UNIVERSIDADE ESTADUAL DE CAMPINAS
Instituto de Biologia

ELENICE APARECIDA FORTES

SISTEMÁTICA DO CLADO EPERUA *S.L*. E REVISÃO TAXONÔMICA DO GÊNERO *EPERUA* (LEGUMINOSAE, DETARIOIDEAE)

SYSTEMATICS OF THE EPERUA *S.L.* CLADE AND TAXONOMIC REVISION OF THE GENUS EPERUA (LEGUMINOSAE, DETARIOIDEAE)

CAMPINAS
2024

ELENICE APARECIDA FORTES

SISTEMÁTICA DO CLADO EPERUA *S.L.* E REVISÃO TAXONÔMICA DO GÊNERO *EPERUA* (LEGUMINOSAE, DETARIOIDEAE)

SYSTEMATICS OF THE EPERUA *S.L.* CLADE AND TAXONOMIC REVISION OF THE GENUS EPERUA (LEGUMINOSAE, DETARIOIDEAE)

Tese apresentada ao Instituto de Biologia da Universidade Estadual de Campinas como parte dos requisitos exigidos para a obtenção do título de Doutora em Biologia Vegetal.

Thesis presented to the Institute of Biology the University of Campinas in partial fulfillment of the requirements for the degree of Doctor, in the area of Plant Biology.

Supervisor/Orientador: Prof. Dr. Vidal de Freitas Mansano

ESTE TRABALHO CORRESPONDE À VERSÃO FINAL DA TESE DEFENDIDA PELA ALUNA ELENICE APARECIDA FORTES, E ORIENTADA PELO PROF. DR. VIDAL DE FREITAS MANSANO

CAMPINAS
2024

Ficha catalográfica
Universidade Estadual de Campinas
Biblioteca do Instituto de Biologia
Mara Janaina de Oliveira - CRB 8/6972

F776s
Fortes, Elenice Aparecida, 1996-
Sistemática do clado Eperua s.l. e revisão taxonômica do gênero *Eperua* (Leguminosae, Detarioideae) / Elenice Aparecida Fortes. – Campinas, SP : [s.n.], 2024.

Orientador: Vidal de Freitas Mansano.
Tese (doutorado) – Universidade Estadual de Campinas, Instituto de Biologia.

1. Biogeografia - Amazônia. 2. Fabaceae. 3. Taxonomia vegetal. 4. Sequenciamento de nucleotídeos em larga escala. 5. Hibridização. 6. Escudo das Guianas. I. Mansano, Vidal de Freitas, 1971-. II. Universidade Estadual de Campinas. Instituto de Biologia. III. Título.

Informações Complementares

Título em outro idioma: Systematics of the Eperua s.l. clade and taxonomic revision of the genus *Eperua* (Leguminosae, Detarioideae)
Palavras-chave em inglês:
Biogeography - Amazon River Region
Fabaceae
Plant taxonomy
High-throughput nucleotide sequencing
Hybridization
Guiana Shield
Área de concentração: Biologia Vegetal
Titulação: Doutora em Biologia Vegetal
Banca examinadora:
Vidal de Freitas Mansano [Orientador]
Ana Paula Fortuna Perez
Juliana Santos Silva
Leandro Cardoso Pederneiras
Samantha Koehler
Data de defesa: 27-02-2024
Programa de Pós-Graduação: Biologia Vegetal

Identificação e informações acadêmicas do(a) aluno(a)
- ORCID do autor: https://orcid.org/0000-0001-8307-6534
- Currículo Lattes do autor: http://lattes.cnpq.br/4769103586073490

Campinas, 27 de fevereiro de 2024

COMISSÃO EXAMINADORA

Profa. Dra. Ana Paula Fortuna Perez

Profa. Dra. Juliana Santos Silva

Prof. Dr. Leandro Cardoso Pederneiras

Profa. Dra. Samantha Koehler

Prof. Dr. Vidal de Freitas Mansano

Os membros da Comissão Examinadora acima assinaram a Ata de defesa, que se encontra no processo de vida acadêmica do aluno.

A Ata da defesa com as respectivas assinaturas dos membros encontra-se no SIGA/Sistema de Fluxo de Dissertação/Tese e na Secretaria do Programa de Biologia Vegetal do Instituto de Biologia da Universidade Estadual de Campinas.

AGRADECIMENTOS

Agradeço à orientação do professor Dr. Vidal de Freitas Mansano em todas as etapas do meu doutorado. Também sou grata pela orientação dos professores Dr. Jeff Doyle, Dra. Chelsea Specht e Dr. Jacob B. Landis durante o programa de doutorado sanduíche na Universidade de Cornell.

Expresso minha gratidão ao Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq (processo 140508/2020-1) pela bolsa de doutorado concedida ao longo dos meus quatro anos de estudo. O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Código de Financiamento 001, bolsa Capes Print Nº 88887.695281/2022-00. Meus agradecimentos também ao Funbio – Conservando o Futuro 2020 e Instituto HUMANIZE pela bolsa que apoiou as atividades de campo e laboratório, e ao Sigma Xi [G03152021120198803] pelo prêmio recebido que auxiliou na compra de materiais para o estudo filogenético.

Sou grata à UNICAMP, ao Instituto de Biologia e ao Programa de Pós-graduação em Biologia Vegetal pelo suporte na execução do projeto. Também agradeço à Universidade de Cornell, especialmente ao laboratório Specht, pelo grande apoio estrutural na extração e preparação do DNA para sequenciamento.

Meus agradecimentos vão aos curadores e funcionários dos herbários nacionais e internacionais pelo apoio durante as visitas, empréstimos de materiais, e amostragem de material para extração de DNA.

Agradeço aos membros do comitê de acompanhamento pelo suporte durante a execução do projeto, e aos membros da qualificação, pré-banca e banca pelas valiosas contribuições e sugestões nos manuscritos.

Por fim, agradeço aos meus familiares, amigos e colegas que me apoiaram ao longo dessa trajetória.

RESUMO

Este estudo busca ampliar o conhecimento do gênero *Eperua* (Leguminosae, Detarioideae, Detarieae) por meio de uma revisão taxonômica e nomenclatural e estudo filogenômico. *Eperua* é um gênero arbóreo com distribuição majoritária na Amazônia. Pertence ao clado Eperua *s.l.*, o qual inclui também outros três gêneros africanos arbóreos (*Augouardia*, *Eurypetalum* e *Stemonocoleus*). As espécies de *Eperua* podem ser agrupadas em dois tipos de flores aqui denominadas tubulares e não tubulares. A inflorescência também varia e pode ser curta e ereta ou longa e pendente. Espécies com corola não tubular, principalmente aquelas com inflorescências longas e pendentes estão associadas à polinização por morcegos, enquanto as espécies com corolas tubulares, com inflorescências curtas e eretas, estão associadas à polinização por abelhas. A revisão taxonômica revelou seis novos táxons para a ciência (*E. cerradoensis*, *E. froesii*, *E. reddeniae*, *E. manauensis*, *E. grandiflora* subsp. *ciliata*, *E. glabriflora* var. *gynopubescens)* e *E. praesagata* foi sinonimizada a *E. glabra*. No total são reconhecidas 19 espécies, cinco subespécies, e seis variedades para *Eperua*. A nova monografia ilustra amplamente as espécies, traz um comparativo morfológico detalhado, chaves de identificação atualizadas, além de informações sobre fenologia, distribuição, habitat, estado de conservação e nomes vernaculares. *Eperua cerradoensis* foi descrita no ecótono entre Cerrado e Caatinga, expandindo a distribuição de *Eperua*, anteriormente considerada endêmica da Amazônia. O estudo filogenômico foi baseado em '*target sequencing'* usando uma '*taxon-specific bait*' desenvolvida para Detarioideae. Foram amostradas todas as 23 espécies conhecidas do clado Eperua *s.l.*, a maioria, com múltiplos acessos. Para a reconstrução das árvores filogenéticas foram utilizadas abordagens de coalescência, concatenação e rede. A árvore concatenada foi datada para realizar análises biogeográficas e de reconstrução de caracteres ancestrais. Este estudo resolve com máximo suporte os gêneros *Eurypetalum* e *Eperua* como monofiléticos. As espécies de *Eperua* foram inferidas como monofiléticas, dando mais robustez às decisões taxonômicas, assim como esclareceu a posição filogenética de cinco espécies incluídas pela primeira vez em um estudo filogenético. Foi observada uma alta discordância entre as árvores de genes, principalmente devido a retenção de polimorfismo ancestral. Também foi demonstrado que as relações filogenéticas pouco resolvidas e com baixo suporte estão ligadas a eventos de reticulação, revelando, inclusive, *E. manauensis* como um potencial híbrido. As análises biogeográficas revelam que a dispersão de longa distância da África para América do Sul explica a origem de *Eperua* no Neotrópico. Seu ancestral comum mais recente chegou à Amazônia no Oligoceno tardio e se diversificou principalmente no Escudo das Guianas. A reconstrução ancestral de caracteres indica que o ancestral de *Eperua* provavelmente possuía flores com corola não tubular e inflorescência curta e ereta. Houve múltiplas origens da corola tubular e da inflorescência longa e pendente ao longo da evolução de *Eperua*. O estudo explora como a corola tubular influenciou a diversificação da espécie por meio da especiação simpátrica e discute os fatores que moldaram a distribuição atual de *Eperua* na Amazônia.

Palavras-chave: Amazônia, biogeografia, Fabaceae, taxonomia, sequenciamento de nova geração, captura por hibridização.

ABSTRACT

This study aims to broaden our understanding of the genus *Eperua* (Leguminosae, Detarioideae, Detarieae) through taxonomic and nomenclature revisions and phylogenomic study. *Eperua*, mainly distributed in the Amazonia, belongs to the Eperua *s.l.* clade, which also includes three other African tree genera (*Augouardia*, *Eurypetalum*, and *Stemonocoleus*). *Eperua* species exhibit two floral architectures, nominated tubular corolla and non-tubular corolla, and inflorescences that can be short and erect or long and pendulous. Species with non-tubular corollas, especially those with long, pendulous inflorescences, are associated with bat pollination, while those with tubular corollas are linked to bee pollination. The taxonomic study unveiled new taxa (*E. cerradoensis*, *E. froesii*, *E. reddeniae*, *E. manauensis*, *E. grandiflora* subsp. *ciliata*, *E. glabriflora* var. *gynopubescens*), and *E. praesagata* was synonymized with *E. glabra*. A total of 19 species, five subspecies, and six varieties were recognized for *Eperua*. The comprehensive monograph provides detailed morphological comparisons, an updated key, and information on phenology, distribution, habitat, conservation status, and vernacular names. *Eperua cerradoensis* was described in the ecotone between Cerrado and Caatinga, expanding *Eperua*'s distribution previously considered endemic to the Amazonia. The phylogenomic study used target sequencing with a taxon-specific bait for Detarioideae, encompassing all 23 known species of the Eperua *s.l.* clade, most with multiple accessions. Coalescence, concatenation, and network approaches were employed for phylogenetic tree reconstruction. The concatenated tree was dated for biogeographic and ancestral character reconstruction analysis. This study strongly supports the monophyly of *Eurypetalum* and *Eperua*. The *Eperua* species were inferred as monophyletic, providing more robustness to taxonomic decisions. Additionally, it elucidated the phylogenetic positions of five species included for the first in a phylogenetic study. High discordance among gene trees was observed, primarily due to incomplete lineage sorting. Additionally, poorly resolved relationships with weak support were linked to reticulation events, suggesting *E. manauensis* as a potential hybrid. Biogeographic analyses suggest long-distance dispersal from Africa to South America explains the origin of *Eperua* in the Neotropics. Its most recent common ancestor arrived in the Amazon in the Late Oligocene and diversified primarily in the Guiana Shield. Ancestral character reconstructions suggest the ancestral *Eperua* likely had non-tubular corolla flowers and short, erect inflorescences. The study investigates how the tubular corolla influenced species diversification through sympatric speciation and discusses factors shaping *Eperua*'s current distribution in Amazonia.

Keywords: Amazonia, biogeography, Fabaceae, taxonomy, next-generation sequencing, hybridization capture.

SUMÁRIO

INTRODUÇÃO

Contextualização

O Brasil ocupa a primeira posição entre os países megadiversos em relação ao número de espécies de plantas (FORZZA et al., 2012). Contudo, a perda de habitat e a fragmentação decorrentes do uso da terra configura uma das principais ameaças para essa megadiversidade (MARTINELLI & MORAES, 2013). A Amazônia Legal, por exemplo, sofreu com um aumento acentuado na taxa de desmatamento de acordo com as avaliações do PRODES de 2019 a 2023 comparando as taxas dos oito anos anteriores (INPE, 2023). Apesar deste cenário negativo para a conservação, o Brasil tem feito esforços para mitigar a perda da biodiversidade tornando-se signatário de diversos acordos internacionais como a Estratégia Global para Conservação de Plantas (GSPC, sigla em inglês). Neste acordo foram traçadas 16 metas com objetivo de catalisar o trabalho conjunto, desde o nível local até o nível global, para conhecer, conservar e usar de maneira sustentável a diversidade de plantas, promovendo a conscientização e propiciando recursos humanos e financeiros para a implementação dessa estratégia (CDB, 2011).

Dados os objetivos da GSPC, como a sistemática botânica pode promover a conservação das espécies de plantas? Por definição, esta é uma ciência que tem como objetivo principal reconstruir a história evolutiva da vida, incluindo e abrangendo a taxonomia tradicional, a descrição, identificação, nomenclatura e classificação de organismos; logo, a pesquisa sistemática é a base para adquirir, catalogar e recuperar informações sobre a biodiversidade (SIMPSON, 2010). Por sua vez, a meta 1 da GSPC, “elaborar e disponibilizar uma lista completa das espécies conhecidas de plantas”, está inteiramente ligada com as práticas desta ciência.

Um grande avanço do Brasil para o alcance desta meta foi o trabalho inovador e colaborativo de botânicos nacionais e internacionais no projeto Flora do Brasil 2020 (BFG, 2022). No entanto, o conhecimento da flora do bioma amazônico ainda está muito fragmentado devido à existência de regiões pouco conhecidas para a ciência (CARDOSO ET AL., 2017; HOPKINS, 2007; ter STEEGE et al. 2016) e à falta de taxonomistas trabalhando na Amazônia (CRANE 2004; FUNK, 2006). Logo, de modo a catalogar por completo a flora amazônica e alcançar a meta 1 da GSPC, ainda é preciso muito investimento em taxonomia, coleções físicas e plataformas virtuais de herbários e novas coletas por meio de trabalhos de campo (CARDOSO et al., 2017).

Na Amazônia há grupos de plantas endêmicas pobremente conhecidas sob o ponto de vista taxonômico, como o gênero arbóreo da família Leguminosae *Eperua* Aubl. Anterior aos trabalhos desta tese eram reconhecidas 16 espécies para este gênero, destas, 12 foram registradas até o momento no Brasil e cinco são endêmicas do país (COWAN, 1975; REIS, 2014; ROMERO-GONZÁLEZ & AYMARD, 2019). Nesses casos, revisões taxonômicas aliadas a estudos filogenéticos são essenciais para delimitar e validar agrupamentos taxonômicos, permitindo reconhecer a real riqueza de espécies.

Muito além da mera descrição de espécies, taxonomistas conhecem sobre a distribuição, as particularidades ecológicas e biológicas e as principais ameaças que afetam determinado táxon (ELI et al., 2017). Logo, a importância dos taxonomistas para ações de conservação se deve ao fato de que não se pode conservar efetivamente uma espécie sem uma delimitação taxonômica acurada e sem o conhecimento robusto da sua distribuição (ELI et al., 2017). Além disso, vale ressaltar que é impossível elaborar planos de ações para conservar táxons desconhecidos ou pobremente conhecidos para a ciência (Eli et al., 2017).

Eperua é um importante componente em termos de biomassa nas florestas de terras baixas da Amazônia (COWAN, 1975; ter STEEGE et al., 2013), dentre as espécies, *E. falcata* Aubl. e *E. leucantha* Benth. são consideradas hiperdominantes e estão listadas entre as 20 mais abundantes desse bioma (ter STEEGE et al., 2013). Em contrapartida, outros táxons do gênero podem ser considerados mais raros e são pouco coletados (REIS, 2014). Avaliando as coletas (SpeciesLink e Reflora) realizadas nas duas últimas décadas para *Eperua*, constatou-se que as espécies consideradas pouco coletadas permanecem nessa posição, representando apenas 1% das coletas nesses anos. A falta de coletas em campo e de revisões taxonômicas das plantas da Amazônia pode ser considerado um empecilho para cumprir a meta 1 da GSPC (ver BFG, 2018). Isso é nítido, por exemplo, a partir de revisões taxonômicas novas espécies são continuamente descobertas no Brasil, porém na Amazônia foram descobertas quatro vezes menos novas espécies entre 1990 e 2006 em comparação com os demais biomas (Sobral & Stehmann, 2009).

A avaliação do estado de conservação de todas as espécies de plantas conhecidas compõe a meta 2 da GSPC. No Brasil, essa avaliação é feita por meio de bases de dados de ocorrência das espécies e pela validação desses registros por taxonomistas (MARTINELLI & MORAES 2013; MARTINS et al. 2015; 2017). Apesar da maior biodiversidade do bioma Amazônia no país, a taxa avaliação do estado de conservação das espécies é muito baixa comparando-se aos outros biomas, pois apenas 9% das espécies avaliadas na lista vermelha pelo CNCFLORA se distribuem na Amazônia; e Leguminosae está entre as famílias com mais espécies na categoria "dados insuficientes" (MARTINS et al., 2018). Esse atraso na avaliação do estado de conservação da flora amazônica está intimamente ligado a falta de conhecimento taxonômico robusto, dos quais são obtidos dados sobre a distribuição da espécie, informação essencial para categorizá-las (ELI et al., 2017).

A avaliação do estado de conservação das espécies por si só não é suficiente para evitar sua extinção, porém, inquestionavelmente, é um instrumento legal que guia decisões dentro de um contexto de conservação (ELI et al., 2017). A falta de uma lista funcional e da avaliação do estado de conservação de todas as plantas conhecidas desafia o alcance das metas 7 e 8 da GSPC "conservar pelo menos 75% das espécies ameaçadas *in situ* e *ex situ*, respectivamente", assim como todas as demais (SHARROCK et al., 2018), principalmente quando se refere às espécies com importância socioeconômica.

As espécies de *Eperua* são fontes de produtos da sociobiodiversidade, como o óleo-resina das espécies conhecidas como "copaibarana" (*E. oleifera* Ducke) e "copaíba-jacaré" (*E. purpurea* Benth.), que são utilizados para fins etnofarmacológicos (DEFILIPPS et al., 2004; VEIGA-JUNIOR & PINTO, 2002). Suas madeiras são exploradas comercialmente devido à alta resistência e durabilidade (COWAN, 1975; RICHTER & DALLWITZ, 2000; TRADA, 2020; USEFUL TROPICAL PLANTS, 2014). Além disso, substâncias com atividades biológicas anti-inflamatórias, antioxidantes, inseticidas e bactericidas foram reportadas para as espécies, evidenciando o potencial farmacológico do gênero (LEANDRO & VEIGA-JUNIOR, 2012). A conservação da diversidade genética de espécies com importância socioeconômica como as do gênero *Eperua* compõe a meta 9 da GSPC. Neste contexto, taxonomistas podem promover essa conservação, pois a partir trabalhos de campo fazem coletas de sementes, frutos, depositam material em bancos de DNA e as espécies são levadas para cultivo em jardins botânicos, como, por exemplo, o Instituto de Pesquisas Jardim Botânico do Rio de Janeiro.

O cumprimento das metas da GSPC é uma forma de elevar a importância de conservar as plantas, que são frequentemente sub-representadas no debate sobre conservação e negligenciadas nos esforços em envolver o público em ações ambientais (SHARROCK et al., 2018). Neste cenário, estudos taxonômicos e filogenéticos do gênero *Eperua* podem contribuir diretamente para alcançar essas metas, promovendo o conhecimento e conservação da flora amazônica, uma das florestas tropicais mais importantes para a humanidade (WWF, 2020).

Organização da tese

A presente tese como objetivo aprofundar o conhecimento sobre o gênero *Eperua* explorando duas abordagens distintas: taxonomia e sistemática filogenética. Os resultados da análise taxonômica foram divididos em três artigos, organizados na tese de acordo com sua ordem cronológica de publicação

O primeiro, intitulado "**Untangling nomenclatural issues of some Amazonian trees of *Eperua* Aubl. (Leguminosae, Detarioideae, Detariae)**", traz uma revisão nomenclatural completa dos nomes associados ao gênero *Eperua*.

No segundo artigo, "**Two new species of *Eperua* (Leguminosae, Detarioideae, Detarieae) from the Amazon and Cerrado Biomes discovered in a botanical garden and a backyard**", descrevem duas novas e icônicas espécies para o gênero. A publicação destas espécies, separada da monografia, ressalta suas peculiaridades botânicas. Uma das espécies é encontrada fora da Amazônia, no ecótono Cerrado-Caatinga, e a segunda foi descrita na conhecida Reserva Florestal Adolpho Ducke, onde a descoberta de novas leguminosas não é comum.

O terceiro e último artigo relacionado à taxonomia é intitulado "**A taxonomic revision of the genus *Eperua* (Leguminosae, Detarioideae, Detarieae)**", oferecendo uma revisão completa de todas as espécies conhecidas e a descrição de mais duas novas espécies, além de uma subespécie e uma variedade nova. Todas espécies foram amplamente ilustradas com pranchas de fotografias de campo e de material dissecado e pranchas de desenhos.

Por fim, o último artigo desta tese, ainda em processo de submissão para publicação, explora a sistemática filogenética. Sob o título "**A nuclear phylogenomic study of the Eperua *s.l.* clade (Leguminosae, Detarioideae) provides new insights into plant diversification in Amazonia**", este artigo emprega sequenciamento de segunda geração e inclui uma variedade de análises evolutivas, desde a reconstrução de caracteres ancestrais até análises biogeográficas.

A formatação dos artigos segue as diretrizes e normas de citação específicas de cada revista onde os artigos foram ou serão publicados. Ademais, ao final da tese, são oferecidas conclusões gerais que englobam todos os artigos e suas respectivas contribuições.

ARTIGO I

Status: publicado na revista Phytotaxa.

FORTES, E. A., MANSANO, V. F. Untangling nomenclatural issues of some Amazonian trees of *Eperua* Aubl. (Leguminosae, Detarioideae, Detariae). *Phytotaxa*, v. 542, n. 2, p. 189–198, 5 abr. 2022. DOI: 10.11646/phytotaxa.542.2.6.

Ver direito de reprodução do artigo na tese em Anexo I.

Untangling nomenclatural issues of some Amazonian trees of *Eperua* Aubl. (Leguminosae, Detarioideae, Detariae)

ELENICE A. FORTES[1] & VIDAL F. MANSANO[2]

[1] *Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Rua Monteiro Lobato, 255, 13083-862, Campinas, SP, Brazil.*
forteselenice@gmail.com; https://orcid.org/0000-0001-8307-6534
[2] *Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão, 915, 22460-030, Rio de Janeiro, RJ, Brazil.*
vidalmansano@gmail.com; https://orcid.org/0000-0002-7204-0744

Abstract

Here we present a further nomenclatural revision of the genus *Eperua*. We correct the author of one nomenclatural combination, update the status of seven names as illegitimate, and make three lectotypifications and one second-step lectotypification. These nomenclatural changes are made in response to the International Code of Nomenclature for algae, fungi, and plants that aims at stability of biological nomenclature. The present results show that even revised names may still need to be checked and updated.

Introduction

Eperua is a tree genus of the family Leguminosae, Detarioideae, tribe Detariae (Estrella *et al.* 2018). The genus comprises 16 accepted species, four varieties, and four subspecies (Cowan 1975, Cowan 1985, Romero-González & Aymard 2019). It is endemic to the Amazonian region, distributed in the Guyana Shield and Amazonian basin in the North of Brazil and Southwest of Colombia. *Eperua* species are locally known as “wallaba”, “apa”, “espadeira”, “muirapiranga”, “copaibarana”, and “jacaré copaíba” (Cowan 1975). Several species have commercial value as a source of timber (Cowan 1975, Richter & Dallwitz 2000, TRADA 2021, Useful Tropical Plants Database 2014), oilresins (DeFilipps *et al.* 2004, Ducke 1932), and substances with biological activities (Leandro & Veiga-Junior 2012).

The history of *Eperua* began in 1775 (see Table 1) when Aublet described the first two species in separated genera (*Eperua falcata* Aubl. and *Parivoa grandiflora* Aubl.). The year 1870 was a landmark in the nomenclature of the genus, when Baillon (1870) first formally combined the genus *Parivoa* with *Eperua*. Until that year, *Eperua* had passed through nomenclatural instability as to the combination or separation from *Parivoa*, in addition to the creation of new names (*Panzera* and *Dimorpha*) (Forsyth 1794, Rees 1808, Schreber, 1791, Willdenow 1799). In 1851, Miquel described a third species (*E. rubiginosa* Miq.) and at the end of the nineteenth century, new species were described in the Flora Brasiliensis (Bentham 1870: *E. bijuga* Mart. ex Benth., *E. leucantha* Benth., *E. purpurea* Benth., *E. schomburgkiana* Benth.) and Hooker’s Icones Plantarum (Oliver 1891: *E. jenmanii* Oliv.). In the twentieth century, the number of species of *Eperua* increased from eight to fifteen, and four new varieties and four subspecies were described. At the beginning of that century, Pulle (1906) described the first variety (*E. rubiginosa* var. *grandiflora* Pulle). During the 1930s, Ducke made the first revision and described new species and varieties (Ducke 1932, 1940: *E. oleifera* Ducke, *E. oleifera* var. *campestris* Ducke, *E. bijuga* var. *glabriflora* Ducke). After Ducke, Cowan made the most complete taxonomic and nomenclatural revision (Cowan 1975) and described five species and two subspecies (Cowan 1957, 1958, 1975, and 1985: *E. glabra* R.S.Cowan, *E. grandiflora* subsp. *guyanensis* R.S.Cowan, *E. jenmanii* subsp. *sandwithii* R.S.Cowan, *E. venosa* R.S.Cowan, *E. duckeana* R.S.Cowan, *E. obtusata* R.S.Cowan, *E. praesagata* R.S.Cowan). Then, more than three decades passed since 1985 when Cowan described his last species (*E. praesagata*), and Romero-González and Aymard (2019) described the most recent species (*E. banaensis* G.A.Romero & Aymard) of the genus.

TABLE 1. Timeline and status of the 43 names associated with *Eperua* Aubl. (Leguminosae, Detarioideae, Detariae).

Year	Name	Status
1775	*Eperua* Aublet	correct name
	Eperua falcata Aublet	correct name
	Parivoa Aublet	nom. illeg. superfl.
	Parivoa grandiflora Aublet	≡ *E. grandiflora* (Aubl.) Baill. subsp. *grandiflora*
	Parivoa tomentosa Aublet	synonym *Crudia tomentosa* (Aubl.) J.F.Macbr.
1791	*Dimorpha* Schreber	nom. illeg. superfl.
1799	*Panzera* Willdenow	nom. illeg. superfl.
	Panzera falcata (Aublet) Willdenow	nom. illeg. superfl.
1802	*Dimorpha grandiflora* (Aublet) Willdenow	nom. illeg. superfl.
1808	*Dimorpha falcata* (Aublet) Smith in Rees	nom. illeg. superfl.
	Parivoa grandiflora Rudge	nom. illeg. superfl.
1837	*Eperua decandra* Blanco	synonym *Intsia bijuga* (Colebr.) Kuntze
	Eperua falcata Blanco	synonym *Afzelia rhomboidea* (Blanco) Fern.-Vill.
1850	*Eperua rubiginosa* Miquel	correct name
Jan. 1870	*Eperua grandiflora* (Aublet) Baillon	correct name
Dec. 1870	*Eperua grandiflora* (Aublet) Bentham	incorrect name
1870	*Eperua bijuga* Martius ex Bentham	correct name
	Eperua leucantha Bentham	correct name
	Eperua purpurea Bentham	correct name
	Eperua schomburgkiana R.S. Cowan	correct name
1891	*Eperua jenmanii* Oliver	correct name
1906	*Eperua rubiginosa* var. *grandiflora* Pulle	correct name
	Eperua rubiginosa Miquel var. *rubiginosa*	correct name
1917	*Eperua kourouensis* Benoist	*/= E. grandiflora (Aubl.) Baill. subsp. grandiflora*
1927	*Eperua preussii*	nomem nudum
1930	*Eperua hohenkerkii* Sprague	nomem nudum
1932	*Eperua oleifera* Ducke	correct name
	Eperua oleifera Ducke var. *oleifera*	correct name
	Eperua oleifera var. *campestris* Ducke	correct name
1933	*Eperua stipulata* Kleinhoonte	*/= E. jenmanii*
1940	*Eperua bijuga* var. *glabriflora* Ducke	≡ *E. glabriflora* (Ducke) R.S.Cowan
	Eperua campestris Ducke	≡ *E. oleifera* var. *campestris* Ducke
1957	*Eperua glabra* R.S. Cowan	correct name
1958	*Eperua venosa* R.S. Cowan	correct name
1975	*Eperua grandiflora* subsp. *guyanensis* R.S. Cowan	correct name
	Eperua grandiflora (Aublet) Baillon subsp. *grandiflora*	correct name
	Eperua duckeana R.S. Cowan	correct name
	Eperua glabriflora (Ducke) Cowan	correct name
	Eperua jenmanii subsp. *sandwithii* R.S. Cowan	correct name
	Eperua jenmanii Oliver subsp. *jenmanii*	correct name
	Eperua obtusata R.S. Cowan	correct name
1985	*Eperua praesagata* R.S. Cowan	correct name
2019	*Eperua banaensis* G.A. Romero & Aymard	correct name

During a revision of the 43 names associated with the genus *Eperua*, we saw the need to adequate them to the International Code of Nomenclature for algae, fungi, and plants (ICN) (Turland *et al.* 2018). The present work contributes to the nomenclatural revision of Cowan (1975), and the changes presented here were made mainly in response to the ICN articles 7.1 and 7.2, which determine that all names must be attached to one type. Additionally, we correct the authorship of the nomenclatural combination of one species based on the principle III of priority and verify the legitimacy of generic names attached to *Eperua*.

Material and methods

All the 43 names (Table 1) associated with the genus *Eperua* cited in The Plant List (2013), IPNI (2021), Tropicos (2021), and Plants of the World Online (2019) were checked. We consulted the original publication of all names directly in the journal or in online databases (BHL 2014, Botanicus 2021). We checked all herbaria available online cited in the taxonomic literature (Stafleu & Cowan 1976, 1979, 1981, 1983, 1985, 1986) in which type collectors likely deposited their collections. The nomenclatural revision is in accordance with ICN (Turland *et al.* 2018). Type specimens were analysed from digital images (JSTOR Global Plants and herbaria databases) and during visits to the herbaria IAN, INPA, MG, R, and RB. We provide herbaria barcodes for all exsiccates or the collection numbers when these were not available.

Results

Eperua Aublet (1775: 369). Type:—*Eperua falcata* Aublet (1775: 369).
Parivoa Aublet (1775: 756). Type:—*Parivoa grandiflora* Aublet (1775: 757) [≡*Eperua grandiflora* (Aublet 1775: 757) Baillon (1870: 110)].
Dimorpha Schreber, (1791: 493) nom. illeg. superfl.
Panzera Willdenow (1799: 540) nom. illeg. superfl. Type:—*Panzera falcata* (Aublet 1775: 369) Willdenow (1799: 540) [≡*Eperua falcata* Aublet (1775: 369)].

Eperua banaensis G.A.Romero & Aymard (2019: 341)
Holotype**:—**VENEZUELA. Amazonas: Municipio Autónomo Maroa, cuenca del río San Miguel, alto caño Mee, bana sobre arena blanca al sur de la serranía de Cariche, 106 m, 2˚44’14”N 66˚20’7”W, 18 September 2011, *G.A. Romero et al. 4079* (VEN not seen; isotypes GH not located, MO not seen, TFAV not seen).

Eperua bijuga Martius ex Bentham (1870: 226)
Lectotype (designated by Cowan 1975)**:—**BRAZIL. Pará: In sylvis inundatis ad insulam Marajo, May 1820, *C.F.P. Martius s.n.* (K[000555103] image!; isolectypes LE[00002232] image!, M[0215266] image!, M[0215267] image!, M[0215268] image!, M[0215270] image!).
Residual syntypes:—BRAZIL. Pará: Habitat in inundatis ad ostia fl. Tocantins et Amazonum; Provinciae Paraënsis, s.d., *C.F.P. Martius s.n.* (M[0215265] image!). Crescit in Brasiliae prov. Paraëns. ad Canalem Jabi, 1820, *C.F.P. Martius s.n.* (M[0215269] image!). Unknown locality, s.d., *C.F.P. Martius s.n.* (L[1951212] image!).

Bentham (1870) described *E. bijuga* based on Martius’ collections from two localities: “insulam Marajo” and “ostia fl. Tocantins”. One collection is found at K, one at LE, one at L, and six at M. All collections are from “Provinciae Paraënsis”, the current state of Pará, Brazil. Most of them are from “insulam Marajo” (K, LE, M[0215266], M[0215267], and M[0215268]), one from “ostia fl. Tocantins et Amazonum” (M[0215265]), and one from ad “Canalem Jabi” (M[0215269]). The K exsiccate has a donation stamp “Herbarium Hookerianum 1867” and a label from Herbarium Regium Monacense (M herbarium). All collections at M have the same label with a stamp “vid Bentham 1869”. Cowan (1975) described the K exsiccate as the holotype and those at M as isotypes. However, the fact that one of the type locations - “*ostia fl. Tocantis et Amazonum” -* is restricted to one of the M exsiccates indicates that Bentham used the M exsiccates to describe *E. bijuga*. Therefore, these three unnumbered collections of Martius are syntypes, and here we correct Cowan’s use of holotype to lectotype.

Eperua duckeana R.S. Cowan (1975: 30)
Holotype**:—**BRAZIL. Amazonas: Rio Urubú abaixo da cachoeira Iracema, 7 July 1941, *W.A. Ducke 732* (US[00001144] image!; isotypes F[0057800] image!, IAN[010263]!, MG[017957]!, MO[954041] image!, NY[1171178] image!, R sheet I[000054531]!, & sheet II[000054531a]!, SI[002003] image!).

Eperua falcata Aublet (1775: 369)
Lectotype (designated by Cowan 1975)**:—**FRENCH GUIANA. Cayenne, s.d. [July 1762–July 1764], *J.B.C.F. Aublet* s.n. (BM-inflorescence [000952284] image!).

≡ *Dimorpha falcata* (Aubl.) Forsyth (1794: 391) nom. illeg. superfl.
≡ *Panzera falcata* (Aubl.) Willdenow (1799: 540), nom. illeg. superfl.
≡ *Dimorpha falcata* (Aubl.) Smith in Rees (1808: 656), nom. illeg. superfl.

In his work, *Histoire des plantes de la Guiane Françoise*, Aublet described 576 genera and 1241 plant species (Leandri 1968) based on his collections, including *E. falcata*. We checked all herbaria cited in the taxonomic literature (Stafleu & Cowan 1976) where it is possible to find Aublet's collections, but we found only one specimen of *E. falcata* in BM. There is another sterile collection in P, J.B.C.F. Aublet 8288, originally identified as *E. falcata*, but characteristics of the leaflets indicate that the specimen is probably *E. rubiginosa*. Although there is only one specimen, Cowan (1975) needed to designate a lectotype to *E. falcata* restricted to the inflorescence on the BM sheet, as the vegetative part represents other *Eperua* species, probably *E. rubiginosa*. Cowan (1975) cited "*Cayenne 1775*" as the location and date of the type collection, and the note "*Cayenne Mr. Fusée Aublet 1773*" is handwritten on the sheet. However, none of these years corresponds to the actual collection date, since Aublet collected the sample in French Guiana between July 1762 and July 1764, leaving the country in July 1764 (Aublet 1775, Froidevaux 1897).

Besides the absence of vegetative parts in the sheet, Aublet (1775) presents a poorly detailed description and a plate. Nevertheless, Aublet's description and plate clearly refer to *E. falcata*. Among the diagnostic characteristics of *E. falcata* are falcate leaflets and pendent lateral racemes. These characteristics differentiate it from *E. rubiginosa*, which has straight leaflets and erect lateral racemes. In addition, *E. falcata* is clearly distinct from related species with falcate leaflets and pendent inflorescences such as *E. leucantha* and *E. venosa*. Aublet's plate presents a 3-jugate leaf differing from *E. venosa* that always has 2-jugate leaves. *E. falcata*'s plate and type sheet show long lateral racemes with many brownish buds, contrasting with the noticeable shorter lateral racemes with fewer and larger gray buds of *E. leucantha*.

Eperua glabra R.S. Cowan (1957: 251)
Holotype**:—**GUYANA. Near Chodikar Landing, Amongst Acarai foothills, 250 m elev., 17 October 1952, *N.G.L. Guppy 430* (NY sheet I[00004378] image!, & sheet II[00004379] image!; isotypes K sheet I[000555111] image!, & sheet II[000555109] image!, RB sheet I[00539601]!, sheet II[00545384]!, US[00001145] image!).

Eperua glabriflora (Ducke 1940: 27) R.S. Cowan (1975: 31)
Lectotype (designated by Cowan 1975)**:—**BRAZIL. Amazonas: Estrada do Aleixo, 3 April 1936, *W.A. Ducke 158* (US[00001143] image!; isolectotypes A not seen, F[0057801] image!, K[000555105] image!, MO[954335] image!, NY[00004376] image!, R sheet I[000054528]!, & sheet II[R000054528a]!).
Residual syntypes:—BRAZIL. Amazonas: Estrada do Aleixo, 14 June 1933, *W.A. Ducke s.n. RB23733* (RB[00285289]!). Manáos, Silva non inundabili sed paludosa secus riverlos, 18 August 1931, *W.A. Ducke 14* (WIS[00000392MAD] image!). Manáos, 21 May 1903, *E.A. Goeldi s.n. MG3862* (MG[003862]!, RB[00140284]!, US[00242890] image!, US[00242891] image!). Pará: Lago do Faro, cabeceira de Inajá, lugar húmido e ligeiramente [...]?, 27 January 1927, *W.A. Ducke s.n. RB20313* (RB[00539602]!, U[1243336] image!).

Ducke (1940) cited five syntypes in the original description of *E. bijuga* var. *glabriflora*: Ducke H.B.R.J. (RB old acronym) 23.733, Ducke 158, Ducke 14 at WIS, Goeldi H.A.M.P. (MG old acronym) 3862, and Ducke H.B.R.J. 20313. The collection Ducke 158 at R has a label handwritten by Ducke with the number 158. All other related exsiccates at US, K, MG, MO, NY are probably duplicates, which contain the same label but not handwritten by Ducke. Cowan (1975) chose one of the isosyntypes at US as the lectotype, which is in agreement with ICN Art. 9.2 (Turland *et al.* 2018).

Eperua grandiflora (Aublet 1775: 757) Baillon (1870: 110) subsp. ***grandiflora***
≡ *Parivoa grandiflora* Aublet (1775: 757).
Lectotype (designated by Cowan 1975)**:—**FRENCH GUIANA. Without locality, s.d. [July 1762–July 1764], *J.B.C.F. Aublet s.n.* (BM[000952282] image!, isolectotypes P[00835933] image!, P[00835934] image!).
≡ *Dimorpha grandiflora* (Aubl.) Forsyth (1794: 391) nom. illeg. superfl.
≡ *Dimorpha grandiflora* (Aubl.) Willdenow (1802: 971), nom. illeg. superfl.
= *Eperua kourouensis* Benoist (1916: 273).
Lectotype (designated here)**:—**FRENCH GUIANA Gourdonville, Kourou R., 8 September 1914, *R. Benoist 1595* (P[00835930] image!; isolectotypes, P[00835931] image!, P[00835932] image!).

Aublet (1775) described *E. grandiflora* in a different genus, *Parivoa*. Later, Bentham & Hooker (1865) combined *P. grandiflora* under *Eperua*, but this is not a valid combination according to ICN Art. 35.2 (Turland *et al.* 2018). Bentham (1870) is considered the author of the combination in many taxonomic treatments, plant reference lists, and herbaria labels (e.g. Pulle 1906, Ducke 1940, Cowan 1975, Tropicos (2021), The Plant List, Flora do Brasil 2020). Indeed, Bentham (1870) associated the epithet *grandiflora* to *Eperua* in an observation in the comments about *E. purpurea*. However, earlier in the same year, Baillon

(1870) had clearly associated the epithet *grandiflora* to the genus *Eperua*. Therefore, as already listed in IPNI, Baillon (1870) must be considered the author responsible for the combination because his work was published in January–February of 1870 while the Flora Brasiliensis of Bentham was published only in December of that year.

Since Aublet (1775) coined all genera and species based on his collections, we checked all herbaria cited in the taxonomic literature (Stafleu & Cowan 1976) where it is possible to find Aublet's collections, and we found one specimen of *E. grandiflora* at BM and two at P. The BM specimen has flowers and the P specimens are sterile. In the case of the latter, the collection locality, the 3-jugate straight leaflets, adaxially prominent main vein, conspicuous tertiary venation, and one intramarginal vein provide strong evidence that the specimen is *E. grandiflora*. Besides that, P00835933 specimen has a note handwritten by Aublet, "*Vouapa ouapa*", a vernacular name for *E. grandiflora* cited by him in the original description. Cowan (1975) cited the BM specimen as the holotype and did not mention the P specimens. As we clearly recognize three Aublet's collections of *E. grandiflora*, the BM specimen is a syntype, and here we correct Cowan's use of holotype to lectotype. Lastly, Aublet's description and collection clearly fits *E. grandiflora*, but his plate 303 shows a flower with exserted stamens in a short and erect inflorescence, thus indicating that this is neither *E. grandiflora* nor *E. falcata*, another species that he described in the same publication.

Eperua grandiflora (Aublet 1775: 757) Baillon (1870: 110) subsp. ***guyanensis*** R.S. Cowan. (1975: 34)

Holotype:—GUYANA. Bartica-Potaro. 83 mi Bartica-Potaro road, 23 June 1933, *T.G. Tutin 245* (US[00001146] image!; isotypes BM[000952283] image!, K[000555101] image!, U[0003225] image!).

Eperua jenmanii Oliver (1955: 20) subsp. ***jenmanii***

Lectotype (designated by Cowan 1975):—GUYANA. Essequibo River, August 1884, *G.S. Jenman 2154* (K[000555100] image!).

Residual syntypes:—GUYANA. Demerara, December 1879, *G.S. Jenman 573* (NY[00004380] image!, K[000555099] image!). Without locality, November 1888, *G.S. Jenman 4770* (BM[000065080] image!; K[000555098] image!). *G.S. Jenman 975* and *S. Jenman 3830* not located.

=*Dimorpha grandiflora* (Aublet 1775) Rudge (1807: 179), nom. illeg.

Lectotype (designated here): Unknown country. Without locality, s.d., *J. Martin s.n.* (BM[000065079] image!; isolectotype F[0111407] image!).

=*Eperua stipulata* Kleinhoonte. (1933: 171).

Lectotype (designated here): SURINAM. Saramaca, May 1924, *Febis 6468* (U[0003226] image!; isolectotypes U[0003227] image!, U[0003231] image!).

Dimorpha grandiflora Rudge (1808) is an illegitimate name since it is a later homonym of *Dimorpha grandiflora* Willd. (1802). *D. grandiflora* Willd. (1802) is also a superfluous name of its basyonim *Parivoa grandiflora* Aubl. (1775). As *D. grandiflora* Rudge is an illegitimate name, *E. jenmanii* Oliv., which is its heterotypic synonym, is the correct name for the taxon.

Eperua jenmanii Oliver (1955: 20) subsp. ***sandwithii*** R.S. Cowan (1975: 37)

Holotype:—VENEZUELA. Bolivar: Raudaul Guaiquinima, 200 m elev., 16–19 January 1952, *B. Maguire 33136* (NY[00004381] image!; isotypes F[0057802] image!, GH not seen, P[00252890] image!, RB[00539604]!, US[00001147] image!).

Eperua leucantha Bentham (1870: 225)

Lectotype (designated by Cowan 1975):—BRAZIL. Amazonas: Rio Negro, moist forest at Uanauaca, January 1852, *R. Spruce 2021* (K[000555107] image!; isolectotypes P[00835936] image!, P[00835937] image!).

Residual syntypes:—BRAZIL. Amazonas: Secus Rio Negro, Brasiliae borealis, inter Barcellos et San Gabriel, December 1851, *R. Spruce 2021* (BM[000952281] image!, G[00365211] image!, G[00365212] image!, GH[00103029] image!, K[000555106] image!, M[0215263] image!, P[00835935] image!, W[18890110107] image!).

The original collection cited by Bentham (1870) for *E. leucantha*, Spruce 2021, combined collections made in two different dates: December 1851 and January 1852. However, in order to comprise a single gathering the specimens need to be collected on the same date (Turland *et al.* 2018). Thus, Spruce 2021 must be considered two different collections. As Bentham (1870) did not specify the collection date of Spruce 2021, the exsiccate K000555107 with a handwritten annotation by Spruce is not the holotype as informed by Cowan (1975). We correct here Cowan's use of holotype to lectotype.

Eperua obtusata R.S. Cowan (1975: 33)

Holotype:—VENEZUELA. Amazonas: Capihuara, Rio Casiquiare, 3 October 1943, *L. Williams 16183* (US[00001148] image!).

Eperua oleifera Ducke (1932: 728) var. ***oleifera***

Lectotype (designated by Cowan 1975)**:—**BRAZIL. Amazonas: Borba, Rio Madeira, 16 January 1930, *W.A. Ducke RB23290* (R[000028782]!, isolectotypes F-frag.[0057804] image!, G not seen, INPA [0234506]!, K[000555093] image!, K[000858688] image!, NY[00004382] image!, NY[00004383] image!, NY[01185435] image!, P[00252888] image!, RB sheet I[00585686]!, & sheet II[00539606]!, S collection number S-R-8709 image!, U[0003233] image!, US[00001149] image!).

Residual syntypes:—BRAZIL. Amazonas: Maués, Lago Massauary, 18 December 1927, *W.A. Ducke s.n. RB20217* (RB sheet I[00539607]!, sheet II[00585687]!, & sheet III[00585688]!).

Ducke (1932) described *E. oleifera* listing two of his unnumbered collections and their respective RB old acronym and collection number "H.B.R.J. n 23.290", and "H.B.R.J. n 20.217". Then, it is unclear which collection is the holotype, making it necessary to select a lectotype. The lectotypification made by Cowan (1975) is correct since he chose as lectotype one of the isosyntypes, Ducke s.n. RB 23290 at R.

Eperua oleifera Ducke (1932: 728) var. ***campestris*** Ducke (1932: 728)

Holotype**:—**BRAZIL: Amazonas: Borba, Rio Madeira, campo arenoso, 17 January 1930, *W.A. Ducke s.n. RB23291* (RB sheet I[00539605]!, sheet II[00585835]!, & sheet III[00585836]!; isotypes NY[00004384] image!, P[00835938] image!, R[000028783]!, U[0003232] image!, US[00001150] image!).

Ducke (1932) described *E. oleifera* var. *campestris* presenting one of his unnumbered collections and respective RB old acronym and collection number (H. J. B. R. n. 23.291) as type. Additionally, he informed that the RB23291 exsiccate had a duplicate at P. Thus, the collection Ducke s.n. RB23291 at RB is the holotype, and not the collection at R, as incorrectly cited by Cowan (1975).

Eperua praesagata R.S. Cowan. (1985: 293)

Holotype**:—**BRAZIL: Pará: Rio Trombetas, Cachoeira Porteira, estrada que dá acesso para Perimetral Norte, km 7, mata de várzea de igarapé, 8 June 1978, *N.T. Silva & M.R. Santos 4758* (MG[061723]!; isotypes MO[1714824] image!, NY[00004377] image!, RB[00141558]!, US[00090950] image!).

Eperua purpurea Bentham (1870: 226)

Lectotype (designated by Cowan 1975)**:—**BRAZIL. Amazonas: Panuré, Rio Negro, Uaupés, September 1852, *R. Spruce 2577* (K[000555096] image!; isolectotype P-flower[00835940] image!).

Residual syntypes**:—**BRAZIL. Amazonas: Panuré, Rio Negro, Uaupés, October 1852–January 1853, *R. Spruce 2577* (BM[000952280] image!, BR[0000005172238] image!, F[0057805] image!, G[00365214] image!, G[00365213] image!, GH[00339219] image!, K[000555097] image!, LE[00002233] image!, M ?, NY[00004385] image!, P[00835939] image!, W[18890110503] image!, W[18890146287] image!), February 1853, *R. Spruce 2577* (K[000555095] image!, P-fruit[00835940] image!), s.d., *R. Spruce 2577* (RB[00539608]!).

Spruce 2577, which is the type collection of *E. purpurea* cited by Bentham (1870), combine collections made in three different dates: September 1852, October 1852–January 1853, and February 1853. However, to comprise a single gathering, the specimens need to be collected on the same date (Turland *et al.* 2018) and, thus, Spruce 2577 must be considered different collections. As Bentham (1870) did not specify the collection date, the exsiccate K000555096 with a handwritten annotation by Spruce is not the holotype as informed by Cowan (1975), and we correct here Cowan's use of holotype to lectotype.

Eperua rubiginosa Miquel (1851: 12) var. ***rubiginosa***

Lectotype (designated by Cowan 1975)**:—**SURINAM. Without locality, s.d., *F.W. Hostmann 229* (U[0003237] image!; isolectotypes K[000555108] image!, LE[00002234] image!).

Residual syntypes**:—**SURINAM. Without locality, October 1844, *A. Kappler 1869* (G[00365205] image!, MO[954222] image!, P[03465633] image!, TUB[009759] image!, U[0003235] image!).

Eperua rubiginosa Miquel (1851: 12) var. ***grandiflora*** Pulle (1906: 211)

Holotype**:—**SURINAM. Fluv. Gonini, August 1903, *G.M. Versteeg 48* (U[0003236] image!).

Eperua schomburgkiana Bentham (1870: 226)

Lectotype (designated by Cowan 1975/designated here)**:—**GUYANA. Essequibo & Rupununy, 1838, *Rob. Schomburgk Ser. 1 517* (K[000555112] image!; isolectotypes BM[000065064] image!, G[00365223] image!, G[00365208] image!, K[000555113] image!, K[000555114] image!, P[00252893] image!, W not seen).

In spite of being collected for the first time in Brazil only in 1965 (collection number: Prance *et al.* 1652), Bentham (1870) described *E. schomburgkiana* in the Flora Brasiliensis. He described *E. schomburgkiana* in a comment on the species *E. purpurea*, providing a complete diagnosis and pointing that the plant was found in Guyana by Schomburgk. As there were two collections of *E. schomburgkiana* by Schomburgk, 517 and

317, Cowan (1975) selected the 517 at K as lectotype and cited the exsiccates at BM, G, K, P, and W as isolectotypes. However, Cowan (1975) did not specify which exsiccate refers to the lectotype and isolectotypes at K, which makes the present second-step lectotypification necessary.

Eperua venosa R.S. Cowan. (1958: 147)
Holotype:—VENEZUELA. Bolívar: Angell Falls, *H.R. Kunhardt Jr. 20* (NY[00004386] image!).

Discussion

Here we presented many nomenclatural novelties for some of the 43 names (Table 1) associated with the genus *Eperua*. The novelties concern correct combination authorship, nomenclatural status, and typifications. These nomenclatural changes are made in response to the International Code of Nomenclature for algae, fungi, and plants that aims at biological nomenclature stability (Turland *et al.* 2018). Before the present work, Cowan (1975) studied the genus *Eperua*, tracing its nomenclatural history and revising the associated names. Then, besides the advance in the stability of the names, the present results show that even names once revised still need to be checked and updated.

Priority of publication is a fundamental principle of the ICN (Turland 2019), and the author of the transference of *Parivoa grandiflora* Aubl. to the genus *Eperua* Aubl. is a case of priority that went unnoticed for more than a century. Until now, Bentham (1870) was considered the author of the combination when actually Baillon (1870) was the first to combine the names. Baillon has, therefore, priority (principle III of the ICN, Turland *et al.* 2018) because he published his work at the beginning of 1870, and Bentham published the Flora Brasiliensis at the end of that year. Thus, *Eperua grandiflora* (Aubl.) Baill. is the correct name and must be updated in many plant reference lists and herbarium labels.

The plates used by Aublet (1775) to illustrate *E. falcata* and *E. grandiflora* have some inconsistencies that can lead to misinterpretations in the taxonomy of these species and consequent nomenclatural instability of the entire genus. The genus *Eperua* is not an isolated case: the plates published by Aublet for many other taxa are mixtures, and the descriptions may contain contradictions (Howard 1983). Here we cited characteristics from the original description, plate, and type collections that can help to clarify the circumscriptions of these taxa, and we excluded the ones that were incongruent. The names *Panzera falcata* Willdenow, *Dimorpha* Schreber, *Dimorpha grandiflora* Willdenow, and *Panzera falcata* Smith were just cited as synonyms by Cowan (1975), but here we updated the nomenclatural status as illegitimate superfluous names. These names reflect a past custom from the seventeenth through the nineteenth century of coining different names to the same taxon (Cowan 1975). *Dimorpha grandiflora* Rudge was for the first time here cited as an illegitimate name and, different from the names previously listed, this was a case of a single name used to refer to different taxa. In fact, Rudge (1808) tried to change the circumscription of *D. grandiflora* as he justified that the specimen collected by Martin better represented the taxon. The taxon that Rudge refers to is now recognized as *E. jenmanii*, the species with the largest flower in the genus (Cowan 1975). The confusion can be due to the epithet “grandiflora” of the species now named *E. grandiflora* (Aubl.) Baill., which contradictorily has one of the smallest flowers of the genus (Cowan 1975). However, this epithet made sense when Aublet (1775) first described *P. grandiflora*, as he described a second species, *Parivoa tomentosa* Aubl, with much smaller flowers, which now belongs to another genus (Cowan 1975).

All names must be attached permanently to a nomenclatural type (ICN Art 7.1, Turland *et al.* 2018). However, many *Eperua* names were attached to more than one type, requiring lectotypifications (ICN Art. 9.17, Turland *et al.* 2018). Cowan (1975) did the lectotypification of six names (*E. falcata*, *E. glabriflora*, *E. jenmanii* subsp. *jenmanii*, and *E. oleifera* var. *oleifera*, *E. schomburgkiana*, and *E. rubiginosa* var. *rubiginosa*), but for others that also needed the designation of a lectotype (*E. bijuga*, *E. grandiflora*, *E. oleifera* var. *oleifera*, *E. leucantha*, and *E. purpurea*), he just pointed one of the syntypes as holotype. Thus, here we recognize these pointed holotypes as lectotypifications and correct Cowan’s use of holotype to lectotype. We provided pieces of evidence that the author cited more than one collection in the original description and did not point which was the holotype. In order to narrow to just one type, we also did a second-step lectotypification of *E. schomburgkiana*. Lastly, all names must be attached to a type including synonyms (ICN Art. 7.2, Turland *et al.* 2018). Thus, we needed to point a lectotype to the names *E. korouensis*, *E. stipulata*, and *D. grandiflora* Rudge. Finally, as presented here, Cowan (1975) did many contributions to *Eperua*’s nomenclature. The present results add to Cowan’s (1975) work, bringing nomenclatural novelties that further enhance the nomenclatural stability of names associated with *Eperua*.

Acknowledgements

This paper is part of the first author's Ph.D. thesis supported by a scholarship from Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq (process 140508/2020-1) and by Funbio - Conservando o Futuro 2020 grant.

References

Aublet, J.B.C.F. (1775) *Histoire des plantes de la Guiane Françoise*. Tome I and Tome II. Pierre Françoies Didot jeune, Paris, 976 pp.

Baillon, H.E. (Jan–Feb 1870) Caesalpinées. *In*: Baillon, H.E. (Ed.) *Histoire des plantes*. Tome II. Librairie Hachette & Cie, Paris. pp. 110–111.

Benoist, R. (1916) Descriptions d'espécies nouvelles de légumineuses de la Guyane Française *Notulae Systematicae. Herbier du Museum de Pari*s 3: 271–274.

Bentham, G. (1870) Caesalpinieae. *In:* von Martius, C.F.P. & Eichler, A.G. (Eds.) *Flora Brasiliensis* 15(2). F. Fleischer, Leipzig, pp. 226–228.

BHL (2021) Biodiversity Heritage Library 2019. Available from: https://www.biodiversitylibrary.org (accessed 6 November 2021)

Botanicus (2021) Botanicus Digital Library. Available from: http://botanicus.org/ (accessed 6 November 2019)

Cowan, R.S. (1957) Tropical American Leguminosae-III. *Brittonia* 8: 251–253. https://doi.org/10.2307/2804977

Cowan, R.S. (1958) Leguminosae-Caesalpinioideae. The Botany of the Guayana Highland. *Memoirs of the New York Botanical Garden* 10: 147–149.

Cowan, R.S. (1975) Monograph of the genus *Eperua* (Leguminosae: Caesalpinioideae). *Smithsonian Contributions to Botany* 28: 1–45. https://doi.org/10.5479/si.0081024X.28

Cowan, R.S. (1985) Studies in Tropical American Leguminosae–IX. *Brittonia* 37 (3): 292–294. https://doi.org/10.2307/2806078

DeFilipps, R.A., Maina, S.L. & Crepin, J. (2004) *Medicinal Plants of the Guianas*. National Museum of Natural History, Smithsonian Institution, Washington, DC, 477 pp.

Ducke, W.A. (1932) Espéces nouvelles de plantes de l'Amazonie brésilienne. *Bulletin du Muséum National d'Histoire Naturelle* 4 (6): 728–729.

Ducke, W.A. (1940) Notes on the wallaba trees. *Tropical Woods* 62: 21–28.

Estrella, M. de La, Forest, F., Klitgård, B., Lewis, G.P., Mackinder, B.A., Queiroz, L.P. de, Wieringa, J.J. & Bruneau, A. (2018) A new phylogeny-based tribal classification of subfamily Detarioideae, an early branching clade of florally diverse tropical arborescent legumes. *Scientific Reports* 8: 6884. https://doi.org/10.1038/s41598-018-24687-3

Forsyth, Jr., W. (1794) *A Botanical nomenclator containing a systematical arrangement of the classes, orders, genera, and species of plants as described in the new edition of Linnæsus's Systema naturæ, by Dr. Gmelin*. Printed for T. Cadell, and P. Elmsly, in the Strand, and G. Nicol, Pall-Mall, London, p. 391. https://doi.org/10.5962/bhl.title.127458

Froidevaux, H. (1897) *Étude sur les recherches scientifiques de Fusée Aublet à la Guyane française 1762–1764*. Kessinger Publishing, United States, 52 pp.

Howard, R. (1983) The plates of Aublet's Histoire des plantes de La Guiane Françoise. *Journal of the Arnold Arboretum* 64 (2): 255–292. https://doi.org/10.5962/p.324743

Kleinhoonte, A. (1933) *Eperua stipulata* Kleinh. nov. spec. *Recueil des Travaux Botaniques Néerlandais* 30: 171.

Leandri, J. (1968) Un pharmacien provençal découvre une partie de la flore du Nouveau Monde: J. B. C. Fusée Aublet et l' "Histoire des plantes de la Guyane française". *Adansonia* 8 (2): 137–146.

IPNI (2021) International Plant Names Index. The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Botanic Gardens. Available from http://www.ipni.org. (accessed 6 November 2021)

Leandro, L.M. & Veiga-Junior, V.F. (2012) O Gênero *Eperua* Aublet: uma revisão. *Scientia Amazonia* 1: 14–22.

Miquel, F.A.G. (1851) Caesalpiniae. *In:* Miquel, F.A.G (Ed.) *Stirpes Surinamensis Selectae*. Arnz & Comp, Leiden, pp. 12–13. https://doi.org/10.5962/bhl.title.77484

Oliver, D. (1891) *Hooker's Icones Plantarum*, vol. 20.

Plants of the World Online (2021) Royal Botanical Garden Kew. Available from: http://www.plantsoftheworldonline.org/ (accessed 9 November 2021)

Pulle, A.A. (1906) *An enumeration of the vascular plants known from Surinam*. E.J. Brill, Leiden, 555 pp.

Rees, A. (1808) *The cyclopædia; or, Universal dictionary of arts, sciences, and literature*. Vol. 11. Longman, Hurst, Rees, Orme & Brown, Paternoser-Row, London, 768 pp.

Richter, H.G. & Dallwitz, M.J. (2000) Commercial timbers: descriptions, illustrations, identification, and information retrieval. Available from: http://delta-intkey.com. (accessed 6 November 2021)

Romero-González, G.A. & Aymard, G.A.A. (2019) A new species of *Eperua* (Leguminosae, Detarioideae) from Amazonas state, Venezuela. *Harvard Papers in Botany* 24: 341–347. https://doi.org/10.3100/hpib.v24iss2.2019.n17

Rudge, E. (1807) Description of a new Species of *Dimorpha*. *Transactions of the Linnean Society of London* 9: 179–181. https://doi.org/10.1111/j.1096-3642.1818.tb00337.x

Schreber, J.C.D. (1791) *Genera Plantarum*. vol. 2. Frankfurt ad Moenum, Sumtu Varrentrappii et Wenneri, 872 pp.

Stafleu, F.A. & Cowan, R.S. (1976) Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Volume I: A-G. Regnum Vegetabile 137. Bohn, Scheltema & Holkema, Utrecht, 1136 pp. Available from: https://www.biodiversitylibrary.org/item/103414#page/11/mode/1up (accessed 6 November 2011.

Stafleu, F.A. & Cowan, R.S. (1979) Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Volume II: H-Le. Regnum Vegetabile 98. Bohn, Scheltema & Holkema, Utrecht, 991 pp. Available from: https://www.biodiversitylibrary.org/item/103253#page/11/mode/1up (accessed 6 November 2011)

Stafleu, F.A. & Cowan, R.S. (1981) Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Volume III: Lh-O. Regnum Vegetabile 105. Bohn, Scheltema & Holkema, Utrecht, 980 pp. Available from: https://www.biodiversitylibrary.org/item/104137#page/7/mode/1up (accessed 6 November 2011)

Stafleu, F.A. & Cowan, R.S. (1983) Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Volume IV: P-Sak. Regnum Vegetabile 110. Bohn, Scheltema & Holkema, Utrecht, 1214 pp. Available from: https://www.biodiversitylibrary.org/item/103624#page/7/mode/1up (accessed 6 November 2011)

Stafleu, F.A. & Cowan, R.S. (1985) Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Volume V: Sal-Ste. Regnum Vegetabile 110. Bohn, Scheltema & Holkema, Utrecht, 1066 pp. Available from: https://www.biodiversitylibrary.org/item/104077#page/11/mode/1up (accessed 6 November 2011)

Stafleu, F.A. & Cowan, R.S. (1986) Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Volume VI: Sti-Vay. Regnum Vegetabile 110. Bohn, Scheltema & Holkema, Utrecht, 926 pp. Available from: https://www.biodiversitylibrary.org/item/103683#page/7/mode/1up (accessed 6 November 2011)

The Plant List (2013) Version 1.1. Published on the Internet. Avalaible from: http://www.theplantlist.org/ (accessed 6 November 2021)

TRADA (2021) Timber Research and Development Association, Wallaba. Available from: https://www.trada.co.uk/wood-species/wallaba/ (accessed 6 November 2021)

Tropicos (2021) Missouri Botanical Garden. Available from: https://tropicos.org (accessed 6 November 2021)

Turland, N.J. (2019) *The code decoded. A user's guide to the International code of nomenclature for algae, fungi, and plants*. Advanced Books, Pensoft Publishers, Sofia. https://doi.org/10.3897/ab.e38075

Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (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. Koeltz Botanical Books, Glashütten, 254 pp. https://doi.org/10.12705/Code.2018

Useful Tropical Plants Database (2014) *Eperua*. Avalaible from: http://tropical.theferns.info/query.php?full=eperua (accessed 6 November 2021)

Willdenow, C.L. (1799) *Species plantarum*, ed. 4, 2(1). G.C. Nauk, Berolini, 823 pp.

Willdenow, C.L. (1802) *Species Plantarum*. ed. 4, 3(2). G.C. Nauk, Berolini, 1474 pp.

ARTIGO II

Status: publicado na revista Phytotaxa (open acccess).

FORTES, E. A., SILVA, G. S. da., MANSANO, V. F. Two new species of Eperua (Leguminosae, Detarioideae, Detarieae) from the Amazon and Cerrado Biomes discovered in a botanical garden and a backyard. *Phytotaxa*, v. 591, n. 3, p. 196–208, 5 abr. 2023. DOI: 10.11646/phytotaxa.591.3.2.

Ver direito de reprodução do artigo na tese em Anexo II.

Two new species of *Eperua* (Leguminosae, Detarioideae, Detarieae) from the Amazon and Cerrado Biomes discovered in a botanical garden and a backyard

ELENICE A. FORTES[1,3*], GUILHERME S. DA SILVA[1,4] & VIDAL F. MANSANO[2,5]
[1] *Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Rua Monteiro Lobato, 255, 13083-862, Campinas, SP, Brazil.*
[2] *Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão, 915, 22460-030, Rio de Janeiro, RJ, Brazil.*
[3] *forteselenice@gmail.com; https://orcid.org/0000-0001-8307-6534*
[4] *guilhremecx.cx@hotmail.com; https://orcid.org/0000-0002-4250-0017*
[5] *vidalmansano@gmail.com; https://orcid.org/0000-0002-7204-0744*
[*] *Corresponding author*

Abstract

In this study, we describe two new species of *Eperua*, *E. cerradoensis* and *E. manausensis. Eperua cerradoensis* is the first species of the genus described from the Cerrado Biome (Brazil); all other 16 species, including the other new species described here *E. manausensis*, are endemic to the Amazon region (Amazon basin and the Guiana Shield). Both species have short and erect inflorescences. *Eperua cerradoensis* has a non-tubular corolla, white petals, and exserted stamens, and is most similar to *E. duckeana* and *E. schomburgkiana,* from which it differs by the bracteole size and phenology, flower indumentum, besides other vegetative characteristics. *Eperua manausensis* has a tubular corolla, pink to purple petals, and inserted stamens, and it is most similar to *E. grandiflora* subsp. *guyanensis*, but differs from it by the bracteole position and phenology and flower indumentum. The type localities of both species are very unusual: a backyard (*E. cerradoensis*) and a botanical garden (*E. manausensis*). The two species have been collected in the last five years. These discoveries show that new undescribed species can be found even in more disturbed areas and that comprehensive knowledge of the flora requires new collections and more taxonomists.

Key words: Fabaceae, Eperua *s.l.* clade, Neotropical flora, species description, taxonomy

Introduction

The Neotropical genus *Eperua* Aublet (1775: 369) is a typical genus of the family Leguminosae or Fabaceae that has a single superior carpel with one locule, marginal placentation in two alternating rows on a single placenta (Lewis *et al.* 2009), besides the common pod without any dispersal modifications, compound and alternate leaves with stipules and pulvinus, racemose inflorescences, and showy, dichlamydeous, pentamerous flowers (Barroso *et al.* 1991). The genus belongs to the subfamily Detarioideae, tribe Detarieae (LPWG 2017, Estrella *et al.* 2018). In the tribe Detarieae, it is closely related to three African genera, *Eurypetalum* Harms (1910: 293), *Augouardia* Pellegrin (1924: 309), and *Stemonocoleus* Harms (1905: 76), which together comprise the Eperua *s.l.* clade (Bruneau *et al.* 2001, 2008, Estrella *et al.* 2018, Fougère-Danezan *et al.* 2007, 2010, LPWG, 2017). *Eperua* shares with *Eurypetalum* (sister genus) flowers with one big adaxial petal and other four very small petals and ten basally connate stamens (Fougère-Danezan *et al.* 2010, Obiang-Mbomio & Breteler 2007).

Eperua is known for its endemicity to the Amazon region in Central and Eastern Amazonia and the Guiana Shield (Cowan 1975, 1985, Romero-González & Aymard 2019). Most of the species occur in the Guiana Shield and, in the Amazon basin, the species occur mainly above the Amazon and Negro rivers (Cowan 1975, 1985, Romero-González & Aymard 2019). *Eperua* species inhabit floodplains (“várzea” and “igapó”) and upland (“terra firme”) forests, and some species are restricted to white sand forests (Cowan 1975, 1985, Romero-González & Aymard 2019).

The species within *Eperua* have contrasting morphology concerning the inflorescence arrangement and floral architecture. The inflorescence is always a raceme or a panicle, but it can be short (around 10 cm long) and erect (Fig. 1—A–E, I) or long (more or less between 100-300 cm long) and pendent (Fig. 1—F–G). As for the floral architecture, there are two groups: non-tubular corolla and exserted stamens (Fig. 1—H–J) and tubular corolla and inserted stamens (Fig. 1—B–E). The tubular corolla is formed only by the adaxial petal whose rolled inwardly margins overlap forming a tube. In contrast, in the non-tubular corolla, the margins do not overlap completely and no tube is formed. Species with tubular corollas always have inserted stamens and those with non-tubular corollas always have exserted stamens. Species with short and erect inflorescences have both floral architectures while those with long and pendulous inflorescences have only non-tubular corollas and exserted stamens (Cowan 1975).

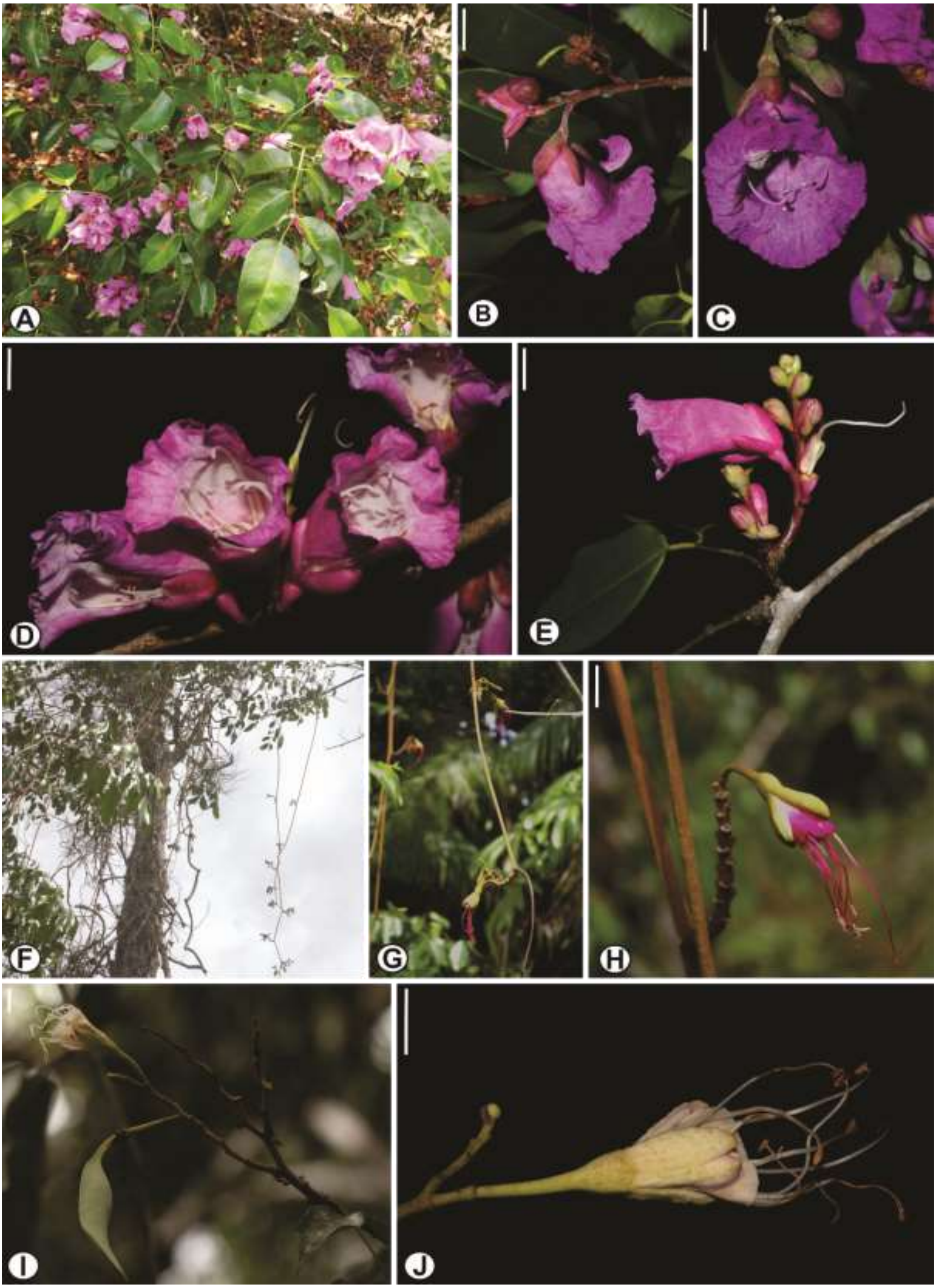


FIGURE 1. Different inflorescence arrangements and flower architectures in the genus *Eperua*. A–E. Short and erect inflorescence, flower with tubular corolla and inserted stamens; F–H. Long and pendulous inflorescence, flower with non-tubular corolla and exserted stamens; I–J. Short and erect inflorescence, flower with non-tubular corolla and exserted stamens. Bar 1 cm; A–C. *E. oleifera*; D–E. *E. glabriflora*; F–H. *E. rubiginosa* Miquel (1851: 12) var. *rubiginosa*; I–J. *E. duckeana*. Photos A–C: F. Farroñay; D: D.B. Cardoso; E–H: E.A. Fortes; I–J: T.C. Monteiro.

According to the last and most complete taxonomic revision of the genus (Cowan 1975), the inflorescence arrangement and floral architecture drive the entire taxonomy of the genus but the species are delimited generally based on inflorescence and flower indumentum and bracteole phenology and position on the pedicels (see Table 1 and 2). The genus comprises 16 species, four subspecies, and four varieties (Cowan 1975, Cowan 1985, Romero- González & Aymard 2019). The two last published species—*Eperua praesagata* and *E. banaensis* – were described by Cowan (1985: 293) and Romero-González & Aymard (2019: 341), respectively. After analyzing Cowan's taxonomy framework, two additional new species came along based on specimens that do not fit the description of any other currently accepted species (see Tables 1 and 2). Thus, in this study, we present morphological descriptions, ecological information, field photographs, and illustrations for the two new species named here *Eperua manausensis* E.A. Fortes & Mansano *sp. nov* and *Eperua cerradoensis* E.A. Fortes, G.S. da Silva & Mansano *sp. nov*.

TABLE 1. Morphological differences between *E. cerradoensis* and its most morphologically similar species *E. duckeana* R.S. Cowan, and *E. schomburgkiana* Benth.

Characters	***E. cerradoensis***	***E. duckeana***	***E. schomburgkiana***
Stipules conation	Joined	Free	Free
Pellucid-punctate blades	Epunctate to inconspicuous pellucid-punctate	Pellucid punctate	Pellucid punctate
Leaflet margin	Revolute	Entire	Entire
Main vein on the adaxial surface	Depressed	Prominent	Prominent
Bracteole size	Larger: 9.8–12.7 × 6.5–9.8 mm	Smaller: 1.9–5.0 × 2.3–4.2 mm	Smaller: 4.9–6.3 × 3.7–5.0 mm
Bracteole phenology	Persistent	Caducous	Caducous
Stamens conation	Joined basally in a tube	Diadelphous sheath 9+1	Diadelphous sheath 9+1
Sheath/tube indumentum	Glabrous	Tomentose	Tomentose
Ovary indumentum	Tomentose	Tomentose	Glabrous
Fruit indumentum	Tomentose	Tomentulose	Glabrous
Fruit margin	Dorsal margin alate	Entire	Entire

Besides their peculiar morphology, these new species have unexpected type localities and distribution. The type locality of *E. cerradoensis* is a backyard in an area of Cerrado in the Eastern region of the state of Maranhão (Brazil), where the species was first registered flowering and fruiting in 2020. It is a common tree in the region, which is characterized by Cerrado physiognomies such as "cerradão" (tall savannah forest), "campo sujo" (grassy vegetation with interspersed small shrubs), typical Cerrado (savannah), "veredas" or "buritizais" (palm swamps), and riparian forest (Spinelli-Araujo *et al.* 2016). This is a remarkable discovery for *Eperua* because it expands the distribution of the genus, formerly thought to be endemic to the Amazon Biome.

In turn, *E. manausensis* occurs in sympatry with *Eperua duckeana* R.S. Cowan (1975: 30) and *E. glabriflora* (Ducke 1940: 27) R.S. Cowan (1975: 30) in "terra firme" forest (uplands) in the Amazon Biome. This species is known from a single specimen (first time collected in 2017) in the Museu da Amazônia (Musa), a botanical garden located in Manaus (Brazil, Amazonas) and associated with the Adolpho Ducke Forest Reserve. Thus, our discoveries provide evidence that undescribed species may be found even in more disturbed areas and that comprehensive knowledge of the flora requires new collections and more taxonomists.

Material & methods

To describe the new species, specimens from the IAN, INPA, RB, UB (image) herbaria (acronyms follow Thiers, 2023) and collected in the field were examined. To compare the new species with other species of the genus, we analyzed representative collections of all *Eperua* species in the RB, INPA, and US herbaria and the last taxonomic revision of *Eperua* (Cowan 1975). Information on distribution, habitat, phenology, and vernacular names was extracted from the exsiccate labels. Distribution maps were prepared using the geographic coordinates provided by the collectors. The coordinate reference system is longitude/latitude and the WGS84 datum. Plant organ and character state terminology follow Beentje (2010); by petalodia we mean the four reduced petals (Cowan 1975).

TABLE 2. Morphological differences between the new species *E. manausensis* and *E. banaensis* G.A. Romero & Aymard, *E. bijuga* Bentham (1870: 226), *E. grandiflora* subsp. *grandiflora*, *E. grandiflora* subsp. *guyanensis, E. jenmanii* Oliver (1891: 20), *E. obtusata* R.S. Cowan (1975: 33), *E. oleifera* Ducke (1932: 728), and *E. purpurea* Bentham (1870: 226), which *E. manausensis* shares short and erect inflorescences, tubular corollas, and inserted stamens. The indumentum is considered scarce when it is puberulous (*E. bijuga*, *E. jenmanii*) or strigulose (*E. banaensis, E. obtusata*), and dense when it is tomentose (*E. manausensis*, *E. grandiflora* subsp. *grandiflora*, *E. oleifera*), pubescent (*E. grandiflora* subsp. *guyanensis, E. grandiflora* subsp. *grandiflora*), or strigose (*E. oleifera*).

Species	Inflorescence indumentum	Bracteole insertion on the pedicels	Bracteole phenology	Stamen indumentum	Ovary indumentum
E. manausensis	Dense indumentum	Lower middle portion	Caducous	Tomentose	Tomentose to villous
E. grandiflora subsp. *guyanensis*	Dense indumentum	At the base of the hypanthium	Persistent	Pubescent to puberulous	Sericeous
E. grandiflora subsp. *grandiflora*	Dense indumentum	Higher portion	Persistent	Irregularly tomentose	Glabrous
E. oleifera	Dense indumentum	Higher portion or at the base of the hypanthium	Persistent	Villous	Glabrous
E. jenmanii	Scarce indumentum or glabrous	Lower middle portion	Persistent	Villous, pubescent to puberulous	Glabrous
E. banaensis	Scarce indumentum	Lower middle portion	Caducous	Glabrous	Sericeous
E. obtusata	Scarce indumentum	Lower portion	Caducous	Glabrous	Sericeous
E. glabriflora	Glabrous	Lower middle portion	Caducous	Tomentose, pubescent to puberulous	Glabrous
E. bijuga	Glabrous	Lower middle portion	persistent	Puberulous	Glabrous
E. purpurea	Glabrous	Middle portion	persistent	Villous	Glabrous

Results and discussion

Eperua cerradoensis E.A. Fortes, G.S. da Silva & Mansano *sp. nov* (Figs. 2–5)

Type:—BRAZIL. Maranhão, Caxias, Povoado Morro Agudo, Segundo Distrito, rio Itapecuru, área rural, 4°32’18”S 43°03’46”W, 24 March 2022, *Gonçalves A.S. 02* (holotype RB[01458708]!, isotypes INPA!, UEC!, US!)

Diagnosis:—*Eperua cerradoensis* has short and erect inflorescences, non-tubular corollas, and exserted stamens. It differs from species with the same type of inflorescence, corolla and stamen by the combination (see Table 1): joined stipules, inconspicuous pellucidpunctate to epunctate leaflets, revolute margins, main vein depressed on the adaxial surface, larger and persistent bracteoles, short and erect inflorescences, stamens joined basally in a tube, glabrous sheath, tomentose ovary, tomentose fruits with alate dorsal margins.

Tree or treelet (1.6–)3.5–11.5 m tall. **Trunk** 10.0–15.7 cm in diameter, bark grayish to brownish, smooth to striate, lenticellate. **Stipules** 15.1–40.9 × 11.8–22.7 mm, joined, foliaceous, semiorbicular, persistent. **Leaves** (4–)5–7jugate, glabrous; **petioles** 2.0–3.8 cm long; **rachis** 15.0–24.0 cm long; **petiolules** 5.3–8.4 mm long; **blades** 7.5–14.1 × 3.5–5.2 cm, coriaceous, glabrous, inconspicuous pellucid-punctate to epunctate, not discolorous, equilateral, lower pair ovate, middle pair ovate to elliptic, upper pair elliptic, apex attenuate to acuminate, mucronate, base asymmetrical, lower pair base rounded, middle pair base rounded to obtuse, upper pair base rounded to obtuse, margin revolute, secondary venation with two intramarginal veins, vein closer to the margin not continuous, main vein straight, depressed on the adaxial surface, tertiary veins slightly conspicuous. **Inflorescences** terminal, raceme, erect, tomentose, whitish, 10.0–20.0 cm long; **bracts** 8.4 × 4.8 mm, ovate, cucullate, apex gland absent, tomentose, whitish, caducous; **bracteoles** 9.8–12.7 × 6.5–

9.8 mm, ovate, cucullate, apex gland absent, tomentose externally and within, whitish, persistent, attached to the lower portion of the pedicels; **pedicel** 18.0–24.4 mm long, 3.0–4.8 mm in diameter, not twisted, tomentose, whitish; **buds** 1.3–1.5 cm long, 1.0 cm in diameter, tomentose, whitish. **Flowers**: **hypanthium** 5.5–7.8 mm long, 7.7–10.6 mm in diameter, cup-shaped, equilateral, tomentose, whitish; **sepal** 2.3–2.9 × 1.3–1.7 cm, elliptic, unequal, the outer ones larger, cucullate, apex gland absent, greenish-white, tomentose, inner sepals scarious marginally, whitish; **adaxial petal** 2.3–3.3 × 5.5–6.5 cm, oblate, non-tubular, apex rounded, base truncate, white, glabrous; **petalodia** 2.7–8.8 × 1.1–3.0 mm; **stamens** exserted, joined basally in a tube, longer filaments 6.0 cm long, shorter filaments 5.1 cm long, tube equilateral, 2.8–3.4 mm long, glabrous, anthers 10.8–12.4 × 2.6–2.9 mm, rectangular; **ovary** 9.6–13.0 × 3.3–3.7 mm, oblanceolate, tomentose, greenish, stipe 5.8–10.5 mm long, tomentose, style 2.7–4.9 cm long, glabrous, stigma capitate. **Legumes** 22.0 × 7.0 cm, stipe 2.6 cm long, elliptic-falcate, apex obtuse, apiculate, dorsal margin alate, yellowish-green, veins absent, tomentose, yellowish. **Seeds** 4 per fruit, 3.2 × 2.0 cm (immature), obovate, whitishbrown.

Phenology:—Flowers in March and September; fruits in September. Flowering probably starts in the rainy season (February-March) and end at the beginning of the dry season (September). The fruits collected in September were not completely mature and, thus, mature fruits are expected by the end of the dry season (October-November).

Distribution:—It has a disjoint distribution in the Eastern region of the state of Maranhão (Brazil) in the Itapecuru and Munin Basins, which are separated from the Amazon Basin by many other basins.

Habitat:—It is the only species that does not occur in the Amazon Biome. *Eperua cerradoensis* was collected in the Cerrado Biome, in the phytofisiognomies of **"**cerradão", secondary forest, ombrophilous lowland forest with a predominance of palm trees, and in open ombrophilous forest, on stony clayey soil, from 57 to 91 m elev. *Eperua cerradoensis* is a common tree on its area of occurrence.

Occurrence in protected areas:—Unknown.

Etymology:—The specific epithet alludes to its occurrence in the Cerrado Biome.

Vernacular names:—Embira de sapo (*Almeida A.B. 134*), imbira de sapo (*Almeida A.B. 152*), pitu (*Oliveira D. 66*), pracateira (*Marinho M.A.O. 606*, *629*, *Santos R.S. 296*).

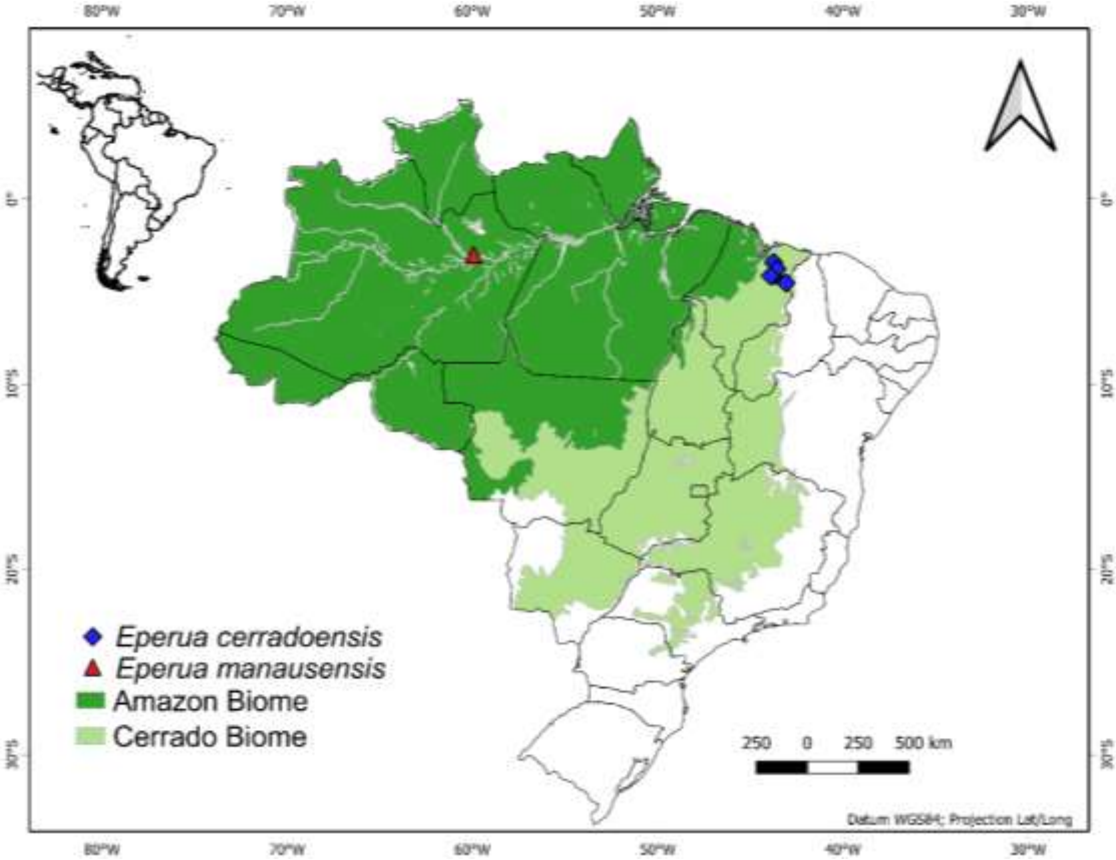


FIGURE 2. Geographic distribution of *Eperua cerradoensis* and *Eperua manausensis.* Biome shape from IBGE (2019).

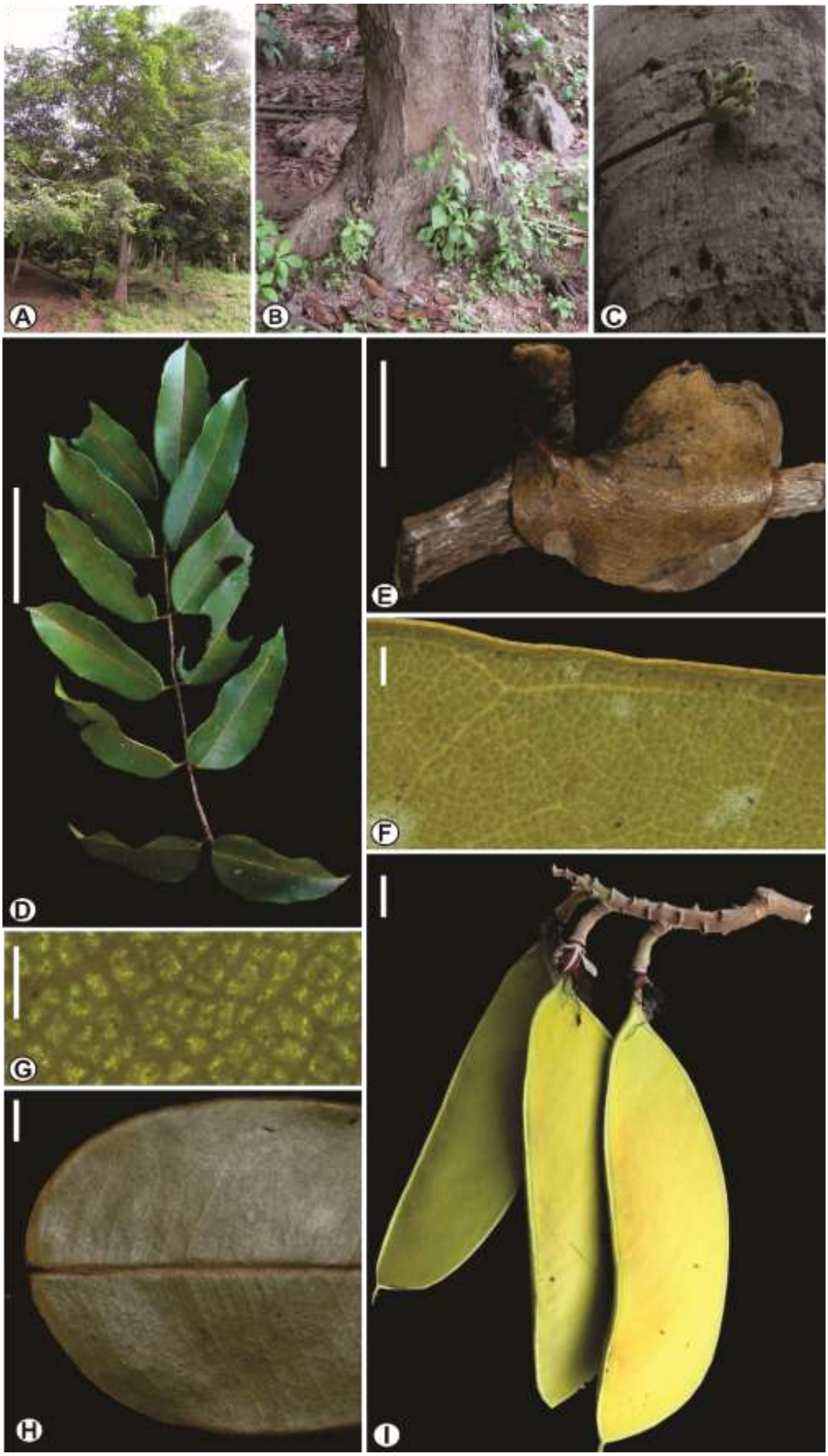


FIGURE 3. *Eperua cerradoensis*: A. habit; B. trunk base; C. bark as a background for a photo of the inflorescence in bud; D. leaf, bar 3 cm; E. stipules, bar 1 cm; F. intramarginal vein, bar 1 mm; G. epunctate leaflet, bar 1 mm; H. adaxial surface of leaflet, bar 1 cm; I. fruits, bar 3 cm. Photos, A–D, I: A.S. Gonçalves; E–H: E.A. Fortes.

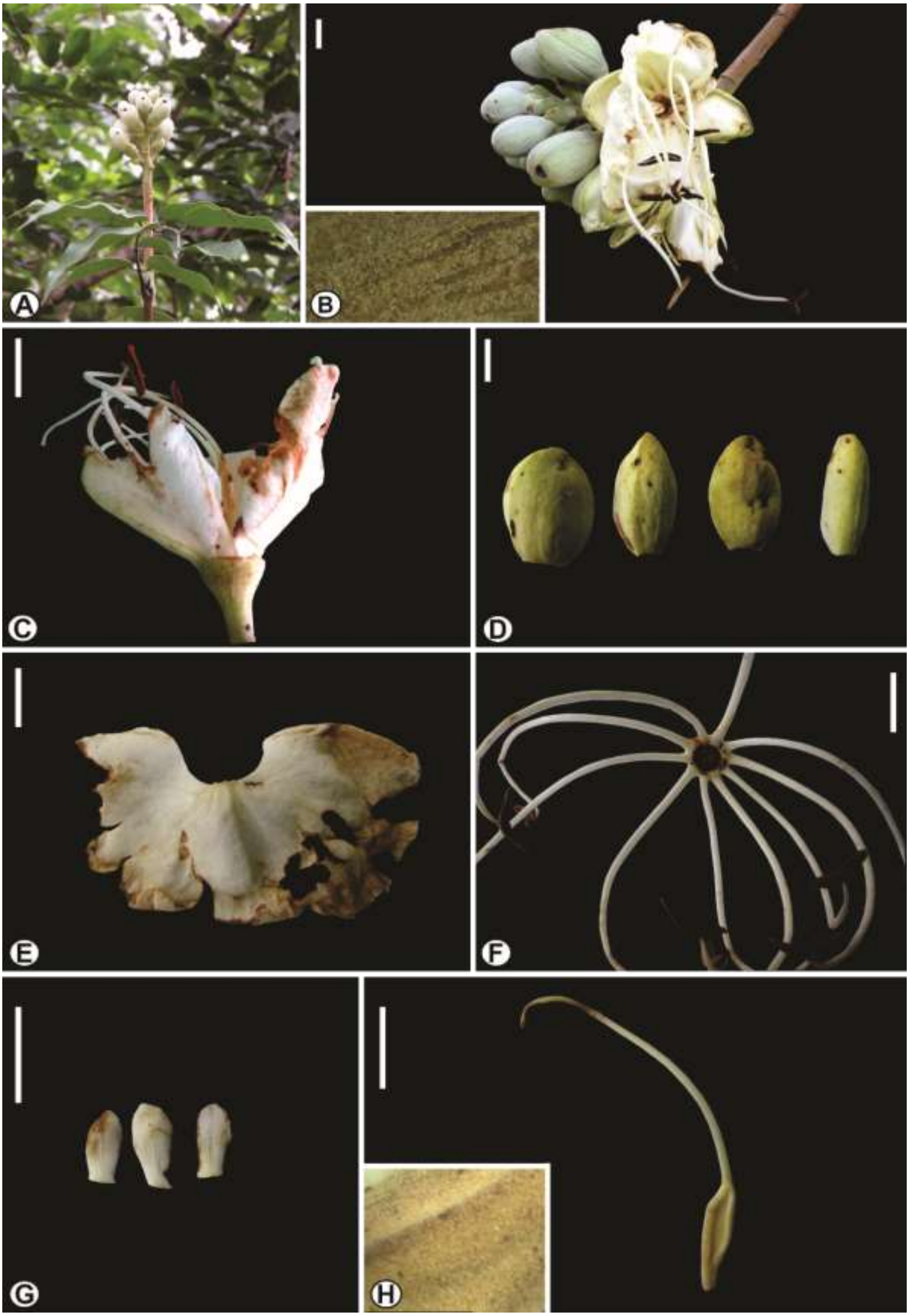


FIGURE 4. *Eperua cerradoensis*: A–B. inflorescence and detail of indumentum, bar 1cm; C. flower, bar 1 cm; D. sepals, bar 1 cm; E. adaxial petal, bar 1 cm; F. stamens, bar 1 cm; G. three of the four petalodia, bar 1 cm; H. carpel and detail of ovary indumentum, bar 1 cm. Photos, A.S. Gonçalves.

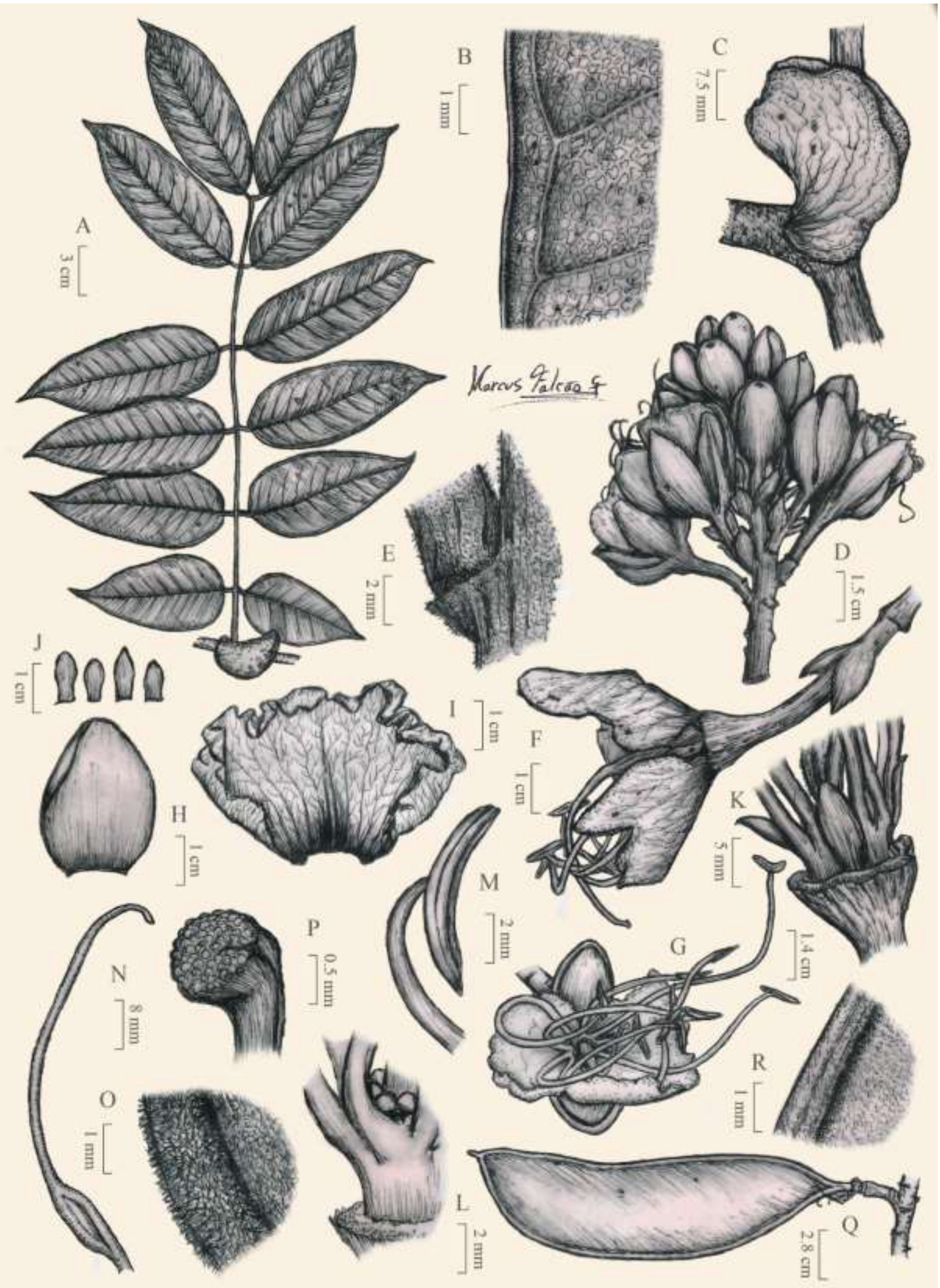


FIGURE 5. *Eperua cerradoensis*: A. leaf; B. detail of leaflet margin, abaxial side, showing the intramarginal vein; C. stipules; D. inflorescence; E. detail of the indumentum of the main axis of the inflorescence and the pedicel; F. flower, lateral view with pair of bracteoles and scar of the caducous bract; G. flower, polar vision; H. sepal; I. petal; J. four petalodia; K. detail of the stamen tube and petalodia (sepals and petals removed); L. detail of the glabrous stamen tube and intrastaminal nectaries; M. anther, side view; N. carpel; O. detail of the ovary indumentum; P. stigma; Q. fruit; R. detail of the fruit indumentum. Specimen: *Gonçalves A.S. 01* and *02*. Illustrated by Marcus Falcão.

Uses:—In the type locality, Povoado Morro Agudo, it is mainly used to make charcoal and fences, and eventually in house construction but this is not a common usage because the local population reported that the plant is very favorable to wood-dwelling termites.

Taxonomic notes:—Besides the collections in the type locality, other sterile collections were found at UB. They match the diagnostic characteristics of *E. cerradoensis* by the foliaceous and joined stipules, (4–)5-jugate leaves, and equilateral leaflets ranging from ovate (lower and middle pairs) to elliptic (middle and upper pairs) in shape with attenuate to acuminate apex and main vein depressed on the adaxial surface.

Eperua cerradoensis, *E. duckeana* and *E. schomburgkiana* Bentham (1870: 226) are a differentiated group in the genus, presenting short and erect inflorescences, non-tubular corollas, and exserted stamens. Besides that, *E. cerradoensis* shares white petals with the two species above and a tomentose ovary with *E. duckena*. *Eperua cerradoensis* differs from the two species by many vegetative and floral characteristics summarized in Table 1.

Specimens examined (Paratypes):—BRAZIL. Maranhão, Caxias, Povoado Morro Agudo, Segundo Distrito, área rural, 4°32’18.2”S 43°03’45.5”W, 18 September 2020, *Gonçalves A.S. 01* (IAN [201061]!, HABIT [collection number 4283]!). Chapadinha, Cajazeiras, conglomerado MA-255, subunidade 1, subparcela 5, indivíduo 16, F6, 60 m elev., 3°46’48”S 43°33’36”W, 30 May 2018, *Marinho M.A.O. 606* (UB [0120836] image!); Cajazeiras, conglomerado MA-255, subunidade 3, subparcela 10, indivíduo 11, F8, 60 m elev., 3°46’48”S 43°33’36”W, 30 May 2018, *Marinho M.A.O. 629* (UB[0120833] image!). Nina Rodrigues, Mangueira, conglomerado MA-202, subunidade 1, subparcela 1, indivíduo 4, F6, 57 m elev., 3°25’12”S 43°44’24.1”W, 05 September 2018, *Almeida A.B. 134* (UB[0120838] image!); Mangueira, conglomerado MA-202, subunidade 3, subparcela 10, indivíduo 13, F8, 57 m elev., 3°25’12”S 43°44’24”W, 05 September 2018, *Almeida A.B. 152* (UB[0120837] image!). Timbiras, comunidade Morada Nova, conglomerado MA-305, subunidade 2, subparcela 1, indivíduo 10, F6, 94 m elev., 4°8’24”S 43°44’24”W, 02 May 2018, *Oliveira D.* 66 (UB[0120834] image!); Bacabalzinho, conglomerado MA-304, subunidade 3, subparcela 1, indivíduo 10, F8, 91 m elev., 4°08’24”S 43°55’12”W, 28 March 2017, *Santos R.S. 296* (UB[0120835] image!).

Eperua manausensis E.A. Fortes & Mansano *sp. nov.* (Figs. 2, 6, 7)

Type:—BRAZIL. Amazonas, Manaus, Reserva Florestal Adolpho Ducke, trilha do Jardim Botânico MUSA, planta marcada JBN 634, 08 June 2017, *Cabral F.N. et al. 1561* (holotype INPA[0284318]!, isotype RB[01459755]!).

Diagnosis:—*Eperua manausensis* has short and erect inflorescences, tubular corollas, and inserted stamens. It differs from species with the same type of inflorescence, corolla, and stamen by the combination: 2–3-jugate leaves, cordate to subcordate leaflet base, two intramarginal veins, vein closer to the margin continuous, tomentose inflorescences, caducous bracteoles attached to the lower middle portion of the pedicels, tomentose stamen sheath, densely tomentose to villous ovary, and puberulous fruit.

Tree 20.0 m tall. **Trunk** 38.0 cm in diameter, bark brownish, lenticellate. **Stipules** 1.8–1.9 × 0.8–1.4 mm, free, nonfoliaceous, ovate to lanceolate, caducous. **Leaves** 2–3jugate, glabrous; **petioles** 0.6–2.9 cm long; **rachis** 3.5–14.6 cm long; **petiolules** 6.2–9.1 mm long; **blades** 5.3–12.8 × 3.5–6.5 cm, coriaceous, glabrous, inconspicuous pellucid-punctate to pellucid-punctate, discolorous, equilateral, lower pair ovate, middle pair elliptic, upper pair elliptic, apex attenuate to acuminate, base symmetrical, lower pair base subcordate to cordate, middle pair base subcordate to rounded, upper pair base subcordate, rounded to obtuse, margin revolute to flat at the apex, secondary venation with two intramarginal veins, vein closer to the margin continuous, main vein straight, prominent only near the base on the adaxial surface, tertiary veins conspicuous. **Inflorescences** axillary, panicle, erect, tomentose, brownish-yellow, 4.6–8.9 cm long, lateral racemes 2.1–3.4 cm long, alternate and distichous; **bracts** not seen, caducous; **bracteoles** 4.9–5.0 × 3.0–3.2 mm, ovate, apex gland present, tomentose externally, pubescent to tomentose within, brownish-yellow, caducous, attached to the lower middle portion of the pedicel; **pedicel** 17.5–18.9 mm long, 1.0 mm in diameter, not twisted, tomentose, brownish-yellow; **buds** 0.7 cm long, 0.4 cm in diameter, tomentose, brownish-yellow. **Flowers**: **hypanthium** 3.8 mm long, 2.8 mm in diameter, cup-shaped, equilateral, tomentose, brownish-yellow; **sepal** 1.6 × 0.5 cm, oblong to elliptic, unequal, the dorsal one larger, cucullate, apex gland absent, pink, tomentose, scarious marginally, brownish-yellow; **adaxial petal** 3.8 × 4.7 cm, flabellate, tubular, apex rounded, base attenuate, pink to purple, glabrous; **petalodia** not seen; **stamens** inserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 3.1 cm long, shorter filaments 2.0 cm long, sheath inequilateral, shorter side 6.5 mm long, longer side 8.0 mm long, sheath tomentose, brownish-yellow, free filaments glabrous, anther 2.2 × 0.8 mm, rectangular; **ovary** 7.1 × 3.7 mm, obovate, densely tomentose to villous, brownish-yellow, stipe tomentose, style 4.0? cm long, glabrous,

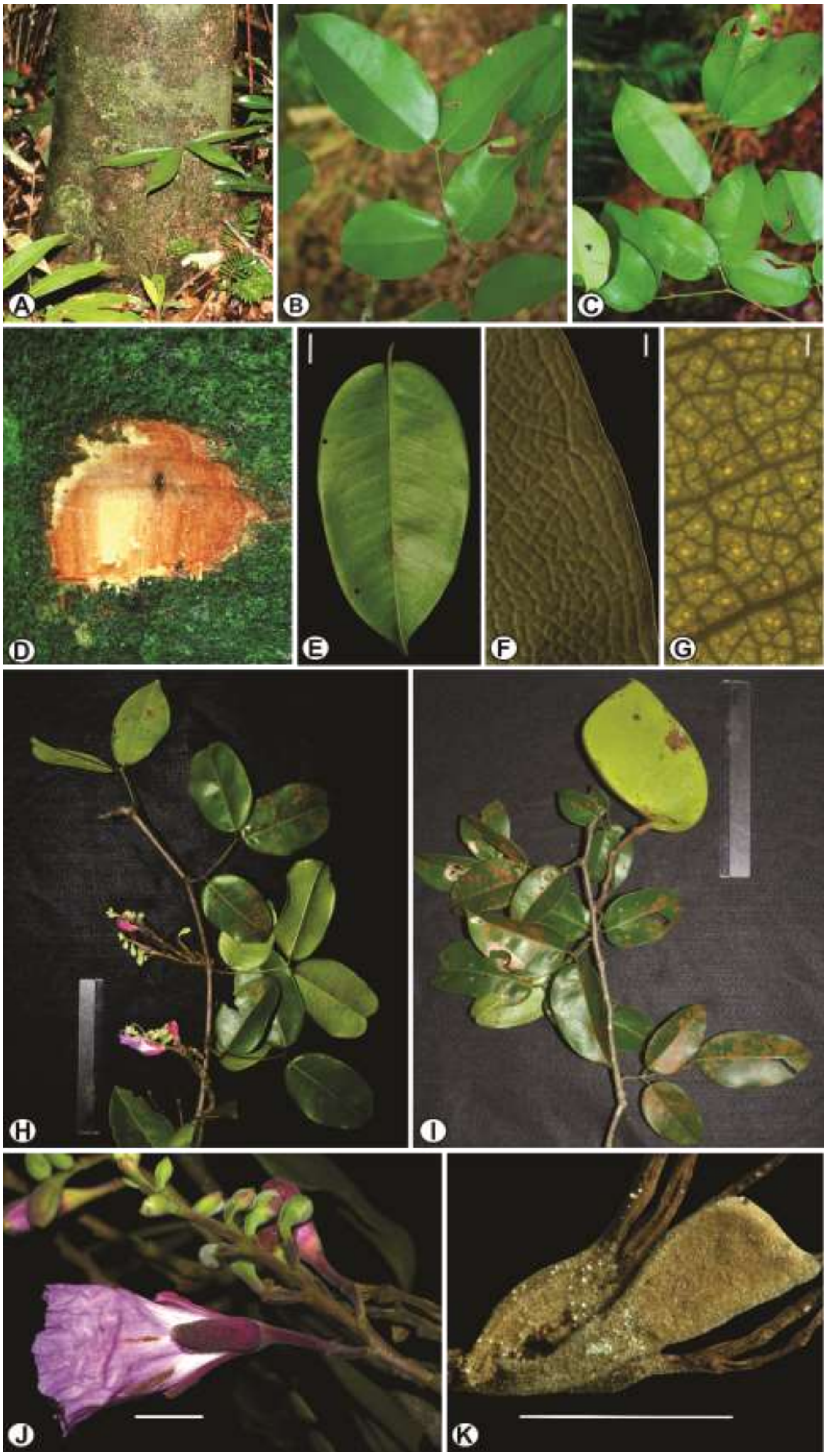


FIGURE 6. *Eperua manausensis*: A. trunk base; B–C. leaves; D. bark; E. leaflet abaxial surface, bar 1 cm; F. intramarginal vein, abaxial side, bar 1 mm; G. pellucid-punctate leaflet, bar 1 mm; H. flowering branch, ruler 15 cm; I. branch bearing a fruit, ruler 15 cm; J. inflorescence with a flower highlighted, bar 1 cm; K. ovary and stamens highlighting the indumentum, bar 1 cm. Photos, A–G, K: E.A. Fortes; H–J: F.N. Cabral.

FIGURE 7. *Eperua manausensis*: A. two-leaved branch showing the leaflet number variation; B. piece of branch showing the pair of stipules; C. detail of the leaflet base, abaxial side; D. detail of the abaxial margin of the leaflet showing the two intramarginal veins; E. inflorescence; F. flower; G. flower bud and bracteoles; H. detail of the indumentum of the inflorescence axis; I. sepal; J. stamen; K. detail of the indumentum at the base of the filament; L. carpel and stamen sheath; M. detail of carpel indumentum; N. fruit; O. detail of the fruit indumentum. A, C–D, O: specimen *Fortes E.A. & Viana G.P. 194b*; E–N: specimen *Cabral F.N. et al. 1561*. Illustrated by Marcus Falcão.

stigma capitate. **Legumes** 11.3–15.9 × 7.7–8.3 cm, stipe 0.9–1.4 mm long, obovate to irregularly elliptic, apex obtuse, apiculate, dorsal margin slightly thickened, brownish-red, with inconspicuous transversal veins, puberulous to puberulent, brownish. **Seeds** 1–2 per fruit.

Phenology:—Flowers in June; fruits in January and June.

Distribution:—It is known from only one specimen collected twice (2017 and 2022) in Musa. This botanical garden has trails, museums, and exhibitions for educational and recreational purposes, but scientific research is also conducted in the area because the garden encompasses native "terra firme" forest vegetation (100 hectares) of the Adolpho Ducke Forest Reserve.

Habitat:—It was collected in "terra firme" forest at 114 m elev. The "terra firme" forest is located at the highest elevations of the Adolpho Ducke Forest Reserve, in well-drained clayey, nutrient-poor soils (Ribeiro *et al.* 1999). *Eperua manausensis* is sympatric with *E. duckeana* and *E. glabriflora*, which are very common in the type locality.

Occurrence in protected areas:—It occurs in the Adolpho Ducke Forest Reserve (Brazil, Amazonas).

Etymology:—The specific epithet alludes its discovery in Manaus (Brazil, Amazonas).

Vernacular names:—Unknown.

Uses:—Unknown.

Taxonomic notes:—*Eperua manausensis* is most similar to *E. grandiflora* (Aublet 1775: 757) Baillon (1870: 110) subsp. *guyanensis* R.S. Cowan (1975: 34), with which it shares the non-glabrous inflorescence, stamen sheath, and ovary; indeed, no other species with short and erect inflorescences share this combination (see Table 2). *Eperua manausensis* differs from *E. grandiflora* subsp. *guyanensis* mainly by the tomentose inflorescence (vs. pubescent, puberulous to glabrescent in *E. grandiflora* subsp. *guyanensis*), larger (4.9–5.0 × 3.0–3.2 mm) and caducous bracteoles attached to the lower middle portion of the pedicel (vs. smaller (1.9–3.0 × 1.5–3.4 mm) and persistent, attached at the base of the hypanthium in *E. grandiflora* subsp. *guyanensis*), tomentose pedicel, hypanthium, and sheath (vs. pubescent, puberulous to glabrescent in *E. grandiflora* subsp. *guyanensis*), and densely tomentose to villous ovary (vs. sericeous in *E. grandiflora* subsp. *guyanensis*).

Specimens examined (Paratypes):—BRAZIL. **Amazonas**, Manaus, Reserva Florestal Adolpho Ducke, MUSA, planta marcada JBN 634 ao lado direito da Casa-Oficina, à 20 m da trilha Branca, 114 m elev., 3°0'22.9"S 59°56'22.7"W, 27 January 2022, *Fortes E.A. & Viana G.P. 194b* (HUEFS!, IAN!, INPA!, MG!, NY!, RB [01458706]!, UEC!, US!).

Acknowledgements

This paper is part of the first author's Ph.D. thesis supported by a scholarship from Conselho Nacional de Desenvolvimento Científico e Tecnológico - (CNPq) [process number 140508/2020-1] and by Funbio – Conservando o Futuro 2020 grant. VFM is grateful to CNPq [process number 303053/2018-6] and the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) [process number E-26-/203.007/2017]. We are very grateful to Anastácia Gonçalves for the collection, information and photos of *E. cerradoensis*; to Fernanda Cabral for the photos of *E. manausensis*; to Mike Hopkins, Mayara Pastore, Thiago Mouzinho, Túlio Martins, Gleison Viana, and José Ribamar for the help in recollecting *E. manausensis*; to Domingos Cardoso, Francisco Farroñay, and Thiago Monteiro for the photos of other *Eperua* species; and to Marcus Falcão for the illustrations.

References

Aublet, J.B.C.F. (1775) *Histoire des plantes de la Guiane Françoise*. Tome I and Tome II. Pierre Françoies Didot jeune, Paris, 976 pp.

Baillon, H.E. (Jan–Feb 1870) Caesalpinées. *In*: Baillon, H.E. (Ed.) *Histoire des plantes*. Tome II. Librairie Hachette & Cie, Paris. pp. 110–111.

Barroso, G.M., Peixoto, A.L., Costa, C.G., Ichaso, C.L.F., Guimarães, E.F. & Lima, H.C. (1991) *Sistemática das angiospermas do Brasil*. Vol 2. Imprensa Universitária, Universidade Federal de Viçosa, Viçosa, pp. 15–100.

Beentje, H. (2010) *The Kew plant glossary an illustrated dictionary of plant terms*. Royal Botanic Gardens, Kew, Richmond, 160 pp.

Bentham, G. (1870) Caesalpinieae. *In:* von Martius, C.F.P. & Eichler, A.G. (Eds.) *Flora Brasiliensis* 15 (2). F. Fleischer, Leipzig, pp.
226–228.

Bruneau, A., Forest, F., Herendeen, P.S., Klitgaard, B.B. & Lewis, G.P. (2001) Phylogenetic relationships in the Caesalpinioideae (Leguminosae) as inferred from chloroplast trnL intron sequences. *Systematic Botany* 26: 487–514.
https://doi.org/10.1043/0363-6445-26.3.487

Bruneau, A., Mercure, M., Lewis, G.P. & Herendeen, P.S. (2008) Phylogenetic patterns and diversification in the caesalpinioid legumes. *Botany* 86: 697–718. https://doi.org/10.1139/B08-058

Cowan, R.S. (1975) Monograph of the genus *Eperua* (Leguminosae: Caesalpinioideae). *Smithsonian Contributions to Botany* 28: 1–45.

Cowan, R.S. (1985) Studies in Tropical American Leguminosae – IX. *Brittonia* 37 (3): 292–294.
https://doi.org/10.2307/2806078

Ducke, W.A. (1932) Espéces nouvelles de plantes de l'Amazonie brésilienne. *Bulletin du Muséum National d'Histoire Naturelle* 4 (6):
728–729.

Ducke, W.A. (1940) Notes on the wallaba trees. *Tropical Woods* 62: 21–28.

Estrella, M. de La, Forest, F., Klitgaard, B., Lewis, G.P., Mackinder, B.A., Queiroz, L.P. de, Wieringa, J.J. & Bruneau, A. (2018) A new phylogeny-based tribal classification of subfamily Detarioideae, an early branching clade of florally diverse tropical arborescent legumes. *Scientific Reports* 8: 6884.
https://doi.org/10.1038/s41598-018-24687-3

Fougère-Danezan, M., Herendeen, P.S., Maumont, S. & Bruneau, A. (2010) Morphological evolution in the variable resin-producing Detarieae (Fabaceae): Do morphological characters retain a phylogenetic signal? *Annals of Botany* 105: 311–325. https://doi.org/10.1093/aob/mcp280

Fougère-Danezan, M., Maumont, S. & Bruneau, A. (2007) Relationships among resin-producing Detarieae *s.l.* (Leguminosae) as inferred by molecular data. *Systematic Botany* 32: 748–761.
https://doi.org/10.1043/06-67.1

Harms, H.A.T. (1905) Zwei neue Gattungen der Leguminosae aus dem tropichen Afrika. *In*: Engler, A. (ed.) *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*. Wilhelm Engelmann, Leipzig, pp. 76–77.

Harms, H.A.T. (1910) Leguminosae africanae. *In*: Engler, A. (ed.) *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*. Wilhelm Engelmann, Leipzig, pp. 293–295.

Instituto Brasileiro de Geografia e Estatística—IBGE (2019) 2019 Biomas e Sistema Costeiro-Marinho do Brasil - 1:250 000. Available from: https://www.ibge.gov.br/geociencias/informacoes-ambientais/estudos-ambientais/15842-biomas.html?edicao=25799&t=downloads/ (accessed: 10 January 2022).

Lewis, G.P., Schrire, B., MacKinder, B. & Lock, M. (2005) *Legumes of the World*. Kew, Royal Botanic Gardens. 577 pp.

LPWG—Legume Working Phylogeny Group (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* 66 (1): 44–77.
https://doi.org/10.5061/dryad.61pd6

Miquel, F.A.G. (1851) Caesalpiniae. *In*: Miquel, F.A.G. (Ed.) *Stirpes Surinamensis Selectae.* Arnz & Comp, Leiden, pp. 12–13. https://doi.org/10.5962/bhl.title.77484

Obiang-Mbomio, D. & Breteler, F.J. (2007) Révision du genre *Eurypetalum* Harms (Fabaceae, Caesalpinioideae). *Adansonia* 29 (1): 67–76.

Oliver, D. (1891) *Hooker's Icones Plantarum*, vol. 20.

Pellegrin, F. (1924) *Augouardia* Pellegrin, genre nouveau de Césalpiniées du Congo. *Bulletin de la Société Botanique de France* 71: 309–311.

Romero-González, G.A. & Aymard, G.A.A. (2019) A new species of *Eperua* (Leguminosae, Detarioideae) from Amazonas state, Venezuela. *Harvard Papers in Botany* 24: 341–347.
https://doi.org/10.3100/hpib.v24iss2.2019.n17

Ribeiro, J.E.L.S., Hopkins, M.J.G., Vicentini, A., Sothers, C.A., Costa, M.A.S., Brito, J.M., Souza, M.A.D., Martins, L.H., Lohmann, L.G.,

Assunção, P.A., Pereira, E.C., Silva, C.F., Mesquita, M.R. & Procópio, L.C. (1999) *Flora da Reserva Ducke. Guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central*. INPA-DFID, Manaus, 816 pp.

Spinelli-Araujo, L., Bayma-Silva, G., Torresan, F.E., Victoria, D., Vicente, L.E., Bolfe, E.L. & Manzatto, C. (2016) *Conservação da Biodiversidade do Estado do Maranhão: Cenário Atual em Dados Geoespaciais*. Embrapa Meio Ambiente, Jaguariúna, 28 pp.

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/ (accessed 10 January 2022)

ARTIGO III

Status: publicado na revista Phytotaxa.

FORTES, E. A., REIS, I. P. dos, TER STEEGE, H., *et al.* A taxonomic revision of the genus Eperua (Leguminosae, Detarioideae, Detarieae). *Phytotaxa*, v. 617, n. 1, p. 1–127, 28 set. 2023. DOI: 10.11646/phytotaxa.617.1.1. Disponível em: https://phytotaxa.mapress.com/pt/article/view/phytotaxa.617.1.1.

Ver direito de reprodução do artigo na tese em Anexo III.

Monograph

https://doi.org/10.11646/phytotaxa.617.1.1

PHYTOTAXA

617

A taxonomic revision of the genus *Eperua* (Leguminosae, Detarioideae, Detarieae)

ELENICE A. FORTES[1]*, ILKA P. DOS REIS[2], HANS TER STEEGE[3,4], GERARDO AYMARD[5,6], RICARDO DE S. SECCO[7], REGINA CÉLIA V. MARTINS-DA-SILVA[8] & VIDAL F. MANSANO[9]
[1]*Programa de Pós-Graduação em Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Rua Monteiro Lobato, 255, Campinas, São Paulo, Brazil, 13083-862. forteselenice@gmail.com; https://orcid.org/0000-0001-8307-6534*
[2]*Programa de Pós Graduação em Ciências Biológicas, área de concentração Botânica Tropical, Universidade Federal Rural da Amazônia e Museu Paraense Emílio Goeldi, Av. Perimetral, 1901, Terra Firme, Belém, Pará, Brasil, CEP 66077-83o. ilkapreis@gmail.com; https://orcid.org/0009-0001-2511-2821*
[3]*Naturalis Biodiversity Center, Leiden, The Netherlands; hans.tersteege@naturalis.nl; https://orcid.org/0000-0002-8738-2659*
[4]*Quantitative Biodiversity Dynamics, Dept. of Biology, Utrecht University, Utrecht, The Netherlands*
[5]*UNELLEZ-Guanare, Programa de Ciencias del Agro y del Mar, Herbario Universitario (PORT), Mesa de Cavacas, estado Portuguesa, Venezuela, 3350; gerardo.aymard@gmail.com; https://orcid.org/ 0000-0001-9405-0508;*
[6]*Compensation International Progress S.A. Ciprogress–Greenlife, Bogotá D.C., Colombia*
[7]*Museu Paraense Emilio Goeldi – MPEG Museu Paraense Emílio Goeldi/Universidade Federal Rural da Amazônia, Programa de Pós-Graduação em Ciências Biológicas – Botânica Tropical, Belém, Pará, Brazil, 66077-830; rsecco@museu-goeldi.br; https://orcid.org/0000-0002-3295-7929*
[8]*Empresa Brasileira de Pesquisa Agropecuária, Embrapa Amazônia Oriental, Laboratório de Botânica, Trav. Enéas Pinheiro, s/n, Marco, CEP 66095-903*
[9]*Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rua Pacheco Leão, 915, Rio de Janeiro, RJ, Brazil, 22460-030 vidalmansano@gmail.com; https://orcid.org/0000-0002-7204-0744*
**Corresponding author*

Magnolia Press
Auckland, New Zealand

ELENICE A. FORTES, ILKA P. DOS REIS, HANS TER STEEGE, GERARDO AYMARD, RICARDO
DE S. SECCO, REGINA CÉLIA V. MARTINS-DA-SILVA & VIDAL F. MANSANO
A taxonomic revision of the genus *Eperua* (Leguminosae, Detarioideae, Detarieae)
(*Phytotaxa* 617)
127 pp.; 30 cm.
28 September 2023
ISBN 978-1-77688-886-3 (paperback)
ISBN 978-1-77688-887-0 (Online edition)

FIRST PUBLISHED IN 2023 BY
Magnolia Press
P.O. Box 41-383
Auckland 1041
New Zealand
e-mail: magnolia@mapress.com
https://www.mapress.com/pt/

© 2023 Magnolia Press
All rights reserved.
No part of this publication may be reproduced, stored, transmitted or disseminated, in any form, or by any means, without prior written permission from the publisher, to whom all requests to reproduce copyright material should be directed in writing.
This authorization does not extend to any other kind of copying, by any means, in any form, and for any purpose other than private research use.

ISSN 1179-3155 (print edition)
ISSN 1179-3163 (online edition)

Abstract

We present a comprehensive taxonomic revision of the tree genus *Eperua*, encompassing several significant findings. We identify and recognize a total of 19 species (including two new species described herein; *E. froesii*, *E. reddeniae*), as well as five subspecies (including one new, *E. grandiflora* subsp. *ciliata*), and six varieties (including one new, *E. glabriflora* var. *gynopubescens*). We also propose the synonymization of *E. praesagata* with *E. glabra* due to the absence of discernible morphological differences, which is supported by molecular data. In addition to these novelties, our revision offers an updated key, illustrations, photos, and maps. Detailed taxonomic comments are provided, discussing morphological similarities and differences between taxa. Furthermore, comprehensive information is provided for each species, including data on phenology, distribution, habitat, conservation status, and vernacular names. *Eperua froesii* is being described from specimens collected more than 50 years ago, while *E. reddeniae* and *E. grandiflora* subsp. *ciliata* from specimens collected recently (2004–2006). This emphasizes the critical role of herbarium collections in biodiversity discovery and underscores the significance of historical specimens. Our taxonomic comments add to Cowan's (1975) revision, in which the author concentrated on listing characteristics considered advanced and less advanced, while here we focus on morphological similarities and differences between taxa. In conclusion, this new taxonomic revision significantly enhances our knowledge of the genus *Eperua* and provides a basis for further research in evolution, ecology, and phytochemistry.

Key words: Eudicots, Eperua, Leguminosae, Detarioideae, Detarieae

Introduction

The Amazonian flora is still relatively poorly known due to the existence of regions little known to science (Hopkins 2007, ter Steege *et al.* 2016, Cardoso *et al.* 2017.). This lack of comprehensive exploration and documentation can contribute to gaps in our knowledge (Hopkins 2007, ter Steege *et al.* 2016, Cardoso *et al.* 2017). Additionally, the limited presence of taxonomists actively working with Amazonian flora further hinders our ability to accurately assess its richness (Crane 2004, Funk 2006). Taxonomic expertise is crucial for identifying general collections and describing new species. The scarcity of taxonomists focusing on the Amazonian flora may lead to a slower pace of species discovery and documentation. It is worth noting that between 1990 and 2006, only a quarter of the newly discovered species were reported from the Amazonia Biome compared to other Brazilian biomes (Sobral & Stehmann 2009). This highlights the need for taxonomists to actively study the Amazonian flora to accurately estimate its species richness (Cardoso *et al.* 2017).

Leguminosae is the richest family in the Amazonian region (BFG 2015, ter Steege *et al.* 2016, Cardoso *et al.* 2017). Indeed, many clades of the subfamily Detarioideae diversified in this biome (Estrella *et al.* 2017, Schley *et al.* 2018), now holding many endemic lineages of this group (ter Steege *et al.* 2016, Cardoso *et al.* 2017, *Fabaceae in* Flora e Funga do Brasil 2022). To understand the evolutionary history of Detarioideae, we need to know its species richness in the Amazonian region as accurately as possible. Although several taxonomic revisions of genera of Amazonian Detarioideae have been conducted in the past, new collections have been made since then, and many of these groups need to be revised. The tree genus *Eperua* is an example. So far, the most comprehensive taxonomic revision for the genus was made by Cowan (1975), with several new taxa being described. Over a thousand new collections have been made since then, including in new areas where the genus had not been previously collected.

Here, we present a new taxonomic revision of the genus *Eperua*. Through an analysis of herbarium specimens, we have identified and described four new taxa for science: *Eperua froesii sp. nov.*, *Eperua reddeniae sp. nov.*, *Eperua grandiflora* subsp. *ciliata* subsp. nov. and *Eperua glabriflora* var. *gynopubescens* var. nov. Of particular significance is the description of *Eperua froesii*, which is based on specimens collected more than 50 years ago. Additionally, *E. reddeniae* and *E. grandiflora* subsp. *ciliata* are described from more recent collections (2004–2006), supporting the crucial role of herbarium collections in discovering and documenting biodiversity (Bebber *et al.* 2010). We also propose synonymizing *E. praesagata* with *E. glabra* due to the lack of discernible morphological differences between them, which is supported by molecular data (ter Steege et al 2023 in press, Fortes *et al.* in prep.). In addition to these novelties, we present an updated key, illustrations, photos, maps, taxonomic comments, information about phenology, distribution, habitat, conservation status, and vernacular names for all species. By focusing on morphological similarities and differences between taxa, our taxonomic comments complement the work of Cowan (1975), who primarily emphasized listing advanced and less advanced characteristics. This new taxonomic revision significantly enhances our knowledge of the genus *Eperua* and provides a basis for further research in evolution, ecology, and phytochemistry.

Systematics and taxonomy

Eperua is a typical genus of the Leguminosae family characterized by a single superior carpel with one locule, and marginal placentation arranged in two alternating rows on a single placenta (Lewis *et al.* 2005). The genus also exhibits common pods without any dispersal modifications, compound and alternate leaves with stipules and pulvinus, racemose inflorescence, and showy, dichlamydeous, pentamerous flowers (Barroso *et al.* 1991). The genus belongs to the subfamily Detarioideae, specifically the tribe Detarieae (LPWG 2017, Estrella *et al.* 2018). Several characteristics shared by *Eperua* species are also typical of the tribe Detarieae. These include the capacity to produce resins composed of sesquiterpenes and diterpenes, leaves with pellucid-punctate leaflets, four free sepals, petal "reduction", and ten stamens (Fougère-Danezan *et al.* 2007, 2010, Estrella *et al.* 2018).

The floral morphology of genera within Detarioideae has a vast diversity and complex patterns. This has challenged the establishment of widely accepted and circumscribed generic groupings (Tucker 2003, Mackinder 2005, Bruneau *et al.* 2014). The use of phylogeny-based tribal classification has helped to overcome some of these challenges, but certain groupings still present difficulties in their morphological recognition (Estrella *et al.* 2018). One such challenging grouping is the Eperua *s.l.* clade, which includes the Neotropical genus *Eperua* and three African genera: *Eurypetalum* Harms, *Augouardia* Pellegr., and *Stemonocoleus* Harms. In the past, these genera were included in phylogenetically unrelated groups (Cowan & Polhill 1981): *Eperua* belonged to the Neotropical Brownea group, *Eurypetalum* belonged to the Hymenostegia group, and *Augouardia* and *Stemonocoleus* were associated with the apetalous Crudia group. The Eperua *s.l.* clade diverges into two lineages. One lineage consists of *Augouardia* and *Stemonocoleus*, while the other lineage comprises *Eperua* and *Eurypetalum* (Bruneau *et al.* 2001, 2008, Fougère-Danezan *et al.* 2007, 2010, LPWG, 2017, Estrella *et al.* 2018, Fortes *et al.* in prep.). *Augouardia* and *Stemonocoleus* have a reduced number of fertile stamens, with three and four stamens, respectively, positioned on the flower`s abaxial side. Additionally, they have an apetalous condition (Fougère-Danezan *et al.* 2010). In contrast, *Eperua* and *Eurypetalum* share a flower with one large, well-developed petal and four vestigial petals, along with ten stamens that are fused at the base (Obiang-Mbomio & Breteler 2007, Fougère-Danezan *et al.* 2010).

Eperua and *Eurypetalum* have been reconstructed as monophyletic genera in the most recent phylogenomic study of the Eperua *s.l.* clade (Fortes *et al.* in prep.). In addition to the phylogenetic evidence, *Eperua* differs from *Eurypetalum* by several morphological characteristics, including longer stamen sheath, larger flowers, more than two ovules per carpel, rarely two, secondary venation with intramarginal vein, mucronate leaflets, untwisted petioles (*vs.* shorter stamen sheath, smaller flowers, two ovules per carpel, secondary venation brochidodromous, non-mucronated leaflets and twisted petioles in *Eurypetalum*) (Fougère-Danezan *et al.* 2010). In addition to these differences, *Eperua* has erect sepals after anthesis, while *Eurypetalum* has reflected sepals.

Eperua can be distinguished from all other Neotropical Leguminosae genera by a single developed petal and four petaloid ones, and ten stamens fused basally in a tube or a diadelphous sheath. Besides these, some other characteristics help recognize it: paripinnate, 1–7-jugate, glabrous leaves, intrapetiolar stipules, no extrafloral nectaries, secondary venation with an intramarginal vein, four free sepals, ovary with a stipe, and elastically dehiscing wood pods with valves twisted after opening, non-arillate seeds.

The taxonomic history of *Eperua* dates back to Aublet's description of *E. falcata* in 1775. In the same work, Aublet (1775) also described *E. grandiflora* in the genus *Parivoa.* Later, Baillon (1870) formally combined the genus *Parivoa* with *Eperua* (Fortes & Mansano 2022). Several species were described in separate floristic treatments before the comprehensive revision by Cowan (1975), including the following works: Bentham (1870), Miquel (1851), Oliver (1891), Pulle (1906), Ducke (1932, 1940), and Cowan (1957, 1958). Details of the nomenclatural history of *Eperua* can be seen in Cowan (1975), with many updates in Fortes & Mansano (2022). In his revision, Cowan (1975) recognized 14 species, four subspecies, and four varieties. Later, Cowan (1985) described *E. praesagata*; Romero-González & Aymard (2019) described *E. banaensis*; and recently Fortes *et al.* (2023) decribed *E. cerradoensis* E.A. Fortes *et al.* and *E. manausensis* E.A. Fortes & Mansano. In the present revision, *Eperua* has 19 species, five subspecies, and six varieties (Table 1). This includes two new species (*E. froesii, E. reddenieae*), one new subspecies (*E. grandiflora* subsp. *ciliata*,), and one new variety (*E. glabriflora* var. *gynopubescens*). Furthermore, *E. praesagata* is synonymized with *E glabra.* All taxonomic results are supported by phylogenetic studies using nuclear and ribosomal data (ter Steege *et al.* 2023 in press, Fortes *et al.* in prep.).

Material and methods

This taxonomic treatment is based on the examination of about 1500 specimens. Collections of the following herbaria were consulted by visits or loans: BH, EAFM, F, IAN, INPA, K, NY, MFS, MG, MO, R, RB, RFA, and US. Images from the selected herbaria were also examined: CAY, COAH, COL, HAMAB, HRCB, HUEFS, K, L, NY, P, SP, U, UB, UDBC, WAG (acronyms follow Thiers *et al.* 2023).

All accepted names are listed following Turland *et al.* (2018), species names are listed alphabetically, and infraspecific names are listed in ascending order of publication date (see Table 1**)**. The list of examined collections is found in the Appendix 2 (collections not seen personally or by image and previously identified as *Eperua* were excluded), and selected materials that show the taxa distribution range is presented with more details in the topic "selected specimens". Information on distribution, habitat, phenology, and vernacular names were extracted from the exsiccate labels. The dots in the distribution maps were obtained from geographic coordinates presented by the collectors, or it was inferred based on the collection locality information using Google Maps (2023). The coordinate reference system is decimal longitude/latitude using the WGS84 datum. Conservation status was assessed using distribution data and the GeoCAT Tool (Bachman *et al.* 2011). For Area of Occupancy (AOO) analysis we used a cell width of 2 km. We categorized the species according to the Extent of Occurrence (EOO) analysis.

The species concept follows Stuessy (2009, pp. 151): "reproductive isolation is fundamental to speciation", and "morphological relationships do reflect genetic and reproductive relationships of a similar degree". All recognized *Eperua* species show unique reproductive characteristics. The species circumscription adopted has phylogenetic support: all species sampled with more than one accession were supported as monophyletic groups (ter Steege *et al.* 2023 in press, Fortes *et al.* in prep.,) The subspecies and variety concepts follows Brummitt (1990) and Wood. *et al.* (2015) synthesized in the World Checklist of Vascular Plants page (https://powo.science.kew.org/about-wcvp): subspecies are largely allopatric or nearly so and differ by characters that are significant for taxonomic species differentiation within the genus; varieties are sympatric and differ by characters that are not significant for taxonomic species differentiation within the genus.

The vegetation types follow Pires & Prance (1985), Adeney *et al.* (2016), Junk *et al.* (2011), and the biogeographical regions of Amazonia are modified after Feldpausch *et al.* (2012). The terms Cerrado Biome and Caatinga Biome follows IBGE (2019). Plant organ and character state terminology follows Beentje (2010). The following specific terms are defined: 1) elliptic: referring to structures with the broader middle part (the apex and base can be obtuse or acute); 2) pellucid-punctate: blades with translucent dots throughout their area (i.e., *E. falcata*, *E. duckeana,* see Figures 3i–n); and inconspicuous pellucid-punctate: blades that have translucent dots, in most cases difficult to see (Figure 3h); 3) secondary venation with one intramarginal vein very close to the margin: the intramarginal vein is so close to the margin that we cannot see tertiary veins between the intramarginal vein and the margin (Figure 3d, e); secondary venation with one intramarginal vein not very close to the margin: there is more space between the intramarginal vein and the margin, and we can see tertiary veins (Figures 3b, c); 4) tertiary veins conspicuous: veins easily seen with the naked eye; tertiary veins very conspicuous: easily seen and prominent on the adaxial surface; and tertiary veins inconspicuous: it is difficult to see the areoles with the naked eye; 5) petalodia: the four reduced petals (Cowan 1975) (Figure 5d, e). The indumentum and fruit colour were described when dried. The filament length measures the filaments` joined and free portion. In this taxonomic revision, the presence and absence of glands in bracts, bracteoles, and sepals were not included in the species delimitations. This decision was made because determining the presence or absence of glands in dried herbarium materials can be challenging.

The macroscopic characteristics of the wood were described following the character list provided by Ruffinatto *et al.* (2015). We analysed samples of the wood collection that have a well-identified exsiccate at the IAN and MG herbaria. The samples were polished in the transverse plane with 120, 180, 320, and 1200 grit sandpaper, respectively. After polishing, they were cleaned with fabric and then analysed and photographed using a stereoscopic lens.

TABLE 1. Index to List of *Eperua* taxa.

List of Eperua taxa
1. *E. banaensis* G.A. Romero & Aymard
2. *E. bijuga* Martius ex Bentham
3. *E. cerradoensis* E.A. Fortes, G.S. da Silva & Mansano
4. *E. duckeana* R.S. Cowan
5. *E. falcata* Aublet
6. *E. froesii* E.A. Fortes, Aymard, H. ter Steege, & Mansano
7. *E. glabra* R.S. Cowan
8. *E. glabriflora* (Ducke) Cowan
8a. *E. glabriflora* (Ducke) Cowan var. *glabriflora*
8b. *E. glabriflora* var. *gynopubescens* E.A. Fortes & Mansano
9. *E. grandiflora* (Aublet) Baillon
9a. *E. grandiflora* (Aublet) Baillon subsp. *grandiflora*
9b. *E. grandiflora* subsp. *guyanensis* R.S. Cowan
9c. *E. grandiflora* subsp. *ciliata* E.A. Fortes & Mansano
10. *E. jenmanii* Oliver
10a. *E. jenmanii* Oliver subsp. *jenmani*i
10b. E. *jenmanii* subsp. *sandwithii* R.S. Cowan
11. *E. leucantha* Bentham
12. *E. manausensis* E.A. Fortes & Mansano
13. *E. obtusata* R.S. Cowan
14. *E. oleifera* Ducke
14a. *E. oleifera* Ducke var. *oleifera*
14b. *E. oleifera* var. *campestris* Ducke
15. *E. purpurea* Bentham
16. *E. red*deniae E.A. Fortes & Mansano
17. *E. rub*iginosa Miquel
17a. *E. r*ubiginosa Miquel var. *rubiginosa*
17b. *E. r*ubiginosa var. *grandiflora* Pulle
18. *E. schomburgkiana* R.S. Cowan
19. *E. v*enosa R.S. Cowan

Results and discussion

Distribution and habitat

The genus *Eperua* is distributed in the Neotropical region, specifically in the Central and Eastern Amazonia and in the Guyana Shield (Figure 7). Only one species, *E. cerradoensis*, occurs outside the Amazonian region, in the Brazilian Cerrado Biome in the Itapecuru, Munin, and Parnaíba Basins (Figures 7, 8). *Eperua falcata, E. grandiflora,* and *E. rubiginosa* are widely distributed in the Guyana Shield, but none occurs in the Orinoco Basin (Figure 9, 11, 12). *Eperua grandiflora* subsp. *guyanensis* (Figure 9), *E. grandiflora* subsp. *ciliata* (Figure 9), *E. jenmanii* subsp. *Jenmanii* (Figure 13), *E. reddeniae*, and *E. schomburgkiana* (Figure 8) are restricted to the Guyana Shield, and do not occur in the Orinoco basin. *Eperua banaensis, E. obtusata* occur between the Orinoco and upper Rio Negro basins (Figure 13); and *E. jenmanii* subsp. *sandwichtii* (Figure 13) and *E. venosa* (Figure 11) are the only ones restricted to the Orinoco Basin in the Guyana Shield. *Eperua glabra* occurs in Guyana Shield (Essequibo basin) and Central Amazonia (Amazon basin) (Figure 12). *Eperua leucantha* (Figure 11) and *E. purpurea* (Figure 14) occur mainly in the Orinoco basin (Atabapo, Inírida, and Guaviare rivers) and Amazon River basin (upper Rio Negro and Guainía rivers). *Eperua leucantha* and *E. purpurea* also reach the westernmost occurrence of the genus in the northern part of western

Amazonia in Colombia (Figure 7, 11, 14). In Central Amazonia, *Eperua glabriflora* (Figure 10), *E. duckeana* (Figure 8), and *E. manausensis* (Figure 9) are found in the Amazon River basin, and the two first species reach the south Guyana Shield. *Eperua oleifera* is the species with the southernmost occurrence; it occurs in Central Amazonia and part of Southern Amazonia in the Madeira River basin (Figures 14). Only *Eperua bijuga* (Figure 10) and *E. froesii* (Figure 8) occur in Eastern Amazonia in the Amazon basin. *Eperua bijuga* can reach the easternmost part of the Guyana Shield.

Eperua species occur in upland forests (*terra-firme*) and floodplain forests (*igapó*, *várzea*). Some species are restricted to the white sand and shrubby communities known as *bana* (*E. banaensis* and *E. obtusata*), *campinarana* (*E. leucantha*, *E. obtusata*, and *E. purpurea*), *campina* (*E. oleifera* var. *campestris*), and *wallaba* forest (*E. grandiflora* subsp. *guyanensis*). The elevation range for *Eperua* species is from sea level up to 1220 m elev., with most specimens found below 200 m. Occurrences above 800 m are rare.

The genus *Eperua* is an essential component of biomass in the lowland forests of the Amazonian region (Cowan 1975; ter Steege *et al.*, 2013, 2020). *Eperua falcata* and *E. leucantha* are considered hyperdominant and rank among the 20 most abundant species in Amazonia (ter Steege *et al.*, 2013). Cowan (1975) suggested that the dominance of one or more *Eperua* species in certain areas could be attributed to the storage of toxic substances in the seeds that serve as a defense mechanism against predation.

Comparative morphology

Eperua species are predominantly medium to large canopy trees reaching 50.0 m tall (Figure 1a, b, d). *Eperua oleifera* var. *campestris* (Figure 1c) and *E. banaensis* are reported mainly as treelets, and the first species often exhibit a spreading branched trunk.

The trunk is terete to buttressed at the base in older and larger trees. The bark is initially smooth but becomes striate, fissured, or scaled in older individuals. However, all species possess lenticels on the bark, which vary from small to very prominent (Figures 2a–c). The inner bark is reddish, while the sapwood is distinct and lighter than the heartwood, often light brown (*E. bijuga*, *E. falcata*, *E. glabriflora*, *E. purpurea*, and *E. rubiginosa* var. *rubiginosa*) (Figure 2b). The heartwood varies in color, ranging from light brown (*E. bijuga*, *E. duckeana*, *E. grandiflora*, *E. leucantha*, *E. praesagata*, *E. purpurea*, and *E. rubiginosa*), brown (*E. jenmanii*), dark brown (*E. falcata* and *E. jenmanii*), purplish brown (*E. falcata*) to reddish brown (*E. falcata*).

Macroscopically, the wood of *Eperua* is characterized by distinct growth rings demarcated by the marginal parenchyma; axial parenchyma vasicentric, scarce; rays visible to the naked eye on the transverse surface, thin and numerous, regularly spaced, larger rays narrower than the wider pores; solitary vessels and in radial multiples of 2–3, medium to large, unobstructed to obstructed by white deposits (Figure 15). The species are very similar, except for *E. purpurea* and *E. jenmanii,* which have larger pores than the other species (Figure 15g, h). The wood of *Eperua* is similar to its related Neotropical Detarioideae genera, such as *Hymenaea* (Chipaia *et al.* 2015) and *Copaifera* (Fontana *et al.* 2018). It is challenging to differentiate these genera based solely on macroscopic wood characteristics.

Branches and branchlets are bifurcate in the same plane (distichous) (Figure 2d). They are horizontally oriented to the trunk, similar to the distichous arrangement of the leaves (Figure 2h). These characteristics give the trees a horizontal spreading canopy appearance (Figure 1b, d).

The number of leaflets per leaf is essential for identifying the species (Figure 2e–h). Most species are multijugate, often up to 5-jugate, although 6-jugate leaves are reported for *E. jenmanii, E. schomburgkiana*, and *E. cerradoensis*, and 7-jugate leaves are restricted to the latter species. There are also 1-jugate (*E. venosa*) and 2-jugate (*E. banaensis, E. biuga, E. glabriflora, E. obtusata,* and *E. venosa*) species.

The venation pattern of the leaflets also aids in species recognition (Figure 3a–e). All species of *Eperua* have a secondary venation with an intramarginal vein. In some species, this vein is very close to the margin (*E. falcata*, *E. leucantha*, *E. venosa*, *E. oleifera*, and *E. purpurea*), while in others, it is not as close to the margin (*E. froesii*, *E. grandiflora*, *E. praesagata*, *E. rubiginosa*, and *E. schmoburgkiana*). Some possess two intramarginal veins, with the vein closer to the margin either continuous (*E. bijuga, E. glabriflora, E. jenmanii*) or not (*E. manausensis, E. cerradoensis, E. bijuga, E. duckeana, E. glabra, E. grandiflora* subsp. *guyanensis*).

A common characteristic in Detarioideae is the presence of dots or translucent glands in the blades, which occurs in most species of *Eperua* (Figure 3f–n). *Eperua oleifera* has the most conspicuous pellucid-punctate leaves; the dots

are visible even to the naked eye. Additionally, *E. duckeana*, *E. falcata*, *E. grandiflora* subsp. *ciliata*, *E. leucantha*, *E. purpurea*, *E. schomburgkiana*, and *E. venosa* also have pellucid-punctate leaves. The remaining species have inconspicuous pellucid-punctate to epunctate leaves (*E. bijuga, E. glabra, E. glabriflora, E.

grandiflora, E. jenmanii, E. praesagata, E. reddeniae, E. rubiginosa, E. cerradoensis, E. manausensis, and *E. froesii*).

Based on floral architecture and inflorescence arrangement, the species can be grouped into three types: I) long and pendulous inflorescence with non-tubular corolla and exserted stamens; II) short and erect inflorescence with nontubular corolla and exserted stamens, and; III) short and erect inflorescence with tubular corolla and inserted stamens (Figure 4). These characteristics play a key role in taxonomy, although species delimitation is generally associated with inflorescence and flower indumentum and phenology and position of the bracteoles on the pedicels (Tables 2–4, see taxonomic notes). All species with tubular corolla have a 1:1 to 2:1 length/width fruit proportion and non-falcate fruits (Figure 6c, e, f), and stamens joined a diadelphous sheath (Figure 5g), but none have falcate leaflets and stamens joined in a tube. The non-tubular corolla group encompasses species with both falcate and non-falcate leaflets, a 3:1 and a 4:1 length/width fruit proportion, falcate fruits (Figure 6 a, b, d), and stamens joined in a tube or in a diadelphous sheath (Figure 5h, i).

The inflorescence is a raceme or a panicle, but it is always a panicle when it is long and pendulous (Figure 4a–c). The lateral racemes are alternate and distichous or alternate and spirally arranged; being always spirally arranged in the long and pendulous inflorescence. The difference between long and short inflorescences lies in the peduncle size. In long inflorescences, the peduncle can vary from 40 cm up to 3 m in length, whereas short inflorescences have a peduncle shorter than 4.0 cm long or sometimes it is sessile.

The tubular corolla in *Eperua* (group III) is formed only by the adaxial petal, whose margins roll inwards, rather than through sympetaly (Figure 4c–g). The stamens are inserted in the corolla tube in this group (Figure 4c–g). All species in this group are heterostaminate, with differences mainly in the size of the filaments. Often, there are five larger filaments alternating with five shorter ones (Figure 4e, f, i). In *E. glabriflora* the difference in filament size is remarkable: there are two longest filaments, three intermediate ones (including the free one), and five shortest ones (Figure 4f). The anthers of the shortest filaments are often smaller. In *E. oleifera* and *E. purpurea,* the smallest filaments anthers differ not only in size but also in shape, and are sterile (Figure 5f). Interestingly, the tubular corolla

and the heteromorphy in the stamens resemble a flower from Bignoniaceae (Cowan 1975).

Groups I and II, which have non-tubular corollas and exserted stamens, share the same number of organs as group III with tubular corolla, but they appear quite different. In these groups, the stamens are always much longer than the adaxial petal, and this petal is as long as the sepals (Figure 4h–l). On the other hand, in the species with tubular corolla, the sepals are much shorter, and the stamens are shorter than the adaxial petal or appear so because they bend downward and remain inside the corolla tube (Figure 4c–g). Interestingly, there are no significant differences between the width or length of the adaxial petal between the species with non-tubular and tubular corolla. However, tubular corolla species have the longest adaxial petals, while non-tubular corolla species have the shortest ones. Therefore, the differences between these two groups can be explained by the proportion of the petal, sepal, and stamens lengths.

The indumentum of the inflorescence axis, stamens, and ovary are the main taxonomic features for the distinguishing species (see the Figures of each species for visual reference). One species, *E. glabra,* is entirely glabrous, except by the ciliate bracts and bracteoles. Five other taxa have glabrous inflorescence (*E. glabriflora* var. *glabriflora, E. glabriflora* var. *gynopubescens, E. grandiflora* subsp. *ciliata, E. jenmanii* subsp. *sandwithii,* and *E. purpurea*). The remaining exhibit varying types of indumentum, which can be dense (tomentose, tomentulose, strigose, or strigulose) or scarce (puberulous or puberulent). Apart from *E. glabra,* other species have glabrous stamens, including *E. banaensis, E. cerradoensis, E. froesii,* and *E. obtusata.* When present, the stamen indumentum ranges from tomentose, sericeous, villous, pubescent, to puberulous. Interestingly, there are more taxa with glabrous ovaries than glabrous stamens. Glabrous ovary occurs in *E. froesii, E. glabra, E. glabriflora* var. *glabriflora, E. grandiflora* subsp. *grandiflora, E. grandiflora* subsp. *ciliata, E. manausensis, E. purpurea, E. jenmanii, E. oleifera,* and *E. schomburgkiana.* In the non-glabrous ovary taxa, the indumentum is either tomentose (both *E. rubiginosa* subspecies, *E. duckeana, E. cerradoensis, E. glabriflora* var. *gynopubescens, E. manausensis,* and *E. reddeniae*) or sericeous (*E. banaensis, E falcata, E. grandiflora* subsp. *guyanensis, E. leucantha, E. venosa,* and *E. obtusata*). When comparing species with tubular corollas to those with non-tubular corollas, no species shares the same combination of ovary and stamen indumentum. This indicates that the indumentum patterns can be used to distinguish between species of these two groups.

FIGURE 1. Types of habitats in the genus *Eperua.* A. *E. schomburgkiana*, medium trees bordering the Demera River, Mabura Hill, Guyana; B. *E. falcata*, huge fruiting tree in Palumeu, Surinam; C. *E. oleifera* var. *campestris*, a small spreading tree, Amazonas state, Brazil. D. *E. falcata*, flowering crown of a huge tree in Palumeu, Surinam. Photos, A: H. ter Steege; B, D: P. Teunissen; C: F. Farroñay.

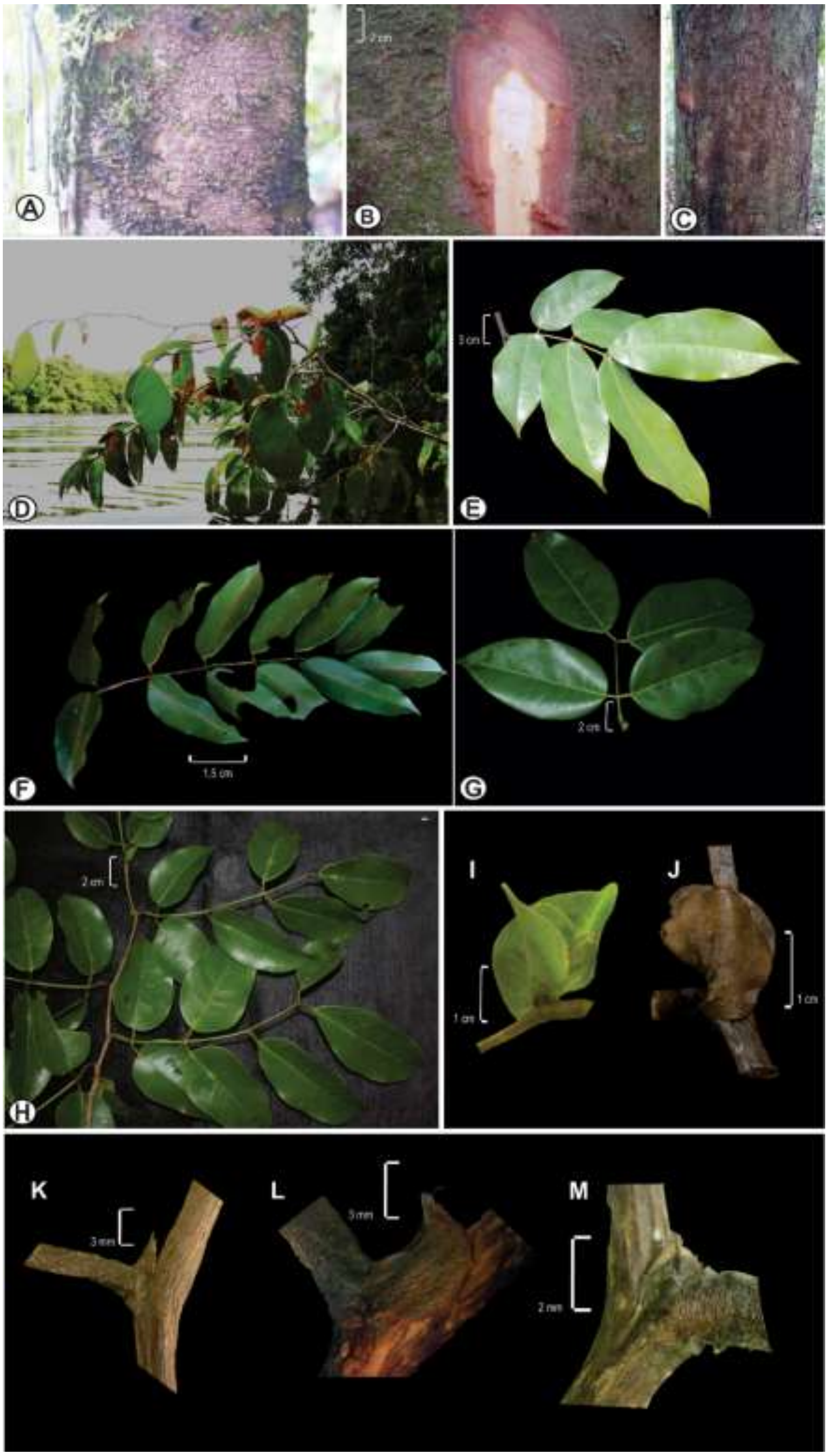


FIGURE 2. Main vegetative characteristics of the genus *Eperua*: A. lenticellate bark, *E. rubiginosa* var. *rubiginosa*; B. trunk with reddish inner bark, and light brown sap-wood, *E. bijuga*; C. smooth to scaled bark, *E. falcata*; D. branchlets bifurcating in the same plane (distichous), *E. bijuga*; E–H. number of leaflets; E. leave 3-jugate with falcate leaflets, *E. falcata*; F. leave 6-jugate with straight leaflets, *E. cerradoensis*; G. leave 2-jugate with straight leaflets, *E. glabriflora* var. *glabriflora*; H. leave 4-jugate with straight leaflets, showing also the alternate and distichous pattern of bifurcation, *E. duckeana*; I–M. types of stipules; I. free foliaceous stipules, *E. duckeana*; J. joined foliaceous stipules, *E. cerradoensis*; K. joined non-foliaceous stipules, *E. purpurea*; L. foliaceous stipules joined at the base, *E. jenmanii* subsp. *sandwithii*; M. free non-foliaceous stipules, *E. rubiginosa* var. *rubiginosa*. Specimens A: *Fortes E.A. & Silva G.S. da 167*; B: *Fortes E.A. et al. 189*; E: *Fortes E.A. & Silva G.S. da 172*; F, J: *Gonçalves A.S. 01*; G: *Fortes E.A. & M. de C. Camelo 150*; H, I: *Fortes E.A. et al. 191b*; K: *Ducke W.A. s.n. RB23288*; L: *Liesner R.L. & Morillo G. 13972*; M: *Fortes E.A. & Silva G.S. da 170*. Photos A, B, E, G–M: E.A. Fortes; C: V.F. Mansano; D: H. ter Steege.

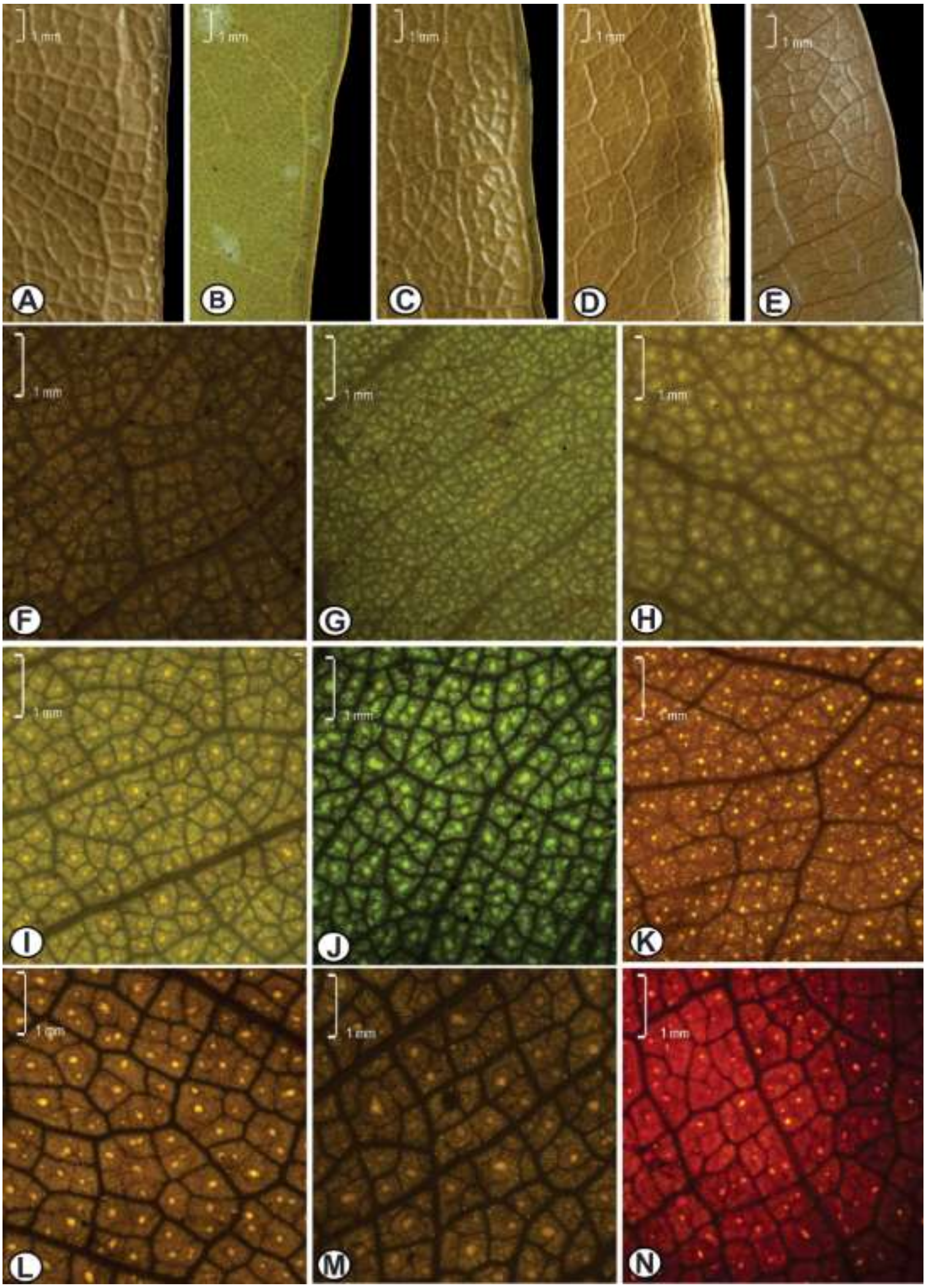


FIGURE 3. Main vegetative characteristics of the genus *Eperua*: A–E. Types of secondary venation; A. two intramarginal veins, vein closer to the margin continuous, *E. jenmanii* subsp. *jenmanii*; B. two intramarginal veins, vein closer to the margin not continuous, *E. cerradoensis*; C. one intramarginal vein not close to the margin, *E. grandiflora* subsp. *grandiflora*; D. one intramarginal vein very close to the margin, *E. leucantha*; E: one intramarginal vein very close to the margin, *E. oleifera* var. *campestris*. F–N. different types of pellucid-punctae blades; F. epuncate, *E. glabriflora* var. *glabriflora*; G. epunctate, *E. cerradoensis*; H. inconspicuous pellucid-punctate, *E. rubiginosa* var. *rubiginosa*; I. pellucid-punctate, *E. manausensis*; J. pellucid-punctate, *E. duckeana*; K. pellucid-punctate, *E. oleifera* var. *campestris*; L. pellucid-punctate, each areole has at least one conspicuous dot, *E. leucantha*; M. pellucid-punctate, each areole has at least one conspicuous dot, *E. venosa*; N. minutely pellucid-punctate, not all areoles have one dot, *E. falcata*. Specimens, A: *Tillett S.S. & Tillett C.L. 45699*; B, G: *Gonçalves A.S. 01*; C: *Goldenberg R. et al. 2632*; D, M: *Maguire B. et al. 42610*; E, K: *Zarucchi J.L. et al. 2842*; F: *Assunção J.M. s.n. RB352959*; H: *Fortes E.A. & Silva G.S. da 170*; I: *Fortes E.A. & Viana G.P. 194b*; J: *Faria S.M. de et al. 2053*; L: *Williams L. 13939*; N: *Anderson C.W. 122*. Photos, E.A. Fortes.

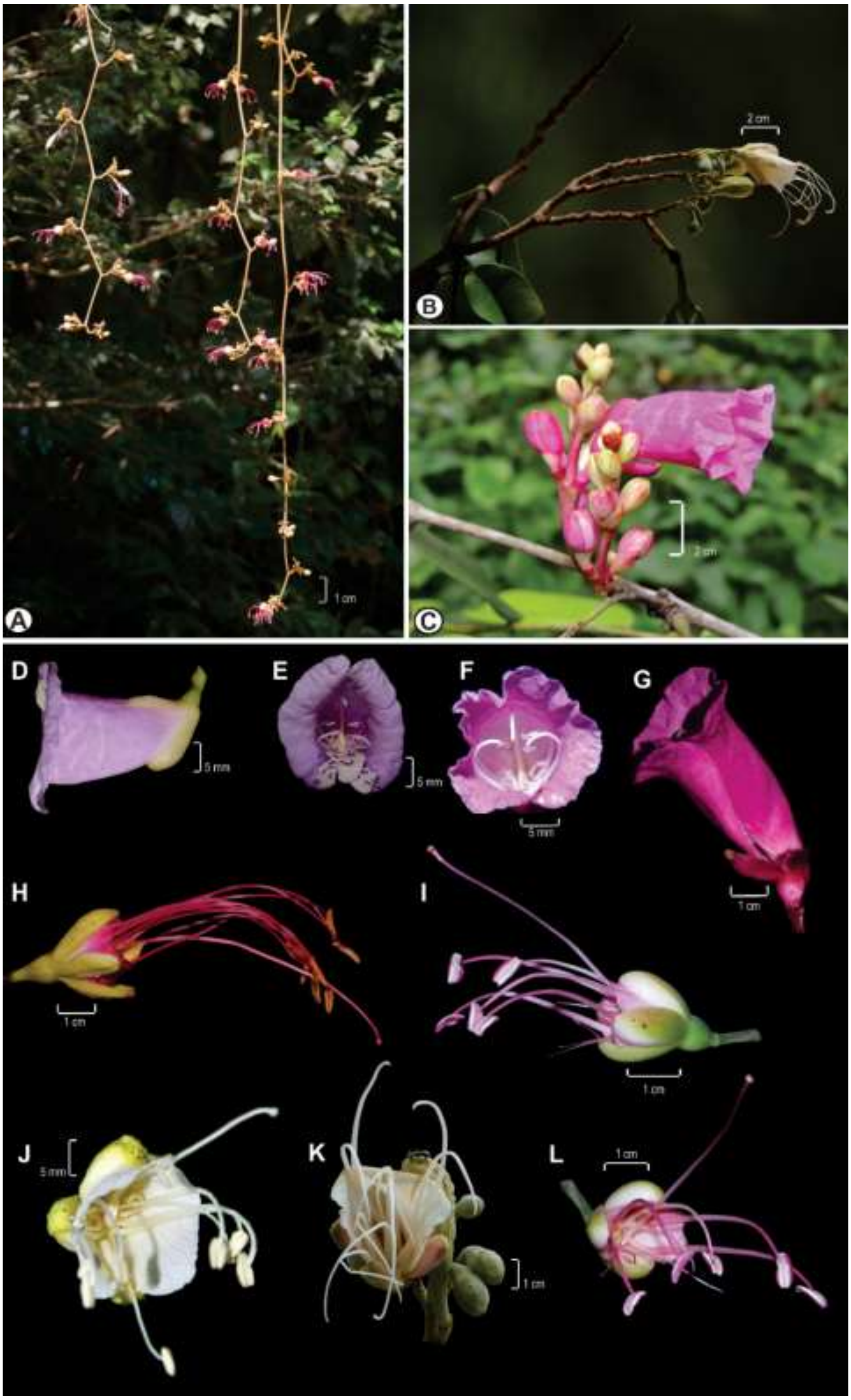


FIGURE 4. Main flowering characteristics of the genus *Eperua***:** A. long and pendulous inflorescence, flower with non-tubular corolla and exserted stamens, *E. rubiginosa* var. *rubiginosa*; B. short and erect inflorescence, flower with non-tubular corolla and exserted stamens, *E. duckeana*; C. short and erect inflorescence, flower with tubular corolla and inserted stamens, *E. glabriflora* var. *glabriflora*; D–G. flowers with tubular corolla and inserted stamens; D. lateral view, *E. grandiflora* subsp. *grandiflora*; E. front view, *E. grandiflora* subsp. *grandiflora*; F. front view, *E. glabriflora* var. *glabriflora*; G. lateral view, *E. glabriflora* var. *glabriflora*; H–L. flowers with non-tubular corolla and exserted stamens; H. lateral view, *E. rubiginosa* var. *rugiginosa*; I. lateral view, *E. falcata*; L. front view, *E. leucantha*; M. front view, *E. duckeana*; N. front view, *E. falcata*. Specimens, C, F: *Fortes E.A. & M. de C. Camelo 150*; D, E: *Goldenberg R. et al. 2632*; H: *Goldenberg R. et al. 2522*. Photos, A: O. Gauberet @Piwigo; B, K: H. ter Steege; C, F: E.A. Fortes; D, E, H: R. Goldenberg; G: F. Farroñay; I, L: D. Sabatier; J: F. Castro-Lima.

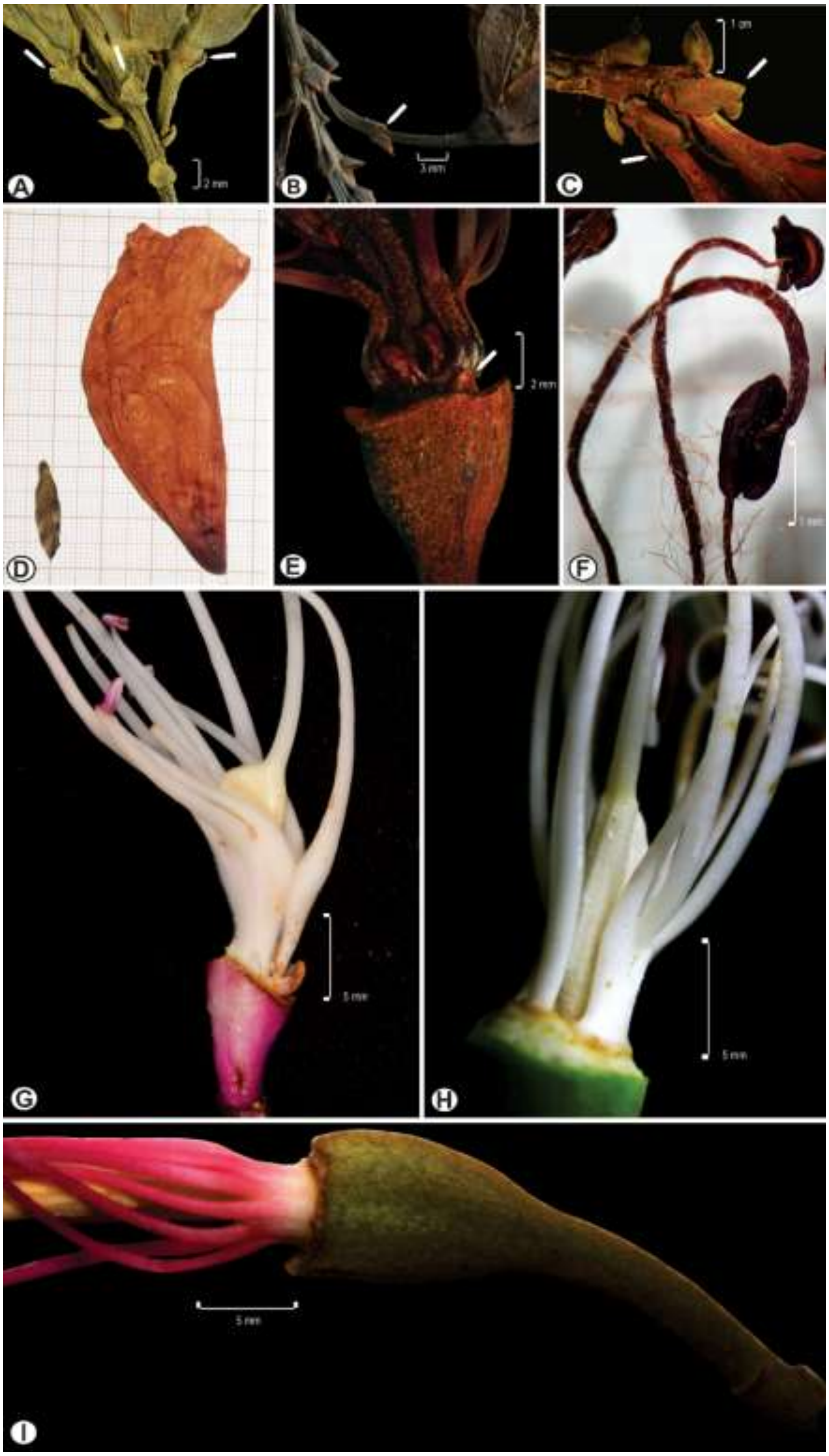


FIGURE 5. Main flowering characteristics of the genus *Eperua***:** A–C: position of the bracteoles on the pedicel; A. attached to the higher portion of the pedicels or at the base of the hypanthium, *E. oleifera* var. *oleifera*; B. attached to the middle portion of the pedicels at slightlydifferent levels, *E. purpurea*; C. attached to the lower portion of the pedicels, *E. jenmanii* subsp. *sandwithii*; D. size differences between the petalodia (smaller) the adaxial petal (bigger), *E. jenmanii* subsp. *jenmanii*; E. size of one petalodia compared with the staminal tube and intrastaminal nectaries (sepals and adaxial petal removed), *E. reddeniae*; F. heteromorphic anthers in *E. purpurea*, the smaller are sterile and the bigger produce pollen; G–I. conation of the stamens; G. joined basally in an inequilateral, diadelphous sheath, *E. glabriflora* var. *glabriflora*; H. joined basally in an equilateral, diadelphous sheath, *E. leucantha*; I. . joined basally in tube, *E. rubiginosa* var. *rubiginosa*. Specimens, A: *Cid-Ferreira C.A. 5791*; B: *Ducke W.A. s.n. RB23288*; C: *Redden K.M. et al. 7059*; D: *Tillett S.S. & Tillett C.L. 45699*; E: *Redden K.M. et al. 3274*; F: *Silva N.T. da 4420*; I: *Fortes E.A. & Silva G.S. da 167*. Photos, A–F, I: E.A. Fortes; G: F. Farroñay; H: H. Ter Steege.

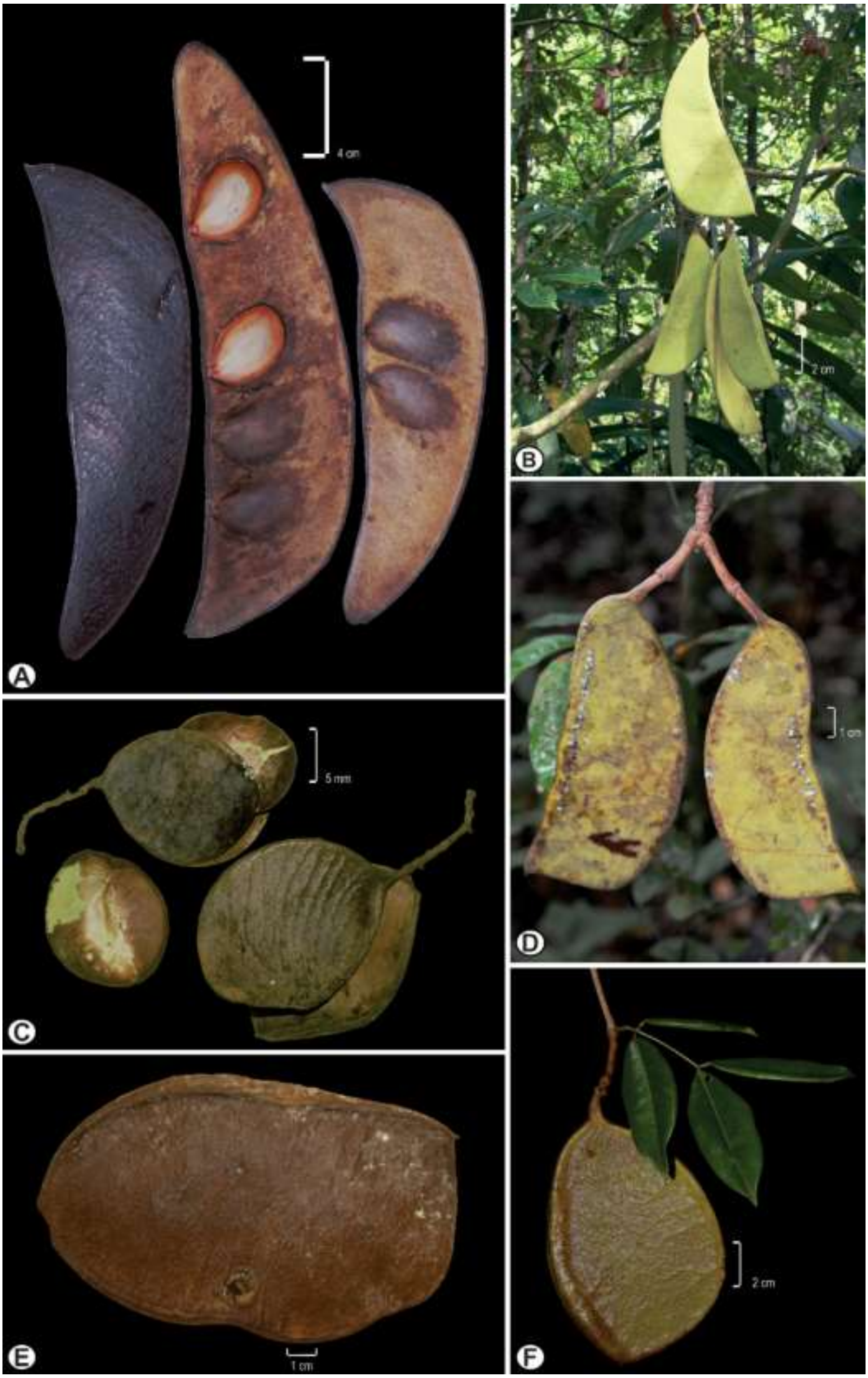


FIGURE 6. Main fruiting characteristics of the genus *Eperua*. A. falcate fruit, 4:1 length/width proportion, *E. falcata*; B. falcate fruit, 4:1 length/width proportion, *E. leucantha*; C. non-falcate one-seeded fruit, 1:1 length/width proportion, *E. grandiflora*; D. falcate fruit, 3:1 length/width proportion, *E. duckeana*; E. non-falcate fruit, 2:1 length/width proportion, *E. jenmanii*; E. non-falcate fruit, 1:1 length/width proportion, *E. glabriflora* var. *glabriflora*. Specimens, D: *Fortes E.A. et al. 191b*; E: *Redden K.M. et al. 1760*. Photos, A, C: D. Sabatier; B: H. ter Steege; D, E: E.A. Fortes; F: H.C. Lima.

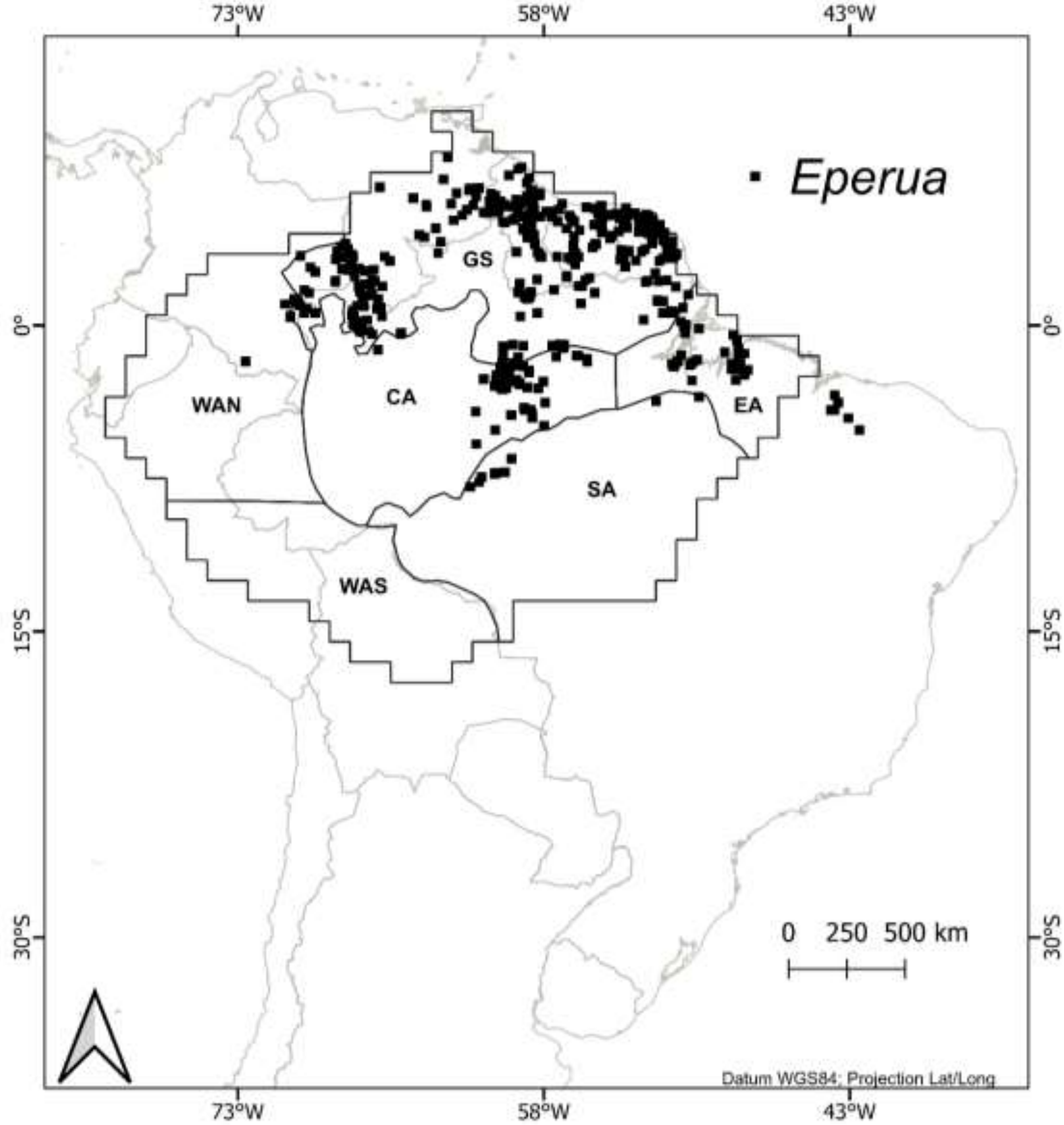


FIGURE 7. Geographic distribution of *Eperua* (Leguminosae, Detarioideae), a genus endemic to the Northern region of South America. The map shows the different biogeographical regions of Amazonia (modified after Feldpausch *et al.* 2012) in which *Eperua* is distributed, and *E. cerradoensis,* which occurs outside of Amazonia in the Cerrado and Caatinga Biome in Brazil. Legend: CA, central Amazonia; EA, eastern Amazonia; GS, Guyana Shield; SA, southern Amazonia; WAN, northern part of western Amazonia; WAS, southern part of western Amazonia.

Eperua has one bract at the base of the pedicels and one pair of bracteoles attached at different levels on the pedicels (Figure 5a–c). The bracteoles are attached to the lower, middle, or higher portion of the pedicels or at the base of the hypanthium. They are caducous or persistent. It is caducous in the non-tubular corolla group, except in *E. cerradoensis* and *E. froesii*. The position and persistence of the bracteoles are stable within each species, serving as important taxonomic characteristics for the group.

The ten stamens in *Eperua* are fused, but the nature of their fusion varies depending on the corolla type. The stamens are joined basally in the non-tubular corolla group forming a tube or a diadelphous sheath 9+1 (Figure 5h, i). In the tubular corolla group, the stamens are joined in a diadelphous sheath, but the sheath is inequilateral, with the middle part longer than the lateral parts (Figure 5g). In contrast, it is equilateral in the non-tubular group (Figure 5h).

The species with non-tubular corollas have falcate fruits with length/width ratio 3:1 to 4:1 (Figure 6a, b). In contrast, those with tubular corollas have a non- falcate fruit with length/width ratio 1:1 to 2:1 (Figure 6c, e, f). Species with a fruit length/width ratio 1:1 to 2:1 often have one or two seeds (Figure 6c), while others can have up to seven (Figure 6a). The seeds do not have specific dispersal structures like pleurogram, aril, or wings. *Eperua glabriflora*, *E. grandiflora*, and *E. bijuga* have the biggest seeds in *Eperua*, and this can be explained because the mature fruits are 1–2-seeded (Figure 6c). The fruit valves have elastic dehiscence, but due to the weight of the seed, they do not disperse far from the tree. Consequently, many seedlings are often observed around the fruiting tree. Flowering and fruiting in all *Eperua* species occur throughout the year, with a peak in flowering during September and peaks in fruiting in November and February.

Reproductive biology

Eperua species have a cossexual sexual system, meaning that all species have flowers with both functional stamensand pistils (Cardoso *et al.* 2018). The flowers possess several characteristics that facilitate cross-pollination by animals. These include approach herkogamy (a spatial separation between the stamens and pistil to prevent self-pollination), nectar guides, nectaries in the hypanthium wall, and gland at the apex of the sepal and bracteoles in some species.

Four species with non-tubular corolla and exserted stamen were reported as bat-pollinated: *E. falcata*, *E. leucantha*, *E. rubiginosa,* and *E. schomburgkiana* (Vogel 1968, Geiselman *et al.* 2004, Fleming *et al.* 2009). Analysing the bat faecal samples from French Guiana, a dominance of pollen from *E. falcata* was observed (Delaval 2005, Geiselman 2010) in the dry and wet season (Geiselman 2010). The pollen from *E. falcata* is the most abundant vegetal item from faecal samples of 12 species of bats in French Guiana. Pollen from *E. rubiginosa* was also found in almost half of the faecal samples collected in the dry season. Those studies heavily indicate those species as bat pollinated. On the other hand, the species with short, erect inflorescences and tubular corolla like *E. bijuga*, *E. purpurea*, *E. jenmanii*, *E. oleifera*, and *E. grandiflora* are generally considered to be bee-pollinated (Vogel 1968, Cowan 1975). However, there are no reproductive experiments to test whether the visitors are pollinators.

Collectors reported, as noted on the exsiccatae labels, visitation by hummingbirds and bees. Hummingbird visitation has been reported in *E. bijuga*: (*Souza L.A.G. de 13_97*), *E. falcata* (*Mori S.A. & Boom B.M. 14745*, *Redden K.M. et al. 4724*), *E glabra* (H. ter Steege pers. obs,), and *E. leucantha* (*Barbosa-Castillo C.E. & Madriñán S. 8407*); honeycreepers visitation in *E. grandiflora* (H. ter Steege pers. obs.); whereas bee visitation in *E. leucantha* (*Spruce R. 2021*), *E. purpurea* (*Spruce R. 2577a*) and *E. oleifera* var. *campestris* (this last one is also visited by large black bees) (*Zarucchi J.L. et al. 2842*).

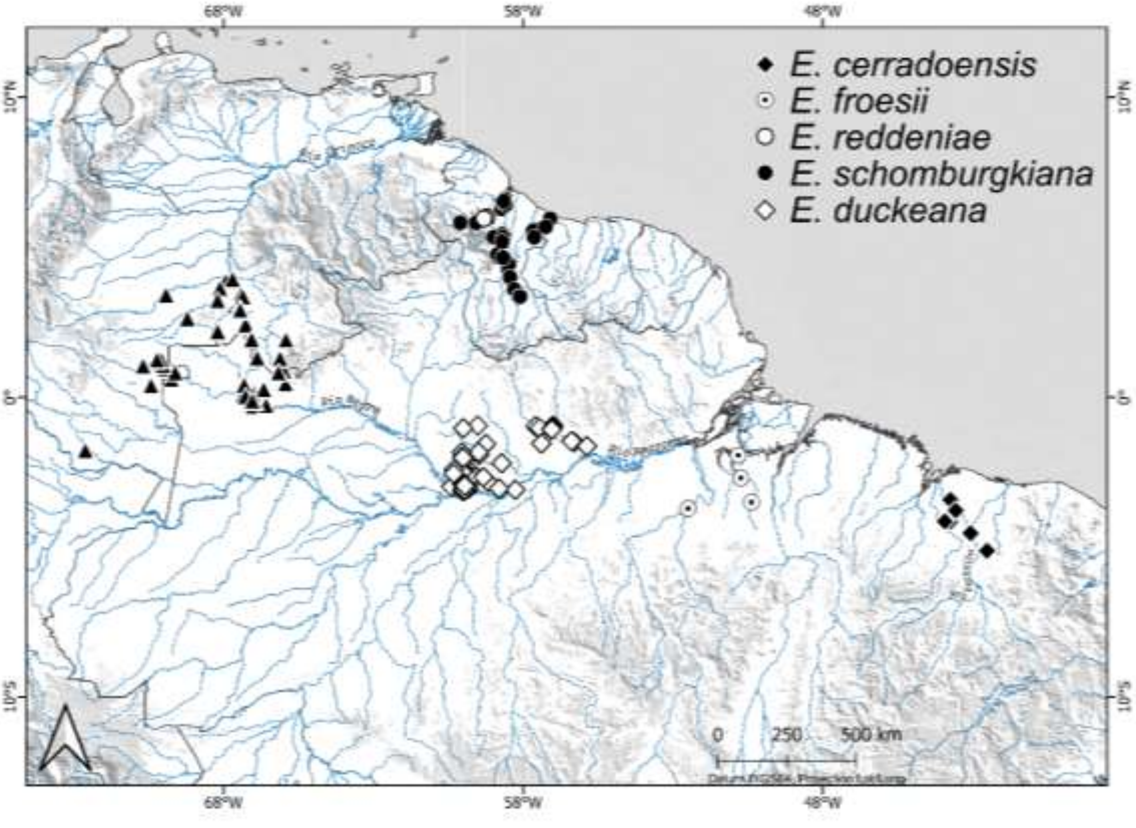


FIGURE 8. Geographic distribution of *Eperua* species with short and erect inflorescence and non-tubular corolla: *Eperua cerradoensis*, *E. duckeana*, *E. froesii*, *E. reddeniae*, and *E. schomburgkiana*.

Economic and sociobiological uses

Eperua has more than a hundred vernacular names (see Appendix 1). Among these, *E. falcata*, *E. jenmanii*, *E. leucanta*, *E. purpurea*, and *E. rubiginosa* var. *rubiginosa* are known by multiple names. The extensive list of names can be attributed to the species' utilization by local communities for various purposes, including timber, medicinal applications, and ornamental potential.

Eperua grandiflora, *E. leucantha*, *E. falcata*, and *E. oleifera* are exploited for medicinal purposes. They are commonly used in baths to promote hair growth, reduce fever, heal wounds, and relieve pain (DeFilipps *et al.* 2004, Useful Tropical Plants 2014). The oil resins of *E. oleifera* and *E. purpurea* resemble and are often confused with those of the genus *Copaifera* used for ethnopharmacological purposes (Veiga-Junior & Pinto 2002); indeed, *E. oleifera* is known as "copaíba preta" and "copaíba jacaré". Additionally, several species contain substances with biological antiinflammatory, antioxidant, insecticidal, and bactericidal properties, underscoring the pharmacological potential of the genus (Leandro & Veiga-Junior 2012).

The wood of *E. duckeana*, *E. falcata*, *E. glabriflora*, *E. grandiflora*, *E. jenmanii* subsp. *jenmanii*, *E. leucantha*, *E. purpurea*, and *E. rubiginosa* var. *rubiginosa* are used in general construction, including houses, bridges, and street light and telephone poles. In Guyana, *Eperua* wood is especially used to make shingles to cover roofs. *Eperua* wood is known for its density and durability, even when subjected to underground conditions (*E. leucantha, Williams L. 15801*), or submersion in water (*E. rubiginosa,* Useful Tropical Plants 2014). *Eperua falcata*, *E. grandiflora*, *E. jenmanii*, and *E. schomburgkiana* have rapid growth and long-lasting wood, making them commercially valuable (Useful Tropical Plants 2014, TRADA 2022). Besides timber use, the wood of *E. grandiflora* subsp. *guyanensis* and *E. jenmanii* subsp. *jenmanii* are used as firewood; and the bark of *E. purpurea* is used for Yuruparí horns, and the ash of its bark is used to make pots and vases.

Thanks to their remarkable flowering features, collectors have recognized *E. bijuga*, *E. falcata*, *E. leucantha,* and *E. purpurea* as potential ornamental trees. Indeed, *E. purpurea*, known as "guapa" in Colombia, is considered one of the world's most beautiful flowering trees, with its purple flower clusters contrasting with the bright green foliage (Useful Tropical Plants 2014).

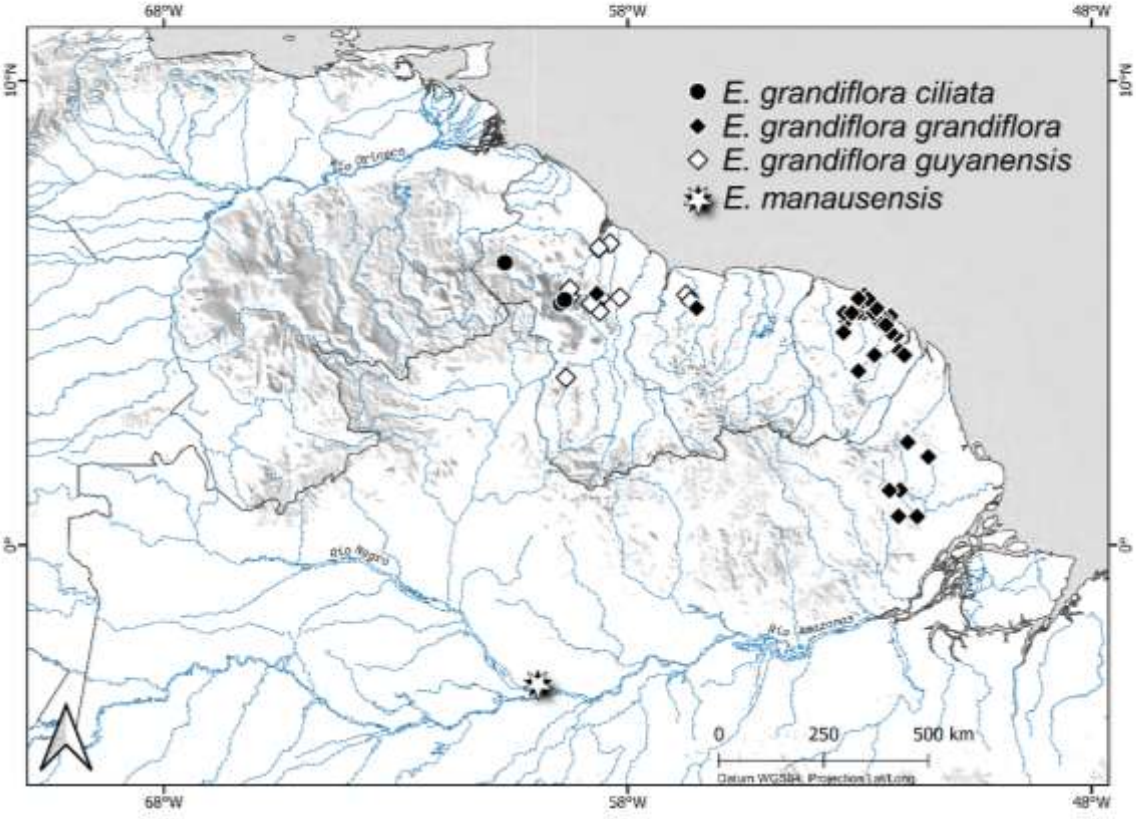


FIGURE 9. Geographic distribution of *Eperua grandiflora* subsp. *grandiflora, E. grandiflora* subsp. *guyanensis, E. grandiflora* subsp. *ciliata,* and *E. manausensis.*

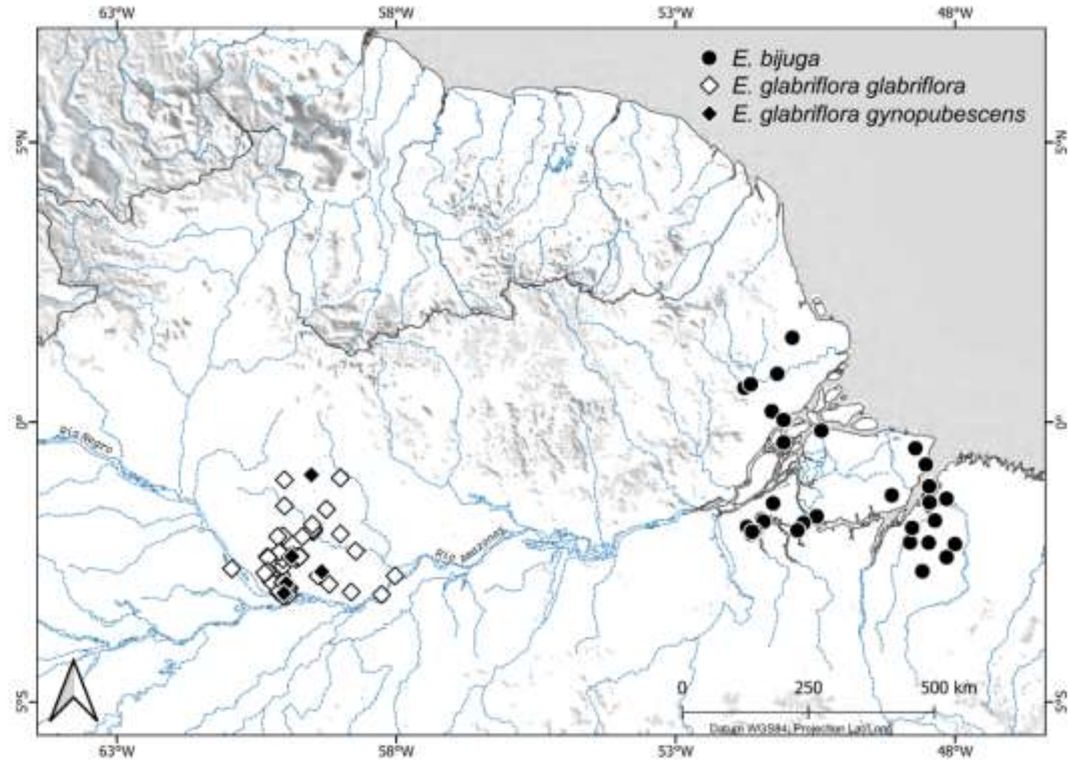


FIGURE 10. Geographic distribution of *Eperua bijuga*, *E. glabriflora* var. *glabriflora*, and *E. glabriflora* var. *gynopubescens*.

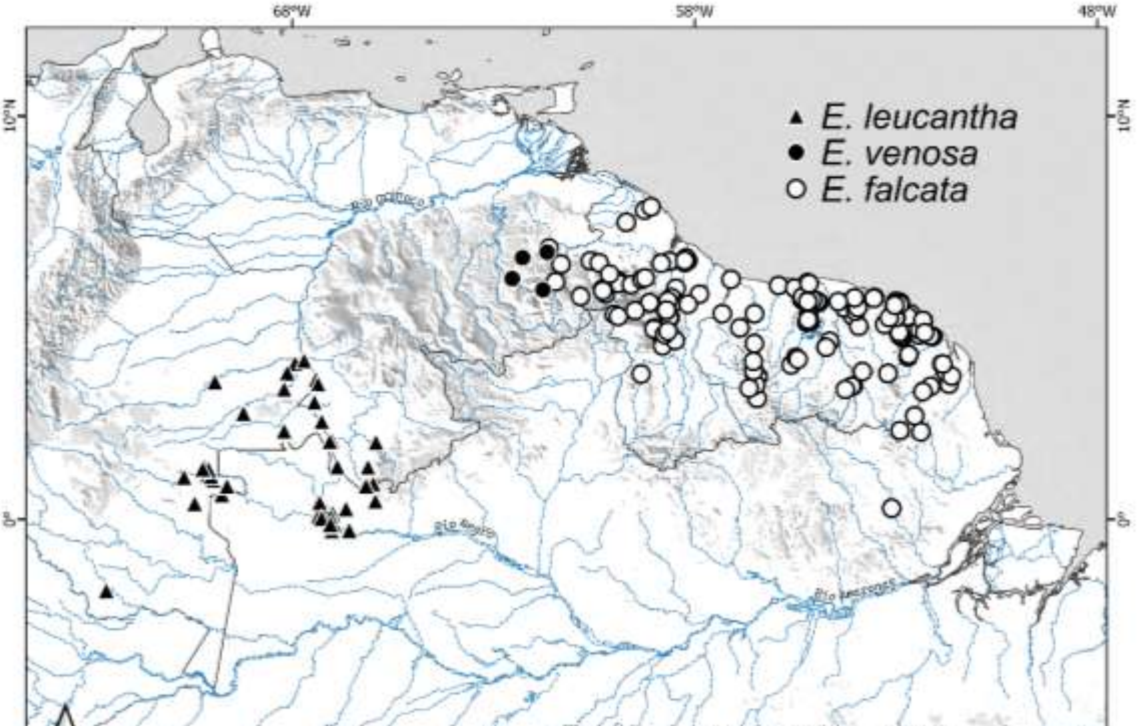


FIGURE 11. Geographic distribution of *Eperua falcata*, *E. leucantha*, and *E. venosa*.

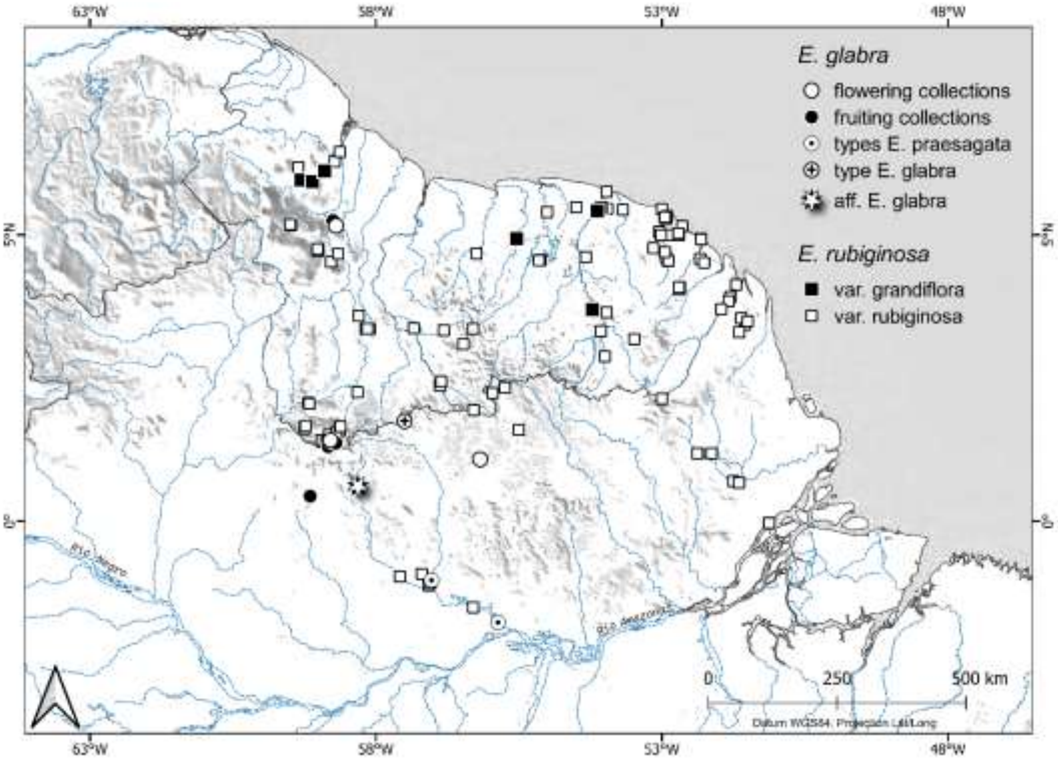


FIGURE 12. Geographic distribution of *Eperua glabra*, *E. rubuginosa* var *rubiginosa*, and *E. rubiginosa* var. *grandiflora*.

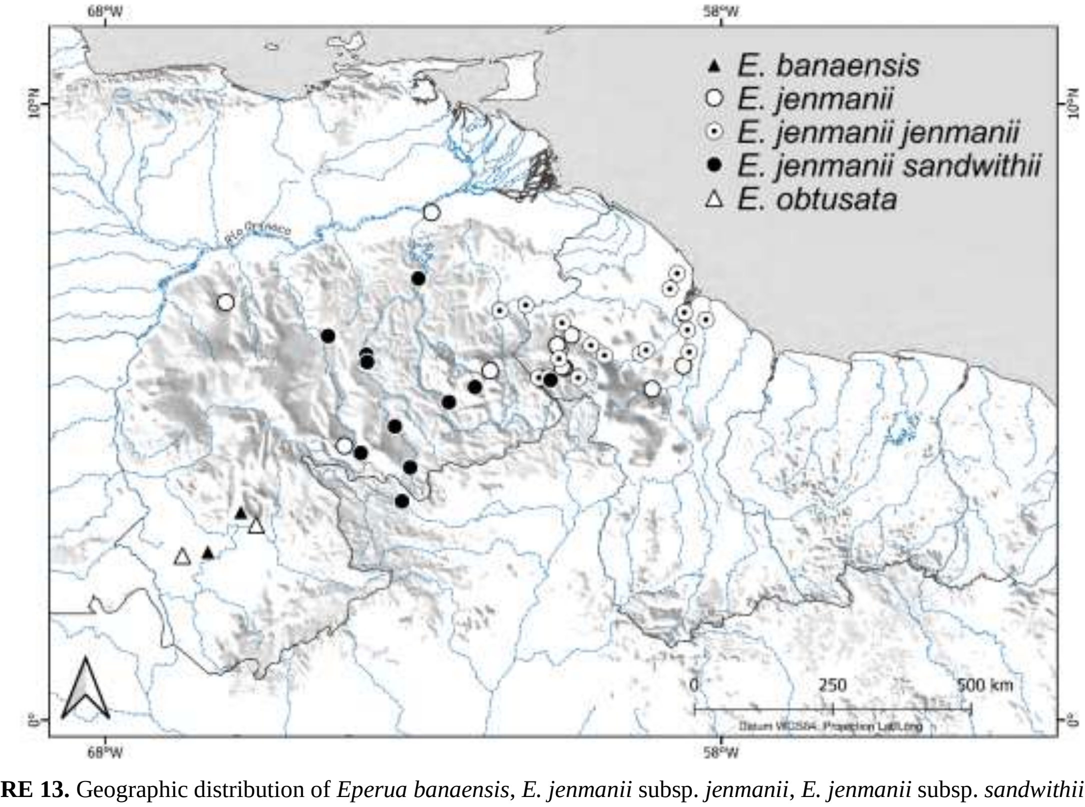


FIGURE 13. Geographic distribution of *Eperua banaensis*, *E. jenmanii* subsp. *jenmanii*, *E. jenmanii* subsp. *sandwithii*, and *E. obtusata*.

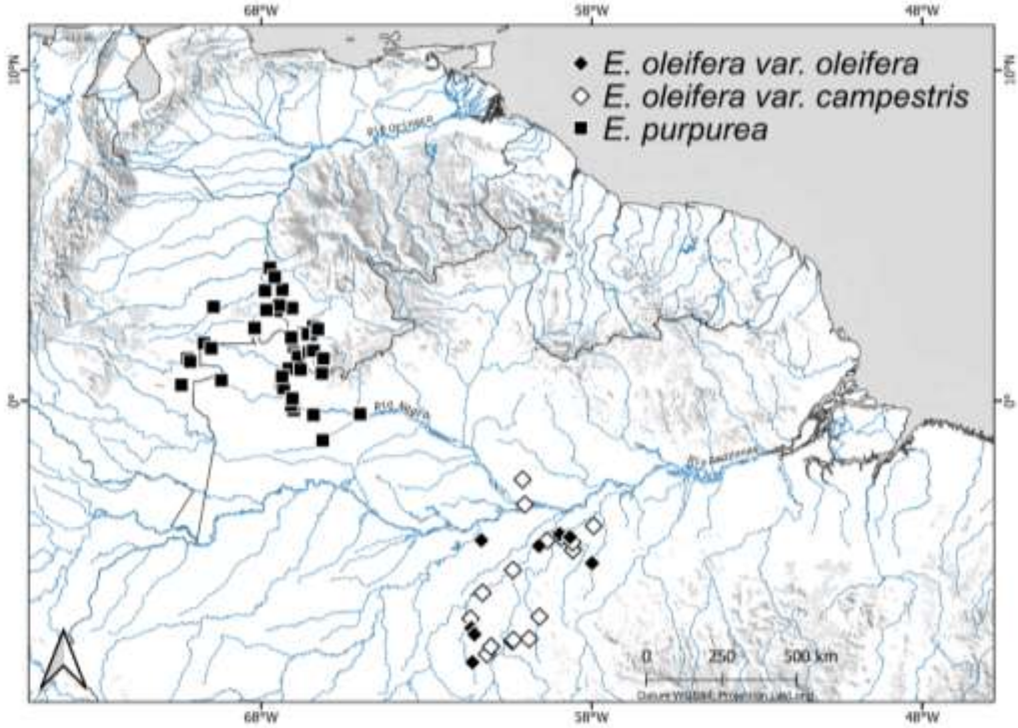


FIGURE 14. Geographic distribution of *Eperua purpurea, E. oleifera* var. *campestris*, and *E. oleifera* var. *oleifera*.

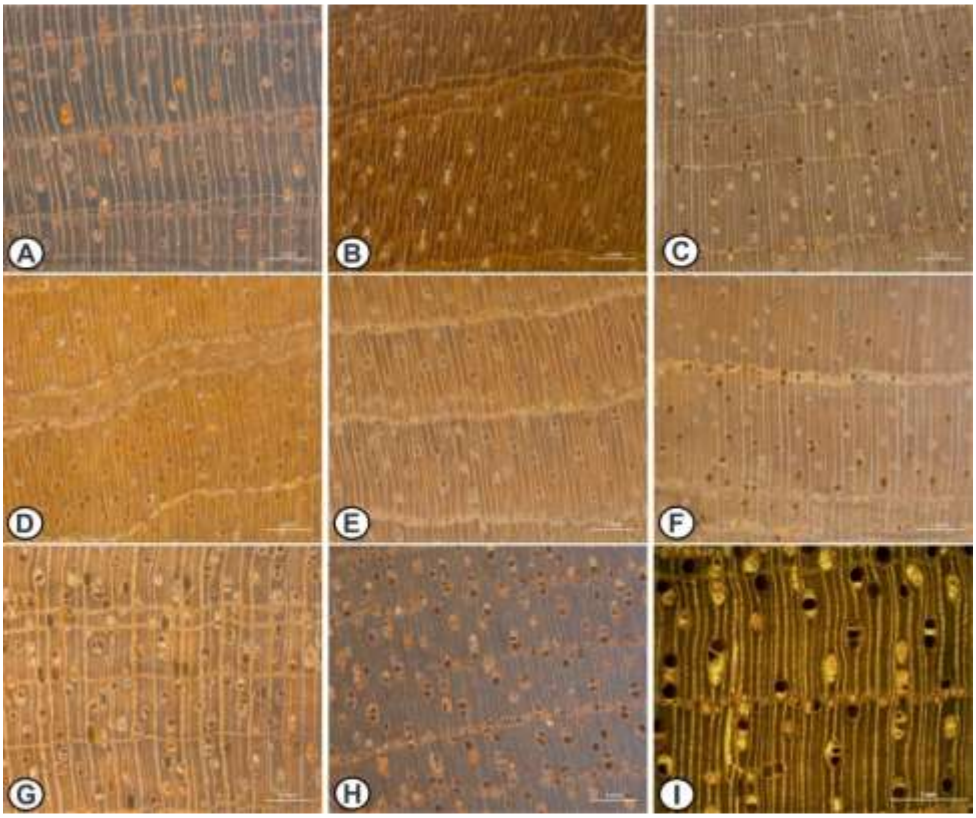


FIGURE 15. Transverse macroscopic image of the *Eperua* wood. A. *E. falcata* (*Stahel G. 22:* MGw2436, exsicate IAN38271); B. *E. leucantha* (*Nascimento O.C. do 691*: MGw1851, voucher MG63683), C. *E. rubiginosa* var. *rubiginosa* (*Cavalcante P.B. 870*: MGw92, voucher MG24706); D. *E. glabra* (*Silva N.T. da & Santos M.R. 4758*: MGw1698, voucher MG61723); E. *E. bijuga* (*Rosa N.A. 1288*: MGw1204, voucher MG52858); F. *E. grandiflora* subsp. *grandiflora* (*Rosa N.A. 1183*: MGw1262, voucher MG52753); G. *E. purpurea* (*Silva N.T. da 4420*: MGw2120, voucher MG56377); H. *E. jenmanii* (*Stahel G. 334*: MGw2702, voucher IAN38557); I. *E. duckeana* (*Oliveira E. 2737*: IANw2237, voucher IAN115520). Bars 1 mm. Figure I (*Eperua duckeana*) was taken in a higher magnification than others, see bars. A–H: images from stereomicroscope Discovery.V8—Zeiss, camera MOTIC SMZ-161), I: image from stereomicroscope Stemi SV 6—Zeiss, camera MOTICAM 5.0 MP.

Taxonomic treatment

Eperua Aublet (1775: 369). Type:—*Eperua falcata* Aublet (1775: 369).

Parivoa Aublet (1775: 756). Type:—*Parivoa grandiflora* Aublet (1775: 757) [≡*Eperua grandiflora* (Aublet 1775: 757) Baillon (1870: 110)]

Dimorpha Schreber (1791: 493) nom. illeg. superfl.

Panzera Willdenow (1799: 540) nom. illeg. superfl. Type:—*Panzera falcata* (Aublet 1775: 369) Willdenow (1799: 540) [≡*Eperua falcata* Aublet (1775: 369)]

Small to very large trees (2.0–50.0 m tall); trunk with bark lenticellate, fissured, striate, scaled, or smooth; branchlets glabrous, rarely puberulent, puberulous to strigulose in *E. oleifera*. **Stipules** 2, intrapetiolar, entirely joined, joined at the base, or free, pellucid-punctate, foliaceous or non-foliaceous, when foliaceous ovate-falcate, obovate-falcate, elliptic-falcate, falcate to semiorbicular, base attenuate, subcordate to cordate, when non-foliaceous ovate to lanceolate, base truncate, persistent to caducous. **Leaves** alternate and distichous, paripinnate, 1- to 7-jugate, usually glabrous, petioles, rachis and petiolules terete to canaliculate, glabrous, rarely puberulous in *E. oleifera*; blades coriaceous to chartaceous, glabrous, pellucid-punctate to epunctate, discolorous or not, equilateral, or inequilateral and falcate, elliptic, ovate to lanceolate, apex usually attenuate to acuminate, but acute, obtuse to rounded in two species, base symmetrical to asymmetrical, or oblique, usually lower pair base more rounded and upper pair base more cuneate, margin flat to revolute, secondary venation with one or two intramarginal veins, usually vein closer to the margin not continuous, main vein straight or curved in falcate leaflets, prominent to depressed on the adaxial side, 10–40 secondary veins, spacing uniform, angle uniform, intersecondary veins conspicuous, tertiary veins regular polygonal reticulate, conspicuous to inconspicuous, areoles smaller and concave or larger and plane. **Inflorescences** a raceme or panicle, terminal, axillary, sometimes ramiflorous or cauliflorous, short and erect or long and pendulous, glabrous or with indumentum, lateral racemes alternate, distichous or spirally arranged, peduncle sessile up to 4.0 cm long in short and erect inflorescences, or up to 3.0 m long in long and pendulous inflorescences; one bract at the base of the pedicel; one pair of bracteoles attached to different portions of the pedicels, imbricate, free, not enclosing the developed flower buds, apex gland present or absent. **Flowers** alternate and spirally arranged, pedicellate, hypanthium cup-shaped or tubular, inner wall with nectar-producing glands; sepals four, free, unequal, the outer ones larger, apex gland present or absent, inner surface glabrous, outer surface glabrous or with indumentum, inner sepals scarious marginally; petals five, adaxial petal superinvolute forming a tube or involute but not forming a tube, flabellate, oblate to broadly obovate, apex rounded to truncate, base attenuate to truncate, white, cream, greenish, lilac, purple, pink to red, glabrous or with indumentum in *E. venosa*, other four petals reduced to petalodia, up to 7.5 mm long; stamens 10, all fertile or up to 5 staminodial, inserted when the adaxial petal is tubular, exserted in the non-tubular ones, filaments heteromorphic, joined basally in a tube, or in a diadelphous sheath with dorsal one free, usually glabrous on the free part, anthers all equal or dimorphic; ovary with stipe inserted centrally in the hypanthium, glabrous or with indumentum, style usually longer than the largest filaments, glabrous, adaxial groove present, stigma obtuse to capitate, entire or 2-lobed. **Fruit** legume, with stipe, equilateral or inequilateral and falcate, wood, flattened, glabrous or with indumentum, dehiscent, valves twisted after opening, seeds 1-few, flattened.

Etymology:—*Eperua* is derived from the fruit shape of its type species, *E. falcata.* The term "eperu" is a Galibi name for the fruit of *E. falcata* (Aublet 1775), which translates to "sabre" in English. This refers to a curved-blade sword (Collins 2023), resembling the curved shape of the fruit.

Key to all species, subspecies and varieties of *Eperua*

1. Leaflets secondary venation with one intramarginal vein very close to the margin..**2**
- Leaflets secondary venation with two intramarginal veins or, if one intramarginal vein, vein not very close to the margin....**7**
2. Inflorescence long and pendulous, corolla non-tubular, fruits elliptic-falcate, narrowly elliptic-falcate, or lanceolate-falcate..**3**
- Inflorescence short and erect, corolla tubular, fruits oblanceolate to obovate, never falcate..**5**
3. Blades minutely pellucid-punctate, not all areoles have one dot, inflorescences with lateral racemes pendulous, adaxial petal nonwhite and glabrous..***E. falcata***
- Blades pellucid-punctate, each areole has at least one conspicuous dot, inflorescences with lateral racemes erect to patent, adaxial petal non-white and sericeous at the base, or white and glabrous..4
4. Petals deep-rose, sericeous at the base.. ***E. venosa***
- Petals white, glabrous..***E. leucantha***

5. Leaflets abaxial surface densely papillate-ceriferous, inflorescence glabrous..***E. purpurea***
- Leaflets abaxial surface not densely papillate-ceriferous, inflorescence strigose to tomentose, rarely pubescent.. **(*E. oleifera*)**
6. Treelet, shrub, leaflets basal pair with base obtuse to rounded, rarely cordate or subcordate............ ***E. oleifera* var. *oleifera***
- Tall tree, leaflets basal pair with base rounded, subcordate to cordate... ***E. oleifera* var. *campestris***
7. Inflorescence long and pendulous, corolla non-tubular..**8**
- Inflorescence short and erect, corolla tubular or non-tubular..**10**
8. Inflorescence glabrous, fruits glabrous... ***E. glabra***
- Inflorescence tomentulose, coppery, fruits tomentose, coppery...**9 (*E. rubiginosa*)**
9. Leaves (2–)3(–4)-jugate, pedicel 0.6–2.0 mm in diameter.. ***E. rubiginosa* var. *rubiginosa***
- Leaves (3–)4–5-jugate, pedicel 2.0–3.3 mm in diameter..***E. rubiginosa* var. *grandiflora***
10. Corolla non-tubular, stamens exserted, fruits oblanceolate-falcate...**11**
- Corolla tubular, stamens inserted, fruits oblong, obovate, orbicular, elliptic, never falcate..**15**
11. Flowers with ovary tomentose, fruit tomentose or tomentulose..**12**
- Flowers with ovary glabrous, fruits glabrous..**14**
12. Main vein depressed on the adaxial surface, bracteoles 9.8–12.7 × 6.5–9.8 mm**,** persistent, stamens entirely glabrous... ***E. cerradoensis***
- Main vein prominent on the adaxial surface, bracteoles 1.9–5.0 × 2.3–4.2 mm**,** caducous, stamens sheath non-glabrous.....**13**
13. Stipules free, blades pellucid-punctate, rarely inconspicuous pellucid-punctate, stamens sheath tomentose......***E. duckeana***
- Stipules joined at the base, blades inconspicuous pellucid-punctate to epunctate, stamens sheath irregularly tomentose...***E. reddeniae***
14. Stipules entirely joined, leaflets with main vein depressed on the adaxial surface, stamens joined basally in a tube, glabrous…..***E. froesii***
- Stipules free, leaflets with main vein prominent on the adaxial surface, stamens joined basally in a diadelphous sheath 9+1, irregularly tomentose.. ***E. schomburgkiana***
15. Apex of the leaflets acute, obtuse, rounded to emarginate, stamens glabrous..**16**
- Apex of the leaflets attenuate, acuminate to caudate, stamens non-glabrous..**17**
16. Treelets, leaflets elliptic to obovate, bracteoles 7.0–8.0 × 7.0–8.0 mm, flowers with hypanthium 5.0 mm long, ovary more than twice (7–8 mm long) longer than the stipe (2.0–3.0 mm long)..***E. banaensis***
- Tall trees, leaflets oblong to elliptic, bracteoles 2.0 × 1.0–2.0 mm, flowers with hypanthium 2.0–3.0 mm long, ovary almost as long (5.0 mm long) as the stipe (4.0 mm long)...***E. obtusata***
17. Inflorescence glabrous..**18**
- Inflorescence non-glabrous (puberulous, strigulose, tomentose, pubescent, or strigose)...**21**
18. Leaflets blades with margin revolute, bracteoles caducous..**19 (*E. glabriflora*)**
- Leaflets blades with margin flat, bracteoles persistent...**20**
19. Flowers with ovary always glabrous... ***E. glabriflora* var. *glabriflora***
- Flowers with ovary glabrous or tomentose in the same inflorescence.................................***E. glabriflora* var. *gynopubescens***
20. Leaves 3–5-jugate, bracteoles attached to the lower portion of the pedicels.......................... ***E. jenmanii* subsp. *sandwithii***
- Leaves 2–3-jugate, bracteoles attached at the base of the hypanthium.. ***E. grandiflora* subsp. *ciliata***
21. Lower pair of leaflets with base subcordate to cordate, ovary tomentose to villous......................................***E. manausensis***
- Lower pair of leaflets with base obtuse to rounded, rarely subcordate, ovary glabrous or sericeous in *E. grandiflora* subsp. *guyanensis*...**22**
22. Stipules joined at the base, leaves 3–5-jugate, bracteoles attached to the lower portion of the pedicels...***E. jenmanii* subsp. *jenmanii***
- Stipules free, leaves 2–3(–4)-jugate, bracteoles attached to the lower middle portion of the pedicels, or to the higher portion of the pedicels, or at the base of the hypanthium...**23**
23. Inflorescence puberulous, bracteoles attached to the lower middle portion of the pedicels....................................***E. bijuga***
- Inflorescences pubescent to tomentose, sometimes puberulous, bracteoles attached to the higher portion of the pedicels or at the base of the hypanthium.. 24 (***E. grandiflora***)
24 Leaflets with margin revolute, flowers with ovary sericeous, fruits puberulous ....***E. grandiflora* subsp. *guyanensis***
- Leaflets with margin flat, flowers with ovary glabrous, fruits glabrous.............................. ***E. grandiflora* subsp. *grandiflora***

1. ***Eperua banaensis*** G.A.Romero & Aymard (2019: 341) (Figures 13, 16a, d)

Type**:—**VENEZUELA. Amazonas: Municipio Autónomo Maroa, cuenca del río San Miguel, alto caño Mee, bana al sur de la serrania de Cariche, 106 m, 2˚44’14”N 66˚20’7”W, 18 September 2011, *Romero G.A. et al. 4079* (holotype VEN not seen, isotypes GH not located, MO not seen, TFAV not seen).

Treelet 2.0–5.0 m tall. **Trunk** not seen. **Stipules** free, non-foliaceous, caducous. **Leaves** 2-jugate; **petioles** 1.7–4.0 cm long; **rachis** 2.0–4.5 cm long; **petiolules** 6.4–9.0 mm long; **blades** 8.2–14.0 × 3.7–6.6 cm, coriaceous, glabrous, pellucid-punctate, discolorous, slightly inequilateral, lower pair oblong, elliptic to narrowly elliptic, upper pair elliptic to obovate, apex apiculate, obtuse, rounded to emarginated, mucronate, base asymmetrical (upper pair) to symmetrical, lower pair base obtuse, upper pair base obtuse to cuneate, margin flat, **secondary venation** with one intramarginal vein, main vein slightly curved, depressed to prominent on the adaxial surface, tertiary veins conspicuous, areoles larger, concave. **Inflorescences** cauliflorous or ramiflorous, racemose or cauliflorous flowers, erect, strigulose, 1.5–11.0 cm long; **bracts** caducous, not seen; **bracteoles** 7.0–8.0 × 7.0–8.0 mm, ovate, apex gland absent, puberulent externally, caducous, attached to the lower portion of the pedicels; **pedicel** ca. 10 mm long, diameter not seen, not twisted, pubescent; **buds** not seen. **Flowers**: **hypanthium** 5.0 mm long, diameter not seen, cup-shaped, inequilateral, pubescent; **sepal** 2.3–2.7 × 0.8–0.9 cm, oblong to ovate, unequal, the outer ones larger, cucullate, apex gland present on the outer ones, purple, pubescent, inner sepals scarious marginally; **adaxial petal** 5.0 × 7.0 cm, flabellate, tubular, apex rounded, crisped, base attenuate, purple, abaxially glabrous, adaxially with two white, lanose structures near the margins; **petalodia** 6.0–7.0 × 2.6–3.5 mm; **stamens** inserted, joined basally in a diadelphous sheath, dorsal one free, filaments 2.3–4.0 cm long, sheath inequilateral, glabrous, anthers 6.5–7.5 × 2.0–3.0 mm, rectangular; **ovary** 7.0–8.0 × 2.5 mm, oblong-obovate, sericeous, ovule not seen, stipe 2.0–3.0 mm long, glabrous, style ca. 3.5 cm long, stigma bilobate. **Legumes** not seen (description based on Romero & Aymard 2019 and selected materials).

Phenology:—Flowering in September and November; fruiting in February.

Habitat:—White sand shrubby communities in low Venezuelan *bana*, common in the ecotone *bana*-forest, on white sand soil, at 106 m elev.

TABLE 2. Morphological differences between *Eperua* species with short and erect inflorescence and tubular corolla: *E. banaensis*, *E. bijuga*, *E. glabriflora*, *E. grandiflora*, *E. jenmanii*, *E. manausensis*, *E. obtusata*, *E. oleifera*, and *E. purpurea*. Legend, *sometimes entirely villous or pubescent to puberulous.

Species	Stipules conation	Secondary venation	Inflorescence indumentum	Bracteoles insertion on the pedicels	Bracteoles phenology	Stamens indumentum	Ovary indumentum	Distribution
E. manausensis	Free	Two intramarginal veins	Dense indumentum	Low to middle	Caducous	Tomentose	Tomentose to villous	Central Amazonia
E. grandiflora	Free	One or two intramarginal veins	Dense indumentum or glabrous	High or at the base of the hypanthium	Persistent	Irregularly tomentose, pubescent to puberulous*	Glabrous or sericeous	Guyana Shield
E. oleifera	Entirely joined	One intramarginal vein very close to the margin	Dense indumentum	High or at the base of the hypanthium	Persistent	Villous	Glabrous	Central Amazonia
E. jenmanii	Joined at the base	Two intramarginal veins	Scarce indumentum or glabrous	Low	Persistent	Villous, pubescent to puberulous	Glabrous	Guyana Shield
E. banaensis	Free	One intramarginal vein	Scarce indumentum	Low	Caducous	Glabrous	Sericeous	Guyana Shield
E. obtusata	?	One intramarginal vein	Scarce indumentum	Low	Caducous	Glabrous	Sericeous	Guyana Shield
E. glabriflora	Free	Two intramarginal veins	Glabrous	Low to middle	Caducous	Tomentose, pubescent to puberulous	Glabrous	Central Amazonia
E. bijuga	Free	Two intramarginal veins	Glabrous	Low to middle	Persistent	Puberulous	Glabrous	Eastern Amazonia
E. purpurea	Entirely joined	One intramarginal vein very close to the margin	Glabrous	Middle	Persistent	Villous	Glabrous	Central Amazonia / Guyana Shield

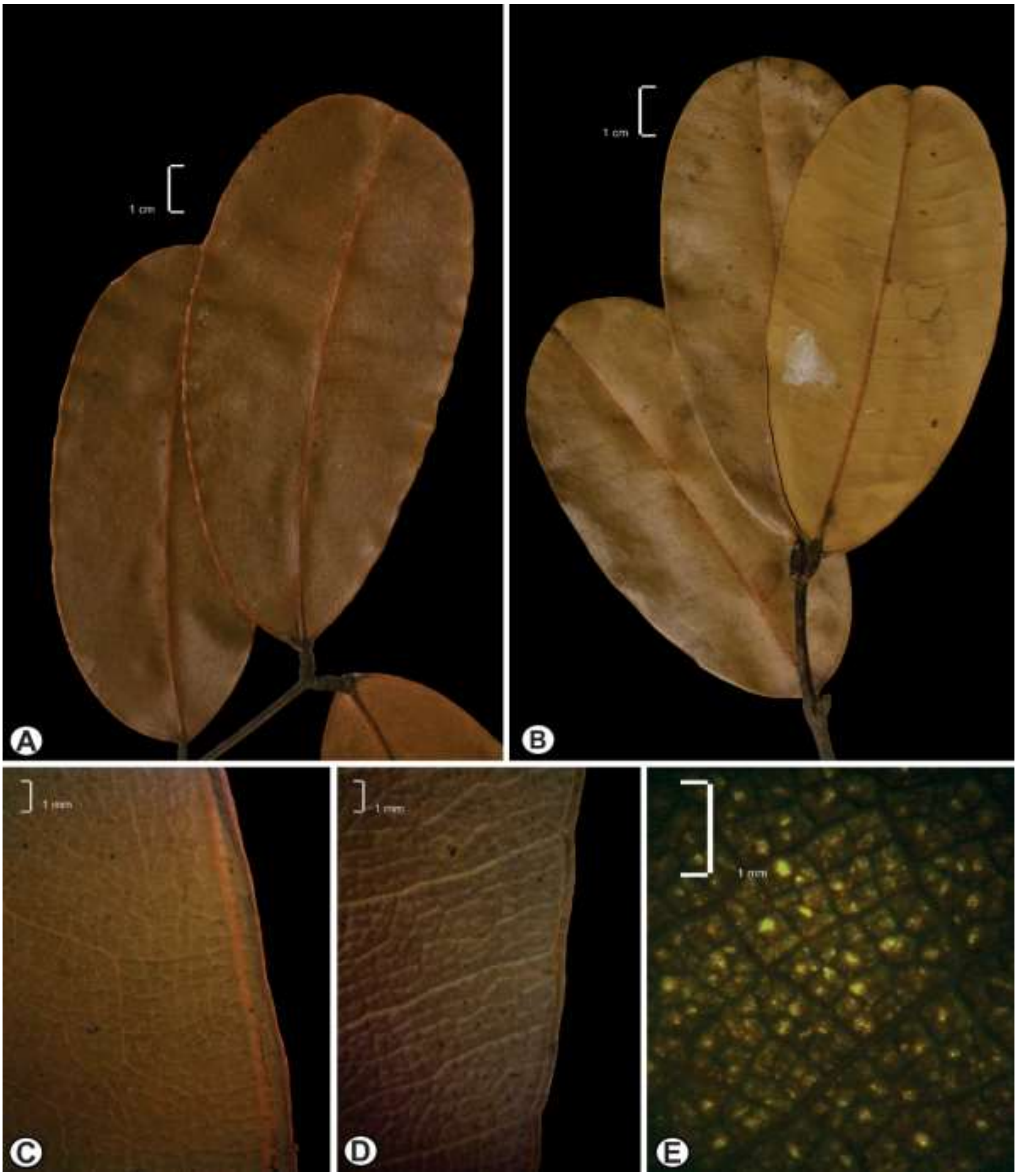


FIGURE 16. *Eperua banaensis* and *Eperua obtusata*: A. leaflets, upper leaflet obovate, *E. banaensis*; B. leaflets, upper pair elliptic to oblong, *E. obtusata*; C. intramarginal vein with one intramarginal vein, *E. obtusata*; D. intramarginal vein with one intramarginal vein, *E. banaensis*; E. pellucid-punctate blade, *E. obtusata*. Specimens, A, D: *Collela M. et al. 1864*; B, C, E: *Coomes D. 207*. Photos E.A. Fortes.

Conservation status:—Categorized as Data Deficient (DD) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022) due to the lack of access to its collections.

Occurrence in protected areas:—Unknown.

Etymology:—The specific epithet relates to its habitat in the *banas* (Romero & Aymard 2019).

Vernacular names:—Unknown.

Uses:—Unknown.

Distribution:—Venezuela (Amazonas).

Taxonomic notes:—*E. banaensis* and *E. obtusata* are distinct from other species of the genus due to their leaflets with rounded, obtuse, acute to emarginate apices. All other species in the genus have attenuate, acuminate to caudate apices. Morphologically, they share 2-jugate leaves, short and erect inflorescence, tubular corolla, inserted stamens, and the same pattern of indumentum on reproductive organs. Among the species with tubular corolla, *E. bananesis* and *E. obstusata* are the only ones with the combination glabrous sheath and indumented ovary (Table 2). We recognize *E banaensis* as a treelet from low Amazonian *campinarana* or *bana*, while *E. obtusata* as a tall tree found in the tall *campinarana*. Additionally, *E. banaensis* differs from *E. obtusata* by the elliptic to obovate leaflets (vs. oblong to elliptic in *E. obtusata*), larger [7.0–8.0 × 7.0–8.0 mm] bracteoles (vs. smaller [ca. 2.0 × 1.0–2.0 mm] in *E. obtusata*), and longer [5.0 mm long] hypanthium (vs. shorter [2.0–3.0 mm long] in *E. obtusata*), petal with two white, lanose structures near the margins (vs. absent in *E. obtusata*), ovary twice the length [7.0–8.0 mm long] of the stipe [2.0–3.0 mm long] (vs. relatively the same length [5.0 mm long] as the stipe [4 mm long] in *E. obtusata*), glabrous stipe (vs. sericeous in *E. obtusata*), and bilobate stigma (vs. truncate in *E. obtusata*). Romero & Aymard (2019) referred the collection *Colella M. et al. 1864* as *E. obtusata*, and did not mention *Guanchez-Meza F.J. 2163*. Here we recognized these collections also as *E. banaensis* for being treelets from the *bana* and having elliptic to obovate leaflets. In addition to the type collection, we recognized one more sample (*Coomes D. 207*) as *E. obtusata*. This collection differs from *E. banaensis* by being tall trees from the tall *campinarana* with elliptic to obtuse leaflets.

Selected specimens:—VENEZUELA. Amazonas, Casiaquire, rio Casiaquire, dos vueltas abajo de Capihuara, 06 February 1991, *Collela M. et al. 1864* (K, NY). San Fernando de Atabapo, Zona 10, cuesta de arenisca de grano fino al pié del cerro Duida, 360 m elev., 3°23’0”N, 65°40’0”W, 10 November 1982, *Guanchez-Meza F.J. 2163* (MO).

2. ***Eperua bijuga*** Martius ex Bentham (1870: 226) (Figures 10, 17, 18)

Type (designated by Cowan 1975)**:**—BRAZIL. Pará: In sylvis inundatis ad insulam Marajo, May 1820, *Martius C.F.P. s.n.* (lectotype K[000555103] image!, isolectypes LE[00002232] image!, M[0215266] image!, M[0215267] image!, M[0215268] image!, M[0215270] image!).

Tree 3.0–33.0 m tall. **Trunk** 18.0–31.8 cm in diameter, bark brown, striate. **Stipules** 1.1–14.2(–18.3) × 0.5–10.0(–13.0) mm, free, foliaceous or non-foliaceous, caducous to persistent. **Leaves** 2(–3)-jugate; **petioles** 0.6–3.1(–6.8) cm long; **rachis** (1.3–)2.0–6.4(–9.3) cm long; **petiolules** 4.4–12.3 mm long; **blades** (3.1–)6.4–17.6(–22.4) × 2.8–9.2 cm, coriaceous, glabrous, sparsely pellucid-punctate, sometimes pellucid-punctate or epunctate, slightly discolorous, equilateral, lower pair elliptic to ovate, rarely lanceolate, smaller, upper pair elliptic, apex attenuate to acuminate, sometimes acute, mucronate, base symmetrical, rarely slightly asymmetrical, with one pair of glands, lower pair base obtuse, rarely rounded, subcordate or cordate, upper pair base obtuse, rarely rounded or cuneate, margin flat, **secondary venation** with two intramarginal veins, vein closer to the margin not continuous, sometimes continuous, main vein straight, prominent near the base, sometimes depressed, on the adaxial surface, tertiary veins conspicuous, areoles smaller, concave. **Inflorescences** terminal, rarely axillary or ramiflorous, panicle or raceme, erect, puberulous, trichomes white, 1.2–3.6 cm long, lateral racemes 0.9–2.6 cm long, alternate and spirally arranged or distichous; **bracts** 3.0–3.7 × 4.5 mm, oblate, apex gland absent, puberulous, trichomes white, caducous, rarely persistent; **bracteoles** 3.3–5.0 × 2.1–6.3 mm, oblate, sometimes broadly ovate, apex gland absent, puberulent externally, glabrous within, sometimes puberulent within, trichomes white, persistent, rarely caducous, attached to the lower middle portion of the pedicels; **pedicel** 3.3–9.5 mm long, 1.0–2.2 mm in diameter, not twisted, puberulent, trichomes white; **buds** 1.0–2.3 cm long, 0.6–1.7 cm in diameter, puberulous, trichomes white. **Flowers**: **hypanthium** 1.6–3.6 mm long, 2.5–7.6 mm in diameter, cup-shaped, inequilateral, puberulent to puberulous, trichomes white; **sepal** 1.3–3.0 × 0.5–1.3 cm, oblong to obovate, unequal, the outer ones more robust, the dorsal one larger, cucullate, apex gland absent, green, puberulent, inner sepals scarious marginally, trichomes white; **adaxial petal** 3.8–8.0 × 3.0–7.3 cm, flabellate, tubular, apex rounded, crisped, base attenuate, lilac with white nectar guide, pink, rose, purple, purple-red to red, glabrous; **petalodia** 0.8–7.3 × 0.4–1.4 mm; **stamens** inserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 3.0–5.2 cm long, shorter filaments 1.7–3.1 cm long, sheath inequilateral, shorter side 5.5–17.3 mm long, longer side 8.9–24.0 mm long, sheath puberulous, free filament glabrous, trichomes white, anthers 3.2–5.0 × 0.7–2.3 mm, rectangular; **ovary** 5.3–11.8 × 1.8–5.1 mm, falcate, rarely obovate or oblong-obovate, glabrous, 1? ovule, stipe 2.8–9.5(–13.4) mm long, glabrous, style 2.4–3.8 cm long, stigma capitate, sometimes obtuse. **Legumes** 7.6–15.4 × 4.6–8.6 cm, stipe 1.0–2.5 mm long, oblong, apex obtuse, sometimes truncate, rarely rounded, apiculate, margin thickened, brown, rarely redbrown or dark-brown, with transversal veins, glabrous, foveate. **Seeds** 1–2 per fruit, 4.0–7.3 × 3.2–4.7 cm, ovate to inequilateral ovate, dark-brown.

Phenology:—Flowering from March to August; fruiting throughout the year.

Distribution:—Brazil (Pará and Amapá), and one collection from French Guiana without locality.

FIGURE 17. *Eperua bijuga*: A. trunk base; B. trunk; C. bark of a younger specimen; D. bark of an older specimen; E. sapwood and heartwood; F. leaves; G. fruits. Specimens, A–G: *Fortes E.A. et al. 189*. Photos, E.A. Fortes.

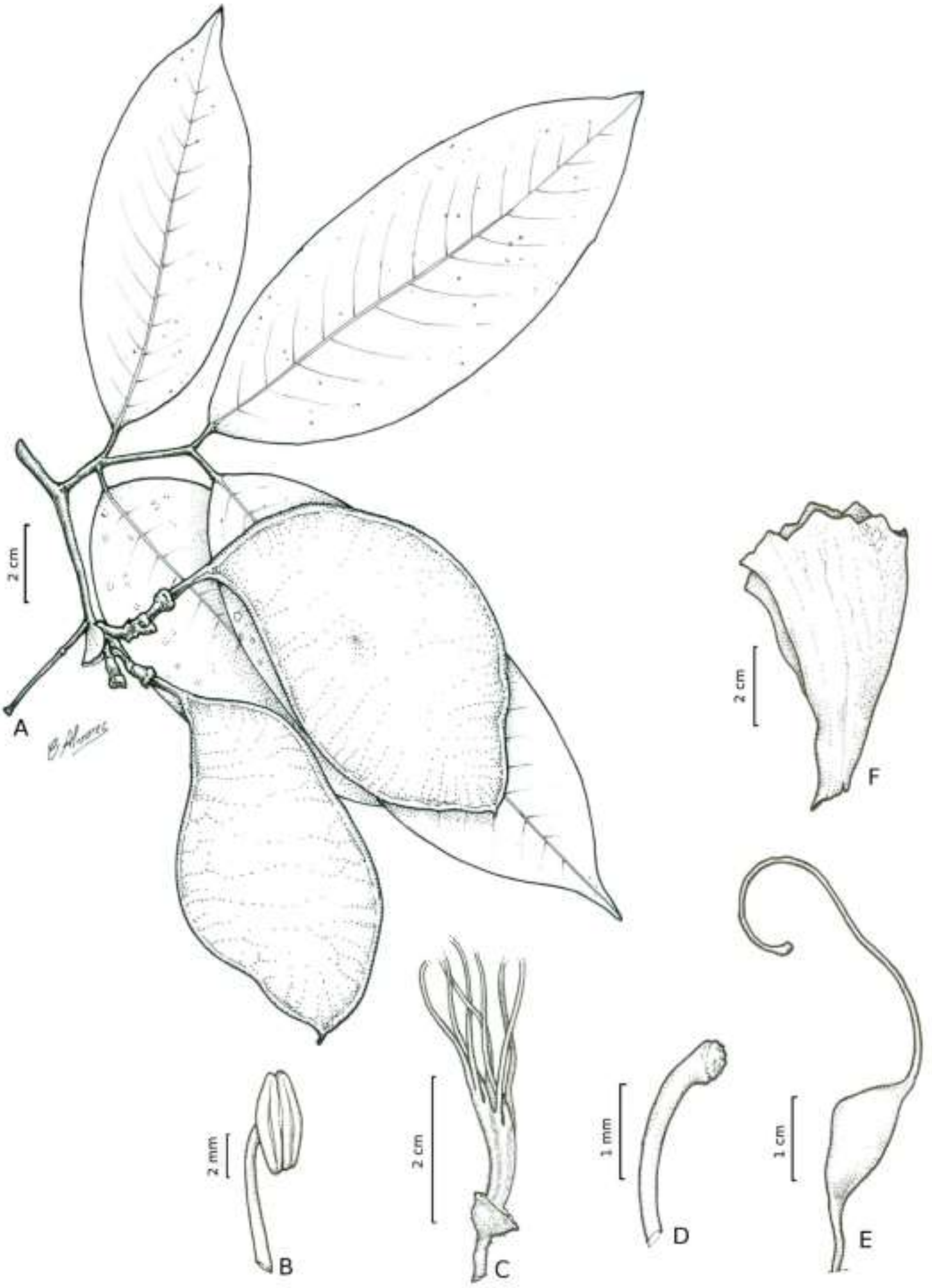


FIGURE 18. *Eperua bijuga*: A. fruiting branchlet; B. anther and part of the filament; C. puberulent to puberulous hypanthium and puberulous sheath; D. detail of a capitate stigma; E. glabrous stipe and ovary; F. adaxial petal. Specimens, A: *Ferreira G.C. & Ribeiro B.G.S. 496*, B–F: *Fróes R. de L. 32988*. Illustrated by Carlos Alvarez.

Habitat:—Floodplain forests, mainly in *igapó* forest, but also in *várzea* forest. It is also found in the Amapá (Brazil) savannas in river-associated vegetation.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 129,115.212 km^2 and the estimated area of occupancy is 148.000 km^2.

Occurrence in protected areas:—Floresta Nacional de Caxiuanã (Brazil, Pará) and Floresta Nacional do Amapá (Brazil, Amapá) (Silva *et al.* 2015).

Etymology:—The specific epithet relates to its 2-jugate leaves.

Vernacular names:—apá (*Rabelo B.V. et al. 3307*, *Rosa N.A. 1288*), muirapiranga (*Oliveira E. 4929*, *Cruz E.D. 1123*), muirapironga (*Oliveira E. 4929*).

Uses:—it is described as potentially ornamental (*Souza L.A.G. de 13_97*).

Taxonomic notes:—*Eperua bijuga* differs from all other species by its 2-jugate leaves, non-falcate leaflets with flat margin and one pair of glands at the adaxial base, tubular corolla, puberulous inflorescences, and persistent bracteoles. Among the species with tubular corolla, *E. bijuga* shares some characteristics with *E. glabriflora*, *E. grandiflora* subsp. *grandiflora*, *E. grandiflora* subsp. *ciliata*, *E. jenmanii*, *E. oleifera*, and *E. purpurea*, such as a non-glabrous sheath and glabrous ovary. However, *E. bijuga* is distinguished by its falcate ovary (vs. oblong or oblong-obovate in the others). *Eperua bijuga* is most morphologically similar to *E. glabriflora*. Both species share 2-jugate leaves, nonfalcate leaflets with two intramarginal veins, and a corolla of similar size and shape. However, *E. bijuga* differs by its puberulous to puberulent inflorescence, buds, sepals, and hypanthium (vs. glabrous in *E. glabriflora*), and smaller and persistent bracteoles (vs. larger and caducous in *E. glabriflora*).

Selected specimens:—BRAZIL. **Amapá**, Ferreira Gomes, Mangabeira, 29 May 2019, *Rocha A.E.S. & Costa-Neto S.V. da 2165* (MG). Macapá, braço do rio Macacoari, July 1982, *Rabelo B.V. & Cardoso J.O. 1261* (HAMAB, MG, NY, US). Porto Grande, Cupixi, Estrada Perimetral Norte, 15 December 1985, *Rabelo B.V. et al. 3307* (HAMAB, INPA, NY). Tartarugarzinho, Rio Apurena, 22 July 1951, *Fróes R. de L. & Black G.A. 27607* (IAN, NY, R). **Pará**, Afuá, rio urucu, 14 November–04 December 1992, *Maciel U.N. et al. 2147* (MG). Ananindeua, vila Marituba, Igarapé Marituba, 03 May 1991, *Almeida S.S. et al. 458* (MG). Belém, Tapanã, beira da estrada, 02 May 1975, *Oliveira E. 6291* (MG, RB); IPEAN. Reserva do Aurá. L.166–70-sn, 03 June 1968, *Pires J.M. & Silva N.T. 11785* (HUEFS, IAN, RB, MFS). Breves, Araurá. Rio Maratana, afluente do rio aramé (Ilha Breves), margem inundada, 01 December 1922, *Ducke W.A. s.n. RB16927* (P, RB, U). Melgaço, Floresta Nacional de Caxiuanã, Ima 6, rio Curuzinho, 1°72’25”S 51°43’11”W, 20 April 2004, *Freitas M.A. de et al. 1093* (INPA, MG, NY, RB). Moju, Experimental Field Station of Embrapa Amazônia Oriental, PA-150, km 34, 2°10’50”S 48°0’0”W, 15 May 2008, *Torke B.M. 432* (IAN, RB). Mosqueiro, Rio Pará, 20 June 1943, *Ducke W.A. 1260* (IAN, F,K, MG, MO, NY, R, US); unknown locality, 13 October 1923, *Ducke W.A. s.n. RB16928* (RB, U). Muaná, Trajeto Monte Alegre/Santo André, 24 April 1982, *Dantas M. & Silva N.T. da 1182* (IAN). Portel, FLONA de Caxiuanã,margem do igarapé Caquajó, 1°57’00.0”S 51°35’00.0”W, 08 July 2007, *Félix-da-Silva M.M. et al. 241* (IAN, MG); região do Anapú, Rio Tapacú, 10 May 1956, *Fróes R. de L. 32776* (IAN); região do Anapú, Rio Maparauá, 05 August 1956, *Fróes R. de L. 32938* (IAN, MG). Salvaterra, Ilha do Marajó Rio Paracauarí, margem do campo de pastagem do Sítio Caçador, 06 September 1969, *Oliveira E. 4929* (IAN); Marajó, margem direita do Rio Jubim, próximo da Rod. Salvaterra-Joanes, a 16 Km de Joanes, 24 April 1980, *Rosa N.A. 3628* (INPA, MG, NY). Santa Isabel do Pará, Caraparú, 25 April 1977, *Silva M.G. da 3391* (MG). Soure, insula Marajó, 13 April 1927, *Ducke W.A. s.n. RB20312* (K, RB, U, US). Tailândia, Fazenda Borba Gato, near Rio Acará, 30 km W of Tomé-Açú-Paragominas road, approx. 30 km S of Tomé-Açú, 2°40’00.0”S 48°35’00.0”W, 08 November 1980, *Daly D.C. et al. 889* (INPA, IAN, K, MG, NY, US). Tomé Açu, margem do rio Acará, 02 January 1978, *Nascimento O.C. do 398* (MG, NY, US). **Rio de Janeiro** (cultivated), Rio de Janeiro, Arboreto do Jardim Botânico do Rio de Janeiro, 09 August 1991, *Fontella H. & Caruso J. 2770* (RB). **FRENCH GUIANA (cultivated?).** unknown locality, undated, *s.c. s.n. P03465139* (P).

3. ***Eperua cerradoensis*** E.A. Fortes, G.S. da Silva & Mansano (2023: 199) (Figure 8; Fortes *et al.* 2023 Figures 3–5)

Type:—BRAZIL. Maranhão, Caxias, Povoado Morro Agudo, Segundo Distrito, rio Itapecuru, área rural, 4°32’18”S 43°03’46”W, 24 March 2022, *Gonçalves A.S. 02* (holotype RB[01458708]!, isotypes INPA!, UEC!, US!).

Tree or treelet (1.6–)3.5–11.5 m tall. **Trunk** 10.0–15.7 cm in diameter, bark grayish to brownish, smooth to striate, lenticellate. **Stipules** 15.1–40.9 × 11.8–22.7 mm, entirely joined, foliaceous, semiorbicular, persistent. **Leaves** (4–)5–7-jugate; **petioles** 2.0–3.8 cm long; **rachis** 15.0–24.0 cm long; **petiolules** 5.3–8.4 mm long; **blades** 7.5–14.1 × 3.5–5.2 cm, coriaceous, glabrous, inconspicuous pellucid-punctate to epunctate, not discolorous, equilateral, lower pair ovate, middle pair ovate to elliptic, upper pair elliptic, apex attenuate to acuminate, mucronate, base asymmetrical, lower pair base rounded, middle pair base rounded to obtuse, upper pair base rounded to obtuse, margin revolute, secondary venation with two intramarginal veins, vein closer to the margin not continuous, main vein straight, depressed on the adaxial surface, tertiary veins slightly conspicuous. **Inflorescences** terminal, raceme, erect, tomentose, whitish, 10.0–20.0 cm long; **bracts** 8.4 × 4.8 mm, ovate, cucullate, apex gland absent, tomentose, whitish, caducous; **bracteoles** 9.8–12.7 × 6.5–9.8 mm, ovate, cucullate, apex gland absent, tomentose externally and within, whitish, persistent, attached to the lower portion of the pedicels; **pedicel** 18.0–24.4 mm long, 3.0–4.8 mm in diameter, not twisted, tomentose, whitish; **buds** 1.3–1.5 cm long, 1.0 cm in diameter, tomentose, whitish. **Flowers**: **hypanthium** 5.5–7.8 mm long, 7.7–10.6 mm in diameter, cup-shaped, equilateral, tomentose, whitish; **sepal** 2.3–2.9 × 1.3–1.7 cm, elliptic, unequal, the outer ones larger, cucullate, apex gland absent, greenish-white, tomentose, inner sepals scarious marginally, whitish; **adaxial petal** 2.3–3.3 × 5.5–6.5 cm, oblate, non-tubular, apex rounded, base truncate, white, glabrous; **petalodia** 2.7–8.8 × 1.1–3.0 mm; **stamens** exserted, joined basally in a tube, longer filaments 6.0 cm long, shorter filaments 5.1 cm long, tube equilateral, 2.8–3.4 mm long, glabrous, anthers 10.8–12.4 × 2.6–2.9 mm, rectangular; **ovary** 9.6–13.0 × 3.3–3.7 mm, oblanceolate, tomentose, greenish, stipe 5.8–10.5 mm long, tomentose, style 2.7–4.9 cm long, glabrous, stigma capitate. **Legumes** 22.0 × 7.0 cm, stipe 2.6 cm long, elliptic-falcate, apex obtuse, apiculate, dorsal margin alate, yellowish-green, veins absent, tomentose, yellowish. **Seeds** 4 per fruit, 3.2 × 2.0 cm (immature), obovate, whitishbrown.

Phenology:—Flowering in March and September; fruiting in September.

Distribution:—Described as having a distribution restricted to the Eastern region of Maranhão (Brazil) in the Itapecuru and Munin Basins in the Cerrado Biome (Fortes *et al.* 2023). Additional collections (*Lui Y. et al. 2* and *178*) of *E. cerradoensis* were found near the type location, in the municipality of Altos (Piauí, Brazil) within the Parnaiba Basin. Although the locality is considered part of the Caatinga Biome, it is situated at the border of the Cerrado Biome (IBGE 2019).

Habitat:—The only species not occurring in the Amazonian region. *E. cerradoensis* was collected in the phytofisiognomies of *cerradão* (a type of savanna woodland), secondary forest, ombrophilous lowland forest with a predominance of palm trees, and in the open ombrophilous forest in the Cerrado Biome; and in semideciduous seasonal forest within the Caatinga Biome. It grows in stony clayey soils and is found at elevations ranging from 57 to 152 meters.

Conservation status:—Categorized as Vulnerable (VU) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 7,323.777 km$_2$ and the estimated area of occupancy is 24.000 km$_2$.

Occurrence in protected areas:—Unknown.

Etymology:—The specific epithet alludes to its occurrence in the Cerrado Biome (Fortes *et al.* 2023).

Vernacular names:—Embira de sapo (*Almeida A.B. 134*), imbira de sapo (*Almeida A.B. 152*), pitu (*Oliveira D. 66*), pracateira (*Lui Y. et al. 2*, *Marinho M.A.O. 606*, *629, Santos R.S. 296*).

Uses:—In the type locality, Povoado Morro Agudo, it is mainly used to make charcoal and fences (Fortes *et al.* 2023). It also can be used in house construction, but this is not a common usage because the local population reported that the plant is very favorable to wood-dwelling termites (Fortes *et al.* 2023).

Taxonomic notes:—*Eperua duckeana*, *E. froesii*, *E. cerradoensis*, *E. reddeniae*, and *E. schomburgkiana* are the only species within the short and erect inflorescence group that have a non-tubular corolla, exserted stamens, and falcate fruit with a 3:1 proportion (vs. tubular corolla, included stamens, non-falcate fruit with a 1:1 to 2:1 length/ width proportion in other short and erect inflorescence species). They also share multijugate leaves with straight leaflets and inflorescence with dense indumentum. Furthermore, *E. cerradoensis* shares white petals with *E. duckeana* and *E. schomburgkiana*; glabrous stamens joined at the base forming a tube with *E. froesii*; and tomentose ovary with *E. duckena.* The similarities and differences between species of this group are summarized in Table 3. *Eperua cerradoensis* is a distinct species by the completely glabrous stamens joined basally in a tube, tomentose ovary and fruits, and other vegetative characteristics. It is found primarily in the Cerrado Biome, differing from other species with distribution restricted to the Amazonian region (see Table 3, and Figure 8).

Specimens examined :—BRAZIL. Maranhão, BRAZIL. Maranhão, Caxias, Povoado Morro Agudo, Segundo Distrito, área rural, 4°32’18.2”S 43°03’45.5”W, 18 September 2020, Gonçalves A.S. 01 (IAN, HABIT). Chapadinha, Cajazeiras, conglomerado MA-255, subunidade 1, subparcela 5, indivíduo 16, F6, 60 m elev., 3°46’48”S 43°33’36”W, 30 May 2018, Marinho M.A.O. 606 (UB); Cajazeiras, conglomerado MA-255, subunidade 3, subparcela 10, indivíduo 11, F8, 60 m elev., 3°46’48”S 43°33’36”W, 30 May 2018, Marinho M.A.O. 629 (UB). Nina Rodrigues, Mangueira, conglomerado MA-202, subunidade 1, subparcela 1, indivíduo 4, F6, 57 m elev., 3°25’12”S 43°44’24.1”W, 05 September 2018, Almeida A.B. 134 (UB); Mangueira, conglomerado MA-202, subunidade 3, subparcela 10, indivíduo 13, F8, 57 m elev., 3°25’12”S 43°44’24”W, 05 September 2018, Almeida A.B. 152 (UB). Timbiras, comunidade Morada Nova, conglomerado MA-305, subunidade 2, subparcela 1, indivíduo 10, F6, 94 m elev., 4°8’24”S 43°44’24”W, 02 May 2018, Oliveira D. 66 (UB); Bacabalzinho, conglomerado MA-304, subunidade 3, subparcela 1, indivíduo 10, F8, 91 m elev., 4°08’24”S 43°55’12”W, 28 March 2017, Santos R.S. 296 (UB). **Piauí**, Altos, Paleobotanical Site of St. Benedict, located in the Homoni village and is 19 km southwest of the headquarters of the municipality of Altos-PI, access made by BR 343 to the county seat, 152 m elev., 5°7’10.92”S 42°31’4”W, 15 March 2018, *Lui Y. et al. 2* (HUEFS); *Lui Y. et al. 178* (HUEFS).

TABLE 3. Morphological differences between *Eperua* species with short and erect inflorescence and non-tubular corolla: *E. cerradoensis*, *E. duckeana*, *E. froesii*, *E. reddeniae*, and *E. schomburgkiana*.

Characters	*E. froesii*	*E. cerradoensis*	*E. schomburgkiana*	*E. duckeana*	*E. reddeniae*
Stipules conation	Entirely joined	Entirely joined	Free	Free	Joined at the base
Pellucid-punctate blades	Epunctate to inconspicuous pellucid-punctate	Epunctate to inconspicuous pellucid-punctate	Pellucid-punctate, sometimes inconspicuous pellucid-punctate	Pellucid-punctate	Inconspicuous pellucid-punctate to epunctate
Leaflet margin	Flat to slightly revolute	Revolute	Flat	Flat	Flat to slightly revolute
Main vein on the adaxial surface	Depressed	Depressed	Prominent	Prominent	Prominent
Tertiary venation	Inconspicuous	Slightly conspicuous	Conspicuous	Conspicuous	Conspicuous
Inflorescence indumentum color	Brownish-yellow to reddish-brown	Whitish	Coppery	Brownish-yellow	Coppery
Bracteoles size	Smaller 4.5–9.0 × 2.9–6.1 mm	Larger: 9.8–12.7 × 6.5–9.8 mm	Smaller: 4.5–6.3 × 3.0–5.0 mm	Smaller: 1.9–5.0 × 2.3–4.2 mm	Smaller: 2.1–3.8 × 2.3–2.4 mm
Bracteoles phenology	Persistent to caducous	Persistent	Caducous	Caducous	Caducous
Petal color	White to light-red	White	White	White	Purple to pink
Stamens conation	Joined basally in a tube	Joined basally in a tube	Diadelphous sheath 9+1	Diadelphous sheath 9+1	Diadelphous sheath 9+1
Sheath/tube indumentum	Glabrous	Glabrous	Irregularly tomentose	Tomentose	Irregularly tomentose
Ovary indumentum	Glabrous	Tomentose	Glabrous	Tomentose	Tomentose
Fruit indumentum	Glabrous	Tomentose	Glabrous	Tomentulose	Tomentulose
Fruit margin	Slightly thickened	Dorsal margin alate	Entire	Entire	Entire
Distribution	Eastern/Southern Amazonia	Cerrado and Caatinga Biomes	Guyana Shield	Central Amazonia	Guyana Shield

4. ***Eperua duckeana*** R.S. Cowan (1975: 30) (Figures 8, 19, 20)

Type:—BRAZIL. Amazonas: Rio Urubú abaixo da cachoeira Iracema, 7 July 1941, *Ducke W.A. 732* (holotype US[00001144]!, isotypes F[0057800] image!, IAN[010263]!, MG[017957]!, MO[954041] image!, NY[1171178] image!, R sheet I[000054531]!, & sheet II[000054531a]!, SI[002003] image!).

Tree 3.5–35.0 m tall. **Trunk** 5.0–60.0 cm in diameter, bark brownish, reddish-brown to grayish-brown, smooth to striate, lenticellate. **Stipules** 5.3–38.7 × (1.3–)3.4–26.9 mm, free, foliaceous, caducous to persistent. **Leaves** 3–5-jugate; **petioles** 0.6–2.9 cm long; **rachis** (3.7–)6.8–19.5(–24.0) cm long; **petiolules** 3.6–10.4 mm long; **blades** 4.7–14.7 × 2.0–10.3 cm, coriaceous, glabrous, pellucid-punctate, rarely inconspicuous pellucid-punctate, discolorous, sometimes slightly discolorous, equilateral, lower pair elliptic, sometimes lanceolate, rarely ovate or broadly elliptic, middle pair elliptic, sometimes lanceolate, rarely narrowly elliptic, upper pair elliptic, rarely lanceolate, obovate, or narrowly elliptic, apex attenuate to acuminate, mucronate, base asymmetrical, rarely oblique, lower pair base cuneate, obtuse, rounded to subcordate, middle pair base obtuse to rounded, sometimes cuneate to subcordate, rarely cordate, upper pair base obtuse to cuneate, margin flat, **secondary venation** with two intramarginal veins, sometimes one, vein closer to the margin not continuous, main vein straight, very prominent on the adaxial surface, tertiary veins conspicuous, areoles smaller, concave. **Inflorescences** terminal, rarely axillary or on the branchlets, panicle, sometimes raceme, erect, tomentose, brownish-yellow, 6.0–20.0 cm long, lateral racemes 2.3–18.0 cm long, alternate and distichous; **bracts** caducous, not seen; **bracteoles** 1.9–5.0 × 2.3–4.2 mm, ovate, rarely semiorbicular, cucullate, apex gland absent, tomentose externally, glabrous within, brownish-yellow, falling early, attached to the lower middle portion of the pedicels; **pedicel** 15.0–23.3 mm long, 1.0–2.8 mm in diameter, not twisted, tomentose to pubescent, brownish-yellow or coppery; **buds** 0.8–1.8 cm long, 0.4–0.9 cm in diameter, tomentose, brownish-yellow. **Flowers**: **hypanthium** 3.3–10.6 mm long, 2.9–7.4 mm in diameter, cup-shaped, sometimes tubular, equilateral, tomentose, brownish-yellow; **sepal** 0.8–1.9 × 0.3–0.9 cm, elliptic, sometimes oblong or ovate, unequal, the outer ones larger, cucullate, apex gland absent, greenish, green, greenish with rose spots, white to cream, tomentose externally, brownish-yellow, inner sepals scarious marginally; **adaxial petal** 1.2–2.4 × 1.9–3.3 cm, oblate, non-tubular, apex truncate or rounded, base truncate, white, whitish, greenish, cream to white-lilac, glabrous; **petalodia** 0.4–1.6 × 0.4–1.0 mm; **stamens**, exserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 1.7–4.9 cm long, shorter filaments 1.2–3.4 cm long, sheath slightly inequilateral to equilateral, shorter side 3.0–8.1 mm long, longer side 6.1–8.7 mm long, sheath entirely tomentose, free filaments glabrous, brownish-yellow, shorter stamens anthers 2.7 × 0.7 mm, rectangular, longer stamens anthers 2.2–4.1 × 0.7–1.3 mm, rectangular; **ovary** 5.9–9.9 × 1.8–4.5 mm, oblaceolate, tomentose, brownish-yellow, stipe 2.9–9.1 mm long, tomentose, style 2.7–4.3 cm long, stigma obtuse to capitate. **Legumes** 7.5– 22.0 × (1.3–)4.0–8.4 cm, stipe 1.1–2.5 cm long, with remnants of the androecium, oblanceolate-falcate, apex obtuse, sometimes acute, apiculate, margin entire, dull brown, veins absent, sometimes with inconspicuous transversal veins, tomentulose, rarely tomentose or tomentulose to glabrescent with long scattered trichomes, brownish-yellow. **Seeds** 2–4 per fruit, 3.1–4.5 × 1.7–3.0 cm, ovate to oblong, reddish-brown.

Phenology:—Flowering in March and from May to December with a peak from August to September; fruiting from January to March and from May to December with a peak in August.

Distribution:—Brazil in the states of Amazonas and Pará.

Habitat:—Mainly *terra-firme* forest, sometimes in *igapó* and *várzea* forests, and *campinaranas*, on sandy and clayey soil, from 7 to 250 m elev.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 88,736.968 km$_2$ and

the estimated area of occupancy is 204.000 km$_2$.

Occurrence in protected areas:—Reserva Florestal Adolpho Ducke (Brazil, Amazonas).

Etymology:—The specific epithet is a tribute to Adolpho Ducke, who revised and described new species and varieties for the genus *Eperua* (Ducke 1932, 1940, Cowan 1975).

Vernacular names:—envira iodo (*Marra D.M. & Neves A.F. 78*), muirapiranga branca (*Coelho D. s.n. INPA20747*, *Rodrigues W.A. & Chagas J. 1725*, *Rodrigues W.A. & Osmarino 6769*), muirapiranga da folha miúda (*Rodrigues W.A. & Chagas J. 1725*, *Rodrigues W.A. & Lima J. 2233*, *Rodrigues W.A. & Osmarino 6769*), murajiboia *(Mello F.C. de & Ribamar s.n. INPA58309*), pau de óleo (*Silva S.F. da 205a*).

Uses:—Used in constructions due to its heavy, soft, and resinous wood (*Rodrigues W.A. & Chagas J. 1725*).

Taxonomic notes:—*Eperua duckeana*, *E. froesii*, *E. cerradoensis*, *E. reddeniae*, and *E. schomburgkiana* are the only species with short and erect inflorescence that exhibit a non-tubular corolla, exserted stamens, falcate fruit with a length-to-width ratio of 3:1 (vs. tubular corolla, included stamens, non-falcate fruit with a length-to-width ratio of 1:1 to 2:1 in other short and erect inflorescence species). They also share multijugate leaves with straight leaflets and inflorescence covered in dense indumentum. Furthermore, *E. duckeana* stands out as a distinct species due to its stamens fused at the base in a sheath of 9+1, tomentose sheath and ovary, and tomentulose fruits. These features and other vegetative characteristics contribute to its differentiation from other species. Additionally, *E. duckeana* has a specific distribution in the Central Amazonia region. Please refer to Table 3 for a summary of the similarities and differences among these species.

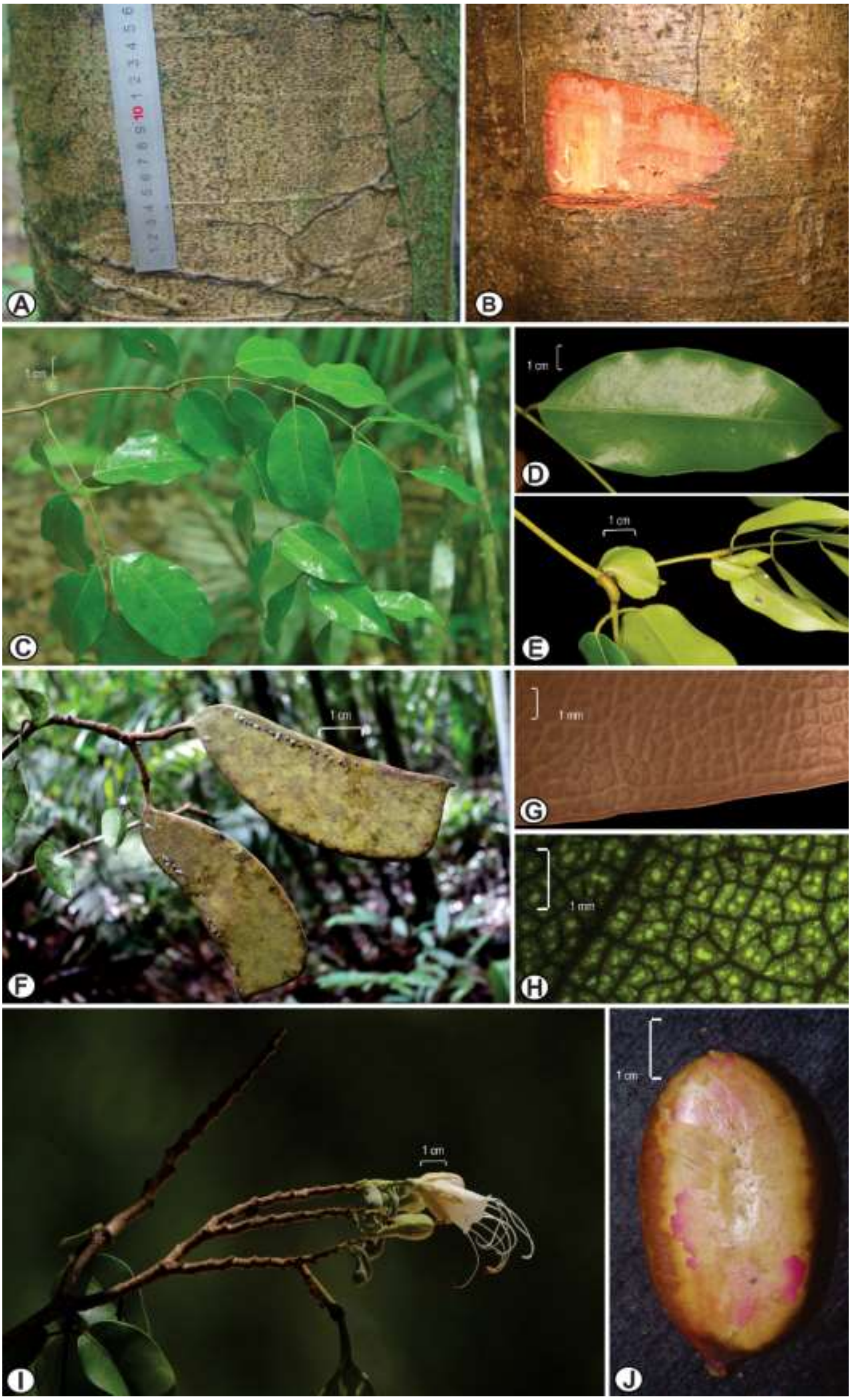


FIGURE 19. *Eperua duckeana*: A. bark; B. sap-wood and heartwood; C. leaves; D. detail prominent main vein on the adaxial surface; E. foliaceous stipules; F. fruits; G. intramarginal veins; H. pellucid-punctate leaflet; I. inflorescence; J. seed. Specimens, A–H, J: *Fortes E.A. et al. 191b*. Photos, A, B, F–H, J: E.A. Fortes; C: M. Pastore; D, E: F. Farroñay; I: H. ter Steege.

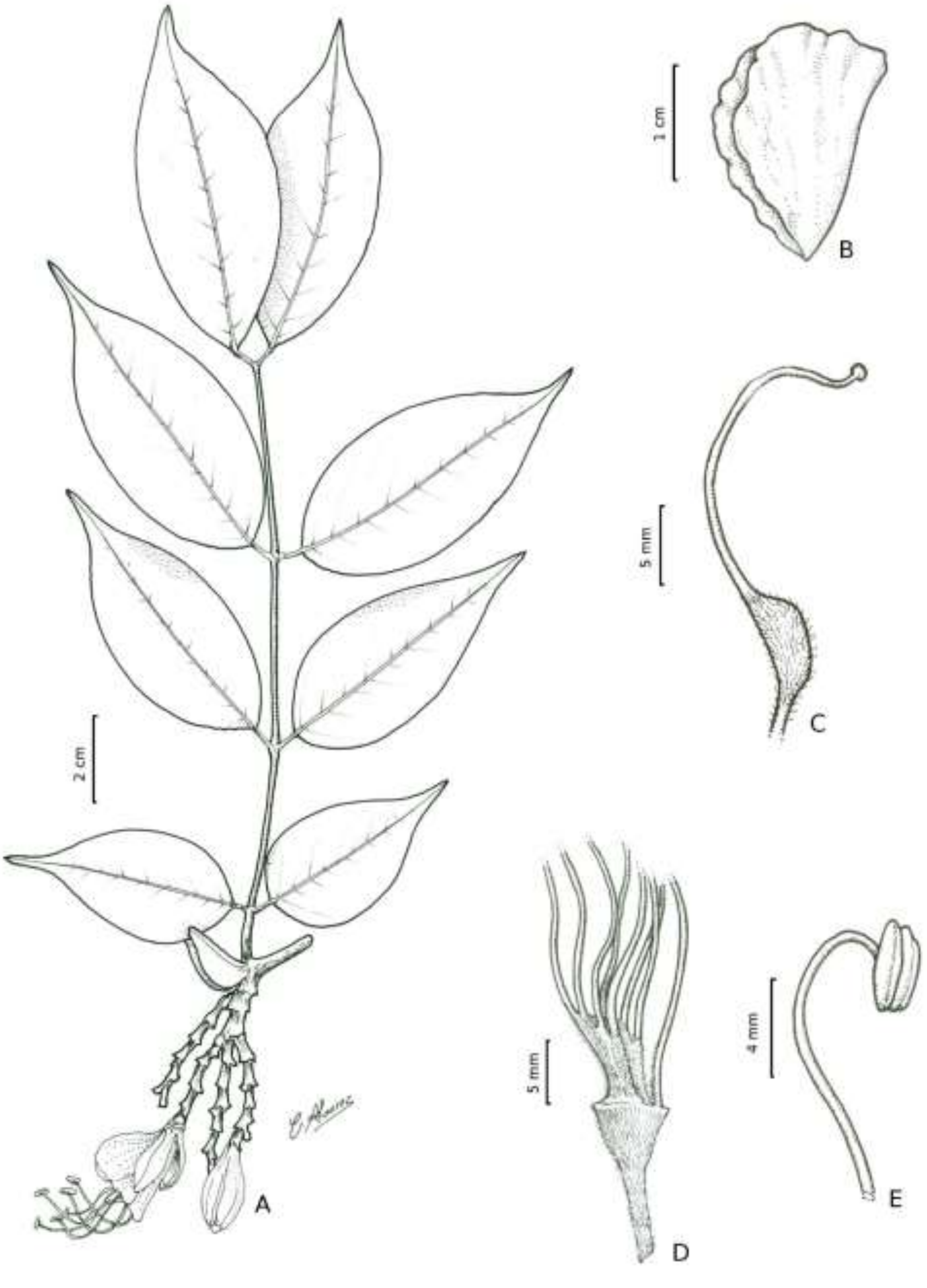


FIGURE 20. *Eperua duckeana*: A. flowering branchlet; B. adaxial petal; C. carpel with tomentose ovary and stipe, glabrous style, capitate stigma; D. tomentose hypanthium and pedicel, stamens joined in a diadelphous sheath 9+1, tomentose sheath, free filaments glabrous; E. anther and part of the filament. Specimen, A–E: *Ducke W.A. 732*. Illustrated by Carlos Alvarez.

Selected specimens:—BRAZIL. **Amazonas**, Itapiranga, rio Pitinga, margem direita, 24 August 1979, *Cid-Ferreira C.A. et al. 703* (INPA, NY, US). Manaus, Reserva Florestal Adolpho Ducke, , L4 após km 3350, 129 m elev., 2°56’59”S 59°56’10”W, 21 January 2022, *Fortes E.A. et al. 190b* (INPA, RB, UEC, US); Reserva Florestal Adolpho Ducke, Igarapé Ipiranga, pique do INPA, sentido oeste-leste, 2°53’0”S 59°58’0”W, 05 July 1993, *Ribeiro J.E.L.S. et al. 1037* (HUEFS, INPA, K, MO, NY, R, RB, SP, U); ZF3, Distrito Agropecuário da SUFRAMA, rodovia BR 174, Km 64, depois 34 Km Leste na ZF3, fazenda Esteio, reserva nº 1302, árvore nº 775, 2°26’0”S 59°48’0”W, 24 September 1981, *Nascimento J.R.M. et al. 1302.775* (INPA, NY); IFAM, Campus Manaus-Zona Leste, 05 November 2011, *Kinupp V.F. et al. 4542* (EAFM). Presidente Figueiredo, no entorno do Lago da Rebio Uatumã, Balbina, 13 August 2008, *Silva M.C.R. da et* *al. 40* (INPA). São Sebastião do Uatumã, RDS Uatumã, Igapó de topografia alta, situado nas margens do rio Abacate, 7 m elev., 2°11’37’’S 58°43’10’’W, 15 May 2016, *Lobo G.S. 14* (INPA). **Pará**, Oriximiná, cachoeira da Porteira, entrada Perimetral Norte, 1°3’17.4”S 57°2’28”W, 09 June 2000, *Faria S.M. de et al. 2053* (HSTM, RB); Porto Trombetas, rio Mapuera, cachoeira da Égua, Ilha, 11 December 1907, *Ducke W.A. 9088* (RB). **Rio de Janeiro** (cultivated), Seropédica, Embrapa-Agrobiologia, 14 September 2001, *Faria S.M. de & C. C.F. da 2186* (RB).

5. ***Eperua falcata*** Aublet (1775: 369) (Figures 11, 21, 22)

Type (designated by Cowan 1975):—FRENCH GUIANA. Cayenne, s.d. [July 1762–July 1764], *Aublet J.B.C.F.* s.n. (lectotype BM-inflorescence [000952284] image!).

≡ *Dimorpha falcata* (Aubl.) Forsyth (1794: 391) nom. illeg. superfl.

≡ *Panzera falcata* (Aubl.) Willdenow (1799: 540), nom. illeg. superfl.

≡ *Dimorpha falcata* (Aubl.) Smith in Rees (1808: 656), nom. illeg. superfl.

Tree 8.0–40.0 m tall. **Trunk** 20.0–70.0 cm in diameter, bark grayish to reddish, smooth, lenticelate. **Stipules** 1.4–4.3 × 1.3–3.1 mm, joined, non-foliaceous, caducous to persistent. **Leaves** (2–)3–4-jugate; **petioles** 1.2–9.7 cm long; **rachis** 1.2–11.9 cm long; **petiolules** 2.5–6.5 mm long; **blades** 2.6–17.5 × 2.4–6.8 cm, chartaceous, sometimes coriaceous, glabrous, minutely pellucid-punctate, not all areoles have one dot, not discolorous to discolorous, inequilateral, all pairs elliptic-falcate, apex acuminate, sometimes caudate, mucronulate, base asymmetrical, lower pair base obtuse to rounded, middle pair base obtuse, rounded or cuneate, upper pair base obtuse to cuneate, rarely rounded, margin flat, rarely slightly revolute, **secondary venation** with one intramarginal vein very close to the margin, main vein curved, depressed, rarely prominent near the base on the adaxial surface, tertiary veins conspicuous, areoles larger, plane. **Inflorescences** terminal, rarely axillary, panicle, main axis and lateral racemes pendulous, main axis strigulose, sometimes glabrous, lateral racemes tomentose, brownish, 66.0–300.0 cm long, lateral racemes (1.1–)2.5–8.8(–11.0) cm long, alternate and spirally arranged; **bracts** 2.9–3.2 × 1.3–1.8 mm, ovate, apex gland absent, tomentose, brownish, caducous; **bracteoles** 2.3–6.1 × 2.3–4.0 mm, broadly ovate, sometimes ovate, apex gland absent, tomentose, brownish, caducous, attached to the higher portion of the pedicels; **pedicel** 8.3–19.3 mm long, 0.7–1.5 mm in diameter, twisted, tomentose, brownish; **buds** 0.8–1.8 cm long, 0.4–0.9 cm in diameter, tomentose, brownish. **Flowers**: **hypanthium** 3.6–5.3 mm long, 3.3–6.3 mm in diameter, cup-shaped, equilateral, tomentose, brownish; **sepal** 1.0–1.8 × 0.5–1.2 cm, elliptic to oblong, unequal, the outer ones larger, cucullate, apex gland absent, pink, red, redidish-green to greenish, tomentose, inner sepals scarious marginally, brownish; **adaxial petal** 1.0–2.0 × 1.2–2.5 cm, oblate, non-tubular, apex rounded, base truncate or subcordate, gibbous, pink, pale-pink, purple, reddish, greenish to red, glabrous; **petalodia** 0.5–1.9 × 0.7–1.2 mm; **stamens** exserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 3.7–4.6 cm long, shorter filaments 1.5–2.4 cm long, sheath equilateral, 2.1–7.3 mm long, sheath and free filaments base villous, middle to upper free filaments glabrous, brownish, anthers 5.7–6.0 × 1.6–2.0 mm, rectangular; **ovary** 4.7–8.8 × 2.2–4.4 mm, oblong to obovate, sericeous, brownish, stipe 3.6–6.2 mm long, sericeous, style 2.2–4.5 cm long, stigma capitate. **Legumes** 19.0–38.0 × 5.1–10.8 cm, stipe 1.8–2.6 cm long, elliptic-falcate, sometimes lanceolate-falcate, apex acute, margin entire to slightly thickened, dark brown, veins absent or with some slightly conspicuous veins, strigulose, rarely glabrous, trichomes brownish. **Seeds** 1–4 per fruit, 3.5–4.6 × 1.9–2.4 cm, oblong, ovate to irregular, dark-brown.

Phenology:—Flowering and fruiting throughout the year, with a flowering peak from September to December and a fruiting peak from October to December**.**

Distribution:—Occurring throughout the Guyana Shield: Brazil (Amapá), French Guiana (Cayenne, Saint- Laurent-du-Maroni), Guyana (Barima-Waini, Cuyuni-Mazaruni, Demerara-Mahaica, East Berbice-Corentyne, Pomeroon-Supenaam, Potaro-Siparuni, Upper Demerara-Berbice), Surinam (Brokopondo, Coronie, Kabalebo, Nickerie, Para, Paramaribo, Patamaca, Sipaliwini), and Venezuela (Bolívar). Cultivated in Trinidad and Tobago, Indonesia, and Panama.

Habitat:—Non-flooded, inundated and periodically inundated forests, and savannas. It can occur from sea level up to elevations of 500 m, and sometimes even up to 800 meters. It grows mainly on white, brown, and mixed sand soils, although it can also be found on bauxite, laterite, and clayey soils. Along with *E. grandiflora*, *E. falcata* comprise the *Eperua* dominant forest known as *wallaba* forest in Guyana and Surinam.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for this species is 501,331.224 km$_2$, and the estimated area of occupancy is 664.000 km$_2$.

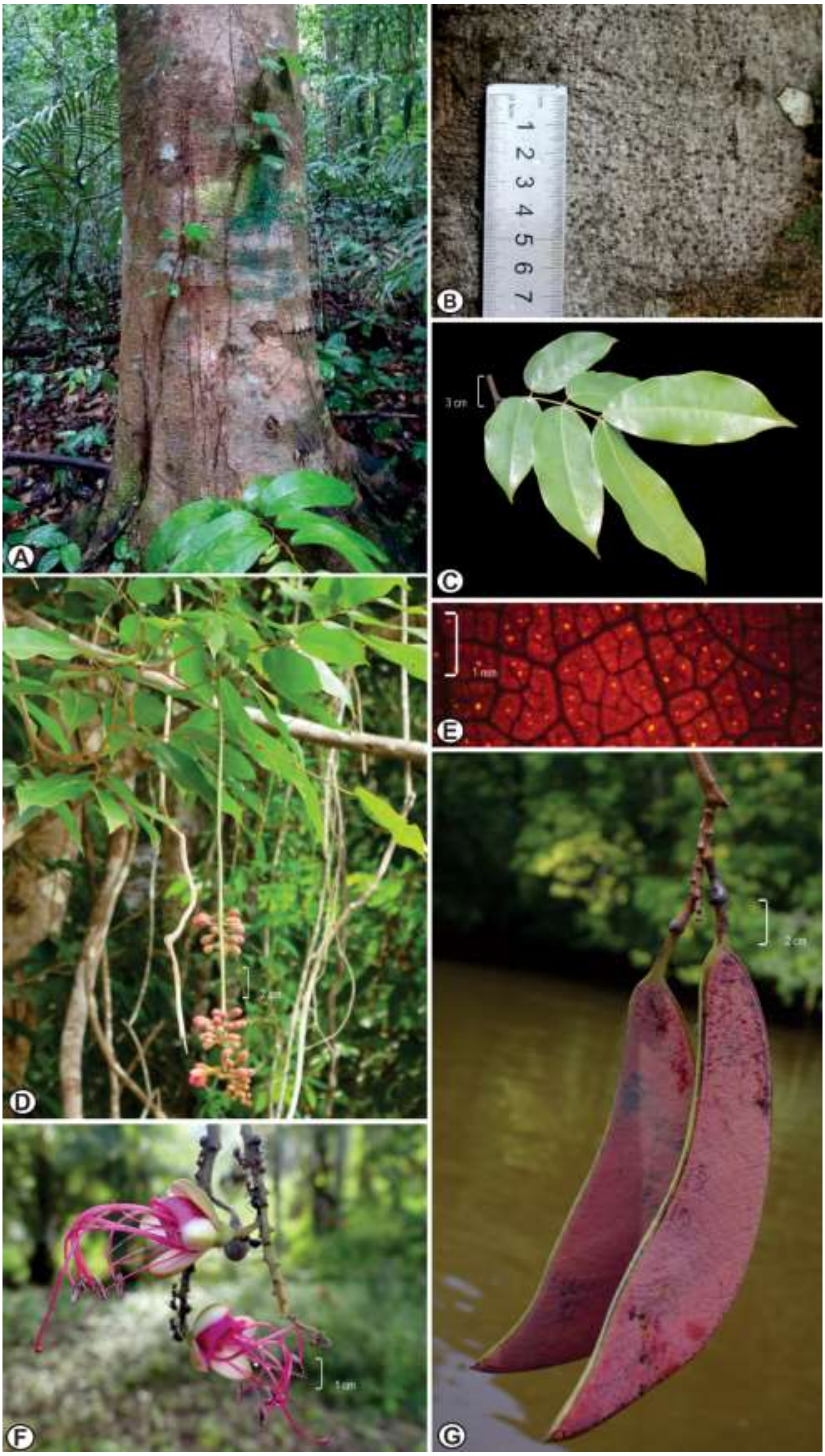


FIGURE 21. *Eperua falcata*: A. trunk base. B. bark; C. leaf; D. inflorescence; E. flowers; D. inflorescence; E. pellucid-punctate leaflet; F. flowers; G. fruits. Specimens, B, C, E, G: *Fortes E.A. & Silva G.S. da* 172. Photos, A. J. Luber; B, C, E, G: E. A. Fortes; D: S.A. Mori; F: J. Perret.

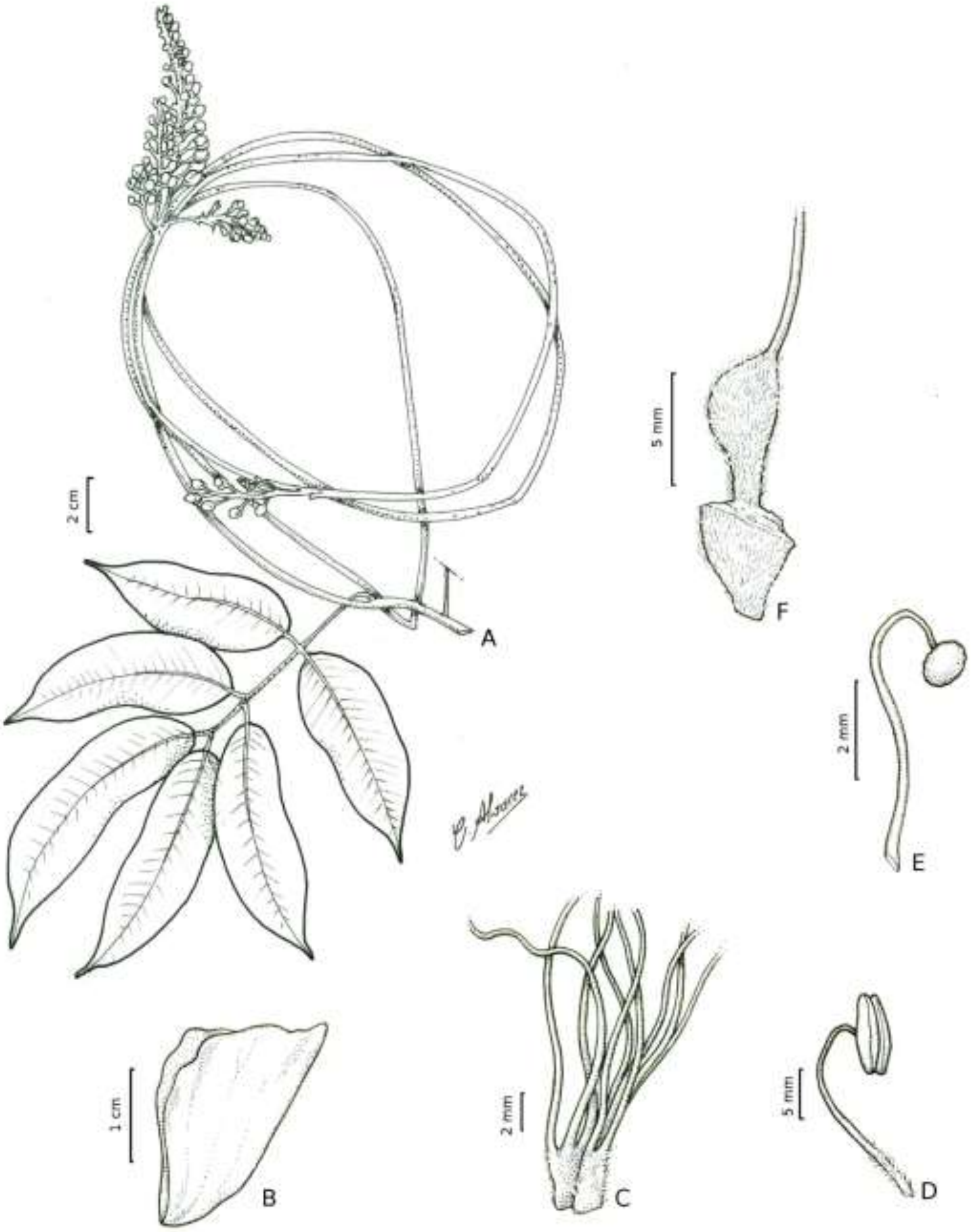


FIGURE 22. *Eperua falcata*: A. flowering branchlet; B. adaxial petal; C. stamens joined in a diadelphous sheath 9+1, villous sheath, free filaments glabrous; D. anther and part of the free filament; E. glabrous style and capitate stigma; F. tomentose hypanthium and sericeous ovary. Specimens, A: *Irwin H.S. & Pires J.M. 48613*; B–F: *Irwin H.S. et al. 48277*. Illustrated by Carlos Alvarez.

Occurrence in protected areas:—Parque Nacional Montanhas do Tumucumaque (Brazil, Amapá), Réserve Naturelle des Nouragues (French Guiana, Régina), Iwokrama Rainforest Reserve (Guyana, Potaro-Siparuni), Kaieteur National Park (Guyana, Potaro-Siparuni), Mabura Hill Forest Reserve (Guyana, Upper Demerara-Berbice), Brownsberg Nature Reserve (Surinam, Brokopondo), and Central Surinam Nature Reserve (Surinam, Kabalebo).

Etymology:—The specific epithet is derived from its elliptic-falcate fruits (Bentham 1870).

Vernacular names:—apa (*Irwin H.S. et al. 48277*, *Irwin H.S. et al. 48408*, *Irwin H.S. & Pires J.M. 48613*, *Maguire B. et al. 48408*), apa-roxo (*Pires J.M. & Westra L.Y.T. 48876*), bioudou or bi-oudou (*BAFOG 51*, *7062*, *7064*, *7254*, *7298*, *Mori S.A. et al. 23384*, *Petrov I. s.n. P03465196*, *Vieillescazes A. 616*), biouolou-wata (*BAFOG 143*), birihoedoe (*Stahel G. 22*), bi-udu or biudu (*Hoffman B. 6522*, *Puig H. 10263*, *10285*), caraota (*Blanco C.A. 603*, *Meijeraan J.W. 42*), falcaha (*Angel G. 19*), itoeli-walaba (*Stahel G. 66*), kergwalaba (*Jimenez-Saa J.H. 14330*), mahomillo-negro (*Steyermark J.A. 86692*), ouapa (*Oldeman 1212*), rosa-de-montaña (*Foldats E. 2645),* soft-wallaba (*Berlo M. van* collections, *Redden K.M. et al. 1050*, *1058*, *1059*), tapaka (*Grenand P. 610*, *Puig H. 10263*, *10285*), walaba (*Berlo M. van collections, Bhikhi C.R. et al. 79, Borsboom N.W.J. 12025*, *12044*, *B.W. 1171*, *Florschütz J. & Florschütz P.A. 217*, *Jimenez-Saa J.H. 14275, 43360 (1627), Lindeman J.C. & Roon A.C. 1980/860, Lobato M. 9, Maguire B. 24778*, *Ogtrop F. van 1, Reuder & Roberts 12329*, *Sabajo P.H. & Roberts L. 11192, Vreden C.C.J. 13673*), walaba-kharemeroe (*Stahel G. 22*), walaba-koeleroe (*Stahel G. 23*), walaba-of-bijlhout (*Versteeg G.M. 393*), wallaba (*Andel T.R. van et al.* collections, *BAFOG 6033*, *Evans R. et al. 2154*, *Evans R. & Lewis G. 1871*, *Kelloff C.L. et al. 1300*, *Kelloff C.L. & Roesel C.C. 1155*, *Junker L. 507*, *Little E.L. Jr. 16825*, *McDowell T. & Gopaul D. 2451*, *Persaud A.C. 243*, *Pipoly J.J. & Boyan R. 8701*, *Redden K.M. et al. 4572*, *Stoffers A.L. et al. 62*), wapa (*Angel G. 19*, *158*, *176*, *BAFOG 6033*, *Dutrève B. 437*, *Garnier F.A. 138*, *Hallé F. 4143*, *Hoff M. 5895*, *Kodjoed J.-F. 140, Larpin D. 187, Loubry D. 1811*, *Mori S.A. et al. 23384*, *Paget D. 49*, *Petrov I. 124*, *Prévost M.F. 4221*, *4232*, *Puig H. 10285*, *Sauvain M. 743,Thiel J.* collections, *Vieillescazes A. 616*), wapa blone (*Thiel J.* collections), wapa-de-crique (*BAFOG 143*), wapa-graj (*Bena P. 1274*), wapa-gras (*BAFOG 1274*), wapa-huileux (*BAFOG 1274*), wapa-rouge (*Thiel J.* collections), warapa (*Andel T.R. van et al. 665*), watapa (*Andel T.R. van et al. 1007*), water-wallaba (*Redden K.M. et al. 3265*), white-sand-wallaba (*Hoffman B. 4599*), zwarte-walaba (*Stahel G. 22*, *22a*).

Uses:—*Eperua falcata* is highly valued for its wood, which is extensively used in Guyana and Surinam for general construction, bridge construction, light and telephone poles, shutter windows, and roof shingles. The following herbarium specimens provided information of the utilization of its wood: *Andel T.R. van et al. 665*, *1007*, *3073*, *Berlo M.* collections, *Bhikhi C.R. et al. 79, Redden K.M. et al. 1050*, *1058*, *1059*.

Taxonomic notes:—*Eperua falcata* is the only species with long and pendulous inflorescences with pendulous lateral racemes (Table 4). Morphologically, it shares the following similarities with *E. leucantha* and *E. venosa:* joined stipules, leaflets with secondary venation with one intramarginal vein very close to the margin, long and pendulous inflorescences, non-tubular corolla, exserted stamens joined in a diadelphous sheath, and sericeous ovary. *Eperua falcata* also shares multijugate leaves with *E. leucantha* and non-white flowers with *E. venosa*. However, notable differences set *E. falcata* apart from these two species. *Eperua falcata* has smaller adaxial petals (1.0–2.0 × 1.2–2.5 cm) compared to *E. leucantha* (1.9–3.3 × 2.9–6.3 cm) and *E. venosa* (2.5–3.4 × 4.7–6.0 cm). Additionally, *E. falcata* has minutely pellucid-punctate leaflets with not all areoles having a dot, whereas *E. leucantha* and *E. venosa* have pellucid-punctate leaflets with each areola having at least one dot. Further distinctions include the lower and middle pairs of leaflets in *E. falcata* tending to have less asymmetrical and more rounded to obtuse bases (vs. more asymmetrical, obtuse to cuneate, rarely rounded in *E. leucantha*), longer [(1.1–)2.5–8.8(–11.0) cm long] and pendulous lateral racemes (vs. shorter [0.5–2.5(–3.1) cm long] and patent to erect in *E. leucantha*), brownish buds (vs. grayish white in *E. leucantha*), pink to purple petals (vs. white in *E. leucantha*), villous sheath (vs. sericeous in *E. leucantha*). From *E. venosa*, *E. falcata* also differs by multijugate leaves (vs. always 1–2(–3)-jugate in *E. venosa*), brownish buds (vs. grayish-white in *E. venosa*), glabrous adaxial petal (vs. sericeous at the base in *E. venosa*), and villous staminal sheath (vs. sericeous in *E. venosa*).

Eperua falcata and *E. leucantha* are allopatric species (Figure 11). *Eperua falcata* occurs in the Guyana Shield, with its westernmost occurrence in the Venezuelan state of Bolívar. It is a widespread and extensively collected species, although no flowering collections have been reported beyond the Bolívar state. In contrast, in Venezuela, *E. leucantha* occurs exclusively in the southeastern part of the Amazonas state. *Eperua falcata* is parapatric with *E. venosa,* which is restricted to the region of Gran Sabana in Venezuela, while *E. falcata* borders this region (Figure 11).

Selected specimens:—BRAZIL. **Amapá**, Laranjal do Jari, Parque Nacional do Tumucumaque, 0°16’35”N 53°6’24”W, 14 January 2005, *Pereira L.A. & Cardoso J.O. 825* (RB). Oiapoque, nas margens da rodovia BR156 entre Oiapoque e Calçoene, a 21 km de Oiapoque, 3°40’33.2”N 51°46’14.1”W, 04 December 2021, *Fortes E.A. & Silva G.S. da 165* (IAN, RB). **CAMEROON (cultivated)**. Victoria Botanical Garden, 12 February 1927, *Fairchild D.G. s.n.* (US1716064, BR0000017324229). **FRENCH GUIANA**. **Cayenne**, Camopi, Trois sauts (haut Oyapock), saut Mansa, 31 December 1974, *Grenand P. 610* (CAY, US). Cayenne, Quesnel-Chantier F.R.G., 11 December 1979, *J. Thiel 619* (CAY); Exploitation forestière F.R.G., 02 February 1981, *Thiel J. 792* (CAY). Kourou, montagne des Singes, 23 November 1981, *Cremers G.A. 7659* (CAY, P, US). Montsinéry-Tonnegrande, crique Serpent, rive gauche à 1 m au dessus de la crique, February 1954, *BAFOG 143* (U). Régina, station des Nouragues (cam inselberg),

TABLE 4. Morphological differences between *Eperua* species with long and pendulous inflorescence and non-tubular corolla: *E. falcata, E. glabra, E. leucantha, E.venosa,* and *E. rubiginosa*.

Characters	*E. falcata*	*E. leucantha*	*E.venosa*	*E. rubiginosa*	*E. glabra*
Stipules conation	Joined	Joined	Joined	Free or joined	Free
Secondary venation	Intramarginal vein very close to the margin	Intramarginal vein very close to the margin	Intramarginal vein very close to the margin	One or two intramarginal veins not very close to the margin	One or two intramarginal veins not very close to the margin
Main vein	Curved	Curved	Curved to straight	Straight	Straight
Inflorescence indumentum	Main axis strigulose, sometimes glabrous, lateral racemes tomentose	Main axis strigulose, puberulous to pubescent, lateral racemes strigulose to tomentulose	Main axis puberulent to strigulose, lateral racemes strigose, pubescent to tomentulose	Main axis and lateral racemes tomentulose	Main axis and lateral racemes glabrous
Lateral racemes position	Pendulous	Patent to erect	Erect	Erect, rarely patent	Patent to erect
Bracteoles insertion on the pedicels	Higher portion	Middle portion	Middle to high portion	Lower portion	Lower portion
Bracteoles phenology	Caducous	Caducous	Caducous	Caducous	Caducous
Petal indument	Glabrous	Glabrous	Sericeous at the base	Glabrous	Glabrous
Stamens conation	Diadelphous sheath 9+1	Diadelphous sheath 9+1	Diadelphous sheath 9+1	Joined basally in a tube	Joined basally in a tube
Stamens indumentum	Villous	Sericeous, sometimes tomentose	Sericeous to tomentose	Glabrous, sometimes tomentulose in the sinuses	Glabrous
Ovary indumentum	Sericeous	Sericeous	Densely sericeous	Tomentose	Glabrous
Distribution	Guyana Shield	Guyana Shield / Central Amazonia	Guyana Shiled	Guyana Shield	Guyana Shield / Central Amazonia

trail CE-CO, 40–20 m elev., 4°5’30”N 52°41’0”W, 23 September 2007, *Geiselman C.K. 94* (NY). Roura, placer Boulanger, basin de la Comté, 12 November 1979, *Thiel J. 582* (CAY). Saint-Élie, Saut Takari-Tanté, bassin du Sinnamary, 34 m elev., 4°37’0”N 52°56’0”W, 17 November 1989, *Hoff M. 5895* (CAY); Saut Dalles, bassin du Sinnamary, 0 m elev., 4°33’0’’N 52°54’0’’W, 01 November 1991, *Loubry D. 1287* (CAY). Saint-Georges, Saut Maripa, bassin de l’Oyapock, August 1973, *Garnier F.A.138* (CAY). **Saint-Laurent-du-Maroni**, Mana, Chantier Laussat—S.F.M., bassin de La Mana, 28 November 1979, *Thiel J. 593* (CAY). Maripasoula, rivière Grand Inini, bassin de l’Inini, 3°40’0”N 53°50’0”W, 07 July 1990, *Sabatier D. & Prévost M.F. 3070* (CAY). Saint-Laurent-du-Maroni, bassin du Bas-Maroni, 14 April 1961, *Aubréville A. 1961/236* (P, U, US). Saül, Monts La Fumée, 200–400 m elev., 3°37’0”N 53°12’0”W, 12 October 1982, *Boom B.M. & Mori S.A. 1985* (CAY). **GUYANA**. **Barima-Waini**, Kariakau, Kariako Village, Barama River, 145 m elev., 7°22’0”N 59°42’0”W, 22 December 1995, *Andel T.R. van et al. 665* (U, WAG); Morebo, Barima River, N.W. district, December 1908, *Anderson C.W. 122* (RB). **Cuyuni-Mazaruni**, Bartica, Essequibo River, Moraballi Creek, near Bartica, 23 September 1929, *Sandwith N.Y. 329* (RB, U, US). Imbaimadai vicinity, Mazaruni River, 0.55 miles South West of Partang River base camp, 485 m elev., 5°41’17”N 60°17’10.2”W, 23 November 2002, *Redden K.M. et al. 1238* (U, US); Pakaraima Mts., Mazaruni River, NW of Chi-Chi Falls, along stream between two tepuis, approx. 1.5km above base camp 2, 762 m elev., 5°35’48.6”N 60°12’49”W, 12 February 2004, *Redden K.M. et al. 1643* (U, US); Mazaruni River, unnamed falls (possible Carin Crow Falls), 0.67 miles W of base camp, 61 m elev., 5°57’4.3”N 59°19’5.2”W, 09 October 2004, *Redden K.M. et al. 3265* (US); Kako River, 536 m elev., 5°31’29”N 60°50’19”W, 12 May 2009, *Redden K.M. et al. 6552* (NY, US). **Demerara-Mahaica**, Soesdyke-Linden Hwy, 0–3 km N Kuru-Kuru Cr, 16–19 km S Georgetown-Timehri Hwy, 10–20 m elev., 6°22’0”N 58°15’0”W, 10 November 1991, *Gillespie L.J. 4250* (INPA, MO, US). **East Berbice-Corentyne**, White Hill on Corentyne River, 10–50 m elev., 5°6’0”N 57°19’0”W, 24 April 1990, *McDowell T. & Gopaul D. 2451* (U, US). **Pomeroon-Supenaam**, along road between Wyaka and Mainstay, 7°15’0”N 58°31’59.9”W, 23 April 1989, *Gillespie L.J. & Persaud H. 1169* (US). **Potaro-Siparuni**, Iwokrama Rainforest Reserve, N side of Burro-Burro R., 60–90 m elev., 4°33’0”N 58°50’0”W, 27 September 1995, *Clarke H.D. 255* (CAY, U, US); Pakaraima Mts, Mt. Wokomung, Suruwabaru Creek, 1–2 km from juncture with Yuarba River, 675–750 m elev., 5°2’0”N 59°54’0”W, 07 November 1993, *Henkel T.W. et al. 4142* (CAY, U, US); Kaieteur National Park, above falls, 474 m elev., 5°10’28.0”N 59°28’54.1”W, 29 August 2006, *Redden K.M. et al. 3860* (CAY, US). **Upper Demerara-Berbice**, Berbice, Dubulay ranch, 10 m elev., 5°35’0”N 57°53’0”W, 19 October 1997, *Jansen-Jacobs M.J. 5623* (U, US). Mabura Hill Forest Reserve, 13 km S of Mabura Hill, 60 m elev., 5°10’0’’N 58°42’0’’W, 13 April 1996, *Clarke H.D. 1633* (CAY, U, US). **Upper Takatu-Upper Essequibo**, Cut Line AB from Lethem-Kurupukari road on 270°, 75 m elev., 4°34’58”N 58°44’45”W, 21 April 1992, *Pennington R.T. et al. 372* (CAY, U, US). **INDONESIA (cultivated)**. **Java**, Borgor City, cultivated in the Botanic Gardens Buitenzorg-Java, 30 May 1941, *Wit I.i. H.C. de 70a* (L). **PANAMA (cultivated)**. **Panamá**, Ciudad de Panamá, Parque Natural Summit, 80 m elev., 15 February 2008, *Ibáñez A. et al. 5358* (MA). **SURINAM**. **Brokopondo**, Brownsberg, Boschreserve (Forest Reserve), sectie O, 10 September 1917, *B.W. 3210* (IAN, U). **Coronie**, Vosberg, January 1947, *Burger D. 8* (U, WAG). **Kabalebo**, Central Surinam Nature Reserve, lower Rechter Cooppename River, 50–75 m elev., 4°21’41.2”N 56°31’8.2”W, 23 February 2004, *Clarke H.D. & Rhodes J. 11085* (U). **Nickerie**, unknown city, Corantijne, 11 December 1949, *Landsbosbeheer 902* (U). **Para**, Carolina, Blakawatra, 5°22’59”N 54°55’0”W, 28 November 1921, *B.W. 5524* (U). Oost, Powakka, Property of Makosi family, 5°26’38.4”N 55°4’37”W, 21 May 2012, *Berlo M. van et al. 63* (L). Zuid, Zanderij, September 1942, *Stahel G. 22* (IAN, RB, U, WAG); banks of Sabakoe Creek, ca. 100 m W from Zanderrij to Kraka road, 4.9 km from intersection with Zanderij Hwy, 25 m elev., 5°25’0”N 55°11’30”W, 10 July 1994, *Evans R. & Lewis G. 1871* (CAY, IAN, INPA, MO, P, RB, U, US). Jodensavanne-Mapane kreek area (Surinam R.), Bij kamp aan Mapane-kreek, 19 September 1953, *Lindeman J.C. 4649* (F, U). **Paramaribo**, Forest surrounding of Carolina, 50 km, South-East of Paramaribo, 11 August 1874, *Outer R.W. den 963* (L, U). **Patamaca**, B.S.H. ekspl. Patamaca, 02 November 1967, *Borsboom N.W.J. 12025* (WAG). **Sipaliwini**, Boven Saramaca, Tafelberg (Table Mountain), 15 September 1944, *Maguire B. 24778* (F, U, US). Boven Suriname, Berlijn, January 1844, *Focke H.C. 945* (U). Coeroeni, vinicity of camp on W bank of Zuid River, across river from central Surinam Nature Preserve, ca. 10 km straight-line distance SSE of Kayserberg airstrip, 240 m elev., 3°0’3”N 56°27’3”W, 14 June 2003, *Rosário C.S. & Rosário D.O. 2011* (MG, MO). Kabalebo, Tafelberg (Table Mountain), summit, trail from Augustus Creek to Lisa Creek, ca. 0.5 km from Lisa Creek, ca. 200 m from western rim of tepuí, 575 m elev., 3°55’0”N 56°12’30”W, 25 June 2001, *Evans R. 3209* (MO, US). Nickerie, Fallawatra, 03 November 1971, *Jimenez-Saa J.H. 14275* (U).Tapanahony, vicinity of Ulemari River, 13 km upstream from its confluence with Litani River, 150 m elev., 3°13’17”N 54°15’31”W, 04 April 1998, *Evans R. & Peckham H. 2814* (L, U). **TRINIDAD AND TABAGO (cultivated).** Botanical Gardens, 19 August 1927, *Broadway W.E. s.n. US1343487* (US). **VENEZUELA**. **Bolívar**, El Dorado, ±65 km S. of El Dorado, 200 m elev., 25 August 1966, *Meijeraan J.W. 42* (WAG). 90 km from El Dorado towards Sta. Elena, 28 December 1956, *Foldats E. 2645* (US).

6. ***Eperua froesii*** E.A. Fortes, Aymard, H. ter Steege, & Mansano, *sp. nov.* (Figures 8, 23–25)

Type:—BRAZIL. Pará: Rios Pacajá and Muirapiranga, Km 3,5–6,5, line SW of Ilha de Breu, 23 September 1965, *Prance G.T. et al. 1458* (holotype IAN[117052]!, isotypes K [000807973] image!, MO [1780623] image!, NY[01171288]!, U [0083421] image!, US [00243011]!).

Diagnosis:—*Eperua froesii* has short and erect inflorescences, non-tubular corollas, and exserted stamens. It differs from species with the same type of inflorescence, corolla, and stamen by the combination (see Table 3): stipules entirely joined, epunctate to inconspicuous pellucid punctate leaflets, flat to slightly revolute margins, depressed main vein on the adaxial surface, inconspicuous tertiary venation, brownish-yellow to reddish-brown inflorescence indumentum, white to light-red petals, stamens joined basally in a tube, glabrous stamens, ovary, and fruit.

Tree 20.0–25.0 m tall. **Trunk** and bark not seen. **Stipules** entirely joined, caducous, 5.6–44.5 × 10.1–44.0 mm, foliaceous, or 4.0–5.2 × 3.0–4.7 mm, non-foliaceous, persistent to caducous. **Leaves** 4–5-jugate; **petioles** 1.0–2.5 cm long; **rachis** 11.0–23.0 cm long; **petiolules** 4.2–7.6 mm long; **blades** 5.3–13.4 × 2.5–5.8 cm, coriaceous, glabrous, epunctate to inconspicuous pellucid-punctate, not discolorous to slightly discolorous, equilateral, lower pair elliptic to ovate, middle pairs elliptic, narrowly elliptic to ovate, upper pair elliptic, apex attenuate to acuminate, base symmetrical to asymmetrical, lower pair base obtuse to rounded, middle pair base obtuse to rounded, upper pair base obtuse to cuneate, margin flat to slightly revolute, **secondary venation** with one or two intramarginal veins (sometimes inconspicuous in developed leaves), vein closer to the margin continuous or not continuous, main vein straight, depressed on the adaxial surface, tertiary veins inconspicuous, areoles smaller concave. **Inflorescences** terminal or axillary, panicle, erect, puberulous, pubescent to tomentose (strigulose in infructescence), brownish-yellow to reddish-brown, 3.2–6.1(–7.2 in infructescence) cm long, lateral racemes 1.0–2.7(–6.0 in infructescence) cm long, alternate and distichous; **bracts** 3.6–4.1 × 2.6–4.4 mm, ovate, concave, apex gland absent, strigose to tomentose, brownish-yellow to reddish-brown; **bracteoles** 4.5–9.0 × 2.9–6.1 mm, ovate to oblate, cucullate, apex gland absent, pubescent to tomentose, brownishyellow to reddish-brown, persistent to caducous, attached to the lower middle portion of the pedicels; **pedicel** 4.0–6.6 mm long, 1.6–3.4 mm in diameter, not twisted, tomentose, brownish-yellow to reddish-brown; **buds** 0.7–1.9 cm long, 0.5–1.0 cm in diameter, tomentose, brownish-yellow to reddish-brown. **Flowers**: **hypanthium** 4.3–4.9 mm long, 4.8– 6.4 mm in diameter, cup-shaped, equilateral, tomentose, brownish-yellow to reddish-brown; **sepal** 1.0–1.5 × 0.5–0.8 cm, elliptic to oblong, unequal, the dorsal one larger, cucullate, apex gland absent, green, tomentose, tomentulose to puberulous externally, brownish-yellow to reddish-brown, inner sepals scarious marginally; **adaxial petal** 0.9–1.4 × 1.2–1.8 cm, oblate, non-tubular, apex rounded, base truncate, white to light-red, glabrous; **petalodia** 0.6–0.8 × 0.4–0.5 mm; **stamens** exserted, joined basally in a tube, filaments 1.9–2.5 cm long, tube equilateral, 1.0–1.6 mm long, glabrous, anthers 4.6–5.4 × 1.0–1.3 mm, rectangular; **ovary** 5.0–8.6 × 2.6–3.1 mm, oblong to obovate, glabrous, stipe 5.9–9.5 mm long, glabrous, style 1.2(pre-anthesis)–2.0, stigma capitate, papillose. **Legumes** 13.2–23.5 × 3.8–9.8 cm, stipe 2.0–2.5 cm long, oblanceolate, apex obtuse, apiculate, margin slightly thickened, dark-brown, veins absent, glabrous. **Seeds** not seen.

Phenology:—Flowering in September and October; fruiting in October and November.

Distribution:—Occurring in Pará (Brazil) along the Acaraí River, a tributary of the Xingu River, and Pacajá, Anapu, and Muirapiranga (connected with Alto Anapu River) rivers, which are tributaries of the Tocantins River. **Habitat:—**Floodplain forests, likely occurring in both *igapó* and *várzea* forests. The floodplain forests of the Xingu and Tocantins rivers are considered *Igapó* due to their clear-water rivers (Junk 2011), while the floodplains near Portel in the Anapu river region are classified as *várzea* forests (Junk 2011) due to Amazon River influence.

Conservation status:—Categorized as Near Threatened (NT) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 21,015.730 km$_2$ and the estimated area of occupancy is 16.000 km$_2$.

Occurrence in protected areas:—Unknown.

Etymology:—The specific epithet is a tribute to Ricardo de Lemos Fróes, a Brazilian botanist (1891–1960) who collected the first two specimens of *E. froesii* in 1955–56, along with many other species of *Eperua.*

Vernacular names:—Ipê do Bento (*Prance G.T. et al. 1458*).

Uses:—Unknown.

Taxonomic notes:—*Eperua froesii, E. cerradoensis, E. duckeana, E. reddeniae,* and *E. schomburgkiana* are part of the group with short and erect inflorescences, non-tubular corolla, exserted stamens, falcate fruit with a length/width ration of 3:1 (vs. tubular corolla, included stamens, non-falcate fruit with a length/width ratio of 1:1 to 2:1 in other species with short and erect inflorescence). They also share multijugate leaves with straight leaflets and inflorescence with dense indumentum. *E. froesii* shares characteristics such as stamens joined in a glabrous tube with *E. cerradoensis*, and glabrous ovary with *E. schomburgkiana*. Please refer to Table 3 for a summary of the similarities and differences among these species. *Eperua froesii* is this group`s only species with entirely glabrous stamens, ovary, and fruits. It was previously identified as *E. schomburgkiana* mainly by the glabrous ovary and fruit. However, besides the allopatric distribution (*E. froesii* is restricted to the Eastern Amazonia, and *E. schomburgkiana* occurs in the Guyana Shield, see Figure 8), *E. froesii* is a different species by the entirely joined stipules (vs. free in *E. schomburgkiana*), stamens joined in a tube (vs. in a diadelphous sheath 9+1 in *E. schomburgkiana*), and glabrous stamens (vs. irregularly tomentose sheath in *E. schomburgkiana*). The separation of the species is also supported by phylogenetic studies using nuclear and ribosomal data (ter Steege *et al.* 2023 in press, Fortes *et al.* in prep).

We chose the collection *Prance G.T. et al. 1458* as the holotype over *Fróes R. de L. 32452* because the former collection has more preserved flowers. Both collections could potentially be the type of *E. froesii* because they have glabrous stamens joined basally in a tube and glabrous ovary, which are the key characteristics to differentiate *E. froesii* from *E. schomburgkiana* and other species of the group.

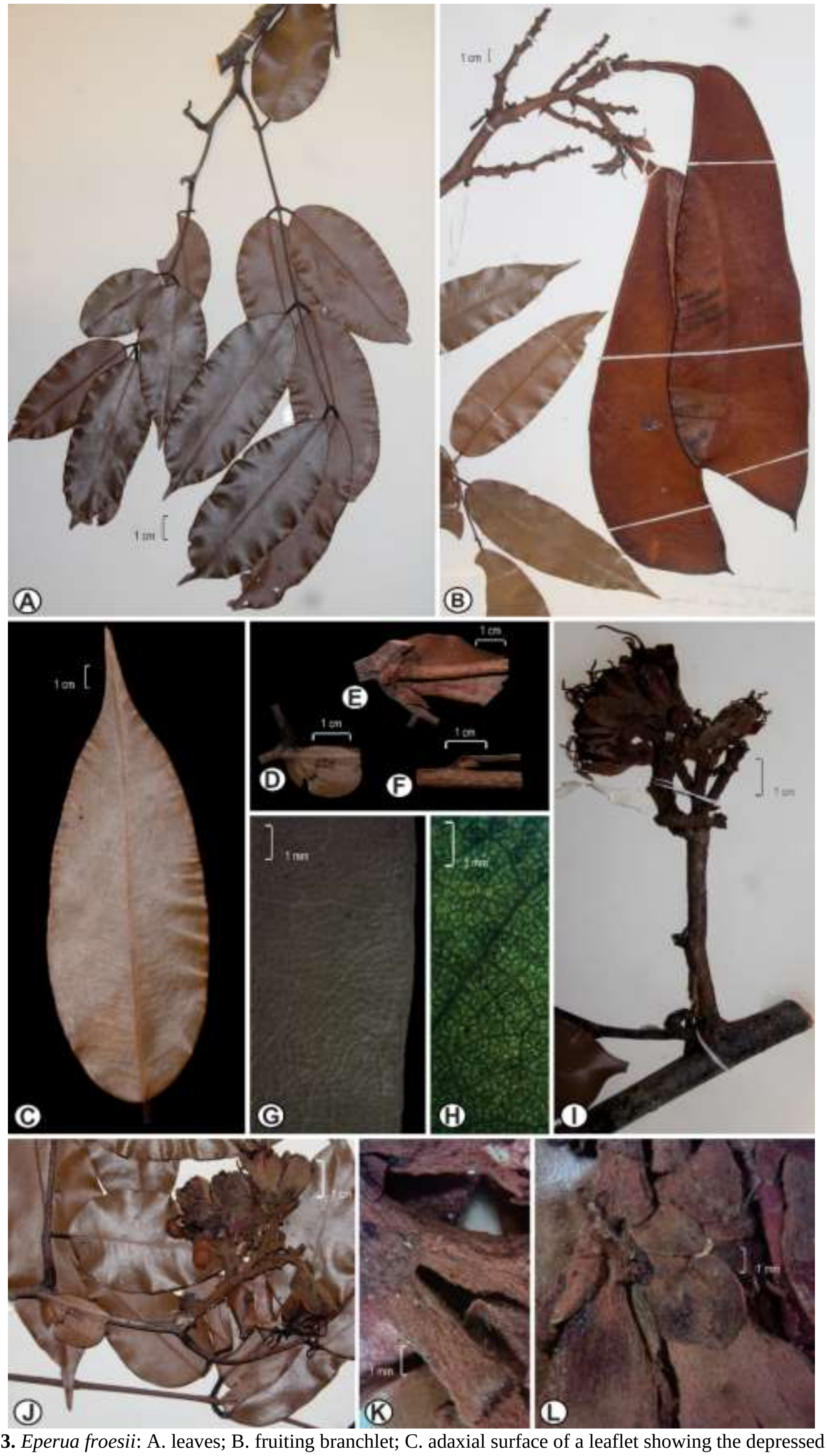


FIGURE 23. *Eperua froesii*: A. leaves; B. fruiting branchlet; C. adaxial surface of a leaflet showing the depressed main vein; D–E. foliaceous joined stipules, showing the variation in size; G. intramarginal vein, abaxial surface; H. inconspicuous pellucid-punctate leaflet; I, J. inflorescences; K. detail of the inflorescence indumentum; L. part of a flower showing one bract at the base of the pedicel, a pair of bracteoles, and the hypanthium. Specimens, A, D–L: *Prance G.T. et al. 1458*; B–C: *Prance G.T. et al. 1652*. Photos, E.A. Fortes.

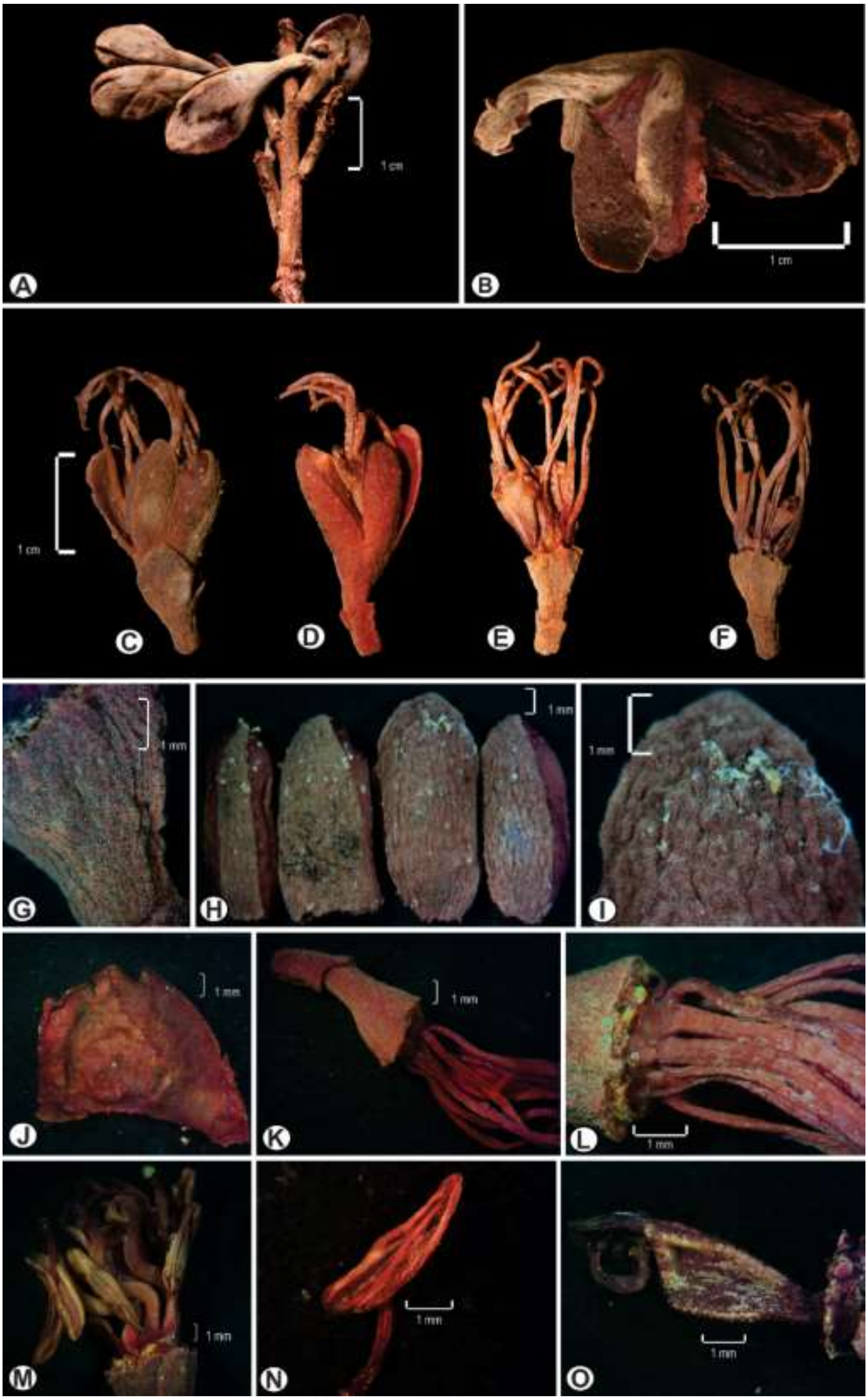


FIGURE 24. *Eperua froesii*: A. inflorescence; B. flower with bracteoles attached to the lower portion of the pedicels; C. flower showing the bracteoles, sepals, and exserted stamens. D. flower showing the scar of the bracteoles in the middle portion of the pedicel, hypanthium, and sepals; E. flower showing the hypanthium, adaxial petal and stamens (bracteoles and sepals removed); F. flower showing the hypanthium, stamens joined at the base, and ovary (bracteoles, sepals, and adaxial petal removed); G. detail of the hypanthium indumentum; H. sepals; I. detail the sepal indumentum; J. adaxial petal (partially broken on the left); K. detail of a flower showing the bracteoles scars, hypanthium, stamens, and ovary; L. detail of the base of the stamens joined in a tube; M. stamens in a bud (sepals and adaxial petal removed); N. anther and part of the filament; O. glabrous carpel. Specimens, A, B: *Fróes R. de L. 33051*; C–O: *Prance G.T. et al. 1458*. Photos, E.A. Fortes.

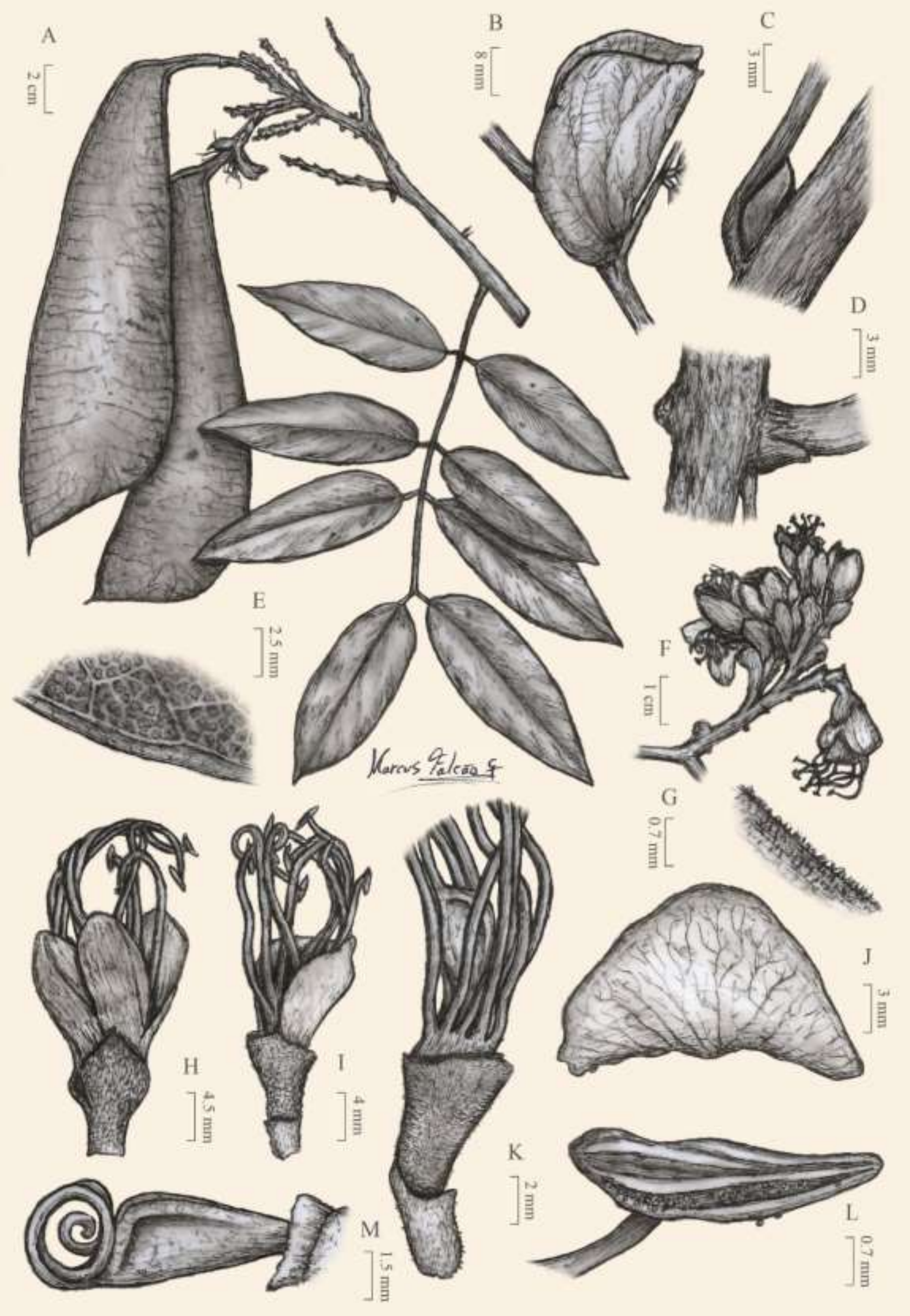


FIGURE 25. *Eperua froesii*: A. fruiting branchlet; B. big joined foliaceous stipules; C. medium joined foliaceous stipules; D. nonfoliaceous joined stipules; E. detail of leaflet margin, abaxial side, showing the intramarginal vein; F. inflorescence; G. inflorescence indumentum; H. flower showing the bracteoles, sepal, and exserted stamens; I: flower showing the hypanthium, adaxial petal, and stamens (bracteoles and sepals removed); J. adaxial petal; K. part of a flower showing the bracteole scars at the middle portion of the pedicels, hypanthium, and glabrous stamens joined at the base in tube; L. anther and part of the filament; M. glabrous carpel. Specimens, A, D: *Prance G.T. et al. 1652*; B, C, E–L: *Prance G.T. et al. 1458.* Illustrated by Marcus Falcão.

Eperua froesii shows some contrasting morphological characteristics within the species with short and erect inflorescence and non-tubular corollas. While most species have clearly white petals (*E. cerradoensis*, E. *duckeana*, and *E. schomburgkiana*) and *E. reddeniae* has non-white petals (pink to purple), *E. froesii* shows a range of petal colors from white (*Prance G.T. et al. 1458*) to light-red (*Fróes R. de L. 32418*). Another variation is the stipule type, which is entirely joined in *E. froesii*, ranging from foliaceous (Figure 23d–f, 25b, c) to non-foliaceous (Figure 25d). Foliaceous stipules are found in flowering branches (*Fróes R. de L. 32418*, *Prance G.T. et al. 1458*), and the non-foliaceous stipules are found in flowering, fruiting and sterile branches (*Fróes R. de L. 32418*, *32452*, *Prance G.T. et al. 1458*, *1652*). Further collections are needed to fully understand the petal color and the stipule patterns in *E. froesii*.

Specimens examined (Paratypes):—BRAZIL. **Pará**, Portel, região do Anapú, rio Pracajaí, à beira do rio, 10 October 1956, *Fróes R. de L. 33051* (IAN[097476]!, K[000807978]image!). Rio Acaraí, afl. do Xingú, região onde foi feito um levantamento estatístico florestal pelo IAN, SPVEA e FAO, 29 November 1955, *Fróes R. de L. 32418* (INPA[0005049]!, NY[1171155] image!, R[collection number 106671]!); *Fróes R. de L. 32452* (IAN[090190]!); rios Pacajá and Muirapiranga, west bank of rio Pacajá., 15 October 1965, *Prance G.T. et al. 1652* (F[V0111469F]!, IAN[117165]!, K[000807974, 000807976] image!, NY[01171289]!, U[0181543] image!, US[00243010]!).

7. ***Eperua glabra*** R.S. Cowan (1957: 251) (Figures 12, 26, 28)

Type:—GUYANA. Near Chodikar Landing, Amongst Acarai foothills, 250 m elev., 17 October 1952, *Guppy N.G.L. 430* (holotype NY sheet I[00004378] image!, & sheet II[00004379] image!; isotypes K sheet I[000555111] image!, & sheet II[000555109] image!, RB sheet I[00539601]!, sheet II[00545384]!, US[00001145]!).

=*Eperua praesagata* R.S. Cowan. (1985: 293) syn. nov.

Type:—BRAZIL: Pará: Rio Trombetas, Cachoeira Porteira, estrada que dá acesso para Perimetral Norte, km 7, mata de várzea de igarapé, 8 June 1978, *Silva N.T. & Santos M.R. 4758* (holotype MG[061723]!, isotypes MO[1714824] image!, NY[00004377] image!, RB[00141558]!, US[00090950]!).

Tree 7.0–37.0(–51.0) m tall. **Trunk** 20.0–60.0 cm in diameter, bark variegated to grey-brown, striate, lenticellate. **Stipules** free, 10.3–25.0(–30.0) × 6.9–14.0(–20.0) mm, foliaceous, or 0.8–1.4 × 0.4–0.8 mm, free, non-foliaceous, caducous. **Leaves** 3–5-jugate; **petioles** 0.8–4.2 cm long; **rachis** 6.4–19.0 cm long; **petiolules** (1.3–)3.7–9.1 mm long; **blades** 6.0–15.1 × 2.6–7.8 cm, chartaceous to coriaceous, glabrous, epunctate to inconspicuous pellucid-punctate, discolorous, equilateral to inequilateral, lower pair ovate, sometimes lanceolate or elliptic, middle pair ovate to elliptic, sometimes lanceolate, upper pair elliptic, apex acuminate to caudate, base symmetrical to asymmetrical, sometimes slightly asymmetrical, lower pair base subcordate, obtuse, subcordate to rounded, middle pair base obtuse to rounded, upper pair base obtuse to cuneate, rare rounded, margin flat, secondary venation with one or two intramarginal veins, vein closer to the margin continuous or not, main vein straight to slightly curved, prominent to depressed on the adaxial surface, tertiary veins conspicuous to inconspicuous, areoles smaller to larger, concave. **Inflorescences** terminal, panicle, main axis pendulous, lateral racemes patent to erect, glabrous, 93.0–300.0 cm long, lateral racemes 1.7–5.2 cm long, alternate and spirally arranged; **bracts** 0.9–1.9 × 2.2–2.3 mm, oblate, cucullate, apex gland absent, glabrous, ciliate, caducous; **bracteoles** 2.3–2.9 × 1.4–2.5 mm, ovate, cucullate, apex gland absent, ciliate, caducous, attached to the lower portion of the pedicels; **pedicel** 16.7–27.0 mm long, 1.0–2.4 mm in diameter, not twisted, glabrous; **buds** 0.7–1.1 cm long, 0.4–0.6 cm in diameter, glabrous. **Flowers**: **hypanthium** 4.5–7.3 mm long, 3.5–7.8 mm in diameter, cup-shaped to tubular, equilateral, glabrous; **sepal** 1.1–2.2 × 0.5–1.2 cm, elliptic to oblong, unequal, the outer ones larger, cucullate, apex gland absent, purplish-green, glabrous; **adaxial petal** 1.5–3.0 × 2.2–5.0 cm, flabellate, nontubular, apex rounded, base truncate, red, rose, pink to cream at base, cream to greenish at the base and pink marginally, glabrous; **petalodia** 0.5–1.6 × 0.4–0.9 mm; **stamens** exserted, joined basally in a tube, longer filaments 5.0–7.8 cm long, shorter filaments 2.3–4.0 cm long, tube equilateral to slightly inequilateral, 2.1–3.8 mm long, anthers 5.0–9.0 × 0.7–2.0 mm, rectangular; **ovary** 5.2–12.5 × 2.2–3.5 mm, oblanceolate, glabrous, 5 ovules, stipe 5.5–10.9 mm long, glabrous, style 4.2–6.0 cm long, stigma capitate to obtuse. **Legumes** 17.0–30.5 × 4.8–10.0 cm, stipe 2.1–4.6 cm long, falcate-elliptic to falcate-oblanceolate, apex obtuse, apiculate, margin thickened, sometimes dorsal margin alate, with transversal veins or veins absent, glabrous, dark-brown to reddish-brown. **Seeds** 4 per fruit, 4.6–5.8 × 2.3–2.6 cm, oblate, oblong, dark-brown.

Phenology:—Flowering in February, May to July, September, and October; fruiting in January, May, and from September to November.

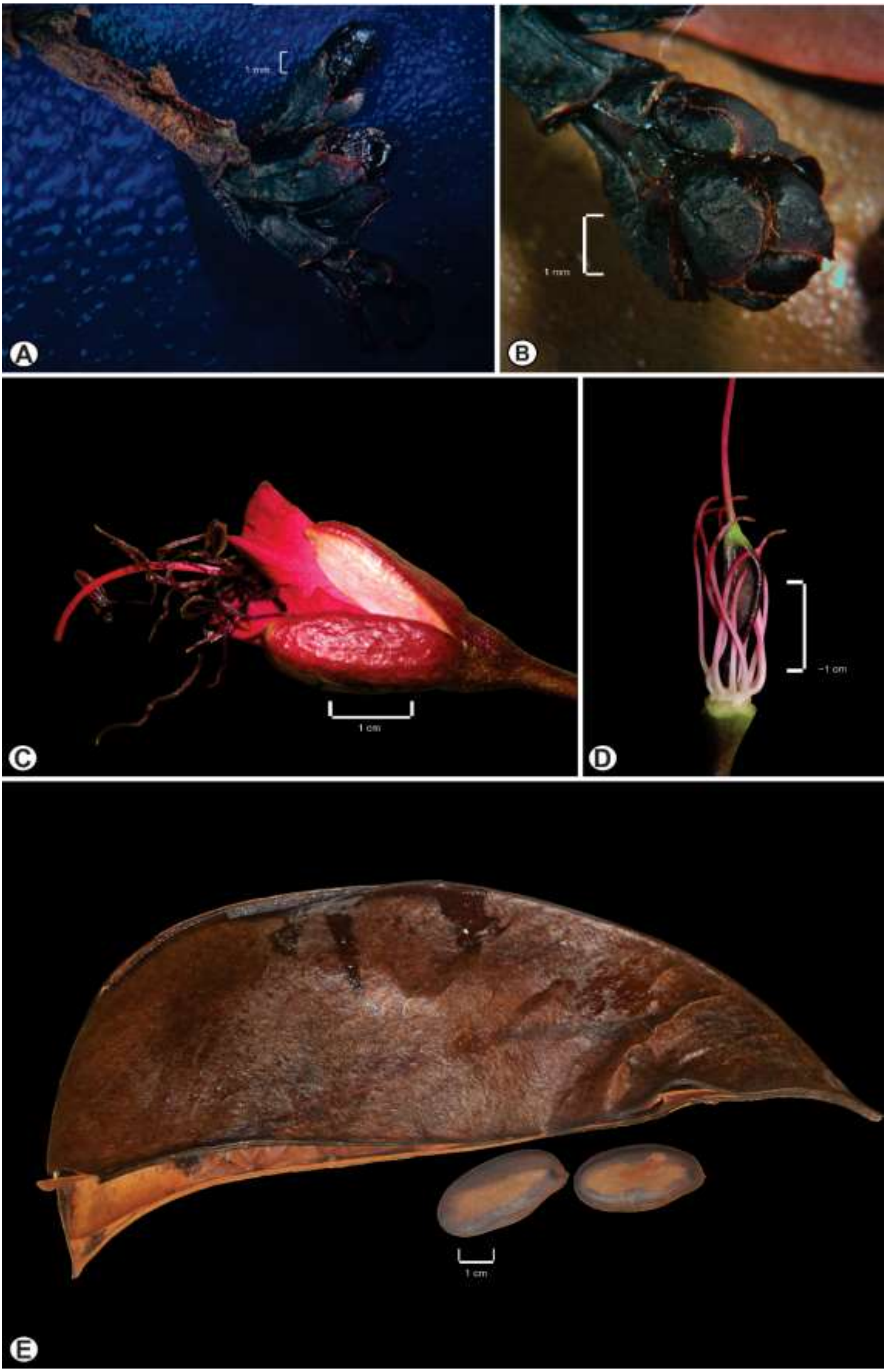


FIGURE 26. *Eperua glabra*: A. glabrous inflorescence; B. detail of a young lateral raceme in buds showing ciliate bracts and bracteoles. Specimens, A, B: *Redden K.M. et al.* 3192; E: *Henkel T.W. et al. 4655*. Photos, A, B, E: E.A. Fortes; C, D: H. ter Steege.

FIGURE 27. *Eperua aff. glabra*: A. flowering branchlet and a young fruit; B. inflorescence indumentum. Specimen, *Silva F.A. et al. 869*. Photos, E.A. Fortes.

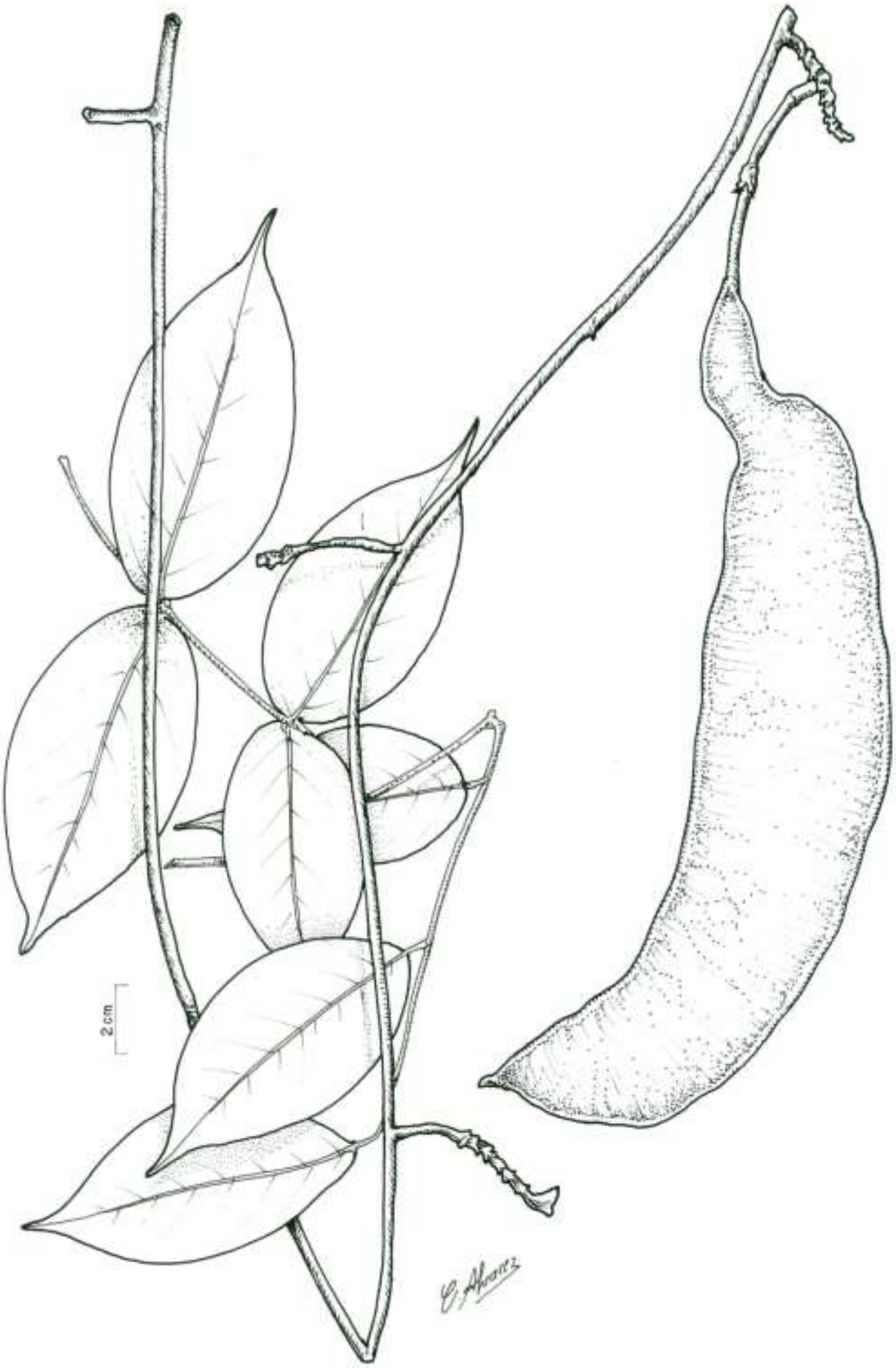


FIGURE 28. *Eperua glabra*: fruiting branchlet showing the erect lateral racemes. Specimen, *Guppy N.G.L. 430* (holotype of *E. glabra*). Illustrated by Carlos Alvarez.

Distribution:—Brazil (Pará and Roraima), Guyana (Upper Takatu-Upper Essequibo, East Berbice-Corentyne, and Upper Demerara-Berbice). One sterile collection made further in Surinam (*Oldenburger F.H.F. et al. 1203*) was sampled in the full ribosomal phylogeny for the genus (ter Steege *et al.* 2023 in press) and was nested within *Eperua glabra* specimens. It resembles *E. glabra* by the vegetative characteristics, but fertile collections are needed in Surinam to morphologically confirm the presence of the species in this country.

Habitat:—Upland (*terra-firme*) and inundated (gallery, and *igapó*) forests on clayey, brown and white mixed sandy, and brown sandy soils, from 200 to 250 m elev.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The occurrence extent of estimated for the species is 316,238.548 km$_2$ and the estimated area of occupancy is 40.000 km$_2$.

Occurrence in protected areas:—Parque Nacional Montanhas do Tumucumaque (Brazil), Mabura Hill Forest Reserve (Guyana, Upper Demerara-Berbice).

Etymology:—The specific epithet relates to its entirely glabrous inflorescences and flowers.

Vernacular names:—Brazil: espadeiro (*Rodrigues I.A. et al. 1000*). Guyana: wallaba (*Redden K.M. et al. 1054*) [although it is more often used to refer to *E. falcata*], wataba (*Redden K.M. et al. 1054*), wataja (*Guppy N.G.L. 430*).

Uses:—Unknown.

Taxonomic notes:—*Eperua glabra* and *E. praesagata* were described by Cowan (1957, 1985, respectively). These are the only entirely glabrous species within *Eperua*. They have long and pendulous inflorescence, non-tubular corolla, and exserted stamens, and share multijugate leaves with equilateral leaflets with *E. rubiginosa*. In Cowan`s (1985) diagnosis of *E. praesagata*, its differentiation from *E. glabra* was based mainly on organ sizes (including filaments, anthers, stipules, and petioles sizes), besides the number of leaflets, and petal colour (see Table 5), but the key characteristics in the genus that allow to differentiate species are related to organ indumentum and bracteole position. Moreover, the organ size variations and leaflets number are not sufficient for distinguishing between the two species, particularly due to the limited number of collections available. Apart from the holotypes of both species, there are three additional flowering collections with entirely glabrous inflorescences and flowers. However, it is not possible to confirm if it is *E. praesagata* or *E. glabra* because these new collections have overlapping characteristics between both species (see Table 5). There are seven fruiting collections (including the type collection of *E. glabra,* and one paratype of *E. praesagata*) with glabrous fruits in glabrous, long, and pendulous inflorescences. Still we did not recognize a pattern that allows us to separate them into two species.

The type locality of *E. glabra* is the Acarai Mountains on the Brazil-Guyana border, while the type locality of *E. praesagata* is in the Trombetas River in Oriximiná, Pará, Brazil (see Figure 12). Indeed, Cowan (1985, pg. 293) reported that the type locality of *E. glabra* is at a "relatively short distance north of the type locality" of *E. praesagata*. Subsequent collections of entirely glabrous specimens were made in various locations, including at the type locality of *E. glabra,* in the Acari Mountains and Chokidar river (*Henkel T.W. et al. 4655, Redden K.M. et al. 3187, 3192, Smith A.C. 2882*); further North from Brazil/Guyana border in the Mabura Hill Forest Reserve region (*Polak A.M. 218, Redden K.M. et al. 1054*); also, in Marapi River near the type locality of *E. praesagata* (*Pena B.S. 499*); and one collection further West in Roraima state (Brazil), but also near the border between Guyana and Brazil (*Rodrigues I.A. et al. 1000*). These two species are indeed sympatric and occupy the same habitat. Collections were made in upland (*terra-firme*) and inundated (*várzea*, gallery) forests in the Acarai Mountains and the Chokidar river. The holotype of *E. praesagata* (*Silva N.T. & Santos M.R. 4758*) was collected in inundated forests, but the paratype (*Cid-Ferreira C.A. et al. 1419*) is from upland forests. In conclusion, there is no reason to keep *E. praesagata* as a different species from *E. glabra*: their morphology overlaps, as well as their distributions and habitat; and they appeared paraphyletic in the phylogeny when considered different taxa (ter Steege *et al.* 2023 in press, Fortes *et al.* in prep.,). For all these reasons, they are synonymized here.

There is one collection, *Silva F.A. et al. 869* (MG[245424]!), from Januari River in the Estação Ecológica Grão-Pará, Roraima, Brazil, which bears a resemblance to *E. glabra* by the long and pendulous inflorescence with glabrous main axis, and glabrous stamens and ovary. However, it differs from *E. glabra* by its puberulent lateral racemes and bracts, puberulous bracteoles, pedicel, buds, and hypanthium, and puberulent to glabrescent sepals (Figure 27). Phylogenetically, this collection is nested within *E. glabra* (Fortes *et al.* in prep.). Further collections and studies are needed to determine this collection's taxonomic rank.

Selected specimens:—BRAZIL. **Pará**, Oriximiná, rio Trombetas, Tapagem, margem direita a 15 Km acima da mineração Santa Patrícia, 09 July 1980, *Cid-Ferreira C.A. et al. 1419* (EAFM, INPA, MG, MO, NY, RB, US); Distrito de Marapi, rio Marapi, ponto 32, 07 September 1974, *Pena B.S. 499* (IAN). **Roraima**, São João da Baliza, BR 210, Km 135, a 6Km do rio Jatapú, lado esquerdo, 0°44’14”N 59°15’15”W, 16 January 1983, *Rodrigues I.A. et al. 1000* (IAN). **GUYANA**. **Upper Demerara-Berbice**, Waraputa compartment, c. 25 km S of Mabura, 5°15’0”N 58°45’0”W, 09 January 1991, *Polak A.M. 218* (U); Mabura Hill Forest Reserve, 5°9’33.8”N 58°41’51.8”W, 20 October 2002, *Redden K.M. et al. 1054* (U, US). **Upper Takatu-Upper Essequibo**, Acarai Mts, Watuwau Creek 8–10 km upstream of juncture with Chodikar River, 1°22’0”N 58°42’0”W, 22 February 1994, *Henkel T.W. et al. 4655* (CAY, U, US); Chodikar River, 239 m elev., 1°23’39.3”N 58°47’7.5”W, 04 May 2004, *Redden K.M. et al. 3187* (NY, US); Chodikar River, 243 m elev., 1°24’53.3”N 58°47’43.2”W, 04 May 2004, *Redden K.M. et al. 3192* (US); basin of Chodikar Creek (Essequibo tributary), 1°18’0”N 58°49’59”W, 8–22 January 1938, *Smith A.C. 2882* (F, P, U, US).

TABLE 5. Morphological differences between *E. praesagata* and *E. glabra* assigned by Cowan (1985) in the diagnosis of the former species; and morphological characteristics of recent collections with glabrous, long and pendulous inflorescence, and glabrous flower with non-tubular corolla and exserted stamens.

Characters	*E. praesagata* (Cowan 1985)	*E. glabra* (Cowan 1957, 1975)	*Pena B.S. 499*	*Redden K.M. et al. 1054*	*Redden K.M. et al. 3192*
Stipules size (cm)	"minute"	2.5 × 1.5	Not seen	13.0 × 10.0	Not seen
Stipules shape	Non-foliaceous	Foliaceous	Not seen	Foliaceous	Not seen
Leaflet pair number	4–6	3–4	3	4–5	3
Petioles size (cm)	Shorter: 1–1.7	Larger: (1–)2.5–3.5	2.7–4.2	1.5–3.9	1.2–1.3
Blades size (cm)	Larger: 7–11.5 × 3.5–4.5	Smaller: 9.5–14.5 × 5.0–7.0	11.1–15.1 × 5.9–6.4	6.6–9.7 × 2.6–3.7	6.5–9.4 × 2.6–4.4
Pedicel length	3.0	2.5	1.9–2.7	1.7	Not seen
Petal color	Red	Mostly cream-colored but greenish at the base and rose-colored marginally	"Róseo" (rose)	Not seen	Pink, cream at base
Filaments size (cm)	4.0	7.8	2.4-5.0	2.3 (broken?)	Not seen
Anthers size (mm)	5–6.5 × 1–1.8	9.0 × 2.0	Not seen	Not seen	Not seen

8. ***Eperua glabriflora*** (Ducke 1940: 27) R.S. Cowan (1975: 31)

≡ *Eperua bijuga* Martius ex Bentham (1870: 226) var. *glabriflora* Ducke (1940: 27).

Type (designated by Cowan 1975)**:**—BRAZIL. Amazonas: Estrada do Aleixo, 3 April 1936, *Ducke W.A. 158* (lectotype US[00001143]!, isolectotypes A not seen, F[0057801] image!, K[000555105] image!, MO[954335] image!, NY[00004376] image!, R sheet I[000054528]!, & sheet II[R000054528a]!).

Tree 3.0–37.5 m tall. **Trunk** 10.0–54.3 cm in diameter, bark dark-yellow-brown, yellowish, brownish, lenticellate to slightly scaled. **Stipules** 1.3–3.7 × 0.7–2.7 mm, free, non-foliaceous, caducous to persistent. **Leaves** 2(3)-jugate; **petioles** 0.9–6.4 cm long; **rachis** 1.7–15.5 cm long; **petiolules** 4.0–13.8 mm long; **blades** 6.2–23.0 × 2.7–17.0 cm, coriaceous, glabrous, epunctate, rarely pellucid-punctate, not discolorous, rarely discolorous, equilateral, lower pair elliptic, sometimes ovate, rarely broadly ovate, smaller, middle pair elliptic, upper pair elliptic, rarely broadly elliptic, obovate or ovate, apex acuminate, mucronate, base symmetrical, lower pair base obtuse to rounded, rarely subcordate to cordate, middle pair base obtuse to subcordate, upper pair base obtuse, sometimes rounded, rarely subcordate or cuneate, margin revolute, sometimes flat to slightly revolute at the base, **secondary venation** with two intramarginal veins, vein closer to the margin continuous, main vein straight, depressed on the adaxial surface, tertiary veins conspicuous, areoles smaller, concave. **Inflorescences** terminal or axillary, sometimes on ramiflorous, panicle, rarely raceme, erect, glabrous, 3.0–14.9 cm long, lateral racemes 1.0–6.4(–10.6) cm long, alternate and distichous, sometimes spirally arranged; **bracts** 4.7–5.3 × 5.6–7.2 mm, broadly ovate, concave, apex gland present, glabrous, caducous; **bracteoles** 5.3–10.3 × 3.1–6.5 mm, ovate, rarely broadly ovate, cucullate, apex gland present, glabrous, caducous, attached to the lower middle portion of the pedicels; **pedicel** (2.0–)3.0–9.3 mm long, 0.9–3.4 mm in diameter, not twisted, glabrous; **buds** 0.7–1.7 cm long, 0.4–0.9 cm in diameter, glabrous. **Flowers**: **hypanthium (**1.2–)2.0–4.2 mm long, (1.2–)2.1–7.0 mm in diameter, cup-shaped, inequilateral, glabrous; **sepal** 0.8–2.0 × 0.3–1.1 cm, elliptic to oblong, unequal, the outer sepals more robust, the dorsal one larger, cucullate, apex gland present on the outer ones, *purple, sometimes pale-purple to pink-reddish*, or *greenish*, glabrous, pellucid-punctate, inner sepals scarious marginally; **adaxial petal** 2.4–5.6 × 2.1–6.7 cm, flabellate, tubular, apex rounded, cripsed, base attenuate, *purple, lilac to red* or *purple, red, greenish* to *white, glabrous;* **petalodia** 0.4–3.5 × 0.2–0.8 mm, white to pink with inner white; **stamens** inserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 2.0–4.2 cm long, shorter filaments 1.4–2.8 cm long, sheath inequilateral, shorter side 2.7–10.0 mm long, longer side 4.4–13.6 mm long, sheath tomentose, pubescent to puberulous, free filaments glabrous, brownish-yellow, shorter stamens anthers 1.1–2.8 × 0.5–1.8 mm, rectangular, longer stamens anthers 1.7–3.6 × 0.6–2.2 mm, rectangular; **ovary** 3.3–7.5 × 1.7–4.4 mm, obovate, *glabrous*, *fovoate* or *tomentose*, brownish-yellow, 2–4 ovules, stipe 3.1–7.7 mm long, *glabrous* or *tomentose*, style 1.9–3.5 cm long, stigma obtuse to capitate. **Legumes** 3.5–15.4 × 5.2–13.8 cm, stipe 0.9–2.6 cm long, obovate to orbicular, sometimes oblongelliptic, apex obtuse to truncate, sometimes rounded, dorsal margin thickened, brown to dark-brown, veins absent, rarely with some inconspicuous transversal veins, glabrous, foveate to rugose. **Seeds** 1 per fruit, 4.3–10.8 × 3.8–7.7 cm, oblate, orbicular to obovate, brown to dark-brown.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 52,541.927 km$_2$ and the estimated area of occupancy is 228.000 km$_2$.

Eperua glabriflora has two varieties: *E. glabriflora* var. *glabriflora* and *E. glabriflora* var. *gynopubescens*.

8a. ***Eperua glabriflora*** (Ducke) R.S. Cowan var. ***glabriflora*** (Figures 10, 29, 30)

Sepal purple, sometimes pale-purple to pink-reddish; **Adaxial petal** purple, lilac to red; **ovary** glabrous, fovoate, stipe glabrous.

Phenology:—Flowering throughout the year, except in October, with a peak in July; fruiting from February to March and from May to November.

Distribution:—Brazil (Amazonas, one collection in Pará).

Habitat:—Upland forest, both in *terra-firme* forest and *campinarana*, on the sand and clayish soils, from sea level to 125 m elev.

Occurrence in protected areas:—Reserva Florestal Adolpho Ducke, Reserva Biológica de Uatumã, Reserva Florestal ZF-3 (Brazil, Amazonas).

Etymology:—*Eperua glabriflora* was first described as a variety of *E. bijuga*. The glabrous pedicel, hypanthium, and sepals of *E. glabriflora* differentiate it from the type variety, then the epithet *glabriflora* probably derives from that characteristic.

Vernacular names:—espadeira (*Ducke W.A. s.n. RB20313*), morapiranga (*Boom B.M. et al. 8699*), muirapiranga (*Cid-Ferreira C.A. et al. 271*, *Cid-Ferreira C.A. et al. 4*, *Coêlho L.F. s.n. INPA6516*, *Ducke W.A. 14*, *14a*, *158 (II^{a} col)*, *s.n. RB23733*, *Elias J. & Aloisio 462*, *Ferreira E. 57-29*, *Haroldo s.n. INPA57650*, *Jorge s.n. INPA57656*, *INPA57656*, *Krukoff B.A. 8006*, *Magalhães F.M.M. 223*, *Mello F.C. de s.n. INPA55353*, *Monteiro O.P. & Mello F. s.n. INPA50065*, *Oliveira A.A. de et al. 1032*, *Oliveira A.R. de s.n. INPA58701*, *Pessoal do C.P.F. INPA6065*, *INPA6280*, *Prance G.T. et al. 23446*, *Reis L.Q. s.n. INPA57645*, *INPA57694*, *Ribeiro J.E.L.S. 881*, *Rodrigues W.A. & Osmarino 6932*, *Rodrigues W.A. & Osmarino 7005*, *Rodrigues W.A. & Osmarino 7903*, *Rodrigues W.A. 562*, *s.n. INPA1043*, *Silva S.S. da et al. 3402.2791.2*), muirapiranga da folha grande (*Oliveira A.R. de* collections, *Rodrigues W.A. & Osmarino* 5982, *Rodrigues W.A. & Osmarino* 7921).

Uses:—general construction (*Rodrigues W.A. s.n. INPA1043*).

Taxonomic notes:—*Eperua glabriflora*, along with *E. grandiflora* subsp. *ciliata* and *E. purpurea* are the only species with tubular corolla and glabrous inflorescences. *Eperua glabriflora* differs from them and all other species by the combination of 2-jugate leaves, non-falcate leaflets with revolute margin, tubular corolla, glabrous inflorescence, and caducous bracteoles attached to the lower middle portion of the pedicels (Table 2). *Eperua glabriflora* resembles *E. bijuga* by the corolla size and shape, 2-jugate leaves, and the non-falcate leaflets with two intramarginal veins. However, it differs by the revolute leaflet margins (vs. flat in *E. bijuga*); glabrous inflorescence, buds, hypanthium, and sepals (vs. puberulous to puberulent in *E. bijuga*); larger and caducous bracteoles (vs. smaller and persistent in *E. bijuga*); and shorter obovate ovary (vs. longer and falcate in *E. bijuga*).

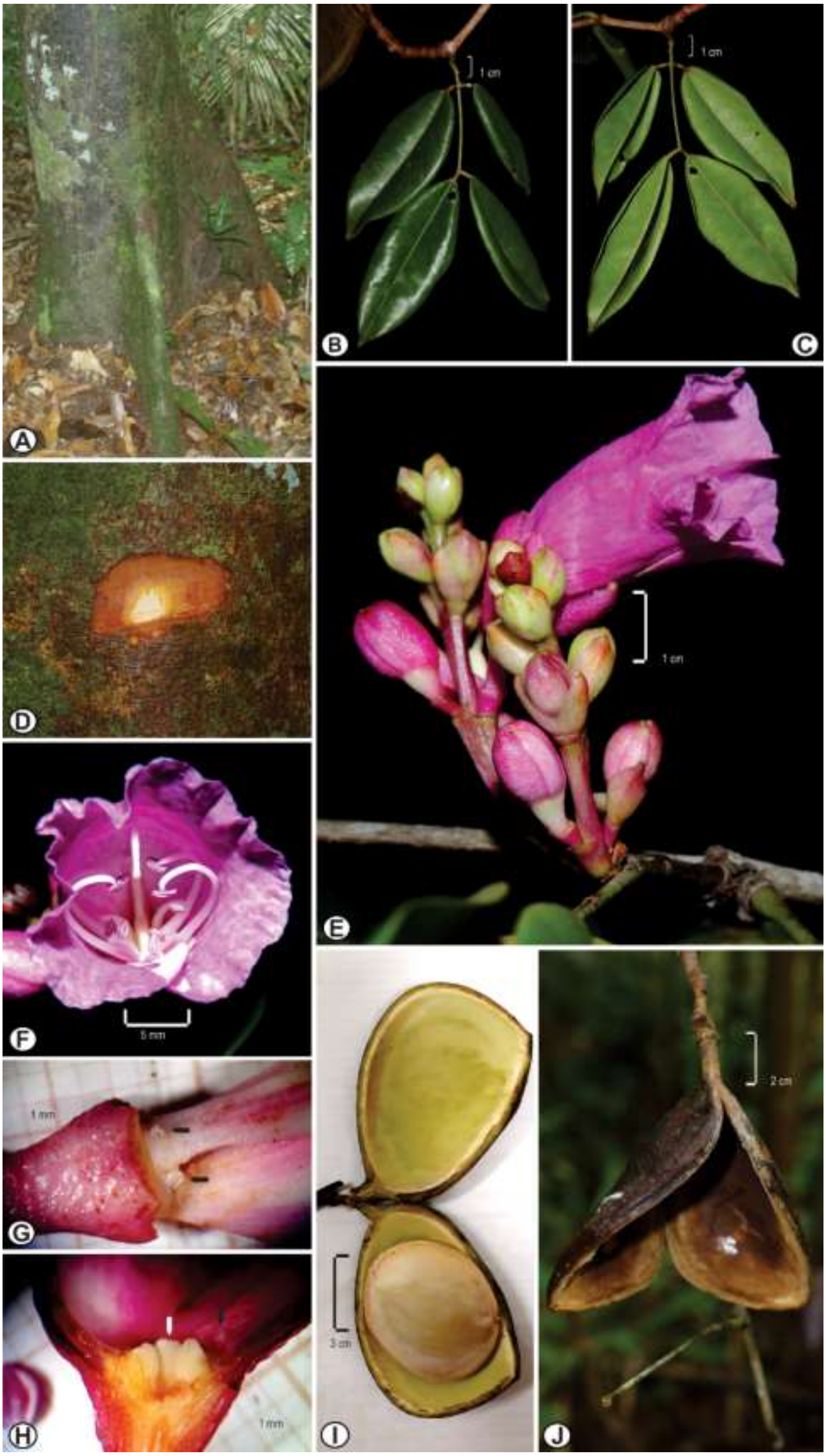


FIGURE 29. *Eperua glabriflora* var. *glabriflora*: A. trunk base; B. leaf, adaxial surface; C. leaf, abaxial surface; D. bark, sapwood, and heartwood; E. inflorescence; F. front view of the flower; G. hypanthium and petalodia (black arrows); H. inner hypanthium and nectary ring (white arrows); I. one-seeded fruit; J. fruit after opening. Specimens A, D, J: *Fortes E.A. et al. 192b*; E–I: *Fortes E.A. & M. de C. Camelo 150*. Photos, A, D–H: E.A. Fortes; B, C: F. Farroñay; H: M. Pastore.

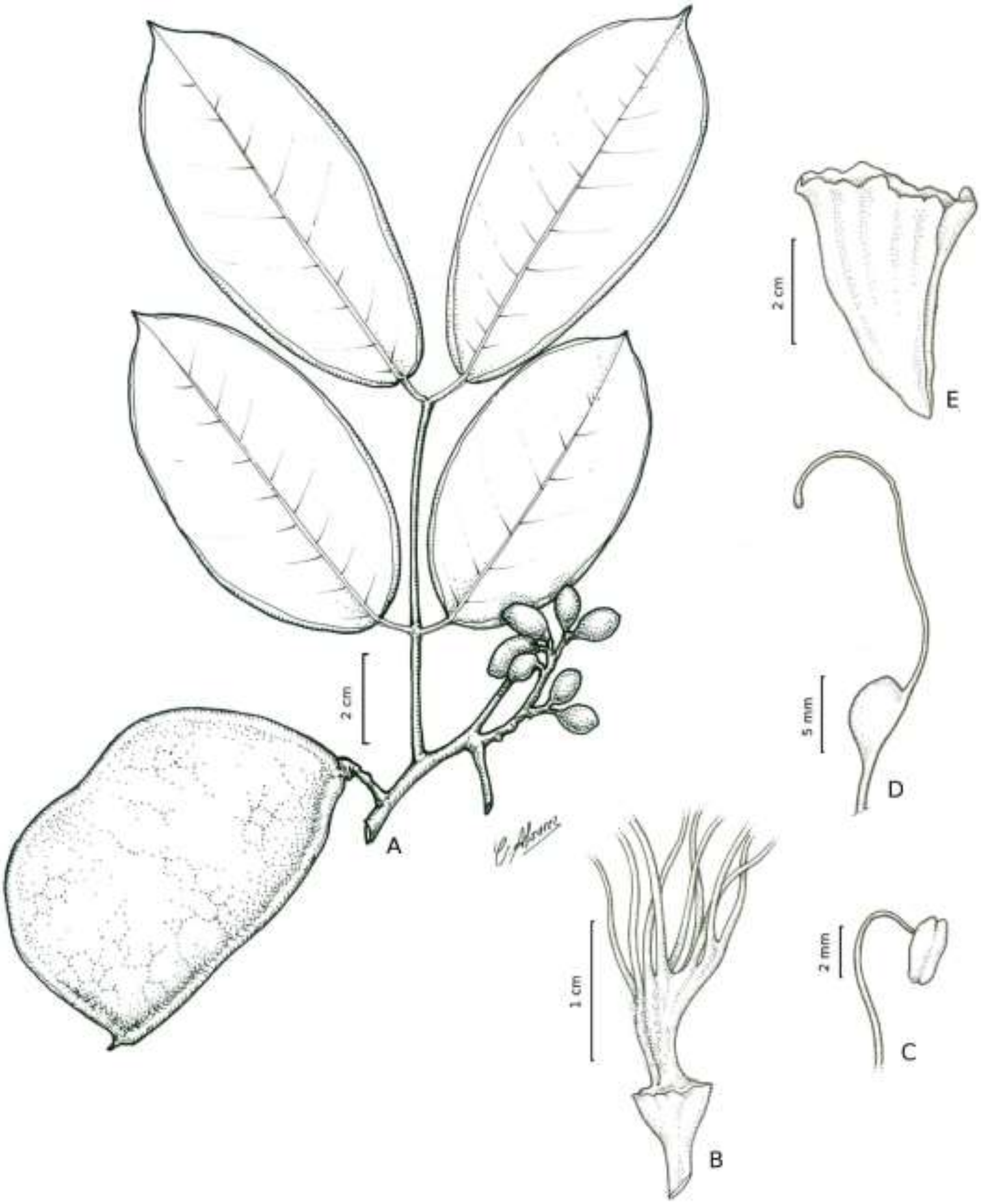


FIGURE 30. *Eperua glabriflora* var. *glabriflora*: A. flowering and fruiting branchlet; B. hypanthium and base of the stamens joined in a diadelphous sheath; C. anther and part of the filament; D. glabrous carpel; E. adaxial petal. Specimens, A: *Fróes R. de L. 24926*; B–E: *Ducke W.A. 158*. Illustrated by Carlos Alvarez.

Specimens examined:—BRAZIL. **Amazonas**, Itacoatiara, Km 75–70 da rod. Manaus-Itacoatiara, 17 October 1963, *Oliveira E. 2709* (IAN). Itapiranga, rio Uatumã, margem esquerda, subindo o rio, atrás do igarapé do Catitu, 18 July 1979, *Cid-Ferreira C.A. et al. 484* (INPA, MG, NY, RB00140230, US). Manaus, Distrito Agropecuário da SUFRAMA rodovia BR-174, km 64 depois de 23 km leste na ZF3, fazenda Esteio, reserva no. 1202, arv. No. 3150, 2°24’0”S 59°52’0”W, 03 July 1980, *Costa J.C. da et al. S.n INPA1202.3150* (NY); Reserva ZF3, BR 174, Km 63, área do Projeto TEAM, parcela do Cabo Frio sub-parcela 16, indivíduo n° 444, 24 August 2004, *Oliveira et al. A.C.A. 369* (INPA); Reserva Florestal Adolpho Ducke, quadra 21, tree #2896, 07 May 1965, *Rodrigues W.A. & Osmarino 6932* (INPA, US). Novo Airão, km 23, KM 19, 18 November 2012, *Kinupp V.F. et al. 4552* (EAFM). Presidente Figueiredo, estrada da UHE de Balbina, entrando 8 Km no vicinal ao lado do campo de pouso, 1°30’0”S 60°0’0”W, 22 September 1986, *Cid-Ferreira C.A. et al. 8239* (INPA, MG, MO, NY, UFACPZ, US); ramal ZF5 (SUFRAMA), BR-174, Km 83, 2°25’23”S 60°17’36”W, 11 June 2011, *Marra D.M. et al. 584* (EAFM); Rebio Uatumã, ramal da Morena, corredeira da Anta próximo ao Projeto de Desenvolvimento Sustentável (PDS), 1°0’0”S 59°0’0”W, 06 July 2007, *Sakagawa S. & Mesquita J.R. 366* (INPA, RB00716854). **Pará**, Lago do Faro, cabeceira de Inajá, lugar húmido e ligeiramente [...]?, 27 January 1927, *Ducke W.A. s.n. RB20313* (RB, U). **Rio de Janeiro (cultivated)**, Rio de Janeiro, Jardim Botânico do rio de Janeiro, Arboreto canteiro 26^{a}, 04 February 2020, *Fortes E.A. & Camelo M. De C. 150* (RB).

8b. ***Eperua glabriflora*** *var.* ***gynopubescens*** E.A. Fortes & Mansano, var. nov. (Figures 10, 31)

Type:—BRAZIL. Amazonas, Itapiranga, rio Pitinga, margem direita, 24 August 1979, *Cid-Ferreira C.A. et al. 659* (holotype INPA[0034257]!, isotypes MG[076037]!, MO[1780613] image!, NY[1171206] image!, R[000049194]!, RB[00266154], US[00242870] image!).

Diagnosis:—*Eperua glabriflora* var. *gynopubescens* is similar to var. *glabriflora,* except for the indumentum of the ovary. The new variety can be differentiated from the type one by the flowers with glabrous or tomentose ovary in the same inflorescence (vs. always glabrous in var. *glabriflora*). **Sepal** greenish; **Adaxial petal** purple, red, greenish to white; **ovary** and stipe tomentose or glabrous in the same inflorescence.

Phenology:—Flowering in April, August, and September; fruiting in August.

Distribution:—Brazil (Amazonas).

Habitat:—*Campinarana,* gallery and *terra-firme* forests.

Occurrence in protected areas:—Reserva Florestal Adolpho Ducke (Brazil, Amazonas).

Etymology:—The specific epithet relates to its tomentose ovary.

Vernacular names:—Unknown.

Uses:—Unknown.

Specimens examined:—BRAZIL. **Amazonas**, Manaus, Reserva Florestal Adolpho Ducke, Manaus-Itacoatiara, km 26, ramal ao Acará, 2°53’0”S 59°58’0”W, 25 April 1988, *Ramos J.F. 1855* (HUEFS[0197835] image!, INPA[0179539]!, MG!, MO[1721976]!, NY[1171186] image!, SP[024676] image!, RB[00140240]!, U[0061219] image!); rio Tarumá, 07 August 1949, *Fróes R. De L. 24926* (IAN[050817, 50817^{a}]!). Pedra Branca, rio Urubú, 17 September 1949, *Fróes R. De L. 25266* (IAC[collection number 25266], IAN[144635]!).

9. ***Eperua grandiflora*** (Aublet 1775: 757) Baillon (1870: 110) (Figures 9, 32, 33, 34)

≡ *Parivoa grandiflora* Aublet (1775: 757).

Type (designated by Cowan 1975)**:**—FRENCH GUIANA. Unknown locality, s.d. [July 1762–July 1764], *Aublet J.B.C.F. s.n.* (lectotype BM[000952282] image!, isolectotypes P[00835933] image!, P[00835934] image!).

≡ *Dimorpha grandiflora* (Aubl.) Forsyth (1794: 391) nom. Illeg. Superfl.

≡ *Dimorpha grandiflora* (Aubl.) Willdenow (1802: 971), nom. Illeg. Superfl.

= *Eperua kourouensis* Benoist (1916: 273).

Type (designated by Fortes & Mansano 2022)**:**—FRENCH GUIANA Gourdonville, Kourou R., 8 September 1914, *Benoist R. 1595* (lectotype P[00835930] image!, isolectotypes, P[00835931] image!, P[00835932] image!).

Tree 3.0–40.0 m tall. **Trunk** 20.0–100.0 cm in diameter, bark gray, greyish-black, reddish, red, lenticellate, smooth to caled. **Stipules** 1.9–11.3(–27.1) × 1.3–10.0(–21.2) mm, free, foliaceous, sometimes non-foliaceous, caducous to persistent. **Leaves** 2–3(–4)-jugate; **petioles** 0.6–2.6 cm long; **rachis** 3.0–11.7 cm long; **petiolules** 1.4–9.3 mm long; **blades** 3.8–15.8 × 1.6–6.9(–9.6) cm, coriaceous, glabrous, epunctate, inconspicuous pellucid-punctate to minutely pellucid-punctate, discolorous to not discolorous, equilateral, lower pair ovate, elliptic to lanceolate, middle pair narrowly elliptic to elliptic, upper pair elliptic to narrowly elliptic, apex attenuate, acuminate to caudate, base symmetrical to oblique, par of glands absent or with one pair of glands, lower pair base obtuse, rounded to subcordate, middle pair base obtuse to rounded, upper pair base obtuse, *margin flat to slightly revolute, rarely very revolute* or *very revolute, rarely flat,* **secondary venation** with one or two intramarginal veins, vein closer to the margin continuous or not, main vein straight, prominent to depressed on the adaxial surface, tertiary veins conspicuous to inconspicuous, areoles smaller, concave. **Inflorescences** terminal or axillary, panicle or raceme, erect, *pubescent to tomentose, sometimes puberulous,* or *pubescent, puberulous to glabrescent,* or *glabrous,* brownish-yellow, 2.3–9.8 cm long, lateral racemes 1.2–6.0 cm long, alternate and distichous; **bracts** 2.1–4.7 × 1.6–4.0 mm, ovate to broadly ovate, cucullate, apex gland present or absent, *tomentose, pubescent to puberulous externally, glabrous within,* or *glabrous, ciliate,* brownish-yellow, caducous to persistent;

FIGURE 31. *Eperua glabriflora* var. *gynopubescens*: A. flowering branchlet and detail of the tomentose carpel; B, C. ovary indumentum. Specimen, *Ramos J.F. 1855*. Photos, E.A. Fortes.

bracteoles *2.3–3.9 × 2.0–3.7 mm*, or *1.9–3.0 × 1.5–3.4 mm*, or *4.7–5.6 × 3.8–5.9 mm*, ovate to broadly ovate, cucullate, apex gland present or absent, *pubescent to tomentose, rarely puberulous externally, glabrous within*, or *pubescent to puberulous on both sides to glabrous within*, brownish-yellow, persistent, attached to the higher portion of the pedicels or at the base of the hypanthium, at slightly different levels; **pedicel** 3.0–10.3 mm long, 0.5–1.6 mm in diameter, not twisted, *puberulous*, *pubescent to tomentose*, or *glabrous*, brownish-yellow; **buds** 0.4–1.3 cm long, 0.3–0.6 cm in diameter, *pubescent to puberulous, sometimes glabrescent*, or *glabrous*, brownish-yellow. **Flowers**: **hypanthium** 1.5–2.8 mm long, 1.9–4.1 mm in diameter, cup-shaped, inequilateral to equilateral, *tomentose, pubescent to puberulous*, or *glabrous*, brownish-yellow; **sepal** 0.5–1.4 × 0.2–0.8 cm, elliptic, ovate, lanceolate to oblanceolate, unequal, the dorsal one larger, cucullate, apex gland present or absent, green, purple-green, purplish, brown-purple, brown to burgundy, *pubescent, puberulous to glabrescent*, or *glabrous*, trichomes brownish-yellow; **adaxial petal** 1.5–4.3 × 1.4–5.1 cm, flabellate, tubular, apex rounded, base attenuate, pale-pink, pink, purple, pale-purple, lilac, whitish inner, to white with purple guide nectar, glabrous; **petalodia** 0.2–1.2 × 0.2–0.5 mm; **stamens**, inserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 0.9–2.7 cm long, shorter filaments 0.5–1.3 cm long, sheath inequilateral, shorter side 2.5–5.0 mm long, longer side 4.0–11.0 mm long, *sheath irregularly tomentose, pubescent to puberulous, sometimes irregularly villous to entirely villous*, or *pubescent to puberulous*, or *irregularly villous*, free filament glabrous, free filament glabrous, brownish-yellow, anthers 1.1–2.6 × 0.3–1.1 mm, rectangular; **ovary** 1.7–5.4 × 1.3–3.7 mm, obovate, *glabrous* or *sericeous*, stipe 1.6–5.1 mm long, glabrous, style 1.2–2.1 cm long, stigma obtuse, papillate. **Legumes** 6.0–12.4 × 4.3–9.2 cm, stipe 0.8–1.4 cm long, oblong, elliptic to obovate, apex truncate, obtuse to rounded, margin thickened, dark-brown, transversal veins present or absent, *glabrous* or *puberulous*, very rugose. **Seeds** 1–2 per fruit, 3.4–4.5 × 4.9–7.4 cm, oblate, dark-brown.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 378,125.077 km_2 and the estimated area of occupancy is 208.000 km_2.

Eperua grandiflora has three subspecies presented here: *E. grandiflora* subsp. *grandiflora*, *E. grandiflora* subsp. *guyanensis*, and *E. grandiflora* subsp. *ciliata* subsp. nov.

9a. ***Eperua grandiflora*** (Aubl.) Baill. subsp. ***grandiflora***

Leaves, margin flat to slightly revolute, rarely very revolute. **Inflorescences** pubescent to tomentose, sometimes puberulous; **bracts** tomentose, pubescent to puberulous externally, glabrous within; **bracteoles** 2.3–3.9 × 2.0–3.7 mm, pubescent to tomentose, rarely puberulous externally, glabrous within; **pedicel** puberulous, pubescent to tomentose; **buds** pubescent to puberulous, sometimes glabrescent. **Flowers**: **hypanthium** tomentose, pubescent to puberulous; **sepal** pubescent, puberulous to glabrescent; **stamens** sheath irregularly tomentose, pubescent to puberulous, sometimes irregularly villous to entirely villous; **ovary** glabrous. **Legumes** glabrous.

Phenology:—Flowering in January, April, May, and from July to November; fruiting from January to April, in

July, and from September to December.

Distribution:—Brazil (Amapá), French Guiana (Cayenne, Saint-Laurent-du-Maroni), Guyana (Upper Demerara-Berbice), and Surinam (Sipaliwini).

Habitat:—Mainly in upland forests, sometimes in floodplains, from sea level to 990 m elev.

Occurrence in protected areas:—Parque Nacional Montanhas do Tumucumaque (Brazil, Amapá), Réserve Naturelle Nationale de la Trinité (French Guiana, Saint-Laurent-du-Maroni), Parque Nacional do Monte Roraima (Brazil-Roraima, Guyana- Cuyuni-Mazaruni), Mabura Hill Forest Reserve (Guyana, Upper Demerara-Berbice). **Etymology:—**The specific epithet relates to the species bigger flower compared with *Parivoa tomentosa* Aubl. (synonym of *Crudia tomentosa* (Aubl.) J.F.Macbr.). But, after the combination of *Pariova* into *Eperua* the epithet became meaningless, as *E. jenmanii* is the species that has the biggest flowers in the genus.

Vernacular names:—apá (*Dambrós L.A. 307, Rabelo B.V. et al. 3308*), bii adu (Djuka) (*Lescure J.P. 746*), wap seinõ (*Grenand P. 3082*), wapa (*Thiel J.* collections), wapa tapaka (Wayãpi) (*Lescure J.P. 746*).

Uses:—Unknown.

Taxonomic notes:—*Eperua grandiflora* differs from other species with short and erect inflorescence and tubular corolla by the combination of the following characteristics: free stipules, intramarginal vein not very close to the margin, inflorescence with dense indumentum (subsp. *grandiflora* and subsp. *guyanensis*) or glabrous (subsp. *ciliata*), persistent bracteoles inserted high on the pedicels or at the base of the hypanthium, and non-glabrous sheath (Table 2). According to Cowan (1975), the type subspecies differs from the subsp. *guyanensis* mainly by the flat leaflet margins (vs. revolute in subsp. *guyanensis*), glabrous ovary (vs. sericeous in subsp. *guyanensis*), and its distribution range along the Brazil-French Guiana border, coastal French Guiana and south-central Suriname (vs. central to south-central Guyana). Most specimens of each subspecies follow the pattern above, but we found two specimens with intermediary morphotypes: *Pipoly J.J. & Boyan R. 8799* from Guyana, with revolute leaflet margins and glabrous ovary, and *Redden K.M. et al. 1053* from Guyana, with flat leaflet margins and puberulous fruits. Considering only the indumentum of the phylogenetic signal, there is an overlap in the distribution range and the vegetative characteristics, which justify the maintenance of subsp. *guyanensis* as an infraspecific category of *E. grandiflora.* ovary, the first collection can be identified as subsp. *grandiflora*, and the second one as subsp. *guyanensis* (puberulous fruits indicate a non-glabrous ovary). In the phylogenetic analysis, the subspecies appeared as a separated lineage, with the specimen *Redden K.M. et al. 1053* nesting within subsp. *guyanensis* (Fortes et al in prep). Although this is a phylogenetic signal, there is an overlap in the distribution range and the vegetative characteristics, which justify the maintenance of subsp. *guyanensis* as an infraspecific category of *E. grandiflora.* Most specimens of *E. grandiflora* subsp. *grandiflora* has irregularly tomentose, pubescent to puberulous sheaths, but we found one specimen with irregularly villous sheath (*W.J. Hahn* 3744) and one with entirely villous sheath (*Goldenberg R. et al. 2632*, Figure 34). These specimens were recorded in the same distribution range as the type subspecies. These described characteristics do not support them as a different species or an infraspecific category of *E. grandiflora.* Additionally, in the phylogenetic analysis, these two collections appeared as sister groups within *E. grandiflora* subsp. *grandiflora* (Fortes *et al.* in prep).

Selected specimens:—BRAZIL. **Amapá**, Lourenço, Calçoene, rio Araguari, 2°13’0”N 51°58’0”W, 02 September 1961, *Pires J.M. et al. 50673* (F, IAN, K, MG, NY, R, S, SP, U, US). Pedra Branca do Amapari, Parque Nacional Montanhas do Tumucumaque, rio Amapari, acima da base Jupará, 1°11’16”N 52°22’8”W, 15 September 2018, *Goldenberg R. et al. 2632* (RB, UPCB).Porto Grande, Cupixi, a cerca de 40 km a sudoeste da localidade de Serra do Navio, proximidade do rio Cupixi, 13 m elev., 0°37’0”N 52°10’0”W, 19 November 1983, *Dambrós L.A. 307* (HRB, INPA, RB). Serra do Navio, Parque Nacional das Montanhas do Tumucumaque, margens do rio Amapari acima da base do ICMBio, 115 m elev, 1°10’26”N 52°21’34”W, *Forzza R.C. et al. 9951* (RB, HAMAB, UPCB, NY). **FRENCH GUIANA**. **Cayenne**, Cayenne, Quesnel-Chantier F.R.G., 10 December 1979, *Thiel J. 603* (CAY); exploitation forestière F.R.G., km 8, 10 March 1981, *Thiel J. 815* (CAY). Kourou, rivière Kourou, bassin du Kourou, 15 October 1981, *Thiel J. 890* (CAY); montagne des Singes - 1, km 8, région littorale, 21 October 1981, *Thiel J. 900* (CAY). Macouria, Matiti, Point-Quadrat MAT, 5°0’0”N 52°38’0”W, 20 November 2001, *Prévost M.F. 4278* (CAY, MO). Montsinéry-Tonnegrande, Montagne des Chevaux, Carrière SCC, 28 m elev., 4°44’34”N 52°26’12”W, 11 January 2009, *Tostain O. et al. 2457* (CAY). Régina, station des Nouragues (camp inselberg), trail CE near camp, 20–40 m elev., 4°5’30”N 52°41’0”W, 08 August 2008, *Geiselman C.K. 165* (NY). Roura, route de l’Est, km 0.5, basin de l’Orapu, 23 April 1981, *Thiel J. 826* (CAY). Saint-Élie, piste de St.Elie, CD-21, 100 m elev., 5°0’0”N 53°10’0”W, 15 September 1987, *Hahn W.J. 3744* (CAY, U, US, WAG). Sinnamary, crique Paracou, 03 November 1996, *Hallé F. 4425* (MPU, U); piste de Saint-Élie, km 11.5, 14 October 1980, *Thiel J. 736* (CAY). **Gourdonville**, unknown locality, 08 September 1914, *Benoist R. 1595* (P). **Saint-Laurent-du-Maroni**, Mana, St-Elie Réserve Naturelle des Montagnes de la Trinité-Plateau- Tabulaire, bassin de la Mana, 400–630 m elev., 4°35’0”N 53°21’0”W, July 1999, *Poncy O. 2652* (CAY). **GUYANA**. **Upper Demerara-Berbice**, Mabura hill and vinicity, 50–60 m elev., 5°25’0”N 58°40’0”W, 5°25’0”N 58°40’0”W, *Pipoly J.J. & Boyan R. 8799* (U, US). **SURINAM**. **Sipaliwini**, Nickerie, Fallawatra, 18 January 1972, *Jimenez-saa J.H. 1698 (L.B.B. 14431)* (U).

9b. ***Eperua grandiflora*** subsp. ***guyanensis*** R.S. Cowan (1975: 34)

Type:—GUYANA. Bartica-Potaro. 83 mi Bartica-Potaro road, 23 June 1933, *Tutin T.G. 245* (holotype US00001146!, isotypes, BM000952283 image!, K000555101 image!, U0003225 image!).

Leaves margin very revolute, rarely flat. **Inflorescences** pubescent, puberulous to glabrescent; **bracts** tomentose, pubescent to puberulous externally, glabrous within; **bracteoles** 1.9–3.0 × 1.5–3.4 mm, pubescent to puberulous on both sides to glabrous within; **pedicel** puberulous, pubescent to tomentose; **buds** pubescent to puberulous, sometimes glabrescent. **Flowers**: **hypanthium** tomentose, pubescent to puberulous; **sepal** pubescent, puberulous to glabrescent; **stamens** sheath entirely pubescent to puberulous; **ovary** sericeous. **Legumes** puberulous.

Phenology:—Flowering from February to April, in June, July, and from September to November; fruiting in January, April, May, August, and October.

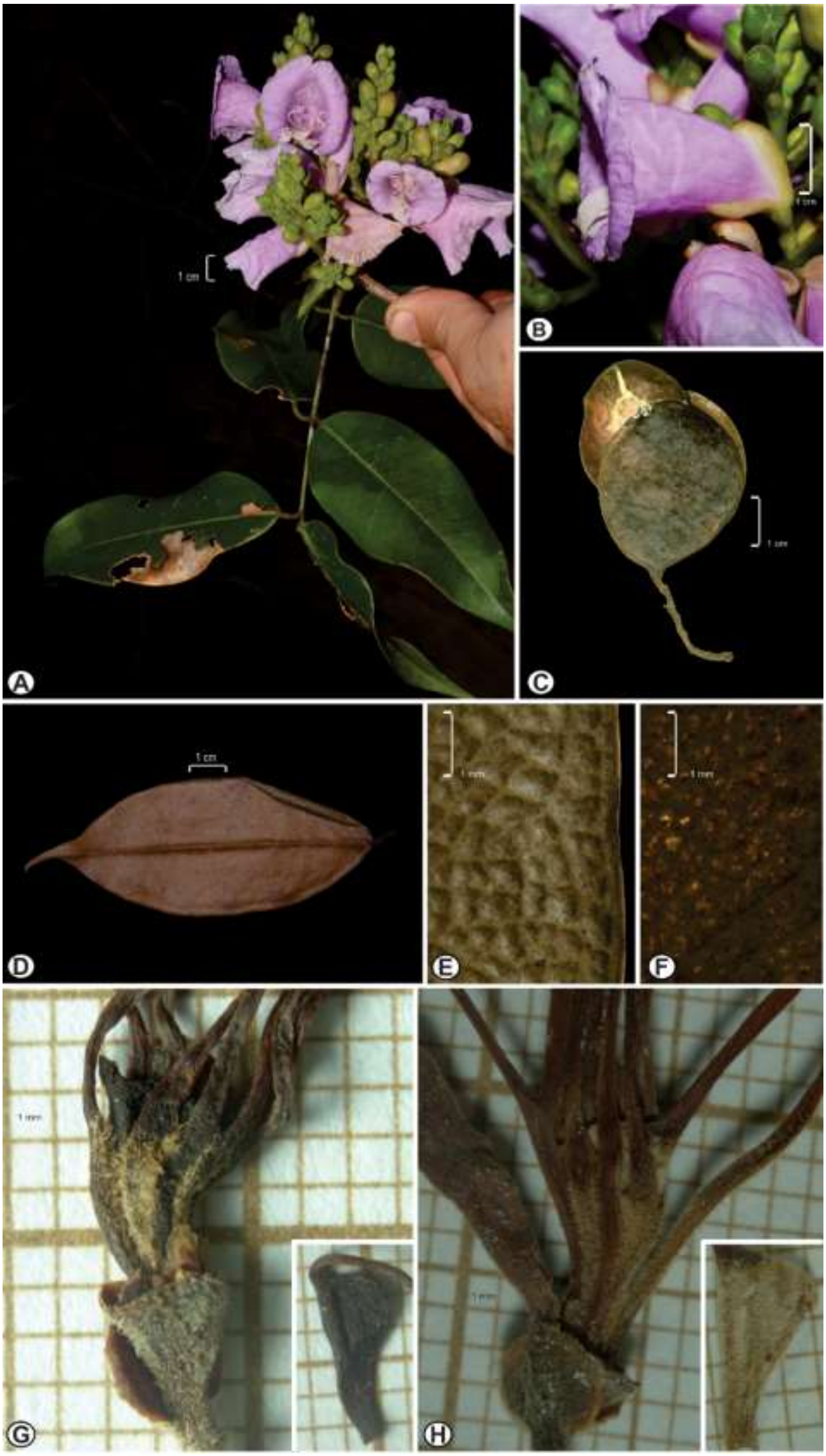


FIGURE 32. *Eperua grandiflora*: A. flowering branchlet, subsp. *grandiflora*; B. flower, lateral view, subsp. *grandiflora*; C. one-seeded fruits, subsp. *grandiflora*; D. leaflet with revolute margin, subsp. *guyanensis*; E. intramarginal vein, abaxial surface, subsp. *grandiflora*; F. epunctate leaflet blade, subsp. *grandiflora*; G. flower showing the stamens and ovary indumentum, subsp. *grandiflora*; H flower showing the stamens and ovary indumentum, subsp. *guyanensis*. Specimens, A, B: *Goldenberg R. et al. 2632*; D, H: *Zartman C.E. 7928*; E, F: *Forzza R.C. et al. 9951*; G: *Pires J.M. et al. 50878*. Photos, A, B: R Goldenberg; C: D. Sabatier; D–H: E.A. Fortes.

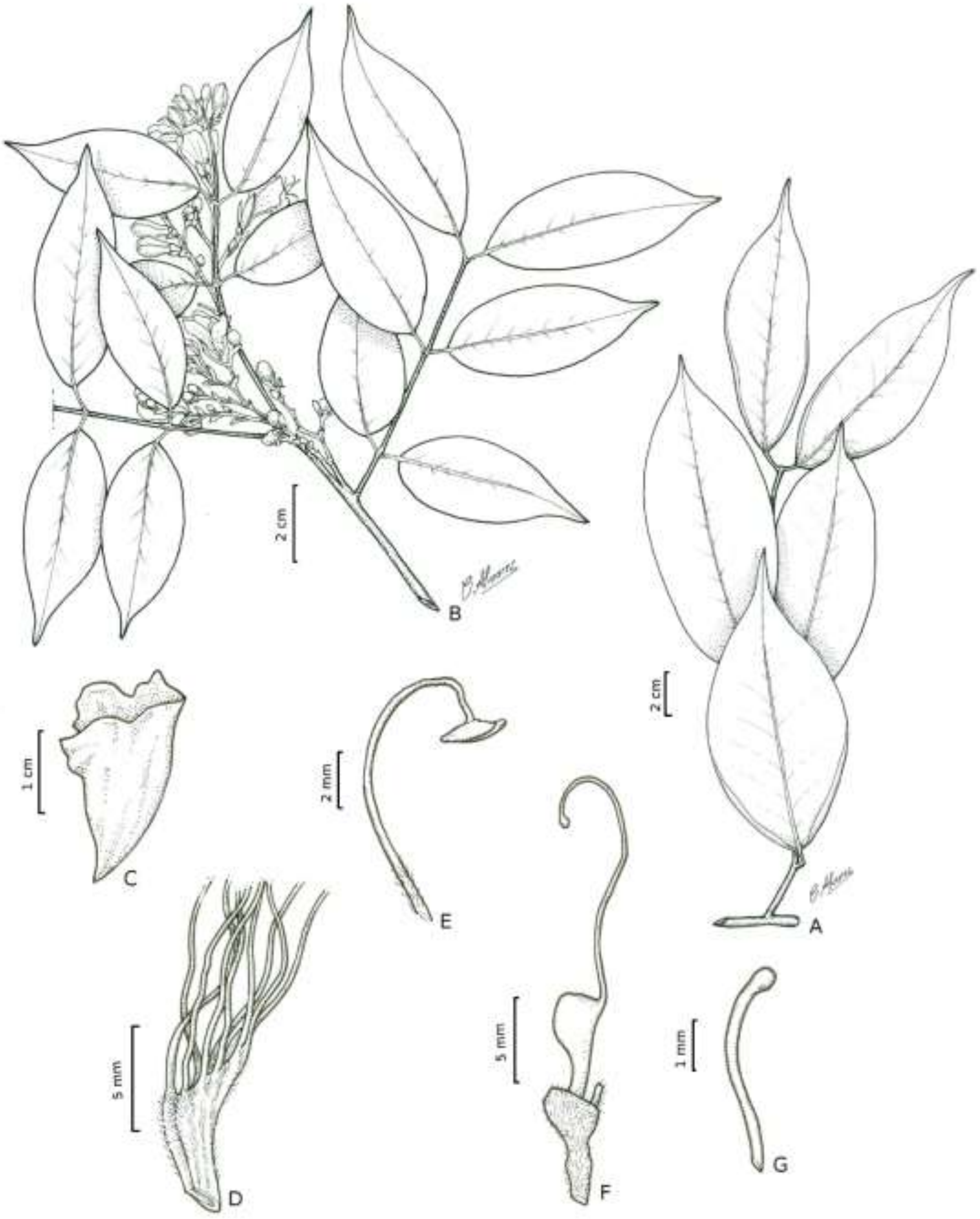


FIGURE 33. *Eperua grandiflora.* Leaf with revolute leaflets, subsp. *guyanensis*; B. flowering branchlet, leaflets with flat margins, subsp. *grandiflora*; D. base of the stamens joined in a sheath, subsp. *grandiflora*; E. anther and filament, subsp. *grandiflora*; F. hypanthium and glabrous carpel, subsp. *grandiflora*; G. style and stigma, subsp. *grandiflora*. Specimens A: *Tutin T.G. 245*; B–G: *Pires J.M. et al. 51659*. Illustrated by Carlos Alvarez.

Distribution:—Guyana (Cuyuni-Mazaruni, Essequibo Islands–West Demerara, Pomeroon-Supenaam, Potaro-Siparuni, Upper Demerara-Berbice) and Surinam (Nickerie).

Habitat:—White sand ecosystems in *wallaba* forest, from sea level to 200 m elev, on white and brown sand, sometimes on white sand-brown loamy sand-bauxite mosaic.

Occurrence in protected areas:—Mabura Hill Forest Reserve (Guyana, Upper Demerara-Berbice), Pibiri Forest Reserve (Guyana, Upper Demerara-Berbice).

FIGURE 34. *Eperua grandiflora* var. *grandiflora*: A. flowering branchlet; B. base of the leaflet; C. free non-foliaceous stipules; D. intramarginal vein, abaxial surface; E. detail of the inflorescence; F. flower, lateral view; G. flower, frontal view; H. part of a flower showing the bracteoles and sepals; I. adaxial petal; J. stamens joined in a diadelphous sheath; K. detail of the stamen indumentum; L. anther and part of the filament; M. glabrous carpel; N. stigma. Specimen, *Goldenberg R. et al. 2632*. Illustrated by Marcus Falcão.

Etymology:—The specific epithet relates to its distribution in Guyana.

Vernacular names:—ituri-wallaba (*Ek R.C. & Zagt R. 855*, *Forest Department 2311*, *Redden K.M. et al. 1053*, *Sandwith N.Y. 314*, *Tutin T.G. 245*), wapa-courbaril (*Coup C. CL203*).

Uses:—Guyana: firewood (*Tutin T.G. 245*), light poles (*Redden K.M. et al. 1053*), fences, posts, electricity poles, and roof shingles (H. ter Steege pers. obs.).

Taxonomic notes:—See taxonomic notes of the type subspecies.

Selected specimens:—GUYANA. **Cuyuni-Mazaruni**, Bartica, Essequibo River, Moraballi Creek, near Bartica, 20 September 1929, *Sandwith N.Y. 314* (RB, U). **Essequibo-Demerara Ocidental**, 4 km from Santa Mision, 0–200 m elev., 6°30'0"N 58°23'W, 25 November 1992, *Görts-van Rijn A.R.A. et al. 403* (CAY, U, US). **Pomeroon-Supenaam**, Waraputa compartment, c. 25 km S of Mabura, 0–100 m elev., 5°15'0"N 58°45'0"W, 10 October 1991, *Polak A.M. et al. 364* (U). **GUYANA**. **Potaro-Siparuni**, Kuribrong, 112 m elev., 5°21'0"S 59°15'0"W, April 2010, *Zartman C.E. 7928* (INPA, RB). **Upper Demerara-Berbice**, Mabura Hill area, 150–200 m elev., 5°20'0"N 58°40'0"W, 05 June 1986, *Pipoly J.J. 7560* (CAY, F, INPA, MO, P, U, US, WAG); Mabura Hill Forest Reserve, main trail, 69 m elev., 5°9'33.8"N 58°41'51.8"W, 20 October 2002, *Redden K.M. et al. 1053* (U, US). **SURINAM**. **Nickerie**, Arkonikreek, Nickerie rivier, 28 August 1976, *Teunissen P.A. 16010* (U).

9c. ***Eperua grandiflora*** subsp. ***ciliata*** E.A. Fortes & Mansano, subsp. nov. (Figures 9, 35, 36, 37)

Type:—GUYANA. Potaro-Siparuni, Potaro River below Waratuk Falls, 107 m elev., 5°16'57"N 59°21'39"W, 05 September 2006, *ReddenK.M. et al. 4029* (holotype US[00963900]!).

Diagnosis:—*Eperua grandiflora* subsp. *ciliata* shares with other subspecies of *E. grandiflora* the free stipules, 2–3- jugate leaves, and persistent bracteoles attached to the higher portion of the pedicels or at the base of the hypanthium. It also shares irregularly villous sheath, and glabrous ovary and fruits with subsp. *grandiflora*. *Eperua grandiflora* subsp. *ciliata* differs from other subspecies by the glabrous inflorescences, pedicel, hypanthium, and sepals (vs. with indumentum in subsp. *grandiflora* and subsp. *guyanensis*), bracts and bracteoles glabrous with ciliate margin (vs. with indumentum in subsp. *grandiflora* and subsp. *guyanensis*), and larger [4.7–5.6 × 3.8–5.9 mm] bracteoles (vs. smaller [1.3–3.9 × 1.5–3.7 mm] in subsp. *grandiflora* and subsp. *guyanensis*).

Leaves, margin flat. **Inflorescences** glabrous; **bracts** glabrous, ciliate; **bracteoles** 4.7–5.6 × 3.8–5.9 mm, glabrous, ciliate; **pedicel** glabrous; **buds**, glabrous. **Flowers**: **hypanthium, sepal** glabrous; **stamens**, sheath irregularly villous; **ovary** glabrous. **Legumes** glabrous.

Phenology:—Flowering in September.

Distribution:—Potaro River in the Esequibo River basin (Guyana, Potaro-Siparuni). It is sympatric with *E. jenmanii*, which also occurs in the same basin.

Habitat:—It occurs in floodplain (riparian) forests, and *wallaba* forests, on white sand soils from 107 to 498 m elev.

Occurrence in protected areas:—Kaieteur National Park (Guyana).

Etymology:—The specific epithet relates to its ciliate bracts and bracteoles.

Vernacular names:—unknown

Uses:—unknown.

Taxonomic notes:—*Eperua grandiflora* subsp. *ciliata* is known by only three specimens which shows some sympatry with *E. grandiflora* subsp. *guyanensis.* In the upcoming phylogeny of the genus *E. grandiflora* subsp. *ciliate* was sampled with one accession that appears as a sister group to the other two subspecies of *E. grandiflora* (Fortes *et al.* in prep.). This lineage grouping the three subspecies of *E. grandiflora* received maximum phylogenetic support.

Specimens examined (paratype):—GUYANA. **Cuyuni-Mazaruni**, Pakaraima Mts., Mazaruni River, trail approx. 0.8 miles North from mining camp, 570 m ele., 6°5'4"N 60°39'2"W, 21 February 2004, *Redden K.M. et al. 2059* (NY[03777031] image!, US [01952126]!). **Potaro-Siparuni**, Tukeit Landing below Kaieteur Falls on Potaro River, 498 m elev., 5°12'16"N 59°27'11"W, 02 September 2006, *Redden K.M. et al. 3962* (CAY[109805] image!, US[00963896]!).

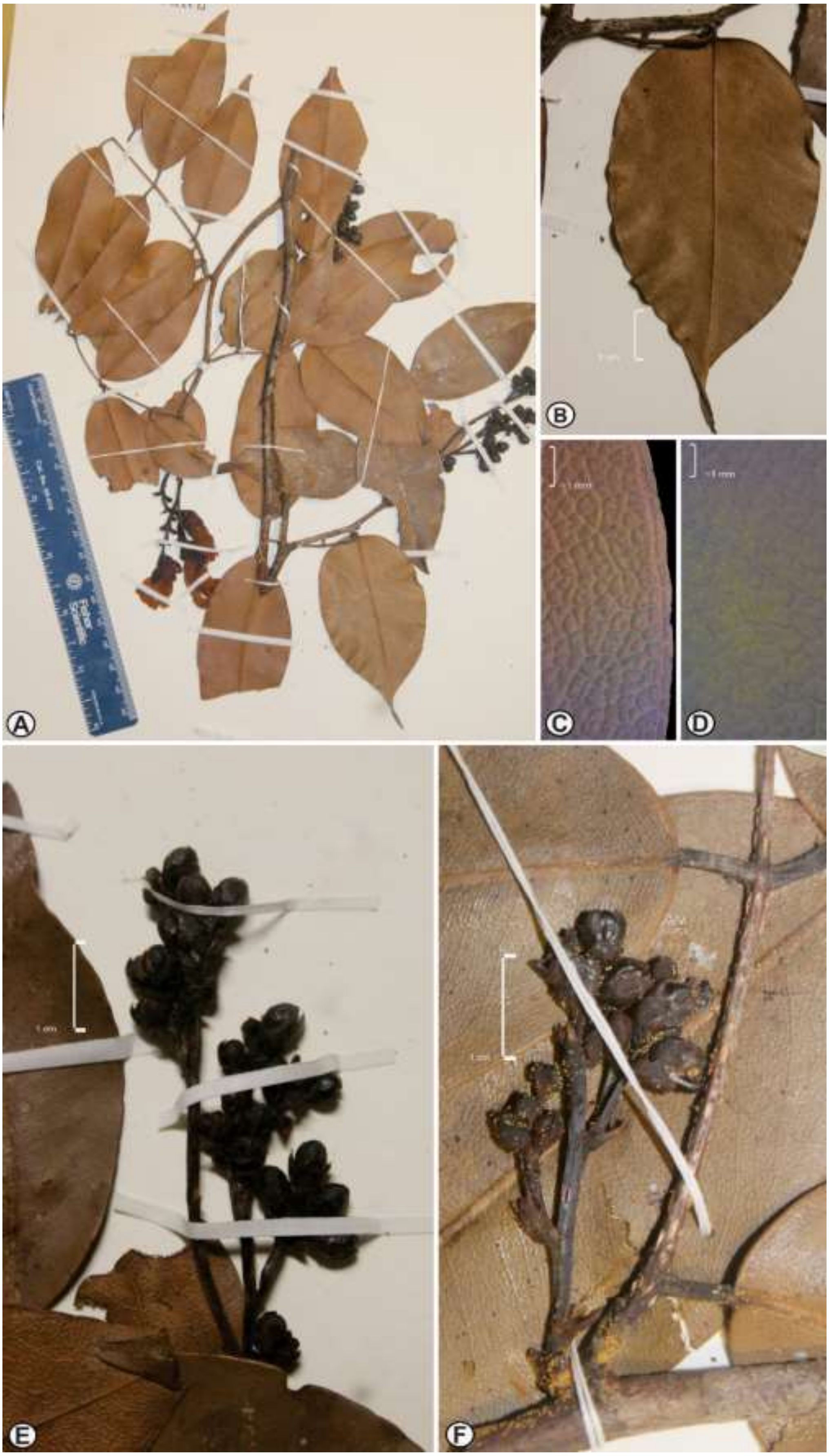


FIGURE 35. *Eperua grandiflora* subsp. *ciliata.* A. flowering branchlet; B. leaflet, abaxial surface; C, D. inflorescence in buds. Specimens, A–E: *Redden K.M. et al. 4029*; F: *Redden K.M. et al. 3962.* Photos E.A. Fortes.

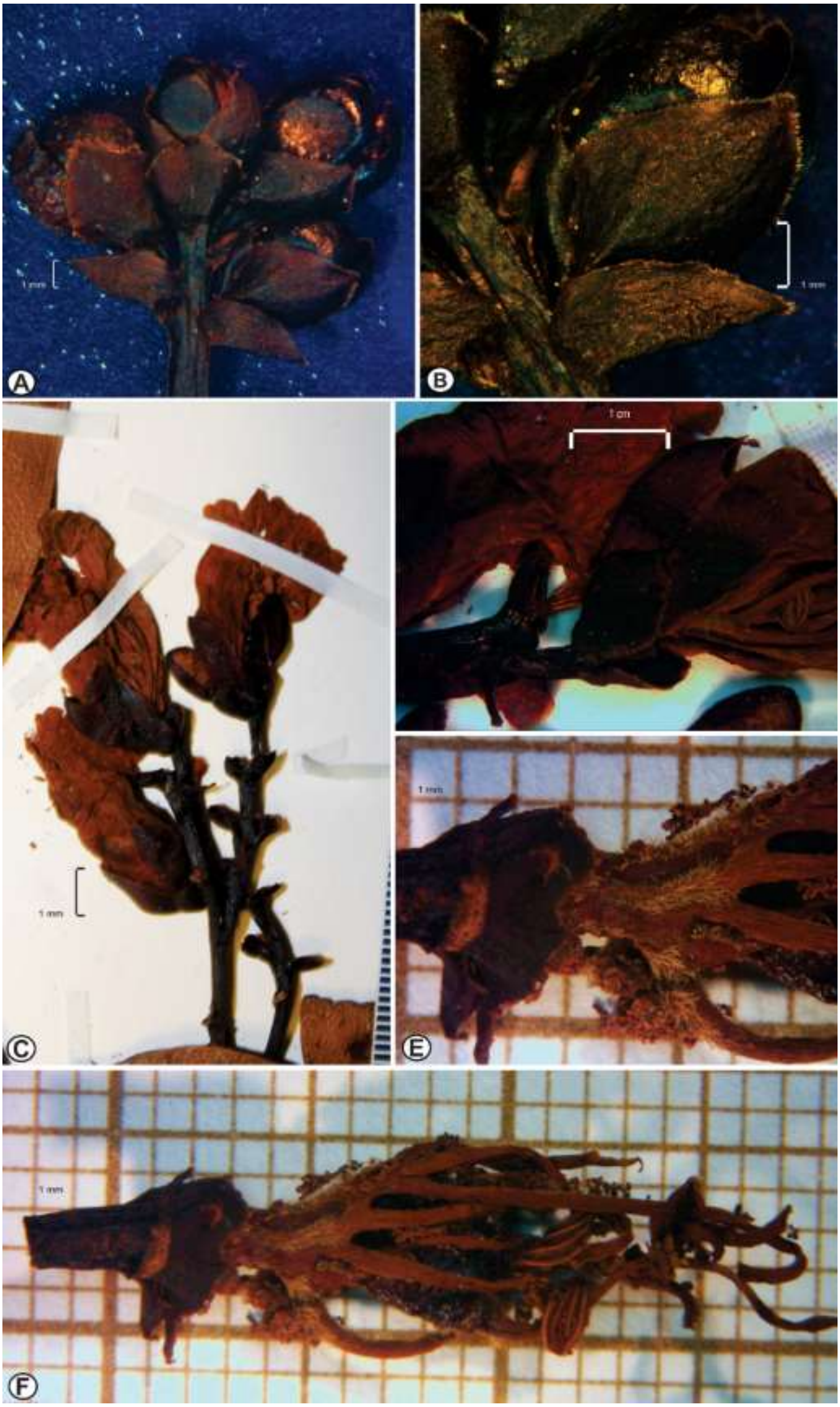


FIGURE 36. *Eperua grandiflora* subsp. *ciliata*: A. part of the inflorescence in buds; B. detail of the ciliate bracts and bracteoles; C. inflorescence showing the flowers, bracts, and bracteoles; D. detail of a flower showing the bract (at the base of the pedicel) and bracteoles (at the base of the hypanthium); E. detail of the hypanthium and stamen indumentum; F. flower showing the glabrous hipanthium, villous sheath, and glabrous ovary. Specimen, A–F: *Redden K.M. et al. 4029*. Photos, E.A. Fortes.

FIGURE 37. *Eperua grandiflora* subsp. *ciliata*: A. leaf; B. intramarginal vein, abaxial surface; C. inflorescence with flowers in bud; D. inflorescence with flowers at anthesis; E. detail of a bud showing one ciliate bract at the base and two ciliate bracteoles covering the bud (left); F. flower showing one bract at the base of the pedicel and two bracteoles at the base of the hypanthium; G. stamens joined in a diadelphous sheath; H. detail of the stamen indumentum; I. anther and part of the filament; J. glabrous carpel. Specimen, A, B, D–J: *Redden K.M. et al. 4029*; C: *Redden K.M. et al. 3962*. Illustrated by Marcus Falcão.

10. ***Eperua jenmanii*** Oliver (1891: 1955) (Figures 13, 38, 39)

Type (designated by Cowan 1975)**:**—GUYANA. Essequibo River, August 1884, *Jenman G.S. 2154* (lectotype K[000555100] image!). =*Dimorpha grandiflora* Rudge (1807: 179), nom. illeg.

Type (designated by Fortes & Mansano 2022): Unknown locality, s.d., *Martin J. s.n.* (lectotype BM[000065079] image!, isolectotype F[0111407] image!)

=*Eperua stipulata* Kleinhoonte. (1933: 171).

Type (designated by Fortes & Mansano 2022): SURINAM. Saramaca, May 1924, *Febis 6468* (lectotype U[0003226] image!, isolectotypes U[0003227] image!, U[0003231] image!)

Tree 5.0–30.0 m tall. **Trunk** 8.5–79.6 cm in diameter, bark gray to pale-brown. **Stipules** 3.7–25.4(–31.2) × 2.3–31 mm, joined at the base, sometimes free or entirely joined, foliaceous or non-foliaceous, persistent. **Leaves** 3–5-jugate; **petioles** 0.8–3.0 cm long; **rachis** 6.0–20.0(–25.8) cm long; **petiolules** 6.0–10.4 mm long; **blades** 5.5–16.2 × 2.2–6.6 cm, coriaceous, glabrous, epunctate to pellucid-punctate, discolorous, equilateral, lower pair elliptic, ovate to lanceolate, middle pair elliptic to narrowly elliptic, upper pair elliptic to narrowly, apex acuminate to attenuate, mucronate, rarely caudate, base symmetrical, with one pair of inconspicuous abaxially gland, lower pair base obtuse to rounded, rarely subcordate, middle pair base obtuse to rounded, upper pair base obtuse to cuneate, margin flat to slightly revolute, **secondary venation** with two intramarginal veins, vein closer to the margin continuous, main vein straight, depressed, prominent near the base to entirely prominent on the adaxial surface, tertiary veins conspicuous, areoles smaller, concave, to larger, plane. **Inflorescences** terminal, axillary or cauliflorous, erect, raceme, rarely panicle, *puberulent* or *glabrous*, trichomes white, 1.3–7.2 cm long; **bracts** (1.7–)3.0–5.3(–8.5) × (1.1–)3.5–5.8 mm, ovate, broadly ovate to oblate, cucullate, apex gland absent, *puberulent externally, glabrous within* or *glabrous in both sides*, *ciliate*, trichomes white, persistent; **bracteoles** (2.3–)3.6–9.0 × (1.0–)2.0–6.9 mm, ovate to broadly ovate, apex gland absent, *puberulent externally*, *glabrous within* or *glabrous in both sides*, *ciliate*, trichomes white, persistent, attached to the lower portion of the pedicels at slightly different levels; **pedicel** 4.5–16.9 mm long, 1.0–2.4 mm in diameter, not twisted, *puberulent, sometimes puberulent to glabrescent* or *glabrous*, trichomes white; **buds** 0.8–2.2 cm long, 0.4–1.1 cm in diameter, *puberulous* or *glabrous*, trichomes white. **Flowers**: **hypanthium** 1.8–4.8 mm long, 2.9–6.8 mm in diameter, cupshaped, inequilateral, *puberulent*, *sometimes puberulent to glabrescent*, or *glabrous*, trichomes white; **sepal** 1.4–3.1 × 0.4–1.3 cm, oblong, elliptic to obovate, unequal, the dorsal one larger, cucullate, apex gland present on the outer ones, pink, magenta, purple to reddish-purple, *puberulent to glabrescent* or *glabrous*, scarious marginally, trichomes white; **adaxial petal** 3.2–11.7 × 4.0–9.6 cm, obovate to broadly obovate, tubular, apex rounded, crisped, base attenuate, gibbous, lavender, purple to pink, whitish marginally, glabrous; **petalodia** 0.3–5.9 × 0.3–1.3 mm, lavender to white; **stamens** inserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 3.0–7.6 cm long, shorter filaments 2.2–5.6 cm long, sheath inequilateral, shorter side *9.1–15.0(–23.0)* or *4.5–13.0* mm long, longer side *10.3–26.0* or *6.1–18.0* mm long, sheath irregularly villous, pubescent to puberulous, free filaments glabrous, trichomes white, shorter stamens anthers 1.4–3.0 × 0.8–1.6 mm, rectangular, longer stamens anthers 2.5–4.1 × 1.0–2.6 mm, rectangular; **ovary** 4.0–11.0 × 2.4–5.1 mm, obovate, glabrous, stipe 3.4–10.0 mm long, glabrous, style 2.5–4.9 cm long, stigma obtuse to capitate, papillose. **Legumes** 6.0–17.0 × 5.6–11.2 cm, stipe 1.0–2.7 cm, oblong to obovate, apex truncate, rounded to obtuse, dorsal side apiculate, dorsal margin thickened, dark redsish-brown to reddish-brown, with transversal veins, sometimes inconspicuous, glabrous, rugose. **Seeds** 1–2 per fruit, 4.6–6.0 × 2.5–3.9 cm, elliptic, ovate to oblong, reddish-brown.

Distribution:—*E. jenmanii* occurs in Guyana (Cuyuni-Mazaruni, Upper Demerara-Berbice), mainly in the Mazaruni River and lower Esequibo River in Esequibo River basin region, and Venezuela (Bolívar), mainly in the Caura, Paragua, and Caroni rivers in the Orinoco River basin region. There are some sterile collections in French Guiana (*Sabatier D. 1879, Sauvain M. 479*) and Surinam (*Febis 6468, Hoffman B. 6146*) that resembles *E. jenmanii*, but flowering and fruiting collections are needed to confirm the distribution of the species in those areas..

Habitat:—Floodplain (riverine) forests, sometimes reaches upland forests and *wallaba* forests, from 5-225(–1220) m elev. **Conservation status:—**Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 264,200.096 km$_2$ and the estimated area of occupancy is 176.000 km$_2$.

Vernacular names:—arekuna (*Cardona F.2158*), baboen walaba (*Febis 6468*), caraoto (*Beruordi 2130, Stergios B. 11719*), itoeli walaba (*Stahel G. 334*), tumay-yek (*Steyermark J.A. 60376*), opá (*Cardona F. 2158*), opá-yek (*Steyermark J.A. 60376*, *60754*), water wallaba (*Redden K.M. et al. 2074*).

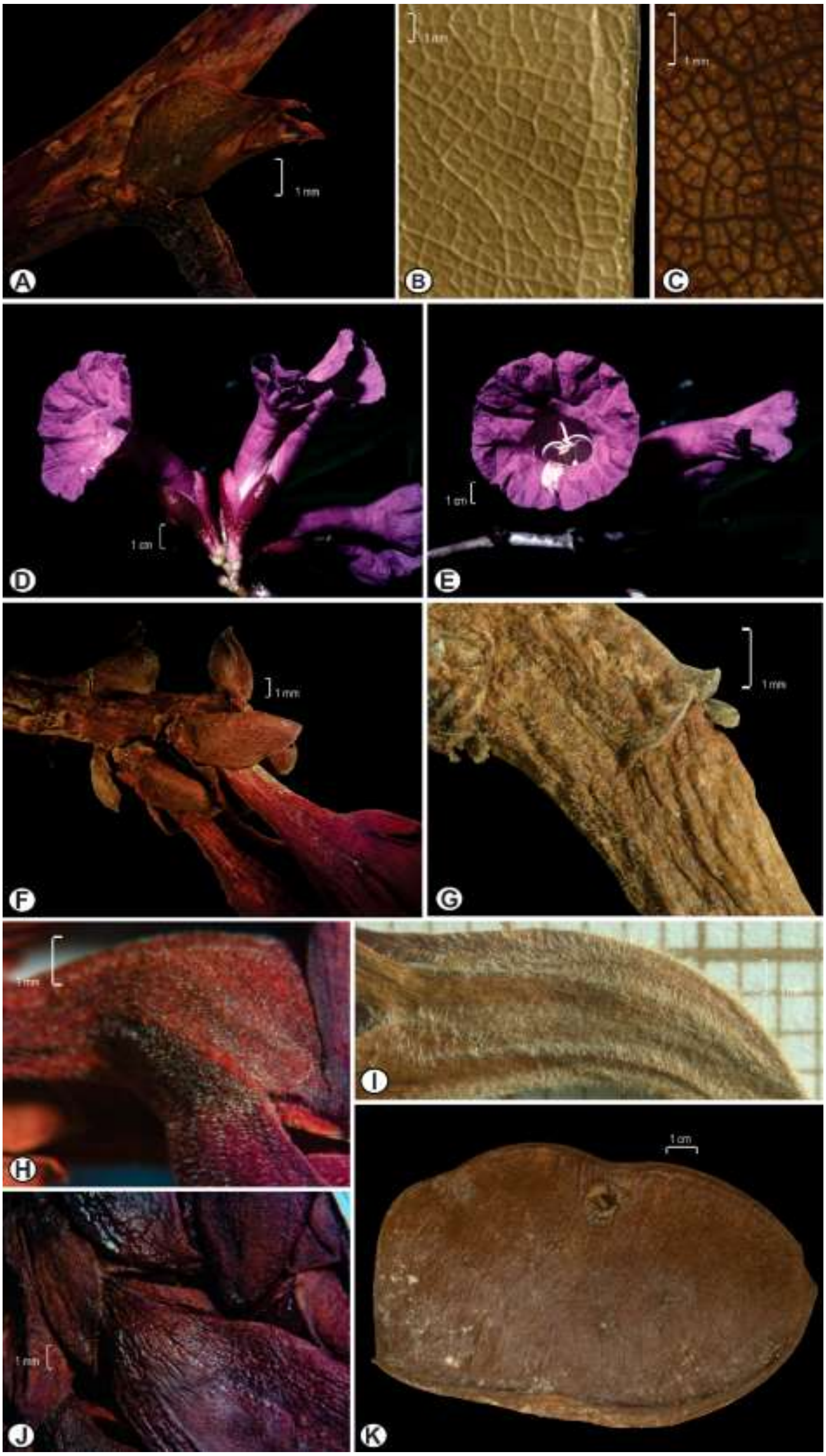


FIGURE 38. *Eperua jenmanii*: A. stipules, subsp. *sandwithii*; B. intramarginal veins, abaxial surface of the leaflet, subsp. *jenmanii*; C. inconspicuous pellucid-punctate leaflets, subsp. *jenmanii*; D. flowers, lateral view; E. flowers, front view; F. bracteoles attached to the lower portion of the pedicel, subsp. *sandwithii*; G. detail of the inflorescence indumentum, subsp. *jenmanii*; H. detail of the hypanthium indumentum, subsp. *jenmanii*; I. detail of the sheath indumentum, subsp. *jenmanii*; J. detail of the glabrous hypanthium and ciliate bracteoles, subsp. *sandwithii*; K. fruit, subsp. *jenmanii*. Specimens, A, J: *Liesner R.L. & Morillo G. 13972*; B, C, G, I: *Tillett S.S. & Tillett C.L. 45699*; F: *Redden K.M. et al. 7059*; H: *Stergios B. et al. 6152*; K: *Redden K.M. et al. 1760*. Photos, D, E: Westra; A–C, F–K: E.A. Fortes.

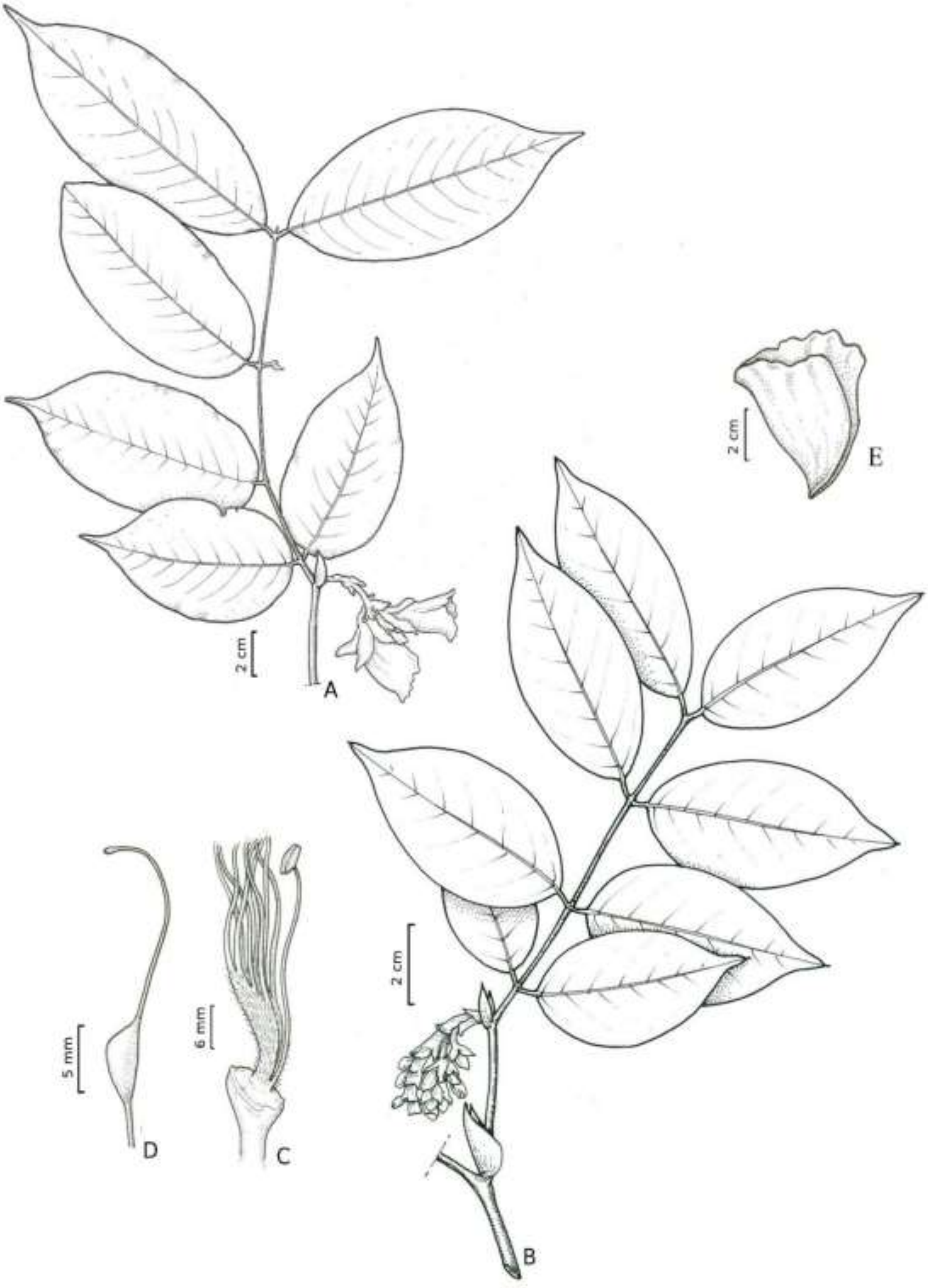


FIGURE 39. *Eperua jenmanii.* A. inflorescence and leaf, subsp. *jenmanii*; B. inflorescence and leaf, subsp. *sandwithii*; C. stamens joined in a diadelphous sheath 9+1, subsp. *sandwithii*; D. glabrous carpel, subsp. *sandwithii*; E. adaxial petal, subsp. *sandwithii*. Specimens, A: *Jenman G.S. 573*; B: *Prance G.T. et al. 10871*; C–E: *Maguire B. 33136*. Illustrated by Carlos Alvarez.

Specimens examined:—GUYANA. **Cuyuni-Mazaruni**, Essequibo River, W bank, Wolga 1 km S, to lower 0.5 km of Kamwatta Creek, 5 m elev., 6°27’0”N 58°36’0”W, 01 April 1993, *Henkel T.W. et al. 1863* (US). **Upper Demerara-Berbice**, Berbice River, 230 km upriver from mouth, N of Kwakwani, Aroiama mining Co. land concession, 70 m elev., 5°39’36”N 58°0’0”W, May 1995, *SI/MAB 60818* (US). **VENEZUELA**. **Bolívar**, Cedeño, Majawana village along the Río Majagua, tributary of the Río Erebato, 05

March 1992, *Boom B.M. 10297* (NY); Ciudad Guayana, orillas de Caroni and upstream from the woods of Ikabaru, October 1947, *Cardona F. 27015* (US). Wooded slopes of Quebrada O-paru-má, between Santa Teresita de Kavanayén and Río Pacairao (tributary of rio Mouak), 1065–1220 m elev., 20–21 November 1944, *Steyermark J.A. 60376* (F). *Eperua jenmanii* has two subspecies: *E. jenmanii* subsp. *jenmanii* and *E. jenmanii* subsp. *sandwithii*.

10a. ***Eperua jenmanii*** Oliv. subsp. ***jenmanii***

Inflorescences puberulent; **bracts** and **bracteoles** puberulent externally, glabrous within, trichomes white; **pedicel** puberulent, sometimes puberulent to glabrescent, trichomes white; **buds** puberulous, trichomes white. **Flowers**: **hypanthium** puberulent, sometimes puberulent to glabrescent; **stamens** sheath shorter side 9.1–15.0(–23.0) mm long, longer side 10.3–26.0 mm long.

Phenology:—Flowering in May and from July to December; fruiting in February, March, September, and November.

Distribution:—Esequibo River basin in Guyana (mainly Mazaruni River and lower Esequibo River region) and there are two collections in Venezuela bordering Guyana in Cuyuni River and El Dorado road. It is cultivated in Trinidad and Tobago.

Habitat:—Mainly floodplains (riverine) forests, sometimes in dry evergreen forest (*wallaba* forest), on alluvial, laterite, red sand, mixed brown and white sand soils, at sea level to 550 m elev.

Occurrence in protected areas:—Unknown.

Etymology:—The specific epithet is a tribute to G.S. Jenamn, who was the superintendent of the botanical gardens and government botanist at Georgetown in Guyana during 1879–1902 (Stafleu & Cowan 1979), and collected the type specimen.

Vernacular names:—fine leaf walaba (*Hoffman B. & Roberts L. 2502*), ituri wallaba (*Tutin T.G. 459*), mahomillo (*Steyermark J.A. 86665*), water wallaba (*Redden K.M. et al. 3213, Henkel T.W. & Chin M. 478*).

Uses:—Guyana: used for firewood and roof shingles (*Tutin T.G. 459*).

Taxonomic notes:—The two *E. jenmanii* subspecies, namely *jenmanii* and *sandwithii*, can be differentiated from other species with 3-to 5-jugate leaves and non-falcate leaflets by their secondary venation with two intramarginal veins and vein closer to the margin continuous. The two subspecies have the largest petals in the genus. Among the species with tubular corolla, *E. jenmanii* distinguishes by its persistent bracts (vs. caducous in *E. bijuga*, *E. glabriflora*, *E. banaensis*, *E.obtusata*, and *E. oleifera*), bracteoles attached to the lower portion of the pedicels (vs. at the base of the hypanthium or to the higher portion of the pedicels in *E. grandiflora* and *E. oleifera*, or the middle one in *E. purpurea*), villous to glabrescent sheath (vs. glabrous in *E banaensis* and *E. obtusata*, puberulous in *E. bijuga*, puberulous to pubescent in *E. glabriflora*, and in *E. grandiflora* subsp. *guyanensis*, tomentose in *E. manausensis*), and glabrous ovary (vs. sericeous in *E. banaensis*, *E. grandiflora* subsp. *grandiflora*, and *E. obtusata*).

Specimens examined:—GUYANA. **Cuyuni-Mazaruni**, Kamakusa, Mazaruni River, 0.59 miles SE of base camp, 105 m elev., 5°55'0"N 59°52'59"W, 30 September 2004, *Redden K.M. et al. 3213* (U, US)**.**Pakaraima Mts., SW-side of Kamarang, 450 m elev., 5°52'0"N 60°38'0"W, 09 November 1979, *Maas P.J.M. & Westra L.Y.T. 3981* (U, US). **Demerara-Mahaica**, Ramsaroop Farm-resort 2 km E of Timehri Airport, vicinity of main house, 5–15 m elev., 6°30'0"N 58°15'0"W, 25 January 1992, *Hoffman B. & Capellaro C. 844* (INPA, US). **Essequibo Islands-West Demerara**, Groete River 2–4 km either side of mouth of Black Creek, 8–16 m elev., 6°37'0"N 58°36'0"W, 23 August 1993, *Henkel T.W. & Williams R. 2715* (U, US). **Pomeroon-Supenaam**, Takutu concession of Willems Timber Comp, 0–100 m elev., 7°0'0"N 58°49'59"W, 12 November 1991, *Polak A.M. et al. 520* (U). **GUYANA**. **Potaro-Siparuni**, Garraway Stream, 102.5 miles on Bartica-Potaro road, 38 m elev., 5°22'25.2"N 59°7'20.6"W, 12 March 2004, *Redden K.M. et al. 2202* (US). **Upper Demerara-Berbice**, Rockstone, 15 July–1 August 1921, *Gleason H.A. 837* (US). Unknown city, Essequibo River from Monkey Jump to Persaud timber concession, 5 m elev., 6°19'60"N 58°33'0"W, 22 May 1993, *Henkel T.W. & Williams R. 2128* (US). **TRINIDAD AND TOBAGO (cultivated)**. Trindade, *s.c. 1350* (US). **VENEZUELA**. **Bolívar**, Río Venamo, between río Cuyuni (Anacoco) and Cano Apanao, 18 July 1983, *Stergios B. et al. 6152* (US); along road S of El dorado between km 42 and 65, 229 m elev., 26 July 1960, *Steyermark J.A. 86665* (S, US).

10b. ***Eperua jenmanii*** Oliv. subsp. ***sandwithii*** R.S. Cowan (1975: 37)

Type:—VENEZUELA. Bolivar: Raudaul Guaiquinima, 200 m elev., 16–19 January 1952, *Maguire B. 33136* (holotype NY[00004381] image!; isotypes F[0057802] image!, GH not seen, P[00252890] image!, RB[00539604]!, US[00001147]!).

Inflorescences glabrous; **bracts** and **bracteoles** glabrous, ciliate, **pedicel**, **buds**, and **hypanthium** glabrous; **stamens** sheath shorter side 4.5–13.0 mm long, longer side 6.1–18.0 mm long.

Phenology:—Flowering in January, March, April, May, July, August, September, and November; fruiting in March, May, September, October, and December.

Distribution:—Unlike the type subspecies it occurs mainly in the Orinoco River basin in Venezuela (Caura, Caroni, Paragua rivers). But it was also collected in Brazil's upper Uraricoera River and the Kako River in Guyana.

Habitat:—Floodplain forests (e.g. in *Mora* dominated forest), on white sand and laterite soils, at 107–1000 m elev.

Occurrence in protected areas:—Unknown.

Etymology:—The epithet *sandwithii* is a tribute to N.Y. Sandwith, a botanist who collected and revised the genus *Eperua* in Guyana (Cowan 1975, Sandwith 1931).

Vernacular names:—concha-de-suela (*Blanco C.A. 598*, *Liesner R.L. & González A.C. 5860*), opai-yek (*Maguire B. et al. 46734*), tehuwadu (Maiongong name, *Milliken W. 2106*), tumai-yek (*Steyermark J.A. 75537*).

Uses:—Unknown.

Taxonomic notes:—*Eperua jenmanii* subsp. *sandwithii* differs from the type subspecies by its glabrous bracts, bracteoles, inflorescence, and hypanthium (vs. puberulent in subsp. *jenmanii*), and the stamens sheath tends to be smaller (vs. larger in subsp. *jenmanii*). Cowan (1975) described this subspecies as having epunctate leaflets, but the isotype at RB herbarium clearly shows pellucid-punctate glands in the leaflets. Furthermore, observations revealed that both subspecies have blades ranging from epunctate to pellucid-punctate.

Specimens examined:—BRAZIL. **Roraima**, Alto Alegre, environs of the Maiongon village close to the FUNAI PIN Uaikas on the (alto) rio Uraricoera, 300 m elev., 3°33'0"N 60°28'0"W [inaccurate coordinate not in upper Uraricoera River, not added to map], September 1994, *Milliken W. 2106* (INPA, K, MIRR, NY); vicinity of Uaicá airstrip, rio Uraricoera, river margin, 2°53'0"N 63°36'0"W–3°33'0"N 63°11'0"W, 07 March 1971, *Prance G.T. et al. 10871* (F, INPA, K, MG, NY, R, U, US). **VENEZUELA**. **Bolívar**, Aripao, rio Caura, 5 –20 km sur (rio arriba) del campamento las Pavas (salto Para), 220–240 m elev., 6°15'0"N 64°25'0"W, May 1982, *Morillo G. & Liesner R.L. 8886* (US); Caño Pablo, tributary of Río Caura, ca 6–9 km east of Río Caura ca 10 km east south of Las Pavas (Salto Para), 240 m elev., 6°14'0"N 64°23'0"W, 10 May 1982, *Liesner R.L. & Morillo G. 13972* (US). Barceloneta, Sierra Ichun: María Espuma (Salto Ichun) along the rio Ichun, tributary of rio Paragua, 500–625 m elev., 4°46'0"N 63°18'0"W, 29 December 1961, *Steyermark J.A. 90416* (US). Gran Sabana, Chimatá Massif, vinicity of base camp, near Río Tirica, lower southwestern slopes of Chimantá-tepuí (Torono-tepuí), 1000 m elev., 24 May 1953, *Steyermark J.A. 75537* (F).

11. ***Eperua leucantha*** Bentham (1870: 225) (Figures 11, 40, 41)

Type (designated by Cowan 1975)**:—**BRAZIL. Amazonas: Rio Negro, moist forest at Uanauaca, January 1852, *Spruce R. 2021* (lectotype K[000555107] image!, isolectotypes P[00835936] image!, P[00835937] image!).

Tree 6.0–32.1 m tall. **Trunk** 6.0–50.0 cm in diameter, bark grayish to brown, smooth to striate, lenticellate. **Stipules** 2.5–4.0 × 1.2–3.5 mm, joined, non-foliaceous, caducous. **Leaves** 2–3(–4)-jugate; **petioles** 1.0–5.9 cm long; **rachis** (2.0–)4.0–15.5 cm long; **petiolules** 3.6–11.1 mm long; **blades** 6.5–19.0 × 3.1–9.0 cm, chartaceous, sometimes coriaceous, glabrous, pellucid-punctate, each areole has at least one conspicuous dot, not discolorous, slightly discolorous to discolorous, inequilateral, lower pair elliptic-falcate, middle pair elliptic-falcate, upper pair ellipticfalcate, apex acuminate, mucronate, base asymmetrical, lower pair base obtuse to rounded, rarely subcordate, middle pair base obtuse to cuneate, rarely rounded, upper pair base cuneate, sometimes obtuse, margin flat, sometimes slightly revolute, **secondary venation** with one intramarginal vein very close to the margin, main vein curved, prominent near the base, sometimes depressed on the adaxial surface, tertiary veins conspicuous, areoles larger, plane. **Inflorescences** terminal or axillary, panicle, main axis pendulous, lateral patent to erect, racemes main axis strigulose, puberulous to pubescent, lateral racemes strigulose to tomentulose, grayish-white, 46.5–300.0 cm long, lateral racemes 0.5–2.5(–3.1) cm long, alternate and spirally arranged; **bracts** 1.4 × 1.4 mm, ovate, apex gland absent, tomentose, grayish-white, caducous; **bracteoles** 1.6–5.1 × 0.8–1.2 mm, linear to ovate, apex gland absent, tomentulose, grayish-white, caducous, attached to the middle portion of the pedicels; **pedicel** (6.0–)8.7–17.0(–22.1) mm long, 1.1–1.8 mm in diameter, twisted, strigulose to tomentulose, rarely puberulous, grayish-white; **buds** 0.9–2.3 cm long, 0.6–1.9 cm in diameter, strigulose to tomentulose, rarely puberulous to glabrescent, grayish-white. **Flowers**: **hypanthium** 2.7–6.1 mm long, 3.4–6.4 mm in in diameter, cup-shaped, equilateral, strigulose to tomentulose, grayish-white; **sepal** 1.4–2.5 × 0.4–1.3 cm, oblong to elliptic, unequal, the outer ones larger, cucullate, apex gland absent, green to light-green, puberulous to strigulose, sometimes tomentulose, inner sepals scarious marginally, grayish-white; **adaxial petal** 1.9–3.3 × 2.9–6.3 cm, oblate, non-tubular, apex rounded, base truncate, white, rarely greenish-white, glabrous; **petalodia** (0.4–)0.8–2.3 × (0.2–)1.0–1.8 mm; **stamens** exserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 1.1–3.7 cm long, shorter filaments 3.4–5.0 cm long, sheath equilateral, 3.0–6.4 mm long, sheath sericeous, sometimes tomentose, free filaments glabrous, brownish-yellow, anthers 3.8–6.8 × 0.9–3.0 mm, rectangular; **ovary** 5.2–9.2 × 2.0–3.5 mm, narrowly obovate, sericeous, brownish-yellow, 7 ovules, stipe 2.3–7.0 mm long, sericeous, style 3.0–4.6 cm long, stigma capitate, papilate. **Legumes** 15.0–28.5 × 5.0–10.0 cm, stipe 0.3–1.0 cm long, elliptic-falcate, sometimes narrowly elliptic-falcate, apex acute, margin entire, brownish-yellow to reddish-brown, veins absent, sometimes with inconspicuous transversal veins, strigulose, sometimes puberulous, trichomes white. **Seeds** 2–7 per fruit, 2.9–6.3 × 1.5–2.6 cm, elliptic to oblong, dark-brown.

Phenology:—Flowering from January to May, in July, and from September to December, with a peak in October and November; fruiting from January to April, in June, July, and from September to December.

Distribution:—Likewise *E. purpurea*, *E. leucantha* occurs in the northwest of Amazonas state in Brazil, south of Amazonas state in Venezuela, and southwest of Colombia Amazonas, Guainía, Vaupés, and Vichada departments.

Habitat:—Very frequent in the Amazonian forests known as *sabatena*, *varillal*, or *campinaranas* on white and brown sand mixed soils, but also reported in *terra-firme* (Aymard *et al.* 2009) and floodplains forests, from 50 to 370 m elev.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 268,709.161 km$_2$ and

the estimated area of occupancy is 252.000 km$_2$.

Occurrence in protected areas:—Resguardo Indígena Atabapo (Colombia, Guainía), Reserva Nacional Natural Puinawai (Colombia, Guainía), Gran Resguardo Indígena del Vaupés (Colombia, Vaupés), Reserva Natural Agua Linda (Colombia, Vichada), Reserva Biológica do Morro dos Seis Lagos (Brazil, Amazonas), Parque Nacional do Pico da Neblina (Brazil, Amazonas), and Parque Nacional Serrania La Neblina (Venezuela, Amazonas).

Etymology:—The specific epithet relates to the white color of its petals.

Vernacular names:—acanã (*Cavalcante P.B. 669*, *Rodrigues W.A. 905*), dzawaka (*Stropp J. & Assunção P. 200*, *289*, *342*, *344*, *345*, *640*), espadeira (*Nascimento O.C. do et al. 29*), iauácano (*Rodrigues W.A. 1075*), iuacanã (*Rodrigues W.A. 905*), jauacaná (*Spruce R. 2021*), jauácano (*Ducke W.A. s.n. RB23289*), kanoneyoa-ke (Guanano) (*Acero E. & Rodríguez R. 948*), kieraiku (*Landinez A. 7*), o-kö-ges (Kubeo) (*Schultes R.E. & Cabrera I. 17872*), palocolorado, palo-rojo (*Landinez A. 7*), shaquiparo (*Delgado H. 30*), tö-ee (Puinave) (*Schultes R.E. & Cabrera I. 17872*), tuic (*Imamoto M. 15*), yaauaka (*Stergios B. 18584*), yabakaike (Kubeo) (*Acero E. & Rodríguez R. 948*), yacuana (*Marcano-Berti L. & Salcedo P. 40-979*), yaguácana (*Clark H.L. 6983*, *Stergios B. 18409*), yaguácana-blanco (*Clark H.L. 7019*, *7020*, *7023*), yaguácana rojo (*Clark H.L.7021*), yaguana (*Williams L. 14390*), yahuana (Baniba) (*Williams L. 14390*, *14942*), yauácano (*Ducke W.A. 164*, *s.n. RB23732*), yaua-kuanã (*Trivellato C. & Gonçalves G.G. 31*), yévaro blanco (*Cárdenas-López D. 21951*), yévaro sabanero (*Cárdenas-López D. 21936*).

Uses:—Venezuela: bridge construction (*Williams L. 13939*, *15801*), poles (*Williams L. 13939*), the wood is very durable even when buried into the ground, and it is very heavy and not useful in watercrafts (*Williams L.15801*). Colombia: timber (*Cárdenas-López D. 21951*). According to *Souza L.A.G. de et al. 28*, it has ornamental potential especially because of its flowers.

Taxonomic notes:—*Eperua leucantha* is morphologically similar to *E. falcata* and *E. venosa*, with which it shares joined stipules, secondary venation with one intramarginal vein very close to the margin, long and pendulous inflorescences, non-tubular corolla, exserted stamens joined in a diadelphous sheath, and sericeous ovary (Table 4). Additionally, *E. leucantha* shares multijugate leaves with *E. falcata*, and erect lateral racemes and sericeous sheath with *E. venosa*. Differences between *E. leucantha* and *E. falcata* are listed in the taxonomic notes of the last species. *Eperua leucantha* differs from *E. venosa* by its shorter [2.7–6.1 mm long] hypanthium (vs. longer [6.8–11.3 mm long] in *E. venosa*), and white glabrous petal (vs. deep rose-colored petals basally sericeous in *E. venosa*).

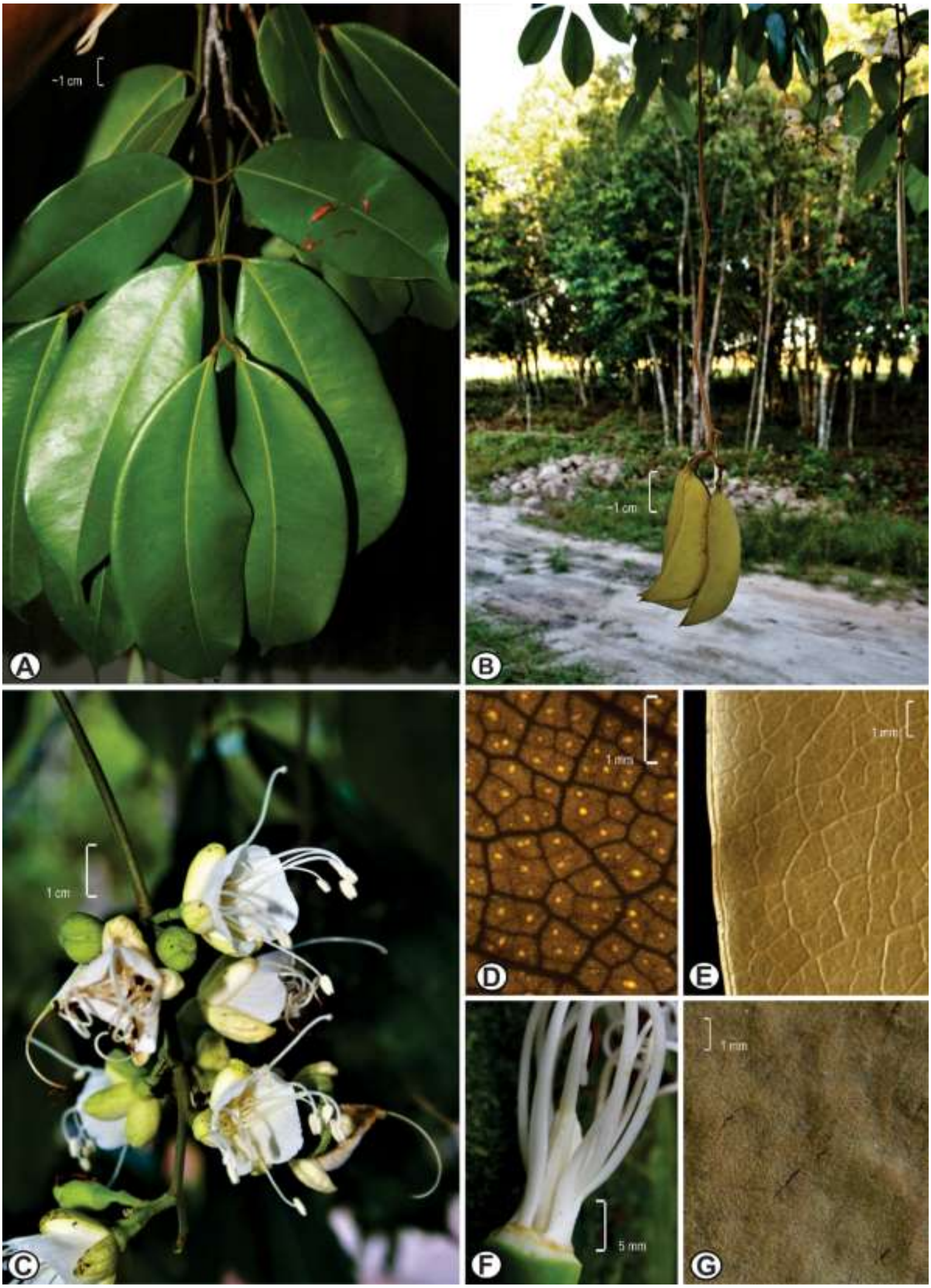


FIGURE 40. *Eperua leucantha*: A. leaf; B. fruits in a pendulous inflorescence; C. inflorescence; D. pellucid-punctate leaflet; E. intramarginal vein, abaxial surface; F. base of the stamens and carpel; G. detail of the fruit indumentum. Specimens, D: *Williams L. 13939*; E: *Maguire B. et al. 42610*; G: *Nascimento O.C. do et al. 29*. Photos, A–C, F: F. Castro-Lima; D, E, G: E.A. Fortes.

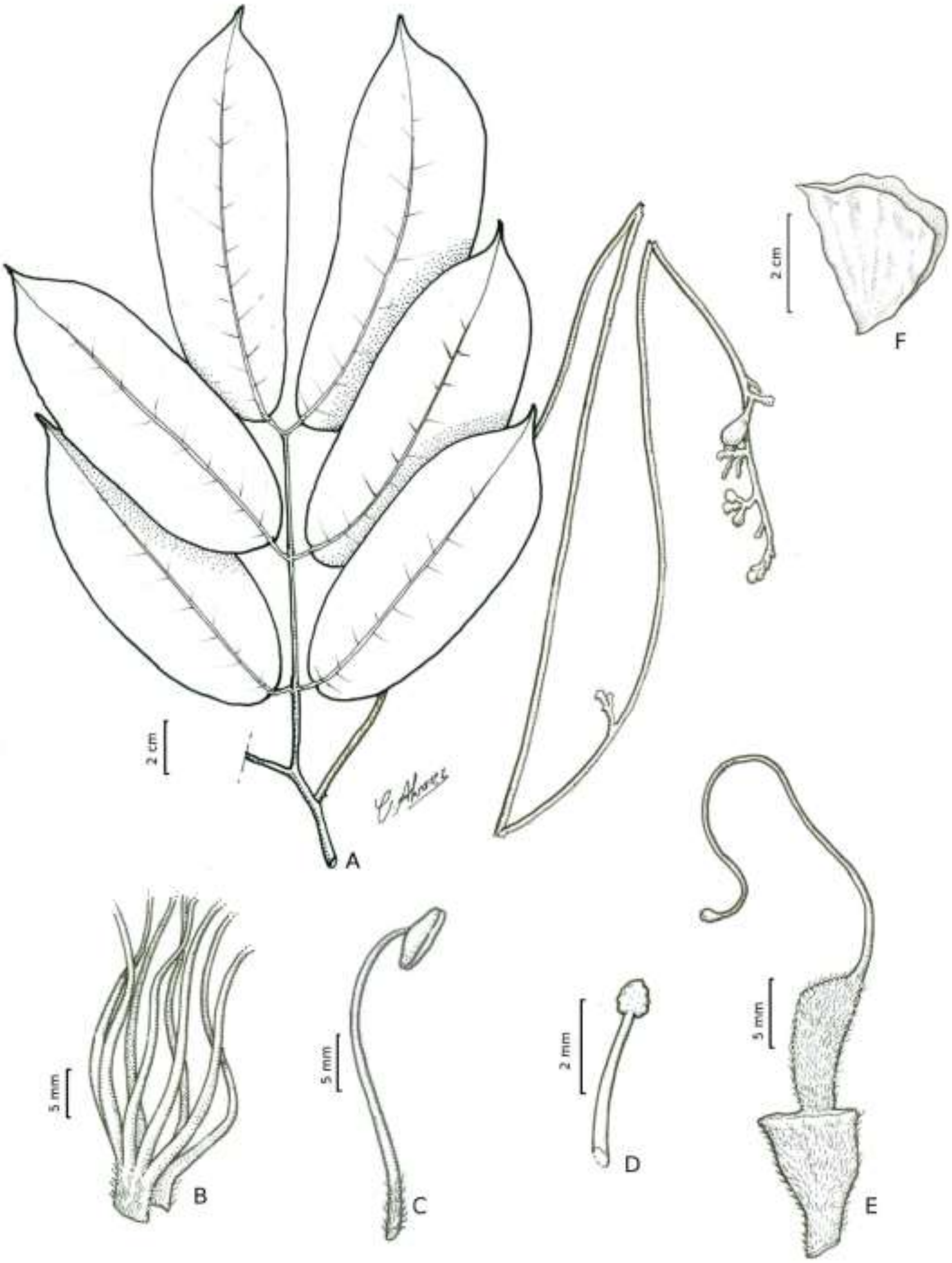


FIGURE 41. *Eperua leucantha*: A. flowering branchlet; B. base of the stamens joined in a diadelphous sheath; C. anther and filament; D. capitate stigma; E. carpel and hypanthium; F. adaxial petal. Specimen, A–F: *Fróes R. de L. 21104*. Illustrated by Carlos Alvarez.

Selected specimens:—BRAZIL. **Amazonas**, São Gabriel da Cachoeira, porto de Camanaús, 18 October 1978, *Madison M.T. et al. 397* (INPA); São Felipe, rio Negro, 11 October 1952, *Fróes R. de L. 28826* (IAN); alto rio Negro, caatinga da Ilha das Flores, 17 February 1959, *Rodrigues W.A. 905* (INPA, U, US). **COLOMBIA**. **Amazonas,** El Encanto, corregimiento departamental de la Chorrera, comunidad de Santa Rosa, río Igará-Parana, 151 m elev., 1°45’40”N 72°37’16”W, 15 March 2020, *Cárdenas-López D. & Marín N. 52950* (COAH). **Guainía**, Cacahual, comunidad indígena Cacahual, río Atabapo sector cñ. Garza, 11 May 2007, *Cárdenas-López D. 20677* (COAH). Inírida, Puerto Inírida, via aeropuerto, vitina km 4, 05 March 2010, *Castro F. 8510* (COAH, UDBC). La Guadalupe, comunidad indígena El Porvenir, alto río Negro, zona limítrofe entre Colombia, Brasil y Venezuela, 14 October 2009, *Cárdenas-López D. et al. 24050* (COAH).

Maimachi, Serrania de Naquen, Caño Ima, 350 m elev., 2°12’0”N 68°12’0”W, 26 July 1992, *Cortés-Ballen R. et al. 149* (COAH, COL, UDBC). Pana Pana, río Guaviare, Barranco Murciélago, 100–600 m elev., 25 November 1976, *Delgado H. 30* (UDBC). **Vaupés**, Mitú, rio Vaupés, Miriti, 01 November 1993, *Martínez X. et al. 3476-2* (COL). Yavaraté, Río Yutica, 0°49’57”N 69°37’9”W, 12 February 1979, *Acero E. & Rodríguez R. 948* (COL, UDBC). **Vichada**, Reserva Natural Agua Linda, afloramiento rocoso adyacente a la Reserva Morrocoy y Bosque de galería del Caño Morrocoy, 07 April 2008, *Castro F. 5010* (UDBC). **VENEZUELA**. **Amazonas**, Casiaquire, ríos Pacimoni - Yatua, Río Yatua near Cano Tauavaca, 100–140 m elev., 04 December 1953, *Maguire B. et al. 36508* (F). Maroa, rio Guainía, 127 m elev., 17 February 1942, *Williams L. 14390* (F, IAN, US). San Carlos de Río Negro, 20 km s of conf. of rio Negro and brazo Casiquiare, 4.3 km NNE of San Carlos on Solano road, 119 m elev., 1°56’0”N 67°3’0”W, 21 February 1979, *Clark H.L. 7019* (US); Neblina Base camp, rio Mawarinuma, 140 m elev., 0°50’0”N 66°10’0”W, 27 November 1984, *Boom B.M. & Weitzman A.L. 5186* (INPA, U, US). Yavita, along road from Maroa to Yavita, ca. 7 km from Maroa, 2°54’42”N 67°26’55”W, 25 February 1998, *Acevedo-Rodríguez P. et al. 10408* (US).

12. ***Eperua manausensis*** E.A. Fortes & Mansano (2023: 204) (Figure 9, Fortes *et al.* 2023 Figures 6, 7)

Type:—BRAZIL. Amazonas, Manaus, Reserva Florestal Adolpho Ducke, trilha do Jardim Botânico MUSA, planta marcada JBN 634, 08 June 2017, Cabral F.N. *et al.* 1561 (holotype INPA[0284318]!, isotype RB[01459755]!).

Tree 20.0 m tall. **Trunk** 38.0 cm in diameter, bark brownish, lenticellate. **Stipules** 1.8–1.9 × 0.8–1.4 mm, free, nonfoliaceous, ovate to lanceolate, caducous. **Leaves** 2–3-jugate, glabrous; **petioles** 0.6–2.9 cm long; **rachis** 3.5–14.6 cm long; **petiolules** 6.2–9.1 mm long; **blades** 5.3–12.8 × 3.5–6.5 cm, coriaceous, glabrous, inconspicuous pellucidpunctate to pellucid-punctate, discolorous, equilateral, lower pair ovate, middle pair elliptic, upper pair elliptic, apex attenuate to acuminate, base symmetrical, lower pair base subcordate to cordate, middle pair base subcordate to rounded, upper pair base subcordate, rounded to obtuse, margin revolute to flat at the apex, secondary venation with two intramarginal veins, vein closer to the margin continuous, main vein straight, prominent only near the base on the adaxial surface, tertiary veins conspicuous. **Inflorescences** axillary, panicle, erect, tomentose, brownish-yellow, 4.6–8.9 cm long, lateral racemes 2.1–3.4 cm long, alternate and distichous; **bracts** not seen, caducous; **bracteoles** 4.9–5.0 × 3.0–3.2 mm, ovate, apex gland present, tomentose externally, pubescent to tomentose within, brownish-yellow, caducous, attached to the lower middle portion of the pedicel; **pedicel** 17.5–18.9 mm long, 1.0 mm in diameter, not twisted, tomentose, brownish-yellow; **buds** 0.7 cm long, 0.4 cm in diameter, tomentose, brownish-yellow. **Flowers**: **hypanthium** 3.8 mm long, 2.8 mm in diameter, cup-shaped, equilateral, tomentose, brownish-yellow; **sepal** 1.6 × 0.5 cm, oblong to elliptic, unequal, the dorsal one larger, cucullate, apex gland absent, pink, tomentose, scarious marginally, brownish-yellow; **adaxial petal** 3.8 × 4.7 cm, flabellate, tubular, apex rounded, base attenuate, pink to purple, glabrous; **petalodia** not seen; **stamens** inserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 3.1 cm long, shorter filaments 2.0 cm long, sheath inequilateral, shorter side 6.5 mm long, longer side 8.0 mm long, sheath tomentose, brownish-yellow, free filaments glabrous, anther 2.2 × 0.8 mm, rectangular; **ovary** 7.1 × 3.7 mm, obovate, densely tomentose to villous, brownish-yellow, stipe tomentose, style 4.0? cm long, glabrous, stigma capitate. **Legumes** 11.3–15.9 × 7.7–8.3 cm, stipe 0.9–1.4 mm long, obovate to irregularly elliptic, apex obtuse, apiculate, dorsal margin slightly thickened, brownish-red, with inconspicuous transversal veins, puberulous to puberulent, brownish. **Seeds** 1–2 per fruit.

Phenology:—Flowering in June; fruiting in January and June.

Distribution:—Brazil (Amazonas)

Habitat:—Upland (*terra-firme*) forest at 114 m elev.

Conservation status:—Categorized as Data Deficient (DD) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022) due to its recently circumscription and being known by only one specimen. **Occurrence in protected areas:—**Reserva Florestal Adolpho Ducke (Brazil, Amazonas).

Etymology:—The specific epithet is related to its first collection in the Museu da Amazônia, a botanical garden located in the city of Manaus (Brazil, Amazonas) and associated with the Adolpho Ducke Forest Reserve (Fortes *et al.* 2023).

Vernacular names:—Unknown.

Uses:—Unknown.

Taxonomic notes:—*Eperua manausensis* differs from other species with short and erect inflorescence and tubular corolla by the following combination of characteristics: free stipules, two intramarginal veins, vein closer to the margin continuous, tomentose inflorescence, caducous bracteoles attached to the lower middle portion of the pedicels, tomentose sheath, tomentose to villous ovary. Additionally, it differs from other species with tubular corolla by its 2–3-jugate leaves, and cordate to subcordate leaflet base.

Specimens examined (Paratypes):—BRAZIL. **Amazonas**, Manaus, Reserva Florestal Adolpho Ducke, MUSA, planta marcada JBN 634 ao lado direito da Casa-Oficina, à 20 m da trilha Branca, 114 m elev., 3°0'22.9"S 59°56'22.7"W, 27 January 2022, *Fortes E.A. & Viana G.P. 194b* (HUEFS, IAN, INPA, MG, NY, RB [01458706]!, UEC, US).

13. *Eperua obtusata* R.S. Cowan (1975: 33) (Figure 13, 16b, c, e, 42)

Type:—VENEZUELA. Amazonas: Capihuara, Rio Casiquiare, 3 October 1943, *Williams L. 16183* (lolotype US[00001148]!).

Tree 10.0–20.0 m tall. **Trunk**, bark smooth, lenticellate. **Stipules** 7.3 × 2.3 mm, free, non-foliaceous, caducous. **Leaves** 2-jugate; **petioles** 2.6–4.5 cm long; **rachis** 3.4–5.3 cm long; **petiolules** 4.5–7.5 mm long; **blades** 8.0–13.0 × 4.0–5.9 cm, coriaceous, glabrous, pellucid-punctate, discolorous, equilateral, lower pair elliptic to oblong, upper pair elliptic, apex rounded to obtuse, base asymmetrical, lower pair base obtuse to cuneate, upper pair base cuneate, margin flat to slightly revolute, **secondary venation** with one intramarginal vein, main vein straight, prominent to depressed on the adaxial surface, tertiary veins conspicuous, areoles larger, plane. **Inflorescences** axillary or ramiflorous, raceme, erect, strigulose, brownish- yellow, 7.5–9.5 cm long; **bracts** not seen, caducous; **bracteoles** ca. 2.0 × 1.0–2.0 mm, ovate, strigulose to tomentose externally, brownish-yellow, caducous, attached to the lower portion of the pedicel; **pedicel** 8.0–10.0 mm long, 0.8–1.1 mm in diameter, not twisted, strigulose, brownish-yellow; **buds** 0.5 cm long, 0.2 cm in diameter, strigulose, brownish-yellow. **Flowers**: **hypanthium** 2.0–3.0 mm long, 3.3–4.6 mm in diameter, cup-shaped, equilateral, strigulose, brownish-yellow; **sepal** 1.6–2.0 × 0.4 cm, oblong to elliptic, unequal, the outer ones larger, apex gland present, strigulose, inner ones scarious marginally, brownish-yellow; **adaxial petal** 3.5–5.0 × 6.5 cm, flabellate, tubular, apex rounded, base attenuate, glabrous; **petalodia** 4.0–5.0 × 1.5–1.8 mm; **stamens** inserted, joined basally in a diadelphous sheath, dorsal one free, filaments 11.5–26.0 cm long, sheath inequilateral, 6.5–10.0 mm long, glabrous, anther 2.6–3.5 × 1.2–1.5 mm, rectangular; **ovary** 5.0 × 2.0 mm, obovate, sericeous, brownish-yellow, stipe 4.0 mm long, sericeous, style 3.4 cm long, stigma truncate . **Legumes** not seen.

Phenology:—Flowering in October**.**

Distribution—Casiquiare River region in Venezuela (Amazonas).

Habitat:—Tall *campinarana* and *terra-firme* forest, on sandy soil, from 106 to 306 m elev. Coomes & Gribb (1996) cited *E. obtusata* as one of the dominant species in the tall *campinarana* of La Esmeralda (Venezuela).

Conservation status:—Categorized as Data Deficient (DD) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022) due to the lack of access to its collections.

Occurrence in protected areas:—Unknown.

Etymology:—*Eperua obtusata* and *E. banaensis* are the only species with leaflets with an obtuse apex, and the specific epithet *obtusata* relates to that characteristic.

Vernacular names:—Unknown.

Uses:—Unknown.

Taxonomic notes:—*Eperua banaensis* and *E. obtusata* are the only species in the genus with rounded, obtuse, acute to emarginate leaflet apex in the genus, whereas all other species have an attenuate, acuminate to caudate apex. They share 2-jugate leaves, short and erect inflorescence, tubular corolla, inserted stamens, and the same pattern of reproductive organ indumentum. Among the species with a tubular corolla, *E. banaensis* and *E. obstusata* are distinguished by the combination of glabrous sheaths and indumented ovaries (Table 2). Differences between them are listed in the taxonomic notes of *E. banaensis*.

Specimens examined:—VENEZUELA. **Amazonas**, Casiaquire, Capihuara, 03 October 1943, *Williams L. 16183* (US). San Fernando de Atabapo, La Esmeralda, 5 Km North of village, near savanna Morichal, 106 m elev., 3°10'0''S 65°33'0''W, undated, *Coomes D. 207* (K).

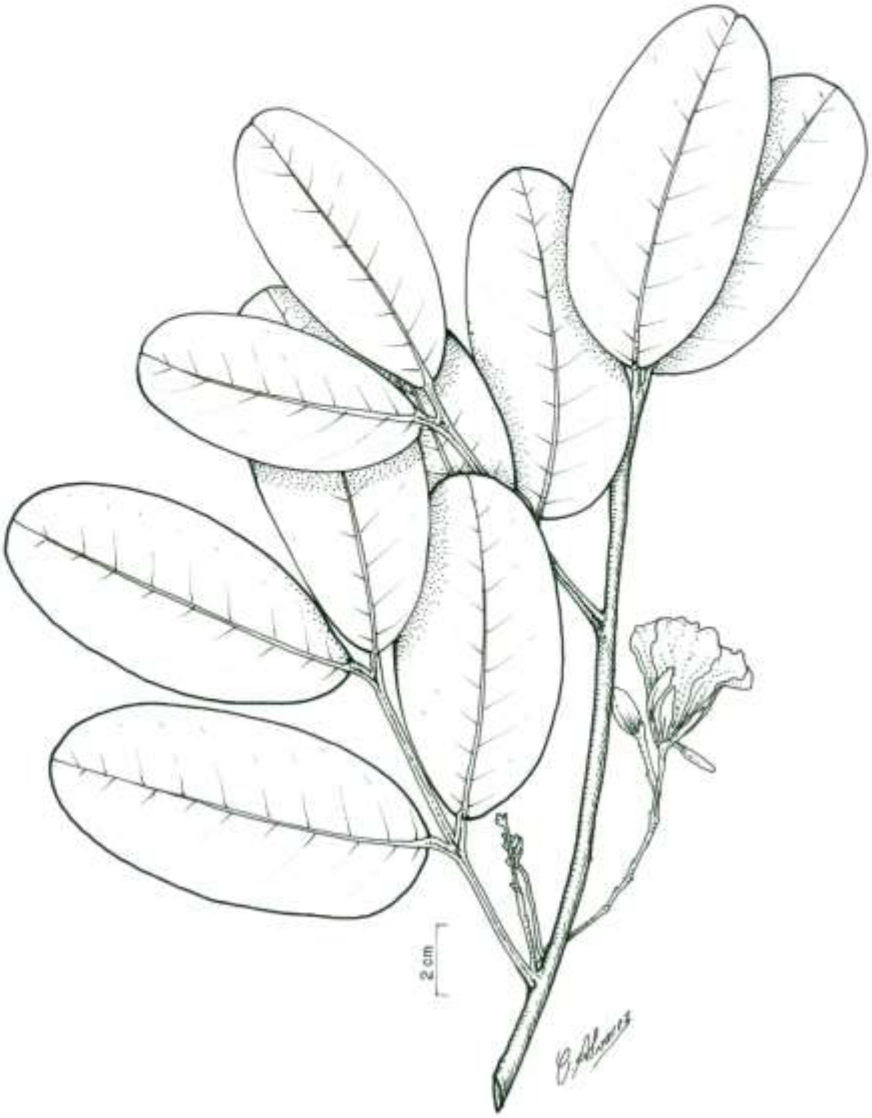


FIGURE 42. *Eperua obtusata*: flowering branchlet showing the 2-jugate leaves, and axillary inflorescence. Specimen, *Williams L. 16183* (holotype). Illustrated by Carlos Alvarez.

14. ***Eperua oleifera*** Ducke (1932: 728)

Type (designated by Cowan 1975)**:**—BRAZIL. Amazonas: Borba, Rio Madeira, 16 January 1930, *Ducke W.A. RB23290* (lectotype R[000028782]!, isolectotypes F-frag.[0057804] image!, G not seen, INPA collection number 234506 image!, K[000555093] image!, K[000858688] image!, NY[00004382] image!, NY[00004383] image!, NY[01185435] image!, P[00252888] image!, RB sheet I[00585686]!, & sheet II[00539606]!, S collection number S-R-8709 image!, U[0003233] image!, US[00001149]!).

Tree 18.0–30.0 m tall, or *treelet, or shrub 1.5–9.0 m tall*. **Trunk** 3.0–60.0 cm in diameter, bark grayish, brown with grey spots, striate. **Stipules** 1.5–4.3 × 1.3–4.0 mm, joined, non-foliaceous, persistent. **Leaves** (2–)3–4(–5)-jugate; **petioles** 0.8–4.2 cm long; **rachis** 1.6–16.6 cm long; **petiolules** 2.2–8.1 mm long; **blades** 4.6–13.7 × 2.6–7.7(–10.6) cm, coriaceous to chartaceous, glabrous, very nitid adaxially, conspicuous pellucid-punctate, discolorous, sometimes not discolorous, equilateral, lower pair elliptic, sometimes broadly elliptic to ovate, middle pair elliptic, sometimes broadly elliptic to ovate, upper pair elliptic, sometimes broadly elliptic to ovate, apex acuminate, sometimes retuse, base symmetrical, sometimes asymmetrical, lower pair base *rounded, subcordate to cordate*, or *obtuse to rounded*, rarely *cordate*, middle pair base *rounded, subcordate to cordate*, or *obtuse, sometimes rounded*, upper pair base *obtuse, rounded, subcordate to cordate*, or *obtuse to cuneate, sometimes rounded*, margin flat, **secondary venation** with one intramarginal vein very close to the margin, main vein straight, depressed on the adaxial surface, tertiary veins *very conspicuous, prominent on the adaxial surface, rarely not prominent*, or *conspicuous to inconspicuous, not prominent on the adaxial surface, rarely prominent*, areoles conspicuous, larger, plane. **Inflorescences** terminal or ramiflorous, sometimes axillary, panicle, sometimes raceme, erect, strigose to tomentose, rarely pubescent, brownish-yellow, 3.0–12.3 cm long, lateral racemes 0.9–6.2 cm long, alternate and distichous; **bracts** 1.0–2.8 × 0.5–1.8 mm, ovate, rarely broadly ovate, apex gland absent, tomentose to tomentulose externally, glabrous within, brownish-yellow, caducous to persistent; **bracteoles** 1.0–2.8 × 0.8–1.9 mm, ovate, apex gland absent, tomentose externally, glabrous within, brownishyellow, persistent, attached to the higher portion of the pedicels or at the base of the hypanthium; **pedicel** 3.7–14.1 mm long, 0.4–1.4 mm in diameter, not twisted, tomentulose to tomentose, sometimes tomentulose, rarely pubescent, brownish-yellow; **buds** 0.5–1.0 cm long, 0.3–0.7 cm in diameter, tomentose, brownish-yellow. **Flowers**: **hypanthium** 0.9–3.4 mm long, 1.2–4.0 mm in in diameter, cup-shaped, equilateral, tomentulose to tomentose, sometimes strigose, brownish-yellow; **sepal** 0.4–1.0 × 0.2–0.7 cm, elliptic to ovate, rarely oblong, unequal, the dorsal one larger, cucullate, apex gland absent, pale-green, yelowish-green to reddish-pink, strigulose, tomentulose to tomentose externally, scarious marginally, brownish-yellow; **adaxial petal** 1.7–3.8 × 2.0–5.7 cm, flabellate, tubular, apex rounded, crisped, base attenuate, gibbous, lilac, bluish-lavender, purple, pink-purple to pink, glabrous; **petalodia** 0.1–1.3 × 0.1–0.6 mm; **stamens** inserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 0.7–1.8 cm long, shorter filaments 1.5–3.7 cm long, sheath inequilateral to slightly inequilateral, shorter side 2.2–6.7 mm long, longer side 1.7–8.5 mm long, sheath villous, sometimes pubescent basally, free filaments glabrous, brownish-yellow, shorter stamens anthers 0.3–1 .2 × 0.3–1.0 mm, square to ovate, apiculate, longer stamens anthers 0.9–2.0 × 0.2–1.2 mm, rectangular, apiculate, rarely ovate with acute apex; **ovary** 1.4–7.6 × 0.8–3.5 mm, obovate, glabrous, 3–8 ovules, stipe 1.4–4.2 mm long, glabrous, style 1.3–2.5 cm long, stigma capitate to obtuse, villous to papillose. **Legumes** 6.5–11.8 × 3.3–6.0 cm, stipe 0.5–1.8 cm long, oblanceolate to obovate, apex obtuse to truncate, apiculate, margin entire, cinnamon, brown to purplish-brown, veins absent, glabrous, pitted. **Seeds** 1–2 per fruit, 2.9 × 1.4 cm, elliptic, dark-brown, nitid, pitted reticulate.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 155,436.182 km$_2$ and the estimated area of occupancy is 112.000 km$_2$.

Eperua oleifera has to varieties: *E. oleifera* var. *oleifera* and *E. oleifera* var. *campestris*.

14a. ***Eperua oleifera*** Ducke var. ***oleifera*** (Figures 14, 44, 45)

Tree 18.0–30.0 m tall. **Blades:** lower pair base obtuse to rounded, rarely cordate, middle pair base obtuse, sometimes obtuse to cuneate, sometimes rounded, tertiary veins conspicuous to inconspicuous, not prominent in the adaxial surface, rarely prominent.

Phenology:—Flowering in January, from May to August, and in November; fruiting in July and August.

Distribution:—Southeast of Amazonas state in the Madeira River basin (Brazil).

Habitat:—Mainly in upland (*terra-firme*) forests on sandy soils, but also in flooded forests at ca. 100 m elev.

Occurrence in protected areas:—Unknown.

Etymology:—The specific epithet relates to the oil resin that is extracted from its trunk (Ducke 1932).

Vernacular names:—jacaré-copahiba (*Ducke W.A. 213, 235, s.n. RB23290, s.n. RB20217*), copaíba-jacaré (*Coêlho L.F. s.n. INPA39594*), copaíba preta (*Coêlho L.F. s.n. INPA42008*).

Uses:—Unknown.

Taxonomic notes:—*Eperua oleifera* can be differentiated from other species of *Eperua* by the 3-jugate leaves with straight and adaxially nitid and conspicuous pellucid-punctate leaflets. Among the species with tubular corollas,

E. oleifera differs by the combination tomentose to strigose inflorescences, strigulose, tomentulose to tomentose sepals, bracteoles attached to the higher portion of the pedicels or at the base of the hypanthium, villous sheath, and glabrous ovary (see Table 2).

Selected specimens:—BRAZIL. **Amazonas**, Borba, Axinim, rio madeira, 07 May 1936–05 July 1936, *Ducke W.A. 213* (F, K, MO, NY, R, S, US). Manicoré, distrito de Santo Antônio do Matupi, área de manejo do Sr. Amadeu S. Vidal, faz. Mão de Bronze, rodovia transamazônica 234, 106.7 m elev., 7°54'31"S 61°36'28"W, 25 August 2014, *Amoêdo A.B. et al. 49* (EAFM). Maués, along rio Apoquitaua, just above mouth of rio Pacoval, 3°47'0"S 57°56'0"W, 27 July 1983, *Zarucchi J.L. et al. 3209* (F, INPA, HFSL, MG, MO, NY, RB, UFACPZ, US). **Rio de Janeiro (cultivated)**, Rio de Janeiro, Jardim Botânico do Rio de Janeiro, 01 July 1989, *Gonçalves V.F. s.n. RB422083* (RB).

14b. ***Eperua oleifera*** Ducke var. ***campestris*** Ducke (1932: 728) (Figures 14, 43, 45)

Type:—BRAZIL: Amazonas: Borba, Rio Madeira, campo arenoso, 17 January 1930, *Ducke W.A. s.n. RB23291* (holotype RB sheet I[00539605]!, sheet II[00585835]!, & sheet III[00585836]!; isotypes NY[00004384] image!, P[00835938] image!, R[000028783]!, U[0003232] image!, US[00001150]!).

Treelet, or shrub 1.5–9.0 m tall. **Blades:** lower pair base rounded, subcordate to cordate, middle pair base rounded, subcordate to cordate, upper pair base obtuse, rounded, subcordate to cordate, tertiary veins very conspicuous, prominent in the adaxial surface, rarely not prominent.

Phenology:—Flowering mainly in April, from June to September, and in November, with a flowering peak in August; fruiting from May to August, in October, and November.

Distribution:—Southeast of Amazonas state in the Madeira River basin (Brazil).

Habitat:—White sand *campina* and *campinarana*, in upland and fooldplains areas, at ca. 100 m elev.

Occurrence in protected areas:—Unknown.

Etymology:—The specific epithet relates to its habitat in the *campinas*.

Vernacular names:—copaiba jacaré (*Pessoal do Proj. Radam 13234*).

Uses:—Unknown.

Taxonomic notes:—*Eperua oleifera* var. *campestris* differs from the type variety by being a treelet or shrub (vs. tall tree in var. *oleifera*) with the lower and middle pair of leaflets having a rounded, cordate to subcordate base (vs. rounded to obtuse, rarely cordate or subcordate, in var. *oleifera*), and very conspicuous tertiary veins (vs. conspicuous to inconspicuous in var. *oleifera). Eperua oleifera* var. *campestris* presents strigose to tomentose inflorescence (vs. tomentose, indumentum tending to be denser, in var. *oleifera*), and it is the only reproductive difference, justifying its permanency as a variety.

Selected specimens:—BRAZIL. **Amazonas**, Apuí, rodovia Transamazônica, igarapé Coca-cola, 7°26'5"S 61°2'23"W, 18 August 2009, *Assunção P.A.C.L. & Carvalho F.A. de 1118* (INPA). Borba, rio Madeira, 09 November 1935, *Ducke W.A. 13* (K). Manaus, rio Negro basin September 1948, *Schultes R.E. & López F. 10337* (IAN, NY, US); 5 Km S of Borba, 4°23'0"S 59°35'0"W, 26 June 1983, *Zarucchi J.L. et al. 2842* (HFSL, INPA, K, MG, MO, NY, RB, UFACPZ, US); Axinim, basin of rio Abacaxis, ca. 4km from mouth of igarapé Surubim, 4°31'0"S 58°34'0"W, 04 July 1983, *Zarucchi J.L. et al. 2941* (INPA, K, MG, MO, NY, RB, UFACPZ, US). Manicoré, BR 230, rod. Transamazônica, a 243 Km de Humaitá, 7°40'0.1"S 61°10'0"W, 24 April 1985, *Cid-Ferreira C.A. 5791* (F, HRCB, INPA, K, MG, MO, RB, US). Maués, campina Socoró, 4°17'2"S 58°34'40"W, 07 August 2015, *Demarchi L.O. et al. 529* (INPA). Novo Aripuanã, BR 230, rod. Transamazônica entre os Kms 350 e 400 ao leste de Humaitá, 30 April 1985, *Cid-Ferreira C.A. 5913* (F, HRCB, INPA, K, MG, MO, NY, RB, US); Nova Prainha, 23 July 1976, *Mota C.D.A. da & Monteiro O.P. s.n. INPA60692* (INPA). Nova Olinda do Nortes, rio Abacaxis, Igarapé do Socoró, campina Socoró, 4°17'2"S 58°34'40"W, 07 August 2015, *Holanda A.S.S. et al. 799* (INPA). **Rio de Janeiro (cultivated)**, Rio de Janeiro, Arboreto do Jardim Botânico do Rio de Janeiro, nº 317, canteiro A, séc. XXV, 25 April 1985, *Carvalho I.R. & Ricardo C.C. s.n. RB243379* (INPA, RB).

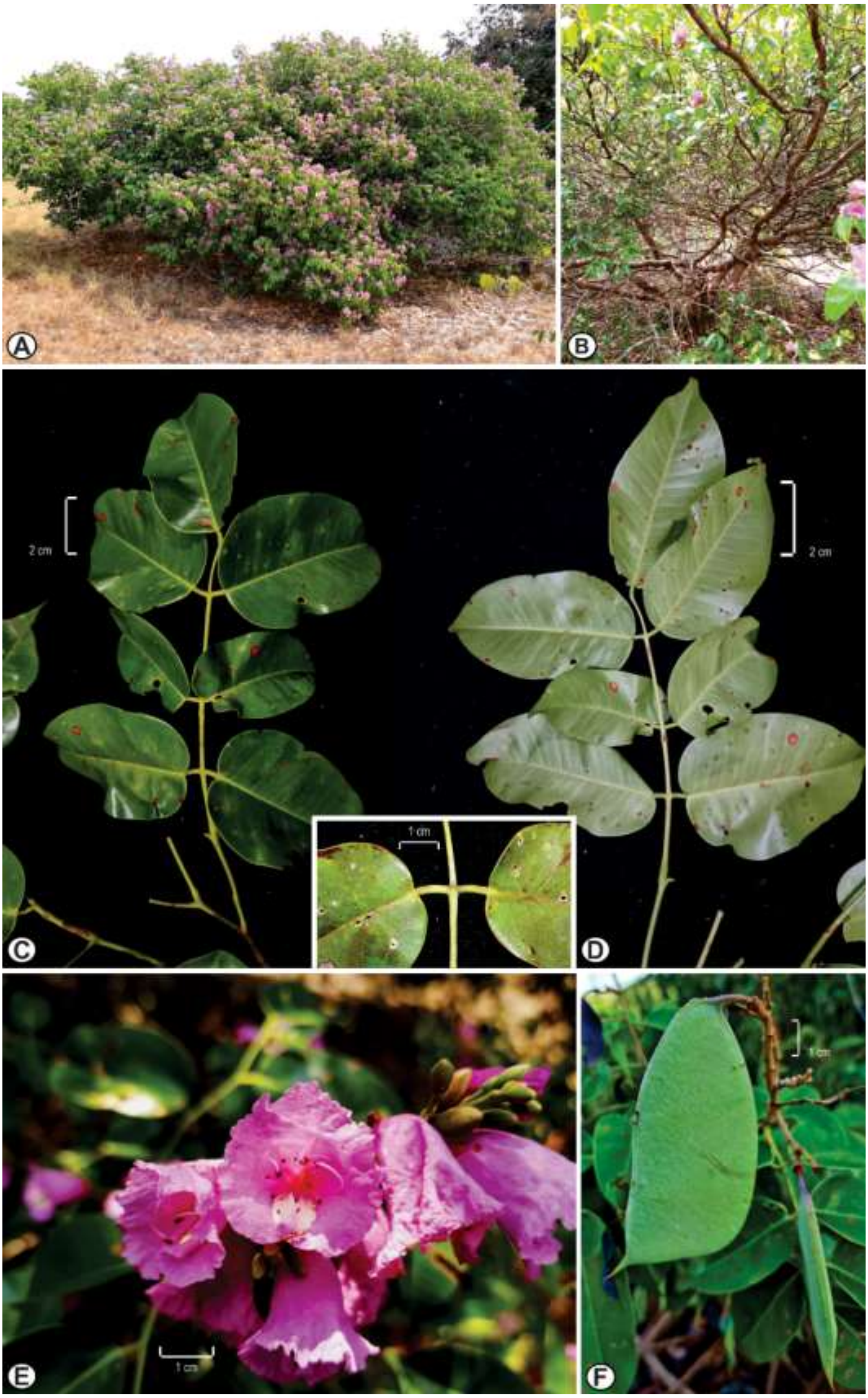


FIGURE 43. *Eperua oleifera* var. *campestris*: A. habit; B. bifurcate trunk; C. leaf, adaxial surface, and detail of the leaflet base; D. leaf, abaxial surface; E. flowers; F. fruits. Photos, F. Farroñay.

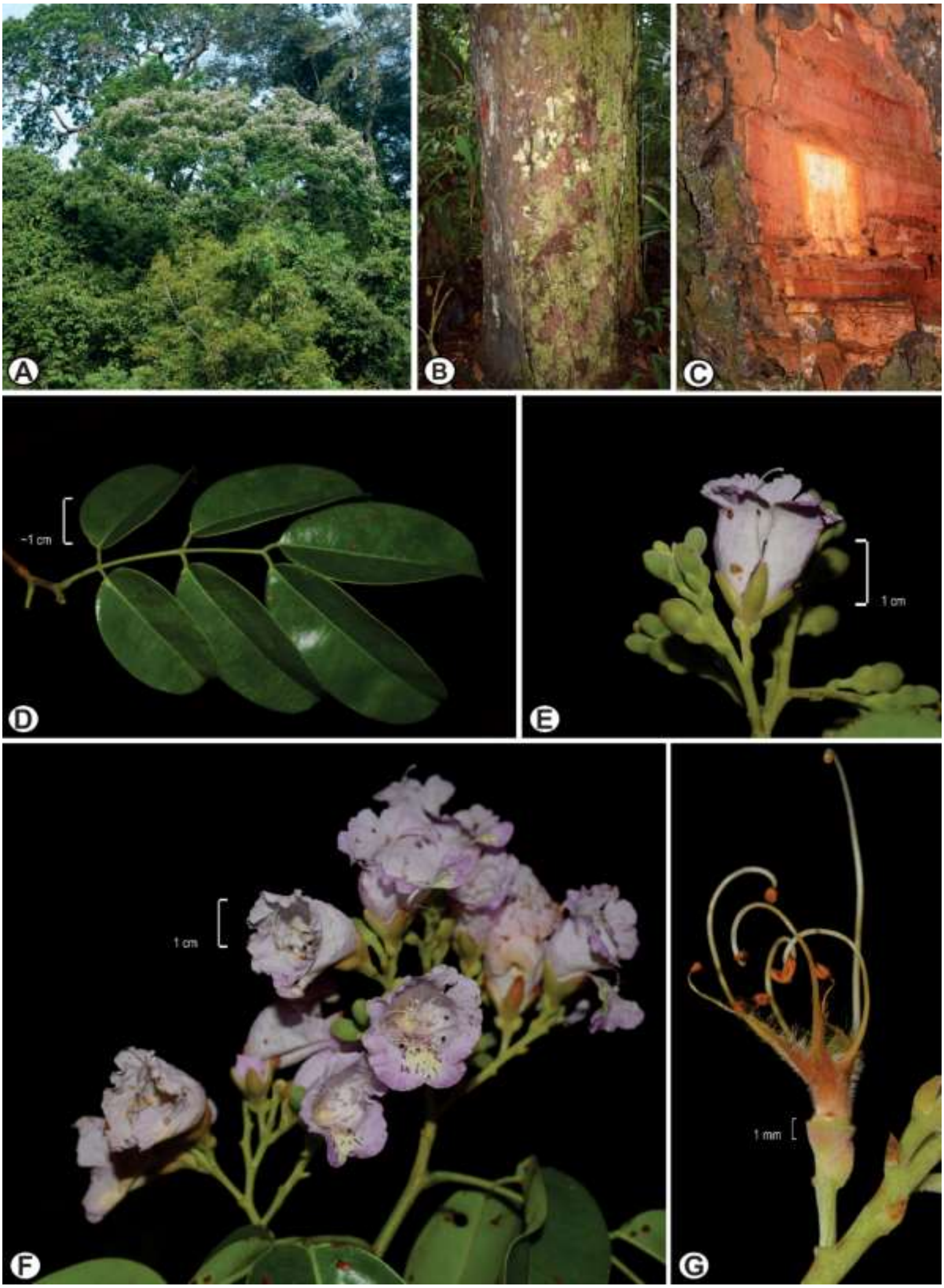


FIGURE 44. *Eperua oleifera* var. *oleifera*: A. habit; B. trunk; C. inner bark and sap-wood and heartwood; D. leaf; E. flower, lateral view; F. inflorescence; G. stamens joined in a diadelphous sheath. Photos, F. Farroñay.

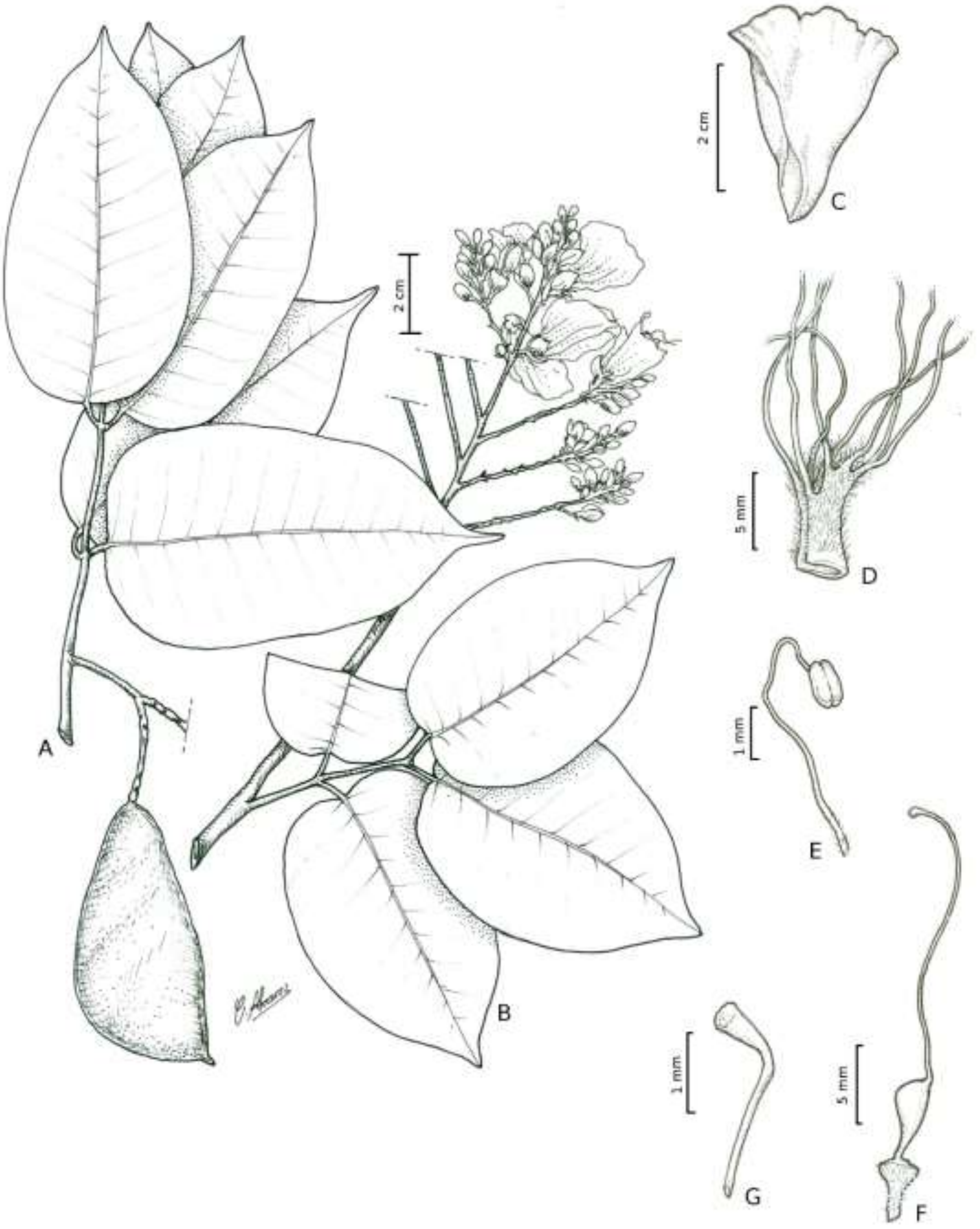


FIGURE 45. *Eperua oleifera*. A. fruiting branchlet, var. *oleifera*.; B. flowering branchlet, var. *campestris*; C adaxial petal, var. *campestris*; D. base of the stamens joined in a diadelphous sheath, var. *campestris*; E. anther and filament, var. *campestris*; F. carpel, var. *campestris*; G. stigma, var. *campestris*. Specimens, A: *Zarucchi J.L. et al. 2935*; B: *Zarucchi J.L. et al. 2842*; C–E: *Schultes R.E. & López F. 10337*. Illustrated by Carlos Alvarez.

15. ***Eperua purpurea*** Bentham (1870: 226) (Figures 14, 46, 47)

Type (designated by Cowan 1975)**:**—BRAZIL. Amazonas: Panuré, Rio Negro, Uaupés, September 1852, *Spruce R. 2577* (lectotype K[000555096] image!, isolectotype P-flower[00835940] image!).

Tree (2.0–)15.0–30.0(–50.0) m tall. **Trunk** 30.0–100.0 cm in diameter, bark grayish, smooth, lenticelate, to fissured. **Stipules** 1.9–4.2 × 1.5–4.1 mm, joined, non-foliaceous, persistent. **Leaves** 2–3-jugate; **petioles** 0.7–3.8 cm long; **rachis** 0.7–10.7 cm long; **petiolules** 2.8–8.4 mm long; **blades** 4.0–14.3 × 2.2–6.7(–10.5) cm, coriaceous, upper surface glabrous, nitid, lower surface densely papillate-ceriferous except on the marginal vein, pellucid-punctate, strongly discolorous, equilateral, lower pair elliptic, sometimes ovate, rarely broadly elliptic, middle pair elliptic, sometimes ovate, rarely broadly elliptic, upper pair elliptic, rarely broadly elliptic or ovate, apex acuminate, retuse, base symmetrical, lower pair base obtuse to rounded, middle pair base obtuse to rounded, sometimes subcordate, rarely cordate, upper pair base obtuse, sometimes rounded, margin flat to slightly revolute, **secondary venation** with one intramarginal vein very close to the margin, main vein straight, depressed on the adaxial surface, tertiary veins inconspicuous to conspicuous only adaxially, areoles inconspicuous. **Inflorescences** terminal, rarely axillary, panicle or raceme, erect, glabrous, 2.2–9.0 cm long, lateral racemes 1.2–9.6 cm long, congested racemes, alternate and distichous; **bracts** 0.9–3.2 × 0.4–3.2 mm, ovate, apex gland absent, glabrous, pellucid punctate externally, sericeous, pubescent to glabrescent within, brownish-yellow, persistent, rarely caducous; **bracteoles** 1.4–3.3(–8.9) × 0.4–3.2 mm, ovate, apex gland absent, glabrous externally, pubescent to sericeous within, ciliate, brownish-yellow, persistent, attached to the middle portion of the pedicels at slightly different levels; **pedicel** 7.4–20.0 mm long, 0.5–1.2 mm in diameter, not twisted, glabrous; **buds** 0.7–1.4 cm long, 0.3–1.0 cm in diameter, glabrous. **Flowers**: **hypanthium** 1.6–4.1 mm long, 1.6–4.8 mm in diameter, cup-shaped, equilateral, glabrous; **sepal** 0.7–1.5 × 0.3–0.8 cm, elliptic to ovate, rarely obovate, unequal, the outer ones larger, cucullate, apex gland absent, purple to red, glabrous, pellucidpunctate; **adaxial petal** 1.9–4.4 × 2.9–5.6 cm, flabellate, tubular, apex rounded, base attenuate, gibbous, pink purple to purple, glabrous; **petalodia** 0.2–1.5 × 0.1–0.7 mm; **stamens** inserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 1.5–3.2 cm long, shorter filaments 0.8–1.6 cm long, sheath inequilateral, shorter side 3.2–7.7 mm long, longer side 4.2–8.9 mm long, sheath and one-third of the free filaments villous, brownish-yellow, shorter stamens anthers 0.4–1.0 × 0.4–1.0 mm, square, apiculate, longer stamens anthers 1.2–1.8 × 0.4–1.0 mm, rectangular; **ovary** 2.4–5.0 × 0.9–2.5 mm, obovate, glabrous, 3 ovules, stipe 1.6–3.6 mm long, glabrous, style 1.2–3.0 cm long, stigma capitate. **Legumes** 11.0–17.0 × 3.9–7.9 cm, stipe 0.5–1.0 cm long, obovate, apex obtuse to truncate, apiculate, dorsal margin alate, fuscous, veins absent or with inconspicuous veins, glabrous. **Seeds** 2 per fruit, 3.8–4.4 × 1.9–3.0 cm, elliptic to obovate, dark-brown to reddish-brown.

Phenology:—Flowering from January to June and from August to November, with a pick in October and November; fruiting from January to May and from September to November.

Distribution:—Northwest of Amazonas state in Brazil, south of Amazonas state in Venezuela, and southwest of Colombia Amazonas, Guainía, and Vaupés departments.

Habitat:—Frequent in the Amazonian forests known as *campinarana* or *varillal* on white and brown sand mixed soils, but also reported in *terra-firme* (Aymard *et al.* 2009), and gallery forests, from 79 to 320(–750) m elev.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 195,184.753 km^2 and the estimated area of occupancy is 216.000 km^2.

Occurrence in protected areas:—Resguardo Indígena Río Atabapo (Colombia, Guainía), Parque Nacional Natural Río Puré (Colombia, Amazonas), Parque Nacional do Pico da Neblina (Brazil, Amazonas), and Parque Nacional Serranía La Neblina (Venezuela, Amazonas).

Habitat:—Frequent in the Amazonian forests known as *campinarana* or *varillal* on white and brown sand mixed soils, but also reported in *terra-firme* (Aymard *et al.* 2009), and gallery forests, from 79 to 320(–750) m elev. **Conservation status:—**Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 195,184.753 km^2 and the estimated area of occupancy is 216.000 km^2.

Occurrence in protected areas:—Resguardo Indígena Río Atabapo (Colombia, Guainía), Parque Nacional Natural Río Puré (Colombia, Amazonas), Parque Nacional do Pico da Neblina (Brazil, Amazonas), and Parque Nacional Serranía La Neblina (Venezuela, Amazonas).

Selected specimens:—BRAZIL. **Amazonas**, Santa Isabel do Rio Negro, Tapuruquara, basin of rio Negro, 27 October 1971, *Prance G.T. et al. 15609* (INPA, K, MG, NY, P, R, U, US). São Gabriel da Cachoeira, rio Içana, próximo a Serra do Grilo, 05 November 1987, *Farney C. de S. et al. 1899* (HAMAB, INPA, K, NY, US); rio Marié, Tapuruquara Mirim, 16 October 1978, *Madison M.T. et al. 319* (INPA, RB); Uaupés, R. Negro, estrada Perimetral Norte, 13 March 1975, *Pires J.M. & Marinho L.R. 15783* (IAN). **Rio de Janeiro (cultivated)**, Jardim Botânico do Rio de Janeiro, 1246 - XXVI-E, undated, *s.c. s.n. RB89490* (RB). **COLOMBIA**. **Amazonas**, Leticia, PNN Amacayacu, 12 August 1995, *Etter A.3* (COAH). **Guainía**, Cacahual, comunidad indígena Cacahual, zona de rebalse del río Atabapo, 18 August 2004, *Cárdenas-López D. et al. 15350* (COAH). Inírida, río Atabapo, Caño Chaquita, localidad La Esperanza, 23 May 1979, *Rodríguez R. & Acero E. 207* (COL, UDBC). La Guadalupe, corremiento de San Felipe, comunidad El Porvenir, alto rio Negro, em cercanias de la Piedra del Cocui (zona limiftrofe entre Colombia, Brasil y

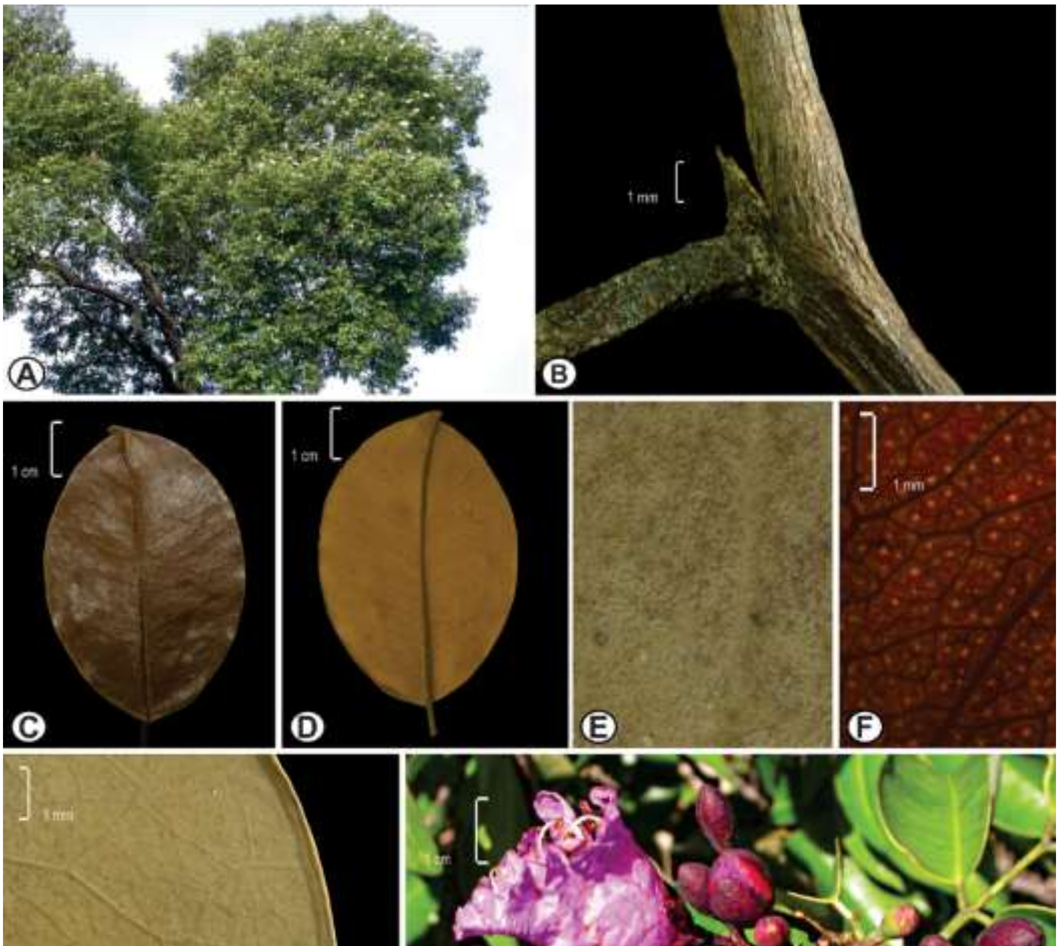


FIGURE 46. *Eperua purpurea*: A. fruiting tree; B. joined stipules; C. leaflet, adaxial surface; D, E. leaflet, abaxial surface; F. pellucidpunctate blade; G. intramarginal vein, abaxial surface; H. inflorescence; I. flowers, front view; J. sheath indumentum. Specimen C, D: *Stropp J. & Assunção P. 639*; B, E–G, J: *Ducke W.A. s.n. RB23288*. Photos, A, H, I: H. ter Steege G–G: E.A. Fortes.

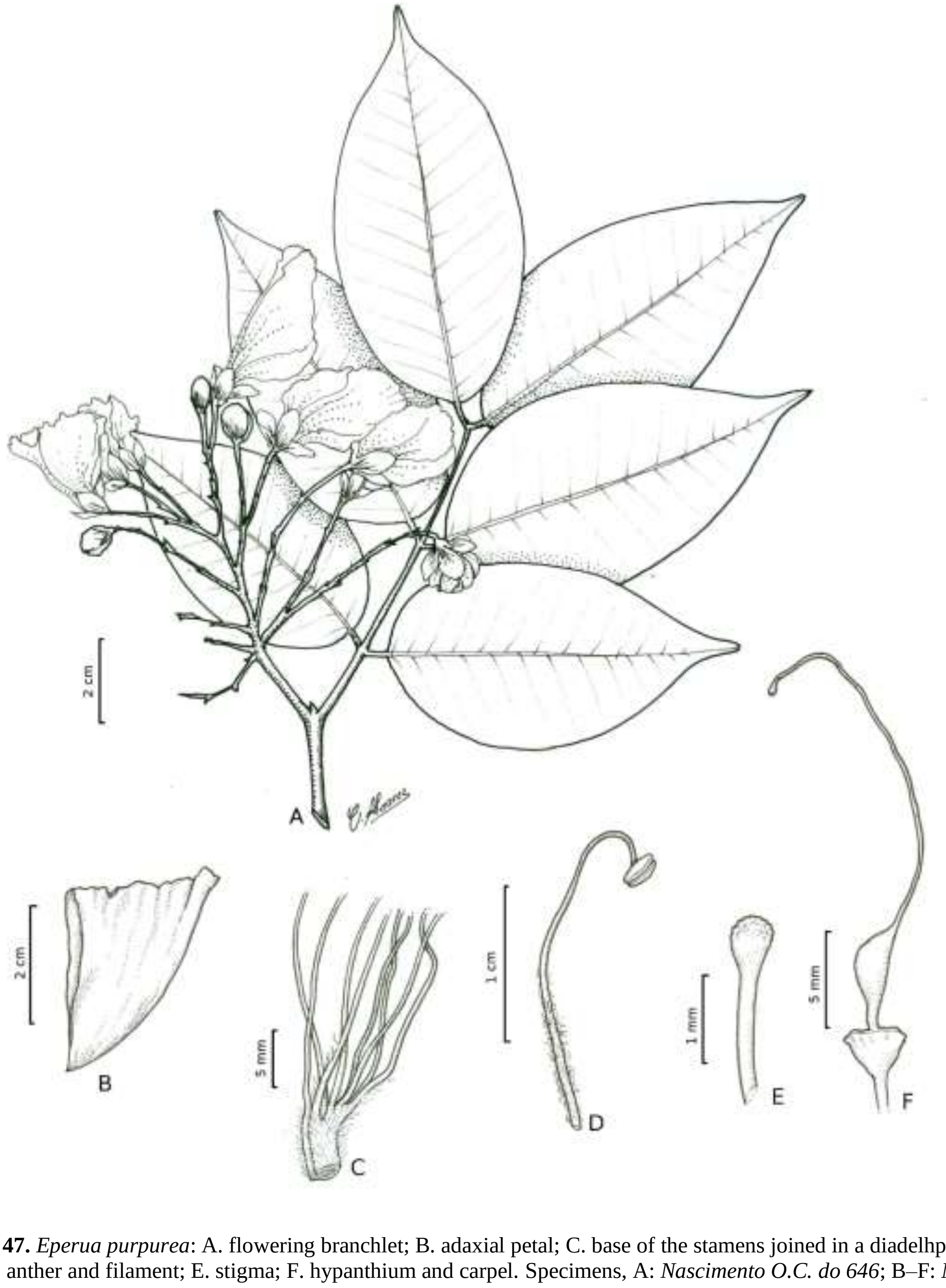


FIGURE 47. *Eperua purpurea*: A. flowering branchlet; B. adaxial petal; C. base of the stamens joined in a diadelhpus sheath; D. anther and filament; E. stigma; F. hypanthium and carpel. Specimens, A: *Nascimento O.C. do 646*; B–F: *Maguire B. et al. 60112*. Illustrated by Carlos Alvarez.

Venezuela), 200 m elev., 1°19'12"N 66°53'4"W, 15 October 2009, *Cárdenas-López D. et al. 24076* (COAH, NY). Maimachi, Serrania de Naquen, alrededores del campamento La Planada, 320 m elev., 2°12'0"N 68°11'59"W, 14 August 1992, *Cortés-Ballen R. et al. 336* (COAH, COL, UDBC). Pana Pana, bosque ubicado a 15min, caminando desde la rivera del río Isana, a 15 min en lancha desde la comunidad de Punta Tigre, 09 May 2014, *Aymard G. 14571* (COAH). Puerto Colombia, corregimiento de Cano Colorado, medio rio Guainia, Cano Mahimachi, Serrania de Naquen, 300 m elev., 2°9'13.4"N 68°14'7"W, 20 October 2009, *Cárdenas-López D. et al. 24415* (COAH, US). San Filipe, rio Negro, below confluence of rio Guainia and rio Casiquiare, 192 m elev., 24 October 1952, *Schultes R.E. et al. 17955* (COL, U, US). **Vaupés**, Mitú, confluencia de los ríos Vaupés y Papurí, Yaravaté, bosque entre el río Vaupés y el caño Ardilla, 120 m elev., 0°37'0"N 69°12'0"W, 30 November 2004, *Bernal R. et al. 3683* (COL). **VENEZUELA**. **Amazonas**, Casiaquire, pueblo de Maroa, 90 m elev., 2°43'0"N 67°32'0"W, 24 February 1979, *Huber O. 3376* (US).

Maroa, rio Guainia, along trail to Guzman Blanco 1–5 km, Southeast of Moroa, 120–140 m elev., 09 October 1957, *Maguire B. et al. 41776* (IAN, RB, U, US). San Carlos de Río Negro, Neblina Base camp, rio Negro, Neblina Base camp, rio Mawarinuma, 140 m elev., 0°50’0”N 66°10’0”W, 28 November 1984, *Boom B.M. & Weitzman A.L. 5185* (F, INPA, MO, U, US); 18 - rio Yatuá, 84 m elev., 1°16’33.3”N 66°6’51.1”W, 05 February 2005, *Redden K.M. et al. 3560* (US). Yavita, along road from Maroa to Yabita, ca. 700 m from Yabita, 2°54’42”N 67°26’55”W, 19 February 1998, *Acevedo-Rodríguez P. et al. 10235* (US).

16. ***Eperua reddeniae*** E.A. Fortes & Mansano, *sp. nov.* (Figures 8, 48, 49, 50)

Type:—GUYANA. Cuyuni-Mazaruni, Mazaruni River, small islands along river, 90 m elev., 6°0’12.6”N 59°13’28.9”W, 11 October 2004, *Redden K.M. et al. 3274* (holotype US[00808373]!, isotypes CAY[109816, 109817] image!, INPA[0220628]!)

Diagnosis:—*Eperua reddeniae* has short and erect inflorescences, non-tubular corollas, and exserted stamens. It differs from species with the same type of inflorescence, corolla, and stamen by the combination (see Table 3): stipules joined at the base, inconspicuous pellucid punctate to epunctate leaflets, slightly revolute margins, coppery inflorescence indumentum, pink to purple petals, stamens joined basally in a diadelphous sheath, dorsal one free, sheath irregularly tomentose in the middle-high portion and glabrous at the base, tomentose ovary, tomentulose fruits with entire margins.

Tree 8–20.0 m tall. **Trunk** 20.0 cm in diameter, bark not seen. **Stipules** 10.9–19.2 × 6.3–12.2 mm, joined at the base, foliaceous, persistent. **Leaves** 4–5-jugate; **petioles** 1.0–1.5 cm long; **rachis** 10.2–15.0 cm long; **petiolules** 6.2–8.2 mm long; **blades** 5.3–11.8 × 2.8–5.0 cm, coriaceous, glabrous, pellucid-punctate to epunctate, discolorous, equilateral, lower pair elliptic to ovate, middle pair elliptic, upper pair elliptic, apex attenuate to acuminate, mucronate, base symmetrical to asymmetrical, lower pair base subcordate to obtuse, middle pair base obtuse, upper pair base obtuse, margin flat to slightly revolute, **secondary venation** with two intramarginal veins, sometimes one, vein closer to the margin not continuous, main vein straight, prominent on the adaxial surface, tertiary veins conspicuous, areoles smaller, concave. **Inflorescences** terminal or axillary, panicle, erect, tomentose, coppery, 13.1–16.0 cm long, lateral racemes 2.1–11.8 cm long, alternate and distichous; **bracts** caducous, not seen; **bracteoles** 2.1–3.8 × 2.3–2.4 mm, ovate, cucullate, apex gland absent, tomentose on both sides, coppery, caducous, attached to the lower middle portion of the pedicels; **pedicel** 18.4–26.2 mm long, 1.3–2.1 mm in diameter, not twisted, tomentose, coppery; **buds** 1.1–1.5 cm long, 0.6–0.7 cm in diameter, tomentose, coppery. **Flowers**: **hypanthium** 4.3–6.3 mm long, 4.9–6.1 mm in diameter, cupshaped, equilateral, tomentose, coppery; **sepal** 1.9–2.7 × 0.6–1.2 cm, elliptic to oblong, unequal, the outer ones larger, cucullate, apex gland absent, green, tomentose externally, coppery, inner sepals scarious marginally; **adaxial petal** 2.0–2.1 × 3.2–4.0 cm, oblate, non-tubular, apex rounded, base truncate, pink to purple, glabrous; **petalodia** 0.5–0.8 × 0.8–1.0 mm; **stamens**, exserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 4.2–5.0 cm long, shorter filaments 3.0 cm long, sheath equilateral, 5.2–8.0 mm long, sheath irregularly tomentose in the middlehigh portion and glabrous at the base, free filaments glabrous, coppery, anthers 5.2–6.6 × 1.0–1.5 mm, rectangular; **ovary** 9.2–12.0 × 4.0–4.2 mm, oblaceolate, tomentose, cream (fresh) to coppery (dried), stipe 8.8–15.0 mm long, tomentose, style 3.5–5.0 cm long, stigma obtuse to capitate. **Legumes** 21.0 × 7.6 cm, stipe not seen, oblanceolatefalcate, apex acute, apiculate, margin entire, coppery, veins absent, tomentulose, coppery. **Seeds**, 4.3 × 2.6 cm, ovate to oblong.

Phenology:—Flowering in September and October.; fruiting in October

Distribution:—Guyana (Cuyuni-Mazaruni).

Distribution and habitat:—Floodplain **(**gallery) forests on mixed brown and white sand soils, at 63–90 m elev.

Conservation status:—Categorized as Data Deficient (DD) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022) as it is known by only two specimens.

Occurrence in protected areas:—Unknown.

Etymology:—The specific epithet is a tribute to Karen Redden, a botanist who studied Detarieae groups and the Guyana Shield Flora, besides collecting a lot of species of *Eperua* (over eighty specimens and 11 species), including the type specimen of this new species.

Vernacular names:—Described as having the common name “tricel” in the *Redden K.M. et al. 3260* collection label. However, a similar name, “trysil”, is the vernacular name of the locally quite common species, *Pentaclethra macroloba* Kuntze, and likely the name “tricel” was mistakenly coined by the collectors (ter Steege pers. obs.)

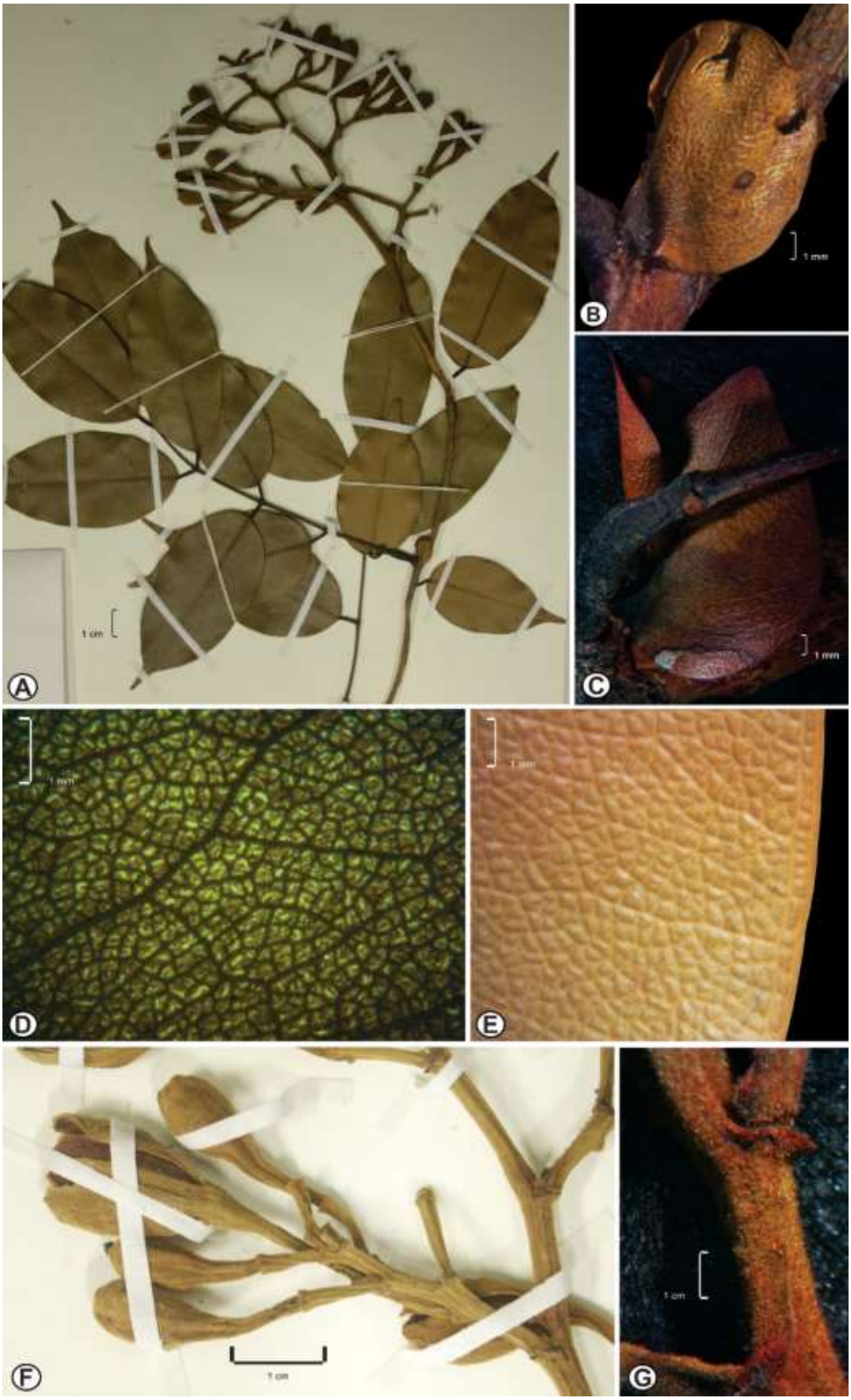


FIGURE 48. *Eperua reddeniae*: A. flowering branchlet; B., C. foliaceous stipules joined at the base; D. inconspicuous pellucid-punctate blade; E. intramarginal vein, abaxial surface; F. lateral raceme in buds; G. detail of the inflorescence indumentum. Specimen, A, B, D–G: *Redden K.M. et al. 3260*; C: *Redden K.M. et al. 3274*. Photos, E.A. Fortes.

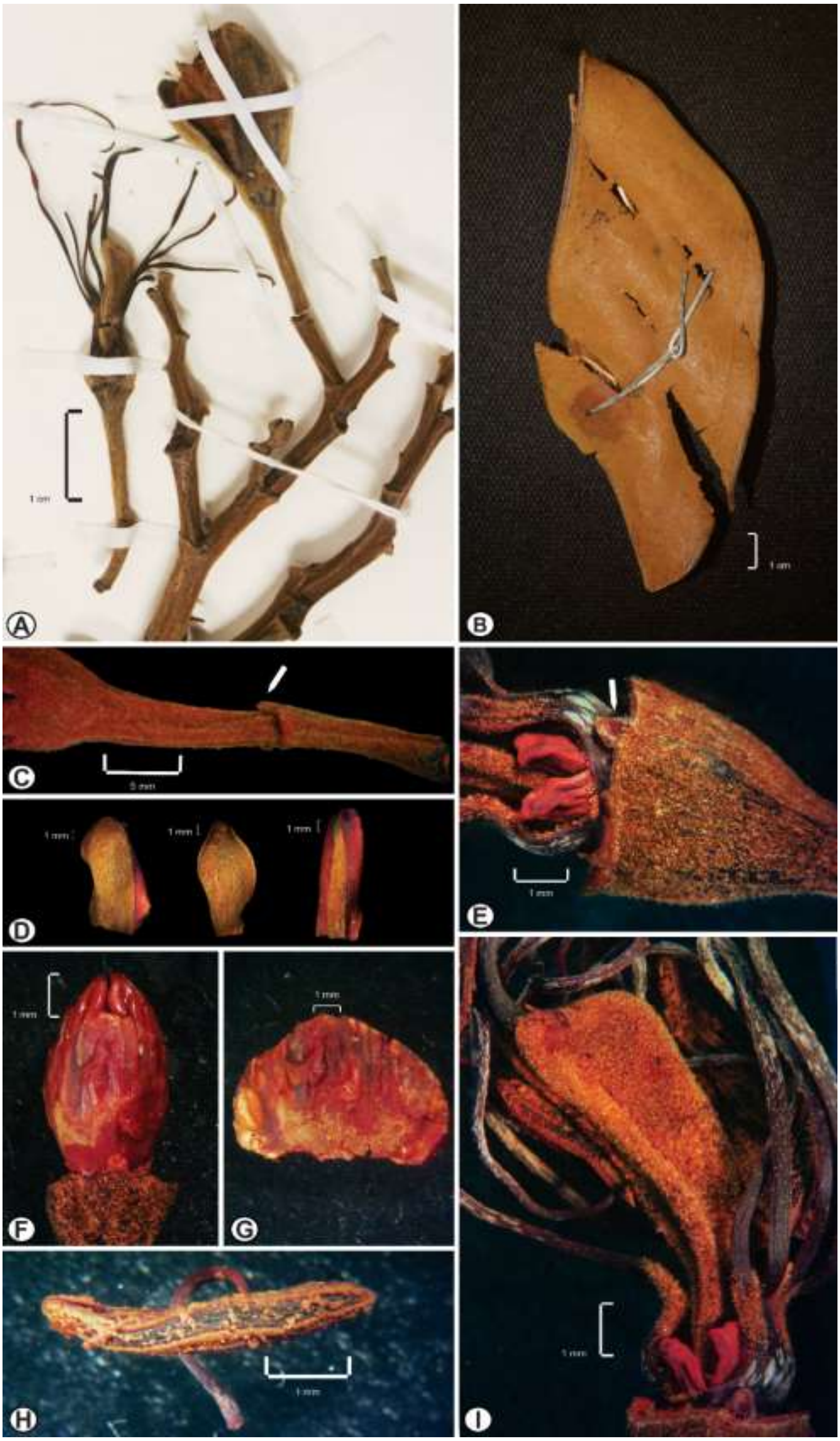


FIGURE 49. *Eperua reddeniae*: A. flower in pre-anthesis and other showing the carpel and stamens (sepals and adaxial petal removed); B. fruit; C. pedicel showing the bracteoles scar (white arrow) on its middle portion; D. sepals; E. detail of the hypanthium, petalodia (white arrow), base of the stamens, and intrastaminal nectaries; F. bud showing the adaxial petal and part of the anthers (sepals removed); G. adaxial petal from a bud; H. anther and part of the filament; I. base of the stamens joined in a diadelphous sheath (free stamen on the left) and tomentose carpel. Specimens, *Redden K.M. et al. 3274*. Photos, E.A. Fortes.

FIGURE 50. *Eperua reddeniae*: A. fruiting branchlet; B. joined foliaceous stipules; C. detail of leaflet margin, abaxial side, showing the intramarginal vein; D. detail of a lateral raceme in buds; E. detail of the inflorescence axis indumentum; F. flower in pre-anthesis showing the bracteole scars at the middle portion of the pedicels; G–I. sepals; J. flower showing the stamens joined basally in a diadelphous sheath, the tomentose ovary, and one petalodia right above the hypanthium (sepals and adaxial petal removed); K. detail of the base of the stamens and one petalodia at the bottom right, the free stamen is at the middle, through the sheath aperture it is possible to see the intrastaminal nectaries; L. adaxial petal from a bud; M. anther and part of the filament. Specimens, A, C, D, E: *Redden K.M. et al. 3260*; B, E–N: Young fruit. Illustrated by Marcus Falcão.

Uses:—Unknown.

Taxonomic notes:—*Eperua reddeniae*, *E. froesii*, *E. cerradoensis*, *E. duckeana* and *E. schomburgkiana* are the only species with short and erect inflorescences that have non-tubular corolla, exserted stamens, falcate fruit with a 3:1 length/width proportion (vs. tubular corolla, included stamens, non-falcate fruit with a 1:1 to 2:1 length/width proportion in other short and erect inflorescence species). They also share multijugate leaves with straight leaflets and inflorescence with dense indumentum. Additionally, *E. reddeniae* shares caducous bracteoles and stamens joined in a diadelphous sheath 9+1 with *E. duckeana* and *E. schomburgkiana*; and irregularly tomentose sheath with *E. schomburgkiana*. Similarities and differences between species of this group are summarized in Table 3. The flower of *E. reddeniae* is most similar to *E. duckeana* by the non-glabrous sheath, ovary, and fruits, and the diadelphous stamen sheath. Besides the allopatric distribution (*E. reddeniae* is restricted to Guyana, and *E. duckeana* to the Central Amazonia, Figure 8), *E. reddeniae* differs from *E. duckeana* mainly by the coppery inflorescence indumentum (vs. brownish-yellow in *E. duckeana*), pink to purple petals (vs. white in *E. duckeana*), and irregularly tomentose sheath (vs. entirely tomentose in *E. duckeana*).

Specimens examined (Paratypes):—GUYANA. **Cuyuni-Mazaruni**, Mazaruni River, unnamed falls (possible Carin Crow Falls), 0.26 miles NW of base camp, 63 m elev., 5°57'25"N 59°18'41.8"W, 09 September 2004, *Redden K.M. et al. 3260* (US[00889812]!).

17. ***Eperua rubiginosa*** Miquel (1851: 12) (Figures 12, 51, 52)

Type (designated by Cowan 1975)**:**—SURINAM. Without locality, s.d., *Hostmann F.W. 229* (lectotype U[0003237] image!; isolectotypes K[000555108] image!, LE[00002234] image!).

Tree 6.0–30.0(–40.0) m tall. **Trunk** 12.0–50.0(–91.0) cm in diameter, bark grayish, lenticellate. **Stipules** *1.2–3.5(– 4.1) × 0.7–2.2, free,* or *1.3–7.7 × 3.0–5.0 mm, joined at the base*, non-foliaceous, caducous. **Leaves** *(2–)3(–4)* or *(3–5)4–5-jugate*; **petioles** (0.4–)0.8–3.8(–8.0) cm long; **rachis** *(2.3–)4.0–15.2(–18.5)* or *7.3–25.0* cm long; **petiolules** (2.0–)4.9–12.5 mm long; **blades** 5.1–16.0(–19.0) × 2.3–7.8 cm, coriaceous, glabrous, epunctate to inconspicuous pellucid-punctate, rarely pellucid-punctate, not discolorous to discolorous, equilateral, lower pair elliptic, sometimes lanceolate or ovate, middle pair elliptic, rarely lanceolate or ovate, upper pair elliptic, rarely lanceolate or obovate, apex attenuate to acuminate, mucronate, sometimes caudate, base symmetrical, lower pair base obtuse to rounded, rarely subcordate, middle pair base obtuse, rarely rounded, subcordate or cordate, upper pair base obtuse to cuneate, margin flat to slightly revolute, rarely revolute, **secondary venation** with *one intramarginal vein, sometimes two, thevein closer to the margin not continuous,* or, *two intramarginal veins, sometimes one, the vein closer to the margin continuous or not*, main vein straight, depressed on the adaxial surface, tertiary veins inconspicuous to conspicuous, areoles smaller, concave. **Inflorescences** terminal, sometimes axillary, panicle, main axis pendulous, lateral racemes erect, rarely patent, tomentulose, coppery, *46.0–280.0(–500.0)* or *40.0–150.0* cm long, lateral racemes 1.8–11.5(–16.5) cm long, alternate and spirally arranged; **bracts** not seen; **bracteoles** 1.9–3.8 × 1.2–2.3 mm, ovate, cucullate, apex gland absent, tomentose, coppery, caducous, attached to the lower portion of the pedicels; **pedicel** 9.7–33.0 mm long, *0.6–2.0* or *2.0–3.3* mm in diameter, not twisted, tomentose, coppery; **buds** 0.6–2.1 cm long, 0.3–1.2 cm in diameter, tomentose, coppery. **Flowers**: **hypanthium** 3.1–9.6 mm long, *2.8–5.9* or *4.9–7.0* mm in diameter, cupshaped, equilateral, tomentose, coppery; **sepal** *1.0–1.8(2.1) × 0.3–1.1* or *1.7–2.3 × 0.6–1.0* cm, elliptic to oblong, unequal, the outer ones larger, dorsal one cucullate, apex gland present on the outer ones, coppery, tomentose, inner sepals scarious marginally, coppery; **adaxial petal** 1.0–2.6 × 1.6–5.0 cm, oblate, non-tubular, apex rounded, crisped, base truncate, reddish, pink, magenta, purple-red to red, glabrous, punctate, papillose; **petalodia** 0.3–2.5 × 0.2–1.2 mm; **stamens** exserted, joined basally in a tube, longer filaments 3.0–6.8 cm long, shorter filaments 2.2–5.5 cm long, tube equilateral, 0.4–4.8 mm long, glabrous, sometimes tomentulose in the sinuses, coppery, anthers 4.1–9.3 × 0.4–1.6 mm, rectangular; **ovary** 4.2–13.0 × 1.6–4.3 mm, oblanceolate, tomentose, coppery, 5 ovules, stipe 3.9–15.5 mm long, tomentose, style 2.0–7.4 cm long, stigma capitate. **Legumes** 13.4–30.3 × 3.3–10.0 cm, stipe 1.0–4.9 cm long, with flower remnants, falcate-oblanceolate, apex acuminate, acute to rounded, dorsal margin thickened, ventral margin entire, coppery, veins absent, tomentose, coppery. **Seeds** 1–3 per fruit, 2.0–5.0 × 0.7–3.0 cm, oblate, oblong, ovate to orbicular, dark-brown, centrally reddish-brown.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 632,928.628 km^2 and the estimated area of occupancy is 436.000 km^2.

Eperua rubiginosa has to varieties presented here: *E. rubiginosa* var. *rubiginosa* and *E. rubiginosa* var. *grandiflora*.

17a. ***Eperua rubiginosa*** Miq. var. ***rubiginosa***

Stipules 1.2–3.5(–4.1) × 0.7–2.2, free. **Leaves** (2–)3(–4); **rachis** (2.3–)4.0–15.2(–18.5) cm long; **secondary venation** with one intramarginal vein, sometimes two, the vein closer to the margin not continuous. **Inflorescences** 46.0–280.0(–500.0) cm long; **pedicel** 0.6–2.0 mm in diameter. **Flowers**: **hypanthium** 2.8–5.9 mm in diameter; **sepal** 1.0–1.8(2.1) × 0.3–1.1 cm.

Phenology:—Flowering throughout the year with a flowering pick from August to December; fruiting throughout the year, mainly from October to November.

Distribution:—Brazil (Amapá, Pará), French Guiana (Cayenne, Saint-Laurent-du-Maroni), Guyana (Cuyuni-

Mazaruni, Potaro-Siparuni, Upper Demerara-Berbice, Upper Takatu-Upper Essequibo), and Surinam (Brokopondo, Kabalebo, Marowijne, Para, Sipaliwini).

Habitat:—Mainly in floodplains forests (*igapó*, swamp forest), sometimes in *terra-firme* forest, rarely in *wallaba* forest, on white and brown sand, stony clayey, sandy stony, and laterite soils, from sea level to 350 m elev.

Occurrence in protected areas:—Parque Indígena Tumucumaque, Parque Nacional Montanhas do Tumucumaque (Brazil), Réserve Naturelle de Nouragues (French Guiana, Cayenne).

Etymology:—The specific epithet relates to its inflorescence, flowers, and fruit color indumentum.

Vernacular names:—apa (*Irwin H.S. & Westra L.Y.T. 47471*, *Pires J.M. & Westra L.Y.T. 48849*), bioudou (*BAFOG 6239*, *BAFOG 7831*, *BAFOG 7937*, *IFAT 7831*, *IFAT 7937*), eturi wallaba (*Redden K.M. et al. 6012*), franga (boni), ouapa (créole) (*Schnell R.A.A. 11456*), iperana-apá (*Rosa N.A. 1183*), ituri wallaba (*Fanshawe D.B. 4840*), oever wallaba (*Maguire B. et al. 54014*), ouapa (nom créole) (*Oldeman R.A.A. 1552*), tapaka (*Grenand P. 1521*), uapá (*Candido J. s.n. IAN44221*, *IAN44221a*), walaba (*BAFOG 219*, *Landsbosbeheer 311*, *Lanjouw J. 1209*, *738*, *Lanjouw J. & Lindeman J.C. 324*, *Mennega A.M.W. 102*), wallaba (*Evans R. et al. 1929*, *Junker L. 249*), wapa (*Angel G. 126*, *Fleury M. 1129*, *Hoff M. 5964*, *Oldeman R.A.A. 1520*, *Thiel J. 891*, *892*), wapa riviére (*Angel G. 126*, *Bordenave B. 228*, *Paget D. 51*, *Thiel J. 891*, *892*, *Prévost M.F. 4038*, *Benoist R. s.n. P03465703*).

Uses:—Brazil: wood used for house construction (*Fortes E.A.* collections), shingles, fencing, and poles (*Pires J.M. & Westra L.Y.T. 48849*).

Taxonomic notes:—*Eperua rubiginosa* shares with *E. glabra* the multijugate leaves with straight leaflets, long and pendulous inflorescences, erect lateral racemes, caducous bracteoles attached to the lower portion of the pedicels, nontubular corolla, and exserted stamens joined in a tube. However, *E. rubiginosa* differs by the tomentulose inflorescence (vs. glabrous in *E. glabra*) and tomentose ovary and fruit (vs. glabrous in *E. glabra*) (see Table 4).

Selected specimens:—BRAZIL. **Amapá**, Macapá, Fazendinha, Parque Zoobotânico, IEPA, rodovia JK, 10 ki, empreendimento AHE, Santo Antônio do rio Jari, 17 August 2010, *Carim M.J.V. & Guimarães J.R.S. 533* (HAMAB). Oiapoque, nas margens da rodovia BR156 entre Oiapoque e Calçoene, a 23 km de Oiapoque, 3°42’11.8”N 51°46’24.1”W, 04 December 2021, *Fortes E.A. & Silva G.S. da 167* (IAN, RB); nas margens do rio Oiapoque próximo à ponte BR-GF, lado brasileiro, 3°51’22.1”N 51°49’29.7”W, 05 December 2021, *Fortes E.A. & Silva G.S. da 168* (IAN, RB). Pedra Branca do Amapari, Parque Nacional Montanhas do Tumucumaque, acima da Base Jupará, 105 m elev., 1°11’16”S 52°22’8”W, 08 November 2018, *Goldenberg R. et al. 2522* (MG, RB); rio Amapari, between Munguba and Serra do Navio, 0°42’0”N 51°45’0”W, 25 September 1961, *Pires J.M. et al. 51182* (IAN, INPA, K, MG, NY, U, US). Serra do Navio, rio Araguari, between camps 12 and 13, 04 October 1961, *Pires J.M. et al. 51501* (IAN, MG, NY, US). **Pará**, Óbidos, rio Paru do Oeste (Tirió), barranco à beira do rio, 26 June 1960, *Cavalcante P.B. 870* (MG, NY). Oriximiná, distrito de Porto Trombetas, km 6, cachoeira da Porteira, 1°5’23”S 57°2’84”W, 17 September 2003, *Faria S.M. de et al. 2450* (HSTM, MBM, RB). **FRENCH GUIANA**. **Cayenne**, Cayenne, unknown locality, October 1910, 1948, *Santini 1948* (L). Kourou, riviére Kourou, bassin du Kourou, 10 October 1980, *Thiel J. 729* (CAY). Régina, station des Nouragues (cam inselberg), trail XV detour near RG on Grand Plateau, 40–20 m elev., 4°5’30”N 52°41’0”W, 10 October 2008, *Geiselman C.K. 169* (NY). Roura, rivière la Counamama, 4°31’0”N 52°16’0”W, 06 October 2000, *Prévost M.F. 4038* (CAY). Saint-Élie, Saut takaritante, bassin du sinnamary, m elev., 4°37’0”N 52°56’0”W, 19 November 1989, *Hoff M. 5964* (CAY). Saint-Georges, crique Gabaret, 3°55’0”N 51°47’59”W, 07 December 2005, *Delnatte C. 325* (CAY, COL, MPU). Sinnamary, pointe Combi, région littorale, riviére Sinnamary, 24 November 1979, *Thiel J. 588* (CAY). **Saint-Laurent-du-Maroni**, Grandi-Santi, 25 August 1961, *Schnell R.A.A. 11456* (CAY, P, U, US). Mana, unknown locality, 06 December 1979, *Thiel J. 601* (CAY). Maripasoula, camp no. 1 ouman fou langa soula—bassin du haut marouini Saint-Laurent-du-Maron, 2°52’59.9”N 54°0’0”W, 24 August 1987, *Granville J-J. de 9666* (CAY, US). **GUYANA**. **Cuyuni-Mazaruni**, Iwokrama Rainforest Reserve, between Pakutau Falls and Ireng Creek on Siparuni R., 75 m elev., 4°45’0’’N 59°01’0’’W, 09 November 1995, *Clarke H.D. 442* (US). **Potaro-Siparuni**, Kaieteur National Park, plot Study #1, NE from end of airstrip at headwaters of Korume Creek, 300–350 m elev., 5°10’0”N 59°28’59.9”W, 11–19 March 1997, *Kelloff C.L. & McKee G.S. 1246* (US) **Upper Demerara-Berbice**, Fairview Landing E bank of Essequibo River, near end of Mabura road, 91 m elev., 4°40’0”N 58°40’0”W, 19 July 1990, *McDowell T. 3271* (INPA, US). **Upper Takatu-Upper Essequibo**, Acarai Mts., 4 km S of Sipu River, area near camp at base of Acarai Mts., 245 m elev., 1°23’0”N 58°56’0”W, 08 September 1998, *Clarke H.D. et al. 7639* (U, US); Essequibo region, Kuyuwuni river watershed, Airshalton Landing, upstream 2–3 km N & S banks, 250 m elev., 2°03’00”N 59°10’0”W, 22 November 1993, *Henkel T.W. et al. 3100* (U, US); Essequibo River, 222 m elev., 2°15’21.1”N 58°19’26.5”W, 27 April 2004, *Redden K.M. et al. 3130* (US);. **SURINAM**. **Brokopondo**, van Blommesteijn Lake, Island south, 48 m elev., 4°33.8’0”N 55°7.2’0”W, 11 April 2011, *Bhikhi C.R. et al. 873* (U). **Kabalebo**, Central SURINAM Nature Reserve, unnamed tributary of Coppename River 200 m South of Driefoetoe Sula, 50–75 m elev., 4°45’0”N 59°1’0”W, 10 March 2004, *Clarke H.D. & Rhodes J. 11375* (US). **Marowijne**, Albina, ad ripas fluv. Marowijne. S of Albina, 19 September 1948, *Lanjouw J. & Lindeman J.C. 324* (IAN, U). **Para**, unknown locality, undated, *Voltz F. s.n. U1302936* (U). **Sipaliwini**, Coeroeni, N side of Kuruni Island, E of trail from airstrip to N branch of Kuruni River around island, ca. 30 airline km E of confluence on Corantijn River, 180 m elev., 3°22’12”N 57°20’36”W, 10 November 1994, *Evans R. et al. 1929* (CAY, IAN, INPA, P, RB, U, US). Goddo, unknown locality, 19 August 1908, *Tresling J.H.A.T. 334* (RB, U). Raleigh vallen- Voltzberg Nature Reserve on the Coppename River, 145 kms SW of Paramaribo, vicinity of Lolopasi Hut, left bank of the Coppename River, 21 November 1976, *Mori S.A. & Bolten A. 8673* (U).

17b. ***Eperua rubiginosa*** Miq. var. ***grandiflora*** Pulle (1906: 211)

Type:—SURINAM. Fluv. Gonini, August 1903, *Versteeg G.M. 48* (holotype U[0003236] image!).

Stipules 1.3–7.7 × 3.0–5.0 mm, joined at the base. **Leaves** (3–)4–5-jugate; **rachis** 7.3–25.0 cm long; **secondary venation** with two intramarginal veins, sometimes one, the vein closer to the margin continuous or not. **Inflorescences** 40.0–150.0 cm long; **pedicel** 2.0–3.3 mm in diameter. **Flowers**: **hypanthium** 4.9–7.0 mm in diameter; **sepal** 1.7–2.3 × 0.6–1.0 cm.

Phenology:—Flowering in March, May, June, August, and October; fruiting in January, February, March, and October.

Distribution:—Previously known in Surinam (Marowijn and Sipaliwini), here we recognize two collections occurring in French Guiana (*Redden K.M. et al. 6005, Schnell R.A.A. 11456*).

Habitat:—Floodplains (riparian vegetation and riverbanks) forests on loamy sandy soil, below 100 m elev.

Occurrence in protected areas:—Unknown.

Etymology:—The specific epithet relates to its flower that is larger than the type variety.

Vernacular names:—panga (*Andel T.R. van et al. 4979*).

Uses:—Surinam: used with Pikin fóo kaka in herbal baths for protection from cutlass slashes (*Andel T.R. van et al. 4979*).

Taxonomic notes:—The most noticeable difference between the two varieties is in the pedicels’ diameter. *Eperua rubiginosa* var. *grandiflora* has a thicker pedicel (>2 mm in diameter), and the type variety has a thinner pedicel (>2 mm in diameter, mainly bellow 1.5 mm). The flower of *E. rubiginosa* var. *grandiflora* looks more robust and it has generally larger sepals. Vegetatively, although there is no precise difference, var. *grandiflora* has bigger joined stipules (vs. free in var. *rubiginosa*), generally 4 or 5, rare 3, leaflets pairs (vs. generally 3, sometimes 4, in var. *rubiginosa*), larger rachis (vs. shorter in var. *rubiginosa*), and in most of the cases, secondary venation with two intramarginal veins (vs. one in var. *rubiginosa*).

Selected specimens:—FRENCH GUIANA. **Saint-Laurent-du-Maroni**, Maroni River near St. Larent., 59 m elev., 5°28’45”N 54°3’43”W, 05 May 2007, *Redden K.M. et al. 6005* (CAY, US). **GUYANA**. **Cuyuni-Mazaruni**, Mazaruni River, unnamed falls (possible Carin Crow Falls), 0.25 miles NW of base camp, 59 m elev., 5°57’23.2”N 59°18’43”W, 09 October 2004, *Redden K.M. et al. 3261* (INPA, COL, US); Mazaruni River, small islands around falls, 49 m elev., 5°55’57.9”N 59°6’35.3”W, 12 October 2004, *Redden K.M. et al. 3286* (US); Mazaruni River, 1.15 miles NE of base camp, 16 m elev., 6°06’50.1”N 58°53’53.9”W, 14 October 2004, *Redden K.M. et al. 3304*. **SURINAM**. **Marowijne,** Albina, Bigiston, Gonkíiki/Poitikondée, 0?°52’26”N 54°7’48”W 09 March 2006, *Andel T.R. van et al. 4979* (U). **Sipaliwini**, Jacob Kondre, Saramacca river, 16 June 1944, *Maguire B. 23804* (F, U, US). Gonini, 25 February 1918, *Gonggrijp J.W. 3700* (U); fluv. Gonini, 11 August 1903, *Versteeg G.M. 48* (CAY, U).

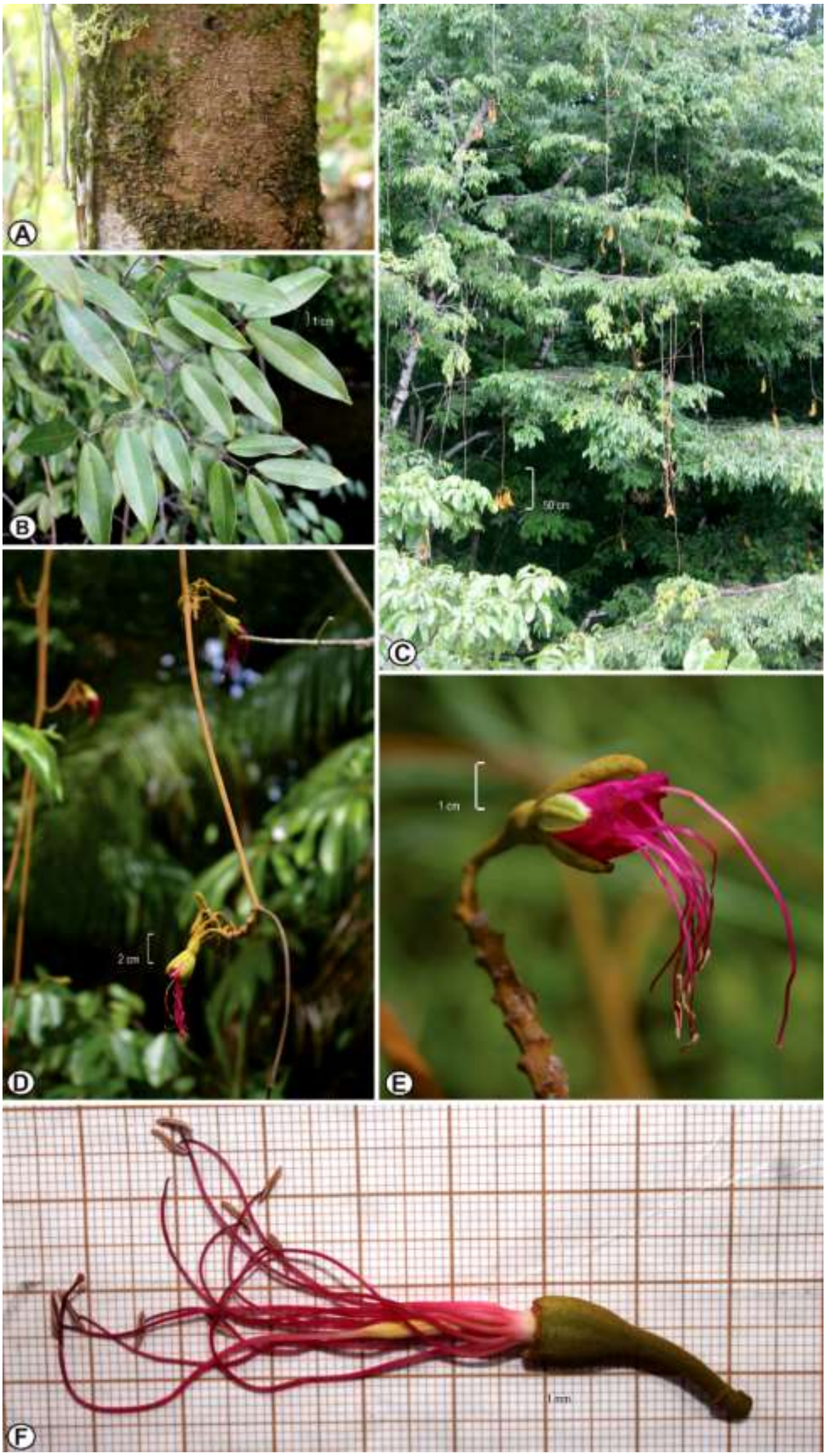


FIGURE 51. *Eperua rubiginosa* var. *rubiginosa*: A. bark; B. leaves; C. fruiting tree; D. terminal portion of a long and pendulous inflorescence with erect lateral racemes; E. flower, lateral view; F. hypanthium, stamens, and carpel. Specimen, A, B, D–F: *Fortes E.A. & Silva G.S. da 167*. Photos, E.A. Fortes.

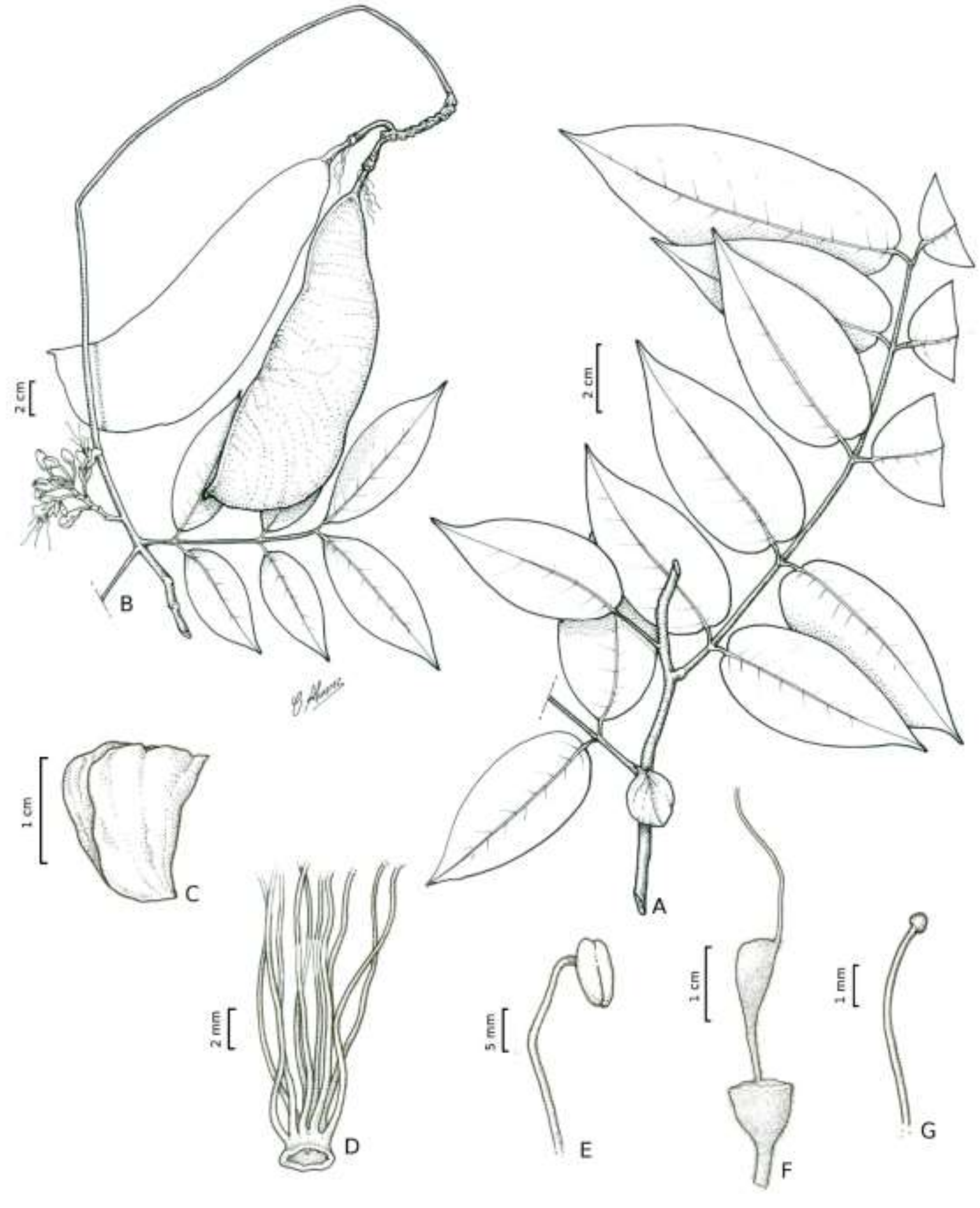


FIGURE 52. *Eperua rubiginosa*: A. leaf, var. *grandiflora*; B. flowering and fruiting branchlet, var. *rubiginosa*; C. adaxial petal, var. *rubiginosa*; D. base of the stamens joined in a tube, var. *rubiginosa*; E. anther and part of the filament, var. *rubiginosa*; F. hypanthium and carpel, var. *rubiginosa*; G. stigma and part of the style, var. *rubiginosa*. Specimens, A: *Hostmann F.W.R. 229*-A; B: *Fróes R. de L. 26638*; C–G: *Pires J.M. et al. 51182*. Illustrated by Carlos Alvarez.

18. ***Eperua schomburgkiana*** Bentham (1870: 226) (Figures 8, 53)

Type (designated by Cowan 1975/Fortes & Mansano 2022)**:**—GUYANA. Essequibo & Rupununy, 1838, *Schomburgk Rob. Ser. 1 517* (lectotype K[000555112] image!, isolectotypes BM[000065064] image!, G[00365223] image!, G[00365208] image!, K[000555113] image!, K[000555114] image!, P[00252893] image!, W not seen).

Tree (3.0–)4.0–35.0 m tall. **Trunk** and bark not seen. **Stipules** (6.2–)10.3–30.0(–44.0) mm, free, foliaceous, persistent to caducous. **Leaves** (3–)4–7-jugate; **petioles** 1.0–3.6 cm long; **rachis** (7.3–)10.0–23.5(–30.0) cm long; **petiolules** 5.2–11.9 mm long; **blades** 5.9–18.5 × (1.7–)2.7–7.2 cm, coriaceous, glabrous, pellucid-punctate, sometimes inconspicuous pellucid-punctate, discolorous to not discolorous, equilateral, lower pair elliptic, narrowly elliptic to ovate, rarely lanceolate, middle pair elliptic, narrowly elliptic to ovate, rarely lanceolate, upper pair elliptic to narrowly elliptic, apex attenuate, acuminate to caudate, base symmetrical to asymmetrical, lower pair base obtuse to rounded, sometimes subcordate, middle pair base obtuse to rounded, upper pair base obtuse to cuneate, margin flat, **secondary venation** with one intramarginal vein, sometimes two intramarginal veins, vein closer to the margin not continuous, main vein straight, prominent only near the base to entirely prominent on the adaxial surface, tertiary veins conspicuous, areoles smaller, concave. **Inflorescences** terminal, rarely axillary, panicle, rarely raceme, erect, tomentose, coppery, 4.0–11.5 cm long, lateral racemes 1.9–7.2 cm long, alternate and distichous; **bracts** 4.1–5.9 × 3.4–5.6 mm, ovate, broadly ovate to orbicular, apex gland absent?, tomentose externally, coppery, caducous; **bracteoles** 4.5–6.3 × 3.0–5.0 mm, ovate, cucullate, apex gland absent, tomentose externally, coppery, caducous, attached to the middle portion of the pedicels; **pedicel** 10.8–26.2 mm long, 1.4–2.7 mm in diameter, not twisted, tomentose, copery; **buds** 1.0–2.2 cm long, 0.5–1.0 cm in diameter, tomentose, coppery. **Flowers**: **hypanthium** 3.8–6.4 mm long, 4.7–7.3 mm in diameter, cup-shaped, equilateral, tomentose, coppery; **sepal** 1.6–2.6 × 0.4–1.7 cm, elliptic to oblong, unequal, the dorsal one larger, apex gland absent, tomentose externally, coppery, inner sepals scarious marginally; **adaxial petal** 2.0–3.2 × 2.9–5.0 cm, oblate, non-tubular, apex rounded, base truncate, white, glabrous; **petalodia** 1.1–1.8 × 1.1–1.6 mm; **stamens** exserted, joined basally in a diadelphous sheath, dorsal one free, longer filaments 3.0–4.5 cm long, shorter filaments 2.9–3.5 cm long, sheath equilateral, 7.0–12.0 mm long, sheath irregularly tomentose on both sides to glabrous externally and entirely tomentose in the inner surface, free filaments glabrous, coppery, anthers 4.0–6.1 × 1.0–2.2 mm, rectangular; **ovary** 6.0–15.0 × 2.4–5.0 mm, oblanceolate, glabrous, stipe 6.3–13.7 mm long, glabrous, style 2.2–3.7 cm long, stigma capitate, papillose. **Legumes** 12.0–23.0 × 4.0–7.5 cm, stipe 1.3–2.0 cm long, oblanceolate-falcate, apex obtuse, apiculate, margin entire, brown to reddish brown, veins absent, glabrous, foveate. **Seeds** 1–3 per fruit, 3.5–5.0 × 1.8–3.6 cm, elliptic, oblong to irregularly oblong, brown to reddish-brown.

Phenology:—Flowering in March and from June to December, with a peak in September; fruiting throughout the year, except in June and August.

Distribution:—Throughout Guyana (Cuyuni-Mazaruni, East Berbice-Corentyne, Essequibo Islands-West Demerara, Macouria, Potaro-Siparuni, Upper Demerara-Berbice, Upper Takatu-Upper Essequibo) and in Surinam (Nickerie, Sipaliwini).

Habitat:—Mainly in floodplain forests (e.g. Mora forests and swamps), sometimes in *wallaba* forests, on alluvial soil, predominately white sand, but also brown sand mixed, loamy and laterite soils, from sea level to 130 m elev.

Conservation status:—Categorized as Least Concern (LC) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The estimated extent of occurrence for the species is 61,910.701 km$_2$ and the estimated area of occupancy is 156.000 km$_2$.

Occurrence in protected areas:—Iwokrama Rainforest Reserve (Guyana, Potaro-Siparuni) and Conservation International concession on the Essequibo River (Guyana, Upper Takatu-Upper Essequibo).

Etymology:—The specific epithet is a tribute to Schomburgk, who first collected the species in Guyana (Bentham 1870).

Vernacular names:—bimiti wallaba (*Mori S.A. et al. 8162*), clump wallaba (*Redden K.M. et al. 6011*), cutlass (*Redden K.M. et al. 3258*, *3272*), ituri wallaba (*Mori S.A. et al. 8162*), machetta (*Mori S.A. et al. 8162*), maseta (*Redden K.M. et al. 3258*), museta (*Redden K.M. et al. 3272*), wallaba (*Anderson C.W. 182*), water wallaba (*Mori S.A. et al. 8162*, *Pennington R.T. 373*, *Persuad A.C. 14*, *166*, *183*, *Schulz J.P. 7708*).

Uses:—unknown.

Taxonomic notes:—*Eperua schomburgkiana***,** *E. cerradoensis*, *E. duckeana*, *E. froesii*, and *E. reddeniae* are the only short and erect inflorescence species that have non-tubular corolla, exserted stamens, falcate fruit with a 3:1 proportion (vs. tubular corolla, included stamens, non-falcate fruit with a 1:1 to 2:1 length/width proportion in other short and erect inflorescence species). They also share multijugate leaves with straight leaflets and inflorescence with dense indumentum. Similarities and differences between species of this group are summarized in Table 3. *Eperua schomburgkiana* is a well-differentiated species by the stamens joined basally in a sheath 9+1, irregularly tomentose sheath, glabrous ovary and fruits, besides other vegetative characteristics (see Table 3).

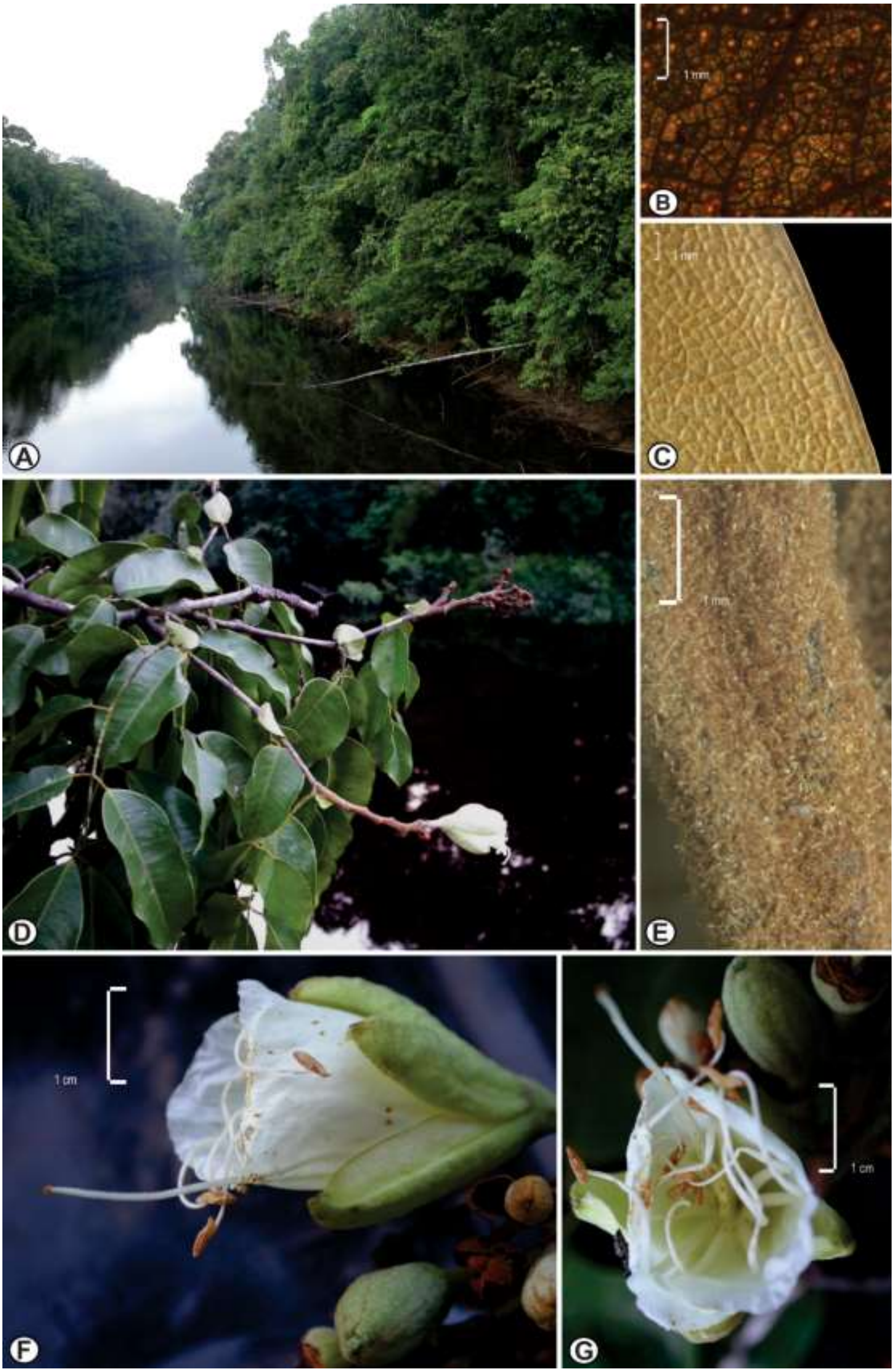


FIGURE 53. *Eperua schomburgkiana*: A. habitat; B. pellucid-punctate leaflet blade; C. intramarginal vein, abaxial surface; D. inflorescence; E. detail of the inflorescence indumentum; F. flower, lateral view; G. flower, front view. Specimens, B, C: *Anderson C.W. 182*; E: *Sandwith N.Y. 142*. Photos, A, D, F, G: H. ter Steege; B, C, E: E.A. Fortes.

Selected specimens:—GUYANA. **Cuyuni-Mazaruni**, Bartica, Moorie island in the Essequibo River near Bartica, 5–25 m elev.,18 August 1976, *Mori S.A. et al. 8162* (U, US); Essequibo River, Moraballi Creek, near Bartica, 28 August 1929, *Sandwith N.Y. 142* (RB, P, U, US). W bank of Essequibo River 0–2 km south of Wolga settlement, 0–15 m elev., 6°27’0”N 58°37’59”W, 24 December 1992, *Henkel T.W. & Chin M. 669* (U, US); Marshall Falls, Mazaruni River, 37 m elev., 6°17’5.6”N 58°43’15.5”W, 06 March 2004, *Redden K.M. et al. 2115* (US). **East Berbice - Corentyne**, Canje River, Cow Savanna E of Digitima Creek, 1–25 m elev., 5°36’0”N 57°35’0”W, 12 April 1987, *Pipoly J.J. et al. 11448* (CAY, MO, U, US). **Essequibo Islands-West Demerara**, Esequibo, along bank of river, 7.5 km. from Lanaballi, 1–10 m elev., 6°60’0”N 57°75’0”W, 10 September 1992, *Tiwari S. 851* (NY). **Potaro-Siparuni**, Iwokrama Forest Reserve, Burro-Burro River, 3.42 miles from Whitewater base camp, 65 m elev., 4°40’58”N 58°50’47.3”W, 02 November 2002, *Redden K.M. et al. 1142* (US); Micobe Road and adjacent forest next to Potaro River, 22 m elev., 5°20’29”N 58°58’51”W, 14 September 2006, *Redden K.M. et al. 4231* (NY, US). **Upper Demerara-Berbice**, Lower 3 km of Macouria River, N and S banks, 15 m elev., 6°25’0”N 58°34’0”W, 07 December 1992, *Henkel T.W. & Chin M. 388* (U, US); Essequibo River, E bank, upstream 2–4 km from Bartica, island shore and mainland, 0–5 m elev., 6°25’0”N 58°35’0”W, 31 March 1993, *Henkel T.W. et al. 1798* (US); CI concession, Himara Creek, 130 m elev., 3°22’0”N 58°11’0”W, 14 September 2008, *Redden K.M. et al. 6011* (US). **Upper Takatu-Upper Essequibo**, Conservation International concession on the Essequibo River, 108 m elev., 3°35’18”N 58°17’58”W, 21 January 2007, *Redden K.M. et al. 5138* (F, NY, U, US). Essequibo & Rupununy, 1838, *Schomburgk Rob. Ser. I 517* (BM, G, K, P, W). **SURINAM**. **Nickerie**, Corantijn, ten N. mondingen New River, 01 September 1935, *Rombouts H.E. 170* (U). **Sipaliwini**, Wonatobo falls, Corantijn River, 26 June 1956, *Schulz J.P. 7708* (U, US).

19. ***Eperua venosa*** R.S. Cowan. (1958: 147) (Figures 11, 54, 55)
Type**:—**VENEZUELA. Bolívar: Angell Falls, undated, *Kunhardt H.R. Jr. 20* (holotype NY[00004386]!).

Tree 10.0–30.0 m tall. **Trunk** 60.0 cm in diameter, bark not seen. **Stipules** 3.0–4.3 × 2.0–3.7 mm, joined, nonfoliaceous, caducous, caducous. **Leaves** 1–2(–3)-jugate; **petioles** 1.3–3.4 cm long; **rachis** 2.4–5.1 cm long; **petiolules** 6.5–9.4 mm long; **blades** 6.6–21.0 × 3.3–9.3 cm, coriaceous, glabrous, pellucid-punctate, each areole has at least one conspicuous dot, not discolorous, equilateral to inequilateral, lower pair elliptic, slightly falcate, apex acuminate, base symmetrical to asymmetrical, lower pair base obtuse, upper pair base obtuse to cuneate, margin flat, **secondary venation** with one intramarginal vein very close to the margin, main vein curved to straight, prominent to depressed on the adaxial surface, tertiary veins very conspicuous, areoles larger, plane. **Inflorescences** terminal or axillary, panicle, main axis pendulous, lateral racemes erect, main axis puberulent to strigulose, lateral racemes strigose, pubescent to tomentulose, grayish-white, 145.0–162.0 cm long, lateral racemes 2.0–5.2 cm long, alternate and spirally arranged; **bracts** not seen; **bracteoles** 4.1–5.8 × 3.8–5.1 mm, ovate to oblate, cucullate, apex gland absent, strigose externally, grayish-white, caducous, attached to the middle to high portion; **pedicel** 7.0–15.0 mm long, 2.5–7.6 mm in diameter, not twisted?, pubescent, strigose to tomentose, grayish-white; **buds** 2.0 cm long, 1.0 cm in diameter, pubescent to tomentose, grayish-white. **Flowers**: **hypanthium** 6.8–11.3 mm long, 4.2–6.5 mm in diameter, tubular to cup-shaped, equilateral, pubescent, strigose to tomentose, grayish-white; **sepal** 1.6–2.2 × 0.6–2.2 cm, elliptic to oblong, unequal, the outer ones larger, cucullate, apex gland absent, green with purple spots, pubescent, strigose to tomentose, scarious marginally, grayish-white; **adaxial petal** 2.5–3.4 × 4.7–6.0 cm, oblate, non-tubular, apex rounded, base attenuate, gibbous, deep-rose, sericeous at the base, glabrous in other parts, pellucid-punctate; **petalodia** 0.4–0.8 × 0.5–0.8 mm; **stamens** exserted, joined basally in a diadelphous sheath, dorsal one free sheath equilateral, 6.7–10.0 mm long, sheath sericeous to tomentose, free filaments glabrous, reddish-white, anthers 4.0–9.0 × 1.5–1.9 mm, rectangular; **ovary** 7.3–10.0 × 3.2–4.9 mm, oblanceolate, densely sericeous, reddish-white, stipe 3.5–7.0 mm long, tomentose to sericeous, style length not seen, stigma capitate to bilobate. **Legumes** oblanceolate-falcate, puberulous (young fruit). **Seeds** not seen.

Phenology:—Flowering in August and September; fruiting in February.

Distribution:—Endemic to Venezuela (Bolívar), known only in the region of Gran Sabana.

Habitat:—Forests, being frequent in forest borders (*Maguire B. et al. 53597*), it is also found bordering savanna (*Steyermark J.A. 115541*), from 87 to 1160 m elev.

Conservation status:—Categorized as Vulnerable (VU) according to the IUCN criteria (IUCN 2012, IUCN Standards and Petitions Committee 2022). The extent of estimated occurrence for the species is 6,325.304 km$_2$ and the estimated area of occupancy is 16.000 km$_2$.

Occurrence in protected areas:—Parque Nacional Canaima (Venezuela, Bolívar).

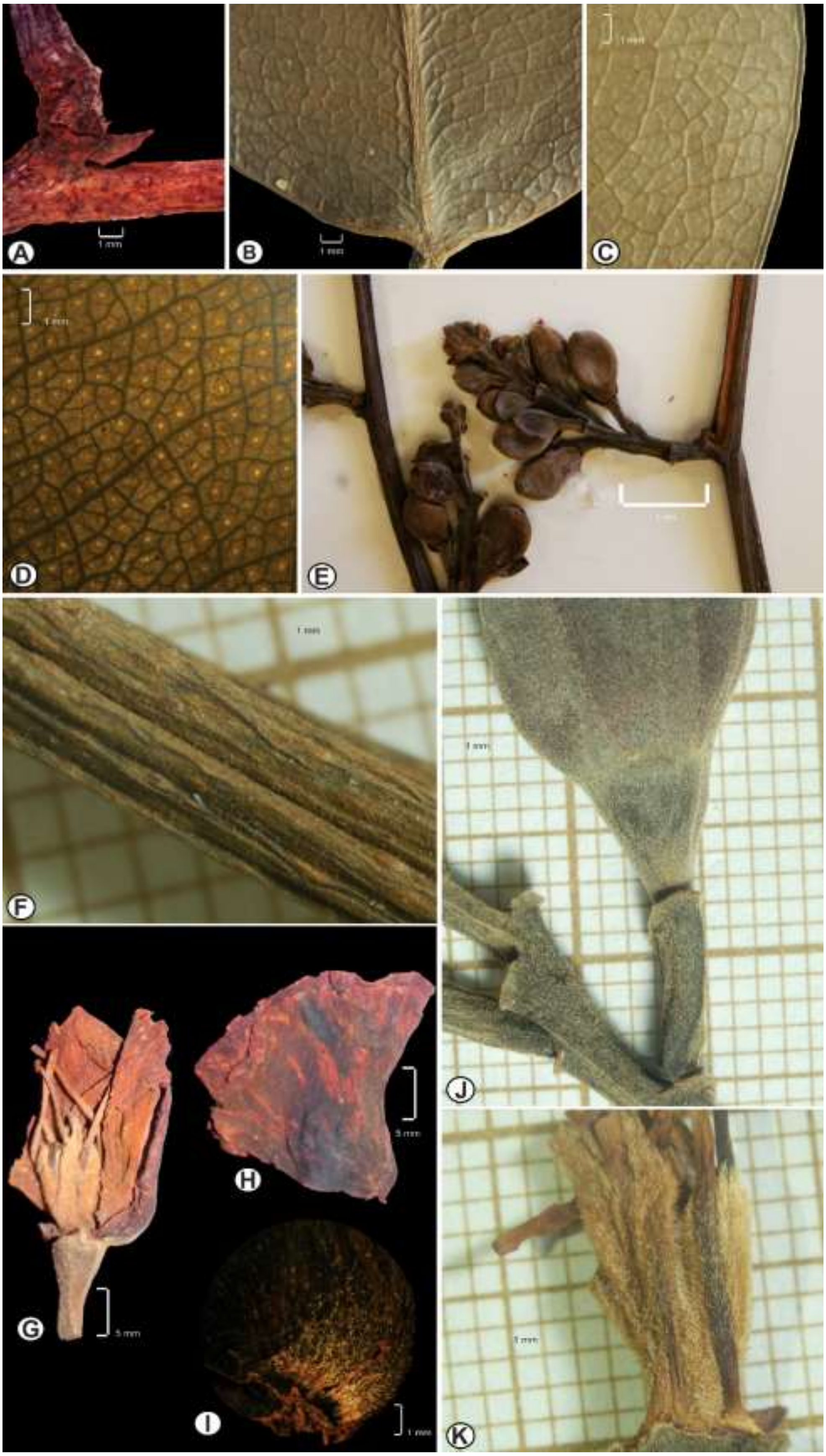


FIGURE 54. *Eperua venosa*: A. joined stipules; B. leaflet base showing the tertiary veins prominent on the adaxial surface; C. intramarginal vein, abaxial side; D. pellucid-punctate leaflet blade; E. lateral raceme; F. detail of the indumentum of the inflorescence main axis; G. flower showing the sheath, adaxial petal and sepal (some sepals were removed); H. adaxial petal (bent); I. detail of the indumentum at the base of the petal; K. sheath and ovary. Specimens, A–F, J, K: *Maguire B. et al. 53597*; G–I: *Kunhardt H.R. Jr. 20* (holotype). Photos, E.A. Fortes.

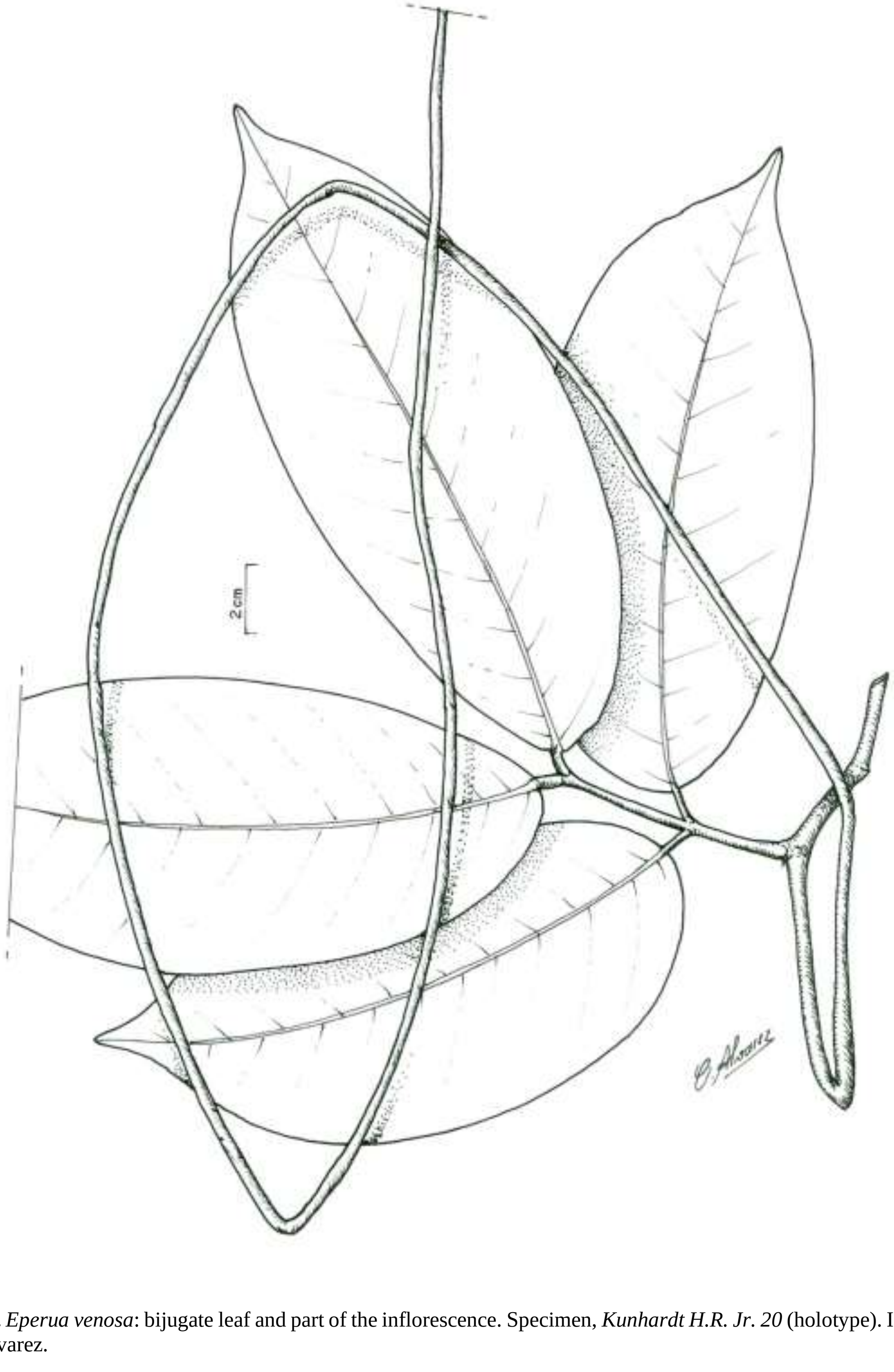


FIGURE 55. *Eperua venosa*: bijugate leaf and part of the inflorescence. Specimen, *Kunhardt H.R. Jr. 20* (holotype). Illustrated by Carlos Alvarez.

Etymology:—The specific epithet relates to its very conspicuous tertiary veins on the adaxial blade surface.

Vernacular names:—Unknown.

Uses:—Unknown.

Taxonomic notes:—*Eperua venosa* is the only species in the genus with basally sericeous petals. It is morphologically similar to *E. leucantha* and *E. falcata,* with which it shares joined stipules, secondary venation with one intramarginal vein very close to the margin, long and pendulous inflorescences, non-tubular corolla, exserted stamens joined in a diadelphous sheath, and sericeous ovary (Table 4). Besides that, *E. venosa* shares non-white petals with *E. falcata*, patent to erect lateral racemes and sericeous sheath with *Eperua leucantha.* However apart from the petal indumentum, *Eperua venosa* differs from *E. falcata* and *E. leucantha* by other characteristics that are listed in their taxonomic notes.

Selected specimens:—VENEZUELA. **Bolívar**, Gran Sabana, Angel Falls, undated, *Kunhardt H.R. 20* (NY), 7 kms al norte de la Misión de Santa Teresita de Kavanayén, 1160 m elev., 20 February 1978, *Steyermark J.A. 115541* (F). Rio Uiri-yuk, El Foco, alto Río Cuyuni, 30 August 1962, *Maguire B. et al. 53514* (NY, US). Triana Savanna, cerro Pitón, cordillera Epicara, rio Chicanán, 05 September 1962, *Maguire B. et al. 53597* (RB, U, US).

Acknowledgements

This paper is part of the first author's Ph.D. thesis supported by a scholarship from Conselho Nacional de Desenvolvimento Científico e Tecnológico—(CNPq) [process number 140508/2020-1], by a sandwich scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—(CAPES) [CAPES-PRINT process number 88887.695281/2022-00], and by Funbio—Conservando o Futuro 2020/HUMANIZE grant. VFM is grateful to CNPq [process number 303053/2018-6] and the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) [process number E-26-/203.007/2017]. We are very grateful to the staff from F, K, MO, NY, US herbaria for loans of herbarium specimens; to the staff from BH for asking and receiving loans from F, K, MO, NY, and US; to the staff from IAN, INPA, MFS, MG, R, and RB herbaria for the great assistance during visits; and to the staff from COAH and UB for the images of herbarium specimens. We are also very grateful to the people that shared field photos of *Eperua*; and to Carlos Alvarez and Marcus Falcão for the illustrations.

References

Adeney, J.M., Christensen, N.L., Vicentini, A. & Cohn-Haft, M. (2016) White-sand ecosystems in Amazonia. *Biotropica* 48: 7–23.

https://doi.org/10.1111/btp.12293

Aublet, J.B.C.F. (1775) *Histoire des plantes de la Guiane Françoise*. Tome I and Tome II. Pierre Françoies Didot jeune, Paris, 976 pp.

Aymard, G., Schargel, R., Berry, P.E. & Stergios, B. (2009) Estudio de los suelos y la vegetación (estructura, composición florística y diversidad) en bosques macrotérmicos no inundables, estado Amazonas Venezuela (aprox. 01° 30' - 05° 55' N; 66° 00' - 67° 0' O). *Biollania* (Ed. Esp.) 9: 6–251.

Bachman, S., Moat, J., Hill, A.W., Torre, J. & Scott, B. (2011) Supporting Red List threat assessment with GeoCAT: geospacial conservation assessment tool. *Zookeys* 150: 117–126.

https://doi.org/10.3897/zookeys.150.2109

Baillon, H.E. (1870) Caesalpinées. *In*: Baillon, H.E. (Ed.) *Histoire des plantes*. Tome II. Librairie Hachette & Cie, Paris. pp. 110–111.

Barroso, G.M., Peixoto, A.L., Costa, C.G., Ichaso, C.L.F., Guimarães, E.F. & Lima, H.C. (1991) *Sistemática das angiospermas do Brasil*. Vol 2. Imprensa Universitária, Universidade Federal de Viçosa, Viçosa, pp. 15–100.

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

https://doi.org/10.1073/pnas.1011841108

Beentje, H. (2010) *The Kew plant glossary an illustrated dictionary of plant terms*. Royal Botanic Gardens, Kew, Richmond, 160 pp.

Benoist, R. (1916) Descriptions d'espécies nouvelles de légumineuses de la Guyane Française *Notulae Systematicae. Herbier du Museum de Paris* 3: 271–274.

Bentham, G. (1870) Caesalpinieae. *In:* von Martius, C.F.P. & Eichler, A.G. (Eds.) *Flora Brasiliensis* 15(2). F. Fleischer, Leipzig, pp. 226–228.

BFG [The Brazil Flora Group] (2015) Growing knowledge: an overview of seed plant diversity in Brazil. *Rodriguésia* 66: 1085–1113.

https://doi.org/10.1590/2175-7860201566411

Bruneau, A., Forest, F., Herendeen, P.S., Klitgaard, B.B. & Lewis, G.P. (2001) Phylogenetic relationships in the Caesalpinioideae (Leguminosae) as inferred from chloroplast trnL intron sequences. *Systematic Botany* 26: 487–514.

https://doi.org/10.1043/0363-6445-26.3.487

Bruneau, A., Mercure, M., Lewis, G.P. & Herendeen, P.S (2008) Phylogenetic patterns and diversification in the Caesalpinioid legumes. *Botany* 86: 697–718.

https://doi.org/10.1139/B08-058

Bruneau, A., Klitgaard, B.B., Prenner, G., Fougère-Danezan, M. & Tucker, S.C. (2014) Floral evolution in the Detarieae (Leguminosae): phylogenetic evidence for labile floral development in an early-diverging legume lineage. *International Journal of Plant Sciences* 175: 392–417.

https://doi.org/10.1086/675574

Cardoso, D., Särkinen T., Alexander, S., Amorim, A.M., Bittrich, V., Celis, M., Daly, D.C., Fiaschi, P., Funk, V.A., Giacomin, L.L., Goldenberg, R., Heiden, G., Iganci, J., Kelloff, C.L., Knapp, S., de Lima, H.C., Machado, A.F.P., dos Santos, R.M., Mello-Silva, R., Michelangeli, F.A., Mitchell, J., Moonlight, P., de Moraes, P.L.R., Mori, S.A., Nunes, T.S., Pennington, T.D., Pirani, J.R., Prance, G.T., de Queiroz, L.P., Rapini, A., Riina, R., Rincon, C.A.V., Roque, N., Shimizu, G., Sobral, M., Stehmann, J.R., Stevens, W.D., Taylor, C.M., Trovó, M., van den Berg, C., van der Werff, H., Viana, P.L., Zartman, C.E. & Forzza, R.C. (2017) Amazon plant diversity revealed by a taxonomically verified species list. *PNAS* 114: 10695–10700.

https://doi.org/10.1073/pnas.1706756114

Cardoso, J.C.F., Viana, M.L., Matias, R., Furtado, M.T., Caetano, A.P. de S., Consolaro, H. & Brito, V.L.G. de (2018) Towards a unified terminology for angiosperm reproductive systems. *Acta Botanica Brasilica* 32: 329–348.

https://doi.org/10.1590/0102-33062018abb0124

Chipaia, F. da C., Reis, A.R.S., Reis, L.P., Carvalho, J.C. de & Silva, E.F.R. da (2012) Descrição anatômica macroscópica de madeira de oito espécies florestais comercializadas no município de Altamira-PA, Brasil. *Journal of Bioenergy and Food Science* 2: 18–24.

https://doi.org/10.13140/RG.2.1.1862.6086

Collins English dictionary (2023) Available from: http://www.collinsdictionary.com/english/creative (accessed 23 May 2023)

Coomes, D.A. & Gribb, P.J. (1996) Amazonian Caatinga and related communities at La Esmeralda, Venezuela: Forest Structure, physiognomy and floristics, and control by soil factors. *Vegetatio* 122: 167–191.

https://doi.org/10.1007/BF00044699

Cowan, R.S. (1957) Tropical American Leguminosae-III. *Brittonia* 8: 251–253.

https://doi.org/10.2307/2804977

Cowan, R.S. (1958) Leguminosae-Caesalpinioideae. The Botany of the Guayana Highland. *Memoirs of the New York Botanical Garden* 10: 147–149.

Cowan, R.S. (1975) Monograph of the genus *Eperua* (Leguminosae: Caesalpinioideae). *Smithsonian Contributions to Botany* 28: 1–45.

https://doi.org/10.5479/si.0081024x.28

Cowan, R.S. & Polhill, R. (1981) Tribe 4. Detarieae DC. *In*: Polhill, R. & Raven, P.H. (Eds.) *Advances in Legume Systematics*. Kew, Royal Botanic Gardens, pp. 117–134.

Cowan, R.S. (1985) Studies in Tropical American Leguminosae – IX. *Brittonia* 37 (3): 292–294.

https://doi.org/10.2307/2806078

Crane, P.R. (2004) Documenting plant diversity: Unfinished business. *Philosophical Transactions of the Royal Society B: Biological Sciences* 359: 735–737.

https://doi.org/10.1098/rstb.2003.1441

DeFilipps, R.A., Maina, S.L. & Crepin, J. (2004) *Medicinal Plants of the Guianas*. National Museum of Natural History, Smithsonian Institution, Washington, DC, 477 pp.

Ducke, W.A. (1932) Espéces nouvelles de plantes de l'Amazonie brésilienne. *Bulletin du Muséum National d'Histoire Naturelle* 4 (6): 728–729.

Ducke, W.A. (1940) Notes on the wallaba trees. *Tropical Woods* 62: 21–28.

Estrella M., De La, Forest, F., Wieringa, J.J., Fougère-Danezan, M. & Bruneau, A. (2017) Insights on the Evolutionary Origin of Detarioideae, a Clade of Ecologically Dominant Tropical African Trees. *New Phytologist* 214: 1722–1735.

https://doi.org/10.1111/nph.14523

Estrella, M. de La, Forest, F., Klitgaard, B., Lewis, G.P., Mackinder, B.A., Queiroz, L.P. de, Wieringa, J.J. & Bruneau, A. (2018) A new phylogeny-based tribal classification of subfamily Detarioideae, an early branching clade of florally diverse tropical arborescent legumes. *Scientific Reports* 8: 6884.

https://doi.org/10.1038/s41598-018-24687-3

Fabaceae in Flora e Funga do Brasil (2022) Jardim Botânico do Rio de Janeiro. Disponível em, Available from: https://floradobrasil.jbrj. gov.br/FB115 (accessed 6 July 2022)

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J.W., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K., Alexiades, M., Almeida, S., Amaral, I., Andrade, A., Aragão, L.E.O.C., Araujo Murakami, A., Arets, E.J.M.M., Arroyo, L., Aymard C., G.A., Baker, T.R., Bánki, O.S., Berry, N.J., Cardozo, N., Chave, J., Comiskey, J.A., Alvarez, E., de Oliveira, A., Di Fiore, A., Djagbletey, G., Domingues, T.F., Erwin, T.L., Fearnside, P.M., França, M.B., Freitas, M.A., Higuchi, N., Honorio C., E., Iida, Y., Jiménez, E., Kassim, A.R., Killeen, T.J., Laurance, W.F., Lovett, J.C., Malhi, Y., Marimon, B.S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Mendoza, C., Metcalfe, D.J., Mitchard, E.T.A., Neill, D.A., Nelson, B.W., Nilus, R., Nogueira, E.M., Parada, A., Peh, K.S.-H., Pena Cruz, A., Peñuela, M.C., Pitman, N.C.A., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Reitsma, J.M., Rudas, A., Saiz, G., Salomão, R.P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Sonké, B., Stropp, J., Taedoumg, H.E., Tan, S., ter Steege, H., Terborgh, J., Torello-Raventos, M., van der Heijden, G.M.F., Vásquez, R., Vilanova, E., Vos, V.A., White, L., Willcock, S., Woell, H. & Phillips, O.L. (2012) Tree height integrated into pantropical forest biomass estimates. *Biogeosciences* 9: 3381–3403.

https://doi.org/10.5194/bg-9-3381-2012

Fleming, T.H., Geiselman, C. & Kress, W.J. (2009) The Evolution of bat Pollination: A Phylogenetic Perspective. *Annals of Botany* 104 (6): 1017–1043.

https://doi.org/10.1093/aob/mcp197

Fontana, C., Pérez-de-Lis, G., Santini-Junior, L., Botosso, P.C., Nabais, C., Tomazello-Filho, M. & Lousada, J.L.P.C. (2018) Wood anatomy and growth ring boundaries of *Copaifera lucens* (Fabaceae). *IAWA Journal* 39: 395–405.

https://doi.org/10.1163/22941932-20170209

Fortes, E.A. & Mansano, V.F. (2022) Untangling nomenclatural issues of some Amazonian trees of *Eperua* Aubl. (Leguminosae, Detarioideae, Detariae). *Phytotaxa* 542 (2): 189–198.

https://doi.org/10.11646/phytotaxa.542.2.6

Fortes, E.A., Silva, G. da S. & Mansano, V. (2023) Two new species of *Eperua* (Leguminosae, Detarioideae, Detarieae) from the Amazon and Cerrado Biomes discovered in a botanical garden and a backyard. *Phytotaxa* 591 (3): 196–208.

https://doi.org/10.11646/phytotaxa.591.3.2

Forsyth Jr., W. (1794) *A Botanical nomenclator containing a systematical arrangement of the classes, orders, genera, and species of plants as described in the new edition of Linnæsus's Systema naturæ, by Dr. Gmelin*. Printed for T. Cadell, and P. Elmsly, in the Strand; and G. Nicol, Pall-Mall, London. p. 391.

https://doi.org/10.5962/bhl.title.127458

Fougère-Danezan, M., Maumont, S. & Bruneau, A. (2007) Relationships among resin-producing Detarieae *s.l.* (Leguminosae) as inferred by molecular data. *American Society of Plant Taxonomists* 32: 748–761.

https://doi.org/10.1600/036364407783390755

Fougère-Danezan, M., Herendeen, P.S., Maumont, S. & Bruneau, A. (2010) Morphological evolution in the variable resin-producing Detarieae (Fabaceae): Do morphological characters retain a phylogenetic signal? *Annals of Botany* 105: 311–325.

https://doi.org/10.1093/aob/mcp280

Funk, V. (2006) Floras: A model for biodiversity studies or a thing of the past? *Taxon* 55: 581–588.

https://doi.org/10.2307/25065635

Google Maps (2023) Available from: https://www.google.com.br/maps/ (accessed 23 May 2023)

Hopkins, M.J.G. (2007) Modelling the known and unknown plant biodiversity of the Amazon Basin. *Journal of Biogeography* 34: 1400–1411.

https://doi.org/10.1111/j.1365-2699.2007.01737.x

Instituto Brasileiro de Geografia e Estatística—IBGE (2019) 2019 Biomas e Sistema Costeiro-Marinho do Brasil - 1:250 000. Available from: https://www.ibge.gov.br/geociencias/informacoes-ambientais/estudos-ambientais/15842-biomas.html?edicao=25799&t=dow nloads/ (accessed 10 January 2022)

IUCN (2012) IUCN Red List Categories and Criteria: Version 3.1. Second edition. IUCN, Gland, Cambridge.

IUCN Standards and Petitions Committee (2022) Guidelines for Using the IUCN Red List Categories and Criteria. Version 15.1. Prepared by the Standards and Petitions Committee. [https://www.iucnredlist.org/documents/RedListGuidelines.pdf]

Junk, W.J., Piedade, M.T.F., Schöngart, J., Cohn-Haft M., Adeney, J.M. & Wittmann, F. (2011) A Classification of Major Naturally-Occurring Amazonian Lowland Wetlands. *Wetlands* 31: 623–640.

https://doi.org/10.1007/s13157-011-0190-7

Kleinhoonte, A. (1933) *Eperua stipulata* Kleinh. nov. spec. *Recueil des Travaux Botaniques Néerlandais* 30: 171.

Leandro, L.M. & Veiga-Junior, V.F. (2012) O gênero *Eperua* Aublet: uma revisão. *Scientia Amazonia* 1: 14–22.

Lewis, G.P., Schrire, B., MacKinder, B. & Lock, M. (2005) *Legumes of the World*. Kew, Royal Botanic Gardens, 577 pp.

LPWG (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* 66 (1): 44–77. https://doi.org/10.5061/dryad.61pd6

Mackinder, B.A. (2005) Tribo Detarieae. *In*: Lewis, G.P., Schrire, B., Mackinder, B. & Lock, M. (Eds.) *Legumes of the World*. Kew, Royal Botanic Gardens, pp. 69–109.

Miquel, F.A.G. (1851) Caesalpiniae. *In:* Miquel, F.A.G. (Ed.) *Stirpes Surinamensis Selectae*. Arnz & Comp, Leiden, pp. 12–13.

https://doi.org/10.5962/bhl.title.77484

Obiang-Mbomio, D. & Breteler, F.J. (2007) Révision du genre *Eurypetalum* Harms (Fabaceae, Caesalpinioideae). *Adansonia* 29: 67–76. [https://edepot.wur.nl/35728]

Oliver, D. (1891) *Hooker's Icones Plantarum* 20. Longman, Rees, Orme, Brown, Green, & Longman, London, 258 pp.

Pires, J.M. & Prance, G.T. (1985) The Vegetation types of the Brazilian Amazon. *In*: Prance, G.T. & Lovejoy, T.E. (Eds.) *Key environments: Amazonia*. Pergamon Press, Oxford, pp. 109–145.

Pulle, A.A. (1906) *An enumeration of the vascular plants known from Surinam*. E.J. Brill, Leiden, 555 pp.

https://doi.org/10.5962/bhl.title.57150

Rees, A. (1808) *The cyclopædia; or, Universal dictionary of arts, sciences, and literature*. Vol. 11. Longman, Hurst, Rees, Orme & Brown, Paternoser-Row, London, 768 pp.

https://doi.org/10.5962/bhl.title.59683

Romero-González, G.A. & Aymard, G.A.A. (2019) A new species of *Eperua* (Leguminosae, Detarioideae) from Amazonas state, Venezuela. *Harvard Papers in Botany* 24: 341–347.

https://doi.org/10.3100/hpib.v24iss2.2019.n17

Rudge, E. (1807) Description of a new Species of *Dimorpha*. *Transactions of the Linnean Society of London* 9: 179–181. https://doi.org/10.1111/j.1096-3642.1818.tb00337.x

Ruffinatto, F., Crivellaro, A. & Wiedenhoeft, A.C. (2015) Review of macroscopic features for hardwood and softwood identification and a proposal for a new character list. *IAWA Journal* 36 (2): 208–241.

https://doi.org/10.1163/22941932-00000096

Sandwith, N.Y. (1931) Contributions to the Flora of Tropical .4merica, VII: New and Noteworthy Leguminosae and Rosaceae from British Guiana. *Kew Bulletin* 1931: 364–366.

https://doi.org/10.2307/4102573

Schreber, J.C.D. (1791) *Genera Plantarum*. vol. 2. Frankfurt ad Moenum, Sumtu Varrentrappii et Wenneri, 872 pp.

Silva, W.L. da S., Costa-Neto, S.V. & Soares, M.V.B. (2015) Diversidade de Leguminosae em Savanas do Amapá. *Biota Amazônia* 5: 83–89.
https://doi.org/10.18561/2179-5746/biotaamazonia.v5n1p83-89

Sobral, M. & Stehmann, J.R. (2009) An analysis of new angiosperm species discoveries in Brazil (1990–2006). *Taxon* 58: 227–232. https://doi.org/10.1002/tax.581021

Stafleu, F.A. & Cowan, R.S. (1979) Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types. Volume II: H-Le. Regnum Vegetabile 98. Bohn, Scheltema & Holkema, Utrecht, 991 pp. Available from: https://www.biodiversitylibrary.org/item/103253#page/11/mode/1up (accessed 6 November 2022)

Stuessy, T.F. (2009) *Plant taxonomy*: *the systematic evaluation of comparative data*. Columbia University Press, New York, 539 pp.

Ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C.V., Magnusson, W.E., Molino, J.-F., Monteagudo, A., Núñez Vargas, P., Montero, J.C., Feldpausch, T.R., Honorio Coronado, E.N., Killeen, T.J., Mostacedo, B., Vasquez, R., Assis, R.L., Terborgh, J., Wittmann, F., Andrade, A., Laurance, W.F., Laurance, S.G.W., Marimon, B.S., Marimon, B.-H., Guimarães Vieira, I.C., Leão Amaral, I., Brienén, R., Castellanos, H., Cárdenas López, D., Duivenvoorden, J.F., Mogollón, H.F., Dionízia de Almeida Matos, F., Dávila, N., García-Villacorta, R., Stevenson Diaz, P.R., Costa, F., Emilio, T., Levis, C., Schietti, J., Souza, P., Alonso, A., Dallmeier, F., Duque Montoya, A.J., Fernández Piedade, M.T., Araujo-Murakami, A., Arroyo, L., Gribel, R., Fine, P.V.A., Peres, C.A., Toledo, M., Aymard C., G.A., Baker, T.R., Cerón, C., Engel, J., Henkel, T.W., Maas, P., Petronelli, P., Stropp, J., Zartman, C.E., Daly, D., Neill, D., Silveira, M., Ríos Paredes, M., Chave, J., Lima Filho, D.de A., Jørgensen, P.M., Fuentes, A., Schöngart, J., Cornejo Valverde, F., Di Fiore, A., Jimenez, E.M., Peñuela Mora, M.C., Phillips, J.F., Rivas, G., Van Andel, T.R., Von Hildebrand, P., Hoffman, B., Zent, E.L., Malhi, Y., Prieto, A., Rudas, A., Ruschel, A.R., Silva, N., Vos, V., Zent, S., Oliveira, A.A., Cano Schutz, A., Gonzales, T., Nascimento, M.T., Ramírez-Angulo, H., Sierra, R., Tirado, M., Umaña Medina, M.N., Van der Heijden, G., Vela, C.I.A., Vilanova Torre, E., Vriesendorp, C., Wang, O., Young, K.R., Baider, C., Balslev, H., Ferreira, C., Mesones, I., Torres-Lezama, A., Urrego Giraldo, L.E., Zagt, R., Alexiades, M.N., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Palacios Cuenca, W., Pauletto, D., Valderrama Sandoval, E., Valenzuela Gamarra, L., Dexter, K.G., Feeley, K., Lopez-Gonzalez, G. & Silman, M.R. (2013) Hyperdominance in the Amazonian tree flora. *Science* 342: 1243092.
https://doi.org/10.1126/science.1243092

ter Steege, H., Vaessen, R.W., Cárdenas-López, D., Sabatier, D., Antonelli, A., Oliveira, S.M. de, Pitman N.C.A., Jorgensen, P.M. & Salomão, R.P. (2016) The discovery of the Amazonian tree flora with an updated checklist of all known tree taxa. *Scientific Reports* 6.
https://doi.org/10.1038/srep29549.

Ter Steege, H., Prado, P.I., de Lima, R.A.F., Pos, E., Coelho, L.de S., Lima Filho, D.de A., Salomão, R.P., Amaral, I.L., Matos, F.D.de A., Castilho, C.V., Phillips, O.L., Guevara, J.E., Carim, M.de J.V., López, D.C., Magnusson, W.E., Wittmann, F., Martins, M.P., Sabatier, D., Irume, M.V., Guimarães, J.R.da S., Molino, J.-F., Bánki, O.S., Piedade, M.T.F., Pitman, N.C.A., Ramos, J.F., Mendoza, A.M., Venticinque, E.M., Luize, B.G., Vargas, P.N., Silva, T.S.F., Novo, E.M.M.de L., Reis, N.F.C., Terborgh, J., Manzatto, A.G., Casula, K.R., Coronado, E.N.H., Montero, J.C., Duque, A., Costa, F.R.C., Arboleda, N.C., Schöngart, J., Zartman, C.E., Killeen, T.J., Marimon, B.S., Marimon-Junior, B.H., Vasquez, R., Mostacedo, B., Demarchi, L.O., Feldpausch, T.R., Engel, J., Petronelli, P., Baraloto, C., Assis, R.L., Castellanos, H., Simon, M.F., de Medeiros, M.B., Quaresma, A., Laurance, S.G.W., Rincón, L.M., Andrade, A., Sousa, T.R., Camargo, J.L., Schietti, J., Laurance, W.F., de Queiroz, H.L., Nascimento, H.E.M., Lopes, M.A., Farias, E.de S., Magalhães, J.L.L., Brienen, R., Aymard C., G.A., Cardenas Revilla, J.D., Vieira, I.C.G., Cintra, B.B.L., Stevenson, P.R., Feitosa, Y.O., Duivenvoorden, J.F., Mogollón, H.F., Araujo-Murakami, A., Ferreira, L.V., Lozada, J.R., Comiskey, J.A., de Toledo, J.J., Damasco, G., Dávila, N., Lopes, A., García-Villacorta, R., Draper, F., Vicentini, A., Valverde, F.C., Lloyd, J., Gomes, V.H.F., Neill, D., Alonso, A., Dallmeier, F., de Souza, F.C., Gribel, R., Arroyo, L., Carvalho, F.A., de Aguiar, D.P.P., do Amaral, D.D., Pansonato, M.P., Feeley, K.J., Berenguer, E., Fine, P.V.A., Guedes, M.C., Barlow, J., Ferreira, J., Villa, B., Peñuela Mora, M.C., Jimenez, E.M., Licona, J.C., Cerón, C., Thomas, R., Maas, P., Silveira, M., Henkel, T.W., Stropp, J., Paredes, M.R., Dexter, K.G., Daly, D., Baker, T.R., Huamantupa-Chuquimaco, I., Milliken, W., Pennington, T., Tello, J.S., Marcelo Pena, J.L., Peres, C.A., Klitgaard, B., Fuentes, A., Silman, M.R., Di Fiore, A., von Hildebrand, P., Chave, J., van Andel, T.R., Hilário, R.R., Phillips, J.F., Rivas-Torres, G., Costa Noronha, J., Prieto, A., Gonzales, T., de Sá Carpanedo, R., Gonzales, G.P.G., Gómez, R.Z., Rodrigues, D.de J., Zent, E.L., Ruschel, A.R., Vos, V.A., Fonty, É., Junqueira, A.B., Dávila Doza, H.P., Hoffman, B., Zent, S., Barbosa, E.M., Malhi, Y., Bonates, L.C.de M., Miranda, I.P.de A., Silva, N., Barbosa, F.R., Vela, C.I.A., Mozombite Pinto, L.F., Rudas, A., Albuquerque, B.W., Umaña, M.N., van der Heijden, G., Young, K.R., Tirado, M., Correa, D.F., Sierra, R., Pedrosa Costa, J.B., Rocha, M., Vilanova Torre, E., Wang, O., Oliveira, A.A., Kalamandeen, M., Vriesendorp, C., Ramirez-Angulo, H., Holmgren, M., Nascimento, M.T., Galbraith, D., Flores, B.M., Scudeller, V.V., Cano, A., Ahuite Reategui, M.A., Mesones, I., Baider, C., Mendoza, C., Zagt, R., Urrego Giraldo, L.E., Ferreira, C., Villarroel, D., Linares-Palomino, R., Farfan-Rios, W., Farfan-Rios, W., Casas, L.F., Cárdenas, S., Balslev, H., Torres-Lezama, A., Alexiades, M.N., Garcia-Cabrera, K., Gamarra, L.V., Valderrama Sandoval, E.H., Ramirez Arevalo, F., Hernandez, L., Sampaio, A.F., Pansini, S., Cuenca, W.P., Oliveira, E.A.de, Pauletto, D., Levesley, A., Melgaço, K. & Pickavance, G. (2020) Biasedcorrected richness estimates for the Amazonian tree flora. *Scientific Reports* 10: 10130.
https://doi.org/10.1038/s41598-020-66686-3

ter Steege, H., Fortes, E.A., Rozendaal, D.M.A., Erkens, R.H.J., Sabatier, D., Aymard, G., Duijm, E., Eurlings, M., Grewe, F., Pombo, M.M., Gomes, Mansano, V.F. & Oliveira, S.M. (2023) Molecular phylogeny and evolution of inflorescence types in *Eperua* (Fabaceae). *American Journal of Botany*. [in press]
https://doi.org/10.1002/ajb2.16229

Thiers, B., Thiers, B.M. & Čokić, B.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/ (accessed 10 March 2023)

TRADA - Timber Research and Development Association (2020) Wallaba. Available from: https://www.trada.co.uk/wood-species/wallaba/ (accessed 14 July 2022)

Tucker, S.C. (2003) Floral development in Legumes. *Plant Physiology* 131: 911–926.

https://doi.org/10.1104/pp.102.017459

Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold,

K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (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. Koeltz Botanical Books, Glashütten, 254 pp.

https://doi.org/10.12705/Code.2018

Useful Tropical Plants Database (2014) *Eperua*. Available from: http://tropical.theferns.info/query.php?full=eperua (aaccessed 14 July 2022)

Veiga-Junior, V.F. & Pinto, A.C. (2002) O gênero *Copaifera* L. *Química Nova* 25: 273–286, 2002.

https://doi.org/10.1590/S0100-40422002000200016

Vogel, S. (1968) Chiropterophilie in der Neotropischen Flora. *Flora, abteilung B* 157: 591–602.

https://doi.org/10.1016/s0367-1801(17)30097-2

Willdenow, C.L. (1799) *Species plantarum*, ed. 4, 2(1). G.C. Nauk, Berolini. 823 pp.

Willdenow, C.L. (1802) *Species Plantarum*. ed. 4, 3(2). G.C. Nauk, Berolini. 1474 pp.

Appendix 1. Index to Vernacular Names.

Name	**Country**	**Taxa**
acanã	Brazil	*E. leucantha*
apa or apá	Brazil	*E. bijuga*, *E. falcata*, *E. grandiflora* subsp. *grandiflora*, *E. rubiginosa* var. *rubiginosa*
apa de crique	French Guiana	*E. falcata*
apa roxo	Brazil	*E. falcata*
apazeiro	Brazil	*E. rubiginosa* var. *rubiginosa*
arekuna	Venezuela	*E. jenmanii* subsp. *sandwithii*
baboen walaba	Surinam	*E. jenmanii*
backaike	Colombia	*E. purpurea*
bifbout	French Guiana	*E. rubiginosa* var. *rubiginosa*
bii adu	French Guiana	*E. grandiflora* subsp. *grandiflora*
bioudou	French Guiana	*E. falcata*, *E. rubiginosa* var. *rubiginosa*
birihoedoe	Surinam	*E. falcata*
bi udu or biudu	French Guiana, Surinam	*E. falcata*
bitimi wallaba	Guyana	*E. schomburgkiana*
boo-ro-go	Colombia	*E. purpurea*
boo-toó-ke	Colombia	*E. purpurea*
caraota	Venezuela	*E. falcata*
caraoto	Venezuela	*E. jenmanii*
biouolou wata	French Guiana	*E. falcata*
clump wallaba	Guyana	*E. schomburgkiana*
concha de suela	Venezuela	*E. jenmanii* subsp. *sandwithii*
copaíba jacaré	Brazil	*E. oleifera* var. *campestris*, *E. oleifera* var. *oleifera*
copaíba preta	Brazil	*E. oleifera* var. *campestris*
cutlas	Guyana	*E. schomburgkiana*
dzawaka	Brazil	*E. leucantha*
embira de sapo, imbira de sapo	Brazil	*E. cerradoensis*
envira iodo	Brazil	*E. duckeana*
espadeira	Brazil	*E. glabriflora*, *E. leucantha*
espadeiro	Brazil	*E. glabra*
Eturi wallaba	Guyana	*E. rubiginosa* var. *rubiginosa*
falcaha	French Guiana	*E. falcata*
fava do matto	Brazil	*E. bijuga*
fine leaf walaba	Guyana	*E. jenmanii* subsp. *jenmanii*
franga	French Guiana	*E. rubiginosa* var. *grandiflora*
gebaro	Brazil	*E. purpurea*
gibarú	Brazil	*E. purpurea*
guapa	Colombia	*E. purpurea*
iacana	Brazil	*E. purpurea*
iauácano	Brazil	*E. leucantha*
iebaro or iebaru	Brazil	*E. purpurea*
ipê do Bento	Brazil	*E. froesii*
iperana-apá	Brazil	*E. rubiginosa* var. *rubiginosa*

Appendix 1. (Continued)

Name	**Country**	**Taxa**
itoeli walaba	Surinam	*E. falcata*, *E. jenmanii*
ituri wallaba	Guyana	*E. grandiflora* subsp. *guyanensis*, *E. rubiginosa* var. *rubiginosa*, *E. schomburgkiana*
iuacanã	Brazil	*E. leucantha*
jacaré-copahiba	Brazil	*E. oleifera* var. *oleifera*
jauacaná	Brazil	*E. leucantha*
jauácano	Brazil	*E. leucantha*
jebaró	Brazil	*E. oleifera* var. *campestris*
jébaru	Brazil	*E. purpurea*
kanoneyoa ke	Colombia	*E. leucantha*
kergwalaba	Surinam	*E. falcata*
Kieraiku	Colombia	*E. leucantha*
machetta	Guyana	*E. schomburgkiana*
mahomillo	Venezuela	*E. jenmanii* subsp. *jenmanii*
mahomillo negro	Venezuela	*E. falcata*
maseta	Guyana	*E. schomburgkiana*
morapiranga	Brazil	*E. glabriflora*
muirapiranga	Brazil	mainly *E. glabriflora*, but also *E. bijuga* and *E. duckeana*
muirapiranga da folha miúda	Brazil	*E. duckeana*
muirapiranga branca	Brazil	*E. duckeana*
muirapiranga branca da miuda	Brazil	*E. duckeana*
muirapiranga da folha grande	Brazil	*E. glabriflora*
muirapiranja	Brazil	*E. glabriflora*
muirapironga	Brazil	*E. bijuga*
murajiboia	Brazil	*E. duckeana*
oever wallaba	Surinam	*E. rubiginosa* var. *rubiginosa*
o-kö-ges	Colombia	*E. leucantha*
opá	Venezuela	*E. jenmanii*
opá-yek or opai-yek	Venezuela	*E. jenmanii*, *E. jenmanii* subsp. *sandwithii*
ouapa	French Guiana	*E. falcata*, *E. rubiginosa* var. *rubiginosa*
palo colorado	Colombia	*E. leucantha*
palo rojo	Colombia	*E. leucantha*
pau de óleo	Brazil	*E. duckeana*
pega pega	Venezuela	*E. purpurea*
pitu	Brazil	*E. cerradoensis*
poé-koó	Colombia	*E. purpurea*
pracateira	Brazil	*E. cerradoensis*
rosa de montaña	Venezuela	*E. falcata*
shaquiparo	Colombia	*E. leucantha*
soft wallaba	Guyana	*E. falcata*
swamp wallaba	Guyana	*E.* cf. *jenmanii*
tapaka	French Guiana	*E. falcata*, *E. rubiginosa* var. *rubiginosa*
tehuwadu	Brazil	*E. jenmanii* subsp. *sandwithii*

Appendix 1. (Continued)

Name	Country	Taxa
tö-ee	Colombia	*E. leucantha*
tricel	Guyana	*E. reddeniae*
tuic	Colombia	*E. leucantha*
tumai-yek	Venezuela	*E. jenmanii* subsp. *sandwithii*
uapá	Brazil	*E. rubiginosa* var. *rubiginosa*
vá-pa	Colombia	*E. purpurea*
vouapa ouapa	French Guyana	*E. grandiflora* subsp. *grandiflora*
waapa	Brazil	*E. purpurea*
walaba	Surinam	*E. falcata*, *E. rubiginosa* var. *rubiginosa*
walaba kharemeroe	Surinam	*E. falcata*
walaba koeleroe	Surinam	*E. falcata*
walaba of bijlhout	Surinam	*E. falcata*
wallaba	Guyana	*E. falcata*, *E. grandiflora* subsp. *grandiflora*, *E. rubiginosa* var. *rubiginosa*, *E. schomburgkiana*
warapa	Guyana	*E. falcata*
wap seinõ	French Guiana	*E. grandiflora* subsp. *grandiflora*
wap waikmuwöiun	French Guiana	*Eperua* sp.
wapa	French Guiana	*E. falcata*, *E. glabra*, *E. grandiflora* subsp. *grandiflora*, *E. rubiginosa* var. *rubiginosa*
wapa blone	French Guiana	*E. falcata*
wapa courbaril	French Guiana	*E. grandiflora* subsp. *guyanensis*
wapa graj or wapa gras	French Guiana	*E. falcata*
wapa huileux	French Guiana	*E. falcata*
wapa panari	Colombia	*E. purpurea*
wapa rivière	Frech Guiana	*E. rubiginosa* var. *rubiginosa*
wapa rouge	French Guiana	*E. falcata*
wapa tapaka	French Guiana	*E. grandiflora* subsp. *grandiflora*
wataba	Guyana	*E. glabra*
wataja	Guyana	*E. glabra*
watapa	Guyana	*E. falcata*
water wallaba	Guyana	*E. falcata*, *E. jenmanii* subsp. *jenmanii*, *E. schomburgkiana*
white sand wallaba	Guyana	*E. falcata*
woupa	French Guyana	*Eperua* sp.
yaauaka	Venezuela	*E. leucantha*
yabakaike	Colombia	*E. leucantha*
yacuana	Venezuela	*E. leucantha*
yaguácana	Venezuela	*E. leucantha*
yaguácana blanco	Venezuela	*E. leucantha*
yaguácana rojo	Venezuela	*E. leucantha*
yaguana	Venezuela	*E. leucantha*
yahuana or yahuanaa	Venezuela	*E. leucantha*
yahyana	Venezuela	*E. leucantha*
yauácano	Brazil	*E. leucantha*

Appendix 1. (Continued)

Name	Country	Taxa
yaua-kuaña	Brazil	*E. leucantha*
yé-ba	Colombia	*E. purpurea*
yebaro	Colombia	*E. purpurea*
yébaro	Brazil	*E. purpurea*
yebaroh	Venezuela	*E. purpurea*
yeberro	Venezuela	*E. purpurea*
yeiaro	Venezuela	*E. purpurea*
yéparo	Venezuela	*E. purpurea*
yévaro	Venezuela	*E. purpurea*
yevaro or yévaro	Venezuela	*E. purpurea*
yévaro blanco	Colombia	*E. leucantha*
yévaro sabanero	Colombia	*E. leucantha*
zwarte walaba	Surinam	*E. falcata*

Appendix 2. Index to Collections.

Collector / number	**Herbarium**	**Species**
Acero E. & Rodríguez R. 945	COL, INPA	*E. purpurea*
Acero E. & Rodríguez R. 948	COL, UDBC	*E. leucantha*
Acevedo-Rodríguez P. et al. 10235	US	*E. purpurea*
Acevedo-Rodríguez P. et al. 10320, 10408	US	*E. leucantha*
Albuquerque B.W.P. de & Elias 67-27	INPA, US	*E. glabriflora*
Albuquerque J.M. de s.n. INPA143010, INPA143037	INPA	*E. glabriflora*
Almeida A.B. 134, 152	UB	*E. cerradoensis*
Almeida S.S. et al. 214	MG	*E. duckeana*
Almeida S.S. et al. 458	MG	*E. bijuga*
Aluisio J. 172	INPA, US	*E. duckeana*
Álvarez A. et al. 1611	COAH	*E. purpurea*
Amaral D.D. et al. 311	MFS, MG	*E. bijuga*
Amoêdo A.B. et al. 49	EAFM	*E. oleifera* var. *oleifera*
Andel T.R. van et al. 665	U, WAG	*E. falcata*
Andel T.R. van et al. 1007, 3073, 4449, 4642, 4724	U	*E. falcata*
Andel T.R. van et al. 4979	U	*E. rubiginosa* var. *grandiflora*
Anderson A.B. 121	INPA	*E. glabriflora*
Anderson C.W. 122	RB	*E. falcata*
Anderson C.W. 182	RB	*E. schomburgkiana*
Angel G. 19	CAY, MPU, L	*E. falcata*
Angel G. 101	CAY, L, MPU	*E. grandiflora* subsp. *grandiflora*
Angel G. 126	CAY, L, MPU	*E. rubiginosa* var. *rubiginosa*
Angel G. 158	CAY, MPU	*E. falcata*
Angel G. 176	CAY, MPU, L	*E. falcata*
Angel G. 184	CAY, MPU, L	*E. rubiginosa* var. *rubiginosa*
Antonelli A.M. et al. 545	INPA	*E. glabriflora*
Appun C.F. 384	K	*E. jenmanii* subsp. *jenmanii*
Ariza-Cortés W. 5713	UDBC	*E. leucantha*
Ariza-Cortés W. 5823	UDBC	*E. leucantha*
Assunção J.M. s.n. RB352959	RB	*E. glabriflora*
Assunção P.A.C.L. & Carvalho F.A. de 1085a, 1118, 1185, 1213, 1218	INPA	*E. oleifera* var. *campestris*
Aublet J.B.C.F. 8288	P	*E. rubiginosa* var. *rubiginosa*
Aublet J.B.C.F. s.n. BM000952282, P00835933, P00835934	BM, P	*E. grandiflora* subsp. *grandiflora*

Appendix 2. Index to Collections.

Collector / number	**Herbarium**	**Species**
Aublet J.B.C.F. s.n. BM000952284	BM	*E. falcata*
Aubréville A. 1961/236	P, U, US	*E. falcata*
Aubréville A. 260	P, U, US	*E. falcata*
Aumeeruddy Y. 24	CAY	*E. falcata*
Aymard G. et al. 14556	COAH	*E. purpurea*
Aymard G. et al. 14571	COAH	*E. purpurea*
B.W. 11, 11a, 482, 1141, 1171, 1297, 1518, 1725, 2750, 3385, 3408, 3434, 3618, 3625, 3972, 4061, 4200, 4324, 4338, 4420, 4528, 4536, 4550, 4791, 4838, 5042, 5060, 5398, 5408, 5420, 5524, 5547, 5549, 5804, 5999, 6905	U	*E. falcata*
B.W. 1609	IAN49658, U, US	*E. falcata*
B.W. 3100	CAY, U	*E. falcata*
B.W. 3210, 4192	IAN, U	*E. falcata*
B.W. 3401, 3970, 5364	U, US	*E. falcata*
B.W. 4416	INPA, U	*E. falcata*
B.W. 5462	IAN 049767-fl, U	*E. rubiginosa* var. *rubiginosa*
B.W. 5515 (leaves =5462)	IAN-fr.	*E. rubiginosa* var. *rubiginosa*
B.W. Nelson et al. 1610	HUEFS, INPA	*E. duckeana*
B.W. s.n. L1951220	L	*E. falcata*
BAFOG 51, 143, 1274, 7062, 7064, 7254, 7298	U	*E. falcata*
BAFOG 219	U	*E. rubiginosa* var. *rubiginosa*
BAFOG 1253	U	*E. grandiflora* subsp. *grandiflora*
BAFOG 6033	CAY, P	*E. falcata*
BAFOG 6239	CAY	*E. rubiginosa* var. *rubiginosa*
BAFOG 7831	U, P (03465694)	*E. rubiginosa* var. *rubiginosa*
BAFOG 7937	U	*E. rubiginosa* var. *rubiginosa*
Bahia T.R. 27	IAN	*E. oleifera* var. *campestris*
Baraloto C. 559	CAY	*E. falcata*
Baraloto C. 719	CAY	*E. rubiginosa* var. *rubiginosa*
Barbosa-Castillo C.E. & Madriñán S. 8407	COL	*E. leucantha*
Baronas-Colmenares A. 3026	COAH	*E. leucantha*
Barrier S. 3809, 4062, 4304, 4312, 4320, 4327, 4328, 4337, 4338, 4342	CAY	*E. falcata*
Bastos M. 2228	RB	*E. grandiflora* subsp. *grandiflora*
L.H. Bailey & E.Z. Baileys s.n.	BH	*E. falcata*

Appendix 2. Index to Collections.

Collector / number	**Herbarium**	**Species**
L.H. Bailey & E.Z. Baileys s.n.	BH	*E. jenmanii*
Bena P. 1273B	CAY	*E. falcata*
Bena P. 1274	CAY	*E. falcata*
Benoist R. 596	P	*E. falcata*
Benoist R. 1595	P	*E. grandiflora* subsp. *grandiflora*
Benoist R. s.n. P03465215	P	*E. falcata*
Benoist R. s.n. P03465703	P	*E. rubiginosa* var. *rubiginosa*
Berg C.C. 783	U	*E. grandiflora* subsp. *grandiflora*
Berlo M. van & Babooll M. 12, 14, 18, 19, 21, 24, 25, 18, 30, 31	L	*E. falcata*
Berlo M. van & Babooll M. 13, 15, 16, 17, 20, 22, 23, 26, 27, 29	L	*Eperua* sp.
Berlo M. van & Kartoikromo R. 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52	L	*E. falcata*
Berlo M. van & Pengtai W. 53, 54, 55, 56, 57, 58, 59, 60,61, 62	L	*E. falcata*
Berlo M. van & Rampersaud D. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11	L	*E. falcata*
Berlo M. van & Simon C. 32, 33, 34, 35, 36, 37, 38, 39, 40, 41	L	*E. falcata*
Berlo M. van et al. 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 80, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90	L	*E. falcata*
Bernal R. et al. 3683	COL	*E. purpurea*
Berry P.E. et al. 5737	U, US	*E. purpurea*
Beruordi 2130	US	*E. jenmanii*
Betancur J. & Jaramillo L.F. 9941	COAH, COL	*E. leucantha*
Bhikhi C.R. et al. 79	U	*E. falcata*
Bhikhi C.R. et al. 873, 887	U	*E. rubiginosa* var. *rubiginosa*
Billiet F. & Jadin B. 1248	CAY	*E. falcata*
Bisby F.A. 1220	INPA, K	*E. duckeana*
Black G.A. 49-8301	ALCB, IAN, INPA, IPA, K, NY, P	*E. rubiginosa* var. *rubiginosa*
Black G.A. 54-17621	IAN, P	*E. rubiginosa* var. *rubiginosa*
Blanco C.A. 598	US	*E. jenmanii* subsp. *sandwithii*
Blanco C.A. 603	US	*E. falcata*
Bonadeu F. et al. 323	MG, RB	*E. bijuga*
Boom B.M. 10297	NY	*E. jenmanii*
Boom B.M. & Mori S.A. 1769, 1797, 1798, 1799, 1957, 1962, 1964, 1971, 1972, 1978, 1980, 1985, 1986, 1991, 2002	CAY	*E. falcata*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Boom B.M. & Mori S.A. 1805	CAY	*Eperua* sp.
Boom B.M. & Weitzman A.L. 5185	F, INPA, MO, U, US	*E. purpurea*
Boom B.M. & Weitzman A.L. 5186	INPA, U, US	*E. leucantha*
Boom B.M. & Weitzman A.L. 5475	U, US	*E. leucantha*
Boom B.M. et al. 5343	US	*E. leucantha*
Boom B.M. et al. 5857	MO, U, US	*E. purpurea*
Boom B.M. et al. 8699	K, NY, U, US	*E. glabriflora*
Boon H.A. 1199	U	*E. falcata*
Boon H.A. 1209	U	*E. grandiflora* subsp. *grandiflora*
Bordenave B. 228	CAY, P, S, U	*E. rubiginosa* var. *rubiginosa*
Bordenave B. 549	CAY	*E. falcata*
Bordenave B. 569	CAY	*E. grandiflora* subsp. *grandiflora*
Bordenave B. 600	CAY	*E. falcata*
Bordenave B. et al. 5079	CAY, U	*E. grandiflora* subsp. *grandiflora*
Borsboom N.W.J. 12025	WAG	*E. falcata*
Borsboom N.W.J. 12044	U, WAG	*E. falcata*
Botanisch Laboratorium Leiden 765	L	*E. falcata*
Briolange s.n. RB176742	RB	*E. oleifera* var. *campestris*
Broadway W.E. s.n. LY0226357, LY0226358, LY0226359, LY0226360, LY0226361, LY0226362, LY0226363, LY0226365; LY0226364; LY0226366, LY0226367, LY0226368, LY0226369, US1343487	LY, US	*E. falcata*
Broadway W.E. s.n. L1951161, LY0226372, LY0226370, LY0226373, LY0226374	L, LY	*E. jenmanii* subsp. *jenmanii*
Burger D. 8	U, WAG	*E. falcata*
Burgos A. 131	CAY	*E. rubiginosa* var. *rubiginosa*
Cabral F.N. 1527	INPA	*E. duckeana*
Cabral F.N. et al. FC990	INPA, UEC	*E. leucantha*
Cabral F.N. et al. 1561	INPA, RB	*E. manausensis*
Cadamuro L. & Solacroup F. 191	CAY	*E. grandiflora* subsp. *grandiflora*
Calderón C.E. et al. 2533	EAFM, HRCB, INPA, K, MO, NY, US	*E. oleifera* var. *campestris*
Calderón C.E. et al. 2925	INPA, MO, NY, US	*E. duckeana*
Campos P. & Mello A.T. 1162	INPA	*E. glabriflora*
Candido J. s.n. IAN44221, IAN44221a	IAN	*E. rubiginosa* var. *rubiginosa*
Cárdenas-López D. 20677, 21295, 21936, 21951	COAH	*E. leucantha*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Cárdenas-López D. 21898, 21937, 24105	COAH	*E. purpurea*
Cárdenas-López D. & Aguirre-Santoro J. 24577	COAH, NY	*E. leucantha*
Cárdenas-López D. & Marín N. 52950	COAH	*E. leucantha*
Cárdenas-López D. et al. 15350, 15460, 21946	COAH	*E. purpurea*
Cárdenas-López D. et al. 21013	COAH, UDBC	*E. leucantha*
Cárdenas-López D. et al. 23672, 24050, 24105, 42486, 43206, 44178, 50772, 53044	COAH	*E. leucantha*
Cárdenas-López D. et al. 24076	COAH, NY	*E. purpurea*
Cárdenas-López D. et al. 24415	COAH, US	*E. purpurea*
Cardona F. 818	F, US	*E. jenmanii* subsp. *sandwithii*
Cardona F. 985	US	*E. jenmanii*
Cardona F. 2158	US	*E. jenmanii*
Cardoso D.B.S.O. et al. 2897	ALCB, HUEFS, INPA	*E. glabriflora*
Cardoso D.B.S.O. et al. 3310	INPA, HUEFS	*E. leucantha*
Carim M.J.V. & Guimarães J.R.S. 532	HAMAB	*E. rubiginosa* var. *rubiginosa*
Carim M.J.V. & Guimarães J.R.S. 533	HAMAB	*E. rubiginosa* var. *rubiginosa*
Carvale P. 870	INPA	*E. rubiginosa* var. *rubiginosa*
Carvalho C. 178	MG	*E. bijuga*
Carvalho F.A. de 2099	INPA	*E. oleifera* var. *campestris*
Carvalho F.A. de et al. 1530	INPA	*E. leucantha*
Carvalho I.R. & Costa R.C. 317	INPA, RB	*E. oleifera* var. *campestris*
Carvalho I.R. & Ricardo C.C. s.n. RB243379	INPA, RB	*E. oleifera* var. *campestris*
Castaño N. et al. 13072	COAH	*E. purpurea*
Castilho C.V. et al. 38	INPA	*E. glabriflora*
Castilho C.V. et al. 294	INPA	*E. glabriflora*
Castilho C.V. et al. 640	INPA	*E. glabriflora*
Castro F. 5010	UDBC	*E. leucantha*
Castro F. 8510	COAH, UDBC	*E. leucantha*
Castro S.Y. 1787	COAH	*E. leucantha*
Castro S.Y. 1855	COAH	*E. purpurea*
Cavalcante P.B. 669	CGMS, INPA, MG	*E. leucantha*
Cavalcante P.B. 870	MG, NY	*E. rubiginosa* var. *rubiginosa*
Cavalcante P.B. 2230 & Augustin D. 4103	MG, MO	*E. bijuga*
Cavalcante P.B. 2235 & Augustin D. 4108	MG, MO	*E. bijuga*
Cavalcante P.B. 2538	K, MG, NY, US	*E. rubiginosa* var. *rubiginosa*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Christenson G.M. et al. GMC-1381	US	*E. leucantha*
Cid-Ferreira C.A. 5791	F, HRCB, INPA, K, MG, MO, RB, US	*E. oleifera* var. *campestris*
Cid-Ferreira C.A. 5913	F, HRCB, INPA, K, MG, MO, NY, RB, US	*E. oleifera* var. *campestris*
Cid-Ferreira C.A. 6919	INPA, K, NY	*E. duckeana*
Cid-Ferreira C.A. 7584	F, HUNEB, INPA, K, MO, NY, RBR, US	*E. glabriflora*
Cid-Ferreira C.A. 9330	INPA, K, NY, US	*E. purpurea*
Cid-Ferreira C.A. 9730	F, HAMAB, INPA, K, MG, MO, NY, RB, UFACPZ, US	*E. duckeana*
Cid-Ferreira C.A. et al. 4	INPA, MG, MO, NY, R, RB00141504, US	*E. glabriflora*
Cid-Ferreira C.A. et al. 271	INPA, MG, MO, NY, R, RB00140259, US	*E. glabriflora*
Cid-Ferreira C.A. et al. 484	INPA, MG, NY, RB00140230, US	*E. glabriflora*
Cid-Ferreira C.A. et al. 659	INPA, MG, MO, NY, R, RB00266154, US	*E. glabriflora* var. *gynopubescens*
Cid-Ferreira C.A. et al. 703	INPA, NY, US	*E. duckeana*
Cid-Ferreira C.A. et al. 1419	EAFM, INPA, MG, MO, NY, RB, US	*E. glabra*
Cid-Ferreira C.A. et al. 6754	INPA, K, MO, NY, US	*E. glabriflora*
Cid-Ferreira C.A. et al. 7655	INPA, K, MBM, MG, MIRR, NY, US	*E. duckeana*
Cid-Ferreira C.A. et al. 7662	F, INPA, K, MBM, MIRR, MG, MO, NY, US	*E. rubiginosa* var. *rubiginosa*
Cid-Ferreira C.A. et al. 7734	F, INPA, K, MBM, MG, MIRR, MO, NY, US	*E. duckeana*
Cid-Ferreira C.A. et al. 7762	MBM, HUEFS, INPA, MO, NY, US	*E. rubiginosa* var. *rubiginosa*
Cid-Ferreira C.A. et al. 7872	INPA, K, MIRR, MG, MO, NY, US	*E. duckeana*
Cid-Ferreira C.A. et al. 8047	HUEFS, INPA, K, MG, MO, MIRR, NY, RBR, US	*E. rubiginosa* var. *rubiginosa*
Cid-Ferreira C.A. et al. 8239	INPA, MG, MO, NY, UFACPZ, US	*E. glabriflora*
Clark H.L. 6983	US	*E. leucantha*
Clark H.L. 7011	NY (3196792), US	*E. purpurea*
Clark H.L. 7019, 7020, 7021	US	*E. leucantha*
Clark H.L. 7023	NY, US	*E. leucantha*
Clark H.L. 7036	US	*E. purpurea*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Clarke H.D. 191	CAY, U, US	*E. rubiginosa* var. *rubiginosa*
Clarke H.D. 255	CAY, U, US	*E. falcata*
Clarke H.D. 393	US, CAY	*E. falcata*
Clarke H.D. 442	US	*E. rubiginosa* var. *rubiginosa*
Clarke H.D. 1353	CAY, U, US	*E. schomburgkiana*
Clarke H.D. 1633, 2613	CAY, U, US	*E. falcata*
Clarke H.D. 2743	CAY, U, US	*E. schomburgkiana*
Clarke H.D. 2788, 3101	US	*E. rubiginosa* var. *rubiginosa*
Clarke H.D. 4084	US	*E. falcata*
Clarke H.D. & Rhodes J. 11085	U	*E. falcata*
Clarke H.D. & Rhodes J. 11375	US	*E. rubiginosa* var. *rubiginosa*
Clarke H.D. et al. 762	US	*E. falcata*
Clarke H.D. et al. 7639, 7748, 7918	U, US	*E. rubiginosa* var. *rubiginosa*
Clarke H.D. et al. 7968, 8809	US	*E. rubiginosa* var. *rubiginosa*
Coelho C.A. 1024	INPA	*E. oleifera* var. *campestris*
Coêlho D. s.n. INPA4308	IAN, INPA, US	*E. duckeana*
Coêlho D. s.n. INPA20747	INPA	*E. duckeana*
Coêlho L.F. & Coêlho D. s.n. INPA21165	INPA	*E. glabriflora*
Coêlho L.F. & Mello F. 270	INPA53847, MG56800	*E. leucantha*
Coêlho L.F. 6	SP	*E. glabriflora*
Coêlho L.F. 94	INPA	*E. glabriflora*
Coêlho L.F. et al. 794	INPA	*E. duckeana*
Coêlho L.F. s.n. INPA5212	IAN, INPA, US	*E. duckeana*
Coêlho L.F. s.n. INPA6516	INPA, MG	*E. glabriflora*
Coêlho L.F. s.n. INPA39594	INPA, RB	*E. oleifera* var. *oleifera*
Coêlho L.F. s.n. INPA42008	INPA	*E. oleifera* var. *oleifera*
Collela M. et al. 1864	K, NY (3196795)	*E. banaensis*
Coomes D. 207	K	*E. obtusata*
Cordeiro M.R. & Batista J. 2642	IAN	*E. bijuga*
Cordeiro M.R. 301	IAN	*E. leucantha*
Córdoba M.P. et al. 93	COAH, COL	*E. purpurea*
Córdoba M.P. et al. 258	COL	*E. leucantha*
Córdoba M.P. et al. 275	COAH	*E. leucantha*
Cortés-Ballen R. et al. 149	COAH, COL, UDBC	*E. leucantha*
Cortés-Ballen R. et al. 336	COAH, COL, UDBC	*E. purpurea*
Costa J.C. da et al. s.n INPA1202.3150	NY (01171211)	*E. glabriflora*
Costa J.C. da et al. s.n INPA1202.3257	(NY (01171201)	*E. glabriflora*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Costa J.C. da et al. s.n INPA1202.3271	NY (01171197)	*E. glabriflora*
Costa J.C. da et al. s.n INPA1202.3437	US (3338936)	*E. glabriflora*
Costa J.C. da et al. s.n INPA1202.3446	NY (1171199), US (1171199)	*E. glabriflora*
Coup C. CL203	MPU	*E. grandiflora* subsp. *guyanensis*
Cremers G.A. & Pétronelli P. 11724	CAY	*E. grandiflora* subsp. *grandiflora*
Cremers G.A. 7659	CAY, P, US	*E. falcata*
Cremers G.A. 9907	CAY, P, U, US	*E. rubiginosa* var. *rubiginosa*
Crevoux s.n. P03465221	P	*E. falcata*
Cruz E.D. 1123	RB	*E. bijuga*
Cruz J.S. de la 1373	F, MO, US	*E. falcata*
Cruz J.S. de la 1704	BH, F, MO, US	*E. grandiflora* subsp. *guyanensis*
Cruz J.S. de la 2091	F, US	*E. schomburgkiana*
Cruz J.S. de la 2172	BH, F, MO, US	*E. schomburgkiana*
Cunha N.M.L. et al. 1032	INPA, NY	*E. glabriflora*
Cunha O. et al. 209	INPA	*E. glabriflora*
Dahlgren B.E. & Persuad A.C. s.n. F519811	F	*E. falcata*.
Daly D.C. & Cardoso J. 3808	HAMAB, K, MG, MO, NY, US	*E. falcata*
Daly D.C. et al. 889	INPA, IAN, K, MG, NY, US	*E. bijuga*
Daly D.C. et al. 5473	INPA, MG, RB	*E. purpurea*
Dambrós L.A. 307	HRB, INPA, RB	*E. grandiflora* subsp. *grandiflora*
Dambrós L.A. s.n. HCDAL259	HCDAL	*E. grandiflora* subsp. *grandiflora*
Dantas M. & Silva N.T. da 1182	IAN	*E. bijuga*
D'Apolito-Junior C. & Vicentini A. 23	INPA	*E. duckeana*
Delgado H. 30	UDBC	*E. leucantha*
Delnatte C. 325	CAY, COL, MPU	*E. rubiginosa* var. *rubiginosa*
Delnatte C. et al. 302	CAY, MPU	*E. falcata*
Demarchi L.O. & Ramos J.F. 989	INPA, RB	*E. duckeana*
Demarchi L.O. et al. 529	INPA	*E. oleifera* var. *campestris*
Demarchi L.O. et al. 583	INPA	*E. oleifera* var. *campestris*
Deward G. 112	CAY, P, U	*E. rubiginosa* var. *rubiginosa* (leaves), *E. falcata* (inflorescence*)*
Deward G. 172	CAY, P	*E. rubiginosa* var. *rubiginosa*
Dick C.W. 2	INPA, MBM, NY	*E. glabriflora*
Dick C.W. 157	INPA, NY, US	*E. glabriflora*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Dioinizia F. et al. 182	INPA, NY, PACA-AGP	*E. duckeana*
Ducke W.A. 13	K	*E. oleifera* var. *campestris*
Ducke W.A. 14	WIS	*E. glabriflora*
Ducke W.A. 14a	F (660050)	*E. glabriflora*
Ducke W.A. 52	F, NY	*E. purpurea*
Ducke W.A. 73	F, IAN, MG, MO, NY, R, S, US	*E. oleifera* var. *campestris*
Ducke W.A. 158	F, K, MO, NY, R, S, US	*E. glabriflora*
Ducke W.A. 158 (II^{a} col)	IAN, MG	*E. glabriflora*
Ducke W.A. 164	F, NY	*E. leucantha*
Ducke W.A. 213	F, K, MO, NY, R, S, US	*E. oleifera* var. *oleifera*
Ducke W.A. 235	NY	*E. oleifera* var. *oleifera*
Ducke W.A. 244	NY, US	*E. duckeana*
Ducke W.A. 732	F, IAN, MG, MO, NY, R, US	*E. duckeana*
Ducke W.A. 1260	IAN, F, K, MG, MO, NY, R, US	*E. bijuga*
Ducke W.A. 9022	MG, RB	*E. rubiginosa* var. *rubiginosa*
Ducke W.A. 9088	RB	*E. duckeana*
Ducke W.A. s.n. RB16927	P, RB, U	*E. bijuga*
Ducke W.A. s.n. RB16928	RB, U	*E. bijuga*
Ducke W.A. s.n. RB16929	P, RB	*E. bijuga*
Ducke W.A. s.n. RB20217	RB	*E. oleifera* var. *oleifera*
Ducke W.A. s.n. RB20312	K, RB, U, US	*E. bijuga*
Ducke W.A. s.n. RB20313	RB, U	*E. glabriflora*
Ducke W.A. s.n. RB23288	K, RB, P, U, US	*E. purpurea*
Ducke W.A. s.n. RB23289	K, RB, US	*E. leucantha*
Ducke W.A. s.n. RB23290	F, K, INPA, NY, P, R, RB, S, U, US	*E. oleifera* var. *oleifera*
Ducke W.A. s.n. RB23291	K, INPA, NY, P, R, RB, U, US	*E. oleifera* var. *campestris*
Ducke W.A. s.n. RB23732	RB, P, U	*E. leucantha*
Ducke W.A. s.n. RB23733	RB	*E. glabriflora*
Ducke W.A. s.n. RB23734	K, P, RB, U, US	*E. duckeana*
Ducke W.A. s.n. RB166884	RB	*E. purpurea*
Dutrève B. 437	CAY	*E. falcata*
Ek R.C. & Granvendeel B. 721	U	*E. grandiflora* subsp. *guyanensis*
Ek R.C. & Zagt R. 855	U	*E. grandiflora* subsp. *guyanensis*
Ek R.C. et al. 1082	U	*E. falcata*
Elburg J.P. 9822	U	*E. falcata*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Elias J. & Aloisio 462	INPA	*E. glabriflora*
Equipe-Fito 1202.1542	INPA	*E. glabriflora*
Etter A. 3	COAH	*E. purpurea*
Evans R. 3209	MO, US	*E. falcata*
Evans R. & Lewis G. 1871	CAY, IAN, INPA, MO, P, RB, U, US	*E. falcata*
Evans R. & Peckham H. 2814	L, U	*E. falcata*
Evans R. et al. 1929	CAY, IAN, INPA, P, RB, U, US	*E. rubiginosa* var. *rubiginosa*
Evans R. et al. 2154	U	*E. falcata*
Evans R. et al. 2372	P, US	*E. falcata*
Fairchild D.G. s.n.	US1716064, 1716066? BR0000017324229	*E. falcata*
Falcão-da-Silva M. et al. 628	MG	*E. bijuga*
Fanshawe D.B. 2104	US	*E. rubiginosa* var. *grandiflora*
Fanshawe D.B. 4840	U	*E. rubiginosa* var. *rubiginosa*
Faria S.M. de & C.F. da C. 2186	RB	*E. duckeana*
Faria S.M. de et al. 1726, 1727, 2053	HSTM, RB	*E. duckeana*
Faria S.M. de et al. 2450	HSTM, MBM, RB	*E. rubiginosa* var. *rubiginosa*
Faria S.M. de et al. 2451	RB	*E. duckeana*
Faria S.M. de et al. 2459	HSTM, K, RB	*E. duckeana*
Farney C. de S. & Mota C.D.A. 1929	F, INPA, MO, NY, RB, US	*E. rubiginosa* var. *rubiginosa*
Farney C. de S. et al. 1751	HAMAB, INPA, K, MG, MO, NY, RB, US	*E. purpurea*
Farney C. de S. et al. 1899	HAMAB, INPA, K, NY, US	*E. purpurea*
Farney C. de S. et al. 1905	F, HAMAB, INPA, K, MO, NY, RB, US	*E. leucantha*
Farroñay F. 1870	INPA	*E. oleifera* var. *oleifera*
Farroñay F. 1887, 1901	INPA	*E. oleifera* var. *campestris*
Febis 6468	U	*E. jenmanii*
Félix-da-Silva M.M. et al. 101, 392, 567	MG	*E. bijuga*
Félix-da-Silva M.M. et al. 241	IAN, MG	*E. bijuga*
Ferreira A. s.n. P00312196	P	*E. purpurea*
Ferreira A.J.C. et al. s.n. INPA1104.285	INPA?, NY 1171189	*E. glabriflora*
Ferreira A.J.C. et al. s.n. INPA1202.5460	INPA?, NY 1171215	*E. glabriflora*
Ferreira E. 57-29	INPA, MG	*E. glabriflora*
Ferreira G.C. & Freitas J.C. 103	IAN	*E. bijuga*
Ferreira G.C. & Ribeiro B.G.S. 496	IAN	*E. bijuga*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Fittkau E.J. & Coelho D. s.n. INPA12913	INPA	*E. rubiginosa* var. *rubiginosa*
Fleury M. 489	CAY, US	*E. falcata*
Fleury M. 1129	CAY	*E. rubiginosa* var. *rubiginosa*
Florschütz J. & Florschütz P.A. 217	U	*E. falcata*
Focke H.C. 323a	L	*E. rubiginosa* var. *rubiginosa*
Focke H.C. 945	U	*E. falcata*
Foldats E. 2645	US	*E. falcata*
Fontella H. & Caruso J. 2770	RB	*E. bijuga*
Forbes E.S. et al. 339	U, US	*E. falcata*
Forest Department 2311	U	*E. grandiflora* subsp. *guyanensis*
Forest Department 7174	U	*E. rubiginosa* var. *rubiginosa*
Foresta H. de 137	CAY	*E. falcata*
Foresta H. de hf261	CAY, US	*E. grandiflora* subsp. *grandiflora*
Fortes E.A. & M. de C. Camelo 150	RB	*E. glabriflora*
Fortes E.A. & Silva G.S. da 165, 166, 171, 172	IAN, RB	*E. falcata*
Fortes E.A. & Silva G.S. da 167, 168, 169, 170	IAN, RB	*E. rubiginosa* var. *rubiginosa*
Fortes E.A. & Viana G.P. 194b	HUEFS, IAN, INPA, MG, NY, RB, UEC, US	*E. manausensis*
Fortes E.A. et al. 189	IAN	*E. bijuga*
Fortes E.A. et al. 190b, 191b	RB, INPA, UEC, US	*E. duckeana*
Fortes E.A. et al. 192b	RB, INPA, UEC, US	*E. glabriflora*
Fortes E.A. et al. 193b	RB, INPA, UEC, UEFS, US	*E. glabriflora*
Forzza R.C. et al. 9385	RB	*E. rubiginosa* var. *rubiginosa*
Forzza R.C. et al. 9951	HAMAB, NY, RB, UPCB	*E. grandiflora* subsp. *grandiflora*
Forzza et al. R.C. 10684	HAMAB, HUEFS, MG, NY, RB	*E. rubiginosa* var. *rubiginosa*
Freitas M.A. de et al. 1093	INPA, MG, NY, RB	*E. bijuga*
Fróes R. de L. 21104	F, IAN, K, NY, US	*E. leucantha*
Fróes R. de L. 21206	IAC, IAN, K, NY, US	*E. purpurea*
Fróes R. de L. 22317	IAC, IAN, INPA, U	*E. purpurea*
Fróes R. de L. 24926	IAN	*E. glabriflora* var. *gynopubescens*
Fróes R. de L. 24949	IAN	*E. duckeana*
Fróes R. de L. 25266	IAC, IAN	*E. glabriflora* var. *gynopubescens*
Fróes R. de L. 25330	IAC, IAN	*E. duckeana*
Fróes R. de L. 25698	IAC, IAN	*E. rubiginosa* var. *rubiginosa*

Appendix 2. (Continued)

Collector / number	Herbarium	Species
Fróes R. de L. 26638	IAN, K, US	*E. rubiginosa* var. *rubiginosa*
Fróes R. de L. 26639	IAN, US	*E. rubiginosa* var. *rubiginosa*
Fróes R. de L. 26649	IAN, RB, US	*E. rubiginosa* var. *rubiginosa*
Fróes R. de L. 26687	IAN, NY, P, RB, SP, US	*E. falcata*
Fróes R. de L. 26687a	IAN, SP, US	*E. falcata*
Fróes R. de L. 28826	IAN	*E. leucantha*
Fróes R. de L. 32418	INPA, NY, R	*E. froesii*
Fróes R. de L. 32452	IAN	*E. froesii*
Fróes R. de L. 32776, 32930, 32962, 33130	IAN	*E. bijuga*
Fróes R. de L. 32938	IAN, MG	*E. bijuga*
Fróes R. de L. 32988	IAN, US	*E. bijuga*
Fróes R. de L. 33051	IAN, K	*E. froesii*
Fróes R. de L. & Black G.A. 27281	IAN, NY, P, US	*E. bijuga*
Fróes R. de L. & Black G.A. 27607	IAN, NY, R	*E. bijuga*
Galeano M.P. et al. 1303	COAH, COL	*E. leucantha*
Garnier F.A. 138	CAY	*E. falcata*
Gaui T.D. 178, 179	INPA	*E. duckeana*
Geiselman C.K. 94	NY (02531350)	*E. falcata*
Geiselman C.K. 95	NY (02531351)	*E. falcata*
Geiselman C.K. 106	NY (02531305)	*E. rubiginosa* var. *rubiginosa*
Geiselman C.K. 165	NY (02531283)	*E. grandiflora* subsp. *grandiflora*
Geiselman C.K. 169	NY (02531331)	*E. rubiginosa* var. *rubiginosa*
Genoyer P. 500	MPU (198107)	*E. falcata*
Genoyer P. 505	MPU (198113)	*Eperua* sp.
Gentry A.H. & Stein B.A. 46526	F, MO, U, US	*E. leucantha*
Gentry A.H. & Stein B.A. 46763	US	*E. leucantha*
Gillespie L.J. 4250	INPA, MO, US	*E. falcata*
Gillespie L.J. & Persuad H. 1559	CAY, F, U, US	*E.* cf. *jenmanii*
Gillespie L.J. & Smart D.R. 2767	CAY, US	*E. falcata*
Gillespie L.J. et al. 2588	CAY, F, U, US	*E. schomburgkiana*
Gleason H.A. 332	US	*E. schomburgkiana*
Gleason H.A. 718	US	*E. jenmanii* (flowers) *E. falcata* (leaves)
Gleason H.A. 837	US	*E. jenmanii* subsp. *jenmanii*
Goeldi E.A. s.n. MG1158	US, RB00140284	*E. rubiginosa* var. *rubiginosa*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Goeldi E.A. s.n. MG3862	MG003862, US, RB00140284	*E. glabriflora*
Goldenberg R. et al. 2522	MG, RB	*E. rubiginosa* var. *rubiginosa*
Goldenberg R. et al. 2632	RB, UPCB	*E. grandiflora* subsp. *grandiflora*
Gonçalves A.S. 01	IAN	*E. cerradoensis*
Gonçalves A.S. 02	INPA, RB, UEC, US	*E. cerradoensis*
Gonçalves V.F. s.n. RB422083	RB	*E. oleifera*
Gonggrijp J.W. 2577, 5515	U	*E. rubiginosa* var. *rubiginosa*
Gonggrijp J.W. 3700	U	*E. rubiginosa* var. *grandiflora*
Görts-van Rijn A.R.A. et al. 403	CAY, U, US	*E. grandiflora* subsp. *guyanensis*
Granville J-J. de B3674	CAY, P, U	*E. rubiginosa* var. *rubiginosa*
Granville J-J. de 4528, 6708	CAY	*E. falcata*
Granville J-J. de 4528A	CAY, P	*E. falcata*
Granville J-J. de 8251	CAY, P, U	*E. falcata*
Granville J-J. de 8288	CAY, P, U	*E. rubiginosa* var. *rubiginosa*
Granville J-J. de 9666	CAY, US	*E. rubiginosa* var. *rubiginosa*
Granville J-J. de et al. 8184	CAY, P, U, US	*E. rubiginosa* var. *rubiginosa*
Grazzioli V. 6	CAY	*E. falcata*
Gregório B.S. 309, 310	INPA	*E. glabriflora*
Grenand P. 610	CAY, US	*E. falcata*
Grenand P. 1521	CAY	*E. rubiginosa* var. *rubiginosa*
Grenand P. 3060	CAY, P	*E. falcata*
Grenand P. 3082	CAY, P	*E. grandiflora* subsp. *grandiflora*
Grenand P. 3133	CAY	*E. falcata*
Grewal M.S. & Persuad R. 189	U	*E. falcata*
Guanchez-Meza F.J. 2163	MO	*E. banaensis*
Guppy N.G.L. 430	K, NY, RB, US	*E. glabra*
Hahn W.J. & Tiwari S. 5181	CAY, U, US	*E. falcata*
Hahn W.J. 3744	CAY, U, US, WAG	*E. grandiflora* subsp. *grandiflora*
Hahn W.J. 3747	CAY, P, U, US	*E. falcata*
Hahn W.J. et al. 3902	US	*E. falcata*
Hall C.J.J. van 11	WAG	*E. falcata*
Hallé F. & Kaiser R. 4361	U	*E. falcata*
Hallé F. 4143	CAY	*E. falcata*
Hallé F. 4404	MPU, U	*E. falcata*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Hallé F. 4425	MPU, U	*E. grandiflora* subsp. *grandiflora*
Hallé F. 4449	MPU, U	*E. rubiginosa* var. *rubiginosa*
Hallé F. 732	US	*E. rubiginosa* var. *rubiginosa*
Haroldo s.n. INPA57650	INPA	*E. glabriflora*
Heckel M. s.n. MPU1220190	MPU	*E. falcata*
Helstone E.M.C. 8095	U	*E. grandiflora* subsp. *guyanensis*
Henkel T.W. & Chin M. 388	U, US	*E. schomburgkiana*
Henkel T.W. & Chin M. 478	CAY, US	*E. jenmanii* subsp. *jenmanii*
Henkel T.W. & Chin M. 560	US	*E. schomburgkiana*
Henkel T.W. & Chin M. 649	U, US	*E. rubiginosa* var. *rubiginosa*
Henkel T.W. & Chin M. 669	U, US	*E. schomburgkiana*
Henkel T.W. & Williams R. 2128	US	*E. jenmanii* subsp. *jenmanii*
Henkel T.W. & Williams R. 2474, 2752	US	*E. schomburgkiana*
Henkel T.W. & Williams R. 2715	U, US	*E. jenmanii* subsp. *jenmanii*
Henkel T.W. et al. 1798	US	*E. schomburgkiana*
Henkel T.W. et al. 3100	U, US	*E. rubiginosa* var. *rubiginosa*
Henkel T.W. et al. 4142	CAY, U, US	*E. falcata*
Henkel T.W. et al. 4587	U, US	*E. rubiginosa* var. *rubiginosa*
Henkel T.W. et al. 4598	CAY, U, US	*E. rubiginosa* var. *rubiginosa*
Henkel T.W. et al. 4655	CAY, U, US	*E. glabra*
Hitchcock A.S. 17089	US	*E. schomburgkiana*
Hoff M. 5895, 7070	CAY	*E. falcata*
Hoff M. 5906	CAY, US	*E. rubiginosa* var. *rubiginosa*
Hoff M. 5964, 6735, 6890	CAY	*E. rubiginosa* var. *rubiginosa*
Hoff M. 6767	CAY, P	*E. rubiginosa* var. *rubiginosa*
Hoffman B. & Capellaro C. 844	INPA, US	*E. jenmanii* subsp. *jenmanii*
Hoffman B. & Roberts L. 2502	US	*E. jenmanii* subsp. *jenmanii*
Hoffman B. & Rodrigues M.T. 4837	US	*E. falcata*
Hoffman B. 4599	U, US	*E. falcata*
Hoffman B. 5914, 5928	US	*E. rubiginosa* var. *rubiginosa*
Hoffman B. 6522	L, MO, US	*E. falcata*
Hoffman B. et al. 718	CAY, U, US	*E. falcata*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Holanda A.S.S. et al. 799	INPA	*E. oleifera* var. *campestris*
Hollowell T.H. & Redden K.M. 561	CAY, NY, US	*E. falcata*
Hopkins M.J.G. 1581	HUEFS, INPA, MG, P, PEUFR, VIC	*E. glabriflora*
Hort Bot Bogoriensis II.0 9	L (1951223)	*E. falcata*
Hostmann F.W.R. & Kappler A. 1689	G, MO, P, TUB, U	*E. rubiginosa* var. *rubiginosa*
Hostmann F.W.R. 229	CAY, K, U	*E. rubiginosa* var. *rubiginosa*
Huber O. 3376	US	*E. purpurea*
Hulk J.F. 227	U	*E. falcata*
Humbert H. 27386	P, US	*E. leucantha*
Humbert H. 27386	US	*E. purpurea*
Ibáñez A. et al. 5358, 5648	MA	*E. falcata*
IFAT 7831, 7937	MG	*E. rubiginosa* var. *rubiginosa*
Imamoto M. 15	COAH	*E. leucantha*
Irwin G.T. et al. 57579	P, U, US, WAG	*E. rubiginosa* var. *rubiginosa*
Irwin H.S. & Pires J.M. 48613	IAN, MG, NY, U, US	*E. falcata*
Irwin H.S. & Westra L.Y.T. 47471	IAN, K, MG, NY, U, US	*E. rubiginosa* var. *rubiginosa*
Irwin H.S. et al. 48277	F, IAN, MG, NY, US	*E. falcata*
Irwin H.S. et al. 48408	IAN, MG, NY, U, US	*E. falcata*
Irwin H.S. et al. 55448	P, U	*E. falcata*
Irwin H.S. et al. 55467	F, MO, NY?, RB, SP, U, US	*E. falcata*
Irwin H.S. et al. 55716	MO, U, US	*E. falcata*
Irwin H.S. et al. 57579	P, US	*E. rubiginosa* var. *rubiginosa*
Jacquemin H. 2439	CAY	*E. grandiflora* subsp. *grandiflora*
Jaimes-Roncancio M.S. 1110	COAH	*E. leucantha*
Jansen-Jacobs M.J. 5623	U, US	*E. falcata*
Jansen-Jacobs M.J. et al. 1437	CAY, F, INPA, MO, P, U, US	*E. rubiginosa* var. *rubiginosa*
Jansen-Jacobs M.J. et al. 6813	L	*E. falcata*
Jansen-Jacobs M.J. et al. 6984	U	*E. falcata*
Jenman G.S. 2154	K	*E. jenmanii* subsp. *jenmanii*
Jenman G.S. 4770	BM, K	*E. jenmanii* subsp. *jenmanii*
Jenman G.S. 573	K, NY	*E. jenmanii* subsp. *jenmanii*
Jimenez-Saa J.H. 14275, 14330	U	*E. falcata*
Jimenez-Saa J.H. 14358	U, P	*E. falcata*
Jimenez-Saa J.H. 14414, 1623 (L.B.B. 14356)	U	*E.* cf. *grandiflora*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Jimenez-Saa J.H. 1627 (143360)	F	*E. falcata*
Jimenez-Saa J.H. 1698 (L.B.B. 14431)	U	*E. grandiflora* subsp. *grandiflora*
Jorge s.n. INPA57656	INPA	*E. glabriflora*
Junker L. 249	WAG	*E. rubiginosa* var. *rubiginosa*
Junker L. 507, 526	L	*E. falcata*
Kappler A. 1689	G, MO, P, TUB, U, W	*E. rubiginosa* var. *rubiginosa*
Kelloff C.L. & McKee G.S. 1246	US	*E. rubiginosa* var. *rubiginosa*
Kelloff C.L. & Roesel C.C. 1155	CAY, U, US	*E. falcata*
Kelloff C.L. et al. 1179, 1183, 1259	US	*E. rubiginosa* var. *rubiginosa*
Kelloff C.L. et al. 1298	F, US	*E. rubiginosa* var. *rubiginosa*
Kelloff C.L. et al. 1331	US	*E. rubiginosa* var. *rubiginosa*
Killip E.P. 37477	US	*E. jenmanii* subsp. *sandwithii*
Kinupp V.F. & H. Lorenzi 3261	EAFM, R	*E. glabriflora*
Kinupp V.F. et al. 3860	EAFM, RB	*E. duckeana*
Kinupp V.F. et al. 3887, 4542	EAFM	*E. duckeana*
Kinupp V.F. et al. 4552	EAFM	*E. glabriflora*
Klitgaard B.B. & Hopkins M. 32	HUEFS, INPA, K, RB	*E. duckeana*
Koch A.K. et al. 235	IAN, MG	*E. bijuga*
Kodjoed J.-F. 140	CAY	*E. falcata*
Krukoff B.A. 8006	K, MO, NY, P, U	*E. glabriflora*
Kuhlmann J.G. s.n. RB46435	RB	*E. oleifera*
Kunhardt H.R. 20	NY	*E. venosa*
Kurtz B.C. s.n. RB292421	RB	*E. oleifera* var. *campestris*
Landinez A. 7	COAH, COL	*E. leucantha*
Landsbosbeheer 52, 53, 1402	U	*E. falcata*
Landsosbeheer 162	IPA, U	*E. rubiginosa* var. *rubiginosa*
Landsbosbeheer 311, 603, 704	U	*E. rubiginosa* var. *rubiginosa*
Landsbosbeheer 806	U	*E. schomburgkiana*
Landsbosbeheer 902	U	*E. falcata*
Lang H. & Persuad A.C. 272	F	*E. falcata*
Lang H. & Persuad A.C. s.n. F559241	F	*E. jenmanii* subsp. *jenmanii*
Lang H. 70	US	*E. jenmanii* subsp. *jenmanii*
Lanjouw J. & Lindeman J.C. 324	IAN, U	*E. rubiginosa* var. *rubiginosa*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Lanjouw J. 738	U	*E. rubiginosa* var. *rubiginosa*
Lanjouw J. 1209	U, US	*E. rubiginosa* var. *rubiginosa*
Larpin D. 187	CAY	*E. falcata*
Le Prieur M. s.n. US2494924	US	*E. rubiginosa* var. *rubiginosa*
Lemos M.C. 128	INPA	*E. duckeana*
Lescure J.P. 746	CAY	*E. grandiflora* subsp. *grandiflora*
Lescure J.P. 793	CAY, P	*E. rubiginosa* var. *rubiginosa*
Lescure s.n. P03465650	P	*E. grandiflora* subsp. *grandiflora*
Leter G. 11	U	*E. falcata*
Liesner R.L. & González A.C. 5860	L, US	*E. jenmanii* subsp. *sandwithii*
Liesner R.L. & Morillo G. 13972	US	*E. jenmanii* subsp. *sandwithii*
Liesner R.L. & Morillo G. 13981	US	*E. jenmanii*
Liesner R.L. 3742, 4049	US	*E. purpurea*
Liesner R.L. 3743, 6079, 16263, 16285	US	*E. leucantha*
Lima H.C. de et al. 2824	RB	*E. oleifera* var. *campestris*
Lima H.C. de et al. 3163, 3221	INPA, MO, NY, RB	*E. purpurea*
Lima H.C. de et al. 3170, 3237	INPA, MO, NY, RB	*E. leucantha*
Lima H.C. de et al. 8202	HUEFS, RB	*E. duckeana*
Lima H.C. de et al. s.n. RB224026	RB	*E. oleifera* var. *campestris*
Lima L.F.G. et al. 290, 291	MG, RB	*E. bijuga*
Lima R.R. de et al. 97	MO, NY	*E. glabriflora*
Lindeman J.C. & Roon A.C. 1980/860	U	*E. falcata*
Lindeman J.C. 4649	F, U	*E. falcata*
Lindeman J.C. 6344	U	*E. rubiginosa* var. *rubiginosa*
Lindeman J.C. 7257 (L.B.B.)	U	*Eperua* sp.
Lindeman J.C. et al. 1975/769	U	*E. falcata*
Little Jr. E.L. 16795	U	*E. jenmanii* subsp. *jenmanii*
Little Jr. E.L. 16824	US	*E. falcata*
Little Jr. E.L. 16825	U, US	*E. falcata*
Little Jr. E.L. 16842	U, US	*E. falcata*
Lobão A. & Cordeiro M. 1112	IAN	*E.* cf. *grandiflora*
Lobão A. et al. 1002	HAMAB, IAN, RB	*E. falcata*
Lobão A. et al. 889	HAMAB, RB	*E. rubiginosa* var. *rubiginosa*
Lobato L.C.B. & Ferreira L. 4007, 4062	MG	*E. bijuga*
Lobato L.C.B. et al. 566	MG	*E. bijuga*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Lobato M. 9	WAG	*E. falcata*
Lobato M. s.n. WAG1633816	WAG	*E. falcata*
Lobo G.S. 14	INPA	*E. duckeana*
Loubry D. 1115, 1118, 1168, 1172, 1287	CAY	*E. falcata*
Loubry D. 1323	CAY, MPU	*E. rubiginosa* var. *rubiginosa*
Loubry D. 1368	CAY, MPU	*E. falcata*
Loubry D. 1473	CAY	*E. rubiginosa* var. *rubiginosa*
Loubry D. 1480	CAY	*E. falcata*
Loubry D. 1493	CAY, MPU	*E. falcata*
Loubry D. 1605	CAY, MPU	*E. grandiflora* subsp. *grandiflora*
Loubry D. 1811	CAY, U	*E. falcata*
Loubry D. 1851	CAY, MPU	*E. rubiginosa* var. *rubiginosa*
Loubry D. 1865	CAY, MPU	*E. grandiflora* subsp. *grandiflora*
Loubry D. 2343	CAY, MPU	*E. falcata*
Loubry D. 40, 700	CAY	*E. falcata*
Loubry D. 707	CAY	*E. rubiginosa* var. *rubiginosa*
Loureiro A.A. et al. s.n. INPA35822, INPA48178	INPA	*E. glabriflora*
Loureiro A.A. s.n. INPA48178	INPA	*E. duckeana*
Luetzelburg P. von 20211	R	*E. rubiginosa* var. *rubiginosa*
Luetzelburg P. von 20397, 20399, 21247	R	*E. rubiginosa* var. *rubiginosa*
Lui Y. et al. 2, 178	HUEFS	*E. cerradoensis*
Luiz 23	MG	*E. glabriflora*
Maas P.J.M. & Westra L.Y.T. 3981	U, US	*E. jenmanii* subsp. *jenmanii*
Maas P.J.M. et al. 6741	INPA, K, MG, MO, NY, RB, U, US	*E. leucantha*
Macedo M.T.S. 17506, 17508	INPA	*E. oleifera* var. *oleifera*
Maciel U.N. et al. 2147	MG	*E. bijuga*
Mackenzie C.A. et al. s.n. INPA2108.18	INPA, NY	*E. glabriflora*
Mackenzie C.A. et al. s.n. INPA2107.25	NY	*E. glabriflora*
Mackenzie C.A. et al. s.n. INPA2108.129, INPA2108.154	NY	*E. duckeana*
Madison M.T. et al. 319	INPA, RB	*E. purpurea*
Madison M.T. et al. 397	INPA	*E. leucantha*
Madison M.T. et al. 6319	K, NY, U, US	*E. purpurea*
Madison M.T. et al. 6397	F, K, NY, U, US	*E. leucantha*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Magalhães F.M.M. 223	INPA	*E. glabriflora*
Maguire B. 23804	F, U, US	*E. rubiginosa* var. *grandiflora*
Maguire B. 24720, 24778	F, U, US	*E. falcata*
Maguire B. 29311	RB	*E. purpurea*
Maguire B. 29486	NY, P, US	*E. purpurea*
Maguire B. 33136	F, NY, RB, P, US	*E. jenmanii* subsp. *sandwithii*
Maguire B. 36452	IAN, U	*E. purpurea*
Maguire B. et al. 36307	US	*E. leucantha*
Maguire B. et al. 36508	F	*E. leucantha*
Maguire B. et al. 41776	IAN, RB, U, US	*E. purpurea*
Maguire B. et al. 41922	US	*E. purpurea*
Maguire B. et al. 42610	F, MO, RB, P, U, US	*E. leucantha*
Maguire B. et al. 46734	US	*E. jenmanii* subsp. *sandwithii*
Maguire B. et al. 48408	U	*E. falcata*
Maguire B. et al. 53514	NY, US	*E. venosa*
Maguire B. et al. 53597	RB, U, US	*E. venosa*
Maguire B. et al. 54014	F, RB, P, U, US	*E. rubiginosa* var. *rubiginosa*
Maguire B. et al. 54401	F, SP, MO, U	*E. falcata*
Maguire B. et al. 60112	IAN, NY, US	*E. purpurea*
Maguire B. et al. 60130	F, IAN, NY, US	*E. leucantha*
Maguire B. et al. 60421	IAN, NY, US	*E. purpurea*
Marcano-Berti L. & Salcedo P. 40-979	US	*E. leucantha*
Marcano-Berti L. & Salcedo P. 65-979, 72-979	US	*E. purpurea*
Marinho M.A.O. 606, 629	UB	*E. cerradoensis*
Marra D.M. & Neves A.F. 78	EAFM	*E. duckeana*
Marra D.M. et al. 258, 322, 584, 1089	EAFM	*E. glabriflora*
Martin s.n. BM000065079	BM, F	*E. jenmanii* subsp. *jenmanii*
Martinelli G. et al. 7169	INPA, MG, MO, NY, RB, US	*E. duckeana*
Martinelli G. et al. 7180	NY, RB	*E. rubiginosa* var. *rubiginosa*
Martinelli G. et al. 7254	INPA, MG, MO, NY, RB, US	*E. duckeana*
Martínez X. 3476	COAH	*E. leucantha*
Martínez X. et al. 3325-3, 3325-5, 3476-2	COL	*E. leucantha*
Martins-da-Silva R.C.V. & Ferreira G.C. 3	IAN	*E. bijuga*
Martins-da-Silva R.C.V. & Ferreira G.C. 9	IAN, K	*E. bijuga*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Martius C.F.P. s.n.	K000555103, LE00002232, M0215266, M021526, M0215268, M0215270	*E. bijuga*
Martius C.F.P. s.n.	M0215265	*E. bijuga*
Martius C.F.P. s.n.	M0215269	*E. bijuga*
Martius C.F.P. s.n.	L1951212	*E. bijuga*
Mattos J.R. & Nadruz M.C. 505	RB01214719	*E. glabriflora*
McDowell T. & Gopaul D. 2451	U, US	*E. falcata*
McDowell T. & Gopaul D. 3710	INPA, US	*E. falcata*
McDowell T. 3271	INPA, US	*E. rubiginosa* var. *rubiginosa*
McDowell T. 3271a	MO, US	*E. falcata*
McDowell T. 3335	CAY, INPA, U, US	*E. schomburgkiana*
McDowell T. 3714	CAY, U, US	*E. jenmanii* subsp. *jenmanii*
Medeiros H. et al. 3109, 3144, 3229	RB	*E.* cf. *grandiflora* subsp. *grandiflora*
Meijeraan J.W. 42	WAG	*E. falcata*
Mélinon M. 216	P (03465199)	*E. rubiginosa* var. *rubiginosa*
Mélinon M. s.n. F540062	F V0111380F	*E. falcata*
Mélinon M. s.n. P03465212	P	*E. falcata*
Mélinon M. s.n. P03465213, P03465687, P02851506	P	*E. falcata*
Mélinon M. s.n. US00242843, P03465184, MPU1220187, MPU1220186, R67023	MPU, P, US	*E. falcata*
Mélinon M. s.n. US1112766, P03465214	P, US	*E. falcata*
Mello F.C. de & Coêlho D. INPA3913	IAN, INPA, US	*E. duckeana*
Mello F.C. de & Ribamar s.n. INPA58309	INPA	*E. duckeana*
Mello F.C. de & Ribamar s.n. INPA58312	INPA	*E. glabriflora*
Mello F.C. de s.n. INPA55353	INPA	*E. glabriflora*
Melo M.F.F. et al. 709	INPA	*E. glabriflora*
Mennega A.M.W. 102	U	*E. rubiginosa* var. *rubiginosa*
Mennega A.M.W. 441	U	*E. falcata*
Mexia Y.E.J. 5982	BH, F, IAN, K, MO, NY, U, US	*E. bijuga*
Miller J.S. 1707	F, U, US	*E. leucantha*
Milliken W. 2106	INPA, K, MIRR, NY	*E. jenmanii* subsp. *sandwithii*
Molino J.F. 1665, 1667, 1673, 1677, 1772, 1785, 1787, 1791, 1808, 1810, 1812, 1814, 1816, 1819, 1821, 1837, 1843	CAY	*E. falcata*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Monteiro O.P. & Mello F. s.n. INPA50065	INPA	*E. glabriflora*
Monteiro O.P. s.n. INPA27363	INPA, U, US	*E. duckeana*
Montoya-Jiménez M. 2728	COAH	*E. leucantha*
Mori S.A. & Bolten A. 8673	U	*E. rubiginosa* var. *rubiginosa*
Mori S.A. & Boom B.M. 14745	CAY, MO, US	*E. falcata*
Mori S.A. & Cardoso J. 17120	HAMAB, MG, NY	*E. rubiginosa* var. *rubiginosa*
Mori S.A. & Smith N.P. 25162	CAY, F, MO, NY, P, U, US	*E. grandiflora* subsp. *grandiflora*
Mori S.A. et al. 8056	U	*E. falcata*
Mori S.A. et al. 8162	U, US	*E. schomburgkiana*
Mori S.A. et al. 20363	INPA, MO, NY	*E. glabriflora*
Mori S.A. et al. 20631	INPA, NY, US	*E. glabriflora*
Mori S.A. et al. 21517	CAY, P, US	*E. falcata*
Mori S.A. et al. 23384	CAY	*E. falcata*
Mori S.A. et al. 23617	CAY, NY	*E. rubiginosa* var. *rubiginosa*
Mori S.A. et al. 26526, 26530, 26531, 26546, 26551, 26647, 26668, 26673, 26674, 26675	CAY	*E. falcata*
Morillo G. & Liesner R.L. 8886	US	*E. jenmanii* subsp. *sandwithii*
Mota C.D.A. da & Monteiro O.P. s.n. INPA60692, INPA60907, INPA60936	INPA	*E. oleifera* var. *campestris*
Mota C.D.A. da 717	INPA	*E. duckeana*
Mota C.D.A. da s.n. INPA60612, INPA61611	INPA	*E. oleifera* var. *campestris*
Mutchnick P. 753	US	*E. falcata*
Mutchnick P. & Allicock B. 438	U, US	*E. falcata*
Mutchnick P. & Allicock B. 446	CAY, U, US	*E. rubiginosa* var. *rubiginosa*
Mutchnick P. & Allicock B. 536	U, US	*E. schomburgkiana*
Mutchnick P. & Allicock B. 726	US, CAY	*E. schomburgkiana*
Mutchnick P. & Allicock B. 728	US	*E. schomburgkiana*
Mutchnick P. & Funk V.A. 675	US	*E. schomburgkiana*
Mutchnick P. et al. 216	CAY, U, US	*E. falcata*
Nadruz M.C. & Fabiano 3316	RB01377761	*E. glabriflora*
Nadruz M.C. 98	RB	*E. bijuga*
Nascimento J.R.M. et al. 1202.6089	INPA	*E. glabriflora*
Nascimento J.R.M. et al. 1302.2492	INPA, NY	*E. glabriflora*
Nascimento J.R.M. et al. 1302.675, 1302.775, 1302.798	INPA, NY	*E. duckeana*
Nascimento J.R.M. et al. 1302.783	NY	*E. duckeana*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Nascimento O.C. do 398	MG, NY, US	*E. bijuga*
Nascimento O.C. do 646	MG, MO, NY, RB, US	*E. purpurea*
Nascimento O.C. do 691	HRCB, MG, NY	*E. leucantha*
Nascimento O.C. do et al. 29	IAN, RB	*E. leucantha*
Nascimento O.C. do et al. 101	IAN, INPA, MG, NY, RB	*E. purpurea*
Nee M.H. 30850	NY, MG, US	*E. leucantha*
Nelson B.W. P21121	INPA, MG, MO, NY, P, U, US	*E. glabriflora*
Nelson B.W. & Lima J.F. P21068	INPA, MG, MO, NY, P, R, S, U, US	*E. glabriflora*
Nelson B.W. et al. 1610	HUEFS, INPA	*E. duckeana*
Neves D.M. et al. 1983	HUEFS, RB	*E. bijuga*
Niel F. van 281	WAG	*E. falcata*
Norden N. & Delnatte C. 12	CAY	*E. falcata*
Occhioni P. s.n. RFA5911	RFA	*E. oleifera var. campestris*
Ogtrop F. van 1	WAG	*E. falcata*
Oldeman R.A.A. 218	CAY, P, U	*E. falcata*
Oldeman R.A.A. 677	CAY, P, US	*E. falcata*
Oldeman R.A.A. 1093	CAY	*E. falcata*
Oldeman R.A.A. 1212	CAY, L, P	*E. falcata*
Oldeman R.A.A. 1389	CAY, P, U	*E. rubiginosa* var. *rubiginosa*
Oldeman R.A.A. 1520	CAY, U	*E. rubiginosa* var. *rubiginosa*
Oldeman R.A.A. 1552	CAY, L, P	*E. rubiginosa* var. *rubiginosa*
Oldeman R.A.A. 1598, 1606, 1613, 1640	CAY, P, U	*Eperua* sp.
Oldeman R.A.A. 2664	CAY, P, US	*E. rubiginosa* var. *rubiginosa*
Oldenburger F.H.F. et al. 568	U	*E. rubiginosa* var. *rubiginosa*
Oldenburger F.H.F. et al. 1203	U	*E.* cf. *glabra*
Oliveira A.A. de et al. 941	ESA	*E. glabriflora*
Oliveira A.A. de et al. 1576	ESA, UNIP	*E. glabriflora*
Oliveira A.A. de et al. 3448	UNIP	*E. glabriflora*
Oliveira A.C.A. 409	INPA	*E. duckeana*
Oliveira A.C.A. et al. 242, 368, 369	INPA	*E. glabriflora*
Oliveira A.R. de s.n. INPA 59696, INPA58701, INPA59614, INPA73462, INPA73463, INPA73464, INPA73465, INPA73466	INPA	*E. glabriflora*
Oliveira D. 66	UB	*E. cerradoensis*
Oliveira E. 2709	IAN	*E. glabriflora*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Oliveira E. 2737	IAN	*E. duckeana*
Oliveira E. 4929	IAN	*E. bijuga*
Oliveira E. 6291	MG, RB	*E. bijuga*
Oliveira J. et al. 379	MG	*E. bijuga*
Ooststroom S.J. van 12734	L	*E. falcata*
Outer R.W. den 963	L, U	*E. falcata*
Paget D. 49	CAY	*E. falcata*
Paget D. 50	CAY	*Eperua* sp.
Paget D. 51	CAY	*E. rubiginosa* var. *rubiginosa*
Pena B.S. 326	IAN	*E. oleifera* var. *campestris*
Pena B.S. 499	IAN	*E. glabra*
Pena B.S. 691	IAN	*E. oleifera* var. *campestris*
Pennington R.T. & Whitmore T.C. 336	U, US	*E. rubiginosa* var. *rubiginosa*
Pennington R.T. 373	U	*E. schomburgkiana*
Pennington R.T. et al. 372	CAY, U, US	*E. falcata*
Pereira E. da C. et al. 0, 68, 85, 91, 116	INPA	*E. duckeana*
Pereira L.A. & Cardoso J.O. 825	RB	*E. falcata*
Perez-C. A. et al. 795	CAY	*E. falcata*
Perrottet? s.n. P03465689, P03465690	P	*E. rubiginosa* var. *rubiginosa*
Persaud A.C. 243	F	*E. falcata*
Persuad A.C. 14, 166, 183	F	*E. schomburgkiana*
Pessoal do C.P.F. INPA6065	INPA, K, MG, US	*E. glabriflora*
Pessoal do C.P.F. INPA6280	IAN, INPA, US	*E. glabriflora*
Pessoal do Proj. Radam 13234	IAN	*E. oleifera* var. *campestris*
Petrov I. 124	CAY	*E. falcata*
Petrov I. s.n. P03465196, P03465198	P	*E. falcata*
Phillippe L.R. et al. 26998	CAY	*E. falcata*
Pipoly J.J. & Boyan R. 8585	CAY, INPA, MO, US	*E. grandiflora* subsp. *guyanensis*
Pipoly J.J. & Boyan R. 8591	CAY, INPA, US	*E. falcata*
Pipoly J.J. & Boyan R. 8701	CAY, US	*E. falcata*
Pipoly J.J. & Boyan R. 8799	U, US	*E. grandiflora* subsp. *grandiflora*
Pipoly J.J. & Boyan R. 8821	U, US	*E. falcata*
Pipoly J.J. & Boyan R. 8948	U, US	*E. grandiflora* subsp. *guyanensis*
Pipoly J.J. & Boyan R. 8967	P, U, US	*E. grandiflora* subsp. *guyanensis*
Pipoly J.J. & Gharbarran G. 9533	MO, US	*E. schomburgkiana*
Pipoly J.J. & Godfrey H. 7482	CAY, COL, MO, US	*E. falcata*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Pipoly J.J. 7534	CAY, MO, US	*E. falcata*
Pipoly J.J. 7542	COL, MO, U, US	*E. falcata*
Pipoly J.J. 7560	CAY, F, INPA, MO, P, U, US, WAG	*E. grandiflora* subsp. *guyanensis*
Pipoly J.J. et al. 11383	CAY, COL, F, MO, U, US	*E. schomburgkiana*
Pipoly J.J. et al. 11406	MO, US	*E. schomburgkiana*
Pipoly J.J. et al. 11448	CAY, MO, U, US	*E. schomburgkiana*
Pipoly J.J. et al. 11493	MA, MO, U, US	*E. schomburgkiana*
Pipoly J.J. et al. 11498	CAY, MO, U, US	*E. schomburgkiana*
Pires J.M. & Marinho L.R. 15679	IAN, MG, RB	*E. leucantha*
Pires J.M. & Marinho L.R. 15783	IAN	*E. purpurea*
Pires J.M. & Marinho L.R. 15914	IAN	*E. purpurea*
Pires J.M. & Silva N.T. 7878a	IAN	*E. leucantha*
Pires J.M. & Silva N.T. 11758	IAN	*E. bijuga*
Pires J.M. & Silva N.T. 11785	HUEFS, IAN, RB, MFS	*E. bijuga*
Pires J.M. & Westra L.Y.T. 48849	F, K, IAN, MG, NY, US	*E. rubiginosa* var. *rubiginosa*
Pires J.M. & Westra L.Y.T. 48876	IAN, K, MG, NY, US	*E. falcata*
Pires J.M. 468	IAN, INPA, IPA, NY, P, US	*E. purpurea*
Pires J.M. 481	ALCB, IAN	*E. leucantha*
Pires J.M. 531	IAC, IAN, NY, US	*E. leucantha*
Pires J.M. 978	IAC, IAN	*E. leucantha*
Pires J.M. et al. 50673	F, IAN, K, MG, NY, R, S, SP, U, US	*E. grandiflora* subsp. *grandiflora*
Pires J.M. et al. 50878	IAN, K, MG, NY, RB, U, US	*E. grandiflora* subsp. *grandiflora*
Pires J.M. et al. 51182	IAN, INPA, K, MG, NY, U, US	*E. rubiginosa* var. *rubiginosa*
Pires J.M. et al. 51307	IAN, INPA, K, MG, NY, U, US	*E. grandiflora* subsp. *grandiflora*
Pires J.M. et al. 51501	IAN, MG, NY, US	*E. rubiginosa* var. *rubiginosa*
Pires J.M. et al. 51659	F, IAN, K, NY, U, US	*E. grandiflora* subsp. *grandiflora*
Poeppig E.F. 2949	NY	*E. bijuga*
Polak A.M. 218	U	*E. glabra*
Polak A.M. 235	U	*E. grandiflora* subsp. *guyanensis*
Polak A.M. 252	U	*E. grandiflora* subsp. *guyanensis*
Polak A.M. 258, 391	U	*E. falcata*
Polak A.M. et al. 364	U	*E. grandiflora* subsp. *guyanensis*
Polak A.M. et al. 520	U	*E. jenmanii* subsp. *jenmanii*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Poncy O. 2652	CAY	*E. grandiflora* subsp. *grandiflora*
Poole J.M. 2115	INPA, MG, NY, RB	*E. leucantha*
Prance G.T. et al. 1458	IAN, K, MO, NY, U, US	*E. froesii*
Prance G.T. et al. 1652	F, IAN, K, NY, U, US	*E. froesii*
Prance G.T. et al. 3072	F, INPA, K, MG, NY, R, U, US	*E. duckeana*
Prance G.T. et al. 3709	F, INPA, K, MG, NY, R, S, US	*E. glabriflora*
Prance G.T. et al. 3720	INPA, NY	*E. duckeana*
Prance G.T. et al. 4637	F, INPA, K, MG, NY, R, U, US	*E. glabriflora*
Prance G.T. et al. 4977	F, INPA, K, MG, NY, P, R, U, US	*E. duckeana*
Prance G.T. et al. 10871	F, INPA, K, MG, NY, R, U, US	*E. jenmanii* subsp. *sandwithii*
Prance G.T. et al. 15025	INPA, K, MG, MO, NY, R, U, US	*E. duckeana*
Prance G.T. et al. 15513	INPA, K, MG, NY, P, R, U, US	*E. purpurea*
Prance G.T. et al. 15609	INPA, K, MG, NY, P, R, U, US	*E. purpurea*
Prance G.T. et al. 15684	INPA, K, MG, NY, P, R, U, US	*E. leucantha*
Prance G.T. et al. 18041	INPA, MG, MO, NY, P, U, US	*E. glabriflora*
Prance G.T. et al. 23446	F, INPA, K, MG, MO, NY, P, R, U, US	*E. glabriflora*
Prance G.T. et al. 23592	INPA, NY	*E. duckeana*
Prévost M.F. 321	CAY, MPU, P, U, US	*E. falcata*
Prévost M.F. 1723	CAY, INPA, P, US	*E. falcata*
Prévost M.F. 2577	CAY	*E. rubiginosa* var. *rubiginosa*
Prévost M.F. 2614	CAY	*E. rubiginosa* var. *rubiginosa*
Prévost M.F. 3143, 3178	CAY	*Eperua* sp.
Prévost M.F. 3176, 3179	CAY	*E. falcata*
Prévost M.F. 4038	CAY	*E. rubiginosa* var. *rubiginosa*
Prévost M.F. 4232	CAY, MO, US	*E. falcata*
Prévost M.F. 4278	CAY, MO	*Eperua* sp.
Prévost M.F. 4745, 4748	CAY	*Eperua* sp.
Pruski J.F. et al. 3258	K, HUEFS, INPA, NY, US	*E. duckeana*
Puig H. 10263, 10285	CAY	*E. falcata*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Purwanto Y. 729	CAY	*E. grandiflora* subsp. *grandiflora*
Purwanto Y. 743	CAY	*E. grandiflora* subsp. *grandiflora*
Queiroz L.P. de & Ferreira J.R.M. 13893	HUEFS, RB	*E. duckeana*
Queiroz L.P. de & Ferreira J.R.M. 13898	HUEFS	*E. duckeana*.
Queiroz L.P. de 13046	IAN, HUEFS	*E. bijuga*
Quiceno M.P. 30	COAH	*E. purpurea*
Rabelo B.V. & Cardoso J.O. 1261	HAMAB, MG, NY, US	*E. bijuga*
Rabelo B.V. & Nonato R. 630	HAMAB, MG	*E. bijuga*
Rabelo B.V. & Penafort C. 971	HAMAB, MG, NY, US	*E. bijuga*
Rabelo B.V. et al. 2850	HAMAB, K, MG, MO, NY, US	*E. falcata*
Rabelo B.V. et al. 3307	HAMAB, INPA, NY	*E. bijuga*
Rabelo B.V. et al. 3308	HAMAB, INPA, NY	*E. grandiflora* subsp. *grandiflora*
Ramos J.F. 1855	HUEFS, INPA, MG, MO, NY, SP, RB, U	*E. glabriflora* var. *gynopubescens*
Rech M. 4	P (03465697)	*E. rubiginosa* var. *rubiginosa*
Redden K.M. & Perry C. 1090	U, US	*E. falcata*
Redden K.M. et al. 1050, 1391, 2205, 3222, 3265, 4572, 4724	US	*E. falcata*
Redden K.M. et al. 1053, 1077	U, US	*E. grandiflora* subsp. *guyanensis*
Redden K.M. et al. 1054	U, US	*E. glabra*
Redden K.M. et al. 1058, 1059, 1109, 1238, 1239, 1643, 3197, 3245	U, US	*E. falcata*
Redden K.M. et al. 1108, 3105, 3175	U, US	*E. rubiginosa* var. *rubiginosa*
Redden K.M. et al. 1125	U, US	*E. schomburgkiana*
Redden K.M. et al. 1142, 2115, 2163, 3258, 3272, 6011, 6237	US	*E. schomburgkiana*
Redden K.M. et al. 1705, 1760, 2202, 5922, 6900	US	*E. jenmanii*
Redden K.M. et al. 1708	U, US	*E. jenmanii*
Redden K.M. et al. 1729	NY, US	*E. jenmanii*
Redden K.M. et al. 2059	NY (03777031), US	*E. grandiflora* subsp. *ciliata*
Redden K.M. et al. 2074	U, US	*E. jenmanii*
Redden K.M. et al. 2164, 3130, 3165, 3193, 5082, 6012, 6253	US	*E. rubiginosa* var. *rubiginosa*
Redden K.M. et al. 3156	U, US	Inflorescence and flowers, fruits in the fruit collection: *E. rubiginosa* var. *rubiginosa* Mounted fruit*:* problably *E. glabra*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Redden K.M. et al. 3187	NY (3196791), US	*E. glabra*
Redden K.M. et al. 3192	US	*E. glabra*
Redden K.M. et al. 3213	U, US	*E. jenmanii* subsp. *jenmanii*
Redden K.M. et al. 3241	CAY, U, US	*E. schomburgkiana*
Redden K.M. et al. 3250	INPA, US	*E. schomburgkiana*
Redden K.M. et al. 3260	US	*E. reddeniae*
Redden K.M. et al. 3261	INPA, COL, US	*E. rubiginosa* var. *grandiflora*
Redden K.M. et al. 3266, 4550	US	*E. jenmanii* subsp. *jenmanii*
Redden K.M. et al. 3270	CAY, COL, US	*E. falcata*
Redden K.M. et al. 3274	CAY, INPA, US	*E. reddeniae*
Redden K.M. et al. 3278	INPA, US	*E. jenmanii* subsp. *jenmanii*
Redden K.M. et al. 3286, 3304	US	*E. rubiginosa* var. *grandiflora*
Redden K.M. et al. 3388, 3396, 3560, 3694, 3697	US	*E. purpurea*
Redden K.M. et al. 3454, 3589, 3605, 3723	US	*E. leucantha*
Redden K.M. et al. 3860	CAY, US	*E. falcata*
Redden K.M. et al. 3962	CAY, US	*E. grandiflora* subsp. *ciliata*
Redden K.M. et al. 4029	US	*E. grandiflora* subsp. *ciliata*
Redden K.M. et al. 4231	NY (3196794), US	*E. schomburgkiana*
Redden K.M. et al. 5079	CAY, US	*E. schomburgkiana*
Redden K.M. et al. 5138	F, NY (03060744), U, US	*E. schomburgkiana*
Redden K.M. et al. 5974	CAY, US	*E. falcata*
Redden K.M. et al. 6005	CAY, US	*E. rubiginosa* var. *grandiflora*
Redden K.M. et al. 6123	CAY, MO, US	*E. schomburgkiana*
Redden K.M. et al. 6468	NY (03235876), US	*E. jenmanii* subsp. *jenmanii*
Redden K.M. et al. 6552	NY (03701883), US	*E. falcata*
Redden K.M. et al. 7059	CAY, US	*E. jenmanii* subsp. *sandwithii*
Reis I.P. & Quindere P.L. 7, 8	RB	*E. glabriflora*
Reis I.P. 9, 10, 11	HUTO, IAN	*E. bijuga*
Reis L.Q. s.n. INPA57645, INPA57694, INPA58591	INPA	*E. glabriflora*
Reuder & Roberts 12329	U	*E. falcata*
Ribamar J.R. do & Ramos J. 163	INPA	*E. duckeana*
Ribamar J.R. do & Ramos J. 197	COL	*E. purpurea*
Ribeiro B.G.S. 837	IAN	*E. leucantha*
Ribeiro J.E.L.S. & Pereira E. da C. 1209	INPA	*E. glabriflora*
Ribeiro J.E.L.S. 881	HUEFS, INPA, R	*E. glabriflora*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Ribeiro J.E.L.S. 921	INPA, UEC	*E. glabriflora*
Ribeiro J.E.L.S. et al. 894	INPA, K, R, UB	*E. duckeana*
Ribeiro J.E.L.S. et al. 1037	HUEFS, INPA, K, MO, NY, R, RB, SP, U	*E. duckeana*
Ribeiro J.E.L.S. et al. 1104	HUEFS, INPA, K, MG	*E. duckeana*
Richard C. s.n. P03465179	P	*E. bijuga*
Riéra B. 34	CAY	*E. falcata*
Riéra B. 454, 1349	CAY	*Eperua* sp.
Riéra B. 877bis	CAY	*E. falcata*
Roa T. A. 376	COL, UDBC	*E. purpurea*
Roa T. A. 945	COAH, COL, UDBC	*E. purpurea*
Rocha A.E.S. & Costa-Neto S.V. da 2165	MG	*E. bijuga*
Rodrigues A. 3	CAY	*E. falcata*
Rodrigues I.A. et al. 1000	IAN	*E. glabra*
Rodrigues J.S. 178	IAN, US	*E. leucantha*
Rodrigues M. dos S. 378	IAN	*E. bijuga*
Rodrigues W.A. 501	INPA, MG	*E. duckeana*
Rodrigues W.A. 562	INPA, MG, US	*E. glabriflora*
Rodrigues W.A. 905	INPA, U, US	*E. leucantha*
Rodrigues W.A. 1075	INPA	*E. leucantha*
Rodrigues W.A. 1807	INPA, US	*E. duckeana*
Rodrigues W.A. 2446	INPA	*E. glabriflora*
Rodrigues W.A. 8686	INPA, US	*E. duckeana*
Rodrigues W.A. s.n. INPA1043	INPA, MG21416	*E. glabriflora*
Rodrigues W.A. & Chagas J. 1725	HST, INPA, US	*E. duckeana*
Rodrigues W.A. & Chagas J. 2261	INPA	*E. glabriflora*
Rodrigues W.A. & Chagas J. 3061	US	*E. glabriflora*
Rodrigues W.A. & Coelho D. 7846	INPA	*E. glabriflora*
Rodrigues W.A. & Coelho D. 9610	INPA, MO	*E. oleifera* var. *oleifera*
Rodrigues W.A. & Lima J. 2233	INPA, US	*E. duckeana*
Rodrigues W.A. & Lima J. 2387	INPA	*E. duckeana*
Rodrigues W.A. & Osmarino 2396, 7903, 7921	INPA	*E. glabriflora*
Rodrigues W.A. & Osmarino 5723, 6932	INPA, US	*E. glabriflora*
Rodrigues W.A. & Osmarino 5982	HST, INPA, US	*E. glabriflora*
Rodrigues W.A. & Osmarino 6769	INPA, US	*E. duckeana*
Rodrigues W.A. & Osmarino 7005	HEPH, INPA, US	*E. glabriflora*
Rodrigues W.A. et al. 10690	HFSL, INPA, K, MG, MO, NY, RB, US	*E. leucantha*
Rodríguez M. et al. 1714	COAH	*E. leucantha*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Rodríguez R. & Acero E. 207	COL, UDBC	*E. purpurea*
Rombouts H.E. 170	U	*E. schomburgkiana*
Rombouts H.E. 177	U	*E. rubiginosa* var. *rubiginosa*
Rombouts H.E. 725	U	*E. rubiginosa* var. *rubiginosa*
Romero G. A. et al. 4079	GH, MO, VEN?, TFAV	*E. banaensis*
Romero-Castañeda R. 3487	COL	*E. leucantha*
Roosmalen M.G.M. van et al. 1305	INPA	*E. purpurea*
Roosmalen M.G.M. van et al. 1367	INPA	*E. purpurea*
Rosa N.A. 1183	MG	*E. rubiginosa* var. *rubiginosa*
Rosa N.A. 1288	MG	*E. bijuga*
Rosa N.A. 3628	INPA, MG, NY	*E. bijuga*
Rosário C.S. & Rosário D.O. 2011	MG, MO	*E. falcata*
S. 311	U1302897	*E. rubiginosa* var. *rubiginosa*
s.c. 12144 (P03465157, P03465159, P03465154)	P	*E. rubiginosa* var. *rubiginosa*
s.c. 12144 (P03465678)	P	*E. rubiginosa* var. *rubiginosa*
s.c. 1350 (1337617)	US	*E. jenmanii* subsp. *jenmanii*
s.c. 313 (P03465699)	P	*E. rubiginosa* var. *rubiginosa*
s.c. 323 (L1951216, L1951221)	L	*E. falcata*
s.c. 3777 (P03465138)	P	*Eperua* sp.
S.c. 7254 (P03465208)	P	*E. falcata*
s.c. 7260 (P03465205)	P	*E. falcata*
s.c. 7937 (P02771548)	P	*E. rubiginosa* var. *rubiginosa*
s.c. s.n. INPA7807	INPA	*E. purpurea*
s.c. s.n. L1951167	L	*E. rubiginosa* var. *rubiginosa*
s.c. s.n. NY01514877	NY	*E. falcata*
s.c. s.n. P03465139	P	*E. bijuga*
s.c. s.n. P03465148	P	*E. falcata*
s.c. s.n. P03465152	P	*E. falcata*
s.c. s.n. P03465204	P	*E. falcata*
s.c. s.n. P03465218	P	*E. falcata*
s.c. s.n. P03465226	P	*E. falcata*
s.c. s.n. P03465228	P	*E. falcata*
s.c. s.n. RB89490	RB	*E. purpurea*
s.c. s.n. U1302890	U	*E. rubiginosa* var. *rubiginosa*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
s.c.s.n. MPU1220188, MPU1220189	MPU	*E. falcata*
s.c.s.n. MPU1220191	MPU	*E. rubiginosa* var. *rubiginosa*
s.c.s.n. P02851526, P02851524	P	*Eperua*
s.c.s.n. P03465207	P	*E. falcata*
s.c.s.n. P03465686, P03465691	P	*E. rubiginosa* var. *rubiginosa*
s.c.s.n. RB89492	RB	*E. bijuga*
Sabajo P.H. & Roberts L. 11192	U	*E. falcata*
Sabatier D. & Prévost M.F. 3070	CAY	*E. falcata*
Sabatier D. & Prévost M.F. 3132, 3381	CAY	*Eperua* sp.
Sabatier D. & Prévost M.F. 4812	CAY, L	*E. falcata*
Sabatier D. & Prévost M.F. 4814	CAY, L	*E. falcata*
Sabatier D. 21, 521, 715, 1790	CAY	*E. falcata*
Sabatier D. 116, 1879	CAY	*Eperua* sp.
Sabatier D. 1018	CAY, P	*E. rubiginosa* var. *rubiginosa*
Sabatier D. 2328	CAY, US	*E. grandiflora* subsp. *grandiflora*
Sagot 183	P	*E. falcata*
Sagot s.n. MPU1220192	MPU	*E. falcata*
Sagot s.n. P03465201	P	*E. falcata*
Sagot s.n. P03465640	P	*E. grandiflora* subsp. *grandiflora*
Sakagawa S. & Mesquita J.R. 366	INPA, RB00716854	*E. glabriflora*
Sakagawa S. et al. 658	INPA, RB	*E. leucantha*
Sampaio A.J. 5760	R	*E. rubiginosa* var. *rubiginosa*
Sampaio A.J. 5818	R	*E. rubiginosa* var. *rubiginosa*
Sandwith N.Y. 137	RB, S, U	*E. falcata*
Sandwith N.Y. 142	RB, P, U, US	*E. schomburgkiana*
Sandwith N.Y. 314	RB, U	*E. grandiflora* subsp. *guyanensis*
Sandwith N.Y. 329	RB, U, US	*E. falcata*
Santini 1948	L	*E. rubiginosa* var. *rubiginosa*
Santos J.L. dos & Lima R.P. de 853	HUEFS, INPA, MG, MBM, R, UEC, US	*E. glabriflora*
Santos J.L. dos et al. s.n. INPA1202.4387	NY	*E. glabriflora*
Santos R.S. 296	UB	*E. cerradoensis*
Sastre C.H.L. 6123	CAY, P, U	*E. falcata*
Sauvain M. 479	CAY, P	*Eperua*
Sauvain M. 743	CAY, U, P	*E. falcata*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Schnell R.A.A. 11456	CAY, P, U, US	*E. rubiginosa* var. *grandiflora*
Schomburgk M.R. 1842-3 (982)	P	*E. grandiflora* subsp. *guyanensis*
Schomburgk R.H. 515	F	*E. rubiginosa* var. *rubiginosa*
Schomburgk R.H. 928	P	*E. grandiflora* subsp. *guyanensis*
Schomburgk Rob. or Rich. 317	K	*E. schomburgkiana*
Schomburgk Rob. Ser. I 517	BM, G, K, P, W	*E. schomburgkiana*
Schultes R.E. 9779	IAN, R, US	*E. purpurea*
Schultes R.E. & Cabrera I. 17872	COL, U, US	*E. leucantha*
Schultes R.E. & Cabrera I. 19324	COL, US	*E. purpurea*
Schultes R.E. & Cabrera I. 19338	COL	*E. purpurea*
Schultes R.E. & López F. 10337	IAN, NY, US	*E. oleifera* var. *campestris*
Schultes R.E. & López F. 9657b	IAN, K, US	*E. purpurea*
Schultes R.E. & Pires J.M. 9066	IAN, K, US	*E. purpurea*
Schultes R.E. et al. 17955	COL, U, US	*E. purpurea*
Schultes R.E. et al. 18268	U, US, WAG	*E. purpurea*
Schulz J.P. 7708	U, US	*E. schomburgkiana*
Schulz J.P. 10237, s.n. U1303081	U	*E. falcata*
Secco R.S. et al. 1010	MG	*E. bijuga*
Silva A.S.L. da & Rosário C. da S. 3836	MG	*E. bijuga*
Silva A.S.L. da et al. 3113	MG, MO	*E. bijuga*
Silva A.S.L. da et al. 3665	HAMAB, MG, SP	*E. bijuga*
Silva A.S.L. da et al. 3666	MG	*E. bijuga*
Silva A.S.L. da et al. 4443	IAN, MG	*E. bijuga*
Silva A.S.L. da & Gomes A. de O. 4365	MG	*E. bijuga*
Silva A.S.L. da & Silva M.C. da 2392	NY, RB, MG, MO, SP	*E. bijuga*
Silva A.V.V. da et al. 2108.130.2	INPA, K, NY	*E. duckeana*
Silva F.A. et al. 869	HSTM, MG	*E.* aff. *glabra*
Silva J.A.C. da et al. 1331, 1593	INPA	*E. glabriflora*
Silva J.A.C. da et al. 1418	INPA	*E. duckeana*
Silva J.A.C. da et al. 762	INPA	*E. leucantha*
Silva J.M. da et al. 3402.1357	INPA, NY	*E. glabriflora*
Silva M.C.R. da et al. 40	INPA	*E. duckeana*
Silva M.G. da & Pinheiro A.A.N. 5103	HAMAB, MAC, MG, NY	*E. bijuga*
Silva M.G. da 3391	MG	*E. bijuga*
Silva N.T. da & Santos M.R. 4758	F, MG, MO, NY, RB, US	*E. glabra*
Silva N.T. da 3751, 3772	IAN	*E. leucantha*
Silva N.T. da 3773	IAN	*E. purpurea*
Silva N.T. da 4420	MG, MO, NY, RB, US	*E. purpurea*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Silva S.F. da 205a	INPA	*E. duckeana*
Silva S.S. da 1301.4850.2	INPA, NY, US	*E. glabriflora*
Silva S.S. da 1301.4850.2	US	*E. glabriflora*
Silva S.S. da et al. 2303.1246.2	INPA, NY, US	*E. glabriflora*
Silva S.S. da et al. 3402.2079.2	INPA, NY, US	*E. glabriflora*
Silva S.S. da et al. 3402.2791.2	INPA, NY	*E. glabriflora*
Silva V.G. da & Mesquita J.R.F. 168	INPA	*E. glabriflora*
Silva V.G. da 75	INPA	*E. duckeana*
Smith A.C. 2741	F, U, US	*E. rubiginosa* var. *rubiginosa*
Smith A.C. 2882	F, P, U, US	*E. glabra*
Smith J.F. et al. 4131	CAY	*E. rubiginosa* var. *rubiginosa*
Sothers C.A. 243	HUEFS, INPA	*E. duckeana*
Souza F. de 48	INPA	*E. rubiginosa* var. *rubiginosa*
Souza I.M. 398, 403, 404A-B	HUEFS	*E. glabriflora*
Souza I.M. 416, 417	HUEFS	*E. duckeana*
Souza J.A. de 172	INPA, US	*E. duckeana*
Souza J.A. de s.n. INPA59559	INPA	*E. glabriflora*
Souza J.E. da C. KF995	INPA	*E. duckeana*
Souza L.A.G. de & Cortês A. 7	INPA	*E. leucantha*
Souza L.A.G. de & Cortês A. 8	INPA	*E. purpurea*
Souza L.A.G. de 13_97	INPA	*E. bijuga*
Souza L.A.G. de 582	INPA	*E. glabriflora*
Souza L.A.G. de et al. 28	INPA	*E. leucantha*
Souza M.A.D. de 1773	IAN	*E. rubiginosa* var. *rubiginosa*
Souza M.A.D. de 1780	IAN	*E. falcata*
Splitgerber F.L. 765	L	*E. falcata*
Splitgerber F.L. s.n. L1951162	L	*E. jenmanii* subsp. *jenmanii*
Splitgerber F.L. s.n. L1951218	L	*E. falcata*
Spruce R. 2021	BM, G, GH, K, M, P, W	*E. leucantha*
Spruce R. 2577	BM, F, G, GH, K, LE, M, NY, P, RB, W	*E. purpurea*
Spruce R. 6214	MO	*E. leucantha*
Stahel G. 22	BH, IAN, RB, U, WAG	*E. falcata*
Stahel G. 22a	IAN, U	*E. falcata*
Stahel G. 23	IAN, INPA, U, WAG	*E. falcata*
Stahel G. 334	IAN, MO, RB, U, WAG	*E. jenmanii*
Stahel G. 66	IAN, L, RB, U, WAG	*E. falcata*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Steege H. ter & Cornelissenr J.H.C. 183	U	*E. schomburgkiana*
Steege H. ter & Cornelissenr J.H.C. 184	U	*E. grandiflora* subsp. *guyanensis*
Steege H. ter & Cornelissenr J.H.C. 185	U	*E. falcata*
Steege H. ter 447	CAY, U	*E. grandiflora* subsp. *guyanensis*
Stergios B. & Matínez O. 9491	MO, US	*E. purpurea*
Stergios B. 11719	MO, US	*E. jenmanii*
Stergios B. 18387	MO	*E. purpurea*.
Stergios B. 18409, 18584	MO	*E. leucantha*
Stergios B. et al. 15492	MO, US	*E. leucantha*
Stergios B. et al. 6152	US	*E. jenmanii* subsp. *jenmanii*
Stergios B. et al. 9814	INPA	*E. purpurea*
Stergios B. et al. 9967	MO	*E. purpurea*
Steyermark J.A. & Luteyn J.L. 129765	U	*E. purpurea*
Steyermark J.A. & Luteyn J.L. 129766	F, U	*E. leucantha*
Steyermark J.A. 60376	F	*E. jenmanii*
Steyermark J.A. 60754	F (V0111457F)	*E. jenmanii*
Steyermark J.A. 75537	F	*E. jenmanii* subsp. *sandwithii*
Steyermark J.A. 76074	F	*E. jenmanii* subsp. *sandwithii*
Steyermark J.A. 86665	S, US	*E. jenmanii* subsp. *jenmanii*
Steyermark J.A. 86692	P, US	*E. falcata*
Steyermark J.A. 90416, 90724	US	*E. jenmanii* subsp. *sandwithii*
Steyermark J.A. 90458	US	*E. jenmanii*
Steyermark J.A. 102733	US	*E. leucantha*
Steyermark J.A. 115541	F	*E. venosa*
Stoffers A.L. et al. 62	CAY, U, US	*E. falcata*
Stoffers A.L. et al. 74	CAY, F, MG, U, US	*E. grandiflora* subsp. *guyanensis*
Stropp J. & Assunção P. 200, 289, 342, 344, 345	EAFM	*E. leucantha*
Stropp J. & Assunção P. 234	EAFM	*E. purpurea*
Stropp J. & Assunção P. 639	INPA, RB	*E. purpurea*
Stropp J. & Assunção P. 640	INPA	*E. leucantha*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Temple A. 216	MPU (MPU198120)	*E. falcata*
Thiel J. 13, 53, 98, 267, 543, 546, 546bis, 549, 550, 550bis, 551, 551bis, 552, 552bis, 553, 553bis, 554, 554bis, 556, 556bis, 557, 557bis, 560, 560bis, 561, 561bis, 561ter, 563, 564, 569, 575, 579, 580, 582, 583, 584, 593, 594, 596, 597, 598, 600, 605, 606, 608, 609, 611, 612, 613, 619, 621, 622, 623, 624, 625, 627, 628, 629, 630, 631, 632, 633, 634, 635, 639, 640, 641, 643, 644, 645, 646, 647, 648, 649, 651, 652, 653, 654, 655, 656, 658, 659, 708, 710, 723, 740, 742, 743, 744, 745, 747, 749, 750, 761, 762, 763, 765, 767, 768, 770, 775, 779, 781, 782, 783, 785, 787, 788, 792, 794, 797, 798, 800, 806, 832, 833, 835, 836, 852, 856, 857, 860, 861, 863, 864, 867, 868, 869, 870, 877, 879, 882, 883, 885, 889, 893, 925, 926, 928, 929, 930, 931, 932, 933, 956, 977, 978, 1176, 1177	CAY	*E. falcata*
Thiel J. 736, 815, 826, 827, 828, 890, 900	CAY	*E. grandiflora* subsp. *grandiflora*
Thiel J. 574, 586, 587, 588, 599, 601, 664, 665, 729, 735, 891, 892, 940	CAY	*E. rubiginosa* var. *rubiginosa*
Thiel J. 547, 547bis, 548, 558, 558bis, 602, 603, 604, 607, 610, 614, 615, 616, 617, 618, 620, 626, 636, 637, 638, 660, 661, 663, 691, 706, 707, 711, 712, 724, 725, 730, 731, 733, 734, 739, 751, 752, 753, 759, 764, 766, 769, 771, 772, 778, 780, 784, 793, 795, 796, 799, 801, 802, 803, 805, 812, 813, 820, 825, 829, 830, 842, 843, 854, 858, 862, 865, 866, 875, 880, 884, 887, 888, 895, 939, 943, 944, 946, 947, 949, 950, 954, 955, 957, 1178	CAY	*Eperua* sp.
Tillett S.S. & Tillett C.L. 45304	F, RB, US	*E. falcata*
Tillett S.S. & Tillett C.L. 45305	US	*E. jenmanii* subsp. *jenmanii*
Tillett S.S. & Tillett C.L. 45474	P, US	*E. jenmanii* subsp. *jenmanii*
Tillett S.S. & Tillett C.L. 45699	RB (115087)	*E. jenmanii* subsp. *jenmanii*
Tillett S.S. & Tillett C.L. 45791	RB (115086)	*E. falcata*
Tillett S.S. & Tillett C.L. 45794	IAN, US	*E. falcata*
Tiwari S. 851	NY	*E. schomburgkiana*
Tiwari S. 924	NY, US	*E. jenmanii* subsp. *jenmanii*
Tiwari S. 957	NY	*E. schomburgkiana*
Toriola-Marbot D. 631	CAY	*E. falcata*
Torke B.M. 432	IAN, RB	*E. bijuga*
Tostain O. et al. 2457	CAY	*E. grandiflora* subsp. *grandiflora*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Tresling J.H.A.T. 96	U	*E. rubiginosa* var. *rubiginosa*
Tresling J.H.A.T. 102	U	*E. rubiginosa* var. *rubiginosa*
Tresling J.H.A.T. 334	RB, U	*E. rubiginosa* var. *rubiginosa*
Tripp E.A. et al. 3350	NY, US	*E. falcata*
Trivellato C. & Gonçalves G.G. 31	EAFM	*E. leucantha*
Tutin T.G. 245	BM, K, U, US	*E. grandiflora* subsp. *guyanensis*
Tutin T.G. 459	US	*E. jenmanii* subsp. *jenmanii*
Ulitzka M. 25B	CAY	*E. falcata*
Vaillant S. s.n. P03465185, P03465705, P03465707, P03465693, P03465706, P03465695, P03465692	P	*E. rubiginosa* var. *rubiginosa*
Vaillant S. s.n. US2624144	US	*E. falcata*
Versteeg G.M. 48	CAY, U	*E. rubiginosa* var. *grandiflora*
Versteeg G.M. 157	U	*E. rubiginosa* var. *rubiginosa*
Versteeg G.M. 393	U	*E. falcata*
Versteeg G.M. 855	U	*E. rubiginosa* var. *rubiginosa*
Vicentini A. et al. 981	F, INPA, MG, P	*E. glabriflora*
Vicentini A. 2909, 2921	INPA	*E. oleifera* var. *oleifera*
Vieillescazes A. 616	CAY	*E. falcata*
Vieira M.G. et al. 178	EAFM, INPA, MG, MO, NY, R, RB	*E. oleifera* var. *campestris*
Villiers J.-F. 4386, 5266, 5273, 5409, 5447, 6333, 6355, 6357	CAY	*E. falcata*
Vogel S. 336	INPA	*E. leucantha*
Voltz F. s.n. U1302934, U1302936, U1302937	U	*E. rubiginosa* var. *rubiginosa*
Vreden C.C.J. 13673	U	*E. falcata*
Wachenheim G. & Hahn W. 328	U, US	*E. falcata*
Wachenheim G. 405	US	*E. falcata*
Wachenheim G. s.n. P03465191, P03465193	P	*E. falcata*
Weitzman A.L. & Hahn W.J. 328	U, US	*E. falcata*
Went F.A.F.C. 116	U	*E. rubiginosa* var. *rubiginosa*
Wessels J.G. Boer 1377	U	*Eperua* sp.
William 501	IAN	*E. duckeana*
Williams L. 13939	RB, U, US, WAG	*E. leucantha*
Williams L. 13990	F, RB, US	*E. purpurea*

Appendix 2. (Continued)

Collector / number	**Herbarium**	**Species**
Williams L. 14390	F, IAN, US	*E. leucantha*
Williams L. 14940, 15811	US	*E. leucantha*
Williams L. 14942	F, US	*E. leucantha*
Williams L. 14942a	F	*E. leucantha*
Williams L. 15801	F, US	*E. leucantha*
Williams L. 16183	US	*E. obtusata*
Wit H.C. de I.i. 70	L (1951226)	*E. falcata*
Wit H.C. de I.i. 70a	L (1951225)	*E. falcata*
Wurdack K.J. et al. 4681	US	*E. rubiginosa* var. *rubiginosa*
Wurdack K.J. et al. 4785	CAY, US	*E. schomburgkiana*
Wurdack K.J. et al. 5446	US	*E. jenmanii subsp. jenmanii*
Zartman C.E. 7885	INPA	*E. leucantha*
Zartman C.E. 7928	INPA, RB	*E. grandiflora* subsp. *guyanensis*
Zartman C.E. 7935	INPA	*E. grandiflora* subsp. *guyanensis*
Zartman C.E. et al. 5987	INPA, RB00716941	*E. glabriflora*
Zartman C.E. et al. 7014	INPA	*E. glabriflora*
Zarucchi J.L. & Balick M.J. 1765	COL, MO, US	*E. leucantha*
Zarucchi J.L. 2505	COAH, COL, U	*E. leucantha*
Zarucchi J.L. et al. 2842	HFSL, INPA, K, MG, MO, NY, RB, UFACPZ, US	*E. oleifera* var. *campestris*
Zarucchi J.L. et al. 2935	INPA, MG, NY, RB, US	*E. oleifera* var. *campestris*
Zarucchi J.L. et al. 2941	INPA, K, MG, MO, NY, RB, UFACPZ, US	*E. oleifera* var. *campestris*
Zarucchi J.L. et al. 3209	F, INPA, HFSL, MG, MO, NY, RB, UFACPZ, US	*E. oleifera* var. *oleifera*

ARTIGO IV

Submetido para publicação na revista Molecular Phylogenetics and Evolution.

FORTES, E. A., LANDIS, J. L., ter STEEGE, H., SPECHT, C. D., DOYLE, J. J., MANSANO, V. de F. A nuclear phylogenomic study of the Eperua *s.l.* clade (Leguminosae, Detarioideae) provides new insights into plant diversification in Amazonia. *Molecular Phylogenetics and Evolution*.

A nuclear phylogenomic study of the Eperua *s.l.* clade (Leguminosae, Detarioideae) provides new insights into plant diversification in Amazonia

Elenice A. Fortes[1], Jacob B. Landis[2,3], Hans ter Steege[4,5], Chelsea D. Specht[2], Jeff J. Doyle[2], and Vidal de F. Mansano[6]
[1]Instituto de Biologia, Universidade Estadual de Campinas, Campinas, SP, Brazil
[2]School of Integrative Plant Science, Section of Plant Biology and the L.H. Bailey Hortorium, Cornell University, Ithaca NY 14853 USA
[3]BTI Computational Biology Center, Boyce Thompson Institute, Ithaca NY 14853, USA
[4]Naturalis Biodiversity Center, Leiden, The Netherlands
[5]Quantitative Biodiversity Dynamics, Dept. of Biology, Utrecht, Utrecht University, The Netherlands
[6]Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro, 22460-030, RJ, Brazil

Eperua is a genus of Neotropical trees that form a major component of tropical lowland forests in Amazonia, especially along the Guiana Shield and in white-sand substrates. The genus is placed in the Eperua *s.l.* clade (Leguminosae, Detarioideae) along with three African tropical tree genera. *S*pecies in *Eperua* exhibit one of two drastically different floral architectures, each associated with different pollinators. Prior phylogenetic studies of *Eperua* have revealed an unstructured topology concerning floral architectures. Still, no investigations have been conducted into the evolution of traits or the origins and dispersal of *Eperua* in Amazonia. Using target capture sequencing with taxon-specific baits, we inferred the most comprehensive phylogeny for the Eperua *s.l.* clade sampling all 23 known species, among which five have been sampled for the first time. Maximum likelihood, coalescence, concatenation, and network methods were used to investigate sources of incongruence impacting resolution and support. With the primary focus on *Eperua*, we reconstructed the biogeographic history and investigated the evolution of the two floral types. Gene tree discordance leading to unresolved relationships is linked to reticulation events between sympatric lineages, potentially facilitated by pollinators or floral visitors. Biogeographical analyses suggest *Eperua* originated in the Neotropics via long-distance dispersal from Africa, primarily diversifying in the Guiana Shield due to altitude, climate, dispersal, and niche occupancy limitations. Our analyses of ancestral geographic areas and corolla morphotype reconstructions provide evidence that speciation in *Eperua* has occurred in sympatry, likely driven by pollinator shifts resulting from drastic changes in floral architecture.

Keywords: Biogeography, Fabaceae, Hyb-Seq, Hybridization, PhyloNetwork, pollinator syndrome, Trait evolution, Taxon-specific baits

1. Introduction

Species-level phylogenies are needed to understand the origin and diversification of rainforest inhabitants (Plana, 2004; Vargas and Dick, 2020), especially in Amazonia where a limited fossil record exists (Wesselingh et al., 2010). Previous studies have demonstrated that, besides dispersal (Dexter et al., 2017), a combination of rapid speciation and the gradual accumulation of lineages are drivers of plant diversification in Amazonia (Erkens et al., 2007; Richardson et al., 2001; Schley et al., 2018; Vargas and Dick, 2020). A similar pattern has been observed in African rainforests (Plana, 2004). Notably, rapid speciation during the Quaternary period is associated with numerous lineages of species-rich genera (~300 species) in Amazonia, such as *Inga* Mill. (Leguminosae) (Richardson et al., 2001) and *Guatteria* Ruiz & Pav. (Annonaceae) (Erkens et al., 2007). Conversely, smaller to medium-sized genera (with ≤ 100 species) are suggested to have undergone ancient diversification, primarily dating back to the Miocene (Schley et al., 2018; Vargas and Dick, 2020), with a low rate of extinction leading to a gradual accumulation of lineages (Schley et al., 2018).

The tropical tree clade Eperua *s.l.* (Detarioideae, Leguminosae) serves as an exemplary model for studying the origin and diversification of rainforests, given its trans-Atlantic distribution, with three endemic genera in Africa (*Augouardia* Pellegr., *Eurypetalum* Harms, and *Stemonocoleus* Harms) and one genus in South America (*Eperua* Aubl.) (Fougère-Danezan et al., 2010; LPWG—Legume Working Phylogeny

Group, 2017). The Neotropical *Eperua,* comprising 19 species, represents the most speciose of the genera, while the African genera collectively account for only four species (*Eurypetalum* Harms with two, and *Augouardia* and *Stemonocoleus* with one each) (Fortes et al., 2023a; Obiang-Mbomio and Breteler, 2007; POWO, 2023). The African genera are distributed in the Guineo-Congolian lowland forests, while *Eperua* is found in the lowland forests of Amazonia with one species in the ecotone of the Amazonia-Caatinga-Cerrado biomes in Brazil (Fortes et al., 2023a, 2023b). Many related clades within Detarioideae, including its crown node, are also primarily associated with humid forest types, with numerous species being dominant components of rainforests on both continents (Arellano-Peña et al., 2023; Backéus et al., 2006; Newbery et al., 2013; ter Steege et al., 2013).

Most *Eperua* species are confined to the Guiana Shield, inhabiting white-sand ecosystems such as *campinarana, bana*, and wallaba forests, as well as upland (terra-firme) and floodplain forests (igapó, várzea) (Fortes et al., 2023a). *Eperua* represents a significant component of the Amazonian forests in the Guiana Shield and the Upper Rio Negro-Orinoco region (Arellano-Peña et al., 2023; Richards, 1941). Two species, *E. falcata* Aubl. and *E. leucantha* Benth., are listed among the 20 most abundant species in Amazonia, while other species, including *E. purpurea* Benth.*, E. grandiflora* (Aubl.) Baill.*, E. jenmanii* Oliv.*, E. rubiginosa* Miq.*, E. glabriflora* (Ducke) R.S. Cowan*,* and *E. duckeana* R.S. Cowan are prevalent in the Amazon and estimated to maintain large populations (ter Steege et al., 2019, 2013). Given *Eperua*'s dominant role in the Amazonian flora, understanding its history can enhance our knowledge of the origins and mechanisms underlying the diversification of the world's richest flora (ter Steege et al., 2016). Previous findings in the biogeography of Detarioideae suggest that the Eperua *s.l.* clade originated in Africa approximately 46.9 Ma (95% HPD 37.6–54.2 Ma), before migrating to South America, leading to the origin of *Eperua* (Estrella et al., 2017). However, the biogeographical origins and dispersal mechanisms within *Eperua* in Amazonia were not addressed with only two species sampled.

A recent comprehensive phylogeny of *Eperua* utilizing complete nuclear ribosomal DNA and partial plastome sequences provided novel insights into phylogenetic relationships and evolutionary patterns by including multiple accessions from 15 of the 19 recognized *Eperua* species (ter Steege et al., 2023). However, the monophyly of *Eperua* and *Eurypetalum* could not be established using ribosomal DNA due to the limited sampling of *Eurypetalum*, leaving the sister relationship to *Eperua* weakly supported. This study provides significant evidence that species do not group together based on some of the more charismatic reproductive traits, such as long and pendulous (vs. short and erect) inflorescences or tubular (vs. non-tubular) corolla.

Corolla and inflorescence morphology play a key role in the taxonomy of *Eperua* (Fortes et al., 2023a) and are associated with different pollinators (Delaval et al., 2005; Fleming et al., 2009; Geiselman, 2010; Vogel, 1968). Ter Steege et al. (2023) suggest that the long and pendulous inflorescence likely originated once from a short and erect inflorescence. However, the ancestral floral architecture (tubular or non-tubular) within *Eperua* and its role in the speciation process remain unclear. Among the 19 *Eperua* species, ten exhibit a non-tubular corolla morphology, while the remaining nine display a tubular corolla (Fortes et al., 2023a). Notably, the long and pendulous inflorescences are limited to five species, each with a non-tubular corolla (Fortes et al., 2023a). Non-tubular corollas and long, pendulous inflorescences are associated with bat pollination (Fleming et al., 2009; Vogel, 1968), as confirmed by fecal content analysis of floral-visiting bats in French Guiana (Delaval et al., 2005; Geiselman, 2010). However, field studies to observe the visitors of species with tubular corollas are lacking which are needed to confirm the mellitophilous hypothesis (Vogel, 1968). The extreme contrast in floral architecture without any known intermediary forms and the apparent homoplasy of this trait (Fortes et al., 2023a; ter Steege et al., 2023) imply an underlying mechanism under directional selection and leading to parallel evolution. In that a shift from insect to vertebrate pollination is expected based on floral morphology, and bat pollination has been shown to independently evolve numerous times from various ancestral pollination conditions (Fleming et al., 2009), one hypothesis is that bat-pollinated species with non-tubular corollas constitute the plesiomorphic morphology of *Eperua* which is found in approximately half of the species in the genus and in both species of its sister genus *Eurypetalum* (Fortes et al., 2023a; Obiang-Mbomio and Breteler, 2007).

The present study provides a comprehensive phylogeny for the Eperua *s.l.* clade based on a nuclear phylogenomic approach using the Detarioideae v.1 nuclear exon capture kit (Ojeda et al., 2019) and encompassing all 23 recognized species with multiple accessions when available. Building upon a well-resolved and strongly supported topology, we reconstructed the biogeographic history of the clade, focusing specifically on the genus *Eperua*, and investigated the evolution of corolla and inflorescence morphology. Through these analyses, we aim to elucidate relationships in the Eperua *s.l.* clade, specifically to determine whether these are phylogenetic or reticulate. We then use this information to address the following key questions: i) where did *Eperua* originate, and how did the genus disperse into Amazonia? and ii) what is the evolutionary history of floral architecture in *Eperua*?

2. Material and methods

2.1 Taxon Sampling

We generated sequences for 119 accessions, including all four genera and 23 species of the Eperua *s.l.* clade (Fortes et al., 2023a; Obiang-Mbomio and Breteler, 2007; POWO, 2023), and four additional species from the closely related Hymenaea and Detarium clades as outgroups (Estrella et al., 2018; LPWG—Legume Working Phylogeny Group, 2017) (See Table S1). For most sampled species, multiple accessions were included, encompassing the geographical and morphological diversity according to the most recent taxonomic revisions and herbarium collections (Cowan, 1975; Fortes et al., 2023a, 2023b; Obiang-Mbomio and Breteler, 2007; Romero-González and Aymard, 2019). Of the 119 accessions, 32 were fresh silica-dried material, and 87 were herbarium specimens (See Table S1).

2.2 DNA Extraction and Library Preparation

Genomic DNA was extracted using the cetyltrimethylammonium bromide (CTAB) method (Cullings, 1992; Doyle and Doyle, 1987). DNA quality was assessed with a 1.2% agarose gel run at 120 volts for 35 minutes, and concentration was measured using Qubit 3.0 Fluorometer (Life Technologies, Grand Island, NY, USA) with the double-stranded Broad Range DNA kit. Samples with an average fragment size above 1000 bp were sheared to a target size of 400 bp using the Covaris E220 evolution Focused-ultrasonicator (Covaris, Woburn, MA, USA) with a duty cycle of 10%, intensity of 4, and cycles per burst of 200 for 55sec. A double-sided-size selection was performed with homemade ampure beads to remove fragments larger than 600 bp and smaller than 300 bp (Rowan et al., 2017). After the double-sided-size selection, DNA concentration was again measured using the Qubit 3.0 Fluorometer.

Dual-indexed libraries were prepared with the KAPA Hyper Prep kit (F. Hoffmann-La Roche Ltd) with 50-250 ng of DNA as input following a modified protocol to accommodate 1/5th volume reactions (Valderrama et al., 2022, 2020) (protocol available at https://osf.io/fkj2x). The NEBNext® Multiplex Oligos for Illumina® (96 Unique Dual Index Primer Pairs Set 4, New England Biolabs, Inc) were used in combination with a Stubby Adapter (see the Supplementary Material Data) during library preparation. After checking the concentration of the indexed libraries, eight samples were pooled, with each library comprising 250 ng with the entire pool totaling 2 µg and concentrated with a Savant DNA120 SpeedVac concentrator to a total of 7 µL, using manual operating mode and low drying rate. Pools were then enriched with the Detarioideae v.1 nuclear exon capture kit (Ojeda et al., 2019), which targets 1021 exons from 289 target loci (genes). The enrichment procedures followed the manufacturer's instructions (myBaits Manual v5.02, Arbor Biosciences, Ann Arbor, MI, USA) with a hybridization temperature of 60°C for 24 h. For 12 libraries, the Roche Universal Blocking Oligo Kit (5 µL) and SeqCap EZ Developer Reagent (5 µL) were used to reduce binding to repetitive plant sequences. A combination of the Blockers Mix supplied with the baits and the SeqCap EZ Developer Reagent (5 µL) were used for the remaining four libraries. The captured libraries (119 individuals in 16 reactions) were quality-assessed and sequenced on a partial lane of Illumina NovaSeq PE150 by Novogene Corporation Inc (Sacramento, CA, USA), targeting 1.0 GB per sample.

2.3 Reads Processing, Assembly, and Alignment

Raw reads were trimmed to remove adapter sequences and low-quality bases with fastp v0.12.4 (Chen et al., 2018) using auto-detection for adapter sequences, minimum length of 75, polyG trimming, compression level (-z) of 4, and base quality value (-q) of 20. The HybPiper v2.1.3 (Johnson et al., 2016) pipeline with default settings was used to map cleaned reads to the 1,021 target exons with BWA v0.7.17 (Li and Durbin, 2009), followed by locus assemblies. The number of reads and assembled exons for silica-dried samples were compared with herbarium specimens using a GLM-generalized linear model (Nelder and Wedderburn, 1972) with a quasi-Poisson distribution. The quality of the distribution fit was verified using the half-normal probability plot with the simulation envelope of the hnp v1.2-6 package (Moral et al., 2017). Means were compared using the Tukey test (p = 0.05), specially designed for GLM from the Multcomp v1.4-25 package (Hothorn et al., 2008).

Retrieved contigs from HybPiper were aligned for each exon with Mafft v7.520 (Katoh and Standley, 2013) using a maximum iteration of 5000, automatically selecting the appropriate strategy (-- auto), automatically adjusting directionality, gap opening penalty at group-to-group alignment (--op) 3, and the --leavegappyregion option. Before tree inference, alignments were cleaned with trimAl v1.4.1 (Capella-Gutiérrez et al., 2009) using the heuristic selection of the automatic method based on similarity statistics (-automated1).

2.4 Phylogenetic Inference

Individual exon trees were inferred with RAxML-NG v1.1.0 (Kozlov et al., 2019) using the GTRGAMMA model of molecular evolution and 100 bootstrap replicates (BS). The phylogenetic signal of each exon was evaluated with Gotree v0.4.3 (Lemoine and Gascuel, 2021) by counting the number of nodes with bootstrap support greater than 70%. A total of 85 exons with more than 30 nodes with bootstrap support greater than 70% were selected and the presence of recombination was tested for them with Phipack v1.1 (Bruen, 2005). A concatenated phylogeny was inferred from the exons recovered for more than 50% of the accessions (883) and from well-supported exons with no signal of recombination (62) by combining exon alignments with catfasta2phyml v1.2.0 (Nylander, 2018) and using RAxML-NG v1.1.0 with the GTRGAMMA model of molecular evolution and 1000 bootstraps. Three partitioning schemes and models of molecular evolution were specified with PartitionFinder v2.1.1 (Lanfear et al., 2017). The species tree was inferred with ASTRAL III v5.7.1 (Zhang et al., 2018) using the individual exon trees produced by RAxML-NG. Species tree support was calculated as local posterior probabilities (LPP) from quartet frequencies (Sayyari and Mirarab, 2016).

PhyParts v0.0.1 (Smith et al., 2015) was used to assess the topological conflict between the gene trees and the species tree with the rooted each exon tree from Gotree 0.4.3. The resulting pie charts were mapped onto the species tree using "phypartspiecharts.py" (available at https://github.com/mossm atters/MJPythonNotebooks).

To evaluate potential competing signals in the concatenated and species trees, different subsets of exons and accessions were used: i) 883 exons and 114 accessions, excluding four accessions with low exon coverage (less than 200) and 90 exons assembled for less than 50% of the accessions (total alignment length was 283,069 bp); ii) 62 exons from 114–115 accessions, including only exons that generated trees with ≥ 30 nodes with support > 70 and that showed no signal for recombination (total alignment length 47,506 bp).

A phylogenetic network was inferred with SNaQ (Solís-Lemus and Ané, 2016) implemented in the Julia v0.6.4 (Bezanson et al., 2017) package PhyloNetworks v0.11.0 (Solís-Lemus et al., 2017). The starting tree was the inferred species tree from Astral III based on 883 exons and with a single accession per species (25 tips), choosing the accession with the highest gene recovery for each lineage. The concordance factor table was obtained with Julia (function '*countquartetsintrees*') using the 883 exon trees with the 25 accessions generated in RAxML-NG v1.1.0 as input. To identify the optimal number of hybrid nodes supported by the data, SNaQ was run with increasing numbers of hybrid nodes (no hybridization up to 5 nodes) until the optimum was reached and with no improvement in the negative log-pseudolikelihood (Solís-Lemus and Ané, 2016). For each analysis with a specified number of hybridization events, ten independent SNaQ searches were conducted, with the highest negative log-pseudolikelihood retained. The negative log-pseudolikelihood for each value of hybridizations (0 to 5) is shown in Fig. S1 plotted with ggplot2 v3.4.3 package (Wickham, 2016). To access whether the "network-like" (phylogenetic network, h > 0) or the "tree-like" (model including only ILS, h = 0) was a better fit to the gene tree topologies Tree Incongruence Checking in R (TICR) (Stenz et al., 2015) was used with the package phylolm v2.6.2 (Tung Ho and Ané, 2014) in R and with the functions 'test.tree.preparation' and 'test.one.species.tree'. The inputs for this analysis were the starting tree and the CF table used previously to run SNaQ.

2.5 Lineage Divergence Time Analyses

Multiple Bayesian runs were conducted to jointly infer the topology and divergence times using BEAST v1.10 (Suchard et al., 2018). Different parameters were tested, such as using a partitioned alignment, no partitions, a Birth-Death tree prior, and a Yule tree prior; however, all of these runs failed to converge even after 2 billion generations. Therefore, a starting tree was used to estimate the divergence times for a fixed topology.

Starting Tree: The appropriate starting tree was estimated using the concatenated tree from 883 exons for 114 accessions. Aiming to include one accession per species with the highest exon coverage, tips were dropped to ultimately include 27 accessions using the R package phytools v0.6-99, function '*drop.tip*' (Revell 2012). Using the 27-tip tree and following the recommendations of Bagley (2013) and Portik (2018), we generated an ultrametric starting tree using three calibration points obtained from Estrella et al. (2017) (Table S2) and the function '*chronos*' from the R package Ape v5.7-1 (Paradis and Schliep, 2019).

BEAST analysis: The final BEAST analysis was performed using the concatenated matrix of 30 exons for the 27 accessions included above. Exons selected were those that produced trees with ≥ 35 nodes with bootstrap support >70% and without any recombination signal. The GTR+G model of molecular evolution was used along with an uncorrelated relaxed clock model with lognormal distribution, Birth-Death process of speciation. To keep the topology constant while estimating other parameters, the operators narrow exchange, wide exchange, Wilson Balding, and subtree slide were deselected following the recommendations of the Beast community (https://beast.community/faq.html#starting-tree-and-fixing-trees). Two secondary calibration points were included according to the ages estimated by Estrella et al. (2017): I) crown Eperua *s.l.* clade with a normal distribution prior, a mean of 45.8, and a standard deviation of 5.2; II) MRCA of *Hymenaea* and *Guibourtia* with a normal distribution prior, a mean of 37.5, and a standard deviation of 4.15. One MCMC analysis comprised four independent runs with 500 million generations on a GPU with a Beagle installation (Ayres et al., 2012), sampling trees every 50,000 generations. The convergence of the runs was checked using an effective sample size (ESS) with a threshold value of 200 using Tracer v1.7.2 (Rambaut et al., 2018). The maximum clade credibility tree was summarized by calculating the average ages and the highest posterior density intervals (95% HDP) with TreeAnnotator v1.8.4 (Rambaut and Drummond, 2016) using a burn-in level of 25%.

2.6 Phylogenetic Comparative Methods

The dated maximum clade credibility tree was used to perform ancestral state reconstruction and biogeographic analysis of *Eperua*. Stochastic character mapping (Huelsenbeck et al., 2003) was used to reconstruct ancestral character states using the function make.simmap (Q matrix = “empirical”, vQ=0.01,prior=list(use.empirical=T)) with the R package phytools v0.6-99. Taxa were coded according to the morphological patterns in the clade [Table S3, (Fortes et al., 2023a; Obiang-Mbomio and Breteler, 2007)]: i) corolla type: tubular corolla (five petals, adaxial petal forming a tube and stamens inserted in the corolla), non-tubular corolla (five petals, adaxial petal not forming a tube and stamens exserted from the perianth), or apetalous flowers (no petals, stamens exserted from the perianth) ; ii) inflorescence type: short (around 10 cm long, most less than 20 cm long) and erect or long (around 80 cm to 3 m long, never shorter than 50 cm) and pendulous; and iii) habitat preferences: specialist to white-sand forests (species primarily inhabiting white-sand forests, occasionally inhabiting other soil formations such as clay soil and terrace formations), generalists (species occurring in white-sand forests and in clay soil and terrace formation forests), and non-specialists (species primarily inhabiting in clay soil and terrace formation forests outside white-sand forests).

Three models were tested for each multistate trait (corolla type and habitat): equal-rates (ER), all-rates-different (ARD), and symmetric (SYM); and two models (ER and ARD) for the two-state trait (inflorescence type). The simplest model, ER, was chosen for the inflorescence trait because the deltaAIC value of the ARD model was 1.8, indicating the two models are essentially equivalent, and there is no justification for using a more complex model (Table S4). The ER model was preferred for habitat because the more complex models received a higher deltaAIC (2.298 and 5.999 for the SYM and ARD models, respectively) (Table S4). However, for the corolla trait, the best model was the SYM model, which had a deltaAIC of 0.814, better than ER; both the ER and SYM models fit the data better than the ARD model, but with no evidence that one model was better than the other, the ER model was used (Table S4). One thousand stochastic character maps were generated with the ER model to estimate each internal node's posterior probabilities across the two traits.

The ancestral distribution ranges of extant species of the Eperua *s.l.* clade were inferred with the R package BioGeoBEARS v1.1.3 (Matzke, 2013). The DEC (Ree and Smith, 2008), DIVALIKE (Ronquist, 1997), and BAYAREALIKE (Landis et al., 2013) models were compared to see which provided a better fit to the data. The incorporation of the founder event (+J parameter) was shown to confer equal likelihood values on the data for each model using the Likelihood Ratio Test. The best model was chosen using Akaike Information Criterion (AIC), selecting the one with the lowest value (Burnham and Anderson, 2002). A maximum of three areas was set as the maximum number of areas occupied by the ingroup extant species, with species often inhabiting just one or two areas. Biogeographical areas were selected using the province classification of (Morrone, 2014; Morrone et al., 2022) for the Neotropical area, the region classification of (Marshall et al., 2021) for the tropical African area, and the biogeographic world region of (Morrone and Ebach, 2022) for one outgroup distributed in Asia (Table S3). To determine the ingroup taxa range accurately, the geographic coordinates of each species were plotted in QGIS v3.30.3 (QGIS.org, 2022) using the biogeographical areas' shapefiles from (Marshall et al., 2021; Morrone et al., 2022; Morrone and Ebach, 2022) as a background (Fig. S2-S3). Coordinates for the species of *Eperua* were obtained from the most recent monograph (Fortes et al., 2023a); while coordinates for the species of *Augouardia, Eurypetalum,* and *Stemonocoleus* were obtained from GBIF (GBIF.org, 2023) using the R packages rgbif v3.7.8 (Chamberlain, 2019), Taxonstand v2.4 (Cayuela et al., 2021), and CoordinateCleaner v3.0.1 (Zizka et al., 2019).

3. Results

3.1 Bait capture efficiency

We obtained an average of 7.0 (SD = 4.5, range of 0.6–28.4) million reads per accession, of which 21.6% (SD = 9.8%, range of 1.8–43.8%) were on target (Table S5, S6). Of the 1,021 targeted nuclear exons, we assembled an average of 820.3 (SD =183.2, range of 0–933) exons per accession. Of the 119 accessions, only five had fewer than 498 assembled exons (one with 161, three with 1–5 loci, and one with no exons recovered) (Fig. S4). Poorly performing accessions were all from highly-fragmented herbarium samples with low concentrations of DNA, collected 30–80 years ago. Fresh material performed better (number of reads and number of assembled exons) than the more fragmented herbarium samples (DNA fragments <300 bp) but did not differ from the better-preserved herbarium specimens (DNA fragments >400 bp) (see Table S5, $p<0.01$).

3.2 Exon phylogenetic signal

We describe phylogenetic relationships based on four categories of support: maximum support (BS 100%, LPP 1.0), high support (BS ≥90%, LPP ≥0.95), medium support (BS ≥70%<90%, LPP ≥0.6>0.95), and weak support (BS <70%, LPP >0.6). The inferred species tree (Fig. 1) and concatenated tree (Fig. 2) from the 883 exons/114 accessions dataset showed greater resolution and higher nodal support compared to trees inferred with a subset (62) of the exons (Fig. S5, Fig. S6). Neither dataset produced a tree that resolved the relationships for the two clades formed by *E. rubiginosa* + *E.glabra* R.S. Cowan and *E. cerradoensis* Fortes, G.S. da Silva & Mansano + *E. froesii* Fortes, Aymard, ter Steege & Mansano*,* (here named Long & Non-tubular clade II and Short & Non-tubular clade, respectively)*.* The hypothesis of these two clades either as one lineage (in the concatenated tree, BS 68%) or as two separate lineages (in the species tree, LPP 0.57) received low support (Figs. 1, Fig. 2, Fig. 3). Within the Short & Mixed clade some clades received medium to low support (BS 71%–78%, LPP 0.53–0.94) (Fig. 3). *Eperua glabriflora* was reconstructed as paraphyletic with *E. manausensis* (sampled with only one accession) in the concatenated tree (Fig. 2). The species tree resolved *E. glabriflora* as monophyletic and *E. manausensis* as its sister species (LPP 0.87). *Eperua schomburgkiana* Benth. was recovered as sister to the clade of *E. duckeana* + *E. glabriflora* + *E. manausensis* in the species and concatenated trees but received low to medium support (BS 71%, LPP 0.53). *Eperua grandiflora* was inferred as sister to the clade of *E. glabriflora* + *E. manausensis* + *E. duckeana* + *E. schomburgkiana* received medium support (BS 71%) in the concatenated tree, but maximum support in the species tree; the same occurred with *E. jenmanii* being sister to the resulting clade of the previously mentioned five species (BS 78%, LPP 1.0).

For the inferred trees with a subset of 62 exons with no signal for recombination, relationships between the Short & Mixed clade, Long & Non-tubular clade II, and Short & Non-tubular clade, and within the Short & Mixed clade are poorly resolved and with low support (Fig. S5, Fig. S6). All species were inferred as monophyletic in the species tree, with most receiving maximum support, except for *E. rubiginosa* (LPP 0.99), *E. glabra* (LPP 0.88), *E. reddeniae* (LPP 0.81), and *E. jenmanii* (LPP 0.76) (Fig. S5). In contrast, the concatenated tree inferred some species as paraphyletic (Fig. S6). *Eperua glabra* showed paraphyly with *E. rubiginosa*, and one accession of *E. jenmanii* was inferred as sister to *E. schomburgkiana* + *E. reddeniae* with almost no support (BS 34%), while all other accessions of the species grouped with maximum support. *Eperua manausensis* was recovered as sister to *E. duckeana* with low support (BS 57 %), and all accessions of *E. glabriflora* formed a clade with maximum support, which differs from relationships seen in the concatenated tree from the 883 exon dataset in which *E. manausensis* was grouped within *E. glabriflora* with maximum support.

The quartet scores of the 883 exon species tree illustrated by pie charts (Fig. 1) show gene tree discordance mainly for the Short & Mixed clade, where the second most favored topology and other topologies together are equally or more prevalent compared to the primary topology. The phyparts analysis, which counts the number of concordant and conflicting gene trees for each node, confirms the quartet score results with many nodes showing a higher proportion of low-frequency topologies that diverge from the primary topology. This is particularly evident in the Short & Mixed clade (Fig. S7). There is no correlation between the date of species cladogenesis event and the percentage of gene tree concordance (Fig. 5). Nevertheless, all cladogenesis events leading to the origin of the extant species in the Mixed clade received less than 10% of gene tree concordance (ranging from 0.5–7.0%) (Fig. 5). A small percentage (1.0%) was also observed in the cladogenesis events originating *E. glabra* and *E. rubiginosa* in the Long and Non-tubular clade II (Fig. 5). In contrast, all other species cladogenesis events received between 15.4% and 65.3% of gene tree concordance (Fig. S5).

3.3 Phylogenetic network

The Tree Incongruence Checking in R (TICR) analysis suggested an excess of outlier quartets (p = 0, X2 = 39132.05) with a p-value <0.01 (expected 126.5 quartets, observed 2316.0 quartets), indicating that the observed CF values do not fit the coalescent model but a model incorporating hybridization/introgression.

The negative log-pseudolikelihood in SNaQ plateaued with four hybridization events (Fig. S1). The network with four hybridization events includes four potential reticulation events (Fig. S8): i) *E. manausensis*, which is 53.5% sister to *E. glabriflora*, and 46.5% sister to *E. duckeana*; ii) the ancestor of *E. rubiginosa* + *E. glabra*, which is 78.6% sister to *E. cerrradoensis* + *E. glabra*, and 21.4% sister to *E. reddeniae*; iii) the ancestral of *E. duckeana* + *E. manauensis* + *E. glabriflora*, which is 91.7% sister to *E. schomburgkiana*, and 8.34% sister to *E. grandiflora* subsp. *grandiflora*; and iv) the ancestor of the clades Short & Mixed clade, Long & Non-tubular clade II and Short & Non-tubular clade, which is 97.7% sister to the Long & Non-tubular clade I, and 2.33% sister to *Augouardia letestui* Pellegr. The network with three hybridization events includes the same reticulation events, except for the last one, with minor changes in the percentage of gene pool inheritance (Fig. 4).

3.4 Monophyly and genera relationships

The Eperua *s.l.* clade was recovered with maximum support in the species and concatenated trees, and all four genera were recovered as monophyletic with maximum support (Fig. 1, Fig. 2). *Augoaurdia* was recovered as sister to *Stemonocoleus*, and *Eurypetalum* as sister to *Eperua, with* both lineages receiving maximum support. In *Eurypetalum,* species *Eu. tessmanii* Harms and *Eu. unijugum* Harms were recovered as reciprocally monophyletic with maximum support.

One accession, K.M. Redden 3187 (US herbarium), was reconstructed in ambiguous positions. In the first scenario, it was positioned as a sister to all *E. glabra* accessions with strong support (BS 98) in the concatenated tree derived from 883 exons (Fig. 2) and with moderate support (PP 0.88) in the species tree from 62 exons (Fig. S5). In both trees, all *E. rubiginosa* accessions grouped in a clade received strong (BS 98) and maximum (LPP 1) supports, respectively. In the second scenario, K.M. Redden 3187 was grouped with *E. rubiginosa* complex and sister to var. *rubiginosa*, with moderate support (PP 0.72) in the species tree based on 883 exons (Fig. 1), and weak support (BS 50) in the concatenated tree based on 62 exons (Fig. S6). Notably, in this second scenario, *E. rubiginosa*+ K.M Redden 3187 received maximum support in the species tree (Fig. 1) and low support (BS 55) in the concatenated tree (Fig. S5). While this accession is identified as *E. glabra* (Fortes et al. 2023a), there is a possibility of a mix of leaf material with *E. rubiginosa*, as reported for other *Eperua* specimens (see Appendix 2, Index to Collections in the last revision for the genus Fortes et al. 2023a). This speculation arises because both species are similar vegetatively, co-occur at the same collection site, and were collected on the same day by the same collector, K.M. Redden (e.g., *E. rubiginosa*, K.M. Redden et al. 3193, US herbarium). Considering this, the paraphyly of *E. rubiginosa* and *E. glabra* is weakly supported by the position of the sample K.M. Redden 3187. It contradicts the results of all the other six *E. glabra* accessions and 14 *E. rubiginosa* accessions included in the phylogenies.

All other species of *Eperua* for which multiple accessions were included were recovered as monophyletic with maximum support. Only one accession was included for *E. bananensis* G.A. Romero & Aymard, *E. cerradoensis*, *E. manausensis*, and *E. obtusata* R.S. Cowan and thus species monophyly was not tested for these taxa. *Eperua cerradoensis* was recovered as sister to *E. froesii* with maximum support; *E. manausensis* was recovered as sister to *E. glabriflora* with medium support (LPP 0.87) in the species tree; and *E. banaensis* and *E. obtusata* were recovered as sister species with maximum support and were sister to all but Long & Tubular clade I. Concerning infraspecific ranks, the subspecies of *E. grandiflora* were recovered as monophyletic with maximum support, and the newly described subspecies, *E. grandiflora* subsp. *ciliata* Fortes & Mansano, sampled with only one accession, was recovered as sister to the other two subspecies in the trees from 883 exons (Fig. 1, Fig. 2) and in an unresolved position in the trees from 62 exons (Fig. S11, Fig. S12); the varieties of *E. oleifera* Ducke and *E. rubiginosa* were also recovered as monophyletic with maximum support. The two subspecies of *E. jenmanii* (*jenmanii* and *sandwithii*) and the variety of *E. glabriflora* were not recovered to be monophyletic (Fig. 1, Fig. 2).

3.5 Relationships in the genus <u>Eperua</u>

Eperua has six well-defined clades that received maximum support in the trees reconstructed from 883 exons and the Short & Mixed clade (Fig. 1) that received an LPP of 0.97 in the species tree (Fig.1, Fig. 2). All but the Mixed clade consist of two or three morphologically similar species with sympatric and/or parapatric distributions (Fig. 2, Fig. 5, Figs. S2). The Short & Mixed clade comprises eight species with a representative mixture of floral morphologies (Fig. 5). Species within the other clades share either a non-tubular (Fig. 1c, g, j, l, m) or a tubular corolla (Fig. 1b, q, s), and/or a short (Fig. 1b, j, r) or a long inflorescence (Fig. 1f, l, m) such that all species within the clades have the same combination of morphologies (Fig. 5). Conversely, the Short & Mixed clade consists of species that all have a short inflorescence type but that have either tubular (Fig. 1c) or non-tubular corollas (Fig. 1b, Fig. 5). All species in the Short & Mixed clade also have their stamens joined in a non-glabrous diadelphous sheath (Fig. 1b), something unique to this clade and Short & Tubular clade I. The Short & Tubular clades I and II and *E. falcata* in the Long & Non-tubular clade I all share reticulate pollen. The Short & Mixed clade has punctate or punctate-rugulose pollen, the last type is also characteristic of *E. leucantha* and *E. venosa* in the Long & Non-tubular clade I. The Long & Non-tubular clades II and Short & Non-tubular clade share verrucose pollen and stamens joined in a tube, which do not occur in the other clades. Within *Eperua,* we recognize synapomorphies only for the Long & Non-tubular clade I (reticulate homobrochate pollen), Short & Tubular clade II (obtuse to rounded leaflet apices, Fig. 1p), and the Long and Non-tubular clade I (falcate leaflets, Fig. 1o) (Fig. 5).

While the sister genera of *Eperua* occur in West-Central Africa in the Guineo-Congolian regions (Fig. 2, Fig S3), *Eperua* is restricted to Northern South America with a distribution predominantly in the Guiana Shield (Fig. 2, Fig. S2). The genus occurs in seven Neotropical provinces (Morrone, 2014; Morrone et al., 2022), with the Short & Mixed clade occurring in six, with the Long & Non-tubular clade I concentrated in four Guiana Shield provinces, and the other clades restricted to one to three provinces (Fig. 2, Figs. S2). The Short & Non-tubular clade is the only clade occurring entirely outside of the Guiana Shield in the Pará and the Xingu-Tapajós provinces (Fig. 2, Fig. S2).

3.6 Lineage divergence times

The Eperua *s.l.* clade originated between the middle Eocene (47.6 Ma, 95% HPD 56–39 Ma) in a post-Gondwana period. In the late Eocene (40.3 Ma, 95% HPD 48–32 Ma) the MRCA of *Eperua* + *Eurypetalum* diverged (Fig. 6). The origin of *Eperua* is dated to the late Oligocene (27.7 Ma, 95% HPD 34–21 Ma) (Fig. 6). Most extant *Eperua* species and their MRCA originate between the late Oligocene and late Miocene (5–26 Ma), *E. duckeana*, *E. glabriflora*, and *E. manausensis* are the most recently originated species dating to the late Tertiary in the Pliocene (5–2 Ma) (Fig. 6).

3.7 Trait evolution

The most likely morphotype for the ancestor of the Eperua *s.l.* clade is a short and erect inflorescence and flowers with a non-tubular corolla (arrows in Fig. 7a, Fig. 7b); the majority of the backbone nodes are reconstructed with this phenotype and a long and pendulous inflorescence and tubular corolla are considered apomorphies for species of *Eperua.* The tubular corolla appears to have originated four times from an ancestor with a non-tubular corolla (asterisks in Fig. 7a): once in the ancestors of each of the Short & Tubular clades I and II, and twice in the Short & Mixed clade (in *E. bijuga* and in the MRCA of *E. jenmanii* + *E.grandiflora* + *E. schomburgkiana* + *E. duckeana* + *E. manausensis* + *E. glabriflora*). Reversion to a non-tubular corolla appears to have occurred twice in the Short & Mixed clade, in *E. schomburgkiana* and in *E. duckeana*. The long and pendulous inflorescence, always found with a non-tubular corolla flower (Fig. 5), originated twice, in the MRCAs of the Long & Non-tubular clades I and II (Fig. 7a). The apetalous condition of the MRCA of the apetalous genera *Augouardia* and *Stemonocoleus* (Fig. 1 v, x) also likely originated from an ancestor with a non-tubular corolla with five petals (Fig. 7a).

Regarding habitat preferences of *Eperua*, the MRCA appears to have inhabited white-sand forests, along with subsequent ancestors (Fig. 7c). The habitat preferences underwent a major shift only with the MRCA of the clade encompassing the Short & Mixed clade, Long & Non-tubular clade II, and Short and Non-tubular clade (blue arrow in Fig. 7c), which likely occurred outside white-sand forests in clay soil and terrace formation forests. Only the MRCA of *E. jenmanii* + *E. grandiflora* + *E. schomburgkiana* + *E. duckeana* + *E. glabriflora* + *E. manausensis* returned to inhabit white-sand forests (purple arrow in Fig. 7c). However, neither the MRCA nor subsequent ancestors and extant species regained the status of specialists in this habitat.

3.8 Ancestral area reconstruction

The AIC model selection supported the DEC as the best model (Table S7). According to the Likelihood Ratio test, adding the jump parameter (+J) increased the model's fit (p-value <0.01, Table S8). Ancestral range estimations under the DEC+J model showed the most likely ancestral area for the MRCA of Eperua *s.l.* and of *Eperua* + *Eurypetalum* comprises Guineo-Congolian (West Central) subregion in Africa (Fig. 7d). This favored area received a high likelihood according to the pie chart graph (Fig. S9).

Regarding the MRCA of *Eperua*, the most likely ancestral area under the DEC+J model encompasses the Guianan province in the Neotropical region (Fig. 7d). Most of the internal nodes were reconstructed within a single province, either Guianan or Guianan Lowlands, with dispersal playing a main role in the origin of several lineages. Numerous cladogenesis events occurred in sympatry within these provinces, giving rise to the main clades. Additionally, several dispersal events to other provinces occurred, often involving a gain of one or two areas, notably toward extant species (Fig. 7d).

A likely vicariance event led to the origin of *E. oleifera* and *E. purpurea* in the Short & Tubular clade I (Fig. 7d). The MRCA of this clade, initially confined to the Guianan province, dispersed to the Imeri and Madeira provinces. Subsequently, a lineage restricted to the Guianan and Imeri province diverged, originating *E. purpurea*, while another lineage restricted to the Madeira province originated *E. oleifera*.

The MRCA of the Long & Non-tubular clade I was also restricted to the Guianan province (Fig. 7d). One lineage leading to *E. falcata* dispersed to the Guianan Lowlands and Roraima provinces. In this clade, *E. leucantha* also dispersed beyond the Guianan province, reaching the Imeri province.

A lineage originating the MRCA of the Long & Non-tubular clade II, Short & Non-tubular clade, and Short & Mixed clade migrated from the Guianan province to the Guianan Lowlands province (Fig. 7d). Subsequent dispersal events to new provinces (Xingu-Tapajós, Pará, Roraima, and Imeri) occurred, along with two returns to the Guianan Lowlands, explaining the current distribution of species in these clades. Migration events to the Roraima province gave rise to *E. bijuga* and to the MRCA of *E. duckeana.* + *E. glabriflora* + *E. manausensis.* Additionally, a migration event from the Guianan Lowlands province to the Xingu-Tapajós province gave rise to the MRCA of the Short & Non-tubular clade. Subsequently, one lineage remained in the Xingu-Tapajós province, originating *E. froesii*, while another migrated to the Pará and Caatinga provinces, originating *E. cerradoensis* (Fig. 7d).

4. Discussion

The phylogenetic inferences in this study represent the most complete for the Eperua *s.l.* clade to date, including all 23 known species and incorporating a phylogenomic approach using nuclear data. Five species were placed in a phylogenetic context for the first time—*E. banaensis, E. cerradoensis*, *E. manauensis*, *E. obtusata,* and *E. reddeniae*. Of these, *Eperua banaensis* and *E. obtusata* form a distinctive group within the genus based on their obtuse to rounded leaflet apex (Fig. 1p), a characteristic not found in any other species (Cowan, 1975; Fortes et al., 2023a; Romero-González and Aymard, 2019). As expected from this morphological uniqueness, they were inferred to be sister species and together form a distinct lineage diverging early from the majority of *Eperua* species (Fig. 1, Fig. 2). *Eperua cerradoensis,* which is characterized by its distribution in the ecotone Cerrado-Caatinga in Brazil (Fig. S2), was inferred as sister to *E. froesii* with which it shares non-tubular corolla, short and erect inflorescences, stamens joined in a glabrous tube, and joined stipules (Fortes et al., 2023a). Conversely, *E. reddeniae* and *E. manauensis* were inferred to be more closely related to species in the Short & Mixed clade, which are not morphologically similar

(Fortes et al., 2023a). Beyond clarifying the phylogenetic position of these species, our study firmly resolved *Eurypetalum* and *Eperua* as reciprocally monophyletic (Fig. 1, Fig. 2). Before this, phylogenetic relationships of species comprising the two genera remained unresolved, even with targeted nuclear ribosomal sampling for *Eperua* (ter Steege et al., 2023). This could be attributed to a limited signal from these loci and the lack of sampling of key *Eurypetalum* species *Eu. unijugum* in addition to sister genera *Augouardia* and *Stemonocoleus*. Nonetheless, our phylogenomic analyses align with the backbone of the ribosomal phylogeny of *Eperua* (ter Steege et al., 2023), most notably the recovery of species monophyly.

4.1 Unresolved phylogenetic relationships are explained by reticulation events

Our phylogenetic inferences, based on 883 gene trees and a concatenated matrix of 283,069 bp, fully resolved the relationships between genera and resolved most of the phylogenetic relationships within *Eperua*. Quartet scores (Fig. 1) and gene tree discordance analyses (Fig. S7) provide evidence of a high level of gene tree discordance, which can be attributed to incomplete lineage sorting (ILS) and hybridization (Degnan and Rosenberg, 2009; Edwards, 2009). Nevertheless, there are nodes, such as the early internal nodes of *Eperua*, that receive maximum LPP support (Fig. 1) despite the high degree of gene tree discordance (Fig. S7). This is likely due to the percentage of concordant gene trees in these nodes that are sufficient to resolve relationships with high confidence (Sayyari and Mirarab, 2016). This was not the case with the position of the Long & Non-tubular clade II as sister to the Short & Mixed clade, nor with *E. schomburgkiana* as sister to *E. duckeana* + *E. glabriflora* + *E. manauensis*, which received low support (LPP 0.57, 0.53, respectively). The coalescent approach, which assumes ILS, does not resolve gene tree conflict in those nodes providing evidence that a different biological source of conflict is involved in the lack of resolution, perhaps violating the expectation of a tree-like relationship (Naciri and Linder, 2015). Indeed, the TICR test supports (p-value <0.01) a model incorporating hybridization instead of only ILS, and the two lineages mentioned above are involved in the inferred hybridization events (Fig. 4, S8). This suggests that hybridization is likely the primary source of gene tree conflicts leading to the non-resolved relationships in *Eperua*. Other studies of the Amazonian legume tree genera *Brownea* (Schley et al., 2020)*, Zygia, Jupunba*, and *Inga* (Schley et al., 2023) also inferred ancient and recent reticulation events, bringing to light the importance of such events for tree species diversification.

The hypothesis of the Long & Non-tubular clade II and Short & Tubular clade either as one lineage (in the concatenated tree, BS 68%) or as two separate lineages (in the species tree, LPP 0.57) received low support (Figs. 1, Fig. 2, Fig. 3). The network analysis suggests that the ancestor of the Long & Non-tubular clade II resulted from a reticulation event, being 20.9–21.4% sister to *E. reddeniae* (Short & Mixed clade) and 78.6–79.1% sister to the Short & Non-tubular clade (Fig. 4, Fig. S8). Morphological similarities—such as stamens joined in a tube and verrucose pollen exine (Fig. S5)—and the percentage of gene inheritance indicate that Long & Non-tubular clade II and Sohrt & Non-tubular are closely related, and the hypothesis of an ancient reticulation event serves as a valid explanation as to why Long & Non-tubular clade II appears as a sister of the Short & Mixed clade with low support. A second reticulation event inferred among lineages within the Short & Mixed clade highlights the lack of support for the positioning of *E. schomburgkiana*: the ancestor of *E. duckeana* + *E. glabriflora* + *E. manausensis* is 4.4–8.3% sister to *E. grandiflora* and 91.7–95.6% sister to *E. schomburgkiana* (Fig. 4, Fig. S8). Another unresolved relationship in the tree-like topologies pertains to the relationship of *E. manausensis*, which appears as either sister to *E. glabriflora* (Fig. 1: LPP 0.87, Fig. S11: LPP 0.96), within *E. glabriflora* (Fig. S5, BS 100), or as sister to *E. duckeana* (Fig. S6, BS 57). Network analyses reveal that *E. manausensis* is more closely related to *E. glabriflora* and vertically inherited 45.8–46.5% of its genetic pool from *E. duckeana*, also offering an explanation for the uncertain position and lack of resolution in our tree-like topologies (Fig. 4, Fig. S8).

The phylogenetic networks with three and four hybridization events share a common set of three hybrid nodes with a similar percentage of gene pool inheritance (Fig. 4, Fig. S8). Even though the network with four hybridization events is statistically preferred (negative log-pseudolikelihood h4=3,313, h3=3,631), the inference of the fourth hybrid node between *A. letestui* and the ancestor of an *Eperua* lineage—including the Short & Mixed clade and Long & Non-tubular clade II and Short & Non-tubular clade—can be considered biologically unlikely due to their allopatric distribution across different continents (Fig. 7d). Additionally, the *Eperua* lineage hybrid node was inferred as receiving a small percentage of its gene pool vertically (2.3%), which makes differentiating introgression event from retention of ancestral polymorphisms (i.e., ILS) difficult (Bravo et al., 2019; Steenwyk et al., 2023). Indeed, the MRCA of the Eperua *s.l.* clade shows a large amount (58.8%, Fig. S7) of gene tree conflict, which could support ILS. Otherwise, the hybrid nodes inferred within *Eperua* are biologically feasible, as they are inferred to occur between sympatric lineages that likely share a common pollinator or flower visitors based on floral morphology (Fig. 4). Reticulation mediated by local pollinator sharing also have been reported in figs (Gardner et al., 2023). *Eperua* is a tree genus with strong evidence for biotic cross-pollination and no indications of vegetative reproduction (Delaval et al., 2005; Fleming et al., 2009; Fortes et al., 2023a; Geiselman, 2010; Vogel, 1968), which reinforces the hypothesis of vertical gene transference through pollinators or floral visitors that carry genetic material (pollen) from closely related sympatric species (Gardner et al., 2023).

Distinguishing between introgression and hybridization in a network requires an assessment of the fraction of the gene pool vertically inherited along with relevant biological factors (Solís-Lemus et al., 2017). Based on these metrics, a small proportion of inferred events suggest introgression (sensu Solís-Lemus et al., 2017), such as in the hybrid ancestor node of *E. duckeana* + *E. glabriflora* + *E. manausensis,* which received less than 10% of the sampled genes from proposed hybrid parent *E. grandiflora* (Fig. 4, Fig. S8). The hybrid node ancestor of the Long & Non-tubular clade II (*E. rubiginosa* + *E. glabra*) inherited a higher amount of its gene pool (20.9–21.4%) from *E. reddeniae* (Fig. 4, Fig. S8) indicating potential for both hybridization or introgression. *Eperua reddeniae* and *E. rubiginosa* are the only species with coppery inflorescence indumentum (Fortes et al., 2023a), which could be morphological evidence of their genetic relatedness. On the other hand, *E. manausensis* recovered as a hybrid node between *E. duckeana* and *E. glabriflora* reveals a potential case of hybridization, with similar proportions of genes being inherited from both proposed ancestors (43.5–45.8% and 54.2–56.5%, respectively, Fig. 4, Fig. S8). *Eperua duckeana* and *E. glabriflora* are closely related sympatric species (Fortes et al., 2023a) that recently diverged (95% HPD 2.0–4.3 Ma) (Fig. 6). Documented hybridization events occur mostly between young lineages because of ongoing isolation that takes millions of years (Mallet, 2005), which provides further evidence of *E. manausensis* being an extant hybrid. *Eperua manauensis* shares with *E. glabriflora* the short and erect inflorescence, pink tubular corolla, similar fruit shape and size, and revolute leaflet margin; while the non-glabrous inflorescence, ovary, and fruits are traits shared with *E. duckeana* (Fortes et al., 2023a, 2023b). This potential hybrid is known from only one individual in the Adolpho Ducke Forest Reserve, whereas proposed parentals *E. glabriflora* and *E. duckeana* are both extremely common (Fortes et al., 2023b). Further investigation is required to determine whether *E. manausensis* is a rare outcome of hybridization between *E. duckeana* and *E. glabriflora*, or if other hybrid individuals with similar characteristics are present and have not yet been collected.

4.2 Phylogenetic relationships supported by morphological, distribution and habitat patterns

Incorporating morphological and ecological characteristics into a phylogenetic context provides evidence of relationships. The presence of morphological synapomorphies can indicate a shared evolutionary history (Assis and Rieppel, 2011). Conversely, the absence of morphological synapomorphies for proposed monophyletic groups points to a labile character evolution, as observed in Eperua *s.l.* and in the Daniellia group tribe Detariae (Fougère-Danezan et al., 2010). Although there is a lack of identifiable morphological synapomorphies, ecologically Eperua *s.l.* is restricted to lowland tropical forests, and the species are either trees or treelets (Fortes et al., 2023a; Obiang-Mbomio and Breteler, 2007; POWO, 2023). This adaption can be viewed as a case of niche reduction and conservatism present early in the evolutionary history of the lineage, likely due to the loss of the capacity to survive in other environments common to other Detarioideae clades such as higher elevations (>500 m), Seasonally Dry Tropical Forests (SDTFs), and savannah (Estrella et al., 2017). The phylogenetic splitting of the two lineages, one grouping *Augouardia* and *Stemonocoleus* and the other grouping *Eperua* and *Eurypetalum,* is morphologically supported (Fougère-Danezan et al., 2010). *Augouardia* and *Stemonocoleus* share apetalous flowers with fewer fertile stamens positioned abaxially (Fougère-Danezan et al., 2010). In contrast, *Eperua* and *Eurypetalum* have one large adaxial petal, four reduced petals, and ten stamens joined basally (Fortes et al., 2023a; Fougère-Danezan et al., 2010).

Relationships reconstructed within the Short and Mixed clade do not align with morphological similarities, but recent cladogenesis events and high gene tree discordance evidence closely related species still undergoing genetic differentiation. In the Mixed clade, morphologically similar species were not reconstructed as sister species as observed in other clades (see Fig. 5). *Eperua bijuga* and *E. glabriflora* share all characteristics plotted in Fig 5, but are distantly related within the Mixed clade; as well *E. duckena* and *E. schomburgkiana* share all characteristics, except by the ovary indumentum, but they are not sister species. In the Mixed clade, most of the species cladogenesis events are younger than in other clades (11.1–3.0 Ma), and these splits show a higher gene tree discordance (see graph in Fig. 5). Trees, especially those with a large effective population size and long lifespans, might require over 50 Ma years to achieve monophyly of all loci (Naciri and Linder, 2015). Six species within the Short & Mixed clade—*E. grandiflora*, *E. glabriflora*, *E. jenmanii*, *E. duckeana*, *E. bijuga*, *E. schomburgkiana*—have an average estimated population of 186 million individuals (ter Steege et al., 2013). Then, this substantial population size and more recent speciation could explain the higher gene tree discordance in the Mixed clade.

4.3 The origin and dispersal of <u>*Eperua*</u> in Amazonia

Our reconstructions of the ancestral area of Eperua *s.l.* using the DEC+J model most likely encompasses the Guineo-Congolian African region (Fig. 7, Fig. S9). This area received a high probability and is in line with previous findings of Detarioideae biogeography (Estrella et al., 2017). Estrella et al. (2017) sampled 73 out of 81 Detarioideae genera and reconstructed Eperua *s.l.* to have originated in Africa during the middle Eocene (HPD 95% 37–54 Ma) with a single subsequent dispersal to South America.

Dispersal from Africa to America in a post-Gondwana scenario is primarily explained by long-distance dispersal (LDD), boreotropical dispersal, or stepping-stone dispersal (Pennington and Dick, 2004). Given that 47.6 Ma (95% HPD 39–56 Ma) ago, when Eperua *s.l.* originated, South America and Africa were geographically isolated—

islands chains between the two continents are hypothesized to have existed only until the late Cretaceous, ca. 76 Ma (Morley, 2000, 2003)—and since there are no fossils or related lineages in high latitudes, the most plausible hypothesis is LDD. Indeed, other lineages in Leguminosae (Lavin et al., 2004), other angiosperm families, and animal lineages are hypothesized to have dispersed to South America via LDD (Hughes et al., 2013; Renner, 2004; Särkinen et al., 2007; Schley et al., 2021; Tosso et al., 2018; Vargas and Dick, 2020).

The MRCA of *Eperua* arrived in Amazonia during the late Oligocene (27.7 Ma, 95% HPD 34–21 Ma) and successfully established and diversified, likely due to prior adaptation to the tropical climate—clades within Detarioideae, including the crown node, are mostly associated with humid forest types (Estrella et al., 2017)—and ecological opportunity for trees (Wellborn and Langerhans, 2015). Currently, *Eperua* represents the most speciose genus in Eperua *s.l.* with some species being the dominant component of a vegetation type known as Wallaba forest in Guiana—wallaba is a common name for some species of the genus—and in the *campinarana* forests of the Upper Rio Negro-Orinoco region (Arellano-Peña et al., 2023; Richards, 1941; ter Steege et al., 2013). In the evolutionary history of Detarioideae, a possible early diversification associated with higher extinction rates may have resulted in many old and species-poor clades (Estrella et al., 2017), explaining the existence of a high percentage of monospecific genera (28 out of 81, or 34.6%) or with 2–5 species (19 genera, or 23.4%) in the subfamily, such as the Eperua *s.l.* genera *Augouardia*, *Eurypetalum*, and *Stemonocoleus* (Estrella et al., 2018). Indeed, Detarioideae is richer in species and genera in Africa than in Asia and America, but several of the monospecific or species-poor genera are found in Africa (Estrella et al., 2018; LPWG—Legume Working Phylogeny Group, 2017). In addition to local extinctions during the glacial maximum, low species richness in those lineages can be explained by fewer niche opportunities for trees because the geographic region harbors fewer mountains and a lower associated vegetation complexity (Plana, 2004).

The most likely ancestral area for the MRCA of *Eperua* and subsequent ancestral nodes is within two Guiana Shield provinces (Guianan and Guianan Lowlands province), areas that can be considered a center of diversification for the genus (Fig.

7d). The majority of reconstructed internal nodes include one province of the Guiana Shield (Guianan, Guianan Lowlands, Roraima), which reflects the present richness of the genus in the region, with 14 out of the 19 species occurring in these forests (Fortes et al., 2023a). Previous studies have demonstrated that the Guiana Shield is also a center of diversification for other Amazonia dominant groups, such as Lecythidaceae (Vargas and Dick, 2020). This region remained climatically and geographically stable during the Miocene (Wesselingh et al., 2010), while other regions were subjected to intense landscape transformations (Hoorn, 1994). This stability facilitated the establishment of newly arrived species, such as *Eperua*, which arrived during the late Oligocene (27.7 Ma, 95% HPD 34–21 Ma) and whose diversification mostly dates back to the Miocene (Fig. 5).

In addition to the Guiana Shield, another main element to consider in the diversification of *Eperua* is its occurrence in the white-sand forests. These vegetations are found in patches throughout Amazonia (Adeney et al., 2016) and *Eperua* inhabits those from Guiana Shield and Central-Southern Amazonia regions. Six taxa within *Eperua* are specialists in these habitats (e.g., *E. banaensis, E. grandiflora* subsp. *guyanensis* R.S. Cowan*, E. falcata, E. leucantha, E. obtusata*, *E. oleifera* var. *campestris*, and *E. purpurea*,) while others may occur in these ecosystems (e.g., *E. jenmanii*, *E. schomburgkiana, E. glabriflora*). Notably, species from the first three diverging lineages (Short & Tubular clades I and II, Long & Non-tubular clade I) within the genus are specialists of the white-sands, and stochastic character mapping reveals that the MRCA of *Eperua* and most other internal nodes likely occurred there (Fig. 7c). Plants from the white-sand forests need to cope with soil drought (ter Steege, 1990), which species of *Eperua* are adapted to given their dominance in associated vegetation (Arellano-Peña et al., 2023; Richards, 1941; ter Steege et al., 2013).

Biogeographical analysis showed that dispersal played a main role in shaping the current distribution of *Eperua* within adjacent South American provinces (Fig 7d). However, *Eperua* has not dispersed widely outside the Guiana Shield, likely due to its limited seed dispersal combined with altitudinal, climate, and ecological opportunity limitations. The genus dispersed outside Guiana Shield provinces during the late Miocene, with *E. froesii* in Xingu-Tapajos province and *E. cerradoensis* in the Pará and

Caatinga provinces (Fig 6, Fig. 7d). Additionally, only other two species, *E. bijuga* and *E. oleifera,* expanded their range outside of the Guiana Shield in the Pará and Madeira provinces, respectively (Fig. 7d). *Eperua* fruits, characterized as legumes, showcase explosive dehiscence that is evident in the twisted valves of dried, opened fruits (Cowan 1975, Fortes et al., 2023). However, the considerable size and weight of the seeds confines their dispersal range and contribute to the high abundance of seedlings near the parental plant (Forget, 1992, 1989; Fortes et al., 2023a). This restricted dispersal capability has been hypothesized as a primary determinant of the species' constrained geographical distribution (ter Steege et al., 2023). The absence of *Eperua* in the western and southern regions of Amazonia can also be attributed to niche conservatism in the white-sand forests within the Guiana Shield—only six of the 19 species do not inhabit this vegetation (Fig. 7c)—, and lack of "ecological opportunity" (after Wellborn and Langerhans, 2015) upon dispersal outside the region. Amazonia during the Miocene is believed to have been more botanically diversified than the present (Hoorn, 1994; Jaramillo et al., 2006; Wesselingh et al., 2010), with many diversification events of extant plants dating back to this period (Conceição Oliveira et al., 2021; Erkens et al., 2007; Schley et al., 2021, 2018), potentially restricting "ecological opportunity". Perhaps *Eperua* was more widely distributed in western Amazonia before the Andes uplift, during a period when the white-sand ecosystems dominated these areas before being covered by the Andean-derived sediments (Ab'Sa´ber, 1982; Struwe et al., 1997). The genus is a lowland element, with most species occurring below 200 m in regions characterized by high precipitation and little seasonality, except for *E. cerradoensis* (Cowan, 1975; Fortes et al., 2023a, 2023b). The Andes' uplift since the late Oligocene and early Miocene (Hoorn et al., 2010) likely acted as a barrier, hindering *Eperua'*s dispersal to Central America. The Acre system formation greatly disconnected the Guiana and Brazilian Shields during 7–10 Ma period (Hoorn et al., 2010), could have limited southward dispersal*.*

4.4 The diversification of Eperua primarily explained by sympatric speciation due to pollinator shift resulted in drastic floral architecture changes

The transition from a non-tubular to a tubular corolla occurred four times, while the reverse happened twice (Fig. 6a), resulting in the occurrence of a sister or closely related species with distinct floral architectures currently coexisting in sympatry (Fig. 5) (Fortes et al., 2023a). The change in corolla form is likely one of the main drivers of the diversification of *Eperua* by enabling sympatric speciation by shifts in pollinator—species with tubular corollas are typically associated with insect pollination (Vogel, 1968), while those with non-tubular corollas are usually linked to bat pollination (Delaval et al., 2005; Fleming et al., 2009; Geiselman, 2010; Vogel, 1968). For pollinator-mediated speciation to evolve in close geographical proximity, a shift conferring reproductive isolation is required to stop gene flow (Van Der Niet et al., 2014). There is no known intermediary form between the non-tubular and tubular corolla in *Eperua*, with the position of the anthers and stigma being completely different between the two types (Fortes et al., 2023a). This drastic change in floral form presumably hampers gene flow. It has been estimated that at least a quarter of documented divergence events in angiosperm species-level phylogenies are marked by pollinator shifts (Van der Niet and Johnson, 2012).

The change to tubular corollas in Detarioideae represents a novelty restricted to *Eperua*, resembling the sympetalous flower of Bignoniaceae (Cowan, 1975; Fortes et al., 2023a). This morphological feature represents a highly specialized flower due to the arrangements of the stigma and stamens, the presence of nectar guides, and a nectariferous tissue on the hypanthium wall (Fortes et al., 2023a). The tubular corolla exhibits an identical organ number and relatively comparable adaxial petal dimensions when compared to the non-tubular corolla type, but differs in the proportion of the petal, sepal, carpel, and stamens—the sepals are shorter than the adaxial petal, as well as are the stamens and the carpel (Fortes et al., 2023a). In contrast, in the non-tubular corolla type, the adaxial petal is as long as the sepals and much shorter than the stamens and carpel (Fortes et al., 2023a). The differences described above are not related to organ identity and number nor purely to organ size but to a more complex change in size and position of the stamens and carpel involving the adaxial petal, resulting in a contrasting floral architecture. Developmental mechanisms underlying these differences remain unknown. Homeotic mutations are known to alter floral morphology in plants, for example affecting floral organ proportions in *Antirrhinum* L. (Delgado-Benarroch et al., 2009), which suggests a relationship between genes controlling organ size and organ identity (Delgado-Benarroch et al., 2009; Weiss et al., 2005).

Bat pollination plays an important role in *Eperua* diversity, being associated with a non-tubular corolla found in 10 of the 19 species. Among the species with non-tubular corolla, half also exhibit a distinctive long (ranging from 40 cm up to 3 m in length) and pendulous inflorescence that originated twice in the genus (Fig. 7b). This characteristic is considered a specialization for bat pollination, facilitating flower accessibility within the canopy (ter Steege et al., 2023). The long and pendulous inflorescence is a rarity among Detarioideae genera, only being observed in the Neotropical *Ecuadendron* D.A.Neill and the African *Englerodendron* Harms in addition to *Eperua*. Size and pollen ornamentation also differ across pollination syndromes in Detarioideae and other legume subfamilies (Banks and Rudall, 2016). The pollen of the non-tubular corolla species is bigger and/or rougher than the pollen of tubular corolla species (ter Steege et al., 2023), traits typically associated with bat pollination (Fleming et al., 2009; Stroo, 2000). The main advantages of bat pollination include transporting substantial amounts of pollen with multiple genotypes across a large area, reducing genetic subdivision between populations (Fleming et al., 2009). Bat pollination is common in lowland habitats in the tropics (Fleming et al., 2009), with the Neotropical region inhabited by 108 species of flower-visiting bats (Nowak, 1994; Simmons, 2005). The origin of Neotropical nectar-feeding bats dates to the late Eocene and Miocene (39–12 Ma) (Dávalos, 2004; Jones et al., 2005; Teeling et al., 2005), which corresponds to the arrival of the lineage that formed *Eperua* in South America during the early Oligocene and early Miocene (34–21 Ma).

Conclusions

Our comprehensive phylogenetic study of the Eperua *s.l.* clade, including all 23 known species, clarified the placement of previously unsampled species and confirmed the monophyly of *Eurypetalum* and *Eperua*. Gene tree discordance leading to unresolved relationships in the species tree is most likely explained by hybridization and introgression, potentially facilitated by shared pollinators or floral visitors. We showed that phylogenetic relationships are supported by morphological characters in most clades within *Eperua,* and cladogenesis events combined high gene tree discordance evidence closely related species still undergoing genetic differentiation. Our biogeographical analyses suggest *Eperua* originated in the Neotropics via long-distance dispersal from Africa, primarily originating and subsequently diversifying in the Guiana Shield. Since the arrival of *Eperua* in South America, dispersal has played a main role in shaping its current distribution within adjacent South American provinces. However, *Eperua* has not dispersed widely outside the Guiana Shield, likely due to its limited seed dispersal combined with altitudinal, climate, and ecological opportunity limitations. Our findings of the ancestral reconstructions of areas and corolla morphotypes provide evidence that speciation in *Eperua* occurred in sympatry, likely driven by a pollinator shift resulting from drastic changes in floral architecture.

Acknowledgments

This paper is part of the first author’s Ph.D. thesis supported by a scholarship from Conselho Nacional de Desenvolvimento Científico e Tecnológico - (CNPq) [process number 140508/2020-1], by a sandwich scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – (CAPES) [CAPES-PRINT process number 88887.695281/2022-00], and by Sigma Xi and Funbio – Conservando o Futuro 2020/HUMANIZE grants. VFM is grateful to CNPq [process number 303053/2018-6] and the Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro - (FAPERJ) [process number E-26-/203.007/2017]. The authors are very grateful to the staff from F, IAN, INPA, K, MO, NY, R, RB, and, especially, US herbaria for exsiccate samples for DNA extraction. They also thank the BTI Computational Biology Center for computational resources and Gisel De La Cerda for assistance with laboratory protocols.

References

Ab’Sa´ber, A.N., 1982. The paleoclimate and paleoecology of Brazilian Amazonia, in: Prance, G.T. (Ed.), Biological Diversification of the Tropics. Columbia Univ. Press, New

York, pp. 41–59.

Adeney, J.M., Christensen, N.L., Vicentini, A., Cohn-Haft, M., 2016. White-sand Ecosystems in Amazonia. Biotropica. https://doi.org/10.1111/btp.12293

Arellano-Peña, H., Cárdenas-López, D., Stropp, J., Castaño-Arboleda, N., Romero-González, G., Castro-Lima, F., Lozano, A., Montilla, M.C., ter Steege, H., Aymard-Corredor, G.A., 2023. The Forests of the Upper Rio Negro (North-Western Amazon) and Adjacent South-Western Orinoco Basins: A Phytosociological Classification, in: Zinck, J.A., Huber, O., García Montero, P., Medina, E. (Eds.), Psammic Peinobiomes. Ecological Studies . Springer, Cham, pp. 55–109. https://doi.org/10.1007/978-3-031-20799-0_3

Assis, L.C.S., Rieppel, O., 2011. Are monophyly and synapomorphy the same or different? Revisiting the role of morphology in phylogenetics. Cladistics 27, 94–102. https://doi.org/10.1111/j.1096-0031.2010.00317.x

Ayres, D.L., Darling, A., Zwickl, D.J., Beerli, P., Holder, M.T., Lewis, P.O., Huelsenbeck, J.P., Ronquist, F., Swofford, D.L., Cummings, M.P., Rambaut, A., Suchard, M.A., 2012. BEAGLE: An application programming interface and high-performance computing library for statistical phylogenetics. Syst Biol 61. https://doi.org/10.1093/sysbio/syr100

Backéus, I., Pettersson, B., Strömquist, L., Ruffo, C., 2006. Tree communities and structural dynamics in miombo (Brachystegia-Julbernardia) woodland, Tanzania. For Ecol Manage 230. https://doi.org/10.1016/j.foreco.2006.04.033

Bagley, J.C., 2013. Off to a good start: how to generate starting trees for BEAST analyses using R [WWW Document]. https://justinbagley.rbind.io/2013/10/10/off-to-a-good-start-how-to-generate-starting-trees-for-beast-analyses-using-r/.

Banks, H., Rudall, P.J., 2016. Pollen structure and function in caesalpinioid legumes. Am J Bot 103, 423–436. https://doi.org/10.3732/ajb.1500248

Bezanson, J., Edelman, A., Karpinski, S., Shah, V.B., 2017. Julia: A fresh approach to numerical computing. SIAM Review 59. https://doi.org/10.1137/141000671

Bravo, G.A., Antonelli, A., Bacon, C.D., Bartoszek, K., Blom, M.P.K., Huynh, S., Jones, G., Lacey Knowles, L., Lamichhaney, S., Marcussen, T., Morlon, H., Nakhleh, L.K., Oxelman, B., Pfeil, B., Schliep, A., Wahlberg, N., Werneck, F.P., Wiedenhoeft, J., Willows-Munro, S., Edwards, S. V., 2019. Embracing heterogeneity: Coalescing the tree of life and the future of phylogenomics. PeerJ 2019. https://doi.org/10.7717/peerj.6399

Bruen, T., 2005. PhiPack: PHI test and other tests of recombination.

Burnham, K.P., Anderson, D.R., 2002. Information and Likelihood Theory: a basis for model selection and inference, in: Burnham, K.P., Anderson, D.R. (Eds.), Multimodel Inference: A Practical Information-Theoretic Approach. Springer, New York, NY, pp. 49–97.

Capella-Gutiérrez, S., Silla-Martínez, J.M., Gabaldón, T., 2009. trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics 25. https://doi.org/10.1093/bioinformatics/btp348

Cayuela, A.L., Macarro, I., Stein, A., Oksanen, J., 2021. Taxonstand: Taxonomic Standardization of Plant Species Names. R package version 2.4.

Chamberlain, S., 2019. Package 'rgbif' - Interface to the Global “Biodiversity” Information Facility API. CRAN Repository.

Chen, S., Zhou, Y., Chen, Y., Gu, J., 2018. Fastp: An ultra-fast all-in-one FASTQ preprocessor, in: Bioinformatics. https://doi.org/10.1093/bioinformatics/bty560

Conceição Oliveira, L., Picanço Rodrigues, D., Fortune Hopkins, H.C., Peter Lewis, G., John Gilbert Hopkins, M., 2021. Phylogeny and historical biogeography of the pantropical genus Parkia (Leguminosae, Caesalpinioideae, mimosoid clade). Mol Phylogenet Evol 163. https://doi.org/10.1016/j.ympev.2021.107219

Cowan, R.S., 1975. A monograph of the genus Eperua (Leguminosae: Caesalpinioideae).

Cullings, K.W., 1992. Design and testing of a plant-specific PCR primer for ecological and evolutionary studies, Molecular Ecology.

Dávalos, L.M., 2004. Phylogeny and biogeography of Caribbean mammals. Biological Journal of the Linnean Society. https://doi.org/10.1111/j.1095-8312.2003.00302.x

Degnan, J.H., Rosenberg, N.A., 2009. Gene tree discordance, phylogenetic inference and the multispecies coalescent. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2009.01.009

Delaval, M., Henry, M., Charles-Dominique, P., 2005. Interspecific competition and niche partitioning: Example of a neotropical rainforest bat community. Revue d'Ecologie (La Terre et la Vie) 60. https://doi.org/10.3406/revec.2005.1253

Delgado-Benarroch, L., Weiss, J., Egea-Cortines, M., 2009. The mutants compacta ähnlich, Nitida and Grandiflora define developmental compartments and a compensation mechanism in floral development in Antirrhinum majus. J Plant Res 122. https://doi.org/10.1007/s10265-009-0236-6

Dexter, K.G., Lavin, M., Torke, B.M., Twyford, A.D., Kursar, T.A., Coley, P.D., Drake, C., Hollands, R., Pennington, R.T., 2017. Dispersal assembly of rain forest tree communities across the Amazon basin. Proc Natl Acad Sci U S A 114. https://doi.org/10.1073/pnas.1613655114

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

Edwards, S. V., 2009. Is a new and general theory of molecular systematics emerging? Evolution (N Y). https://doi.org/10.1111/j.1558-5646.2008.00549.x

Erkens, R.H.J., Chatrou, L.W., Maas, J.W., van der Niet, T., Savolainen, V., 2007. A rapid diversification of rainforest trees (Guatteria; Annonaceae) following dispersal from Central into South America. Mol Phylogenet Evol 44, 399–411. https://doi.org/10.1016/j.ympev.2007.02.017

Estrella, M. de la, Forest, F., Klitgård, B., Lewis, G.P., Mackinder, B.A., De Queiroz, L.P., Wieringa, J.J., Bruneau, A., 2018. A new phylogeny-based tribal classification of subfamily Detarioideae, an early branching clade of florally diverse tropical arborescent legumes. Sci Rep 8. https://doi.org/10.1038/s41598-018-24687-3

Estrella, M. de la, Forest, F., Wieringa, J.J., Fougère-Danezan, M., Bruneau, A., 2017. Insights on the evolutionary origin of Detarioideae, a clade of ecologically dominant tropical African trees. New Phytologist 214, 1722–1735. https://doi.org/10.1111/nph.14523

Fleming, T.H., Geiselman, C., Kress, W.J., 2009. The evolution of bat pollination: A phylogenetic perspective. Ann Bot 104, 1017–1043. https://doi.org/10.1093/aob/mcp197

Forget, P.-M., 1992. Regeneration Ecology of Eperua grandiflora (Caesalpiniaceae), a Large-Seeded Tree in French Guiana. Biotropica 24. https://doi.org/10.2307/2388668

Fortes, E.A., Reis, I.P. dos, ter Steege, H., Aymard, G., Secco, R. de S., Martins-da-Silva, R.C.V., Mansano, V.F., 2023a. A taxonomic revision of the genus Eperua (Leguminosae, Detarioideae, Detarieae). Phytotaxa 617, 1–127.

https://doi.org/10.11646/phytotaxa.617.1.1

Fortes, E.A., Silva, G.S. da., Mansano, V.F., 2023b. Two new species of Eperua (Leguminosae, Detarioideae, Detarieae) from the Amazon and Cerrado Biomes discovered in a botanical garden and a backyard. Phytotaxa 591, 196–208. https://doi.org/10.11646/phytotaxa.591.3.2

Fougère-Danezan, M., Herendeen, P.S., Maumont, S., Bruneau, A., 2010. Morphological evolution in the variable resin-producing Detarieae (Fabaceae): Do morphological characters retain a phylogenetic signal? Ann Bot 105, 311–325. https://doi.org/10.1093/aob/mcp280

GBIF.org, 2023. GBIF Occurrence Download: https://doi.org/10.15468/dl.hehv63, https://doi.org/10.15468/dl.ga3jgd, https://doi.org/10.15468/dl.des4gs, https://doi.org/10.15468/dl.rngbkr [WWW Document]. Available from: https://www.gbif.org.

Geiselman, C.K., 2010. Diet and reproduction of sympatric nectar-feeding bat species (Chiroptera: Phyllostomidae) in French Guiana. Columbia University.

Hoorn, C., 1994. An environmental reconstruction of the palaeo-Amazon River system (Middle-Late Miocene, NW Amazonia), Palaeogeography, Palaeoclimatology, Palaeoecology.

Hoorn, C., Wesselingh, F.P., Ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T., Antonelli, A., 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. Science (1979). https://doi.org/10.1126/science.1194585

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biometrical Journal. https://doi.org/10.1002/bimj.200810425

Huelsenbeck, J.P., Nielsen, R., Bollback, J.P., 2003. Stochastic mapping of morphological characters. Syst Biol 52. https://doi.org/10.1080/10635150390192780

Hughes, C.E., Pennington, R.T., Antonelli, A., 2013. Neotropical Plant Evolution: Assembling the Big Picture. Botanical Journal of the Linnean Society. https://doi.org/10.1111/boj.12006

Jaramillo, C., Rueda, M.J., Mora, G., 2006. Cenozoic plant diversity in the neotropics. Science (1979) 311. https://doi.org/10.1126/science.1121380

Johnson, M.G., Gardner, E.M., Liu, Y., Medina, R., Goffinet, B., Shaw, A.J., Zerega, N.J.C., Wickett, N.J., 2016. HybPiper: Extracting coding sequence and introns for phylogenetics from high-throughput sequencing reads using target enrichment. Appl Plant Sci 4. https://doi.org/10.3732/apps.1600016

Jones, K.E., Bininda-Emonds, O.R.P., Gittleman, J.L., 2005. Bats, clocks, and rocks: diversification patterns in Chiroptera. Evolution (N Y) 59. https://doi.org/10.1111/j.0014-3820.2005.tb00932.x

Katoh, K., Standley, D.M., 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Mol Biol Evol 30. https://doi.org/10.1093/molbev/mst010

Kozlov, A.M., Darriba, D., Flouri, T., Morel, B., Stamatakis, A., 2019. RAxML-NG: A fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics 35. https://doi.org/10.1093/bioinformatics/btz305

Landis, M.J., Matzke, N.J., Moore, B.R., Huelsenbeck, J.P., 2013. Bayesian analysis of biogeography when the number of areas is large. Syst Biol 62. https://doi.org/10.1093/sysbio/syt040

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., Calcott, B., 2017. Partitionfinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol Biol Evol 34. https://doi.org/10.1093/molbev/msw260

Lavin, M., Schrire, B.P., Lewis, G., Pennington, R.T., Delgado-Salinas, A., Thulin, M., Hughes, C.E., Matos, A.B., Wojciechowski, M.F., 2004. Metacommunity process rather than continental tectonic history better explains geographically structured phylogenies in legumes, in: Philosophical Transactions of the Royal Society B: Biological Sciences. https://doi.org/10.1098/rstb.2004.1536

Lemoine, F., Gascuel, O., 2021. Gotree/Goalign: Toolkit and Go API to facilitate the development of phylogenetic workflows. NAR Genom Bioinform 3. https://doi.org/10.1093/nargab/lqab075

Li, H., Durbin, R., 2009. Fast and accurate short read alignment with Burrows-Wheeler transform. Bioinformatics 25. https://doi.org/10.1093/bioinformatics/btp324

LPWG—Legume Working Phylogeny Group, 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny: The Legume Phylogeny Working Group (LPWG). Taxon 66, 44–77. https://doi.org/10.12705/661.3

Mallet, J., 2005. Hybridization as an invasion of the genome. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2005.02.010

Marshall, C.A.M., Wieringa, J.J., Hawthorne, W.D., 2021. An interpolated biogeographical framework for tropical Africa using plant species distributions and the physical environment. J Biogeogr 48, 23–36. https://doi.org/10.1111/jbi.13976

Matzke, N.J., 2013. Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. Front Biogeogr 5. https://doi.org/10.21425/f5fbg19694

Moral, R.A., Hinde, J., Demétrio, C.G.B., 2017. Half-normal plots and overdispersed models in R: The hnp package. J Stat Softw 81. https://doi.org/10.18637/jss.v081.i10

Morley, R.J., 2003. Interplate dispersal paths for megathermal angiosperms. Perspect Plant Ecol Evol Syst 6, 5–20. https://doi.org/10.1078/1433-8319-00039

Morley, R.J., 2000. Origin and evolution of tropical rainforests. Wiley, Chichester, UK.

Morrone, J.J., 2014. Biogeographical regionalisation of the neotropical region. Zootaxa 3782, 1–110. https://doi.org/10.11646/zootaxa.3782.1.1

Morrone, J.J., Ebach, M.C., 2022. Toward a terrestrial biogeographical regionalisation of the world: historical notes, characterisation and area nomenclature. Aust Syst Bot 35, 89–126. https://doi.org/10.1071/SB22002

Morrone, J.J., Escalante, T., Rodriguez-Tapia, G., Carmona, A., Arana, M., Mercado-Gomez, J.D., 2022. Biogeographic regionalization of the Neotropical region: New map and shapefile. An Acad Bras Cienc 94. https://doi.org/10.1590/0001-3765202220211167

Naciri, Y., Linder, H.P., 2015. Species delimitation and relationships: The dance of the seven veils. Taxon 64. https://doi.org/10.12705/641.24

Nelder, J.A., Wedderburn, R.W.M., 1972. Generalized linear models. Royal Statistical Society 135, 370–384.

Newbery, D.M., Van Der Burgt, X.M., Worbes, M., Chuyong, G.B., 2013. Transient dominance in a central african rain forest. Ecol Monogr 83. https://doi.org/10.1890/12-1699.1

Nowak, R.M., 1994. Walker's bats of the world. Johns Hopkins University Press, Baltimore.

Nylander, J.A.A., 2018. catfasta2phyml [WWW Document]. https://github.com/nylander/catfasta2phyml.

Obiang-Mbomio, D., Breteler, F.J., 2007. Révision du genre Eurypetalum Harms (Fabaceae, Caesalpinioideae).

Ojeda, D.I., Koenen, E., Cervantes, S., de la Estrella, M., Banguera-Hinestroza, E., Janssens, S.B., Migliore, J., Demenou, B.B., Bruneau, A., Forest, F., Hardy, O.J., 2019. Phylogenomic analyses reveal an exceptionally high number of evolutionary shifts in a florally diverse clade of African legumes. Mol Phylogenet Evol 137, 156–167. https://doi.org/10.1016/j.ympev.2019.05.002

Paradis, E., Schliep, K., 2019. Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35. https://doi.org/10.1093/bioinformatics/bty633

Pennington, R.T., Dick, C.W., 2004. The role of immigrants in the assembly of the South American rainforest tree flora, in: Philosophical Transactions of the Royal Society B: Biological Sciences. https://doi.org/10.1098/rstb.2004.1532

Plana, V., 2004. Mechanisms and tempo of evolution in the African Guineo-Congolian rainforest, in: Philosophical Transactions of the Royal Society B: Biological Sciences. Royal Society, pp. 1585–1594. https://doi.org/10.1098/rstb.2004.1535

Portik, D., 2018. BEAST Divergence Dating using a Fixed Tree Topology [WWW Document]. https://osf.io/7y59t/.

POWO, 2023. Plants of the World Online. Facilitated by the Royal Botanic Gardens [WWW Document]. http://www.plantsoftheworldonline.org/ .

QGIS.org, 2022. QGIS Geographic Information System. QGIS Association. Open Source Geospatial Foundation Project.

Rambaut, A., Drummond, A.J., 2016. TreeAnnotator v1.8.4. Http://Beast.Bio.Ed.Ac.Uk/.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G., Suchard, M.A., 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Syst Biol 67. https://doi.org/10.1093/sysbio/syy032

Ree, R.H., Smith, S.A., 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. Syst Biol 57. https://doi.org/10.1080/10635150701883881

Renner, S., 2004. Plant dispersal across the tropical Atlantic by wind and sea currents, in: International Journal of Plant Sciences. https://doi.org/10.1086/383334

Revell, L.J., 2012. phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol Evol 3. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Richards, P.W., 1941. Lowland tropical podsols and their vegetation. Nature 148, 129–131. https://doi.org/10.1038/148129a0

Richardson, J.E., Pennington, R.T., Pennington, T.D., Hollingsworth, P.M., 2001. Rapid diversification of a species-rich genus of neotropical rain forest trees. Science (1979) 293. https://doi.org/10.1126/science.1061421

Romero-González, G.A., Aymard, G.A., 2019. A New Species of Eperua (Leguminosae, Detarioideae) from Amazonas State, Venezuela. Harv Pap Bot 24, 341–347. https://doi.org/10.3100/hpib.v24iss2.2019.n17

Ronquist, F., 1997. Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. Syst Biol 46. https://doi.org/10.1093/sysbio/46.1.195

Rowan, B.A., Seymour, D.K., Chae, E., Lundberg, D.S., Weigel, D., 2017. Methods for genotyping-by-sequencing, in: Methods in Molecular Biology. https://doi.org/10.1007/978-1-4939-6442-0_16

Särkinen, T.E., Newman, M.F., Maas, P.J.M., Maas, H., Poulsen, A.D., Harris, D.J., Richardson, J.E., Clark, A., Hollingsworth, M., Toby Pennington, R., 2007. Recent oceanic long-distance dispersal and divergence in the amphi-Atlantic rain forest genus Renealmia L.f. (Zingiberaceae). Mol Phylogenet Evol 44, 968–980. https://doi.org/10.1016/j.ympev.2007.06.007

Sayyari, E., Mirarab, S., 2016. Fast Coalescent-Based Computation of Local Branch Support from Quartet Frequencies. Mol Biol Evol 33. https://doi.org/10.1093/MOLBEV/MSW079

Schley, R.J., de la Estrella, M., Pérez-Escobar, O.A., Bruneau, A., Barraclough, T., Forest, F., Klitgård, B., 2018. Is Amazonia a 'museum' for Neotropical trees? The evolution of the Brownea clade (Detarioideae, Leguminosae). Mol Phylogenet Evol 126, 279–292. https://doi.org/10.1016/j.ympev.2018.04.029

Schley, R.J., Nicholls, J.A., Kidner, C., 2023. Do Reticulate Relationships Between Tropical Trees Drive Diversification? Insights from Inga (Fabaceae). https://doi.org/10.1101/2023.09.12.557345

Schley, R.J., Pennington, R.T., Pérez-Escobar, O.A., Helmstetter, A.J., de la Estrella, M., Larridon, I., Sabino Kikuchi, I.A.B., Barraclough, T.G., Forest, F., Klitgård, B., 2020. Introgression across evolutionary scales suggests reticulation contributes to Amazonian tree diversity. Mol Ecol 29, 4170–4185. https://doi.org/10.1111/mec.15616

Schley, R.J., Qin, M., Vatanparast, M., Malakasi, P., de la Estrella, M., Lewis, G., Klitgård, B., 2021. The diversification of Pterocarpus; (Leguminosae: Papilionoideae) was influenced by biome-switching and infrequent long-distance dispersal. bioRxiv.

Simmons, N.B., 2005. Order Chiroptera, in: Wilson, D.E., Reeder, D.M. (Eds.), Mammal Species of the World. A Taxonomic and Geographic Reference. Johns Hopkins University Press, Baltimore, pp. 312–529.

Smith, S.A., Moore, M.J., Brown, J.W., Yang, Y., 2015. Analysis of phylogenomic datasets reveals conflict, concordance, and gene duplications with examples from animals and plants. BMC Evol Biol 15. https://doi.org/10.1186/s12862-015-0423-0

Solís-Lemus, C., Ané, C., 2016. Inferring Phylogenetic Networks with Maximum Pseudolikelihood under Incomplete Lineage Sorting. PLoS Genet 12. https://doi.org/10.1371/journal.pgen.1005896

Solís-Lemus, C., Bastide, P., Ané, C., 2017. PhyloNetworks: A package for phylogenetic networks. Mol Biol Evol 34, 3292–3298. https://doi.org/10.1093/molbev/msx235

Steenwyk, J.L., Li, Y., Zhou, X., Shen, X.X., Rokas, A., 2023. Incongruence in the phylogenomics era. Nat Rev Genet. https://doi.org/10.1038/s41576-023-00620-x

Stenz, N.W.M., Larget, B., Baum, D.A., Ané, C., 2015. Exploring tree-like and non-tree-like patterns using genome sequences: An example using the inbreeding plant species Arabidopsis thaliana (L.) heynh. Syst Biol 64. https://doi.org/10.1093/sysbio/syv039

Stroo, A., 2000. Plant Systematics and Evolution Pollen morphological evolution in bat pollinated plants, Plant Syst. Evol.

Struwe, L., Maas, P.J.M., Albert, V.A., 1997. Aripuana cullmaniorum, a new genus and species of Gentianaceae from white sands of southeastern Amazonas, Brazil. Harv Pap

Bot 2, 235–253.

Suchard, M.A., Lemey, P., Baele, G., Ayres, D.L., Drummond, A.J., Rambaut, A., 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. Virus Evol 4. https://doi.org/10.1093/ve/vey016

Teeling, E.C., Springer, M.S., Madsen, O., Bates, P., O'Brien, S.J., Murphy, W.J., 2005. A molecular phylogeny for bats illuminates biogeography and the fossil record. Science (1979) 307. https://doi.org/10.1126/science.1105113

ter Steege, H., 1990. A monograph of Wallaba, Mora and Greenheart. Wageningen, Netherlands.

ter Steege, H., Fortes, E.A., Rozendaal, D.M.A., Erkens, R.H.J., Sabatier, D., Aymard, G., Duijm, E., Eurlings, M., Grewe, F., Pombo, M.M., Gomes, V.F., Mansano, V. de F., de Oliveira, S.M., 2023. Molecular phylogeny and evolution of inflorescence types in Eperua . Am J Bot. https://doi.org/10.1002/ajb2.16229

ter Steege, H., Henkel, T.W., Helal, N., Marimon, B.S., Marimon-Junior, B.H., Huth, A., Groeneveld, J., Sabatier, D., Coelho, L. de S., Filho, D. de A.L., Salomão, R.P., Amaral, I.L., Matos, F.D. de A., Castilho, C. V., Phillips, O.L., Guevara, J.E., Carim, M. de J.V., Cárdenas López, D., Magnusson, W.E., Wittmann, F., Irume, M.V., Martins, M.P., Guimarães, J.R. da S., Molino, J.F., Bánki, O.S., Piedade, M.T.F., Pitman, N.C.A., Mendoza, A.M., Ramos, J.F., Luize, B.G., Moraes de Leão Novo, E.M., Núñez Vargas, P., Silva, T.S.F., Venticinque, E.M., Manzatto, A.G., Reis, N.F.C., Terborgh, J., Casula, K.R., Honorio Coronado, E.N., Montero, J.C., Feldpausch, T.R., Duque, A., Costa, F.R.C., Arboleda, N.C., Schöngart, J., Killeen, T.J., Vasquez, R., Mostacedo, B., Demarchi, L.O., Assis, R.L., Baraloto, C., Engel, J., Petronelli, P., Castellanos, H., de Medeiros, M.B., Quaresma, A., Simon, M.F., Andrade, A., Camargo, J.L., Laurance, S.G.W., Laurance, W.F., Rincón, L.M., Schietti, J., Sousa, T.R., de Sousa Farias, E., Lopes, M.A., Magalhães, J.L.L., Mendonça Nascimento, H.E., Lima de Queiroz, H., Aymard C, G.A., Brienen, R., Revilla, J.D.C., Vieira, I.C.G., Cintra, B.B.L., Stevenson, P.R., Feitosa, Y.O., Duivenvoorden, J.F., Mogollón, H.F., Araujo-Murakami, A., Ferreira, L.V., Lozada, J.R., Comiskey, J.A., de Toledo, J.J., Damasco, G., Dávila, N., Draper, F., García-Villacorta, R., Lopes, A., Vicentini, A., Alonso, A., Dallmeier, F., Gomes, V.H.F., Lloyd, J., Neill, D., de Aguiar, D.P.P., Arroyo, L., Carvalho, F.A., de Souza, F.C., do Amaral, D.D., Feeley, K.J., Gribel, R., Pansonato, M.P., Barlow, J., Berenguer, E., Ferreira, J., Fine, P.V.A., Guedes, M.C., Jimenez, E.M., Licona, J.C., Peñuela Mora, M.C., Villa, B., Cerón, C., Maas, P., Silveira, M., Stropp, J., Thomas, R., Baker, T.R., Daly, D., Dexter, K.G., Huamantupa-Chuquimaco, I., Milliken, W., Pennington, T., Ríos Paredes, M., Fuentes, A., Klitgaard, B., Pena, J.L.M., Peres, C.A., Silman, M.R., Tello, J.S., Chave, J., Cornejo Valverde, F., Di Fiore, A., Hilário, R.R., Phillips, J.F., Rivas-Torres, G., van Andel, T.R., von Hildebrand, P., Noronha, J.C., Barbosa, E.M., Barbosa, F.R., de Matos Bonates, L.C., Carpanedo, R. de S., Dávila Doza, H.P., Fonty, É., GómeZárate z, R., Gonzales, T., Gallardo Gonzales, G.P., Hoffman, B., Junqueira, A.B., Malhi, Y., Miranda, I.P. de A., Pinto, L.F.M., Prieto, A., Rodrigues, D. de J., Rudas, A., Ruschel, A.R., Silva, N., Vela, C.I.A., Vos, V.A., Zent, E.L., Zent, S., Weiss Albuquerque, B., Cano, A., Carrero Márquez, Y.A., Correa, D.F., Costa, J.B.P., Flores, B.M., Galbraith, D., Holmgren, M., Kalamandeen, M., Nascimento, M.T., Oliveira, A.A., Ramirez-Angulo, H., Rocha, M., Scudeller, V.V., Sierra, R., Tirado, M., Umaña Medina, M.N., van der Heijden, G., Vilanova Torre, E., Vriesendorp, C., Wang, O., Young, K.R., Ahuite Reategui, M.A., Baider, C., Balslev, H., Cárdenas, S., Casas, L.F., Farfan-Rios, W., Ferreira, C., Linares-Palomino, R., Mendoza, C., Mesones, I., Torres-Lezama, A., Giraldo, L.E.U., Villarroel, D., Zagt, R., Alexiades, M.N., de Oliveira, E.A., Garcia-Cabrera, K., Hernandez, L., Palacios Cuenca, W., Pansini, S., Pauletto, D., Ramirez Arevalo, F., Sampaio, A.F., Sandoval, E.H.V., Valenzuela Gamarra, L., Levesley, A., Pickavance, G., Melgaço, K., 2019. Rarity of monodominance in hyperdiverse Amazonian forests. Sci Rep 9. https://doi.org/10.1038/s41598-019-50323-9

ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P., Guevara, J.E., Phillips, O.L., Castilho, C. V., Magnusson, W.E., Molino, J.F., Monteagudo, A., Vargas, P.N., Montero, J.C., Feldpausch, T.R., Coronado, E.N.H., Killeen, T.J., Mostacedo, B., Vasquez, R., Assis, R.L., Terborgh, J., Wittmann, F., Andrade, A., Laurance, W.F., Laurance, S.G.W., Marimon, B.S., Marimon, B.H., Vieira, I.C.G., Amaral, I.L., Brienen, R., Castellanos, H., López, D.C., Duivenvoorden, J.F., Mogollón, H.F., Matos, F.D.D.A., Dávila, N., García-Villacorta, R., Diaz, P.R.S., Costa, F., Emilio, T., Levis, C., Schietti, J., Souza, P., Alonso, A., Dallmeier, F., Montoya, A.J.D., Piedade, M.T.F., Araujo-Murakami, A., Arroyo, L., Gribel, R., Fine, P.V.A., Peres, C.A., Toledo, M., Aymard C., G.A., Baker, T.R., Cerón, C., Engel, J., Henkel, T.W., Maas, P., Petronelli, P., Stropp, J., Zartman, C.E., Daly, D., Neill, D., Silveira, M., Paredes, M.R., Chave, J., Lima Filho, D.D.A., Jørgensen, P.M., Fuentes, A., Schöngart, J., Valverde, F.C., Di Fiore, A., Jimenez, E.M., Mora, M.C.P., Phillips, J.F., Rivas, G., Van Andel, T.R., Von Hildebrand, P., Hoffman, B., Zent, E.L., Malhi, Y., Prieto, A., Rudas, A., Ruschell, A.R., Silva, N., Vos, V., Zent, S., Oliveira, A.A., Schutz, A.C., Gonzales, T., Nascimento, M.T., Ramirez-Angulo, H., Sierra, R., Tirado, M., Medina, M.N.U., Van Der Heijden, G., Vela, C.I.A., Torre, E.V., Vriesendorp, C., Wang, O., Young, K.R., Baider, C., Balslev, H., Ferreira, C., Mesones, I., Torres-Lezama, A., Giraldo, L.E.U., Zagt, R., Alexiades, M.N., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Cuenca, W.P., Pauletto, D., Sandoval, E.V., Gamarra, L.V., Dexter, K.G., Feeley, K., Lopez-Gonzalez, G., Silman, M.R., 2013. Hyperdominance in the Amazonian tree flora. Science (1979) 342. https://doi.org/10.1126/science.1243092

ter Steege, H., Vaessen, R.W., Cárdenas-López, D., Sabatier, D., Antonelli, A., De Oliveira, S.M., Pitman, N.C.A., Jørgensen, P.M., Salomão, R.P., 2016. The discovery of the Amazonian tree flora with an updated checklist of all known tree taxa. Sci Rep 6. https://doi.org/10.1038/srep29549

Tosso, F., Hardy, O.J., Doucet, J.L., Daïnou, K., Kaymak, E., Migliore, J., 2018. Evolution in the Amphi-Atlantic tropical genus Guibourtia (Fabaceae, Detarioideae), combining NGS phylogeny and morphology. Mol Phylogenet Evol 120, 83–93. https://doi.org/10.1016/j.ympev.2017.11.026

Tung Ho, L.S., Ané, C., 2014. A linear-time algorithm for gaussian and non-gaussian trait evolution models. Syst Biol 63. https://doi.org/10.1093/sysbio/syu005

Valderrama, E., Landis, J.B., Skinner, D., Maas, P.J.M., Maas-van de Kramer, H., André, T., Grunder, N., Sass, C., Pinilla-Vargas, M., Guan, C.J., Phillips, H.R., Almeida, A.M.R. de, Specht, C.D., 2022. The genetic mechanisms underlying the convergent evolution of pollination syndromes in the Neotropical radiation of Costus L. Front Plant Sci 13. https://doi.org/10.3389/fpls.2022.874322

Valderrama, E., Sass, C., Pinilla-Vargas, M., Skinner, D., Maas, P.J.M., Maas-van de Kamer, H., Landis, J.B., Guan, C.J., Specht, C.D., 2020. Unraveling the Spiraling

Radiation: A Phylogenomic Analysis of Neotropical Costus L. Front Plant Sci 11. https://doi.org/10.3389/fpls.2020.01195

Van der Niet, T., Johnson, S.D., 2012. Phylogenetic evidence for pollinator-driven diversification of angiosperms. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2012.02.002

Van Der Niet, T., Peakall, R., Johnson, S.D., 2014. Pollinator-driven ecological speciation in plants: New evidence and future perspectives. Ann Bot 113, 199–211. https://doi.org/10.1093/aob/mct290

Vargas, O.M., Dick, C.W., 2020. Diversification History of Neotropical Lecythidaceae, an Ecologically Dominant Tree Family of Amazon Rain Forest, in: Rull, V., Carnaval, A.C. (Eds.), Neotropical Diversification: Patterns and Processes. pp. 791–806. https://doi.org/10.1007/978-3-030-31167-4_29

Vogel, S., 1968. Chiropterophilie in der neotropischen Flora. Flora oder Allgemeine botanische Zeitung. Abt. B, Morphologie und Geobotanik 157. https://doi.org/10.1016/s0367-1801(17)30097-2

Weiss, J., Delgado-Benarroch, L., Egea-Cortines, M., 2005. Genetic control of floral size and proportions. International Journal of Developmental Biology. https://doi.org/10.1387/ijdb.051998jw

Wellborn, G.A., Langerhans, R.B., 2015. Ecological opportunity and the adaptive diversification of lineages. Ecol Evol. https://doi.org/10.1002/ece3.1347

Wesselingh, F.P., Hoorn, C., Kroonenberg, S.B., Antonelli, A., Lundberg, J.G., Vonhof, H.B., Hooghiemstra, H., 2010. On the Origin of Amazonian Landscapes and Biodiversity: A Synthesis, in: Amazonia, Landscape and Species Evolution: A Look into the Past. Wiley Blackwell, pp. 421–431. https://doi.org/10.1002/9781444306408.ch26

Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, Media.

Yang, C.X., Liu, S.Y., Zerega, N.J.C., Stull, G.W., Gardner, E.M., Tian, Q., Gu, W., Lu, Q., Folk, R.A., Kates, H.R., Guralnick, R.P., Soltis, D.E., Soltis, P.S., Wang, Y.H., Yi, T.S., 2023. Phylogeny and Biogeography of Morus (Moraceae). Agronomy 13. https://doi.org/10.3390/agronomy13082021

Zhang, C., Rabiee, M., Sayyari, E., Mirarab, S., 2018. ASTRAL-III: Polynomial time species tree reconstruction from partially resolved gene trees. BMC Bioinformatics 19. https://doi.org/10.1186/s12859-018-2129-y

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., Svantesson, S., Wengström, N., Zizka, V., Antonelli, A., 2019. CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. Methods Ecol Evol 10. https://doi.org/10.1111/2041-210X.13152

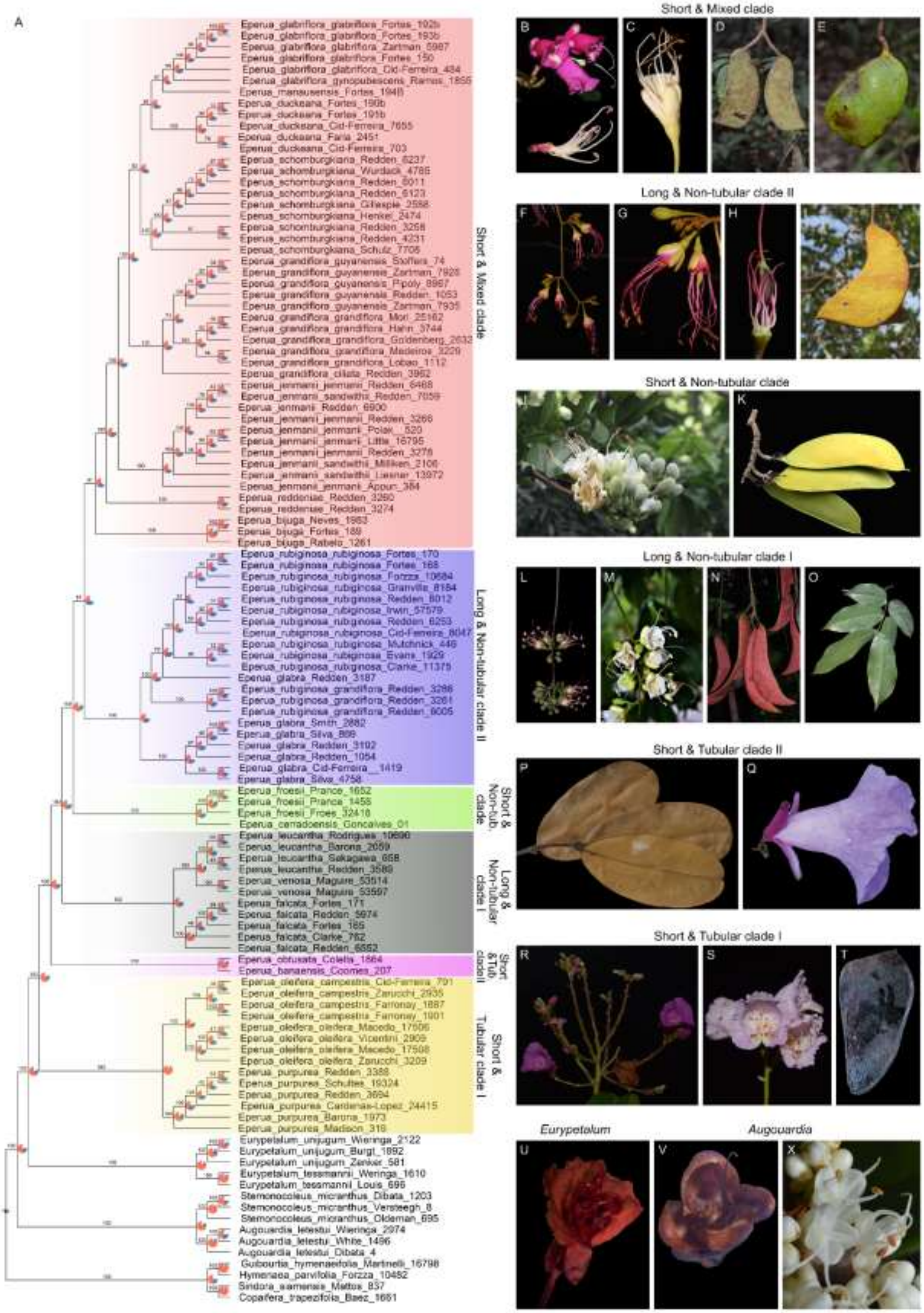

A
Eperua_glabriflora_glabriflora_Fortes_192b
Eperua_glabriflora_glabriflora_Fortes_193b
Eperua_glabriflora_glabriflora_Zartman_5987
Eperua_glabriflora_glabriflora_Fortes_150
Eperua_glabriflora_glabriflora_Cid-Ferreira_484
Eperua_glabriflora_gynopubescens_Ramos_1856
Eperua_manausensis_Fortes_194B
Eperua_duckeana_Fortes_190b
Eperua_duckeana_Fortes_191b
Eperua_duckeana_Cid-Ferreira_7655
Eperua_duckeana_Faria_2451
Eperua_duckeana_Cid-Ferreira_703
Eperua_schomburgkiana_Redden_6237
Eperua_schomburgkiana_Wurdack_4786
Eperua_schomburgkiana_Redden_6011
Eperua_schomburgkiana_Redden_6123
Eperua_schomburgkiana_Gillespie_2588
Eperua_schomburgkiana_Henkel_2474
Eperua_schomburgkiana_Redden_3268
Eperua_schomburgkiana_Redden_4231
Eperua_schomburgkiana_Schulz_7706
Eperua_grandiflora_guyanensis_Stoffers_74
Eperua_grandiflora_guyanensis_Zartman_7928
Eperua_grandiflora_guyanensis_Pipoly_8967
Eperua_grandiflora_guyanensis_Redden_1053
Eperua_grandiflora_guyanensis_Zartman_7935
Eperua_grandiflora_grandiflora_Mori_25162
Eperua_grandiflora_grandiflora_Hahn_3744
Eperua_grandiflora_grandiflora_Goldenberg_2632
Eperua_grandiflora_grandiflora_Madeiros_3229
Eperua_grandiflora_grandiflora_Lobao_1112
Eperua_grandiflora_ciliata_Redden_3962
Eperua_jenmanii_jenmanii_Redden_6488
Eperua_jenmanii_sandwithii_Redden_7059
Eperua_jenmanii_Redden_6900
Eperua_jenmanii_jenmanii_Redden_3266
Eperua_jenmanii_jenmanii_Polak_520
Eperua_jenmanii_jenmanii_Little_16795
Eperua_jenmanii_jenmanii_Redden_3278
Eperua_jenmanii_sandwithii_Milliken_2106
Eperua_jenmanii_sandwithii_Liesner_13972
Eperua_jenmanii_jenmanii_Appun_384
Eperua_reddeniae_Redden_3260
Eperua_reddeniae_Redden_3274
Eperua_bijuga_Neves_1983
Eperua_bijuga_Fortes_189
Eperua_bijuga_Rabelo_1261
Eperua_rubiginosa_rubiginosa_Fortes_170
Eperua_rubiginosa_rubiginosa_Fortes_168
Eperua_rubiginosa_rubiginosa_Forzza_10684
Eperua_rubiginosa_rubiginosa_Granville_8184
Eperua_rubiginosa_rubiginosa_Redden_8012
Eperua_rubiginosa_rubiginosa_Irwin_57579
Eperua_rubiginosa_rubiginosa_Redden_6253
Eperua_rubiginosa_rubiginosa_Cid-Ferreira_8047
Eperua_rubiginosa_rubiginosa_Mutchnick_446
Eperua_rubiginosa_rubiginosa_Evans_1929
Eperua_rubiginosa_rubiginosa_Clarke_11375
Eperua_glabra_Redden_3187
Eperua_rubiginosa_grandiflora_Redden_3286
Eperua_rubiginosa_grandiflora_Redden_3261
Eperua_rubiginosa_grandiflora_Redden_6005
Eperua_glabra_Smith_2882
Eperua_glabra_Silva_868
Eperua_glabra_Redden_3192
Eperua_glabra_Redden_1054
Eperua_glabra_Cid-Ferreira__1419
Eperua_glabra_Silva_4758
Eperua_froesii_Prance_1652
Eperua_froesii_Prance_1458
Eperua_froesii_Froes_32418
Eperua_cerradoensis_Goncalves_01
Eperua_leucantha_Rodrigues_10690
Eperua_leucantha_Barona_2059
Eperua_leucantha_Sakagawa_658
Eperua_leucantha_Redden_3589
Eperua_venosa_Maguire_53514
Eperua_venosa_Maguire_53597
Eperua_falcata_Fortes_171
Eperua_falcata_Redden_5974
Eperua_falcata_Fortes_165
Eperua_falcata_Clarke_762
Eperua_falcata_Redden_6552
Eperua_obtusata_Coletta_1864
Eperua_banaensis_Coomes_207
Eperua_oleifera_campestris_Cid-Ferreira_791
Eperua_oleifera_campestris_Zarucchi_2935
Eperua_oleifera_campestris_Farronay_1887
Eperua_oleifera_campestris_Farronay_1901
Eperua_oleifera_oleifera_Macedo_17506
Eperua_oleifera_oleifera_Vicentini_2909
Eperua_oleifera_oleifera_Macedo_17508
Eperua_oleifera_oleifera_Zarucchi_3209
Eperua_purpurea_Redden_3388
Eperua_purpurea_Schultes_19324
Eperua_purpurea_Redden_3694
Eperua_purpurea_Cardenas-Lopez_24415
Eperua_purpurea_Baruna_1973
Eperua_purpurea_Madison_318
Eurypetalum_unijugum_Wieringa_2122
Eurypetalum_unijugum_Burgt_1892
Eurypetalum_unijugum_Zenker_581
Eurypetalum_tessmannii_Wieringa_1610
Eurypetalum_tessmannii_Louis_696
Stemonocoleus_micranthus_Dibata_1203
Stemonocoleus_micranthus_Versteegh_8
Stemonocoleus_micranthus_Oldeman_695
Augouardia_letestui_Wieringa_2974
Augouardia_letestui_White_1496
Augouardia_letestui_Dibata_4
Guibourtia_hymenaeifolia_Martinelli_16798
Hymenaea_parvifolia_Forzza_10482
Sindora_siamensis_Mattos_837
Copaifera_trapezifolia_Baez_1661
Short & Mixed clade
Long & Non-tubular clade II
Short & Non-tub. clade
Long & Non-tubular clade I
Short &Tub. cladeII
Short & Tubular clade I
Short & Mixed clade
B
C
D
E
Long & Non-tubular clade II
F
G
H
Short & Non-tubular clade
J
K
Long & Non-tubular clade I
L
M
N
O
Short & Tubular clade II
P
Q
Short & Tubular clade I
R
S
T
Eurypetalum
Augouardia
U
V
X

Fig. 1. A. Coalescent-based species tree analysis of the Eperua *s.l.* clade obtained from 883 exons and 114 accessions. Branch lengths are proportional to coalescent units in the ASTRAL result. Pie charts illustrate the quartet scores for each node for the 883 exons, with red representing the current topology, blue the second most favored topology, and azure the remaining one. Numbers above the branches show local posterior probabilities [pp1*100, following the representation of Sayyary and Mirarab (2016)]. Equal branch lengths were used to allow the reader to distinguish support values. Species B, E: *Eperua glabriflora*; C, D: *E. duckeana*; F-H: *E. rubiginosa*; I, J: *E. cerradoensis*; K, M, N: *E. falcata*; L: *E. leucantha*; O: *E. obtusata*; P: *E. banaensis*; Q, S: *E. oleifera* var. *campestris*; R: *E. oleifera* var. *oleifera*; T: *Eurypetalum tessmanii*; U, V: *Augouardia letestui*. Photos B: H.C.Lima; C: T.C. Monteiro; D, E, N, T, U: E.A. Fortes; F: R. Goldenberg; G: H. ter Steege; H: P. Teunissen; I, J: A. Gonçalves; K, M: D. Sabatier; L: F. Castro-Lima; P: G.A. Romero-González; Q, R: F. Farroñay; V: Bidault.

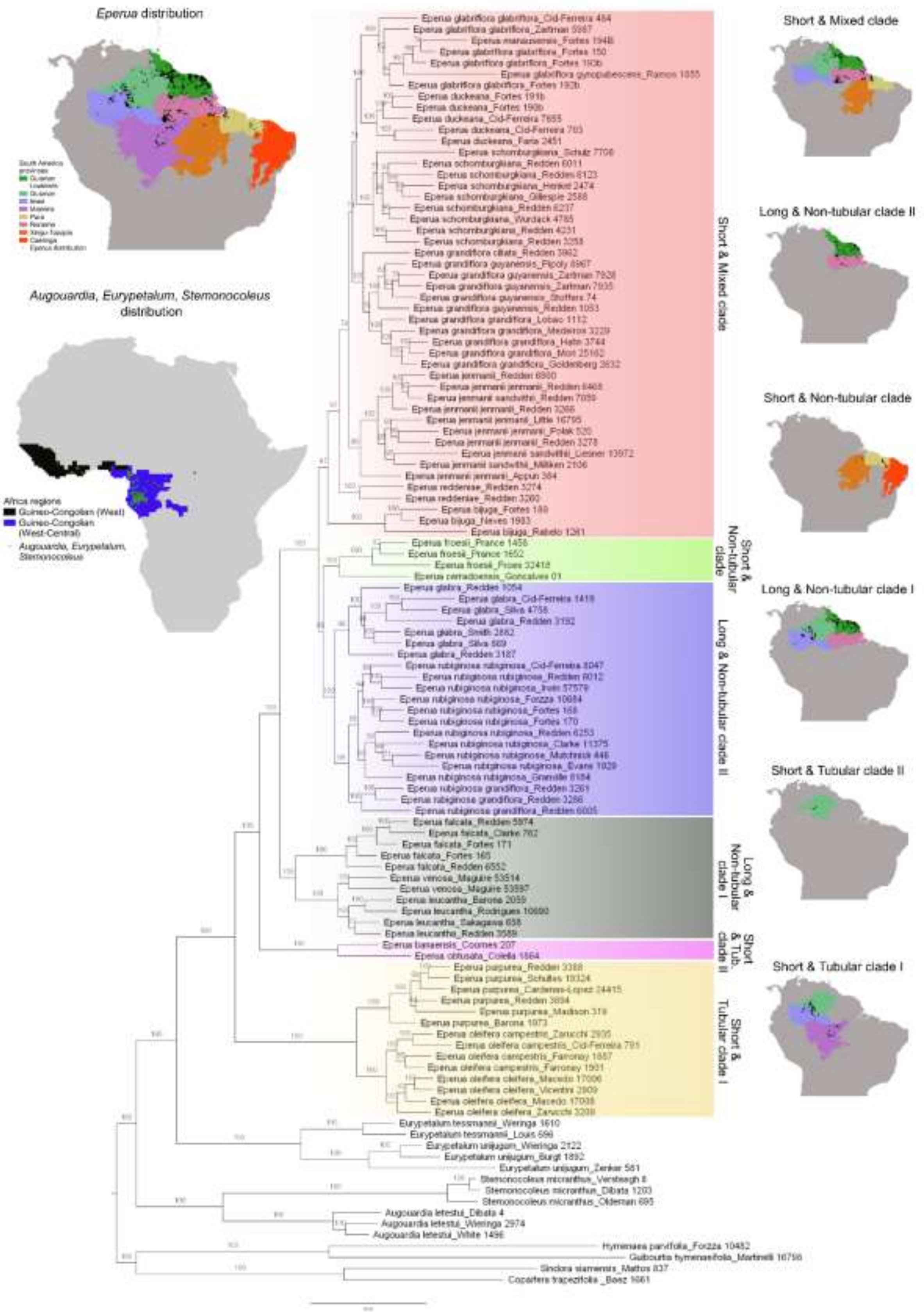

Eperua distribution
South America provinces
Guianan Lowlands
Guianan
Imeri
Madeira
Pará
Roraima
Xingu-Tapajós
Caatinga
Eperua distribution
Augouardia, Eurypetalum, Stemonocoleus distribution
Africa regions
Guineo-Congolian (West)
Guineo-Congolian (West-Central)
Augouardia, Eurypetalum, Stemonocoleus
Eperua glabriflora glabriflora_Cid-Ferreira 484
Eperua glabriflora glabriflora_Zartman 5987
Eperua manausensis_Fortes 194B
Eperua glabriflora glabriflora_Fortes 150
Eperua glabriflora glabriflora_Fortes 193b
Eperua glabriflora gynopubescens_Ramos 1855
Eperua glabriflora glabriflora_Fortes 192b
Eperua duckeana_Fortes 191b
Eperua duckeana_Fortes 190b
Eperua duckeana_Cid-Ferreira 7655
Eperua duckeana_Cid-Ferreira 793
Eperua duckeana_Faria 2451
Eperua schomburgkiana_Schulz 7706
Eperua schomburgkiana_Redden 6011
Eperua schomburgkiana_Redden 6123
Eperua schomburgkiana_Henkel 2474
Eperua schomburgkiana_Gillespie 2588
Eperua schomburgkiana_Redden 6237
Eperua schomburgkiana_Wurdack 4785
Eperua schomburgkiana_Redden 4231
Eperua schomburgkiana_Redden 3258
Eperua grandiflora ciliata_Redden 3962
Eperua grandiflora guyanensis_Pipoly 8967
Eperua grandiflora guyanensis_Zartman 7928
Eperua grandiflora guyanensis_Zartman 7935
Eperua grandiflora guyanensis_Stoffers 74
Eperua grandiflora guyanensis_Redden 1053
Eperua grandiflora grandiflora_Lobão 1112
Eperua grandiflora grandiflora_Medeiros 3229
Eperua grandiflora grandiflora_Hatin 3744
Eperua grandiflora grandiflora_Mori 25162
Eperua grandiflora grandiflora_Goldenberg 3632
Eperua jenmanii_Redden 6900
Eperua jenmanii jenmanii_Redden 6468
Eperua jenmanii sandwithii_Redden 7059
Eperua jenmanii jenmanii_Redden 3266
Eperua jenmanii jenmanii_Little 16795
Eperua jenmanii jenmanii_Polak 520
Eperua jenmanii jenmanii_Redden 3278
Eperua jenmanii sandwithii_Lesner 13972
Eperua jenmanii sandwithii_Milliken 2106
Eperua jenmanii jenmanii_Appun 384
Eperua reddeniae_Redden 3274
Eperua reddeniae_Redden 3260
Eperua bijuga_Fortes 189
Eperua bijuga_Neves 1983
Eperua bijuga_Rabelo 1261
Short & Mixed clade
Eperua froesii_Prance 1458
Eperua froesii_Prance 1652
Eperua froesii_Froes 32418
Eperua cerradoensis_Goncalves 01
Short & Non-tubular clade
Eperua glabra_Redden 1054
Eperua glabra_Cid-Ferreira 1418
Eperua glabra_Silva 4758
Eperua glabra_Redden 3192
Eperua glabra_Smith 2882
Eperua glabra_Silva 569
Eperua glabra_Redden 3187
Eperua rubiginosa rubiginosa_Cid-Ferreira 8047
Eperua rubiginosa rubiginosa_Redden 6012
Eperua rubiginosa rubiginosa_Irwin 57579
Eperua rubiginosa rubiginosa_Forzza 10684
Eperua rubiginosa rubiginosa_Fortes 168
Eperua rubiginosa rubiginosa_Fortes 170
Eperua rubiginosa rubiginosa_Redden 6253
Eperua rubiginosa rubiginosa_Clarke 11375
Eperua rubiginosa rubiginosa_Mutchnick 446
Eperua rubiginosa rubiginosa_Evans 1029
Eperua rubiginosa rubiginosa_Granville 6184
Eperua rubiginosa grandiflora_Redden 3261
Eperua rubiginosa grandiflora_Redden 3286
Eperua rubiginosa grandiflora_Redden 6005
Long & Non-tubular clade II
Eperua falcata_Redden 5974
Eperua falcata_Clarke 782
Eperua falcata_Fortes 171
Eperua falcata_Fortes 165
Eperua falcata_Redden 6552
Eperua venosa_Maguire 53514
Eperua venosa_Maguire 53597
Eperua leucantha_Barona 2059
Eperua leucantha_Rodrigues 10690
Eperua leucantha_Sakagawa 658
Eperua leucantha_Redden 3589
Long & Non-tubular clade I
Eperua banaensis_Coomes 207
Eperua obtusata_Colella 1664
Short & Tub. clade II
Eperua purpurea_Redden 3388
Eperua purpurea_Schultes 10324
Eperua purpurea_Cardenas-Lopez 24415
Eperua purpurea_Redden 3894
Eperua purpurea_Madison 319
Eperua purpurea_Barona 1973
Eperua oleifera campestris_Zarucchi 2935
Eperua oleifera campestris_Cid-Ferreira 791
Eperua oleifera campestris_Farroñay 1887
Eperua oleifera campestris_Farroñay 1931
Eperua oleifera oleifera_Macedo 17006
Eperua oleifera oleifera_Vicentini 2909
Eperua oleifera oleifera_Macedo 17038
Eperua oleifera oleifera_Zarucchi 3208
Short & Tubular clade I
Eurypetalum tessmannii_Wieringa 1610
Eurypetalum tessmannii_Louis 696
Eurypetalum unijugum_Wieringa 2122
Eurypetalum unijugum_Burgt 1892
Eurypetalum unijugum_Zenker 581
Stemonocoleus micranthus_Versteegh 8
Stemonocoleus micranthus_Dibata 1203
Stemonocoleus micranthus_Oldeman 695
Augouardia letestui_Dibata 4
Augouardia letestui_Wieringa 2974
Augouardia letestui_White 1496
Hymenaea parvifolia_Forzza 10482
Guibourtia hymenaeifolia_Martinelli 16756
Sindora siamensis_Mattos 837
Copaifera trapezifolia _Baez 1661
Short & Mixed clade
Long & Non-tubular clade II
Short & Non-tubular clade
Long & Non-tubular clade I
Short & Tubular clade II
Short & Tubular clade I

Fig. 2. Concatenated-based tree analysis using ML of the Eperua *s.l.* clade obtained from 883 exons and 114 accessions. Branch lengths are proportional to the number of substitutions. Number in the branches show the bootstrap support obtained from the RAxML analyses.

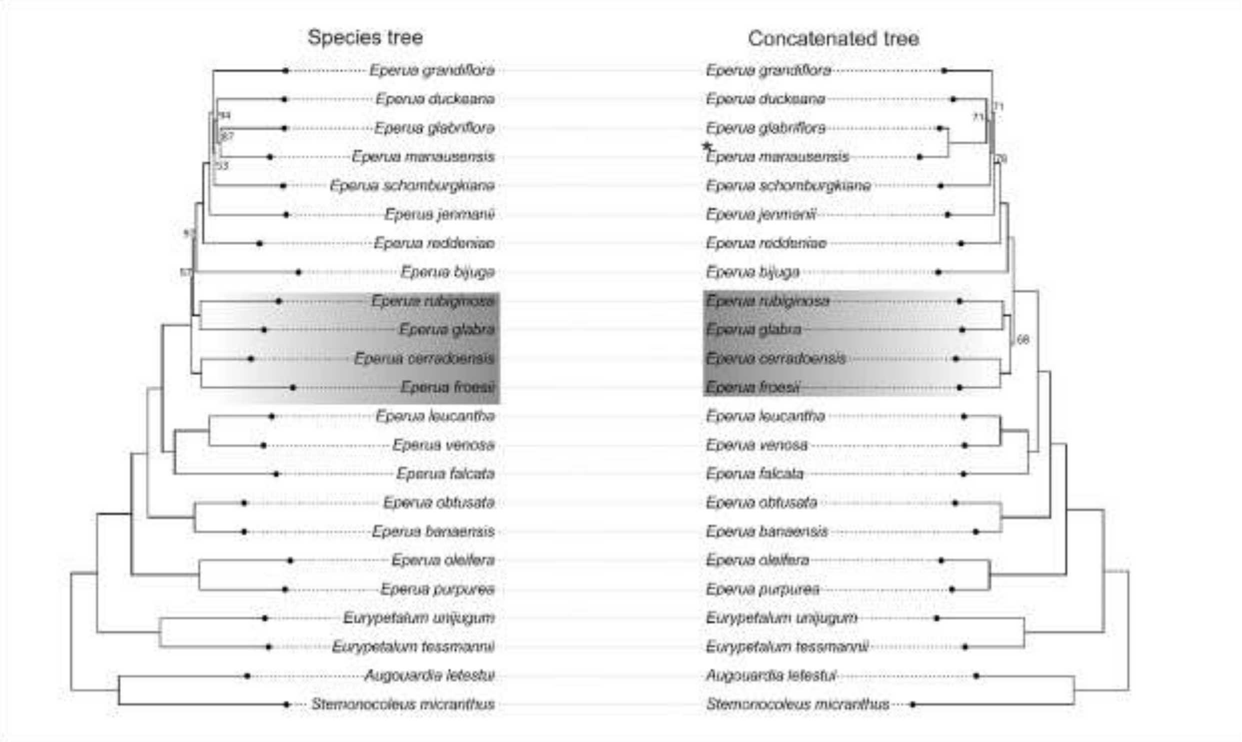


Fig. 3. Comparison between the concatenated and the species trees. The main incongruence in the tree is highlighted in the black square. Also, *Eperua manausensis* showed inside *E. glabriflora* in the concatenated tree. All branches received maximum support except the ones with the support annotated (bootstrap support in the concatenated tree and local posterior probabilities in the species tree [pp1 *100]).

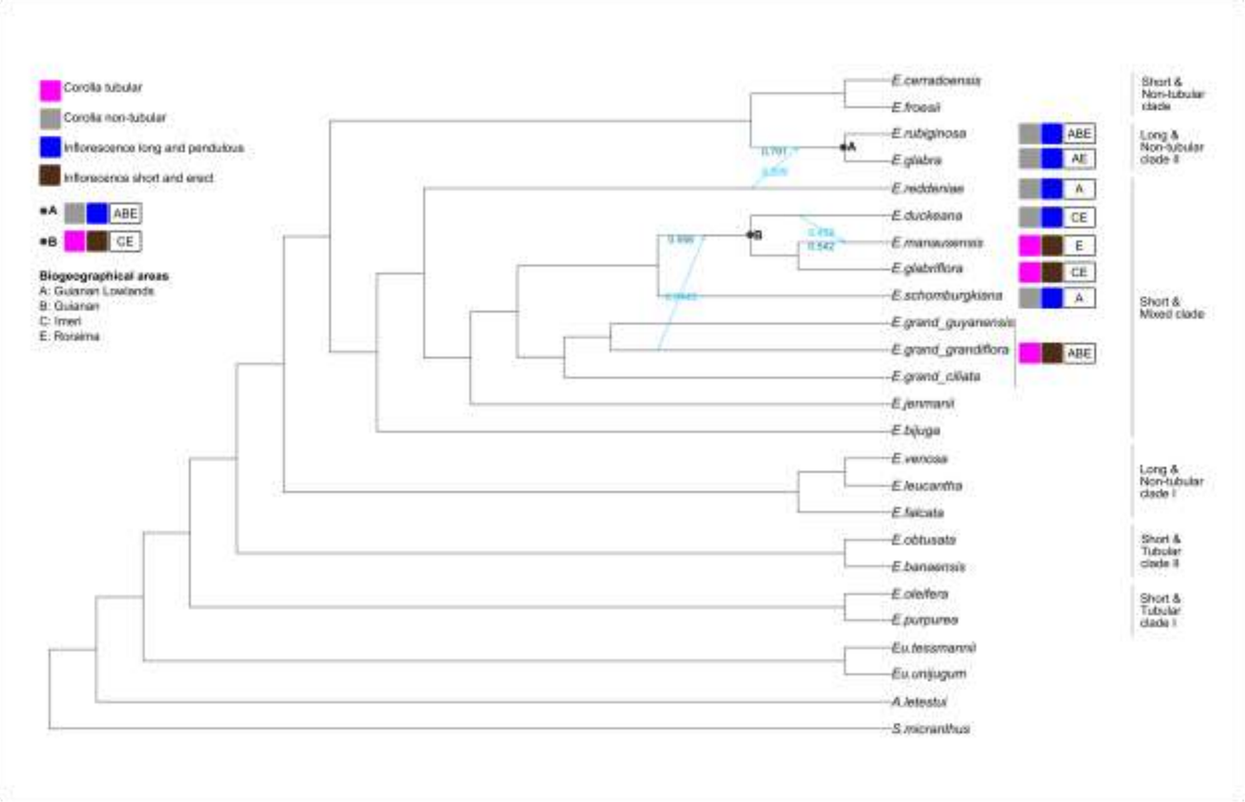


Fig. 4. Rooted phylogenetic network with three hybridization events (h = 3), estimated using SNaQ in the Julia package PhyloNetworks. Species and ancestral nodes involved in reticulation events are illustrated according to the corolla and inflorescence types and distribution area. Black edges: major tree; blue colored arrows: minor hybrid edges, annotated by their estimated γ (light blue numbers).

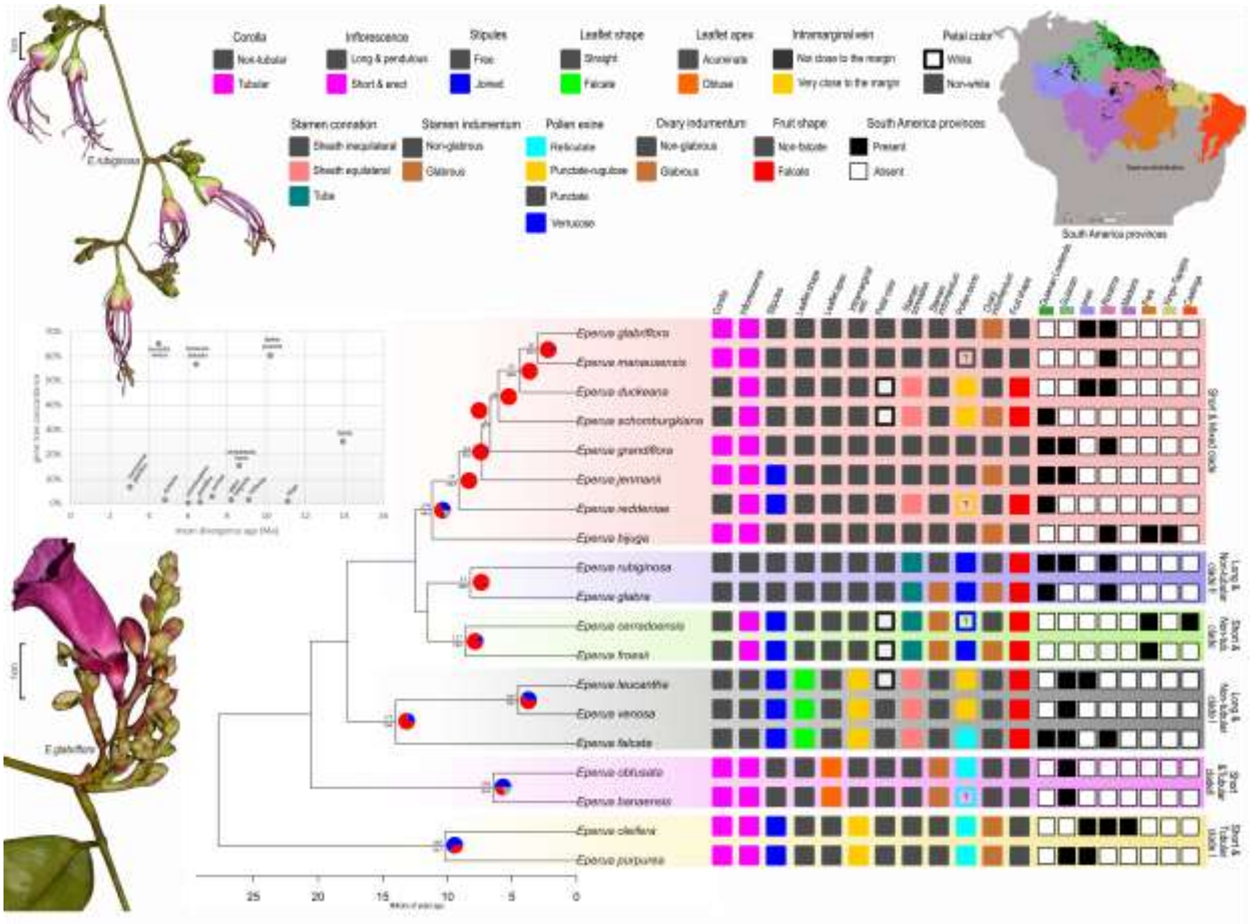


Fig. 5. Main morphological characteristics of the genus *Eperua.* Pollen morphology is based on (Banks and Rico, 1999), (Cowan, 1975), and (ter Steege et al., 2023), other morphological characteristics are based on Fortes et al. (2023a), and the biogeographical provinces are based on (Morrone, 2014; Morrone et al., 2022). The pie charts display (results from Phyparts, Fig. S7) the proportion of exons that support that clade (blue), the proportion that support the main alternative for that clade (green), the proportion that supports the remaining alternatives (red), and the proportion that have no support for conflicting bipartition (grey).

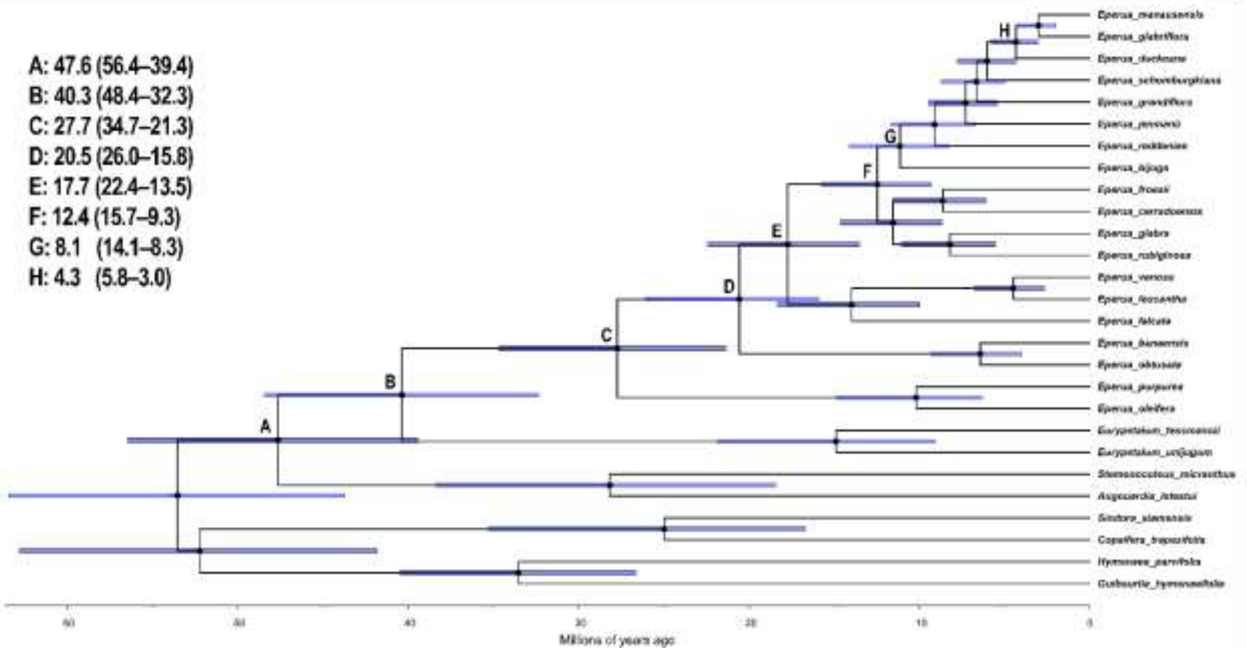


Fig. 6. Calibrated maximum clade credibility tree of the Eperua *s.l.* clade obtained in Beast from a concatenated matrix of 30 exons and 27 accessions. Node bars show 95% highest posterior density (HPD) for node ages.

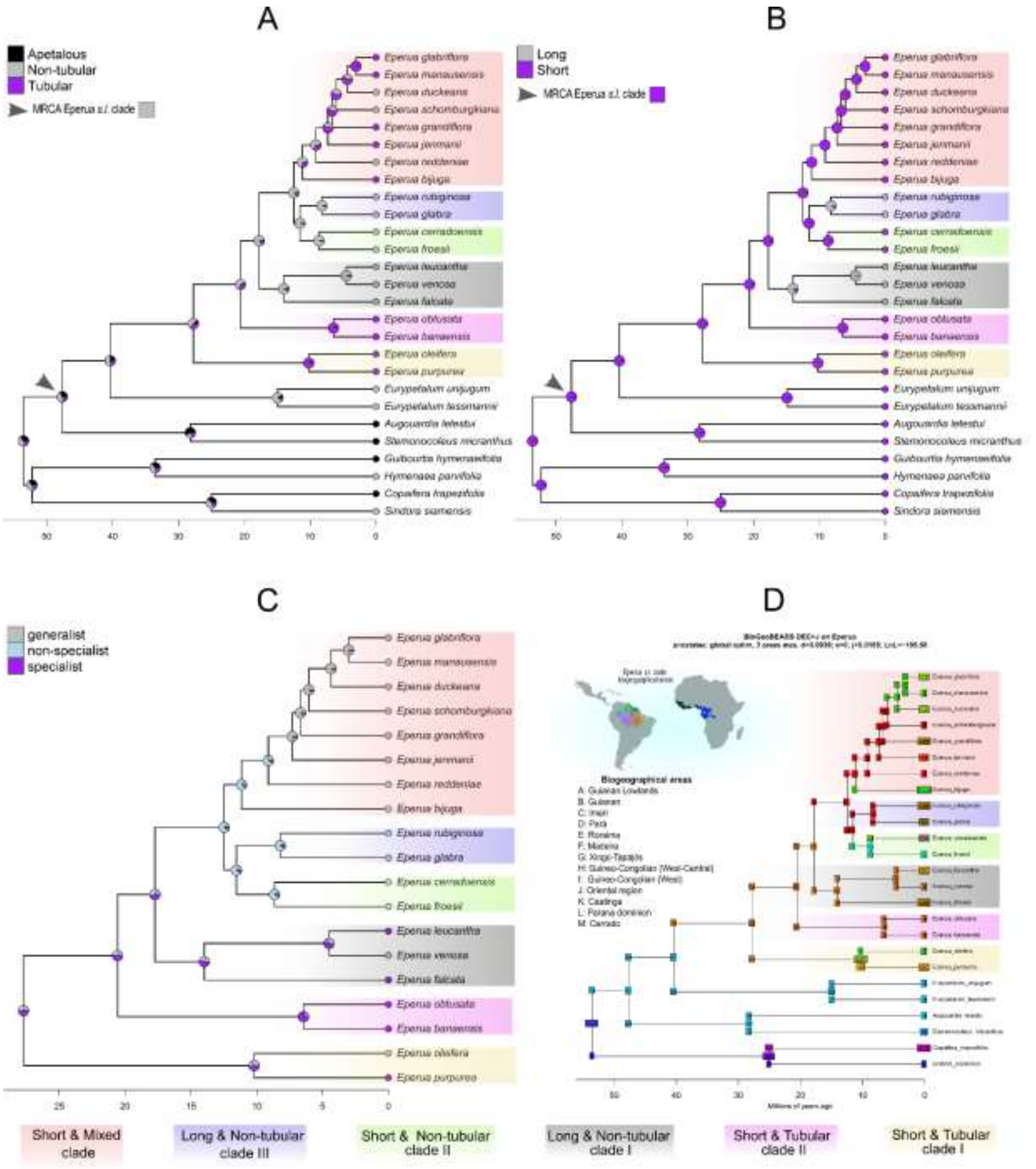


Fig. 7. Ancestral state reconstruction and biogeographic analysis of the Eperua *s.l.* clade. (A-C) Ancestral state reconstructions on the dated MCC tree from BEAST v.1.10.4., posterior probabilities at nodes from 100 stochastic character maps under ER model; (A) corolla type: tubular corolla (five petals, adaxial petal forming a tube and stamens inserted in the corolla), non-tubular corolla (five petals, adaxial petal not

forming a tube and stamens exserted from the perianth), or apetalous flowers (no petals, stamens exserted from the perianth) ; (B) inflorescence type: short (around 10 cm long, most less than 20 cm long) and erect or long (around 80 cm to 3 m long, never shorter than 50 cm) and pendulous; (C) habitat preferences: specialist to white-sand forests (species primarily inhabiting white-sand forests, occasionally inhabiting other soil formations such as clay soil and terrace formations), generalists (species occurring in white-sand forests and in clay soil and terrace formation forests), and non-specialists (species primarily inhabiting in clay soil and terrace formation forests outside white-sand forests); (D) BioGeoBEARS results showing the most probable geographic ranges of ancestral nodes of the Eperua *s.l.* clade under DEC+J model. Biogeographical areas after Morrone 2014, 2022a, and Marshall 2019.

Supplementary Material

1 Supplementary data

Stubby Adapter sequences:

5'-/5Phos/GATCGGAAGAGCACACGTCTGAACTCCAGTC-3'

5'-ACACTCTTTCCCTACACGACGCTCTTCCGATC*T-3'

```
5'-   G A T C G G A A G A G C A C A C G T C T G A A C T C C A G T C -3'
      | | | | | | | | | | | |                 |         | | |
3'- T C T A G C C T T C T C G C A G C A C A T C C C T T T C T C A C A -3'
```

2 Supplementary Figures and Tables

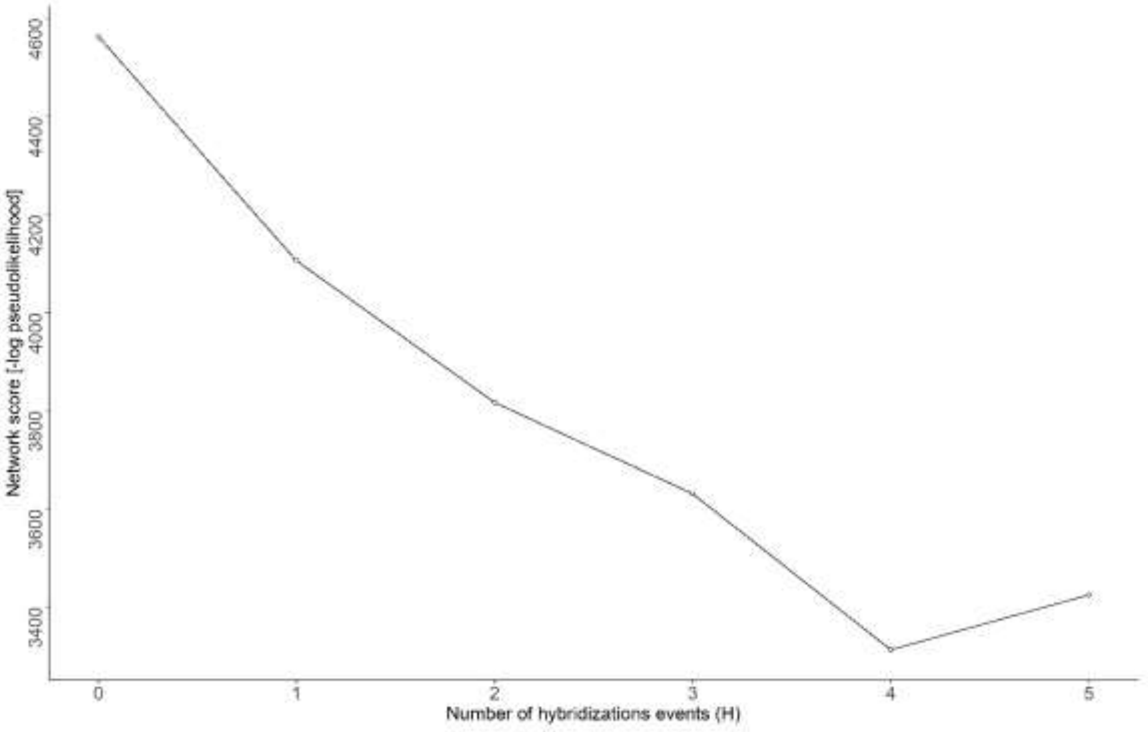


Figure S1. Negative log pseudolikelihood profile for each number of hybridization events inferred using SNaQ in the Julia package PhyloNetworks.

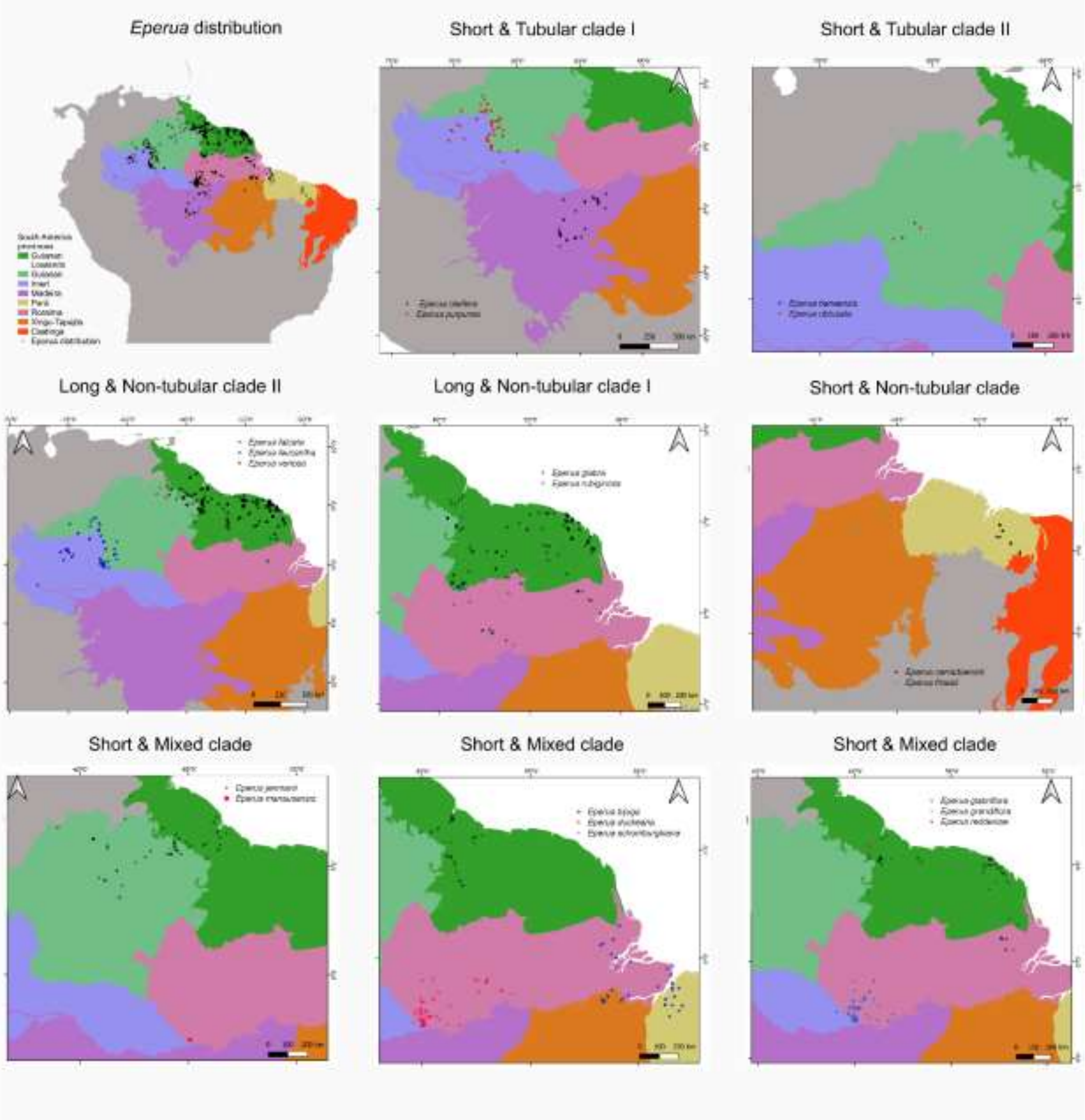


Figure S2. Geographic distribution of the genus *Eperua* across South America provinces from (Morrone, 2014; Morrone et al., 2022). Coordinates obtained from Fortes et al (2023a). The only point of *E. falcata* in the Roraima province refers to the collection Pereira L.A. & Cardoso J.O. 825 (RB herbarium).

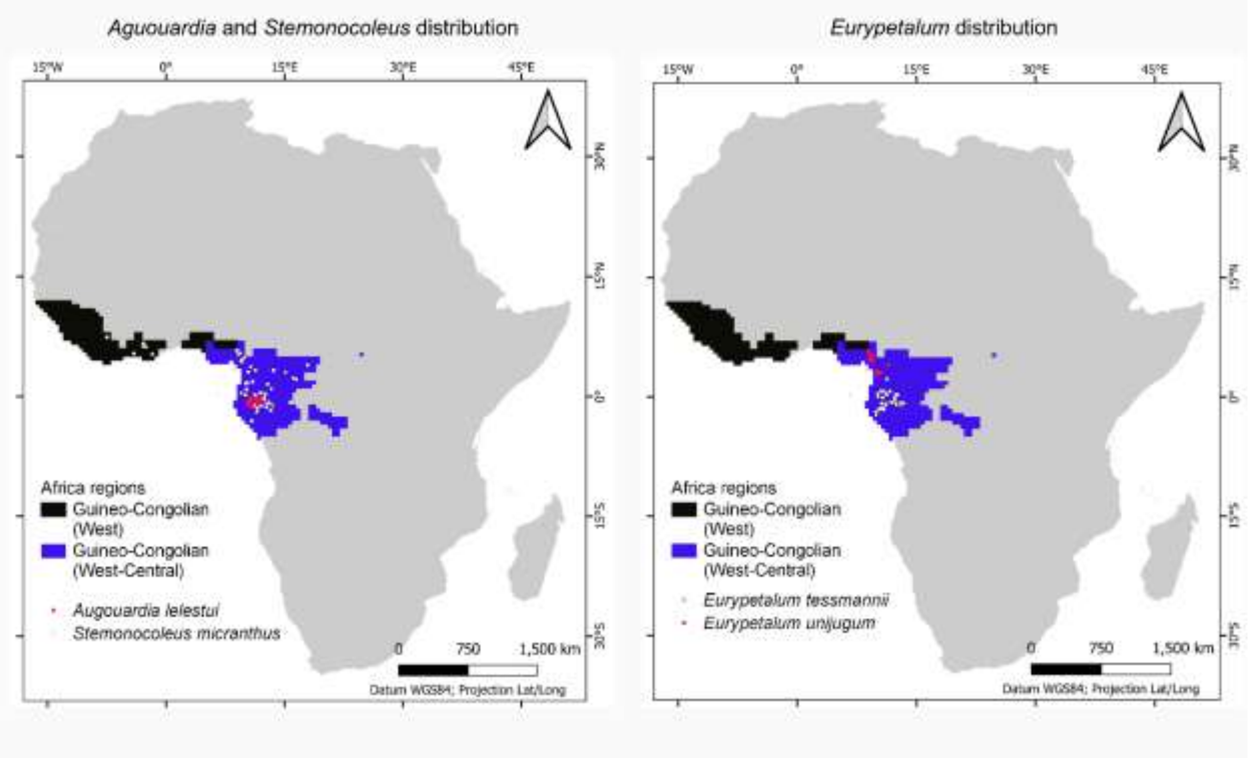


Figure S3. Geographic distribution of the genera *Agugouardia, Eurypetalum,* and *Stemonocoleus* across South America provinces from (Morrone, 2014; Morrone et al., 2022). Coordinates obtained from Fortes et al (2023a). Coordinates were obtained from GBIF (GBIF.org, 2023) using the R packages rgbif v3.7.8 (Chamberlain, 2019), Taxonstand v2.4 (Cayuela et al., 2021), and CoordinateCleaner v3.0.1 (Zizka et al., 2019).

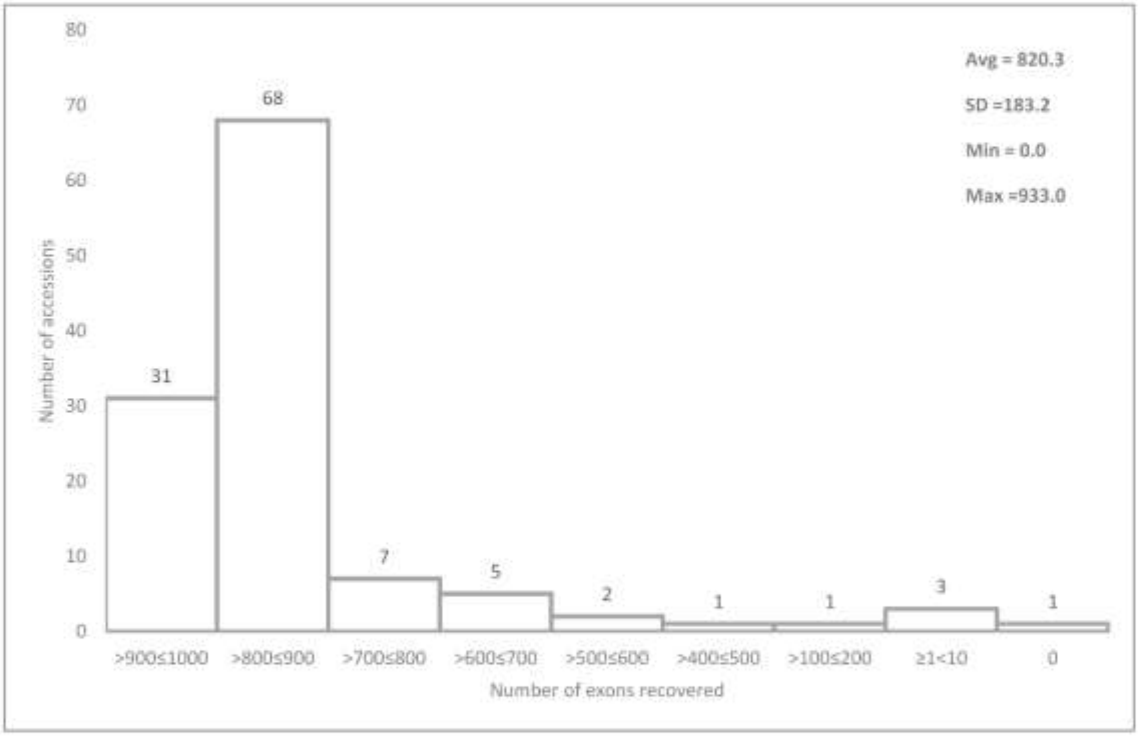


Figure S4. Numbers of exons recovered per accession using Hybpiper. It was used target capture sequencing with the Detarioideae v.1 nuclear exon capture kit to sequence 119 collections comprising all species of the Eperua *s.l.* clade. Avg: average, SD: standart deviation; Min: minimum number of accessions recovered; Max: maximum number of exons recovered.

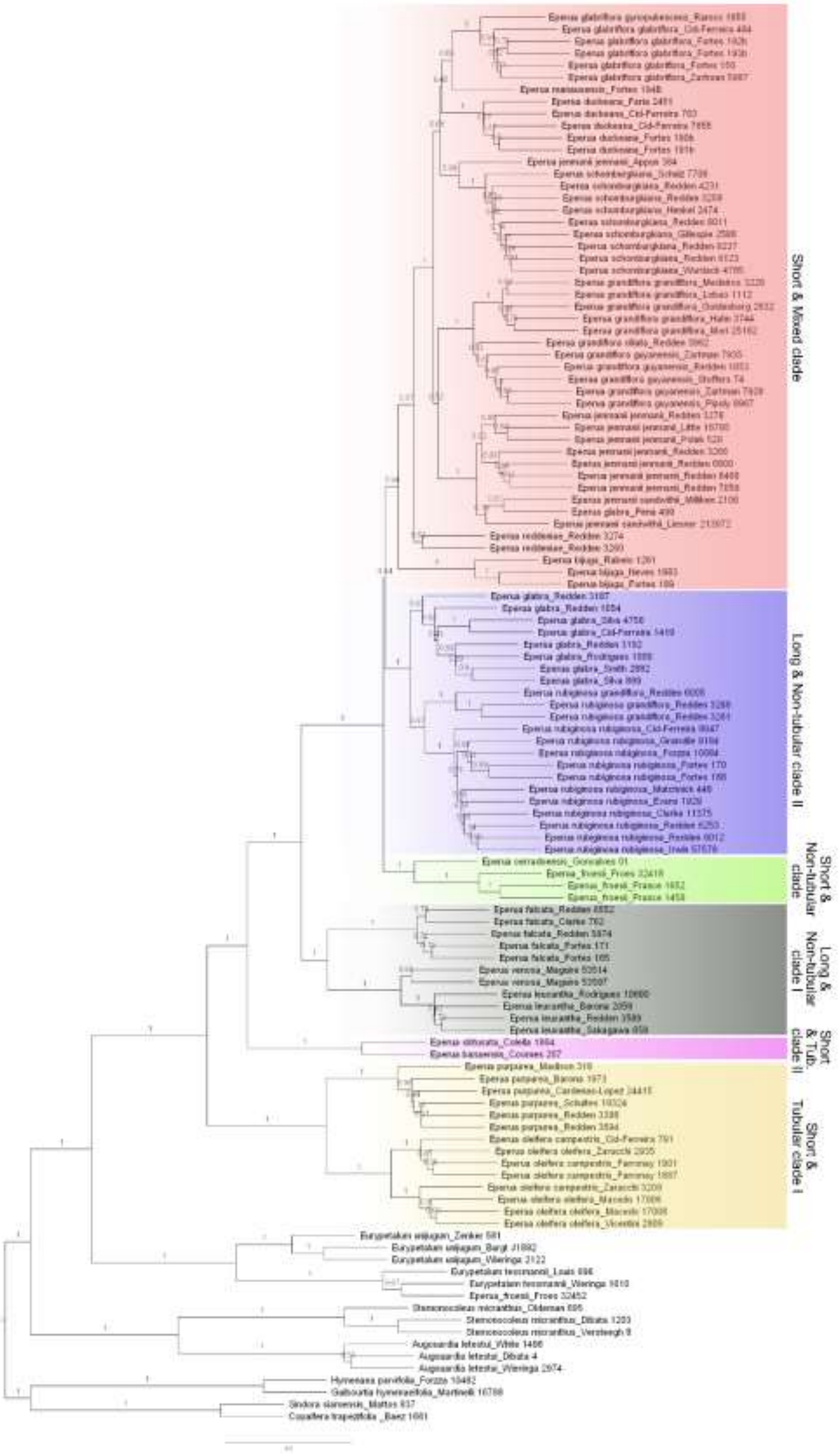

Eperua glabriflora puripubescens_Ramos 1855
Eperua glabriflora glabriflora_Cid-Ferreira 484
Eperua glabriflora glabriflora_Fortes 192b
Eperua glabriflora glabriflora_Fortes 193b
Eperua glabriflora glabriflora_Fortes 150
Eperua glabriflora glabriflora_Zartman 5887
Eperua manausensis_Fortes 1948
Eperua duckeana_Faria 2451
Eperua duckeana_Cid-Ferreira 703
Eperua duckeana_Cid-Ferreira 7855
Eperua duckeana_Fortes 190b
Eperua duckeana_Fortes 191b
Eperua jenmanii jenmanii_Appun 364
Eperua schomburgkiana_Schulz 7709
Eperua schomburgkiana_Redden 4231
Eperua schomburgkiana_Redden 3259
Eperua schomburgkiana_Henkel 2474
Eperua schomburgkiana_Redden 8011
Eperua schomburgkiana_Gillespie 2586
Eperua schomburgkiana_Redden 8227
Eperua schomburgkiana_Redden 6123
Eperua schomburgkiana_Wurdack 4785
Eperua grandiflora grandiflora_Medeiros 3220
Eperua grandiflora grandiflora_Lobao 1112
Eperua grandiflora grandiflora_Oostenberg 2832
Eperua grandiflora grandiflora_Hahn 3744
Eperua grandiflora grandiflora_Mori 25162
Eperua grandiflora ciliata_Redden 5962
Eperua grandiflora guyanensis_Zartman 7935
Eperua grandiflora guyanensis_Redden 1053
Eperua grandiflora guyanensis_Stoffers 74
Eperua grandiflora guyanensis_Zartman 7928
Eperua grandiflora guyanensis_Pipoly 6967
Eperua jenmanii jenmanii_Redden 3276
Eperua jenmanii jenmanii_Little 15700
Eperua jenmanii jenmanii_Polak 520
Eperua jenmanii jenmanii_Redden 3266
Eperua jenmanii jenmanii_Redden 0900
Eperua jenmanii jenmanii_Redden 8468
Eperua jenmanii jenmanii_Redden 7058
Eperua jenmanii sandwithii_Milliken 2100
Eperua glabra_Pena 490
Eperua jenmanii sandwithii_Liesner 213972
Eperua reddeniae_Redden 3274
Eperua reddeniae_Redden 3260
Eperua bijuga_Ribeiro 1261
Eperua bijuga_Neves 1983
Eperua bijuga_Fortes 189
Eperua glabra_Redden 3187
Eperua glabra_Redden 1054
Eperua glabra_Silva 4758
Eperua glabra_Cid-Ferreira 1419
Eperua glabra_Redden 3192
Eperua glabra_Rodrigues 1559
Eperua glabra_Smith 2982
Eperua glabra_Silva 899
Eperua rubiginosa grandiflora_Redden 6005
Eperua rubiginosa grandiflora_Redden 3268
Eperua rubiginosa grandiflora_Redden 3261
Eperua rubiginosa rubiginosa_Cid-Ferreira 9047
Eperua rubiginosa rubiginosa_Granville 9194
Eperua rubiginosa rubiginosa_Forzza 10084
Eperua rubiginosa rubiginosa_Fortes 170
Eperua rubiginosa rubiginosa_Fortes 188
Eperua rubiginosa rubiginosa_Maguire 446
Eperua rubiginosa rubiginosa_Evans 1929
Eperua rubiginosa rubiginosa_Clarke 11375
Eperua rubiginosa rubiginosa_Redden 6253
Eperua rubiginosa rubiginosa_Redden 6012
Eperua rubiginosa rubiginosa_Irwin 57579
Eperua cerradoensis_Goncalves 01
Eperua_froesii_Froes 32418
Eperua_froesii_Prance 1652
Eperua_froesii_Prance 1458
Eperua falcata_Redden 6552
Eperua falcata_Clarke 762
Eperua falcata_Redden 5874
Eperua falcata_Fortes 171
Eperua falcata_Fortes 165
Eperua venosa_Maguire 53514
Eperua venosa_Maguire 53597
Eperua leucantha_Rodrigues 10660
Eperua leucantha_Barona 2059
Eperua leucantha_Redden 3589
Eperua leucantha_Sakagawa 658
Eperua obtusata_Colella 1864
Eperua baresensis_Cousses 287
Eperua purpurea_Madison 318
Eperua purpurea_Barona 1973
Eperua purpurea_Cardenas-Lopez 24415
Eperua purpurea_Schultes 10324
Eperua purpurea_Redden 3388
Eperua purpurea_Redden 3594
Eperua oleifera campestris_Cid-Ferreira 791
Eperua oleifera oleifera_Zaracchi 2935
Eperua oleifera campestris_Farroney 1901
Eperua oleifera campestris_Farroney 1887
Eperua oleifera campestris_Zaracchi 3209
Eperua oleifera oleifera_Macedo 17006
Eperua oleifera oleifera_Macedo 17008
Eperua oleifera oleifera_Vicentini 2809
Eurypetalum unijugum_Zenker 581
Eurypetalum unijugum_Bargt J1882
Eurypetalum unijugum_Wieringa 3122
Eurypetalum tessmannii_Louis 896
Eurypetalum tessmannii_Wieringa 5610
Eperua_froesii_Froes 32452
Stemonocoleus micranthus_Oldeman 695
Stemonocoleus micranthus_Dibata 1203
Stemonocoleus micranthus_Versteegh 8
Augouardia letestui_White 1488
Augouardia letestui_Dibata 4
Augouardia letestui_Wieringa 2974
Hymenaea parvifolia_Forzza 10482
Guibourtia hymenaeifolia_Martinelli 16788
Sindora siamensis_Mattos 837
Copaifera trapezifolia _Baez 1081
Short & Mixed clade
Long & Non-tubular clade II
Short & Non-tubular clade
Long & Non-tubular clade I
Short & Tub. clade II
Short & Tubular clade I

Figure S5. Coalescent-based species tree analysis of the Eperua *s.l.* clade obtained from 62 exons (no signal for recombination) and 114 accessions. Branch lengths are proportional to coalescent units in the ASTRAL result. Numbers above the branches show local posterior probabilities.

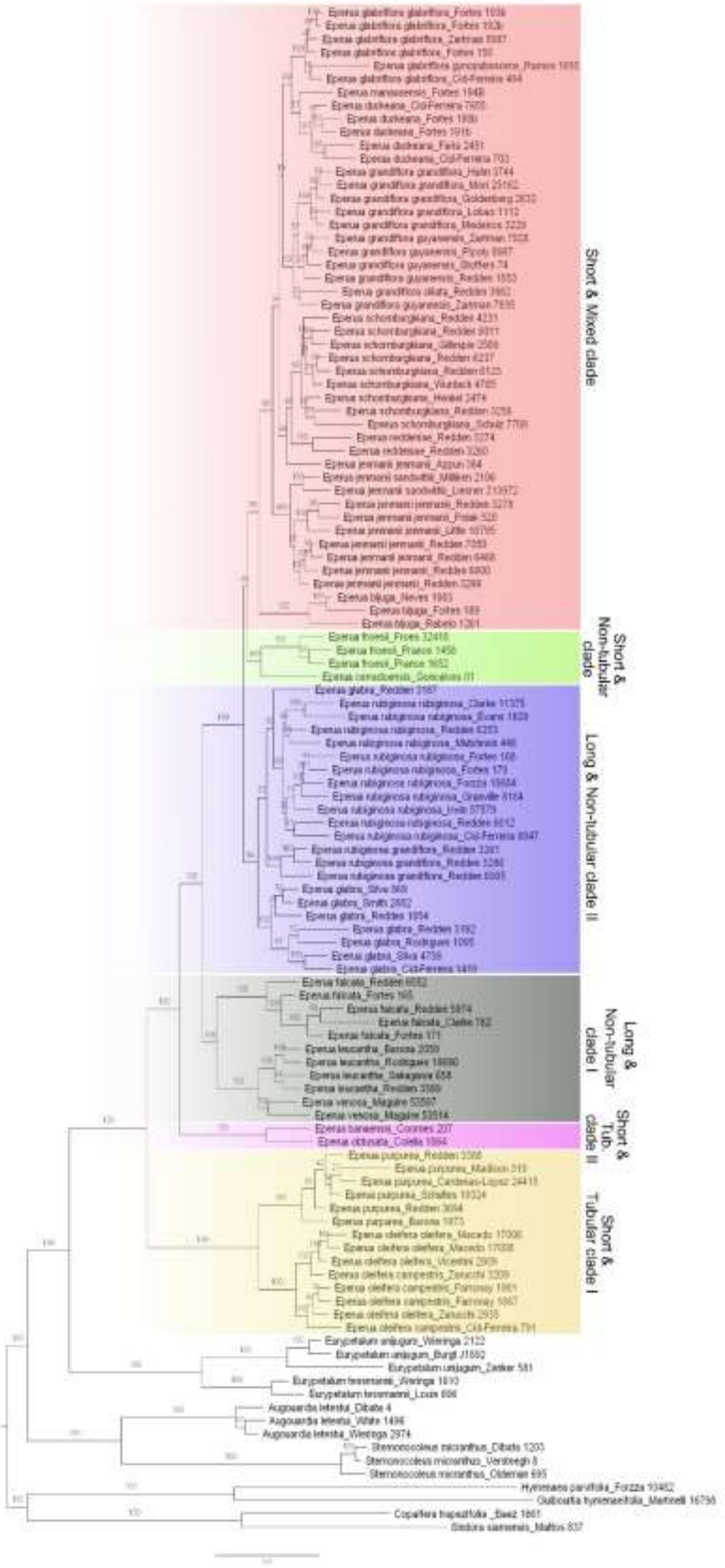

Eperua glabriflora glabriflora_Fortes 1036
Eperua glabriflora glabriflora_Fortes 1036
Eperua glabriflora glabriflora_Zartman 7087
Eperua glabriflora glabriflora_Fortes 150
Eperua glabriflora guncophaseoma_Ramos 1016
Eperua glabriflora glabriflora_Cid-Ferreira 464
Eperua manausensis_Fortes 1948
Eperua duckeana_Cid-Ferreira 7605
Eperua duckeana_Fortes 1936
Eperua duckeana_Fortes 1916
Eperua duckeana_Faria 2451
Eperua duckeana_Cid-Ferreira 703
Eperua grandiflora grandiflora_Hahn 3744
Eperua grandiflora grandiflora_Mori 25162
Eperua grandiflora grandiflora_Goldenberg 2632
Eperua grandiflora grandiflora_Lobao 1112
Eperua grandiflora grandiflora_Medeiros 3229
Eperua grandiflora guyanensis_Zartman 7528
Eperua grandiflora guyanensis_Pipoly 8987
Eperua grandiflora guyanensis_Stoffers 74
Eperua grandiflora guyanensis_Redden 1553
Eperua grandiflora ciliata_Redden 3902
Eperua grandiflora guyanensis_Zartman 7535
Eperua schomburgkiana_Redden 4231
Eperua schomburgkiana_Redden 9011
Eperua schomburgkiana_Gillespie 2566
Eperua schomburgkiana_Redden 4237
Eperua schomburgkiana_Redden 0125
Eperua schomburgkiana_Vourlack 4785
Eperua schomburgkiana_Henkel 2474
Eperua schomburgkiana_Redden 3258
Eperua schomburgkiana_Schulz 7706
Eperua reddeniae_Redden 3274
Eperua reddeniae_Redden 3260
Eperua jenmanii jenmanii_Appun 384
Eperua jenmanii sandwithii_Milliken 2106
Eperua jenmanii sandwithii_Liesner 213972
Eperua jenmanii jenmanii_Redden 3278
Eperua jenmanii jenmanii_Polak 520
Eperua jenmanii jenmanii_Little 10795
Eperua jenmanii jenmanii_Redden 7093
Eperua jenmanii jenmanii_Redden 6468
Eperua jenmanii jenmanii_Redden 6800
Eperua jenmanii jenmanii_Redden 3288
Eperua bijuga_Neves 1903
Eperua bijuga_Fortes 189
Eperua bijuga_Rabelo 1261
Short & Mixed clade
Eperua froesii_Froes 32416
Eperua froesii_Prance 1456
Eperua froesii_Prance 1652
Eperua cerradoensis_Goncalves 01
Short & Non-tubular clade
Eperua glabra_Redden 2187
Eperua rubiginosa rubiginosa_Clarke 11325
Eperua rubiginosa rubiginosa_Evans 1829
Eperua rubiginosa rubiginosa_Redden 6253
Eperua rubiginosa rubiginosa_Melchers 446
Eperua rubiginosa rubiginosa_Fortes 168
Eperua rubiginosa rubiginosa_Fortes 179
Eperua rubiginosa rubiginosa_Forzza 18684
Eperua rubiginosa rubiginosa_Granville 8184
Eperua rubiginosa rubiginosa_Irwin 57579
Eperua rubiginosa rubiginosa_Redden 6612
Eperua rubiginosa rubiginosa_Cid-Ferreira 8347
Eperua rubiginosa grandiflora_Redden 3261
Eperua rubiginosa grandiflora_Redden 3286
Eperua rubiginosa grandiflora_Redden 6005
Eperua glabra_Silva 369
Eperua glabra_Smith 2882
Eperua glabra_Redden 1934
Eperua glabra_Redden 3192
Eperua glabra_Rodrigues 1095
Eperua glabra_Silva 4739
Eperua glabra_Cid-Ferreira 1419
Long & Non-tubular clade II
Eperua falcata_Redden 6052
Eperua falcata_Fortes 165
Eperua falcata_Redden 5974
Eperua falcata_Clarke 782
Eperua falcata_Fortes 171
Eperua leucantha_Barona 2050
Eperua leucantha_Rodrigues 18690
Eperua leucantha_Sakagawa 658
Eperua leucantha_Redden 3589
Eperua venosa_Maguire 53597
Eperua venosa_Maguire 53514
Long & Non-tubular clade I
Eperua banaensis_Coomes 207
Eperua obtusata_Colella 1984
Short & Tub. clade II
Eperua purpurea_Redden 3366
Eperua purpurea_Madison 515
Eperua purpurea_Cardenas-Lopez 24418
Eperua purpurea_Schultes 18324
Eperua purpurea_Redden 3094
Eperua purpurea_Barona 1873
Eperua oleifera oleifera_Macedo 17006
Eperua oleifera oleifera_Macedo 17008
Eperua oleifera oleifera_Vicentini 2909
Eperua oleifera campestris_Zanucchi 3209
Eperua oleifera campestris_Farroway 1861
Eperua oleifera campestris_Farroway 1867
Eperua oleifera oleifera_Zanucchi 2938
Eperua oleifera campestris_Cid-Ferreira 791
Short & Tubular clade I
Eurypetalum unijugum_Wieringa 2122
Eurypetalum unijugum_Burgt J1880
Eurypetalum unijugum_Zenker 581
Eurypetalum tessmannii_Wieringa 1810
Eurypetalum tessmannii_Louis 896
Augouardia letestui_Dibata 4
Augouardia letestui_White 1496
Augouardia letestui_Wieringa 2974
Stemonocoleus micranthus_Dibata 1200
Stemonocoleus micranthus_Versteegh 8
Stemonocoleus micranthus_Oldeman 695
Hymenaea parvifolia_Forzza 10482
Guibourtia hymenaeifolia_Martinelli 16756
Copaifera trapezifolia _Baez 1861
Sindora siamensis_Maxwell 837

Figure S6. Concatenated-based species tree analysis using ML of the Eperua *s.l.* clade obtained from 62 (no signal for recombination) exons and 115 accessions. Branch lengths are proportional to the number of substitutions. The number in the branches shows the bootstrap support obtained from the RAxML analyses.

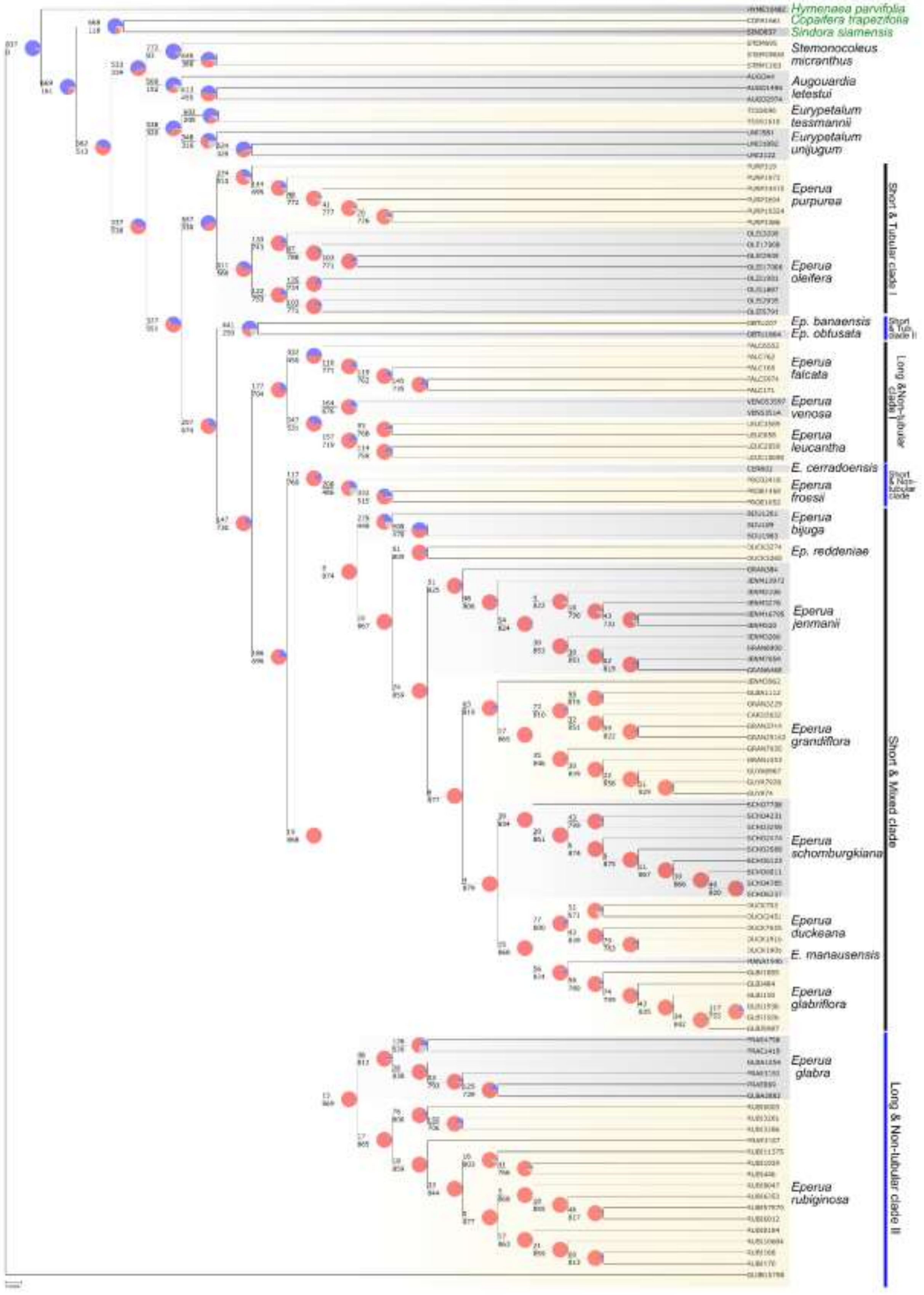

Hymenaea parvifolia
Copaifera trapezifolia
Sindora siamensis
Stemonocoleus micranthus
Augouardia letestui
Eurypetalum tessmannii
Eurypetalum unijugum
Eperua purpurea
Eperua oleifera
Ep. banaensis
Ep. obtusata
Eperua falcata
Eperua venosa
Eperua leucantha
E. cerradoensis
Eperua froesii
Eperua bijuga
Ep. reddeniae
Eperua jenmanii
Eperua grandiflora
Eperua schomburgkiana
Eperua duckeana
E. manausensis
Eperua glabriflora
Eperua glabra
Eperua rubiginosa
Short & Tubular clade I
Short & Tub. clade II
Long &Non-tubular clade I
Short & Non-tubular clade
Short & Mixed clade
Long & Non-tubular clade II

Figure S7. Coalescent-based species tree (Astral III) of the Eperua *s.l.* clade obtained from 883 exons with summary of conflicting and concordant exons. For each branch, the top number indicates the number of exons concordant with the species tree at that node, and the bottom number indicates the number of exons in conflict with that clade in the species tree. The pie charts at each node present the proportion of exons that support that clade (blue), the proportion that support the main alternative for that clade (green), the proportion that supports the remaining alternatives (red), and the proportion that have no support for conflicting bipartition (grey). The collector's name and collection number details are documented in Table S1.

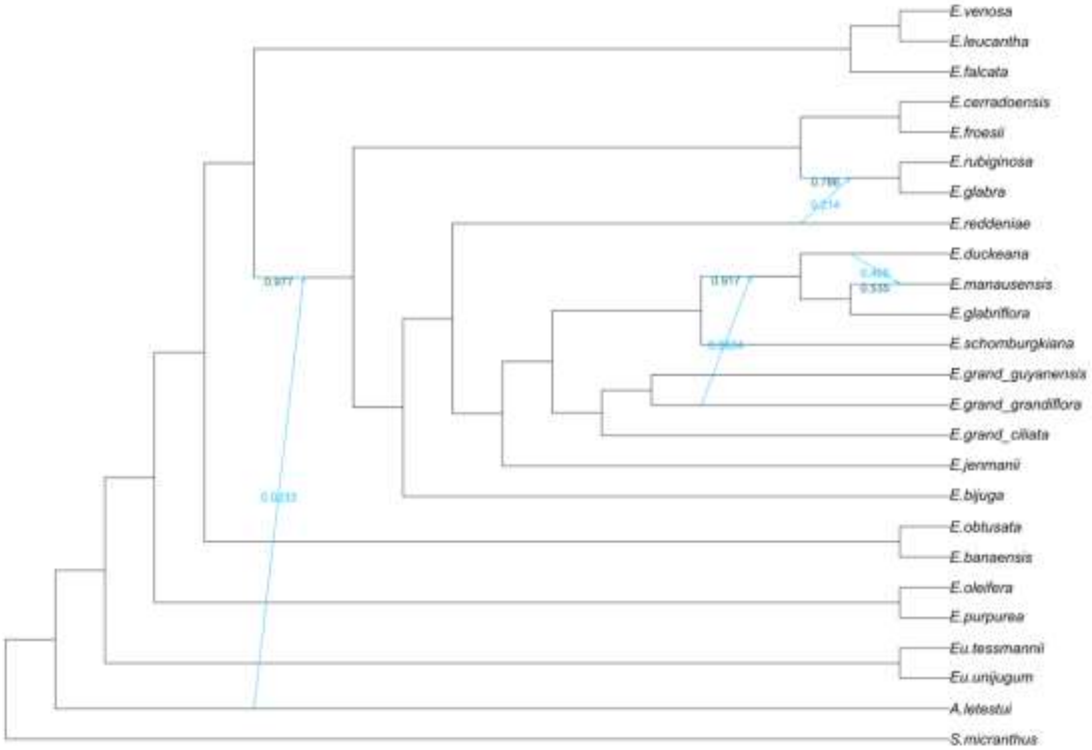


Figure S8. Rooted phylogenetic network with four hybridization events (h = 4), estimated using SNaQ in the Julia package PhyloNetworks. Black edges: major tree; blue colored arrows: minor hybrid edges, annotated by their estimated γ (light blue numbers).

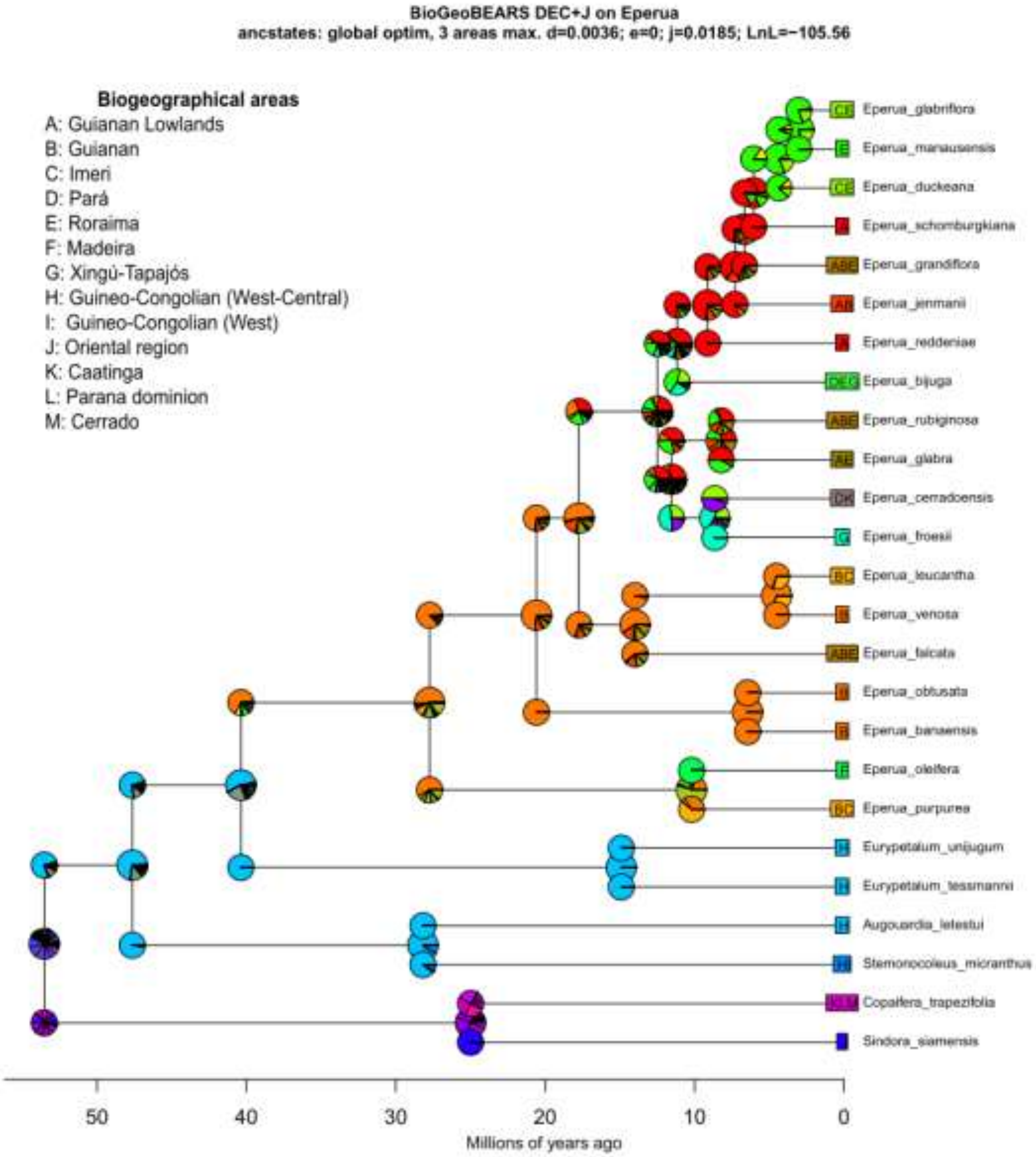


Figure S9. BioGeoBEARS results showing the pie charts of the relative probability of all possible geographic ranges of ancestral nodes of the Eperua *s.l.* clade under DEC+J model. Biogeographical areas after Morrone 2014, 2022a, and Marshall 2019: A) Guianan Lowlands [30]; B) Guianan [31]; C) Imeri [32]; D) Pará [34]; E) Roraima [35]; F) Madeira [36]; G) Xingú-Tapajós [40]; H) Guineo-Congolian (West-Central); I) Guineo-Congolian (West); J) Oriental region; K) Caatinga [41]; L) Parana dominion: Araucaria Forest [45], Atlantic [46], Parana [49], Southern Espinhaco [50]; M) Cerrado [42].

TABLE S1. Specimens sampled in the phylogeny with their respective collector number, collection locality, herbarium barcode, and type of tissue in which (F) refers to fresh material dried in silica gel (F) and (H) to herbarium specimens.

Species	**Code ID**	**Collector Number**	**Collection Date**	**Collection Locality**	**Collection Barcode**	**Type of tissue**
Augouardia letestui Pellegr.	AUGOA4	Dibata J.J. 4	04 January 1987	Gabon, Moyen-Ogooué, 13 km ENE de Belle Vue	WAG1703304	H
	AUGO2974	Wieringa J.J. et al. 2974	29 October 1994	Gabon, Ngounié, Fougamou, Bendolo river	WAG1703270	H
	AUGO1496	White L.J.T. (series 1) 1496	15 October 1996	Gabon, Ogooué-Ivindo, Lope Reserve	WAG1703267	H
Copaifera trapezifolia Hayne	COPA1661	Baez 1661	15 May 2018	Brasil, Rio de Janeiro, Valença Mata, Parque Estadual da Serra da Concórdia	RB01389019	F
Eperua bijuga Mart. ex Benth.	BIJU1261	Rabelo B.V. & Cardoso J.O. 1261	July 1982	Brazil, Amapá, Macapá, braço do rio Macacoari	US00242791	H

	BIJU1983	Neves D.M. et al. 1983	28 August 2014	Brazil, Pará, Melgaço, Flona Caxiuanã, Estação Científica Ferreira Penna	RB00903502	H
	BIJU189	Fortes E.A. et al. 189	28 December 2021	Brazil, Pará, Moju, Reserva da Embrapa	IAN201278	F
Eperua cerradoensis E.A. Fortes, G.S. da Silva & Mansano	CERR01	Gonçalves A.S. 01	18 September 2020	Brazil, Maranhão, Caxias, Povoado Morro Agudo	IAN201061	F
Eperua duckeana R.S.Cowan	DUCK703	Cid-Ferreira C.A. et al. 703	24 August 1979	Brazil, Amazonas, Itapiranga, rio Pitinga	US00242804	H
	DUCK190b	Fortes E.A. et al. 190b	21 January 2022	Brazil, Amazonas, Manaus, Reserva Florestal Adolpho Ducke	RB01458703	F
	DUCK191b	Fortes E.A. et al. 191b	21 January 2022	Brazil, Amazonas, Manaus, Reserva Florestal Adolpho Ducke	RB01458704	F

	DUCK2451	Faria S.M. de et al. 2451	17 September 2003	Brazil, Pará, Oriximiná, distrito de Porto Trombetas	RB00116251	H
	DUCK7655	Cid-Ferreira C.A. et al. 7655	12 August 1986	Brazil, Pará, Oriximiná, rio Mapuera	US00501058	H
Eperua falcata Aubl.	FALC165	Fortes E.A. & Silva G.S. da 165	04 December 2021	Brazil, Amapá, Oiapoque	RB01459756	F
	FALC171	Fortes E.A. & Silva G.S. da 171	05 December 2021	Brazil, Amapá, Oiapoque, rio Oiapoque	RB01460612	F
	FALC5974	Redden K.M. et al. 5974	25 April 2007	French Guiana, Cayenne, Sinnamary	US00998737	H
	FALC6552	Redden K.M. et al. 6552	12 May 2009	Guyana, Cuyuni-Mazaruni, Kako River	US01952468	F
	FALC762	Clarke H.D. et al. 762	04 January 1996	Guyana, Upper Demerara-Berbice, Mabura Hill	US00687666	H
Eperua froesii Fortes, Aymard, ter Steege & Mansano	FROE32452	Fróes R. de L. 32452	29 November 1955	Brazil, Pará, rio Acaraí, afl. do Xingú	IAN090190	H

	FRO32418	Fróes R. de L. 32418	29 November 1955	Brazil, Pará, rio Acarí, afl. do Xingú	R106671	H
	FROE1652	Prance G.T. et al. 1652	15 October 1965	Brazil, Pará, rios Pacajá and Muirapirang	IAN117165	H
	FROE1458	Prance G.T. et al. 1458	23 September 1965	Brazil, Pará, rios Pacajá and Muirapiranga	IAN117052	H
Eperua glabra R.S.Cowan	GLBA499	Pena B.S. 499	07 September 1974	Brazil, Pará, Oriximiná, Distrito de Marapi, rio Marapi	IAN148578	H
	GLBA1054	Redden K.M. et al. 1054	20 October 2002	Guyana, Upper Demerara-Berbice, Mabura Hill Forest Reserve	US00889535	H
	GLBA2882	Smith A.C. 2882	8–22 January 1938	Guyana, Upper Takatu-Upper Essequibo, basin of Shodikar Creek (Essequibo tributary)	V0111391F	H
	PRAE1419	Cid-Ferreira C.A. et al. 1419	09 July 1980	Brazil, Pará, Oriximiná, rio	US00242958	H

				Trombetas,		
	PRAE4758	Silva N.T. da & Santos M.R. 4758	08 June 1978	Brazil, Pará, Oriximiná, rio Trombetas, cachoeira Porteira	MG061723	H
	PRAE1000	Rodrigues I.A. et al. 1000	16 January 1983	Brazil, Roraima, São João da Baliza	IAN158522	H
	PRAE3187	Redden K.M. et al. 3187	04 May 2004	Guyana, Upper Takatu-Upper Essequibo, Chodikar River	US00904615	H
	PRAE3192	Redden K.M. et al. 3192	04 May 2004	Guyana, Upper Takatu-Upper Essequibo, Chodikar River	US00904614	H
	PRAE869	Silva F.A. et al. 869	25 September 2021	Brazil, Pará, Oriximiná, ESEC do Grão-Pará, margem do rio Jauari	MG0245424	H
Eperua glabriflora (Ducke) R.S.Cowan var. *glabriflora*	GLBI484	Cid-Ferreira C.A. et al. 484	18 July 1979	Brazil, Amazonas, Itapiranga, rio Uatumã	RB00140230	H

	GLBI192b	Fortes E.A. et al. 192b	23 January 2022	Brazil, Amazonas, Manaus, Reserva Florestal Adolpho Ducke	RB01458707	F
	GLBI193b	Fortes E.A. et al. 193b	24 January 2022	Brazil, Amazonas, Manaus, Reserva Florestal Adolpho Ducke, MUSA	RB01458705	F
	GLBI5987	Zartman C.E. et al. 5987	12 August 2006	Brazil, Amazonas, Presidente Figueiredo, Rebio Uatumã, rio Barretos	RB00716941	H
	GLBI150	Fortes E.A. & Camelo M.C. 150	04 February 2020	Brazil, Rio de Janeiro (cultivated), Rio de Janeiro, Jardim Botânico do rio de Janeiro	RB01429074	F
Eperua glabriflora var. *gynopubescens* Fortes & Mansano	GLBI1855	Ramos J.F. 1855	25 April 1988	Brazil, Amazonas, Manaus, Reserva Florestal Adolpho Ducke	INPA0179539	H
Eperua grandiflora (Aubl.)	GRAN3229	Medeiros H. et al.	26 November	Brazil, Amapá,	RB0138873	H

Baill. subsp. *grandiflora*		3229	2017	Pedra Branca do Amapari, Parque Nacional das Montanhas do Tumucumaque	3	
	GRAN25162	Mori S.A. & Smith N.P. 25162	14 September 2000	French Guiana, Cayenne, Régina, Pic Matécho, ca. 22.5 km NE of Les Eaux Claires	US00754207	H
	GRAN3744	Hahn W.J. 3744	15 September 1987	French Guiana, Cayenne, Saint-Élie, piste de St.Elie, CD-21	US00518410	H
	GLBA1112	Lobão A. & Cordeiro M. 1112	03 November 2005	Brazil, Amapá, Parque Nacional Montanhas do Tumucumaque, rio Mutum	IAN181270	H
	CARD2632	Goldenberg R. et al. 2632	15 September 2018	Brazil, Amapá, Pedra Branca do Amapari, Parque	RB01406159	H

				Nacional Montanhas do Tumucumaque		
Eperua grandiflora subsp. *guyanensis* R.S.Cowan	GUYA74	Stoffers A.L. et al. 74	28 October 1982	Guyana, Essequibo Islands–West Demerara, ca. 3 km from Mabura Hill	US00501049	H
	GUYA7928	Zartman C.E. 7928	April 2010	Guyana, Potaro-Siparuni, Kuribrong	INPA0237096	H
	GUYA8967	Pipoly J.J. & Boyan R. 8967	20 November 1986	Guyana, Upper Demerara-Berbice, Mabura Hill concession	US00508872	H
	GRAN7935	Zartman C.E. 7935	April 2010	Guyana, Potaro-Siparuni, Kuribrong	INPA0237097	H
	GRAN1053	Redden K.M. et al. 1053	20 October 2002	Guyana, Upper Demerara-Berbice, Mabura Hill Forest Reserve	US00742054	H
Eperua grandiflora subsp. *ciliata* Fortes & Mansano	JENM3962	Redden K.M. et al. 3962	07 March 1971	Guyana, Potaro-Siparuni, Tukeit Landing below Kaieteur Falls on	US00963896	H

				Potaro River		
Eperua jenmanii subsp. jenmanii Oliv.	JENM3278	Redden K.M. et al. 3278	11 October 2004	Guyana, Cuyuni-Mazaruni, Mazaruni River	INPA0220629	H
	JENM3266	Redden K.M. et al. 3266	09 October 2004	Guyana, Cuyuni-Mazaruni, Mazaruni River	US00889825	H
	JENM520	Polak A.M. et al. 520	12 November 1991	Guyana, Pomeroon-Supenaam, Takutu concessionof Willems Timber Comp	U1243245	H
	JENM16795	Little Jr. E.L. 16795	02 September 1955	Guyana, unknown, Boerasirie area, 5–25 miles West of Georgtown	U1243247	H
	GRAN6900	Redden K.M. et al. 6900	08 July 2010	Guyana, Cuyuni-Mazaruni, banks of Cara Creek, tributary of Kako River, near border with Venezuela	US01074208	F

	GRAN6468	Redden K.M. et al. 6468	09 May 2009	Guyana, Cuyuni-Mazaruni, Kako River	US03469553	F
	GRAN384	Appun C.F. 384	unknown date	Guyana, Essequibo	K000555115	H
Eperua jenmanii subsp. *sandwithii* R.S.Cowan	JENM2106	Milliken W. 2106	September 1994	Brazil, Roraima, Alto Alegre, alto rio Uraricoera	INPA0187773	H
	JENM13972	Liesner R.L. & Morillo G. 13972	10 May 1982	Venezuela, Bolívar, Aripao, Caño Pablo, tributary of Río Caura	US00242902	H
	JENM7059	Redden K.M. et al. 7059	25 July 2010	Guyana, Cuyuni-Mazaruni, Kako River	US01074211	F
Eperua leucantha Benth.	LEUC10690	Rodrigues W.A. et al. 10690	13 October 1987	Brazil, Amazonas, São Gabriel da Cachoeira	US00501048	H
	LEUC658	Sakagawa S. et al. 658	27 october 2008	Brazil, Amazonas, São Gabriel da Cachoeira, Reserva Biológica do Morro dos Seis Lagos	RB00717091	H

	LEUC2059	Barona A. et al. 2059	12 November 2015	Colombia, Guainia, Inírida, Comunidad de Sejalito, Rio Inírida	COAH	F
	LEUC3589	Redden K.M. et al. 3589	05 February 2005	Venezuela, Amazonas, San Carlos do Río Negro, 18 - rio Yatuá	US01001200	H
Eperua manausenis E.A. Fortes & Mansano	MANA194b	Fortes E.A. & Viana G.P. 194b	27 January 2022	Brazil, Amazonas, Manaus, Reserva Florestal Adolpho Ducke, MUSA	RB01458706	F
Eperua obtusata R.S. Cowan	OBTU1864	Colella M. et al. 1864	06 February 1991	Venezuela, Amazonas, Casiaquire, rio Casiaquire	K000544652	H
	OBTU207	Coomes D. 207	unknown date	Venezuela, Amazonas, San Fernando de Atabapo, La Esmeralda	K000834024	H
Eperua oleifera var.	OLEI1887	Farroñay F. 1887	11 June 2022	Brazil, Amazonas,	INPA029361	F

campestris Ducke				Manicoré	0	
	OLEI1901	Farroñay F. 1901	11 June 2022	Brazil, Amazonas, Manicoré	INPA0293613	F
	OLEI5791	Cid-Ferreira C.A. 5791	24 April 1985	Brazil, Amazonas, Manicoré	RB00140265	H
	OLEI2935	Zarucchi J.L. et al. 2935	01 July 1983	Brazil, Amazonas, Borba, Axinim, basin of rio Abacaxis	RB00140092	H
Eperua oleifera Ducke var. *oleifera*	OLEI2909	Vicentini A. 2909	10 June 2022	Brazil, Amazonas, Manicoré	INPA0293697	F
	OLE17008	Macedo M.T. de S. 17508	15 June 2022	Brazil, Amazonas, Manicoré	INPA0293652	F
	OLEI17006	Macedo M.T. de S. 17506	15 June 2022	Brazil, Amazonas, Manicoré	INPA0293650	F
	OLEI3209	Zarucchi J.L. et al. 3209	27 July 1983	Brazil, Amazonas, Maués, along rio Apoquitaua	RB00140099	H
Eperua purpurea Benth.	PURP319	Madison M.T. et al. 319	16 October 1978	Brazil, Amazonas, São Gabriel da Cachoeira, rio Marié, Tapuruquara Mirim	INPA0084638	H

	PURP1973	Barona A. et al. 1973	11 November 2015	Colombia, Guainia, Inírida, Comunidad de Sejalito, Rio Inírida	COAH	F
	PURP24415	Cárdenas-López D. et al. 24415	20 October 2009	Colombia, Guainia, Puerto Colombia, rio Guainia	US01323838	H
	PURP19324	Schultes R.E. & Cabrera I. 19324	14–24 May 1958	Colombia, Vaupés, rio Vaupes, between Mitu and Javareté	US00242973	H
	PURP3388	Redden K.M. et al. 3388	28 January 2005	Venezuala, Amazonas, San Carlos do Río Negro, 06 - rio Pasimoni	US01001000	H
	PURP3694	Redden K.M. et al. 3694	12 February 2005	Venezuala, Amazonas, San Carlos do Río Negro, rio Casiquiare	US00963721	H
Eperua reddeniae Fortes & Mansano	DUCK3274	Redden K.M. et al. 3274	11 October 2004	Guyana, Cuyuni-Mazaruni, Mazaruni River	INPA0220628	H
	DUCK3260	Redden K.M. et al.	09 September	Guyana, Cuyuni-	US0088981	H

		3260	2004	Mazaruni, Mazaruni River	2	
Eperua rubiginosa var. *grandiflora* Pulle	RUBI6005	Redden K.M. et al. 6005	05 May 2007	French Guiana, Saint-Laurent-du-Maroni, Saint-Laurent-du-Maroni, Maroni River	US01928426	H
	RUBI3261	Redden K.M. et al. 3261	09 October 2004	Guyana, Cuyuni-Mazaruni, Mazaruni River	INPA0220627	H
	RUBI23804	Maguire B. 23804	16 June 1944	Surinam, Sipaliwini, Jacob Kondre, Saramacca River	V0111448F	H
	RUBI3286	Redden K.M. et al. 3286	12 October 2004	Guyana, Cuyuni-Mazaruni, Mazaruni River	US00825906	H
Eperua rubiginosa var. *rubiginosa* Miq.	RUBI168	Fortes E.A. & Silva G.S. da 168	05 December 2021	Brazil, Amapá, Oiapoque, rio Oiapoque	RB01459763	F
	RUBI170	Fortes E.A. & Silva G.S. da 170	05 December 2021	Brazil, Amapá, Oiapoque, rio Oiapoque	RB01459770	F

RUBI10684	Forzza R.C. et al. 10684	19 August 2019	Brazil, Amapá, Pedra Branca do Amapari, Parque Nacional das Montanhas do Tumucumaque, rio Amapari	RB01429423	H
RUBI8047	Cid-Ferreira C.A. et al. 8047	25 August 1986	Brazil, Pará, Oriximiná, rio Cachorro	US00501062	H
RUBI8184	Granville J-J. de et al. 8184	13 September 1985	French Guiana, Saint-Laurent-du-Maroni, riviére Grand Inini en aval et en amont de Degrad Fourmi	US00799084	H
RUBI446	Mutchnick P. & Allicock B. 446	30 November 1994	Guyana, Potaro-Siparuni, Iworama, Siparuni River, Pakatu Falls	US00873174	H
RUBI6253	Redden K.M. et al. 6253	03 October 2008	Guyana, Upper Takatu-Upper	US01074188	H

				Essequibo, CI concession, Himara Creek		
	RUBI6012	Redden K.M. et al. 6012	14 September 2008	Guyana, Upper Takatu-Upper Essequibo, CI concession, Himara Creek	US0107435 9	F
	RUBI11375	Clarke H.D. & Rhodes J. 11375	10 March 2004	Surinam, Kabalebo, Central Surinam Nature Reserve, tributary of Coppename River	US0093867 9	H
	RUBI57579	Irwin G.T. et al. 57579	25 September 1963	Surinam, Kayser airstrip, 45 km du confluent avec Riv. Lucie	US0024300 4	H
	RUBI1929	Evans R. et al. 1929	10 November 1994	Surinam, Sipaliwini, Coeroeni, N side of Kuruni Island	RB0014160 0	H
Eperua schomburgkiana Benth.	SCHO3258	Redden K.M. et al. 3258	09 October 2004	Guyana, Cuyuni-Mazaruni, Mazaruni	US0088981 3	H

			River		
SCHO2588	Gillespie L.J. et al. 2588	31 October 1989	Guyana, East Berbice - Corentyne, upper Canje River	US00515083	H
SCHO2474	Henkel T.W. & Williams R. 2474	10 August 1993	Guyana, Essequibo Islands - West Demerara, W bank Essequibo River, 0-1 km N of Wolga settlement	US00512171	H
SCHO4231	Redden K.M. et al. 4231	14 September 2006	Guyana, Potaro-Siparuni, Micobe Road and adjacent forest next to Potaro River	US00963910	H
SCHO4785	Wurdack K.J. et al. 4785	11 October 2008	Guyana, Upper Demerara-Berbice, CI concession, along Essequibo River	US01087612	H
SCHO6011	Redden K.M. et al. 6011	14 September 2008	Guyana, Upper Demerara-Berbice, CI concession,	US01074366	F

				Himara Creek		
	SCHO6123	Redden K.M. et al. 6123	24 September 2008	Guyana, Upper Takatu-Upper Essequibo, CI concession, Himara Creek	US01074185	F
	SCHO6237	Redden K.M. et al. 6237	30 September 2008	Guyana, Upper Takatu-Upper Essequibo, CI concession, line 12	US01074184	F
	SCHO7708	Schulz J.P. 7708	26 June 1956	Surinam, Sipaliwini, Wonatobo falls, Corantijn River	US00243019	H
Eperua venosa R.S. Cowan	VEN53514	Maguire B. et al. 53514	30 August 1962	Venezuela, Bolívar, rio Uiri-yuk, El Foco, alto Río Cuyuni	US00243022	H
	VENO53597	Maguire B. et al. 53597	05 September 1962	Venezuela, Bolívar, Triana Savanna, cerro Pitón, rio Chicanán	US00243020	H
Eurypetalum tessmannii Harms	TESS696	Louis A.M. 696	14 November 1983	Gabon, Ogooué-Ivindo, about 50 km	WAG1633441	H

				SE of Achouka, Région des Abeilles		
	TESS3457	Reitsma J.M. 3457	18 May 1987	Gabon, Ogooué-Ivindo, ca 20 km NE of Koumameyong	WAG1633440	H
	TESS1610	Weringa J.J. 1610	18 September 1992	Gabon, Ogooué-maritime, Rabi-Kounga, Rabi, N of Shell Camp	US1188000	H
Eurypetalum unijugum Harms	UNI2122	Wieringa J.J. et al. 2122	06 February 1994	Cameroon, South Region, 23 km SE of Kribi, along road to HEVECAM	WAG8002076	F
	UNIJ581	Zenker G. 581	March 1914	Cameroon, South Region, Bipindi	NY3196802	H
	UNIJ1892	Burgt X.M. van der 1892	18 October 2015	Cameroon, South Region, Korup National Park	K001091352	H
Guibourtia hymenaeifolia (Moric.) J.Léonard	GUIB16798	Martinelli G. et al. 16798	22 December 2010	Brazil, Mato Grosso do Sul, Porto Murtinho	RB00609015	F
Hymenaea parvifolia Huber	HYME1048	Forzza R.C. 10482	26 June 2019	Brazil, Pará,	RB0142303	F

	2			Belterra, Floresta Nacional do Tapajós	0	
Sindora siamensis Teijsm. ex Miq.	SIND837	Mattos 837	May 2019	Brazil, Rio de Janeiro (cultivated), Rio de Janeiro, Jardim Botânico do rio de Janeiro	RB01411231	F
Stemonocoleus micranthus Harms	STEM1203	Dibata J.J. 1203	13 August 1996	Gabon, Ogooué-Lolo, Bambidie, route B3	WAG1635815	H
	STEM695	Oldeman R.A.A. 695	02 December 1963	Ivory Coast, Abidjan, near O.R.S.T.O.M., 17 km W of Abidjan	WAG1635801	H
	STEMONO8	Versteegh C. et al. 8	09 May 1969	Ivory Coast, Abidjan, Orstom, c. 17km W of Abidjan	WAG1635806	H

TABLE S2. Secondary calibration points obtained from (Estrella et al., 2017) used to prepare the starting tree for lineage divergence times analysis with BEAST 1.10.4 using the function ‘chronos’ from the R package Ape (Paradis & Schliep, 2019).

Node	Age.min	Age.max	Soft.bounds
29	37.6882	54.2709	FALSE
53	30.9475	44.3145	FALSE
52	25.4875	34.4392	FALSE

TABLE S3. Character table of the Eperua *s.l.* clade: Inflorescence and corolla type after Fortes et al. 2023, and Fougère-Danezan et al. (2010): Biogeographical areas after Morrone 2014, 2022a, and Marshall 2019: A) Guianan Lowlands [30]; B) Guianan [31]; C) Imeri [32]; D) Pará [34]; E) Roraima [35]; F) Madeira [36]; G) Xingú-Tapajós [40]; H) Guineo-Congolian (West-Central); I) Guineo-Congolian (West); J) Oriental region; K) Caatinga [41]; L) Parana dominion: Araucaria Forest [45], Atlantic [46], Parana [49], Southern Espinhaco [50]; M) Cerrado [42]; Habitat in white sand (WS) forests: specialist: species specialist of WS forests; non-specialists: species that do not inhabit WS forests, but clay and terrace formations; generalists: species that inhabit WS forests and other soil formations (clay and terrace formation).

Species	Inflorescence type	Corolla type	Biogeographical areas	Habitat in WS forests
Augouardia letestui	Short	Apetalous	H	*
Copaifera trapezifolia	Short	Apetalous	KLM	*
Eperua banaensis	Short	Tubular	B	specialist
Eperua bijuga	Short	Tubular	DEG	non-specialist
Eperua cerradoensis	Short	Non-tubular	DK	non-specialist
Eperua duckeana	Short	Non-tubular	CE	generalist
Eperua reddeniae	Short	Non-tubular	A	non-specialist
Eperua falcata	Long	Non-tubular	ABE	specialist
Eperua froesii	Short	Non-tubular	G	non-specialist
Eperua glabra	Long	Non-tubular	AE	non-specialist

Eperua glabriflora	Short	Tubular	CE	generalist
Eperua grandiflora	Short	Tubular	ABE	generalist
Eperua jenmanii	Short	Tubular	AB	generalist
Eperua leucantha	Long	Non-tubular	BC	specialist
Eperua manausenis	Short	Tubular	E	non-specialist
Eperua obtusata	Short	Tubular	B	specialist
Eperua oleifera	Short	Tubular	C	generalist
Eperua purpurea	Short	Tubular	BC	specialist
Eperua rubiginosa	Long	Non-tubular	ABE	non-specialist
Eperua schomburgkiana	Short	Non-tubular	A	generalist
Eperua venosa	Long	Non-tubular	B	generalist
Eurypetalum tessmannii	Short	Non-tubular	H	*
Eurypetalum unijugum	Short	Non-tubular	H	*
Guibourtia hymenaeifolia	Short	Apetalous	*	*
Hymenaea parvifolia	Short	Non-tubular	J	*
Sindora siamensis	Short	Non-tubular	*	*
Stemonocoleus micranthus	Short	Apetalous	HI	*

TABLE S4. Results of the model test for the evolution of the inflorescence and corolla in the Eperua *s.l.* clade and the habitat preferences in the genus *Eperua*. Legend: * not evaluated.

	Corolla type			Inflorescence type			Habitat preferences		
Model	logL	AIC	delta.AIC	logL	AIC	delta.AIC	logL	AIC	delta.AIC
ER	-22.4383	54.547	0.8135	-10.939	24.062	0.000	-17.240	40.481	0.000
ARD	-26.2733	56.877	3.1435	-11.031	25.879	1.816	-19.240	46.480	5.999
SYM	-23.8665	53.733	0.0000	*	*	*	-18.389	42.779	2.298

Table S5. Bait capture efficiency for fresh material and herbarium samples. Legend, All: the total of 119 accessions sequenced in this work; F: fresh material dried in silica gel samples (32); H: herbarium specimens' samples (83); Hp: preserved (DNA fragments

>300 bp) herbarium specimens samples (21 of 83). Different letters (a, b) indicate a significant difference between treatments by Tukey's test ($p \leq 0.01$): Number of loci assembled X^2=(df=2; deviance=731.11; p<0.001); Number of reads X^2=(df=2; deviance= 45,756,132; p<0.001).

	Number of reads (millions)				Reads on target (%)				Number of exons assembled			
	All	F[a]	H[b]	Hp[a]	All	F	H	Hp	All	F[a]	H[b]	Hp[a]
AVG	7.0	9.3	5.8	7.9	21.6	26.0	19.5	29.8	820.3	924.3	791.2	899.9
SD	4.5	5.0	3.3	3.2	9.8	9.7	9.5	9.1	183.2	27.2	213.2	15.7
MIN	0.6	3.5	1.7	2.3	1.8	8.2	1.8	9.8	0.0	835.0	0.0	863.0
MAX	28.4	28.4	13.3	13.3	43.8	43.8	38.3	41.9	933.0	960.0	917.0	923.0

Table S6. Statistics of the capture for the samples included in this study using Hybpiper v2.1.3. Legend: F: fresh material dried in silica gel samples; H: herbarium specimens; Hp: preserved (DNA fragments >300 bp) herbarium specimens; POT: percentage of reads on target; EM: number of exons mapped; EWC: number of exons with contigs; EWS: number of exons with sequences; At25pct, At50pct, At75pct, and At150pct: number of genes with sequences > 25%, >50%, >75%, >150% of the mean target length, respectively; PWL: paralog warnings Long; PWD: paralog warnings depth; EnoSC: exons without stitched contigs; ESC: exons with stitched contigs; ESCS: exons with stitched contigs skipped; ECW: exons with chimera warning.

Sample type	Name	Num Reads	Reads Mapped	POT	EM	EWC	EWS	25pct	50pct	75pct	150pct	PWL	PWD	EnoSC	ESC	ESCS	ECW
Hp	AUGO1496	5644114	1232395	21.8	990	909	891	888	861	774	0	136	156	752	139	0	0
Hp	AUGO2974	9096176	1818748	20	1005	943	923	922	898	821	0	158	179	819	104	0	0
H	AUGOA4	3501450	342910	9.8	959	755	730	725	629	454	0	41	49	562	168	0	0
H	BIJU1261	1695236	169797	10	903	636	607	578	434	244	0	22	22	474	133	0	0
F	BIJU189	9969710	2978700	29.9	1000	944	920	919	899	828	0	154	173	796	124	0	0
H	BIJU1983	8858446	1600297	18.1	979	911	884	882	854	765	0	118	141	702	182	0	0
H	CARD2632	9815742	2510715	25.6	996	933	907	904	883	802	0	162	188	762	145	0	0

F	CERR01	20393638	6208251	30.4	1009	957	933	929	909	837	1	174	197	827	106	0	0
F	COPA1661	3694436	310266	8.4	973	835	812	811	781	654	0	75	85	684	128	0	0
F	DUCK190b	4578550	702227	15.3	982	897	876	874	849	772	1	150	166	747	129	0	0
F	DUCK191b	7456070	3027039	40.6	979	940	917	915	891	813	1	151	186	769	148	0	0
H	DUCK2451	1825340	350269	19.2	945	787	764	761	702	573	0	66	75	604	160	0	0
H	DUCK3260	8760988	2366932	27	987	916	891	889	865	773	2	173	214	715	176	0	0
H	DUCK3274	6176714	1643542	26.6	972	906	877	875	851	760	3	160	201	678	199	0	0
H	DUCK703	2229076	272523	12.2	936	787	761	759	704	558	1	70	81	582	179	0	0
Hp	DUCK7655	8782754	1651392	18.8	1002	920	897	894	873	785	0	141	168	755	142	0	0
F	FALC165	5191254	1611537	31	978	923	906	904	883	799	0	170	201	731	175	0	0
F	FALC171	7495416	3286648	43.8	983	940	917	915	895	820	0	184	215	764	153	0	0
Hp	FALC5974	12895242	3784851	29.4	999	945	918	916	898	826	1	172	205	767	151	0	0

F	FALC6552	7905610	3283723	41.5	986	940	912	909	886	797	2	161	201	713	199	0	0
H	FALC762	11074936	3812117	34.4	1001	958	932	930	916	842	0	192	229	801	131	0	0
H	FRO32418	566736	90592	16	875	516	499	480	368	217	0	13	13	398	101	0	0
H	FROE1458	2602356	628269	24.1	945	874	851	849	810	693	0	93	113	644	207	0	0
Hp	FROE1652	8205140	2086761	25.4	990	915	892	890	864	764	0	133	164	708	184	0	0
H	FROE32452	14555574	277968	1.9	284	42	2	2	1	0	0	0	0	1	1	0	0
H	GLBA1054	3857218	792591	20.5	967	888	860	858	834	729	1	130	156	674	186	0	0
H	GLBA1112	8714884	1402745	16.1	989	910	883	880	852	757	1	124	150	691	192	0	0
H	GLBA2882	6303942	1426822	22.6	961	898	871	868	839	731	2	116	150	674	197	0	0
H	GLBA499	1247770	79464	6.4	470	46	5	3	2	0	0	0	0	4	1	0	0
F	GLBI150	10744686	3651736	34	992	950	923	921	902	837	1	170	193	823	100	0	0
H	GLBI1855	1790238	192679	10.8	914	588	560	538	409	232	0	19	20	423	137	0	0

F	GLBI192b	3472738	873302	25.1	968	908	884	881	857	774	0	133	160	720	164	0	0
F	GLBI193b	6383452	1660210	26	986	928	899	897	874	805	0	153	180	781	118	0	0
H	GLBI484	6128944	797383	13	980	881	847	844	810	693	0	97	114	642	205	0	0
H	GLBI5987	3927232	993981	25.3	973	896	871	868	846	760	0	128	153	716	155	0	0
H	GRAN1053	4150074	944318	22.8	962	892	863	860	835	734	0	114	138	672	191	0	0
Hp	GRAN25162	6836596	2515997	36.8	982	937	909	907	882	805	1	159	184	760	149	0	0
H	GRAN3229	5278676	1146458	21.7	976	908	879	876	848	752	0	128	157	700	179	0	0
Hp	GRAN3744	11683288	3470951	29.7	1000	943	915	913	892	812	1	162	187	778	137	0	0
H	GRAN384	4358506	588638	13.5	970	863	837	834	793	675	0	99	120	645	192	0	0
F	GRAN6468	11185176	3317549	29.7	989	943	915	913	891	816	0	167	192	796	119	0	0
F	GRAN6900	8777200	1430153	16.3	996	919	894	892	873	788	0	147	165	770	124	0	0
Hp	GRAN7935	5159504	2113322	41	973	922	896	893	866	782	0	144	174	739	157	0	0

F	GUIB16798	17134272	2356022	13.8	996	926	897	895	865	755	0	98	111	770	127	0	0
Hp	GUYA74	5123660	2015702	39.3	973	923	893	890	865	784	0	140	169	746	147	0	0
H	GUYA7928	9235192	2459571	26.6	989	932	903	900	874	791	0	142	165	742	161	0	0
H	GUYA8967	16487014	1664788	10.1	1004	915	883	880	857	765	0	133	161	708	175	0	0
F	HYME10482	5806020	708845	12.2	986	897	868	864	836	740	1	100	112	737	131	0	0
H	JENM13972	919384	98431	10.7	901	598	578	562	459	280	0	20	22	462	116	0	0
H	JENM16795	1755608	333346	19	940	805	785	785	727	586	1	66	78	601	184	0	0
H	JENM2106	5861308	577603	9.9	971	847	825	821	769	634	1	81	97	615	210	0	0
H	JENM3266	7618482	2389044	31.4	987	925	894	891	861	775	1	132	157	744	150	0	0
H	JENM3278	8177602	862153	10.5	976	844	824	821	778	658	0	98	113	646	178	0	0
H	JENM3962	8451012	1078131	12.8	974	897	864	860	830	718	0	101	126	663	201	0	0
H	JENM520	1827824	324497	17.8	936	822	802	798	743	602	0	71	88	583	219	0	0

F	JENM7059	7871806	2646768	33.6	984	940	915	913	888	809	0	154	178	778	137	0	0
Hp	LEUC10690	8559664	3584586	41.9	998	944	920	920	894	825	0	193	236	774	146	0	0
F	LEUC2059	8798214	2471681	28.1	991	921	898	897	876	791	1	175	208	741	157	0	0
H	LEUC3589	12892986	1849098	14.3	1002	906	878	876	848	747	0	146	181	683	195	0	0
H	LEUC658	5523102	1621807	29.4	981	913	888	887	863	773	0	160	187	719	169	0	0
F	MANA194b	28413212	6345738	22.3	1016	960	933	931	910	847	1	200	241	808	125	0	0
H	OBTU1864	1982030	374678	18.9	933	719	695	684	562	347	0	33	34	525	170	0	0
H	OBTU207	20843466	3353697	16.1	1011	930	908	906	881	792	1	152	177	756	152	0	0
F	OLE17008	7667006	1548108	20.2	988	926	907	907	884	813	1	154	171	782	125	0	0
F	OLEI17006	11003886	3561507	32.4	993	942	919	918	895	830	1	161	186	801	118	0	0
F	OLEI1887	14040876	5489308	39.1	994	946	918	917	894	820	0	165	188	795	123	0	0
F	OLEI1901	5121020	1003539	19.6	989	920	900	898	875	795	0	147	165	786	114	0	0

F	OLEI2909	11288644	3728617	33	985	941	916	915	896	820	1	157	182	795	121	0	0
Hp	OLEI2935	5055496	2088320	41.3	970	923	903	901	872	775	1	141	162	729	174	0	0
H	OLEI3209	15807016	3075842	19.5	993	924	896	893	868	776	0	135	161	723	173	0	0
H	OLEI5791	8355600	2510943	30.1	984	925	898	896	869	776	2	144	165	730	168	0	0
H	PRAE1000	1517112	140079	9.2	833	196	161	129	61	29	0	0	0	143	18	0	0
H	PRAE1419	4399072	469817	10.7	946	793	765	753	653	461	1	41	49	572	193	0	0
H	PRAE3187	3360730	628560	18.7	950	852	830	827	787	660	0	94	123	623	207	0	0
H	PRAE3192	3434860	512195	14.9	939	766	737	726	622	417	0	33	39	544	193	0	0
H	PRAE4758	1425004	165504	11.6	918	691	667	655	563	386	0	33	41	511	156	0	0
H	PRAE869	10412608	1403938	13.5	988	903	878	876	856	754	2	126	151	700	178	0	0
H	PURP19324	2642136	470595	17.8	941	837	811	809	767	632	0	87	106	608	203	0	0
F	PURP1973	8581442	2879472	33.6	989	937	913	912	889	814	2	158	179	792	121	0	0

H	PURP24415	4684158	676629	14.4	954	835	805	802	744	581	0	62	79	592	213	0	0
H	PURP319	10439838	681216	6.5	963	737	696	680	567	372	0	29	34	512	184	0	0
H	PURP3388	4775584	655640	13.7	958	849	821	815	769	632	0	80	102	634	187	0	0
H	PURP3694	2506318	538420	21.5	947	853	827	823	776	647	0	76	98	614	213	0	0
H	RUBI10684	5035172	1075108	21.4	977	907	883	882	862	770	1	150	172	737	146	0	0
H	RUBI11375	1998060	486347	24.3	938	835	811	807	747	593	0	79	95	599	212	0	0
F	RUBI168	8825572	1210167	13.7	1000	914	897	895	873	781	2	163	189	747	150	0	0
F	RUBI170	9614024	3731989	38.8	995	940	918	917	899	817	2	169	201	760	158	0	0
H	RUBI1929	3025456	590596	19.5	940	847	823	821	765	611	0	74	90	601	222	0	0
H	RUBI23804	3631300	77660	2.1	506	55	4	3	2	0	0	0	0	4	0	0	0
H	RUBI3261	5956618	1124429	18.9	976	888	861	859	829	728	2	124	156	662	199	0	0
H	RUBI3286	3693628	1046944	28.3	965	901	878	876	848	758	2	141	170	709	169	0	0

H	RUBI446	3806540	486881	12.8	954	853	829	826	779	644	1	88	108	622	207	0	0
Hp	RUBI57579	3177580	1215889	38.3	977	910	888	887	867	784	1	159	183	759	129	0	0
Hp	RUBI6005	10061746	2853043	28.4	1002	933	909	908	889	807	0	164	192	789	120	0	0
F	RUBI6012	5251770	1064069	20.3	977	908	887	886	868	784	0	164	184	761	126	0	0
H	RUBI6253	3184870	614724	19.3	960	881	856	853	825	712	0	120	144	656	200	0	0
Hp	RUBI8047	2318724	804531	34.7	968	883	863	861	832	741	1	136	158	699	164	0	0
H	RUBI8184	6852678	1011446	14.8	992	889	865	862	835	731	1	112	138	684	181	0	0
Hp	SCHO2474	10342336	2691574	26	1004	941	911	909	888	811	0	163	184	805	106	0	0
Hp	SCHO2588	4213322	1333293	31.6	982	921	896	894	874	793	0	146	167	763	133	0	0
H	SCHO3258	6567702	864466	13.2	981	886	860	857	824	712	0	103	125	664	196	0	0
H	SCHO4231	8522516	773761	9.1	983	873	850	847	818	699	0	99	118	665	185	0	0
Hp	SCHO4785	5485200	2046255	37.3	979	925	894	892	870	771	1	140	163	741	153	0	0

F	SCHO6011	4906468	1061919	21.6	980	910	879	876	851	765	0	140	159	747	132	0	0
F	SCHO6123	7328082	1431917	19.5	981	921	889	886	864	784	0	140	160	765	124	0	0
F	SCHO6237	8298066	1683445	20.3	984	921	891	887	870	787	0	143	166	742	149	0	0
H	SCHO7708	1803346	199619	11.1	929	721	704	693	580	386	0	27	33	554	150	0	0
F	SIND837	6344118	522368	8.2	974	842	817	817	786	664	0	92	98	697	120	0	0
H	STEM1203	3252770	584926	18	973	869	845	841	813	706	1	81	94	674	171	0	0
Hp	STEM695	7433404	2379450	32	1003	938	917	916	893	811	0	109	123	801	116	0	0
H	STEMONO8	5635720	1055057	18.7	989	900	871	869	838	731	1	86	100	700	171	0	0
Hp	TESS1610	13254258	1555609	11.7	1003	897	880	877	854	761	1	136	149	733	147	0	0
H	TESS3457	11080188	195070	1.8	198	31	0	0	0	0	0	0	0	0	0	0	0
H	TESS696	2863342	501918	17.5	963	834	815	809	748	605	0	67	74	613	202	0	0
Hp	UNI2122	12089772	1188433	9.8	990	900	871	869	843	738	1	112	126	716	155	0	0

F	UNIJ1892	13156004	3848916	29.3	999	941	917	916	893	812	1	153	172	794	123	0	0
H	UNIJ581	1718082	327480	19.1	929	672	628	598	443	236	0	14	14	458	170	0	0
H	VEN53514	4383078	795218	18.1	970	866	846	845	805	692	0	107	130	640	206	0	0
Hp	VENO53597	10683744	3343919	31.3	1008	935	911	911	889	809	0	187	232	764	147	0	0

Table S7. Comparison between biogeographical models for ancestral area reconstruction of the Eperua *s.l.* clade with the R package BioGeoBEARS: DEC received the lowest AIC and AICc values (showed in bold).

Models	Free parameters				Log-Likelihood	AIC	AICc	AIC weights	AICc weights
	Number	d	e	j					
DEC	2	0.0048	0.006	0.000	-110.3	224.5	225.1	0.001	0.024
DEC+J	3	0.0036	0.000	0.018	-105.6	**217.1**	**218.3**	0.015	0.98
DIVALIKE	2	0.0100	0.010	0.000	-116.2	236.5	237	0.000	6.10E-05
DIVALIKE+J	3	0.0100	0.010	0.000	-116.2	238.4	239.6	0.005	2.30E-05
BAYAREALIKE	2	0.0100	0.010	0.000	-132.7	269.4	270	0.424	4.20E-12
BAYAREALIKE+J	3	0.0100	0.010	0.000	-131.4	268.8	269.9	0.555	5.90E-12

Table S8. Likelihood model test for the null hypothesis that the addition of the founder (J) parameter confers equal likelihoods on the data for DEC, DIVALIKE, BAYAREALIKE models.

null	LnLalt	LnLnull	DFalt	DFnull	DF	Dstatistic	pval	AIC1	AIC2	AICwt1	AICwt2	AIC weight ratio model1	AIC weight ratio model2
DEC	**-106**	**-110**	**3**	**2**	**1**	**9.39**	**0.0022**	**217**	**225**	**0.98**	**0.024**	**40.34**	**0.025**
DIVALIKE	-116	-116	3	2	1	0.06	0.8100	238	237	0.27	0.73	0.38	2.64
BAYAREALIKE	-131	-133	3	2	1	2.65	0.1000	269	269	0.58	0.42	1.38	0.72

DISCUSSÃO

A presente tese apresenta novidades nomenclaturais para nomes associados ao gênero *Eperua*. Foram corrigidas a autoria de uma combinação, atualizados o status nomenclatural de alguns nomes e realizadas tipificações. Também foi corrigido o uso do termo holótipo, indevidamente assinalado a síntipos, por Cowan (1975). Este trabalho complementa a revisão nomenclatural feita por Cowan (1975), trazendo mais estabilidade a nomes associados ao gênero *Eperua.*

Dentre as principais descobertas da revisão taxonômica está a descrição de quatro novas espécies —*E. cerradoensis, E. froesii, E. manausensis, E. reddeniae*— e a sinonimização de *E. praesagata* a *E. glabra.* A descrição de *E. cerradoensis* para o ecótono Cerrado-Caatinga é um marco para o estudo da taxonomia do gênero *Eperua* porque amplia a distribuição do gênero, anteriormente considerada endêmica da região Amazônica.

Em *Eperua,* as espécies *E. cerradoensis, E. froesii, E. reddeniae* fazem parte de um grupo de espécies do gênero com inflorescência curta e ereta, e flores não-tubulares. A primeira espécie foi descrita a partir de coletas recentes (2020), já as outras foram baseadas em coletas mais antigas da década de 50 e 60 (*E. froesii*) e início dos anos 2000 (*E. reddeniae*). Todas essas três espécies apresentam diferenças marcantes quanto a morfologia e suporte molecular. Ocorrendo no Pará, as coletas de *E. froesii* foram identificadas como *E. schomburgkiana* por Cowan (1975). No entanto, além da distribuição alopátrica (*E. froesii* é restrita à Amazônia Oriental e *E. schomburgkiana* ocorre no Escudo das Guianas, veja Figura 8), *E. froesii* é uma espécie com diferenças marcantes nas estípulas, união dos estames e indumento dos estames. Além disso, molecularmente, *E. froesii,* está posicionada distante de *E. schomburgkiana* e mais relacionada a *E. cerradoensis.*

Eperua praesagata foi sinonimizada a *E. glabra* devido a sobreposição de características morfológicas e distribuição, e suporte filogenético. A coleta Silva F.A. et al. 869 (MG[245424]!), é um forte indício de que *E. glabra* é uma espécie complexa e com ampla variação morfológica. No entanto, a falta de coletas férteis é uma realidade para *E. glabra,* e mais coletas sãos necessárias para ampliar o conhecimento das variações presentes nesta espécie.

As análises filogenômicas apresentadas nesta tese foram baseadas em uma amostragem abrangente do clado de Eperua *s.l*, incluindo todas as 23 espécies conhecidas, a maioria, com múltiplo acessos. Pela primeira vez, cinco espécies foram integradas em um contexto filogenético—*E. banaensis*, *E. cerradoensis*, *E. manauensis*, *E. obtusata* e *E. reddeniae*. Além de esclarecer a posição filogenética dessas espécies, o estudo também confirmou que *Eurypetalum* e *Eperua* são monofiléticos com máximo suporte filogenético. As árvores filogenéticas reconstruídas neste estudo corroboram os resultados anteriores de ter Steege et al. (2023) baseados em DNA ribossomal.

As inferências filogenéticas, baseadas em 883 árvores gênicas e uma matriz concatenada de 283.069 pb, resolveram completamente as relações entre os gêneros e a maioria das relações filogenéticas dentro de *Eperua*. Os resultados indicam que a hibridização provavelmente é a principal fonte de conflitos entre árvores gênicas que levam às relações não resolvidas em *Eperua*. Outros estudos dos gêneros de árvores leguminosas amazônicas *Brownea* (SCHLEY et al., 2020), *Zygia*, *Jupunba* e *Inga* (SCHLEY et al., 2023) também inferiram eventos de reticulação antigos e recentes, destacando a importância desses eventos para a diversificação das espécies arbóreas.

As reconstruções da área ancestral do clado Eperua *s.l.*, utilizando o modelo DEC+J, sugerem que essa área provavelmente engloba a região Guineo-Congolesa na África. Esta região recebeu uma alta probabilidade, o que está em concordância com descobertas anteriores sobre a biogeografia de Detarioideae (ESTRELLA et al., 2017). A dispersão da África para a América em um cenário pós-Gondwana é principalmente atribuída à dispersão de longa distância, dispersão boreotropical ou dispersão do tipo "*stepping stones"* (PENNINGTON & DICK, 2004). Considerando que a origem do clado Eperua *s.l.* remonta a cerca de 47,6 milhões de anos, época em que a América do Sul e a África estavam geograficamente isoladas—ilhas entre os dois continentes são hipotetizadas apenas até o final do Cretáceo, cerca de 76 milhões de anos atrás (MORLEY, 2003, 2000)—e como não existem fósseis ou linhagens relacionadas em altas latitudes, a hipótese mais plausível é a dispersão de longa distância.

A análise biogeográfica revelou que a dispersão exerceu um papel crucial na determinação da distribuição atual de *Eperua* nas províncias sul-americanas da região amazônica. No entanto, a dispersão de *Eperua* para além do Escudo das Guianas foi limitada, possivelmente devido à sua capacidade restrita de dispersão de sementes, aliada a limitações altitudinais, climáticas e de oportunidades ecológicas. O ancestral comum mais recente de Eperua chegou à Amazônia durante o final do Oligoceno (27,7 Ma, 95% HPD 34-21 Ma) e conseguiu estabelecer-se e diversificar-se com sucesso, provavelmente devido a uma adaptação prévia ao clima tropical—clados dentro de Detarioideae estão principalmente associados a tipos de florestas úmidas (ESTRELLA et al., 2017). Adicionalmente, *Eperua* encontrou oportunidades ecológicas favoráveis, definidas como a combinação de disponibilidade de nicho e discordância de nicho (WELLBORN & LANGERHANS, 2015), especialmente nas florestas de areia branca do Escudo das Guianas.

A transição de uma corola não tubular para uma tubular ocorreu quatro vezes na filogenia, enquanto o oposto ocorreu duas vezes, resultando na ocorrência de uma espécie irmãs ou intimamente relacionadas com arquiteturas florais distintas atualmente coexistindo em simpatria. A mudança na forma da corola é provavelmente um dos principais impulsionadores da diversificação de *Eperua*, ao permitir especiação simpátrica por meio de mudanças no polinizador—espécies com corolas tubulares estão tipicamente associadas à polinização por insetos (VOGEL, 1968), enquanto aquelas com corolas não tubulares estão geralmente ligadas à polinização por morcegos (DELAVAL et al., 2005; FLEMING et al., 2009; GEISELMAN, 2010; VOGEL, 1968).

CONCLUSÃO

Esta tese reforça a importância das coletas botânicas e das coleções que as abrigam para o estudo da taxonomia e da evolução com base no sequenciamento de DNA. Levando em consideração limitações financeiras e de tempo, o acesso digital aos herbários foi fundamental para realizar um estudo prévio das mesmas, tornando mais eficiente as visitas às coleções.

Novas coletas foram a base para a descrição de novas espécies (*E. manauensis* e *E. cerradoensis*), assim como para a expansão do conhecimento sobre espécies já conhecidas. Coletas mais antigas, datadas entre 20 e 50 anos atrás, também possibilitaram a descrição de novas espécies (*E. froesii*, *E. reddeniae*). Isso não apenas reforça a importância dos herbários na descoberta científica, mas também destaca a relevância do trabalho ativo dos taxonomistas. Mesmo com a publicação da nova monografia para o gênero *Eperua*, alguns táxons ainda permanecem pouco esclarecidos devido à escassez de coletas férteis (*E. banaensis*, *E. glabra*, *E. grandiflora, E. manausensis*, E*. obtusata*), ressaltando mais uma vez a necessidade de novas coletas férteis e o contínuo suporte ao trabalho dos taxonomistas.

A necessidade de coletas férteis é fundamental para uma circunscrição robusta e para garantir a correta identificação das espécies em *Eperua*. A delimitação das espécies do gênero se baseia principalmente em características florais. Portanto, a chave de identificação foi desenvolvida com base em caracteres reprodutivos, principalmente. *Eperua purpurea*, *E. oleifera*, *E. bijuga* e *E. glabriflora* são facilmente identificadas por características vegetativas. No entanto, para as demais espécies, uma identificação mais precisa na ausência de flores somente pode ser realizada na presença de frutos associada à informação sobre o tipo de inflorescência. Materiais estéreis, especialmente na região das Guianas, dificilmente são identificados com acurácia, já que espécies simpátricas podem apresentar características foliares semelhantes (e.g. *E. jenmanii* e *E. schomburgkiana*, *E. rubiginosa* e *E. glabra*).

Pranchas com fotografias de campo, lupa e ilustrações são úteis para o reconhecimento das espécies. A nova monografia de *Eperua* oferece uma extensa ilustração das espécies, apresentando também, pela primeira vez, um amplo comparativo morfológico entre elas por meio de tabelas e comentários taxonômicos. Isso representa uma distinção em relação à última revisão publicada para o gênero por Cowan em 1975.

Com base em informações de etiquetas foi possível caracterizar as espécies quanto suas preferências de habitat, nomes populares, usos, fenologia e distribuição. Notou-se uma grande dificuldade na categorização do tipo de habitat das espécies, devido a descrição muito generalizada em muitas coletas, além da falta de informação sobre o tipo de solo e influência de inundações. A partir dos dados de distribuição foi possível inferir os status de conservação da maioria das espécies baseadas na área de ocorrência. Uma análise mais acurada levando em consideração outros fatores é necessária para um status de conservação mais acurado. A ocorrência das espécies em unidades de conservação foi registrada, o que pode facilitar futuras avaliações. Observou-se uma escassez de registro das espécies em unidades de conservação, que por ser resultado de falta de coletas em UCs aliada a não descrição pelos coletores de que a área de coleta pertence a uma UC.

A maioria dos materiais usados para a extração de DNA provém de amostras de exsicatas de herbário. A baixa concentração e a alta fragmentação do DNA na maioria dessas amostras não foram obstáculos para um sequenciamento bem-sucedido. Isso se deve à utilização de sequenciamento de segunda geração do tipo target, através de 'baits' ou iscas específicas para o táxon, desenvolvidas para a subfamília Detarioideae, que não exigem fragmentos longos nem alta concentração de DNA. Algumas amostras de herbário, mesmo antigas, são comparáveis às amostras coletadas em sílica em relação ao número de ‘reads’ e loci sequenciados. Esses resultados evidenciam a importância da boa manutenção das coleções de herbários.

O estudo filogenômico incluindo *Eperua* e gêneros próximos do clado Eperua *s.l.* é o mais abrangente até o momento, amostrando todas as 23 espécies conhecidas, a maioria, com múltiplos acessos. Este estudo resolve com máximo suporte os gêneros *Eurypetalum* e *Eperua* como monofiléticos. As espécies de *Eperua* foram inferidas como monofiléticas, dando mais robustez às decisões taxonômicas, assim como esclareceu a posição filogenética de cinco espécies incluídas pela primeira vez em um estudo filogenético. Dentre as principais conclusões deste trabalho pode-se citar a alta discordância entre as árvores de genes, principalmente devido a *incomplete lineage sorting* (ILS), resolvida por meio uma abordagem de coalescência. Foi demonstrado que as relações filogenéticas pouco resolvidas e com baixo suporte estão ligadas a eventos de reticulação. Inclusive as análises revelam *E. manauensis* como um potencial híbrido.

As análises evolutivas revelam que a dispersão de longa distância da África para a América do Sul explica a origem de *Eperua* no Neotrópico. Seu ancestral comum mais recente chegou à Amazônia no Oligoceno tardio e se diversificou principalmente no Escudo das Guianas, provavelmente devido ao clima tropical similar a área de ocorrência de seus ancestrais e nichos disponíveis. A limitação de distribuição de *Eperua* além do Escudo pode ser atribuída a altitude e clima, além de restrições de dispersão e nicho.

Reconstrução ancestral de caracteres revelam que a mudança no tipo de corola é provavelmente um dos principais impulsionadores da evolução de *Eperua*, pois facilitou a especiação simpátrica alterando as preferências dos polinizadores; espécies com corolas tubulares estão associadas à polinização por abelhas, enquanto aquelas com corolas não tubulares estão ligadas à polinização por morcegos. A polinização por morcegos, comum em florestas tropicais de baixa altitude, também desempenhou um papel importante na diversificação de *Eperua*, evidente a partir das características prováveis do ancestral comum mais recente (MRCA) e de muitos nós internos possuindo corolas não tubulares. Além disso, todas as espécies com corola não tubular possuem pólen mais robustos e com exina mais ásperas, e algumas dessas apresentam inflorescência longas e pendentes, as quais também são atribuídas a polinização por morcegos. Também foi reconstruída a reversão da polinização por insetos (corola tubular) para polinização por morcegos (corola não tubular) em duas espécies existentes. A origem aproximadamente concomitante de morcegos neotropicais com a chegada de *Eperua* na Amazônia fornece evidências que apoiam a possibilidade de polinização por morcegos em seu MRCA e nós internos.

REFERÊNCIAS

AUBLET, J. B. C. F., "**Histoire des plantes de la Guiane Françoise**", Tome I and Tome II. Pierre Françoies Didot jeune, Paris, 1775, 976 pp.

AB'SA´BER, A. N., "The paleoclimate and paleoecology of Brazilian Amazonia". In: PRANCE, G. T. (Org.), **Biological diversification of the tropics**, New York, Columbia Univ. Press, 1982. p. 41–59.

ADENEY, J. M., CHRISTENSEN, N. L., VICENTINI, A., *et al.* **White-sand Ecosystems in Amazonia**. **Biotropica**. [S.l.], Blackwell Publishing Ltd. , 1 jan. 2016

ARELLANO-PEÑA, H., CÁRDENAS-LÓPEZ, D., STROPP, J., *et al.*, "The Forests of the Upper Rio Negro (North-Western Amazon) and Adjacent South-Western Orinoco Basins: A Phytosociological Classification". In: ZINCK, J. A., HUBER, O., GARCÍA MONTERO, P., *et al.* (Org.), **Psammic Peinobiomes. Ecological Studies** , Cham, Springer, 2023. v. 247. p. 55–109. DOI: 10.1007/978-3-031-20799-0_3.

ASSIS, L. C. S., RIEPPEL, O. "Are monophyly and synapomorphy the same or different? Revisiting the role of morphology in phylogenetics", **Cladistics**, v. 27, n. 1, p. 94–102, fev. 2011. DOI: 10.1111/j.1096-0031.2010.00317.x. .

AYRES, D. L., DARLING, A., ZWICKL, D. J., *et al.* "BEAGLE: An application programming interface and high-performance computing library for statistical phylogenetics", **Systematic Biology**, v. 61, n. 1, 2012. DOI: 10.1093/sysbio/syr100. .

BACKÉUS, I., PETTERSSON, B., STRÖMQUIST, L., *et al.* "Tree communities and structural dynamics in miombo (Brachystegia-Julbernardia) woodland, Tanzania", **Forest Ecology and Management**, v. 230, n. 1–3, 2006. DOI: 10.1016/j.foreco.2006.04.033. .

BAGLEY, J. C. **Off to a good start: how to generate starting trees for BEAST analyses using R**. 10 out. 2013. https://justinbagley.rbind.io/2013/10/10/off-to-a-good-start-how-to-generate-starting-trees-for-beast-analyses-using-r/.

BAILLON, H. E., Caesalpinées. In: Baillon, H.E. (Ed.) **Histoire des plantes**. Tome II. Librairie Hachette & Cie, Paris, Jan–Feb 1870, pp. 110–111.

BANKS, H., RUDALL, P. J. "Pollen structure and function in caesalpinioid legumes", **American Journal of Botany**, v. 103, n. 3, p. 423–436, 1 mar. 2016. DOI: 10.3732/ajb.1500248. .

BARROSO, G. M., PEIXOTO, A. L., COSTA, C. G., ICHASO, C. L. F., GUIMARÃES, E. F. & LIMA, H. C. **Sistemática das angiospermas do Brasil**. Vol 2. Imprensa Universitária, Universidade Federal de Viçosa, Viçosa, 1991, p. 15–100.

BENOIST, R., "Descriptions d'espécies nouvelles de légumineuses de la Guyane Française", **Notulae Systematicae. Herbier du Museum de Paris**, v. 3, p. 271–274, 1916.

BEENTJE, H. **The Kew plant glossary an illustrated dictionary of plant terms**. Royal Botanic Gardens, Kew, Richmond, 2010, 160 pp.

BENTHAM, G. "Caesalpinieae". *In*: von MARTIUS, C. F. P. & EICHLER, A.G. (Eds.) **Flora Brasiliensis** 15(2). F. Fleischer, Leipzig, 1870, pp. 226–228.

BEZANSON, J., EDELMAN, A., KARPINSKI, S., *et al.* "Julia: A fresh approach to numerical computing", **SIAM Review**, v. 59, n. 1, 2017. DOI: 10.1137/141000671. .

BHL, Biodiversity Heritage Library 2019. Available from:

https://www.biodiversitylibrary.org (accessed 6 November 2021)

BILBAO, G., BRUNEAU, A., JOLY, S. "Judge it by its shape: a pollinator-blind approach reveals convergence in petal shape and infers pollination modes in the genus Erythrina", **American Journal of Botany**, v. 108, n. 9, p. 1716–1730, 1 set. 2021. DOI: 10.1002/ajb2.1735. .

BFG - The Brazil Flora Group. Brazilian. Flora 2020: Leveraging the power of a collaborative scientific network. **Taxon**, v. 71, n. 1, 2022. DOI: 10.1002/tax.12640.

BFG - The Brazil Flora Group. Brazilian flora 2020: Innovation and collaboration to meet target 1 of the global strategy for plant conservation (GSPC). **Rodriguesia**, v. 69, n. 4, p. 1513–1527, 2018. DOI: 10.1590/2175-7860201869402.

Botanicus,Botanicus Digital Library. Available from: http://botanicus.org/ (accessed 6 November 2019)

BRAVO, G. A., ANTONELLI, A., BACON, C. D., *et al.* "Embracing heterogeneity: Coalescing the tree of life and the future of phylogenomics", **PeerJ**, v. 2019, n. 2, 2019. DOI: 10.7717/peerj.6399. .

BRUEN, T. **PhiPack: PHI test and other tests of recombination**. . [S.l: s.n.], 2005.

BRUNEAU, A., FOREST, F., HERENDEEN, P. S., KLITGAARD, B. B. & LEWIS, G. P. "Phylogenetic relationships in the Caesalpinioideae (Leguminosae) as inferred from chloroplast trnL intron sequences", **Systematic Botany**, v. 26, p. 487–514, 2001. https://doi.org/10.1043/0363-6445-26.3.487

BRUNEAU, A., MERCURE, M., LEWIS, G.P. & HERENDEEN, P.S. "Phylogenetic patterns and diversification in the caesalpinioid legumes", **Botany**, v. 86, p. 697–718, 2008. https://doi.org/10.1139/B08-058

BURNHAM, K. P., ANDERSON, D. R., "Information and Likelihood Theory: a basis for model selection and inference". In: BURNHAM, K. P., ANDERSON, D. R. (Org.), **Multimodel inference: A Practical Information-Theoretic Approach**, 2. ed. New York, NY, Springer, 2002. p. 49–97. Disponível em: https://link.springer.com/chapter/10.1007/978-0-387-22456-5_2. Acesso em: 10 out. 2023.

CAPELLA-GUTIÉRREZ, S., SILLA-MARTÍNEZ, J. M., GABALDÓN, T. "trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses", **Bioinformatics**, v. 25, n. 15, 2009. DOI: 10.1093/bioinformatics/btp348. .

CARDOSO, D.; SÄRKINEN, T.; ALEXANDER, S., *et al.* Amazon plant diversity revealed by a taxonomically verified species list. **Proceedings of the National Academy of Sciences of the United States of America**, v. 114, n. 40, 2017. DOI: 10.1073/pnas.1706756114.

CAYUELA, A. L., MACARRO, I., STEIN, A., *et al.* "Taxonstand: Taxonomic Standardization of Plant Species Names", **R package version 2.4**, 2021. .

CBD – Convention on Biological Diversity (2011) Global strategy 2011-2020. 09 fevereiro 2011. Disponível em <https://www.cbd.int/gspc/strategy.shtml>. Acesso em 24 Novembro 2023.

CHAMBERLAIN, S. **Package 'rgbif' - Interface to the Global “Biodiversity” Information Facility API**. **CRAN Repository**. [S.l: s.n.]. , 2019

CHEN, S., ZHOU, Y., CHEN, Y., *et al.* "Fastp: An ultra-fast all-in-one FASTQ preprocessor". 34, 2018. **Anais** [...] [S.l: s.n.], 2018. DOI:

10.1093/bioinformatics/bty560.

CONCEIÇÃO OLIVEIRA, L., PICANÇO RODRIGUES, D., FORTUNE HOPKINS, H. C., *et al.* "Phylogeny and historical biogeography of the pantropical genus Parkia (Leguminosae, Caesalpinioideae, mimosoid clade)", **Molecular Phylogenetics and Evolution**, v. 163, 1 out. 2021. DOI: 10.1016/j.ympev.2021.107219. .

COOPER, D. L. M., LEWIS, S. L., SULLIVAN, M. J. P., *et al.* "Consistent patterns of common species across tropical tree communities", **Nature**, v. 625, n. 7996, p. 728–734, 25 jan. 2024. DOI: 10.1038/s41586-023-06820-z. .

COWAN, R. S. "Tropical American Leguminosae-III", **Brittonia,** v. 8, p. 251–253, 1957. https://doi.org/10.2307/2804977

COWAN, R. S. "Leguminosae-Caesalpinioideae. The Botany of the Guayana Highland", **Memoirs of the New York Botanical Garden**, v. 10, p. 147–149, 1958.

COWAN, R. S. "A monograph of the genus *Eperua* (Leguminosae: Caesalpinioideae)", **Memoirs of the New York Botanical Garden,** v. 28, p. 1–45, 1975.

COWAN, R. S. "Studies in Tropical American Leguminosae–IX", **Brittonia,** v. 37, n. 3, p. 292–294, 1985. https://doi.org/10.2307/2806078

CRANE, P. R. Documenting plant diversity: Unfinished business. **Philosophical Transactions of the Royal Society B: Biological Sciences**, v. 359, n. 1444, 2004. DOI: 10.1098/rstb.2003.1441.

CULLINGS, K. W. **Design and testing of a plant-specific PCR primer for ecological and evolutionary studies**. **Molecular Ecology**. [S.l: s.n.], 1992.

DÁVALOS, L. M. **Phylogeny and biogeography of Caribbean mammals**. **Biological Journal of the Linnean Society**. [S.l: s.n.]. , 2004

DEFILIPPS, R. A.; MAINA, S. L. & CREPIN, J. **Medicinal Plants of the Guianas**. Washington, DC: National Museum of Natural History, Smithsonian Institution, 2004, 477 p.

DEGNAN, J. H., ROSENBERG, N. A. **Gene tree discordance, phylogenetic inference and the multispecies coalescent**. **Trends in Ecology and Evolution**. [S.l: s.n.]. , 2009

DELAVAL, M., HENRY, M., CHARLES-DOMINIQUE, P. "Interspecific competition and niche partitioning: Example of a neotropical rainforest bat community", **Revue d'Ecologie (La Terre et la Vie)**, v. 60, n. 2, 2005. DOI: 10.3406/revec.2005.1253. .

DELGADO-BENARROCH, L., WEISS, J., EGEA-CORTINES, M. "The mutants compacta ähnlich, Nitida and Grandiflora define developmental compartments and a compensation mechanism in floral development in Antirrhinum majus", **Journal of Plant Research**, v. 122, n. 5, 2009. DOI: 10.1007/s10265-009-0236-6. .

DEXTER, K. G., LAVIN, M., TORKE, B. M., *et al.* "Dispersal assembly of rain forest tree communities across the Amazon basin", **Proceedings of the National Academy of Sciences of the United States of America**, v. 114, n. 10, 2017. DOI: 10.1073/pnas.1613655114.

DOYLE, J. J., DOYLE, J. L. "A rapid DNA isolation procedure for small quantities of fresh leaf tissue", **Phytochemistry Bulletin** , v. 19, n. 1, p. 11–15, 1987. .

DUCKE, W. A. "Espéces nouvelles de plantes de l'Amazonie brésilienne", **Bulletin du Muséum National d'Histoire Naturelle**, v. 4, n. 6, p. 728–729, 1932.

DUCKE, W. A. "Notes on the wallaba trees", **Tropical Woods**, v. 62, p. 21–28, 1940.

EDWARDS, S. V. **Is a new and general theory of molecular systematics emerging? Evolution**. [S.l: s.n.]. , jan. 2009

ELY, C., V.; BORDIGNON, S. A. de L.; TREVISAN, R., *et al.* Implications of poor taxonomy in conservation. **Journal for Nature Conservation**, v. 36, 2017. DOI: 10.1016/j.jnc.2017.01.003.

ERKENS, R. H. J., CHATROU, L. W., MAAS, J. W., *et al.* "A rapid diversification of rainforest trees (Guatteria; Annonaceae) following dispersal from Central into South America", **Molecular Phylogenetics and Evolution**, v. 44, n. 1, p. 399–411, jul. 2007. DOI: 10.1016/j.ympev.2007.02.017. .

ESTRELLA, M. de la, FOREST, F., KLITGÅRD, B., *et al.* "A new phylogeny-based tribal classification of subfamily Detarioideae, an early branching clade of florally diverse tropical arborescent legumes", **Scientific Reports**, v. 8, n. 1, 1 dez. 2018. DOI: 10.1038/s41598-018-24687-3

ESTRELLA, M. de la, FOREST, F., WIERINGA, J. J., *et al.* "Insights on the evolutionary origin of Detarioideae, a clade of ecologically dominant tropical African trees", **New Phytologist**, v. 214, n. 4, p. 1722–1735, 1 jun. 2017. DOI: 10.1111/nph.14523.

FLEMING, T. H., GEISELMAN, C., KRESS, W. J. "The evolution of bat pollination: A phylogenetic perspective", **Annals of Botany**, v. 104, n. 6, p. 1017–1043, nov. 2009. DOI: 10.1093/aob/mcp197. .

FORGET, P.-M. "Regeneration Ecology of Eperua grandiflora (Caesalpiniaceae), a Large-Seeded Tree in French Guiana", **Biotropica**, v. 24, n. 2, 1992. DOI: 10.2307/2388668

FORSYTH, Jr., W. "A Botanical nomenclator containing a systematical arrangement of the classes, orders, genera, and species of plants as described in the new edition of Linnæsus's Systema naturæ, by Dr. Gmelin", Printed for T. Cadell, and P. Elmsly, in the Strand, and G. Nicol, Pall-Mall, London, 1794, p. 391. https://doi.org/10.5962/bhl.title.127458

FORTES, E. A., REIS, I. P. dos, TER STEEGE, H., *et al.* "A taxonomic revision of the genus Eperua (Leguminosae, Detarioideae, Detarieae)", **Phytotaxa**, v. 617, n. 1, p. 1–127, 28 set. 2023. DOI: 10.11646/phytotaxa.617.1.1. Disponível em: https://phytotaxa.mapress.com/pt/article/view/phytotaxa.617.1.1.

FORTES, E. A., SILVA, G. S. da., MANSANO, V. F. "Two new species of Eperua (Leguminosae, Detarioideae, Detarieae) from the Amazon and Cerrado Biomes discovered in a botanical garden and a backyard", **Phytotaxa**, v. 591, n. 3, p. 196–208, 5 abr. 2023. DOI: 10.11646/phytotaxa.591.3.2

FORZZA, R. C.; BAUMGRATZ, J. F. A.; BICUDO, C. E. M.; *et al.* New brazilian floristic list highlights conservation challenges. **BioScience**, v. 62, n. 1, 2012. DOI: 10.1525/bio.2012.62.1.8.

FOUGÈRE-DANEZAN, M., HERENDEEN, P. S., MAUMONT, S., *et al.* "Morphological evolution in the variable resin-producing Detarieae (Fabaceae): Do morphological characters retain a phylogenetic signal?", **Annals of Botany**, v. 105, n. 2, p. 311–325, fev. 2010. DOI: 10.1093/aob/mcp280. .

FOUGÈRE-DANEZAN, M., MAUMONT, S. & BRUNEAU, A. "Relationships among resin-producing Detarieae s.l. (Leguminosae) as inferred by molecular data",

Systematic Botany, v. 32, p. 748–761, 2007. https://doi.org/10.1043/06-67.1

FROIDEVAUX, H. **Étude sur les recherches scientifiques de Fusée Aublet à la Guyane française 1762–1764**. Kessinger Publishing, United States, 1897, 52 pp.

FUNK, V. A. Floras: A model for biodiversity studies or a thing of the past? **Taxon**. v. 55, n. 3, 2006. DOI: 10.2307/25065635.

GBIF.ORG. **GBIF Occurrence Download: https://doi.org/10.15468/dl.hehv63, https://doi.org/10.15468/dl.ga3jgd, https://doi.org/10.15468/dl.des4gs, https://doi.org/10.15468/dl.rngbkr**. 11 nov. 2023. Available from: https://www.gbif.org.

GEISELMAN, C. K. "Diet and reproduction of sympatric nectar-feeding bat species (Chiroptera: Phyllostomidae) in French Guiana", **Columbia University**, 2010.

HARMS, H. A. T. "Zwei neue Gattungen der Leguminosae aus dem tropichen Afrika". *In*: ENGLER, A. (ed.) **Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie**. Wilhelm Engelmann, Leipzig, 1905, pp. 76–77.

HARMS, H. A. T. "Leguminosae africanae". *In*: ENGLER, A. (ed.) **Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie**. Wilhelm Engelmann, Leipzig, 1910, pp. 293–295.

HOORN, C., WESSELINGH, F. P., TER STEEGE, H., *et al.* **Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity**. **Science**. [S.l: s.n.]. , 2010

HOORN, Carina. **An environmental reconstruction of the palaeo-Amazon River system (Middle-Late Miocene, NW Amazonia)**. **Palaeogeography, Palaeoclimatology, Palaeoecology**. [S.l: s.n.], 1994.

HOPKINS, M. J. G. "Modelling the known and unknown plant biodiversity of the Amazon Basin", **Journal of Biogeography**, v. 34, n. 8, 2007. DOI: 10.1111/j.1365-2699.2007.01737.x.

HOTHORN, T., BRETZ, F., WESTFALL, P. **Simultaneous inference in general parametric models**. **Biometrical Journal**. [S.l: s.n.]. , 2008

HOWARD, R. "The plates of Aublet's Histoire des plantes de La Guiane Françoise", **Journal of the Arnold Arboretum**, v. 64, n. 2, 255–292, 1983. https://doi.org/10.5962/p.324743

HUELSENBECK, J. P., NIELSEN, R., BOLLBACK, J. P. "Stochastic mapping of morphological characters", **Systematic Biology**, v. 52, n. 2, 2003. DOI: 10.1080/10635150390192780. .

HUGHES, C. E., PENNINGTON, R. T., ANTONELLI, A. **Neotropical Plant Evolution: Assembling the Big Picture**. **Botanical Journal of the Linnean Society**. [S.l: s.n.]. , 2013

IBGE - Instituto Brasileiro de Geografia e Estatística—IBGE (2019) 2019 Biomas e Sistema Costeiro-Marinho do Brasil - 1:250 000. 10 January 2022https://www.ibge.gov.br/geociencias/informacoes-ambientais/estudos-ambientais/15842-biomas.html?edicao=25799&t=downloads/

INPE – Instituto Nacional de Pesquisas Espaciais. PRODES: monitoramento do Desmatamento da Floresta Amazônica Brasileira por Satélite. 10 November 2023. http://www.obt.inpe.br/OBT/assuntos/programas/amazonia/prodes.

IPNI. International Plant Names Index. The Royal Botanic Gardens, Kew, Harvard

University Herbaria & Libraries and Australian National Botanic Gardens. 6 November 2021. http://www.ipni.org.

JARAMILLO, C., RUEDA, M. J., MORA, G. "Cenozoic plant diversity in the neotropics", **Science**, v. 311, n. 5769, 2006. DOI: 10.1126/science.1121380. .

JOHNSON, M. G., GARDNER, E. M., LIU, Y., *et al.* "HybPiper: Extracting coding sequence and introns for phylogenetics from high-throughput sequencing reads using target enrichment", **Applications in Plant Sciences**, v. 4, n. 7, 2016. DOI: 10.3732/apps.1600016. .

JONES, K. E., BININDA-EMONDS, O. R. P., GITTLEMAN, J. L. "Bats, clocks, and rocks: diversification patterns in Chiroptera", **Evolution**, v. 59, n. 10, 2005. DOI: 10.1111/j.0014-3820.2005.tb00932.x. .

KATOH, K., STANDLEY, D. M. "MAFFT multiple sequence alignment software version 7: Improvements in performance and usability", **Molecular Biology and Evolution**, v. 30, n. 4, 2013. DOI: 10.1093/molbev/mst010. .

KLEINHOONTE, A. "*Eperua* stipulata Kleinh. nov. spec. " **Recueil des Travaux Botaniques Néerlandais**, v. 30, p. 171, 1933.

KOZLOV, A. M., DARRIBA, D., FLOURI, T., *et al.* "RAxML-NG: A fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference", **Bioinformatics**, v. 35, n. 21, 2019. DOI: 10.1093/bioinformatics/btz305. .

LANDIS, M. J., MATZKE, N. J., MOORE, B. R., *et al.* "Bayesian analysis of biogeography when the number of areas is large", **Systematic Biology**, v. 62, n. 6, 2013. DOI: 10.1093/sysbio/syt040. .

LANFEAR, R., FRANDSEN, P. B., WRIGHT, A. M., *et al.* "Partitionfinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses", **Molecular Biology and Evolution**, v. 34, n. 3, 2017. DOI: 10.1093/molbev/msw260. .

LAVIN, M., SCHRIRE, B. P., LEWIS, G., *et al.* "Metacommunity process rather than continental tectonic history better explains geographically structured phylogenies in legumes". 359, 2004. **Anais** [...] [S.l: s.n.], 2004. DOI: 10.1098/rstb.2004.1536.

LEANDRI, J. "Un pharmacien provençal découvre une partie de la flore du Nouveau Monde: J. B. C. Fusée Aublet et l' "Histoire des plantes de la Guyane française" ", **Adansonia,** v. 8, n. 2, p. 137–146, 1968.

LEANDRO, L. M.; VEIGA-JUNIOR, V. F. DA. "O gênero *Eperua* Aublet: uma revisão", **Scientia Amazonia**, v. 1, n. 2, p. 14–22, 2012.

LEMOINE, F., GASCUEL, O. "Gotree/Goalign: Toolkit and Go API to facilitate the development of phylogenetic workflows", **NAR Genomics and Bioinformatics**, v. 3, n. 3, 2021. DOI: 10.1093/nargab/lqab075. .

LEWIS, G. P., SCHRIRE, B., MACKINDER, B. & LOCK, M. **Legumes of the World**. Kew, Royal Botanic Gardens, 2005, 577 pp.

LI, H., DURBIN, R. "Fast and accurate short read alignment with Burrows-Wheeler transform", **Bioinformatics**, v. 25, n. 14, 2009. DOI: 10.1093/bioinformatics/btp324. .

LPWG - Legume Working Phylogeny 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, 23 fev. 2017. DOI: 10.12705/661.3.

MALLET, J. **Hybridization as an invasion of the genome**. **Trends in Ecology and Evolution**. [S.l.], Elsevier Ltd. , 2005

MARSHALL, C. A. M., WIERINGA, J. J., HAWTHORNE, W. D. "An interpolated biogeographical framework for tropical Africa using plant species distributions and the physical environment", **Journal of Biogeography**, v. 48, n. 1, p. 23–36, 1 jan. 2021. DOI: 10.1111/jbi.13976. .

MARTINELLI, G., MORAES, M. **Livro vermelho da flora do Brasil**. Rio de Janeiro: Andrea Jakobsson Estúdio, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, 2013, 1100p.

MARTINS, E.; LOYOLA, R.; MESSINA, T., *et al.* "Tree red listing in Brazil: lessons and perspectives", **BGjournal**, v. 12, n. 2, 2015.

MARTINS, E., LOYOLA, R., MARTINELLI, G. "Challenges and perspectives for achieving the global strategy for plant conservation targets in Brazil", **Annals of the Missouri Botanical Garden**, v. 102, n. 2, 2017. DOI: 10.3417/D-16-00009A.

MATZKE, N. J. "Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing", **Frontiers of Biogeography**, v. 5, n. 4, 2013. DOI: 10.21425/f5fbg19694. .

MIQUEL, F. A. G. Caesalpiniae. *In*: MIQUEL, F. A. G (Ed.) **Stirpes Surinamensis Selectae**. Arnz & Comp, Leiden, 1851, pp. 12–13. https://doi.org/10.5962/bhl.title.77484

MORAL, R. A., HINDE, J., DEMÉTRIO, C. G. B. "Half-normal plots and overdispersed models in R: The hnp package", **Journal of Statistical Software**, v. 81, 2017. DOI: 10.18637/jss.v081.i10. .

MORLEY, R. J. **Origin and evolution of tropical rainforests.** Chichester, UK, Wiley, 2000.

MORLEY, Robert J. "Interplate dispersal paths for megathermal angiosperms", **Perspectives in Plant Ecology, Evolution and Systematics**, v. 6, n. 1–2, p. 5–20, 2003. DOI: 10.1078/1433-8319-00039. .

MORRONE, J. J. "Biogeographical regionalisation of the neotropical region", **Zootaxa**, v. 3782, n. 1, p. 1–110, 25 mar. 2014. DOI: 10.11646/zootaxa.3782.1.1. .

MORRONE, J. J., EBACH, M. C. "Toward a terrestrial biogeographical regionalisation of the world: historical notes, characterisation and area nomenclature", **Australian Systematic Botany**, v. 35, n. 3, p. 89–126, 1 jul. 2022. DOI: 10.1071/SB22002. .

MORRONE, J. J., ESCALANTE, T., RODRIGUEZ-TAPIA, G., *et al.* "Biogeographic regionalization of the Neotropical region: New map and shapefile", **Anais da Academia Brasileira de Ciencias**, v. 94, n. 1, 2022. DOI: 10.1590/0001-3765202220211167. .

NACIRI, Y., LINDER, H. P. "Species delimitation and relationships: The dance of the seven veils", **Taxon**, v. 64, n. 1, 2015. DOI: 10.12705/641.24. .

NELDER, J. A., WEDDERBURN, R. W. M. "Generalized linear models", **Royal Statistical Society**, v. 135, p. 370–384, 1972. .

NEWBERY, D. M., VAN DER BURGT, X. M., WORBES, M., *et al.* "Transient dominance in a central african rain forest", **Ecological Monographs**, v. 83, n. 3, 2013. DOI: 10.1890/12-1699.1. .

NOWAK, R. M. **Walker’s bats of the world**. Baltimore, Johns Hopkins University Press, 1994.

NYLANDER, J. A. A. **catfasta2phyml**. 2018. https://github.com/nylander/catfasta2phyml.

OBIANG-MBOMIO, D., BRETELER, F. J. **Révision du genre Eurypetalum Harms (Fabaceae, Caesalpinioideae)**. . [S.l: s.n.], 2007. Disponível em: www.adansonia.com.

OJEDA, D. I., KOENEN, E., CERVANTES, S., *et al.* "Phylogenomic analyses reveal an exceptionally high number of evolutionary shifts in a florally diverse clade of African legumes", **Molecular Phylogenetics and Evolution**, v. 137, p. 156–167, 1 ago. 2019. DOI: 10.1016/j.ympev.2019.05.002. .

OLIVER, D. **Hooker’s Icones Plantarum**, vol. 20, 1891

PARADIS, E., SCHLIEP, K. "Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R", **Bioinformatics**, v. 35, n. 3, 2019. DOI: 10.1093/bioinformatics/bty633. .

PELLEGRIN, F. "*Augouardia* Pellegrin, genre nouveau de Césalpiniées du Congo". **Bulletin de la Société Botanique de France**, v. 71, p. 309–311, 1924.

PENNINGTON, R. T., DICK, C. W. "The role of immigrants in the assembly of the South American rainforest tree flora". 359, 2004. **Anais** [...] [S.l: s.n.], 2004. DOI: 10.1098/rstb.2004.1532.

PLANA, V. "Mechanisms and tempo of evolution in the African Guineo-Congolian rainforest". 359, 29 out. 2004. **Anais** [...] [S.l.], Royal Society, 29 out. 2004. p. 1585–1594. DOI: 10.1098/rstb.2004.1535.

PORTIK, D. **BEAST Divergence Dating using a Fixed Tree Topology**. 19 dez. 2018. https://osf.io/7y59t/.

POWO. **Plants of the World Online. Facilitated by the Royal Botanic Gardens**. 14 nov. 2023. http://www.plantsoftheworldonline.org/ .

Pulle, A. A. **An enumeration of the vascular plants known from Surinam**. E.J. Brill, Leiden, 1906, 555 pp.

QGIS.ORG. **QGIS Geographic Information System. QGIS Association**. **Open Source Geospatial Foundation Project**. [S.l: s.n.]. , 2022

RAMBAUT, A., DRUMMOND, A. J. "TreeAnnotator v1.8.4", **Http://Beast.Bio.Ed.Ac.Uk/**, 2016. .

RAMBAUT, Andrew, DRUMMOND, A. J., XIE, D., *et al.* "Posterior summarization in Bayesian phylogenetics using Tracer 1.7", **Systematic Biology**, v. 67, n. 5, 2018. DOI: 10.1093/sysbio/syy032. .

REE, R. H., SMITH, S. A. "Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis", **Systematic Biology**, v. 57, n. 1, 2008. DOI: 10.1080/10635150701883881. .

REES, A. **The cyclopædia; or, Universal dictionary of arts, sciences, and literature**. Vol. 11. Longman, Hurst, Rees, Orme & Brown, Paternoser-Row, London, 1808, 768 pp.

Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten, 254 pp. https://doi.org/10.12705/Code.2018

REIS, I. P. ***Eperua* Aubl. (Leguminosae – Caesalpinioideae, Detarieae)**. Dissertação (Mestrado, Ciências Biológicas) – Museu Paraense Emílio Goeldi, Universidade Federal da Amazônia, Belém, Pará, 2014.

RENNER, S. "Plant dispersal across the tropical Atlantic by wind and sea currents". 165, 2004. **Anais** [...] [S.l: s.n.], 2004. DOI: 10.1086/383334.

REVELL, L. J. "phytools: An R package for phylogenetic comparative biology (and other things)", **Methods in Ecology and Evolution**, v. 3, n. 2, 2012. DOI: 10.1111/j.2041-210X.2011.00169.x. .

RIBEIRO, J. E. L. S., HOPKINS, M. J. G., VICENTINI, A., et al. **Flora da Reserva Ducke. Guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central**. INPA-DFID, Manaus, 1999, 816 pp.

RICHARDS, P. W. "Lowland tropical podsols and their vegetation", **Nature**, v. 148, n. 3744, p. 129–131, 1941. DOI: 10.1038/148129a0. .

RICHARDSON, J. E., PENNINGTON, R. T., PENNINGTON, T. D., *et al.* "Rapid diversification of a species-rich genus of neotropical rain forest trees", **Science**, v. 293, n. 5538, 2001. DOI: 10.1126/science.1061421. .

RICHTER, H. G.; DALLWITZ, M. J. Commercial timbers: descriptions, illustrations, identification, and information retrieval. 2000. 24 Nov. 2023. http://delta-intkey.com.

ROMERO-GONZÁLEZ, G. A., AYMARD, G. A. "A New Species of Eperua (Leguminosae, Detarioideae) from Amazonas State, Venezuela", **Harvard Papers in Botany**, v. 24, n. 2, p. 341–347, 31 dez. 2019. DOI: 10.3100/hpib.v24iss2.2019.n17.

RONQUIST, F. "Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography", **Systematic Biology**, v. 46, n. 1, 1997. DOI: 10.1093/sysbio/46.1.195. .

ROWAN, B. A., SEYMOUR, D. K., CHAE, E., *et al.*, "Methods for genotyping-by-sequencing". **Methods in Molecular Biology**, [S.l: s.n.], 2017. v. 1492. . DOI: 10.1007/978-1-4939-6442-0_16.

RUDGE, E. "Description of a new Species of *Dimorpha*" **Transactions of the Linnean Society of London**, v. 9, p. 179–181, 1807. https://doi.org/10.1111/j.1096-3642.1818.tb00337.x

SÄRKINEN, T. E., NEWMAN, M. F., MAAS, P. J. M., *et al.* "Recent oceanic long-distance dispersal and divergence in the amphi-Atlantic rain forest genus Renealmia L.f. (Zingiberaceae)", **Molecular Phylogenetics and Evolution**, v. 44, n. 3, p. 968–980, set. 2007. DOI: 10.1016/j.ympev.2007.06.007. .

SAYYARI, E., MIRARAB, S. "Fast Coalescent-Based Computation of Local Branch Support from Quartet Frequencies", **Molecular Biology and Evolution**, v. 33, n. 7, 2016. DOI: 10.1093/MOLBEV/MSW079. .

SCHLEY, R. J., DE LA ESTRELLA, M., PÉREZ-ESCOBAR, O. A., *et al.* "Is Amazonia a ‘museum’ for Neotropical trees? The evolution of the Brownea clade (Detarioideae, Leguminosae)", **Molecular Phylogenetics and Evolution**, v. 126, p. 279–292, 1 set. 2018. DOI: 10.1016/j.ympev.2018.04.029. .

SCHLEY, R. J., NICHOLLS, J. A., KIDNER, C. "Do Reticulate Relationships Between Tropical Trees Drive Diversification? Insights from Inga (Fabaceae)", 2023. DOI: 10.1101/2023.09.12.557345. Disponível em: https://www.researchgate.net/publication/373947041.

SCHLEY, R. J., PENNINGTON, R. T., PÉREZ-ESCOBAR, O. A., *et al.* "Introgression across evolutionary scales suggests reticulation contributes to Amazonian tree diversity", **Molecular Ecology**, v. 29, n. 21, p. 4170–4185, 1 nov. 2020. DOI: 10.1111/mec.15616. .

SCHLEY, R. J., QIN, M., VATANPARAST, M., *et al.* "The diversification of Pterocarpus; (Leguminosae: Papilionoideae) was influenced by biome-switching and infrequent long-distance dispersal", **bioRxiv**, n. 31670193, 2021. .

SCHREBER, J. C. D. **Genera Plantarum**. vol. 2. Frankfurt ad Moenum, Sumtu Varrentrappii et Wenneri, 1791, 872 pp.

SHARROCK, S.; HOFT, R.; DE SOUZA DIAS, B. F. "An overview of recent progress in the implementation of the Global Strategy for Plant Conservation – a global perspective", **Rodriguesia**, v. 69, n. 4, 2018. DOI: 10.1590/2175-7860201869401

SIMMONS, N. B., "Order Chiroptera". In: WILSON, D. E., REEDER, D. M. (Org.), **Mammal species of the world. A taxonomic and geographic reference**, Baltimore, Johns Hopkins University Press, 2005. p. 312–529.

SIMPSON, M. G. **Plant Systematics**. 2 Ed. Elsevier, 2010, 754 p.

SMITH, S. A., MOORE, M. J., BROWN, J. W., *et al.* "Analysis of phylogenomic datasets reveals conflict, concordance, and gene duplications with examples from animals and plants", **BMC Evolutionary Biology**, v. 15, n. 1, 2015. DOI: 10.1186/s12862-015-0423-0. .

SOBRAL, M.; STEHMANN, J. R. "An analysis of new angiosperm species discoveries in Brazil (1990-2006) ", **Taxon**, v. 58, n. 1, 2009. DOI: 10.1002/tax.581021.

SOLÍS-LEMUS, C., ANÉ, C. "Inferring Phylogenetic Networks with Maximum Pseudolikelihood under Incomplete Lineage Sorting", **PLoS Genetics**, v. 12, n. 3, 1 mar. 2016. DOI: 10.1371/journal.pgen.1005896. .

SOLÍS-LEMUS, C., BASTIDE, P., ANÉ, C. "PhyloNetworks: A package for phylogenetic networks", **Molecular Biology and Evolution**, v. 34, n. 12, p. 3292–3298, 1 dez. 2017. DOI: 10.1093/molbev/msx235. .

SPINELLI-ARAUJO, L., BAYMA-SILVA, G., TORRESAN, F.E., et al. **Conservação da Biodiversidade do Estado do Maranhão: Cenário Atual em Dados Geoespaciais**. Embrapa Meio Ambiente, Jaguariúna, 2016, 28 pp.

STAFLEU, F. A. & COWAN, R. S. **Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types**. Volume I: A-G. Regnum Vegetabile 137. Bohn, Scheltema & Holkema, Utrecht, 1976, 1136 pp.

STAFLEU, F. A. & COWAN, R. S. **Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types**. Volume II: H-Le. Regnum Vegetabile 98. Bohn, Scheltema & Holkema, Utrecht, 1979, 991 pp.

STAFLEU, F. A. & COWAN, R. S. **Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types**. Volume III: Lh-O. Regnum Vegetabile 105. Bohn, Scheltema & Holkema, Utrecht, 1981, 980 pp.

STAFLEU, F. A. & COWAN, R. S. **Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types**.

Volume IV: P-Sak. Regnum Vegetabile 110. Bohn, Scheltema & Holkema, Utrecht, 1983, 1214 pp.

STAFLEU, F. A. & COWAN, R. S. **Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types.** Volume V: Sal-Ste. Regnum Vegetabile 110. Bohn, Scheltema & Holkema, Utrecht, 1985, 1066 pp.

STAFLEU, F. A. & COWAN, R. S**. Taxonomic literature: a selective guide to botanical publications and collections with dates, commentaries and types.** Volume VI: Sti-Vay. Regnum Vegetabile 110. Bohn, Scheltema & Holkema, Utrecht, 1986, 926 pp.

STEENWYK, J. L., LI, Y., ZHOU, X., *et al.* **Incongruence in the phylogenomics era**. **Nature Reviews Genetics**. [S.l: s.n.]. , 2023

STENZ, N. W. M., LARGET, B., BAUM, D. A., *et al.* "Exploring tree-like and non-tree-like patterns using genome sequences: An example using the inbreeding plant species Arabidopsis thaliana (L.) heynh", **Systematic Biology**, v. 64, n. 5, 2015. DOI: 10.1093/sysbio/syv039. .

STROO, A. **Plant Systematics and Evolution Pollen morphological evolution in bat pollinated plants**. **Plant Syst. Evol**. [S.l: s.n.], 2000.

STRUWE, L., MAAS, P. J. M., ALBERT, V. A. "Aripuana cullmaniorum, a new genus and species of Gentianaceae from white sands of southeastern Amazonas, Brazil", **Harvard Papers in Botany**, v. 2, n. 2, p. 235–253, 1997. .

SUCHARD, M. A., LEMEY, P., BAELE, G., *et al.* "Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10", **Virus Evolution**, v. 4, n. 1, 2018. DOI: 10.1093/ve/vey016. .

TEELING, E. C., SPRINGER, M. S., MADSEN, O., *et al.* "A molecular phylogeny for bats illuminates biogeography and the fossil record", **Science**, v. 307, n. 5709, 2005. DOI: 10.1126/science.1105113. .

TER STEEGE, H. **A monograph of Wallaba, Mora and Greenheart**. Netherlands, Wageningen, 1990.

TER STEEGE, Hans, FORTES, E. A., ROZENDAAL, D. M. A., *et al.* " Molecular phylogeny and evolution of inflorescence types in Eperua ", **American Journal of Botany**, 4 out. 2023. DOI: 10.1002/ajb2.16229. .

TER STEEGE, Hans, HENKEL, T. W., HELAL, N., *et al.* "Rarity of monodominance in hyperdiverse Amazonian forests", **Scientific Reports**, v. 9, n. 1, 1 dez. 2019. DOI: 10.1038/s41598-019-50323-9. .

TER STEEGE, Hans, PITMAN, N. C. A., SABATIER, D., *et al.* "Hyperdominance in the Amazonian tree flora", **Science**, v. 342, n. 6156, 2013. DOI: 10.1126/science.1243092. .

TER STEEGE, Hans, VAESSEN, R. W., CÁRDENAS-LÓPEZ, D., *et al.* "The discovery of the Amazonian tree flora with an updated checklist of all known tree taxa", **Scientific Reports**, v. 6, 13 jul. 2016. DOI: 10.1038/srep29549. .

The Plant List Version 1.1. Published on the Internet. 2013. http://www.theplantlist.org/

Thiers, B.Index herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden’s Virtual Herbarium. 2023 [continuously updated.

http://sweetgum.nybg.org/ih/

TOSSO, F., HARDY, O. J., DOUCET, J. L., *et al.* "Evolution in the Amphi-Atlantic tropical genus Guibourtia (Fabaceae, Detarioideae), combining NGS phylogeny and morphology", **Molecular Phylogenetics and Evolution**, v. 120, p. 83–93, 1 mar. 2018. DOI: 10.1016/j.ympev.2017.11.026. .

TRADA - Timber Research And Development Association. Wallaba. Disponível em <https://www.trada.co.uk/wood-species/wallaba/>. Acesso em 24 novembro 2023.

TUNG HO, L. S., ANÉ, C. "A linear-time algorithm for gaussian and non-gaussian trait evolution models", **Systematic Biology**, v. 63, n. 3, 2014. DOI: 10.1093/sysbio/syu005. .

TROPICOS (2021) Missouri Botanical Garden. 6 November 2021. https://tropicos.org

Useful Tropical Plants Database. *Eperua.* 2014. Disponível em <http://tropical.theferns.info/query.php?full=eperua>. Acesso em 24 novembro 2020.

TURLAND, N. J. **The code decoded. A user's guide to the International code of nomenclature for algae, fungi, and plants.** Advanced Books, Pensoft Publishers, Sofia, 2019. https://doi.org/10.3897/ab.e38075

TURLAND, N. J., WIERSEMA, J. H., BARRIE, F. R., et al. **International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017**, 2018.

VALDERRAMA, E., LANDIS, J. B., SKINNER, D., *et al.* "The genetic mechanisms underlying the convergent evolution of pollination syndromes in the Neotropical radiation of Costus L.", **Frontiers in Plant Science**, v. 13, 8 set. 2022. DOI: 10.3389/fpls.2022.874322. .

VALDERRAMA, E., SASS, C., PINILLA-VARGAS, M., *et al.* "Unraveling the Spiraling Radiation: A Phylogenomic Analysis of Neotropical Costus L", **Frontiers in Plant Science**, v. 11, 14 ago. 2020. DOI: 10.3389/fpls.2020.01195. .

VAN DER NIET, T., JOHNSON, S. D. **Phylogenetic evidence for pollinator-driven diversification of angiosperms**. **Trends in Ecology and Evolution**. [S.l: s.n.]. , jun. 2012

VAN DER NIET, T., PEAKALL, R., JOHNSON, S. D. "Pollinator-driven ecological speciation in plants: New evidence and future perspectives", **Annals of Botany**, v. 113, n. 2, p. 199–211, jan. 2014. DOI: 10.1093/aob/mct290. .

VARGAS, O. M., DICK, C. W., "Diversification History of Neotropical Lecythidaceae, an Ecologically Dominant Tree Family of Amazon Rain Forest". In: RULL, V., CARNAVAL, A. C. (Org.), **Neotropical Diversification: Patterns and Processes**, [S.l: s.n.], 2020. p. 791–806. DOI: 10.1007/978-3-030-31167-4_29.

VEIGA JUNIOR, V. F. ;PINTO, A. C. "O gênero *Copaifera* L. ", **Química Nova**, v. 25, n. 2, 2002. DOI: 10.1590/s0100-40422002000200016.

VOGEL, S. "Chiropterophilie in der neotropischen Flora", **Flora oder Allgemeine botanische Zeitung. Abt. B, Morphologie und Geobotanik**, v. 157, n. 4, 1968. DOI: 10.1016/s0367-1801(17)30097-2. .

WEISS, J., DELGADO-BENARROCH, L., EGEA-CORTINES, M. **Genetic control of floral size and proportions**. **International Journal of Developmental Biology**. [S.l: s.n.]. , 2005

WELLBORN, G. A., LANGERHANS, R. B. **Ecological opportunity and the**

adaptive diversification of lineages. **Ecology and Evolution**. [S.l.], John Wiley and Sons Ltd. , 1 jan. 2015

WESSELINGH, F. P., HOORN, C., KROONENBERG, S. B., *et al.*, "On the Origin of Amazonian Landscapes and Biodiversity: A Synthesis". **Amazonia, Landscape and Species Evolution: A Look into the Past**, [S.l.], Wiley Blackwell, 2010. p. 421–431. DOI: 10.1002/9781444306408.ch26.

WICKHAM, H. **ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York**. [S.l: s.n.], 2016. v. 35.

WILLDENOW, C. L. **Species plantarum**, ed. 4, 2(1). G.C. Nauk, Berolini, 1799, 823 pp.

WILLDENOW, C. L. **Species Plantarum**. ed. 4, 3(2). G.C. Nauk, Berolini, 1802, 1474 pp.

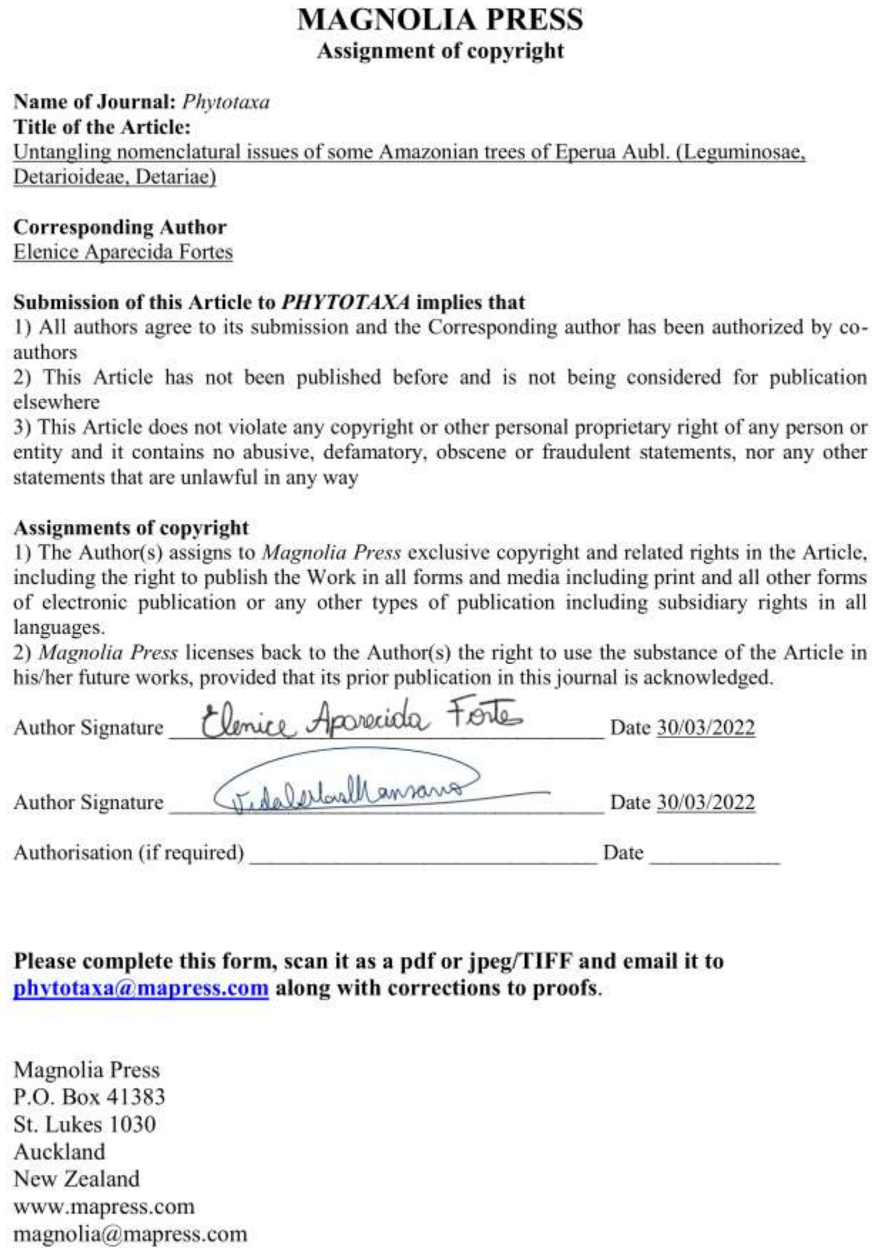
WWF – World Wide Fund For Nature. Why is the Amazon rainforest important: The vital links between the Amazon rainforest, global warming and you. 2023 Disponível em:<https://wwf.panda.org/knowledge_hub/where_we_work/amazon/about_the_amazon/why_amazon_important/ > Acesso em 18 novembro 2023.

YANG, C. X., LIU, S. Y., ZEREGA, N. J. C., *et al.* "Phylogeny and Biogeography of Morus (Moraceae)", **Agronomy**, v. 13, n. 8, 1 ago. 2023. DOI: 10.3390/agronomy13082021. .

ZHANG, C., RABIEE, M., SAYYARI, E., *et al.* "ASTRAL-III: Polynomial time species tree reconstruction from partially resolved gene trees", **BMC Bioinformatics**, v. 19, 2018. DOI: 10.1186/s12859-018-2129-y. .

ZIZKA, A., SILVESTRO, D., ANDERMANN, T., *et al.* "CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases", **Methods in Ecology and Evolution**, v. 10, n. 5, 2019. DOI: 10.1111/2041-210X.13152.

ANEXO I



MAGNOLIA PRESS

Assignment of copyright

Name of Journal: *Phytotaxa*
Title of the Article:
Untangling nomenclatural issues of some Amazonian trees of Eperua Aubl. (Leguminosae, Detarioideae, Detariae)

Corresponding Author
Elenice Aparecida Fortes

Submission of this Article to *PHYTOTAXA* implies that

1) All authors agree to its submission and the Corresponding author has been authorized by co-authors

2) This Article has not been published before and is not being considered for publication elsewhere

3) This Article does not violate any copyright or other personal proprietary right of any person or entity and it contains no abusive, defamatory, obscene or fraudulent statements, nor any other statements that are unlawful in any way

Assignments of copyright

1) The Author(s) assigns to *Magnolia Press* exclusive copyright and related rights in the Article, including the right to publish the Work in all forms and media including print and all other forms of electronic publication or any other types of publication including subsidiary rights in all languages.

2) *Magnolia Press* licenses back to the Author(s) the right to use the substance of the Article in his/her future works, provided that its prior publication in this journal is acknowledged.

Author Signature Elenice Aparecida Forte Date 30/03/2022

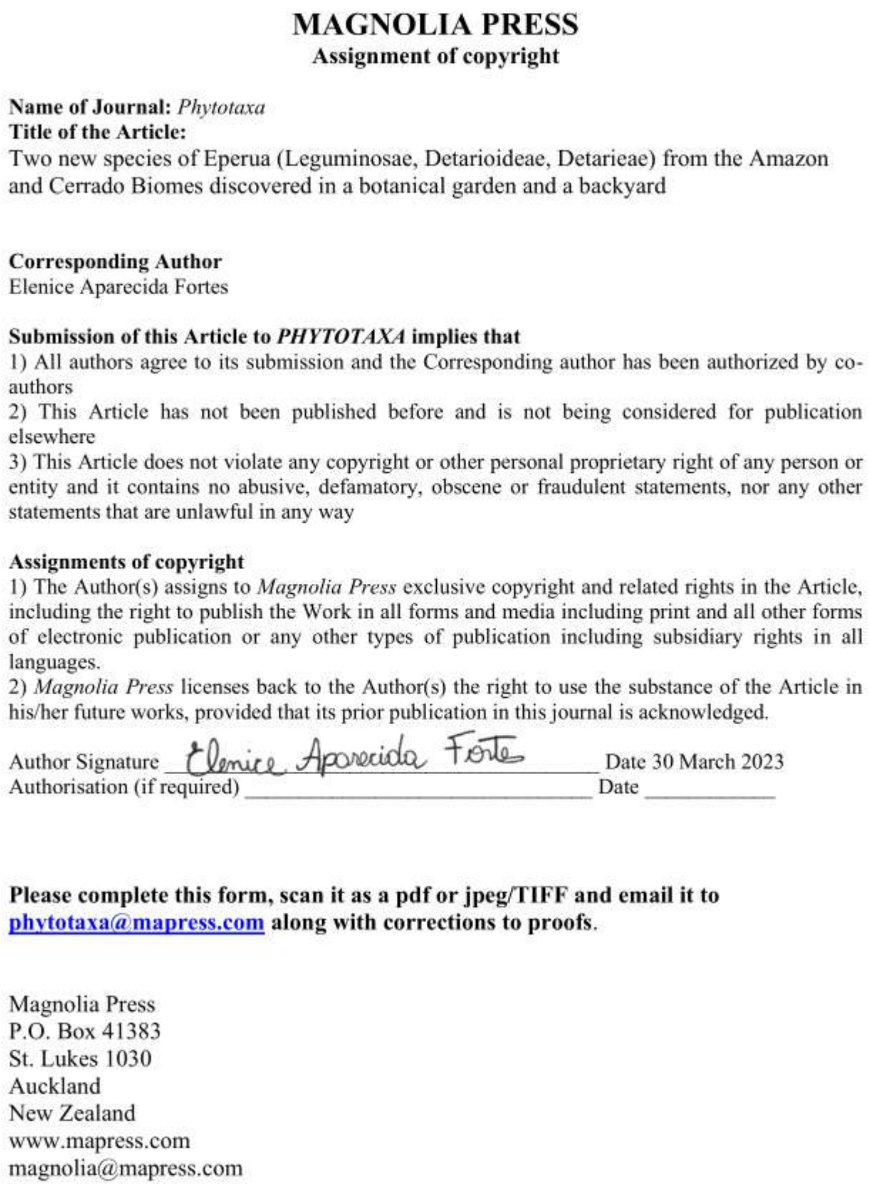
Author Signature ____________ Date 30/03/2022

Authorisation (if required) ____________ Date ____________

Please complete this form, scan it as a pdf or jpeg/TIFF and email it to phytotaxa@mapress.com along with corrections to proofs.

Magnolia Press
P.O. Box 41383
St. Lukes 1030
Auckland
New Zealand
www.mapress.com
magnolia@mapress.com

Anexo II



MAGNOLIA PRESS

Assignment of copyright

Name of Journal: *Phytotaxa*
Title of the Article:
Two new species of Eperua (Leguminosae, Detarioideae, Detarieae) from the Amazon and Cerrado Biomes discovered in a botanical garden and a backyard

Corresponding Author
Elenice Aparecida Fortes

Submission of this Article to *PHYTOTAXA* implies that

1) All authors agree to its submission and the Corresponding author has been authorized by co-authors
2) This Article has not been published before and is not being considered for publication elsewhere
3) This Article does not violate any copyright or other personal proprietary right of any person or entity and it contains no abusive, defamatory, obscene or fraudulent statements, nor any other statements that are unlawful in any way

Assignments of copyright

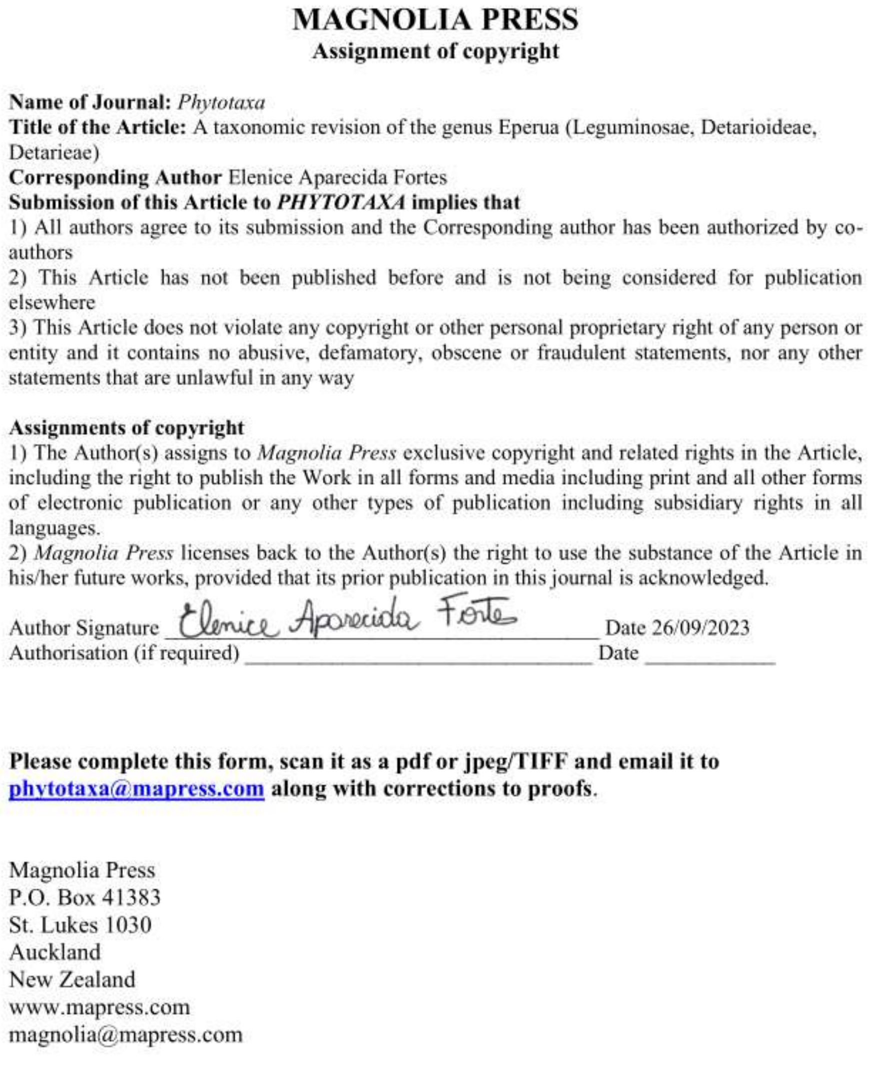
1) The Author(s) assigns to *Magnolia Press* exclusive copyright and related rights in the Article, including the right to publish the Work in all forms and media including print and all other forms of electronic publication or any other types of publication including subsidiary rights in all languages.
2) *Magnolia Press* licenses back to the Author(s) the right to use the substance of the Article in his/her future works, provided that its prior publication in this journal is acknowledged.

Author Signature Elenice Aparecida Forte Date 30 March 2023
Authorisation (if required) ________________________________ Date ___________

Please complete this form, scan it as a pdf or jpeg/TIFF and email it to phytotaxa@mapress.com along with corrections to proofs.

Magnolia Press
P.O. Box 41383
St. Lukes 1030
Auckland
New Zealand
www.mapress.com
magnolia@mapress.com

Anexo III



MAGNOLIA PRESS

Assignment of copyright

Name of Journal: *Phytotaxa*
Title of the Article: A taxonomic revision of the genus Eperua (Leguminosae, Detarioideae, Detarieae)
Corresponding Author Elenice Aparecida Fortes
Submission of this Article to *PHYTOTAXA* implies that
1) All authors agree to its submission and the Corresponding author has been authorized by co-authors
2) This Article has not been published before and is not being considered for publication elsewhere
3) This Article does not violate any copyright or other personal proprietary right of any person or entity and it contains no abusive, defamatory, obscene or fraudulent statements, nor any other statements that are unlawful in any way

Assignments of copyright
1) The Author(s) assigns to *Magnolia Press* exclusive copyright and related rights in the Article, including the right to publish the Work in all forms and media including print and all other forms of electronic publication or any other types of publication including subsidiary rights in all languages.
2) *Magnolia Press* licenses back to the Author(s) the right to use the substance of the Article in his/her future works, provided that its prior publication in this journal is acknowledged.

Author Signature Elenice Aparecida Fortes Date 26/09/2023
Authorisation (if required) ______________________________ Date ___________

Please complete this form, scan it as a pdf or jpeg/TIFF and email it to phytotaxa@mapress.com along with corrections to proofs.

Magnolia Press
P.O. Box 41383
St. Lukes 1030
Auckland
New Zealand
www.mapress.com
magnolia@mapress.com

Anexo IV

Ministério do Meio Ambiente
CONSELHO DE GESTÃO DO PATRIMÔNIO GENÉTICO
SISTEMA NACIONAL DE GESTÃO DO PATRIMÔNIO GENÉTICO E DO CONHECIMENTO TRADICIONAL ASSOCIADO

Certidão
Cadastro nº AB4CAFE

Declaramos, nos termos do art. 41 do Decreto nº 8.772/2016, que o cadastro de acesso ao patrimônio genético ou conhecimento tradicional associado, abaixo identificado e resumido, no Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado foi submetido ao procedimento administrativo de verificação e não foi objeto de requerimentos admitidos de verificação de indícios de irregularidades ou, caso tenha sido, o requerimento de verificação não foi acatado pelo CGen.

Número do cadastro:	**AB4CAFE**
Usuário:	**UNICAMP**
CPF/CNPJ:	**46.068.425/0001-33**
Objeto do Acesso:	**Patrimônio Genético**
Finalidade do Acesso:	**Pesquisa**

Espécie

Eperua bijuga
Eperua sp
Eperua duckeana
Eperua falcata
Eperua glabra
Eperua glabriflora
Eperua grandiflora
Eperua jenmanii
Eperua leucantha
Eperua oleifera
Eperua praesagata
Eperua purpurea
Eperua rubiginosa

Título da Atividade:	**O papel da evolução da inflorescência e dos padrões biogeográficos na história evolutiva do clado tropical Eperua s.l. (Leguminosae, Detarioideae)**

Equipe

Elenice Aparecida Fortes	**UNICAMP**
Vidal de Freitas Mansano	**Instituto de Pesquisas Jardim Botânico do Rio de Janeir**

Parceiras no Exterior

Cornell University

Envios de Amostra

Espécie:	**Eperua bijuga**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**

Anexo IV (continuação)

Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Eperua sp**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab 111, Plant Science 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Eperua duckeana**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Eperua falcata**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Eperua glabra**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Eperua glabriflora**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Eperua grandiflora**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Eperua jenmanii**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Eperua leucantha**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Eperua oleifera**

Anexo IV (continuação)

Tipo do Patrimônio Genético: **-**
Forma do Patrimônio Genético: **Outra**
Instituição Destinatária: **Cornell University**
Sede da Instituição Destinatária: **Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie: **Eperua praesagata**
Tipo do Patrimônio Genético: **-**
Forma do Patrimônio Genético: **Outra**
Instituição Destinatária: **Cornell University**
Sede da Instituição Destinatária: **Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie: **Eperua purpurea**
Tipo do Patrimônio Genético: **-**
Forma do Patrimônio Genético: **Outra**
Instituição Destinatária: **Cornell University**
Sede da Instituição Destinatária: **Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie: **Eperua rubiginosa**
Tipo do Patrimônio Genético: **-**
Forma do Patrimônio Genético: **Outra**
Instituição Destinatária: **Cornell University**
Sede da Instituição Destinatária: **Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**

Data do Cadastro: **02/09/2022 06:48:27**
Situação do Cadastro: **Concluído**

Conselho de Gestão do Patrimônio Genético
Situação cadastral conforme consulta ao SisGen em **8:29** de **27/11/2023**.

SISTEMA NACIONAL DE GESTÃO
DO PATRIMÔNIO GENÉTICO
E DO CONHECIMENTO TRADICIONAL
ASSOCIADO - **SISGEN**

Anexo V

Ministério do Meio Ambiente
CONSELHO DE GESTÃO DO PATRIMÔNIO GENÉTICO
SISTEMA NACIONAL DE GESTÃO DO PATRIMÔNIO GENÉTICO E DO CONHECIMENTO TRADICIONAL ASSOCIADO

Certidão
Cadastro nº AFEB16F

Declaramos, nos termos do art. 41 do Decreto nº 8.772/2016, que o cadastro de acesso ao patrimônio genético ou conhecimento tradicional associado, abaixo identificado e resumido, no Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado foi submetido ao procedimento administrativo de verificação e não foi objeto de requerimentos admitidos de verificação de indícios de irregularidades ou, caso tenha sido, o requerimento de verificação não foi acatado pelo CGen.

Número do cadastro:	**AFEB16F**
Usuário:	**UNICAMP**
CPF/CNPJ:	**46.068.425/0001-33**
Objeto do Acesso:	**Patrimônio Genético**
Finalidade do Acesso:	**Pesquisa**

Espécie

Guibourtia hymenaeifolia
Hymenaea parvifolia
Sindora siamensis
Copaifera trapezifolia

Título da Atividade:	**O papel da evolução da inflorescência e dos padrões biogeográficos na história evolutiva do clado tropical Eperua s.l. (Leguminosae, Detarioideae)**

Equipe

Elenice Aparecida Fortes	**UNICAMP**
Vidal de Freitas Mansano	**Instituto de Pesquisas Jardim Botânico do Rio de Janeir**

Parceiras no Exterior

Cornell University

Envios de Amostra

Espécie:	**Guibourtia hymenaeifolia**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Hymenaea parvifolia**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Sindora siamensis**
Tipo do Patrimônio Genético:	**-**

Anexo V (continuação)

Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**
Espécie:	**Copaifera trapezifolia**
Tipo do Patrimônio Genético:	**-**
Forma do Patrimônio Genético:	**Outra**
Instituição Destinatária:	**Cornell University**
Sede da Instituição Destinatária:	**Specht Lab, 111 Plant Science, 236 Tower Road, Ithaca, New York, 14853, Estados Unidos**

Data do Cadastro:	**05/09/2022 10:39:37**
Situação do Cadastro:	**Concluído**

Conselho de Gestão do Patrimônio Genético
Situação cadastral conforme consulta ao SisGen em **8:30** de **27/11/2023**.

SISTEMA NACIONAL DE GESTÃO
DO PATRIMÔNIO GENÉTICO
E DO CONHECIMENTO TRADICIONAL
ASSOCIADO - SISGEN

Anexo VI

COORDENADORIA DE PÓS-GRADUAÇÃO
INSTITUTO DE BIOLOGIA
Universidade Estadual de Campinas
Caixa Postal 6109. 13083-970, Campinas, SP, Brasil
Fone (19) 3521-6378. email: cpgib@unicamp.br

DECLARAÇÃO

Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada "***Sistemática do clado Eperua s.l. e revisão taxonômica do gênero Eperua (Leguminosae, Detarioideae)***", desenvolvida no Programa de Pós-Graduação em Biologia Vegetal do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

gov.br
Documento assinado digitalmente
ELENICE APARECIDA FORTES
Data: 05/03/2024 11:52:42-0300
Verifique em https://validar.iti.gov.br

Assinatura: ________________________________
Nome do(a) aluno(a): Elenice Aparecida Fortes

gov.br
Documento assinado digitalmente
VIDAL DE FREITAS MANSANO
Data: 05/03/2024 15:22:35-0300
Verifique em https://validar.iti.gov.br

Assinatura: ___________________________
Nome do(a) orientador(a): Vidal de Freitas Mansano

Data: 05 de março de 2024

Anexo VII

Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada **Sistemática do clado Eperua s.l. e revisão taxonômica do gênero Eperua (Leguminosae, Detarioideae)**, não infringem os dispositivos da Lei n.° 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 05 de março de 2024

gov.br
Documento assinado digitalmente
ELENICE APARECIDA FORTES
Data: 05/03/2024 11:52:42-0300
Verifique em https://validar.iti.gov.br

Assinatura : ___________________________________
Nome do(a) autor(a): **Elenice Aparecida Fortes**
RG n.° 19924007

gov.br
Documento assinado digitalmente
VIDAL DE FREITAS MANSANO
Data: 05/03/2024 15:25:39-0300
Verifique em https://validar.iti.gov.br

Assinatura : ___________________________________
Nome do(a) orientador(a): **Vidal de Freitas Mansano**
RG n.° 19630609