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Valner Matheus Milanezi Jordão

Estudos Morfométricos e Ecológicos para a Delimitação de Táxons Associados ao Complexo *Machaerium acutifolium* (Leguminosae, Papilionoideae, Clado Dalbergia)

São José do Rio Preto
2023

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Dissertação apresentada como parte dos requisitos para obtenção do título de Mestre em Biodiversidade, junto ao Programa de Pós-Graduação em Biodiversidade do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista "Júlio de Mesquita Filho", Campus de São José do Rio Preto.

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Financiadora: CAPES

Comissão Examinadora

Profa. Dra. Daniela Sampaio Silveira
UNESP – Campus de São José do Rio Preto

Prof. Dr. Haroldo Cavalcante de Lima
JBRJ – Instituto de Pesquisa Jardim Botânico do Rio de Janeiro

Prof. Dr. Vinicius Castro Souza
USP – Escola Superior de Agricultura "Luiz de Queiroz"

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Devemos considerar as características próprias e a natureza geral das plantas do ponto de vista de sua morfologia, seu comportamento sob condições externas, seu modo de geração e todo o curso de suas vidas.

Teofrasto, c. 371-c.287 a.C.

RESUMO

Machaerium Pers. (Leguminosae Juss) apresenta cerca de 130 espécies e uma distribuição predominantemente na América tropical. No Brasil, são encontradas 74 espécies, sendo destas 44 endêmicas. Entre as espécies mais representativas do gênero, *Machaerium acutifolium* Vogel. representa um grupo-chave para uma análise de reconstrução biogeográfica de biomas neotropicais megadiversos, contudo, possui um histórico taxonômico complexo. Para solucionar os problemas de circunscrição em grupos de difícil delimitação, estudos taxonômicos vêm utilizando análises morfométricas para a identificação dos caracteres considerados diagnósticos para a delimitação de táxons. Combinados com abordagens ecológicas, esses dados podem contribuir para a compreensão de como os fatores abióticos podem influenciar na distribuição geográfica das espécies e, se esses fatores podem levar a alterações específicas nos padrões de variação morfológica. Dessa forma, o presente trabalho pretendeu elucidar as relações morfotípicas do complexo *Machaerium acutifolium* com base na análise dos tipos nomenclaturais e seus sinônimos (*M. acutifolium* var. *enneandrum*; *M. acutifolium* var. *muticum; M. acutifolium* var. *pseudacutifolium*; *M. junglandifolium* e *Sweetia atrata*) bem como das espécies morfologicamente relacionadas, *M. mucronulatum* Mart. ex Benth. e *M. opacum* Vogel. Para a realização das análises morfológicas e morfométricas, foram realizadas quatro expedições de campo, onde o complexo possui maior distribuição (Bahia, Distrito Federal Espírito Santo, Minas Gerais e São Paulo), além do estudo de materiais depositados nos herbários nacionais CEN, CEPEC, HUEFS, R, RB, SJRP e UB e a análise de imagens em alta resolução tanto de amostras depositadas em herbários nacionais quanto internacionais. Cinquenta variáveis morfológicas foram escolhidas para medições e os dados obtidos foram analisados por meio da Análise de Agrupamento (Dendrograma), Ordenação (PCA) e pelo Index de Critério Bayesiano (NMMs) pelo programa R versão 4.3. Para a produção das análises ecológicas foram utilizadas duas variáveis bioclimáticas, Precipitação Anual (BIO 12) e Sazonalidade da Precipitação – Coeficiente de Variação (BIO 15). Foram realizadas as tipificações de quatro nomes relacionados à *M. mucronulatum* e *M. opacum*. Como resultado das análises morfométricas e dos estudos taxonômicos, também são apresentadas três novas espécies de *Machaerium* com ocorrência para as regiões Nordeste e Sudeste do Brasil e características dos Domínios da Caatinga e do Cerrado.

Palavras Chaves: Dalbergieae. Diversidade. *Machaerium*. Sistemática de Fanerógamas. Taxonomia integrativa.

ABSTRACT

Machaerium Pers. (Leguminosae Juss) includes 130 species and a distribution predominantly in tropical America. In Brazil, 74 species occur of which 44 are endemic. Among the most representative species of the genus, *Machaerium acutifolium* Vogel represents a key group for a biogeographic reconstruction analysis of megadiverse Neotropical biomes, however, it has a complex taxonomic history. To solve circumscription problems in groups that are difficult to delimit, taxonomic studies have used morphometric analyzes to identify characters considered diagnostic for delimiting taxa. Combined with ecological approaches, these data can contribute to the understanding of how abiotic factors can influence the geographic distribution of species and, if these factors can lead to specific alterations in the patterns of morphological variation. Thus, the present work intended to elucidate the morphotypic relationships of the *Machaerium acutifolium* complex based on the analysis of the nomenclatural types and their synonyms (*M. acutifolium* var. *enneandrum*; *M. acutifolium* var. *muticum*; *M. acutifolium* var. *pseudacutifolium*; *M. junglandifolium* and *Sweetia atrata*) as well as the morphologically related species, *M. mucronulatum* Mart. ex Benth. and *M. opacum* Vogel. In order to develop the morphological and morphometric analyses, four field expeditions were carried out, where the complex has the greatest distribution (Bahia, Distrito Federal Espírito Santo, Minas Gerais and São Paulo), in addition to the study of materials deposited in the national herbaria CEN, CEPEC, HUEFS, R, RB, SJRP and UB and the analysis of high-resolution images of both samples deposited in national and foreign herbaria. Fifty morphological variables were chosen for measurements and the data obtained were analyzed using Cluster Analysis (Dendrogram), Ordering (PCA) and Bayesian Criterion Index (NMMs) using the R program version 4.3. Two bioclimatic variables were used to produce the ecological analyses, Annual Precipitation (BIO 12) and Seasonality of Precipitation – Coefficient of Variation (BIO 15). Typification of four names related to *M. mucronulatum* and *M. opacum* were performed. As a result of the morphometric analyzes and taxonomic studies, three new species of *Machaerium* occurring in the Northeast and Southeast regions of Brazil and characteristics of the Caatinga and Cerrado Domains are also presented.

Keywords: Dalbergieae. Diversity. Integrative taxonomy. *Machaerium.* Phanerogams Systematics.

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LISTA DE ABREVIATURAS E SIGLAS

BIC Bayesian Information Criterion

BIO Bioclimatic Variables

NMM Normal Mixture Models

PCA Principal Component Analysis

LISTA DE SÍMBOLOS

cm Centímetro

m Metro

SUMÁRIO

1. ORGANIZAÇÃO DO MANUSCRITO

Esta dissertação está dividida em três capítulos que foram escritos no formato de artigos científicos. Como norma da biblioteca do Instituto de Biociências, Letras e Ciências Exatas, somente a Introdução Geral está em português, seguindo as normas da ABNT e os demais capítulos foram escritos em inglês seguindo as normas prévias da revista Systematic Botany.

No Capítulo I, "Integrated analysis in the *Machaerium acutifolium* complex (Leguminosae, Papilionoideae, Clado Dalbergia) suggest a new infrageneric circumscription" são apresentadas as análises realizadas por meio de dados morfométricos e ecológicos.

O Capítulo II, intitulado "Taxonomy and nomenclature of the *Machaerium acutifolium* complex and related species (Leguminosae: Papilionoideae: Clado Dalbergia) complementa o capítulo I ao apresentar atualizações nomenclaturais e descrições atualizadas para todas as espécies referentes ao complexo investigado.

Por fim, o Capítulo III, "A remarkable new species of *Machaerium* (Leguminosae, Papilionoideae) from Northeast and Southeast Brazil.", é resultado do estudo cuidadoso realizado nos herbários mais representativos da Caatinga e Cerrado, onde foi possível identificar mais uma nova espécie para o gênero, não relacionada ao complexo *Machaerium acutifolium* Vogel.

2. INTRODUÇÃO GERAL

Com 796 gêneros e com 22.450 espécies, Leguminosae Juss. é a terceira maior família de angiospermas em número de espécies, depois de Asteraceae e Orchidaceae, com distribuição cosmopolita e que apresenta uma grande variedade de formas e hábitos, agrupando desde ervas até grandes árvores de dossel (Lewis *et al*., 2005; LPWG, 2017; LDP, 2021). A família desempenha um importante papel ecológico principalmente em ecossistemas que apresentam sazonalidade climática, tanto em regiões temperadas, quanto tropicais (Schrire *et al*., 2005).

Estudos filogenéticos sustentam as leguminosas como um grupo monofilético (Wojciechowski, 2003; Wojciechowski *et al*., 2004; Lewis *et al*., 2005; LPWG 2017), onde são reconhecidas seis subfamílias, Caesalpinioideae DC., Cercidoideae LPWG, Detarioideae Burmeist, Dialioideae LPWG, Duparquetioideae LPWG e Papilionoideae DC. (LPWG 2017), que se originaram quase que simultaneamente, descartando a hipótese da existência de subfamílias basais e outras derivadas (Koenen *et al*., 2020).

De todas as subfamílias, apenas Papilionoideae permaneceu filogeneticamente inalterada após os estudos mais recentes, apresentando estados de caráter considerados particularmente valiosos para a identificação de seus membros como nectários extraflorais, a presença de estípulas e brácteas, folhas pari e imparipinadas, pré-floração imbricada com a pétala adaxial mais externa, flores geralmente papilionadas, e filamentos do androceu geralmente unidos por uma bainha (LPWG, 2017).

Apesar dos avanços em estudos moleculares, algumas relações em Papilionoideae ainda permanecem obscuras, principalmente nas linhagens que representam clados formados por representantes das tribos tradicionalmente aceitas Dalbergieae, Sophoreae e Swartzieae que são pouco conhecidos, dificultando o esclarecimento das relações existentes entre elas (Pennington *et al*., 2001; Cardoso *et al*., 2013).

Dentre os principais gêneros lenhosos da tribo Dalbergieae, *Machaerium* Pers. tem cerca de 130 espécies e apresenta uma distribuição predominantemente neotropical, embora, a espécie *Machaerium lunatum* (L.f.) Ducke, seja anfiatlântica, e alcance a costa oeste africana (Lozano; Klitgaard, 2006). Neste gênero, há o reconhecimento de dois grupos de espécies: o primeiro ocorrendo desde o sul do México até a Região Amazônica e o segundo, com espécies distribuídas pelo centro sul do continente americano até o norte da Argentina (Filardi, 2011; Filardi; Lima, 2014).

No Brasil, país centro de diversidade do gênero, são encontradas 74 espécies de *Machaerium*, sendo 60% delas endêmicas (Filardi *et al*., 2020). O gênero consiste em árvores,

arbustos e lianas, que são comumente encontrados em formações florestais (Hoehne, 1941; Ducke, 1949; 1953; Rudd, 1977; 1987a; 1987b; Filardi *et al*. 2013; Filardi; Lima, 2014).

Machaerium apresenta dificuldade de delimitação devido a sua expressiva variedade morfológica, que pode ser expressa de forma máxima na existência de espécimes arbóreos e lianescente pertencente a uma mesma espécie (Filardi, 2011; Filardi *et al*., 2020). Assim, dentre as espécies do gênero existe uma variação expressiva no número, dimensões e padrões de venação dos folíolos, na forma e na consistência de estípulas e de bractéolas, na coloração e indumento das pétalas, na adelfia do androceu e por fim, nos tipos de frutos, que variam de sâmaras anemocóricas a núculas adaptadas para a dispersão pela água. Hoehne, 1941; Ducke, 1949; 1953; Rudd, 1977; 1987a; 1987b; Filardi *et al*. 2013; Filardi; Lima, 2014).

Além disso, esse gênero apresenta uma grande importância ecológica e econômica no continente Sul-Americano uma vez que diversos autores estudaram as relações ecológicas entre *Machaerium* e insetos e descobriram grupos de espécies correlatas e ainda, outros trabalhos apresentaram o potencial de polinização dessas espécies ao indicar que muitas possuem um potencial na produção melífera (Fernandes *et al*., 1987; Lorenzi, 1992; Mendonça-Filho, 2002).

Alguns estudos mais antigos, destacaram o potencial medicinal das espécies amazônicas *M. kegelii* Meisn. e *M. lunatum* (Rudd, 1977; 1987b) e em trabalhos mais recentes relacionados a *M. acutifolium,* foi possível observar o seu potencial para agir como larvicida natural contra o *Aedes aegypti* além de apresentar compostos que podem ser considerados como fortes candidatos no tratamento do fungo *Candida parapsilosis* (Dias *et al*., 2020; Melo *et al*., 2021).

Além da importância medicinal, *M. acutifolium* se destaca por ser um grupo-chave para análises biogeográficas, pois em seu amplo padrão de distribuição, juntamente com os padrões observados para outras espécies de Leguminosae com as mesmas características de ocorrência, fundamentaram a proposta para o estabelecimento de uma unidade fitogeográfica denominada Florestas Tropicais Sazonalmente Seca (SDTF, Seasonally Dry Tropical Forests), que se baseia em hipóteses relacionadas à biogeografia de vicariância (Prado, 2000 *apud* Cardoso e Queiroz, 2010; Pennington *et al*., 2000).

Devido a seu amplo padrão de distribuição geográfica, ocorrendo em quase todos os domínios fitogeográficos brasileiros e em outros cinco países da América do Sul, *Machaerium acutifolium* apresenta uma grande plasticidade fenotípica, levando ao reconhecimento de diferentes táxons ao longo do tempo que foram todos sinonimizados nos trabalhos de Filardi e Lima (2014) e Filardi *et al*. (2020) (Tabela 1).

Taxon	Local da coleta	Ano de publicação	Status nomenclatural	Sinonimização
Machaerium acutifolium Vogel	Brasil – "Brasil merid."	1837	Nome aceito	-
Machaerium acutifolium var. *muticum* (Benth.) Benth.	Brasil – Minas Gerais	1862	Sinônimo heterotípico de *M. acutifolium*	Filardi & Lima 2014
Machaerium muticum Benth.	Brasil – Minas Gerais	1837	Basiônimo de *M. acutifolium* var. *muticum*	Filardi & Lima 2014
Machaerium junglandifolium Rusby	Bolívia – Tumpasa	1910	Sinônimo heterotípico de *M. acutifolium*	Filardi & Lima 2014
Sweetia atrata Mohlenbr.	Paraguai – Caaguazú	1963	Sinônimo heterotípico de *M. acutifolium*	Filardi et al. 2020
Machaerium acutifolium var. *enneandrum* (Hoehne) Rudd	Brasil – Mato Grosso	1973	Sinônimo heterotípico de *M. acutifolium*	Filardi et al. 2020
Machaerium enneandrum Hoehne	Brasil – Mato Grosso	1938	Basiônimo de *M. acutifolium* var. *enneandrum*	Filardi et al. 2020
Machaerium acutifolium var. *pseudacutifolium* (Pittier) Rudd.	Venezuela – Guárico	1973	Sinônimo heterotípico de *M. acutifolium*	Filardi & Lima 2014
Machaerium pseudacutifolium Pittier	Venezuela – Guárico	1941	Basiônimo de *M. acutifolium* var. *pseudacutifolium*	Filardi & Lima 2014

Tabela 1. Histórico nomenclatural de *Machaerium acutifolium* Vogel.

Além disso, Ducke (1949) ao propor uma espécie nova para o estado do Amazonas, *Machaerium hoehneanum*, incluiu *M. enneandrum* como seu sinônimo heterotípico e essa problemática nomenclatural permaneceu em aberto até o presente momento, uma vez que no trabalho publicado por Filardi e Lima (2014) os autores não conseguiram localizar o material tipo de *M. enneandrum* depositado no herbário do Museu Nacional (R2580).

Embora uma recente atualização nomenclatural tenha ocorrido (Filardi; Lima, 2014; Filardi *et al*., 2020), diversos autores (Lewis, 1987; Queiroz, 2009; Filardi, 2011) indicaram que *Machaerium acutifolium* ainda possuía uma variação acentuada em sua morfologia e que um estudo morfológico detalhado com esse grupo poderia levar ao reconhecimento de táxons distintos. Essa variação estava contida principalmente na forma e comprimento dos folíolos (folíolos alternos ou subopostos, 3,5–10 cm comprimento, elípticos, lanceolados, oblongo-lanceolados, oval-lanceolados, ápice agudo, acuminado, mucronulado, base arredondada, raro

levemente cordada) e no tamanho dos frutos e superfície do núcleo seminífero (sâmaras de 5–9 cm comprimento com núcleo seminífero proeminente, enrugado ou verrucoso) (Filardi, 2011).

Dessa maneira, devido às variações morfológicas e a grande quantidade de nomes associados, *Machaerium acutifolium* foi considerada como um complexo taxonômico que necessitava ser mais bem estudado e compreendido. Assim, o objetivo deste trabalho foi revisar todo o histórico nomenclatural de *Machaerium acutifolium*, analisar as variedades e morfotipos propostos em estudos anteriores e apresentar uma delimitação atual para a mesma com base em metodologias integrativas, utilizado a morfometria e dados ecológicos para propor uma nova circunscrição a esse complexo.

3. REFERÊNCIAS

BENTHAM, G. Leguminosae. *In*: MARTIUS, C. F. P.; EICHLER, A. W.; URBAN, I. (ed.). **Flora Brasiliensis.** Viena: Editora R. Oldenbourg Verlag, 1862, v. 15, n. 1, p. 1–504.

CARDOSO, D. B. O. S.; QUEIROZ, L. P. DE. Caatinga no contexto de uma metacomunidade: evidências da biogeografia, padrões filogenéticos e abundância de espécies em Leguminosas. In: CARVALHO, C. J. B; ALMEIDA, E. A. B. (org.). **Biogeografia da América do Sul: padrões e processos**. São Paulo: Editora Roca. 2011. cap. 15, p. 241–260. ISBN: 978-85-7241-896-6.

DIAS, L. P. et al. *Machaerium acutifolium* lectin alters membrane structure and induces ROS production in *Candida parapsilosis*. **International Journal of Biological Macromolecules**, v. 163, p. 19-25, 2020.

DUCKE, A. Notas sobre a Flora Neotrópica II - as leguminosas da Amazônia brasileira. **Boletim Técnico do Instituto Agronômico do Norte**, v. 18 p. 1–248, 1949.

DUCKE**,** A. As Leguminosas de Pernambuco e Paraíba. **Memórias do Instituto Oswaldo Cruz**, v. 51, p. 418–461, 1953.

FERNANDES, G.W.; MARTINS R.P.; TAMEIRÃO-NETO, E. Food web relationships invoving *Anadiplosis* sp galls (Diptera: Cecidomyiidae) on *Machaerium aculeatum* (Leguminosae). **Revista Brasileira de Botânica,** v. 10, p. 117-123, 1987.

FILARDI, F. L. R. **Avanços na sistemática de Machaerium Pers.(Leguminosae Papilionoideae Dalbergieae): filogenia e revisão taxonômica das espécies do Domínio Atlântico**. 2011. Tese de Doutorado. Ph. D. thesis. Escola Nacional de Botânica Tropical, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro. 385p.

FILARDI, F. L. R; LIMA, H. C.; KLITGAARD, B. B.; SARTORI, A. L. B. Taxonomy and nomenclature of the neotropical *Machaerium hirtum* complex (Leguminosae, Papilionoideae). **Brittonia**, v. 65, p. 154-170, 2013.

FILARDI, F. L. R.; LIMA, H. C. de. The diversity of *Machaerium* (Leguminosae: Papilionoideae) in the Atlantic Forest: Three new species, nomenclatural updates, and a revised key. **Systematic Botany**, v. 39, n. 1, p. 145–159, 2014.

FILARDI, F.L.R.; LIMA, H.C.; CARDOSO, D.B.O.S. 2020. *Machaerium in* **Flora e Funga do Brasil 2020**. Jardim Botânico do Rio de Janeiro. Disponível em: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB23055. Acesso em: 11 mar. 2023.

HOEHNE, F. C. Leguminosas Papilionadas (*Machaerium* e *Paramachaerium*). **Flora Brasilica**, v. 25, p. 1–99, 1941.

LDP. Legume data portal. Disponível em (https://www.legumedata.org/2021. Acesso em 15. abr. 2023.

LEWIS, G. P. **Legumes of Bahia**. Kew: Royal Botanic Gardens. 1987.

LEWIS, G. P.; SCHRIRE, B.; MACKINDER, B.; LOCK, M. (ed.). **Legumes of the World**. Royal Botanic Gardens Kew, 2005.

LORENZI, H. **Árvores Brasileiras: manual de identificação e cultivo de plantas arbóreas nativas no Brasil.** Plantarum, Nova Odessa, São Paulo, 352 p. 1992.

LOZANO, P.; KLITGAARD, B. B. The genus *Machaerium* (Leguminosae: Papilionoideae: Dalbergieae) in Ecuador. **Brittonia**, v. 58, n. 2, p. 124–150, 2006.

LPWG. The Legume Phylogeny Working Group. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny: The Legume Phylogeny Working Group (LPWG). **Taxon**, v. 66, n. 1, p. 44-77, 2017.

MELO, S. J.; SOUSA, J. P. B.; SÁ, M. G.; MORAIS, L. S.; MAGALHÃES, N. M.; GOUVEIA, F. N.; ALBERNAZ, L. C.; ESPINDOLA, L. S. *Machaerium acutifolium* compounds with larvicidal activity against *Aedes aegypti*. **Pest Management Science**, v. 77, n. 3, p. 1444-1451, 2021.

MENDONÇA FILHO, C. V. **Citotaxonomia de Machaerium Pers. e revisão taxonômica de Machaerium sect. Oblonga (Benth.) Taub. (Leguminosae-Papilionoideae).** 2002. Tese de Doutorado. Tese de Doutorado. Universidade Estadual de Campinas, Campinas.

PENNINGTON, R.T.; PRADO, D. E.; PENDRY, C. A. Neotropical seasonally dry forests and Quaternary vegetation changes. **Journal of Biogeography**, v. 27, n. 2, p. 261–273, 2000.

PENNINGTON, R.T., LAVIN, M., IRELAND, H.E., KLITGAARD, B. & PRESTON, J. Phylogenetic relationships of basal papilionoid legumes based upon sequences of the chloroplast trnL intron. **Systematic Botany**, v. 26, n. 3, p. 537-556, 2001.

PRADO, D. E. Seasonally dry forests of tropical South America: from forgotten ecosystems to a new phytogeographic unit. **Edinburgh Journal of Botany**, v. 57, n. 3, p. 437–461, 2000.

QUEIROZ, L. P. **Leguminosas da caatinga**. Feira de Santana: Universidade Estadual de Feira de Santana. 2009.

RUDD, V. E. The genus *Machaerium* (Leguminosae) in Mexico. **Boletín de la Sociedad Botánica de México**. v. 37, p 119–146, 1977.

RUDD, V. E. Studies in *Machaerium* (Leguminosae) VI: Section I. Machaerium. **Phytologia**, v. 62, p. 283–302. 1987a.

RUDD, V. E. Studies in *Machaerium* (Leguminosae) VII: Section II. Lineata. Part I: Species with wingless fruit. **Phytologia**, v. 64, p. 1–12, 1987b.

SCHRIRE, B. D., LAVIN, M. & LEWIS, G.P. 2005. Global distribution patterns of the Leguminosae: Insights from recent phylogenies. **Biologiske Skrifter**. 55: 375–422.

WOJCIECHOWSKI, M. F. 2003. Reconstructing the phylogeny of legumes (Leguminosae): an early 21st century perspective. *In*: B.B. Klitgaard & A. Bruneau (ed.). **Advances in Legume Systematics part**, v. 10. Royal Botanic Gardens. Kew. 5–35.

WOJCIECHOWSKI, Martin F.; LAVIN, Matt; SANDERSON, Michael J. A phylogeny of legumes (Leguminosae) based on analysis of the plastid matK gene resolves many well-supported subclades within the family. **American journal of botany**, v. 91, n. 11, p. 1846-1862, 2004.

4. Chapter I: Integrated analyzes in the *Machaerium acutifolium* complex (Leguminosae, Papilionoideae, Dalbergieae) suggest a new infrageneric circumscription.

4.1. Resumo

A espécie *Machaerium acutifolium* Vogel (Leguminosae, Papilionoideae) é sem dúvida uma das mais difíceis de serem entendidas do ponto de vista taxonômico, principalmente por ser uma das mais amplamente distribuídas no gênero. Ocorre em pelo menos seis países da América do Sul (Argentina, Bolívia, Brasil, Paraguai, Peru e Venezuela), onde apresenta grande importância ecológica e econômica. Ao longo de sua distribuição, esta espécie apresenta uma evidente plasticidade fenotípica, principalmente no formato e tamanho dos folíolos e frutos que levaram à descrição de diferentes entidades taxonômicas ao longo dos anos: *M. enneandrum* Hoehne; *M. muticum* Benth.*; M. pseudacutifolium* Pittier; *M. junglandifolium* Rusby e *Sweetia atrata* Mohlenbr. Assim, este trabalho teve como objetivo analisar, *Machaerium acutifolium* sob dados morfométricos e ecológicos e testar a hipótese de que a variação morfológica observada conteria mais um táxon associado a este binômio. Para tanto, foi realizado um levantamento bibliográfico das principais publicações, bem como de todos os tipos nomenclaturais e das "*Opus Princeps*" do gênero. A partir desta base de dados, os caracteres diagnósticos do complexo foram delimitados, tendo sido definidos 50 caracteres, 23 vegetativos e 27 reprodutivos, para serem amostrados e analisados com base nos testes exploratórios de Agrupamento (Dendrograma) e Ordenação (PCA). Para avaliação da hipótese, foi adotado o teste Normal Mixture Models (NMMs), que utiliza métodos estatísticos gaussianos com diferentes estruturas de covariância. Para produzir as análises ecológicas, foram utilizadas duas variáveis bioclimáticas, Precipitação Anual (BIO 12) e Sazonalidade da Precipitação – Coeficiente de Variação (BIO 15). Como resultado, dentre os 102 materiais analisados, foram identificados 4 grupos distintos: *Machaerium acutifolium* Vogel, *Machaerium mucronulatum* Mart. ex Benth, *Machaerium* morfotipo 1 e *Machaerium* morfotipo 2.

Palavras-chave: Dalbergieae, diversidade, Fabaceae, estatística, taxonomia.

4.2. Abstract

The species *Machaerium acutifolium* Vogel (Leguminosae, Papilionoideae) is undoubtedly one of the most difficult to understand from a taxonomic point of view, mainly because it is one of the most widely distributed in the genus. It occurs in at least six countries in South America (Argentina, Bolivia, Brazil, Paraguay, Peru, and Venezuela), where it has great ecological and economic importance. Throughout its distribution, this species shows an evident phenotypic plasticity, mainly in the shape and size of leaflets and fruits, which led to the description of different taxonomic entities over the years: *M. enneandrum* Hoehne; *M. muticum* Benth.; *M. pseudacutifolium* Pittier; *M. junglandifolium* Rusby and *Sweetia atrata* Mohlenbr. Thus, this work aimed to analyze *Machaerium acutifolium* under morphometric and ecological data and test the hypothesis that the observed morphological variation would contain another taxon associated with this binomial. For that, a bibliographical survey of the main publications was carried out, as well as of all nomenclatural types and of the "Opus Princeps" of the genre. From this database, the diagnostic characters of the complex were delimited, having defined 50 characters, 23 vegetative and 27 reproductive, to be sampled and analyzed based on exploratory tests of Grouping (Dendrogram) and Ordering (PCA). To evaluate the hypothesis, the Normal Mixture Models (NMMs) test was adopted, which uses Gaussian statistical methods with different covariance structures. To produce the ecological analyses, two bioclimatic variables were used, Annual Precipitation (BIO 12) and Seasonality of Precipitation – Coefficient of Variation (BIO 15). As a result, among the 102 analyzed materials, 4 distinct groups were identified: *Machaerium acutifolium* Vogel, *Machaerium mucronulatum* Mart. ex Benth, *Machaerium* morphotype 1 and *Machaerium* morphotype 2.

Keywords: Dalbergieae, diversity, Fabaceae, statistic, taxonomy.

4.3. Introduction

4.3.1. Integrated morphometric and ecological analysis as a key-tool to solve delimiting problems in species complexes

Tropical areas are classified as megadiverse and strongly impacted by environmental degradation, being disproportionately represented in their botanical collections (Olson et al. 2001; Bebber et al. 2010; Eigenbrod et al. 2015). However, herbaria present an expressive value to the biodiversity comprehension since as more than fifty per cent of new species described annually come from materials deposited in these institutions (Bebber et al. 2010; Heberling et al. 2019). Therefore, plant groups in tropical forests and in developing countries, marked by environmental exploration and deforestation, are considered the focus of biodiversity studies (Grace et al. 2021).

Taxonomy is a very important resource for biodiversity preservation since botanical monographs stimulate species discovery and slow the decline of undescribed biodiversity by providing the baseline information to address the environmental emergencies of the Anthropocene (Grace et al. 2021).

Despite the difficulty, defining properly a species is a fundamental mission in taxonomy and for a long time, alpha taxonomy reaches the main goal of relating the type specimens with taxonomically valid names considered as accepted species (De Queiroz 2007; Schlick-Steiner et al. 2007). However, in some cases due to the complexity of morphological variation, taxonomic treatments based on this classical method have become ineffective (Whitmore 1976 apud Bennett et al. 2008), making it necessary to use an integrative approach which may also include biochemical, ecological, geographic, molecular, and morphometric analyses (De Queiroz 2007; Padial et al. 2010; Damasco et al. 2019).

Statistical analyzes based on morphometric data have been used in taxonomy to characterize differences in morphology between two or more taxa, generally for a species complex where some structure can be divided into separate character states, presenting in many cases more accurate results, when compared with those obtained by classical morphological analyzes (Andres-Sanches et al. 2009; Steven and Subramanyam 2009). Combining with ecological information, this method can explain how abiotic factors influence the geographic distribution of a species complex and whether these factors can lead to specific changes in phenotypic variation (Doyen and Slobodchikoff 1974; Robbiati et al. 2017).

This approach has been used to resolve delimiting problems of several groups of angiosperms specially in Leguminosae family, resulting in new morphological limits for

species complexes and in various cases, presenting remarkable new species to science (Casiva et al. 2002; De La Estrella et al. 2009; Knaus 2010; Sousa et al. 2010; Ceolin, G. B. and Miotto 2012; Meireles and Lima 2013; Souza et al. 2014; Egan 2015; Gomero et al. 2016; Guerra et al. 2016, Castro-Bonilla et al. 2022; Crameri et al. 2022).

4.3.2. *Machaerium acutifolium* complex

Machaerium acutifolium Vogel (Leguminosae, Papilionoideae) is undoubtedly one of the most difficult species to understand from a taxonomic point of view, as it is one of the most widely distributed species in the genus. It occurs in at least six countries in South America, in Argentina, Bolivia, Brazil, Paraguay, Peru and Venezuela where it displays large ecological and economic importance (Filardi 2011).

Described by Vogel in 1837, this species was characterized by strictly arboreal habit, foliaceous and early deciduous stipules, leaves reaching from 7 to 21 leaflets, petiole and leaf rachis varying from sub-glabrous to puberulent and by leaflets with apex acute to acuminate, with length between 1.2 to 5.5 cm (Vogel 1837; Sartori and Tozzi 1998; Filardi 2011; Filardi et al. 2020).

Concerning the reproductive characters, flowers present an externally sericeous-nigrescent indumentum and internally white with greenish streaks standard petal with monadelphous androecium and samaras with seed chamber crumpled to verrucous (Vogel 1837; Sartori and Tozzi 1998; Filardi 2011; Filardi et al. 2020).

In Brazil, *M. acutifolium* occurs in vegetations known as Caatinga (*stricto sensu*), campos rupestres (rocky fields), Cerrado (*lato sensu*), riparian or gallery forests, seasonal deciduous and semideciduous forests, reaching altitudes up to 1.000 m (Filardi et al. 2020). Across its distribution in almost all biomes in Brazil, there is an evident phenotypic plasticity, mainly in the shape and size of the leaflets and fruits that led to the description of different taxonomic entities over the years (Bentham 1837; Bentham 1862; Loefgren 1895; Rudd 1973; 1977; Filardi 2011).

Consequently, this species has a complex taxonomic history, with eight names related to it as synonyms : *Machaerium acutifolium* var. *muticum* (Benth.) Benth., *Machaerium muticum* Benth., *Machaerium junglandifolium* Rusby, *Sweetia atrata* Mohlenbr., *Machaerium acutifolium* var. *enneandrum* (Hoehne) Rudd, *Machaerium enneandrum* Hoehne, *Machaerium acutifolium* var. *pseudacutifolium* (Pittier) Rudd., *Machaerium pseudacutifolium* Pittier and shares a great number of morphological characters with three other close related species (*M.*

mucronulatum Mart. ex Benth. and *M. opacum* Vogel) (Vogel 1837; Bentham 1837; Bentham 1862; Loefgren 1895; Rusby 1910; Pittier 1941; Ducke 1949; Rudd 1973; 1977; Filardi 2011, Filardi and Lima 2014).

Recent taxonomic treatments contributed to establish a more precise morphological limits for *M. acutifolium* (Filardi 2014; Filardi et al. 2020) but several authors have indicated that this species still had a noticeable variation in the morphology and a detailed investigation with this group could lead to the recognition of distinct taxa (Lewis 1987; Queiroz 2009; Filardi and Lima 2014).

Hence, this study aimed to investigate the *Machaerium acutifolium* complex based on an integrative taxonomic approach, through morphometrical and ecological data to evaluate if there are more than one distinguished taxon in this group of specific and infraspecif names.

4.4. Materials and Methods

4.4.1. Complex delimitation

Before choosing the materials and morphological characters to produce the morphometry, a review was made of all nomenclatural types as well as the "*opus princeps*" of *Machaerium* from the tropical America, highlighting the Brazilian species. That way we would have means of identifying erroneous determinations in herbaria and not include materials out of the species complex in the analysis and, we also would be able to propose new taxonomic entities.

Initially, we used the publications of Ducke 1944, Filardi 2011, Filardi and Lima 2014 and Filardi et al. 2020 to define the complex and then, based on the observations we made in the materials deposited in herbaria, we were able to refine this definition, adding or removing taxa, for a more precise statistical analysis.

After studying the materials from the Caatinga and Cerrado biomes, we observed that *Machaerium mucronulatum* Mart. ex Benth. should be included in the morphometrics analysis because this species presents several shared vegetative characters with *M. acutifolium*.

Also, we observed and included in the analysis two other morphotypes, from the Caatinga biome because mostly of all the analyzed materials were indicated as *Machaerium acutifolium* however, only few vegetative aspects could lead to this determination (e.g., shape of the leaflets), since almost all reproductive characters already indicated great differences from *M. acutifolium*.

4.4.2. Plant Material

We investigated *Machaerium* collections belongs to BHCB, CEN, CEPEC, CGMS, HEPH, HUEFS, INPA, MG, R, RB, SJRP and UB through visits and permute. Images in high resolution available in the Reflora Virtual Herbarium (http://reflora.jbrj.gov.br/reflora/herbarioVirtual), SpeciesLink (https://specieslink.net/search/index) and GBIF (https://www.gbif.org/) by herbaria A, ALCB, CESJ, EAC, ESA, K, L, M, MBM, MO, NY, P, UEC, US, and VIES were also analyzed (acronyms based on Thiers 2020), which together hold most type specimens and recent collections of the neotropical *Machaerium*.

Of these, we selected 102 specimens representing the following entities: *Machaerium acutifolium* (n = 79), *Machaerium mucronulatum* (n = 4), *Machaerium* morphotype 1 (n = 13) and *Machaerium* morphotype 2 (n = 6). In this sample, 52 materials represent flowering specimens being 40 of *Machaerium acutifolium*, seven of *Machaerium* morphotype 1 and five of *Machaerium* morphotype 2, and 50 represent fruiting specimens being 40 of *Machaerium acutifolium*, four of *Machaerium mucronulatum*, six of *Machaerium* morphotype 1 and one of *Machaerium* morphotype 2 for measurements of flower and fruit characters.

The vegetative, flowering, and fruiting specimens were chosen to represent the observed morphological and geographical variation, although the selection of specimens was partly limited by a lack of fully developed and intact flowers or immature fruits. The complete list of the examined material from the morphometric study of the complex is in the supplementary material, at the end of this chapter.

4.4.3. Morphological measurements

We assessed 23 vegetative characters besides with 27 reproductive characters of mature samples (Table 1 and supplementary material). Continuous characters were measured three times on a given collection, then were recorded as sample medians. One or two flowers, when the material had a large amount of it, per collection were withdrawn, rehydrated, and dissected under a stereomicroscope Leica DFC295. Measurements of continuous characters were made on digital images of leaves and fruits and dissected flower organs using Image-Pro Plus (Media Cybernetics, Silver Spring, USA) version 6.0.

Code	**Character**
Leaf	

PL	Petiole length (after pulvinus to insertion of first basal leaflet)
RL	Rachis length (after the insertion of the first basal leaflet up terminal leaflet's pulvinulum)
Basal leaflet	
BPL	Basal pulvinulum length
LBL	Length of basal leaflet (not including pulvinulum)
WBL	Width of basal leaflets at widest point
DBL	Distance from the base to the maximum width of the basal leaflet
RLWB	Ratio of basal leaflet length to width
RBW	Ratio of distance from the base to the maximum width of the basal leaflet
ABL	Area of basal leaflet
Middle leaflet	
MPL	Middle pulvinulum length
LML	Length of middle leaflet (not including pulvinulum)
WML	Width of middle leaflets at widest point
DML	Distance from the base to the maximum width of the middle leaflet
RLWM	Ratio of middle leaflet length to width
RMW	Ratio of distance from the base to the maximum width of the middle leaflet
AML	Area of middle leaflet
Terminal leaflet	
TPL	Terminal pulvinulum length
LTL	Length of terminal leaflet (not including pulvinulum)
WTL	Width of terminal leaflet at widest point
DTL	Distance from the base to the maximum width of the terminal leaflet
RLWT	Ratio of terminal leaflet length to width
RTW	Ratio of distance from the base to the maximum width of the terminal leaflet
ATL	Area of terminal leaflet
Flower	
BRL	Bracteole length
BRW	Bracteole width
CLL	Calyx length
CLW	Calyx width
SPL	Standard petal length
SPW	Standard petal width
WPL	Wing petal length

WPW	Wing petal width
KPL	Keel petal length
KPW	Keel petal width
SSL	Filament sheath length
SFL	Stamens filament length
ATHL	Anther length
ATW	Anther width
NEL	Nectary length
NEW	Nectary width
GSL	Gynoecium stipe length
OVL	Ovary length
OVW	Width of ovary at widest point
STL	Style length
Fruit	
SFL	Stipe length
SCL	Seed chamber length
SCW	Seed chamber width
WFL	Wing length
WFW	Wing width
TFL	Total fruit length
RSCW	Ratio of seed chamber length to wing length

Table 2. Morphological characters of leaves and leaflets (n = 23) and of flowers and fruits (n = 27).

4.4.4. Morphometrical analysis

We created a database for each analyzed sample and include information provided by the labels of the exsiccate: Id – used to indicate which material represented the information obtained in the analysis; taxon name; collector; collector number; barcode or herbarium registration number; country; state, department or province; city; locality; original latitude and longitude, when indicated and municipal latitude and longitude, when originals were missing, and subsequently all label's information. We were careful to include the material following the setting of a sample referring to a collector/collector number, so in that way, we would not analyze samples referring to a duplicate.

We analyzed the results of all measurements using multidimensional statistical methods that are designed for complex data sets. These methods consider the co-varying nature of data and can evidence the structures that underlie the data (Legendre and Legendre 2012).

They are classified in three ways, quantitative, semiquantitative and qualitative data. Quantitative data describe the variability of the structure of the assemblage as a whole and it is related with multinormally distribution; semiquantitative is based on ranked observations instead of quantitative values relationships, and qualitative data is neither quantitative nor ordered, it represents, for example color, locality, and geological substrate (Legendre and Legendre 2012).

In this study, we selected only quantitative date and to analyze them we applied Clustering, represented by the Dendrogram, and Ordination, represented by the Principal Component Analysis (PCA). In both analyses, we used the Bray-Curtis dissimilarity index that can analyze quantitative and semiquantitative data and, it is an asymmetrical coefficient that can deal with missing data, giving more emphasis to more abundant specimens (Bray and Curtis 1957; Beals 1984; Faith et al. 1987; Gomero et al. 2016; Lima 2019).

Boxplot graphics were presented to discuss the most representative characters obtained in the PCA analysis. We recorded the median and where the morphological characteristics were grouped in the sampled morphotypes, highlighting the outliers (discordant or absent data).

Finally, to test the hypothesis that there is more than one taxon in *Machaerium acutifolium* complex, we selected the most represented characters form the vegetative PCA and we performed the Normal Mixture Modeling test (NMMs) that combine model-based hierarchical clustering and the Bayesian Information Criterion (BIC) in comprehensive strategies for clustering analysis (Scrucca et al. 2016, Damasco et al. 2019).

All the analyses were developed using the R program version 2023.3.0. Analyses were produced using ade4, cowplot, factoextra, FactoMineR, ggdendro, ggplot2, mclust, tibble, tidyverse, vegan and viridis packages and the graphics were made using ggplot and ggplot2 functions (Dray and Dufour 2007; Sebastien et al. 2008; Scrucca et al. 2016, Wickham 2016; Villanueva and Chen 2019; Wickham et al. 2019; Kassambara and Mundt 2020; Wilke 2020; Oksanen et al. 2021; Simon et al. 2021; Müller and Wickham 2023; R Development Core Team 2023).

4.4.5. Ecological analysis

We extracted climate data from the WorldClim v.2.1 model layers database (Fick and Hijmans 2017) to establish of each analyzed specimen that presented correct georeferenced point and we add the additional material examinated in Chapter II following the same settings

of all morphotypes analyzed, using the raster package (Hijmans et al. 2005), in R software (R Development Core Team 2010). To obtain the graphics and edit them, the packages ggbiplot and ggplot2 were used and the colors were defined using the viridis package.

The following variables were used to assess the association between environment and morphology: Annual Precipitation (BIO12) and Seasonality of Precipitation – Coefficient of Variation (BIO 15). To generate the distribution map, we used the rasterVis and maptools packages, including the raster file of the bioclimatic variable BIO 12 showing the distribution according to precipitation, following the models developed in Leguminosae (Toledo et al. 2012) and then we combined this variable with BIO 15 to assess if there is any relation concerning the distribution of the analyzed samples.

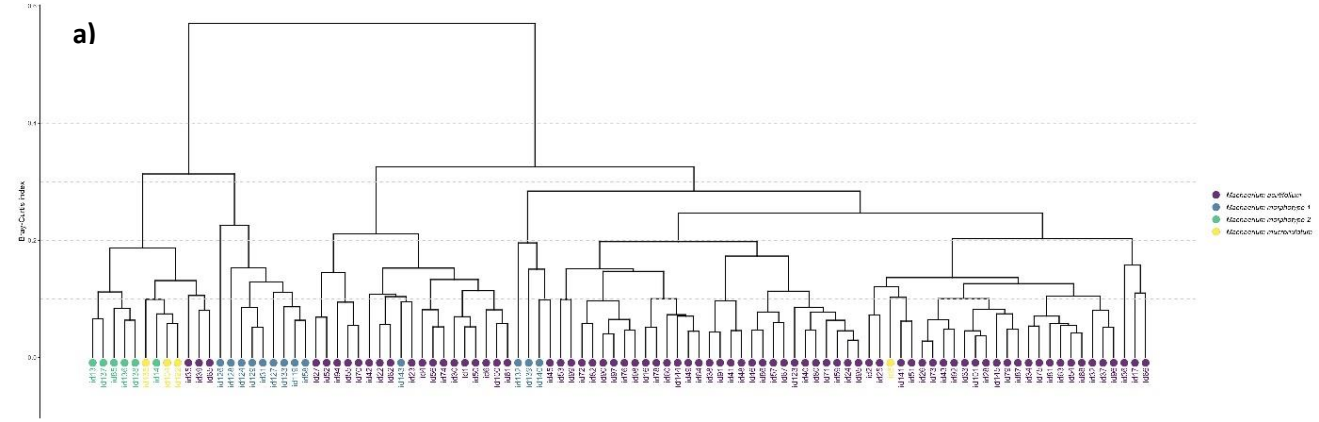
For that, we include 92 materials from *Machaerium acutifolium* 21 from *Machaerium mucronulatum*, 26 from *Machaerium* morphotype 1, and 15 from *Machaerium* morphotype 2.

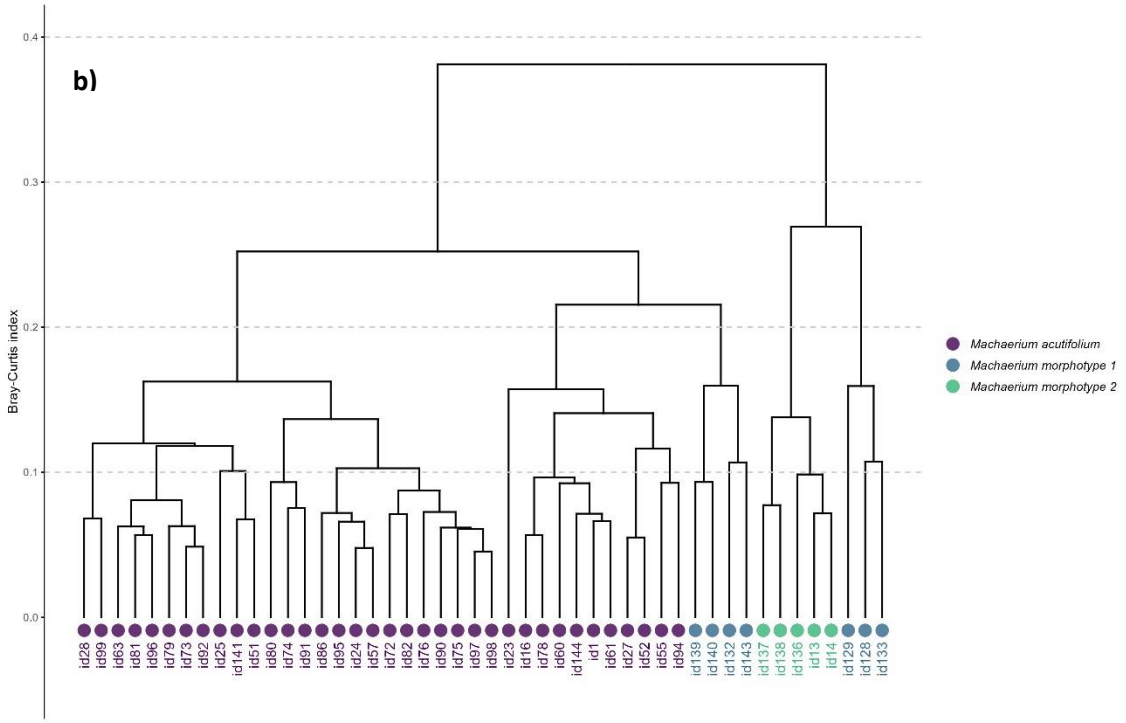
4.5. Results and Discussion:

4.5.1. Clustering analysis:

Clustering is an operation by which the set of objects or descriptors is partitioned in two or more subsets (clusters), using pre-established rules of agglomeration or division (Legendre and Legendre 2012). In general, this analysis is presented in a dendrogram graphic that summarizes a great amount of data and presents it in simpler visualization.

Here, we provided three different dendrograms, the first with only vegetative characters, the second including vegetative and floral characters and the third including vegetative and fruit characters. There is no complete sample from *Machaerium mucronulatum* with vegetative and flower characters, but this reproductive piece was analyzed separately and included in Chapter II.





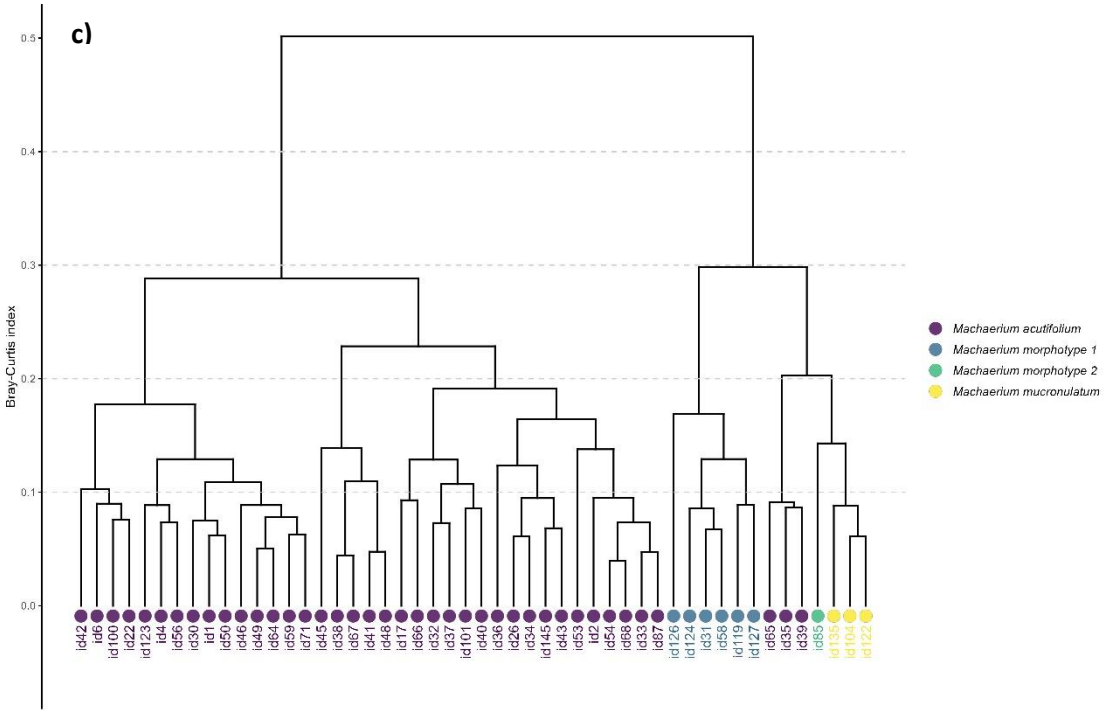


Figure 1. Dendrograms; a) Vegetative characters. b) Vegetative and floral characters. c) Vegetative and fruit characters.

Machaerium presents generally a wide variation in vegetative characters, and these differences were a manner that Bentham in 1862 used to propose five series for the genus, although Filardi (2011) proved by molecular analysis, that most of these series were not monophyletic. Based on this statement, we did not observe in the vegetative dendrogram (Figure 1a), a clear separation in the morphotypes here proposed, on the contrary, we observed an overlap on *Machaerium acutifolium*, *M. mucronulatum* and *Machaerium* morphotype 1. Only *Machaerium* morphotype 2 showed a preliminary separation, being grouped five on its six samples in a cluster and the explanation for that is these samples present, generally, smaller leaflets.

When we included reproductive characters, the dendrogram conformation changed and we were able to observe a more detailed separation within the morphotypes. Regarding the floral characters (Figure 1b), the dendrogram presented a complete separation to *Machaerium acutifolium* from both morphotypes. This time, materials indicated as *Machaerium acutifolium* as well as morphotype 2 formed individuals cluster, meanwhile morphotype 1 formed two cluster. This configuration can be explained because most materials from this morphotype

present five leaflets, but we were able to include samples with seven and in addition, flowers from these samples frequently present being slightly greater.

As concerning fruit characters, we were able to include at least one of each morphotypes in all analysis. That way we observed in the vegetative and fruit dendrogram a cluster including all materials from *Machaerium* morphotype 1 and another with *M. mucronulatum* (Figure 1c). Even though we included only a sample that corresponds to morphotype 2, we noticed that it was in a distant point from *M. acutifolium* samples, and it was grouped close to *M. mucronulatum* cluster but because these two morphotypes present a higher Bray-Curtis index (~ 0.15) they were categorized in different groups.

This time *Machaerium acutifolium* was grouped in two clusters and the explanation for that is because the samples that formed the smaller group (id 35, id 39, id 65) were collected in Piauí state, in Caatinga biome and the leaflets and fruits present smaller values, especially in width.

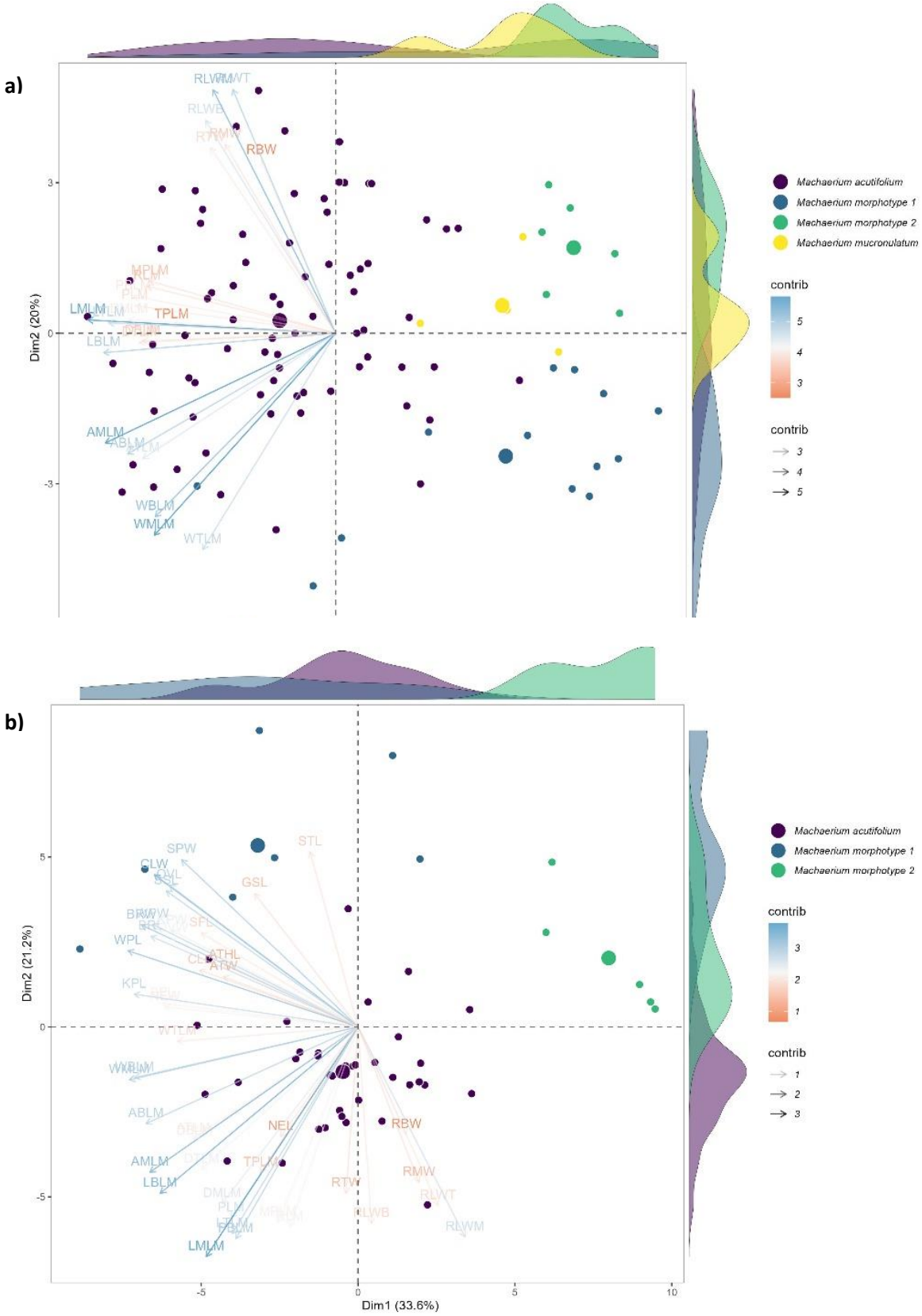
4.5.2 Ordination analysis:

Ordination in reduced space is an operation by which the objects or descriptors are represented in a space that contains fewer dimensions than in the original data set (Legendre and Legendre 2012). As we choose to include only quantitative date, we decided to present a PCA whereas it can be better applied when Euclidean distance is more appropriate (Gower, 1996).

Following the same standard from Clustering analysis, here we provided three PCAs, the first with only vegetative characters, the second including vegetative and floral characters and the third including vegetative and fruit characters (Figure 2).

After that, referring to the PCAs, we produced bar graphs illustrating a list with ten most representative characters for each analysis. Then we used them to produce boxplot graphs to facilitate the visualization of this variation. Both vegetative and vegetative/fruit analyzes presented the same representative characters and therefore, we indicate them in boxplots in figure 3.

The bar graph for the vegetative (figure 5) was used to produce the Normal Mixture Models (NMMs) analysis in the following session, and the other two graphs can be seen in the supplementary material at the end of this chapter.



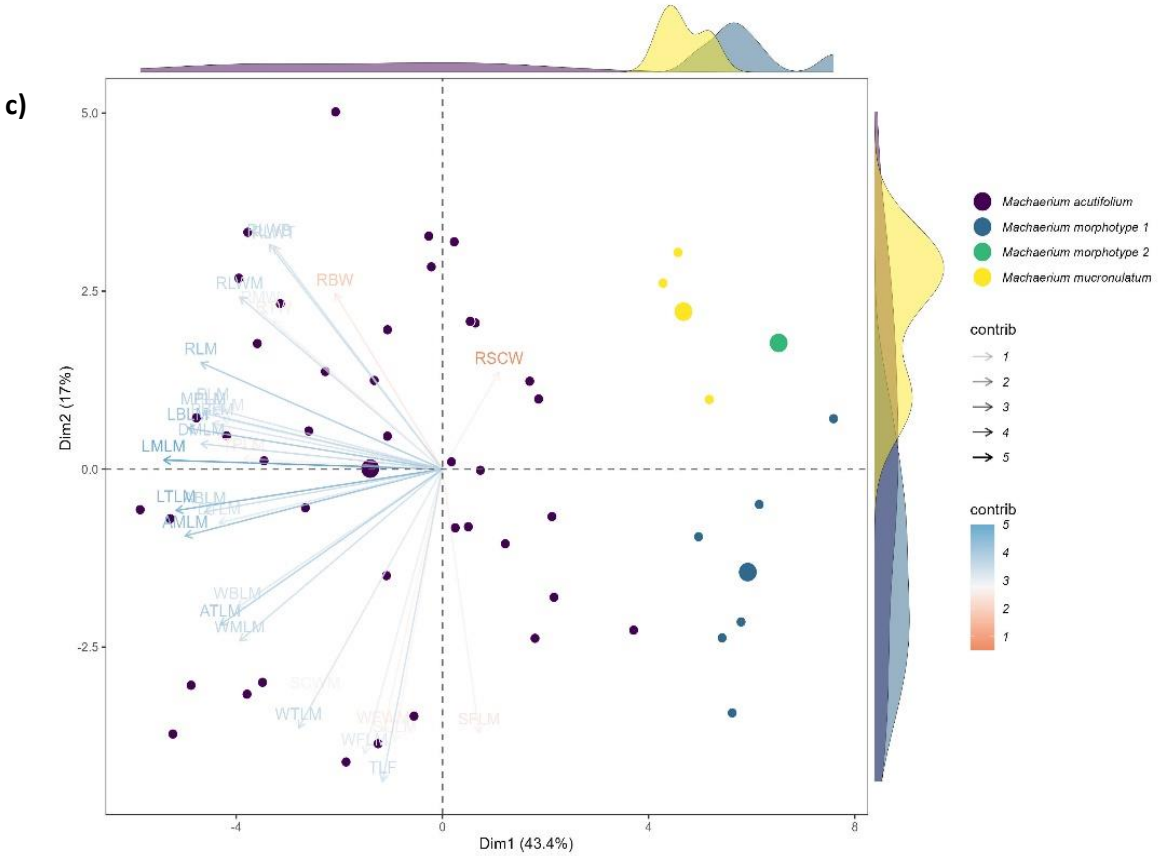


Figure 2. PCAs; a) Vegetative characters. b) Vegetative and floral characters. c) Vegetative and fruit characters. **PLM** – Petiole length; **RLM** – Rachis length; **BPLM** – Basal pulvinulum length; **LBLM** – Length of basal leaflet; **WBLM** – Width of basal leaflets at widest point; **DBLM** – Distance from the base to the maximum width of the basal leaflet; **RLWBM** – Ratio of basal leaflet length to width; **RBWM** – Ratio of distance from the base to the maximum width of the basal leaflet; **ABLM** – Area of basal leaflet; **MPLM** – Middle leaflet pulvinulum length; **LMLM** – Length of middle leaflets; **WMLM** – Width of middle leaflets at widest point; **DMLM** – Distance from the base to the maximum width of the middle leaflet; **RLWM** – Ratio of middle leaflet length to width; **RMWM** – Ratio of distance from the base to the maximum width of the middle leaflet; **AMLM** – Area of middle leaflet; **TPLM** – Terminal leaflet pulvinulum length; **LTLM** – Length of terminal leaflet; **WTLM** – Width of terminal leaflets at widest point; **DTLM** – Distance from the base to the maximum width of the terminal leaflet; **RLWTM** – Ratio of terminal leaflet length; **RTWM** – Ratio of distance from the base to the maximum width of the terminal leaflet to width; **ATLM** – Area of terminal leaflet; **BRL** – Bracteole length; **BRW** – Bracteole width; **CLL** – Calyx length; **CLW** – Calyx width; **SPL** – Standard petal length; **SPW** – Standard petal width; **WPL** – Wing petal length; **WPW** – Wing petal width; **KPL** – Keel petal length; **KPW** – Keel petal width; **SSL** – Stamens filament sheath length; **SFL** – Stamens filament length; **ATHL** – Anther length; **ATW** – Anther width; **NEL** – Nectary length; **NEW** – Nectary width; **GSL** – Gynoecium stipe length; **OVL** – Ovary length; **OVW** – Width of ovary at widest point; **STL** – Style length; **SFL** – Stipe length; **SCL** – Seed chamber length; **SCW** – Seed chamber width; **WFL** – Wing length; **WFW** – Wing width; **TFL** – Total fruit length; **RSCW** – Ratio of seed chamber length to wing length.

In vegetative PCA (Figure 2a), we observed that Dim 1 explains 48.2% of the variation and *Machaerium acutifolium* was largely distributed on the negative axis, meanwhile *M. mucronulatum* and the other morphotypes were all grouped together in the positive axis, except by a single point from *M*. morphotype 1. About Dim 2, that explains 20% of the variation, *M. acutifolium* was dispersed throughout this dimension, overlapping with the other groups and we observed that morphotype 1 was concentrated in the negative part of this axis and the opposite was observed for morphotype 2. Regarding *M. mucronulatum*, its distribution was observed in both axes.

Almost the same organization was observed in vegetative and fruit PCA (Figure 2c). The main differences were that all samples of morphotype 1 was grouped together in the positive axis from Dim 1, that explains 43.4% of the variation and *Machaerium mucronulatum* was completed distributed in the positive part in Dim 2, that explains 17% of the variation.

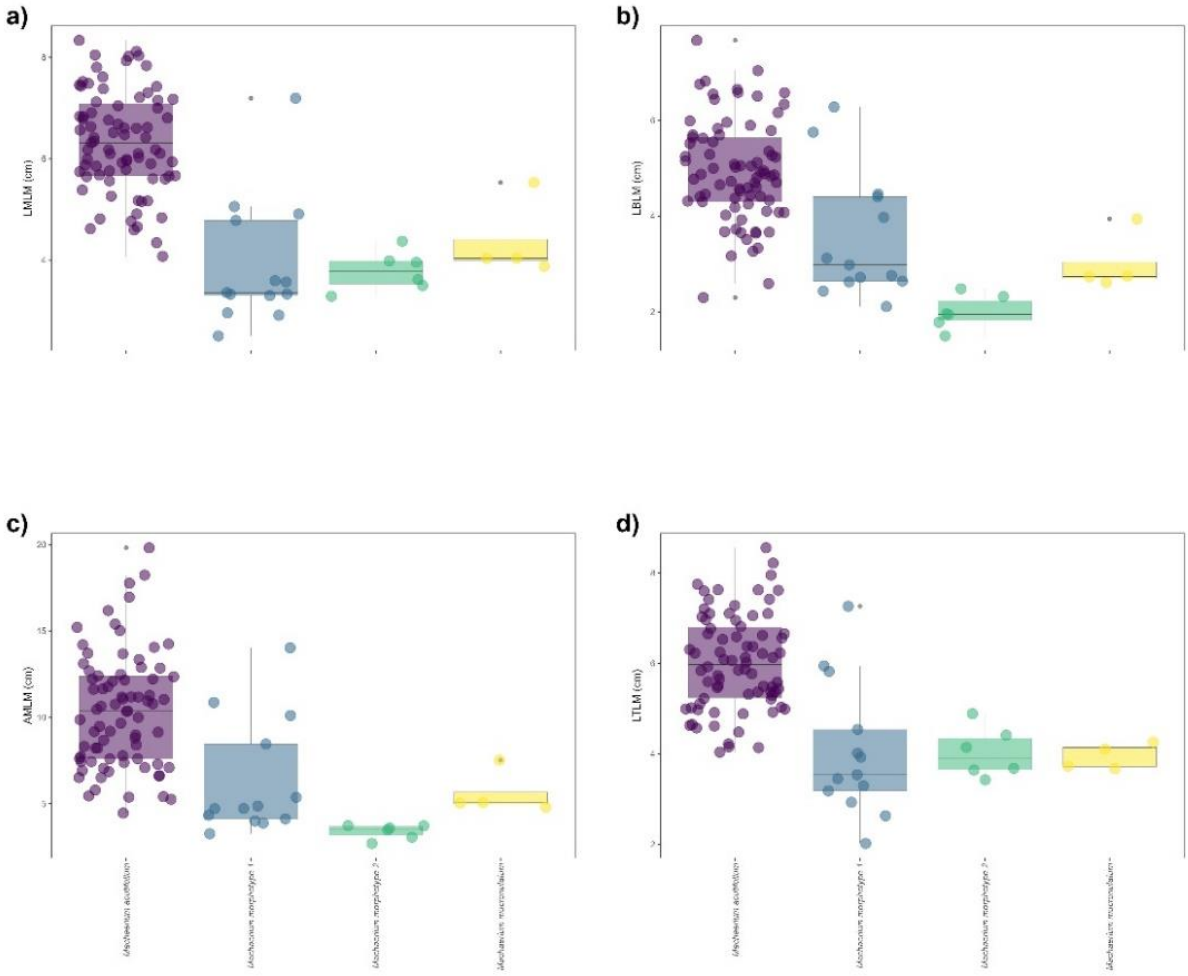


Figure 3. Boxplots of most representative vegetative characters; a) **LMLM** – Length of middle leaflet. b) **LBLM** – Length of basal leaflet. c) **AMLM** – Area of middle leaflet. d) **LTLM** – Length of terminal leaflet.

Concerning the vegetative and floral PCA (Figure 2b), although Dim 1 explains 33.6% of the variation, an interesting organization was observed in Dim 2, that explains 21.2% where *Machaerium acutifolium* was largely concentrated in the negative axis and in the meantime, both morphotype 1 and morphotype 2 were concentrated completely in the positive axis. Dim 1 present numerous overlapping but we observed that only morphotype 2 remained in the positive axis.

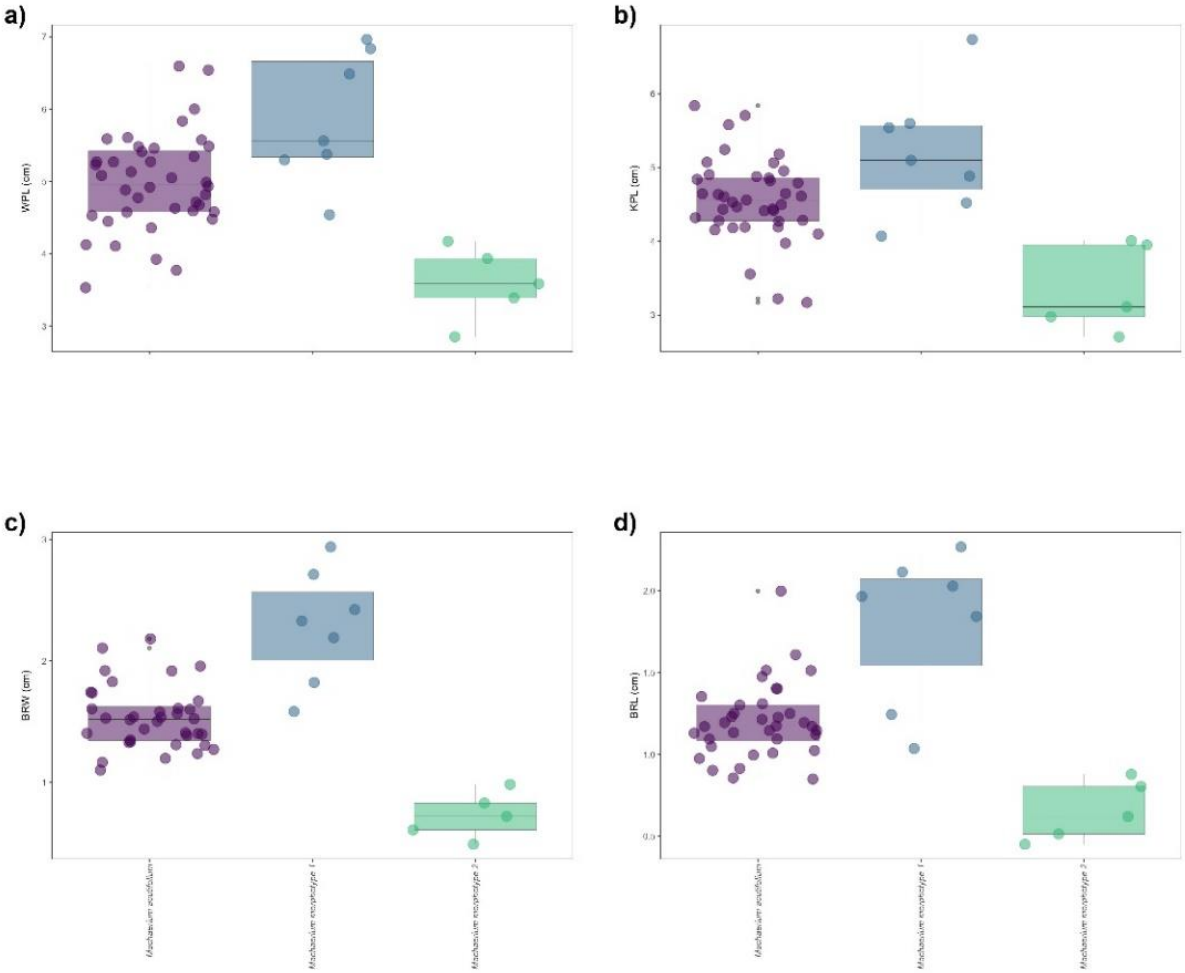


Figure 4. Boxplots of most representative flowers characters; a) **WPL** – Wing petal length. b) **KPL** – Keel petal length. c) **BRW** – Bracteole width. d) **BRL** – Bracteole length.

4.5.3 Normal mixture models analysis:

After recuperating which were the most representative characters for the vegetative PCA (Figure 5), we used them to perform the NMMs analysis. We used The Bayesian Information Criterion (BIC) (Schwarz, 1978) as well as the Classification Criterion to evaluate the best-fit number of morphological groups (Cadena et al. 2018, Damasco et al. 2019).

We preformed a great number of test in the reproductive characters but because of the missing data, we do not have a best number of samples both in floral and in fruit characters to produce a NMM analysis. Only when we added all the 102 vegetative samples, that we were able to produce them.

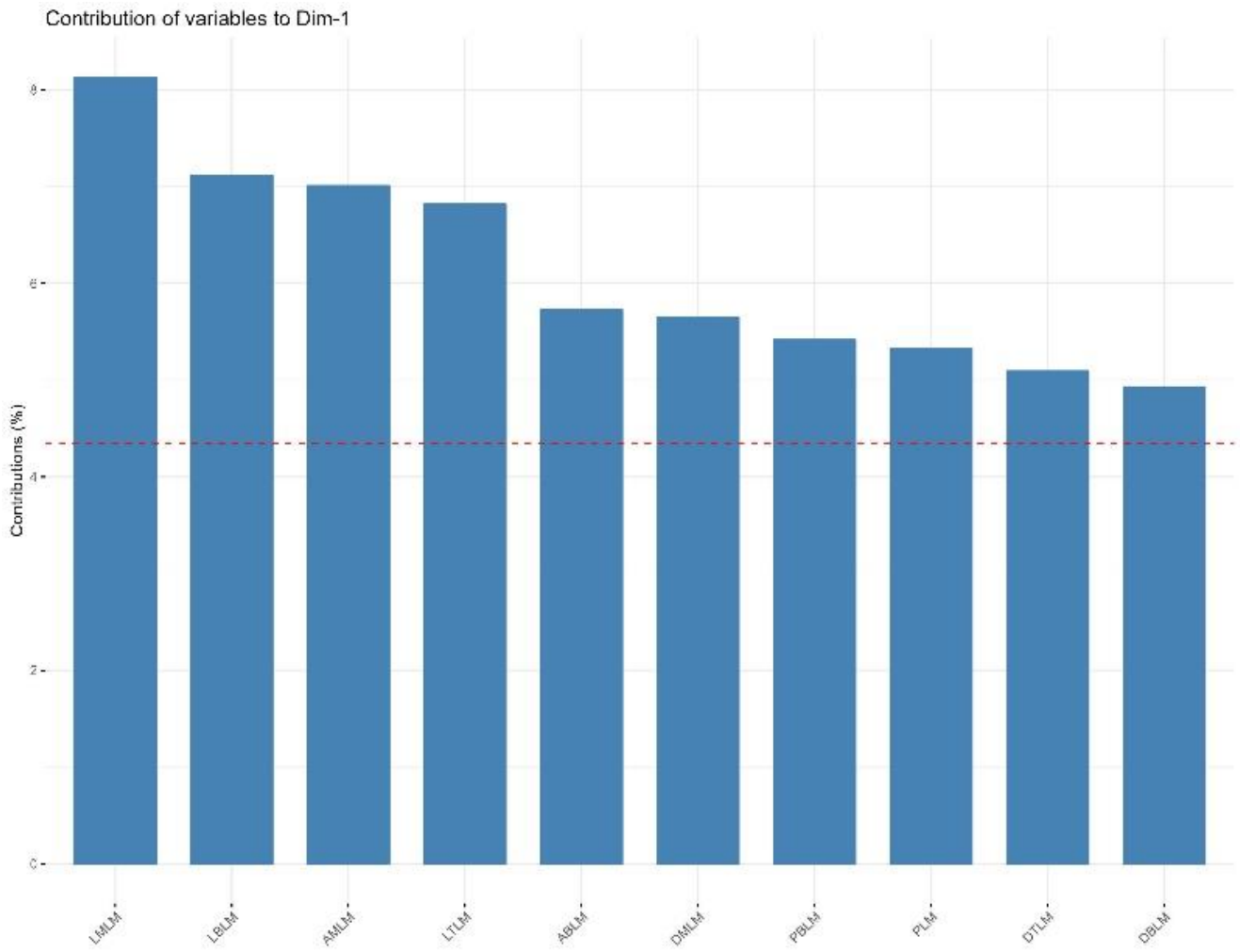


Figure 5. Vegetative bar graph of most representative characters. **PLM** – Petiole length; **PBLM** – Basal pulvinulum length; **LBLM** – Length of basal leaflet; **DBLM** – Distance from the base to the maximum width of the basal leaflet; **ABLM** – Area of basal leaflet; **LMLM** – Length of middle leaflet (not including pulvinulum); **DMLM** – Distance from the base to the maximum width of the middle leaflet; **AMLM** – Area of middle leaflet; **LTLM** – Length of terminal leaflet; **DTLM** – Distance from the base to the maximum width of the terminal leaflet.

When we applied the BIC test (Figure 6), we observed three optimal clusters formed in the vegetative analysis. The best model that explains this variantion was VEE that means the interaction between the variables and the groupings formed was agrupped in an ellipsiodal configuration, with varible volume and equal shape.

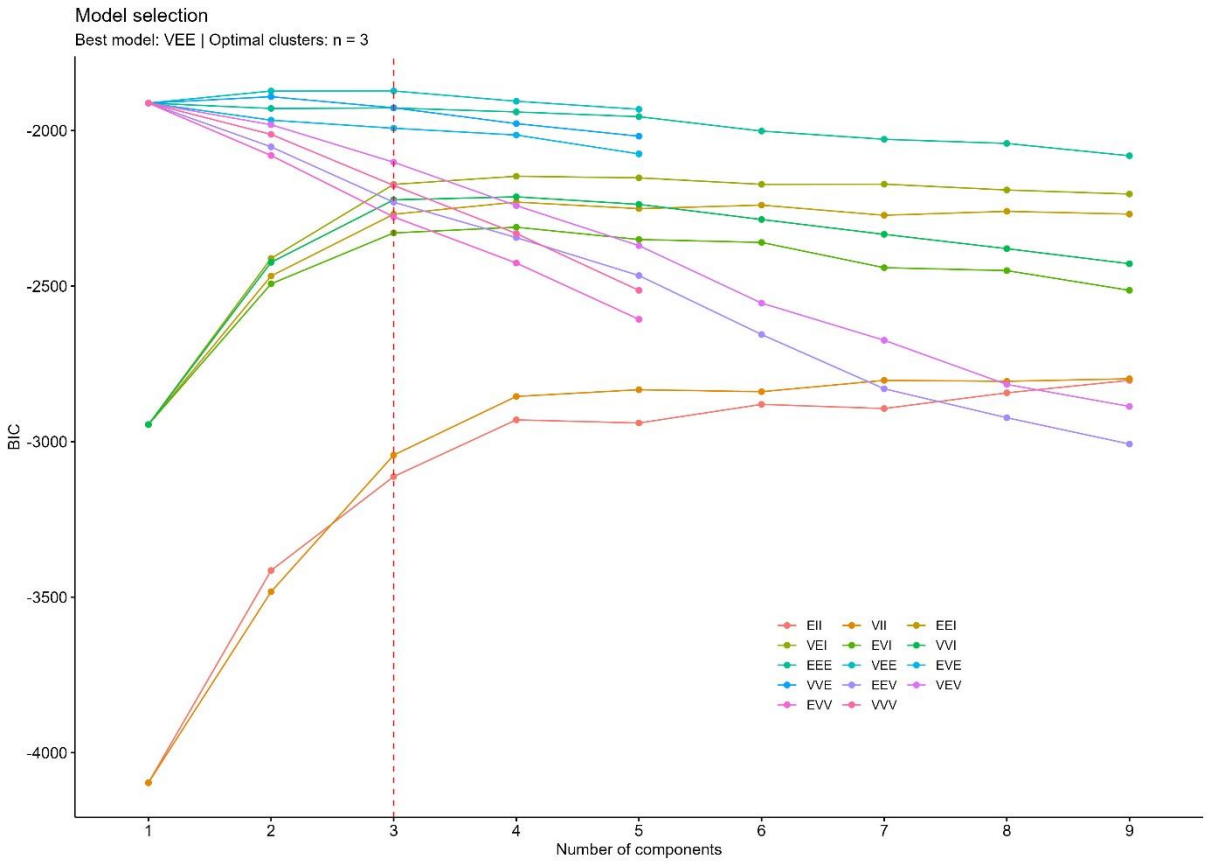


Figure 6. Bayesian Information Criterion of vegetative characters.

To see which groups were formed, we used the Classification Criterion, also included in the mclust package. We produced two graphics from the four most representative characters and the groups formed were indicated in different colors (Figure 7).

Even though this analysis is based on statistical information, diferent from Clustering and Ordernation that were exploratory tests, the Classification Criterion was not able to distingish with precision all morphotypes detected in the previous analyses. For example, in Figure 7a, we observed that one group highlighted in gray presents both morphotype 1, represented in black marking and morphotype 2 represented in red marking. The same was observed in Figure 7b.

However, this analysis was able to return the information that in the *Machaerium acutifolium* species complex, there is at least more than one group which corroborates the exploratory analyses. Indeed, our NMMs results were similar with the vegetative dendrogram and PCA (Figures 1a and 2a) when we obseerved few ordination in the main groups explained by a great number of overllaped characteristcs.

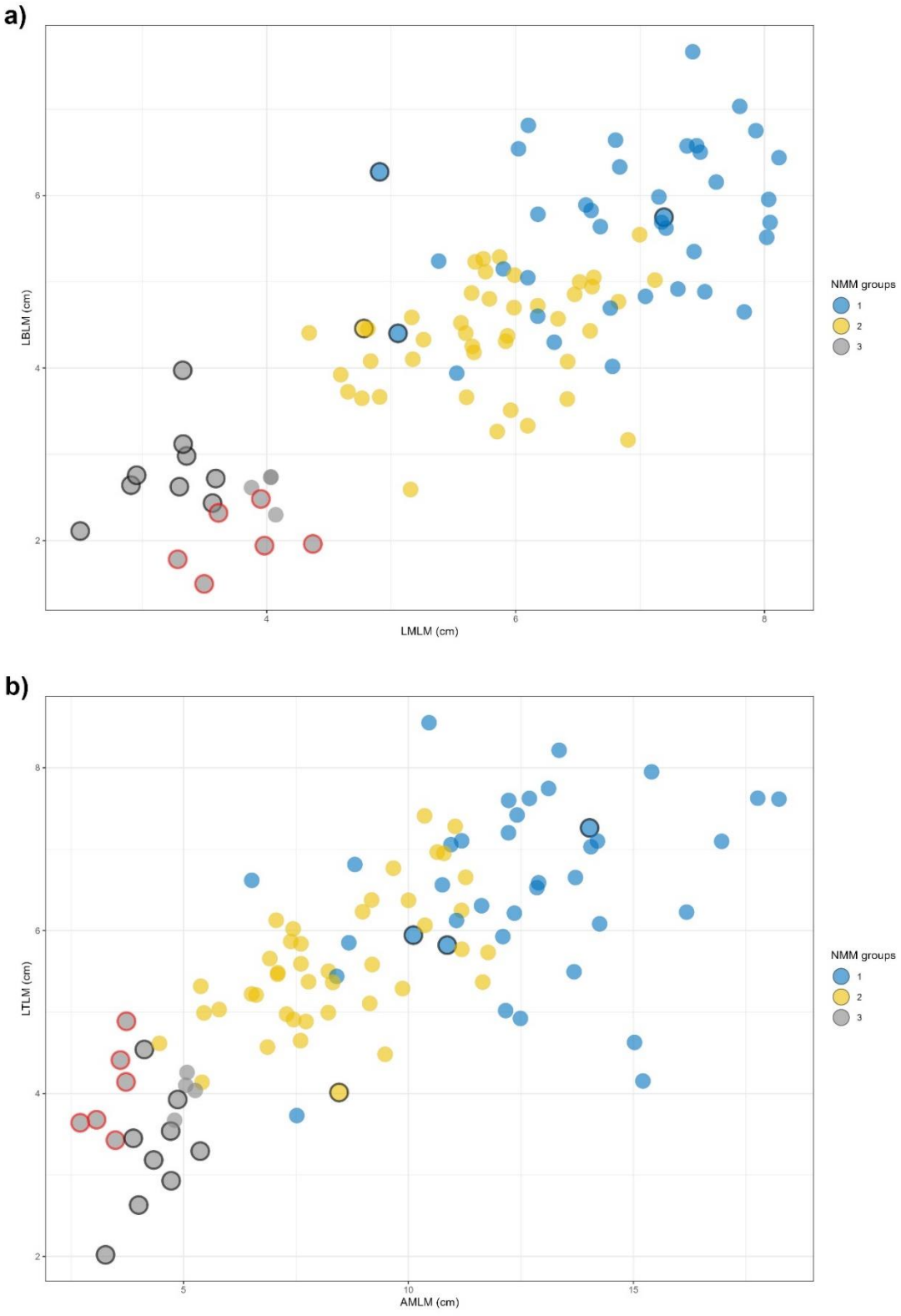


Figure 7. Classification Criterion of the four most representative vegetative characters. a) LBLM and LMLM. b) LTLM and AMLM

4.5.4 Ecological analysis:

By plotting the distribution map including information on annual precipitation (BIO 12), (Figure 8a) we were able to observe that the complex is distributed across deciduous and semideciduous forests, known as seasonally dry tropical forests, savanna and chaco, more precisely presenting a distribution pattern known as "Pleistocene Arc" along with the distribution pattern of several other genera among Leguminosae (Prado and Gibbs 1993; Pennington et al. 2000; Cardoso and Queiroz 2010).

We observed from the map that *M. acutifolium* has the largest distribution area, occurring beyond the Brazilian territory, corroborating the information from (Filardi 2011). However, we did not able to verify the occurrence of this species for Bahia state. Only *M. mucronulatum* and morphotypes 1 and 2 were found in this region, highlighting morphotype 1, with a restricted distribution along the Espinhaço Range.

When we compared Annual Precipitation (BIO12) and Seasonality of Precipitation – Coefficient of Variation (BIO 15) (Figure 8b), we observed another expressive separation between *M. acutifolium* and *M. mucronulatum* from morphotype 1 and morphotype 2. It was explained because these two morphotypes were found in drier location mostly in Caatinga biome.

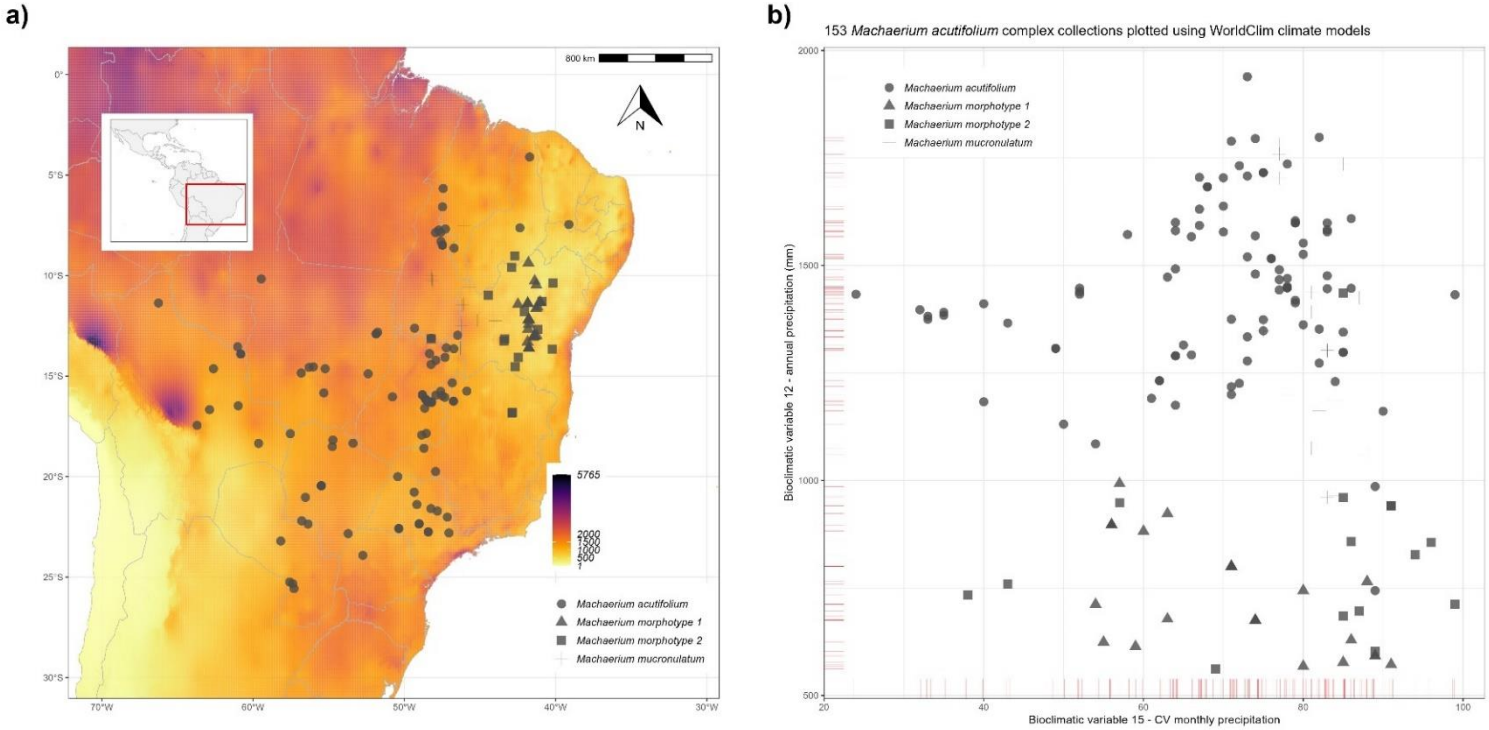


Figure 8. Ecological analysis. a) Distribution map of the complex using BIO 12. b) Comparison between Annual Precipitation (BIO12) and Seasonality of Precipitation – Coefficient of Variation (BIO 15).

Thus, as of the results obtained from the morphometric and ecological data, we were able to understand that morphological variations is related to the geographic distribution of the complex and we can explain that this variation observed represents an association of the phenotypes with the environment, once climatic variables represent important delimiters in the morphological variation along the distribution of the specimens as observed by Toledo et al. (2012) and may be responsible for speciation events, as reported by Ceolin and Miotto (2012).

With that, our results based on integrated analysis highlighted four groups, with morphological, ecological and, distribution distinctiveness.

When evaluating all type materials of the genus in the tropical America region, we concluded that morphotypes 1 and 2 represent distinct taxonomic entities, with unique morphological differences that must be recognized at the species level. Thus, in chapter II, we proposed them respectively as *Machaerium* sp. nov. 1 and *Machaerium* sp. nov. 2

4.6. References:

Andres-Sanchez, S., E. Rico, A. Herrero, M. Santos-Vicente, and M. M. Martinez-Ortega. 2009. Combining traditional morphometrics and molecular markers in cryptic taxa: towards an updated integrative taxonomic treatment for *Veronica* subgenus *Pentasepalae* (Plantaginaceae sensu APG II) in the western Mediterranean. *Botanical Journal of the Linnean Society* 159(1): 68–87.

Beals, E. W. 1984. Bray-Curtis's ordination: an effective strategy for analysis of multivariate ecological data. Pp. 1–55 in *Advances in ecological research*, ed. A. MacFadyen, and E. F. Ford. Cambridge: Academic Press.

Bebber, D. P., M. A. Carine, J. R. I. Wood, A. H. Wortley, D. J. Harris, G. T. Prance, G. Davidse, J. Paige, T. D. Pennington, N. K. B. Robson and R. W, Scotland. 2010. Herbaria are a major frontier for species discovery. *Proceedings of the National Academy of Sciences* 107(51): 22169–22171.

Bennett, J. R., J. R. I. Wood, R. W. Scotland. 2008. Uncorrelated variation in widespread species: species delimitation in *Strobilanthes echinata* Nees (Acanthaceae). *Botanical Journal of the Linnean Society*, 156(1): 131–141.

Bentham, G. 1837. *Commentationes de Leguminosarum Generibus*. Vienna: Zollinger.

Bentham, G. 1860. Synopsis of Dalbergieae a tribe of Leguminosae. *Botanical Journal of the Linnean Society*, 4 (s1): 1–128.

Bentham, G. 1862. Leguminosae. Dalbergieae. Pp 1–350 in *Flora Brasiliensis*, ed. C. F. P. Martius, A. W. Eichler, and I. Urban. Vienna: R. Oldenbourg Verlag.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological monographs*, 27(4): 325–349.

Cadena, C. D., F. Zapata, and I. Jiménez, 2018. Issues and perspectives in species delimitation using phenotypic data: Atlantean evolution in Darwin's finches. *Systematic Biology* 67: 181–194.

Cardoso, D. and L. P. Queiroz. 2010. Caatinga no contexto de uma Metacomunidade: Evidências da Biogeografia, Padrões Filogenéticos e Abundância de Espécies em Leguminosas.

Pp. 241 – 260 in: *Biogeografia da América do Sul: padrões e processos*, org. C. J. B. Carvalho and E. A. B. Almeida. São Paulo: Roca.

Casiva, P. V., B. O. Saidman, J. C. Vilardi, and A. M. Cialdella. 2002. First comparative phenetic studies of Argentinean species of *Acacia* (Fabaceae), using morphometric, isozymal, and RAPD approaches. *American Journal of Botany* 89(5): 843–853.

Castro-Bonilla M. A., M. L. Bueno, P. S. R. Romano, V. F. Dutra, J. N. Fregonezi, and F. C. P. Garcia. 2022. Species delimitation of the Atlantic Forest endemic *Inga subnuda* (Leguminosae, Caesalpinioideae, Mimosoid Clade) subspecies based on morphological, ecological, and palaeoecological data. *Systematic Botany* 47(2): 417–430.

Ceolin, G. B., and S. T. S. Miotto. 2012. Combining ecological and morphometrical approaches to increase the resolution within the *Galactia neesii* (Leguminosae) complex. *Plant Systematics and Evolution* 298 (3): 645–652.

Crameri, S., P. B. Phillipson, N. Rakotonirina, N. Wilding, R. L. Andriamiarisoa, P. P. Lowry II, and A. Widmer. 2022. Taxonomic Studies on Malagasy *Dalbergia* (Fabaceae). III. Two New Species from Southeastern Madagascar and an Emended Description of the Rosewood Species *Dalbergia maritima*. *Systematic Botany* 47(2): 397–416.

Damasco, G., D. C. Daly, A. Vicentini, and P. V. Fine. 2019. Reestablishment of *Protium cordatum* (Burseraceae) based on integrative taxonomy. *Taxon* 68(1): 34–46.

De Queiroz, K. 2007. Species concepts and species delimitation. *Systematic Biology* 56(6): 879–886.

De La Estrella, M., C. Aedo, and M. Velayos. 2009. A morphometric analysis of *Daniellia* (Fabaceae–Caesalpinioideae). *Botanical Journal of the Linnean Society* 159(2): 268–279.

Doyen, J. T., and C. N. Slobodchikoff. 1974. An Operational Approach to Species Classification. *Systematic Zoology*. 23(2): 239–247.

Dray S., and A. Dufour. 2007. The ade4 Package: Implementing the Duality Diagram for Ecologists. *Journal of Statistical Software* 22(4): 1–20.

Ducke, A. 1949. Notas sobre a Flora Neotrópica II - as leguminosas da Amazônia brasileira. *Boletim Técnico do Instituto Agronômico do Norte* 18: 1–248.

Egan, A. N. 2015. Species delimitation and recognition in the *Pediomelum megalanthum* complex (Fabaceae) via multivariate morphometrics. *PhytoKeys* 44: 65–87.

Eigenbrod, F., P. Gonzalez, J. Dash, and I. Steyl. 2015. Vulnerability of ecosystems to climate change moderated by habitat intactness. *Global Change Biology* 21(1): 275–286.

Faith, D. P., P. R. Minchin, and L. Belbin. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetation* 69: 57–68.

Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37(12): 4302–4315.

Filardi, F. L. R. 2011. *Avanços na Sistemática de Machaerium Pers. (Leguminosae Papilionoideae Dalbergieae): Filogenia e Revisão Taxonômica das espécies do Domínio Atlântico*. Doctoral dissertation (dissertation in Botany). Rio de Janeiro: Escola Nacional de Botânica Tropical, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

Filardi, F. L. R. and H.C. Lima. 2014. The diversity of *Machaerium* (Leguminosae: Papilionoideae) in the Atlantic Forest: Three new species, nomenclatural updates, and a revised key. *Systematic Botany* 39(1):145–159.

Filardi, F. L. R., H. C. Lima, D. B. O. S. Cardoso. 2020. *Machaerium in Flora e Funga do Brasil*. Jardim Botânico do Rio de Janeiro. Available from: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB23055 (last accessed August 2023).

Gomero, D. R. A., C. R. García-Dávila, C. G. Hidalgo, G. R. F. L. Pizango, D. D. C. Torres, C. R. Reynel, E. P. Mondragón, and E. N. H. Coronado. 2016. Análisis morfométrico de las especies de *Dipteryx* en la Amazonía Peruana. *Folia Amazónica* 25: 101–118.

Gower, J. C. 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53: 325–338.

Grace, O. M., O. A. Pérez-Escobar, E. J. Lucas, M. S. Vorontsova, G. P. Lewis, B. E. Walker, L. G. Lohmann, S. Knapp, P. Wilkie, T. Sarkinen, I. Darbyshire, E. N. Lughadha, A. Monro, Y. Woudstra, S. Demissew, A. M. Muasya, S. Díaz, W. J. Baker, and A. Antonelli. 2021. Botanical Monography in the Anthropocene. *Trends in Plant Science* 26(5): 433–411.

Guerra, E., M. P. Morim, and J. R. V. Iganci. 2016. A new species of *Abarema* (Fabaceae) from Brazil. *Phytotaxa* 289(1): 77–82.

Heberling, J. M., L. A. Prather, and S. J. Tonsor. 2019. The changing uses of herbarium data in an era of global change: An overview using automated content analysis. *BioScience* 69(10): 812–822.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high-resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25(15): 1965–1978.

Image-Pro Plus. *Photo analysis and professional image software*. Available from: http://www.mediacy.com/imageproplus (last accessed April 2023).

Kassambara, A. and F. Mundt. 2020. factoextra: Extract and Visualize the Results of Multivariate Data Analyses. *R package version* 1.0.7.

Knaus, B. J. 2010. Morphometric architecture of the most taxon-rich species in the US flora: *Astragalus lentiginosus* (Fabaceae). *American Journal of Botany* 97(11): 1816–1826.

Legendre, P., L. Legendre. 2012. *Numerical ecology third edition*. Amsterdam: Elsevier.

Lewis, G. P. 1987. *Legumes of Bahia*. Kew: Royal Botanic Gardens.

Lima, A. N. 2019. *Revisão Taxonômica do gênero Platypodium (Leguminosae, Papilionoideae)*. Master thesis (thesis in Botany). Rio de Janeiro: Escola Nacional de Botânica Tropical, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

Loefgren, A. 1895. Uma synonimia dos nomes populares das plantas indígenas do estado de São Paulo. *Boletim da Comissão Geographica e Geologica de São Paulo* 10: 25.

Meireles, J. E., and H. C. Lima. 2013. A new species of *Ormosia* (Leguminosae, Papilionoideae, Sophoreae) from the Brazilian Atlantic Rain Forest. *Phytotaxa* 143(1): 54–60.

Mendonça Filho, C. V. 2002. *Citotaxonomia de Machaerium Pers. e revisão taxonômica de Machaerium sect. Oblonga (Benth.) Taub. (Leguminosae-Papilionoideae).* 2002. Doctoral dissertation (dissertation in Botany). Campinas: Universidade Estadual de Campinas.

Müller, K., and Wickham, H. 2023. tibble: Simple Data Frames. *R package version* 3.2.1.

Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, P. Solymos, M. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard,

G. Carvalho, M. Chirico, M. Caceres, S. Durand, H. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. Hill, L. Lahti, D. McGlinn, M. Ouellette, E. Ribeiro-Cunha, T. Smith, A. Stier, C. Ter-Braak, and J. Weedon. 2022. *vegan: Community Ecology Package. R package version* 2.6-4.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*, 51(11): 933–938.

Padial, J. M., A. Miralles, I. Riva, and M. Vences. 2010. The integrative future of taxonomy. *Frontiers in Zoology*, 7(1): 1–14.

Pennington. R. T., D. E. Prado, and C. A. Pendry. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* 27 (2) 261 – 273.

Pittier, H. F. 1941. *Boletín de la Sociedad Venezolana de Ciencias Naturales* 7:148.

Prado, D. E. and Gibbs, P. E. 1993. Patterns of species distributions in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden* 80: 902–927.

Queiroz, L. P. D. 2009. *Leguminosas da caatinga.* Feira de Santana: Universidade Estadual de Feira de Santana.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing*. Vienna: Austria. https://www.R-project.org/.

Robbiati, F. O., L. D. Amarilla, A. M. Anton, R. H. Fortunato. 2017. Phenotypic variation in arid and semi-arid zones of southern South America: the case of *Senna* series Aphyllae (Fabaceae, Caesalpinioideae). *Botanical Journal of the Linnean Society* 183: 454–473.

Rudd, V. E. 1973. New taxa and combinations in *Machaerium* (Leguminosae) III. *Phytologia*, 25: 399.

Rudd, V. E. 1977. The genus *Machaerium* (Leguminosae) in Mexico. *Boletín de la Sociedad Botánica de México* 37: 119–146.

Rudd, V. E. 1987a. Studies in *Machaerium* (Leguminosae) VI: Section I. Machaerium. *Phytologia* 62: 283–302.

Rudd, V. E. 1987b. Studies in *Machaerium* (Leguminosae) VII: Section II. Lineata. Part I: Species with wingless fruit. *Phytologia* 64: 1–12.

Rusby, H. H. 1910. New Species from Bolivia, Collected by R. S. Willians. *Bulletin of the New York Botanical Garden*, 6(22): 513.

Sartori, A. L. B., and A. M. A. Tozzi. 1998. As espécies de *Machaerium* Pers. (Leguminosae-Papilionoideae-Dalbergieae) ocorrentes no estado de São Paulo. *Brazilian Journal of Botany*, 21: 211–246.

Schlick-Steiner, B. C., B. Seifert, C Stauffer, E. Christian, R. H. Crozier, and F. M. Steiner. 2007. Without morphology, cryptic species stay in taxonomic crypsis following discovery. *Trends in Ecology & Evolution* 22(8) 391–392.

Sebastien, L., J. Julie, and H. Francois. 2008. FactoMineR: An R Package for Multivariate Analysis. *Journal of Statistical Software* 25(1): 1–18.

Simon, G., R. Noam, R. Robert, P. C. Antônio, S. Marco, and S. Cédric. 2021. Rvision - Colorblind-Friendly Color Maps for R. *R package version* 0.6.2.

Sousa, F. P. S. T., G. P. Lewis, and J. A. Hawkins. 2010. A revision of the South American genus *Apuleia* (Leguminosae, Cassieae). *Kew Bulletin* 65(2): 225–232.

Souza, I. M., L. S. Funch, and L. P. Queiroz. 2014. Morphological analyses suggest a new taxonomic circumscription for *Hymenaea courbaril* L. (Leguminosae, Caesalpinioideae). *PhytoKeys*, n. 38, p. 101–118.

Steven G. N., and R. Subramanyam. 2009. Testing plant barcoding in a sister species complex of pantropical *Acacia* (Mimosoideae, Fabaceae). *Molecular Ecology Resources* 9: 172–180.

Schwarz, G. 1978. Estimating the dimension of a model. *The annals of statistics* 6: 461–464.

Scrucca, L., M. Fop, T. B. Murphy, and A. E. Raftery. 2016. mclust 5: Clustering, classification and density estimation using Gaussian finite mixture models. *R Journal* 8: 289–317.

Thiers, B. 2023. [continuously updated] *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih/ (last accessed August 2023).

Toledo, M., M. Peña-Claros, F. Bongers, A. Alarcón, J. Balcázar, J. Chuviña, C. Leaño, J. C. Licona, and L. Poorter. 2012. Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology* 100: 253–263.

Villanueva R. A. M., and Z. J. Chen. 2019. ggplot2: Elegant Graphics for Data Analysis (2nd ed.). *Measurement: Interdisciplinary Research and Perspectives* 17(3): 160–167.

Vogel, J. R. T. 1837. Dalbergiearum genera brasiliensis. Pp. 177–203 in *Linnaea: Ein Journal für die Botanik in ihrem ganzen Umfange* ed. Von Schlechtendal, Berlin: Dümmler.

Whitmore T. C. 1976. Natural variation and its taxonomic treatment within tropical tree species as seen in the Far East in Tropical trees. *Variation, breeding, and conservation* ed J. Burley, B. T. Styles, eds. London: Academic Press.

Wickham, H. 2016. ggplot2: Elegant Graphics for Data Analysis. *Springer*. New York.

Wickham, H., M. Averick, J. Bryan, W. Chang, L. D. McGowan, R. François, G. Grolemund, A. Hayes, L. Henry, J. Hester, M. Kuhn, T. L. Pedersen, E. Miller, S. M. Bache, K. Müller, J. Ooms, D. Robinson, D. P. Seidel, V. Spinu, K. Takahashi, D. Vaughan, C. Wilke, K. Woo, and H. Yutani. 2019. "Welcome to the tidyverse." *Journal of Open-Source Software* 4(43): 1686.

Wilke, C. 2020. cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'. *R package version* 1.1.1.

4.7. Supplementary material:

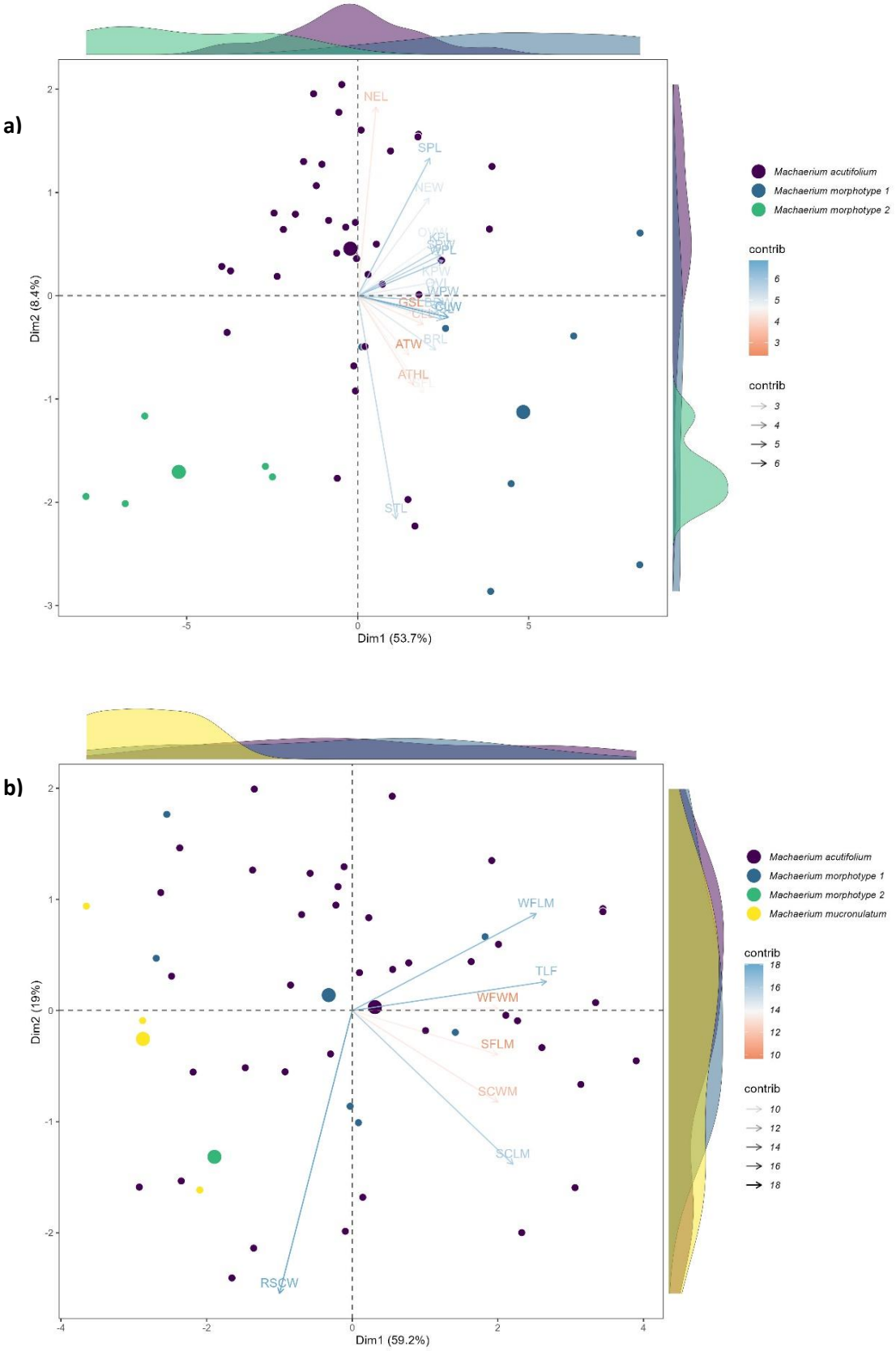


Figure 9. Additional PCAs. a) Flower characters. b) Fruit characters.

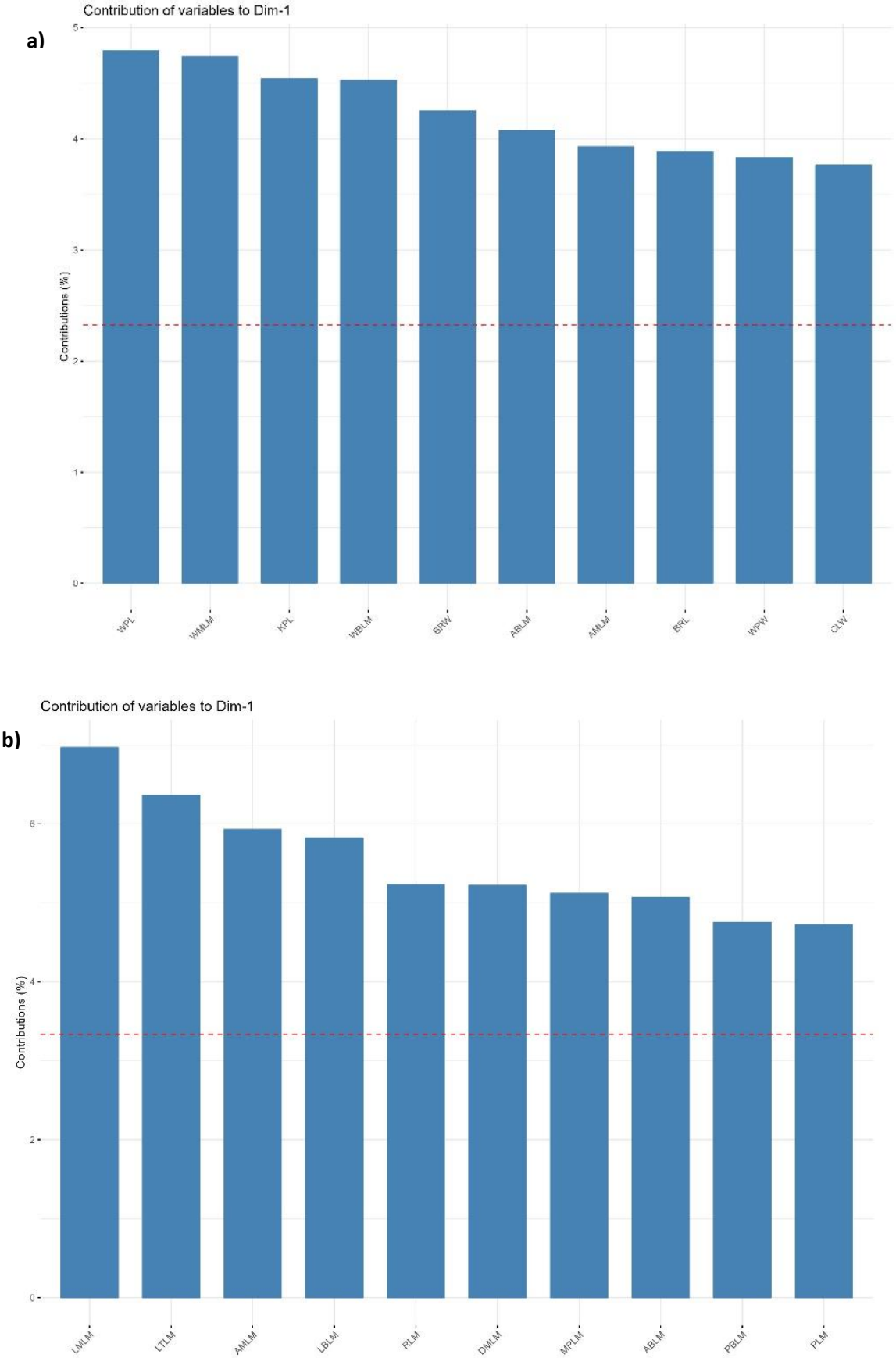


Figure 10. Bar graphs of most representative characters. a) Vegetative and floral. b) Vegetative and fruit.

Examined material from the morphometric study of the *Machaerium acutifolium* complex

Id	Collector	n°	Species	Collection
id1	Jordão, V.M.M.	130	*Machaerium acutifolium*	SJRP
id2	Sellow, F.	s.n.	*Machaerium acutifolium*	K
id3	Kuhlmann, J.G.	424	*Machaerium acutifolium*	R
id4	Williams, R.S.	529	*Machaerium acutifolium*	NY
id5	Pohl, J.E.	560	*Machaerium acutifolium*	K
id6	Pittier, H.	12484	*Machaerium acutifolium*	A
id8	Martius, C.F.P.	s.n.	*Machaerium mucronulatum*	M
id12	Bernadi	20177	*Machaerium acutifolium*	US
id13	Jardim, J.G. et al	31	*Machaerium* sp nov 2	MBM
id14	Arbo, M.M. et al	7357	*Machaerium* sp nov 2	RB
id16	Faria, J.E.Q & Romão, D.R.	9996	*Machaerium acutifolium*	HEPH
id17	Weiser, V.L.	151	*Machaerium acutifolium*	RB
id22	Nobrega, M.G. Ramos, A.E.	1396	*Machaerium acutifolium*	HEPH
id23	Salles, A.H. et al	1486	*Machaerium acutifolium*	HEPH
id24	Stranghetti, V. et al	2328	*Machaerium acutifolium*	SJRP
id25	Goodland, R.	4086	*Machaerium acutifolium*	BHCB
id26	Neto, E.T.	637	*Machaerium acutifolium*	BHCB
id27	Neto, E.T.	2190	*Machaerium acutifolium*	BHCB
id28	Harley, R.M. et al	10930	*Machaerium acutifolium*	NY
id30	Walter, B.M.T. et al	4255	*Machaerium acutifolium*	CEN
id31	Queiroz, L.P. & Nascimento, N.S.	3379	*Machaerium* sp nov 1	HUEFS
id32	Silva, J.A.	528	*Machaerium acutifolium*	CEN
id33	Bernardi	20597	*Machaerium acutifolium*	F
id34	Santos, A.A. et al	2996	*Machaerium acutifolium*	CEN
id35	Fernandes, A.	s.n.	*Machaerium acutifolium*	EAC
id36	Fernandes, A.	s.n.	*Machaerium acutifolium*	EAC
id37	Fernandes, A.	s.n.	*Machaerium acutifolium*	EAC
id38	Fernandes, A. et al.	s.n.	*Machaerium acutifolium*	EAC
id39	Fernandes, A. et al	s.n.	*Machaerium acutifolium*	EAC
id40	Nunes, E. & Cavada, B.S.	s.n.	*Machaerium acutifolium*	EAC
id41	Fernandes, A. et al	s.n.	*Machaerium acutifolium*	EAC
id42	Pereira-Júnior, F.N.	s.n.	*Machaerium acutifolium*	EAC
id43	Balansa, B.	3110	*Machaerium acutifolium*	L
id45	Kinoshita, L.S. et al	03--67	*Machaerium acutifolium*	UEC
id46	Tamashiro, J.Y. et al	323	*Machaerium acutifolium*	UEC
id48	Sobrinho, M.S.	191	*Machaerium acutifolium*	EAC
id49	Queiroz, L.P. et al	10508	*Machaerium acutifolium*	HUEFS
id50	Krukoff, B.A.	10029	*Machaerium acutifolium*	U
id51	Rita	2	*Machaerium acutifolium*	EAC
id52	Nunes, M.S.	17	*Machaerium acutifolium*	CGM
id53	Manzoli, J.V.L.	393	*Machaerium acutifolium*	SJRP
id54	Árbocz, G.F. et al	4071	*Machaerium acutifolium*	ESA
id55	Souza, V.C. et al	20505	*Machaerium acutifolium*	ESA
id56	Sartori, A.	28769	*Machaerium acutifolium*	CGMS

id57	Hatschbach, G.	37488	*Machaerium acutifolium*	HUEFS
id58	Harley, R.M.	22967	*Machaerium* sp nov 1	CEPEC
id59	Ratter, J.A. & Ferreira, A.	2073	*Machaerium acutifolium*	MO
id60	Nobrega, M.G. et al	875	*Machaerium acutifolium*	HEPH
id61	Gottsberger, I.S. & Campos, C.J.	14-221174	*Machaerium acutifolium*	UB
id62	Ratter, J.A. et al	3811	*Machaerium acutifolium*	INPA
id63	Hatschbach, G.	52427	*Machaerium acutifolium*	ESA
id64	Plowmann, T.C.	9335	*Machaerium acutifolium*	NY
id65	Fontana, A.P. & Murilo, F.	8505	*Machaerium acutifolium*	RB
id66	Barroso, G.M. & Guimarães, E.F.	222	*Machaerium acutifolium*	SJRP
id67	Guedes, T.N.	363	*Machaerium acutifolium*	RB
id68	Rezende, A.A. & Ranga, N.T.	s.n.	*Machaerium acutifolium*	SJRP
id70	Brina, A.E. & Costa, L.V.	s.n.	*Machaerium acutifolium*	BHCB
id71	Duarte, A.P. & Mattos, A.	8201	*Machaerium acutifolium*	SJRP
id72	Savassi-Coutinho, A.P. Scalon, V.	797	*Machaerium acutifolium*	RB
id73	Silva, S.S.	101	*Machaerium acutifolium*	RB
id74	Pereira, B.A.S. Alvarenga, D.	2948	*Machaerium acutifolium*	NY
id75	Silva, M.A. et al	2435	*Machaerium acutifolium*	RB
id76	Savassi-Coutinho,A.P., Scalon, V.	693	*Machaerium acutifolium*	SJRR
id78	Ratter, J.A. et al	4314	*Machaerium acutifolium*	UB
id79	Chagas e Silva, F.	1887	*Machaerium acutifolium*	UB
id80	Heringer, E.P.	9448	*Machaerium acutifolium*	UB
id81	Gottsberger, I.S.	2140	*Machaerium acutifolium*	UB
id82	Tannus, J.L.S.	492	*Machaerium acutifolium*	CESJ
id85	Hatschbach, G.	50456	*Machaerium* sp nov 2	NY
id86	Heringer, E.P.	5763	*Machaerium acutifolium*	MG
id87	de Sá, K.L.V.R. et al	233	*Machaerium acutifolium*	MBM
id90	Saraiva, D.P. et al	290	*Machaerium acutifolium*	HUEFS
id91	Ferruccini, M.S. et al	1472	*Machaerium acutifolium*	CEN
id92	Colletta, G.D.	2431	*Machaerium acutifolium*	CEN
id94	Assis, C.S.	s.n.	*Machaerium acutifolium*	CEN
id95	Killeen, T.J. & Guillén, R.	7330	*Machaerium acutifolium*	CEPEC
id96	Sartori, A. et al	2139	*Machaerium acutifolium*	SJRP
id97	Bambil, D.R. et al	17	*Machaerium acutifolium*	SJRP
id98	Pott, A. & Pott, V.J.	14293	*Machaerium acutifolium*	SJRP
id99	Ferreira, B.H.S. et al	16	*Machaerium acutifolium*	SJRP
id100	Sartori, A. et al	580	*Machaerium acutifolium*	SJRP
id101	Zacharias, S.R. & Ferreira, F.	174	*Machaerium acutifolium*	SJRP
id104	Walter, B.M.T.; et al	4420	*Machaerium mucronulatum*	CEN
id119	Carvalho, A.M., et al	2408	*Machaerium* sp nov 1	CEP
id122	Nunes, E. & Martins, P.	s.n.	*Machaerium mucronulatum*	EAC
id123	Hunt, D.R.	6158	*Machaerium acutifolium*	K
id124	Harley, R.M.	16903	*Machaerium* sp nov 1	NY
id126	Querioz, L.P. et al	4991	*Machaerium* sp nov 1	HUEFS
id127	Queiroz, L.P. & Nascimento, N.S.	3330	*Machaerium* sp nov 1	HUEFS
id128	Giulietti, A.M. et al	1806	*Machaerium* sp nov 1	HUEFS

id129	Ganev, W.	1534	*Machaerium* sp nov 1	HUEFS
id130	Ganev, W.	1124	*Machaerium* sp nov 1	HUEFS
id131	Ganev, W.	1343	*Machaerium* sp nov 1	HUEFS
id132	Ganev, W.	1427	*Machaerium* sp nov 1	HUEFS
id133	Melo, E.; et al	4563	*Machaerium* sp nov 1	HUEFS
id135	Yoshida-Arns, K	s.n.	*Machaerium mucronulatum*	HUEFS
id136	Sousa, G. et al	583	*Machaerium* sp nov 2	HUEFS
id137	Passos, L. et al	5271	*Machaerium* sp nov 2	CEPEC
id138	Guedes, M.L. & Xavier, A.B.	11671	*Machaerium* sp nov 2	CEPEC
id139	Pinto, G.C.P	376/83A	*Machaerium* sp nov 1	CEPEC
id140	Harley, R.M, et al	27000	*Machaerium* sp nov 1	CEPEC
id141	Rodriguez, A. & Surubi, J.	631	*Machaerium acutifolium*	CEPEC
id143	Jordão, V.M.M.	263	*Machaerium* sp nov 1	SJRP
id144	Jordão, V.M.M.	141	*Machaerium acutifolium*	SJRP
id145	Jordão, V.M.M.	139	*Machaerium acutifolium*	SJRP

5. Chapter II: Taxonomy and nomenclature of the *Machaerium acutifolium* complex and related species (Leguminosae: Papilionoideae: Dalbergieae)

5.1. Resumo

Machaerium Pers. inclui cerca de 130 espécies distribuídas na América tropical, reunindo árvores, arbustos e lianas que ocorrem desde o sul do México até o norte da Argentina. Dentro do gênero, *M. acutifolium* se destaca devido ao seu amplo padrão de distribuição, ocorrendo em quase todos os biomas do Brasil, além de também estar presente em outros cinco países da América do Sul. Ao longo de sua distribuição, a espécie apresenta uma evidente plasticidade fenotípica, principalmente na forma e tamanho dos folíolos e frutos, levando à descrição de diferentes entidades taxonômicas ao longo dos anos que, posteriormente foram sinonimizadas. Por outro lado, a acentuada variação observada para a espécie pode sugerir a necessidade de estudos mais específicos que possam levar ao reconhecimento de novos táxons. Assim, este trabalho teve como objetivo realizar a revisão taxonômica do complexo taxonômico *Machaerium acutifolium* a partir dos resultados obtidos nas análises integradas apresentadas no capítulo I. Fornecemos descrições completadas para todos os táxons do complexo, bem como para suas espécies afins (*M. mucronulatum* e *M. opacum*) bem como informações sobre habitat, distribuição, fenologia e comentários taxonômicos juntamente com fotografias, ilustrações e mapas de distribuição.

Palavras-chave: Brasil, Caatinga, Cerrado, Dalbergieae, endemismos, Fabaceae.

5.2. Abstract

Machaerium Pers. includes around 130 species distributed in tropical America, gathering trees, shrubs and lianas that occur from southern Mexico to northern Argentina. Within the genus, *M. acutifolium* highlights due to its wide distribution pattern, occurring in almost all biomes in Brazil, in addition to also being present in five other countries in South America. Throughout its distribution, the species presents an evident phenotypic plasticity, mainly in the shape and size of leaflets and fruits, leading to the description of different taxonomic entities over the years that were later synonymized. On the other hand, the marked variation observed for the species may suggest the need for more specific studies that could lead to the recognition of new taxa. Thus, this work aimed to carry out a taxonomic review of the *Machaerium acutifolium* taxonomic complex based on the results obtained in the integrated analyzes presented in chapter

I. We provide complete descriptions for all taxa in the complex, as well as for their related species (*M. mucronulatum* and *M. opacum*) as well as information on habitat, distribution, phenology, and taxonomic comments together with photographs, illustrations, and distribution maps.

Keywords: Brazil, Caatinga, Cerrado, Dalbergieae, endemism, Fabaceae.

5.3. Introduction

Being one of the major woody genera among the Papilionoid legumes, *Machaerium* Pers. presents about 130 species with neotropical distribution, whereas *Machaerium lunatum* (L.f.) Ducke, extending its distribution to west coast of Africa (Lozano and Klitgaard 2006). Within this genus, *Machaerium acutifolium* Vogel is highlighted for presenting a wide geographic distribution, occurring in almost all Brazilian biomes, and is also found in Argentina, Bolivia, Paraguay, Peru, and Venezuela (Filardi 2011).

When working with Atlantic Forest species, Filardi in 2011 included *Machaerium acutifolium* in her thesis by using the broad definition of Atlantic Domain, which includes extra-Amazon rainforests and seasonal forests, in addition to other coastal forest formations (Oliveira Filho et al. 2006). Although she has not fully investigated all the morphological variation of this species since it occurs in the Caatinga and Cerrado biomes and in other South American countries, she had already indicated that an infraspecific treatment with this species needed to be produced.

On the other hand, Lewis (1987) and Queiroz (2009), when working respectively with Leguminosae from Bahia and Leguminosae from Caatinga, indicated in their studies that in these regions, the genus *Machaerium* needed a taxonomic revision, and a detailed analysis could reveal new taxa.

Concerning *Machaerium acutifolium*, Lewis (1987) recognized that for Bahia state, there would be three varieties (*M.* var. *acutifolium*, *M.* var. *enneandrum* (Hoehne) Rudd, and *M.* var. *pseudacutifolium* (Pittier) Rudd), whereas Queiroz (2009), considered for Caatinga, the occurrence of *M.* var. *acutifolium* and *M.* var. *enneandrum*.

Thus, due to morphological variations and the large number of associated names, *Machaerium acutifolium* was treated as a taxonomic complex that was analyzed in Chapter I by integrated approaches and in this chapter, we provided a taxonomic treatment of the species in the complex and associated taxa.

Here we discussed the information concerning *Machaerium acutifolium* Vogel, *M. mucronulatum* Mart. ex Benth., *M. opacum* Vogel and the two new species introduced in Chapter I, *Machaerium* sp. nov. 1 e *Machaerium* sp. nov. 2.

5.4. Materials and Methods

5.4.1 Study of collections and field expeditions

The present study was based on analysis in herbaria BHCB, CEN, CEPEC, CGMS, HEPH, INPA, MBML, MG, OUPR, R, RB, SJRP, and UB through visits, and permute. Images in high resolution available in the Reflora Virtual Herbarium (http://reflora.jbrj.gov.br/reflora/herbarioVirtual), SpeciesLink (https://specieslink.net/search/index) and GBIF (https://www.gbif.org/) by herbaria A, ALCB, ASU, B, BM, ESA, F, G, HAL, K, L, LUS, M, MBM, MEX, MICH, MO, MPU, NY, P, S, SP, SPF, SPSF, U, UEC, UESC, US, VEN, VIES and W were also analyzed (acronyms based on Thiers 2020).

Four field expeditions were carried out to collect botanical material jointly with visits to the main herbaria in Brazil, whose locations are related to the distribution of the complex under study. These expeditions were organized after visiting the R and RB collections, since from that moment on, it was possible to establish the main sites of occurrence of the complex and in which regions field work would be necessary.

Thus, the first field expedition occurred in the Northwest region of São Paulo state, covering mainly the Semideciduous Seasonal Forest in Atlantic Forest biome in the following municipalities: Icem, Itajobi, Mogi-Guaçu and São José do Rio Preto. The second expedition occurred in Brasília, Distrito Federal, where it was possible to visit the CEN and UB collections, two of the main Brazilian Cerrado herbaria. The third expedition occurred in the state of Minas Gerais, addressing mainly the phytophysiognomies of Campos Rupestres and Cerrado "*stricto sensu*" and it was possible to study the collection of the OUPR herbarium, in the city of Ouro Preto.

The fourth expedition occurred in the states of Bahia, Espírito Santo, and Rio de Janeiro, covering mainly Caatinga and Atlantic Forest biomes. On this last trip we were able to visit the collections of CEPEC, HUEFS, as well as MBML and once more RB. All collected material was processed according to the herborization rules (Bridson and Forman, 1998) and incorporated into the SJRP herbarium.

5.4.2 Taxonomic treatment

Since the main objective of this work was to delimit the complex based on integrative taxonomy, the concept of species adopted here followed the work of De Queiroz (2007), as he considers species as metapopulations with independent evolutionary lineages over time, and a species represents a segment of a specific lineage.

Thus, among the criteria listed by this author for the delimitation of species, the diagnostic criterion was utilized here, once considers species as having morphological variances measurable between distinguished taxa and, the ecological criterion that refer to a species that occur the same niche or adaptive zone (Chapter I).

Each species presents a nomenclatural headline, followed by description, illustration, phenology, examined material, field photos (when collected by the author or provided by collaborators), distribution and ecology, vernacular names, and taxon discussion sections.

For the proposition of new species, all nomenclatural types as well as the "*Opus Princeps*" of *Machaerium* from the tropical America were analyzed, highlighting the Brazilian species, specially from Caatinga and Cerrado biomes. The epithets were replaced by "sp. nov.". All of them have the same structure and information as the valid species, but we added a diagnosis, in Latin, between the nomenclatural headline and the description.

New lectotypifications of valid names and synonyms were indicated by "*Lectotype here designated:*" followed by the referring materials presented in the protologues, then the barcodes numbers. The lectotypification followed the norms of the International Code of Nomenclature for Algae, Fungi and Plants (Turland et al. 2018).

For the taxonomic treatment, the main bibliography of the genus was used (Vogel 1837; Bentham 1862; Hoehne 1941; Bastos 1987; Rudd 1987a, 1987b; Mendonça-Filho et al. 2007; Filardi and Lima 2014). The terminology adopted for colors was based on Beentje (2010) and for shape and indumentum on Harris and Harris (1994).

For the descriptions, the total length of the leaves considered the length of the pulvinus, petiole, rachis, and terminal leaflet. Basal leaflets correspond to the first pair of leaflets after the petiole; middle leaflets to the middle pair of leaflets in the leaf, and terminal leaflet, the last leaflet at the apex of the leaf.

In the reproductive organs, the total length of petals included also included the length of the claw and the total length of the fruit considered the length of the stipe, seed chamber and wing.

To describe vegetative organs, inflorescence, and fruit, we used centimeters (cm) and to describe flowers, we used millimeters (mm). The morphological analysis of small-sized structures was carried out with the aid of stereomicroscope Leica MZ16 and the digital images of these structures were captured with the aid of a coupled Leica DFC295 camera and processed in Photoshop CS6.

With the information obtained from the specimens, it was possible to extract data to compose the vernacular names as well as to produce the distribution maps. These were created with the program QGis 3.4.10 with Grass 7.6.1 and doubtful and/or inaccurate locations were disregarded.

5.5. Taxonomy of *Machaerium acutifolium* complex:

5.5.1. *Machaerium acutifolium* Vogel

Machaerium acutifolium Vogel, Linnaea 11: 187. 1837. Type: Brazil. "Brasil merid.", s.d., fr., *F. Sellow s.n.* – (Lectotype designated by Filardi & Lima, 2014: K barcode K000530222 [photo!]; isolectótipos: NY 2645 [photo!]; E [not seen]).

= *Machaerium acutifolium* var. *muticum* (Benth.) Benth., Fl. bras. 15 (1b): 245. 1862. ≡ *Machaerium muticum* Benth., Comm. Legum. Gen. 36. 1837. Type: Brazil. Minas Gerais: São João Baptista, 1837, fl., *J. B. E. Pohl 560* (holotype: W0026191 [photo!]; isotypes: BR0000005197170 [photo!], F0059521 [photo!], K000530224 [photo!], M-0234122 [photo!], NY00016247 [photo!], US00002417 [photo!]).

= *Machaerium juglandifolium* Rusby, Bull. New York Bot. Gard. 6 (22): 513-514. 1910. Type: Bolivia. Tumpasa, 19 Jan 1902, fr., *R.S. Williams 529* (holotype: NY00016226 [photo!]; isotypes: BM00093183 [photo!], US00002431 [photo!]).

= *Sweetia atrata* Mohlenbr., Webbia 17: 233. 1963. Type: Paraguay. Caaguazú, Yhu, Feb 1932, fr., *P. Jörgensen 4796* (holotype: MO-1698477 [photo!], isotype: F0044202 [photo!]).

= *Machaerium acutifolium* var. *enneandrum* (Hoehne) Rudd, Phytologia 25(6): 399. 1973. ≡ *Machaerium enneandrum* Hoehne, Arq. Bot. Estado São Paulo 1: 32. 1938. Type: Brazil. Mato Grosso, Comissão de Linhas Telégrafas Estratégicas de Mato Grosso ao Amazonas, Caminho para Porto Velho do rio Arinos, Nov 1914, fl., *J.G. Kuhlmann 424* (holotype: R000005280 [!], isotype: RB01309901 [!]).

= *Machaerium acutifolium* var. *pseudacutifolium* (Pittier) Rudd, Phytologia 25 (6): 399. 1973. ≡ *Machaerium pseudacutifolium* Pittier, Bol. Soc. Ven. Cien. Nat. 7: 148. 1941. Type: Venezuela. Guárico, Mesa de El Sombrero, in savanna, 10 Sep 1927, fr., *H. Pittier 12484* (holotype: VEN4930 [photo!]; isotype: A00065215 [photo!], M-0234121 [photo!], NY00016255 [photo!], US00002407 [photo!]), WIS00000476MAD [photo!]).

Trees, 2–11 m tall; trunk cylindric; bark fissured, brown. **Branches** cylindric, brown to gray, sub-glabrous to pubescent; lenticels conspicuous; cataphyll absent; stipules not seen. **Leaves** 15.8–29.1 cm long; pulvinus 0.4–0.7 cm long, sub-glabrous to cream-pubescent; petiole 1.6–6.5 cm long, sub-glabrous to cream-pubescent; rachis 5.1–24.4 cm long, sub-glabrous to cream-pubescent; pulvinule 0.1–0.7 cm long, sub-glabrous to cream-pubescent. Leaflets 11–19, alternate to sub-opposite, concolorous, margin entire, chartaceous to coriaceous; adaxial surface

opaque, glabrous; abaxial surface opaque, sub-glabrous to sparse cream-pubescent; midrib sub-glabrous to cream-sericeous-pubescent; secondary veins multiple-brochidodromous. Basal leaflet 2.6–7.6 × 1.3–3.8 cm; oblong-lanceolate, rarely large-ovate; apex acuminate to attenuate, rarely obtuse, often mucronate; base rounded to subcordate, rarely cordate. Middle leaflets 3.5–8.9 × 1.2–3.5 cm; oblong-lanceolate, rarely large-ovate; apex acuminate to attenuate, rarely obtuse, often mucronate; base rounded to subcordate, rarely cordate. Terminal leaflet 3.5–9.1 × 1.3–4.1 cm; oblong-lanceolate, rarely large-ovate; apex acuminate to attenuate, rarely obtuse, often mucronate; base rounded to subcordate, rarely cordate. **Inflorescence** panicle, 10.3–24.2 cm long, axillar or terminal, pendulous, lenticels present; peduncle 2.1–4.2 cm long, cream-pubescent; rachis 8.2–20.0 cm long, cream-pubescent; lateral axis 3.6–8.3 cm long; cream-pubescent; bracts deciduous, not seen. **Flowers** sessilis, 8.6–9.3 mm long; bracteoles 0.8–1.9 x 1.0–2.1 mm, large-ovate, fuscous-tomentose; calyx 1.8–3.8 × 4.1–8.3 mm, dark-greyish-brown-tomentose; corolla white. Banner petal 4.6–7.6 × 3.7–7.0 mm, orbicular to obovate, externally fuscous-tomentose, internally sericeous-tomentose in the apex, apex retuse, base attenuate, claw 1.1–1.7 mm long. Wing petals 3.5–6.5 × 1.5–3.1 mm, elliptic, glabrous, apex obtuse, base slightly auriculate. claw 2.5–3.1 mm long. Keel petals 3.1–5.8 × 1.2–2.9 mm, falcate-oblong, sparse-pubescent in the middle vein dorsally, apex obtuse, base auriculate, 2.1–3.4 claw mm long. Androecium monadelphous, 10 stamens; filament sheath 2.1–4.4 mm long, glabrous; filaments 1.2–2.8 mm long, glabrous; anthers 0.2–0.6 × 0.1–0.5 mm, oblong to triangular. Gynoecium with nectary (0.3) 0.5–1.1 (1.3) × 0.4–0.9 mm, cupulate; stipe 1.2–3.1 mm, glabrous at the base and sparse-pubescent at the apex; ovary 1.6–3.2 × 0.6–1.0 mm, tomentose; style 0.6–1.6 mm long, glabrous; stigma capitate. **Fruit** samara, 3.6–10.0 cm long; stipe 0.3–1.1 cm long, sub-glabrous; seed chamber 1.0–2.3 × 0.6–1.5 cm, oblong-falcate, prominent, verrucose, brown, glabrous; wing 2.3–6.6 × 0.9–2.7 cm, oblong to oblong-falcate, reticulate, brown, glabrous; apex obtuse, short-apiculate.

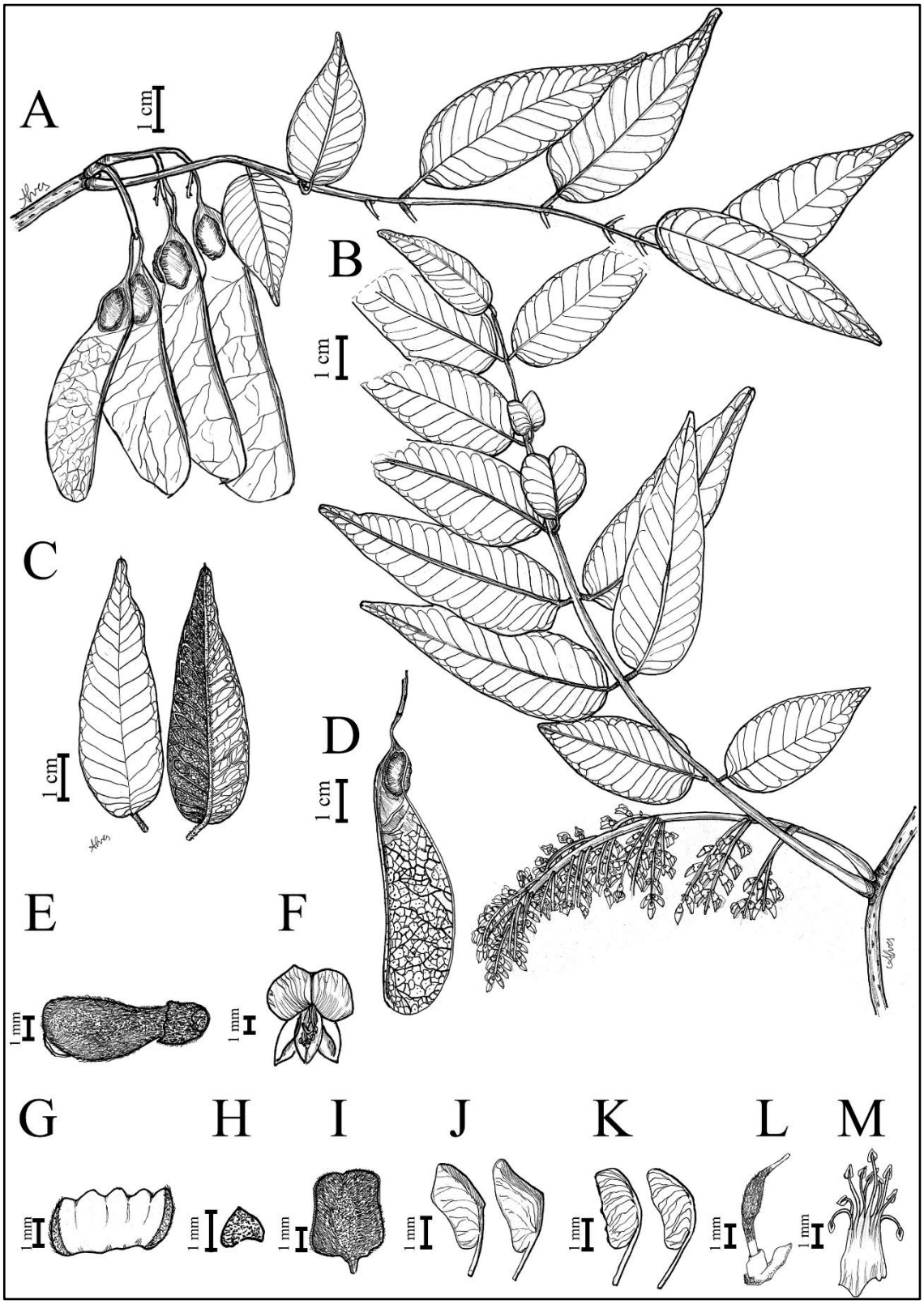


Figure 11. Illustration of *Machaerium acutifolium* Vogel. **A** – Branch with fruits (Sartori, A.L.B. *et al*. 580); **B – M**. Jordão, V.M.M. 130; **B –** Branch with flowers; **C** – Terminal leaflet (respectively adaxial and abaxial surface); **D** – Fruit; **E** – Bud flower; **F** – Opened flower; **G** – Calyx; **H** – Bracteoles; **I** – Banner petal; **J** – Wing petals; **K** – Keel petal; **L** – Gynaecium; **M** – Androecium. (Illustrator: Vieira, J.A.)

Additional material examined – **BOLIVIA.** BENI, Vaca Diez, Nazaret, 80 Km SSE of Riberalta along road to La Paz, 150 m, 11°22'S 66°15'W, 05 Nov 2001, fl., *L.W. Chatrou et al. 382* (BM [digital image], U). – LA PAZ, Nor Yungas, Coroico, 1100 m, Nov or Dec 1912, fl., *O. Buchtien 3792* (US [digital image]); Province of S. Yungas, Basin of Rio Bopi, San Bartolomeu, (near Calisaya), 750–900 m, fr., 1-22 Jul 1939, *B.A. Krukoff 10029* (F [digital image], L [digital image], U [digital image], US [digital image]). – SANTA CRUZ: Ichilo, 5 Km WNW of Buena Vista, El Fraile, 350 m, 17°27'S, 63°42'W, 30 Jan 1988, fr., *M. Nee et al. 36125* (F [digital image], US [digital image]); Ñuflo de Chavez, Perseverancia, Riberas del Río Negro, 5 Km al S, rio Arriba, 257 m, 14°38'S, 62°37'W, 12 Jun 1990, fr., *G. Israel & C. Vargas 572* (F [digital image]); San Xavier, 16 Km de San Xavier hacia San Ramon, cerca de la hacienda Santo Rosario, El Jucio, 535 m, 16°40'11S, 62°51'92''W, 15 Mar 2009, fr., *J.R.I. Wood et al 25688* (UB); Sara, 450 m, 28 Jun 1925 fr., *J. Steinbach 7159* (F [digital image]); Buenavista, 450 m, 01 Sep 1925, fr., *J. Steinbach 7220* (F [digital image]); Chiquitos, Serranía de Santiago, near Santiago de Chiquitos, 1-3 Km SW, of Santiago, trail to "Cachuela", 700 m, 18°21'S, 59°38'W, 22 Nov 1989, fl., *D.C. Daly et al. 6334* (US [digital image]); Velasco, a 15 Km al S de San Ignacio, por el camino a San Miguel, fl., 08 Dec 1994, *T.J. Killeen & R, Guillén 7330* (CEPEC, MO [digital image]); Parque Nacional Noel Kempff M. Pampa húmeda con termiteros, parcela permanente, 2 Km hacia el norte de la casa de guarda parques, 160 m, 13°32'40''S, 61°01'05''W, 13 Nov 1993, fl., *T.J. Killen et al. 6052* (F[digital image], MO [digital image]); 1,5 Km S de la pista Noel Kempff M. Sabana, 290 m, 13°53'55''S, 60°48'36''W, 12 May 1994, fr., *B. Mostacedo et al. 1732* (F [digital image]). **BRAZIL.** CEARÁ: Crato, à margem da estrada Crato – Juazeiro do Norte, fr., 26 Jun 1952, *A. Lima & M Mag. 52-1114* (R). – DISTRITO FEDERAL: Brasília, Fazenda Água Limpa/UnB. Mata de Galeria do Córrego da Onça, 1060 m, 15°57'S, 47°55'W, fl., 22 Nov 1994, *B.M.T. Walter 2273* (CEN); Fazenda Malunga, 15°58'40''S, 47°30'06''W, fl., 22 Nov 2012, *B.R. Teixeira 390* (CEN); Núcleo rural de Tabatinga, 973 m, 15°45'39''S, 47°35'43''W, st., 15 Feb 2003, *J.C.S. Silva 2482* (CEN); Paranoá, DF-285, próximo a ponte de concreto do rio Preto, 930 m, 16°03'02''S, 47°19'26''W, fl., 15 Oct 2002, *J.M. Rezende et al 592* (CEN); Parque Ecológico Burle Marx, 1082 m, 15°44'50''S, 45°52'19''W, fl. 20 Nov 2020, *M. Figueira & B. Schindler 1531* (CEN), São Sebastião. fl., 19 Nov 2016, *F.F.M. Santos 701* (CEN). – GOIÁS: Abadiânia, Fazenda Porto Corumbá, margem direita do rio Corumbá, 900 m, 16°11'54''S, 48°31'55''W, fr., 08 May 2003, *G. Pereira-Silva et al. 7640* (CEN); Alexânia, Cerca de 300 m a Oeste da BR-060, na direção de Corumbá/GO (Estrada de terra à 500 m da ponte sobre o rio Corumbá), 880 m, 16°08'33''S, 48°36'12'', fr., 18 Feb 2003, *G. Pereira-Silva et al. 7177* (CEN); Alto

Paraíso, 6-7 Km E of Alto Paraíso on road to Nova Roma, Chapada dos Veadeiros, elev. ca. 1400 alt., fr., 07 Mar1973, *W.R. Anderson 6507* (UB); Anápolis, Estrada de Anápolis, fr., 26 Mar 1963, *E.P. Heringer 9240* (UB); Barro Alto, Estrada de terra que sai da GO-342 para Barra dos Rios Maranhão e Almas. (Rumo a Fazenda Pontal), fr., 08 Feb 1996, *B.M.T. Walter et al. 3118* (CEN, HUEFS, NY [digital image]); Caiapônia-Aragarças road, 75 Km from Aragarças, near Piranhas, fr., 23 Jul 1966, *D.R. Hunt 6158* (UB); Caldas Novas, cerrado denso em beira de estrada, 600 m, 17°56'S, 48°51'W, fr., 27 Fev 1996, *G. Pereira-Silva et al. 3388* (CEN, HUEFS, UEC[digital image]), margem esquerda do córrego gameleira, próximo a foz, 720 m, 17°'51'S, 48°'33W, fl., 26 Oct 1993, *R.F. Vieira et al. 1661* (CEN, HUEFS, NY [digital image]); Campos Belos, estrada de chão para Pouso Alto, 740 m, 12°58'00''S, 46°28'41''W, fr., 23 Apr 2001, *M.L. Fonseca et al. 2519* (CEN); Cavalcante, 7 Km south of Cavalcante, Chapada dos Veadeiros, fr., 09 Mar 1969, *H.S. Irwin 24108* (UB); Goiânia, Goiás Velha, Km 3, fr., 14 Jul 1964, A.P. Duarte 8200 (UB); Corumbá de Goiás, margem do rio Corumbá, dentro da cidade de Corumbá, local chamado Prainha, 945 m, 15°56'05''S, 48°48'20''W, fl., 23 Nov 2011, *D.P. Saraiva et al. 290* (CEN, HUEFS, K [digital image], RB); Luziânia, margem esquerda do rio Alagado, próximo â captação d'água da Saneago, ponto 16, 740 m, 16°'17'02''S, 48°11'36''W, fl., 07 Nov 2002, *G. Pereira-Silva et al. 6909* (CEN); canteiro de obras, margem direita do rio Corumbá a montante da Barragem, Fazenda Corumbá, 885 m, 16°19'3''S, 48°12'11''W, fr., 10 Dec 2022, *J.M. Rezende et al. 717* (CEN); Niquelândia, Área de influência do AHE Serra da Mesa, estrada de terra Niquelândia, Colinas do Sul/Moquém, Cerca de 24 Km de Niquelândia, 480 m, 14°'25'10''S, 48°13'50''W, fr., 03 Jun 1998, *B.M.T. Walter et al. 4178* (CEN); São Domingos, Fazenda Flor do Ermo, 470 m, 13°38'23''S, 46°43'34''W, fr., 22 Mar 2000, *A.C. Sevilha et al. 1933* (CEN); São João da Aliança, 4 Km by road S of São João da Aliança, Serra Geral do Paraná, 1070 m, fr., 21.III.1973, W.R. Anderson 7622 (UB); Silvânia, Estação Florestal Experimental, Cerradão, 16°36'S, 48°39'W, fr., 12 Jan 1989, *D. Alvarenga et al. 130* (UB); margem direita do rio Antas (próxima à ponte de madeira), 820 m, 16°17'23''S, 48°'26'26''W, fr., 11 Mar 2003, *G. Pereira-Silva et al. 7343* (CEN); Teresina de Goiás, Comunidade Limoeiro, 13°35'36''S, 47°13'03''W, fr., 20 Apr 2008, *N.P. Massarotto 18* (UB); 4 Km road S of Teresina, Chapada dos Veadeiros, 1000 m, fr., 18 Mar 1979, *W.R. Anderson 7362* (UB). – MARANHÃO: Balsas, reservas de cerrado entre plantios de soja, ao sul da vila Kissy, 470 m, 08°38'S, 46°43'W, fr., 24 Feb 1996, *B.M.T. Walter et al. 3212* (CEN); projeto de colonização agrícola Batavo/Campo, região próxima ao córrego Tem Medo, 470 m, 08°38'S, 46°43'W, fl., 10 Nov 1996, *B.M.T. Walter et al. 3554* (CEN); Carolina, estrada Goiatins-Carolina, Km 5, 230 m, 07°40'48''S, 47°17'05W, fr., 31 Aug 2008, *G.*

Pereira-Silva et al. 13676 (CEN). – MATO GROSSO: Caneeleiro, Near Base Camp, 12°49’S, 51°46’W, fr. 05 Dec 1968, *R.M. Harley & R. de Castro 11300* (NY [digital image], UB); 66,9 Km North along road from Base Camp, 12°49’S, 51°46’W, fl. 01 Nov 1968, *R.M. Harley et al. 10930* (UB); Cuiabá, São José da Serra, 13 Nov 1975 fl., fr., G. Hatschbach 37488 (CEPEC); Diamantino, 14,5 Km da estrada Diamantino-Nobres, cerca de 500 m antes do córrego Piraputanga, Fazenda Piraputanga, 14°34’S 56°18’W, fr., 17 May 1997 (CGMS); Nobres, Área rural ca. 47 km NE de Nobres, 14°32’28’’S, 56°00’54’’W, fr., 02 Apr 2019, *J.B.A Bringel et al. 1534* (CEN); Nova Xavantina, Fazenda Brasil, beira da represa do rio Bacaba, 14°53’17’’S, 52°22’89’’W, fr., 28 Mar 1999, *G.F. Árbocz et al. 3690* (CGMS); Pantanal, Rio Paraguai, Fazenda Acurizal 17°52’S, 57°32’W, fr., Jun 1979, *G.T. Prance & G.B. Schaller s.n*. (CGMS, NY [digital image]); Xavantina, Close to the Base Camp of the Expedition, c. 270 Km N of Xavantina, on the Xavantina–São Félix Road, 12°54’S, 51°52’W, fr., 04 Jul 1968, *J.A. Ratter et al. 2073* (U [digital image], UB); Cachimbo road, fl., 14 Nov 1967, *Philcox et al. 3017* (UB). – MATO GROSSO DO SUL: Alcinópolis, 4 Km de Alcinópolis, estrada para Coxim, fr., 29 Apr 2001, *A.L.B. Sartori, et al. 580* (CGMS); Aquidauana, acampamento Batista, Distrito de Piraputanga, 20°27’04’’S, 55°29’02’’W, fr., 18 Feb 2008, *W.M. Ramos & F.R.O. Rodrigues 355* (CGMS), estrada Park de Piraputanga, 20°27’41’’S, 55°29’25’’W, fl., 16 Dec 2007, *W.M. Ramos & F.F. Fernandes 292* (CGMS); fazenda Santa Ana, Distrito de Piraputanga, 20°27’38’’S, 55°29’25’’W, fr., 18 Feb 2008, *W.M. Ramos 134* (CGMS); 17 Mar 2008, *W.M. Ramos & F.R.O. Rodrigues 318* (CGMS); *Ramos & F.R.O. Rodrigues 326* (CGMS); fazenda São Benedito, 21°01’64’’S, 56°32’13’’W, fr., 06 Jul 2006, *C.A. Polido et al. 3* (CGMS); Bela Vista, Rod. BR–060, 40 Km N de Bela Vista, 11 Feb 1993, fr., *G. Hatschbach et al. 58886* (CEPEC); Bodoquena, estrada Bodoquena/Miranda, st., 19 Jul 2006, *C.A. Polido et al. 5* (CGMS); Campo Grande, Cerradão, fr. 26 Jun 1995, *C.A.C. Ferreira 2947* (CGMS); Coxins, Conglomerado MS-87, Subunidade 1, Subparcela 2, Indivíduo 24, 18°10’48’’S, 54°43’12’’W, fr., 24 Apr 2018, *J.A. da Silva 528* (CEN); Dourados, Fazenda Paradouro, fl., 28 Oct 1999, *A. Sciamarelli, Z.V. Pereira 770* (CGMS). – MINAS GERAIS: Paracatu, entre Paracatu e João Pinheiro, fr., 28 Jul 1964, *A.P. Duarte, &, A. Mattos 8201* (CEN, UB, RB); Margem do Escuro Paracatu fr., 18 Jun1960, *E.P. Heringer 7620A* (UB); Rio da Prata, Margem do Rio, fl., 25 Nov 1960, *E.P. Heringer 9448* (UB); Perdizes, Gerônimo, Estação Ambiental Galheiro, fr., 20 Dec 2002, *S. Mendes et al*. 425 (UB); céu cavalo, Estação Ambiental Galheiro, fr., 14 Feb 2003, *E.H. Amorim et al. 576* (UB); Prata, 16 Km south of Prata highway BR-14, fl., 30 Sep 1967, *R. Goodland 4025* (UB); Serra da Anta, ca. 5 Km N.W. of Paracatu, 800 m, fr., 04 Feb 1970, *H.S. Irwin et al. 25968* (UB, NY [digital image]); Tupaciguara, 26 Km south of Tupaciguara on

Highway BR-180, fl., 06 Oct 1967, *R. Goodland 4086* (UB); Uberaba, 11 Km north of Uberaba on Highway BR-106, fr., 04 Jul 1967, *R. Goodland 3067* (UB); Unaí, fragmento de cerradão no Km 11 da rodovia Unaí/Paracatu, 650 m, 16°15'S, 46°45'W, fl., 22 Oct 1995, *B.A.S. Pereira & D. Alvarenga 2948* (EAC [digital image], CEN, NY [digital image]) – PARANÁ: São Jerônimo da Serra, Arredores de São Jerônimo da Serra, fl., 08 Dec 1995, *F. Chagas e Silva 1887* (UB); Próximo à Vila Nova, beira de estrada, fr., 01 May 1999, *E.M. Francisco et al. s.n* (R); Reserva Indígena São Gerônimo, fr., 08 Jul 2002, *K.L.V.R. de Sá, et al. 233* (R); fr., 06 Mar 2009, *K.L.V.R. de Sá, et al. 448* (UB); Turnera do Oeste, 510 m, 23°55'S, 52°44'42''W, 27 Nov 2012, fl., *M.G Caxambu & F.F. Sanches 4491* (DVPR [digital image]). – RONDÔNIA: Vilhena, Fundos da cidade, Nos Fundos da cidade, 07 Jan 1979, fr., *M.G. da Silva 4210* (INPA, MAC [digital image]) – SÃO PAULO: Araraquara, Conglomerado SP-225, Subunidade 3, Subparcela 4, indivíduo 3, 21°35'30''S, 48°14'24''W, fr., 28 Feb 2020, *G.C. Camargo 84* (CEN); Bauru, Mata próxima ao IPMet, 628 m, 55°01'39''S, 28°21'27''W, fr., 07 Jan 2016, *G.D. Colletta 2461* (CEN); reserva ao lado do IPET (UNESP), 628 m, 49°01'39''S, 22°21'27''W, fl. 25 Nov 2015, *G.D. Colletta 2431* (CEN, ESA, UEC [digital image]); Botucatu, 18 Km north of Botucatu, (14 Km east of São Manuel). Along the São Manuel, Piracicaba Highway, Near ex-RR station, 550 m, 22°45'S, 48°25'W, st., 30 Aug 1970, *I.S. Gottesberger, 319* (UB), 18 Km north of Botucatu, (14 Km east of São Manuel). Along the São Manuel, Piracicaba Highway, near ex-RR station, 550 m, 22°45'S, 48°25'W, st., 30 Aug 1970, *I.S. Gottesberger, 320* (UB); fl. 24 Nov 1970, *I.S. Gottesberger, 2140* (UB); 18 Km north of Botucatu, (14 Km east of São Manuel); fl. 22 Nov 1974, *I.S. Gottesberger, 14-221174* (UB); Moji-Guaçu, Fazenda Campininha, near Padua Sales, fl., 17 Nov 1978, *J.A. Ratter et al., 4314* (UB); Pirassununga, Cachoeira de Emas, fr., 09 Apr 1993, *A. Sartori 28769* (CEN, LUSC [digital image], UEC [digital image]); São Carlos, Conglomerado: SP_227_P32. subunidade 4, subparcela 7, indivíduo 2, 21°42'45''S, 47°48'45''W, fl., 14 Oct 2020, *M. Piazza 936* (CEN). – TOCANTINS: Babaçulândia, margem esquerda do rio Tocantins, 170 m, 07°51'05''S, 47°35'48''W, fr., 22 Apr 2008, *G. Pereira-Silva et al. 13207* (CEN); Barra do Ouro, Estrada Barra do Ouro rio Tauá (Ponte Suspensa) Km 11, Kms marcados a partir da igreja Divino Pai Eterno, 190 m, 07°44'13''S 47°43'43''W, fr., 25 Sep 2009, *G. Pereira-Silva et al. 14652* (CEN); Goiatins, estrada Goiatins, Carolina via balsa, Km 11, 200 m, 07°37'37''S, 47°21'16''W, fr., 23 Sep 2009, *G. Pereira-Silva et al. 14636* (CEN); Itacajá, Estrada Itacajá – Itapirantins, Km 16, 280 m, 08°26'31''S, 47°54'29''W, fr., 28 Aug 2008, *G. Pereira-Silva et al. 13636* (CEN); Reserva Indígena Krahó, Aldeia Pedra Branca, aproximadamente 900 m a NE da aldeia, 08°18'12''S, 47°34'56''W, fr., 09 May 2000, *A.A. Santos et al. 702* (CEN);

Comunidade Indígena Krahò, Aldeia Pedra Branca, cerca de 2 km a SE da Aldeia, fl. e fr., 16 Oct 2000, *A.A. Santos et al. 818* (CEN, HUEFS); Palmeirante, , 156 m, 07°51’53’’S, 47°56’11’’W, fr., 07 Mar 2005, *G. Pereira-Silva et al. 9853* (CEN); Palmeirópolis, T 87, Fazenda São Cristóvão, propriedade Sr. Rubens de Oliveira Gomes, 1220 m, 13°06’58’S, 48°13’36’’W, fr., 27 Feb 2008, J.*B. Pereira & G.A. Moreira 53* (CEN); Paraná, 2ª parada sentido rio São Domingos; próximo ao bar, ao lado do rio, fr., 28 Mar 2004, *A.C. Sevilha et al. 3891* (CEN); Talismã, Conglomerado TO-643. subunidade 2, subparcela 1, indivíduo 2, 12°37’00’’S, 49°19’12’’W, fr., 26 Nov 2017, *E.R.S. Jesus 113* (CEN); Tocantinópolis, margem esquerda do rio Tocantins, canteiro de obras da AHE estreito, 160 m, 06°34’54’’S, 47°28’15’’W, fr., 19 Feb 2005, *G. Pereira-Silva et al. 9388* (CEN); Tupiratins, estrada de terra seguindo da BR-153 em direção à Itacajá, 272 m, 08°29’06’’S, 47°28’41’’W, fr., 26 Aug 2008, *A.A. Santos et al. 2996* (CEN). **PARAGUAY.** ALTO PARANÁ, Mbaracayú, in región Yerbalium de Maracayú, Paraguaria euro-austra, 1898-1899, fl., fr., *E. Hassler 5977* (BM [digital image], F [digital image]). – AMAMBAY, Circa Bella Vista, 15 Apr 1980, fr., *L. Bernardi 20597* (F[digital image], MO [digital image]); Pedro Juan Caballero, Zwischen Rio Apa und Rio Aquidaban, 1908-1909, fl., *K. Fiebring 4273* (BM [digital image]); Ruta 3, 41 Km N del rio Aquidabán, 15 Dec 1999, fl., *M.S. Ferrucci et al. 1472* (ALCB [digital image], ASU [digital image], CEN, ESA [digital image], U [digital image]). – CAPITAL, Asunción, Santísima Trinidad, Horto botánico, 22 Nov 1942, fl., *C.V.P. Morin 906* (MICH [digital image]); Dans le bois, Dec 1876, fl., *B. Balansa 1382* (F[digital image]) – CONCEPCIÓN Circa Colonia Sebastián Miranda, 35–40 Km NE Paao Barreto, 05 Mar 1980, fr., *L. Bernardi 20177* (L [digital image], US [digital image]). – CORDILLERA. Caacupé, 05 Mar 1883, fr., *B. Balansa 4427* (F [digital image], P [digital image]); San Bernardino, 1919, fl., *E. Hassler 12359* (BM [digital image], L [digital image], US [digital image]); Valenzuela, campo monteralo, 25 May 1945, fr., *T. Rojas 12745* (US [digital material]) – PARAGUARÍ, Yaguaron, 17 Jun 1879, fr., *B. Balansa 3110* (BM [digital image], F, [digital image], L [digital image], P [digital image], U [digital image], US [digital image]); 15 Dec 1965, fl., *T.M. Pedersen 7550* (US [digital image]); Paraguaria septentrionalis, 1901-1902, fl., *E. Hassler 7750* (BM [digital image], F [digital image]), s.l., s.d., fr., *E. Hassler, 2955* (F [digital image]). **PERU**. CUZCO: Concepción, Rosario Mayo, 1250 m, 06 Aug 1968, fr., *R.A. Chávez* 204 (F [digital image], US [digital image]). **VENEZUELA**. Bolívar: Los Chacharos, 4 km up stream on Río Asa from Raudal Cotua, 02 Aug 1960, fr. *J.A. Steyermark 86811* (US [digital image]).

Phenology – The species presents flowers from September to January and fruits throughout the year.

Vernacular names – Besides of all species studied for this complex, *Machaerium acutifolium* is the only one that presents a great variety of vernacular names (Table 2).

COUNTRY	LOCALITY	VERNACULAR NAME
BOLIVIA	Santa Cruz	Nagal
BRAZIL	Goiás	Jacarandá
	Maranhão	Violeta
	Mato Grosso	Cancileiro-do-cerrado
	Minas Gerais	Jacarandá, Jacarandá-branco-do-cerrado, Jacarandá-do-campo, Jacarandá-do-cerrado, Jacarandá-grande, Jacarandá-tã, Jacarandá-tinga, Pé-de-banco.
	São Paulo	Jacarandá, Jacarandá-bico-de-pato, Jacarandá-do-cerrado, Jacarandá-flecha, Jacarandá-papagaio, Sapeuva
	Tocantins	Faveirinha
PARAGUAY	Asunción	Tapé-hú, Tapih-ih-jhu
VENEZUELA	Bolívar	Tucurito

Table 3. Vernacular names of *Machaerium acutifolium* Vogel.

Distribution and Ecology – *Machaerium acutifolium* is registered in Argentina (Burkart 1943), Bolivia, Brazil, Paraguay, Peru, and Venezuela. In Brazil, it occurs in Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraná, Piauí, Rondônia, São Paulo and Tocantins.

Although all materials analyzed until this moment for Bahia represent *Machaerium* sp. nov. 1 and *Machaerium* sp. nov. 2, discussed later in this chapter, we do not disconsider the occurrence of *M. acutifolium* for this state since great part of its western portion has Cerrado vegetation and there are records of collections on the borders between Bahia/Goiás/Tocantins.

Thus, in Brazil, this species occurs predominantly in the Cerrado biome. In the Atlantic Forest, it is more associated with seasonal semideciduous forests and in the Amazon, it is

restricted to bordering regions in areas of Cerrado (Pará and Rondônia). It is commonly located in forest edges, gallery forests and in regeneration environments (Rosa et al. 2014).

Concerning the soil, in the Cerrado and Atlantic Forest, it can be found in red, red-yellow latosol, quartzarenic neosol, gravelly, sand-stone outcrops, sandy, clay-stony, and sandy-clay soils. In the Amazon, it can be found in clay and more fertile soils (Ducke 1949). Regarding altitude, it is often found at elevations between 350 and 700 meters but can be found at altitudes between 1000 and 1400 meters (Chapada dos Veadeiros – Brazil; Andes Mountains – Peru).

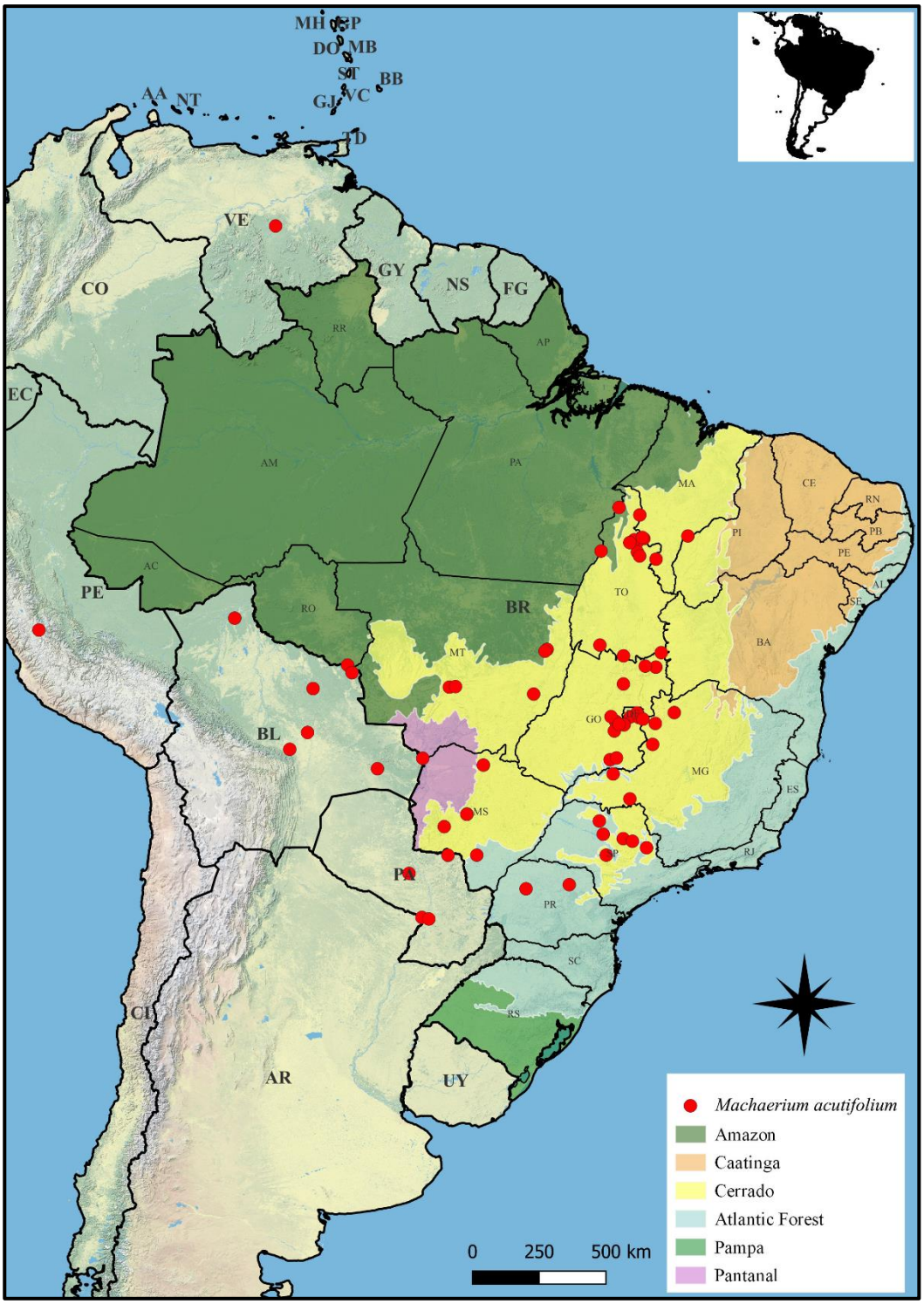


Figure 12. Distribution map of *Machaerium acutifolium* Vogel.

Taxon discussion — *Machaerium acutifolium* can be recognized by the strictly arboreal habit, 11–19-leaflets, petiole, and rachis glabrous to puberulent and, generally blackish when dehydrated, leaflets generally alternates and oblong-lanceolates. In the reproductive characters, the flowers vary in length of about 8–9 mm, the banner, externally is sericeous-nigrescent and internally white with generally greenish streaks; the androecium is monadelphous, with a

glabrous filaments sheath and filaments, and concerning to the fruits, the seed chamber is prominent and verrucose.

Due to its geographic distribution as well as a great phenotypic plasticity, several names have been proposed and are now included in the synonymy of *Machaerium acutifolium* (Filardi and Lima 2014; Filardi et al 2020).

Initially, this species was published by Vogel in March 1837 in "Linnaea" and in the same year, Bentham published in June the name *M. muticum* in "Commentationes de Leguminosarum Generibus" which was later recognized in 1862 in the work "Flora Brasiliensis", by the same author, as an infraspecific taxon of *M. acutifolium*, at the variety level.

In 1973, Rudd proposed that the names *M. enneandrum* (published in 1938, type material: Mato Grosso, Brazil) and *M. pseudacutifolium* (published in 1941, type material: Guárico, Venezuela) should also be recognized as infraspecific taxa at the variety level from *M. acutifolium*.

In a recent taxonomic review for the genus (Filardi 2011; Filardi and Lima 2014), the authors included *M. muticum* and *M. pseudacutifolium* in addition to the name *M. juglandifolium* (published in 1910, type material: Tumpasa, Bolivia) in the synonymy of *M. acutifolium* and in 2020, Filardi and collaborators recognized two other names under the synonym, the variety *M.* var. *enneandrum* and now the name *Sweetia atrata* (published in 1932, type material: Paraguay).

Although the nomenclatural update has contributed to the delimitation of the morphological limits of this species, it still did not fully explain the variation observed by Filardi (2011) and Filardi and Lima (2014), mainly in relation to the shape and size of the leaflets (leaflets 3.5–10 cm long; elliptical, lanceolate, oblong-lanceolate, oval-lanceolate; apex acute, acuminate, mucronulate) and the size of the fruits and surface of the seminiferous nucleus (samaras 5–9 cm long with seminiferous nucleus sparse-puberulent to glabrous, prominent, wrinkled, verrucous), and Queiroz (2009) working exclusively with materials from Caatinga, recognized two varieties but indicated that more careful treatment could result in the recognition of new different taxa.

Thereby, the explanation for this great phenotypic plasticity lies in the fact that many of the materials collected in the Cerrado of western Bahia, Goiás, Tocantins and Maranhão, are

representatives of *M. mucronulatum* and the materials from the Caatinga, mainly from the Chapada Diamantina, represent *Machaerium* sp. nov.1 and *Machaerium* sp. nov. 2.

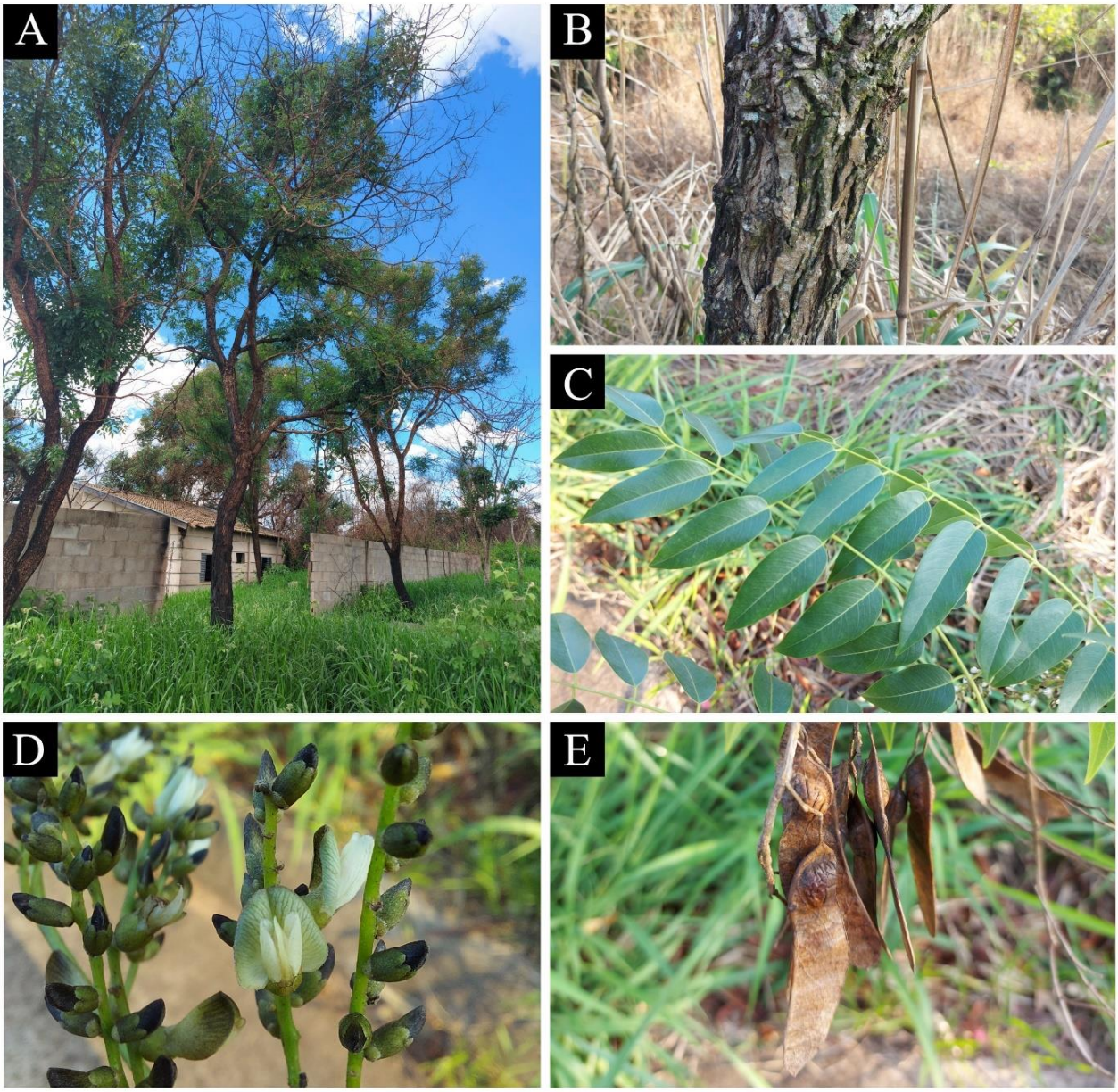


Figure 13. Field images of *Machaerium acutifolium* Vogel. A. Habitat, Seasonal Semideciduous Forests, at Itajobi, São Paulo. B. Trunk detailing the bark. C. Leaves. D. Inflorescence detailing a flower. E. Fruit. (A– E Jordão, V.M.M.).

5.5.2. *Machaerium mucronulatum* Mart. ex Benth.

Machaerium mucronulatum Mart. ex Benth., Comm. Legum. Gen.: 36. 1837. Tipo: Brazil. In Chapada do Paranam, et ad Rio Fermoso provinciarum Minas Geraes et Pernambuco, 1837, fl., *C.F.P. von Martius s.n.* (Lectotype here designated: M-0234172 [photo!]; isolectotype M-0234171 [photo!]).

Trees or shrubs, 1–6.5 m tall; trunk ramified; bark fissured, brown. **Branches** cylindric, brown, puberulent to tomentose; lenticels conspicuous; cataphyll absent; stipules not seen. **Leaves** 10–22 cm long; pulvinus 0.4–0.7 cm long, ferruginous-pubescent; petiole 1.5–4.7 cm long, ferruginous-pubescent to ferruginous-tomentose; rachis 4.3–12.5 cm long, ferruginous-pubescent to ferruginous-tomentose; pulvinule 0.1–0.3 cm long, ferruginous-pubescent. Leaflets 11–15, opposite to sub-opposite, rarely alternate, discolors, margin entire, chartaceous to coriaceous; adaxial surface lustrous, sub-glabrous to ferruginous-pubescent; abaxial surface opaque, ferruginous-pubescent to ferruginous-villous; midrib villous at close to the pulvinule than sparce pubescent; secondary veins multiple-brochidodromous. Basal leaflet 2.0–4.7 × 1.0–2.9 cm; ovate to ovate-lanceolate; apex attenuate and mucronulate; base subcordate to cordate. Middle leaflets 1.3–6.6 × 1.2–3.1 cm; lanceolate to oblong-lanceolate; apex attenuate and mucronulate; base subcordate to cordate. Terminal leaflet 2.9–5.5 × 0.9–2.3 cm; elliptic to obovate; apex attenuate and mucronulate; base acute to subcordate. **Inflorescence** panicle 4.5–12.7 cm long, axillar or terminal, pendulous, lenticels absent; peduncle 1.8–3.5 cm long, ferruginous-pubescent; rachis 5.5–10.2 cm long, ferruginous-pubescent; lateral axis 2.2–3.3 cm long; ferruginous-pubescent; bracts foliaceous, not seen. **Flowers** 8–10 mm long; bracteoles 1.6–1.7 × 1.2–1.3 mm, large-ovate, ferruginous-tomentose; calyx 3.5–3.6 × 6.3–7.1 mm, ferruginous-tomentose; corolla white. Banner petal 6.4–6.7 × 5.6–6.9 mm, orbicular, externally ferruginous-tomentose, internally glabrous to tomentose in the apex, apex retuse, base attenuate, claw 2,1 mm long. Wing petals 4.9–5.3 × 2.2–2.8 mm, slightly-oblong, sub-glabrous in the middle vein dorsally, apex obtuse, base slightly auriculate, claw 3.9 mm long. Keel petals 4.5–4.7 × 2.1–2.7 mm, falcate-oblong, ferruginous-tomentose in the middle vein dorsally, apex acute, base auriculate, claw 3.7–3.9 mm long. Androecium monadelphous, 10 stamens; filament sheath 4.9–5.0 mm long, glabrous; filaments 2.0–2.4 mm long, glabrous; anthers 0.4 × 0.3–0.4 mm, oblong or triangular. Gynoecium with nectary 0.4–0.6 × 0.6–0.7 mm, cupulate; stipe 3.0–3.3 mm, glabrous at the base to sparse tomentose toward the ovary; ovary 3.0–4.1 × 1.0–1.2 mm, ferruginous-tomentose; style 1.2 mm long, glabrous; stigma captade. **Fruit** samara, 6.5–7.2 cm long; stipe 0.5–0.9 cm long, sub-glabrous to ferruginous-sericeous; seed chamber 1.0–

1.7 × 0.8–1.1 cm, oblong-falcate, prominent, brown, sub-glabrous; wing 2.2–4.4 × 1.1–1.7 cm, oblong-falcate, reticulate, brown, sub-glabrous; apex obtuse, rarely short-apiculate.

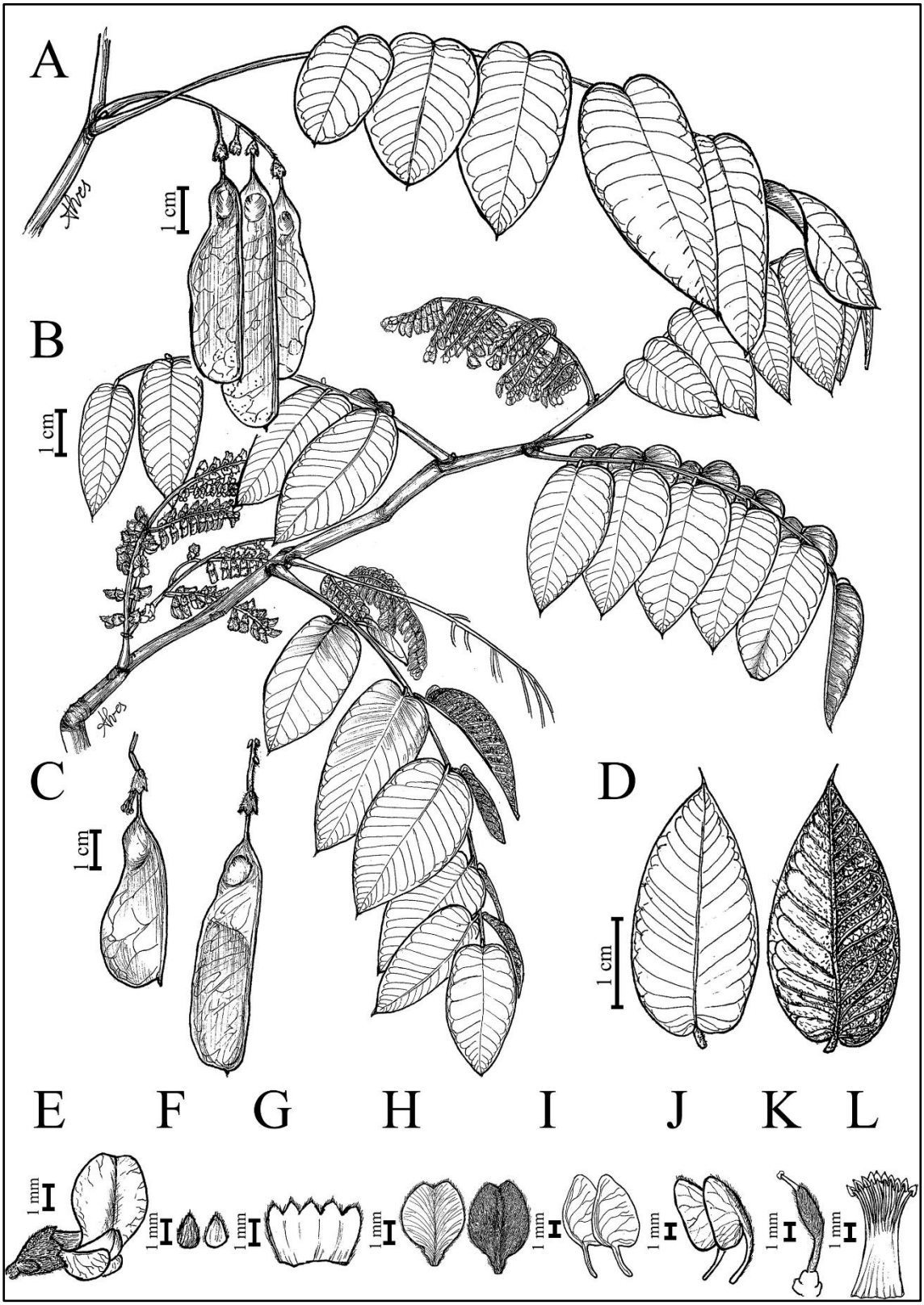


Figure 14. Illustration of *Machaerium mucronulatum* Mart. ex Benth. **A** – Branch with fruits (Pereira, B.A.S. *et al*. 1576); **B – L**. Heringer, E.P. 9821; **B –** Branch with flowers; **C** – Immature and mature samaras; **D** – Leaflets

(respectively adaxial and abaxial surface); **E** – Flower; **F** – Bracteoles; **G** – Calyx; **H** – Banner petal; **I** – Wing petals; **J** – Keel petal; **K** – Gynaecium; **L** – Androecium. (Illustrator: Vieira, J.A.)

Additional material examined – **BRAZIL**. BAHIA: Barreiras, 12°04'S, 45°05'W, 21 Nov 1980, fr. *S.B. da Silva 159* (CEPEC, RB); cerrado ralo com vestígios de fogo, 12°14'24''S, 45°10'48''W, 19 Jul 2017, st., *J.F. Araújo 146* (UB); Km 87 da rodovia Barreiras/Ibotirama, 10 Feb 1991, fr., *B.A.S. Pereira et al. 1576* (UB); Catolândia, Campo Sujo, 12°14'24''S, 44°38'24''W, 06 Jul 2017, st., *E.O. Moura 1246* (UB); Cristópolis, Cerrado Denso em regeneração com presença de antropização, 12°14'24''S, 44°06'00''W, 11 Jul 2017, st., *J.F. Araújo 107* (UB); Espigão Mestre, ca. 100 Km SW of Barreiras, 800 m, 07 Mar 1972, fr., *W.R. Anderson et al. 36777* (NY [digital image], RB, UB, US [digital image]); Formosa do Rio Preto, Coaceral, remanescente na beira de estrada numa área de cultivo intenso, 892 m, 10°33'68''S, 45°41'21''W, 26 Mar 2000, fr., *R.M. Harley et al. 53764* (CEPEC), Fazenda Estrondo, reserva, Arbóreo Denso, 810 m, 11°27'4''S, 46°9'42''W, 03 Feb 2000, fr., *N.G. Jesus et al. 823* (CEN); rodovia Anel da Soja, Reserva de Cerrado entre plantios de soja, 710 m, 11°26'S, 46°04'W, fr., 15 Nov 1995, *B.M.T. Walter et al. 2935* (CEN); Tabocas do Brejo Velho, ca. 101 Km W de Ibotirama na Br-242, Cerrado Arbustivo, 12°15'S, 43°59'W, 11 Oct 1994, fl., *L.P. de Queiroz & N.S. Nascimento 4071* (HUEFS, NY [digital image], VIES [digital image]). – GOIÁS: São Domingos, Parque Estadual de Terra Rouca, Módulo RAPELD, Parcela 3500W, s.d., fr., *A.M.C. Teixeira & J.R.R. Pinto 16* (UB), Parque Estadual de Terra Rouca, Cerrado sensu stricto, 13°36'44''S, 46°17'23'', 687 m, 03 Nov 2013, fl., *C.B.R. Munhoz, et al. 7432* (UB); São Domingos, Parque Estadual de Terra Rouca, Cerrado sensu stricto, 13°36'44''S, 46°17'23'', 687 m, 03 Nov 2013, fl., *C.B.R. Munhoz, et al. 7503* (HUEFS, UB) – MARANHÃO: Balsas, Projeto de Colonização Agrícola Gerais de Balsas, Região de Vila Kissy, próximo ao rio Tem Medo (Lote 23), 08°38''S, 46°43'W, 19 Mar 2000, fr., *B.M. Walter et al. 4420* (CEN, HUEFS); BR-230 entre Patos Bons e São Domingos de Jaboatão, 05 Dec 1980, fr., *E. Nunes & P. Martins s.n* (HUEFS). – MINAS GERAIS: Chapada de Pirapora, 26 Sep 1964, fl., *E.P. Heringer & L.R. Guimarães 9821* (UB); São Gonçalo do Abaeté, Rodovia BR-365 Km 261, 20 Mar 1980, fr., *G. Hatschbach 42811* (INPA). TOCANTINS: Palmas, Serra do Lajeado, próximo ao Córrego Brejao, Cerrado sobre latossolo, 10°0'00''S, 48°13'00''W, 15 Apr 1994, fr. *A.E. Ramos et al. 731* (HEPH, UB); Palmas, Córrego Brejo da Lagoa, 10°17'45''S, 48°7'40'', 15 Apr 1994, fr., *A. E. Ramos et al. 331* (UB); Palmas, Parque Estadual da Serra do Lajeado, fragmento florestal de aproximadamente 10 ha., próximo a uma das entradas do parque, 10°11'14''S 48°10'43''W, 687 m, 01 Feb 2020, fr., *M.S. Martins 158*

(CEN, UB); Palmas, Parque Estadual da Serra do Lajeado, parcela permanente: 27, 01 Feb 2021, fr., *M.S. Martins et al. 186* (CEN, UB).

Phenology – The species flowering from September to November and fruiting from November to April.

Vernacular names – *Machaerium mucronulatum* is known as Jacarandá and Violete in Bahia and Maranhão state.

Distribution and Ecology – *Machaerium mucronulatum* occurs in the Bahia, Goiás, Maranhão, Minas Gerais, and Tocantins. Here we expand its distribution, verifying that this species also occurs in the states Goiás, Maranhão and Tocantins. In addition, we did not find material occurring in Pernambuco, as cited in Filardi et al. (2020) thus we decided to exclude the occurrence of *M. mucronulatum* for this state. It occurs in Cerrado "*stricto sensu*" and it is commonly found in regeneration environments. As concerning the soil and the altitude, the species be found on sandy-clay soil with superficial gravel at elevation between 470 to 810 meters.

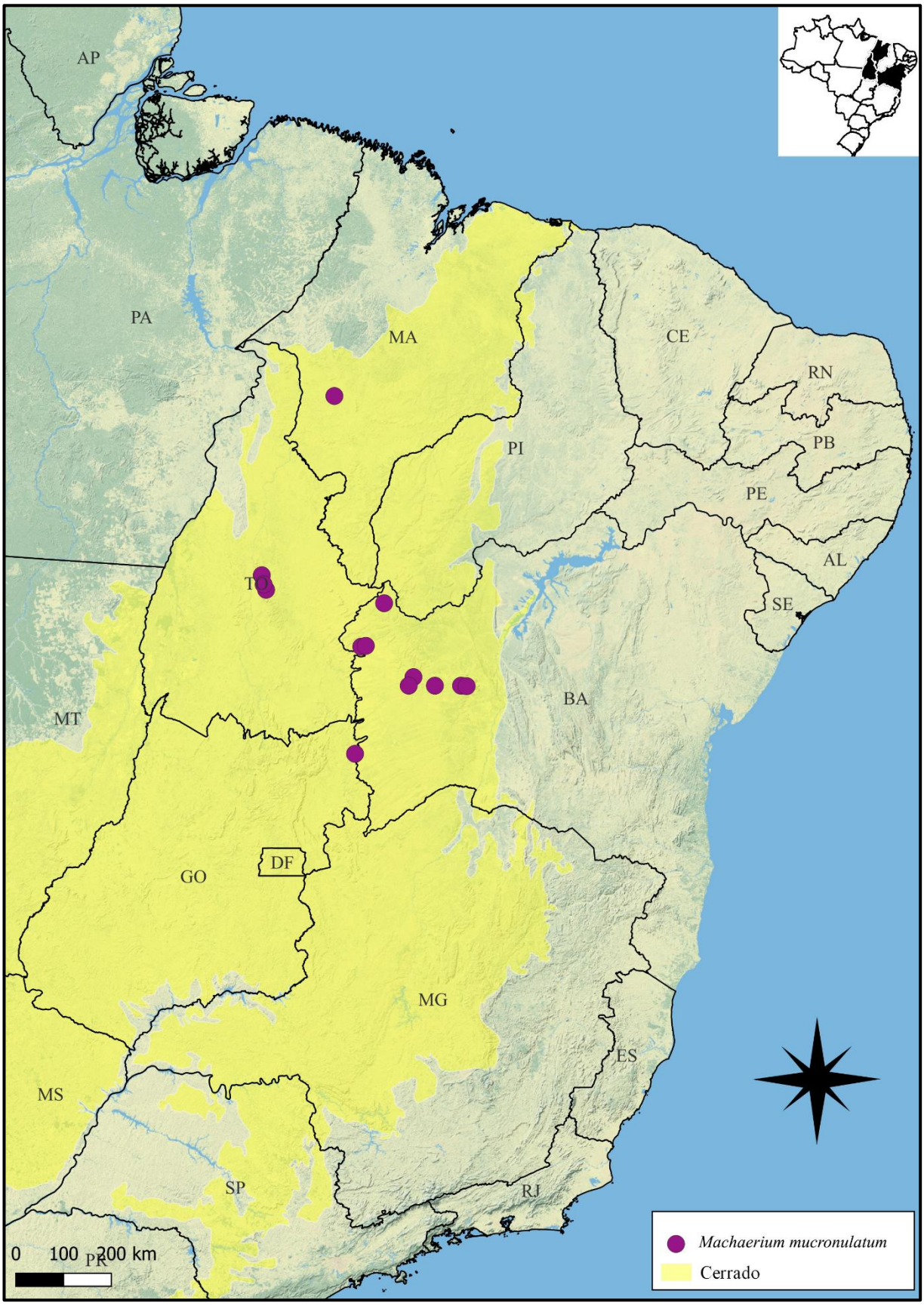


Figure 15. Distribution map of *Machaerium mucronulatum* Mart. ex Benth.

Taxon discussion — Machaerium mucronulatum can be recognized by short pulvinulus; leaflets base cordate, opposite to subopposite, ferruginous indumentum when dehydrated. In the reproductive characters, the flowers vary in length of 8–10 mm; monadelphous androecium, with a glabrous filaments sheath and filaments and as concerning the fruits, samaras present seed chamber prominent.

M. mucronulatum was published in 1837 by Bentham in "*Commentationes de Leguminosarum Generibus*". The author provided a rich description of the leaves, inflorescences, and flowers although, at that moment, the fruits had not been observed. Later in 1859, this species was included in "*Flora Brasiliensis*". That time, Bentham once more was not able to see materials presenting fruits, but he provided a very informative discussion to separate *M. acutifolium* from *M. mucronulatum* and *M. opacum* "*Differt a* M. acutifolio *foliolis brevius petiolulatis, evidentius cordatis, magis coriaceis et mucrone; a* M. opaco*, foliolis angustioribus tenuioribus acutis mucronatisque".* Later in the same publication, it was presented a remarkable illustration, the first one for that species presenting flowers and fruits, updating the knowledge of *M. mucronulatum* morphology.

However, 1859 was the last time *M. mucronulatum* was included in a taxonomic treatment for Brazil. Rudd in 1973 indicated the type deposited in München herbarium, but no recent studies on this species was done until now. The result of this was although there was a significant number of materials of this species in the Cerrado collections, all of them were determined as *M. acutifolium* or *M. opacum*. Before starting this study, in Reflora Virtual Herbarium there was only one material (E.P. Heringer 8716/910, Minas Gerais, HEPH [digital image]) indicated as *M. mucronulatum*, but it came to be a *M. acutifolium* specimen.

To clarify this matter, we provided here, in the end of taxon discussion section of *M. opacum* a table comparing different morphological characters among *M. acutifolium, M. mucronulatum*, and *M. opacum* (Table 3).

5.5.3. *Machaerium opacum* Vogel

Machaerium opacum Vogel, Linnaea 11: 187. 1837. TYPE: BRAZIL. “Brasil merid.”, s.d., fr., *F. Sellow s.n.* – (Lectotype here designated: K000530234 [photo!]; isolectotype: P00734126 [photo!]).

= *Machaerium campestre* Mart. ex Benth., Comm. Legum. Gen.: 36. 1837. TYPE: BRAZIL. Minas Gerais, in campis Taboliero interioribus deserti Serro Frio provinciae Minas Gerais, s.d., fl., *C.F.P. Martius s.n.* (Lectotype here designated: M0234177 [photo!]).

= *Machaerium opacum* var. *rotundatum* Vogel, Linnaea 11: 203. 1837. BRAZIL. Brasilia, s.d., fl., *F. Sellow s.n.* – (Lectotype here designated: US00002415 [photo!]).

Trees, 2–11 m tall; trunk cylindric or ramified; bark fissured, brown. **Branches** cylindric, brown, sub-glabrous to tomentose; lenticels conspicuous; cataphyll present; stipules not seen. **Leaves** 13.4–27.2 cm long; pulvinus 0.3–0.4 cm long, strong pale yellow-pubescent to strong pale yellow-tomentose; petiole 1.2–4.7 cm long, strong pale yellow-pubescent to strong pale yellow-tomentose; rachis 10.2–16.7 cm long, strong pale yellow-pubescent to strong pale yellow-tomentose; pulvinule 0.2–0.3 cm long, strong pale yellow-pubescent. Leaflets 9–15, alternate to sub-opposite, concolorous or slightly discolours, margin entire, coriaceous; adaxial surface opaque, sub-glabrous to strong pale yellow-pubescent; abaxial surface opaque, strong pale yellow-pubescent to strong pale yellow-tomentose; midrib strong pale yellow-sericeous-tomentose; secondary veins multiple-brochidodromous. Basal leaflet 2.5–5.1 × 1.9–3.0 cm; ovate; apex obtuse and slightly retuse; base subcordate to cordate. Middle leaflets 5.8–7.9 × 2.7–4.1; ovate to oblong-lanceolate; apex obtuse and slightly retuse, rarely acuminate; base subcordate to cordate. Terminal leaflet 5.1–7.5 × 3.4–4.3 ovate to oblong-lanceolate; apex obtuse and slightly retuse, rarely acuminate; base rounded to subcordate. **Inflorescence** panicle, 12.1–17.5 cm long, axillar or terminal, pendulous, lenticels absent; peduncle 2.9–3.1 cm long, strong pale yellow-pubescent to strong pale yellow-tomentose; rachis 9.3–12.2 cm long, strong pale yellow-pubescent to strong pale yellow-tomentose; lateral axis 4.6–12.3 cm long; strong pale yellow-pubescent to strong pale yellow-tomentose; bracts foliaceous, 3.6 × 5.7 mm, large-ovate, sub-glabrous to pubescent at the apex. **Flowers** 7,4 mm long; bracteoles 3.0 × 2.0 mm, ovate, strong pale yellow-tomentose; calyx 2.9 x 5.4 mm, strong pale yellow-tomentose; corolla white. Banner petal 4.6 × 4.8 mm, orbicular, externally tomentose, internally glabrous to tomentose in the apex, apex emarginate, base attenuate, claw 2.0 mm long. Wing petals 4.5 × 1.9 mm, oblong, sparsely pubescent in the middle vein dorsally, apex obtuse, base slightly

truncate, claw 2.5 mm long. Keel petals 4.0–4.1 × 1.7–1.9 mm, falcate-oblong, pubescent in the middle vein dorsally, apex acute, base auriculate, claw 2.9 mm long. Androecium monadelphous, 10 stamens; filament sheath 3.6 mm long, glabrous; filaments 2.3–2.4 mm long, sparsely pilose; anthers 0.4 × 0.3 mm, triangular. Gynoecium with nectary 0.7 × 7.5 mm, cupulate; stipe 1.5 mm, tomentose; ovary 3.3 × 1.0 mm, primrose-tomentose; style 1.9 mm long, glabrous; stigma punctate. **Fruit** samara, 6.5–8.8 cm long; stipe 0.8–1.0 cm long, sub-glabrous; seed chamber 1.2–2.0 × 1.0–1.5 cm, oblong, prominent, rarely verrucose, brown, glabrous; wing 4.1–6.1 × 1. 8–2.0 cm, oblong rarely oblong-falcate, reticulate, brown, glabrous; apex obtuse.

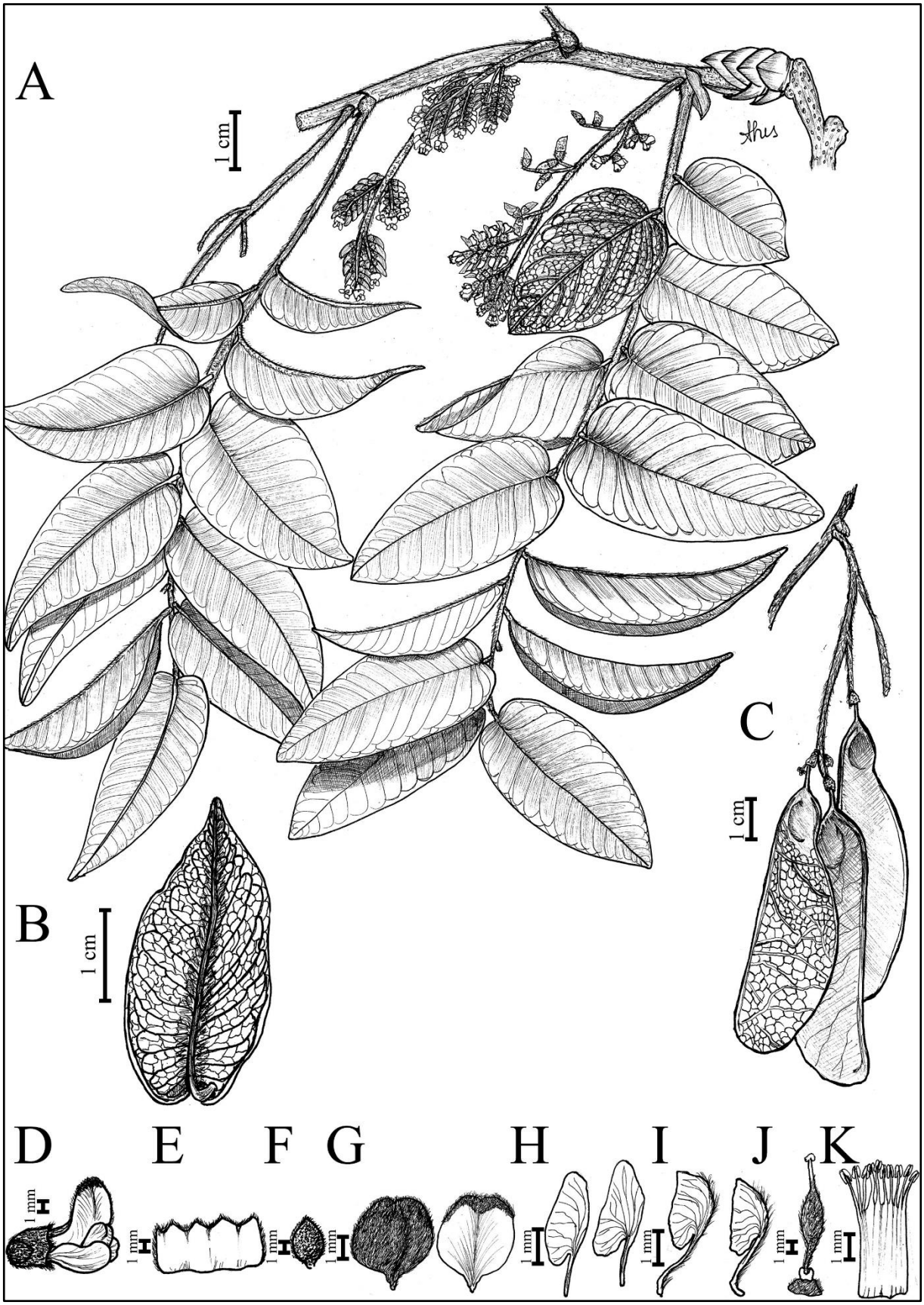


Figure 16. Illustration of *Machaerium opacum* Vogel. **A** – Branch with flowers (Queiroz, L.P. et al. 2120); **B –** Abaxial surface of the leaflet; **C** – Fruits; **D** – Flower; **E** – Calyx; **F** – Bracteoles; **G** – Banner petal; **H** – Wings petal; **I** – Keel petals; **J** – Gynaecium; **K** – Androecium. (Illustrator: Vieira, J.A.)

Additional material examined – **BRAZIL.** BAHIA: Barreira, Cachoeira Acaba-Vida, ca. de 91 km da sede, 710 m, 12°53’41’’S, 45°36’03’’W, 04 Feb 2000, fr., *M.R. Fonseca et al. 1275* (CEN, CEPEC, HUEFS, NY [digital image], SPF, UESC); 46 Km E da cidade de Barreira, Cerrado, 12°09’27’’S, 44°37’03’’W, 03 Nov 1987, fl., *L.P. Queiroz 2120* (ALCB [digital image], CEN, HUEFS, MBM [digital image], NY [digital image], UB); Caetité, ca de 7 Km N de Caetité, na estrada para Maniaçu, 13°59’S, 42°28’W, 28 Oct 1993, fr., *L.P. Queiroz & N.S. Nascimento 3635* (HUEFS); ca 2 Km S de Caetité, na estrada para Brejinho das Ametistas, 14°05’S, 45°32’W, 27 Oct 1993, fl., *L.P. Queiroz & N.S. Nascimento 3573* (HUEFS); Formosa do Rio Preto, Cerrado próximo ao rio Riachão, solo arenoso, 530 m, 11°07’17’’S, 45°28’W, 07 Apr 1989, fr., *B.M.T. Walter 224 et al.* (CEN, SP, UB); ESEC Serra Geral do Tocantins, acampamento da Vila dos Prazeres, 605 m, 10°47’33’’ S, 46°04’51’’W, 05 Oct 2018, fl., *M.F. Simon et al. 3564* (CEN, HUEFS, HUTO); Rio de Contas, estrada Fazendola-Caiambola, 1350 m, 13°30’S, 41°52’W, 24 Dec 1999, fl., *F.H.F. Nascimento 313* (CEN, CEPEC, HUEFS, IPA, VIC [digital image]); São Desidério, Oeste, Roda Velha, 12°21’S, 44°58’W, 16 Feb 2017, fl., *M.L. Guedes 25508* (ALCB [digital image], CEN), ca 2 a 3 Km do povoado Cabeceira Grande, 688 m, 13°39’33’’S, 45°01’57’’W, 21 May 2010, fr., *E. Melo et al. 8146* (HUEFS). – DISTRITO FEDERAL: Brasília, centro Olímpico da UnB, 15°53’S, 47°52’W, 04 Oct 1993, fl., *T.C.U. Brasília 1110* (UB), condomínio Residencial, 1100 m, 04 Mar 2000, fr., *G. Pereira Silva & G. Abdala 4247* (CEN); em frente à primeira barragem da CAESB JBB, 1150 m, 15°52’S, 47°51’W, 22 May 1996, fr., *V.J. Caetano 41* (HEPH); Parque Ecológico Burle Marx, 1100 m, 15°45’55’’S, 47°54’14’’W, 07 Nov 2020, fl., *M. Figueira & B. Schindler 1534* (CEN); Planaltina - EMBRAPA CPAC - BR-20 km 15 - Brasília-Fortaleza, 1175 m, 15°35’30’’S, 47°42’30’’W, 30 Mar 1980, st., *J.A. Silva & J. Fonseca 19* (CEN); Reserva Ecológica de Águas Emendadas, BR-020, 23 Nov 1976, fr., *K.A. Okada 777* (CEN); Reserva Ecológica do IBGE, estrada para o córrego do Roncador, cerca de 300 m da entrada, 1105m, 15°56’43’’S, 47°52’31’’W, 23 Oct 2017, fl., *H.C. Lima et al. 8566* (ALCB [digital image], CEN, HUEFS, RB); 2 km à esquerda do posto Colorado, 14 km à direita do primeiro desvio, 960 m, 15°46’S, 47°55’W, 08 Apr 1994, fr., *R.F. Vieira 1854* (CEN, HUEFS, NY [digital image]). – GOIÁS: Alexânia, Estrada de acesso à foz do rio Galinha, 905 m, 06 Aug 2003, fr., *J.M. Rezende et al. 912* (CEN); Aparecida de Goiânia, Caminho para Chácara Jatobá, 26 Apr 2003, fr., *J.F.B. Pastore & J.B.A. Bringel 573* (CEN); Barro Alto, área de mineração da Anglo American, 918 m, 15°06’07’’S, 49°00’40’’W, 21 Nov 2012, fr., *M.F. Simon et al. 1780* (CEN); Caldas Novas, alternativa 4 régua de leitura de vazão da Hidrometria, 600 m, 17°56’S, 48°51’W, 27 Feb 1996, fr., *G. Pereira-Silva et al. 3389* (CEN, HUEFS, UEC [digital image]), Parque estadual Serra de

Caldas Novas, 14 Aug 2009, fl., *D.I. Junqueira 553* (CEN, UB); 24 Jan 2010, fr., *D.I. Junqueira 638* (CEN, UB); Rodovia Caldas Novas–Ipameri, 2,5 Km leste do Ribeirão Pirapitinga, 690 m, 17°42’S, 48°32’W, 28 Aug 1996, st., *G. Pereira-Silva et al. 3599* (CEN, UEC [digital image]); Campinaçu, Conglomerado: GO-111. subunidade 3, subparcela 1, indivíduo 9, 13°51’36’’S, 48°36’00’’W, 26 Apr 2018, fr., *L. Lerner 1279* (CEN); Cavalcante, após o canteiro de obras da barragem de Cana Brava, cerca de 2,5 Km do eixo da barragem, na direção do Rio do Carmo, 370 m, 13°23’45’’S, 48°07’45’’W, 23 Jan 2001, fr., *B.M.T. Walter et al. 4754* (CEN); Cerrado, ca. 12 Km S. of Pirenópolis, 1000 m, 01 Dec 1965, fl., fr., *H.S. Irwin et al. 10877* (UB); Colinas do Sul, a 1 Km do entroncamento da estrada que vai a ponte do rio Tocantins para Minaçu, a 21 Km da usina, 640 m, 14°12’S, 48°04’W, 12 Mar 1992, fr., *T.B. Cavalcanti et al. 1195* (CEN); Estrada de terra de acesso às linhas de transmissão Serra da Mesa-Samambaia. Na altura das torres 40 a 48. Cerca de 10km ao sul da Barragem de Serra da Mesa, 530 m, 13°53’S, 48°19’W, 17 Jul 1998, fr., *B.M.T. Walter et al. 4251* (CEN, HUEFS); Formosa, Fazenda Santa Fé, Km 35 da rodovia Formosa/Alvorada do Norte, 700 m, 15°20’S, 46°50’W, 26 Apr 1996, fr., *B.A.S. Pereira & D. Alvarenga 2970* (RB); Fazenda Vargem-Grande, a 190 Km de Brasília, localizada na margem direita do rio Praim ou Paraim, região do vale do Paranã, do lado esquerdo da rodovia BR-020, no sentido Brasília-Fortaleza, 08 Jun 1992, st., *I.C.A. Mendes 106* (UB), Margem direita do rio Bezerra, cerca de 1 km a Leste da Lagoa Perta Pé (área do Exército), 820 m, 15°59’06’’S, 47°11’35’’W, 05 Mar 2002, fr., *G. Pereira-Silva et al. 6006* (CEN); Goiás, Goiás Velho, base da Serra Dourada, s.d., fr., *A.P. Duarte & A. Mattos 8183* (RB, UB); Padre Bernardes, 02 Nov 1976, fl., *E.P Heringer 16179* (UB); Hidrolândia, entrada na BR-153 sentido a Goiânia, passando posto de combustível, próximo ao condomínio Terras do Boi, 780 m, 16°53’25’’S, 49°14’32’’W, 15 Feb 2016, fr., *R.L.G. Coelho et al. 808* (CEN, CVRD, ESA); Luziania, margem esquerda do rio Corumbá, chapada entre o rio Alagado e o Corumbá, 900 m, 16°15’15’’S, 48°08’40’’W, 30 Jun 2003, fr., *G. Pereira-Silva et al. 7930* (CEN); Minaçu, canteiro de obras, Km 2, 350 m, 13°29’44’’S, 48°13’14’’W, 11 Jul 2001, fr., *G. Pereira-Silva et al. 5235* (CEN); São Domingos, mata à beira da estrada, 13°33’51’’S, 46°43’18’’W, 13 Mar 2004, fr., *A.A. Santos et al. 2352* (CEN); Parque Estadual de Terra Ronca – Módulo RAPELD, parcela 1500W, indivíduo 284, 766 m, Nov 2019, fr., *A.M.C. Teixeira & J.R.R. Pinto 16* (UB); Sandy cerrado, Rio da Prata, ca. 6 Km S. of Posse, 800 m, 14°S, 46°W, 04 Apr 1966, fr., *H.S. Irwin 14343* (UB); Santo Antônio do Descoberto, margem direita do rio Descoberto, próximo a Barra com o Córrego Engenho das Lages, 900 m, 16°05’39’’S, 48°16’27’’W, 17 Feb 2003, fr., *G. Pereira-Silva et al. 7085* (CEN); Rocky campo ca. 7 Km E. of Cabeceiras, 1000 m, 16°S, 47°W, 18 Nov 1965, fl., *H.S. Irwin 10496* (UB); Uruaçu, ao norte

da cidade de Uruaçu, passando pelo córrego Macaco, na direção, das fazendas Laje ou Jacaré, 470 m, 14°20’S, 49°02’W, 09 Feb 1996, fr., *B.M.T. Walter et al. 3169* (CEN, NY [digital image], UEC [digital image]), estrada Uruaçu-Niquelândia, cerca de 4 km da ponte nova sobre o lago de Serra da Mesa, 560 m, 14°33’15’’S, 49°00’16’’W, 13 Oct 1997, fl., *B.M.T. Walter et al. 3890* (CEN, HUEFS, UEC [digital image]), região das fazendas GZ, à direita da GO-237, no rumo Uruaçu-Niquelândia, 450 m, 14°33’S, 49°02’W, 26 Jun 1996, fr., B.M.T. *Walter et al. 3349* (CEN); 15 Km N. of Corumbá de Goiás on road to Niquelândia, Goiás in valley of Rio Corumbá, 1150 m, 17 Jan 1968, fr., *H.S. Irwin et al. 18689* (UB); 75 Km N of Corumbá de Goiás, on road to Niquelândia, Goiás in valley of Rio Maranhão, 700 m, 23 Jan 1968, fr., *H.S. Irwin 19043* (UB). – MATO GROSSO DO SUL: Ribas do Rio Pardo, conglomerado: MS-498. subunidade 2, subparcela 1, indivíduo 1, 20°20’24’’S, 53°38’24’’W, 11 May 2018, fr., *J.A. da Silva 900* (CEN) – MINAS GERAIS: Cerrado a 500 Km de Brasília para Belo Horizonte, 19 Jun 1964, fr., *J.M. Pires 57999* (UB); Formoso, Parque Nacional Grande Sertão Veredas. 10 Km a Noroeste da fazenda do Sr. Edgar, próximo ao Rio Carinhanha, 760 m, 15°09’S, 45°47’ W, 31 Jul 1989, fr., *B.M.T. Walter et al. 327* (CEN); Francisco Sá, 30 Km antes da cidade, 16°25’S, 42°18’W, 19 Apr 2012, fr., *E.R. Souza et al. 857* (HUEFS); Grão Mogol, assentamento Americana, 18 Nov 2014, fl., *A.B. Giroldo & J.B. Pereira 313* (CEN, UB), beira de estrada, baixada com lagoa intermitente, com cerrado adjacente, 844 m, 16°22’38’’S, 43°00’10’’W, 26 May 2005, fr., *A.C. Sevilha et al. 4482* (CEN); Joaquim Felício, Serra do Cabral, subida do Morro da SCAI, Parque Estadual da Serra do Cabral, 1045 m, 17°43’05’’S, 44°11’26’’W, 12 Nov 2010, fl., *N.F.O. Mota et al. 1624* (HUEFS); Morada Nova de Minas, Cerrado recorte acima do cerrado virgem da fazenda Boa Vista, a 18,2 Km da cidade, 18°35’S, 45°22’W, 12 Nov 1991, fl., *R.F. Vieira et al. 932* (CEN, HEPH, NY [digital image]); Paraopeba, margem da rodovia I. 15 Km de Paraopeba, 25 Sep 1960, st., *E.P. Heringer 7722* (UB); Perdizes, Estação Ambiental Galheiro, 26 Oct 2002, fl., *E.H. Amorim et al. 286* (UB); Prata, Parque Florestal Buriti dos Bois, 16 Jul 2010, fr., *A.C.B. Marcondelli s.n.* (SJRP); Rio Pardo de Minas, Areião, ponto 1, 830 m, 15°26’13’’S, 42°30’36’’W, 22 May 2005, fr., *A.C. Sevilha et al. 4205* (CEN); ponto 10, 976 m, 15°26’40’’S, 42°27’19’’W, 25 May 2005, fr., *A.C. Sevilha et al. 4380* (CEN); Unaí, Região da ponte sobre o rio Preto, a 29 km do entroncamento BsB/Unaí/Palmital, na direção de Palmital, divisa DF/MG, 850 m, 16°02’15’’S, 47°18’34’’W, 14 Feb 2002, fr., *B.M.T. Walter et al. 5048* (CEN). – PIAUÍ: 18 Km from Guibués, on the road to Santa Filomena, 09°44’S, 45°23’W, 21 Jul 1997, st., *S. Bridgewater et al. S606* (UB). – TOCANTINS: Arraiais, conglomerado TO_696 - coleta extra, 13°08’35’’S, 47°09’36’’W, 16 Dec 2018, fr., *G.P.E. Rocha 1214* (CEN); Dianópolis, 603 m, 11°42’32’’S, 46°20’10’’W, 30

Sep 2009, fl., *T.B. Cavalcanti et al. 3427* (CEN); Mateiros, Refrgião do Jalapão. Proximidades do riacho Formiga, fazenda do Seu Vicente, 10°20'S, 46°29'W, s.d., fr., *A.B. Sampaio & P.L. Simpson 456* (CEN, MBM [digital image], UB).

Phenology – This species presents flowers from August to February and fruits from October to July.

Vernacular names – *Machaerium opacum* is known as Jacarandá-do-campo and Jacarandá-preto in Minas Gerais; Jacarandá-do-cerrado e Jacarandá-muchiba in Goiás; Jacarandá-do-campo and Vinhático-cascudo in Distrito Federal as well as Jacarandá, Jacarandá-bravo and Jacarandá-do-campo in Bahia.

Distribution and Ecology – This species occurs in the Bahia, Distrito Federal, Goiás, Mato Grosso do Sul, Minas Gerais, and Tocantins. It occurs in Cerrado "*stricto sensu*" and it is commonly found in gallery forests and in regeneration environments. Concerning the soil and the altitude, it can be found on sandy-clay soil with superficial gravel and rocky outcrops at elevation between 450 to 1,400 meters.

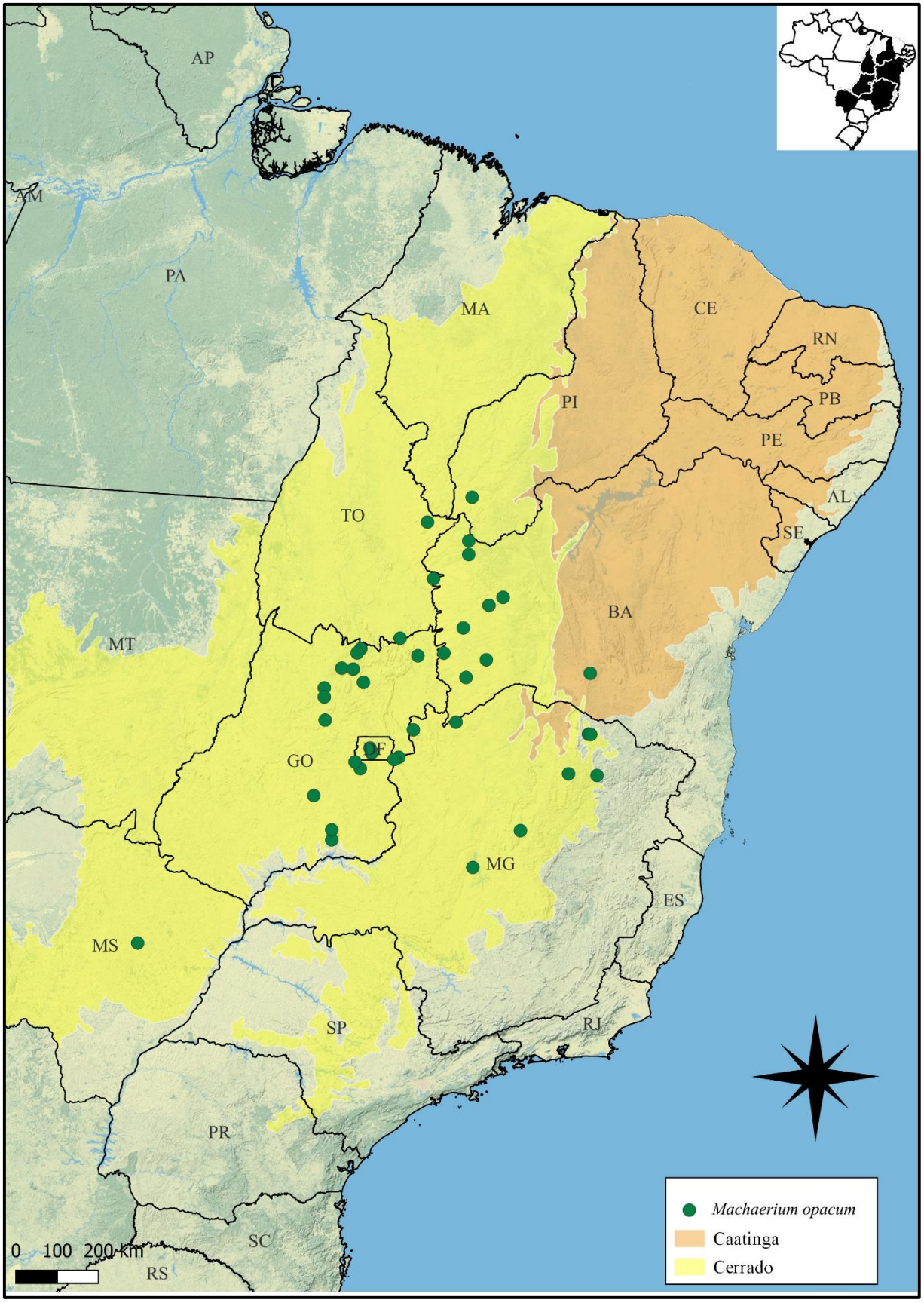


Figure 17. Distribution map of *Machaerium opacum* Vogel

Taxon discussion — *Machaerium opacum* can be recognized by the presence of cataphylls, short pulvinulum (0.2–0.3 cm long.), base of the leaflets cordate to subcordate, leaflets alternate, adaxial surface sub-glabrous to pubescent, abaxial surface tomentose. About reproductive characters, the species has flowers with 7–8 mm length, monadelphous androecium, with filaments sheath and filaments glabrous and samaras with seed chamber prominent, rarely verrucose.

Machaerium opacum and *M. opacum* var. *rotundatum* were published on "Linnaea" in 1837, by Vogel and both materials were collected by *Sellow* but without a collector number. In Filardi et al. 2020, the authors synonymized this variety under *M. opacum*, but the type materials had not been indicated since then. In the protologue for *M. opacum*, Vogel described this species as having 13 up to 17 leaflets, and the Sellow's materials analyzed in Kew (K000530234) and in Paris (P00734126) herbarium correspond to this description. As for *M. opacum* var. *rotundatum* the variation described is from 8 up to 11 leaflets, which corresponds to the material deposited in the Smithsonian Institute herbarium (US00002415).

In the same year, 1837, Bentham published in "Commentationes de Leguminosarum Generibus" the name *Machaerium campestre* and the author indicated two materials: Martius s.n., "*In campis Taboliero interioribus deserti Serro Frio provinciae Minas Geraes*"; and Pohl s.n., "*Ad Pongo alto er Ourofino*". In 1987, Lewis in his book "Legumes of Bahia" synonymized this name under *M. opacum*, however he did not indicate a lectotype. Pohl's material was not found, but Martius's material is in the M herbarium and, therefore, it was used for lectotypification.

Regarding morphology, *Machaerium opacum* is easily distinguished from *M. acutifolium*, however, it was included in this treatment since we observed materials of *M. mucronulatum* determinated as *M. opacum*, and even some materials of *M. opacum*, with vegetative morphological overlaps that led to determinate these samples as *M. acutifolium*. To clarify this matter, we provided here, a table comparing different morphological characters among *M. acutifolium*, *M. mucronulatum*, and *M. opacum* (Table 3).

	M. acutifolium	*M. mucronulatum*	*M. opacum*
Cataphylls	absent	absent	present
Pulvinulum (length)	0,1–0,7 cm	0,1–0,3 cm	0,2–0,3 cm
Leaflets	alternate	opposite	alternate
Adaxial surface	glabrous	sparse pubescent	sparse pubescent
Leaflet's apex	acuminate, mucronate	attenuate, mucronulate	obtuse, slightly retuse
Leaflet's base	rounded	subcordate to cordate	subcordate to cordate
Terminal leaflet	oblong-lanceolate	elliptic to obovate	ovate to oblong-lanceolate
Flower (length)	8-9 mm	9-10 mm	7-8 mm
Seed chamber	prominent and verrucose	prominent	prominent rarely verrucose
Distribution	Argentina, Bolivia, Brazil, Paraguay, Peru, and Venezuela.	Brazil (Bahia, Goiás*, Maranhão* and Tocantins*).	Brazil (Distrito Federal, Goiás, Mato Grosso do Sul, Minas Gerais and Tocantins).

Table 4. Comparison of morphological characters among *Machaerium acutifolium*, *M. mucronulatum*, and *M. opacum.* New occurrences (*).

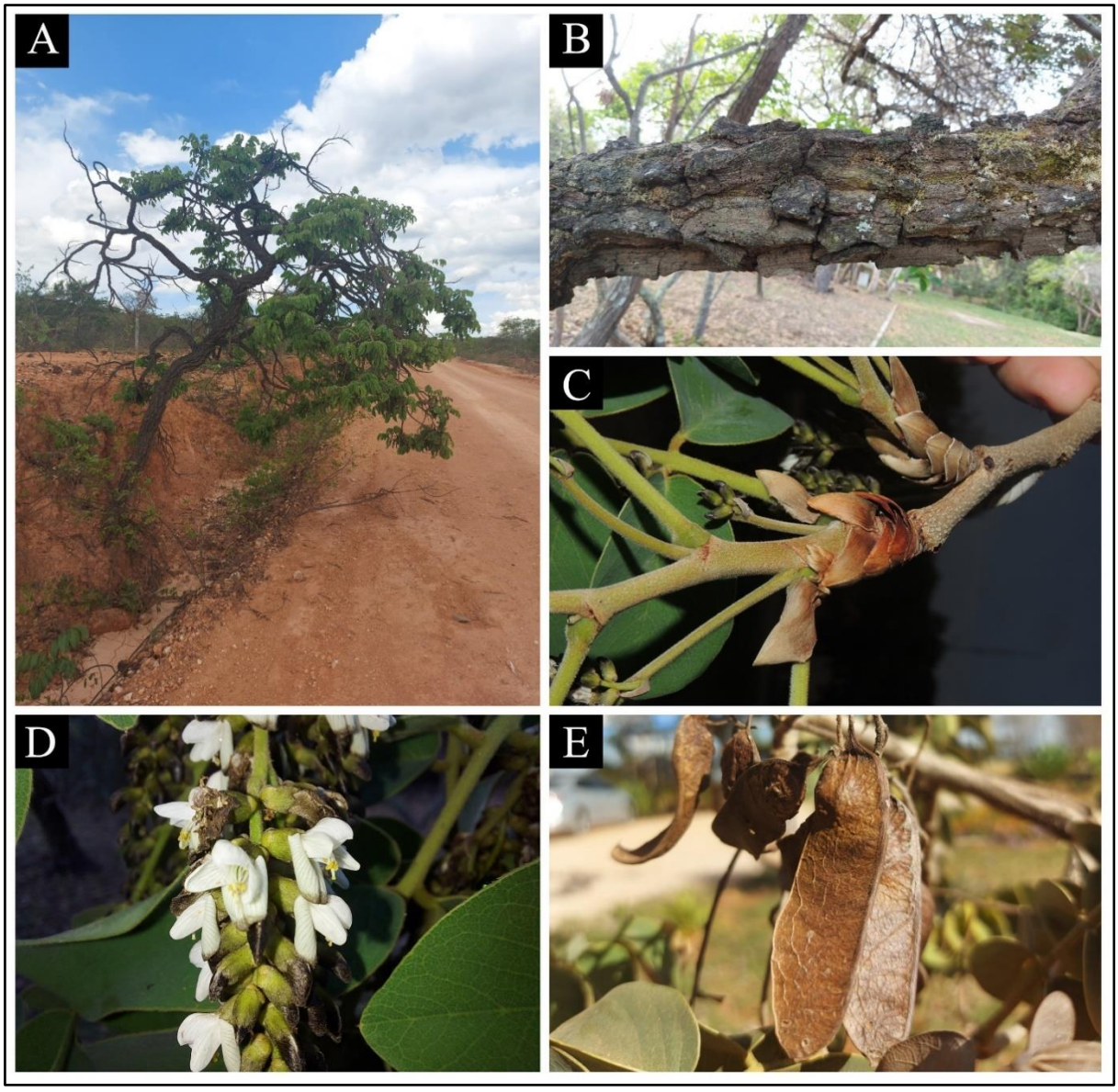


Figure 18. Field images of *Machaerium opacum* Vogel. A. Habitat, Cerrado, at Montes Claros, Minas Gerais. B. Trunk detailing the bark. C. Cataphyll. D. Inflorescence detailing flowers. E. Fruit. (A–B; D–E: Jordão, V.M.M; C: Monzoli, J.V.L).

5.5.4. *Machaerium* sp. nov. 1

Machaerium sp. nov. 1 Milezi-Jordão, D. Sampaio & Filardi **sp. nov.** Type: Brazil. Bahia. Rio de Contas, Rodovia BA-148, 13°36’23’’S, 41°46’02’’W, 930 m., 11.XI.2022, fl. *V.M.M. Jordão et al 263* (holotype: SJRP00026078; isotypes: HUEFS, INPA, K, MBM, NY, RB, UB).

Diagnosis – Machaerium sp. nov. 1 Milezi-Jordão, D. Sampaio & Filardi; *Machaerium acutifolium* Rudd affini, sed habitu (frutex vel scandent frutex), numerum foliolum 5 (7-9) et forma (ovatus vel lanceolatus), bracteola forma (ovatus) differt.

Shrubs to scandent shrubs 1–5 m tall; bark cylindric, brown, with lenticels conspicuous. **Branches** cylindric, brown, sub-glabrous to sericeous pubescent; lenticels conspicuous; cataphyll absent; stipules foliaceous, triangular, pubescent. **Leaves** 8.2–15.3 (20.2) cm long; pulvinus 0.3–0.4 cm long, sub-glabrous to sparse yellow-brown-pubescent; petiole 1.3–3.9 cm long, sub-glabrous to yellow-brown-pubescent; rachis 1.6–6.9 cm long, sub-glabrous to yellow-brown-pubescent; pulvinule 0.1–0.3 cm long, sub-glabrous to yellow-brown-pubescent. Leaflets 5 (7–9), opposite to subopposite rarely alternate, concolorous, margin entire, coriaceous; adaxial surface opaque, sub-glabrous; abaxial surface opaque, sub-glabrous; midrib sub-glabrous to fulvo-sericeous; secondary veins multiple-brochidodromous. Basal leaflet 2.1–6.2 × 1,9–3,0 cm; ovate to lanceolate; apex acuminate to obtuse, short-mucronate; base subcordate to cordate. Middle leaflets 1.6–7.3 × 1.0–3.5 cm; ovate to lanceolate; apex acuminate to obtuse, mucronate; base subcordate to cordate. Terminal leaflet 1.8–7.3 × 1.2–4.1 cm; ovate to lanceolate; apex acuminate to obtuse, short-mucronate; base subcordate, rarely rounded. **Inflorescence** panicle, 2.5–10.5 cm long, axillar or terminal, lenticels absent; peduncle 0.8–1.2 cm long, yellow-brown-pubescent; rachis 1.7–9.3 cm long, yellow-brown-pubescent; lateral axis 1.8–3.2 cm long; yellow-brown-pubescent; bracts deciduous, not seen. **Flowers** 7,9–8,8 mm long; bracteoles 1.2–2.2 × 1.5–2.9 mm, ovate, yellow-brown-tomentose; calyx 2.4–4.0 × 6.0–10.3 mm, yellow-brown-tomentose; corolla white. Banner petal 4.8–8.4 × 6.3–8.3 mm, orbicular, externally yellow-brown-tomentose, internally glabrous to tomentose in the apex, apex retuse, base attenuate, claw 1.5–1.7 mm long. Wing petals 4.5–6.9 × 1.9–3.8 mm, oblong-falcate, yellow-brown-tomentose in the middle vein dorsally, apex obtuse, base auriculate, claw 3.2–3.7 mm long. Keel petals 4.0–6.7 × 1.9–2.8 mm, falcate, yellow-brown-tomentose in the middle vein dorsally, apex acute, base auriculate, claw 2.3–2.7 mm long. Androecium monadelphous, 10 stamens; filament sheath 2.8–5.3 mm long, glabrous; filaments 1.1–3.5 mm long, sub-glabrous; anthers 0.4–0.7 × 0.3–0.4 mm, oblong to triangular. Gynoecium with nectary 0.3–0.7 × 0.7–1.0 mm, cupulate; stipe 1.0–3.6 mm, glabrous; ovary

2.6–4.9 × 0.8–1.3 mm, yellow-brown-tomentose; style 1.1–2.1 mm long, glabrous; stigma capitate. **Fruit** samara 4.1–8.4 cm long; stipe 0.6–1.1 cm long, sub-glabrous to sparsely-pubescent; seed chamber 1.0–1.8 × 0.6–1.2 cm, oblong-falcate, prominent, brown, sub-glabrous; wing 2.5–5.5 × 1.0–2.0 cm, oblong-falcate rarely oblong, reticulate, brown, glabrous; apex obtuse, apiculate.

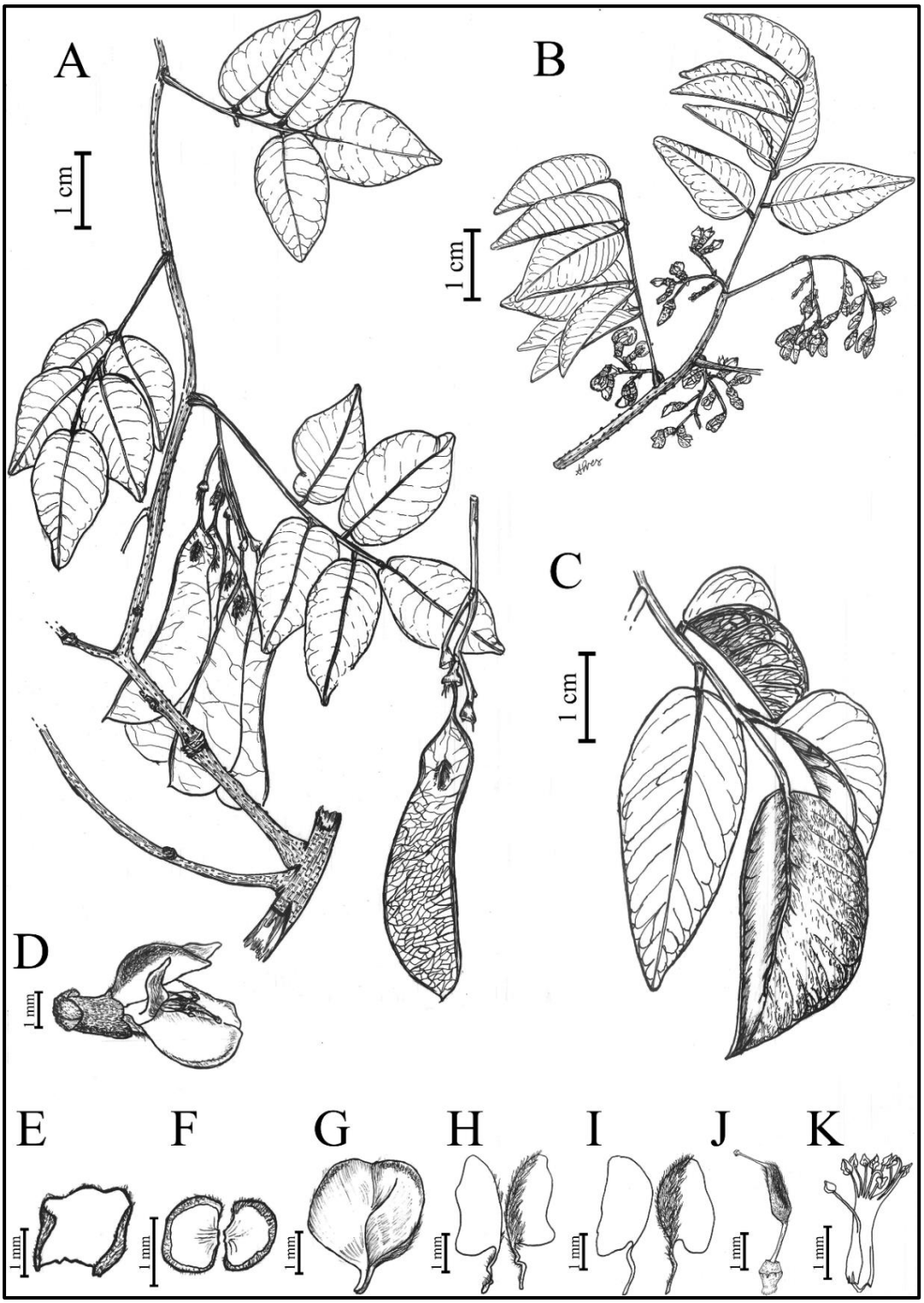


Figure 19. Illustration of *Machaerium* sp. nov. 1. **A** – Branch with fruits (Giulietti, A.M. et al. 1806); **B–K.** Jordão, V.M.M. et al. 263; **B** – Branch with flowers; **C** – Branch in early stage of development; **D** – Flower; **E** – Calyx;

F – Bracteoles; **G** – Banner petal; **H** – Wing petals; **I** – Keel petals; **J** – Gynaecium; **K** – Androecium. (Illustrator: Vieira, J.A.)

Additional material examined – **BRAZIL**. BAHIA: Abaíra, Catolés, próximo à máquina de café de Mariano, 13°18'S, 41°51'W, 02 Dec 1992, fr., *W. Ganev 1614* (HUEFS); Água de Rega, Serra da Água de Reta, ca. 26 Km N. of Seabra, road to Água de Rega, near Rio Riachão, 1000 m, 23 Feb1971, fr., *H.S. Irwin et al. 30774* (F [digital image], NY [digital image], UB); 23 Feb1971, fr., *H.S. Irwin et al. 30829* (UB); Catolés, Rodovia BA-148, 930 m, 13°36'23''S, 41°46'02''W, 11 Nov 2022, st., *V.M.M. Jordão et al. 264* (SJRP); Delfino, 26 Km North West of Lagoinha, (which is 5.5 Km S.W. Delfino), on side road to Minas do Mimoso, 650 m, 10°16'S, 41°23'W, 07 Mar 1974, fr., *R.M. Harley 16930* (CEPEC); Gentio do Ouro, Serra do Açuruá, estrada para Xique-Xique, 2 Km antes de Gameleira do Açuruá, 10 Sep 1990, st., *H.C. Lima et al. 3937* (CEPEC); Iraquara, ca. 4 Km S de Água de Rega na estrada para Lagoa da Boa Vista, 960 m, 12°12'16''S, 41°46'54''W, 23 Jul 1993, fr., *L.P. Queiroz & N.S. Nascimento 3390* (HUEFS); Lençóis, entroncamento BR–242 Bonital Km 14, 940 m, 12°40'S, 41°49'W, 14 Sep 1992, fl., *L. Coradin et al. 8617* (CEN, RB); Morro do Chapéu, BA–052, Km 349, próximo ao rio Vereda, fazenda 3M, 09 Sep 1990, fr., *H.C. Lima et al. 3918* (CEPEC); BA–426, 29 Km al NE do Morro do Chapéu, camino a Várzea Nova, 800 m, 11°20'S, 41°W, 17 Jan 1997, fr., *M.M. Arbo et al. 7452* (CEPEC); ca. 16 Km along the Morro do Chapéu to Utinga road, S.W. of Morro do Chapéu, open scrubby, 980 m, 11°38'S, 41°17'W, 01 Jun 1980, fr., *R.M. Harley 22967* (CEPEC); ca 85 Km na estrada Jacobina/Morro do Chapéu, 22 Feb 1993, fr., *J.G. Jardim et al. 33* (CEPEC); estrada para Morrão, 1123 m, 11°34'S, 41°11'11''W, 04 Apr 2002, fr., *C. Correia et al. 94* (HUEFS); Fazenda Guariba, 1067 m, 11°20'23''S, 41°04'37W, 29 Apr 2011, fr., *E. Melo et al. 9629* (HUEFS); Mucugê, a 14 km de Mucugê, 16 Dec 1984, fr., *G.P. Lewis et al. s.n.* (CEPEC, RB); Chapada Diamantina, 12°59'28''S, 41°15'W, 15 Feb 2003, fr., *M.L. Guedes s.n.* (CEPEC); estrada Mucugê-Guiné, 1000 m, 17 Dec 1984, fr., *G.P. Lewis et al. s.n.* (CEPEC); estrada Mucugê-Barra Estiva, ca. 16 Km de Mucugê, 1040 m, 13°04'20''S, 41°29'06''W, 01 Feb 2003, fr., *F. França et al. 4170* (HUEFS); estrada para Cascavel, ca. de 2 Km de Mucugê, BA–142, 1000 m, 13°00'30''S, 41°23'41''W, 18 Mar 2004, fr., *L.P. Queiroz et al. 9179* (HUEFS); Remanso, ca 48 Km de Remanso, na estrada para Casa Nova, 481 m, 09°22'10''S, 41°47'49''W, 11 Oct 2004, fl., fr., *L.P. Queiroz et al. 9678* (HUEFS); Rio de Contas, ca 8 Km a leste da cidade 13 Nov 2000, fr. *C.V. Mendonça-Filho & R. Belinello 659* (BHCB); ca 18 Km N de Rio de Contas, próximo ao entroncamento para Brumadinho, 13°19'S, 41°56'W, 29 Oct 1993, fl., fr., L.P. *Queiroz & N.S, Nascimento 3686* (HUEFS); 31 Km de Jussiape em direção ao Rio de Contas, 960 m, 13°36'56''S,

41°45’54’’W, 30 Jan 2005, fr., *J. Paula-Souza et al. 5107* (HUEFS); Seabra, Rocks and sandy banks at margin of Rio Riachão, ca. 27 Km N. of Seabra, road to Água de Rega, 1000 m, 26 Feb 1971, fr., *H.S. Irwin et al. 31140* (NY [digital image], UB); Umburanas, Distrito de Delfino, estrada para a Serra do Curral Frio (mapeado como Curral Frio), entrando à direita, logo depois de deixar a estrada BA-220, Delfino-Umburanas, 757 m, 10°28’10’’S, 41°16’29’’W, 28 May 2010, fr., *D. Cardoso et al. 2985* (HUEFS).

Phenology – The species flowers from September to November and presenting fruits from December to October.

Vernacular names – no name applied.

Distribution and Ecology – *Machaerium* sp. nov. 1 is only known for Chapada Diamantina at Espinhaço Range, an erosional landform that runs from North to South in the middle of Bahia state and it is an extension of the Espinhaço Mountain Range in Brazil. This species occurs in the Caatinga biome, especially in arboreal Caatinga, in the vegetation locally known as “Carrasco” and can be found in gallery forests on sandy and clay soils at elevations between 600 and 1,200 meters.

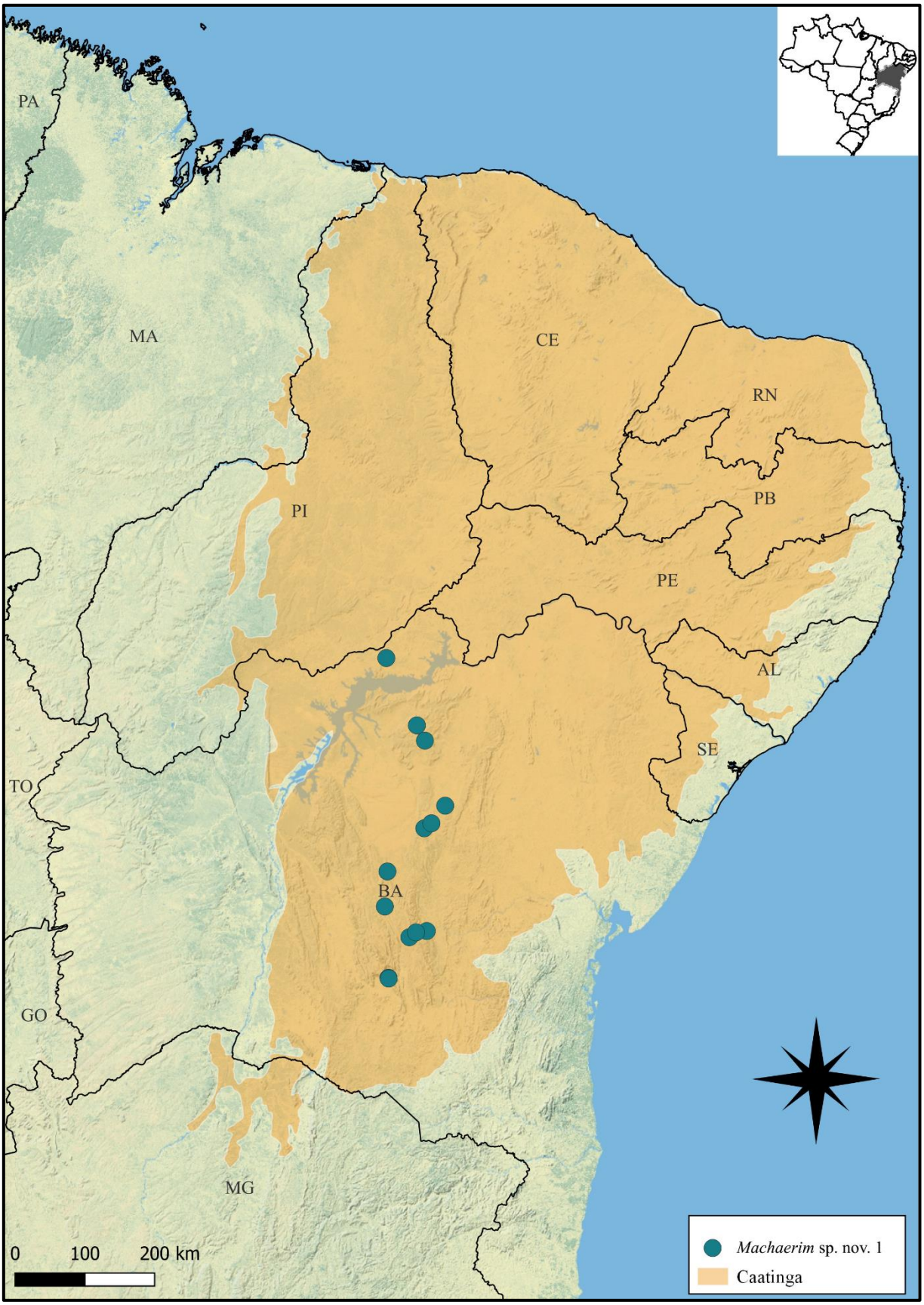


Figure 20. Distribution map of *Machaerium* sp. nov. 1.

Taxon discussion — Machaerium sp.nov.1 can be recognized by the strictly shrubby habit, 5 (-7–9) leaflets; leaflets ovate to lanceolate; apex acuminate to obtuse, mucronate, base subcordate to cordate. The flowers vary in length of about 7–8 mm; with bracteoles ovate; glabrous monadelphous androecium, and samaras with seed chamber prominent.

Working with a broad definition of Atlantic Domain, which includes extra-Amazon rainforests and seasonal forest, in addition to other coastal forest formations (Oliveira-Filho et al. 2006), Filardi (2011) included *Machaerium acutifolium* in her PhD Thesis. Although she did not fully investigate all the morphological variation of this species, that it also occurs in the Caatinga, Cerrado and other South American countries, she indicated that an infraspecific treatment could contribute to the better understanding of the morphological limits of this species.

Other previews suggested similar ideas. Lewis (1987) working with legumes of Bahia, indicated three varieties for *Machaerium acutifolium* (var. *acutifolium*, var. *enneandrum* and var. *pseudacutifolium*). In this work, the variety *pseudacutifolium* was included from data provided by Dr. Velva Rudd, who analyzed the material "Black 54-17688". We were able to analyze an online duplicate (NY02148619) and in fact, it refers to a specimen of *M. villosum* Vogel. The only material determined as *M.* var. *enneandrum*, analyzed by Lewis (Irwin et al. 30774 – duplicates in F, NY and UB) refers to *Machaerium* sp. nov. 1.

In the "Leguminosas da Caatinga", by Queiroz (2009), the author includes *Machaerium acutifolium* as a species that occurs in this biome and presented a discussion on the phenotypic plasticity of it, raising the hypothesis that these materials (Harley et al. 21528 [CEPEC, K]; Hatschbach and Zelma [50456]; Mori and Santos 11825 [CEPEC, K]; Irwin 30829 [K]; Harley et al. 16517 [CEPEC, K]; Gardner 1933 [K]; Anderson 9164 [K]; Lewis et al. [1346]; Queiroz and Nascimento 3397 [HUEFS, K]; Harley et al. 16903 [CEPEC, K]; Carvalho et al. [2408]; Lewis et al. CFCR7009 [K, SPF]; Harley et al. 27000 [CEPEC, K]; Irwin et al. 30774 [K] and Coradin et al. 8656 [CEN, K]) could be recognized as separate taxa. Thus, he considered for this biome, the occurrence of only two varieties: var. *acutifolium* and var. *enneandrum*.

Therefore, similarly to Lewis (1987), all materials analyzed and determined as variety *enneandrum* by Queiroz (2009) refer to *Machaerium* sp. nov. 1. (L.P. Queiroz & N.S. Nascimento 3397; R.M. Harley 16903; A.M. Carvalho et al. 2408; G.P. Lewis et al. CFCR 7009; R.M. Harley et al. 27000; Irwin et al. 30774 and L. Coradin et al. 8656).

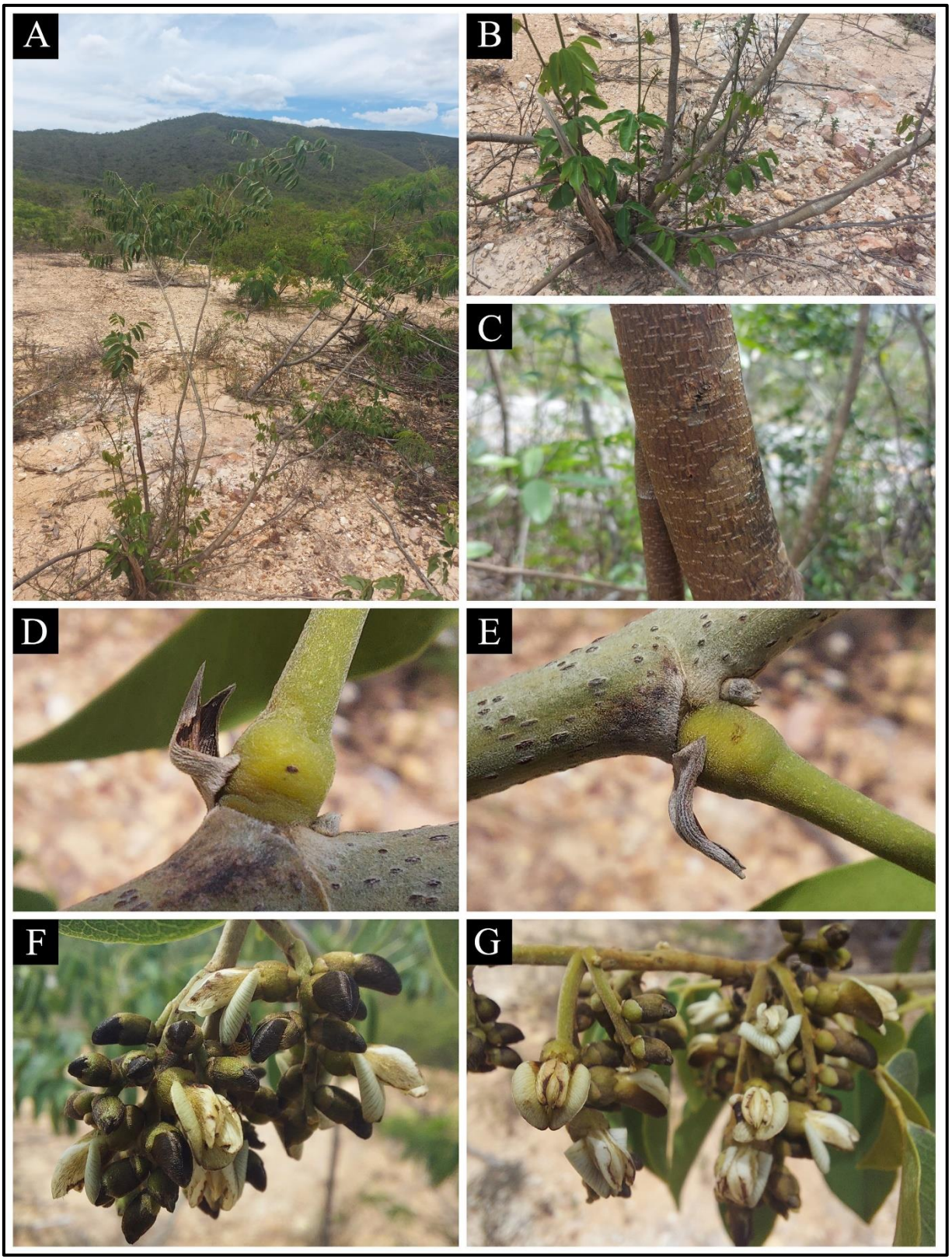


Figure 21. Field images of *Machaerium* sp. nov. 1 Milezi-Jordão & Sampaio. A. Habitat, Caatinga biome, at Rio de Contas, Bahia. B. Shrub habit. C. Lenticel bark. D-E. Stipule. F. Terminal inflorescence. G. Lateral inflorescences. (A– G Jordão, V.M.M.).

5.5.5. *Machaerium* sp. nov. 2

Machaerium sp. nov. 2 Milezi-Jordão, D. Sampaio & Filardi **sp. nov.** Type: Brazil. Bahia. Jacobina ca. de 85 Km na estrada Jacobina/Morro do Chapéu. Carrasco/Campos Gerais de Chapada, 22.II.1993, fl. *J.G. Jardim et al 31* (holotype: CEPEC 57390! isotypes: IPA 56618; MBM 203391[photo!], MO 100219757; NY barcode 00565140 [photo!], RB00180051!).

Diagnosis – *Machaerium* sp. nov. 2 Milezi-Jordão, D. Sampaio & Filardi; *Machaerium acutifolium* Vogel affini habitu, sed folia stipulis adnatis spathulatus, foliolum ovatus vel lanceolatus, bracteola ovatus, androecium monadelphus vel pseudomonadelphus differt.

Trees 1–10 m tall; trunk cylindric; bark fissured, scaly, brown. **Branches** cylindric, brown or gray, sub-glabrous; lenticels conspicuous; cataphyll present; stipules foliaceous, spatulate, sub-glabrous, early deciduous. **Leaves** 13.1–15.4 cm long; pulvinus 0.3–0.4 cm long, sub-glabrous; petiole 0.8–2.8 cm long, sub-glabrous to brownish-yellow-pubescent; rachis 5.1–10.6 cm long, sub-glabrous to brownish-yellow-pubescent; pulvinule 0.1–0.3 cm long, sub-glabrous to brownish-yellow-pubescent. Leaflets 9–13, alternate to subopposite rarely opposite, concolorous, margin entire, chartaceous; adaxial surface opaque, sub-glabrous; abaxial surface opaque, sub-glabrous to pubescent; midrib sub-glabrous to brownish-yellow-sericeous; secondary veins multiple-brochidodromous. Basal leaflet 1.4–2.8 × 0.7–1.7 cm; ovate; apex acuminate or attenuate, rarely obtuse, and slightly retuse, short-mucronate; base rounded. Middle leaflets 3.1–5.7 × 0.9–1.8 cm; lanceolate, rarely ovate; apex acuminate or attenuate, rarely obtuse, and slightly retuse, short-mucronate; base rounded. Terminal leaflet 3.3–5.2 × 1.1–1.6 cm; lanceolate or elliptic; apex acuminate or attenuate, rarely obtuse, and slightly retuse, short-mucronate; base rounded. **Inflorescence** panicle, 6.1–15.8 cm long, axillar or terminal, lenticels absent; peduncle 1.8–2.5 cm long, cream-pubescent; rachis 4.3–13.3 cm long, cream-pubescent; lateral axis 2.5–2.8 cm long; cream-pubescent; bracts foliaceous, 1.6 × 2.4 mm, ovate, sub-glabrous. **Flowers** 5.5–5.8 mm long; bracteoles 0.4–0.8 × 0.4–0.9 mm, ovate, yellow-brown-tomentose; calyx 1.9–2.7 × 3.0–6.0 mm, yellow-brown-tomentose; corolla purple. Banner petal 3.7–4.6 × 3.5–5.3 mm, orbicular to ovate, externally yellow-brown-tomentose, internally glabrous, apex slightly retuse, base slightly truncate, claw 0.7–0.9 mm long. Wing petals 2.8–4.1 × 1.2–2.2 mm, oblong, sub-glabrous to pubescent in the middle vein dorsally, apex obtuse, base auriculate, claw 2.0–2.1 mm long. Keel petals 2.7–4.0 × 1.4–2.2 mm, falcate, sub-glabrous to pubescent in the middle vein dorsally, apex acute, base auriculate, claw 1.6–2.0 mm long. Androecium monadelphous or pseudomonadelphous, 10 stamens; filament sheath 1.4–3.0 mm long, glabrous; filaments 0.9–2.0 mm long, glabrous; anthers 0.3

× 0.2 mm, oblong to triangular. Gynoecium with nectary 0.2–0.5 x 0.2–0.4 mm, cupulate; stipe 1.2–3.1 mm, glabrous; ovary 1.2–2.3 × 0.4–0.8 mm, yellow-brown-villose; style 0.6–1.4 mm long, glabrous; stigma capitate. **Fruit** samara 5.5–7.9 cm long; stipe 0.7–1.0 cm long, sub-glabrous; seed chamber 1.7–2.0 × 0.7–1.0 cm, falcate, prominent, brown, sub-glabrous; wing 3.1–4.9 × 1.3–1.5 cm, oblong-falcate, reticulate, punctate, brown, sub-glabrous; apex obtuse, apiculate rarely short apiculate.

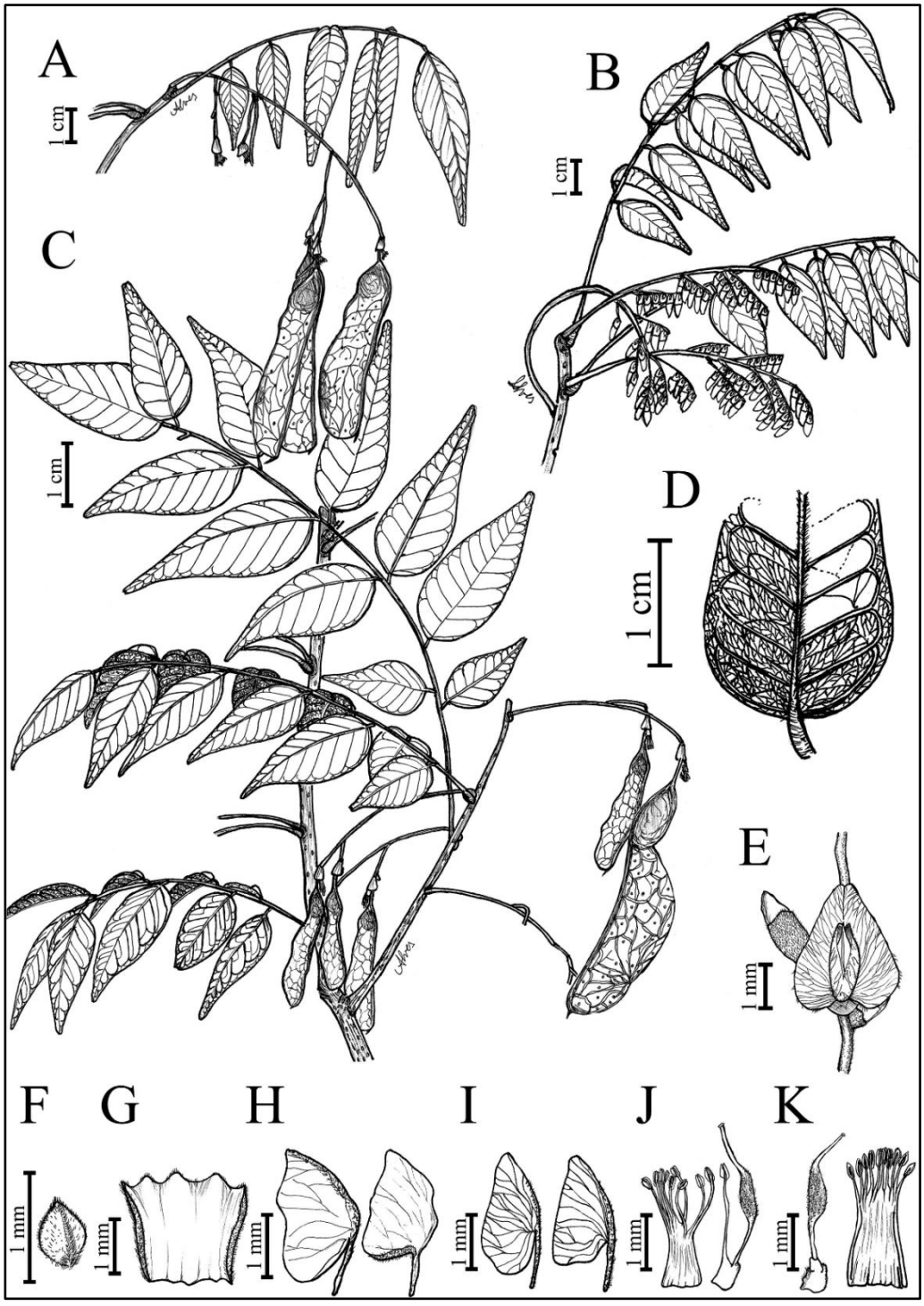


Figure 22. Illustration of *Machaerium* sp. nov. 2. **A** – Branch with immature fruits (Hatschbach, G and Zelma F.J. 50456); **B –** Branch with flowers (Arbo, M.M. et al. 7357); **C** – Branch with mature fruits (Hatschbach, G et al.

55136); **D** – Abaxial surface of the leaflet; **E** – Flower; **F** – Bracteoles; **G** – Calyx; **H** – Wing petals; **I** – Keel petals; **J** – Gynaecium and androecium with stamens pseudomonadelphous (Jardim, J.G. et al. 31); **K** – Gynaecium and androecium with stamens monadelphous (Arbo, M.M. et al. 7357). (Illustrator: Vieira, J.A.)

Additional material examined – **BRAZIL.** BAHIA: Barra do Mendes, caminho de Vandique para Mussambé 11°48'S, 42°03'W, 24 Jan 2000, fr., *M.L. Guedes et al 8160* (ALCB [digital image], CEPEC, HUEFS, UESC); Bom Jesus da Lapa, basin of the Upper São Francisco River, Fazenda Imbuzeiro da Onça, ca. 8 Km from Bom Jesus da Lapa, on by-road to Caldeirão, 500 m, 13°09'S, 43°22'W, 19 Apr 1980 fr., *R.M. Harley 21528* (ALCB [digital image], CEPEC, NY [digital image], U [digital image]); Juá, 14 Feb 1999, fr., *G. Hatschbach et al 55136* (CEPEC, MBM [digital image], MO, SPSF, UPCB, US [digital image]); Caitete, rodovia para Bom Jesus da Lapa, 17 Jun 1986, fr., *G. Hatschbach & F.J. Zelma 50456* (CEPEC, INPA, MBM [digital image], NY [digital image] US [digital image]); Jacobina, BR-324, 12 Km NW de Jacobina, caminho a Umburanas, 600 m, 11°06'S, 40°36'W, 17 Jan 1997, fl., *M.M. Arbo et al 7357* (CEPEC, HUEFS, NY [digital image], RB, UEC [digital image]); Lafayete Coutinho, Rodovia BA-890, 5 Km entroncamento com a rodovia BR-116 (Rio-Bahia), 06 May 1979, fr., *S.A. Mori & T.S. dos Santos 11825* (CEPEC, NY [digital image]); Pindaí, Tanque para Guirapá, 620 m, 14°32'S, 42°40'W, 16 Mar 1981, fr., *G.C.P. Pinto 172/81* (CEPEC, UB); Remanso, Campo Alegre de Lourdes, Angico dos Dias, brejo, 09°35'38''S, 42°54'50''W, 02 Mar 2000, fr., *A. Nascimento et al 260* (ALCB [digital image] CEN, HUEFS, RB, SPF, UESC); Santa Rita de Cássia, Lagoa do Norato, 10°58'37''S, 44°26'39''W, 28 Apr 1990, fr., *H.P. Bautista 1513* (RB, UB); Senhor do Bonfim, side road ca. 2 Km from Estiva, about 12 Km N of Senhor do Bonfim on the BA-130 to Juazeiro, 620 m, 10°23'S, 40°10'W, 27 Feb 1974, fl., *R.M. Harley 16517* (CEPEC, IPA, NY [digital image], U [digital image], US [digital image]); Wagner, Chapada Diamantina, Mata do CETEP, 12°41'S, 41°10'W, 16 Jun 2017, fr., *M.L. Guedes et al 25695* (RB) – MINAS GERAIS: Cristália, Fazenda Curral Velho, 25 Apr 1991, fr., *M.G.C. & S.T.S 139* (BHCH, CEPEC, RB); Januária, 13 Km by road W of Januária on road to Serra das Araras, 575 m, 19 Apr 1973, fr., *W.R. Anderson 9164* (F [digital image], MO, NY [digital image], UB). – PIAUI: São Raimundo Nonato, 13 Feb 1986, fr., *L. Emperaire 2880* (P [digital image], RB). – TOCANTINS: Palmeirópolis, linha de transmissão São Salvador – Canabrava, entre as torres 77 e 79, fazenda do Sr. Joaquim (fazenda esplanada), 370 m, 13°08'55''S, 48°13'12''W, 04 Nov 2009, fr., *B.M.T. Walter et al 5884* (CEN)

Phenology – *Machaerium* sp. nov. 2 presents flowers from January to February, presenting fruits from January to November.

Vernacular names – *Machaerium* sp. nov. 2 is known as Bastião-de-arruda and as Sucupira in Bahia state and as Bainha-de-galinha in Piauí state.

Distribution and Ecology – This species occurs in the states of Bahia, Minas Gerais, Piaui and Tocantins, majority in the Caatinga Biome, but it can be found in transitional regions of Cerrado and Cerrado "*strictu sensu*", in the vegetation locally known as "Carrasco" and "Capoeira" on sandy and clay soils with superficial gravel at elevations between 370 and 600 meters.

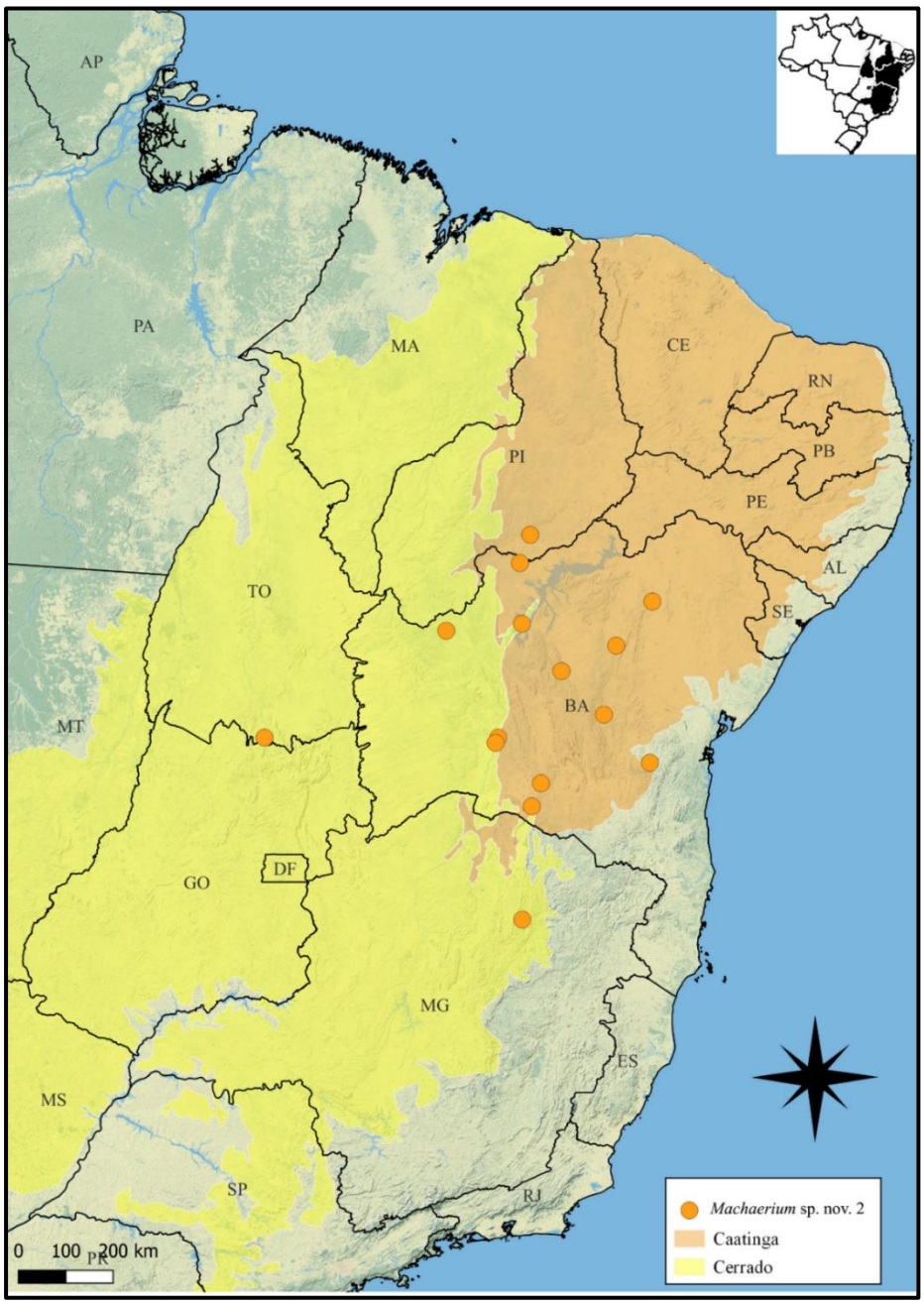


Figure 23. Distribution map of *Machaerium* sp. nov. 2.

Taxon discussion — *Machaerium* sp. nov. 2 can be recognized by the strictly arboreal habit, stipule spathulate; leaflets ovate to lanceolate, smaller width (0,7–1,8 cm long), when

comparing to *M. acutifolium*, and base rounded. In the reproductive characters, flowers are the smallest in the complex (5 mm long); bracteoles ovate; androecium with 10 stamens monadelphous or pseudomonadelphous, with a glabrous filaments sheath and filaments and as concerning the fruits, samaras present seed chamber prominent.

Machaerium sp. nov. 2 was also included in the works by Lewis (1987) and Queiroz (2009) and in these, both authors considered it as *M. acutifolium* var. *acutifolium*. However, when performing the analysis of Chapter I including this morphotype, it was possible to recognize that variety *acutifolium* is a distinct taxon. In view of this, it is worth discussing that this species presents very interesting morphological variations both in vegetative and reproductive characters and that require special attention.

First, in the vegetative aspect, the materials collected at East of Chapada Diamantina, in the Caatinga region, tend to have a lanceolate shape in their leaflets; as for the materials from West of the Chapada, those with distribution in areas of Caatinga, in transitional areas between Caatinga and Cerrado and, Cerrado itself, tend to present a more oval shape. When analyzing the materials collected along the Chapada Diamantina or very close to it, this characteristic tends to overlap.

In the reproductive aspect, another interesting question concerns the welding of the androecium. For *Machaerium* in general, this characteristic tends to be conserved between species (e.g., *M. aculeatum* – diadelphous: 5+5; *M. acutifolium* – monadelphous: 10; *M. androvillosum* – diadelphous, 9+1) (Filardi 2011, Filardi 2014). As for this new species, we found a variation in monadelphous and pseudomonadelphous with 10 stamens. However, we faced a difficulty to locate materials presenting flowers. Great part of collections is vegetative or have immature fruits and therefore it is necessary to analyze more materials that present floral characters to confirm whether this is a continuous variation, or it should be investigated in an infraspecific study.

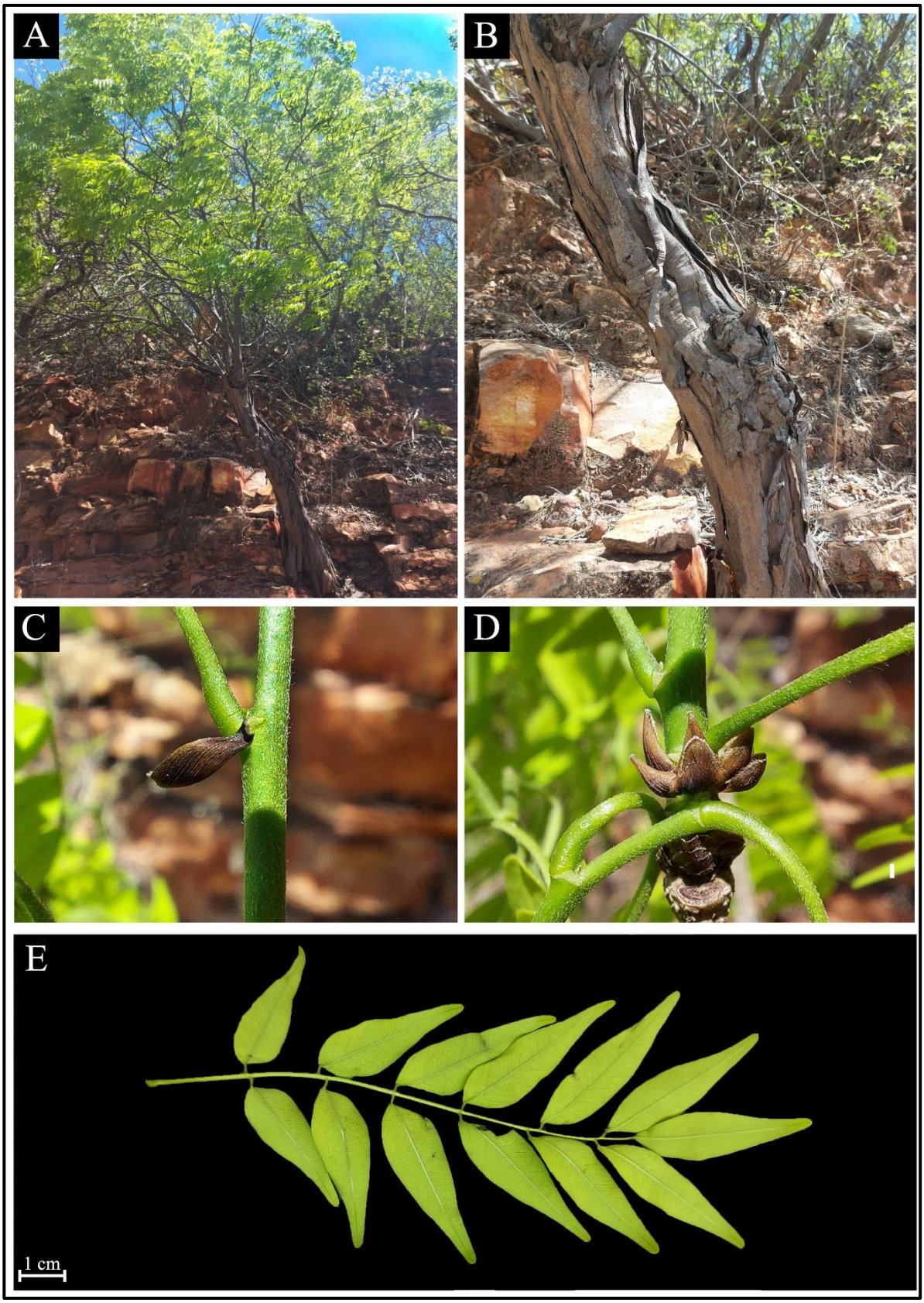


Figure 24. Field images of *Machaerium* sp. nov. 2 Milezi-Jordão, D. Sampaio & Filardi. A. Habitat, Caatinga biome, at Morro do Chapéu, Bahia. B. Bark fissured. C. Stipule. D. Cataphylls. E. Abaxial leaf. (A– E Jordão, V.M.M.).

References:

Bastos, M. N. C. Contribuição ao estudo sistemático de algumas espécies do gênero *Machaerium* Persoon (Leguminosae – Papilionoideae) ocorrentes na Amazônia brasileira. *Boletim do Museu Paraense Emílio Goeldi* 3: 183–278. 1987.

Beentje, H. 2010. *The Kew plant glossary: an illustrated dictionary of plant terms*. London: Royal Botanic Gardens.

Bentham, G. 1837. *Commentationes de Leguminosarum Generibus*. Vienna: Zollinger.

Bentham, G. 1862. Leguminosae. Dalbergiae. Pp 1–350 in *Flora Brasiliensis*, ed. C. F. P. Martius, A. W. Eichler, and I. Urban. Vienna: R. Oldenbourg Verlag.

Bridson, D. F. L., L. Forman. The herbarium handbook. Kew: *Royal Botanic Gardens*, ed. 3, 1998.

De Queiroz, K. 2007. Species concepts and species delimitation. *Systematic biology* 56(6): 879–886.

Ducke, A. 1949 Notas sobre a Flora Neotrópica II - as leguminosas da Amazônia brasileira. *Boletim Técnico do Instituto Agronômico do Norte* 18:1–248.

Filardi, F. L. R. 2011. *Avanços na Sistemática de Machaerium Pers. (Leguminosae Papilionoideae Dalbergieae): Filogenia e Revisão Taxonômica das espécies do Domínio Atlântico*. Doctoral dissertation (dissertation in Botany). Rio de Janeiro: Escola Nacional de Botânica Tropical, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

Filardi, F. L. R., H. C. Lima, B. B. Klitgaard, and A. L. B. Sartori. 2013. Taxonomy and nomenclature of the neotropical *Machaerium hirtum* complex (Leguminosae, Papilionoideae). *Brittonia* 65:154–170.

Filardi, F. L. R. and H.C. Lima. 2014. The diversity of *Machaerium* (Leguminosae: Papilionoideae) in the Atlantic Forest: Three new species, nomenclatural updates, and a revised key. *Systematic Botany* 39(1):145–159.

Filardi, F. L. R., H. C. Lima, D. B. O. S. Cardoso. 2020. *Machaerium in Flora e Funga do Brasil*. Jardim Botânico do Rio de Janeiro. Available from: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB23055 (last accessed August 2023).

Harris, J. G., and M. W. Harris. 2001. *Plant Identification Terminology: An Illustrated Glossary*. Utah: Spring Lake Publishing.

Hoehne, F. C. 1941. Leguminosas Papilionadas (*Machaerium* e *Paramachaerium*). *Flora Brasilica* 25: 1–99.

Lewis, G.P. 1987. Legumes of Bahia. Kew: Royal Botanic Gardens.

Lozano, P., and B. B. Klitgaard. 2006. The genus *Machaerium* (Leguminosae: Papilionoideae: Dalbergieae) in Ecuador. *Brittonia* 58(2): 124–150.

Mendonça-Filho, C. V., H. C. Lima, E. R. Forni-Martins, and A. M. A. Tozzi. 2011. Two new species of *Machaerium* (Leguminosae) from Bahia and Southeastern Brazil. *Novon* 21: 73–77. 2011.

Oliveira-Filho, A. T., J. A. Jarenkow, and M. J. N. Rodal. 2006. Floristic relationships of seasonally dry forests of eastern South America based on tree species distribution patterns. Pp. 159–192 in *Neotropical savannas and seasonally dry forests: plant diversity, biogeography, and conservation*, eds. R. T. Pennington, G. P. Lewis, and J. A. Ratter, J.A. eds, CRC Press.

QGIS. 2019. QGIS Development Team. QGIS Geographic Information System. Open-Source Geospatial Foundation Project. http://qgis.osgeo.org.

Queiroz, L. P. D. 2009. *Leguminosas da caatinga.* Feira de Santana: Universidade Estadual de Feira de Santana.

Rudd, V. E. 1987a. Studies in *Machaerium* (Leguminosae) VI: Section I. Machaerium. *Phytologia* 62: 283–302.

Rudd, V. E. 1987b. Studies in *Machaerium* (Leguminosae) VII: Section II. Lineata. Part I: Species with wingless fruit. *Phytologia* 64: 1–12.

Thiers, B. 2023. [continuously updated] *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih/ (last accessed August 2023).

Turland, N. J., J. H. Wiersema, F. R. Barrie, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, W. H. Kusber, D.-Z. Li, K. Marhold, T. W. May, J. McNeill, A. M. Monro, J. Prado, M. J. Price, and G. F. Smith. 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159*. Glashutten: Koeltz Botanical Books

Vogel, T. 1837. Dalbergiearum genera brasiliensis. *Linnaea* 11: 177–203.

6. Chapter III: A remarkable new species of *Machaerium* (Leguminosae, Papilionoideae) from Northeast and Southeast Brazil with an Emended Key for Species of Brazilian Caatinga.

VALNER MATHEUS MILANEZI JORDÃO[1,4], FABIANA LUIZA RANZATO FILARDI[3] DANIELA SAMPAIO SILVEIRA[2].

[1] Programa de Pós-Graduação em Biodiversidade, Departamento de Ciências Biológicas, Instituto de Biociências, Letras e Ciências Exatas (IBILCE), Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP). CEP: 15054-000, São José do Rio Preto, São Paulo, Brazil; email: valner.jordao@gmail.com

[2] Departamento de Ciências Biológicas, Instituto de Biociências, Letras e Ciências Exatas (IBILCE), Universidade Estadual Paulista "Júlio de Mesquita Filho" (UNESP). CEP: 15054-000, São José do Rio Preto, São Paulo, Brazil; email: daniela.sampaio@unesp.br

[3] Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Diretoria de Pesquisa Científica, Rua Pacheco Leão 915, CEP: 22460-030, Rio de Janeiro, Rio de Janeiro, Brazil. email: ffilardi@jbrj.gov.br

[4] Author for correspondence

6.1. Abstract

Machaerium Pers. includes about 130 species with neotropical distribution, of trees, shrubs and lianas that occurs from southern Mexico to northern Argentina. In Brazil, a center of diversity of the genus, there are about 74 species with 44 endemics. During a careful analysis on the Caatinga collections and a field work in Bahia state, we discovered a remarkable new endemic species to this phytogeographic domain and here we propose it as *Machaerium* sp. nov. 3 Information about habitat, distribution, conservation, phenology, and taxonomy affinities are presented, also with photographs, illustration, and distribution maps. We also present an identification key to all species of this genus that occurs in Caatinga biome.

Keywords— Dalbergieae, diversity, Fabaceae, liana, taxonomy.

6.2. Resumo

Machaerium Pers. inclui cerca de 130 espécies com distribuição neotropical, de árvores, arbustos e lianas que ocorre desde o sul do México até o norte da Argentina. No Brasil, centro de diversidade do gênero, existem cerca de 74 espécies com 44 endemismos. Durante uma análise cuidadosa das coleções da Caatinga e um trabalho de campo no estado da Bahia, descobrimos uma nova espécie endêmica notável para este domínio fitogeográfico e aqui a propomos como *Machaerium* sp. nov. 3 São apresentadas informações sobre habitat, distribuição, conservação, fenologia e afinidades taxonômicas, bem como fotografias, ilustrações, e mapas de distribuição. Apresentamos também uma chave de identificação para todas as espécies desse gênero que ocorrem no bioma Caatinga.

Palavras-chave— Dalbergieae, diversidade, Fabaceae, liana, taxonomia.

6.3. Introduction

Among the Papilionoid legumes, *Machaerium* Pers. is one of the major woody genera and includes about 130 species with neotropical distribution, whereas one species, *Machaerium lunatum* (L.f.) Ducke, extending to west Africa (Lozano and Klitgaard 2006). Within *Machaerium*, it is possible to recognize two groups of species: the first with a geographic range from southern Mexico to the Amazon and the second, occurring from central South America to northern Argentina (Lozano and Klitgaard 2006; Filardi and Lima 2014).

This genus consists of trees, shrubs, and lianas and it is difficult to define due to its expressive morphological variety, which can be maximally expressed in the existence of arboreal and lianescent specimens in the same species (Filardi 2011; Filardi and Lima 2014, Filardi et al. 2020). Thus, among the species of the genus, there are variations in the number of leaflets, patterns of secondary venation, shape and consistency of stipules and bracteoles, as well as in the color and indument of the petals, the adelphia of the androecium and finally in the types of fruits, which varies from anemochory samaras to nutlets adapted for water dispersion. (Bentham 1837; Hoehne 1941; Rudd 1977, 1987a, 1987b; Lozano and Klitgaard, 2006; Mendonça-Filho et al. 2007, Filardi et al. 2013, Filardi and Lima 2014).

In Brazil, the center of its diversity, *Machaerium* occurs especially in seasonally dry forests (Lewis 1987; Sartori and Tozzi 1998, Ribeiro and Lima 2007; Filardi and Lima, 2014). There are 74 species in the country of which 44 are endemic and the major richness and

endemism are found in the Atlantic Forest, with 41 species, and the Amazon Forest, with 33 (Filardi and Lima 2014; Filardi et al 2020). Subsequently, Cerrado appears as the third most diverse phytogeographic domain, followed by Caatinga, Pantanal and Pampas, with respectively twenty-two, twelve, eight and two species each (Filardi et al 2020).

The major richness in the Atlantic Forest can be explained by mainly two recent taxonomic treatments of the genus, describing five new species (Mendonça-Filho et al. 2011; Filardi and Lima 2014). Thus, to understand the real biodiversity of *Machaerium* in Brazil as well as in the Neotropics, it is extremely necessary new taxonomic and systematic studies including the other Brazilian biomes.

Thus, especially in the Caatinga, one of the first works to discuss *Machaerium* richness in this biome considered only 5 species and two varieties (Queiroz, 2009). In this work, the author disregarded the species that occur in other vegetation types, highlighting those that occur exclusively in this domain. In a more recent work (Filardi et al. 2020) the authors increase this number to twelve, considering the species that occur in the Caatinga as well as those that occur in the transitional regions (Caatinga/Cerrado; Caatinga/Atlantic Forest). Although the species richness has increased by 140%, this number still does not clearly represent the diversity of this genus, since some studies indicate that a careful study of the materials present in the Northeast Brazil, can result in the recognition of new taxa (Queiroz, 2009; Filardi, 2011).

That way, during a fieldwork in the state of Bahia in November 2022 as well as the study of herbarium specimens from Caatinga, we were able to discover a remarkable new species, *Machaerium* sp. nov. 3 Filardi & Milezi-Jordão, that is here described, illustrated, and compared with the most morphologically similar species. Data of geographic distribution and conservation status are also presented. Also, we present an updated identification key for all 15 species of *Machaerium* occurring in this phytogeographic domain.

6.4. Materials and methods

The herbarium materials were examined from CEN, CEPEC, HUEFS, R, RB SJRP, and UB. Images in high resolution available in the Reflora Virtual Herbarium (http://reflora.jbrj.gov.br/reflora/herbarioVirtual) and SpeciesLink (https://specieslink.net/search/index) by herbaria ALCB, EAC, K and US were also analyzed (acronyms following Thiers 2020).

Description and illustration were based on dried and hydrated materials using a stereomicroscope Leica DFC295 and on field observations; the terminology of shape, color and indumentum of the structures follows Harris and Harris (2001) and Beentje (2010); inflorescence analysis followed Werbeling (1989); specific *Machaerium* morphological characters were obtained on Hoehne (1941), Rudd, (1977, 1987a, 1987b), Filardi (2011) and Filardi and Lima (2014); and to steam featured, we followed the definitions by Acevedo-Rodrígues et al. (2015).

Geographic distribution and habitat data for the new species described here, were obtained from labels in the exsiccate and analyzed using QGIS version 3.28.4, which was used to create a map based on the coordinate information available.

6.5. Results and Discussion

KEY TO THE SPECIES OF *MACHAERIUM* IN THE BRAZILIAN CAATINGA BIOME:

1. Leaflets with cladodromous pattern 2

1'. Leaflets with brochidodromous or multiple-brochidodromous pattern 3

2. Trees; spinescent stipules parallel or perpendicular to the branch (Panama, Guyanas, Venezuela, Colombia, Brazil, Peru, Bolivia, Paraguay, and Argentina)..... ..... *Machaerium hirtum* (Vell.) Stellfeld

2'. Lianas or scandent-shrubs; spinescent stipules recurved (Brazil: Bahia and Minas Gerais) .. .. *Machaerium sericiflorum* Vogel

3. Branches with spinescent stipules 4

3'. Branches with foliar stipules 6

4. Leaves with 5-7 leaflets, elliptics or ovates (Brazil: Bahia, Espírito Santo, Minas Gerais, Pernambuco, and Rio de Janeiro) ..... *Machaerium leucopterum* Vogel

4'. Leaves with (7) 11-25 (37) leaflets, oblongs..... 5

5. Leaflets with adaxial surface glabrous (Brazil: Bahia, Espírito Santo, and Minas Gerais) ..... *Machaerium ovalifolium* Glaz. ex Rudd

5'. Leaflets with adaxial surface sub-glabrous to sericeous (Brazil: Bahia and Minas Gerais) ... .*Machaerium floridum* (Mart. ex Benth) Ducke

6. Adaxial surface of mature leaflets pubescent to villous 7

6.' Adaxial surface of mature leaflets glabrous to sub-glabrous 11

7. Lianas to scandent shrubs, rarely shrubs 8

7'. Trees 9

8. Secondary veins multiple-brochidodromous; abaxial surface of mature leaflets sericeous; (Brazil: Bahia, Minas Gerais, and Rio de Janeiro) .....*Machaerium punctatum* (Poir.) Pers.

8'. Secondary veins brochidodromous; abaxial surface of mature leaflets villosus to tomentose; (Brazil: Goiás, Bahia, Minas Gerais, Espírito Santo, Rio de Janeiro, and São Paulo) ..... *Machaerium oblongifolium* Vogel

9. Leaflets ovate, leaflet apex obtuse and slightly retuse (Brazil: Bahia, Distrito Federal, Goiás, Mato Grosso do Sul, Minas Gerais, and Tocantins)..... *Machaerium opacum* Vogel

9'. Leaflets lanceolate, elliptic, oblong-lanceolate, leaflet apex mucronulate, acuminate, acute, or attenuate; 10

10. Leaflets base cordate to subcordate; leaflets apex acuminate or attenuate and always mucronulate (Brazil: Bahia, Goiás, Maranhão and Tocantins) .... *Machaerium mucronulatum* Mart. ex Benth

10’. Leaflets base attenuate; leaflets apex acuminate or acute (Brazil: Bahia, Ceará, Distrito Federal, Goiás, Mato Grosso do Sul, Minas Gerais, São Paulo, Paraná) .... *Machaerium villosum* Vogel

11. Lianas to scandent shrubs 12

11’. Trees 14

12. Leaflet base cordate; leaflet apex mucronulate (Brazil: Bahia, Ceará, Maranhão, Minas Gerais and Piauí) .....*Machaerium* sp. nov. 3 Filardi & Milezi-Jordão

12’. Leaflet base acute or rounded; leaflet apex acuminate, acute or cuspidate..... 13

13. Leaflets 7 -13 elliptics (Argentina, Bolivia e Brasil)..... *Machaerium brasiliense* Vogel

13’. Leaflets 5 (7), ovate to lanceolate (Brazil: Bahia) ....*Machaerium* sp. nov. 1 Milezi-Jordão & Sampaio

14. Leaflets 7–13, elliptics (Argentina, Bolivia e Brazil)..... *Machaerium brasiliense* Vogel

14’. Leaflets 11–19, oblong-lanceolate 15

15. Leaflets base cordate to subcordate; leaflets apex acuminate or attenuate and always mucronulate (Brazil: Bahia, Goiás, Maranhão and Tocantins) .... *Machaerium mucronulatum* Mart. ex Benth

15’. Leaflets base rounded; leaflets apex acuminate or acute 16

16. Basal leaflets (first pair of leaflets) oblong-lanceolate; width of the leaflets 1,2–4,1 cm long (Argentina, Bolivia, Brazil, Paraguay, Peru, Venezuela).....*Machaerium acutifolium* Vogel

16’. Basal leaflets (first pair of leaflets) ovate, lanceolate; width of the leaflets 0,7–1,8 cm long (Brazil: Bahia, Minas Gerais, Piaui and Tocantins) ....*Machaerium* sp. nov. 2 Milezi-Jordão & Sampaio

Machaerium sp3 Filardi & Milezi-Jordão, **sp. nov.** Type: Brazil. Bahia, Licínio de Almeida: Estrada de terra próxima a BA-156, cerca de 4 Km da cidade de Licínio de Almeida, 14°42’48’’S, 42°30’33’’W, 875 m, 10 Nov 2022 (fl.), *Jordão, V.M.M. et al.* 234 (holotype: SJRP!; isotype: CEPEC!, HUEFS!, RB!).

Diagnosis – *Machaerium* sp. nov. 3 Filardi & Milezi-Jordão; *Machaerium sericiflorum* Vogel affini habitu et indumentum, sed folia stipulis foliaris, foliolum ovatus vel lanceolatus, venatio brochidodroma, base cordatus, flores sessilis et corolla alba differt.

Lianas to scandent shrubs 1–3 m tall. **Steam** 3 cm diam, cylindrical; cross section with a single cambium; pith in a central position, lobed; exudate reddish. **Branch** cylindrical, unarmed, gray to gray-brown, sub-glabrous to pubescent; lenticels conspicuous; cataphylls present; stipules foliaceous, triangular. **Leaves** 3–12 cm long; pulvinus 0.12 cm long, aureum-villose; petiole 0.5–1 cm long, aureum-villose; rachis 2.5–5.1 cm long, aureum-villose; pulvinule 0.07 cm long, aureum-villose. **Leaflets** 9–13, alternate rarely opposite, discolors, margin slightly revolute, coriaceous; adaxial surface lustrous or opaque, sub-glabrous; abaxial surface opaque, sparse aureum-villose; midrib villose; secondary veins brochidodromous. Basal leaflets 0.9–1.5 × 0.7–1.1 cm; ovate; apex mucronulate, slightly retuse, rarely acuminate; base cordate to subcordate. Middle leaflets 1.1–3.7 × 0.8–3.7 cm; lanceolate to ovate; apex mucronulate, slightly retuse, rarely acuminate; base cordate to subcordate. Terminal leaflet 1.1–5.6 × 0.6–2.2 cm; elliptic; apex mucronulate; base cordate. Inflorescence panicle, 3.2–6.3 cm long, axillar; peduncle 0.9–1.2 cm long, aureum-villose; rachis 4.3–5.1 cm long, aureum-villose; lateral axis 1.6–2.0 cm long, aureum-villose; bracts not seen. **Flowers** sessilis, 7.5 mm long; bracteoles 1.5–1.7 × 1.4–1.5 mm, ovate, tomentose; calyx campanulate, 3.1 x 6.3 mm, aureum-tomentose; corolla white; banner petal 7 x 6 mm, orbicular, externally aureum-sericeous-tomentose, internally glabrous, apex retuse, base attenuate, claw 1.6 mm long; wing petals 7.3–7.6 × 2.2–2.5 mm, oblong, aureum-tomentose dorsally, apex acute, base auriculate, claw 3.0–3.2 mm long; keel petals 6.9–7.1 × 2.1–2.2 mm, strait-oblong, aureum-tomentose dorsally, apex obtuse, base auriculate. Androecium with stamens monadelphous, 10; filament sheath 4.0 mm long, glabrous; filaments 2.3 mm long, glabrous; anthers 0.5 × 0.2 mm, oblong. Gynoecium with nectary cupulate, 0.9 × 0.8 mm; stipe 1.3 mm, glabrous; ovary 2.6 x 0.9 mm, aureum-tomentose; style 0.9 mm long, glabrous; stigma punctate. **Fruit** samara, 5.5–6.0 cm long; stipe 0.6–0.7 cm long, fulvo-pubescent; seed chamber 1.5 – 2.0 × 1.0–1.2 cm, falcate, reticulate-verrucose, brown, sub-

glabrous; wing 3.0–4.2 × 1.4–1.8 cm, oblong to oblong-falcate, reticulate, punctate, brown, sub-glabrous; apex obtuse, apiculate, rarely short-apiculate. Figure 1.

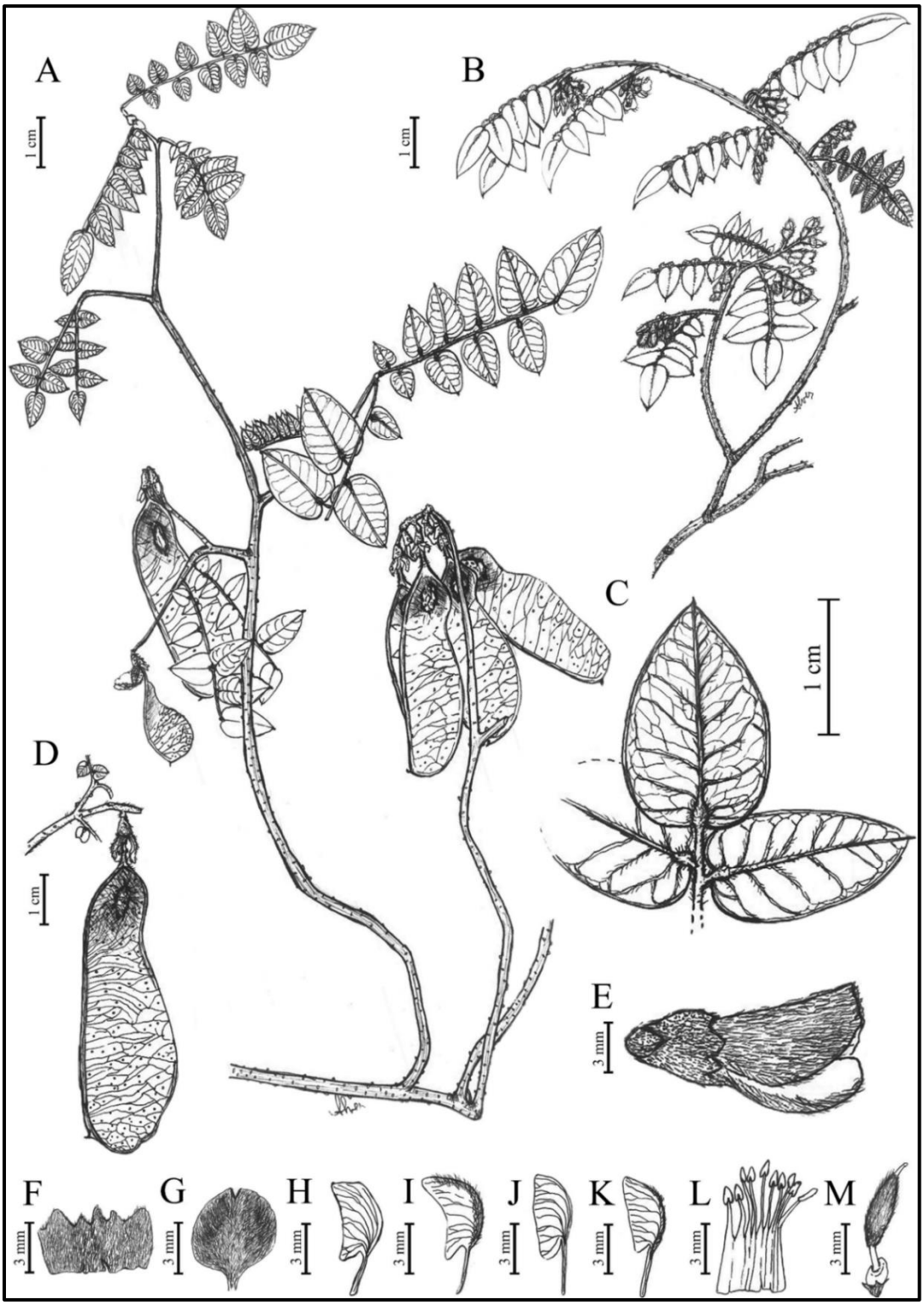


Figure 25. Illustration of *Machaerium* sp. nov. 3. **A, C and D** – Sevilha A.C. et al. 6736.; **B** – Jordão V.M.M. et al. 234. E – M. Alves, L.J. 23.; (Illustrator: Vieira, J.A.); **E** – Flower; **F** – Calyx; **G** – Banner petal; **H** – Inside view of wing petal; **I** – Outside view of wing petal; **J** – Inside view of keel petal; **K** – Outside view of keel petal; **L** – Androecium; **M** – Gynaecium. (Illustrator: Vieira, J.A.)

Distribution and Habitat— *Machaerium* sp. nov. 3 occurs in the states of Bahia, Ceará, Maranhão, Minas Gerais and Piauí, in Northeastern and Southeastern Brazil. It occurs in deciduous forest, including the vegetation locally known as “capoeira”, in arboreal Caatinga, in “Carrasco” vegetation, and the Caatinga-Cerrado transitional vegetation on sandy and clay soil at elevations between 670 and 880 m.

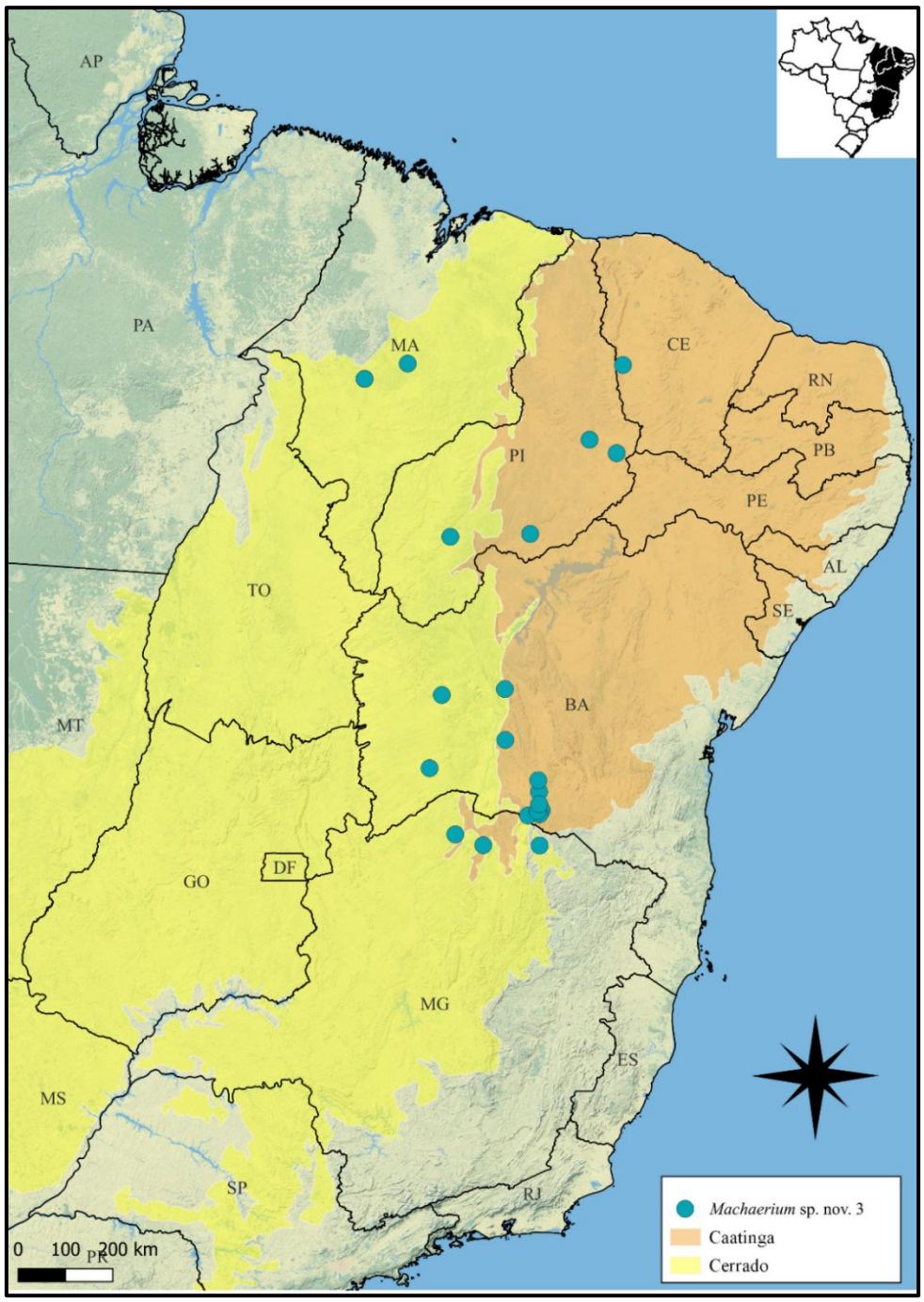


Figure 26. Distribution map of *Machaerium* sp. nov. 3.

Notes— *Machaerium* sp. nov. 3 can be recognized by the liana and scandent habit, stipule foliaceous; leaflets ovate to lanceolate; base cordate; mucron pubescent. In the reproductive

characters, flowers vary in length of about 7–8 mm; bracteoles ovate; corolla white; androecium monadelphous, with a glabrous filaments sheath and filaments and as concerning the fruits, samaras present seed chamber prominent.

Among the species occurring in the Caatinga, *Machaerium* sp. nov. 3 is distinct from all others. As shown in the diagnosis, it presents similarities with *M. sericiflorum* Vogel in terms of habits, however the similarities stop there. Another species, *M. oblongifolium* Vogel, which although it is also distinct, shares similar characteristics concerning the reduced number of leaflets and density of the indumentum in different parts of the plant in young individuals.

Phenology— The species flowers from October to January, presenting fruits from February to August.

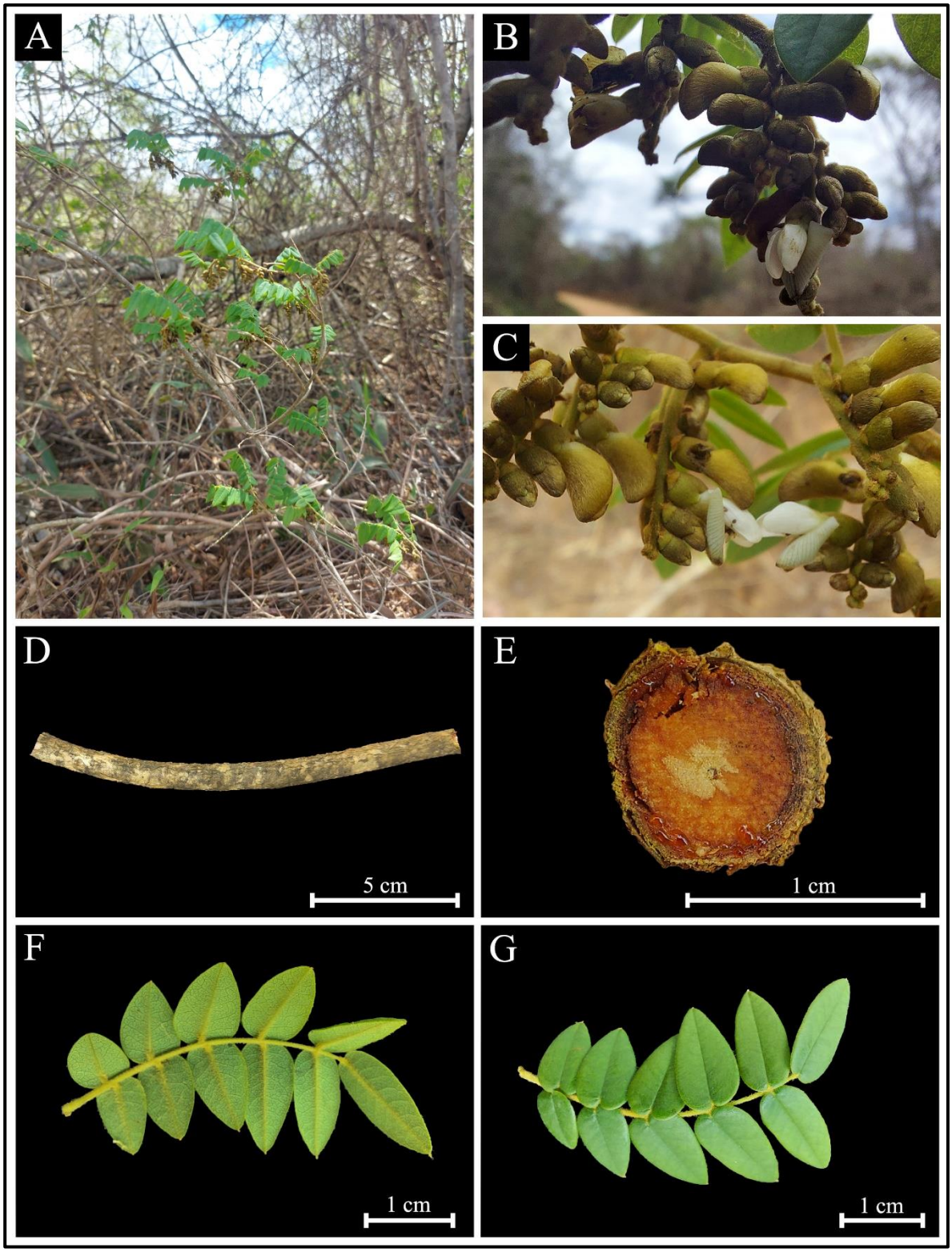


Figure 27. Field images of *Machaerium* sp. nov. 3 Filardi & Milezi-Jordão. A. Habitat, Caatinga biome, at Licínio de Almeida, Bahia. B. Terminal inflorescence. C. Axillar inflorescences. D. Cataphylls. E. Steam's cross section detailing the single cambium. F. Leaf's abaxial surface. G. Leaf's adaxial surface (A– G Jordão, V.M.M.).

Additional Specimens Examined —Brazil. Bahia: Baianópolis, Fazenda São Roque, 02 Dec 2011 (fl.), A.M. Miranda & J. Ferraz 6486 (HUEFS); Bom Jesus da Lapa, Médio São Francisco, ca.2,5 Km E da estrada Bom Jesus da Lapa - Ibotirama em ramal entrando a ca. 9,1 Km N de Bom Jesus da Lapa, [-13.218056°, -43.218056°], 10 Feb 2000 (fr.), L.P. Queiroz et al. 5838 (ALCB [digital image]); Brejinho das Ametistas, [-14.266667°, -42.516667], 12 Dec 2009 (fl.) L.J. Alves et al. 23 (HUEFS); Caetité, [-14.266667°, -42.516667], 13 Mar 1981 (fr.), S.B. Silva 185 (HUEFS); Coribe, Cerca de 10 km L de Coribe. Estrada Coribe/Descoberto, 670 m, [-13.789444°, -44.789444°], 17 Apr 2002 (fr.), F. França et al. 3847 (HUEFS); Ibotirama, Rod. BA-160, 5-10 km de Ibotirama, 500 m, 16 mar 1995 (fr.), G. Hatschbach et al. 61977 (US [digital image]); Licínio de Almeida, Fazenda Xaxá, na margem do rio, 923 m, [-14.655833°, -42.546944°], 07 Aug 2014 (fr.) M.L Guedes et al. 22160 (ALCB [digital image]), Rod. para Urandi, ca. 3,8 km da cidade, 800 m, [-14.713056°, -42.509167°], 31 Mar 2001 (fr.) J.G. Jardim et al. 3281 (HUEFS), Serra Geral, Estrada para Urandi, 7 Km de Licínio de Almeida, 750 m, [-14.74278°, -42745278°], 09 Dec 2009 (fl.), E. Melo et al 7360 (ALCB [digital image]), Serra Geral Licínio de Almeida, estrada, 5km de Licínio de Almeida para Urandi.09 Dec 2009 (fl.), M.L. Guedes et al 16693 (ALCB [digital image], HUEFS), Serra Geral, Rod. BA-S/C Caculé/Licínio de Almeida 38,3km, 850 m [-14.641389°, -42.461389°], 30 Mar 2001 (fr.) J.G. Jardim et al. 3252 (ALCB [digital image], HUEFS); Wanderley, Fazenda Cabecinhas. Conglomerado BA-642, Subunidade 2, Subparcela 1, Indivíduo 9, F8, 809 m, [-12.01°, -44.166667°], 22 Mar 2018 (st.) T.M. Moraes 1547 (UB). —Ceará: Novo Oriente, Baixa Fria - Planalto da Ibiapaba 05 Jan 1991 (fl.) F.S. Araújo 240 (EAC [digital image]), 16 Feb 1991 (fr.) F.S. Araújo 287 (EAC [digital image], UFRN [digital image]), Depois da Cabeça de Onça, Serra da Ibiapaba, 29 Apr 1979 (fr.), A. Fernandes et al. s.n. (EAC [digital image], HUEFS), Estrondo - Planalto da Ibiapaba, 05 Jan 1991 (fl.) F.S. Araújo 241 (EAC [digital image]), Estrondo - Planalto da Ibiapaba, 05 Jan 1991 (fl.) F.S. Araújo 434 (EAC [digital image], UEC [digital image]); Plantas da Comm. Scient. da provícia do Ceará, s.d. (fr.), F. Allemão & M. Cysneiros 419 (R [digital image]).—maranhão: Barra do Corda, Próximo à zona urbana, 10 Nov 1979 (fl.), E. Nunes & P. Martins s.n (EAC [digital image]); Grajaú, Entre Grajaú e Barra do Corda, 12 Nov 1979 (fl.) E. Nunes & P. Martins s.n (EAC [digital image], HUEFS [digital image], US [digital image]); Rodovia a 6 Km da cidade de Grajaú, 21 Apr 1983 (fr.) M.F.F. Silva et al. 1175 (INPA, US [digital image]). —minas gerais: Jaíba, Distrito de Irrigação de Jaíba – Reserva Legal, 12 Dec 1996 (fl.), E.T. Neto 2280 (UEC [digital image]); Januário, Distrito de Fabião, 2 km na estrada partindo do Abrigo do Malhador; [-15.1211°, -44.255556°], 26 Out 1997 (fl.), J.A. Lombardi 2096 (HUEFS); Santo Antônio do Retiro, Sítio 16, ponto 1,

881 m, [-15.3450°, -42.503888°], 21 Mar 2017 (fr.), A.C. Sevilha et al. 6736 (CEN, SJRP). — Piauí: Bom Jesus, Serra do Uuçuí, 06 Jun 1998 (fr.), A. Fernandes s.n (EAC [digital image]); Padre Marcos, Serra Velha, 10 Jan 1995 (st), M.E. Alencar 236 (HUEFS), Serra Velha - Km 2 da vicinal para Alagoinha do Piauí, 420 m, 21 May 1995 (fr.), M.E. Alencar 253 (HUEFS, K [digital image]), Serra Velha - Km 2 da vicinal para Alagoinha do Piauí, 420 m, 22 Jun 1995 (fr.), M.E. Alencar 284 (HUEFS); Picos, BR 316, KM 341, 02 May 1978 (fr.), A. Fernandes & Matos s.n (EAC [digital image], HUEFS); São Raimundo Nonato, Zabelê - Parna, Serra da Capivara, 630 m, [-9.015279°, -42.699401], 22 Jan 1998 (fl.), J.R. Lemos & J. Lima 35 (EAC [digital image], HST, IPA, PEUFR, UFP).

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6.6. Literature Cited

Acevedo-Rodrıguez, P., et al. 2015 (onwards). Lianas and climbing plants of the Neotropics: Cross sections of liana stems. https://naturalhistory.si. edu/research/botany/research/lianas-and-climbing-plants-neotropics/ lianas-cross-sections (accessed Aug 2023).

Beentje, H. 2010. *The Kew plant glossary: an illustrated dictionary of plant terms*. London: Royal Botanic Gardens.

Bentham, G. 1837. *Commentationes de Leguminosarum Generibus*. Vienna: Zollinger.

Filardi, F. L. R. 2011. *Avanços na Sistemática de Machaerium Pers. (Leguminosae Papilionoideae Dalbergieae): Filogenia e Revisão Taxonômica das espécies do Domínio Atlântico*. Doctoral dissertation (dissertation in Botany). Rio de Janeiro: Escola Nacional de Botânica Tropical, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

Filardi, F. L. R., H. C. Lima, B. B. Klitgaard, and A. L. B. Sartori. 2013. Taxonomy and nomenclature of the neotropical *Machaerium hirtum* complex (Leguminosae, Papilionoideae). *Brittonia* 65:154–170.

Filardi, F. L. R. and H.C. Lima. 2014. The diversity of *Machaerium* (Leguminosae: Papilionoideae) in the Atlantic Forest: Three new species, nomenclatural updates, and a revised key. *Systematic Botany* 39(1):145–159.

Filardi, F. L. R., H. C. Lima, D. B. O. S. Cardoso. 2020. *Machaerium in Flora e Funga do Brasil*. Jardim Botânico do Rio de Janeiro. Available from: http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB23055 (last accessed August 2023).

Harris, J. G., and M. W. Harris. 2001. *Plant Identification Terminology: An Illustrated Glossary*. Utah: Spring Lake Publishing.

Hoehne, F. C. 1941. Leguminosas Papilionadas (*Machaerium* e *Paramachaerium*). *Flora Brasilica* 25: 1–99.

Lewis, G.P. 1987. Legumes of Bahia. Kew: Royal Botanic Gardens.

Lozano, P., and B. B. Klitgaard. 2006. The genus *Machaerium* (Leguminosae: Papilionoideae: Dalbergieae) in Ecuador. *Brittonia* 58(2): 124–150.

Mendonça-Filho, C. V., H. C. Lima, E. R. Forni-Martins, and A. M. A. Tozzi. 2011. Two new species of *Machaerium* (Leguminosae) from Bahia and Southeastern Brazil. *Novon* 21: 73–77. 2011.

QGIS. 2019. QGIS Development Team. QGIS Geographic Information System. Open-Source Geospatial Foundation Project. http://qgis.osgeo.org.

Queiroz, L. P. D. 2009. *Leguminosas da caatinga.* Feira de Santana: Universidade Estadual de Feira de Santana.

Ribeiro, R. D., and H. C. Lima. 2007. Taxonomia de *Machaerium incorruptibile* (Vell.) Benth. e espécies afins (Leguminosae – Papilionoideae) na Mata Atlântica. *Rodriguésia* 58: 17–25.

Rudd, V. E. 1977. The genus *Machaerium* (Leguminosae) in Mexico. *Boletín de la Sociedad Botánica de México* 37: 119–146.

Rudd, V. E. 1987a. Studies in *Machaerium* (Leguminosae) VI: Section I. Machaerium. *Phytologia* 62: 283–302.

Rudd, V. E. 1987b. Studies in *Machaerium* (Leguminosae) VII: Section II. Lineata. Part I: Species with wingless fruit. *Phytologia* 64: 1–12.

Sartori, A. L. B., and A. M. A. Tozzi. 1998. As espécies de *Machaerium* Pers. (Leguminosae-Papilionoideae-Dalbergieae) ocorrentes no estado de São Paulo. *Brazilian Journal of Botany*, 21: 211–246.

Thiers, B. 2023. [continuously updated] *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih/ (last accessed August 2023).

Weberling, F. 1989. *Morphology of Flowers and Inflorescences*. Cambridge: Cambridge University Press.

7. CONSIDERAÇÕES FINAIS

Nossos resultados baseados na análise integrada destacaram quatro grupos, com distinções morfológicas, ecológicas e de distribuição e ao avaliar todos os materiais tipo do gênero na região Neotropical, concluímos que os morfotipos 1 e 2 representam entidades taxonômicas distintas, com diferenças morfológicas únicas que devem ser reconhecidas em nível de espécie.

Embora propusemos duas espécies novas, destacamos que são necessários mais estudos sobre biodiversidade aliados à conservação das espécies da Caatinga para que seja possível entender quais são os limites morfológicos para cada táxon.