myrcia* sect. *Aulomyrcia* for use as a framework for further systematic studies with these species and to aid taxonomic decision making.

Keywords— Amazon Forest, Atlantic Forest, Myrteae, Neotropics.

Myrtaceae is composed of 137 genera and *c.* 6500 species (Wilson 2011; POWO 2023) distributed across the tropics ,with its range extending to subtropical and temperate zones, predominantly in the Southern Hemisphere (Thornhill et al. 2015). Myrtaceae is among the richest woody angiosperms families in the Neotropics (Oliveira-Filho & Fontes 2000, Cardoso et al. 2017), and has been cited as a model taxon for studies of evolution, ecology, and conservation in the Atlantic Forest Domain (Murray-Smith et al.

2009, Lucas & Bunger 2015, Staggemeier et al. 2017). All neotropical species of Myrtaceae belong to tribe Myrteae, and all its 51 genera and *c.* 2,500 species bear fleshy fruits (Lucas et al. 2007, Vasconcelos et al. 2017). In Chile occurs the species *Metrosideros stipularis* (Hook. & Arn.) Hook.f. of tribe Metrosidereae (Pillon et al. 2015), *Myrcia* DC. is a species rich genus of Myrtaceae, comprising *c.* 780 neotropical species. It is the second largest genus of tribe Myrteae (POWO, 2023). *Myrcia* is the only genera considered as part of tribe Myrciinae O.Berg.

Phylogenetic studies on *Myrcia* (Lucas et al. 2011) suggested the genus be subdivided into nine sections further corroborated by Lucas et al. (2018). Later Amorim et al. (2019) identified another clade with high support other than the nine clades already formalized. This informal clade is called Clade 10 for the moment.

One of these sections is *Myrcia* sect. *Aulomyrcia* (O.Berg) Griseb., encompassing about 140 species that are mostly represented in the Atlantic and Amazon Forest Domains. In the latter Domain especially in the Guiana Shield region) (Lucas et al. 2016; Lucas et al. 2018). And also in the Cerrado, where species such as *Myrcia amazonica, M. tetraloba* D.F.Lima & E.Lucas, and *M. pinifolia* Cambess. occur (Lima et al. 2017). *Myrcia amazonica* occurs all through South America reaching Central America and the Caribbean. *Myrcia zetekiana* (Standl.) B.Holst is recorded in Panama, reaching the Central American Isthmian & Colombian Coastal Forests Bioregion (One Earth 2023).

Species of *Myrcia* sect. *Aulomyrcia* (*sensu* Staggemeier et al. 2015 and Lucas et al. 2016) are usually trees or shrubs that differ from other clades of *Myrcia* by the combination of monopodial branching, relatively large leaves, that are either opposite distichous, opposite decussate, or verticillate; and inflorescences that vary from asymmetrical pyramidal panicles in leaf axils, to terminal spiral ones with short axes. Their rachis present a reddish or white tomentose indumentum on the inflorescence hypanthium, and abaxial surface of the calyx lobes, persistent subfloral bracts, calyx are usually pentamerous (rarely tetramerous), calyx lobes are free to partially or completely fused, opening regularly or tearing irregularly through the hypanthium, the floral disc is glabrous and narrow, the staminal ring is usually glabrous, with the hypanthium extending somewhat beyond the ovary but sometimes indistinct after deep tearing; the ovary is bi-locular with two ovules per locule; and the fruits are globose (Staggemeier et al. 2015, Lucas et al. 2016, Lucas et al. 2018).

Recent phylogenetic analyses focusing on *Myrcia* sect. *Aulomyrcia* by Staggemeier et al. (2015) identified seven clades within the section, to which the authors informally assigned letters from A to G. These seven clades are further arranged into two larger clades that reflect somewhat the geographical distribution of the species in the section. One clade (A–C) comprises mostly species from the Amazon Forest Domain (AMFD) and the Northern Atlantic Forest Domain (AFD). *Myrcia multiflora* (Lam.) DC. (clade C) is widespread and occurs in the Caatinga, Cerrado and Pampa Domains as well (Santos et al. 2023). *Myrcia racemosa* (O.Berg) Kiaersk. (clade B) is broadly dispersed in the Southern and Northern AFD.

The other group (clades D–G), which loosely represent the formerly accepted *Marlierea* Cambess. comprises mostly Northern and Southern AFD species, while *Myrcia amazonica* DC. (clade G) is widespread. Such pattern of distinct species composition in the AFD was indicated for Myrteae (McVaugh 1956, Wagner et al. 2022). And the sections and lineages within *Myrcia* present their own distinct species composition patterns in the Neotropics (Staggemeier et al. 2015, Lima et al. 2021, Santos et al. 2021).

In the phylogenetic analyses of *Myrcia* section *Aulomyrcia* carried out by Staggemeier et al. (2015), clades F, G, and *Myrcia neodimorpha* E.Lucas & C.E.Wilson emerged in a well-supported clade. According to our recent observations of herbaria specimens and to the phylogeny (Staggemeier et al. 2015), clade F included five species, namely: *Myrcia clavija* Sobral, *M. eumecephylla* (O.Berg) Nied., *M. hexasticha* Kiaersk. (O.Berg), *M. obversa* (D. Legrand) Nied., and *M. tetraphylla* Sobral, while Clade G included *Myrcia amazonica* and *M. riodocensis* G.M. Barroso & Peixoto. *Myrcia neodimorpha* emerged either as sister to clade G, in the Bayesian Inference (BI) or to clade F, in the dated, fossil calibrated BEAST analysis*.*

Lucas et al. (2016) developed a taxonomic conspectus of *Myrcia* sect. *Aulomyrcia* including information on typification, geographic distribution, conservation status and taxonomic notes of species. Within this taxonomic framework, the 124 species of *Myrcia* sect. *Aulomyrcia* included in the study were organized into five further informal groups, based on morphology and distribution, that broadly correspond to the clades from Staggemeier et al. (2015). According to Lucas et al. (2016), a group of 16 species corresponds to clade F of Staggemeier et al. (2015), and another group of six species corresponds to clade G. *Myrcia neodimorpha* was placed in a different group than the Verticillate one in the study by Lucas et al. (2016). From here on we refer to such group of 22 species from clades F, G plus *Myrcia neodimorpha* as the 'Verticillate Group' (see Table 1), as its species bear conspicuous terminal, verticillate inflorescences.

Since the publication of the initial phylogenetic hypothesis of *Myrcia*, systematic and monographic studies focusing on smaller groups have further addressed species, traits, and subgeneric relationships (Santos et al. 2016, 2018, 2019, Wilson, et al. 2016, Santos et al. 2021). Such results were analyzed in the context of morphology and geographic distribution (Amorim et al. 2019; Lima et al. 2021, Burton et al. 2022). The subclades within *Myrcia* sect. *Aulomyrcia* have not yet received detailed morphological review.

The main goal of our study is to develop a phylogenetic analysis of the Verticillate Group providing morphological features such as leaf morpho-anatomy, indumentum characteristics, inflorescence, and flower features to distinguish it, and the putative lineages within it. We aim to test the monophyly of the widespread species *Myrcia amazonica* and to discuss relationships of accessions sampled from throughout its range. A further aim is to examine relationships between this group and other clades of *Myrcia* sect. *Aulomyrcia*. Cohesive and recognizable infrageneric groups recovered within *Myrcia* sect. *Aulomyrcia* will provide a basis for further taxonomic work within the section.

MATERIALS AND METHODS

Sampling— Of the 23 species hypothesized to belong to the Verticillate Group, our sample included nine species (approximately 40% indicated in bold in Table 1). We included nine accessions of *Myrcia amazonica* from different localities (Brazilian states of Amazonas, Bahia, Mato Grosso, Paraná, and São Paulo, plus one from French Guiana) and two of *Myrcia tetraphylla* Sobral (from Bahia and from Espírito Santo) to encompass geographical variation. *Myrcia tetraphylla* is considered a Vulnerable (VU) species according to IUCN criteria (Canteiro & Lucas 2018).

As outgroups we included 22 other species of *Myrcia* in the analyses, nine from other subgroups of *M.* sect. *Aulomyrcia* and 13 from other sections of *Myrcia*, such as *M.* sect. *Aguava* (Raf.) D.F. Lima & E. Lucas, *M.* sect. *Calyptranthes* (Sw.) A.R. Lourenço & E. Lucas, *M.* sect. *Eugeniopsis* (O. Berg) M.F. Santos, *M.* sect. *Gomidesia* (O. Berg) B.S. Amorim & E. Lucas, *M.* sect. *Myrcia*, *M.* sect. *Reticulosae* D.F Lima & E. Lucas, *M.* sect. *Sympodiomyrcia* M.F. Santos & E. Lucas, and *M.* sect. *Tomentosae* E. Lucas & D.F. Lima, and Clade 10. We also included *Eugenia uniflora* L., *Myrceugenia alpigena* (DC.) Landrum, and *Myrtus comunis* L. as outgroups.

For the molecular sampling, we used the nuclear ribosomal internal transcribed spacer

(ITS), and the plastid markers *ndhF*, *psbA-trnH*, *trnL-trnF*, and *trnQ-rps16*, all of which have been successfully used to infer phylogenetic relationships among species of *Myrcia* (e.g., Lucas et al. 2007, 2011, Staggemeier et al. 2015, Santos et al. 2016, Lima et al. 2021). We used a total of 192 sequences; 23 sequences (15%) were generated for this study, and 169 sequences (85%) were obtained from previous studies (Appendix 1). Species names used here follow Santos et al. (2023).

DNA Extraction, Amplification and Sequencing — Total DNA was extracted from 20 mg of leaf tissue dried in silica gel using maceration in liquid nitrogen, following the modified CTAB extraction protocol of Doyle & Doyle (1987). DNA regions amplified for this study were ITS (Sun et al. 1994) from the nuclear genome, and *trnL-trnF* (Taberlet et al. 1991) and *trnQ-rps16* (Shaw et al. 2007) from the plastome. In addition to these markers, sequences from plastid markers *ndhF* (Neyland and Urbatsch 1996) and *psbA-trnH* (Hamilton 1999) were obtained from published studies (Lucas et al. 2007, 2011, Staggemeier et al. 2015, Santos et al., 2016). Amplifications were performed according to the protocols used by Santos et al. (2016) (PCR conditions are described in Table 2). PCR product purification was performed using polyethylene glycol at 20%. Sequencing was performed at GoGenetics (Curitiba – PR, Brazil). Sequences were viewed, edited, and assembled with the program Geneious (Biomatters Ltd.) and verified using the Basic Local Alignment Search Tool (BLAST) (Altschup et al. 1990).

Alignment and phylogenetic analysis — Sequences were aligned using MAFFT (Katoh et al. 2019) under default parameters. Data from nuclear and plastid markers were analyzed independently and then combined in a total matrix dataset including all markers.

Data was analyzed with Bayesian Inference (BI) implemented in Mr. Bayes v.3.2.2 (Huelsenbeck & Ronquist 2001, Ronquist et al. 2012) and Maximum Likelihood analysis

(ML) using RAxML v.8.2.4 (Stamatakis 2006). We choose two analyses because of the possibility to compare results, from different analytical perspective. The best evolutionary models were checked separately for each marker using jModelTest2 (Darriba et al. 2012) and selected under the Akaike information criterion (AIC). All analyses were performed through the CIPRES interface (Miller et al. 2010). The BI was conducted using four Markov-Monte Carlo chains with 10 million generations and a sample frequency of 1000 trees. Results were checked on Tracer 1.6 (Rambaut et al. 2018b) to ensure convergence. ML analysis was estimated using rapid bootstrap strategy with 1000 replicates, combined with a search of the best-scoring ML tree. The GTRCAT model was employed.

Five partitions, representing each molecular region, were applied in both BI and ML analyses. *Myrtus communis* was set as the outgroup. Trees were visualized and edited with FigTree v.1.4.3 (Rambaut 2018a). Values of support were recognized as high when bootstrap (BS) was ≥ 70% and posterior probability (PP) was ≥ 0.95 (Amorim et al., 2019). Data from nuclear and plastid markers were analyzed independently with ML and then the total combined dataset with BI and ML.

RESULTS

Twenty-three new DNA sequences were generated from nine species of *Myrcia*. For the first time *Myrcia neoestrellensis* and a specimen of *M. amazonica* from Bahia, of *M tetraphylla* from Espírito Santo and of *M. umbraticola* from Roraima were included in a phylogenetic analysis.

Phylogenetic Analysis — Information on the data provided by each DNA region is summarized in Table 3. The phylogenetic hypotheses resulting from total combined dataset analysis (BI and ML analyses) and those resulting from independent partitions of the ITS data, and the combined plastid data presented various incongruencies. Although statistical support for many of such incongruencies is low.

The phylogenetic hypotheses resulting from the total combined dataset (BI and ML analyses) is represented in Figure 1. The total combined datasets (ITS + plastid markers) supplied superior resolution and support than the single partition analyses. The combined analysis recovered *Myrcia* as a monophyletic group (PP 1; BS 81%) (Fig. 1). *Myrcia splendens* (Sw.) DC. and *Myrcia* sp*.* [Wagner, 316], representing *M.* sect. *Myrcia*, formed a clade (PP 0.97; BS 54%), sister to another large clade including all remaining species of *Myrcia* sampled here (PP 0.85; BS 52%). This larger clade included two subclades; one subclade presented low support (PP 0.56, BS 26%) and included groups A-C of *Myrcia* sect. *Aulomyrcia* [*sensu* Staggemeier et al. (2015)] and representatives of *M.* sect. *Aguava*, *M.* sect. *Calyptranthes*, *M.* sect. *Eugeniopsis*, *M.* sect. *Gomidesia*, *M.* sect *Reticulosae*, *M.* sect. *Sympodiomyrcia*, and Clade 10 (*sensu* Amorim et al. 2019)*.* The other clade included *M.* sect. *Aulomyrcia* clades D-G [sensu Staggemeier et al. (2015)] with high support (PP 1, BS 97%), which corresponds to former commonly accepted *Marlierea*.

Clades A-C form a monophyletic group that presented high support in the BI (PP 1), and moderate support in the ML analysis (BS 69%). The subclade containing Clade 10, *M.* sect. *Aguava*, *M.* sect. *Calyptranthes, M.* sect. *Eugeniopsis*, *M.* sect. *Gomidesia*, *M.* sect. *Reticulosae*, and *M.* sect. *Sympodiomyrcia* formed a similarly well supported clade with high support in the BI (PP 0.98) and low support in the ML analysis (BS 49%).

In both the BI and ML analysis, the Verticillate Group emerged as monophyletic with high support (PP 1, BS 84%). *Myrcia clavija*, *M. eumecephylla*, *M. obversa*, and *M. tetraphylla* formed a clade corresponding to clade F with high support: (PP 0.99, BS 73%). *Myrcia neodimorpha* appeared in a sister relationship with clade G with low support (PP 0.53, BS 49%), and all accessions of *Myrcia amazonica* plus *M. riodocensis* emerged in clade G with high support (PP 1, BS 81%).

The widespread *Myrcia amazonica* was not recovered as monophyletic (Fig. 1). A specimen from Amazonas (Staggemeier 839) and another from Mato Grosso (Labiak 7171) appeared as successive sisters to a larger clade (PP 1, BS 81%) containing all other samples of *M. amazonica* plus *M. riodocensis* (Fig. 1). These additional samples of *M. amazonica* are placed in two subclades, one of them (PP 0.87, BS 39%) is comprised of four specimens of *Myrcia amazonica* from Paraná (Lucas 130, 189), São Paulo (Lucas 59), and Espírito Santo (Staggemeier 901) together with *M. riodocensis*, which is endemic to Espírito Santo. The other subclade showed high support (PP 1, BS 97%) and is composed of four specimens of *Myrcia amazonica* from Amazonas (Wagner 212), Bahia (Goldenberg 2330), French Guiana (Prévost 4751) and Mato Grosso (Neto 3007).

Regarding the incongruencies between combined dataset analysis (BI and ML analyses) and independent partitions of the ITS data, and the combined plastid data, many of these presented low support. For example, the Verticillate Group was not monophyletic in the ML analysis of the ITS partition (Supplemental Figure S1), as species of clades D and E emerged in a sister relationship with clade F, but support for this was low (BS 27%). However, some relationships from the ITS partition analysis presented high support. For instance: *Myrcia tetraphylla* (ES), *M. obversa*, and *M. eumecephylla*, all species from clade F appear in a clade with high support (BS 94%), as do all *Myrcia amazonica* accessions in another clade (BS 90%). *Myrcia neoestrellensis,* hypothesized to belong to the Verticillate Group, appears in a clade with species of clades D and E (BS 86%) (namely *M. marianae* Staggemeier & E.Lucas (clade D) and *M. excoriata* (Mart.) E.Lucas & C.E.Wilson (clade E).

Myrcia micropetala (Mart.) Nied. appears in a clade with *Myrcia racemosa* (clade B) (BS 96%), as indicated before by Staggemeier et al. (2015).

In the combined plastid dataset ML analysis, the Verticillate Group was not monophyletic (Supplement Figure S2). A large clade emerged containing all species of the Verticillate Group except for one accession of *Myrcia obversa*, but support for this clade was low (BS 30%). The outlier *Myrcia obversa* accession emerged in another clade with *Myrcia neoestrellensis* and species of clades D and E (BS 88%). *Myrcia amazonica* did not emerge as monophyletic, as one group of accessions from the AMFD and the Northern AFD emerged in a clade with species of clade F, but there was no support for this. And the accessions from the Southern AFD emerged in another clade with low support (BS 54%).

DISCUSSION

The Verticillate Group The Verticillate Group is recovered with high support (PP 1, BS 84%) in our total combined dataset analyses, confirming results from previous phylogenetic studies (Staggemeier et al. 2015, Amorim et al. 2019). The subclades F and G *sensu* Staggemeier et al. (2015) were also recovered with high support (PP 0.99, BS 73% and PP 1, BS 81%, respectively). Clade F was highly supported in prior studies (PP 1 in Staggemeier et al. (2015), and PP 0.99 in Amorim et al. (2019)), as was clade G (PP 1, in Staggemeier et al (2015); PP 0.96, BS 82% in Amorim et al. (2019)). *Myrcia neodimorpha* appeared as sister to clade G with low support (PP 0.53, BS 49%) as it has before in the BI analysis in Staggemeier et al. (2015) (PP_{BAYES} 0.41). In the BEAST analysis by Staggemeier et al. (2015) *Myrcia neodimorpha* appeared as sister to clade F, also with low support (PP_{BEAST} 0.67).

The trees resulting from each separate partition, the ITS one and the combined plastid one, did not present the Verticillate Group as monophyletic, but there was low support for these relationships (BS 57% for the ITS and 31% for the combined plastid). Low support and incongruence between different partitions on *Myrcia* phylogenies are common. Discrepancy between plastid versus nuclear data might be a cause of this phenomenon. The signal generated by the plastid data has been known, in Sanger sequencing, to eclipse that from nuclear data in a combined analysis (Fonseca & Lohman, 2020). Results from a phylogenomic study on Myrtales (Maurin et al. 2021) illustrate this conflict with two Myrtaceae tribes, Syzygieae and Myrteae, being distantly related based on nuclear DNA sequences, but closely related using plastid or combined data. This conflicting signal may interfere with statistical support.

Morphological evidence for the Verticillate Group and its subclades. The Verticillate Group can be distinguished from other groups of *M.* sect. *Aulomyrcia* by the combination of opposite distichous, opposite decussate or verticillate leaves, asymmetrical pyramidal panicles in leaf axils, to terminal spiral inflorescences with short axes, and inflorescence branches, bracts, hypanthium, and calyx lobes usually covered with white or red trichomes.

Within the Verticillate Group, combinations of characters help to morphologically distinguish subclades F, G, and *M. neodimorpha* (Fig. 2). Clade F species have opposite distichous, opposite decussate, or verticillate, narrowly elliptic leaves with raised midveins adaxially and abaxially (Fig. 2A), their petioles do not contain accessory vascular bundles, and the midvein vascular cylinder is surrounded by a continuous band of perivascular fibers (Wagner et al. 2023). Cataphylls may be present at the base of inflorescences. Inflorescences are usually terminal spiral panicles, with red or white pubescence (Fig. 2B, C).

Myrcia neodimorpha presents a combination of characters that somehow reflects its uncertain position among clades F and G. It presents opposite decussate, narrowly elliptic leaves that resemble clade F species. Leaf midveins adaxially vary between flat such as clade G species to slightly raised which tends to resemble the raised midveins seen in clade F. *Myrcia neodimorpha* presents petioles with accessory vascular bundles, an anatomic character not found in clade F or G species. Another unique character to this species are cataphylls which occur between leaf nodes and on the base of inflorescence (Fig. 2D). Cataphylls in clade F species usually subtend the terminal inflorescences but do not occur between leaf nodes along branches. *Myrcia neodimorpha* is also distinguished by its terminal spiral panicles subtended by persistent bracts with dense white pubescence (Fig. 2E).

Clade G species have opposite distichous leaves, that are ovate or elliptic with flat, canaliculate midveins adaxially and raised midveins abaxially, their petioles do not contain accessory vascular bundles. Fiber bundles in the midvein vascular cylinder can vary occurring only adaxially in some species, or as a continuous band in others (Wagner et al. 2023). Cataphylls are absent. Inflorescences are asymmetrical pyramidical panicles, that tend to have spiral branching, but can also have opposite or alternate branches, and have tomentose rachis and hypanthium base with red pubescence (Fig. 2F, G). The leaves are usually sparsely pubescent abaxially in this group, with the exception of *Myrcia pyrifolia* that has a glabrous abaxial surface (Fig. 2H), although this species has not yet been included in a phylogenetic analysis.

Phylogenetic status of Myrcia amazonica. Clade G is composed of the widespread *Myrcia amazonica*, that occurs from Santa Catarina in the South of Brazil towards the North through all regions reaching Central America and the Caribbean (GBIF, 2023). In the total combined dataset analyses the species was not recovered as monophyletic.

Accessions of *Myrcia amazonica* from the Brazilian Amazonas state (Staggemeier 839) appeared in a sister relationship (PP 1, BS 81%) with a larger clade containing all other accessions of *M. amazonica* and *M. riodocensis.* Within this larger clade an accession of *Myrcia amazonica* from Mato Grosso (Labiak 7171) appears in a sister relationship with low support (PP 0.52) to a clade containing the remaining accessions of *M. amazonica* and *M. riodocensis* (PP 0.79, BS 40%). Such larger clade is divided in two. Accessions from the Southern AFD appeared in a clade with *Myrcia riodocensis*, but with low support (PP 0.87, BS 39). *Myrcia riodocensis* is endemic to the AFD in Espírito Santo and is very similar to *M. amazonica* but the elliptic leaves are thicker (with a tendency to be more coriaceous), and larger than those of *M. amazonica.* Also, inflorescences tend to be terminal and slightly spiral in *Myrcia riodocensis*, versus inflorescences in the axil of leaves, with opposite distichous or opposite decussate branching in *M amazonica*.
The other subclade is composed of *Myrcia amazonica* accessions from Northern AFD (Goldenberg 2330) and AMFD (Neto 3007; Prévost 4751). When one analyzes herbaria specimens of *Myrcia amazonica* it is not possible to pinpoint the variation in morphology corroborating these lineages detected in the analyses. Morphological patterns to corroborate these clades will require more morphometric analysis. Another pattern for further investigation is that more pubescent specimens tend to occur in the Cerrado, usually having a more densely tomentose red indumentum abaxially on the leaves and inflorescences rachis and bracts.

Geographic occurrence of species in the Verticillate Group. All species in clade F surveyed here occur in the AFD. In the hypothesis based on morphology suggested by Lucas et al. (2016), some Amazonian species such as *Myrcia areolata* (McVaugh) E. Lucas and C.E. Wilson, *M. liesneri* B. Holst, *M. magna* D. Legrand, *M. speciosa* (Amshoff) McVaugh, and *M. zetekiana* (Standl.) B.Holst (the latter occurring in the Central

American Isthmian & Colombian Coastal Forests Bioregion (One Earth 2023) also belong in clade F. Unfortunately, these species have not yet been included in a phylogenetic analysis for this to be tested. *Myrcia neodimorpha* occurs in the AFD, in Espírito Santo and Rio de Janeiro.

In clade G we included in our phylogeny the widespread *Myrcia amazonica* and *M. riodocensis* of the Southern AFD in Espírito Santo as mentioned above. Lucas et al. (2016) suggested other species to belong to clade G, such as *Myrcia pyrifolia, M. salticola* (Steyerm.) McVaugh, and *M. speciosa* (Amshoff) McVaugh from the AMFD, and *M. rubiginosa* Cambess., *M. santateresana* Sobral, endemic to Rio de Janeiro and Espírito Santo, respectively, in the Southern AFD. Again, unfortunately, these species have not yet been included in a phylogenetic study.

The monophyly of Myrcia section Aulomyrcia. *Myrcia* sect. *Aulomyrcia* was not monophyletic in our combined data analyses. Section *Aulomyrcia* groups A-C emerged in a clade with the other sections of *Myrcia* (*M.* sect. *Aguava*, *Calyptranthes*, *Eugeniopsis*, *Gomidesia*, *Reticulosae*, *Sympodiomyrcia*, *Tomentosae*, and Clade 10), but this relationship had low support (BS 20%) in the combined plastid analyses, and in both of the total combined dataset analyses (PP 0.56, BS 26%). In the ITS analysis, *M.* sect. *Aulomyrcia* group A emerged in a sister relationship with low support (BS 34%) to a larger clade including all other groups of *Aulomyrcia* (B-G) and all other sections of *Myrcia*.

Myrcia sect. *Aulomyrcia* was recovered as monophyletic in previous phylogenies (Staggemeier et al. 2015; Amorim et al. 2019; Lima et al. 2021), however, in some of these studies, the support was low (PP_{BAYES} 0.50, PP_{BEAST} 0.88 in Staggemeier et al. (2015). In the more recent phylogenies by Amorim et al. (2019) and Lima et al. (2021) *M.* sect. *Aulomyrcia* emerged as a monophyletic group with high support (PP 0.97, BS

81% and BS 100%, respectively). In this context, the polyphyly noted here is not considered to throw serious doubt on the unity of section *Aulomyrcia.*

Relationships within Myrcia sect. Aulomyrcia. The clade formed by groups D-G was highly supported in our combined dataset analyses (PP 1, BS 97%), as in Staggemeier et al. (2015) (PP_{BEAST} 1) and Amorim et al. (2019) (PP 1, BS 100%). The monophyletic group formed by *Aulomyrcia* groups A-C was highly supported in our BI analysis (PP 1), as in the previous studies mentioned (PP_{BEAST} 0.97 in Staggemeier et al. (2015) and BS 74% in Amorim et al. (2019).

Lucas et al. (2016) hypothesized that *Myrcia neoestrellensis* belonged to clade F. However, in our total combined dataset analyses, *M. neoestrellensis* formed a highly supported clade (PP 1, BS 100%) with *M. excoriata* (of clade E) and *M. marianae* (of clade D). Certain aspects of leaf morphology indicate that *Myrcia neoestrellensis* differs from species of clade F such as having elliptic to obovate leaves (versus narrowly elliptic in clade F), flat midveins adaxially (versus raised midveins in clade F) and visible oil glands (versus inconspicuous in clade F) (Wagner et al. 2023).

Myrcia micropetala is represented here by two accessions from the state of Bahia. One of them (Wagner, 301) formed a clade with *M. racemosa* of clade B with high support in the total combined analyses (PP 0.92, BS 82%); the other one (Paixão, 289) formed a clade with *M. multiflora* (of clade C) with low support in the total combined analyses (PP 0.59, BS 64%) but high support in the combined plastid analysis (BS 72%). Staggemeier et al. (2015) mentioned an exploratory analysis with ITS data where *Myrcia micropetala* appeared in a sister relationship with *M. racemosa*. Morphologically, all three species present light beige twigs and discolored leaves with lustrous adaxial surfaces, which dry with fading color around the veins, however, leaves are much larger and pubescent abaxially in *Myrcia micropetala* (versus glabrous in *M. multiflora* and *M. racemosa).* The grayish tomentose inflorescence rachis and hypanthium of *Myrcia micropetala* is similar to that of *M. racemosa*. In light of this evidence, we feel more comfortable placing *Myrcia micropetala* in clade B with *Myrcia racemosa*.

A clade comprising two *Myrcia micropetala* accessions plus *M. racemosa* and *M. multiflora* was highly supported in the combined plastid data analysis (BS 90%) and total combined analyses (PP 1, BS 84%). This relationship among species of clades B and C was indicated before with high support (PP_{BAYES}. 0.99, PP_{BEAST} 1 in Staggemeier et al. 2015). But the question remains about the *Myrcia micropetala* accession (Paixão 289) grouping with *Myrcia multiflora*. Such phenomenon could be related to different rates of phenotypic and genotypic evolution (Davies & Savolainen 2006), when morphological variation among species in a lineage do not necessarily match patterns seen in molecular data analysis. This would suggest that the morphologies of these species have not stabilized, resulting in a cryptic continuum where intermediate forms are common (Struck & Cerca 2019). These first exploratory results indicate a species complex. Further research is necessary, on a broader sample, with the addition of more accessions of *Myrcia micropetala* and more representatives of clade B and C to clarify these relationships

Despite the relatively small sample and low support at nodes, our study interprets and characterizes the Verticillate Group further, with the combination of molecular and morphological evidence supporting its monophyly. An ampler sample, including as many species as possible of the Verticillate Group, is necessary to understand the systematics and the geographic distribution of species within the group. This is particular significant for the AMFD species which are not well represented here.

CONCLUSION

Our study provides a phylogenetic hypothesis of the Verticillate Group within the context of *Myrcia* section *Aulomyrcia* and *Myrcia.* We discuss the relationships of subclades within the Verticillate Group and provide combinations of morphological characters to identify clades F, G and *Myrcia neodimorpha*. The widespread *Myrcia amazonica* is not monophyletic in our analyses, with *M. riodocensis* emerging amongst the *M. amazonica* accessions. Two subclades are recognized within *Myrcia* section *Aulomyrcia,* namely groups A-C, and groups D-G with high support. *Myrcia neoestrellensis* forms a highly supported clade with *M. excoriata* of group E and *M. marianae* of group D. *Myrcia micropetala* appears in a clade with species of group B and C. For future perspectives we suggest further phylogenetic analysis with a larger sample of species of the Verticillate Group, particularly species that have not been included in phylogenies yet. We suggest further phylogeographic and morphometric studies of the widespread *Myrcia amazonica,* focusing on collection efforts in areas of its range that have not yet been represented. We also suggest further collection of *Myrcia* sect. *Aulomyrcia* species to allow broader sampling for phylogenetic study of the entire section. Lastly, the phylogenetic structure discussed here serves as a basis to discern and confirm further infrageneric lineages within *Myrcia* section *Aulomyrcia and* provide ground for further taxonomic work within the section.

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Author Contributions

MW and DL provided the data and analyses. MW was the primary author, and the creator of the figures. PF and EL helped with input on the preparation for the study, the writing, and the revision process.

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FIG. 1. Phylogenetic hypothesis based on Bayesian-inference analysis of the combined nuclear and plastidial dataset (nuclear ITS and plastid markers *ndhF, psbA-trnH, trnQ-rps16,* and *trnL-trnF*). Sections of *Myrcia* are indicated by background color. The subgroups of *M.* sect. *Aulomyrcia* are indicated by letters corresponding to Staggemeier et al. (2015). Values above branches indicate the Posterior Probabilities (from the BI analysis) and below branches the corresponding bootstrap percentages (from the ML analysis). Species with multiple samples from different localities are indicated by place name abbreviations, collector, and collection number. [AM=Amazonas; BA=Bahia; GF=French Guyana; MT=Mato Grosso; PR=Paraná; SP=São Paulo

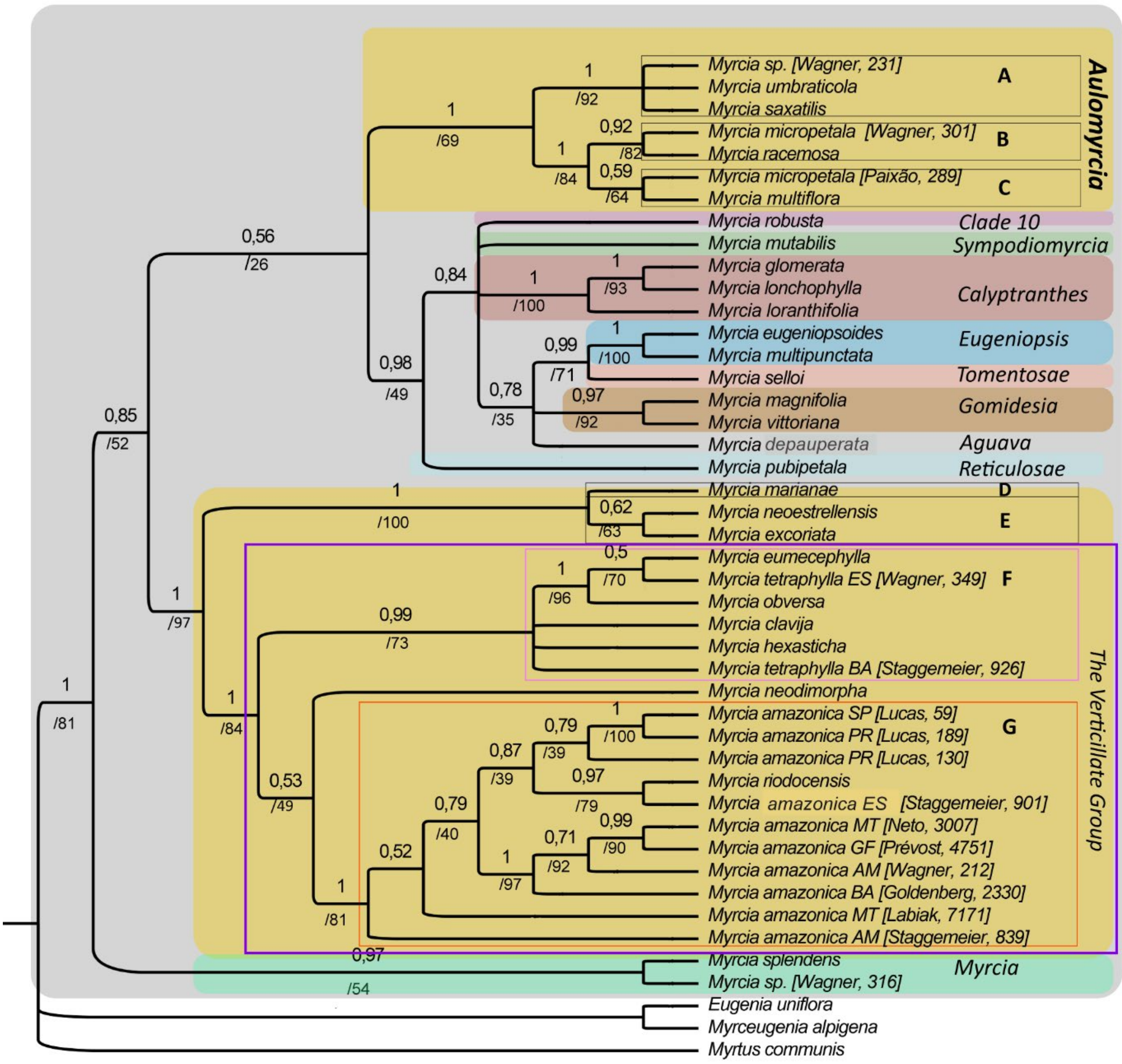
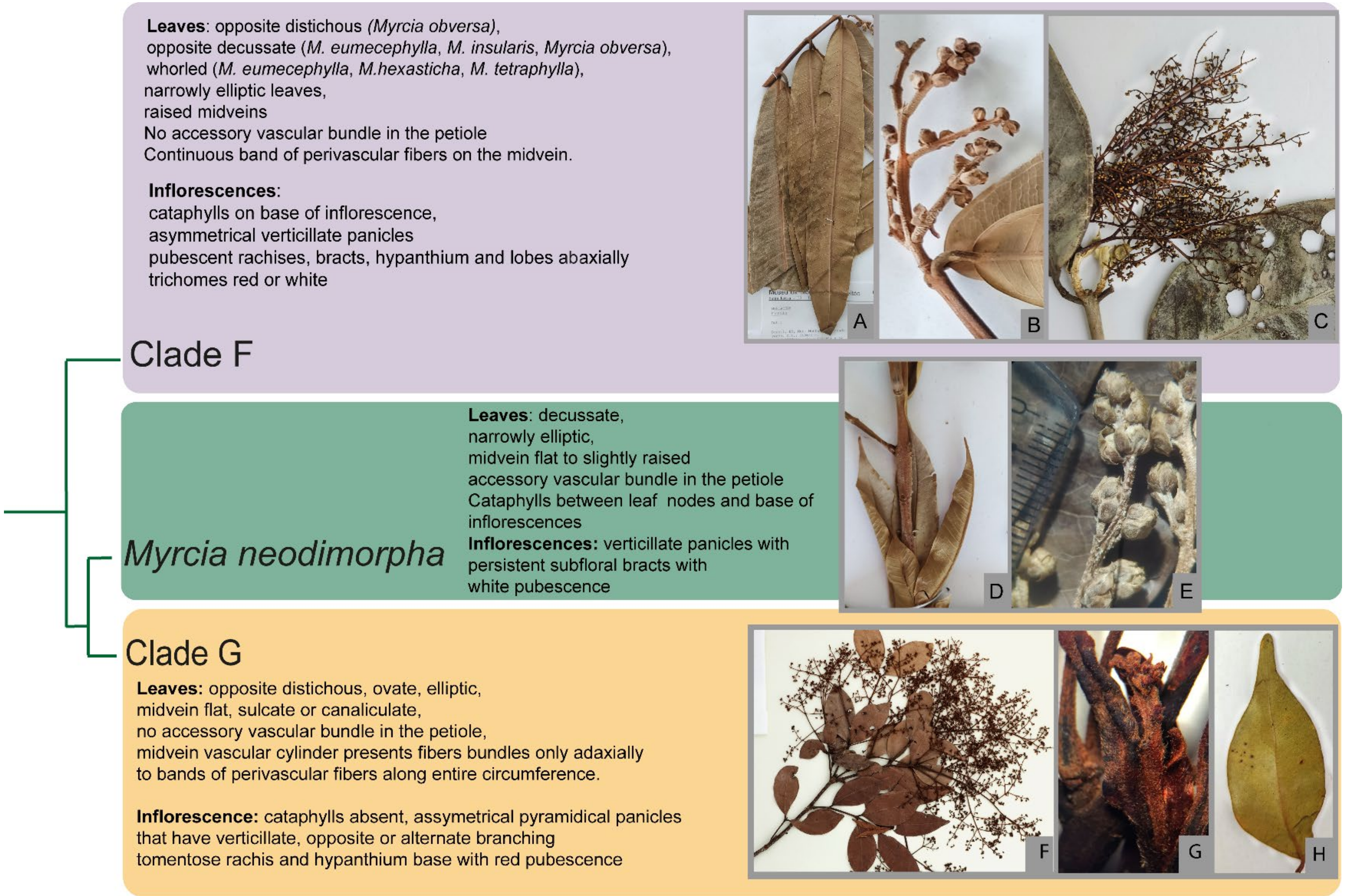


FIG. 2. Diagnostic features of clades F, G and *Myrcia neodimorpha* of the Verticillate Group. A. Decussate, narrowly elliptic leaves of *M. eumecephylla*. B. Inflorescence of *M. eumecephylla*. C. Inflorescence of *M. insularis*. D. Cataphylls on base of the inflorescence of *M. neodimorpha*. E. Flower buds with white pubescence in *M. neodimorpha*. F. *M. amazonica*. G. Red pubescence of young inflorescence rachis and bracts in *M. amazonica*. H. Glabrous leaf of *M. pyrifolia.*



Leaves: opposite distichous (Myrcia obversa),
opposite decussate (M. eumecephylla, M. insularis, Myrcia obversa),
whorled (M. eumecephylla, M.hexasticha, M. tetraphylla),
narrowly elliptic leaves,
raised midveins
No accessory vascular bundle in the petiole
Continuous band of perivascular fibers on the midvein.
Inflorescences:
cataphylls on base of inflorescence,
asymmetrical verticillate panicles
pubescent rachises, bracts, hypanthium and lobes abaxially
trichomes red or white
A
B
C
Clade F
Myrcia neodimorpha
Leaves: decussate,
narrowly elliptic,
midvein flat to slightly raised
accessory vascular bundle in the petiole
Cataphylls between leaf nodes and base of
inflorescences
Inflorescences: verticillate panicles with
persistent subfloral bracts with
white pubescence
D
E
Clade G
Leaves: opposite distichous, ovate, elliptic,
midvein flat, sulcate or canaliculate,
no accessory vascular bundle in the petiole,
midvein vascular cylinder presents fibers bundles only adaxially
to bands of perivascular fibers along entire circumference.
Inflorescence: cataphylls absent, assymetrical pyramidical panicles
that have verticillate, opposite or alternate branching
tomentose rachis and hypanthium base with red pubescence
F
G
H

TABLE 1. Species hypothesized to belong to the Verticillate Group of *Myrcia* sect. *Aulomyrcia* and their geographic distribution. Subclades follow Staggemeier et al. (2015). The nine species included in analysis are indicated in bold.

Species	Subclade	Phytogeographic domain
***Myrcia amazonica* DC.**	G	Amazon Forest, Atlantic Forest, and Cerrado
Myrcia areolata (McVaugh) E.Lucas & C.E.Wilson	F	Amazon
Myrcia badia (O.Berg) N.Silveira	F	Atlantic Forest
***Myrcia clavija* Sobral**	F	Atlantic Forest
Myrcia colpodes Kiaersk.	F	Atlantic Forest
***Myrcia eumecephylla* (O.Berg) Nied.**	F	Atlantic Forest
Myrcia gigantea (O.Berg) Nied.	F	Atlantic Forest
***Myrcia hexasticha* Kiaersk.**	F	Atlantic Forest
Myrcia insularis Gardner	F	Atlantic Forest
Myrcia liesneri B.Holst	F	Amazon
Myrcia magna D.Legrand	F	Amazon
***Myrcia neodimorpha* E.Lucas & C.E.Wilson**		Atlantic Forest
***Myrcia neoestrellensis* E.Lucas & C.E.Wilson**	F	Atlantic Forest
Myrcia neoverticillaris E. Lucas & C.E.Wilson	F	Atlantic Forest
***Myrcia obversa* (D.Legrand) E.Lucas & C.E.Wilson**	F	Atlantic Forest
Myrcia pyrifolia (Desv. ex Ham.) Nied.	G	Amazon
***Myrcia riodocensis* G.M.Barroso & Peixoto**	G	Atlantic Forest
Myrcia rubiginosa Cambess.	G	Atlantic Forest
Myrcia salticola (Steyerm.) McVaugh	G	Amazon
Myrcia santateresana Sobral	G	Atlantic Forest
Myrcia speciosa (Amshoff) McVaugh	F	Amazon
***Myrcia tetraphylla* Sobral**	F	Atlantic Forest
Myrcia zetekiana (Standl.) B.Holst	F	Central American Isthmian Forest

TABLE 2. DNA regions amplified for this study ITS from the nuclear genome, and *trnL-trnF* and *trnQ-rps16* from the plastome their amplification protocol, and primer information for each region.

	ITS	***trnL-trnF***	***trnQ-rps16***
Number of samples*	9	6	8
Amplification protocol	2 min to 94°C; 30 cycles of 1 min to 94°C; 1 min to 50°C; and 1.5 min to 72°C; end 4 min to 72°C	5 min 80°C, 35 cycles of 1 min to 95°C, 1 min to 53°C and 5 min to 65°C; at the end 4 min to 65°C Idem ndhF	5 min 80°C, 35 cycles of 1 min to 95°C, 1 min to 53°C and 5 min to 65°C; at the end 4 min to 65°C Idem ndhF
Primers	ITS u1/ ITS u4	External: trnL(c), trnL(f)	External: trnQ(F), rps16xi (R); internal: MYtrnQ (R); MYrps16 (F)
Primer reference	Sun et al. 1994	Taberlet et al. 1991	Murillo et al. 2012

Table 3. Summary information for each marker: number of samples, length of aligned fragment and substitution model selected under Akaike Information Criterion (AIC).

	ITS	***ndhF***	***psbA-trnH***	***trnL-trnF***	***trnQ-rps16***
Number of samples	42	32	36	40	42
Length of fragment	729	700	656	799	1453
Substitution model	TIM2+I+G	TVM+I	TPM1uf+G	TVM	TVM+G

APPENDIX 1. Sequences employed in the analysis presented here. NA = Not available.

Species	**Voucher**	**ITS**	***ndhF***	***psbA-trnH***	***trnL-trnF***	***trnQ-rps16***
***Eugenia uniflora* L.**	Lucas, E. 207	AM234088	KP722418	AM489828	KP722326	KP722202
Myrceugenia alpigena (DC.) Landrum	Lucas E. 167	AM234098	KP722441	AM489854	KP722376	JN661090

***Myrcia amazonica* DC**	Brazil AM	Staggemeier, V. 839	KP722396	KP722474	KP722304	KP722354	KP722251
***Myrcia amazonica* DC.**	Brazil PR	Lucas, E. 130	JN091215	MW023252	JN091406	JN091340	MW026490
***Myrcia amazonica* DC.**	Brazil PR	Lucas, E. 189	JN091212	KP722437	JN091403	JN091337	KP722213
***Myrcia amazonica* DC.**	Brazil SP	Lucas, E. 59	JN091213	KP722422	JN091404	JN091338	KP722240
***Myrcia amazonica* DC.**	French Guyana	Prévost, M.F. 4751	JN091214	KP722439	JN091405	JN091339	KP722215
***Myrcia amazonica* DC.**	Brazil AM	Wagner, M.A. 212	W212ITS	NA	NA	W212 trnL-trnF	W212trnQ-rps16
***Myrcia amazonica* DC.**	Brazil BA	Goldenberg, R. 2330	G2330ITS	NA	NA	NA	G2330trnQ_rps16
Myrcia amazonica DC.	Brazil MT	Labiak, P. 7171	L7171ITS	NA	NA	NA	L7171trnQ-rps16
***Myrcia amazonica* DC.**		Neto, L.A. 3007	KP722417	KP722495	KP722325	KP722375	KP722272
***Myrcia clavija* Sobral**		Lucas, E. 244	JN091220	KP722442	JN091411	KP722332	KP722217
***Myrcia depauperate* Glaz. Ex P.O. Rosa & Proença**		Mello-Silva, R. 1713	AM234118	KP722421	AM489859	KP722328	KP722230
***Myrcia eugeniopsoides* (D.Legrand & Kausel) Mazine**		Lucas E. 61	AM234107	KP722429	AM489845	JN091327	KP722205

***Myrcia eumecephylla* (O.Berg) Nied.**	Matsumoto, K. 803	JN091223	KP722446	JN091414	JN091349	KP722223
***Myrcia eumecephylla* (O.Berg) Nied.**	Cordeiro, M.J. 310	NA	NA	KP722284	NA	NA
***Myrcia excoriata* Mart.**	Matsumoto, K. 825	JN091203	KP722449	JN091394	JN091328	KP722226
***Myrcia glomerata* (Cambess.) G.P.Burton & E.Lucas**	Lucas, E. 74	KP722378	KP722454	AM489817	KP722334	KP722231
***Myrcia hexasticha* Kiaersk.**	Lucas, E. 194	JN091227	KP722438	JN091418	JN091354	KP722214
***Myrcia lonchophylla* A.R. Lourenço & E.Lucas**	Lucas, E. 84.	NA	NA	AM489818.1	JN091324.1	MK202481.1
***Myrcia loranthifolia* (DC.)G.P.Burton & E.Lucas**	Wagner, M.A. 347	W347ITS	NA	NA	W347trnL-trnF	NA
***Myrcia magnifolia* (O.Berg) Kiaersk.**	Lucas, E. 1182	KP722411.1	KP722489	KP722319	KP722369	KP722266
***Myrcia marianae* Staggemeier & E.Lucas**	Staggemeier, V. 764	KP722381	KP722458	KP722288	KP722337	KP722235
***Myrcia micropetala* (Mart.) Nied.**	Wagner, M.A. 301	W301ITS	NA	NA	W301trnL-trnF	W301trnQ-rps16
***Myrcia micropetala* (Mart.) Nied.**	Paixão, J.L. da 289	NA	NA	JN091422.1	NA	NA
***Myrcia multiflora (*Lam.) DC.**	Staggemeier, V. 867	KP722387	KP722464	KP722294	KP722343	KP698771

***Myrcia multipunctata* Mazine**	Santos, M.F. 836	KU898311.1	KU898368.1	KU898416.1	KU898471.1	KU898526.1
***Myrcia mutabilis* (O.Berg) N.Silveira**	Mazine, F. 1052	JN091233	KP722435	JN091424	KP722344	KP722241
***Myrcia neodimorpha* E.Lucas & C.E.Wilson**	Folli, D. 6649	KP722416	KP722494	KP722324	KP722374	KP722271
***Myrcia neoestrellensis* E.Lucas & C.E.Wilson**	Wagner, M.A. 348	W348ITS	NA	NA	NA	W348trnQ-rps16
Myrcia obversa	Matsumoto, K. 820	JN091206	KP722450	JN091397	JN091331	KP722227
***Myrcia pubipetala* Miq.**	Lucas, E. 86	AM234114	KP722426	AM489855	JN091364	KP722273
***Myrcia racemosa* (O.Berg) Kiaersk.**	Staggemeier, V. 751	KP722380	KP722457	KP722287	KP722336	KP722234
***Myrcia riodocensis* G.M.Barroso & Peixoto**	Staggemeier, V. 917	NA	KP722466	KP722296	KP722346	KP722243
***Myrcia robusta* Sobral**	Lucas, E. 727	KU898289.1	KU898346.1	KU898393.1	KU898448.1	NA
***Myrcia saxatilis* (Amshoff) McVaugh**	Lucas, E. 98	AM234119	KP722427	AM489860	JN091370	KP722203
***Myrcia selloi* (Spreng.) N.Silveira**	Lucas, E. 110	JN091240	KP722436	JN091431	JN091371	KP722212
Myrcia sp.	Wagner, M.A. 231	NA	NA	NA	W231trnL-trnF	W231trnQ-rps16

Myrcia sp.		Wagner, M.A. 316	W316	NA	NA	W316trnL-trnF	W316trnQ-rps16
***Myrcia splendens* (Sw.) DC.**		Lucas, E. 73	AM234122	KP722425	AM489863	JN091374	KP722274
***Myrcia tetraphylla* Sobral**		Staggemeier, V. 926	KP722389	KP722467	KP722297	KP722347	KP698773
Myrcia tetraphylla Sobral		Wagner, M.A. 349	W349ITS	NA	NA	NA	NA
***Myrcia umbraticola* (Kunth) E.Lucas & C.E.Wilson**		Wagner, M.A. 240	W240ITS	NA	NA	W240trnL-trnF	W240trnQ-rps16
***Myrcia vittoriana* Kiaersk.**		Amorim, B. 2008	MH880970.1	NA	MK157129.1	NA	MK202518.1
Myrcia cf santateresana Sobral		Staggemeier, V. 901	KP722401	KP722479	KP722309	KP722359	KP722256
***Myrtus communis* L.**	Cult Kew	Lucas, E. 211	AM234149	KP722420	AM489872	KP722327	KP722221

SUPPLEMENTAL FIGURES

FIG. S1 Maximum-likelihood phylogenetic tree obtained through RAxML based on internal transcribed spacer (ITS); the groups of *Myrcia* sect. *Aulomyrcia* are indicate in the rectangles. Values above branches are bootstrap supports.

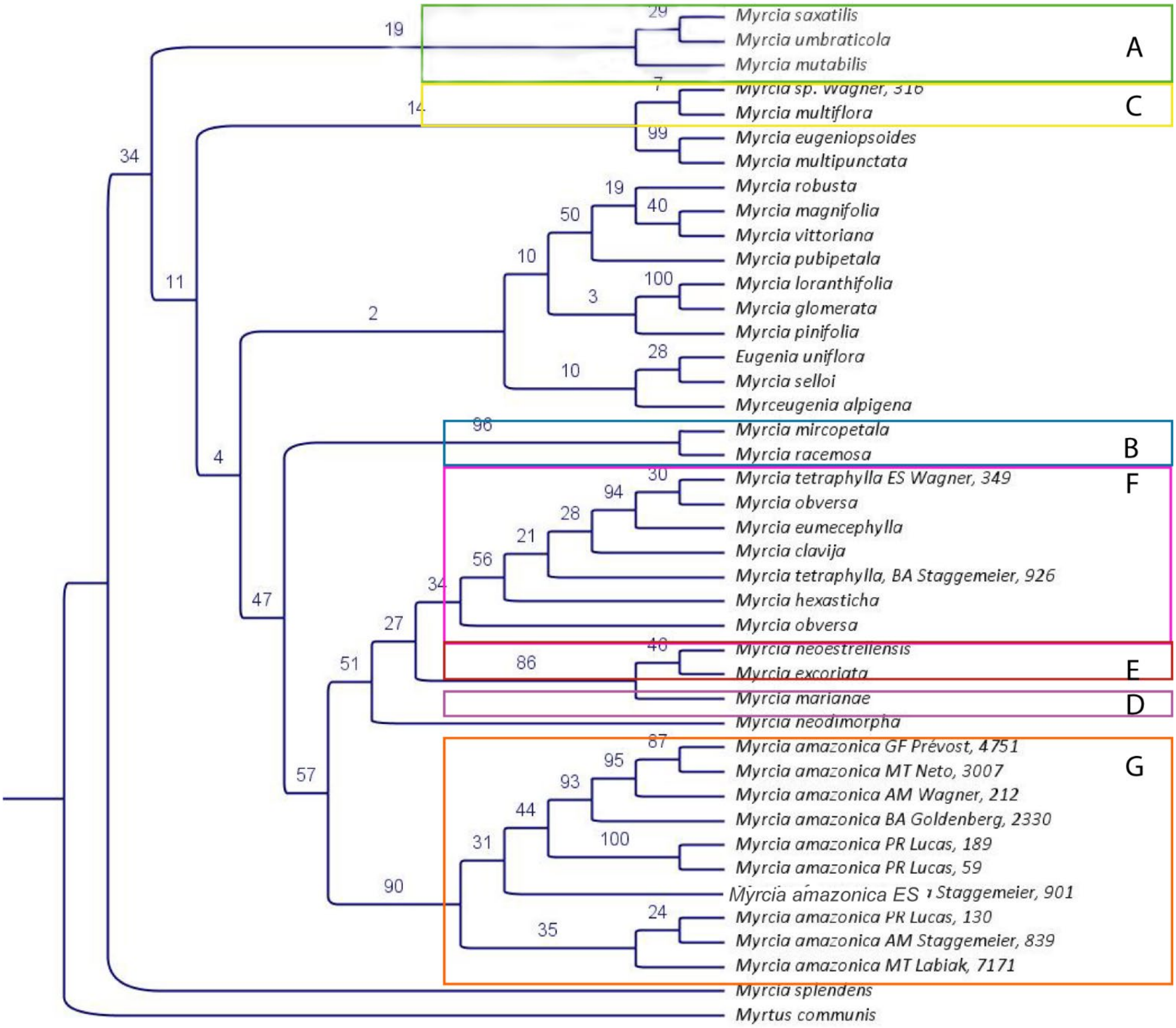
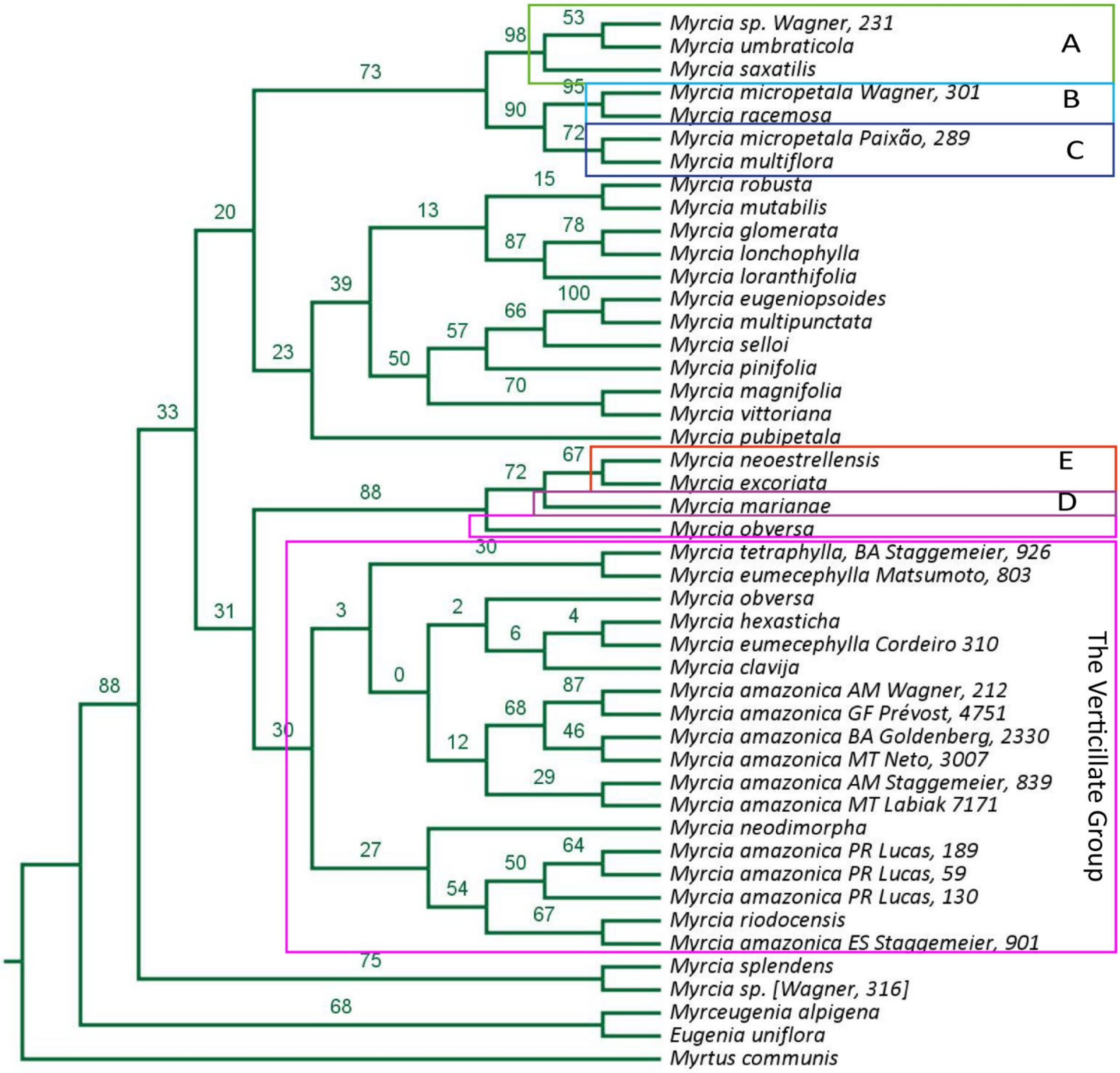


FIG. S2. Maximum-likelihood phylogenetic tree obtained through RAxML based on combined chloroplast markers (*ndhF, psbA-trnH, trnL-trnF, trnQ-rps16*); the groups of *Myrcia* sect. *Aulomyrcia* are indicate in the rectangles. Values above branches are bootstrap supports.



3. CHAPTER 2 - LEAF MORPHOLOGY AND ANATOMY IN *MYRCIA* SECT. *AULOMYRCIA* (MYRTACEAE)

Artigo publicado na revista Botany.

Leaf morphology and anatomy in *Myrcia* sect. *Aulomyrcia* (MYRTACEAE): species circumscription and characterization of clades

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Abstract

Myrcia, a diverse neotropical genus of Myrtaceae, encompasses ca. 780 species. However, species of *Myrcia* are similar and difficult to distinguish. In *Myrcia* sect. *Aulomyrcia,* leaf features help distinguishing clades and species. Our aim is to provide data on leaf features for species of *Myrcia* sect. *Aulomyrcia* clades F, and G. We sampled 31 specimens of 13 species of *Myrcia* sect. *Aulomyrcia* (*Myrcia amazonica, M. eumecephylla*, *M. hexasticha*, *M. insularis*, *M. magna*, *M. micropetala*, *M. neodimorpha*, *M. neoestrellensis*, *M. obversa*, *M. pyrifolia*, *M. riodocensis*, *M. subobliqua,* and *M. tetraphylla).* Samples were subjected to sectioning and staining techniques for morphological and anatomical analysis through stereo and light-microscopy. Leaf blade and petiole morphological and anatomical features were described carefully for the first time for these 13 species. We provided an identification key based on leaf features. Our findings are discussed in the light of *Myrcia* sect. *Aulomyrcia* systematics. We comment on the significance of petiolar and blade features, such as trichomes types and location, phyllotaxis, rhytidome peeling, periderm and lenticels, and petiole, blade, and vascular cylinder shape. Our study brings novel information on leaf structure variation in *Myrcia* sect. *Aulomyrcia*, delivering much needed data for species and clades circumscription and identification.

Keywords: blade, petiole, Myrteae, Neotropics, periderm.

1. Introduction

Myrtaceae is a taxonomically complex angiosperm family. For instance, some clades of Neotropical Myrtaceae present highly similar species, showing such subtle morphological differences among them that one can call the variation cryptic. Species identification can be difficult in such cases because it asks for careful attention to detail.

Leaf and petiolar morphological and anatomical characters can support species circumscription in such challenging clades. These leaf features datasets can be combined with other information on habit, inflorescences, flowers, fruits, and species occurrence data and habitat to retrospectively, not only for species identification but also to interpret phylogenies (e.g., Lucas et al. 2019).

Identification of neotropical Myrtaceae specimens is often challenging, so floristic and ecological studies commonly include multiple undetermined specimens (e.g., Martini et al. 2007; Cola et al. 2020), strongly contributing to the taxonomic impediment and preventing effective management of species diversity in tropical forests (Lucas and Bunger 2015).

Myrtaceae is composed of 137 genera and c. 6500 species with a pantropical distribution (Thornhill et al. 2015; POWO 2022). Most neotropical species of Myrtaceae belong to tribe Myrteae DC., which is constituted exclusively by species with fleshy fruits (McVaugh 1968; Lucas et al. 2005; Vasconcelos et al. 2017a). Tribe Myrteae species are significant components, both in species numbers and abundance, of neotropical phytogeographic domains such as the Amazon Forest (Steege et al. 2013; Cardoso et al. 2017), Atlantic Forest (Murray-Smith et al. 2009; Lucas and Bünger

2015; Staggemeier et al. 2017), Caatinga (Tölke et al. 2011; Lima et al. 2012; Costa et al. 2015; Santos et al. 2021) and Cerrado (Lima et al. 2021).

Myrcia DC. is the second largest genus of tribe Myrteae, encompassing 780 species (POWO 2022) subdivided into nine sections (Lucas et al. 2011, 2018). *Myrcia* sect. *Aulomyrcia* (O.Berg) corresponds to one of these sections and encompasses approximately 140 species (Lucas et al. 2018).

Based on the current phylogenetic knowledge of *Myrcia* sect. *Aulomyrcia* (Staggemeier et al. 2015), there is a link between Amazonian and Northeastern Atlantic Forest species and between Northeastern and Southeastern Atlantic Forest species and seven clades were recognized (informally named from A to G), divided into two main monophyletic subgroups. One is the branch formed by clades A-C of Amazonian and Northeastern Atlantic Forest species. As examples, we cite the Amazonian species *Myrcia umbraticola* (Kunth) E.Lucas & C.E.Wilson of clade A, *Myrcia micropetala* (Mart.) Nied., a species endemic to Bahia and *Myrcia racemosa* (O.Berg) Kiaersk. (widespread in the Atlantic Forest) both belonging to clade B, and the widespread *Myrcia multiflora* (Lam.) DC., belonging to clade C. The other is a branch formed by clades D-G of Northeastern and Southeastern Atlantic Forest species plus a few Amazonian species, and the widely distributed *Myrcia amazonica* DC. Morphologically, the distinction is supported by characters such as leaf morphology, e.g., opposite distichous versus opposite decussate or verticillate phyllotaxis, corky petioles and leaf blade characteristics.

Clades F, G and *Myrcia neodimorpha* E.Lucas and C.E.Wilson emerged as a monophyletic group, consisting of eight species **(Fig. 1**) (Staggemeier et al. 2015). Fifteen other species are hypothesized to belong to these clades in a recent conspectus of the section (Lucas et al. 2016), but they have not been included in a phylogenetic analysis yet. *Myrcia neodimorpha* and species in clades F and G are highly similar in morphology, making it difficult to separate species based only on inflorescence or flower morphology, so that leaf characters can be taxonomically useful.

Most recent studies on leaf morphology and anatomy in Angiosperms focus on taxonomically diagnostic features that are relatively stable, in the sense of environmental changes and leaf adaptation to variation (Ma et al. 2005; Rossatto et al. 2011, Araújo et al. 2020; Santos et al. 2020). One may object to leaf morphology and anatomy being potential diagnostic features for clades because leaves are highly versatile organs that adapt to change. So that the focus should be on stable leaf characters within a clade.

For example, in acaulescent species of *Syagrus* Mart. (Arecaceae), leaflet morphological and anatomical characters were successfully used for species circumscription, corroborating clades recovered in molecular studies (Noblick 2013; Sant'Anna-Santos 2021). Leaf trichomes were successfully used to distinguish between species of subtribe Lychnophorinae of Asteraceae (Wagner et al. 2014) and Zaman et al. (2022) used leaf epidermal micromorphological characters analyzed through Scanning Electron Microscopy and indicated that such characters can help identify species of Lamiaceae that are useful for Traditional Chinese Medicine.

Another objection to using leaves as diagnostic features in Myrtaceae is that phylogenetic studies often indicate high levels of homoplasy in morphological and anatomical characters. Which means that highly similar characters evolved separately many times, making it difficult to sort species groups based on these morphological characters (Vasconcelos et al. 2017b; Giaretta et al. 2019).

However subtle, leaf morphological and anatomical features in Myrtaceae have been used for systematic decisions when combined with other information (Lucas et al. 2019). For example, in the *Campomanesia xanthocarpa* complex, leaf morphology and anatomy, in combination with habit, geographic distribution, and phylogenetic data, was used in species circumscription (Oliveira et al. 2011, 2018). Moreover, among the species of *Leptospermum* J.R.Forst. and G.Forst. (Leptospermeae), leaf morphological and anatomical characters were considered useful as diagnostic characters of the different species (Johnson 1980). Retamales and Scharaschkin (2014) surveyed variation in leaf anatomy and micromorphology of Chilean Myrtaceae, and the combined implications to taxonomy and ecology.

The objective of our study is to analyze and describe the leaf morphology and anatomy in species of *Myrcia* sect. *Aulomyrcia*, with special focus on species of clades F, G, and *Myrcia neodimorpha*. We aimed to find leaf characters to shed light on the affinities shared by species in these clades, in order to enhance the existing taxonomic understanding of lineages within *Myrcia* sect. *Aulomyrcia*.

2. Material and Methods

2.1 Sampling

We analyzed 31 specimens of 13 species of *Myrcia* sect. *Aulomyrcia* (vouchers of specimens are listed in **Table 1**). The samples were obtained from the FLOR herbarium (acronym follows Thiers continuously updated), supplemented with material from field expeditions. We included *Myrcia micropetala* (Mart.) Nied., from the clade B of *M.*

sect. *Aulomyrcia* (Staggmeier et al. 2015), for comparison with species from clades F and G **(Fig. 1)**.

We analyzed three specimens from each species, except in the case of species with limited material. We ensured sample selection from different environments to limit the effect of environmental variation. Habitat type for each specimen is listed in **Table 1**.

We selected leaf characters for analysis based on previous leaf morpho-anatomical studies of *Myrcia* (Gomes and Neves 1997; Gomes et al. 2009), but we also scrutinized material for other leaf characters of likely use specially for section *Aulomyrcia*'s taxonomy, to generate detailed characterizations of the leaves. Characters are listed in **Table 2**. We also consulted leaf morpho-anatomy studies in other genera *of* Myrtaceae for comparison with *Myrcia* characters to decide character relevance in context (Wilson 2011; Al-Edany and Al-Saadi 2012; Oliveira et al. 2011, 2018).

Material collected in the field was fixed in a solution of formalin-acetic acid ethyl alcohol (FAA) 50% (Johansen, 1940), and rinsed in distilled water before storing in 70% ethanol, according to Berlyn and Mickshe (1976). Leaf fragments of voucher specimens were immersed in water and drops of detergent, microwaved on low heat for 1 minute, and then left overnight in room temperature (adapted from Smith and Smith, 1942). After that, samples were dehydrated and stored in 70% ethanol. Before free-hand sectioning, all samples were rehydrated in distilled water.

2.2 Freehand Sections

Freehand paradermal and transverse sections of the leaf blades and petiole median portion were obtained using a razor blade. Sections were cleared in a solution of sodium hypochlorite (Kraus and Arduin 1997), then rinsed in distilled water and stained with 0,025% Toluidine Blue O at pH 4 (O'Brien et al. 1964; Ribeiro and Leitão 2020). Some petiole sections were stained with Sudan III to detect lipids and Lugol's iodine to confirm the presence of starch (Johansen 1940). Semi-permanent slides were mounted with a solution of glycerol and distilled water (50%) (Purvis et al. 1964).

2.3 Historesin embedding

Petioles were embedded in Historesin (Leica) following the manufacturer's instructions, and then sectioned in a rotative microtome. Samples that were previously stored in 70% ethanol were dehydrated in a sequence of ethanol 85% and 95%, kept for one hour in each, before infiltrating in a solution of ethanol 95% and historesin + activator (1:1). Afterwards, samples were kept for 24 hours in 100% historesin solution and activator (1:1), and then embedded in historesin, activator and hardener. For the embedding procedures and proportions, we followed the manufacturer's protocol (Historesin Leica, Leica Biosystems, Wetzlar, Germany). Thin sections of 8-10 µm were obtained in a rotative microtome, then stained with 0,025% Toluidine Blue O at pH 4 (O'Brien et al. 1964) and mounted as permanent slides with synthetic resin, following the standard methods used in plant anatomy.

2.4 Analyses and image capturing

Morphological and anatomical analyses were performed using stereo and optical light microscopes. Images of the material were obtained with Leica apparatus: DM2500 optical light microscope and stereo microscope with integrated LED illumination coupled to a DFC 295 digital camera using LAS 3.8 software.

2.5 Terminology

Morphological and anatomical descriptions follow nomenclature used by Radford et al. (1976) and Wilson (2011). Because appressed simple trichomes can be confused with unequal armed brachiate trichomes, we designated trichomes as brachiate when they present a base that resembles a ‘stalk’ beneath two equal or unequal ‘arms’ forming a T-shape. We considered trichomes to be simple when this base is absent, and the trichome consists of a single elongated cell that is erect (patent) or seldom appressed.

According to Radford 1976, opposite leaves arise from the stem at the same level, the opposite distichous are arranged in two vertical rows on either side of the stem, while opposite decussate have successive leaf pairs at 90 degrees angles apart from each other. More than two leaves arise from the same node in whorled phyllotaxis. Regarding leaf shape, elliptic leaves present the widest axis at midpoint of structure and with margins symmetrically curved. Elliptic leaves present a length to width ratio of 2:1 to 3:2, while narrowly elliptic leaves present a ratio of 6:1 to 3:1. Ovate leaves have the widest axis below middle point in structure, resembling an egg shape and obovate leaves are the opposite of ovate.

3. Results

We chose to present the results as a characterization of leaf blade and petiole in species of *Myrcia* section *Aulomyrcia* focusing on the studied species of clades F and G of the section. The descriptive results are presented in the following four parts: **(3.1) phyllotaxis**, **(3.2) petiole and leaf blade macroscopic morphological characters (3.3) description of petiole and leaf blade anatomical characters, (3.4) diagnostic leaf**

characters for studied clades of *Myrcia* sect. *Aulomyrcia* (3.5), and identification key of studied species.

3.1 Phyllotaxis

In *Myrcia* sect. *Aulomyrcia* phyllotaxy varies from opposite distichous, opposite decussate, or whorled. For example: *Myrcia amazonica* presents opposite distichous phyllotaxis **(Fig. 2A)**, *M. insularis,* opposite decussate **(Fig. 2B)** and *M. hexasticha,* whorled **(Fig. 2C)**. Some species, such as *Myrcia eumecephylla*, can present two types of leaf arrangement, opposite decussate or whorled. Phyllotaxis for each studied species are listed in **Table 3.**

3.2 Petiole and leaf blade macroscopic morphological characters

3.2.1. Petiole

All species present corky petioles with peeling or smooth non-peeling outer layers. For example, *Myrcia tetraphylla* presents a peeling petiole **(Fig. 3A**) and *M. amazonica* presents a non-peeling one **(Fig. 3B)**. All species present lenticels on the petioles **(3B).** Information on petiole outer layers for each species are indicated in **Table 3**.

3.2.2 Leaf blade

Leaf shape of species of *Myrcia* sect. *Aulomyrcia* vary from narrowly elliptic and elliptic to ovate or obovate, with a gradient possible between the states. In *Myrcia micropetala* leaf blades are elliptic **(Fig. 4A)**, in *M. neoestrellensis* blades are elliptic to obovate **(Fig. 4B)**, and in *M. amazonica* they are elliptic to ovate **(Fig. 4C)**. Information on leaf blade shape for each studied species are indicated in **Table 3**.

Leaf apex of species of *Myrcia* sect. *Aulomyrcia* varies between acute, acuminate, caudate or mucronate. *Myrcia micropetala* has a mucronate leaf apex **(Fig. 4A)**, while *M. neoestrellensis* presents an acute one**(Fig. 4B)**. *Myrcia amazonica* presents an acuminate to caudate apex **(Fig. 4C)**. Information on leaf blade apex for each studied species are indicated in **Table 3.**

Leaf blade bases in *Myrcia* sect. *Aulomyrcia* studied species can be either cuneate or cuneate to rounded. *Myrcia neoestrellensis,* for example, presents a cuneate base **(Fig. 4B)**, and *M. amazonica* presents a cuneate to rounded base (**Fig. 4C)**. All species present flat leaf blade margins **(Fig. 4B,C)** except for *M. micropetala*, that presents revolute margins **(Fig. 4A)**. Information on leaf blade bases and leaf blade margins for each species are indicated on **Table 3**.

Most species do not present oil glands visible to the naked eye on either surface, except for *Myrcia neoestrellensis*, which presents conspicuous glands abaxially **(Fig. 4B)**.

Myrcia sect. *Aulomyrcia* leaf blades of species studied here present glabrous adaxial surfaces. And all species present glabrescent abaxial surfaces with few sparse trichomes, as in *M. amazonica* **(Fig. 4D)**, except for *Myrcia micropetala* with a golden tomentose indumentum that is denser along the midvein **(Fig. 4E)**. Abaxial leaf blade indumentum variation among studied species are described in **Table 3**.

Adaxial leaf blade midvein prominence in studied species of *Myrcia* sect. *Aulomyrcia* can be flat or raised. For instance, *Myrcia neodimorpha* presents flat midveins adaxially **(Fig. 4F)**, while *M. eumecephylla* presents raised midveins adaxially **(Fig. 4G)**. Midveins of leaf blades abaxially of all studied species are raised, except for *M. neoestrellensis,* with a flat midvein abaxially. Midvein prominence data for all studied species are presented in **Table 3**.

3.3 Petiole and leaf blade anatomical characters

3.3.1 Trichomes

In all studied species, leaves trichomes occur mostly on the abaxial surfaces, along the midvein and on the petioles. Only non-glandular trichomes are observed and they are simple (erect or appressed) or brachiate (T-shaped). *Myrcia amazonica* presents sparse short erect trichomes with enlarged bases **(Fig. 5A).** *Myrcia magna* presents sparse simple appressed trichomes with tannin-like content **(Fig. 5B)** and brachiate trichomes in the petiole also with tannin-like content **(Fig. 5C)**. The golden tomentose indumentum on the abaxial surface of *Myrcia micropetala* is composed of simple erect trichomes, some with tannin-like content and others without **(Fig.5D).** Petiole trichomes information for each studied species is found on **Table 4** and leaf blade trichomes data on **Table 5**.

3.3.2 Petiole

The leaf petioles of *Myrcia* sect. *Aulomyrcia* studied species present variation in shape, epidermis, cortex, and vascular cylinder characteristics.

Petiole outline shape in cross section can vary between planar (adaxially) and convex (abaxially) in most species **(Fig. 6A-G, J-K),** concave on both surfaces in *Myrcia magna* **(Fig. 6H)**, concave adaxially and convex abaxially in *M. neoestrellensis* **(Fig. 6I)**, and circular in *M. neodimorpha* and *M. micropetala* **(Fig. 6L-M)**. Data on petiole outline for each studied species is presented on **Table 4**.

All studied species present lenticels in the petioles outer layers **(Fig. 7A)** and a layer of epicuticular waxes **(Fig. 7B)**. All species present cuticles with extensions from the outer surface to the anticlinal walls of epidermal cells **(Fig. 7C)**. The petiole epidermis is uniseriate in most species **(Fig. 7C)**, or uniseriate with some biseriate portions (as in *M. obversa* **(Fig. 7D)**. All species present periderm, with alternating layers of suberized and lignified cell walls **(Fig. 7E)**. Data on the petiolar outer layers, epidermis and periderm for each studied *Aulomyrcia* species are indicated on **Table 4**.

Some species present only collenchyma in the petiolar cortex, such as *Myrcia amazonica* **(Fig. 7F)**, others present only sclerenchyma, as in *M. riodocensis* **(Fig. 7G)**, and yet other species present both collenchyma and sclerenchyma.

Xylem bundles shape in the vascular cylinder varies among the studied species, being either an open arch with ends pointing inward **(Fig. 6A-C, G-I, M)**, or a closed ellipse **(Fig. 6.D-F, J-L).** *Myrcia neodimorpha* presents an accessory vascular bundle emerging beside the central cylinder in the petiole **(Fig. 7H)**.

Myrcia obversa, *M. eumecephylla*, and *M. insularis* present cells in pith stained with Sudan III, probably containing lipidic material.

Regarding idioblast types, all species present prismatic crystals in their petiolar cortex and pith **(Fig. 7G)**, except for *Myrcia subobliqua*, which presents prismatic crystals and starch grains as idioblasts, especially around the oil glands **(Fig. 7I)**. Petiolar cortex, vascular cylinder and pith characteristics for each studied species is presented on **Table 4.**

3.3.3 Leaf blade anatomical characters

Some leaf blade anatomical characteristics among studied species of *Myrcia* sect. *Aulomyrcia* are constant and others are variable.

All studied species presented uniseriate epidermis **(Fig. 8A, B)**. Epidermal cells shape in cross section can be square (as in *Myrcia insularis* **Fig. 8A**) or rectangular (as in *M. micropetala*, **Fig. 8B**). Epidermal cell anticlinal walls in paradermal sections are sinuous adaxially and abaxially in all studied species (e.g., adaxially in *Myrcia neodimorpha* **(Fig. 8C)** an abaxially in *Myrcia riodocensis* **(Fig. 8D).** Stomata are paracytic in all studied species **(Fig. 8D)** and occur on the abaxial surface only **(Fig. 8E)**. The leaf blade epidermal characteristics variation among all studied species are summarized in **Table 5**.

All studied species presented dorsiventral mesophyll with palisade parenchyma and spongy parenchyma **(Fig. 8F)**. Oil glands are lodged in the parenchyma on both sides of the leaves **(Fig. 8G)**. Idioblasts containing prismatic crystals are present in all species in the blade's midvein cortex and flanking the vascular bundles on the palisade and spongy parenchyma **(Fig. 8H)**.

Midvein vascular cylinder shape varies among species. It can be an open arch with ends pointing outward (for e.g., in *Myrcia neoestrellensis* **(Fig. 8I)** and *M. micropetala* **(Fig. 8J)**; an open arch with ends pointing inward (for e.g., in *M. insularis* **(Fig. 8K)** or a closed ellipse (for e.g., in *Myrcia tetraphylla* **(Fig. 8L)**. The vascular cylinder can be flanked either by bundles of perivascular fibers, or by entire bands of it. The cortex is formed by collenchyma (e.g., *Myrcia insularis* **Fig. 8K**), or by sclerenchyma cells (e.g., *M. micropetala* **Fig. 8J**). Data on leaf blade midvein characteristics variation for each studied species is presented on **Table 5**.

3.4 Diagnostic leaf characters for studied clades of *Myrcia* sect. *Aulomyrcia.*

Based on the data discussed in prior paragraphs, combinations of morphological and anatomical leaf characters considered diagnostic for subclades of *Myrcia* sect. *Aulomyrcia* represented in this study are indicated in **Table 6**. Our focus was mainly on clades F and G of *Myrcia* sect. *Aulomyrcia* (including *Myrcia neodimorpha).* Thus, species of clade F usually present opposite decussate or whorled phyllotaxis (vs. opposite distichous in clade G species), leaf blades are larger in clade F (approximately 12-25 x 3-12 cm) vs smaller in clade G species (3-9 x 2-4 cm), narrowly elliptic in clade F (vs. elliptic or ovate in clade G) and the midvein is raised adaxially in clade F (vs. flat in clade G). *Myrcia neodimorpha* presents ovate or elliptic leaf blades and flat midvein adaxially (as in species of clade G), with large and coriaceous leaves like those in clade F.

In our analyses we found that *Myrcia obversa* of clade F can also present specimens with opposite distichous phyllotaxis or with opposite decussate arrangements as expected. *Myrcia eumecephylla* can present both opposite decussate (more common) and whorled leaves. But for this species, both phyllotaxis can occur on the same specimen. The whorled leaves are usually near the ends of branches, just below the terminal inflorescences.

We also indicated data on *Myrcia micropetala* **(clade B)** to give it a perspective for comparison. We observed that species from clade F and G differ from *M. micropetala* of clade B by having petioles that lack sclereids in the cortex (vs. petioles with sclereids in the cortex). Also, species in clades F and G present glabrous to sparsely pubescent leaf blades abaxially, while *Myrcia micropetala* of clade B presents a tomentose indumentum, leaf margins are flat in clades F and G (vs. revolute in *Myrcia micropetala* of clade B).

Bellow we provide an identification key based on leaf data of the studied species.

3.5 Identification key for the studied species of *Myrcia* sect. *Aulomyrcia* based on morphological and anatomical characters.

1. Phyllotaxy opposite distichous or opposite decussate **2**

Phyllotaxis whorled **12**

2. Phyllotaxis opposite distichous (or sometimes slightly opposite decussate in *Myrcia obversa*) **3**

Phyllotaxis opposite decussate **9**

3. Uniseriate epidermis in the petiole. Midvein flat adaxially on the leaf blade **4**

Uniseriate epidermis with many biseriate portions in the petiole. Midvein raised adaxially on the leaf blade.. ***Myrcia obversa***

4. Petiole outer layer non-peeling. Collenchyma between leaf blade midvein vascular cylinder and epidermis **5**

Petiole outer layer peeling. Sclerenchyma between leaf blade midvein vascular cylinder and epidermis... ***Myrcia riodocensis***

5. Midvein raised abaxially on the leaf blade. Oil glands on abaxial surface not visible to the naked eye **6**

Midvein flat abaxially on the leaf blade. Oil glands on abaxial surface visible to the naked eye... ***Myrcia neoestrellensis***

6. Idioblasts containing prismatic crystals on petiole cortex. Vascular cylinder shaped as an open arch with ends folding inward on leaf blade midvein.......................................**7**

Idioblasts containing prismatic crystals and starch grains on petiole cortex. Vascular cylinder shaped as a closed ellipse on leaf blade midvein................. ***Myrcia subobliqua***

7. Planar and convex petiole, regular outer surface, with pockets of periderm. Leaf blade with cuneate to rounded base, and glabrous or with simple trichomes with enlarged bases abaxially.. **8**

Petiole concave on both sides, highly irregular outer surface, continuous layer of periderm, thicker in some portions. Leaf blade with cuneate base, and sparsely pubescent with brachiate trichomes abaxially... ***Myrcia magna***

8. Petiole with simple trichomes with enlarged bases, bundles of perivascular fibers concentrated adaxially or in a continuous band. Leaf blade with simple trichomes with enlarged bases abaxially.. ***Myrcia amazonica***

Petiole glabrous, bundles of perivascular fibers around the vascular cylinder (not continuous). Leaf blade glabrous on both surfaces .... ***Myrcia pyrifolia***

9. Midvein raised adaxially and apex acute on the leaf blade **10**

Midvein flat adaxially and apex mucronate on the leaf blade.......................................**11**

10. Petiole with irregular outer surface. Leaf blade base cuneate to cordate, raised secondary veins abaxially, epidermal cells rectangular .... ***Myrcia eumecephylla***

Petiole with regular outer surface. Leaf blade cuneate, flat secondary veins abaxially, epidermal cells square.. ***Myrcia insularis***

11. Petiole with irregular outer surface and accessory vascular bundle. Leaf blade narrowly elliptic, elliptic, or ovate, base rounded to cordate, sparsely pubescent with simple trichomes with enlarged bases and brachiate trichomes abaxially; midvein vascular cylinder shaped as closed ellipse and epidermal cells square***Myrcia neodimorpha***

Petiole with regular outer surface without accessory vascular bundle. Leaf blade elliptic, base cuneate, tomentose with simple trichomes abaxially, midvein vascular cylinder an open arch; epidermal cells rectangular and flattened .... ***Myrcia micropetala***

12. Phyllotaxis whorled with three leaves at each node. Petiole rhytidome non-peeling. Leaf blade apex acute to acuminate (rarely truncate)......................... ***Myrcia hexasticha***

Phyllotaxis whorled with four leaves at each node. Petiole rhytidome non-peeling. Leaf blade apex acuminate ....***Myrcia tetraphylla***

Discussion

In this study, we aimed to find leaf morphological and anatomical characters to support clades circumscription and species identification in *Myrcia* sect. *Aulomyrcia*. Detailed description of leaf morphological and anatomical features of *Myrcia* sect. *Aulomyrcia* are provided for the first time. The 13 species that were represented in this study are*: Myrcia amazonica*, *M. eumecephylla*, *M. hexasticha*, *M. insularis*, *M. magna*, *M. micropetala*, *M. neodimorpha*, *M. neoestrellensis*, *M. obversa, M. pyrifolia*, *M. riodocensis*, *M. subobliqua* and *M. tetraphylla*. We have discussed the characters that help set species apart. Regarding general diagnostic characters, we have complemented combinations of leaf macro-morphological characters already discussed by Staggemeier et al. (2015) and Lucas et al. (2016) with a more in-depth analysis of the morphological variation, and then further with anatomic data. An identification key for these species is also provided, that aids the identification of studied species.

According to Klücking (1988) and Wilson (2011), in Myrteae species, the most common phyllotaxis is opposite distichous (but whorled and alternate are also found); leaves are simple, with entire margins (rarely crenulate), pinnately brochidodromous (rarely camptodromous) with well-defined intramarginal veins.

Leaf anatomical features with published taxonomic value in Myrteae are the presence and location of unicellular simple and brachiate trichomes, anticlinal epidermal cell walls shape, mesophyll type (dorsiventral or isobilateral), shape of the bicollateral vascular cylinder, and secretory cavities or oil glands location (Wilson 2011; Al-Edany and Al-Saadi 2012). *Myrcia* is no different, the three main prior studies of leaf morphological and anatomical features in the genus (Gomes and Neves 1997; Jorge et al. 2000; Gomes et al. 2009) indicate that type and location of trichomes, oil gland structure, and shape of epidermal cells are helpful. Narrowing down to the clades of *Myrcia* sect. *Aulomyrcia*, Staggemeier et al. (2015) indicated morphological features to separate the clades F and G, that were further developed here (see **Table 6**). The particular features to distinguish its clades are phyllotaxis, leaf blade size, shape, and texture, abaxial surface pubescence, and other anatomical features discussed in the following paragraphs.

In our analyses, studied species presented corky petioles when considering the presence of periderm and lenticels, with peeling or non-peeling outer layers. However, in the Conspectus of *Myrcia* sect. *Aulomyrcia* Lucas et al. (2016) suggested that petioles of species from clade G are never corky. However, their comparison was made with species such as *Myrcia saxatilis* (Amshoff) McVaugh (of clade A), which has a strongly conspicuous corky peeling petiole, so causing them to overlook less conspicuous cork in clade G species.

Variation in petiole outline shape in cross section is a valuable character for species identification in *Myrcia* (Jorge et al. 2000). We have created diagrams of petiole outline and xylem bundle shapes for that end. It is important to point out that xylem bundle shapes do correspond to the vascular cylinder shape of petioles. Variation in xylem bundles of the vascular cylinder include open arched with ends pointing inward in most species or a closed ellipse in others.

Adaxial midvein prominence, as suggested by Staggemeier et al. (2015) to separate species in clade F (raised) to species in clade G (flat) must be considered with caution. Midveins can be only slightly raised in *Myrcia insularis* and *M. tetraphylla*, which can be confused with flat midveins. If there is slight prominence, one must consider it raised.

Myrcia magna and *M. neoestrellensis* present adaxially flat midveins. Based on morphological comparison, these two species were considered part of clade F by Lucas et al. (2016). However, Staggemeier et al. (2015) suggested that clade F species have adaxially raised midveins. As these two species were not included in the phylogeny by Staggemeier et al. (2015), their phylogenetic relationships remain unknown.

Staggemeier et al. (2015) found the placement of *Myrcia neodimorpha* to vary from sister to clade G in Bayesian inference to sister to clade F in the maximum clade credibility tree. *Myrcia neodimorpha* presents opposite distichous phyllotaxy and ovate or elliptic leaf blades with adaxially flat midveins, as found in clade G. However, flower and inflorescence characteristics resemble those of clade F, such as large tomentose bracts that cover the buds, which are very similar to those of *Myrcia obversa* in clade F. Anatomically, *Myrcia neodimorpha* presents an accessory vascular bundle emerging besides the petiole central cylinder, which is not found in species of clades F and G studied here. This character is more commonly observed in leaf blade midveins, but it has been previously reported in the petioles of Dipterocarpaceae (Noraini et al. 2016) and Oleaceae (Maksymowych et al. 1983). We understand *Myrcia neodimorpha* to be a separate entity from these two other clades, because of the combination of characters from each clade and the presence of an accessory vascular bundle. The leaves of *Myrcia neodimorpha* may present the clade G leaf characters of ovate or elliptic leaf blades with flat midvein adaxially, but they are large and coriaceous like those of clade F, to which we ultimately believe this species is more closely related to. Leaves are usually smaller and chartaceous in clade G species.

Radford et al. (1976) classified midveins and petioles as channeled or canaliculate when there is a groove in the entire midvein. Studied species occasionally present an adaxial groove in the transition between petiole and the blade or along the entire midvein, which is thus canaliculate. We chose not to use this character in our description because the presence of a groove and their length along the midvein can vary within a species. Staggemeier et al. (2015) suggested that midvein can be canaliculate in species from clade G, but we have observed it in samples from clade F.

Regarding trichomes, we observed thicker lignified walls and tannin-like content in the brachiate trichomes of *Myrcia magna*, *M. neodimorpha*, and *M. obversa*, and in the simple trichomes of *M. micropetala and M. neodimorpha.* The remaining species presented trichomes with thinner walls and no apparent content. Gomes and Neves (1997) have previously described trichomes with lignified cell walls and trichome bases with tannin-like content in *Myrcia spectabilis* and *M. subsericea*.

In our study, all species presented oil glands on both blade surfaces. In petioles some species presented glands distributed along the entire petiole circumference, or at more concentrated densities either abaxially or adaxially. In the study by Gomes and Neves (1997), *Myrcia spectabilis* and *M. subsericea* presented oil gland only adaxially in the leaf blades. According to Costa et al. (2020), in a study with *Myrcia splendens* (Sw.) DC., oil glands location is subject to environmental plasticity related to variation in light and water conditions.

In our analysis, all species presented prismatic crystals in two sizes, smaller ones flanking the vascular bundles in the blades and larger ones in the cortex of petiole and blade midvein. *Myrcia subobliqua,* on the other hand*,* presented prismatic crystals and starch grains especially around oil glands in the petiole. According to the phylogeny of

Myrcia sect. *Aulomyrcia*, sampled specimens that resemble *Myrcia subobliqua* emerged in clade G, but in the conspectus of *Myrcia* sect. *Aulomyrcia* by Lucas et al. (2016), the authors believe *M. subobliqua* to belong to clade C based in the morphology. Further phylogenetic analyses with confirmed *M. subobliqua* samples must be carried out to establish to which clade this species belongs. Prismatic crystals were reported before in *Myrcia* by Jorge et al. (2000), and starch granules by Gomes and Neves (1997).

All studied species present a layer of epicuticular waxes in the petiole though we were unable to determine the ornamentation patterns, noting it only as a gray layer above the cuticle.

Our study presented descriptions of features in taxonomic point of view, but it also indicated which foliar features should be focused on, developing further studies that can put leaves in *Myrcia* sect. *Aulomyrcia* in a phylogenetic context.

Conclusion

Our study provides a thorough analysis of variation of leaf morphological and anatomical characters in a group of species of *Myrcia* sect. *Aulomyrcia*. The leaves of species in clades F and G, and *Myrcia micropetala* (clade B) are strikingly similar at first sight, but we indicated combinations of leaf characters that could support species circumscription in combination with other data. Our results can not only aid in species identification, but also reflect on the systematic implications of these findings. We suggest that future studies include more species from other clades of *Myrcia* sect. *Aulomyrcia* and examine further morphological characters of potential taxonomic value (possibly venation pattern and quantitative data). Future studies are required to examine epicuticular waxes ornamentations and these different degrees of petiolar thickenings with scanning electron microscopy to better understand their significance and potential use for *Myrcia* taxonomy. Moreover, we suggest that additional phylogenetic studies of *Myrcia* sect. *Aulomyrcia* should be carried out with the inclusion of more species of the section to further elucidate to which subclades the species belong to.

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Statements

Data generated or analyzed during this study are provided in full within the published article. The authors declare there are no competing interests.

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Tables and Figures

Table 1 Studied species and specimen vouchers, the corresponding clade of *Myrcia* sect. *Aulomyrcia* they belong to, based on Staggemeier et al. (2015) and Lucas et al. (2016), location and habitat.

Species	Clade	Collector/Number	Location	Habitat
***Myrcia amazonica* DC.**	G	Wagner M.A. 212	Manaus, AM, Brazil	Forest edge
		Wagner M.A. 241	Caracaraí, RR, Brazil	Forest edge
		Pereira O.J. 5812	Presidente Kennedy, ES, Brazil	Sandbank
***Myrcia pyrifolia* (Desv. Ex Ham) Nied.**	G	Wagner M.A. 290	Caracaraí, RR, Brazil	“Campina” wild field with sandy soil, roadside
		Wagner M.A 341	Caracaraí, RR, Brazil	Riverbank of “Igarapé”watercourse.
		Rodrigues P. 8059		
***Myrcia riodocensis* G.M. Barroso & Peixoto**	G	Vervloet R.R. 3038	Governador Lindenberg, ES, Brazil	Forest edge
		Ribeiro M. 294	Conceição da Barra, ES, Brazil	Forest edge
		Gomes J.M.L. 4082	Linhares, ES, Brazil	Sandbank
***Myrcia subobliqua* (Benth.) Nied.**	G	Gillespie L.J. 1431	Cuyuni-Mazaruni, Guyanna	Riverbank
***Myrcia eumecephylla* (O.Berg) Nied.**	F	Fontana A.P. 1720	Santa Teresa, ES, Brazil	On the banks of waterfall
		Demuner 2789	Governador Lindenberg, ES, Brazil	Riverbank
***Myrcia hexasticha* Kiaersk.**	F	Fávero O.A. 355	Iguape, SP, Brazil	Riverbank
		Pessoa S.V.A. 1217	Silva Jardim, RJ, Brazil	Forest edge
		Hatschbach G. 13139	Paranaguá, PR, Brazil	
***Myrcia insularis* Gardner**	F	Silva L.A. 517	Governador Lindenberg, ES, Brazil	Forest edge
		Gomes J.M.L. 3881		
		Gomes J.M.L.	Presidente Kennedy, ES, Brazil	Sandbank

		3419		
Myrcia magna **D.Legrand**	F	Soares E.80	Porto Trombetas, PA	secondary vegetation after removal of primary forest "capoeira"
		Wagner M.A. 237		Forest edge
		Rodrigues, W.4119		Forest edge
Myrcia neoestrellensis **E.Lucas & C.E.Wilson**	F	Wagner M.A 348	Linhares, ES, Brazil	Forest, understory
Myrcia obversa **(D. Legrand) E.Lucas and C.E.Wilson**	F	Pereira O.J. 6222	Vila Velha, ES, Brazil	Sandbank
		Assis A.M. 562	Guarapari, ES, Brazil	
		Pereira O.J. 4305	Conceição da Barra, ES, Brazil	Dry forest
Myrcia tetraphylla **Sobral**	F	Wagner M.A. 349	Linhares, ES, Brazil	Forest edge
		Wagner M.A. 353	Nova Venécia, ES, Brazil	Forest edge
Myrcia neodimorpha **E. Lucas and C.E.Wilson**		Pereira O.J. 4339	Conceição da Barra, ES, Brazil	Sandbank
		Pereira O.J. 6256	Vila Velha, ES, Brazil	Sandbank, water edge
		Manhães V.C. 102	Alegre, ES, Brazil	
Myrcia micropetala**(Mart.) Nied.**		Wagner, M.A. 301	Una, BA, Brazil	Forest edge

Table 2 Morphological and anatomical leaf characters analyzed in species of *Myrcia* sect. *Aulomyrcia*.

Morphological Characters	
Phyllotaxis	
Petiole	***Leaf blade***
Petiole rhytidome: peeling or not	Texture
Petiole shape	Shape
Indumentum	Apex
	Base
	Margin
	Indumentum
	Midvein prominence
Anatomical characters	
Petiole	***Leaf blade***
Epicuticular waxes	Trichome types
Periderm and lenticels	Epidermis: number of layers of cells, cell shape
Epidermis: number of layers of cells and cell shape	Stomata: type and location
Cortex: collenchyma, sclerenchyma	Mesophyll: type and description of parenchyma tissues
Oil glands location	Idioblasts type
Idioblasts type	Midvein vascular cylinder shape,
Vascular cylinder shape	Perivascular fibers
	Collenchyma and Sclerenchyma

Table 3 Petiole and leaf blade morphological characters in species of *Myrcia* sect. *Aulomyrcia*(O.Berg) Griseb.

Species	**Clade**	**Phyllotaxy**	**Petiole**	**Blade Shape**	**Blade Apex**	**Blade Base**	**Blade Margin**	**Indumentum abaxially**	**Midvein adaxially**	**Midvein abaxially**
Myrcia amazonica	G	Opposite distichous	Not peeling	Elliptic to ovate	Acuminate to caudate	Cuneate to rounded	Flat	Glabrescent	Flat	Raised
Myrcia pyrifolia	G	Opposite distichous	Not peeling	Elliptic to ovate	Acuminate to caudate	Cuneate to rounded	Flat	Glabrous	Flat	Raised
Myrcia riodocensis	G	Opposite distichous	Peeling	Elliptic to narrowly elliptic	Acute	Cuneate or cordate	Flat	Glabrous	Flat	Raised
Myrcia subobliqua	G	Opposite distichous	Not peeling	Narrowly elliptic	Acuminate	Cuneate	Flat	Glabrescent	Flat	Raised
Myrcia eumecephylla	F	Opposite decussate or whorled (rare)	Peeling	Narrowly elliptic	Acute	Cuneate to cordate	Flat	Glabrous	Raised	Raised
Myrcia hexasticha	F	Whorled (three leaves)	Not peeling	Narrowly elliptic	Acute to acuminate or truncate (rare)	Cuneate	Flat	Glabrescent	Raised	Raised
Myrcia insularis	F	Opposite decussate	Not peeling	Narrowly elliptic	Acute	Cuneate	Flat	Glabrescent	Raised	Raised
Myrcia magna	F	Opposite distichous	Not peeling	Elliptic	Acute or caudate	Cuneate	Flat	Glabrescent	Flat	Raised
Myrcia neoestrellensis	F	Opposite	Not peeling	Elliptic to	Acute	Cuneate	Flat	Glabrescent	Flat	Flat

		distichous		obovate						
Myrcia obversa	F	Opposite distichous or Opposite decussate	Not peeling	Narrowly elliptic	Acute	Cuneate	Raised	Glabrescent	Raised	Raised
Myrcia tetraphylla	F	Whorled (four leaves)	Peeling	Narrowly elliptic	Acuminate	Cuneate	Flat	Glabrescent	Raised	Raised
Myrcia neodimorpha	Sister species	Opposite decussate	Not peeling	Narrowly elliptic, elliptic or ovate	Mucronate	Rounded to cordate	Flat	Glabrescent	Flat	Raised
Myrcia micropetala	B	Opposite decussate	Not peeling	Elliptic	Mucronate	Cuneate	Revolute	Tomentose	Flat	Raised

Table 4. Petiole anatomical characters among studied species of *Myrcia* sect. *Aulomyrcia*

Petiole anatomy							
Species	**Trichomes**	**Shape**	**Epidermal layers**	**Cortex**	**Idioblast type**	**Perivascular fibers**	**Vascular cylinder shape**
Myrcia amazonica	Simple trichomes with enlarged base	Planar and convex	Uniseriate	Collenchyma	Prismatic crystals	Fiber bundles adaxially	Open arch, ends pointing inward
Myrcia pyrifolia	Glabrous	Planar and convex	Uniseriate	Collenchyma	Prismatic crystals	Fiber bundles around vascular cylinder, not continuous	Open arch, ends pointing inward
Myrcia riodocensis	Simple trichomes	Planar and convex	Uniseriate (sometimes biseriate)	Sclerenchyma	Prismatic crystals	Fiber bundles adaxially	Open arch, ends pointing inward

Myrcia subobliqua	Simple trichomes and brachiate	Planar and convex	Uniseriate	Collenchyma and sclerenchyma	Prismatic crystals and starch	Fiber bundles adaxially	Closed cylinder
Myrcia eumecephylla	Simple trichomes with enlarged base	Planar and convex, irregular outer surface	Uniseriate	Sclerenchyma	Prismatic crystals	Absent	Closed cylinder
Myrcia hexasticha	Glabrous	Planar and convex, irregular outer surface	Uniseriate	Collenchyma and sclerenchyma	Prismatic crystals	Fiber bundles around vascular cylinder, not continuous	Closed cylinder
Myrcia insularis	Simple trichomes and brachiate.	Planar and convex	Uniseriate (sometimes biseriate)	Sclerenchyma	Prismatic crystals	Absent	Open arch, ends pointing inward
Myrcia magna	Brachiate	Concave on both surfaces, irregular outer surface	Uniseriate	Sclerenchyma	Prismatic crystals	Fiber bundles adaxially	Open arch, ends pointing inward
Myrcia neoestrellensis	Glabrous	Concave convex, irregular outer surface	Uniseriate	Collenchyma and sclerenchyma	Prismatic crystals	Absent	Open arch, ends pointing inward
Myrcia obversa	Brachiate	Planar and convex	Uniseriate (sometimes biseriate)	Collenchyma and sclerenchyma	Prismatic crystals	Fiber bundles adaxially	Closed cylinder
Myrcia tetraphylla	Glabrous	Planar and convex	Uniseriate	Sclerenchyma	Prismatic crystals	Fiber bundles around vascular cylinder, not continuous	Closed cylinder
Myrcia neodimorpha	Simple trichomes with enlarged base and brachiate	Circular, irregular outer surface	Uniseriate (sometimes biseriate)	Sclerenchyma	Prismatic crystals	Absent	Closed cylinder (accessory vascular bundle)
Myrcia micropetala	Simpler trichomes	Circular	Uniseriate	Sclerenchyma	Prismatic crystals	Absent	Open arch ends pointing inward

Table 5 Leaf blade anatomical characters in studied species of *Myrcia* sect. *Aulomyrcia.*

Species	**Leaf blade characters**					
	Non-glandular trichomes	**Epidermal cells shape**	**Mesophyll palisade parenchyma**	**Midvein cortex: collenchyma or sclerenchyma presence**	**Midvein vascular bundle shape**	**Midvein perivascular fibers**
Myrcia amazonica	Simple with enlarged base	Squared	1-3	Collenchyma	Open arch, ends pointing inward	Fibers bundle only adaxially or bands of perivascular fibers
Myrcia pyrifolia	Glabrous	Squared	2-3	Collenchyma	Open arch, ends pointing inward	Bands of perivascular fibers
Myrcia riodocensis	Glabrous	Square**d**	1-2	Sclerenchyma (sclereids)	Open arch, ends pointing inward	Bands of perivascular fibers
Myrcia subobliqua	Brachiate	Squared	2	Collenchyma	Closed cylinder	Bands of perivascular fibers
Myrcia eumecephylla	Simple with enlarged base and brachiate	Rectangular	2	Collenchyma	Closed cylinder	Bands of perivascular fibers
Myrcia hexasticha	Glabrous	Rectangular	2-3	Sclerenchyma	Open arch, ends pointing inward	Thick bands of perivascular fibers
Myrcia insularis	Simple with enlarged base and brachiate	Squared	1-3	Collenchyma	Open arch, ends pointing inward	Thick bands of perivascular fibers
Myrcia magna	Simple appressed and brachiate	Squared	1-3	Sclerenchyma	Open arch, ends pointing inward	Bands of perivascular fibers
Myrcia neoestrellensis	Glabrous	Squared	1	Collenchyma	Open arch, ends open	Bands of perivascular fibers
Myrcia obversa	Brachiate	Squared	3	Collenchyma	Closed cylinder	Bands of perivascular fibers
Myrcia tetraphylla	Glabrous	Rectangular	2	Collenchyma	Closed cylinder	Bands of perivascular fibers
Myrcia neodimorpha	Simple trichomes with enlarged base and brachiate	Squared	2	Neither	Closed cylinder	Bands of perivascular fibers
Myrcia micropetala	Simple trichomes	Rectangular	2	Sclerenchyma	Open arch, ends pointing outward	Fibers bundles both adaxially and abaxially

Table 6. Combinations of morphological and anatomical leaf characters that are diagnostic for the studied subclades of *Myrcia* sect. *Aulomyrcia* based our study and those indicated by Staggemeier et al. (2015).

Clades/characters	This Study	Staggemeier et al. 2015
***Myrcia micropetala* (representing clade B)**	Opposite distichous; Opposite decussate Midvein flat Revolute margin Tomentose abaxially Fiber bundles on the midvein adaxially and abaxially, not forming a continuous band Sclereids in the petiole cortex	Leaves smaller Never verticillate, dry green Midvein flat
Clade F	Opposite distichous (*Myrcia obversa*; *M. magna*, *M. neoestrellensis*), Opposite decussate (*Myrcia obversa, M. eumecephylla; M. insularis*), and whorled (*M. eumecephylla*, *M.hexasticha* and *M. tetraphylla*) Narrowly elliptic leaves (exception: *M. magna* elliptic and *M. neoestrellensis* elliptic to obovate) Raised midveins (exceptions: *Myrcia magna* and *Myrcia neoestrellensis* with flat midveins) Flat margins Glabrous to sparsely pubescent abaxially Continuous band of perivascular fibers on midvein	Leaves larger Opposite decussate to whorled leaves, Dry brown Raised midvein
G	Opposite distichous, Ovate, elliptic, or elliptic to narrowly elliptic (rare) blades Midvein flat Flat margin Glabrous to sparsely pubescent abaxially Fibers bundle only adaxially to bands of perivascular fibers along entire circumference	Leaves larger Opposite Dry brown Midvein flat, sulcate or canaliculate
Myrcia neodimorpha	Opposite distichous; Opposite decussate, Midvein flat to slightly raised Margin straight Glabrous to sparsely pubescent abaxially	Raised midvein

	Bands of perivascular fibers along entire circumference

Figures

Figure 1. Schematic illustration of the *Myrcia* section *Aulomyrcia* (O.Berg) Griseb. phylogeny adapted from Staggemeier et al. (2015).

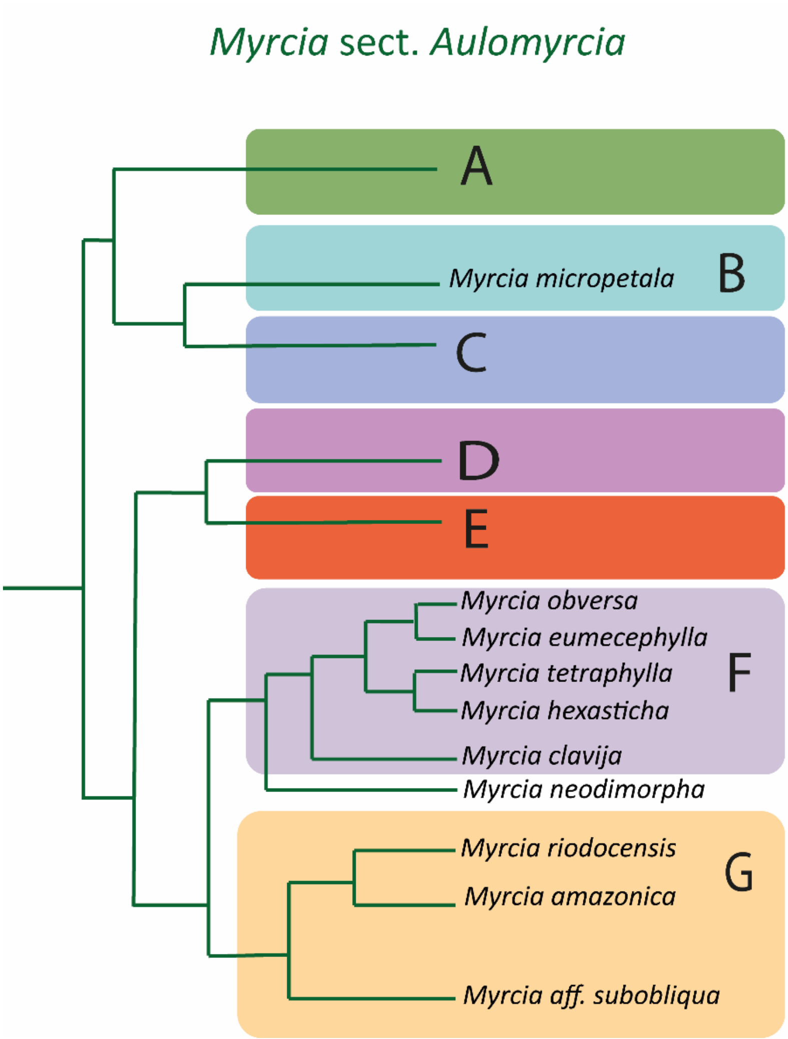


Figure 2. Phyllotaxis in studied species of the *Myrcia* sect. *Aulomyrcia*. A. *M. amazonica*: opposite. **B.** *M. insularis*: decussate. **C.** *M. hexasticha*: whorled ternate (black arrow indicate nodes).

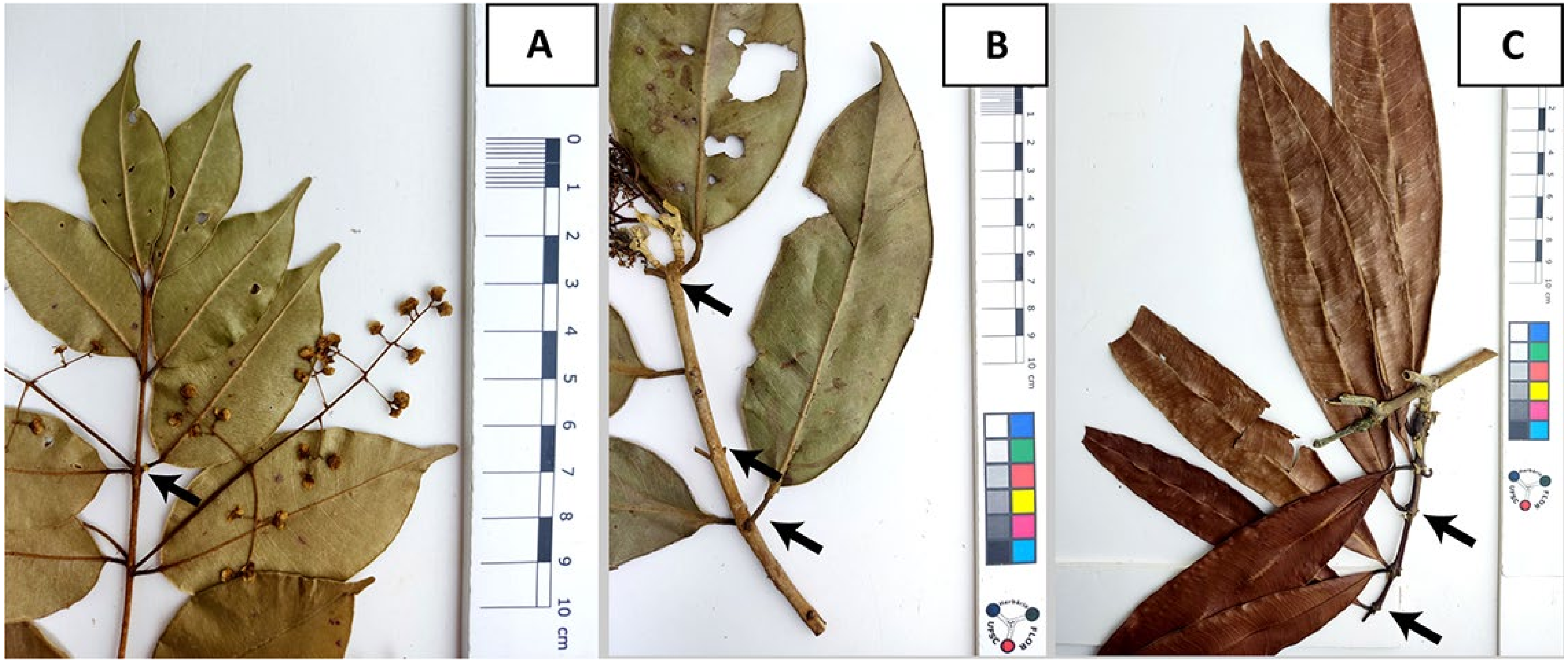


Figure 3 Petiole morphology in *Myrcia* sect. *Aulomyrcia*. **A.** *M. tetraphylla*: peeling petiole (gray bar= 2 mm).**B.** *M.amazonica*: lenticels in the petiole (white arrows), smooth surface (gray bar=0,5 mm).

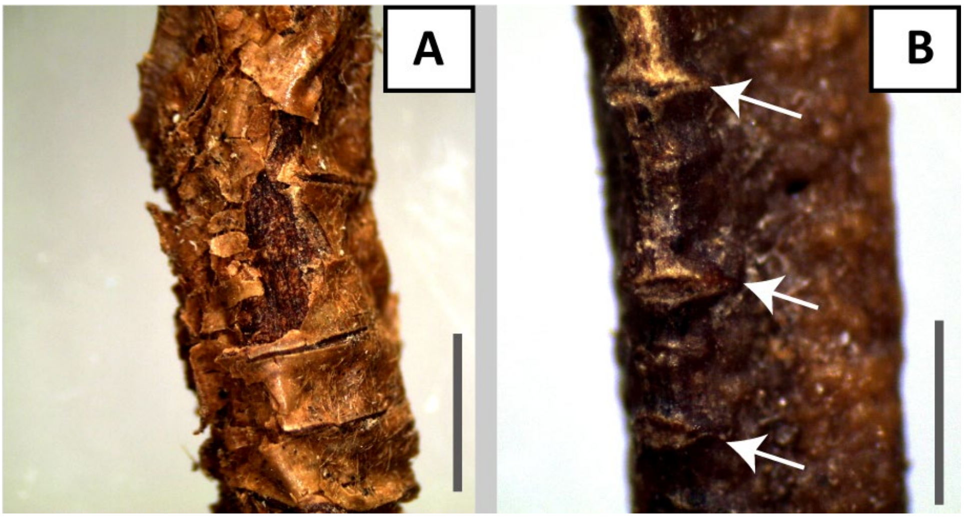
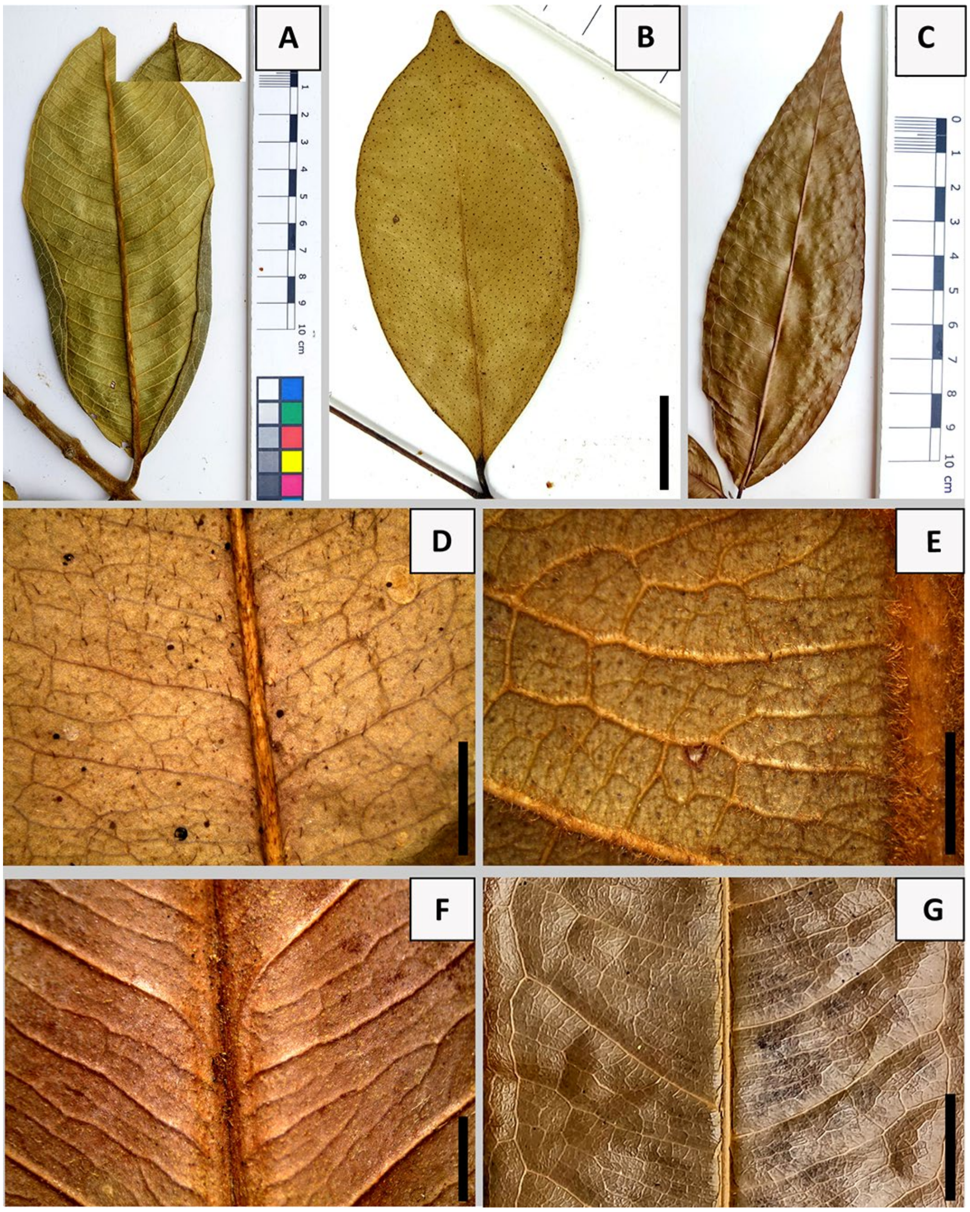


Figure 4. Leaf blade morphological characters in species of the *Myrcia sect. Aulomyrcia*. A. *M. micropetala* leaf blade abaxially: elliptic, margin revolute, mucronate apex (detail) and cuneate base. **B**. *M.neoestrellensis* leaf blade abaxially: elliptic to obovate, margin straight, apex acute, base cuneate, oil glands visible to naked eye on abaxial surface (black bar=2 cm). **C.** *M. amazonica* leaf blade abaxially : elliptic leaves, acuminate apex, cuneate base. **D.** *M. amazonica*: glabrescent abaxial surface, (black bar= 2mm). **E.** *M. micropetala*: tomentose golden indumentum abaxially, (black bar= 2 mm). **F.** *M. neodimorpha* adaxial surface: flat midvein, (black bar = 2 mm). **M.** *M. eumecephylla* adaxial surface : raised midvein, (black bar= 2 cm).


A
B
C
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G

Figure 5 Trichome diversity in leaf blades and petioles of studied species of *Myrcia* sect. *Aulomyrcia*. A. Simple trichomes with enlarged bases in leaf blade of *M. amazonica*. **B.** Simple appressed trichomes with tannin contents in leaf blade of *M. magna*. **C.** Brachiate trichomes with tannin contents in petiole of *M. magna* **D.** Simple trichomes with and without tannin content in leaf blade *M. micropetala*.

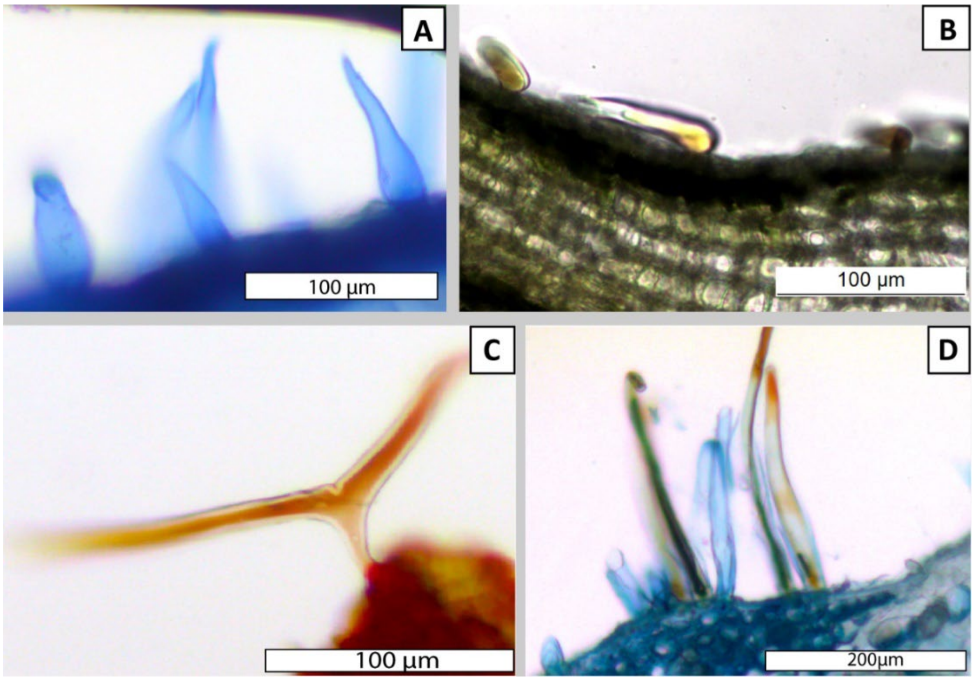


Figure 6. **Diagrams of cross sections of petioles and xylem bundles of each studied species of *Myrcia* sect. *Aulomyrcia*. A**. *M. amazonica*. **B**. *M. pyrifolia*. **C**. *M. riodocensis* **D**. *M. subobliqua* **E.** *M. eumecephylla* **F**. *M. hexasticha* **G.** *M. insularis* **H.** *M. magna* **I.** *M. neoestrellensis* **J.** *M. obversa* **K**. *M. tetraphylla* **L**. *M. neodimorpha* **M.** *M. micropetala* (Scale bar = 1mm)

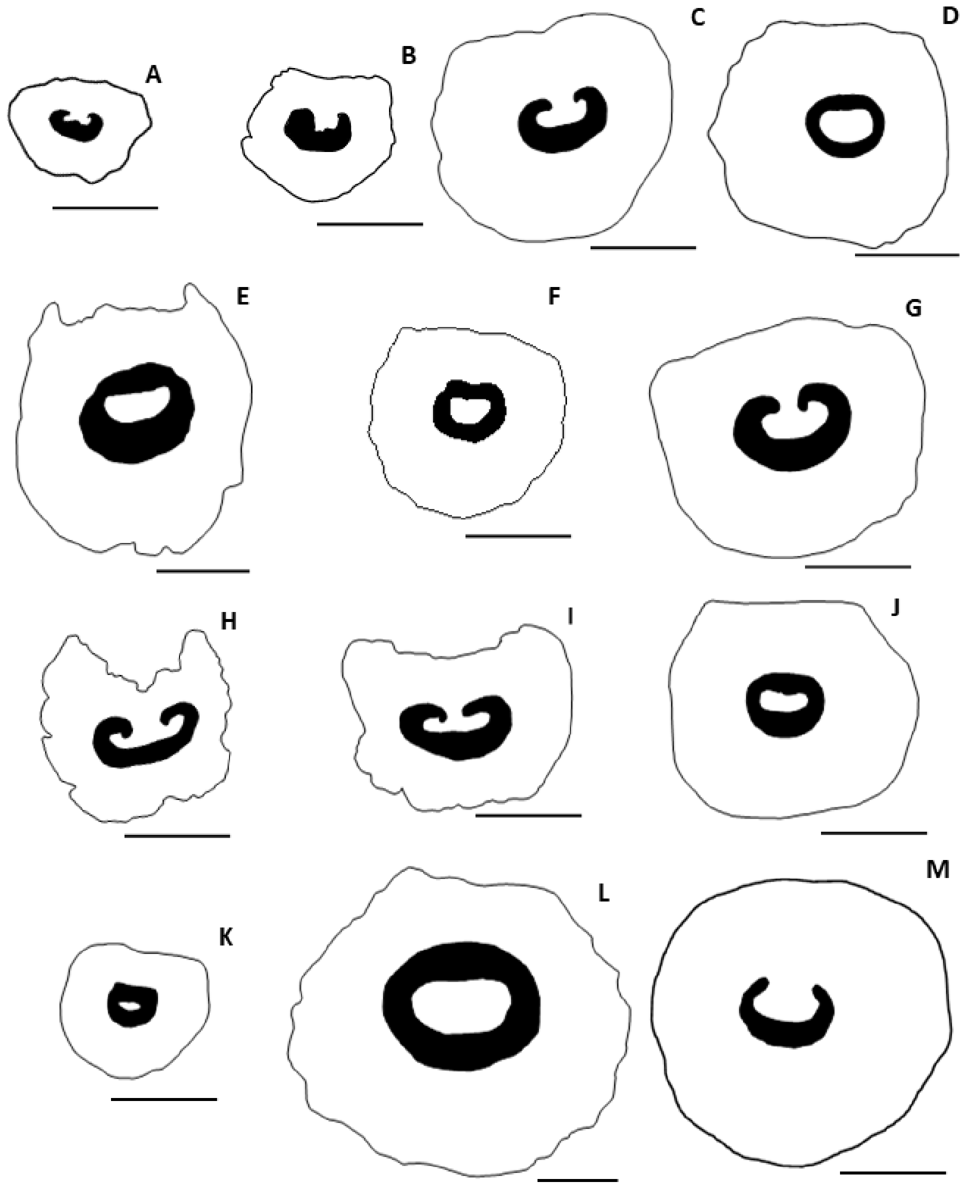


Figure 7 Petiole anatomy of *Myrcia* sect. *Aulomyrcia* studied species. A. Lenticel in *M. riodocensis*. **B.** Epicuticular waxes in the petiole of *M. amazonica.* **C.** Uniseriate epidermis with square epidermal cells and cuticular extensions into anticlinal walls in *M. amazonica*. **D.** Biseriate epidermis in *M. riodocensis*. **E**. Periderm with alternating layers of suberized and lignified walls in *M. micropetala*. **F.** Collenchyma in the cortex of *M. amazonica*. **G.** Sclerenchyma in the cortex of *M. riodocensis* **H.** Oil glands, vascular cylinder, and accessory vascular bundle in *M. neodimorpha* **I.** Idioblasts in the petiole of *M. subobliqua*: starch grains and prismatic crystals around the oil glands. (AVB=Accessory vascular bundle, Col=collenchyma, Cu= cuticle, Ep=epidermis, EW=Epicuticular waxes, OG=Oil glands, Pe=Periderm, PC=Prismatic crystals, Sc=Sclerenchyma, SG=Starch Grains, VC=Vascular cylinder)

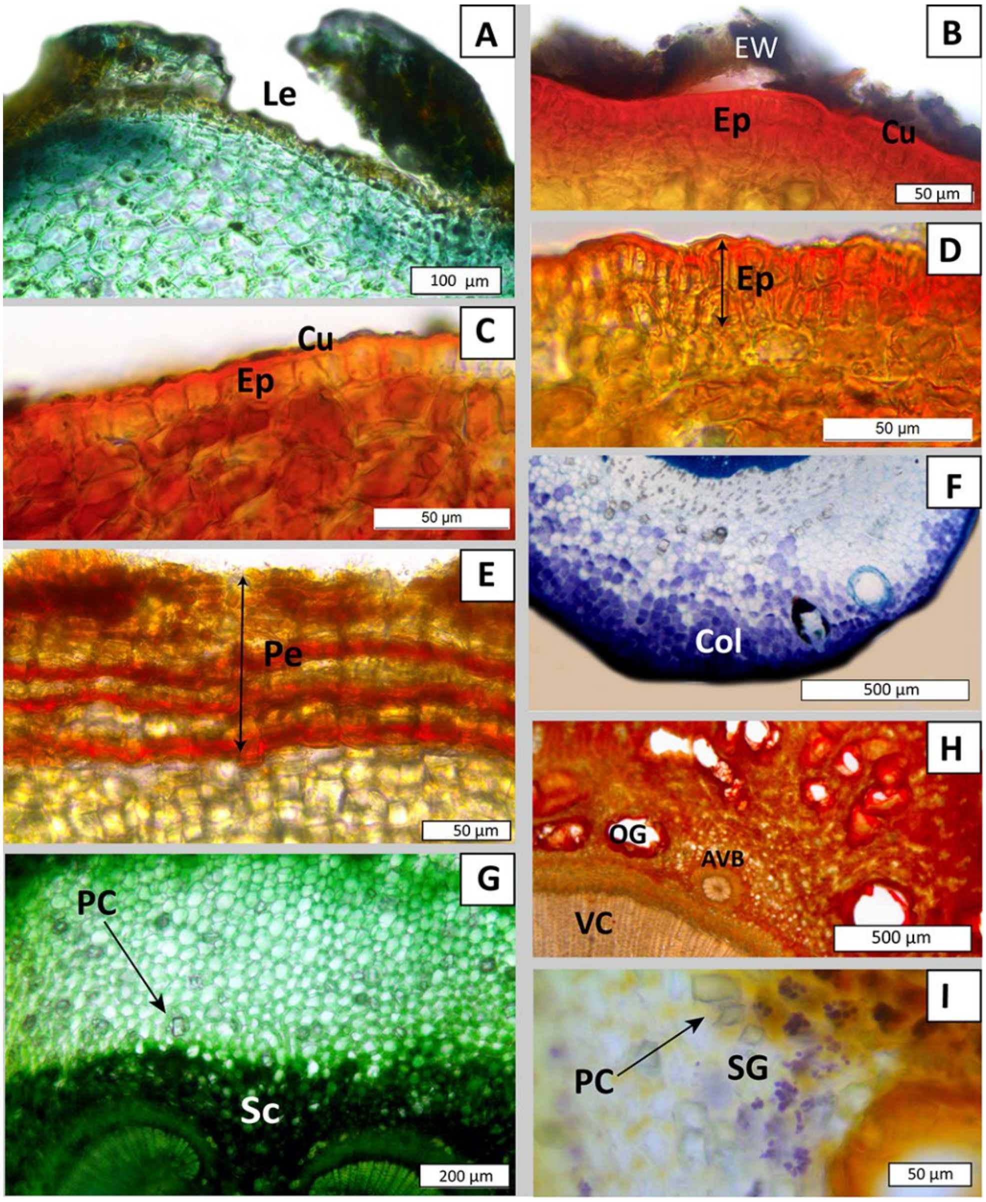
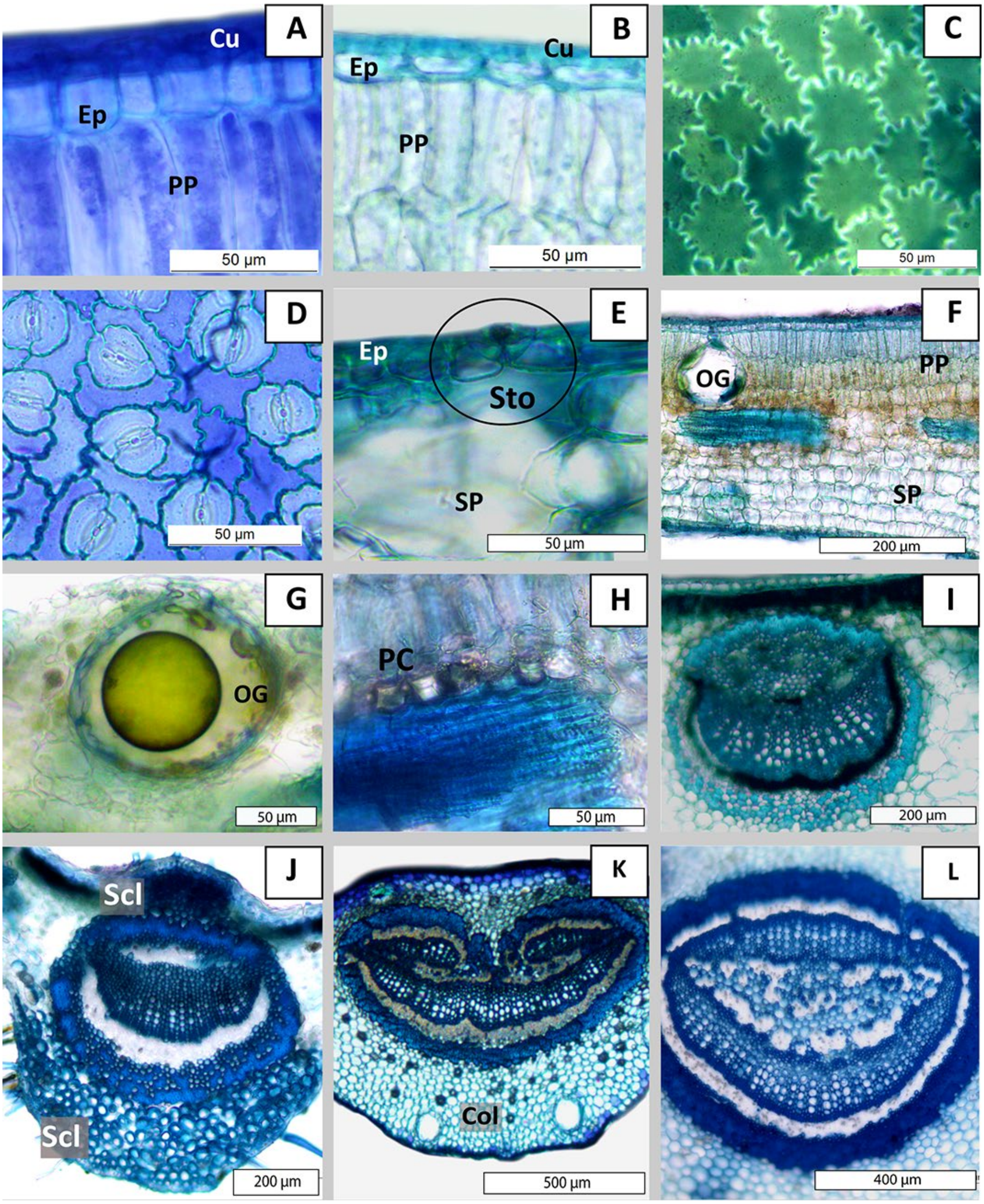


Figure 8. Leaf blade anatomical characters of studied species of *Myrcia* sect. *Aulomyrcia.* **A.** Square epidermal cells of *M. insularis*. **B.** Rectangular epidermal cells of *M. micropetala*. **C.** Sinuous anticlinal walls of epidermal cells on adaxial surface of *M. neodimorpha* **D.** Paracytic stomata on abaxial surface of *M. riodocensis* **E.** Stoma on abaxial surface of *M. neoestrellensis.* **F.** Dorsiventral mesophyll in *M. obversa* three layers of palisade parenchyma and *c.* 7 layers of spongy parenchyma**. G.** Oil gland in the spongy parenchyma of *M. neodimorpha* **H.** Prismatic crystals flanking vascular bundle in *M. amazonica*. **I.** Vascular bundle shaped as open arch with ends pointing outwards in *M. neoestrellensis* **J.** Vascular

bundle shaped as open arch with ends pointing outwards in *M. micropetala* presenting sclerenchyma between the vascular cylinder and epidermis. **K.** Vascular bundle shaped as open arch with ends folding inward in *M. insularis.* **L.** Closed ellipse shaped vascular cylinder and thick continuous perivascular fiber band in the midvein of *M. obversa*

(Col=Collenchyma, Cu=cuticle, EP=epidermis, OG= oil gland, PC=Prismatic crystal, PP=Palisade parenchyma, Sto= Stomata, Sc=Sclerenchyma, SP=Spongy parenchyma)



in

4. CHAPTER 3 – TAXONOMIC STUDY OF *MYRCIA* SECT. *AULOMYRCIA* (MYRTACEAE): THE VERTICILLATE GROUP

CAPÍTULO 3

Artigo será submetido futuramente ao periódico Phytotaxa.

Taxonomic study of *Myrcia* sect. *Aulomyrcia* (Myrtaceae): The Verticillate Group

Abstract

Myrcia consists of ca. 780 species that are divided into nine sections. *Myrcia* section *Aulomyrcia* is one of these sections and encompasses approximately 140 species. This study presents a taxonomic review of 22 species of *Myrcia* section *Aulomyrcia* that are here informally referred to as the Verticillate Group based on their verticillate leaves. Species of the Verticillate Group occur across the neotropical region, mainly in the Atlantic Forest Domain, Amazon Forest Domain, and the Central American Isthmian & Colombian Coastal Forests. We provide monographic information on types, morphological description, geographic distribution, conservation status and phenology. A dichotomous key and representative specimen images are also provided. The twenty-two species considered part of the Verticillate group are the following: *Myrcia amazonica, M. areolata, M. badia, M. clavija, M. colpodes, M. eumecephylla, M. gigantea, M. hexasticha, M. insularis*, *M. liesneri, M. magna, M. neodimorpha, M. neoverticillaris, M. obversa*, *M. pyrifolia, M. riodocensis, M. rubiginosa, M. salticola, M. speciosa, M. santateresana, M. tetraphylla*, and *M. zetekiana.*

Introduction

Myrcia (Candolle 1827: 401) is a large genus of neotropical Myrtaceae that is highly species diverse in the forests of the neotropical region. *Myrcia* comprises ca.780 species (POWO 2023) and belongs to tribe Myrteae, that contains the majority of the neotropical species of Myrtaceae. Recent phylogenetic studies of Myrteae have at least partially elucidated the systematics of the genera that compose it (Lucas *et al.* 2007; Lucas *et al.* 2011; Santos *et al.* 2017, Vasconcelos *et al.* 2017; Amorim *et al.* 2019, Lima *et al.* 2021).

Based on the phylogeny of Lucas *et al.* (2011), *Myrcia* is composed of nine separate clades later formalized as sections (Lucas *et al.* 2018). One of these sections is *Myrcia* section *Aulomyrcia* (O. Berg) Griseb. *Aulomyrcia* was described as a genus by Berg (1855), later recognized as a section by Grisenbach (1864), then as a subgenus by Legrand (1961) and finally again as a section by McVaugh (1968).

Species of *Myrcia* sect. *Aulomyrcia* are trees or shrubs that usually present monopodial branching, relatively large leaves; subfloral bracts are usually persistent and asymmetrical deltate panicles. Inflorescences rachis, hypanthium, and abaxial surface of the calyx lobes are usually pubescent, flowers are frequently pentamerous (rarely tetramerous), calyx lobes are free to partially or completely fused, opening regularly or tearing irregularly through the hypanthium, the floral disc is glabrous and narrow, the staminal ring is usually glabrous, with the hypanthium extending somewhat beyond the ovary but sometimes indistinct after deep tearing following anthesis; the ovary is bi-locular with two ovules per locule; and the fruits are globose (Staggemeier *et al.* 2015, Lucas *et al.* 2016, Lucas *et al.* 2018).

Staggemeier *et al.* (2015) analyzed phylogenetic relationships within *Myrcia* section *Aulomyrcia* and seven clades emerged that were informally named with the letters A-G. Clades F and G. and *Myrcia neodimorpha* E. Lucas & C.E. Wilson emerged in a monophyletic group in the phylogenetic hypothesis of Staggemeier *et al.* (2015) and by our own findings discussed in chapter 1 of this thesis.

Myrcia sect. *Aulomyrcia* currently includes ca. 140 species (Lucas et al. 2018), 124 of these species were treated by Lucas *et al.* (2016) in a taxonomic conspectus that included typification, geographic distribution, conservation status and taxonomic notes. The taxonomic framework resulting from this conspectus organized species of *Myrcia* sect. *Aulomyrcia* into five tentative groups based on morphology and distribution, which corresponds somewhat to the clades from the study of Staggemeier *et al.* (2015). A group of 16 species, according to Lucas *et al.* (2016), corresponds to clade F of Staggemeier *et al.* (2015), and another group of six species corresponds to clade G. *Myrcia neodimorpha* was not associated with either of these groups in the study of Lucas *et al.* (2016). This group of 22 species derived from clades F, G, as identified in both Staggemeier *et al.* (2015) and Lucas *et al.* (2016) and including *Myrcia neodimorpha*, is from here on informally referred to as the 'Verticillate Group' due to the characteristic verticillate arrangement of leaves and inflorescences among its species. The morphological features of the Verticillate Group are indicated in. Figure 1.

Within the Verticillate Group the Clade F species sensu Staggemeier *et al.* (2015) bear red, white or brown indumentum and light brown bark, and have large opposite decussate or verticillate leaves with raised midveins and corky, peeling petioles; inflorescences are asymmetric with unevenly sized branches on each side, with an asymmetrical triangular shape and verticillate branching. Clade G species sensu Staggemeier *et al.* (2015) present red indumentum and bark, opposite distichous leaves with midvein canaliculate and flat adaxially. Petioles are not so conspicuously corky and are usually smooth and non-peeling. *Myrcia neodimorpha* presents large robust leaves, corky petioles and white pubescence on the inflorescences. Table 2 displays key diagnostic features for species in the component subclades of the Verticillate Group.

Species of the Verticillate Group are distributed from Central America (Panama) and the Caribbean throughout South America, mostly in the Amazon Forest Domain (AMFD) and the Atlantic Forest Domain (AFD) but also in the Cerrado Domain (CD) (Ab'Sáber, 2003, Staggemeier *et al.* 2015, Lucas *et al.* 2016) (see Table 1 and Figure 2).

Clade F species occur mostly in the AFD, such as *Myrcia clavija* Sobral, *M. colpodes* Kiaersk., *M. eumecephylla* (O.Berg) Nied, *M. gigantea* (O.Berg) Nied., *M. hexasticha* Kiaersk, *M. insularis* Gardner, *M. neoverticillaris* E. Lucas and C.E. Wilson, *M. obversa* (D. Legrand) E. Lucas and C.E. Wilson and *M. tetraphylla* Sobral, with some species occurring in the AMFD, such as *M. areolata* (McVaugh) E. Lucas & C.E. Wilson, *M. liesneri* B. Holst, *M. speciosa* (Amshoff) McVaugh. *Myrcia zetekiana* (Standl.) B.Holst) occurs in the Central American Isthmian & Colombian Coastal Forests Bioregion (One Earth 2023).

Clade G includes the widespread *Myrcia amazonica* DC., and species from the AMFD such as *Myrcia magna* D. Legrand, *Myrcia pyrifolia* (Desv. Ex Ham) Nied., and *Myrcia salticola* (Steyerm.) McVaugh. Other species occur in the AFD such as *Myrcia riodocensis* G.M. Barroso & Peixoto, *M. rubiginosa* Cambess. and *M. santateresana* Sobral.

The Verticillate Group is composed of twenty-two species, some of which form cryptic morphological complexes. This lineage warrants examination as a distinct group due to this taxonomic complexity, allowing focus on e.g. widespread *Myrcia amazonica* in clade G, and the uncertainty of the sister relationships between clade F and *Myrcia neodimorpha*.

Of the ca. 780 species of *Myrcia,* many have already been taxonomically reviewed and many have been included in phylogenies of *Myrcia* at generic and sectional levels (Santos *et al.* 2016, 2018, 2019, 2021, Wilson *et al.* 2016, Amorim *et al.* 2019, Lima *et al.* 2021).

However as of today there yet remains many species to be treated taxonomically and phylogenetically. In such case, taxonomic studies that provide detail regarding species recognition and provide data on geography, morphology, evolution, and phenology are an invaluable resource. Species identification in the mega species diverse genus *Myrcia* is important for anyone hoping to manage the environments in which it occurs, for ecological or evolutionary study, for conservation or restoration, aiding specialists and non-specialists of Myrtaceae. The objective of our taxonomic study is to provide information for species determination, and also help elucidate the relationships between clades.

Material and Methods

Collections and taxonomic treatments

Myrcia species were targeted from the Amazon (Amazonas and Roraima) and Atlantic Forest (Bahia, Espírito Santo, and Santa Catarina) during four expeditions between 2018 and 2019. Geographic coordinates and elevation were recorded with a GPD Garmin 76. We collected fertile and vegetative material, preserving leaves, flowers, and fruits in 70 % ethanol for morphological analysis. Collected materials were herborized and deposited at INPA and FLOR (acronyms follow Thiers, continuously updated).

Additional specimens were analyzed physically during visits to, and loaned from, the following herbaria: ALCB, CEPEC, CVRD, FLOR, HAS, HUA, HUAM, HUEFS, HURB, ICN, INPA, JUAM, MBM, MBML, MIRR, RB, SAMES, SP, UFRR and VIES (Thiers, continuously updated). Specimens that were not possible to analyze physically were studied through high resolution digital images from databases such as SpeciesLink (2023) and Reflora/Flora do Brasil (2023). Certain species, such as *Myrcia areolata*, *M. badia*, *M. clavija*, *M. colpodes*, *M. rubiginosa*, *M. salticola* and *M. speciosa* are rare in herbaria collections. For such species, descriptions were based on the protologue and on high quality photographs of types and other specimens.

We assembled a database that was managed with the software MonographaR (Reginato 2016) and R (R Core Team 2021) to finalize descriptions, produce distribution maps and phenology graphs. We provide author, protologue and type information, commentaries on taxonomic aspects of the species and conservation status (now fully assessed (IUCN 2023). since the preliminary risk assessments of Lucas et al. 2016), figures, and an identification key.

We used Radford *et al.* (1976), Weberling (1989), Harris & Harris (2001), Ellis *et al.* (2009) and Beentje (2016) as reference for the taxonomic descriptions and structure names and categories. We measured the peduncle length of inflorescences from the point of insertion in the shoot up to its first branching. Trichomes and indumentum nomenclature follows Radford *et al.* (1976). Shapes of structures also follows those suggested by Radford et al. (1976).

Results

Taxonomic treatment

Key to the species of *Myrcia* sect. *Aulomyrcia*: the Verticillate Group.

1)Leaf midveins flat adaxially…**2**

1)Leaf midveins raised adaxially…**3**

2) Plants widespread in the neotropical region or one of unknown origin in Brazil…**4**

2) Plants from the AMFD or the AFD…**5**

3) Plant from the Central American Isthmian & Colombian Coastal Forests Bioregion. Leaves tomentose along the midvein abaxially. Fruit light brown…***Myrcia zetekiana***

3) Plants from the AMFD or from the AFD. Leaves glabrous to slightly pubescent along the midvein abaxially. Fruit dark purple or black…11

4) Plants widespread in the neotropical region. Leaves 3-9 x 1.5-4 cm, opposite distichous, elliptic to ovate. Inflorescence deltate, opposite branching, calyx lobes deltate...***Myrcia amazonica***

4) Plants of unknown origin in Brazil. Leaves 15.2-26.7 x 4-7.2 cm, opposite decussate, lanceolate to narrowly elliptic. Inflorescences narrowly elliptic, alternate branching, calyx lobes circular…***Myrcia badia***

5) Plants from the AMFD…**6**

5) Plants from the AFD…**8**

6) Twigs white. Leaves opposite decussate, leaf blades 4-7 x 1.5-3.5 cm, elliptic; strigillose abaxially …***Myrcia salticola***

6) Twigs reddish brown. Leaves opposite distichous, leaf blades 10–39 × 3.5–11 cm, narrowly elliptic or ovate, glabrous, or sparsely pubescent abaxially…**7**

7) Twigs flattened and grooved. Leaf blades narrowly elliptic to elliptic, apices caudate to rounded, bases cuneate, petioles 0.4-1.3 cm long. Inflorescences terminal and axillary, calyx lobes deltate ….***Myrcia magna***

7) Twigs cylindric and smooth. Leaf blades ovate, apices acuminate, bases obtuse; petioles 0.3–0.4 cm long. Inflorescences terminal, calyx lobes circular…***Myrcia pyrifolia***

8) Cataphylls on base of inflorescences. Bracts elliptic concave, apices cuspidate or acute, and attenuate bases, velutinous and persistent after anthesis. Calyx lobes completely fused in the bud…***Myrcia neodimorpha***

8) Cataphylls absent. Bracts lanceolate or narrowly triangular, apices acute to acuminate. Calyx lobes free in the bud…**9**

9) Twigs ochre to pale yellow. Leaves discolor when dried, light brown adaxially and dark brown abaxially. Inflorescences symmetrically widely triangular and terminal, calyx pentamerous... ***Myrcia santateresana***

9) Twigs reddish brown or beige. Leaves reddish brown or light green on both surfaces when dried. Inflorescences asymmetrically deltate, axillary and terminal, calyx tetramerous or pentamerous…**10**

10) Leaves coriaceous. Inflorescence rachis glabrous. Calyx tetramerous…***Myrcia riodocensis***

10) Leaves chartaceous. Inflorescence rachis tomentose. Calyx pentamerous…***Myrcia rubiginosa***

11) Plants from the AMFD…**12**

11) Plants from the AFD….**13**

12) Leaf apices acute to caudate. Inflorescences terminal, calyx tetramerous...***Myrcia areolata***

12) Leaf apices acuminate or mucronate. Inflorescences subterminal, or axillary and terminal, calyx pentamerous…**14**

13) Leaves verticillate…**15**

13) Leaves opposite distichous and/or opposite decussate…**16**

14)Twigs with villous white trichomes. Leaf blades ovate, or lanceolate to narrowly elliptic, apices evenly to abruptly acuminate. Inflorescences deltate ……..***Myrcia liesneri***

14) Twigs glabrous. Leaf blades widely elliptic to obovate, apices mucronate. Inflorescences oblong…***Myrcia speciosa***

15) Leaves arranged with six–ten leaves per node, leaf blades lanceolate. Inflorescence asymmetrically narrowly triangular. Corolla trimerous. ***Myrcia clavija***

15) Leaves arranged with three, or four leaves per node, leaf blades narrowly elliptic or narrowly elliptic to elliptic. Corolla pentamerous…**17**

16) Leaves lanceolate to narrowly elliptic, distinctly bullate, apices acuminate. Inflorescences triangular, calyx lobes free in the bud…***Myrcia colpodes***

16) Leaves narrowly elliptic or elliptic, not bullate, apices acute or caudate. Inflorescences deltate, calyx lobes partially fused or fused in the bud…**19**

17) Leaves arranged with three leaves per node. Inflorescences thyrsoid panicles, alternate branching, inflorescence units dichasiums...***Myrcia hexasticha***

17) Leaves arranged with four leaves per node. Inflorescences panicles, verticillate branching, inflorescence units monochasiums…**18**

18) Leaf bases cuneate, petioles 0.8-1.7 cm long. Inflorescences panicles, asymmetrically deltate. Fruit spheroid not lobed... ***Myrcia neoverticillaris***

18) Leaf bases narrowly cuneate, petioles 1.5-2 cm long. Inflorescences racemose panicles, oblong. Fruit spheroid and regularly lobed…***Myrcia tetraphylla***

19) Cataphylls on base of inflorescences. Inflorescences terminal and axillary, flower buds yellow…***Myrcia insularis***

19) Cataphylls absent. Inflorescences terminal, flower buds white or reddish-brown…**20**

20) Leaf bases cuneate. Bracts persistent. Calyx lobes fused in the bud. Fruit spheroid with irregularly grooved outer surface…***Myrcia obversa***

20) Leaf bases subcordate or cordate. Bracts caducous. Calyx lobes partially fused in the bud. Fruit spheroid with smooth outer surface…**21**

21) Leaves opposite decussate, rarely verticillate on the apex of twigs, two leaves per node (rarely 3 when verticillate), leaf blades 20-55 x 6-12 cm, narrowly elliptic, bases subcordate to cordate with revolute margins. Inflorescences with opposite decussate branching, flower buds white …***Myrcia eumecephylla***

21) Leaves opposite decussate, never verticillate, two leaves per node. leaf blades 54-62 x 10-27, elliptic, bases cordate with straight margins. Inflorescences opposite distichous branching, flower bud reddish-brown…***Myrcia gigantea***

1. ***Myrcia amazonica*** Candolle (1828: 250). (Figure 2–4)

Aulomyrcia amazonica (Candolle 1828: 250) O. Berg (1855: 41). (Other synonyms of *Myrcia amazonica* are indicated at POWO 2023). TYPE:—BRAZIL. Amazonas: Solimões, s.d., C.F.P. Martius, s.n. (lectotype, designated by McVaugh (1969: 110) M-0136802; isolectotypes, G-DC, M-0136800)

Shrubs or trees, 2–12 m high. *Trichomes* white, reddish-brown, or golden (rare), brachiate and simple. *Twigs* shedding thin membranes, red bark, flat and grooved, sparsely pilose to tomentose; mature twigs shedding thin membranes, red bark, cylindric, glabrous to pilose, *internodes* 2.5–6.5 cm long. *Cataphylls* absent. *Leaves* opposite distichous, two leaves per node, *leaf blades* 3–9 × 1.5–4 cm, elliptic to ovate, apices acute, or acuminate or caudate, bases cuneate to rounded, green or red when dried, chartaceous, midveins flat and canaliculate adaxially, midveins raised abaxially, 8-16 secondary veins pairs, secondary veins flat on both surfaces, intramarginal veins 0.2–2 mm from the margin, glabrous adaxially, glabrous and pilose along the midveins abaxially, *petioles* 0.2–0.7 × 0.1–0.2 cm, cylindric, canaliculate, glabrous to pilose. *Inflorescences* 6–9 × 3.5–7 cm, panicles, axillary and terminal, asymmetrical triangular, branching opposite distichous, peduncle 0.9–3.5 cm long, rachis pilose, inflorescence units monochasiums, 19–80 flowers per inflorescence; *bracts* 0.1–0.6 × 0.1–0.3 cm, elliptic , apices acute to acuminate, bases truncate, pilose abaxially and ciliate, persistent; *flower* pedicels 0.3–0.5 × 0.3–0.5 mm, flat to cylindric, pilose, bracteoles 0.8–1.7

× 0.2–0.6 mm, lanceolate, ciliate. caducous, flower buds 1–3 × 0.6–2 mm, white or beige; hypanthium extending 0.5 mm above the summit of the ovary, not tearing at anthesis, pilose with simple, appressed, red, and white trichomes; calyx pentamerous, lobes free in the bud, 0.9–2 × 1–1.5 mm, deltate, apices acute or rounded, bases truncate, ciliate, glabrous adaxially, pilose abaxially; corolla pentamerous, petals beige, 1–2 × 1–2 mm, ovate, apices rounded, bases truncate, glabrous; staminal ring 0.5 mm wide, glabrous, 31–43 stamens, filaments 2–4 × 0.2 mm, anthers brown, 0.2–0.4 × 0.3 mm, oblong to rounded; style 1–3 mm long, *Fruit* black, 4–10 × 5–9 mm, spheroid, calyx lobes persistent. *Seeds* 2.

Comments:—*Myrcia amazonica* can be recognized by its red bark that sheds as a thin membrane, by flat leaf midvein, small (no more than 2 mm long) flowers, and its 5 equally sized, adaxially glabrous (at most strigose) calyx lobes. In the AMFD, *Myrcia amazonica* can be confused with *M. pyrifolia* (Desv. ex Ham) Nied. *Myrcia amazonica* leaves usually present acuminate apices (versus caudate apices in *M. pyrifolia*); the indumentum in the abaxial surface of leaves is glabrescent to pilose in *M. amazonica* (versus glabrous in *M. pyrifolia*); mature fruit color is black in *M. amazonica* (versus red in *M. pyrifolia*). These species can also be differentiated by their habitats: while *Myrcia amazonica* occurs in the forest understory, *Myrcia pyrifolia* occurs at the edge of rivers. *Myrcia amazonica* presents widespread distribution in the neotropical region reaching Central America and the Caribbean.

Myrcia amazonica distribution is indicated in Figure 3 and the phenology is indicated in Figure 4.

Myrcia amazonica is considered of Least Concern (LC) by IUCN (2023).

Specimens examined:—BOLIVIA. Bení: Riberalta, Solomon, J.C. 6395 (INPA!, MBM!). — BRAZIL. Acre: Brasiléia, Daly, D.C. 6733 (INPA!); Cruzeiro do Sul, Maas, P.J.M. P12652 (FLOR!). Amapá: Porto Grande, Mattos, J. 10083 (HAS!). Amazonas: Manaus, Mello, F. s.n. (INPA!), Mota, C. 227 (INPA!), Prance, G.R. 4841 (INPA!), Ribamar, J. 171 (INPA!), Rodrigues, W. 1681 (INPA!), Rodrigues, W. 4623 (INPA!), Rodrigues, W. 4654 (INPA!), Rodrigues, W. 6018 (INPA!), Vicentini, A. 704 (INPA!), Wagner, M.A. 212 (FLOR!); Presidente Figueiredo, Ferreira, C.A.C. 6963 (INPA!); Rio Preto da Eva, Rodrigues, W. 2224

(INPA!); São Gabriel da Cachoeira, Farney, C. 1887 (INPA!). Bahia: Abaíra, Harley, R.M. 50115 (CEPEC!), Harley, R.M. 50236 (CEPEC!), Harley, R.M. 50330 (CEPEC!); Ganev, W 2585 (HUEFS!); Alagoinhas, Jesus, N.G. 256 (HUEFS!); Arataca, Santos, M.F. 757 (CEPEC!); Barra da Estiva, Fonseca, W.O. 411 (HURB!), Harley, R.M. 15646 (CEPEC!); Bonito, Gasson, P. 6103 (ALCB!); Eunápolis, Belém, R.P. 2619 (CEPEC!), Guedes, M.L. 4245 (CEPEC!); Igatu, Santos, D.L. 51 (HUEFS!); Itamarajú, Monteiro, M.T. 23568 (HUEFS!); Jacobina, Bautista, H.P. 3087 (ALCB!, CEPEC!), Carvalho, A.M. 4145 (CEPEC!), Carvalho, A.M. 4147 (CEPEC!), Carvalho, A.M. 4172 (HUEFS!), França, F. 3063 (HUEFS!), Guedes, M.L. 9356 (ALCB!),Guedes, M.L. 14822 (ALCB!), Stadnik, A. 14 (ALCB!), Stadnik, A. 19 (ALCB!), Stadnik, A. 48 (ALCB!), Stadnik, A. 55 (ALCB!); Lençóis, Carvalho, A.M. 1011 (CEPEC!), Funch, L.S. 923 (HUEFS!), Mello, E. PCD 1673 (ALCB!), Santos, R.B. 46 (HUEFS!), Santos, R.B. 51 (HUEFS!); Maracás, Paganucci, L. 92 (ALCB!); Miguel Calmon, Guedes, M.L. 13262 (ALCB!); Mucugê, Funch, L.S. 1046 (HUEFS!), Funch, R. 200 (HUEFS!), Guedes, M.L. 16922 (ALCB!); Mucurí, Pinheiro, R.S. 2138 (ICN!); Palmeiras, Carvalho, A.M. 2143 (HUEFS!), Costa, G. 100 (HUEFS!), Costa, G. 2329 (HURB!), Fonseca, R.B.S. 39 (HUEFS!), Funch, L.S. 1537 (HUEFS!), Guedes, M.L. 5480 (ALCB!), Guedes, M.L. 5489 (ALCB!); Piatã, Lima, D.F 609 (FLOR!), Roque, N. 933 (ALCB!); Porto Seguro, Euponino, A. 307 (ICN!), Folli, D.A. 880 (CVRD!), Mattos-Silva, L.A. 4990 (CEPEC!, HUEFS!); Rui Barbosa, Cardoso, D. 341 (HUEFS!); Santa Cruz Cabrália, Eupunino, A. 95 (CEPEC!); São José da Vitória, Amorim, A.M. 8354 (CEPEC!); Vitória da Conquista, Mori, S.A. 11285 (CEPEC!). Espírito Santo: Conceição da Barra, Giaretta, A.O. 1040 (VIES!), Pereira, O.J. 5187 (VIES!); Linhares, Folli, D.A. 2438 (CVRD!), Folli, D.A. 34 (CVRD!), Folli, D.A. 4032 (CVRD!), Folli, D.A. 6250 (CVRD!), Folli, D.A. 963 (CVRD!), Lopes, J.C. 286 (INPA!), Silva, L.A. 12 (CVRD!), Silva, L.A. 308 (CVRD!); Presidente Kennedy, Gomes, J.M.L. 1320 (VIES!), Pereira, O.J. 5812 (VIES!), Souza, V. 344 (CVRD!); Rio Bananal, Folli, D.A. 5808 (CVRD!). Goiás: Goiás Velha, Proença, C. 3546 (INPA!). Maranhão: São Luis, Muniz, F.H. 392 (INPA!). Mato Grosso: São José do Rio Claro, Rozza, A. 309 (INPA!); Vila Bela da Santíssima Trindade, Macedo, M. 730 (INPA!). Minas Gerais: Anderson, W.R. 36249 (INPA!); Jaboticatubas, Semir, J. 4710 (SP!); Santa Bárbara, Stehmann, J.R. s.n. (ICN!). Pará: Oliveira, E. 730 (HAS!); Bragança, Mehlig, U. 1389 (INPA!); Concórdia do Pará, Oliveira, E. 442 (HAS!); Oriximiná, Ferreira, C.A.C. 9531 (INPA!), Ferreira, C.A.C. 9534 (INPA!), Ramos, J.F. 2938 (INPA!); Santarém, Calao, V.Y.P. s.n. (INPA!); Tucuruí, Daly, D.C. 975 (INPA!), Miranda, F.E. 405 (INPA!), Miranda, F.E. 425 (INPA!), Miranda, F.E. 435 (INPA!), Revilla, J. 8284 (INPA!), Silva, M.G. 5379 (INPA!). Paraná: Guaratuba, Barboza, E. 3977 (MBM!); Piraquara, Hatschbach, G. 64003 (FLOR!), Kummrow, R. 2067 (FLOR!), Silva, J.M. 1615 (INPA!); São José dos Pinhais, Cordeiro, J. 108 (FLOR!). Pernambuco: Brejo da Madre de Deus, Nascimento, L.M. 188 (CEPEC!), Nascimento, L.M. 464 (CEPEC!), Nascimento, L.M. 468 (CEPEC!), Nascimento, L.M. 486 (CEPEC!), Silva, A.G. 48 (CEPEC!); Camaragibe, Torres, J.E.L. s.n. (HUEFS!). Rondônia: Abuna, Perigolo, N.A. 217 (INPA!); Porto-Velho, Pereira-Silva, G. 13547 (INPA!); Porto Velho, Rocha, G.P.E. 194 (INPA!); Vilhena, Vieira, M.G. 930 (INPA!). Roraima: Caracaraí, Wagner, M.A. 239 (INPA!), Wagner, M.A. 240 (INPA!), Wagner, M.A. 241 (INPA!), Wagner, M.A. 242 (INPA!), Wagner, M.A. 291 (INPA!). Santa Catarina: Itapoá, Mello, A.S. 713 (FLOR!); São Francisco do Sul, Dreveck, S. 1200 (HURB!). São Paulo: Cananéia, Staggemeier, V. 109 (MBM!); Praia Grande, Antar, G.M. 1761 (HUEFS!); São Paulo, Sedulsky, T. 1169 (HUEFS!), Sendulsky, T. 1169 (HUEFS!). COLOMBIA. Antioquia: Anori, Oswaldo, D. 802 (HUA!); Anorí, López A.N. 849 (HUA!); La Ceja, Galeano 353 (HUA!); Maceo, Cardona N.F. 1757 (HUA!); Yolombo, Tobón-Juan Pablo 1630 (JAUM!). Casanare: Tauramena, Uribe, L. 4263 (JAUM!). Chocó: Acandí, Roldán, R. 1188 (HUA!). Bahía Solano, Espina, J. 2871 (HUA!). El Cesar: La Jagua de Ibirico, Velásquez-Rúa, C. 5473 (HUA!). Valle del Cauca: Yotoco, Betancur, J. 17830 (HUA!). VENEZUELA. Táchira: Liesner, R. 10343 (MBM!).

2. ***Myrcia areolata*** (McVaugh 1956: 175) E. Lucas & C.E. Wilson (2016: 656).

Marlierea areolata (McVaugh 1956:175). TYPE:—PERU. Loreto: von 10º S bis zur Mündung, 1923, G. Tessmann 3264 (holotype, G-00223340; isotypes, F-0040039F, NY-0003834, S-052556, US-00153783).

Shrubs or trees 5 m high. *Trichomes* white. *Twigs* shedding thin membranes, red bark, cylindric, mature twigs not seen. *Cataphylls* absent. *Leaves* opposite distichous, 2 leaves per node, *leaf blades* ca. 7.5 cm, elliptic, apices acute to caudate, bases cuneate to rounded, green or red when dried, midveins raised adaxially and raised abaxially, 6–8 secondary veins pairs, secondary veins flat to slightly raised on both surfaces, glabrous on both surfaces. *Inflorescences* terminal; asymmetrical narrowly triangular, calyx tetramerous, lobes free in the bud, ca. 1.7 × 2.5 mm, glabrous adaxially; 75–100 stamens; style ca. 4 mm long.

Comments: —*Myrcia areolata* is similar to *M. amazonica* but differs from it by presenting leaves with raised midveins. It is also recognized by its elliptic and few (6–8)secondary veins pairs, terminal verticillate inflorescences, the flattening of the hypanthium after anthesis and four unequal, internally glabrous calyx lobes, with inner ones presenting membranous margins.

Myrcia areolata type is from Peru, but there is one occurrence record in Brazil, in the state of Pará. The specimen from Pará presents highly similar leaves to the type specimen, but the inflorescences are more loosely arranged.

Myrcia areolata is considered of Least Concern (LC) IUCN (2023).

Specimens examined:—BRAZIL. Pará: Juruti, Ramos, M.B. 454 (INPA!). PERÚ. Loreto, Maynas Province, Michana, Catauga, R.R. 163. (ASU).

3. *Myrcia badia* (O. Berg 1859: 547) N. Silveira (1985: 66).

Aulomyrcia badia O. Berg (1859: 547). TYPE:—BRAZIL. Brasilia, s.d., Riedel, s.n. (holotype LE-00007023)

Twigs reddish brown, sparsely pubescent. *Cataphylls* present on bases of inflorescences, 3 cm long, elliptic. *Leaves* opposite decussate, 2 leaves per node, *leaf blades* 15–27 × 4–7.5 cm, lanceolate to narrowly elliptical, apices acuminate, bases cuneate, chartaceous, midveins flat adaxially, and raised abaxially, glabrous on both surfaces; *petioles* 0.9–1 cm long. *Inflorescences* 7.5 ×13 cm, panicle, terminal, asymmetrical narrowly triangular, alternate branching, glabrous; bracteoles 1.5 mm, lanceolate, flower bud ca. 4.5 mm long, calyx pentamerous, lobes free on the bud, lobes 1.5–3 × 3.5 mm, circular and concave, ciliate; corolla pentamerous.

Comments: —*Myrcia badia* type specimen presents flat midveins, terminal glabrous panicles subtended by foliose cataphylls. *Myrcia badia* is related to clade G species.

Myrcia badia is known only from its type specimen, from an unidentified location in Brazil.

Myrcia badia conservation status is considered Data Deficient (DD) by IUCN (2023).

4. *Myrcia clavija* Sobral (2006: 520). (Figure 5)

TYPE:—BRAZIL Minas Gerais: Descoberto, Res. Biol. Represa do Grama, 15 June 2001. R. Forzza, 2193 (holotype CESJ-37715, isotype RB-391417)

Treelet, 3–8 m high. *Trichomes* brown. *Twigs* brown, cylindric, slightly grooved and peeling thin to thick bark, mature twig golden-brown, cylindric, *internodes* ca. 3 cm long, rachis with graying and brown trichomes. *Cataphylls* absent. *Leaves* verticillate, 6–10 leaves per node, *leaf blades* 16–27 × 1.8–3 cm, lanceolate, apices acuminate, bases obtuse to cordate, discolored when dried, midveins raised on both surfaces, 40–60 secondary veins pairs, secondary veins slightly raised on both surfaces, intramarginal veins 0.8–1 mm from the margin; *petioles* 0.3–0.7 cm long. *Inflorescences* 10–23 cm long, panicles, terminal, asymmetrical narrowly triangular, alternate branching, peduncle ca. 13 cm long, rachis pubescent with grayish and brown trichomes, inflorescences units monochasiums, 50-100 flowers per inflorescence; *bracts* ca. 1.5 × 0.2 cm, sessile flowers; bracteoles 0.2–1.5 × 0.1–0.2 mm, triangular, persistent; calyx pentamerous, lobes free in the bud, lobes 1–1.5 × 1–2 mm, triangular, reflexed, bearing an arista of 1.5–2 mm long that breaks at anthesis, corolla trimerous, petals ca. 2 × 2.5 mm, circular, glabrous to finely ciliate; ca. 50 stamens, filaments ca. 3 mm long, anthers 0.2–0.3 × 0.3 mm, circular; style 5 mm long. *Fruit* black, 10 × 10–12 mm, spheroid to obloid, seeds 1–2.

Comments:—*Myrcia clavija* is recognized by its brown pubescence, and distinctive verticillate phyllotaxis. and the aristate calyx lobes. *Myrcia clavija* resembles *M. tetraphylla*, and *M. neoverticillaris,* and can be distinguished by presenting six–ten leaves per node, (versus four in *M. tetraphylla*, and *M. neoverticillaris*).

It is endemic to the Represa do Gama Biological Reserve in Descoberto, southern Minas Gerais.

Myrcia clavija flowering time is from March to June, and fruiting time from October to November.

Myrcia clavija is considered Critically Endangered (CR) by IUCN (2023).

Specimens examined:—BRAZIL. Minas Gerais: Descoberto, Castro, R.M. 658 (CESJ), Faria, P.C.L. 118 (CESJ).

5. *Myrcia colpodes* Kiaerskov (1893: 80).

TYPE:—BRAZIL. Rio de Janeiro, Praia Grande, 12 March 1862, A.F.M. Glaziou, 832. (lectotype, designated by Lucas *et al.* (2016: 661) C-10015833, isolectotypes BR-5238972, BR-5239917, C-10015834, P-00161301)

*Shrub*s. *Trichomes* reddish-brown and white. *Twigs* beige or reddish-brown, cylindric, glabrous to tomentose, *internodes* ca. 7 cm long. *Cataphylls* absent. *Leaves* opposite distichous, 2 leaves per node, *leaf blade*s 18–23 × 3.5–5 cm, lanceolate to narrowly elliptic, bullate, apices acuminate, bases cordate, discolor, green adaxially, golden brown abaxially, chartaceous to coriaceous, midveins raised on both surfaces, bullate, 20-30 secondary veins pairs, intramarginal veins 3–6 mm from the margin, adaxial surface glabrous, abaxial surface slightly pubescent; *petioles* ca. 0.5 × 0.3 cm. *Inflorescences* 15–23 × 9–15 cm, panicles, terminal, asymmetrical triangular, alternate to verticillate branching, peduncle 4.3–7.2 cm long, rachis glabrous to slightly pubescent, inflorescence unit dichasium; *bracts* ca. 2 cm long, deltate, apices acuminate, bases rounded, pubescent abaxially; *flowers* sessile, bracteoles ca. 3 mm long, lanceolate, glabrous, calyx pentamerous, lobes free in the bud, lobes 1–2 mm, ovate to triangular, apices acute to obtuse; staminal ring 2 mm wide, pubescent, style ca. 7 mm long. *Fruit* ca. 1.2 × 1.2 mm, cylindric, calyx lobes persistent.

Comments:—*Myrcia colpodes* is known by its pubescent young twigs, bullate leaves and long pedunculate terminal inflorescences.

Myrcia colpodes occurs in Rio de Janeiro, Brazil.

According to IUCN criteria (2023) *Myrcia colpodes* is considered Critically Endangered (CR).

Specimens examined:—BRAZIL. Glaziou, A.F.M., s.n. (K).

6. *Myrcia eumecephylla* (O.Berg 1857: 98) Niedenzu (1893: 76). (Figure 6–8)

Aulomyrcia eumecephylla O.Berg (1857: 98). TYPE:—BRAZIL. São Paulo, s.d., F. Sellow s.n. (holotype, B†, lectotype, designated by Lucas *et al.* (2016: 664) LE-00007060)

=*Myrcia limae* G.M. Barroso & Peixoto (1990: 11)

Shrubs to treelets, 2–5 m high. *Trichomes* brown and white, simple and brachiate, sometimes appressed. *Twigs* reddish-brown, cylindric, sometimes flattened, tomentose; mature twigs reddish-brown, cylindric, sometimes angular, glabrous to tomentose, *internodes* 3–5 cm long; *Cataphylls* absent. cm. *Leaves* opposite decussate, rarely verticillate in the apex, 2 leaves per node (rarely 3), *leaf blades* 20–55 × 6–12 cm, narrowly elliptic, apices acute, bases subcordate or cordate, margins slightly revolute in the bases, light green or reddish-brown when dried, chartaceous, midveins raised on both surfaces, 30–32 secondary veins pairs, secondary veins raised on both surfaces, intramarginal veins 2, 0.9–1.9, 3.6–5.8 mm from the margin, glabrous on both surfaces; *petioles* 1.5–3.5 cm long, plane adaxially and convex abaxially, irregular outer surface, tomentose, sheading the bark. *Inflorescences* 7–27 × 4–17 cm, panicles, terminal, asymmetrical triangular, decussate branching, peduncle ca. 0.5 cm long, tomentose, inflorescence unit monochasium, 67–148 flowers per inflorescence; *bracts* ca. 1 × 0.3 cm, deltate, apices acute, bases rounded, tomentose, caducous. *Sessile flowers*, bracteoles 2.8–5.3 × 2.5–3.6 mm, deltate, ciliate, strigose on both sides, persistent, flower buds 6–8 × 4.5–6 mm, white, hypanthium extending 2 mm above the summit of the ovary, tearing at anthesis, tomentose; calyx pentamerous, lobes partially fused before anthesis, 3.4–3.6 × 3.6–4 mm, deltate to shallowly deltate, apices acute to rounded, bases truncate, strigose abaxially; corolla pentamerous, petals beige, 3.5–5 × 2.5–3 mm, deltate, apices acute to rounded, bases truncate, glabrous; staminal rings 2 mm wide, glabrous, ca. 50 stamens, filaments ca. 6.2 mm long, anthers beige, ca. 0.4 mm long, circular; style ca. 9.2 mm long. *Fruit* green, 9–10.5 × 10–12.4 mm, calyx lobes persistent or caducous.

Comments:—*Myrcia eumecephylla* presents mostly opposite decussate phyllotaxis, sometimes verticillate near the inflorescences in the apices of twigs. It is known for its large (up to 55 cm long), subsessile leaves, cordate to sub-cordate bases, and raised adaxial midveins. Its terminal decussate inflorescence presents foliaceous bracts, brown tomentose rachis, and sessile flowers.

Myrcia eumecephylla resembles *M. obversa*. It can be distinguished by its subcordate or cordate leaf bases and slightly revolute margins (versus cuneate bases and straight margins in *M. obversa*).

Myrcia eumecephylla is endemic to Espírito Santo and Bahia in Brazil, its distribution is indicated on Figure 7 and the phenology is indicated in Figure 8.

Myrcia eumecephylla is considered Vulnerable (VU) by IUCN (2023).

Specimens examined:—BRAZIL. Bahia: Belmonte, Folli, D.A. 6929 (CVRD!); Prado, Belém, R.P. 2695 (CEPEC!). Espírito Santo: Águia Branca, Magnago, L.F.S. 1067 (MBML!), Vervloet, R.R. 2730 (MBML!); Colatina, Magnago, L.F.S. 736 (MBML!), Vervloet, R.R. 3411 (MBML!); Conceição da Barra, Ribeiro, M. 294 (SAMES!); Governador Lindemberg, Demuner, V. 2784 (MBML!), Vervloet, R.R. 2991 (MBML!); Jaguaré, Folli, D.A. 7140 (CVRD!); Linhares, Folli, D.A. 6885 (CVRD!), Jesus, M.C.F. 310 (SAMES!), Santos, T.S. 2014 (ICN!), Siqueira, G.S. 121 (CVRD!); Montanha, Assis, A.M. 3516 (MBML!); Nova Venécia, Forzza, R.C. 5138 (CEPEC!); Santa Teresa, Demuner, V. 1329 (MBML!), Fontana, A.P. 1720 (MBML!), Matsumoto, K. 803 (MBML!), Vimercat, J.M. 167 (MBML!); Sooretama, Folli, D.A. 7271 (CVRD!), Menezes, L.F.T. s.n. (SAMES!), Siqueira, G.S. 1209 (CVRD!); Vila Velha, Folli, D.A. 5750 (CVRD!), Folli, D.A. 6414 (VIES!).

7. *Myrcia gigantea* (O.Berg 1859: 548) Niedenzu (1893: 76). (Figures 9–11)

Aulomyrcia gigantea O.Berg (1859: 548). TYPE:— BRAZIL. Bahia: Ilhéus, 1859, L. Riedel s.n. (lectotype, designated by Lucas *et al.* (2016: 666), LE-00007069; isolectotypes, F-0064729F, K-000343087, LE-00007065, LE-00007066, LE-00007067, LE-00007068, LE-00007070, P-00163071, P-00163072).

Trees and shrubs, 6–8 m high. *Trichomes* red simple and short, with enlarged bases. *Twigs* reddish-brown, cylindric, sparsely pubescent with red indumentum; mature twigs reddish-brown, cylindric, glabrous, peeling epidermis. *Cataphylls* absent. *Leaves* opposite decussate, two leaves per node, *leaf blades* 54–65 × 10–27 cm, elliptic, apices acute, bases cordate, reddish-brown when dried, midveins raised on both surfaces, 17–22 secondary veins pairs, secondary veins slightly raised adaxially, and raised abaxially, intramarginal veins 2.5 mm from the margin, glabrous on both surfaces; *petioles* subsessile, cylindric, thicker near the shoot, pubescent with sparse red short trichomes with enlarged bases. *Inflorescences ca.*30 × 21 cm, panicles, terminal, asymmetrical triangular, opposite distichous branching, peduncle ca. 2.5 cm long, rachis strigose, inflorescence units monochasium and dichasium, ca. 400 flowers per inflorescence. *Sessile flowers*, bracteoles ca. 1 × 0.5 mm, lanceolate, strigose abaxially, glabrous adaxially, perennial, flower bud ca. 2.5 x 2 mm, reddish brown, hypanthium extending 1 mm above the summit of the ovary, tearing at anthesis, strigose, calyx pentamerous, lobes partially fused on the bud, lobes two sizes, 0.5–1.5 × 0.9–1,5 mm, shallowly deltate, apices acute to rounded, bases truncate, strigose abaxially, glabrous adaxially; corolla pentamerous, petals white, ca. 2 × 1.5 mm, deltate to ovate, apices rounded, bases truncate, glabrous; staminal ring ca. 0.5 mm wide, glabrous, stamens ca. 30, filaments ca. 3 mm long, anthers reddish brown, ca. 0.3 mm long, circular; ovaries ca. 1 × 1 mm, style ca. 5 mm long. *Fruits* immature green, ca. 7 × 7.5 mm, spheroid, calyx lobes caducous on the fruit. *Seeds* 1.

Comments:—*Myrcia gigantea* can be distinguished from other species of the Verticillate group of *Aulomyrcia* for its large (up to 65 cm) subsessile leaves with cordate bases and raised midveins adaxially, terminal verticillate inflorescences with a red strigose indumentum.

Specimen W. Thomas, 9841 was erroneously determined as *M. gigantea*, and this mistake has been repeated in multiple herbaria for other specimens with large leaves. W. Thomas, 9841 probably corresponds to a *Myrcia eximia* DC., a species of *Myrcia* sect. *Myrcia*, that presents a red indumentum abaxially, while *M. gigantea* presents shiny glabrous leaves.

Myrcia gigantea is endemic to Espírito Santo and Bahia in Brazil. See the distribution map on Figure 10 and the phenology on Figure 11.

Myrcia gigantea is considered Endangered (EN) by IUCN (2023).

Specimens examined:—BRAZIL. Bahia: Camamu, Paixão, J.L. 292 (CEPEC!); Eunápolis, Santos, T.S. 911 (CEPEC!); Ilhéus, Hage, J.L. 1299 (CEPEC!), Hage, J.L. 2144 (CEPEC!). Espírito Santo: Linhares, Monteiro, M.T. 23545 (HUEFS!).

8. *Myrcia hexasticha* Kiaerskov (1893: 72). (Figure 12–14).

TYPE:—BRAZIL. Rio de Janeiro, Jan. 1881, A.F.M. Glaziou 11975 (holotype, C-10015856; isotypes, G-00439824, K-000343357, LE-00007167, P-00161247, R-000009042).

Trees, 5–12 m high. *Trichomes* white and golden brown, simple and brachiate, appressed. *Twigs* cylindric, grooved, shedding thin gray membrane; mature twigs light brown and gray, cylindric, grooved, glabrous and smooth to pubescent near leaf petioles, shedding bark, *internodes* 2.7 cm long. *Cataphylls* on bases of inflorescence, ca. 1.7 × 0.3 cm, lanceolate or spatulate. *Leaves* verticillate, rarely opposite distichous, 3 leaves per node, rarely 2, *leaf blades* 12–25 × 2.6–10.5 cm, narrowly elliptic to elliptic, apices caudate, rarely truncate, bases cuneate to attenuate, reddish-brown to brown when dried, chartaceous , midveins raised on both surfaces, 21–31 secondary veins pairs, secondary veins raised on both surfaces, intramarginal veins 2, outer 0.6–1.8 mm, inner 0.9–3.2 mm from the margin, glabrous on both surfaces, abaxial; *petioles* 0.8–1.4 × 0.2–1.9 cm, plane adaxially and convex abaxially, rarely cylindrical, sometimes slightly canaliculate adaxially, glabrous to sparsely pubescent. *Inflorescences* 12.2–18.5 × 5–14 cm, thyrsoid panicles, terminal, asymmetrical triangular, alternate branching, peduncle 3.2–4.5 cm long, rachis pubescent with small red simple trichomes and brown brachiate appressed trichomes, inflorescence units dichasium, 89–190 flowers per inflorescence; *bracts* 0.9–1 × 0.2–0.3 cm, lanceolate, apices acuminate, bases truncate, pubescent abaxially, persistent. *Sessile flowers*, bracteoles 4, 0.5–0.8 × 0.1–0.4 mm, lanceolate to triangular, puberulent on abaxial surface, persistent, flower buds 1.9–2.5 × 1.4–1.7 mm, yellowish-brown; hypanthium extending 0.2 mm above the summit of the ovary, not tearing at anthesis, glabrous. Calyx pentamerous, lobes free on the bud, lobes 0.9–1.4 × 1.1–1.6 mm, very widely ovate or deltate, apices obtuse or acute, bases truncate, puberulent abaxially; corolla pentamerous, petals white to beige, 1.5–2.3 × 1.7–2.3 mm, ovate, apices rounded, bases truncate, glabrous or puberulent near the apices on abaxial surface; staminal ring ca. 0.4 mm wide, glabrous, 20–22 stamens, filaments 2.3–4.5 mm long, anthers beige, 0.4 × 0.3–0.4 mm, square; style 4.3–5.4 mm long. *Fruit* dark-purple, 8.1–8.9 × 8.8–12.3 mm, spheroid to obloid, sulcate when dried, calyx lobes persistent. *Seeds* 1-2.

Comments: —*Myrcia hexasticha* presents a verticillate ternate leaf arrangement, raised midveins, verticillate terminal inflorescences, and free calyx lobes.

Myrcia hexasticha resembles *M. clavija* and *M. tetraphylla,* the number of leaves per node can help differentiate them, with *M. clavija* presenting six to ten leaves per node and *M. tetraphylla,* four.

Myrcia hexasticha is endemic to the states of São Paulo, Rio de Janeiro and Paraná in Brazil. See the distribution map on Figure 13 and the phenology in Figure 14.

Myrcia hexasticha is considered Vulnerable (VU) by IUCN (2023).

Specimens examined:—BRAZIL. Paraná: Guaraqueçaba, Hatschbach, G. 72725 (MBM!); Paranaguá, Hatschbach, G. 13139 (FLOR!), Hatschbach, G. 45773 (ICN!), Hatschbach, G. 50835 (ICN!), Silva, S.M. (MBM!), Tessmann, G. 1015 (MBM!); Pontal do Paraná, Lucas, E.J. 194 (MBM!). Rio de Janeiro: Silva Jardim, Pessoa, S.V.A. 1217 (RB!). São Paulo: Cananéia, Person, V.G. s/n (MBM!); Iguape, Fávero, O.A. 355 (SP!), Fávero, O.A. s/n (SP!).

9. *Myrcia insularis* Gardner (1842: 536). (Figure 15-17)

TYPE:—BRAZIL. Rio de Janeiro: Ilha do Govenador, 1836, G. Gardner 202 (lectotype, designated by Lucas *et al.* (2016: 670)BM-000953612; isolectotypes, K-000343449, K-000343450, K-000343451, P-001612300).

Trees, 12 m high. *Trichomes* white, red, or golden-brown, simple with enlarged bases and brachiate. *Twigs* and mature twigs gray and reddish brown, cylindric, glabrous, *internodes* 3.7–4.9 cm long; *Cataphylls* on bases of inflorescences, 2.9–3.2 × 0.7–0.9 cm, narrowly elliptic. *Leaves* opposite decussate, 2 leaves per node, *leaf blades* 11–15 × 3.6–5 cm, narrowly elliptic, apices acute, bases cuneate, light brown when dried, chartaceous, midveins raised on both surfaces, 17–25 secondary veins pairs, secondary veins flat adaxially on both surfaces, intramarginal veins 2, outter0.5–1.9, inner 1.9–3.5 mm from the margin, adaxial surface glabrous, abaxial surface slightly pubescent; *petioles* 0.7–1 × 0.1–0.2 cm, plane adaxially and convex abaxially, slightly pubescent. *Inflorescences* 15–17 × 10–15 cm, panicles, terminal and axillary, asymmetrical triangular, opposite, and alternate branching, peduncle 2.9–3.7 cm long, rachis glabrous to slightly pubescent, inflorescence units monochasium and dichasium, ca. 300 flowers per inflorescence; *bracts* 0.1–0.4 × 0.1–0.2 cm, lanceolate, apices acute to acuminate, bases truncate, glabrous. Persistent. *Flower* pedicel ca. 0.1 × 0.1 mm, cylindric, glabrous, bracteoles ca. 0.1 × 0.1 mm, lanceolate, persistent, flower buds 1.8–2.8 × 1.7–2.2 mm, yellow; hypanthium extending 0.3 mm above the summit of the ovary, tears from the bases of lobes into the hypanthium at anthesis. pubescent with reddish-brown short trichomes with enlarged bases, calyx pentamerous, lobes free to partially fused in the bud, lobes 0.8–1.5 × 1–1.5 mm, deltate or ovate, apices acute or rounded, bases truncate, slightly pubescent on both surfaces; corolla pentamerous, petals white to beige, ca. 2 × 2 mm, ovate, apices rounded, bases truncate, glabrous; staminal ring ca. 0.6 mm wide, glabrous, ca. 15 stamens, filaments ca. 2.6 mm long, anthers brown, ca. 0.1 × 0.1 mm, oblong; style ca. 4 mm long. *Fruit* black, 7.2–8.6 mm long, ovoid, smooth surface, calyx lobes caducous. *Seeds* 1-2.

Comments:—*Myrcia insularis* presents decussate leaves, slightly raised midveins, and terminal verticillate, glabrous inflorescence subtended by cataphylls.

Myrcia insularis can be confused with *M. hexasticha.* The two species can be distinguished by the phyllotaxis markedly opposite decussate in *Myrcia insularis* (versus verticillate with three leaves per node in *M. hexasticha*).

Myrcia insularis distribution is from the states of Espírito Santo to Pernambuco, in Brazil, see the map indicated on Figure 16 and the phenology in Figure 17.

Myrcia insularis is considered Vulnerable (VU) by IUCN (2023).

Specimens examined:—BRAZIL. Bahia: Ilhéus, Carvalho, A. M. 4810 (MBM!), Mattos Silva, L.A. 1513 (CEPEC!); Itabuna, Santos, T.S. 928 (ICN!); Santa Cruz Cabrália, Mori, S.A. 12079 (CEPLAC!); Teixeira de Freitas, Santos, T.S. 1619 (CEPEC!); Una, Sartori, A.L.B. 263 (CEPEC!). Espírito Santo: Águia Branca, Magnago, L.F.S. 1689 (MBML!); Governador Lindemberg, Silva, L.A. 517 (VIES!); Linhares, Hatschbach, G. 58026 (MBM!); Nova Venécia, Luber, J. 196 (VIES!); Presidente Kennedy, Gomes, J.M.L. 3381 (VIES!), Gomes, J.M.L. 3419 (VIES!). Pernambuco: São Lourenço da Mata, Almeida, K. 17 (CEPEC!).

10. *Myrcia liesneri* B. Holst (2002: 154).

TYPE:—VENEZUELA. Amazonas: Rio Negro, 4 Dec. 1984, R. Liesner 17494 (holotype, ASU-78739 , isotypes, VEN-332431).

Trees, 4 m high. *Trichomes* are long thin forming villous indumentum. *Twigs* with villous indument to glabrous, *internodes* ca. 5 cm long; *Cataphylls* absent. *Leaves* opposite distichous to opposite decussate, 2 leaves per node, *leaf blades* 12–19 × 4–6.5 cm, lanceolate to narrowly elliptic or ovate, apices evenly to abruptly acuminate, bases rounded to subcordate, discolor, dark green adaxially, pale green abaxially, chartaceous to coriaceous, midveins raised on both surfaces, ca. 25 secondary veins pairs, secondary veins flat to slightly raised adaxially, secondary veins abaxially raised, intramarginal veins 2, outer 0.5–1, inner 2–4 mm from the margin, adaxial surface glabrous, pubescent on midveins when young on both surfaces; *petioles* 0.3–0.5 cm. *Inflorescences* 4–7 cm long, panicles, subterminal, peduncle 2.5–4 cm long, rachis pubescent, 3-5 flowers per inflorescence; bracts caducous. *Flowers* sessile to pedicel ca. 3 mm long, bracteoles 1 mm, deltate, caducous, hypanthium extending 1.5–2 mm above the summit of the ovary, calyx pentamerous, lobes free in the bud, stamens filaments ca. 2.5 mm long, anthers ca. 0.5 mm. *Fruit* obloid to spheroid, calyx lobes persistent.

Comments:—*Myrcia liesneri* is recognized by leaves with short corky petioles, raised midveins adaxially, and conspicuous pellucid dots abaxially.

Myrcia liesneri occurs in the Southern Amazon State in Venezuela in lowland (140–400 m elevation) tropical forests. *Myrcia liesneri* flowers in December.

Myrcia liesneri is considered Data Deficient (DD) IUCN (2023).

Specimens examined:—COLOMBIA. Cumaribo, Marín-C., N.L. 6075 (COAH).

11. *Myrcia magna* D. Legrand (1967: 150). (Figure 18–20)

TYPE:—BRAZIL. Amazonas, Barra do Rio Negro, Oct. 1851, R. Spruce s.n. (holotype, M-0136853; isotypes, F-0064722F, G-00222416, G-00222417, K-000343116, K-000343117, K-000343961, LE-00007074, NY-00386668, P-00161260)

Tree or shrubs, 4–20 m high. *Trichomes* white and brown short and simple, extended, or appressed. *Twigs* reddish-brown, flattened, grooved, sometimes shedding thin membrane, pubescent with brown simple trichomes, mature twigs golden-brown to reddish-brown cylindric, grooved, *internodes* ca. 5 cm long; *Cataphylls absent*. *Leaves* opposite distichous, 2 leaves per node, *leaf blades* 12.3–33 × 3.5–10.5 cm, narrowly elliptic to elliptic, apices caudate or rounded, bases cuneate, brown when dried, chartaceous, midveins flat to slightly raised adaxially, canaliculate, midveins abaxially raised, 11–23 secondary veins pairs, secondary veins flat to slightly raised adaxially, raised abaxially, intramarginal veins 2, outer 0.7–1.2, inner 1.5–4 mm from the margin, glabrous adaxially, glabrous or sparsely pubescent abaxially; *petioles* 0.4–1.3 × 0.1–0.3 cm, concave on both surfaces, sparsely pubescent. *Inflorescences* 10–17 × 3–12 cm, panicles, terminal and axillary, asymmetrical triangular alternate branching, peduncle 0.6–4 cm long, rachis pubescent with very small brown reflexed trichomes or white simple appressed, inflorescence units monochasium, 57-72 flowers per inflorescence; *bracts* ca. 1.6 × 0.9 cm, triangular, caducous, *sessile flowers* mm, bracteoles 0.7–1.3 × 0.6–1 mm, lanceolate, pubescent abaxially, caducous, flower bud 2.2–2.7 × 1.5–1.9 mm, reddish brown, hypanthium extending 0.3 mm above the summit of the ovary, not tearing, sericeous with white appressed trichomes, calyx pentamerous, lobes free in the bud, lobes 1–1.3 × 0.6–1.4 mm, deltate, acute to rounded, truncate, sparsely pubescent; corolla pentamerous, petals beige, ca. 2.5 × 2 mm, very widely ovate, apices rounded, bases truncate, glabrous; staminal ring ca. 0.6 mm wide, slightly pubescent, ca. 16 stamens, filaments ca. 3.7 mm long, anthers beige, ca. 0.4 × 0.3 mm, squared; style ca. 4.2 mm long. *Fruit* dark purple to black, 4.5–10.7 × 5–13.5 mm, obloid, sometimes lobed, calyx lobes persistent. *Seeds* 1.

Comments:—*Myrcia magna* is identified by its red peeling bark that grants its common name “casca fina” meaning thin bark in Portuguese, and terminal to subterminal long (c. 18 cm) asymmetrical panicles.

Myrcia magna occurs in northern Brazil, in the states of Acre, Amazonas, Pará, Roraima e Tocantins. Its distribution is indicated in Figure 19 and the phenology is indicated in Figure 20.

Myrcia magna is considered of Least Concern (LC) by IUCN (2023).

Specimens examined:—BRAZIL. Gentry, A. 12863 (INPA!). Acre: Cruzeiro do Sul, Rosas Junior, A. 267 (INPA!). Amazonas: BR 17 Km 3, Dionisio s.n. (INPA!); Coari, Miralha, J.M.S. 138 (MBM!); Distrito Agropecuário da Suframa, Setz, E. 990 (INPA!); Manaus, Coelho, D. 59 (ICN!), Coelho, D. s.n. (INPA!), Kinupp, V.F. 4946 (RB!), Mello, F. 3 (INPA!), Prance, G.R. 3714 (INPA!), Prance, G.R. 3758 (INPA!), Rodrigues, W. 3550 (HAS!), Rodrigues, W. 4004 (HAS!), Rodrigues, W. 4101 (HAS!), Rodrigues, W. 4119 (HAS!), Rodrigues, W. 4361 (HAS!), Rodrigues, W. 4796 (INPA!), Rodrigues, W. 8644 (INPA!), Willian s.n. (INPA!); Maués, Zarucchi, J.L. 3051 (INPA!); Presidente Figueiredo, Carvalho-Sobrinho, J.G. 1096 (INPA!), Carvalho-Sobrinho, J.G. 1481 (INPA!), Ferreira, C.A.C. 6770 (INPA!), Silva, J.A.C. 1480 (INPA!). Pará: Porto Trombetas, Soares, E. 80 (INPA!). Roraima: Caracaraí, Ferreira, C.A.C. 13167 (INPA!), Wagner, M.A. 237 (FLOR!). Tocantins: Lagoa da Confusão, Haidar, R.F. 1224 (INPA!). VENEZUELA. Amazonas: São Carlos de Rio Negro, Clark, H.L. 7485 (INPA!).

12. ***Myrcia neodimorpha*** E. Lucas & C.E. Wilson (2016: 678). (Figures 21–23)

TYPE:—BRAZIL. Rio de Janeiro: Goiatacazes, Lagoa Fria, 1833, L. Riedel, 314 (lectotype, LE-4017; isolectotypes, G-223338, K-330498, all three designated by Lucas et al. 2016)

Trees, 4–8 m high. *Trichomes* white or golden-brown, long simple or brachiate, appressed or extended forming velutinous indumentum. *Twigs* beige, cylindric, glabrous; mature twigs brown, cylindric, glabrous, *internodes* 2–4 cm long; *cataphylls* verticillate, on bases of inflorescence and between nodes, 1–9 cm long, narrowly elliptic, or lanceolate. *Leaves* opposite decussate, 2 leaves per node, *leaf blades* 11–27 × 5–12 cm, narrowly elliptic to widely elliptic, apices cuspidate, bases cuneate, light green abaxially, chartaceous, midveins adaxially flat, midveins abaxially raised, 16 pairs of secondary veins, secondary veins flat adaxially, and slightly raised abaxially, intramarginal veins 3.1 mm from the margin, glabrous on both surfaces; *petioles* ca. 5 × 2 cm, cylindric, glabrous to pubescent. *Inflorescences* 11–15 × 4–7 cm, panicles, terminal, asymmetrical triangular, verticillate branches 1–2 cm long, lanate, monochasium 25 flowers per inflorescence. *Bracts* 0.7–1.5 × 0.1–0.9 cm, elliptic concave, apices cuspidate or acute, bases attenuate, pubescent, persistent. *Sessile flowers*, bracteoles ca. 9 × 6 mm, elliptic, ciliate, persistent, flower bud 4 × 6 mm, grayish green, hypanthium extending 0.8–2 mm above the summit of the ovary, tearing at anthesis, lanuginose or velutinous, calyx pentamerous, lobes completely fused in the bud, lobes 2–5 × 1.3–2.2 mm, triangular, acuminate, truncate, lanuginose abaxially; corolla pentamerous, petals white, ca. 4 × 6 mm, oblate, apices retuse, bases truncate, lanuginose abaxially; staminal ring ca. 1.5 mm wide, glabrous, c. 55 stamens, filaments ca. 9 mm long, anthers beige, 0.3–0.5 × 0.1 mm, oblong; style ca. 8 mm long. *Fruit* black, 7–11 × 9–11 mm, spheroid, calyx lobes persistent. *Seeds* 1.

Comments:—*Myrcia neodimorpha* can be distinguished by the cataphylls that subtend inflorescences and also occur between leaf nodes. The beige pubescent bracts subtending secondary branches of the inflorescence are also characteristic.

Myrcia neodimorpha is endemic to the Brazilian southeastern states of São Paulo, Rio de Janeiro, and Espírito Santo (Figure 22). Its phenology is shown in Figure 23.

Myrcia neodimorpha is considered vulnerable (VU) by IUCN (2023).

Specimens examined:—BRAZIL. Espírito Santo: Alegre, Couto, D.R. 997 (MBML!), Manhães, V.C. 102 (MBML!), Manhães, V.C. 106 (MBML!); Colatina, Vervloet, R.R. 3411

(MBML!); Conceição da Barra, Pereira, O.J. 4339 (VIES!); Linhares, Folli, D.A. 6649 (CVRD!); Vila Velha, Folli, D.A. 5747 (CVRD!), Pereira, O.J. 6256 (VIES!). São Paulo: Salesópolis, Mattos, J. 13886 (HAS!).

13. *Myrcia neoverticillaris* E. Lucas & C.E. Wilson (2016: 683). (Figures 24–26)

TYPE:—BRAZIL, Bahia: flumen Itahype prope Castel novo, s.d., L. Riedel 534 (lectotype, designated by Lucas *et al.* (2016: 638) LE-00004048, isolectotypes G-00222986, K-000330440, LE [2], P-00217957).

Tree or shrub, 2–9 m high. *Trichomes* reddish-brown simple with enlarged bases, appressed or extended slightly pubescent indumentum. *Twigs* and mature twigs reddish-brown, cylindric, sometimes flattened, glabrous; *internodes* 2.5–4.6 cm long. *Cataphylls* at the base of inflorescences, 1.4–1.6 cm long, lanceolate. *Leaves* verticillate rarely opposite distichous, 4 leaves per node (rarely 3), *leaf blades* 12–21 × 2.5–6 cm, narrowly elliptic, apices acuminate, bases cuneate, reddish-brown when dried, chartaceous, midveins raised on both surfaces, 12–17 secondary vein pairs, secondary veins flat adaxially, raised abaxially; intramarginal veins 2, outer 0.6–0.9, inner 1.9–3 mm from the margin, glabrous on both surfaces; *petioles* 0.8–1.7 × 0.2–0.3 cm, plane adaxially, convex abaxially, glabrous. *Inflorescences* 7–16 × 8–15 cm, panicles, terminal, asymmetrical, triangular, verticillate branching, peduncles ca. 0.9 cm long, rachis slightly pubescent, inflorescence units monochasium ca. 150 flowers per inflorescence; *bracts* ca. 4.5 × 1.2 cm, lanceolate, apices acuminate, bases truncate, tomentose, persistent, *sessile flowers*, bracteoles ca. 1.2 × 0.2 mm, lanceolate, pubescent. persistent, flower buds 2.4–2.8 × 2.0–2.4 mm, dark brown when dried, hypanthium extending 0.4–0.6 mm above the summit of the ovary, tearing at anthesis, glabrous, calyx pentamerous, lobes fused in the bud, lobes 2.1–2.8 × 0.8–1.3 mm, deltate, acute , truncate, glabrous; corolla pentamerous, petals beige, ca. 1.5 × 0.5 mm, oblong, apices rounded, bases truncate, glabrous; staminal ring ca. 0.4 mm wide, glabrous, ca. 25 stamens, filaments ca. 2.5 mm long, anthers beige, ca. 0.2 × 0.2 mm, oblong, styles 3 mm long. *Fruit* black, ca. 9 × 9 mm, spheroid, calyx lobes persistent. *Seeds* 1.

Comments:—*Myrcia neoverticillaris* is characterized by presenting verticillate leaves, with up to four leaves per node, and reddish-brown terminal inflorescences.

Myrcia neoverticillaris is endemic to the state of Bahia, Brazil. Its distribution is indicated in Figure 25 and the phenology is indicated in Figure 26.

Myrcia neoverticillaris is considered Endangered (EN) by IUCN (2023).

Specimens examined:—BRAZIL. Bahia: Aurelino Leal, Thomas, W.W. 12680 (RB!); Ilhéus, Pinheiro, R.S. 1013 (RB!); Santa Cruz Cabrália, Mori, S.A. 10837 (RB!).

14. *Myrcia obversa* (D. Legrand 1962: 28) E. Lucas & C.E. Wilson (2016: 684) (Figures 27–29).

Marlierea obversa D. Legrand (1962: 28)

TYPE:— BRAZIL. Rio de Janeiro: ad vicum Uba, August, 1821, L. Riedel s.n., (lectotype, designated by Lucas *et al.* (2016: 684), LE-00004049, isolectotype, P-05209045).

Trees, 4–8 m high. *Trichomes* beige, simple and brachiate. *Twigs* brown, cylindric, grooved, sparsely pubescent; mature twigs reddish-brown, cylindric, shedding bark, glabrous, *internodes* ca. 2.5 cm long. *Cataphylls* absent. *Leaves* opposite distichous or opposite decussate, 2 leaves per node, leaf blades 9.5–21 × 2–7 cm, narrowly elliptic, apices acuminate or caudate, bases cuneate, light brown when dried, chartaceous, midveins raised on both surfaces, ca.20 secondary veins pairs, secondary veins flat adaxially, slightly raised abaxially, intramarginal veins 2, 0.6–1.2, 2.7–4 mm from the margin, glabrous on both surfaces; *petioles* 0.7–1.5 × 0.2–0.3 cm, plane adaxially, convex abaxially, pubescent to lanuginose with very thin trichomes. *Inflorescences* 10–11× ca. 7.6 cm, panicles, terminal, triangular alternate, peduncles ca. 1.3 cm long, rachis lanuginose, inflorescence units monochasium, 12-30 flowers per inflorescence; *bracts* 1.2–1.5 × 1–7 cm, elliptic or spatulate, apices, persistent, *flower* pedicel 0.6–1 × 1–1.6 mm, bracteoles 2, 4.5–5.6 × 2–2.5 mm, elliptic or circular, caducous, flower buds 5.1–6.1 × 4.1–4.8 mm, hypanthium densely tomentose, calyx pentamerous, lobes fused on the bud, lobes 3.9–4.5 × 3.1–3.4 mm, asymmetrical to oblate, apices rounded, bases truncate, tomentose adaxially; corolla pentamerous, petals beige, ca 2.5 × 3.5 mm, oblate, apices rounded, bases truncate, glabrous; staminal ring ca. 1.8 mm wide, filaments ca. 4.5–6.5 mm long, anthers 0.4–0.5 × 0.3–0.4 mm , very widely obovate, styles ca. 6.5 mm long. *Fruit* black, 7.6–8.5 × 4.8–9.3 mm, spheroid, irregular outer surface, pubescent, calyx lobes persistent.

Comments:—*Myrcia obversa* is recognized by its opposite distichous or opposite decussate leaves, with petioles of young leaves covered by straw colored brachiate trichomes, bracts below buds and inflorescences, thick tomentose inflorescence rachis, large buds (ca. 6 mm width) and fruits (7.6–8.5 × 4.8–9.3 mm).

Myrcia obversa is considered as Vulnerable (VU) by Canteiro and Lucas (2019) according to IUCN criteria (2023).

Myrcia obversa occurs in Brazil from Rio de Janeiro to Bahia, its distribution is indicated on Figure 28 and the phenology is indicated in Figure 29.

Specimens examined:—BRAZIL. Bahia: Camacan, Belém, R.P. 1395 (CEPEC!). Ilhéus, Hage, J.L. 1344 (CEPEC!), Santos, T.S. 3783 (CEPEC!). Itanagra, Mori, S.A. 14129 (CEPEC!); Itacaré, Jardim, J.G. 1837 (CEPEC!), Mori, S.A. 10155 (CEPEC!). Mascote, Gomes, F.S. 1653 (ALCB!). Porto Seguro, Folli, D.A. 6430 (CVRD!), Mattos-Silva, L.A. 2513 (CEPEC!); São José da Vitória, Amorim, A.M. 8324 (CEPEC!). Una, Gomes, F.S. 1378 (ALCB!), Jardim, J.G. 2264 (CEPEC!), 214 (CEPEC!), Mattos-Silva, L.A. 4593 (CEPEC!), Sant'Ana, S.C. 339 (CEPEC!); Uruçuca, Piotto, D. 3156 (CEPEC!). Espírito Santo: Conceição da Barra, Giaretta, A.O. 1159 (SAMES!), Giaretta, A.O. 1351 (RB!), Oliveira, A.G. 644 (SAMES!), Pereira, O.J. 4305 (VIES!), Ribeiro, M. 642 (SAMES!); Guarapari, Assis, A.M. 562 (VIES!); Linhares, Farias, G.L. 250 (CVRD!), Flores, T.B. 956 (CVRD!), Folli, D.A. 1067 (CVRD!), Folli, D.A. 4277 (CVRD!), Folli, D.A. 4861 (CVRD!), Folli, D.A. 6168 (CVRD!), Folli, D.A. 6657 (CVRD!), Matsumoto, K. 820 (CVRD!), Oliveira, A.G. 30 (SAMES!), Peres, A.L.S.S. 339 (RB!), Silva, I.A. 2 (CVRD!), Souza, V. 167 (CVRD!); Praia das Neves, Araújo, D. 5614 (VIES!); Presidente Kennedy, Gomes, J.M.L. 4266 (VIES!); São Mateus, Martins, R.F.A. 95 (SAMES!), Saporetti, A.M.J. 81 (SAMES!); Hatschbach, G. 71530 (MBM!), Sooretama, Siqueira, G.S. 997 (CVRD!); Vila Velha, Pereira, O.J. 6222 (VIES!), Thomaz, L.D. 490 (RB!), Zambom, O. 141 (VIES!); Vitória, Pereira, O.J. 1536 (VIES!). Rio de Janeiro: Silva Jardim, Pessoa, S.V.A. 965 (RB!), Pessoa, S.V.A. 969 (RB!), Pessoa, S.V.A. 977 (RB!).

15. *Myrcia pyrifolia* (Desvaux ex Hamilton 1825: 44) Niedenzu (1893: 76). (Figure 30–32)

Eugenia pyrifolia Desvaux ex Hamilton (1825: 44)

Aulomyrcia pyrifolia (Desvaux ex Hamilton 1825: 44) O.Berg (1855: 44)

TYPE:—GUYANA. Guiana Gallica, s.d., herb. Prof. Desv. s.n. (holotype, P-725813).

Trees, 4–8 m high. *Trichomes* white or reddish-brown. *Twigs* and mature twigs reddish-brown, cylindric, glabrous. *Cataphylls* absent. *Leaves* opposite distichous, 2 leaves per node, *leaf blades* 10–39 × 5–11 cm, ovate, apices acuminate, bases obtuse, light green, reddish when dried, chartaceous, midveins adaxially flat to slightly raised proximally, raised abaxially, ca. 9 secondary veins pairs, secondary veins flat on both surfaces, glabrous on both surfaces; *petioles* 0.3–0.4 × 0.2 cm, plane adaxially, convex abaxially, glabrous. *Inflorescences* 22–27 × 14–16 cm, panicles, terminal, asymmetrical triangular, alternate branching, peduncles ca. 3 cm long, rachis pubescent, inflorescence units monochasiums, *flowers* sessile, hypanthium sericeous with white or red trichomes, calyx pentamerous, lobes free in the flower bud, lobes circular and concave, apices rounded, bases truncate, ciliolate. *Fruit* red and spheroid.

Comments:—*Myrcia pyrifolia* is diagnosed by ovate and acuminate leaf blades and red fruits. It occurs in riverine forests in the AMFD. *Myrcia pyrifolia* can have submersed roots, and their fruit is said to feed fish commonly known as Pacú, (Serrasalmidae family). Information on how to distinguish *Myrcia pyrifolia* from *M. amazonica* is given under the treatment of the latter species.

Myrcia pyrifolia occurs in Northern Brazil, in Amazonas, Mato Grosso, Pará, and Roraima (Figure 31) and the phenology is indicated in Figure 32.

Myrcia pyrifolia is considered of Least Concern (LC) by IUCN (2023).

Specimens examined:—BRAZIL. Amazonas: Barcelos, Ferreira, C.A.C. 11849 (INPA!), Pereira, P.A. 586 (INPA!); Borba, Rodrigues, W. 1615 (INPA!); Camanaus, Silva, M.F. 1678 (INPA!); Cucuí, Silva, M.F. 1263 (INPA!); Ipanoré, Stevenson, D.W. 969 (INPA!); Novo Japurá, Amaral, I.L. 431 (INPA!); Rio Aracá, Acevedo-Rdgz., P. 8059 (INPA!); Rio Marié, Maia, L.A. 456 (INPA!); Rio Xié, Silva, M.F. 1377 (INPA!). Mato Grosso: Novo Mundo, Sasaki, D. 1280 (INPA!). Pará: Oriximiná, Farney, C. 12268 (INPA!); Porto Trombetas, Campbell, D.G. P22420 (INPA!), Soares, E. 240 (INPA!). Roraima: Caracaraí, Perdiz, R.O. 2091 (MIRR!), Perdiz, R.O. 2191 (MIRR!), Perdiz, R.O. 2251 (MIRR!), Perdiz, R.O. 2293 (UFRR!), Schütz Rodrigues, R. 2641 (UFRR!); Rorainópolis, Garcia, S. 254735 (INPA!), Matta, A. 58 (INPA!).

16. *Myrcia riodocensis* G.M. Barroso & Peixoto (1990: 13). (Figures 33–35)

TYPE:—BRAZIL. Espírito Santo, Linhares, 30 Jan. 1972, D. Sucre 8269 (lectotype, designated by Lucas et al (2016: 689) RB-542159, isolectotype, MBML-43499!).

*Tree*s, up to 17 m high. *Trichomes* golden-brown or brown, simple. *Twigs* and mature twigs reddish-brown, cylindric, pubescent. *Cataphylls* absent. *Leaves* opposite-distichous, 2 leaves per node, *leaf blades* 4–18 × 4–6 cm, narrowly to elliptic, apices acute to rounded, seldom caudate, bases cuneate or obtuse to rounded, reddish-brown or light-green when dried, coriaceous, midveins flat adaxially, raised abaxially, 6-26 secondary veins pairs, secondary veins flat on both surfaces, intramarginal veins 2, 0.9–1.4, 2.7–4.2 mm from the margin, adaxial surface glabrous, abaxial surface glabrous; *petioles* 0.5–2.3 × 0.3–0.4 cm, plane adaxially, convex abaxially, glabrous to-slightly pubescent with simple trichomes. *Inflorescences* 3–8 × 1–4.5 cm, panicles, axillary and terminal, asymmetrical deltate, alternate branching to verticillate, peduncles 1-4 cm long, rachis glabrous, inflorescence unit monochasium, 11–30 flowers per inflorescence; *bracts* 2–6 × 1–2.5 cm, narrowly triangular, apices acute or acuminate, bases truncate or cuneate, pubescent, caducous, *flowers* sessile or pedicellate, then pedicel 0.4–0.9 mm long, bracteoles 0.9–1.2 × 0.4–0.8 mm, elliptic or triangular to narrowly triangular, caducous, flower bud 3–4 × 1–3 mm, golden-brown, hypanthium extending 0.2 mm above the summit of the ovary, not tearing after anthesis, glabrous to slightly pubescent, calyx tetramerous, lobes free on the bud, lobes 1–1.7 × 1.3–2.1 mm, elliptic or widely ovate, apices apiculate or rounded, bases truncate, puberulent and ciliate; corolla tetramerous, petals white, ca. 2 × 2–3 mm, oblate, apices rounded, bases truncate, ciliate; staminal ring 0.5–1.5 mm wide, 46 stamens, 2.5–4.5 mm filaments long, anthers 0.3–0.5 × 0.4–0.5 mm , widely obovate; style 4.5–5.5 mm long, *Fruit* black, 9.5–13 × 11–13 mm, spheroid, calyx lobes persistent *Seeds* 1-2.

Comments:—*Myrcia riodocensis* can be recognized by its reddish-brown bark, and its tetramerous flower with apiculate and rounded calyx lobes. *Myrcia riodocensis* is closely related to *M. amazonica*. *Myrcia riodocensis* is endemic to the AFD in Espírito Santo and *M. amazonica* is widespread. *Myrcia riodocensis* differs from *M. amazonica* by its elliptic leaves that are thicker (with a tendency to be more coriaceous), and larger than those of *M. amazonica*. Moreover, in *Myrcia riodocensis* the inflorescences tend to be terminal more frequently and present slightly spiral branching (versus inflorescences axillary more frequently and opposite distichous or opposite decussate branching in *M amazonica*), tetramerous (vs. pentamerous) flowers.

Myrcia riodocensis is endemic to Espírito Santo, its distribution is indicated in Figure 34 and the phenology in Figure 35.

Myrcia riodocensis is considered Endangered (EN) by Canteiro and Lucas (2018) according to IUCN criteria (2023).

Specimens examined:—BRAZIL. Espírito Santo: Conceição da Barra, Ribeiro, M. 300 (SAMES!); Linhares, Farias, G.L. 274 (RB!), Folli, D.A. 3197 (CVRD!), Folli, D.A. 3918 (CVRD!), Folli, D.A. 4866 (CVRD!), Gomes, J.M.L. 3888 (VIES!), Gomes, J.M.L. 4000 (VIES!), Siqueira, G.S. 1008 (CVRD!), Siqueira, G.S. 237 (CVRD!), Staggemeier, V. 917 (RB!), Staggemeier, V.G. 917 (CVRD!), Sucre, D. 8269 (MBML!); Pancas, Luber, J. 155 (VIES!).

17. *Myrcia rubiginosa* Cambess. (1832: 300). (Figure 36, 37)

TYPE:—BRAZIL. Rio de Janeiro, 1816-1821, A.F.C. Saint-Hilaire s.n. (holotype, P-161371, isotype MPU-010964, P-0161369, P-00161370)

Treelets or trees, 9 m high. *Trichomes* reddish-brown. *Twigs* reddish-brown, cylindric, sparsely pubescent, mature twigs reddish-brown, cylindric and glabrous. Cataphylls absent. *Leaves* opposite distichous, 2 leaves per node, 8.5–11.5 cm, narrowly elliptic to elliptic, apices acuminate to caudate, bases cuneate, midveins flat adaxially, raised abaxially, 23–25 secondary veins pairs, secondary veins flat adaxially, slightly raised abaxially, intramarginal veins 5–10 mm from the margin, adaxial surface glabrous, abaxial surface slightly pubescent, pellucid dots adaxially; *petioles* ca. 3× 0.8–1 cm, concave adaxially and convex abaxially. *Inflorescences* 10–15.5 cm, panicles, axillary and terminal, asymmetrical deltate, opposite distichous branching, peduncles ca. 2 × 0.9 cm long, rachis tomentose, ca. 55 flowers per inflorescence; *flowers* subsessile to pedicel 5–8 mm long, calyx pentamerous; lobes free in the bud; corolla pentamerous, petals white, circular, glabrous; anthers circular.

Comments:—*Myrcia rubiginosa* is characterized by its elliptic to narrowly elliptic acuminate to caudate leaves and long pedunculate inflorescences, with the inflorescence rachis covered with reddish-brown pubescence.

Myrcia rubiginosa is considered Data Deficient (DD) by Canteiro and Lucas (2019) according to IUCN criteria (2023).

Myrcia rubiginosa occurs in Rio de Janeiro and Espírito Santo, in Brazil, its distribution is indicated in Figure 37.

Specimens examined:—BRAZIL. Espírito Santo: Santa Teresa, Thomaz, L.D. s.n. (RB!).

18. *Myrcia salticola* (Steyermark 1957: 1007) McVaugh (1969: 123).

Aulomyrcia salticola Steyermark (1957: 1007)

TYPE:—VENEZUELA. Bolívar Salto Iwaracaru-meru, Sororopan-tepui, 15 Nov. 1944, J.A. Steyermark 60213 (holotype, F-64766F; isotypes, NY-00386684, U-5149, US-00048591, VEN-37427)

Trees, 4–5 m high. *Trichomes* gray. *Twigs*, cylindric, *internodes* ca. 2 cm long. *Cataphylls* absent. *Leaves* opposite decussate, 2 leaves per node, *leaf blades* 4–7 × 1.5–3.5 cm, elliptic, apices obtuse or rounded, bases cuneate, discolor, dark green adaxially, light green abaxially, chartaceous, midveins slightly raised adaxially, and raised abaxially, 10–12 secondary veins pairs, secondary veins flat on both surfaces, adaxial surface strigillose or glabrous, abaxial surface strigillose; *petioles* 0.4–0.5 cm long, strigillose. *Inflorescences* 5–6.5 cm long, panicles, terminal, triangular, pubescent; calyx pentamerous, lobes free on the bud, widely elliptic, rounded, strigillose. *Fruit* dark-purple, 5–7 mm long, spheroid, calyx lobes persistent.

Comments:— *Myrcia salticola* is only known to us from the type collection, which is characterized by its elliptical leaves with obtuse apices and grayish pubescent inflorescence.

Myrcia salticola is considered Critically Endangered (CR) by IUCN criteria (2023).

19. *Myrcia santateresana* Sobral (2010: 340) (Figure 38, 39)

TYPE:—BRAZIL. Espírito Santo: Santa Teresa, 3 Feb. 1999, L. Kollmann, 1793 (holotype, MBML-9502, isotype BHBC)

Trees, 9–12 m high. *Trichomes* hyaline and simple on inflorescences. *Twigs* and mature twigs ochre to pale yellow, cylindric, 2 branches per node, *internodes* 9.5–10 cm long; *Cataphylls* absent. *Leaves* opposite distichous, 2 leaves per node, *leaf blades* 8–14 ×3.5–5 cm, elliptic to narrowly elliptic, apices acute to acuminate, bases cuneate, discolor, dark brown adaxially and light green abaxially when dried, midveins flat adaxially, and raised abaxially, 12–15 secondary veins pairs, secondary veins flat adaxially and raised abaxially, intramarginal veins 2, inner 3–4 mm (discontinuous), outer 1 mm from the margin, glabrous on both surfaces; *petioles* 0.8–1 × 0.1-0.2 cm. I*nflorescences* ca. 57 × 60 cm, panicles, terminal, widely triangular, opposite decussate branching, peduncles 3.5–10.5. cm long, rachis glabrous, inflorescence units monochasia, ca. 32 flowers per inflorescence. *Bracts* 0.8–0.3 cm long, lanceolate, caducous. *Flowers* sessile or pedicel ca. 0.5 × 0.3 mm long, bracteoles 0.5–0.7 × 0.3 mm, lanceolate, deciduous, flower buds 1.5–2 × 1.5 mm, calyx pentamerous, lobes 1–1.5 × 1–2 mm, triangular to circular, reflexed after anthesis; corolla pentamerous, petals white, ca. 2 × 2 mm, rounded to obovate, ca. 50 stamens, filaments 1.5–1.8 mm long, anthers 0.4–0.2 mm, style 3–4 mm long. *Fruit* 5–6 mm in diameter, spheroid. *Seeds* 1-2.

Comments:—*Myrcia santateresana* is recognized by its ochre yellow pubescence, discolored leaves, and paired long (up to 57 cm) terminal inflorescence.

Myrcia santateresana is endemic to Espírito Santo in Brazil (See Figure 39).

Myrcia santateresana is considered Critically Endangered (CR) by IUCN (2023).

Specimens examined:—BRAZIL. Espírito Santo: Santa Teresa, Kollmann, L. 2153 (MBML!).

20. *Myrcia speciosa* (Amshoff 1950: 5) McVaugh (1969: 106).

Aulomyrcia speciosa Amshoff (1950: 5). TYPE:—GUYANA. 24 Jan. 1943, D.B. Fanshawe 3836 (holotype, K-344368, isotype, U-8496).

Treelet, 5 m high. *Trichomes* white long. *Twigs* dark brown, flattened, *internodes* ca. 20.5 cm long; *Cataphylls absent*. *Leaves* opposite distichous, 2 leaves per node, 12–25 x 7–10 cm, widely elliptic to obovate, apices mucronate, bases cuneate, light green, chartaceous, midveins raised on both surfaces, 13–17 secondary veins pairs, secondary veins flat adaxially, and raised abaxially, intramarginal veins 3–10 mm from the margin, glabrous on both surfaces; *petioles* 1.5–2.3 × 1.6–3 cm, concave adaxially, convex abaxially, glabrous. *Inflorescences* ca. 32 × 12 cm, congested panicles, axillary and terminal, oblong, opposite branching, peduncles ca. 6 cm long, rachis white sericeous, inflorescence unit dichasium, c. 35 flowers per inflorescence, *flowers* sessile, calyx pentamerous, lobes free on the bud, ca. 9 × 10 mm, circular, apices rounded, bases truncate, pubescent on both sides; corolla pentamerous, petals beige, ca. 1.5 × 1.5 mm, apices rounded, bases truncate, staminal ring pubescent, anthers brown. Fruit unknwon.

Comments:—*Myrcia speciosa* can be recognized by its large widely elliptic leaves with raised midveins, intramarginal veins distant from the margin and oblong inflorescences covered by white pubescence.

Myrcia speciosa is considered Critically Endangered (CR) by Canteiro and Lucas (2018) according to IUCN criteria (2023).

Myrcia speciosa is known from records from Guyana and Brazil, Pará. It flowers in January.

Specimens examined:—BRAZIL. Pará: Cachoeira do Arari, Costa-Coutinho, J.M. da P. 83 (MG). Salinópolis, Zoghbi, M.G.B., s.n. (MG). GUYANA, Cuyuni-Mazaruni, K. M. Redden, 2292 (US).

21. ***Myrcia tetraphylla*** Sobral (2010: 152). (Figure 40–42)

TYPE:—BRAZIL. Bahia, Ilhéus, Una, 26 Aug. 1993, J. G. Jardim 265 (holotype, CEPEC-58815, isotype, RB-352625)

Trees, 8 m high. *Trichomes* golden brown, simple, short reflexed or extended. *Twigs* golden brown, flattened to cylindric, pubescent; mature twigs red, cylindric, peeling, *internodes* 4–5 cm long. *Cataphylls* on base of inflorescences, 0.5–1 × 0.5 cm, elliptic, *leaves* verticillate, 4 leaves per node, rarely 2, *leaf blades* 15–21 × 4–6 cm, narrowly elliptic to elliptic, apices caudate, bases narrowly cuneate, discolor, green adaxially, brown abaxially when dried, coriaceous, midveins raised on both surfaces, 22 secondary veins pairs, secondary veins flat to slightly raised on both surfaces, intramarginal veins 2, 3.1–4.8, 0.5–1.0 mm from the margin, glabrous on both surfaces; *petioles* 1.5–2 cm long, plane adaxially, convex abaxially, glabrous (pubescent when leaf is young). *Leaf blades* 8.5–28.5 × 1–6 cm, racemose panicles, terminal, oblong, verticillate branching, peduncles 1.3–1.9 cm long, rachis pubescent, inflorescence unit monochasium, 15–105 flowers per inflorescence; *bracts* 0.1–1.5 × 0.1–0.3 cm, lanceolate to narrowly elliptic, *flowers* sessile to pedicels 0.8 mm long, bracteoles 0.6–1.0 × 0.1 mm, narrowly triangular, persistent, hypanthium extending 0.5 mm above the summit of the ovary, calyx pentamerous, lobes free on the bud, lobes 0.7–1.5 × 0.5–2 mm, very widely ovate or squared, apices rounded or truncate, bases truncate, pubescent abaxially; staminal ring ca. 0.6 mm wide. *Fruit* 8–12 mm, spheroid and lobed, calyx lobes persistent. *Seeds* 1–2.

Comments:—*Myrcia tetraphylla* is recognized by its verticillate phyllotaxy with up to 4 long petiolate leaves per node and terminal, verticillate inflorescences subtended by lanceolate bracts at their bases.

Myrcia tetraphylla distribution is from Espírito Santo to Bahia in Brazil (see Figure 41) and the phenology is indicated in Figure 42.

Myrcia tetraphylla is considered Vulnerable (VU) by IUCN (2023).

Specimens examined:—Nascimento, F.C.G. 10 (RB!), Staggemeier, V. 926 (RB!). BRAZIL. Bahia: Aurelino Leal, Thomas, W.W. 12680 (CEPEC!); Ilhéus, Carvalho, A.M.V. 4810 (CEPEC!), Carvalho, A.M.V. 4951 (CEPEC!), Mori, S.A. 12887 (CEPEC!); Itabuna, Santos, T.S. 1164 (CEPEC!); Porto Seguro, Amorim, A.M. 6436 (CEPEC!);; Una, Amorim, A.M. 1334 (CEPEC!), Amorim, A.M. 1427 (CEPEC!), Amorim, A.M. 2636 (CEPEC!), Jardim, J.G. 265 (CEPEC!), Jardim, J.G. 6 (CEPEC!), Mori, S.A. 11021 (CEPEC!), Pinheiro, R.S. 1681 (CEPEC!), Pinheiro, R.S. 2260 (CEPEC!), Thomas, W.W. 9416 (CEPEC!), Martini, A. 50 (CEPEC!). Espírito Santo: Alegre, Machado, A.F.P. 889 (HUEFS!); Conceição da Barra, Oliveira, A.G. 1145 (SAMES!).

22. *Myrcia zetekiana* (Standl. 1925: 296) B.Holst (2005: 296). (Figure 43)

Eugenia zetekiana Standl. (1925: 296)

Aulomyrcia zetekiana (Standl.) Amshoff (1958: 170). TYPE:—PANAMA. Canal Zone, North Frijoles, 19 Dec. 1923, P.C. Standley 27503 (holotype, US-8153, isotypes, BM-645689)

Shrubs, 2.5–4.5 m high. *Twigs* reddish-brown, tomentose; *internodes* 2–5 cm long. *Cataphylls* between leaf nodes, ca. 0.7 cm, lanceolate. *Leaves* opposite distichous, 2 leaves per node, 30 × 6.5–9.5 cm, lanceolate to narrowly elliptic, apices acuminate or acute, bases rounded, light green, coriaceous, midveins raised on both surfaces, 20 secondary veins pairs, secondary veins adaxially, secondary veins raised on both surfaces, intramarginal veins 2 mm from the margin, glabrous adaxially, tomentose abaxially along midveins; *petioles* 0.6–1.2 cm, tomentose. *Inflorescences* 7–8 cm, panicle, terminal, oblong or narrowly triangular, peduncles 1.5–2 cm long, rachis velutinous with reddish trichomes, 30–60 flowers per inflorescence;

flowers subsessile, hypanthium extending ca. 0.3 mm above the summit of the ovary, calyx pentamerous, lobes partially fused before anthesis, widely elliptic, apices rounded. *Fruit* 1.5–1.8 mm, ellipsoid, calyx lobes persistent. *Seeds* 2.

Comments:—*Myrcia zetekiana* is identified by its large leaves (up to 30 cm), large flowers (*ca.* 0.5 cm) and pubescent fruit.

Myrcia zetekiana occurs in the Central American Isthmian & Colombian Coastal Forests Bioregion (One Earth 2023).

Myrcia zetekiana is considered Near Threatened (NT) by IUCN (2023).

Specimens examined:—COLOMBIA. Segovia-Antioquía: El Río, Renteria, E. 1590 (HUA!).

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Supplemental material

Collector list

(1) *Myrcia amazonica*, (2) *Myrcia areolata,* (3) *Myrcia badia*, (4) *Myrcia clavija,* (5) *Myrcia colpodes,* (6) *Myrcia eumecephylla*, (7) *Myrcia gigantea*, (8) *Myrcia hexasticha*, (9) *Myrcia insularis*, (10) *Myrcia liesneri*, (11) *Myrcia magna*, (12) *Myrcia neodimorpha,* (13) *Myrcia neoverticillaris,* (14) *Myrcia obversa,* (15) *Myrcia pyrifolia,* (16) *Myrcia riodocensis*, (17) *Myrcia rubiginosa,* (18) *Myrcia salticola*, (19) *Myrcia santateresana,* (20) *Myrcia speciosa*, (21) *Myrcia tetraphylla*, (22) *Myrcia zetekiana.*

Acevedo-Rdgz., P. 8059 (16) Almeida, K. 17 (9) Amaral, I.L. 431 (16) Amorim, A.M. 1334 (20); 1427 (20); 2636 (20); 6436 (20); 8324 (15); 8354 (1) Anderson, W.R. 36249 (1) Antar, G.M. 1761 (1) Araujo, D. 5614 (15) Assis, A.M. 562 (15) Assis, A.M. 3516 (6) Aymard, G. 8182 (10) Barboza, E. 3977 (1) Bautista, H.P. 3087 (11) Belém, R.P. 1395 (15); 2619 (1); 2695 (6) Betancur, J. 17830 (1) Calao, V.Y.P. s.n. (1) Campbell, D.G. P22420 (16) Cardona N., F. 1757 (1) Cardoso, D. 341 (1) Carvalho 4810 (20); 4951 (20) Carvalho-Sobrinho, J.G. 1096 (11); 1481 (11) Carvalho, A. M. 4810 (9) Carvalho, A.M. 1011 (1); 2143 (1); 4145 (1); 4147 (1); 4172 (1) Castro, R.M. 658 (4) Clark, H.L. 7485 (11) Coelho, D. 59 (11); s.n. (11) Cordeiro, J. 108 (1) Costa, G. 100 (1); 2329 (1) Costa-Coutinho, J.M. da P. 83 (20) Couto, D.R. 997 (12) Daly, D.C. 6733 (1); Demuner, V. 1329 (6); 2784 (6) Dionisio s.n. (11) Dreveck, S. 1200 (1) Espina, J. 2871 (1) Euponino, A. 307 (1) Eupunino, A. 95 (1) Faria, P.C.L. 118 (4) Farias, G.L. 250 (15); 274 (17) Farney, C. 12268 (16); 1887 (1) Fávero, O.A. 355 (8); s/n (8) Fernandes, T. 918 (18) Ferreira, C.A.C. 11849 (16); 13167 (11); 6770 (11); 9531 (1); 9534 (1) Ferreira, C.A.C. 6963 (1) Flores, T.B. 956 (15) Folli, D.A. 1067 (15); 2438 (1); 319 (13); 3197 (17); 34 (1); 3918 (17); 4032 (1); 4277 (15); 4861 (15); 4866 (17); 5747 (12); 5750 (6); 5808 (1); 6168 (15); 6250 (1); 6414 (6); 6430 (15); 6649 (12); 6657 (15); 6885 (6); 6929 (6); 7140 (6); 7271 (6); 880 (1); 963 (1) Fonseca, R.B.S. 39 (1) Fonseca, W.O. 411 (1) Fontana, A.P. 1720 (6) Forzza, R.C. 5138 (6) França, F. 3063 (1) Funch, L.S. 1046 (1); 1537 (1); 923 (1) Funch, R. 200 (1) Galeano 353 (1) Ganev, W 2585 (1) Garcia, S. 254735 (16) Gasson, P. 6103 (1) Gentry, A. 12863 (11) Giaretta, A.O. 1040 (1); 1159 (15); 1351 (15) Glaziou, A. 1880 (5); s.n. (5) Gomes, F.S. 1378 (15); 1653 (15) Gomes, J.M.L. 1320 (1); 3381 (9); 3419 (9); 3888 (17); 4000 (17); 4266 (15) Guedes, M.L. 13262 (1); 14822 (1); 16922 (1); 4245 (1); 5480 (1); 5489 (1); 9356 (1) Hage, J.L. 1299 (7); 1344 (15); 2144 (7)

Haidar, R.F. 1224 (11) Harley, R.M. 15646 (1); 50115 (1); 50236 (1); 50330 (1) Hatschbach, G. 13139 (8); 45773 (8); 50835 (8); 58026 (9); 64003 (1); 71530 (15); 72725 (8) Jardim, J.G. 1837 (15); 214 (15); 2264 (15); 265 (20); 6 (20) Jesus, M.C.F. 310 (6) Jesus, N.G. 256 (1) Kinupp, V.F. 4946 (11) Kollmann, L. 2153 (19) Kummrow, R. 2067 (1) Liene 3914 (5) Liesner, R. 10343 (1) Lima, D.F 609 (1) Lopes, J.C. 286 (1) López A., N. 849 (1) Luber, J. 155 (17); 196 (9) Lucas, E.J. 194 (8) Maas, P.J.M. P12652 (1) Macedo, M. 730 (1) Machado, A.F.P. 889 (20) Magnago, L.F.S. 1067 (6); 1689 (9); 736 (6) Maia, L.A. 456 (16) Manhães, V.C. 102 (12); 106 (12) Martini, A. 50 (20) Martins, R.F.A. 95 (15) Matsumoto, K. 803 (6); 820 (15) Matta, A. 58 (16) Mattos-Silva, L.A. 2513 (15); 4593 (15); 4990 (11) Mattos Silva, L.A. 1513 (9) Mattos, J. 10083 (1); 13886 (12) Mehlig, U. 1389 (1) Mello, A.S. 713 (1) Mello, E. PCD 1673 (1) Mello, F. 3 (11); s.n. (1) Menezes, L.F.T. s.n. (6) Miralha, J.M.S. 138 (11) Miranda, F.E. 405 (1); 425 (1); 435 (1) Monteiro, M.T. 23545 (7); 23568 (1) Mori, S.A. 10155 (15); 10837 (14); 11021 (20); 11285 (1); 12079 (9); 12887 (20); 14129 (15) Mota, C. 227 (1) Muniz, F.H. 392 (1) Nascimento, F.C.G. 10 (20) Nascimento, L.M. 188 (1); 464 (1); 468 (1); 486 (1) Oliveira, A.G. 1145 (20); 30 (15); 644 (15) Oliveira, E. 442 (1); 730 (1) Oswaldo, D. 802 (1) Paganucci, L. 92 (1) Paixão, J.L. 292 (7) Perdiz, R.O. 2091 (16); 2191 (16); 2251 (16); 2293 (16) Pereira-Silva, G. 13547 (1) Pereira, O.J. 1536 (15); 4305 (15); 4339 (12); 5187 (1); 5812 (1); 6222 (15); 6256 (12) Pereira, P.A. 586 (16) Peres, A.L.S.S. 339 (15) Perigolo, N.A. 217 (1) Person, V.G. s/n (8) Pessoa, S.V.A. 1217 (8); 965 (15); 969 (15); 977 (15) Pinheiro, R.S. 1013 (14); 1681 (20); 2138 (1); 2260 (20) Piotto, D. 3156 (15) Prance, G.R. 3714 (11); 3758 (11); 4841 (1) Proença, C. 3546 (1) Ramos, J.F. 2938 (1) Ramos, M.B. 454 (2) Redden, K. M. 2292 (20). Renteria, E. 1590 (21) Revilla, J. 8284 (1) Ribamar, J. 171 (1) Ribeiro, M. 294 (6); 300 (17); 642 (15) Rocha, G.P.E. 194 (1) Rodrigues, W. 1615 (16); 1681 (1); 2224 (1); 3550 (11); 4004 (11); 4101 (11); 4119 (11); 4361 (11); 4623 (1); 4654 (1); 4796 (11); 6018 (1); 8644 (11) Roldán, R. 1188 (1) Roque, N. 933 (1) Rosas Junior, A. 267 (11) Rozza, A. 309 (1) Sant'Ana, S.C. 339 (15) Santos, D.L. 51 (1) Santos, M.F. 757 (1) Santos, R.B. 46 (1); 51 (1) Santos, T.S. 1164 (20); 1619 (9); 2014 (6); 3783 (15); 911 (7); 928 (9) Saporetti, A.M.J. 81 (15) Sartori, A.L.B. 263 (9) Sasaki, D. 1280 (16) Schütz Rodrigues 2641 (16) Sedulsky, T. 1169 (1) Sellow, F. s.n. (18) Semir, J. 4710 (1) Sendulsky, T. 1169 (1) Setz, E. 990 (11) Silva, A.G. 48 (1) Silva, I.A. 2 (15) Silva, J.A.C. 1480 (11) Silva, J.M. 1615 (1) Silva, L.A. 12 (1); 308 (1); 517 (9) Silva, M.F. 1377 (16) Silva, M.F. 1263 (16); 1678 (16) Silva, M.G. 5379 (1) Silva, S.M. (8) Siqueira, G.S. 1190 (13); 1209 (6); 121 (6); 997 (15) Siqueira, G.S. 1008 (17); 237 (17) Soares, E. 240 (16); 80 (11) Solomon, J.C. 6395 (11) Souza, V. 167 (15); 344 (1) Stadnik, A. 14 (1); 19 (1); 48 (1);

55 (1) Staggemeier, V. 109 (1); 917 (17); 926 (20) Staggemeier, V.G. 917 (17) Stehmann, J.R. s.n. (1) Stevenson, D.W. 969 (16) Sucre, D. 8269 (17) Tessmann, G. 1015 (8) Thomas, W.W. 12680 (14); 9416 (20) Thomaz, L.D. 490 (15); s.n. (19) Tobón-Juan Pablo 1630 (1) Torres, J.E.L. s.n. (1) Uller, H.E. 576 (1) Uribe, L. 4263 (1) Velásquez-Rúa, C. 5473 (1) Vervloet, R.R. 2730 (6); 2991 (6); 3411 (6) Vicentini, A. 704 (1) Vieira, M.G. 930 (1) Vimercat, J.M. 167 (6) Wagner, M.A. 212 (1); 237 (11); 239 (1); 240 (1); 241 (1); 242 (1); 291 (1); 348 (13) Willian s.n. (11) Zambom, O. 141 (15) Zarucchi, J.L. 3051 (11) Zoghbi, M.G.B., s.n. (20).

Tables and Figures

TABLE 1 Species of the Verticillate Group, indicating to which subclade they pertain to and the phytogeographic domain in which they occur.

Species	**Subclade**	**Phytogeographic domain**
***Myrcia amazonica* DC.**	G	Widespread in the neotropical region
***Myrcia areolata* (McVaugh) E.Lucas & C.E.Wilson**	F	Amazon
***Myrcia badia* (O.Berg) N.Silveira**	F	Unknown
***Myrcia clavija* Sobral**	F	Atlantic Forest
***Myrcia colpodes* Kiaersk.**	F	Atlantic Forest
***Myrcia eumecephylla* (O.Berg) Nied.**	F	Atlantic Forest
***Myrcia gigantea* (O.Berg) Nied.**	F	Atlantic Forest
Myrcia hexasticha* Kiaersk	F	Atlantic Forest
***Myrcia insularis* Gardner**	F	Atlantic Forest
***Myrcia liesneri* B.Holst**	F	Amazon
***Myrcia magna* D. Legrand**	G	Amazon
Myrcia neodimorpha* E.Lucas and C.E.Wilson		Atlantic Forest
***Myrcia neoverticillaris* E.Lucas and C.E.Wilson**	F	Atlantic Forest
***Myrcia obversa* (D. Legrand) E.Lucas and C.E.Wilson**	F	Atlantic Forest
***Myrcia pyrifolia* (Desv. ex Ham.) Nied.**	G	Amazon
***Myrcia riodocensis* G.M.Barroso & Peixoto**	G	Atlantic Forest
***Myrcia rubiginosa* Cambess.**	G	Atlantic Forest
***Myrcia salticola* (Steyerm.) McVaugh**	G	Amazon
***Myrcia santateresana* Sobral**	G	Atlantic Forest
***Myrcia speciosa* (Amshoff) McVaugh**	F	Amazon
***Myrcia tetraphylla* Sobral**	F	Atlantic Forest
***Myrcia zetekiana* (Standl.) B.Holst**	F	Isthmian-Atlantic Moist Forest (Panama)

Table 2. Key diagnostic characteristics for species of clades F, G and *Myrcia neodimorpha* of the Verticillate Group.

	Myrcia neodimorpha	**Clade F**	**Clade G**
Indumentum	Cataphylls, inflorescence rachis and bracts with whitish or golden-brown pubescence.	Sparsely pubescent to glabrescent on leaves. Young stems not pubescent Indumentum usually on the inflorescence rachis and bracts, that can be red or white.	Reddish indumentum sparse on the leaves but tomentose on young stems and inflorescence rachis throughout the plant
Petioles	Inconspicuously corky and smooth	Corky and peeling	Inconspicuously corky and smooth
Phyllotaxy	Opposite decussate	Opposite decussate or verticillate	Opposed distichous
Leaf midvein	Flat	Raised	Flat
Cataphylls	Present on inflorescences bases and between leaf nodes	Present on inflorescences bases	absent
Inflorescence	Inflorescence with verticillate branching	Inflorescence with verticillate branching	Inflorescences with alternate branching

FIGURE 1. Distribution of *Myrcia* sect. *Aulomyrcia*: the Verticillate Group species (records depicted by dark dots). Continuous lines represent South American countries boundaries. The color gradient represents elevation.

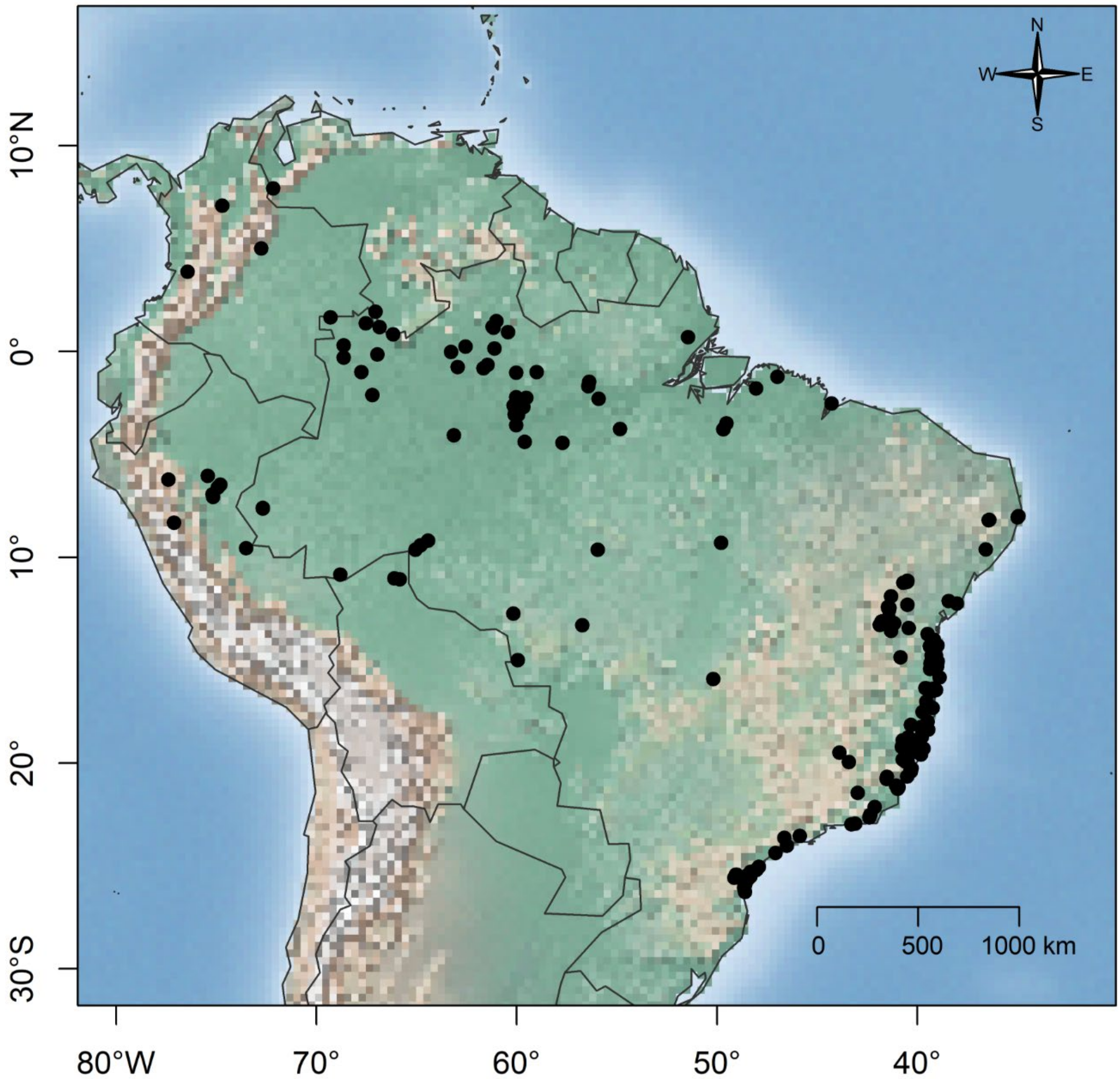


FIGURE 2 Image of representative specimen of *Myrcia amazonica* (Stadnik, A. 48 ALCB).

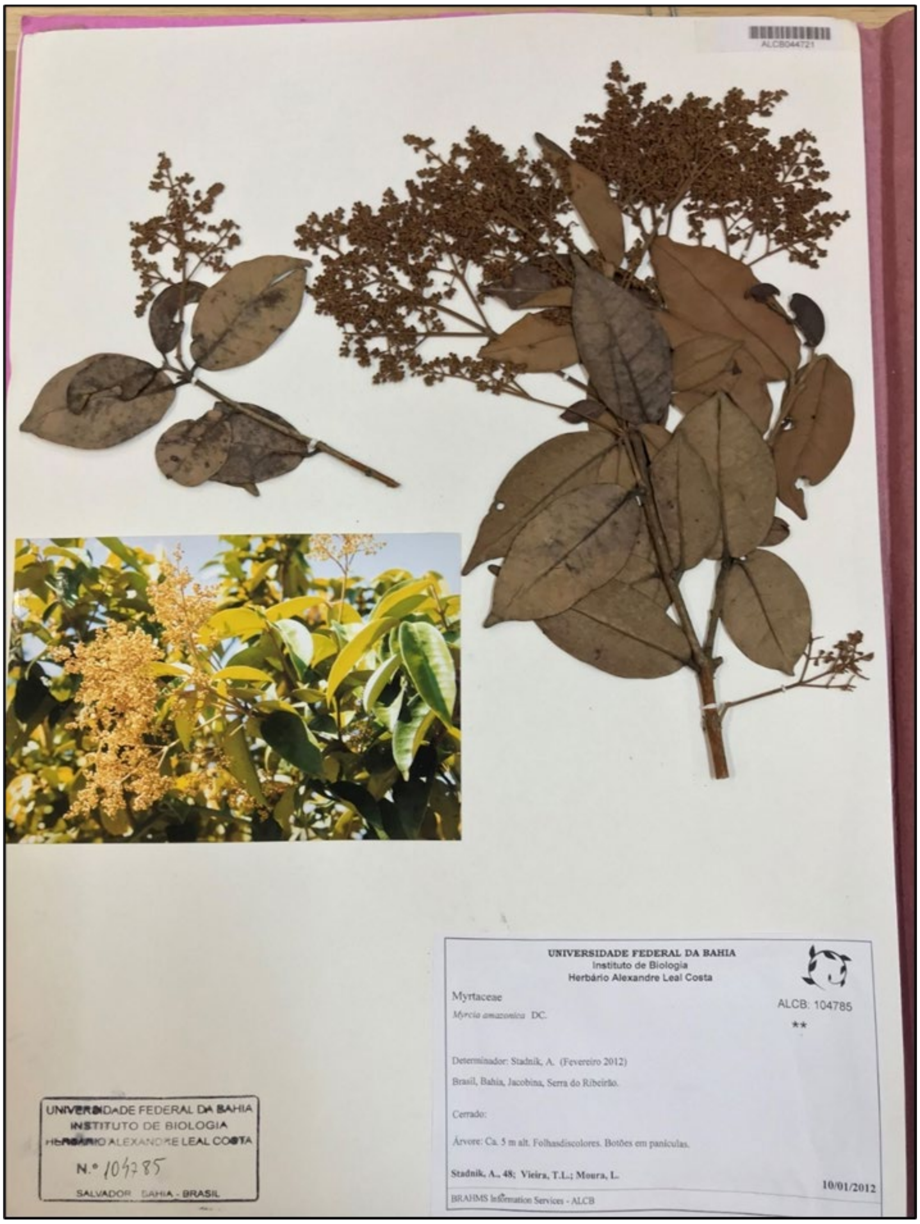


FIGURE 3: Distribution of *Myrcia amazonica* (white dots). Continuous lines represent South American countries and Brazilian states. The grey gradient represents elevation.

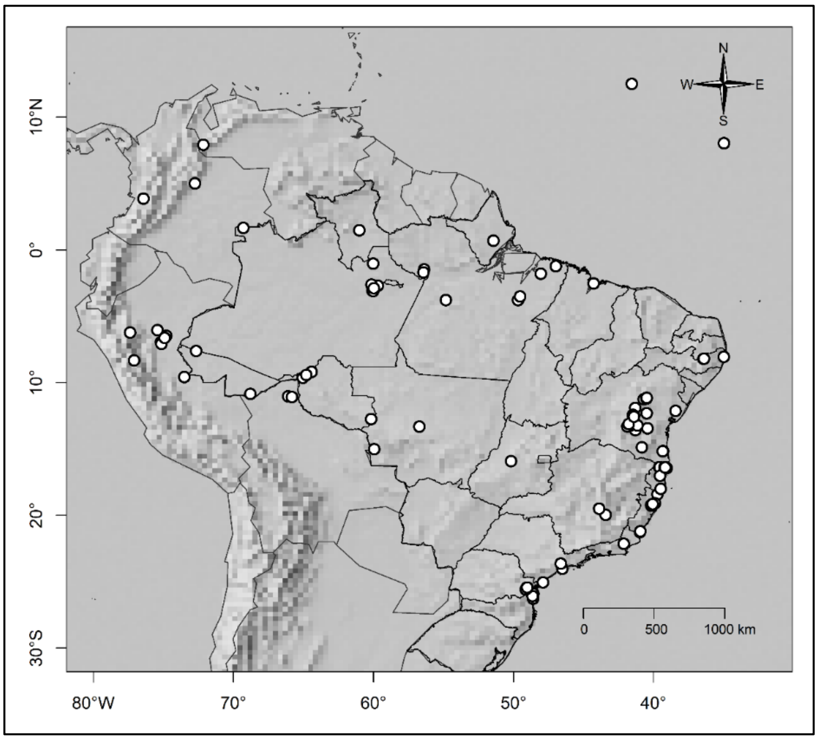


FIGURE 4: Phenology graph of *Myrcia amazonica* (sampling - n=144, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

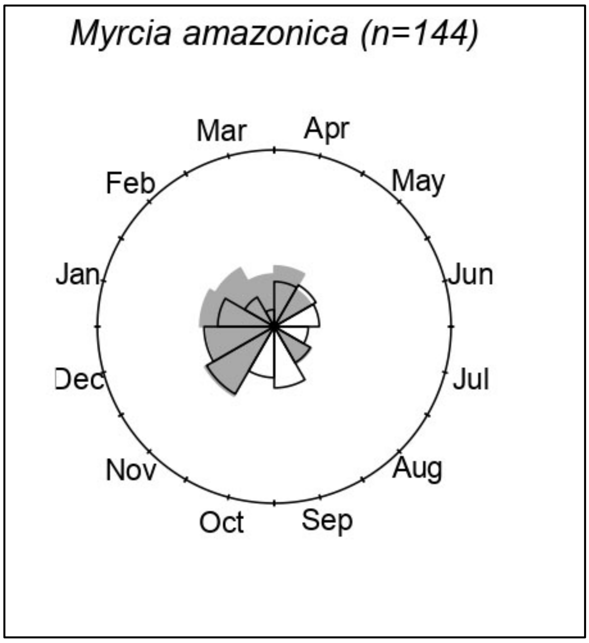


FIGURE 5. Image of representative specimen of *Myrcia clavija* (Paratype: Castro, R.M. 658 CESJ)

FIGURE 6 Image of representative specimen of *Myrcia eumecephylla* (Folli, D.A. 5750 CVRD).

FIGURE 7: Distribution of *Myrcia eumecephylla* (white dots). Continuous lines represent Brazilian States. The grey gradient represents elevation.

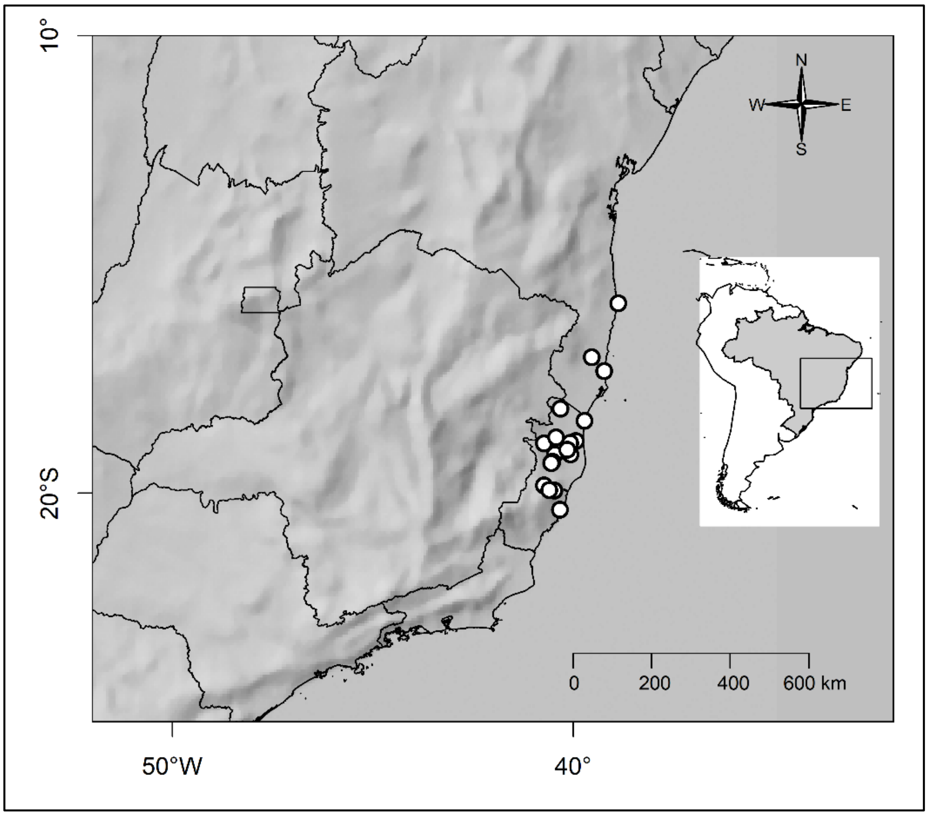


FIGURE 8: Phenology graph of *Myrcia eumecephylla* (sampling n=25, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

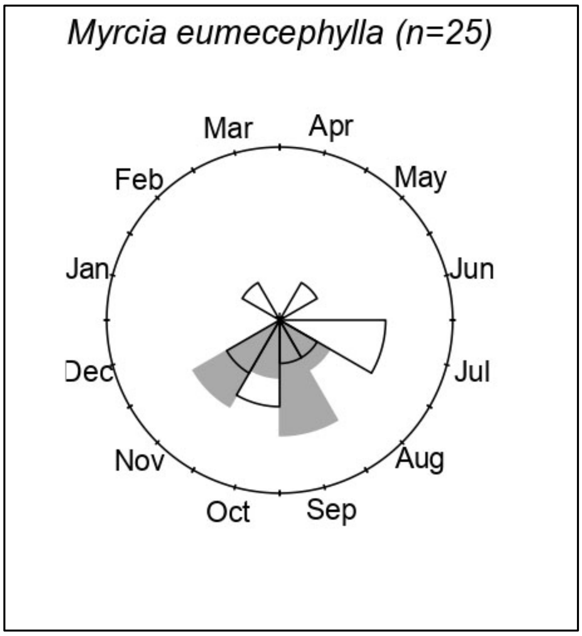


FIGURE 9: Image of representative specimen of *Myrcia gigantea* (holotype: Martius M-0136802).

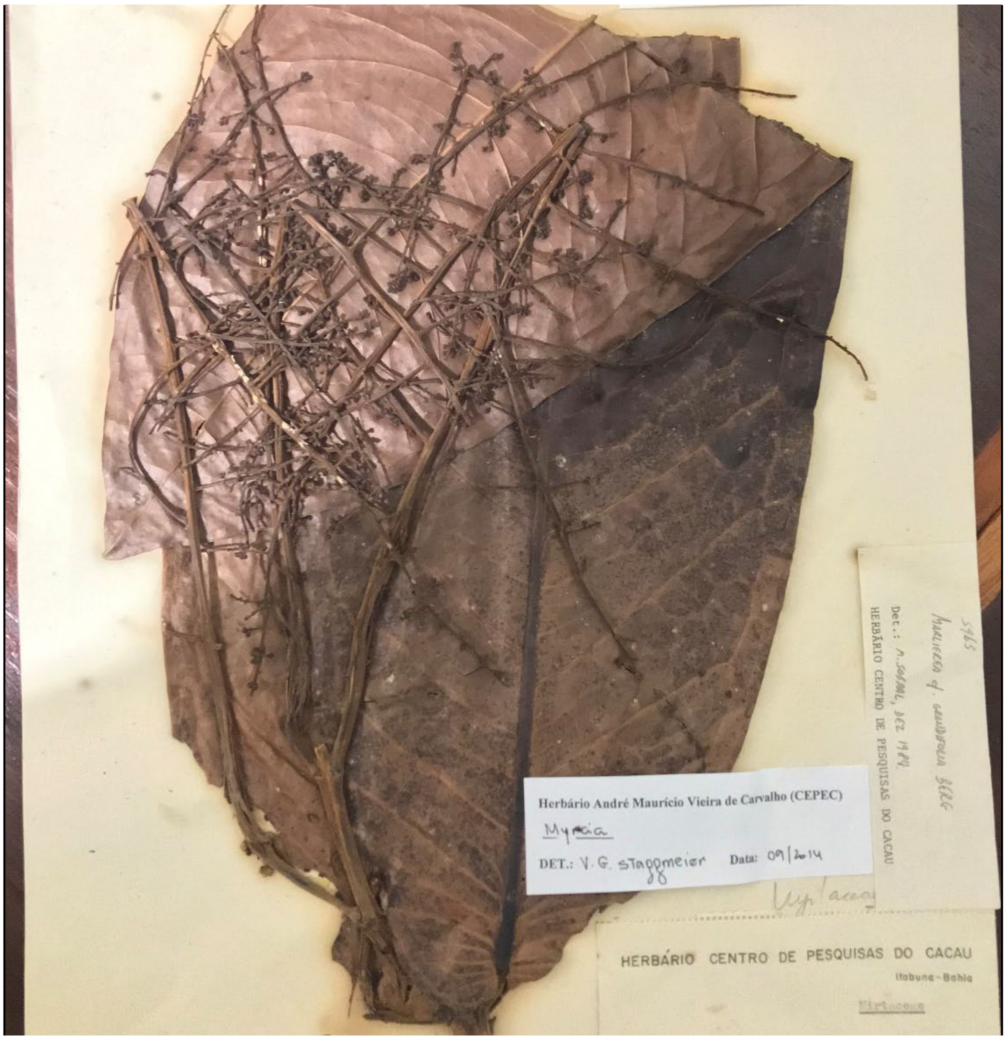


FIGURE 10: Distribution of *Myrcia gigantea* (white dots). Continuous lines represent South American countries. The grey gradient represents elevation.

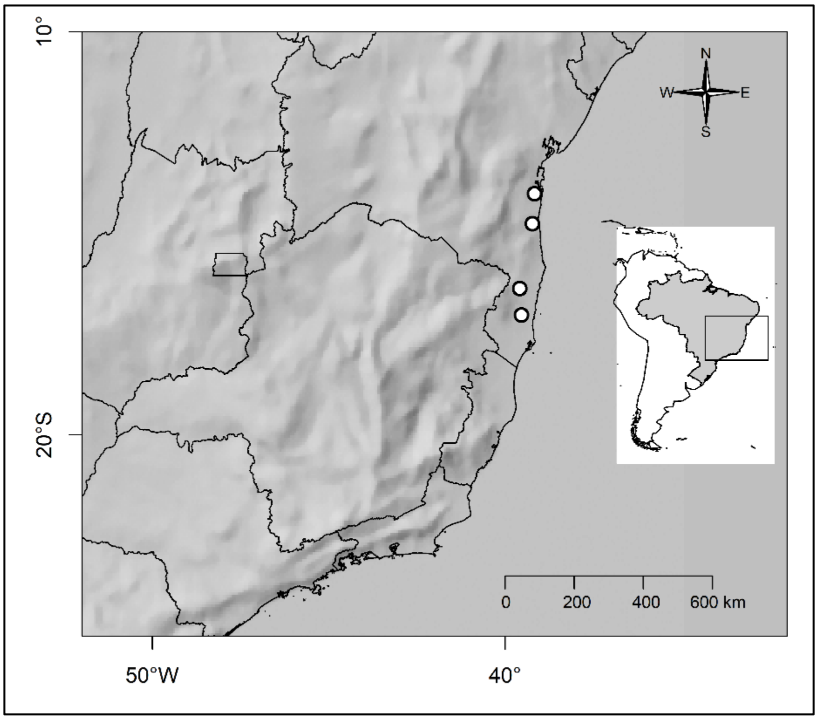


FIGURE 11: Phenology graph of *Myrcia gigantea* (sampling n=5, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

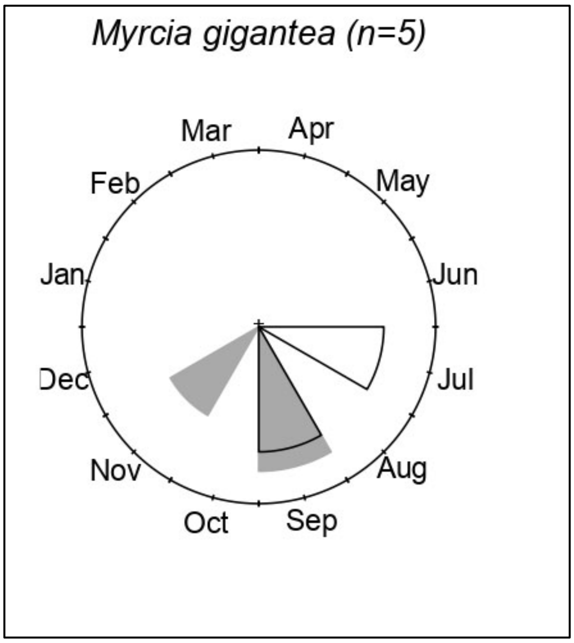


FIGURE 12: Image of representative specimen of *Myrcia hexasticha* (Silva, J.M. 194, HUEM).

FIGURE 13: Distribution of *Myrcia hexasticha* (white dots). Continuous lines represent South American countries. The grey gradient represents elevation.

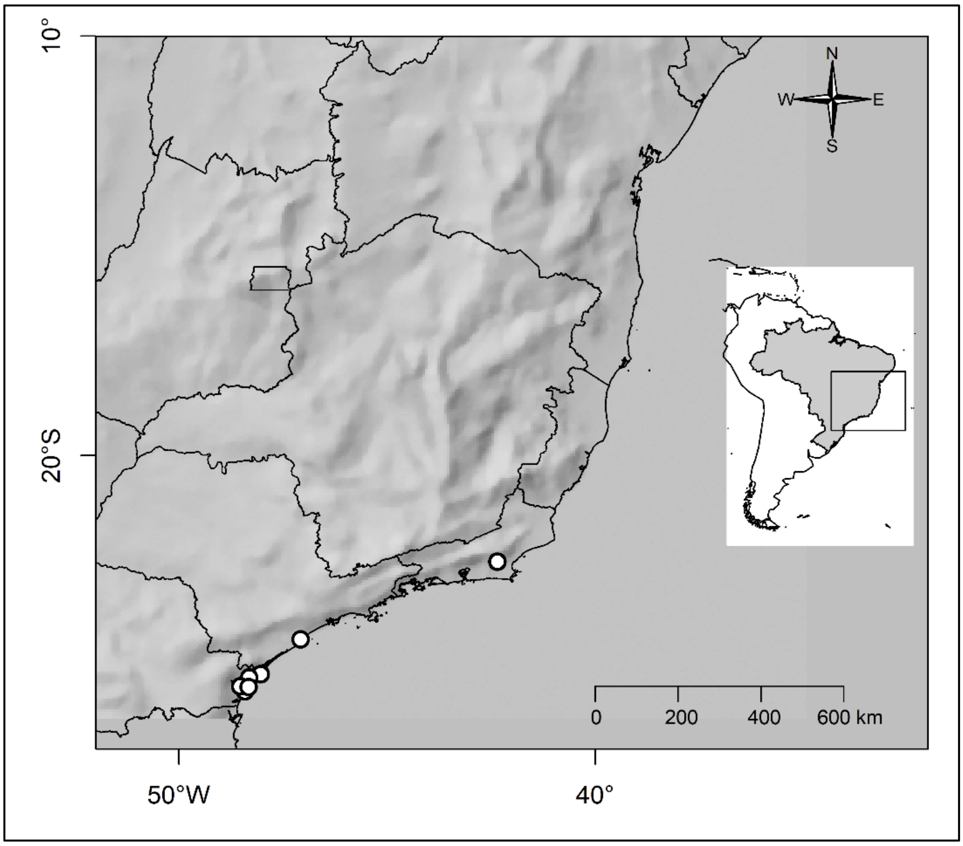


FIGURE 14: Phenology graph of *Myrcia hexasticha* (sampling n=11, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

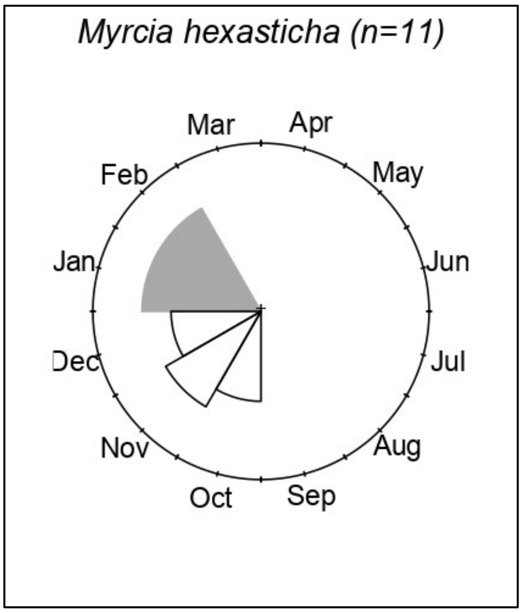


FIGURE 15: Image of representative specimen of *Myrcia insularis* (Gomes, J.M.L. 3419 VIES).

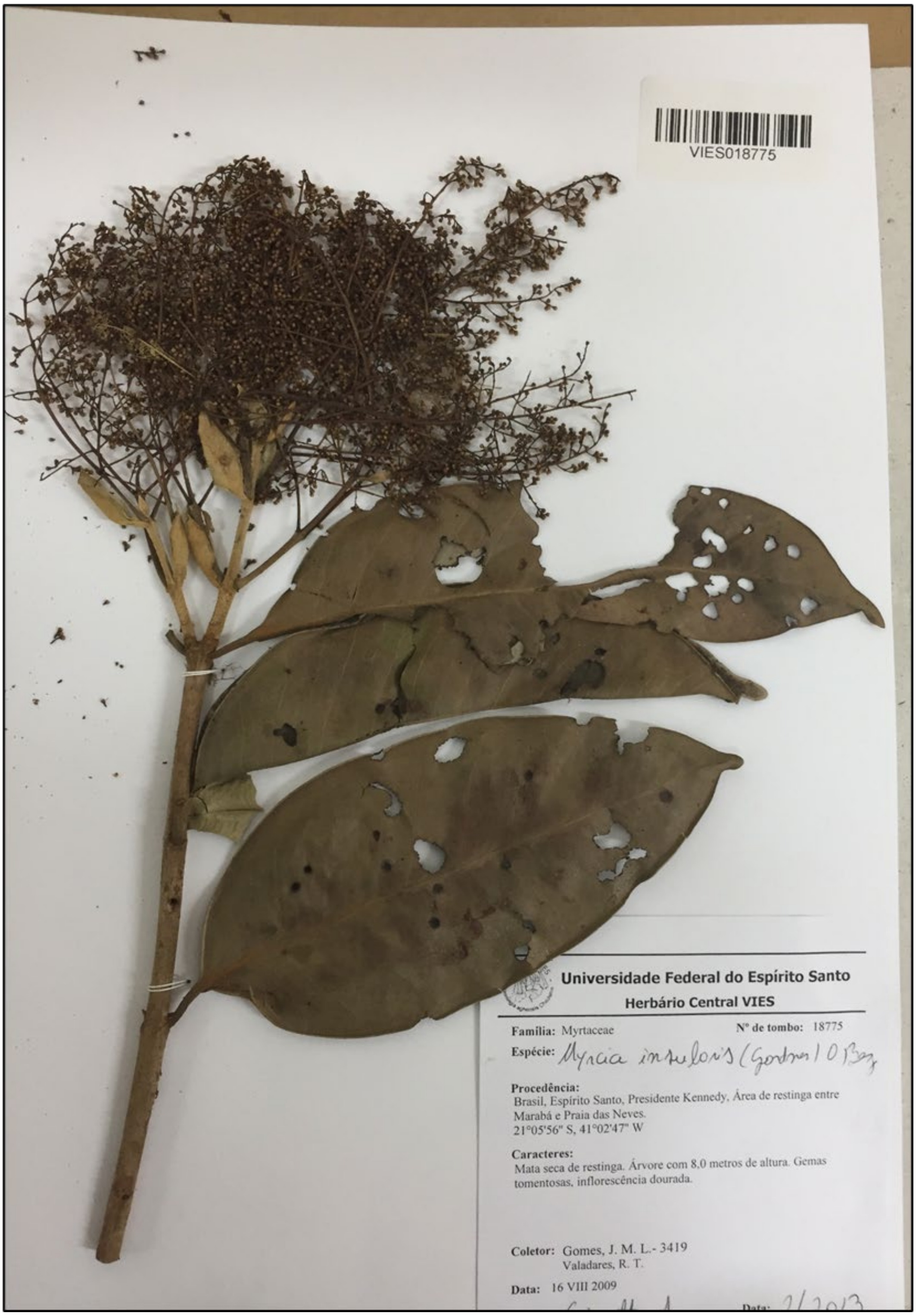


FIGURE 16: Distribution of *Myrcia insularis* (white dots). Continuous lines represent South American countries. The grey gradient represents elevation.

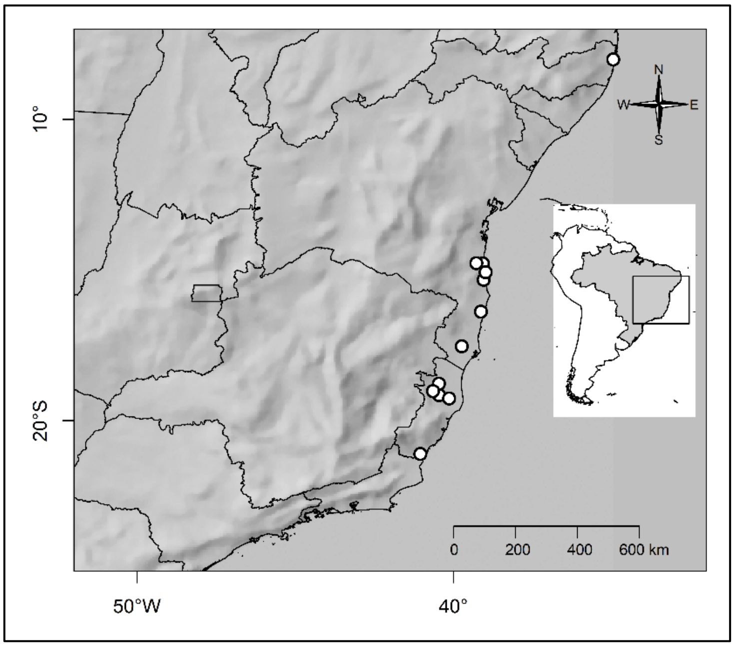


FIGURE 17: Phenology graph of *Myrcia insularis* (sampling n=13, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

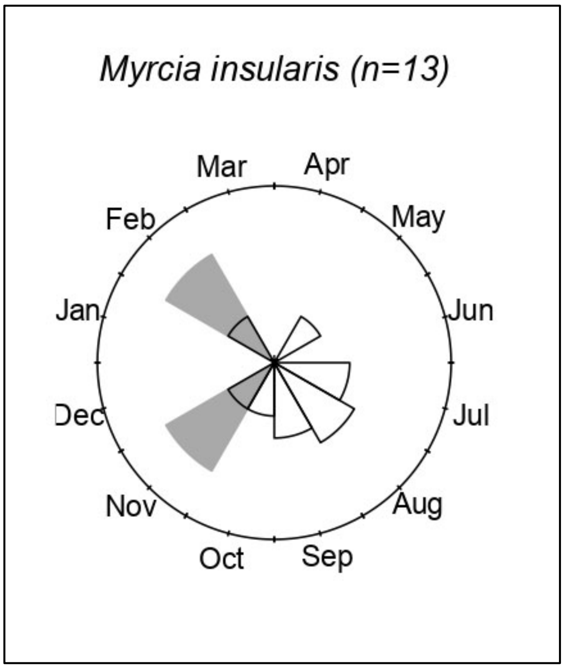


FIGURE 18: Image of representative specimen of *Myrcia magna* (Rodrigues, W. 344 INPA).

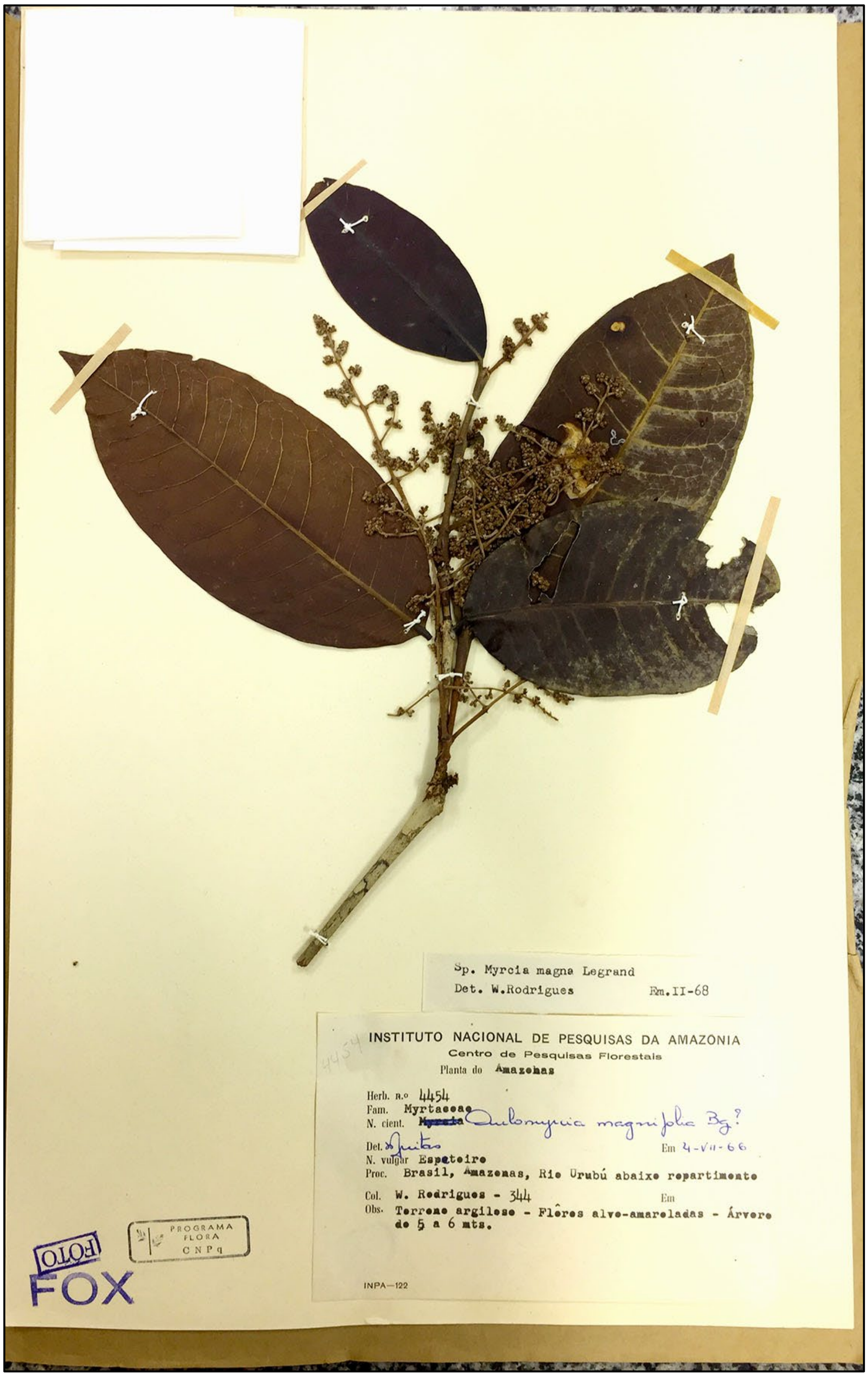


FIGURE 19: Distribution of *Myrcia magna*(black dots). Continuous lines represent South American countries. The grey gradient represents elevation.

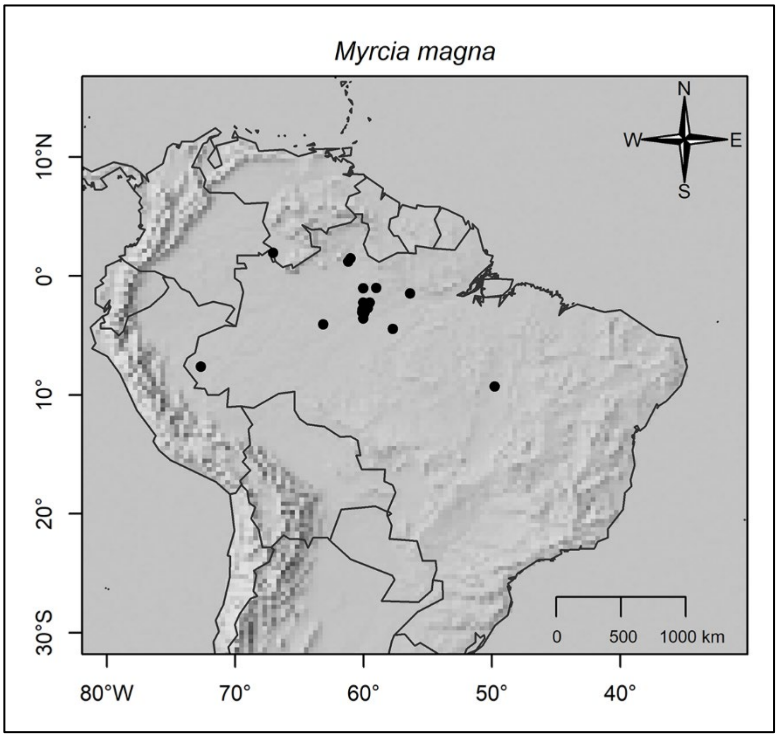


FIGURE 20: Phenology graph of *Myrcia magna* (sampling n=29, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

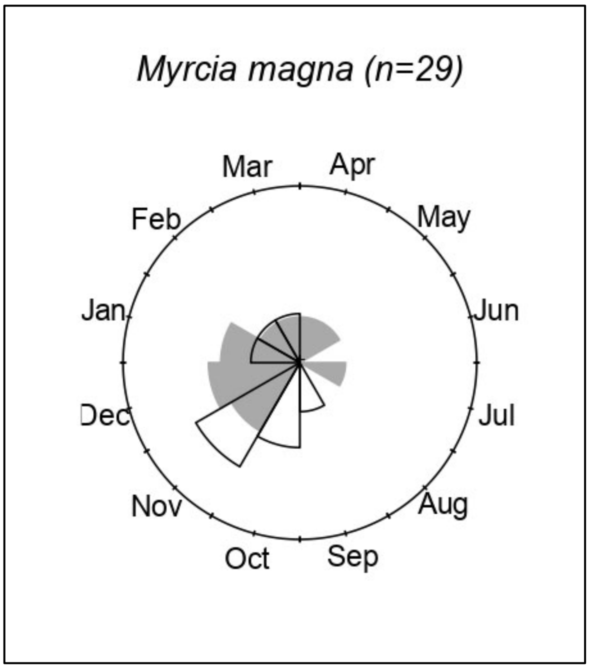


FIGURE 21: Image of representative specimen of *Myrcia neodimorpha* (Manhães, V.C. 106 MBML).

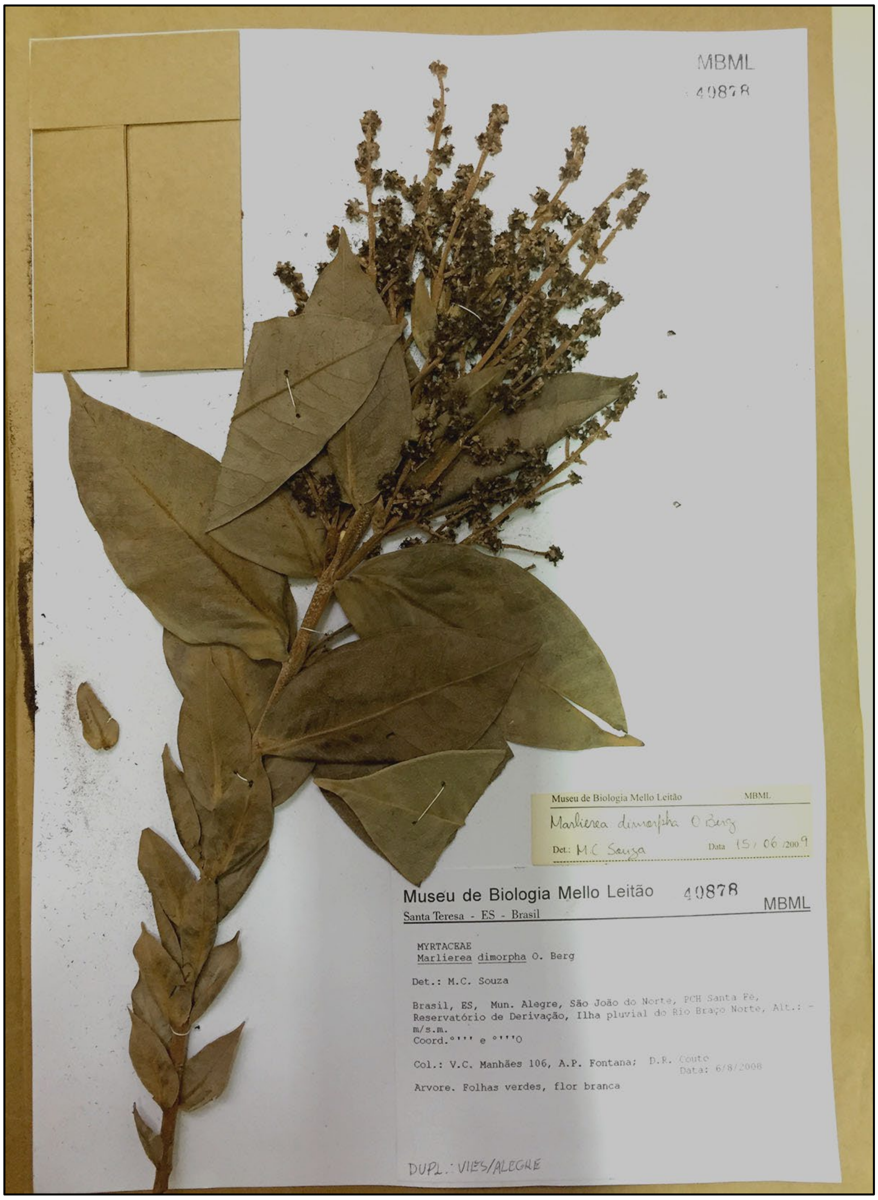


FIGURE 22: Distribution of *Myrcia neodimorpha* (white dots). Continuous lines represent South American countries. The grey gradient represents elevation.

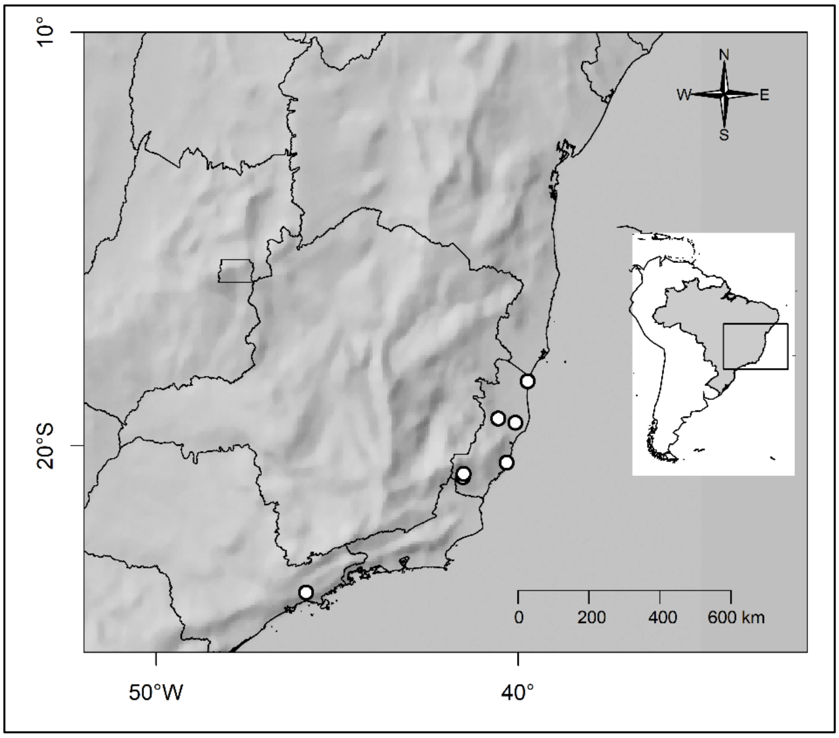


FIGURE 23: Phenology graph of *Myrcia neodimorpha* (sampling n=9, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

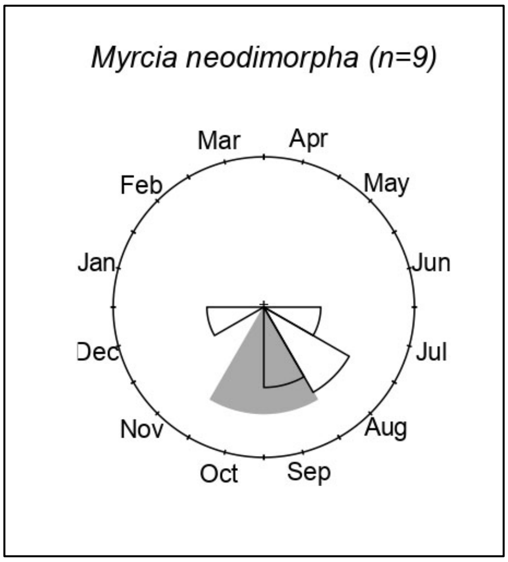


FIGURE 24: Image of representative specimen of *Myrcia neoverticillaris* (Thomas, W.W. 12680 RB).

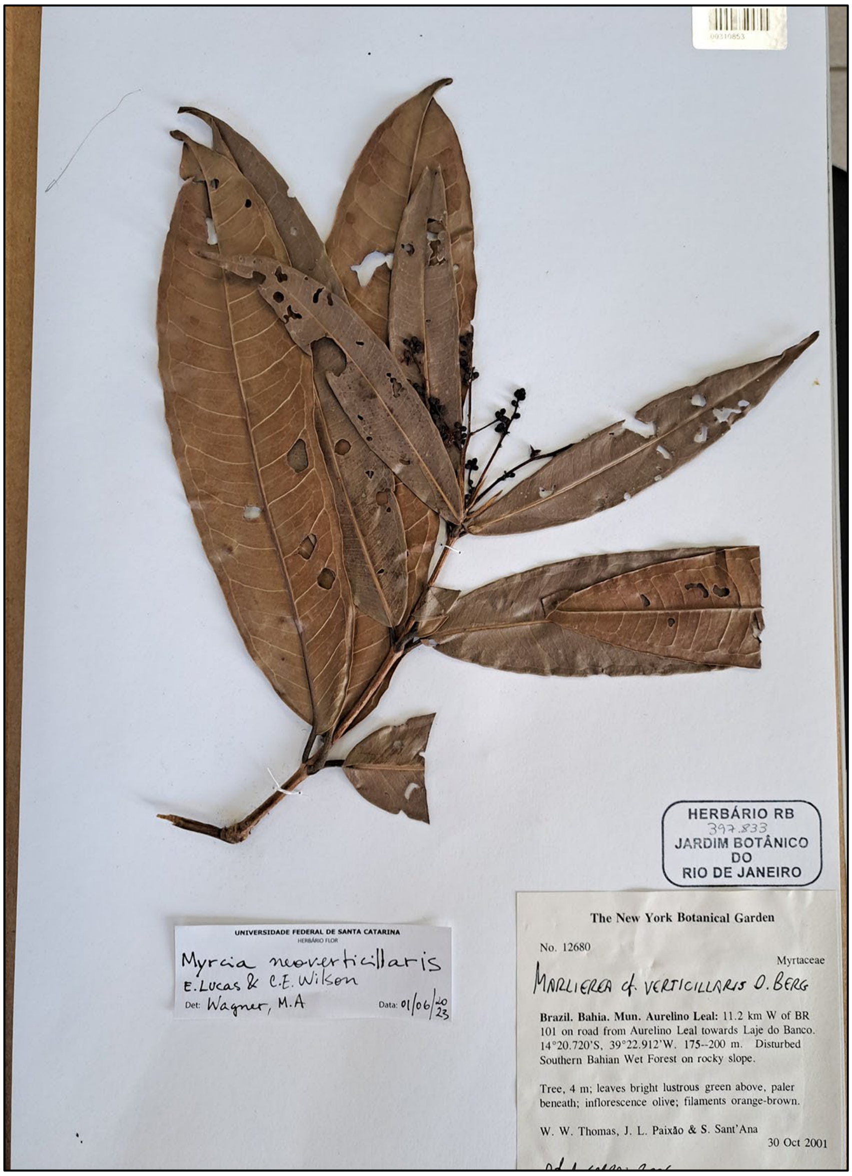


FIGURE 25: Distribution of *Myrcia neoverticillaris* (white dots). Continuous lines represent South American countries. The grey gradient represents elevation.

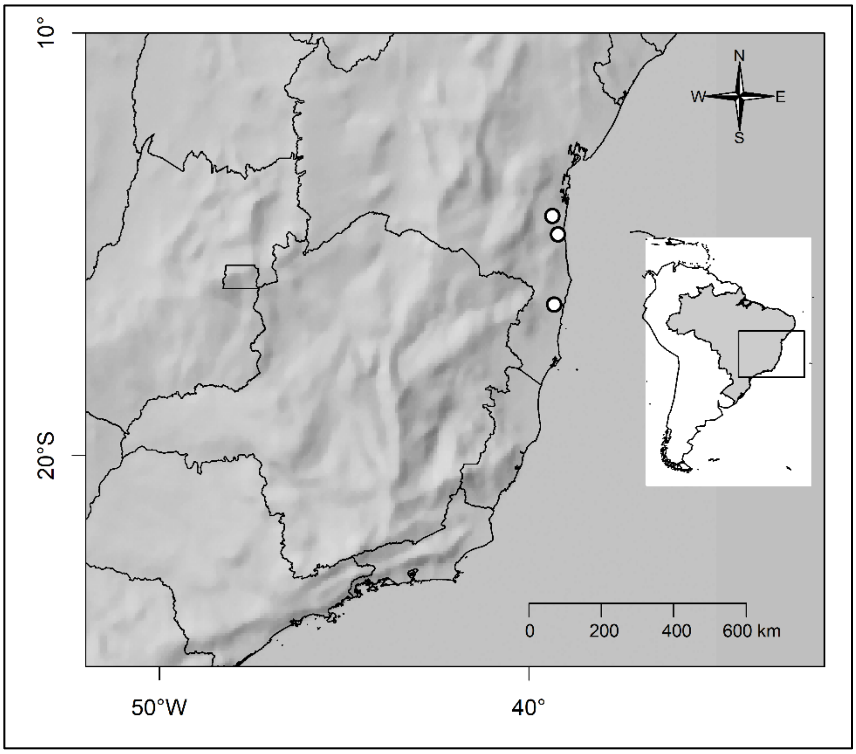


FIGURE 26: Phenology graph of *Myrcia neoverticillaris* (sampling n=3, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

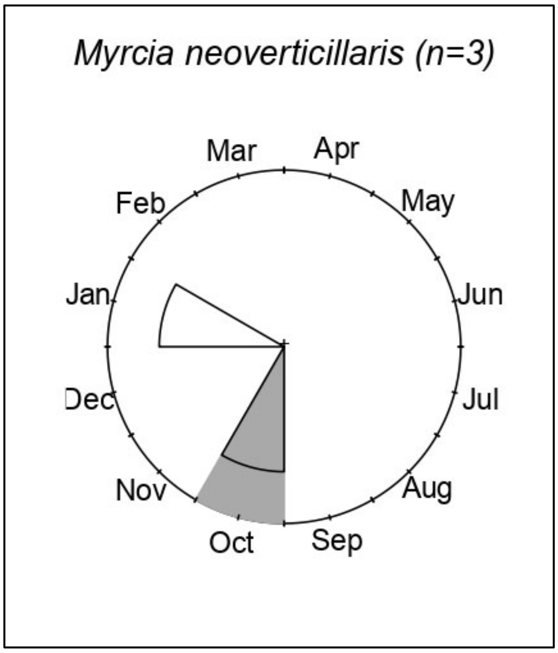


FIGURE 27: Image of representative specimen of *Myrcia obversa* (holotype: Piotto, D. 3156 CEPEC).

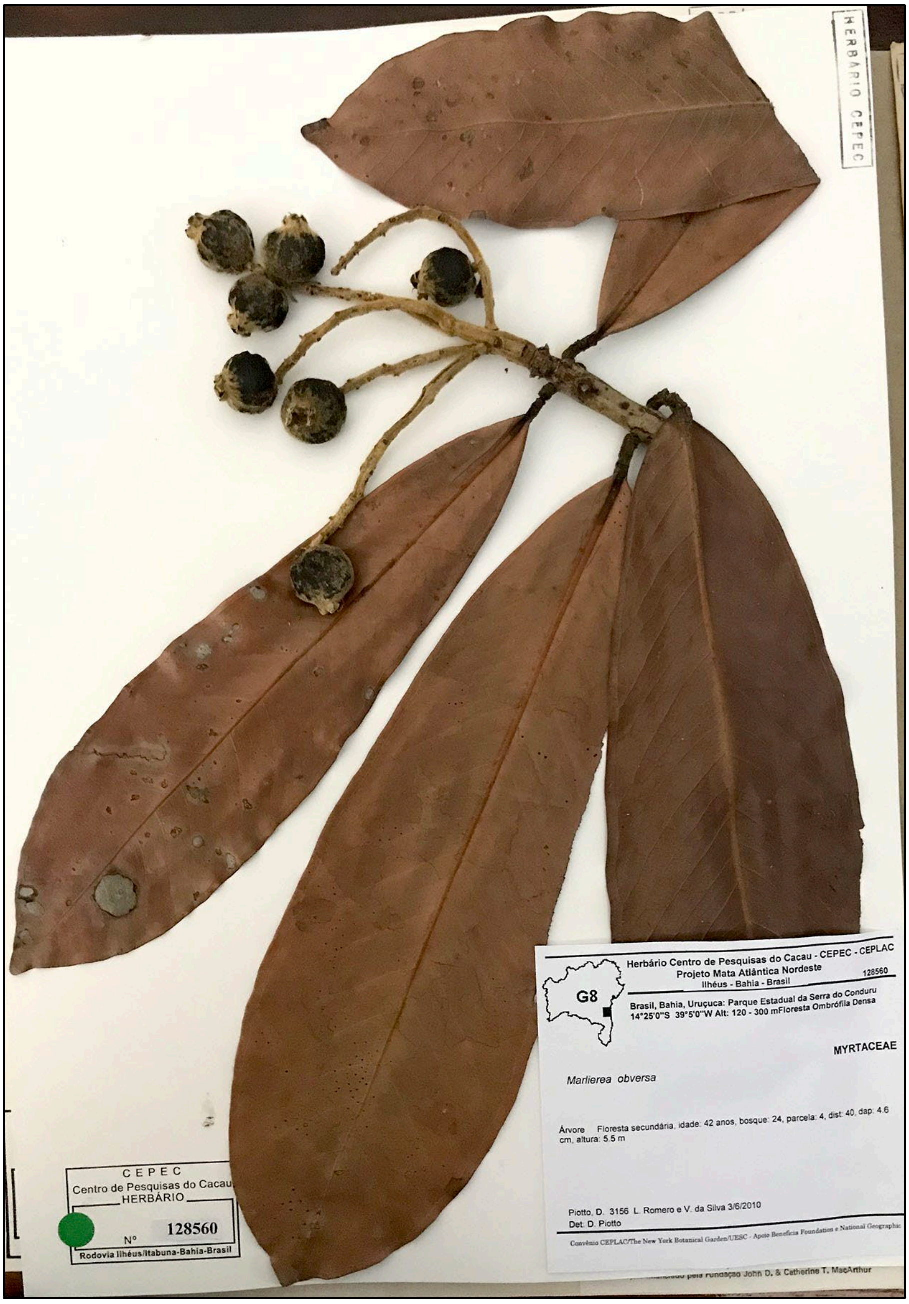


FIGURE 28: Distribution of *Myrcia obversa* (white dots). Continuous lines represent South American countries. The grey gradient represents elevation.

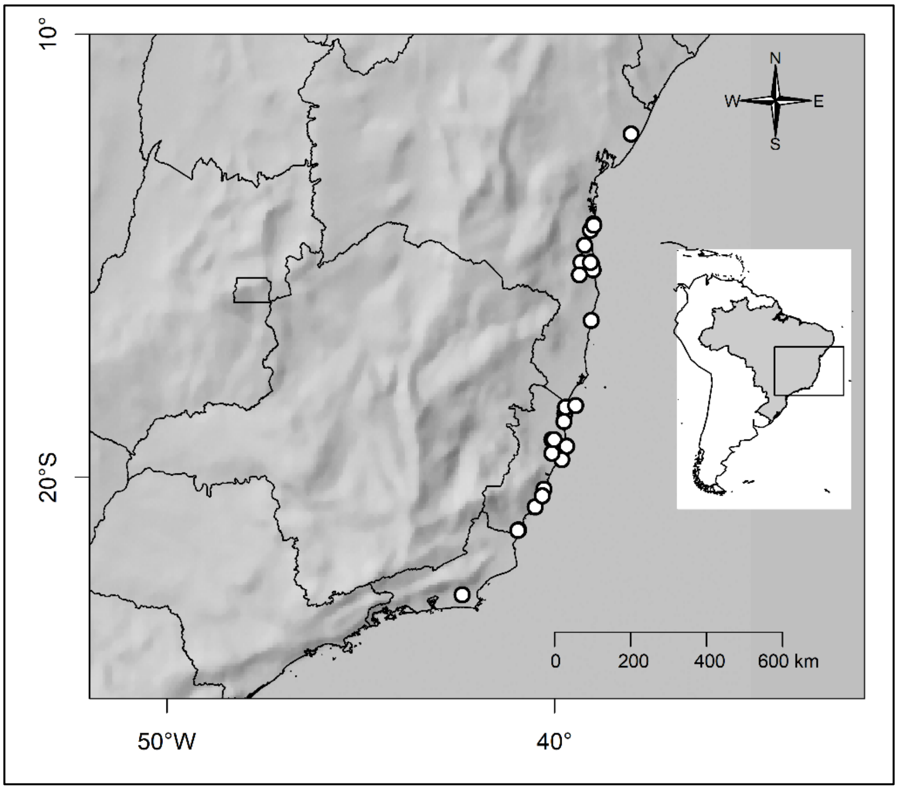


FIGURE 29: Phenology graph of *Myrcia obversa* (sampling n=48, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

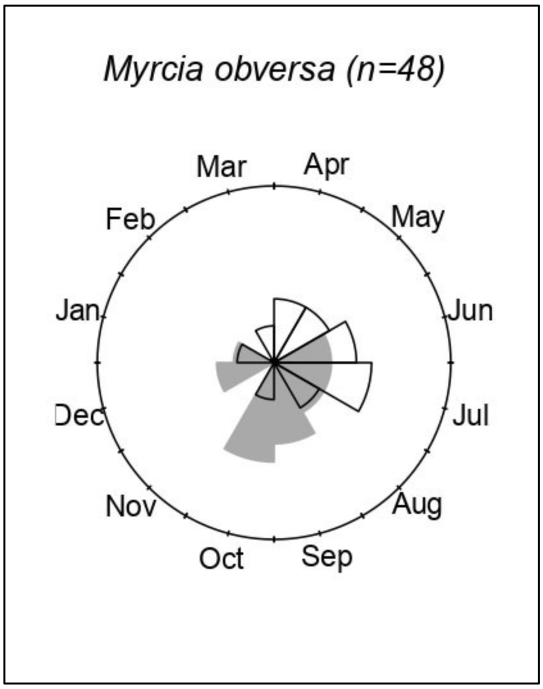


FIGURE 30: Image of representative specimen of *Myrcia pyrifolia* (Perdiz, R.O. 2251-UFRR).

FIGURE 31: Distribution of *Myrcia pyrifolia* (black dots). Continuous lines represent South American countries. The grey gradient represents elevation.

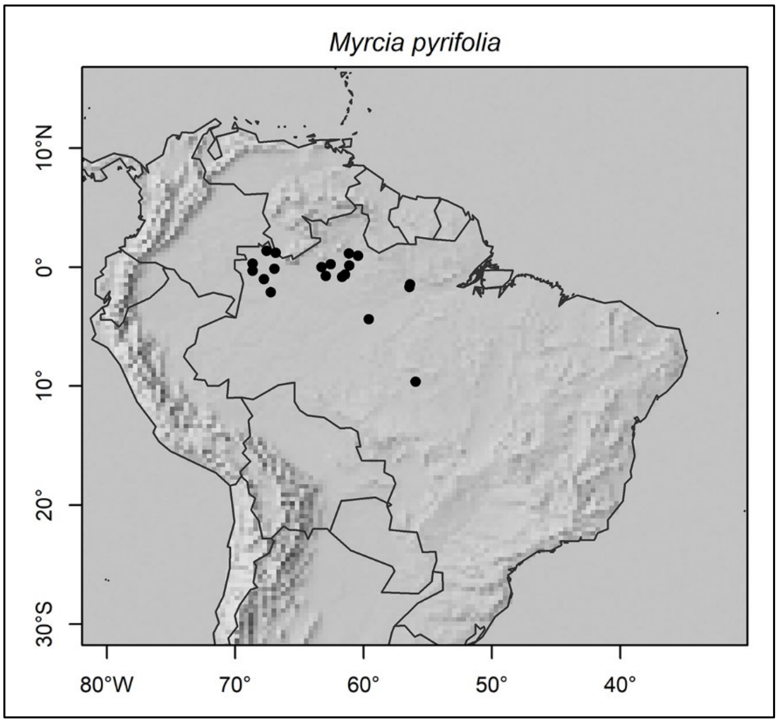


FIGURE 32: Phenology graph of *Myrcia pyrifolia* (sampling n=22, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

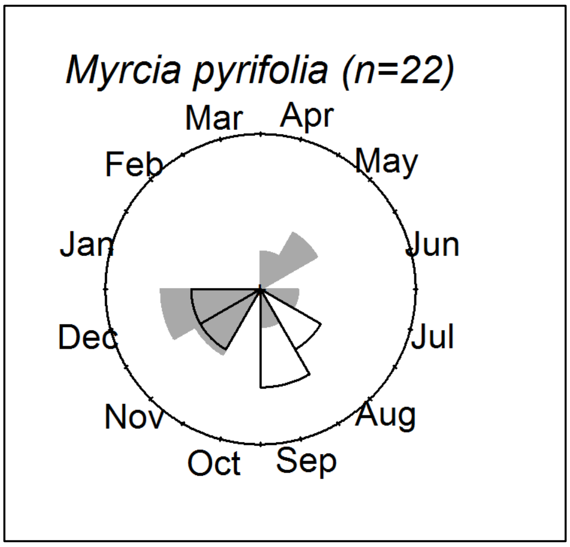


FIGURE 33: Image of representative specimen of *Myrcia riodocensis* (holotype: Sucre, 8269, RB).

FIGURE 34: Distribution of *Myrcia riodocensis* (white dots). Continuous lines represent South American countries. The grey gradient represents elevation.

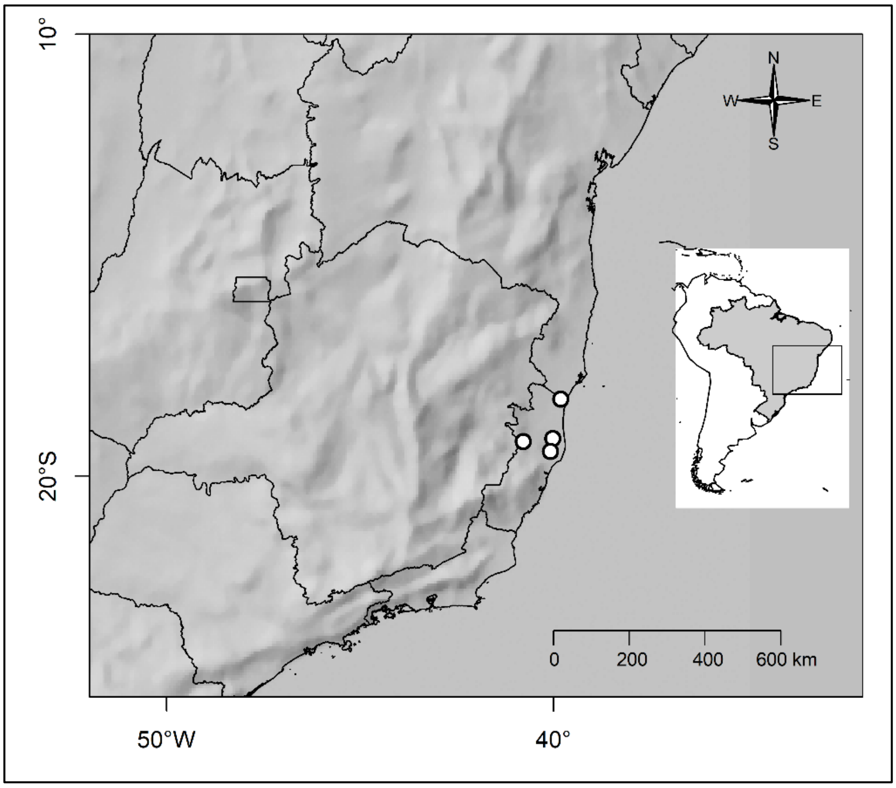


FIGURE 35: Phenology graph of *Myrcia riodocensis* (sampling n=13, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

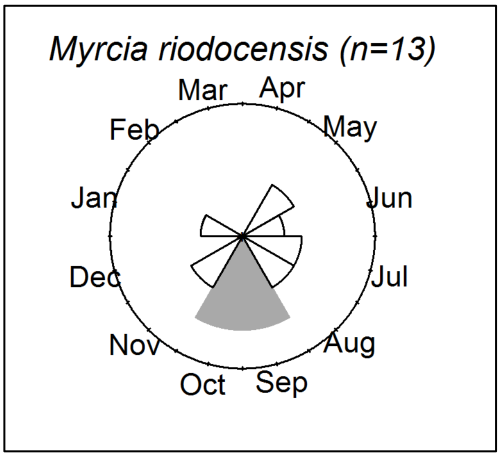


FIGURE 36: Image of representative specimen of *Myrcia rubiginosa*(Thomaz, s.n. RB)

FIGURE 37: Distribution of *Myrcia rubiginosa* (black dots). Continuous lines represent South American countries. The grey gradient represents elevation.

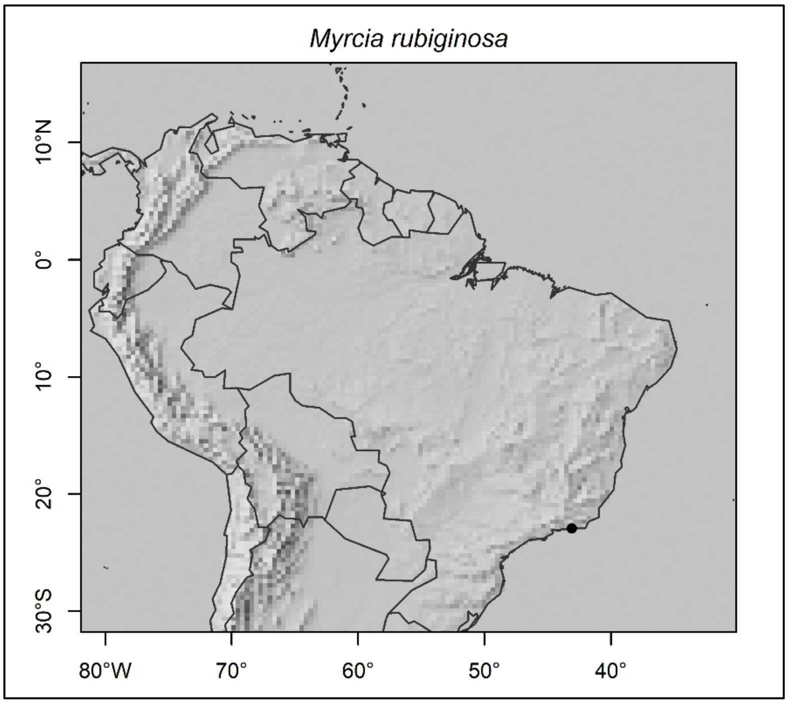


FIGURE 38: Image of representative specimen of *Myrcia santateresana* (holotype: Kollman, L. MBML).

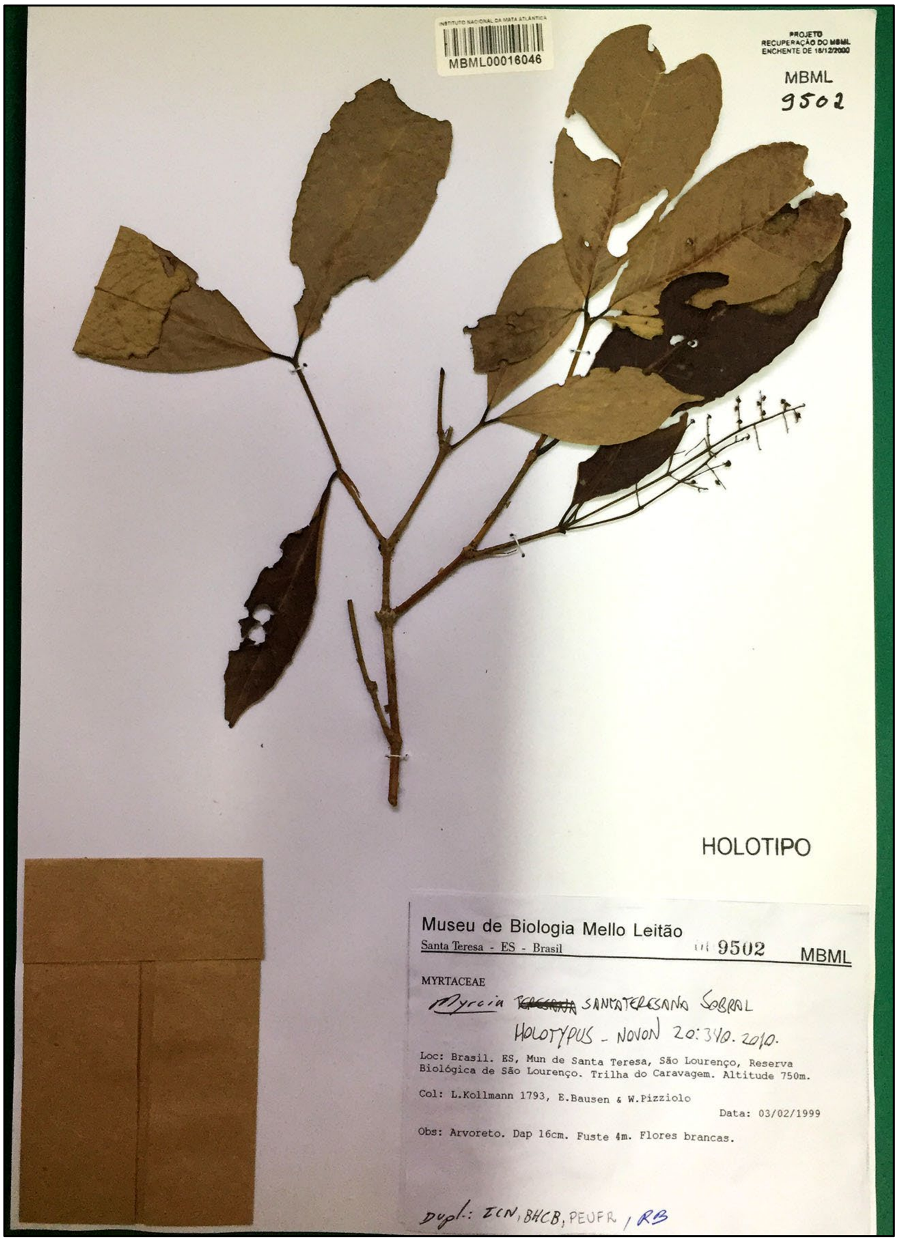


FIGURE 39: Distribution of *Myrcia santateresana* (black dots). Continuous lines represent South American countries. The grey gradient represents elevation.

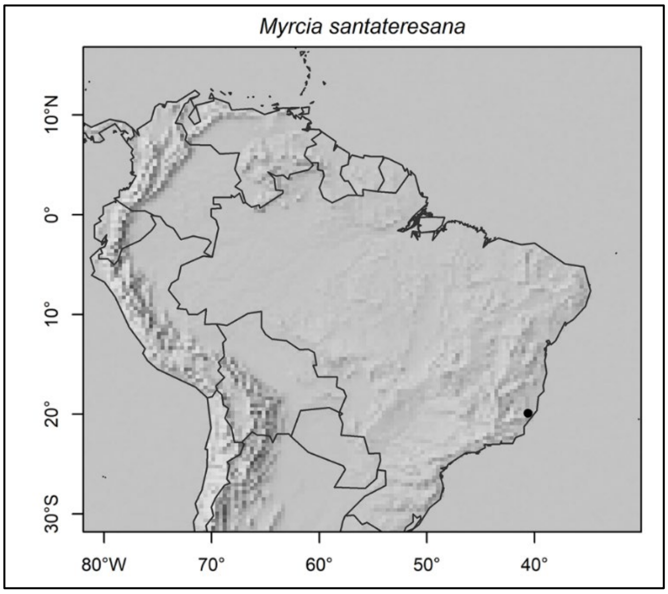


FIGURE 40: Image of representative specimen of *Myrcia tetraphylla* (paratype: Amorim, A.M. CEPEC).

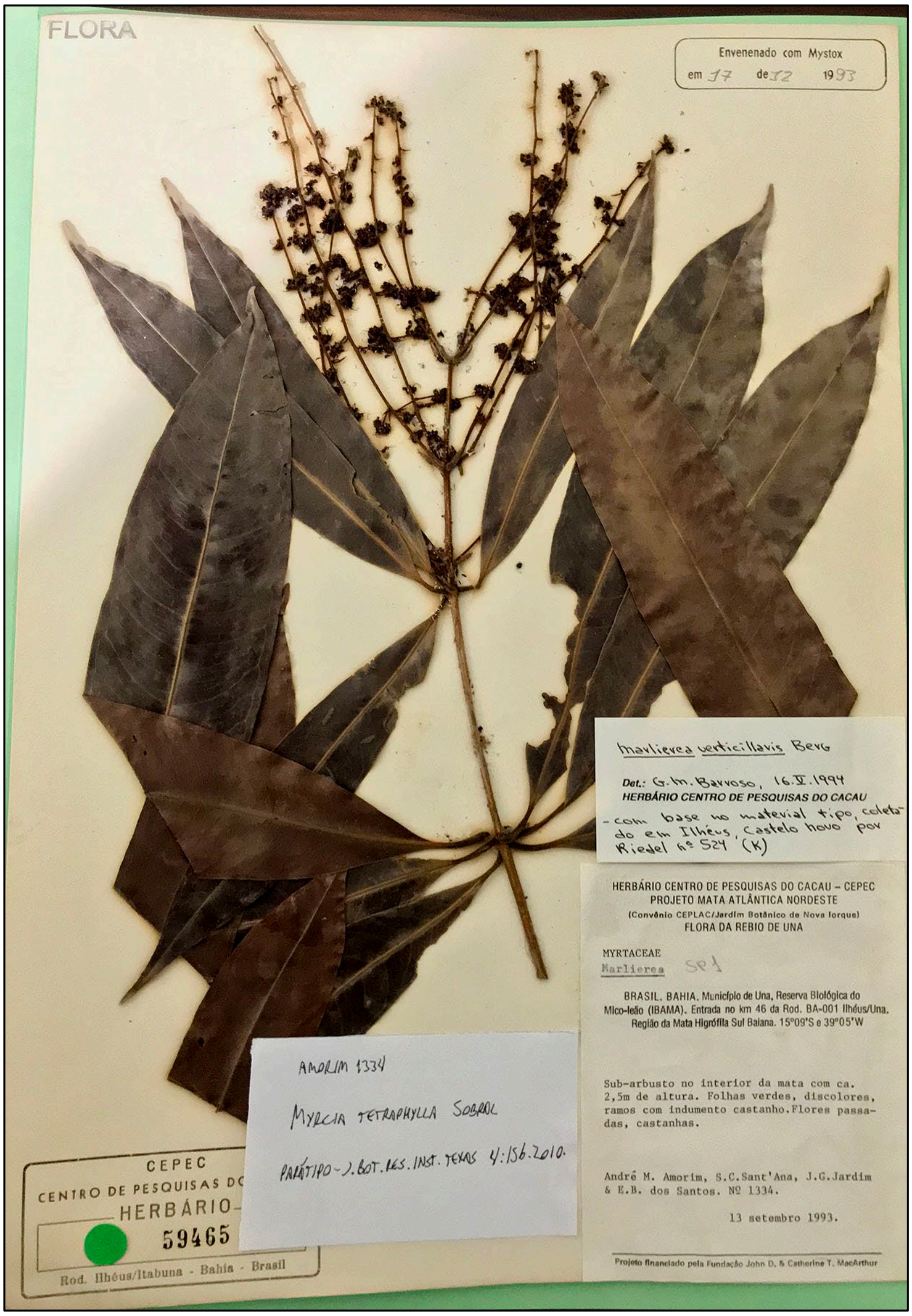


FIGURE 41: Distribution of *Myrcia tetraphylla* (white dots). Continuous lines represent South American countries. The grey gradient represents elevation.

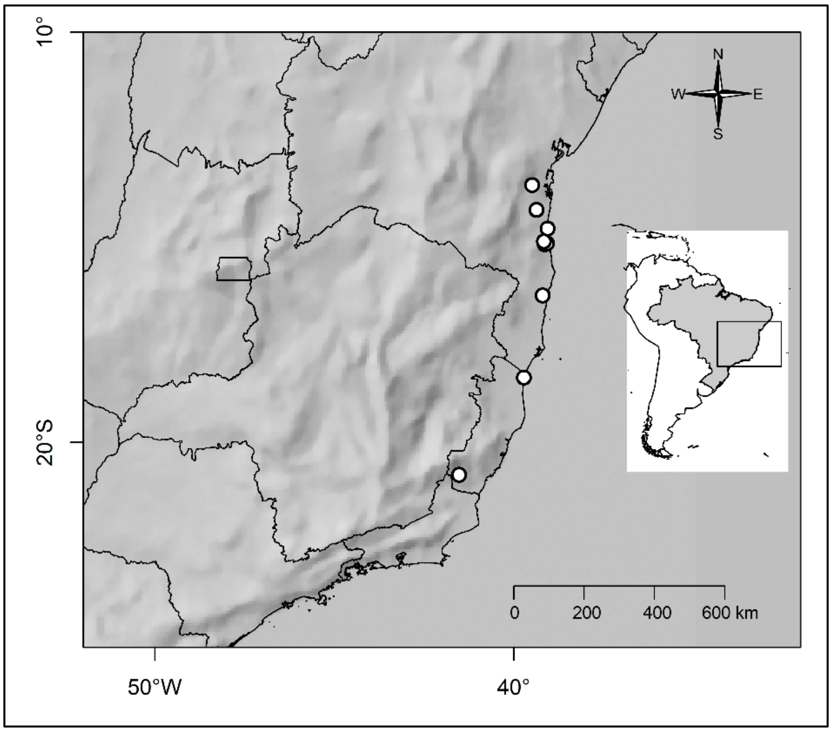


FIGURE 42: Phenology graph of *Myrcia tetraphylla* (sampling n=20, white triangles indicate flowering and dark ones fruiting, triangle size indicates sample size).

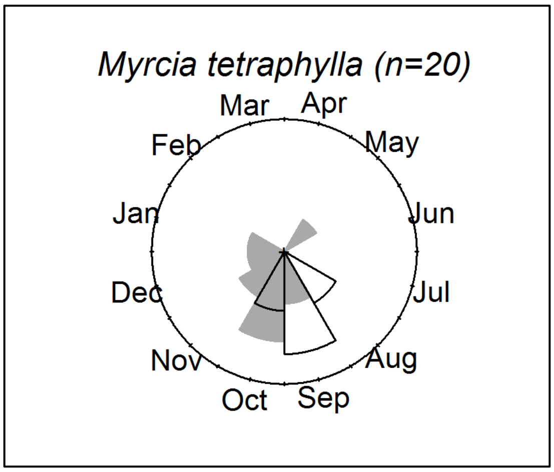
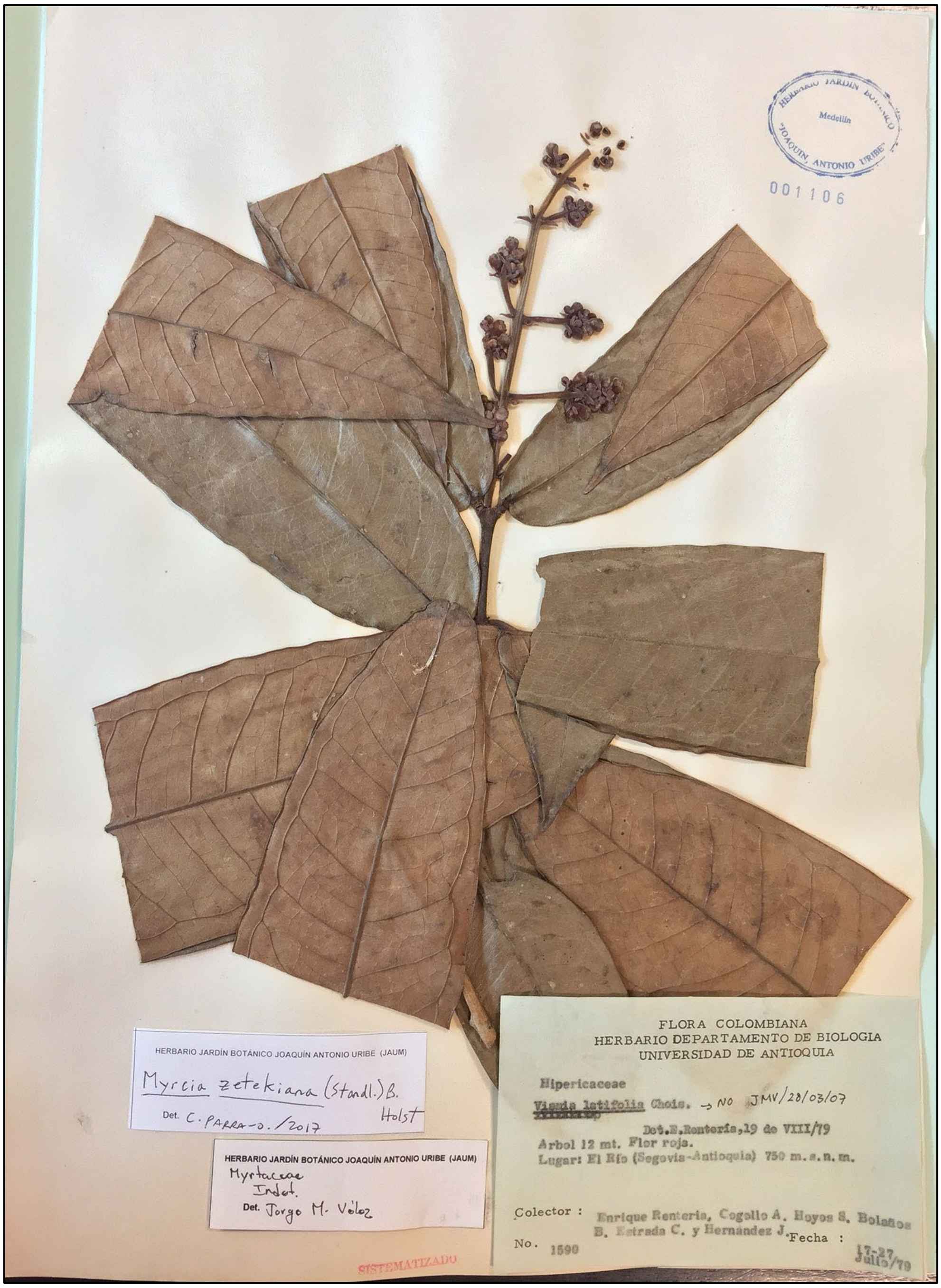


FIGURE 43: Image of representative specimen of *Myrcia zetekiana* (Renteria, E. 1590 JAUM).



5. CONSIDERAÇÕES FINAIS.

O Grupo das Verticiladas é considerado filogeneticamente coeso, emergindo monofilético das análises filogenéticas com bom suporte. As características morfológicas que distinguem o Grupo das Verticiladas são: inflorescências terminais espiraladas com eixo primário curto; padrão de ramificação assimétrico das inflorescências; brácteas persistentes; indumento com tricomas brancos ou vermelhos nas raquis da inflorescência, brácteas abaxialmente, hipanto e lobos do cálice abaxialmente.

Myrcia amazonica DC. não saiu monofilética nas análises, espécimes do Sul da Floresta Atlântica emergiram com *Myrcia riodocensis* mas com baixo suporte. Myrcia riodocensis é endêmica do ES e apresenta folhas maiores e coriáceas, inflorescências terminais. O outro grupo emergiu com espécimes da Floresta Amazônica e do Norte da Floresta Atlântica com alto suporte. Até aqui não foi possível definir características morfológicas destas linhagens Norte/Sul. Sugerimos futuras análises morfométricas e análises filogenética com mais espécimes, de múltiplas localidades. A única variação morfológica observada depois da observação de muitos materiais é que espécimes do Cerrado tem indumento mais denso.

Myrcia neodimorpha emergiu como grupo irmão do clado G mas com baixo suporte. Porém com características morfológicas (folhas grandes, opostas decussadas e inflorescências com brácteas permanente e pubescência branca) que nos levam a acreditar que esta espécie é mais próxima ao clado F. Anatomicamente na folha, *M. neodimorpha* apresenta um feixe vascular acessório ao cilindro central. Essa característica não ocorre nas espécies do clado F e G.

Myrcia neoestrellensis não emergiu no clado F como esperado nas nossas análises e sim no clado E com *Myrcia excoriata. Myrcia neoestrellensis* apresenta folhas elípticas a obovadas (vs. estreitamente elípticas no clado F); venação primária achatada adaxialmente na folha (vs. elevada no clado F); e pontuações pelúcidas conspícuas (vs. inconspícuas no clado F).

As folhas e pecíolos de 13 espécies de *Myrcia* sect. *Aulomyrcia* (*Myrcia amazonica, M. eumecephylla, M. hexasticha, M. insularis, M. magna, M. micropetala, M. neodimorpha, M. neoestrellensis, M. obversa*, *M. riodocensis*, *M. subobliqua*, e *M. tetraphylla*) foram descritas morfológica- e anatomicamente pela primeira vez.

Providenciamos também uma chave dicotômica baseada em dados foliares e peciolares para estas espécies.

Providenciamos um estudo taxonômico do Grupo das Verticiladas, agora contendo 22 espécies (baseando-se nas análises moleculares do primeiro capítulo, *Myrcia neoestrellensis* não é parte do grupo). Neste estudo foram disponibilizadas para as espécies do Grupo das Verticiladas, descrições detalhadas, dados da ocorrência, gráficos da fenologia, imagens e comentários.

As espécies do Grupo das Verticiladas são distintas umas das outras baseando-se em combinações de caracteres do indumento, caracteres foliares e da inflorescência. O Grupo das Verticiladas é um grupo coerente e com um bom suporte morfológico e filogenético.

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