



UNIVERSIDADE ESTADUAL DE CAMPINAS
INSTITUTO DE BIOLOGIA

NALLARETT MARINA DAVILA CARDOZO

**PHYLOGENY AND TAXONOMY OF HENRIQUEZIEAE BENTH. &
HOOK. F (IXOROIDEAE, RUBIACEAE) IN THE GUIANA SHIELD**

**RELAÇÕES FILOGENÉTICAS E TAXONOMIA DA TRIBO
HENRIQUEZIEAE BENTH. & HOOK. F (IXOROIDEAE, RUBIACEAE) NO
ESCUDO DAS GUIANAS**

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ESCUDO DAS GUIANAS**

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RESUMO

O Escudo das Guianas é uma região que se encontra no norte da América do Sul, entre o rio Orinoco e o rio Amazonas. Este maciço representa aproximadamente 13% da área da América do Sul, é uma das formações geológicas mais antigas que data desde o Pré-Cambriano. A família Rubiaceae tem alta diversidade e alto endemismo nestas áreas. Henriquezieae (Ixoroideae, Rubiaceae), cuja distribuição é praticamente restrita ao Escudo das Guianas, apresenta características atípicas dentro de Rubiaceae, como flores principalmente zigomorfas, sementes planas e carentes de endosperma e ovário secundariamente súpero. A tribo encontra-se inserida no Clado Henriquezieae-Posoquerieae-Sipaneeae (subfamília Ixoroideae) que é predominantemente restrito ao Escudo das Guianas. Apesar de existir uma recente hipótese filogenética da tribo as relações a nível infratribal não encontra-se bem resolvidas. Além disso, a última revisão taxonômica da tribo foi realizada em 1984, desde então novas coletas e novas espécies tem surgido, sendo necessária uma atualização taxonômica da tribo. Os objetivos deste trabalho são ampliar a amostragem das espécies em Henriquezieae e incrementar a amostragem de dados moleculares usando sequenciamento de nova geração para resolver as relações dentro da tribo, e postular hipóteses sobre a evolução da morfologia atípica que a tribo apresenta. Além disso, atualizar a taxonomia depois da última revisão taxonômica feita por Rogers em 1984. Nossos resultados mostram que Henriquezieae e os três gêneros que compõem a tribo são fortemente sustentados como monofiléticos. *Gleasonia* é o grupo irmão de *Henriquezia* e *Platycarpum*. Os resultados da reconstrução ancestral da morfologia mostram que os caracteres atípicos em Henriquezieae são apomórficos. Sinapomorfias morfológicas como corola variegada com linhas e/ou macula, endosperma reduzido e fruto leve a fortemente achatado perpendicular ao septo são propostas para a tribo. É apresentado um tratamento taxonômico com 23 espécies, chaves taxonômicas e mapas de distribuição atualizados.

Palavras-chave: filogenia, campinaranas, tepuis, Amazônia.

ABSTRACT

The Guiana Shield is a region in the north of South America, between Orinoco and Amazon River. This area represents approximately 13% of South America, and is one of the oldest geological formations dating from the Precambrian. The Rubiaceae family has high diversity and high endemism in this area. Henriquezieae is a tribe in the Rubiaceae family distributed mainly in the Guiana Shield. It has a variable morphology and presents atypical characteristics within Rubiaceae, such as zygomorphic corollas, seeds flattened and without endosperm and ovary secondarily superior. The tribe belongs to the Clade Henriquezieae-Posoquerieae-Sipaneeae (subfamily Ixoroideae), which is predominantly restricted to the Guiana Shield. Despite a recent phylogenetic hypothesis of the tribe, where it is considered monophyletic, a new sampling is necessary to infer infratribal level relationships. The latest taxonomic revision for the tribe was in 1984, since then new collections and new species have emerged, requiring a taxonomic update of the tribe. Our objectives are to expand the number of species samples and molecular sampling using next generation sequencing to resolve the relationships within the tribe, to postulate hypotheses about the evolution of atypical morphology and to update the taxonomy after the last taxonomic revision by Rogers in 1984. Our results show that Henriquezieae and the three genera in the tribe are strongly supported as monophyletic. *Gleasonia* is the sister group of *Henriquezia* and *Platycarpum*. The results of ancestral morphology reconstruction shows that atypical characters are apomorphic characters in Henriquezieae. Morphological synapomorphies as corolla variegation internally with lines and/or spots, reduced endosperm and fruits slightly to strong flattened perpendicularly to the septum are proposed for the tribe. We also present a taxonomic treatment with 23 species, taxonomic keys, and updated distribution maps.

Keywords: Phylogeny, white-sand forest, tepuis, Amazon basin.

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INTRODUÇÃO GERAL

O Escudo das Guianas é uma região que se encontra no Nordeste da América do Sul, entre o rio Orinoco e o rio Amazonas. Este maciço representa aproximadamente 13% da área da América do Sul, é uma das formações geológicas mais antigas que data desde o Pré-Cambriano (1.65 ± 0.05 Ma, Gibbs & Barron 1993) e é constituído por uma variedade de tipos de rochas ígneas e metamórficas, especialmente granitos e gnaisses (Hammond 2005; Kelloff & Funk 2004).

A fisionomia do Escudo das Guianas é um mosaico heterogêneo variando desde montanhas de 500-2.500 m, algumas com formato de mesas chamadas de tepuis, até terras baixas nos arredores das montanhas com florestas ombrófilas e savanas conhecidas como *llanos* e *campinaranas* (Gibbs & Barron 1993; Kelloff & Funk 2004). Aproximadamente metade da área do escudo das Guianas se encontra no Brasil, o que equivale a 14% do território do país, abrangendo parte dos estados de Amapá, Roraima, Pará e Amazonas (Hammond 2005).

A flora nesta área se caracteriza pelo alto endemismo, uma vez que cerca de 40% das plantas distribuídas na área são endêmicas (Kelloff & Funk 2004). A família Rubiaceae é a quarta família com maior número de espécies no Escudo das Guianas, com um total de 742 espécies, das quais 237 espécies são endêmicas (Funk *et al.* 2007). Além disso, o Escudo das Guianas é um dos lugares nos trópicos com maior endemismo para a família (Govaerts 2009).

Henriquezieae Benth. & Hook.f é uma tribo da família Rubiaceae cuja distribuição é praticamente restrita ao Escudo das Guianas, ocorrendo em seu amplo gradiente altitudinal, em habitats altamente variáveis, incluindo topos de montanhas, sobre rochas, terras baixas e savanas (Rogers 1984). Segundo a última revisão da tribo (Rogers 1984), Henriquezieae compreende três gêneros e um total de 19 espécies, *Gleasonia* Standl. (4 spp.), *Henriquezia* Spruce ex Benth. (3 spp.) e *Platycarpum* Humb. & Bonpl. (12 spp.).

A morfologia de Henriquezieae é considerada atípica dentro de Rubiaceae, por apresentar flores principalmente zigomorfas, sementes planas e carentes de endosperma e ovário secundariamente súpero (Rogers 1984), enquanto que Rubiaceae é reconhecida tradicionalmente por apresentar corola actinomorfa, ovário ínfero e endosperma presente (Robbrecht 1988). Apesar das espécies de Henriquezieae compartilharem este conjunto de características, existe uma ampla variação morfológica para os representantes da tribo. Espécies de *Henriquezia* e *Platycarpum*, por exemplo, apresentam glândulas no pecíolo, que estão ausentes em *Gleasonia*. A corola é principalmente zigomorfa nos três gêneros, porém

algumas espécies de *Gleasonia* são actinomorfas. A posição da cicatriz do perianto nos frutos do tipo cápsula loculicida achatada varia, sendo localizada na base em *Platycarpum*, no meio em *Henriquezia* e no ápice em *Gleasonia* (Rogers 1984).

Essas características tão distintas em Henriquezieae influenciaram no histórico taxonômico da tribo. *Platycarpum* (Bonpland 1811) e *Henriquezia* (Bentham 1854), quando descritas, foram classificadas como Bignoniaceae, por apresentarem corola zigomorfa e frutos achatados. Hooker (1873) observou a similaridade entre *Platycarpum* e *Henriquezia* e propôs a tribo Henriquezieae, possivelmente relacionada às Rubiaceae pela presença de flores pentâmeras, ovário ínfero, estípula interpeciolar na maioria das espécies e folhas opostas ou verticiladas. Schumann (1889, 1891) concordou com a proposta de Hooker (1873) e continuou considerando os dois gêneros como uma tribo de Rubiaceae.

Por outro lado, *Gleasonia* quando descrita foi incluída em Rondeletieae (Rubiaceae), por apresentar corola imbricada e lobos do cálice expandido e colorido. No entanto, Bremekamp (1957), propôs colocar *Gleasonia* na sua própria subfamília dentro de Rubiaceae, Gleasonioideae. Além disso, Bremekamp (1957) propôs elevar a tribo Henriquezieae (composta por *Henriquezia* e *Platycarpum*) à categoria de família, chamando-a assim de Henriqueziaceae, proposta apoiada por Verdecourt (1958). Cronquist (1968) não aceitou o status de família Henriqueziaceae, retornando-a novamente ao status de tribo (Henriquezieae) dentro de Rubiaceae próximo de Cinchoneae. Rogers (1984) sugere que *Gleasonia*, *Henriquezia* e *Platycarpum* compartilham características semelhantes e coloca os três gêneros na tribo Henriquezieae. A tribo Henriquezieae foi classificada dentro da subfamília Cichonoideae por Robbrecht (1988).

Rova et al. (2002), incluíram o primeiro membro de Henriquezieae em estudos moleculares usando sequências de *trnL-F* em estudo do complexo Condamineae-Rondeletieae-Sipaneeae, e chegaram à conclusão que *Gleasonia* forma um clado com *Posoqueria* e *Molopanthera* dentro da subfamília Ixoroideae. Delprete & Cortés (2004), durante o estudo filogenético da tribo Sipaneeae usando marcadores moleculares de cloroplasto e nuclear (*trnL-F* e ITS), proporam que *Gleasonia* e *Platycarpum* (um acesso de cada gênero) junto com *Posoqueria* e *Molopanthera* é o grupo irmão de Sipaneeae. Bremer & Eriksson (2009), em uma ampla análise filogenética molecular da família Rubiaceae usando vários marcadores moleculares, inferiram *Gleasonia* como grupo irmão de Posoquerieae; inferindo a tribo Henriquezieae como grupo irmão de Posoquerieae. Cortés et al. (2009) encontraram a mesma relação entre Posoquerieae e Henriquezieae utilizando marcadores de cloroplasto (*trnL-F* e *rps16*) em análise da posição de Retiniphyllaeae na subfamília

Ixoroideae. Também Kainulainen et al. (2013), usando seis marcadores de cloroplasto em estudo das relações entre as tribos da subfamília Ixoroideae, encontraram a relação entre Henriquezieae (*Henriquezia nitida* apenas amostrado) e Posoquerieae.

Cortés & Motley (2015) realizaram a mais recente e ampla amostragem de Henriquezieae (7 espécies) durante o estudo no Clado Henriquezieae-Posoquerieae-Sipaneeae. O estudo utilizou marcadores de cloroplasto (*trnL-F*, *rps16*) e nuclear (ITS) e também a combinação de marcadores moleculares e morfológicos, a resolução dentro de Henriquezieae quando usaram apenas marcadores moleculares obtiveram que a tribo é monofilética com dois dos gêneros, *Henriquezia* e *Platycarpum*, enquanto que *Gleasonia* a posição foi incerta. Já com a combinação dos dados moleculares e morfológicos a tribo é monofilética com os seus três gêneros (fig. 1).

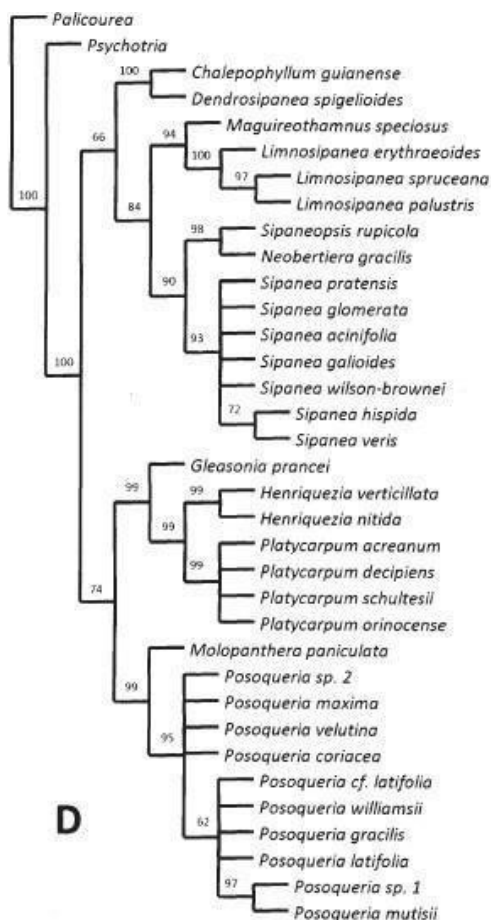


Figura 1: Filogenia do clado Henriquezieae-Posoquerieae-Sipaneeae baseado em dados morfológicos e moleculares (ITS, *trnL-F*, *rps16*), extraído de Cortés & Motley (2015)

Apesar destes estudos recentes, as relações dentro da tribo ainda não estão bem esclarecidas, sendo necessário um estudo filogenético a nível infratribal para entender as relações dentro de cada linhagem de *Henriquezieae*. Além disso, o entendimento das relações genealógicas dentro da tribo *Henriquezieae* permitirá reconstruir os padrões de evolução dos caracteres morfológicos, que é chave para a compreensão dos processos evolutivos da variada morfologia que os gêneros de *Henriquezieae* apresentam.

Neste estudo propomos uma hipótese filogenética para as espécies que compõem os três gêneros da tribo *Henriquezieae* baseados em caracteres moleculares e postulamos hipóteses sobre a evolução dos caracteres morfológicos “atípicos” presentes na tribo em comparação a *Rubiaceae* (Capítulo I). Além disso, atualizamos a taxonomia de *Henriquezieae* depois da última revisão taxonômica feita por Rogers (1984) (Capítulo II).

Foi feita uma amostragem abrangente para aumentar o número de espécies amostradas nesta nova filogenia, nove expedições de campo no Peru, Brasil e fronteira do Brasil e Venezuela foram feitas. Apesar do esforço para coletar no máximo de lugares de ocorrência de *Henriquezieae*, já que muitas das espécies são endêmicas, algumas espécies ocorrem em áreas de difícil acesso como os “tepui” e também de difícil acesso à autorização de coleta, nesse caso utilizamos material de herbário para tentar uma amostragem representativa desta tribo.

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CAPÍTULO I

Phylogeny and morphological character evolution in tribe Henriquezieae Benth. & Hook. F (Ixoroideae, Rubiaceae) in the Guiana Shield

Abstract

Henriquezieae is a tribe that belongs to the coffee family that occurs mainly in the Guiana Shield. Species of Henriquezieae have morphological traits that are atypical for Rubiaceae, such as mainly zygomorphic flowers, secondary superior ovary, and seeds without endosperm. Molecular phylogenetic studies placed this tribe in Ixoroideae subfamily and it belongs to the Henriquezieae-Posoquerieae-Sipaneeae clade. Previous studies using Sanger sequencing, shows that there is a low resolution using chloroplast (*trnL-F* and *rps16*) and nuclear marker (ITS) in Henriquezieae, and the tribe is only resolved as a monophyletic group with all three genera when combining molecular and morphologic data. The objectives of this work are to evaluate the phylogenetic relationships within the tribe Henriquezieae; to propose hypothesis about the evolution of atypical characters in Henriquezieae; and to identify potential synapomorphies for Henriquezieae as well as for *Gleasonia*, *Henriquezia* and *Platycarpum*. We expanded the sampling in the tribe and used next generation sequencing approach (Multiplexed exon capture) to infer a new infratribal level phylogeny for Henriquezieae and used morphology and molecular data in order to infer the morphological ancestral reconstruction in the tribe. Our results show that Henriquezieae and its three genera are monophyletic. We found that *Gleasonia* is sister to *Henriquezia* and *Platycarpum*. The morphological ancestral reconstruction shows that morphological characters considered atypical in Rubiaceae are apomorphic characters in the tribe. We propose synapomorphies for the tribe Henriquezieae such as corolla variegation internally with lines and/or spots, reduced endosperm and fruits slight to strong flattened perpendicularly to the septum. Also we propose synapomorphies each genera. *Gleasonia* has intrapetiolar stipules, trichomes inside ovary and pollen arrangement in tetrad. *Henriquezia* has partially intrapetiolar stipules. *Platycarpum* has adaxial leaves with strigose trichomes and perianth scar at the base of the fruit. Also we hypothesize that diversity in *Platycarpum* could be related with changes in flower and fruit morphology and dispersal mechanism.

Keywords: white-sand forest, tepuis, Amazon basin.

Introduction

The Guiana Shield has fascinated botanists because of its high endemism, since about 40% of plants in the area are endemic (Kelloff & Funk 2004). This area is in the northeast of South America, between the Orinoco and the Amazon River, and its extension represents approximately 13% of the area of South America. The Guiana shield is one of the oldest geological formations dating from the Precambrian (1.65 ± 0.05 Ga, Gibbs & Barron 1993), it consists of a variety of types of igneous and metamorphic rocks, especially granites and gneisses (Hammond 2005; Kelloff & Funk 2004). The physiognomy of the Guiana Shield is a heterogeneous mosaic with mountains of 500-2,500 m, called tepuis, and lowlands around the mountains with rain forests and savannas (Gibbs & Barron 1993; Kelloff & Funk 2004).

Rubiaceae Juss. is the fourth richest family in the Guiana Shield, represented by 742 species, of which 237 species are endemic (Funk et al. 2007). Also the Guiana Shield is one of tropical places with the highest endemic species in Rubiaceae (Govaerts 2009). *Henriquezieae* Benth. & Hook. f. is a tribe in the Rubiaceae family and its distribution is largely confined to the Guayana Shield, occurring in its wide altitudinal gradient in highly variable habitats, including mountain tops, on rocks, lowlands and savannas (Rogers 1984). According to the latest revision of the tribe (Rogers 1984), it comprises three genera and a total of 19 species: *Gleasonia* Standl. with four species, *Henriquezia* Spruce ex Benth. with three species, and *Platycarpum* Humb. & Bonpl. with 12 species.

The morphology in *Henriquezieae* is considered atypical within Rubiaceae, by having mainly zygomorphic corollas, seeds flat and without endosperm, and ovary secondarily superior (Rogers 1984), while Rubiaceae is traditionally recognized for its actinomorphic corolla, inferior ovary, and seeds with endosperm (Robbrecht 1988). Despite the fact that species of *Henriquezieae* share this set of characteristics, there is a wide variation in morphology for the representatives of the tribe, eg. species of *Henriquezia* and *Platycarpum* present glands in the petiole, which are absent in *Gleasonia*; corolla is mainly zygomorphic in the three genera, but some species of *Gleasonia* are actinomorphic; the position of the perianth scars in the fruit varies, it can be located at the base in *Platycarpum*, in the middle in *Henriquezia*, and at the top in *Gleasonia* (Rogers 1984).

These morphological characters so distinct in Henriquezieae influenced the taxonomic history of the tribe. *Platycarpum* (Bonpland 1811) and *Henriquezia* (Bentham 1854) were classified as Bignoniaceae when described, for presenting zygomorphic corolla and flattened fruit. Hooker (1873) noted the similarity between *Platycarpum* and *Henriquezia* and proposed the tribe Henriquezieae, related to Rubiaceae by the presence of pentamerous flowers, inferior ovary, interpetiolar stipule in most species, and opposite or verticillate leaves. Schumann (1889, 1891) agreed with the proposal made by Hooker (1873) and continued considering the two genera as a tribe of Rubiaceae.

On the other hand, *Gleasonia* was included in Rondeletieae (Rubiaceae) when described for presenting imbricate corolla and expanded and colored calyx lobes. However, Bremekamp (1957), proposed placing *Gleasonia* in its own subfamily within Rubiaceae, Gleasonioideae. Besides, Bremekamp (1957) proposed elevating the tribe Henriquezieae (composed of *Henriquezia* and *Platycarpum*) to the family category, naming it Henriqueziaceae. This proposal was supported by Verdecourt (1958), but it was rejected by Cronquist (1968), who returned it to the tribe status (Henriquezieae) within Rubiaceae near Cinchoneae. Rogers (1984) suggested that *Gleasonia*, *Henriquezia* and *Platycarpum* share similar characteristics and places the three genera in the tribe Henriquezieae. The tribe Henriquezieae was classified within the subfamily Cichonoideae by Robbrecht (1988).

Rova et al. (2002) included the first member of Henriquezieae in molecular studies using sequences of *trnL-F* during the study of the Condamineeae-Rondeletiaea-Sipaneeae complex, and concluded that *Gleasonia* form a clade with *Posoqueria* and *Molopanthera*, within the subfamily Ixoroideae. Delprete & Cortés (2004) during the phylogenetic study of the tribe Sipaneeae using chloroplast and nuclear (*trnL-F* and ITS) molecular markers, suggested that *Gleasonia* and *Platycarpum* (one sample of each genera) along with *Posoqueria* and *Molopanthera* is the sister group of Sipaneeae.

Bremer & Eriksson (2009), in an extensive molecular phylogenetic analysis of the Rubiaceae using various molecular markers, inferred that *Gleasonia* is the sister group of Posoquerieae; suggesting the tribe Henriquezieae as sister group of Posoquerieae. Cortés et al. (2009) found the same relationship between Posoquerieae and Henriquezieae using chloroplast markers (*trnL-F* and *rps16*) during the analysis of the subfamily Retiniphyllaeae

in the subfamily Ixoroideae. Also Kainulainen et al. (2013), using six chloroplast markers for the study of the relationships between the tribes of the subfamily Ixoroideae, found the same relationship between Henriquezieae (with only *Henriquezia nitida* sampled) and Posoquerieae.

Cortés & Motley (2015), based on a molecular study of the Henriquezieae-Posoquerieae-Sipaneeae clade tested the monophyly for each tribe and their genera. In their analysis, when they used plastid markers (*rps16* and *trnL-F*), found that *Henriquezia* is a monophyletic group, but *Platycarpum* and *Gleasonia* are not supported as monophyletic. While with nuclear marker (ITS), *Platycarpum* and *Henriquezia* are monophyletic, but *Gleasonia* was not sampled. The tribe Henriquezieae is inferred as monophyletic only when molecular data and morphology were analyzed together. Although there was a great effort by Cortés & Montley (2015) to elucidate the relationships in the clade Henriquezieae-Posoquerieae-Sipaneeae, the relationships within Henriquezieae still needs to be improved, mainly because of low molecular data and species number used previously. Therefore, a phylogenetic infratribal study is necessary in Henriquezieae to understand the relationships within each genera and resolve the phylogenetic position of *Gleasonia*. A better resolution in Henriquezieae is crucial to understand in which way the atypical morphology for Rubiaceae present in this tribe has evolved.

Currently access to next generation sequencing technology has revolutionized modern studies in genomic and molecular biology due to the massive amount of sequences that is possible to obtain (Shendure & Hanlee 2008). This new technique supplies the difficulty of limited molecular data by the high cost and effort of previous sequencing methods, such as Sanger sequencing (Sanger et al. 1977). Also new approaches like focusing in target loci to increment specific variation has emerged (Hodges et al. 2009, Ekblom & Galindo 2011). The multiplexed exon-capture is a method designed initially for animals (Bi et al. 2012), but successfully used in plant (Sass et al. 2016), where a specific pre-existing genome reference is not necessary, using genomes and transcriptomes information of related group to get target loci regions to be used in groups of interest. This method is an alternative to explore the relationships in Henriquezieae to improve the phylogeny resolution that could not be solved up until now with Sanger sequencing.

Our aims in this study are: 1) to evaluate the phylogenetic relationships within the tribe Henriquezieae expanding the sampling in the tribe and using next generation sequencing; 2) to propose hypothesis about the evolution of atypical characters in Henriquezieae; and 3) to identify potential synapomorphies for Henriquezieae as well as for *Gleasonia*, *Henriquezia* and *Platycarpum*.

Material and methods

Taxon sampling

Our data set comprised ~70% of Henriquezieae members, 16 out of 23 species for the tribe (as we recognize in this thesis): *Gleasonia* (2 spp.), *Henriquezia* (2 spp.) and *Platycarpum* (12 spp.). Material for seven species of the tribe was unavailable, which are difficult to collect because of distribution and they are poorly represented in herbarium collections (*Gleasonia duidana*, *Gleasonia cururuensis*, *Gleasonia macrocalyx*, *Henriquezia jenmanii*, *Platycarpum rugosum*, *Platycarpum eglandulosum*, *Platycarpum pierisii*). We also sampled *Pagamea guianensis*, *Psychotria* sp. and *Sipanea galioides* to be used as outgroups. Since the relationship of Henriquezieae within intertribal level is resolved (Cortés & Motley 2015, Kainulainen et al. 2013), we do not focus in a broad sampling in the outgroup. Information of taxa vouchers are listed in table 1.

Table 1: List of taxa used in molecular analysis.

Taxa	Voucher
<i>Gleasonia prancei</i> B.M. Boom	Plinio 5697 (RB)
<i>Gleasonia uaupensis</i> Ducke	Dávila 6434 (UEC, MO, RB)
<i>Henriquezia nitida</i> Spruce ex Benth.	Dávila 6445 (INPA)
<i>Henriquezia verticillata</i> Spruce ex Benth.	Dávila 6415 (INPA, UEC)
<i>Pagamea guianensis</i> Aubl.	Hanh 3227 (INPA)

<i>Platycarpum acreanum</i> G.K.Rogers	Dávila 6321 (UEC)
<i>Platycarpum araracuarensense</i> Dávila*	Eusse 697 (COL)
<i>Platycarpum decipiens</i> Woodson & Steyerml.*	Velazco 882 (MO, PORT)
<i>Platycarpum duckei</i> Steyerml.	Dávila 6353 (UEC)
<i>Platycarpum egleri</i> G.K.Rogers	Dávila 5595 (INPA, MO)
<i>Platycarpum froesii</i> Bremek.	Dávila 6530 (INPA, MO)
<i>Platycarpum loretensis</i> Dávila & L. Kinoshita	Dávila 6318 (AMAZ)
<i>Platycarpum negrense</i> Ducke	Dávila 6423 (INPA, UEC, MO)
<i>Platycarpum orinocense</i> Bonpl.*	Marin 402 (MO)
<i>Platycarpum rhododactylum</i> Woodson & Steyerml.*	Boom 9432 (MO, VEN)
<i>Platycarpum schultesii</i> Steyerml.*	Cárdenas 14774 (COAH, COL)
<i>Platycarpum vriesendorpiae</i> Dávila	Ríos 4302 (AMAZ, MO)
<i>Psychotria</i> sp.	Dávila 6350 (INPA)
<i>Sipanea galoides</i> Wernham	Dávila 6372 (INPA)

*Sampled from herbarium material

Gene selection and probe design

Probe were designed using *Coffea canephora* genome from Coffee Genome hub (<http://coffee-genome.org>), and using transcriptomes from *Psychotria douarrei*, *Morinda citrifolia*, and *Psychotria marginata* downloaded from the 1kp genome database and a bioinformatic pipeline according to Sass et al. (2016). In this process raw reads of transcriptome were cleaned by removing adapters, contaminants, low complexity sequences and PCR duplicates. Then, each of the three transcriptomes were aligned separately to the *C. canephora* CDS exons using NovoAlign v3.01 (<http://novocraft.com>) with -t 502 to allow

highly divergent sequences to map. After mapping, the single nucleotide polymorphisms (SNP) were called using SAMtools v.0.1.18 (Li et al. 2009) and VarScan 2.3.6 (Koboldt et al. 2012) and consensus sequences for each transcriptome were made based on SNP calls. Then, all exons were filtered by being longer than 150 bp and having between 30–70% GC content and being unique by reciprocal BLAST. After filtering, 437 exons from 327 genes were identified to be used as probes, and these probes were prepared to print out in a microarray chip using 1x tiling density by Agilent (Sass et al. 2016). All analysis were conducted in the supercomputer of the Berkeley Research Computing (BRC) at the University of California, Berkeley.

DNA Extraction and fragmentation

We used leaves dried in silica or herbarium material to extract DNA. Dry tissue in silica gel was extracted with CTAB 6% protocol described in Vicentini (2016). Herbarium material was extracted with SDS protocol (Konieczny & Ausubel 1993) and with CTAB 6% protocol in replicate and then concentrated in a speedvac. Extraction product for both methods was observed in gel agarose 1.6% and quantified DNA concentration for each sample with Qubit fluorometer. We obtained 1 and 1.5 ng of DNA per sample (except for herbarium material, which we used the concentration available). DNA obtained from dry silica gel were fragmented with Bioruptor (Diagenode, Liège, Belgium), with cycles of 5 minutes at 4 °C, using intervals of 30 seconds *on* and 30 seconds *off*, resulting in fragments of 300 base pairs on average (100 to 500 bps). In case of herbarium material, sonication was not necessary. DNA fragment sizes were visualized in agarose gel 1.6%.

Library preparation

Library preparation started with a cleaning-up sonicated samples using Solid Reversible Immobilization (SPRI bead clean-up) at 1.8 %. In case of herbarium material, we used SPRI 3%. Then, Meyer & Kircher (2010) protocol was used for steps of Blunt-End repair, adaptor ligation, adaptor fill-in and indexing PCR. DNA enrichment was performed in two separated PCRs with 6-10 cycles. The PCR products were pooled and measured on

Nanodrop, final concentrations varying between 20 and 50 ng/μl in a total of 40 μl per sample. To the DNA hybridization process, a library pool obtained was added between the microarray chip and a gasket and it was left in the oven for 65 hours at 95°C. After, the microarray chip was washed to remove all non-captured DNA, and the captured DNA was eluted with 490 μl of deionized water and recovered with a syringe, and the volume was decreased down to 230 μl in a vacuum centrifuge. The captured library was enriched by carrying out six independent PCRs, using 10, 11, 12 and 14 cycles. After, final concentrations were measured on Qubit and the length distribution of DNA sequences was verified on Bioanalyzer. The success of exon-capture experiment was checked through a qPCR, using primers for three target and three non-target genes to be amplified in a reaction with the captured library, and also using the control DNA (library before hybridization). Finally, all libraries were sequenced in an Illumina HiSeq 4000 platform, at the Genomics Sequencing Laboratory in the University of California, in Berkeley.

Reads processing and alignment

Bioinformatic procedures were conducted at the supercomputer at Research Computing (BRC) of the University of California, Berkeley. In this step raw sequences were cleaned for the removal of low quality sequences, adaptors with indexing barcodes, contaminants and PCR duplicates. Individual references for the baits previously generated were created through an interactive SNP calling process, using Mapsembler for assembled the references, a final SNP call was made and genotypes were called from the SNP call files. All these protocols (commands and scripts) are detailed in Sass et al. (2016). Then each sequenced sample was filtered by gene region and created one file per gene. An interactive script was used to run MAFFT (Katoh 2013) software for all genes individually, using the G-INS-1 method. Finally, a matrix with 437 nuclear regions and it was concatenated for each sample and aligned with MAFFT.

Phylogenetic inference

Two approaches for phylogenetic inference were used, Maximum Likelihood (ML) and Maximum Parsimony (MP). Maximum Likelihood was estimated in RaxML v 8 (Stamatakis 2014), using the best nucleotide substitution model GTR+I+G conducted with jModelTest v. 2.1.6 (Darriba et al. 2012) with the Akaike Information Criterion (Akaike 1974). Support ML was calculated with 1000 bootstrap replicates with rapid bootstrap algorithm recommended by large data (Stamatakis et al. 2008). The RaxML analysis was performed on the CIPRES Science Gateway (Miller et al. 2010). The Maximum Parsimony analysis was performed using PAUP* v4.0 (Swofford et al. 2002) with a plugin implemented in Geneious R9 (Kearse et al. 2012). It was used heuristic search with 100 random addition sequence replicates and the TBR branch swapping with one tree held per replicate parameter. The support for MP was evaluated with 1000 bootstrap replicates (each with 10 random addition sequences replicate).

Topologies were seen and adjusted using FigTree v 1.4.2 (Rambaut 2009). Values for Bootstrap support are defined as moderate support when $\geq 70\%$ and strongly supported when $\geq 90\%$.

Morphological character state reconstruction

Morphological characters based on herbarium specimens or specialized literature were selected. We created a combined tree based on topology of Henriquezieae Maximum Parsimony tree and topology of Maximum Parsimony tree of Posoquerieae and Sipaneeae from Cortés & Motley (2015) analysis. We traced selected characters (table 1) on the combined tree using the parameter *traced character history* on Mesquite 3.02 (Maddison & Maddison 2014).

Table 2: List of morphological characters for ancestral reconstruction in Henriquezieae.

Characters state
1. Stipule position: interpetiolar = 0; partially intrapetiolar = 1; intrapetiolar = 2
2. Stipules colleters: present = 0; absent = 1
3. Petiolar glands: absent = 0; present= 1

4. Leaves adaxial indumentum: soft = 0; strigose = 1
 5. Flower symmetry: zygomorphic = 0; actinomorphic = 1
 6. Internal pubescence corolla: uniformly pubescent = 0; pubescent at mouth = 1; bearded = 2
 7. Corolla variegation internally: with spots or lines = 0; without spots or lines = 1
 8. Pollen arrangement: monad = 0; tetrad = 1
 9. Trichomes inside the ovary: absent = 0; present = 1
 10. Fruit perianth scar: at top of fruit = 0; near top of fruit = 1; at middle of fruit = 2; at base of fruit = 3
 11. Seed endosperm: with endosperm = 0; reduced endosperm = 1
 12. Fruit symmetry: not flattened perpendicularly to the septum = 0; slightly to strong flattened perpendicularly to the septum = 1
-

Table 3: Morphological characters states coding used for ancestral reconstruction. Order of characters state follows organization in table 2.

Species	Character states		
	1	5	12
<i>Chalepophyllum guianense</i> Hook.f.	0000	1110	00000
<i>Dendrosipanea spigelioides</i> Ducke	0000	1110	00000
<i>Gleasonia prancei</i> B.M.Boom	2000	1001	1011
<i>Gleasonia uaupensis</i> Ducke	2000	1001	1011
<i>Henriquezia nitida</i> Spruce ex Benth.	1110	0200	0211
<i>Henriquezia verticillata</i> Spruce ex Benth.	1110	0200	0211
<i>Limnosipanea erythraeoides</i> (Cham.) K.Schum.	0000	1110	00000
<i>Limnosipanea palustris</i> (Seem.) Hook.f.	0000	1110	00000
<i>Limnosipanea spruceana</i> Hook.f.	0000	1110	00000
<i>Maguireothamnus speciosus</i> (N.E.Br.) Steyerl.	0000	1110	00000
<i>Molopanthera paniculata</i> Turcz.	0000	0310	00000
<i>Neobertiera gracilis</i> Wernham	0000	1110	00000
<i>Platycarpum acreanum</i> G.K.Rogers	0111	0200	0311

<i>Platycarpum araracuarens</i> Dávila	011102000311
<i>Platycarpum decipiens</i> Woodson & Steyer.	011102000311
<i>Platycarpum duckei</i> Steyer.	011102000311
<i>Platycarpum egleri</i> G.K.Rogers	011102000311
<i>Platycarpum froesii</i> Bremek.	011102000311
<i>Platycarpum loretensis</i> Dávila & L. Kinoshita	011102000311
<i>Platycarpum negrense</i> Ducke	011102000311
<i>Platycarpum orinocense</i> Bonpl.	011102000311
<i>Platycarpum rhododactylum</i> Woodson & Steyer.	011102000311
<i>Platycarpum schultesii</i> Steyer.	011102000311
<i>Platycarpum vriesendorpiae</i> Dávila	011102000311
<i>Posoqueria cf. latifolia</i> (Rudge) Roem. & Schult.	000001100000
<i>Posoqueria coriacea</i> M.Martens & Galeotti	000001100000
<i>Posoqueria gracilis</i> (Rudge) Roem. & Schult.	000001100000
<i>Posoqueria latifolia</i> (Rudge) Roem. & Schult.	000001100000
<i>Posoqueria maxima</i> Standl.	000001100000
<i>Posoqueria mutisii</i> Standl.	000001100000
<i>Posoqueria sp. 1</i>	000001100000
<i>Posoqueria sp. 2</i>	000001100000
<i>Posoqueria velutina</i> Standl.	000001100000
<i>Posoqueria williamsii</i> Steyer.	000001100000
<i>Sipanea acinifolia</i> Spruce ex Sprague	000011100000
<i>Sipanea galioides</i> Wernham	000011100000
<i>Sipanea glomerata</i> Kunth	000011100000
<i>Sipanea hispida</i> Benth. ex Wernham	000011100000
<i>Sipanea pratensis</i> Aubl.	000011100000
<i>Sipanea veris</i> S.Moore	000011100000
<i>Sipanea wilson-brownei</i> R.S.Cowan	000011100000
<i>Sipaneopsis rupicula</i> (K.Schum.) Steyer.	000011100000

Results

Phylogenetic analysis

We sampled ca. 70% of the members of Henriquezieae in this new phylogeny, and obtained a concatenated matrix of 437 regions with 313,305 pb, of which 271,833 are conserved characters, 20,001 are parsimony informative characters, and 21,471 are parsimony uninformative characters.

Phylogenetic analysis for both Maximum Likelihood and Maximum Parsimony approaches show equal topologies (fig. 1). The Henriquezieae tribe is a monophyletic group with strong support (BS=100) for both ML and MP approaches, as well as all three genera *Gleasonia*, *Henriquezia* and *Platycarpum* (BS=100 for both ML and MP). The internal relationship in Henriquezieae shows two major clades. One clade with *Gleasonia*, and the second clade with *Henriquezia* + *Platycarpum*, both clades are strongly supported (BS=100 for both ML and MP). Also in clade *Henriquezia* + *Platycarpum* we found that *Platycarpum* presents two moderately supported clades (fig. 1). *Platycarpum* clade I with *P. dukei* + *P. negrense* (BS=56 with ML and BS=65 with MP). And *Platycarpum* clade II with two subclades strongly supported, one formed by *P. froesii* + *P. egleri* (BS=100 ML and BS=97 MP), and another subclade formed by *P. acreanum* + *P. lorentensis* (BS=100 for both ML and MP).

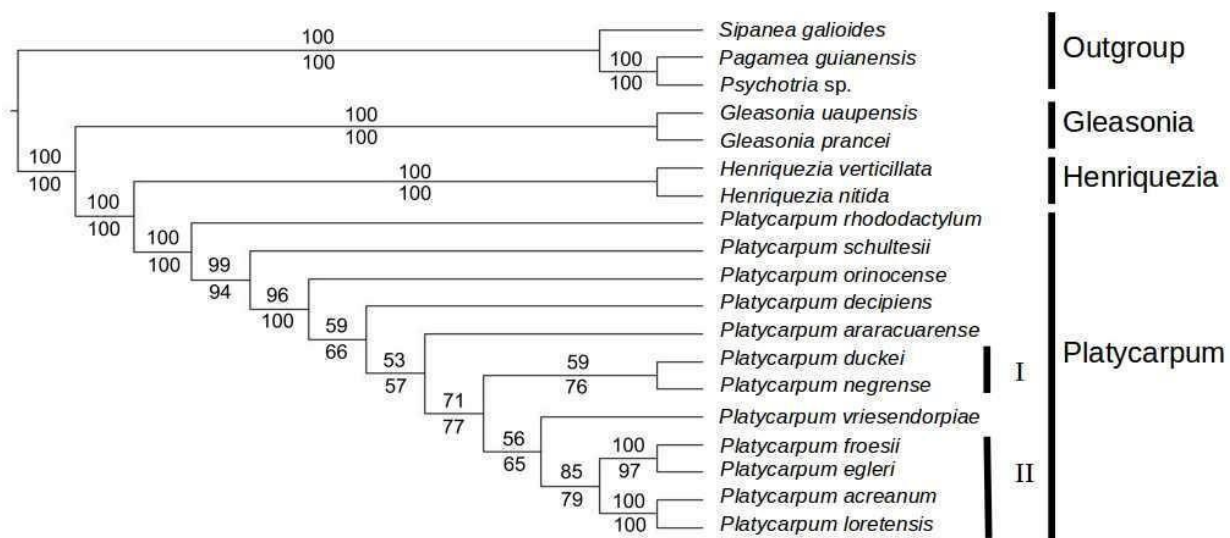


Figure 1. Phylogenetic tree of Henriquezieae based in ML of concatenated matrix with 437 regions. Values on the branches represent bootstrap percentage: above ML and below branches MP.

Ancestral morphological character reconstruction

Combined tree from Henriquezieae Maximum Parsimony tree and topology of Maximum Parsimony tree of Posoquerieae and Sipaneeae from Cortés & Motley (2015) was used to reconstruct 12 selected morphological characters (table 1) shown in figure 2-4. The ancestral morphological reconstruction of vegetative characters shows that intrapetiolar stipules state in *Gleasonia* and partially intrapetiolar stipules state in *Henriquezia* evolved once from interpetiolar stipules states (fig. 2A). Stipules with colleters is the ancestral character state in Henriquezieae, stipules without colleters state evolved only in *Henriquezia* and *Platycarpum* (fig. 2B). The absence of petiolar glands state is a plesiomorphic character in the tribe and presence of petiolar glands state evolved once in Henriquezieae in both genus *Henriquezia* and *Platycarpum* (fig. 2C, 5B). The reconstruction for adaxial surface of leaves shows that the ancestral character state in Henriquezieae is soft adaxial surface leaves, meanwhile strigose adaxial leaves surface state is an apomorphic character state only present in *Platycarpum* (fig. 2D, 5C).

The reconstruction of reproductive characters demonstrates that in Henriquezieae the actinomorphic corolla state evolved only in *Gleasonia*, whereas zygomorphic corolla state maintained in *Henriquezia* and *Platycarpum* such as in the sister tribe Posoquerieae (fig. 3A; 5H-I). The internal corolla uniformly pubescence state only evolved in *Gleasonia*, while bearded corolla state is an apomorphic character present in the clade *Henriquezia* and *Platycarpum* (fig. 3B; 5G-I). Corolla variegation with lines and/or spots evolved in the tribe Henriquezieae (fig. 3C, 5G-I) from non variegation corolla condition. Pollen arrangement in tetrad (fig. 3D) and trichomes inside ovary (fig. 4A) is a condition that only evolved independently in *Gleasonia*. Perianth scar position in fruit of Henriquezieae evolved from perianth at the apex of fruits state to perianth scar near the top of the fruit in *Gleasonia* (fig. 4B, 5J), at the middle of the fruit in *Henriquezia* (fig. 4B, 5K), and at the base of the fruit in *Platycarpum* (fig. 4B, 5L). Seed with reduced endosperm state evolved from seed with endosperm in all Henriquezieae members (fig. 4C). Fruits with slightly to strong flattened perpendicularly to the septum state evolved in all Henriquezieae members from not perpendicularly flattened to the septum on fruits (fig. 4D, 5J-L).

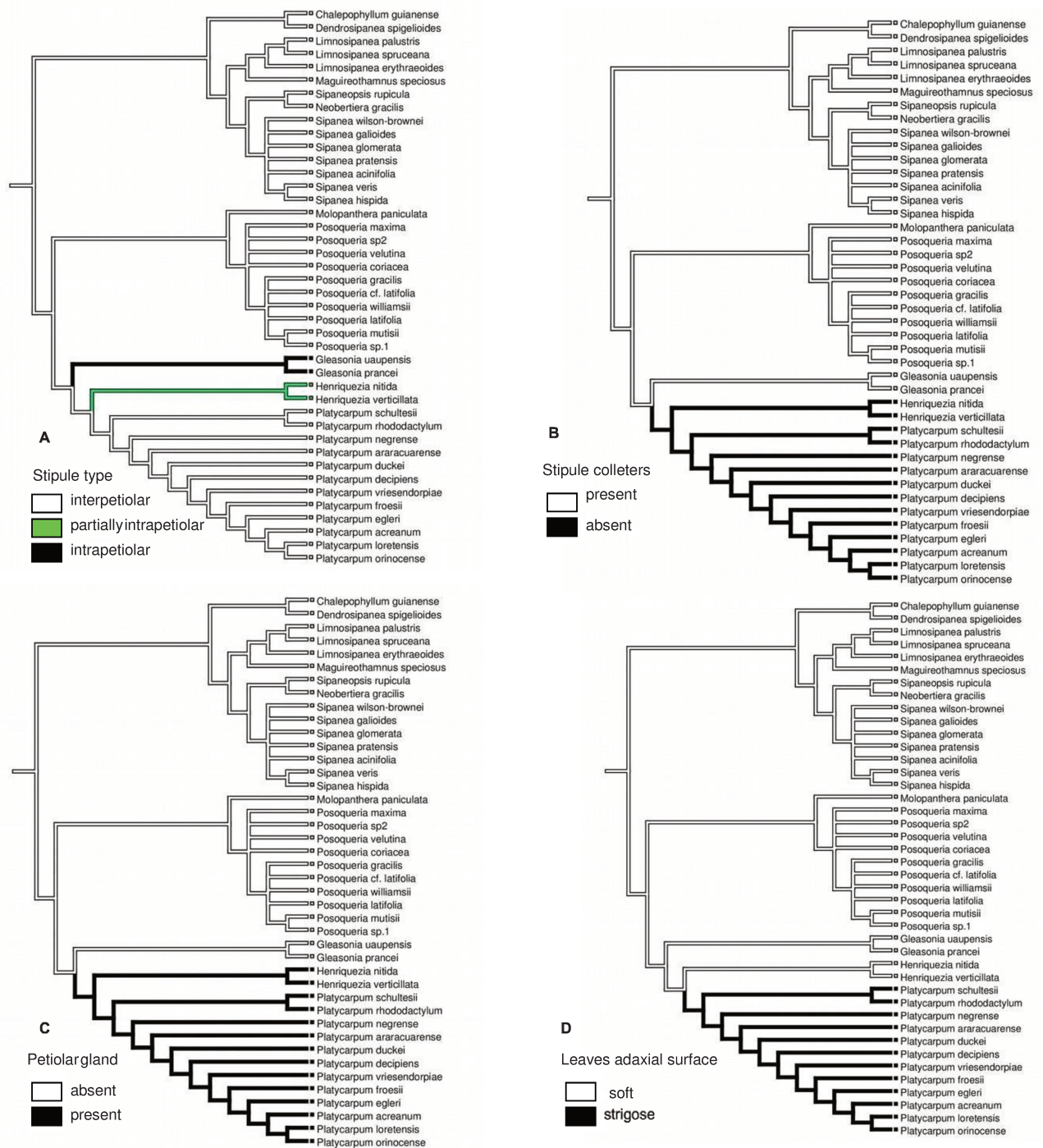


Figure 2: Character state reconstruction of morphological features in Henriquezieae and related tribes. Combined tree from Henriquezieae Maximum Parsimony tree with Maximum Parsimony tree from Cortés & Motley (2015). Stipule type (A); stipule colleters (B); petiolar gland (C); leaves adaxial surface (D).

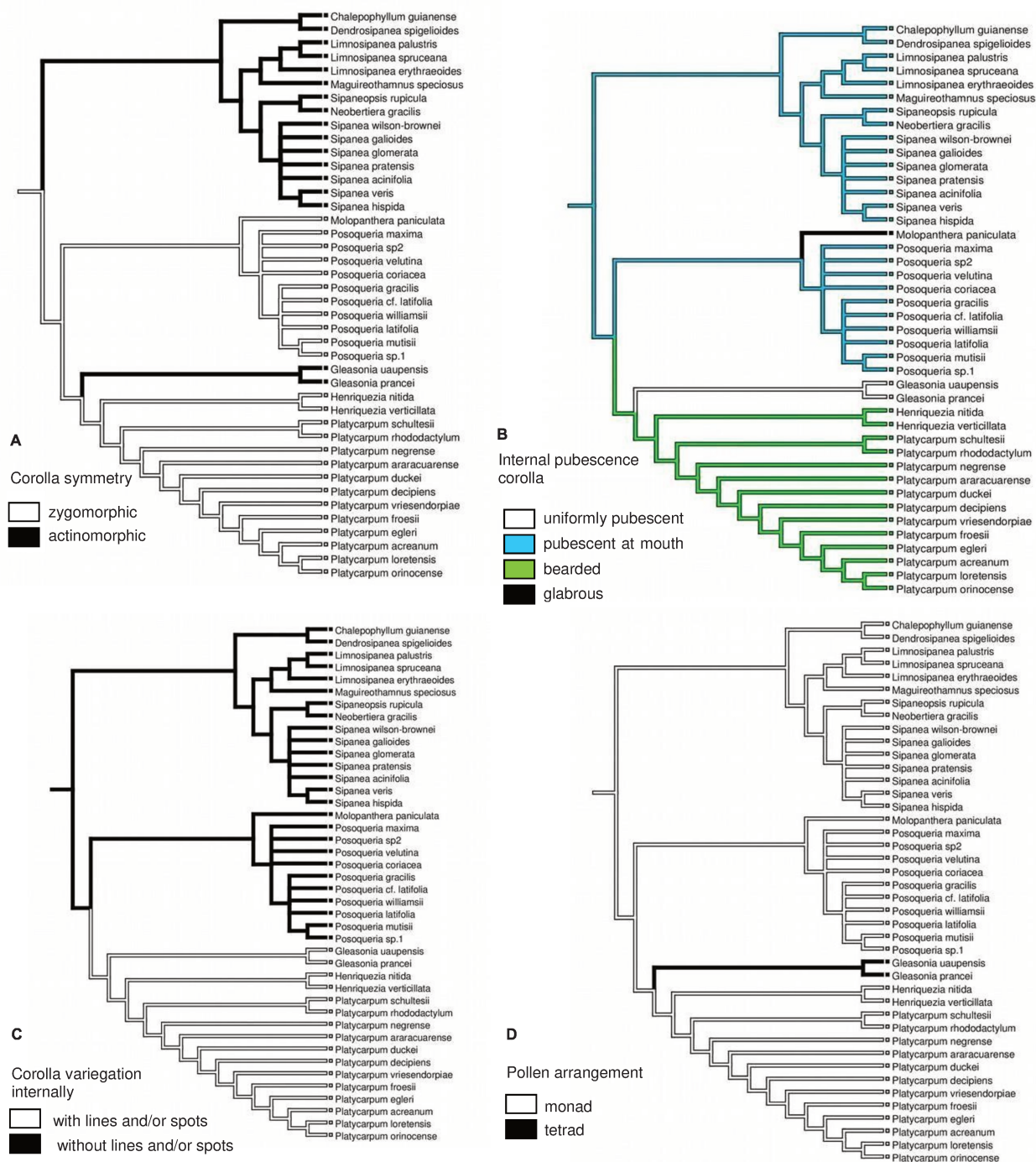


Figure 3: Character state reconstruction of morphological features in Henriquezieae and related tribes. Combined tree from Henriquezieae Maximum Parsimony tree with Maximum Parsimony tree from Cortés & Motley (2015). Corolla symmetry (A); internal pubescence corolla (B); corolla variegation internally (C); pollen arrangement (D).

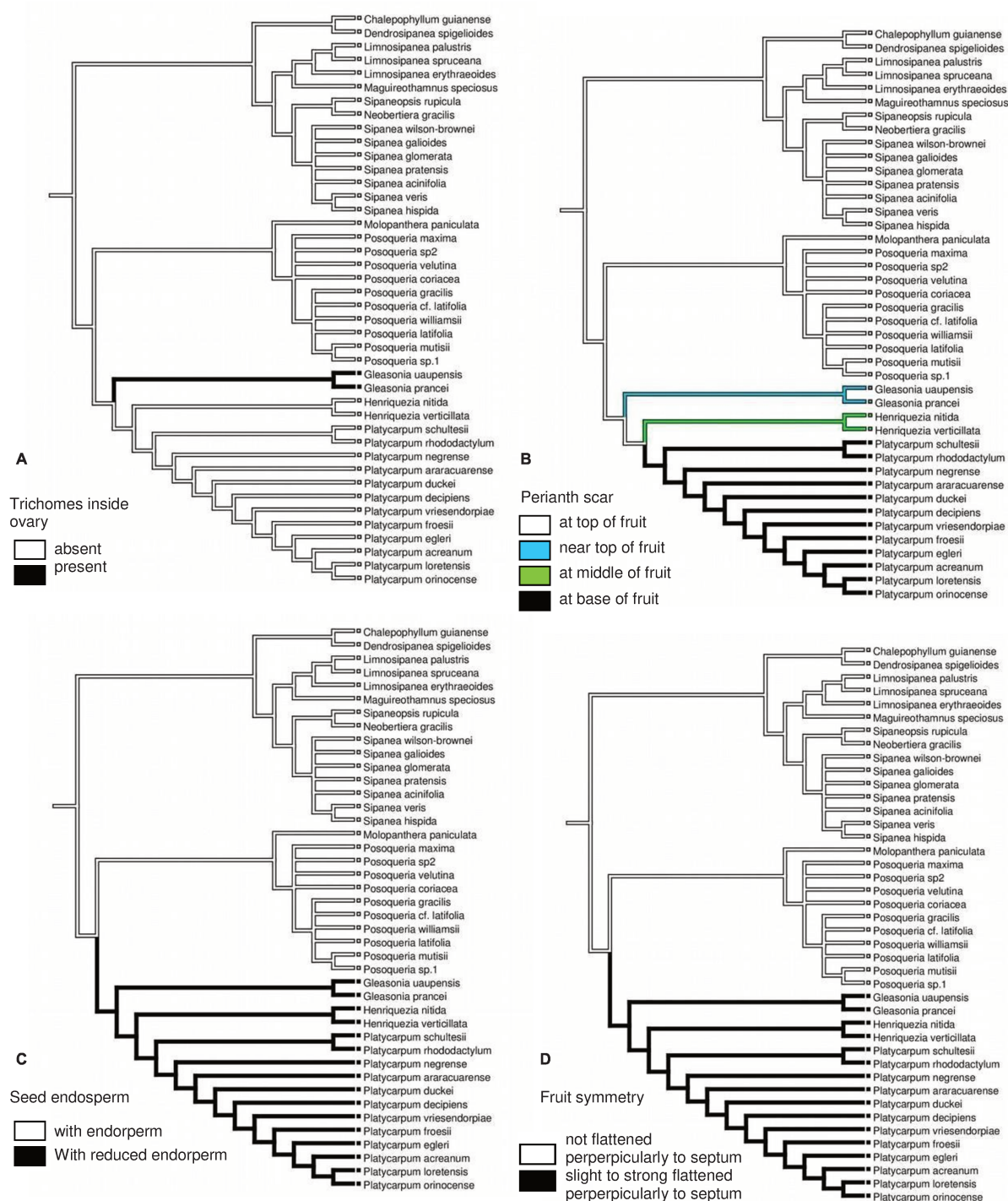


Figure 4. Character state reconstruction of morphological features in Henriquezieae and related tribes. Combined tree from Henriquezieae Maximum Parsimony tree with Maximum Parsimony tree from Cortés & Motley (2015). Trichomes inside ovary (A); perianth scar in the fruit (B); seed endosperm (C); fruit symmetry (D).

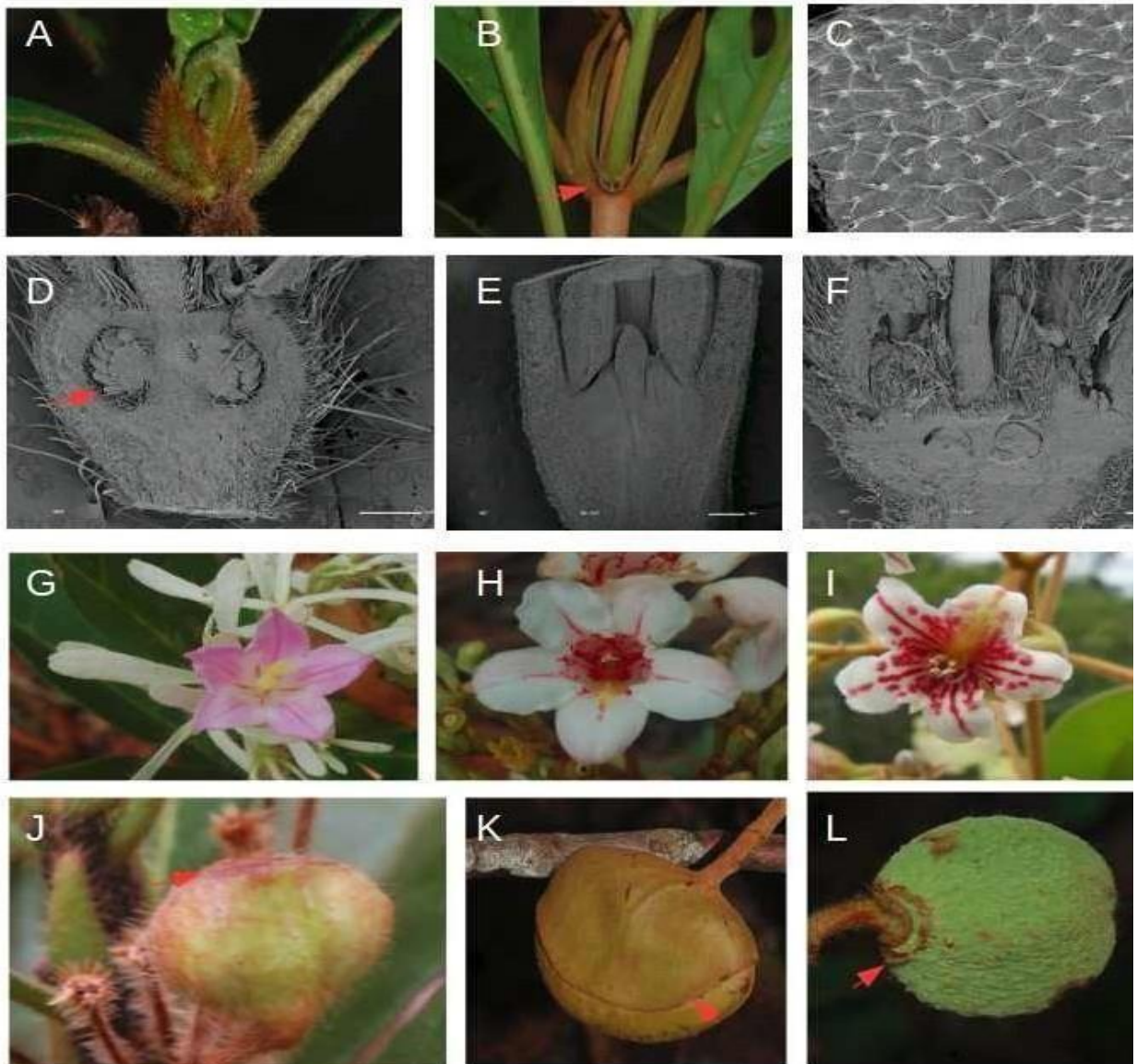


Figure 5. Microphotography and macrophotography of Henriquezieae. A. *Gleasonia uaupensis* intrapetiolar stipules, B. *Henriquezia verticillata* partially intrapetiolar stipules (arrow shows petiolar glands) C. *Platycarpum egleri* with strigose adaxial trichomes. D-F. SEM transection of ovary showing inferior ovary position, D. *Gleasonia uaupensis* (arrow shows trichomes in locules), E. *Henriquezia nitida*, F. *Platycarpum egleri*. G-H Flowers, G. *Gleasonia uaupensis*, H. *Henriquezia nitida*, I. *Platycarpum egleri*, J-L Fruits showing the perianth scar, J. *Gleasonia uaupensis*, K. *Henriquezia nitida*, L. *Platycarpum acreanum*.

Discussion

Phylogenetic analysis

Henriquezieae tribe is a strongly supported monophyletic group in this new phylogenetic hypothesis, corroborating the results found by Cortés & Motley (2015) about the monophyly of the tribe. The internal relationship in the tribe shows *Gleasonia* as sister group of *Henriquezia* and *Platycarpum*, which corroborate Cortés & Motley (2015) analyses when they used molecular and morphological data together, while only using molecular data the position of *Gleasonia* was unresolved. They attributed this due to the low molecular sampling (2,141 characters) and mainly because it was not possible to sample the nuclear region for *Gleasonia*. Using new techniques to get a phylogenomic scale of sequences has increased greatly the resolution in the groups that could not be solved using Sanger sequencing (Sanger et al. 1977). This is the case for Zingiberales reported by Sass et al. (2016), when using the multiplexed exon capture method, the resolution has improved the intra and inter family relationship for Zingiberales.

For *Platycarpum*, the internal relationship knowledge has improved greatly (12 of the 15 species were sampled). We found that *Platycarpum rhododactylum*, which is distributed in rocky places with scrubland vegetation in Venezuela, is the sister species of all the other *Platycarpum* species. Also two clades with moderate support are distinguished in the genus. *Platycarpum* clade I formed by *P. duckei* + *P. negrense*, which are species morphologically different and geographically distant. *Platycarpum duckei* is characterized by its elliptic leaf and its abaxial surface with dense ferruginous-hirsute and papillate surface leaves, and oblate with emarginate apex fruits. It grows in white-sand forest close to flooded areas (locally known as igapó) and is endemic to Borba (Amazonas state, Brazil). *Platycarpum negrense*, on the other hand, has elliptic to oblanceolate leaves, and mostly glaucousness appearance in young stem, stipules and leaves. It grows in white-sand forest in Brazil and Venezuela.

Platycarpum clade II has two subclades strongly supported. One formed by *P. froesii* + *P. egleri*, both with similar morphology and distribution (for similarities and differences see Chapter II). Both species grow in white-sand forest in Amazonas and Roraima state (Brazil),

occurring in sympatry in large open white-sand forest (locally known as campinaranas) in Roraima state (Brazil). The second subclade is also strongly supported, formed by *P. acreanum* + *P. lorentensis*, in this case both are morphologically similar (for similarities and differences see Chapter II) but with different distribution. *Platycarpum acreanum* is an endemic species from white-sand forest in Acre state (Brazil), and *Platycarpum lorentensis* is an endemic species from white-sand forest, swamp forest and peatlands in Loreto department (Peru).

The internal relationship that we found in *Henriquezieae* is in accordance with Cortés & Motley (2015) considering *Henriquezia* + *Platycarpum* clade during their molecular and morphological analysis. However, when they analyzed just plastidial regions (*rps16* and *trnL-F*), only *Henriquezia* was recovered as monophyletic, *Platycarpum* and *Gleasonia* were not supported as such. In comparison when they used the nuclear region ITS, both *Henriquezia* and *Platycarpum* were monophyletic groups, the same results we found in our analysis. In the internal relationship for *Platycarpum* in Cortés & Motley (2015), *Platycarpum decipiens* is sister to all other *Platycarpum* species. However, our analysis with more species sampled indicate that *Platycarpum rhododactylum* is sister to all other species of *Platycarpum*.

Ancestral morphology reconstruction

“*Henriquezieae* is obviously strongly derived *Rubiaceae*” was written by Robbrecht (1988) when he agreed with Roger (1984) that *Henriquezieae* should be classified as a member of *Rubiaceae*. This tribe has been such an interesting group with its morphological peculiarities that it was early classified as *Bignoniaceae* (Bonpland 1811) or the most extreme case as on their own family (*Henriqueziaceae*, Bremekamp 1957).

Characters such as petiolar glands, bearded corolla, stipules without colleter, perianth scar at the base of the fruits are apomorphic character state in the tribe. Characters states such as intrapetiolar stipule, partially intrapetiolar stipules, corolla uniformly pubescent, pollen in tetrad and trichomes inside ovary evolved independently in some genera in the tribe. We found that *Gleasonia* has characteristics shared with traditional *Rubiaceae*, like stipules with colleters, actinomorphic corolla and all species have perianth scar near the top of the fruit, as

mostly Rubiaceae (Robbrecht 1988). However, *Gleasonia* also presents unique characteristics as pollen in tetrads, intrapetiolar stipules and trichomes inside ovary that are not very common in Rubiaceae. Aggregated pollen appears independently in angiosperms, there are 39 families that produce pollen in tetrads, and it is present in 13 genera in Rubiaceae, mostly African genera (Robbrecht 1988; Harder & Johnson 2008). Harder & Johnson (2008) suggested that the tetrad condition arises in plants that are not frequently visited by pollinators. Whereas intrapetiolar stipules is a rare condition in Rubiaceae and known in Condaminea and Isertieae (Robbrecht 1988). Ovary with trichomes inside appears to have emerged independently in some groups of angiosperms, in Monocots the mucilage produced by trichomes is thought to guide the pollen tube during the fertilization (Rudall et al. 1998). In Rubiaceae, it is common in *Jackieopsis* (Puff & Igersheim 1994) but it is not clear if there is a relation with its reproductive biology.

In the *Henriquezia* + *Platycarpum* clade, common characteristics of Rubiaceae are also present such as intrapetiolar stipules (just in *Platycarpum*), ovary without trichomes inside and pollen in monad (Robbrecht 1988). Also some characteristics evolved in both genera, such as absence of colleters, presence of petiolar glands and zygomorphic corolla with bearded and variegate corolla; which are considered atypical characters in Rubiaceae. Cortés & Motley (2015) proposed that the loss of colleters in *Platycarpum* and *Henriquezia* could be balanced with the presence of glands on the petioles. The glands were frequently accompanied with ants during field observation. It is widely documented that the mutualism between ants and plants is a protection to avoid herbivory (Bronstein 1998). On the other hand, changes in flower morphology in *Henriquezia* and *Platycarpum*, such as zygomorphic corolla with bearded corolla and variegate corolla is probably related to attraction of pollinators. It has been attributed that zygomorphic corolla is a trait that could be one of the drivers of angiosperm diversification, as the divergence tend to increase with a more specialized pollination system (Vamosi & Vamosi 2011). Also all three genera in Henriquezieae have differences in fruit morphology, which indicates different dispersal mechanism in each group. *Gleasonia* has capsular globose fruits slightly compressed laterally and no winged seeds, which indicate an autochoric dispersal mechanism. *Henriquezia* has capsular fruits compressed laterally with no winged seed and with floating capacity; documented by Roger (1984) and personal observations, which suggests a hydrochoric

dispersal mechanism. *Platycarpum* has capsular fruits complete flattened with winged seeds, which suggest an anemochoric dispersal mechanism.

Another variation that occurs in all tree genera in Henriquezieae is the number of species. The richest genus in Henriquezieae is *Platycarpum* (15 spp.), and the least diverse is *Gleasonia* (5 spp.) and *Henriquezia* (3 spp.). As we mentioned, changes in flower morphology, probably as a strategy to attract pollinators, occurred in *Henriquezia* and *Platycarpum*. In addition, a reduction of flower size is seen in *Platycarpum* (ca. 3 cm) in comparison with *Henriquezia* (ca. 8 cm), which probably diversified the pollinator assembly and led to an increase in the diversification in *Platycarpum*. Another difference observed in *Platycarpum* is that seeds became smaller and lighter, in comparison to *Henriquezia*, which probably changed the dispersal mechanism in this genus (anemochoric syndrome). *Platycarpum* species are recorded for white-sand forest that can be flooded, facilitating a secondary dispersal by water too. Therefore, changes in flowers to attract pollinators and changes in dispersal strategies facilitating wind and aquatic dispersal mechanism probably increased the diversity in *Platycarpum*. This assumptions need to be investigated to better understand the evolutionary history of this group.

Synapomorphies

We found that the tribe Henriquezieae are supported by three morphological synapomorphies, such as corolla variegation internally with lines and/or spots, reduced endosperm and fruits slightly to strong flattened perpendicularly to the septum. Also each genera in Henriquezieae are supported by morphological synapomorphies. *Gleasonia* has intrapetiolar stipules, trichomes inside ovary and pollen arrangement in tetrad. *Henriquezia* has partially intrapetiolar stipules. *Platycarpum* has adaxial leaves with strigose trichomes and perianth scar at the base of the fruit. Also we observed that the *Henriquezia-Platycarpum* clade are supported with morphological features such as petiolar glands, zygomorphic corolla and bearded corolla.

Conclusion

We conclude that Henriquezieae and its three genera are monophyletic. We resolved that *Gleasonia* is sister to *Henriquezia* and *Platycarpum*. Characters considered atypical in Henriquezieae are apomorphic characters. We propose synapomorphies for the tribe Henriquezieae such as corolla variegation internally with lines and/or spots, reduced endosperm and fruits slightly to strongly flattened perpendicularly to the septum. Also morphological synapomorphies for *Gleasonia* are intrapetiolar stipules, ovary with trichomes inside and pollen arrangement in tetrad. *Henriquezia* has partially intrapetiolar stipules. *Platycarpum* has adaxial leaves with strigose trichomes and perianth scar at the base of the fruit. Also we postulate that the diversity in *Platycarpum* could be related to changes in flower and fruit morphology, and dispersal mechanism.

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CAPÍTULO II

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A new revision of tribe Henriquezieae Benth. & Hook. f (Rubiaceae)

Abstract

The tribe Henriquezieae is revised here, based in herbarium material and field sampled. Twenty-three species are recognized for the tribe, which encompasses *Gleasonia* (5 spp.), *Henriquezia* (3 spp.) and *Platycarpum* (15 spp.), and four varieties in *Platycarpum*. We synonymized *Platycarpum maguire* in *P. decipiens*. Varieties in *Gleasonia duidana*, *Henriquezia nitida*, *Platycarpum orinocense* and *Platycarpum schultesii* were not recognized because all the characters used to separate them are not discrete among all material analyzed. Two new species, *Platycarpum araracuarensense* and *P. piresii*, and one variety, *Platycarpum schultesii* var. *egleorides* are here described. We improved descriptions of reproductive characters previously unknown for *Gleasonia prancei* and *Platycarpum acreanum*. The important characters for species recognition in Henriquezieae are variation in leaf indumentum, corolla size and fruit size.

Keywords: *Gleasonia*, *Henriquezia*, *Platycarpum*, Ixoroideae, Guiana Shield, Amazon.

Introduction

Henriquezieae Benth. & Hook. F is a remarkable tribe because it has an atypical morphology for Rubiaceae. It is characterized by petiolar glands, zygomorphic corolla, bearded corolla with red macula and secondary superior ovary with perianth scar at the base, in the middle and near at the apex of the fruit (Rogers, 1984; Steyermark, 1952). It comprises three genera, *Gleasonia*, *Henriquezia* and *Platycarpum*. It is distributed along the Guiana Shield and in the Amazon basin, occurring throughout the altitudinal gradient of the Guiana Shield, in highly variable habitats, including mountain tops, rocks, lowlands, and savannas (Rogers, 1984). In the Amazon basin, Henriquezieae occurs in poor soils of white-sand forests, swamp forests and peatlands (Dávila & Kinoshita, 2016).

Platycarpum (Bonpland, 1811) and *Henriquezia* (Bentham, 1854) when described were considered as Bignoniaceae. Hooker (1873) created the tribe Henriquezieae for both genera and related them to Rubiaceae. Schumann (1889, 1891) agreed with the proposal made by Hooker (1873) and continued considering the two genera as a tribe of Rubiaceae. Meanwhile *Gleasonia* was described as a Rubiaceae in tribe Rondeletieae (Standley, 1931). Later, Bremekamp (1957) proposed a family Henriqueziaceae for *Platycarpum* and *Henriquezia*. And also Bremekamp (1957) created a subfamily Gleasonioideae to accommodate *Gleasonia*. Rogers (1984) completed the most recent taxonomic revision of the tribe Henriquezieae, using morphology, anatomy, and chromosomic characteristics. Rogers did a profound study about the relationship of all genera circumscribed in the tribe, as well as a comparison of the tribe with Rubiaceae and other families to which Henriquezieae supposedly belonged. Rogers (1984) circumscribed Henriquezieae as a tribe of Rubiaceae with three genera, *Gleasonia*, *Henriquezia* and *Platycarpum*.

Studies based on molecular phylogeny support the position of Henriquezieae in Rubiaceae. Currently the tribe is placed in the subfamily Ixoroideae (Rubiaceae), nested in the Guayanan clade that encompasses Henriquezieae-Posoquerieae-Sipaneeae (Bremer & Eriksson, 2009; Cortés & Motley, 2015).

After Rogers taxonomic revision (1984), new materials have been collected and new species have been discovered. Boom (1985) described *Gleasonia prancei*, Dávila & Kinoshita (2016) described *Platycarpum lorentensis*, and Dávila *et al.* (Submitted) described *Platycarpum vriesendorpiae*. In addition, in this treatment we describe two more new species and one variety for *Platycarpum*. Therefore, it is necessary to update the taxonomic comprehension of the tribe Henriquezieae.

Our goals in this new revision of the tribe Henriquezieae are to complement taxonomic descriptions for species with incomplete material, to analyze morphological limits inside species, and to update the identification key and the distribution maps.

Material and methods

Morphological analyses were conducted based in herbarium materials (A, AMAZ, COL, COAH, F, GH, HB, IAC, IAN, INPA, K, MICH, MO, NY, R, RB, UDBC, UEC,

UFACPZ, UMSM, US, VEN) (acronyms according to the *Index Herbariorum*, Thiers 2016) and field study. Our criteria to recognize species are morphological differentiation. The recognition of varieties was done when morphologic variation was related to geographic distribution. Terminology is according to Harris & Harris (2001), Hickey (1973) for leaf pattern, and trichome nomenclature follows Payne (1978). Measurements were taken from mature leaves, opened flowers, and mature fruits. Information from labels was extracted for color of flowers and fruits, flowering and fructification time, and distribution and ecological data. We conducted Scanning Electronic Microscopy for leaf surface details at the Missouri Botanical Garden and at the Universidade Estadual de Campinas. We prepared distribution maps in QGIS V. 2.0.1 (2013), for voucher without coordinates the georeferencing was made using label information and Google Earth.

Taxonomic treatment of *Henriquezieae*

Henriquezieae Benth. & Hook. f. Gen. Pl. 2(1): 8, 12. 1873. TYPE: *Henriquezia* Spruce ex Benth.

Shrubs, treelets or trees, usually with red exudate; young stem circular, triangular or angled; glabrous or pubescence in one or two layers; stipules intrapetiolar, interpetiolar or partially attached at petioles, lanceolate, triangular, deltoid, oblong or linear. Leaves decussate or whorled; petioles with or without glands, colleters present or absent at internal base of stipules; leaf blade with size variation from young to mature leaves, apex being variable from acuminate to emarginate at same individual. Inflorescence terminal, usually cymose, congested cymose or cymose with axis not completely developed, glabrescent or with one or two layers of trichomes, usually with a pair of foliaceous bracts at the base of inflorescence, and flowers with linear bracteoles. Flowers slightly actinomorphic or zygomorphic; calyx lobed 4-5(-6), being shorter or longer than corolla, fusiform, obovate, spatulate or rarely differentiated in claw and limb; corolla funnelform; reddish to purple or white with internal lines or/and macula, sometimes one (two) yellow bearded lobe; filaments 5, anthers narrow elliptic, dorsifixed and antrorse; inferior ovary becoming secondary half-superior or superior

in fruit, 2-locular, with two or many ovules per locule; style tomentose, stigma bifid. Fruit capsular, woody, slightly to strong flattened perpendicularly to the septum, bilocular, loculicidal, perianth scar near at the apex, at the middle or at base of fruit, glabrescent or hirsute and tomentose. Seeds two to many, with reduced endosperm, circular, elliptic or D-shaped, sometimes with narrow marginal wing, papillae in surface.

Henriquezieae is a monophyletic group (see chapter I) and it can be recognized because its corolla with lines or/and macula, fruits slightly to strong flattened perpendicularly to the septum and reduced endosperm.

Key to genera of Henriquezieae

- 1a. Stipules intrapetiolar (fig. 1C), showy calyx lobes (fig. 1F-G), perianth scar near at the apex of fruits (fig. 1J)..... *Gleasonia*
- 1b. Stipules interpetiolar or partially attached to petioles (fig. 3D, 6D), calyx lobe without highlighting lobes (fig. 3F, 6H), perianth scar at the central or basal portion of fruits (fig. 3H, 6I).2
- 2a. Petioles with two circular glands (fig. 3D), perianth scar a line horizontally or inverted U-shape in the middle of fruits (fig. 3H)..... *Henriquezia*
- 2b. Petioles with U-shaped glands, inverted U-shape, or rectangular glands (fig. 6G), perianth scar at the base of fruits (fig. 6I)..... *Platycarpum*

Gleasonia Standley, Field Mus. Nat. Hist., Bot. Ser. 7: 372. 1931. TYPE: *Gleasonia duidana* Standl.

Shrubs to trees; young stem circular, striate or ribbed, glabrous to hirsute, yellow to dark brown; stipules intrapetiolar, deltoid to lanceolate, 2- or 4-lobate, glabrescent to dense hirsute, with black colleters at internal base. Leaves decussate; petioles without glands; lamina elliptic, obovate or lanceolate, acute to rounded at apex, truncate at base. Inflorescence cymose with incomplete developed axis, glabrescent to hirsute, yellow to tawny, with linear or lanceolate bracts. Flowers slightly actinomorphic to zygomorphic; calyx lobe 5, showy,

white to reddish, spatulate or unguiculate, surface with conspicuous reticulate venation; corolla infundibuliform, pink or violet, hispid externally, internally with purple lines in the throat, unequal corolla lobes; filaments 5, inserted in the middle portion of the corolla tube; inferior ovary, style tomentose. Fruit capsular, perianth scar at apex of the fruit, brown when dry, with 3-4 vertical costa externally, glabrescent or sparse hirsute. Seeds more than 2, papillae in surface.

Gleasonia is distinguished by its intrapetiolar stipules, presence of colleters at petiolar base, calyx with showy lobes and fruit with perianth scar near at the top of the fruit (fig. 1C, E, F, I, L). *Gleasonia* is distributed from South of Venezuela to North of Brazil (fig. 2). It grows from lowlands in forested and open white-sand forest, and highlands like mountain “tepui” (1800 m). *Gleasonia* is a monophyletic genus and it is the sister of *Henriquezia* and *Platycarpum* (see chapter 1). Potential sinapomorphies for this genus are intrapetiolar stipules, pollen in tetrad and trichomes inside ovary (see Chapter I).

Key to the species of *Gleasonia*

- 1a. Stipules 4-lobate.....*G. prancei* B.M.Boom
- 1b. Stipules 2-lobate 2
 - 2a. Stipules with ant nest *G. uaupensis* Ducke
 - 2b. Stipules without ant nest..... 3
 - 3a. Calyx lobe with inconspicuous reticulated venation.....*G. cururuensis* Egler
 - 3b. Calyx lobe with conspicuous reticulated venation. 4
 - 4a. Calyx lobe spatulate, 3–5.3 × 0.5–1.2 cm, pedicel
absent.....*G. duidana* Standl.
 - 4b. Calyx lobe unguiculate, 4–9 × 0.7–2.4 cm, pedicel
present.....*G. macrocalyx* Ducke

1. *Gleasonia cururuensis* Egler, Bol. Mus. Paraense Hist. Nat. Bot. 14: 4, pl. 1, I-N. 1961.
TYPE: Brazil. Pará: Alto Tapajós, Rio Cururú, Ereri, entre lagedos, 25 Jul. 1959 (fl, fr), *Egler 1032* (holotype, MG!; isotypes, HB!, IAN not seen, NY!, NY neg. 6173!, photo of IAN at NY!).

Trees or treelets, 3.5–11 m, to 8 cm dbh; exudate not seen; young stems circular, striate, glabrescent to sparse yellow-hirsute; stipules 2-lobate, lobes 2.0–2.7 cm long, adaxially glabrescent, abaxially glabrescent to dense yellowish-hirsute; ant nest absent. Leaves decussate; petioles (0.6–)1.5–2.5 cm long, dense yellow-hirsute or glabrescent; lamina 10.0–20.0(–22) × 4.5–9.0 cm, elliptic to obovate, acuminate to acute at apex, attenuate at base, with venation eucamptodromous, 11–17 pairs of secondary veins, midrib and secondary veins impressed adaxially and prominent abaxially, indumentum sparse yellowish bent trichomes adaxially, and sparse tawny bent trichomes abaxially, more dense hirsute in veins. Inflorescences 11–13 × 10–14 cm; peduncle 2.3–2.5 cm; axes pubescent in two layers, longer layer dense yellow-hirsute, shorter layer all surface yellow-tomentose; pedicels absent. Flowers with hypanthium obconic, 3.0–4.5 cm long., all surface yellow-hirsute; calyx lobes 5, these spatulate, 1.7–2.7 × 0.4–0.7 cm, acute or rounded at apex, pubescence in two layers, shorter layer creamy-tomentose covering all surface, longer layer sparse brown-hirsute, with inconspicuous reticulate venation; corolla infundibular, 2.5–4.0(–4.7) cm long, externally light pink to purple, pubescence in two layers, longer layer dense yellow-hirsute, shorter layer all surface yellow-strigillose, internally corolla tube glabrous, lobes with pubescence in two layers, longer layer tomentose, shorter layer yellowish-puberulous, corolla lobes unequal, 0.8–1.5 × 0.6–1.4 cm, with crenate margins. Fruits capsular, 2–2.2 × 2.1–2.2 cm, widely elliptic, perianth scar at the top, surface rugose, glabrescent to hirsute. Seeds not seen.

Illustration. Inflorescence, sepal, open flowers, corolla (Egler, 1961).

Phenology. Flowers in February and fruits in September.

Distribution and habitat. This species occurs in Serra do Cachimbo area (Pará state) and close to Manaus (Amazonas state) in Brazil. This is the southernmost distribution of the genus, and this is close to the boundary between Amazon and Cerrado (fig. 2). It grows in forested and open white-sand forest close to flooded forest (locally known as Igarapé).

Discussion. This species is recognized by its dark leaves when dry, calyx lobe with inconspicuous reticulate venation and dense tomentose indumentum. This species is the only species in the genus that the calyx lobe is completely covered by indumentum and it has inconspicuous reticulate venation.

Additional specimens examined. BRAZIL. **Amazonas:** Itapiranga, rio Uatumã, 13 Ago 1979, *Cid* 254 (INPA, MO, RB); 13 Ago 1979, *Cid* 286 (INPA, MO, RB); Parque

Nacional Jaú, 5 Sep 1998, *Vicentini 1393* (INPA, MO). **Pará:** Northwest edge of Serra do Cachimbo, 25 km by foot NE of Missão Velha on rio Cururú, 14 Feb 1974, *Anderson 10966* (INPA, MO, NY). Alto Tapajós, Rio Cururú, 8 Feb 1960, *Egler 1267* (NY).

2. *Gleasonia duidana* Standley, Field Mus. Nat. Hist., Bot. Ser. 7: 372. 1931. TYPE. Venezuela. Amazonas: Cerro Duida, summit, 5000 ft. 26 Nov.-16 Dec. 1928 (fl), *Tate 467* (holotype, NY!; isotype, F!). *Gleasonia duidana* var. *duidana* Standley, *syn. nov.*

Gleasonia duidana var. *latifolia* Steyermark, Mem. New York Bot. Gard. 17: 239. 1967, *syn. nov.* TYPE. Venezuela. Amazonas: Cerro Yutaje, 1500 m, 21 Feb. 1953 (fl, fr), *B. Maguire & C. Maguire 35344* (holotype, NY!; isotypes, GH!, NY!, U not seen, VEN!).

Gleasonia duidana var. *oblanceolata* Steyermark, Mem. New York Bot. Gard. 17: 239. 1967. TYPE. Venezuela, Bolivar: Cerro Apácará, declives, 800-900 m, 26 Jun. 1946, *Cardona 1610* (holotype, VEN!; isotype, NY!).

Trees up to 16 m or shrubs 1.5–3 m, to 10 cm dbh; external bark striate or angulate; young stems circular, glabrescent to yellow-hirsute at apex; stipules 2-lobate, triangular-shape, free at base, (1–)1.7–3.0 cm long, glabrescent adaxially, sparse to dense bend ferruginous trichomes abaxially, ant nest absent. Leaves decussate; petioles (1.4–)2.0–3.5(–4.5) cm long, glabrescent to dense trichomes; lamina (11–)14–22(–26) × 6–12 cm, elliptic to obovate, acuminate to rounded or obtuse at apex, cuneate at base, with venation eucamptodromous, 10–13 pairs of secondary veins, flat to impressed adaxially, prominent abaxially, glabrescent adaxially with dense to sparse bent trichomes in central veins, dense to sparse ferruginous-hirsute abaxially (0.5–0.7 mm long.), with dense trichomes in central veins. Inflorescences 9–20 × 15–21 cm; peduncle 3–5 cm; bracts deltoid to lanceolate, these 12–15 × 2 mm; pubescence dense ferruginous-hirsute; pedicels absent. Flowers with hypanthium obconic, 0.3–0.8 cm, all surface cover by ferruginous-hirsute indumentum; calyx lobes 5, pinkish, spatulate, 3.0–5.3 × 0.5–1.2 cm, acute to rounded at apex, pubescence in two layers, longer layer yellow adpressed-hirsute, shorter layer puberulent, with conspicuous reticulate venation; corolla funnelform, pink, 2.8–5.2 cm long, externally with pubescence in two layers, longer layer dense hirsute, shorter layer dense tomentose, internally dense pilose at throat, and dense pilose and puberulent in lobes, corolla lobes 5, 0.8–3.5 × 0.9–1.1 cm,

obvate, acute at apex. Fruits capsular, $1.5\text{--}2.5 \times 1.8\text{--}2.0$ cm, rugose, glabrescent to sparsely yellow-hirsute indumentum. Seeds $0.5\text{--}1.5$ cm long, dark when dry.

Illustration. Bremekamp (1957), flower dissection; Egler (1961), stipules and sepal; Gleason (1931), flower; Rogers (1984), wood, vested pits, nodal vascular anatomy, colleters, petiole anatomy, leaf surface, leaf blade anatomy, inflorescence, corolla, fruits, surface details of seed, pollen; Steyermark (1974), inflorescence, infructescence, flower dissection.

Phenology. Flowers from November to March, fruits from May to February.

Distribution and habitat. This species is mainly distributed in the south of Venezuela from lowland to highland “tepui” and less frequently distributed in northern Brazil, in the Amazonas state (fig.2). Because of its wide distribution it occurs in many types of habitats like savannas, white sand-forest, and cloud forest.

Discussion. This species is widely variable and previously it was comprising two varieties due to the variable leaf shape, leaf apex shape, and inflorescence sizes (Steyermark, 1967). However, these limits are less obvious when more specimens are analyzed. We observed that ranges for size and shape leaves use to differentiated varieties are present in duplicates the same sample. e.g. *Huber 11006* has a wide variation of size of leaves and leaf shape in the same individual. Another example is *Steyermark 58098*, when duplicates of the same specimen were observed independently, one of them could be assigned to *G. duidana* var. *duidana* and the other one to *G. duidana* var. *latifolia*, because of the leaf size and inflorescence development. After analysing many specimens we decided not to recognize the limits of these varieties for *Gleasonia duidana*.

Gleasonia duidana is morphologically similar to *G. macrocalyx* and *G. prancei* by its leaves, stipules and calyx lobes. *Gleasonia duidana* has stipules 2-lobate, (1–)1.7–3.0 cm long, and free at base (vs. 2-lobate stipules, 1.2–2.5 cm long., and free at base in *G. macrocalyx*, and vs. 4-lobate stipules, (1–)1.7–3 cm long, united at the base in *G. prancei*). Leaves in *G. duidana* are acuminate to rounded or obtuse at apex (vs. obtuse or rounded (rarely acute) at apex in *G. macrocalyx* and vs. obcordate to retuse or rounded at apex in *G. prancei*). The abaxial leaf indumentum in *G. duidana* has two layers of trichomes, the longer layer yellow adpressed-hirsute and the shorter layer puberulent (vs. glabrous to sparsely hairy in *G. macrocalyx* and *G. prancei*). The calyx lobe in *G. duidana* is spatulate, $3.0\text{--}5.3 \times 0.5\text{--}$

1.2 cm (vs. unguiculate, 4.0–9.0 × 0.7–2.4 cm in *G. macrocalyx*, and vs. oblanceolate to spatulate, 5.0–6.0(–8) × 1.2–1.6 cm in *G. prancei*).

Additional specimens examined. BRAZIL. **Amazonas:** Barcelos, Ubicadas en la ribera izquierda del Río Aracá medio, aprox. 16 km al SE (en línea recta) de la boca del Río Jauarí, Jul 1985, *Huber 10787* (INPA, NY). VENEZUELA. **Amazonas:** Atures. Serranía Parú, Planicie central, SW sector, 7 Mar 1991, *Berry et al. 4999* (MYF, VEN); Rio Negro, Cerro Aracamoni, Capto. La Popa. Escaso en la orilla de la quebrada en el matorral tepuiano, 27–30 Oct 1987, *Carnevali & Santana 2416* (PORT, VEN); Cerro Duida, 1000 m, Jan–Feb 1969, *Farilas et al. 374* (VEN); Cerro Aracamoni, Capto. La Proa, 30 Oct 1987, *Carnevali 2555* (PORT); 28 Jan 2005, Río Pasimoni (de aguas negras), Tamarinuma, a 1,5 Km aguas abajo del campam., *Diaz et al. 7340* (PORT); Atabapo, Meseta de arenisca grande ubicada al Sur del Río Matakuni, aprox. 50 km al NE de su desembocadura en el Río Orinoco, 9 Nov 1991, *Huber 13258* (MYF); Macizo del Marahuaca, gran altiplanicie ubicada en el piedemonte SW del sector meridional del Cerro Marahuaka (Athua-Shiho), 14 Dec 1992, *Huber 13452* (MYF), Atures: Río Coro-Coro, W of Serrania de Yutaje, 8 km N of settlement of Yutaje. E of river on gradual slope, 22 Feb 1987, *Holst et al. 3114* (MO, PORT); Cerro Sipapo (Paráque), in brakes below escarpment, 1500 m, 8 Dec 1948, *Maguire & Politi 27564* (NY, U, VEN); Cerro Sipapo, in low bush bordering Savanna Creek, 1500 m, 10 Dec 1948, *Maguire & Politi 27579* (NY); Cerro Sipapo, in marsh above pool, 1400 m, 15 Dec 1948, *Maguire & Politi 27712* (NY, U, VEN); Cerro Sipapo (Paráque), W mountain, 1800 m, 17 Jan 1949, *Maguire & Politi 28396* (NY, RB, U, VEN); Cerro Duida, on N slopes and ridges of Caño Negro basin, 2000–2300 m, 23 Nov 1950, *Maguire et al. 29711* (NY); Cerro Huachamacari, in cumbre, 1800 m, 8 Dec 1950, *Maguire et al. 30032* (NY); *Maguire et al. 30043* (NY, U); Cerro Yapacana, in cumbre, 1200 m, 3 Jan 1951, *Maguire et al. 30655* (NY, U, VEN); Cerro Guanay, occasional in places in woodland, 900–1100 m, 30 Jan 1951, *Maguire et al. 31680* (NY); Cerro Guanay, occasional on summit, 1800 m, 2 Feb 1951, *Maguire et al. 31720* (NY); Cerro Camani, common on upper slopes, 1800 m, 12 Feb 1951, *Maguire et al. 31800* (NY, VEN); Cerro Yutaje, 1300 m, 8 Feb 1953, *Maguire & Maguire 35089* (NY, U); Cerro Coro-Coro, frequent in savanna, 1500 m, 2 Mar 1953, *Maguire & Maguire 35487* (F, NY, U); Cerro de la Neblina, frequent on banks of Cano Grande, 1100 m, 24 Nov 1957, *Maguire et al. 42205* (NY, VEN); Cerro Sipapo, falda occidental, 1500 m, Feb

1946, *Phelps* 54 (VEN); Atabapo, Río de aguas negras que tiene su fuente en el cerro Marahuaca sur, afluente de Caño Negro, que a su vez desemboca en el Cunucunuma, 17 Oct 1988, *Rodriguez* 2442 (PORT) ; Cerro Yapacana, SW face at base of escarpment, 900 m, 8 Nov 1979, *Rogers* 63 (MICH, NY, VEN); Cerro Duida, summit, along valley forest, 1675 m, 31 Aug 1944, *Steyermark* 58098 (F, NY, VEN); Cerro Yapacana, en la cumbre, 1000-1200 m, 5-7 May 1970, *Steyermark & Bunting* 103140 (U, VEN); Cerro Duida, summit, 4800 ft., 1928 or 1929, *Tate* 1026 (F fragment, NY); Cerro Duida, inmediatamente al N de La Esmeralda, en el alto río Orinoco, 1 Feb 1975, *Tillett* 752-127 (MYF). **Bolivar:** Cerro Sarisariñama, cumbre, porción NE, 1300 m, 10 Feb 1976, *Brewer-Carías s.n.* (VEN); Cerro Appacará, faldas, 1400 m, 12 Nov 1946, *Cardona* 1947 (NY, VEN); Cerro Pauo, en las estribaciones, cerca de la caída del Gran Salto del Río Pauo, 1000 m, Jan 1963, *Cardona* 2988 (VEN); Cedeño. Serranía Guanay, 20-28 Oct 1985, *Huber* 1106 (MYF); Abácapa-tepuí, forested west-facing slopes with sandstone boulders, 850-1100 m, 18 Apr 1953, *Steyermark* 75109 (F, NY, VEN); Abácapa-tepuí, western part, 1250 m, 21 Apr 1953, *Steyermark* 75220 (F, NY, VEN); Sierra Pakaraima, cabeceras del Río Paragua, a lo largo de la frontera Venezolana-Brasilera, 1400 m, 4-5 May 1973, *Steyermark* 107220 (VEN); Cerro Sarisariñama, porción NE, formación de bosque achaparrado y árboles enanos, 1410 m, 10 Feb 1974, *Steyermark et al.* 108888 (VEN); Cerro Sarisariñama, cumbre, porción NE, bosque enano, 1320 m, 13 Feb 1974, *Steyermark et al.* 108914 (VEN); Gran Sabana near Sta. Elena, Mar 1946, *Tamayo s.n.* (F); Gran Sabana, en selvas de galería a orillas de quebradas afluentes del Yari, 13 Mar 1946, *Tamayo* 3115 (VEN); Sarven-tepuí, occasional cloud forest, 1500-1700 m, 10 Jan 1953, *Wurdack* 34065 (NY, RB, U, VEN).

3. *Gleasonia macrocalyx* Ducke, Trop. Woods 50: 40. 1937. TYPE: Brazil. Amazonas: Alto Rio Curicuriary, tributary of the Rio Negro, margem inundável, 26 Nov. 1936 (fr), *Ducke* 304 (holotype, RB!; isotypes, NY!, U not seen, MADw not seen).

Tree; exudate unknown; young stems circular, ribbed, glabrescent; stipules 2-lobate, deltoid, 1.2–2.5 cm long, glabrous except at abaxially margin with dense yellow trichomes; ant nest absent. Leaves decussate; petioles 0.6–2.0 cm long, glabrescent; lamina 11–22 × 5–10 cm, elliptic to obovate, obtuse, rounded to acute at apex, cuneate at base, with venation

eucamptodromous, 5–10 pairs of secondary veins, adaxially with main veins impressed and secondary veins flat, prominent abaxially, glabrous or sparse bent trichomes adaxially, glabrous to sparse adpressed trichomes abaxially. Inflorescences 15–20 × 15–23 cm; peduncle 3–4 cm; glabrescent; linear to lanceolate bracts, these 0.4–2.4 × 0.6–2 cm, with sparse bent trichomes; pedicel present. Flowers with hypanthium obconic, 0.4–0.7 cm, cover with dense antrorse trichomes; calyx lobes 5, white with base red, unguiculate, 4–9 × 0.7–2.4 cm, rounded to emarginated at apex, glabrescent, with conspicuous reticulate venation; corolla not seen. Fruits capsular, 2–3 × 1.5–2.2 cm, sparse tawny trichomes. Seeds 0.5–1.5 cm, dark when dry.

Illustration. Bremekamp (1957), stomata; Egler (1961), sepal, fruit; Rogers (1984), woods anatomy, vessel elements.

Phenology. flowers unknown, fruits in November.

Distribution and habitat. This species is endemic to the Curicuriary river, Amazonas state in Brazil. It grows in riparian forest which may be seasonally flooded (fig. 2).

Discussion. *Gleasonia macrocalyx* is only known from the type collection and another collection with the same date, *Ducke* 359. More collections of *G. macrocalyx* are necessary to better understand the morphological variation within the species, especially the flower morphology. *Gleasonia macrocalyx* resembles *G. duidana* by its 2-lobate stipules and elliptic to obovate leaves, and *G. prancei* by its elliptic to obovate leaves. See *Gleasonia duidana* discussion for differences.

Additional specimens examined. BRAZIL. **Amazonas.** Rio Curicuriary superior ad ripas inundabiles, 26 Nov. 1936, *Ducke* 359 (F, MO, NY).

4. *Gleasonia prancei* B.M. Boom, *Brittonia*, Vol. 37: 3. 1985. TYPE. Brazil. Amazonas: Southern extremity of Northern Plateau of Serra Aracá, 0°51–57'N, 63°21–22'W, elev. 1200 m, cloud forest, 13 Feb. 1984 (fl), *G. T. Prance et al.* 29052 (holotype, INPA!; isotypes, GH!, INPA!, K not seen, MO!, NY !, US!).

Trees 7–10 m tall, 10 cm dbh; red exudate; young stems quadrangular and ribbed, densely yellow- to ferruginous-hirsute; stipules 4-lobate, (1.2–)2.0–3.2(–4.0) cm long, adaxially glabrescent with yellow pubescence at the apex lobe, abaxially mostly glabrescent

or dense bent trichomes; ant nest absent. Leaves opposite; petioles 1.3–2.0(3.6) cm long, dense to sparse yellowish-hirsute indumentum; lamina 14–24 × 8–13 cm, elliptic to widely elliptic or obovate, mostly obcordate to retuse or rounded at apex, attenuate at base, with venation eucamptodromous, 10–12 pairs of secondary veins, midrib and secondary veins impressed adaxially and prominent abaxially, indumentum adaxially sparse bent trichomes, abaxially glabrescent, in veins densely ferruginous. Inflorescences (4–)8–16 × 12–21 cm; peduncle 3–6 cm; axes with pubescence in two layers, longer layer dense yellowish-hirsute, shorter layer ferruginous; pedicels absent. Flowers with hypanthium obconic, 3–4 cm long, dense ferruginous-hirsute; calyx lobe 5, these oblanceolate, 5.0–6.0(–8) × 1.2–1.6 cm, with sparse bent trichomes; conspicuous reticulate venation; corolla infundibular, 3.7–4.0 cm, externally pink, pubescence in two layers, longer layer dense ferruginous-hirsute, shorter layer dense ferruginous-setose, corolla tube internally glabrous, with internal corolla lobes pubescence in two layers, longer layer tomentose and shorter layer yellowish-puberulous, corolla lobes 0.9–1.7 × 0.9–1.5 cm, cucullate; stamens 5, filaments ca. 4 mm long, anthers 8–9 mm long; style ca. 21 mm long, stigmatic lobes 8–9 mm long. Fruits capsular, 2.9–3.3 × 2.7–3.5 cm, oblate, with rugose surface, pubescent with longer layer sparse brown-hirsute, shorter layer sparse grayish-tomentose. Seeds not seen.

Illustration. Boom (1985), terminal shoot showing flowers, calyx lobe, open corolla.

Phenology. Flowers in February and July, fruits in August.

Distribution and habitat. Endemic to Serra do Aracá, Amazonas state (Brazil) (fig.2). It occurs in cloud forest in high rocky places and open areas.

Discussion. *Gleasonia prancei* is morphologically similar to *G. duidana* and *G. macrocalyx*. However, its 4-lobate stipule makes it a unique species with this character in the genus, see *G. duidana* comments for comparison. This is the first time that fruits are described and it complements Boom's (1985) description.

Additional specimens examined. BRAZIL. **Amazonas.** Barcelos. Platô da Serra Aracá, parte SE da Serra Norte. Mata de galeria e campo rupestre ao longo do rio Grande, 12 Feb 1984, *Amaral 1568* (MO, NY, RB); Rio Tuari (afluente do rio Negro), Lago Uirauaçu (= pássaro Grande em Língua Geral), 13 Nov 1987, *Kawasaki et al. 120* (INPA, MO, NY); Arredores do Rio da Serra Aracá, 29 Jan 1978, *Rosa & Lira 2301* (NY); Plateau of northern massif of Serra Aracá. Southern extremity of Northern Plateau of Serra Aracá. Cloud forest,

13 Feb 1984, *Prance et al.* 29044 (INPA, NY); north part of north slope of Serra Aracá, 0°57'N, 63°22'W, cloud forest, 1400 m, 20 Feb 1984, *Prance et al.* 29189 (INPA, NY); Summit of Central Massif of Serra Aracá, 16 Jul 1985, *Prance et al.* 29696 (INPA, NY); Serra do Aracá, porção norte. Floresta Ombrófila Densa Alto Montana, 26 Aug 2001, *Vicentini et al.* 1859 (INPA).

5. *Gleasonia uaupensis* Ducke, Arq. Inst. Biol. Veg. 1: 91, pl. 1-2. 1934. TYPE. Brazil. Amazonas: Baixo Rio Uaupés, catinga de carana do Igarapé Jurupary, 2 Nov. 1921 (fl, fr), *Ducke* 23737 (holotype, RB!).

Trees or treelet 3–16 m tall; exudate red; young stems circular and ribbed, densely hirsute yellow to tawn; stipules 2-lobate, 1.5–3 cm long, adaxially densely yellow-hirsute to glabrescent, abaxially glabrescent to dense yellowish bent trichomes; ant nest present. Leaves opposite; petioles 0.9–2.0 cm long, dense yellow-hirsute; lamina 13–29 × (4.5–)8–11 cm, elliptic to oblanceolate or obovate, acuminate to acute at apex, decurrent at base, with venation eucamptodromous, 9–14 pairs of secondary veins, adaxially midrib impressed and secondary veins flat to impressed, prominent abaxially, indumentum adaxially sparse to dense bent to hirsute trichomes, abaxially dense yellow-hirsute, these same trichomes densely in veins. Inflorescences (7–)10–13 × 8–17 cm; peduncle 1 cm; axes with pubescence in two layers, longer layer all surface yellow-hirsute, shorter layer yellow-pubescent; pedicel absent. Flowers with hypanthium obconic, 0.2–0.4 cm, all surface yellow-hirsute; calyx lobes 5, oblanceolate, 2.7–4.8 × 0.6–1.0 cm, with obtuse to cleft apex, with sparse hirsute or bent trichomes; conspicuous reticulate venation; corolla infundibular, 2.0–3.3 cm long, externally light purple with pubescence in two layers, the longer layer dense yellow-hirsute, shorter layer covering all surface with setose trichomes, tube internally glabrous and internal lobes pubescence in two layers, longer layer tomentose and shorter layer yellowish-puberulous, corolla lobes 0.7–1.3 × 0.6–1.2 cm, cucullate; stamens 5, filaments 3–5 mm long, anthers 4–7 mm long; style 2.0–2.2 mm long, stigmatic lobes 2, 3 mm long. Fruits capsular, 1.2–1.6 × 1.8–2.3 cm, depressed obovate, with surface rugose, pubescence in two layers, shorter layer dense yellow–tomentose, longer layer dense yellow-hirsute or glabrescent. Seeds not seen.

Illustration. Rogers (1084), wood anatomy, resin sacs, petiole anatomy, fruit, surface of endocarp, surface of seed, sectioned seed, embryos, trichomes, pollen, flowering branch, fruiting branch, calyx and corolla.

Phenology. Flowers and fruits in May to November.

Distribution and habitat. This species is distributed in the Upper Rio Negro, Amazonas state, Brazil (fig. 2). It grows in white-sand forest close to the riparian forest.

Discussion. This species is easily differentiated from all other *Gleasonia* species by its yellow or tawny hirsute trichomes covering all parts of the plant. It is the only species that has nest of ants in their stipules. The fruits are depressed obovate in comparison with other species from the genus. We noticed in *Black* 48-2732 a reduction of corolla size and the corolla indumentum is shorter.

Additional specimens examined. BRAZIL. **Amazonas.** Rio Içana, Estacamento (João da Lapa), caatinga baixa, 17 May 1948, *Black* 48-2732 (U, VEN); Lago Jauacana, 30 Nov 2013, *Dávila et al.* 6434 (UEC, MO, RB); *Dávila et al.* 6435 (UEC, MO, RB); Igarapé Jurupary (afluente Rio Uaupes inferior), caatinga, 29 Sep 1935, *Ducke* 40 (A, F, MO, NY, R), *Ducke* 223 (MADw, NY), *Ducke* s.n. (RB34641 at RB, U); Rio Iá trib. to Marié, rather lowland, sand soil, 11 Jun 1947, *Fróes* 22384 (U); Rio Negro, Padauri, Sao Pedro, 27 Oct 1947, *Fróes* 22667 (U); Rio Negro, Matupiri, 11 Nov 1947, *Fróes* 22828 (RB, U); Rio Negro, Preto Matupiri, open country, dry soil, 13 Nov 1947, *Fróes* 22839 (U); Rio Içana, caatinga de Santana, 2 May 1952, *Fróes* 28169 (U); Rio Preto, 19 Apr 1952, *Fróes* 28300 (U, VEN); Rio Negro, São Felipe, Região do Igarapé Touri, caatinga ou mata aberta e baixa, 27 Sep 1952, *Fróes* 28760 (U); Rio Negro, Comunidade Aparecida, Opposite mouth of Igarapé Tuarí, near abandoned portion of Perimetral Norte, 6 Nov. 1987, *Maas et al.* 6943 (INPA, MO, NY, RB); São Gabriel da Cachoeira, 4 Km NW da Ilha Açaí, 25 Jul 1991, *Martinelli & Ramos* 14528 (RB).



Figure 1: Morphology of *Gleasonia*. A-D, F-G, I-J. *Gleasonia uaupensis*, E *G. duidana*, H. *G. macrocalyx*. A. Terminal shoot, B. External and internal bark and red exsudado after cut, C. Intrapetiolar stipule, D. Ant nest in stipules, E. Colleters in petiole, F. Inflorescence cymose with incomplete developed axis, G. Flower with showy calyx lobes, H. Fruit with calyx lobe persistent, arrow show showy unguiculate calyx lobe, I. Internal corolla with lines in lobes and showing yellow stigma, J. Capsular fruits, arrow shows perianth scar near at the apex of fruit.

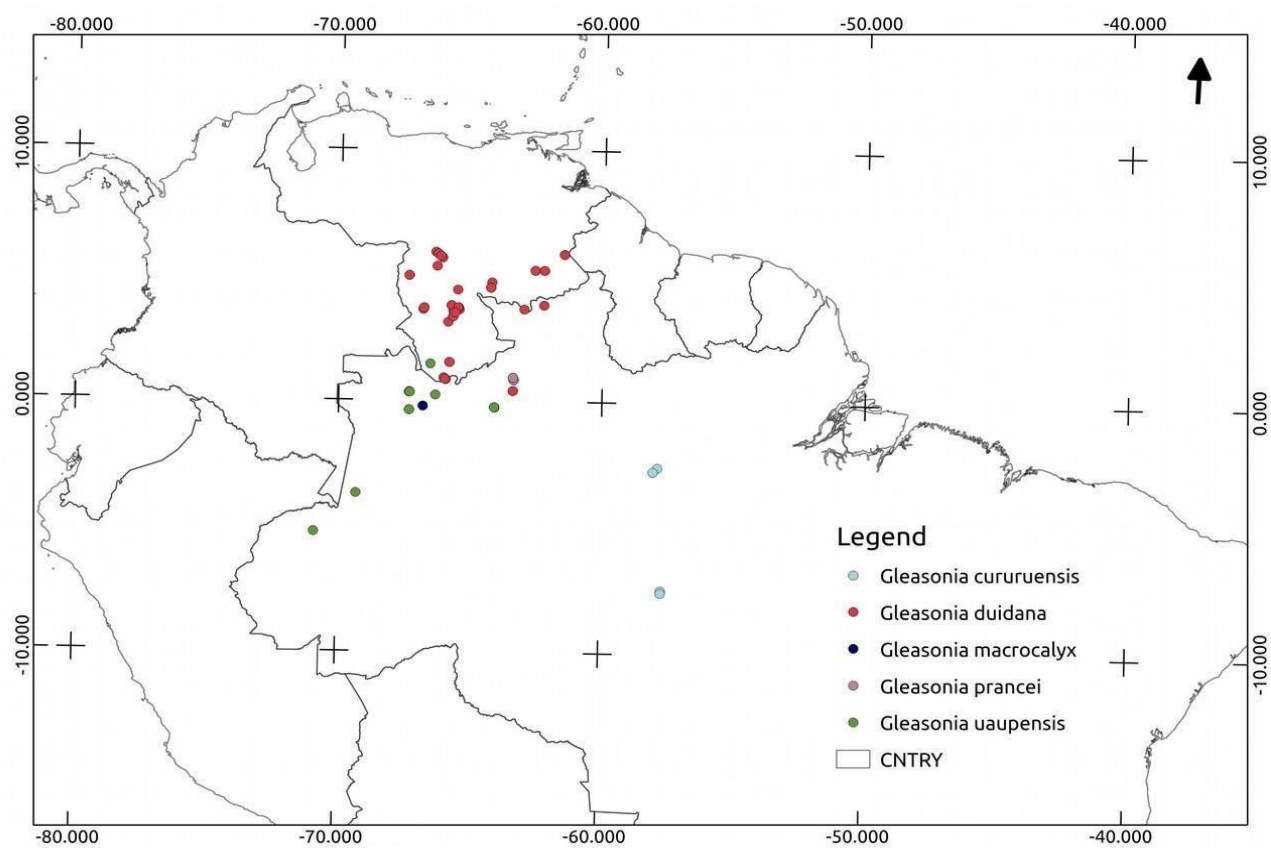


Figure 2: Distribution map of *Gleasonia*

Henriquezia Spruce ex Benth, Hooker's J. Bot. Kew Gard. Misc. 6: 338. 1854. TYPE.

Henriquezia verticillata Spruce ex Benth

Treelets or trees; exudate red; young stems terete, glabrescent to ferruginous-tomentose; stipules paired inserted partly on petiole and partly on stem, persistent, linear, ferruginous-tomentose. Leaves 3-6-whorled; petioles with two circular glands at base; lamina elliptic, lanceolate or oblong, retuse to acuminate at apex, attenuate, cuneate to truncate at base, glabrous adaxially, glabrous to glabrescent abaxially, papillate surface abaxially, with venation brochidodromous. Inflorescences cyme, sparsely or dense ferruginous-tomentose or hirsute. Flowers with hypanthium obconic, calyx 4-5 lobes, regular lobes and not showy, deltoid to lanceolate, yellow-sericeous adaxially, ferruginous-tomentose abaxially; corolla zygomorphic, infundibuliform, almost sigmoid at base, creamy to pinkish, hirsute and tomentose externally, internally white with red or orange-reddish line and macula in the throat, yellow bearded, the throat with ring of trichomes, corolla lobes 5, unequal, ovate to oblong, acuminate to acute at apex; inferior ovary and secondary half-superior in fruit, 2 locule, 4 ovules per locule, tomentose circular disk at apex, stamens 5 unequal, inserted at different heights in the corolla tube. Fruits capsular, oblate in outline, surface rugose, ferruginous tomentose-hirsute, perianth scar a line horizontally or inverted U-shape in the middle of the fruit. Seeds flat, papillate.

Henriquezia is morphologically recognized due to its stipules inserted partly on the petiole and partly on the stem (fig. 3C-D), petioles with two circular glands at the base (fig 3D), zygomorphic corolla and inner corolla white with red macula (fig 3G), capsular fruits with perianth scar at the middle of the fruit (fig. 3H). *Henriquezia* is the smallest genus in Henriquezieae tribe, with only three species. It is distributed in Brazil, Colombia, Venezuela and Guyana (fig. 5), and it occurs close to riverbank in open or forested white-sand forest. *Henriquezia* is a monophyletic group and it is sister of *Platycarpum*. It has as potencial synapomorphy partially intrapetiolar stipules (see chapter I).

Key to the species of *Henriquezia*

- 1a. Leaves narrow lanceolate, acuminate to acute at apex, abaxially leaves with papillate appearance (waxy papillae) *H. jenmanii* K. Schumann
- 1b. Leaves oblong to obovate, acute, round or retuse at apex, abaxially leaves without papillate appearance (without waxy papillae). 2
- 2a. Leaves abaxially brown when dry, calyx lobe 0.4-0.6 cm long..... *H. verticillata* Spruce ex Benth
- 2b. Leaves abaxially yellow when dry, calyx lobe > 1.3 cm long..... *H. nitida* Spruce ex Benth

1. *Henriquezia jenmanii* K. Schumann, Mart. Fl. Bras. 6(6): 135. 1889; Brown, Trans. Linn. Soc. London, Bot. 6: 33, pl. 4. 1901. TYPE. Guyana. Mazaruni-Potaro Region: Mazaruni River, near the mouth, Sep. 1880 (fl), *Jenman* 629 (holotype, K not seen, NY neg. 3207 at NY!; isotypes, BRG not seen).

Trees to 15 m, 20 cm dbh; young stems striate, pubescence in two layers, shorter layer dense ferruginous-tomentose, longer layer dense hirsute; stipules 1.0–1.2 cm, persistent, linear, glabrescent to dense ferruginous-tomentose. Leaves 3–4-whorled; petioles 1.4–2.0 cm long, pubescence with shorter layer sparse to dense ferruginous-tomentose, longer layer dense to sparse hirsute, at base 2 circular glands, 1.2–1.5 mm; lamina 15–32(–36) × 4.2–6.4 cm, narrow lanceolate, acuminate to acute at apex, cuneate at base, glabrous adaxially, glabrous to sparse reddish trichomes abaxially; surface abaxially yellowish-cinereous with waxy papillae, venation brochidodromous, 15–19(–23) pairs of secondary veins, midrib impressed and secondary veins flat adaxially, midrib and secondary veins prominent abaxially, indumentum adaxially and abaxially glabrous or glabrescent with sparse trichomes reddish (0.3 mm), tertiary veins alternate percurrent. Inflorescences 7.5–16.0 × 11.0–18.0 cm; peduncle 2.5–4.0 cm; pubescence two layers, shorter layer dense ferruginous-tomentose, longer layer ferruginous-hirsute, pedicel 0.3–0.4 cm. Flowers with hypanthium obconic, 0.3–0.4 cm long; calyx lobes 5, 1.4–1.6 × 0.4–0.7 cm, lanceolate, acuminate at apex, externally dense ferruginous-tomentose, with a darker central line along middle of lobe, internally dense

yellow-sericeous; corolla infundibuliform, 3.8–5.2 cm long, creamy, externally pubescence in two layers, shorter layer dense whitish-tomentose, longer layer dense creamy hirsute, internally with sparse trichomes, a yellow bearded lobe; corolla lobes 5, 1–1.5 × 0.7–1.2 cm, oblong to ovate, rounded or acute at apex; stamens 5, filaments 7–10 mm long, anthers 5–5.6 mm long; ovary with tomentose circular disk at apex, style 7 mm long, stigmatic lobes 1–mm long. Fruits capsular, 6–10 × 9–12 cm, oblate, surface rugose, ferruginous-tomentose, perianth scar at the middle of fruit. Seeds 5.5–9.5 cm long.

Illustration. Roger (1984), woods and fruit anatomy, embryos.

Phenology. Flower in August and October, fruits in development in September and February.

Distribution and habitat. This species is geographically distant from the other two species of the genus. It occurs in watershed junction of Mazaruni and Esequibo rivers in Guyana (fig. 5). It grows in foreshore of this river with sandy and silty soils.

Discussion. *Henriquezia jenmanii* is morphologically similar to *H. nitida* because of its lanceolate calyx lobe with acuminate apex and a darker central line along the middle of the lobe. *Henriquezia jenmanii* can be distinguished from *H. nitida* by its abaxial leaf with waxy papillae (fig 4A-B), giving a cinereous appearance in *H. jenmanii*, in comparison with the abaxial leaf without wax ornamentation in *H. nitida* (fig. 4E).

Additional specimens examined. GUYANA. Mazaruni-Potaro River junction, foreshore on sandy silt at or below tidal level, 13 Sep 1942, *Forest Dept. F847* (BRG, F, NY); Mazaruni-Esequeibo junction, Bartica Point, alluvium or sand, 18 Feb 1843, *Forest Dept. F1194* (BRG); Mazaruni River, near the mouth, Oct 1899, *Jenman 7524* (BRG); Mazaruni River, Autumn 1898, McConnell & Quelch 711 (BRG, K); Bartica, frequent on low islands and on fringe, often in water, 27 Sep 1979, *Rogers & Persaud 46* (MICH, NY, U, VEN).

2. *Henriquezia nitida* Spruce ex Benth, Trans. Linn. Soc. London 22: 297, pl. 54. 1859.

Henriquezia nitida var. *nitida* Spruce ex Benth, *syn. nov.* TYPE. Venezuela. Amazonas: ad flumina Casiquiari, Vasiva et Pacimoni, 1853-1854 (fl), *Spruce 3690* (holotype, K not seen, NY neg. 3208 at NY!; isotypes, B photo at GH!, B photo at NY!, F fragment!, GH!, NY!).

Henriquezia longisepala Bremekamp, Acta Bot. Neerl. 6: 376. 1957. TYPE. Brazil.

Amazonas: Rio Negro, São Felipe, Igarapé Touri, igapó, 27 Sep. 1952 (fl, fr), *Fróes 28781*

(holotype, U not seen; isotype, IAN not seen, NY neg. 6176 at NY!). *Henriquezia nitida* var. *longisepala* (Bremekamp) Roger, Fl. Neotropica. 39: 92. 1984, *syn. nov.*

Henriquezia macrophylla Ducke, Notizbl. Bot. Gart. Berlin-Dahlem 11: 475. 1932; Arch. Jard. Bot. Rio de Janeiro 6: 92. 1933. *Henriquezia nitida* var. *macrophylla* (Ducke) Steyermark, Mem. New York Bot. Gard. 10: 2006. 1963. *syn. nov.* TYPE. Brazil. Amazonas: Rio Curicuriary, affl. do alto Rio Negro, 28 Nov. 1929 (fl), *Ducke 22815* (holotype, RB!; isotypes, U not seen, US!).

Henriquezia nitida var. *subcuneata* Steyermark, Mem. New York Bot. Gard. 10: 207. 1963. TYPE. Brazil. Amazonas: Rio Negro, Preto, Campina, 18 Nov. 1947, *Fróes 22885* (holotype, NY!; isotype, US!).

Henriquezia oblonga Spruce ex Benth, Trans. Linn. Soc. London 22: 297. 1859. TYPE. Venezuela. Territorio Federal Amazonas: In ripas fl. Atabapo inunds, Jun. 1854, *Spruce 3702* (holotype, K not seen, NY neg. 3209 at NY!). *Henriquezia nitida* var. *oblonga* (Spruce ex Benth) Steyermark, Mem. New York Bot. Gard. 10: 207. 1963.

Treelets or trees 3–20 m, to 20 cm dbh; external bark with scales, inner bark orange; exudate red; young stems terete, dense ferruginous-tomentose; stipules linear, 1.5–2.8-cm, persistent, ferruginous-tomentose. Leaves 3–4-whorled; petioles 1.1–2.2 cm long, sparse to dense ferruginous-tomentose, with two circular glands at base, 1.2–1.5 mm; lamina 15–32(–41) × 5–11(15) cm, elliptic, oblong to obovate, rounded or retuse (rarely acute) at apex, truncate at base, surface adaxially papillate, covered with cinereous wax, which resembles trichomes (fig. 4C-D), glabrous, surface abaxially yellow without waxy papillae, glabrous to sparse whitish-adpressed trichomes (0.1 mm); venation brochidodromous, 13–19 pairs of secondary veins, midrib and secondary veins adaxially and abaxially prominent, reddish when dry, glabrous or glabrescent with whitish-adpressed trichomes (0.1–0.2 mm) on veins, tertiary veins alternate percurrent. Inflorescences 8–25 × 10–12 cm, peduncle 3–5 cm; pubescence ferruginous-tomentose, pedicel 0.6–0.8 cm. Flowers with hypanthium obconic, 0.4–0.6 cm, pubescence the same as inflorescence axes; calyx lobes 4, 1.3–2.5(–2.8) × 0.4–0.6 cm, lanceolate, acuminate, dense yellow-sericeous adaxially, dense yellow-tomentose abaxially, with a dark central line along middle of lobe; corolla (2.6–)4.0–5.8 cm long, creamy to reddish, externally with pubescence longer layer yellow-hirsute, shorter layer cream-

tomentose, internally white, with red or orange macula in the throat, one yellow bearded lobe and the other lobes glabrescent, a ring of creamy trichomes at base, corolla lobes 5, 0.9–1.8 × 0.8–2.0 cm, unequal, acuminate at apex; stamens 5, filaments 15–16 mm long, anthers 7–8 mm long; ovary with tomentose circular disk at apex, style 24–33 mm long, stigmatic lobes 1–2 mm, yellow pubescence. Fruits capsular, 5.0–10.5 × 7–13 cm, oblate in outline, with surface ferruginous-tomentose, perianth scar horizontally at the middle. Seeds 5.0–8.0 × 3.0–4.2 cm.

Illustration. Bremekamp (1957), pollen; Rogers (1984), wood anatomy, petiole anatomy, SEM of pollen, pictures of fruit, SEM seed surface details, line draw of flowering branch, calyx, corolla, pistil; Steyermark & Taylor (2004), flowering branch and fruit.

Phenology. Flowers from October to January and fruits from November to March.

Distribution and habitat. This species occurs in southeast of Colombia, south of Venezuela and north of Brazil (fig. 6). It is an emergent tree in white sand-forest, usually this species is recorded in white-sand forest with open canopy and periodically flooded.

Discussion. This species resembles *Henriquezia jenmanii* because of its calyx lobe, for differences see comments in *H. jenmanii*. We did not recognize the varieties in this species because the limits are not consistent when all collections are analyzed together. *Henriquezia nitida* var. *macrophylla* apparently is the extreme size in leaves for *H. nitida* individuals. We observed that leaves from juvenile individuals or new leaves can overlap the limits of leaves giving for *Henriquezia nitida* var. *macrophylla* (41 × 15 cm). While for *Henriquezia nitida* var. *longisepala* the limits given for calyx lobe (1.7–2.8 cm) overlap between varieties. We observed one population of *Henriquezia nitida* in Campinas, Rio Negro (Amazonas state in Brazil), that appears to have a gradual variation on calyx lobe sizes, Dávila *et al.* 6445 has a calyx lobe measuring 2.5 cm, which is close to limits defined for *H. nitida* var. *longisepala*. (1.7–2.8 cm), and it is longer in comparison with other collections of the same population. But it is not clear if this long calyx lobes variation is a morphological plasticity influenced by habitat occurrence. This collection was made between the limits of a white sand-forest with seasonal flooded and forested white-sand forest.

Additional specimens examined. BRAZIL. **Amazonas:** São Gabriel da Cachoeira, Rio Içana Comunidade Jauacanã, 29 Jun 2009, Caddah *et al.* 546 (INPA); Comunidade Monte Cristo, 17 Jun 2009, Carvalho 1592 (INPA); Borda do Igarapé da Lagoa do Jauacanã, 30 Nov

2013, *Dávila et al.* 6437 (INPA); 30 Nov 2013, *Dávila et al.* 6445 (INPA); Rio Vaupés, 11 May 1942, *Fróes* 12573/297 (A, F); upper Rio Negro basin, Rio Xié, Cachoeira Cumatí, 29 Nov-7 Dec 1947, *Schultes & López* 9227 (F, GH, K). COLOMBIA. **Guainía:** Inírida, comunidade de Cacahual, zona de rebalse del río Atabapo, 18 Aug 2004, *Cárdenas et al.* 15359 (COAH, UDBC); carretera entre Huesito-Puerto Caribe, río Inírida a río Guainía, 2 Oct 2005, *Cárdenas et al.* 16938 (COAH); *Cárdenas et al.* 16941 (COAH); 2 Oct 2005, *Cárdenas et al.* 16956 (COAH); *Cárdenas et al.* 16959 (COAH); Río Inirida, comunidad de Almidón, 7 Oct 2005, *Cárdenas et al.* 17079 (COAH); Río Atabapo, comunidad de Cacahual Bosque bajo abierto de 8 m., 8 Oct 2005, *Cárdenas et al.* 17079 (COAH); 17 Dec 2005, *Cárdenas et al.* 18044 (COAH); comunidad indígena de Chaquita, arbustal de 2 m en la margen derecha de caño Chaquita, afluente del río Atabapo, zona limítrofe con Venezuela, 4 Apr 2006, *Cárdenas et al.* 18673 (COAH); Caño Palo, 4 Jan 2007, *Cárdenas et al.* 20404 (COAH); río Atabapo, sector entre Maviso y comunidad Chaquita, 9 May 2007, *Cárdenas et al.* 20555 (COAH); Rio Atabapo, frequent along drowned river margin just above Cacagual, 19 Nov 1953, *Maguire et al.* 36268 (MICH, MO, NY); Rio Atabapo, ca. 20 km above San Fernando de Atabapo, 7 Mar 1978, *Rogers* 41, 42 (MICH, NY, VEN); Rio Atabapo, ca. 10 km below mouth of Rio Temi, periodically inundated white sand, 19 Nov 1979, *Rogers* 100 (MICH, NY, VEN), *Rogers* 101 (MICH); Rio Atabapo, ca. 50 km above San Fernando, white sand, 19 Nov 1979, *Rogers* 102 (MICH, VEN); Rio Guainia basin, Rio Naquieni, vicinity of Cerro Monachi, Jun 1948, *Schultes & Lopez* 10090 (GH); Rio Guainia, Puerto Colombia, Raudel Sapo, 31 Oct-2 Nov 1952, *Schultes et a.* 18222 (ECON, GH). VENEZUELA. **Amazonas:** Reserva Forestal El Sipapo, en sabana inundable, May 1971, *Blanco* 1202 (NY, VEN); Dept. Casiquiare, alrededores de Yavita, orilla inundada del Rio Temi, 6-19 Jul 1969, *Bunting et al.* 4039 (U, VEN); Rio Atabapo cerca de la desembocadura del Rio Atacavi, en las orillas del rio con el tronco sumergido en agua negra durante la estacion lluviosa, 4 Sep 1960, *Foldats* 3706 (F NY, US); Rio Atabapo 15 km above San Fernando de Atabapo, 17 Oct 1950, *Maguire* 29261 (NY); Rio Temi, below Yavita, caatinga, 20 Oct 1950, *Maguire* 29322 (F, NY); Cerro Yapacana, occasional along Caio Catua at NW base of mountain, 125 m, 19 Nov 1953, *Maguire et al.* 36557 (NY, RB, US); Rio Pacimoni, 50 km above mouth, 27 Nov 1953, *Maguire et al.* 36640 (NY); Atabapo, Planicie inundable Riverina del Caño Yagua, Nov 1989, *Marin* 459 (PORT); Savannah behind base camp. 9, 11 Feb 2005, *Redden et al.* 3683 (PORT);

Cerro Yapacana, along Caio Catua, 7-9 Nov 1979, *Rogers 61* (MICH, NY, VEN), 64 (MICH); Rio Guainia, Maroa, along shore ca. 2 km upstream from town, 15 Nov 1979, *Rogers 82* (MICH); Rio Temi, between Yavita and Santa Cruz, 17-18 Nov 1979, *Rogers 83* (MICH), *Rogers 85* (MICH, NY, VEN), *Rogers 88* (MICH), *Rogers 89* (MICH), *Rogers 92* (MICH, VEN), *Rogers 94* (MICH), *Rogers 99* (MICH); Santa Cruz, forested area within white sand savanna, 18 Nov 1979, *Rogers 96* (MICH, VEN); Region of Yavita, Vargas, Nov 1845, Spruce s.n (F); a lo largo del Rio Temi, alrededores de Yavita, 22 Apr 1970, *Steyermark & Bunting 102956* (F, NY, VEN); Rio Atacavi, El Amidon, en los limites del Departamento Atabapo y Casiquiare. Rio Atacavi. Frente 2, Nov 1989, *Velazco et al. 243* (PORT); Yavita, entre palmas en las sabanetas, 29 Jan 1942, *Williams 14076* (F, US, VEN); Rio Caname, 11 Nov 1989, *Yanez et al. 92* (PORT).

3. *Henriquezia verticillata* Spruce ex Bentham, Hooker's J. Bot. Kew Gard. Misc. 6: 338. 1854. TYPE. Brazil. Amazonas: Secus Rio Negro inter Barcellos et San Isabel, Dec. 1851 (fl), *Spruce 1957* (holotype, K not seen, NY neg. 3211 photo at NY!; isotypes, F fragments!, GH!, NY!, RB!).

Henriquezia obovata Spruce ex Bentham, Trans. Linn. Soc. London 22: 296, pl. 53. 1859. TYPE. Venezuela. Amazonas: In sylvis secus Guainiam, Jun. 1854 (fr), *Spruce s.n.* (holotype, K not seen).

Henriquezia verticillata var. *apiculata* Steyermark, Mem. New York Bot. Gard. 10: 204. 1963. TYPE. Brazil. Amazonas: Manaus, Igarape Mindu Superiorem (fl), 19 Nov. 1935, *Ducke 81* (holotype, US!; isotypes, A!, F!, MO!, NY!, R!).

Trees up to 30–40 m tall, to 40 cm dbh, with external bark ribbed and inner bark yellow; red exudate; Young stems terete, glabrescent to ferruginous–tomentose; stipules linear, 1.5–4.0 (6)–0.1–0.2 cm, caducous or persistent, dense tomentose. Leaves 4–5–whorled; petioles 1.0–2.5 cm long, ferruginous–tomentose, at base two circular glands, 1.2–1.5 mm; lamina 10–20 (45) × 4.5–8.5(11.5) cm, oblong to obovate, acute to rounded or retuse at apex, attenuate to truncate at base, surface adaxially without wax covering and not papillate surface (fig. 4F), brown when dry, surface abaxially without waxy papillae (fig. 4G–H), brown when dry; venation brochidodromous, 11–17 pairs of secondary veins, with dense or sparse

ferruginous-tomentose indumentum, midrib and secondary veins adaxially and abaxially prominent, tertiary veins alternate percurrent, indumentum adaxially and abaxially glabrescent or whitish bent trichomes (0.4–0.7 mm). Inflorescences 8–20 × 10–13 cm; peduncle 2.6–4 cm; pubescence dense ferruginous-tomentose, pedicel 0.3–0.7 cm. Flowers with hypanthium obconic, 0.3–0.5 cm, short tube 0.2–0.5 cm, calyx 4 lobes, deltoid 0.4–0.6 × 0.2–0.4 cm, adaxially yellow-sericeous, next to the apex sericeous and puberulent, abaxially dense ferruginous-tomentose; corolla funnelform, 4.1–5.8 cm long, externally yellow, pubescence in two layers, longer layer hirsute and shorter layer tomentose, internally white with red or orange macula in the throat, one yellow bearded lobe and the other lobes glabrescent, a ring of creamy trichomes at base, corolla lobes 1.0–2.0 × 0.7–1.8 cm, unequal, acute; stamens 5, filaments 9–12 mm long, anthers 6–8 mm long; ovary with tomentose circular disk at apex, style 17–20 mm long, stigmatic lobes 2, 1–2 mm, with yellow indumentum. Fruits capsular, 6.4–7.2 × 8.0–12.0 cm, oblate in outline, with surface ferruginous-tomentose, perianth scar at the middle. Seeds 4–5 × 3–4 cm.

Illustration. Bentham (1959), line draw of flowering branch, flower, fruit and seed; Bremekamp (1957), floral diagram, fruit, stomata, testa; Rogers (1984), pictures of habit and leaves, inflorescence drawn, stipule anatomy, petiole anatomy, leaf surface, leaf anatomy, fruit and seed pictures; Schumann (1889, 1891), line draw of inflorescence and flower.

Phenology. Flowers from October to December and fruits from June to November.

Distribution and habitat. This species is distributed from southeast of Colombia, south of Venezuela to Manaus and North of Brazil (Amazonas state) (fig. 5).

Discussion. This species has a similar distribution of *Henriquezia nitida* but it does not share the same habitat. *Henriquezia verticillata* is an emergent tree in seasonally flooded forest with closed canopy that reaches 30 m high. While *Henriquezia nitida* is an emergent tree in white-sand forest with open canopy that reaches 10–15 m high. This species can be differentiated by its brown leaves when dry, usually more leaves per node (4–5) than the other two species in the genus (3–4), calyx lobe < 0.6 cm (vs. >1.3 cm long in *H. nitida* and *H. jenmanii*).

Additional specimens examined. BRAZIL. **Amazonas:** Along Aracá River (a black water tributary of Rio Negro), 8 Aug 1996, *Acevedo-Rodríguez et al.* 8117 (MO, INPA); Reserva Florestal Ducke, Manaus-Itacoatiara, Km 26, 25 Nov 1994, Assunção 91 (INPA, MO,

NY, RB); Manaus, Igarapé do Parque 10, 14 Nov 1955, *Coelho* 2904 (INPA, RB); 9 Jan 1956, *Coelho* 3298 (INPA, RB); 3 Apr 1956, *Coelho* 3805 (INPA, RB); São Gabriel da Cachoeira, Rio Negro, Cabeçudo, 24 Nov 2013, Dávila et al. 6415 (UEC, MO); Rio Taruma, lower falls, near Manaus, river shore, 12 Nov 1942, *Ducke s.n.*, (MICH); Manaus, Jun 1932, *Ducke* 36 (F, MADw); Manaus, silva paludo secus rivulas, 8 Dec 1927, *Ducke* 21683 (MICH, K, U); Manaus, Cachoeira do Mindú, 22 Oct 1929, *Ducke* 22813 (MICH, NY, R, RB, US); Santa Isabel do Rio Negro, mata da baixa inundável, 13 Nov 1929, *Ducke* 22814 (RB); Mun. Sao Gabriel, Rio Marie, Macubeta, 31 Jan 1942, *Fróes* 580 (NY); Rio Negro, Cucui, 15 Dec 1945, *Fróes* 21518 (F, NY, US); Rio Negro, Preto Maboaby, terra firme, highland, high forest, 8 Nov 1947, *Fróes* 22784 (NY, U), 17 Nov 1947, *Fróes* 22872 (NY); vicinity of Manaus, Cachoeira Baixa Tarumã, 25 Mar 1971, *Prance et al.* 11601 (GH, INPA); Manaus, margem do Igarapé do Pensador, 11 July 1955, *Rodrigues* 2844 (INPA); upper Rio Negro, 20 mi below Sao Gabriel, periodically inundated forest, 20 Jan 1978, *Rogers* 4 (NY); 20 mi below Sao Gabriel, on beach, 20 Jan 1978, *Rogers* 5 (MICH, NY); approx. 30 mi below Sao Gabriel, periodically inundated forest, 23 Jan 1978, *Rogers* 6 (NY); upper Rio Negro basin, above mouth of Uaupés, near Sao Joaquim, 6 Nov 1947, *Schultes & Pires* 8990 (F); vicinity of Manaus, Cachoeira Baixa de Tarumã, 11-14 Apr 1972, *Schultes & Rodrigues* 26141A (ECON, GH, INPA); Reserva Florestal Ducke, Manaus-Itacoatiara, Km 26. Igarapé do Aracá, próximo ao acampamento, margem do Igarapé. 12 Nov 1993, *Vicentini et al.* 370 (INPA, MO, NY, RB).

COLOMBIA. **Amazonas:** Fronteira Brasil-Colombia, confluência dos rios Traíra e Apaporis, cachoeira Urumutum, a 1:30 minutos e Vila Bittencourt, 12 Nov 1982, *Amaral et al.* 567 (INPA, MO, RB).

VENEZUELA. **Amazonas:** Rio Guainía, near Maroa, occasional along river, 27 Nov 1953, *Maguire et al.* 36432 (NY, US, VEN); Cerca de la boca del Casiquiare rio Negro, 5 Feb 1977, *Morillo* 5316 (VEN); Rio Negro, San Carlos de Rio Negro, stretch of periodically inundated shore, 28 Feb-1 Mar 1978, *Rogers* 18 (MICH, NY, U, VEN), *Rogers* 19-25, *Rogers* 34, *Rogers* 40 (MICH); Maroa, 1 km E of Rio Guainía, 15 Nov 1979, *Rogers* 70 (MICH).

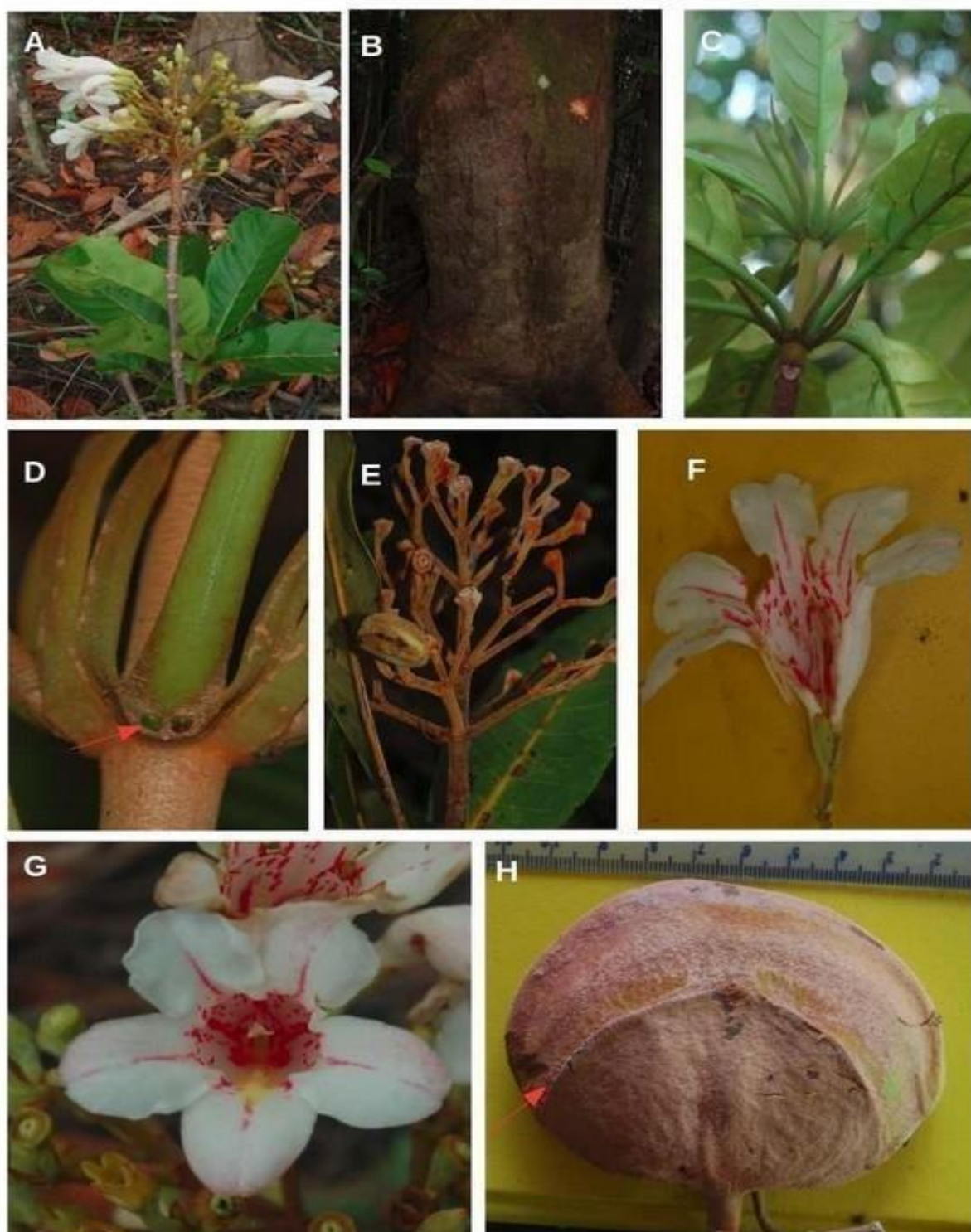


Figura 3: Morphology of *Henriquezia*. A-G. *Henriquezia verticillata*, H. *H. nitida*. A. Terminal branch with flowers, B. External bark, C. Young stem showing phyllotaxy and stipules, D. Petiole base, arrow shows glands at petiole base, E. Cymose inflorescence, F. Open flower, G. Open corolla showing the throat with red lines and macula and yellow bearded corolla, H. Mature woody capsular fruit, arrow shows the perianth scar in the middle of the fruit.

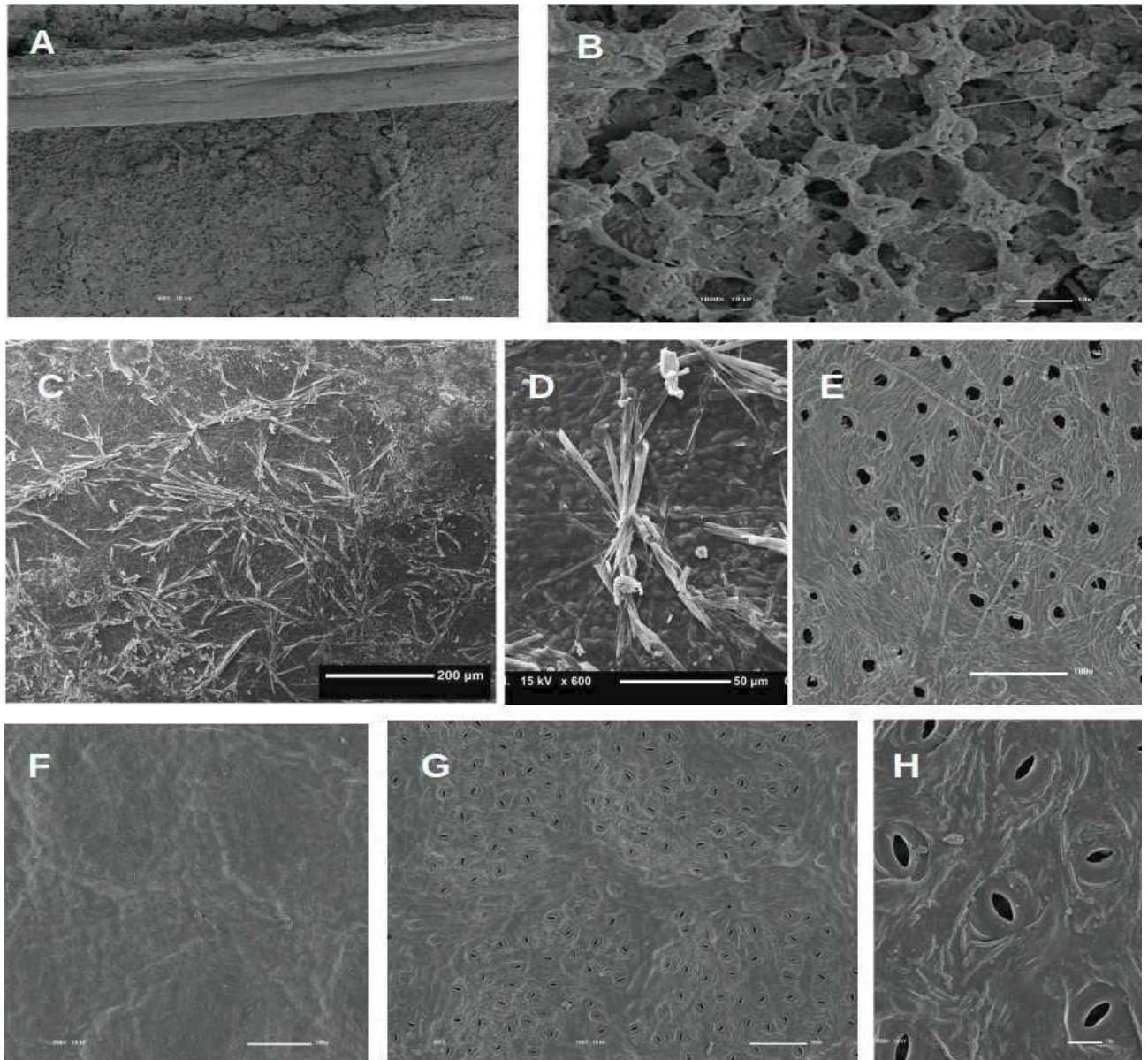


Figure 4: A-B. *Henriquezia jenmanii*, C-E. *H. nitida*, F-H. *H. verticillata*. A. Abaxial leaf view, B. Wax ornamentation of abaxial leaf, C. Adaxial leaf view, D. Adaxial surface papillate with wax ornamentation, which has appearances of trichomes, E. Abaxial leaf view showing stomata, F. Adaxial leaf view, G. Abaxial leaf view showing stomata, H. a close-up view of stomata.

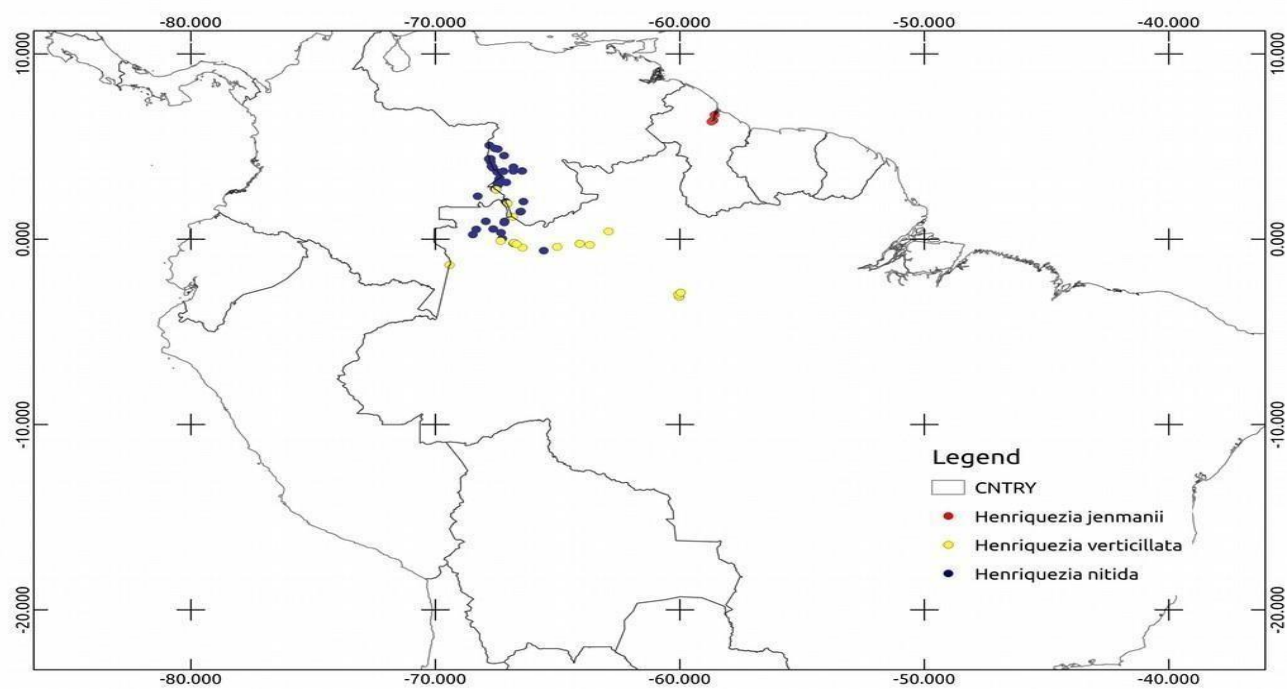


Figure 5: Distribution map of *Henriquezia*.

Platycarpum Bonpl., Pl. Aequin. 2: 81, pl. 104. 1811; TYPE: *Platycarpum orinocense* Bonpl.

Shrubs or trees, exudate red, translucent or absent; young stems circular, triangular, or angled, pubescence in one or two layers; stipules interpetiolar, lanceolate, triangular or ovate. Leaves decussate or whorled; petioles usually one gland or three, rarely without gland (*P. eglandulosum*); lamina elliptic, obovate or rounded, adaxially strigose or strigillose, abaxially glabrescent or pubescence in one or two layers, villous, tomentose, hispid or hirsute, sometimes abaxial surface papillose. Inflorescences cymose or congested cymose, 3–5 order branching, foliar bracts at base of inflorescence, bracteoles linear or lunate. Flowers with hypanthium obconic; calyx 4–5 lobes, regular lobes not showy, these oblong, deltoid or fusiform; corolla zygomorphic, infundibular or funnelform, white, creamy, yellowish or pinkish, externally with pubescence in two layers, internally white or pink with red lines and macula in the throat, glabrescent, a ring of trichomes at the height of filament insertion, one or rarely two yellow-bearded lobes, corolla lobes 4–5, acuminate, acute or rounded with cucullate margin; stamens 5, inserted at two different heights in the corolla tube, anthers acuminate at the apex and cordate at the base; ovary inferior in flower and secondary superior in fruit, with tomentose circular disk at apex, style with two stigmatic lobes. Fruits capsular, elliptic, oblate, oblong or ovate, perianth scar at the base on the fruit, markedly flattened, parallel to woody septum, with surface verrucose or rugose, pubescence in one or two layers, dehiscence loculicidal. Seeds D-shaped, reniform or elliptic, with surface pitted, with marginal wing.

Platycarpum is characterized by its interpetiolar stipules (fig. 6D), adaxial leaves with strigose or strigillose trichomes (fig. 7-8), glands at the petiole base (fig. 6G), zygomorphic corollas (fig. 6H), and capsular fruits with perianth scar at the base of fruit (fig. 6I). The genus occurs in Colombia, Venezuela, Guyana, Peru and Brazil (fig. 9A-B), from lowland savannas or open and forested white sand-forest to highland on mountains “tepui” with shrubby or open areas. *Platycarpum* is a monophyletic group and is close related to *Henriquezia*, and both form a clade in the internal relationship of the tribe (see Charter I). The synapomorphies proposed for the genus are leaves with strigose adaxial surface and perianth scar at the base of the fruits (see chapter I).

Key to the species of *Platycarpum*

- 1a. Petioles without glands.....*P. eglandulosum* Steyermark
- 1b. Petioles with glands 2
 - 2a Petioles with than three glands.....*P. rugosum* Steyermark
 - 2b. Petioles with only one gland. 3
 - 3a. Inflorescence congested cymose, calyx lobe 4.....*P. rhododactylum*
Wood. & Steyermark
 - 3b. Inflorescence cymose, calyx lobe 5. 4
 - 4a. Abaxial lamina glaucous 5
 - 5a. Abaxial lamina with venation white-tomentose areoles.....6
 - 6a. Fruits oblate, 2.5–3.0 cm long...*P. egleri* G.K.Rogers
 - 6b. Fruits ellipsoid, 1.3–2.3 cm long.....*P. schultesii*
Steyermark
 - 5b. Abaxial lamina without venation white-tomentose areoles..7
 - 7a. Fruits 4.3–5.7 cm long.....*P. decipiens* Wood.
& Steyerm.
 - 7b. Fruits less than 3.6 cm long.....*P. negrense* Ducke
 - 4b. Abaxial lamina brown, golden, ferruginous or white-creamy (not
glaucous)..... 8
 - 8a. Lamina abaxially with one type of trichomes 9
 - 9a. Leaves with more than 20 secondary veins, abaxial
lamina with golden-villous
trichomes.....*P. vriesendorpiae* Dávila
 - 9b. Leaves with less than 18 pairs of secondary veins,
abaxial leaves with ferruginous or white-creamy
trichomes10
 - 10a. Abaxial surface papillate..... 11

- 11a. Leaves oblanceolate.....*P. loretensis*
Dávila & L. Kinoshita
- 11b. Leaves elliptic or wide-elliptic to
obovate12
- 12a. Leaves 20–21 × 7.3–10 cm,
abaxially ferruginous-
villous.....*P. piresii*Dávila
- 12b. Leaves 12–17 × 4.5–5.8 cm,
abaxially ferruginous
hirsute.....*P. duckei* Steyermark
- 10b. Abaxial surface not papillate13
- 13a. Petioles 1.4–1.6 cm long, calyx lobe
2.8–3.0 cm.....*P. araracuarensense* Dávila
- 13b. Petioles 0.3–1.0 cm long, calyx lobe
0.5–0.6 cm.....*P. froesii* Bremekamp
- 8b. Lamina abaxially with two types of trichomes 14
- 14a. Phyllotaxy decussate, fruits 3.0–3.9 cm
long.....*P. orinocense* Bonpl.
- 14b. Phyllotaxy 3-whorled, fruits 4.5–5.5 cm long...
.....*P. acreanum* G.K.Rogers

1. *Platycarpum acreanum* G.K.Rogers, Fl. Neotropica. Monogr. 39: 101. 1984. TYPE. Brazil. Acre: Cruzeiro do Sul, próximo do novo aeroporto, mata de terra firme, solo argilo-arenoso, 6 Feb. 1976, *Monteiro & Damião 146* (holotype, INPA!), Fig. 10

Trees 5–35 m tall, ca. 40 cm dbh, with outer bark fissured, with red exudate; young stems terete to angled and striate, with pubescence in two layers, longer layer dense ferruginous-hirsute, 2.0–2.4 mm long, shorter layer densely white or ferruginous-tomentose (1 mm long); stipules lanceolate, 2.9–3.8(–4.8) × 0.7 cm, caducous, adaxially pubescence in two layers,

longer layer dense ferruginous-hirsute, 1.8–2.3 mm, abaxially sericeous with pubescence yellowish. Leaves 3–whorled; petioles 1.1–1.6 cm long, pubescence the same as young stem, near abaxial base with one gland, this U-shaped to slightly rectangular, 0.3–0.4 cm long, dark when dry; lamina 19.3–23.5 × 6.3–10.0 cm, narrowly elliptic to oblong, rounded to retuse at apex, cuneate at base, adaxially sparse one layer of strigose cinereous trichomes, abaxially with two layers of trichomes, longer layer dense ferruginous-villous, (1.1–1.8 mm long), shorter layer sparse cinereous-tomentose, surface with elongated cinereous papillae; venation eucamptodromous, 19–23 pairs of secondary veins, midrib and secondary veins flattened adaxially and prominent abaxially, with dense tomentose-hirsute indumentum, intersecondary and tertiary veins conspicuous, reticulate white-tomentose areoles absent. Inflorescences cymose, 10.0–15.5 cm long, with 4 orders of branching, with foliar bracts at base of inflorescence, these 9.0 × 2.2 cm, bracteoles 0.8–1.0 cm long, these with pubescent in two layers, longer layer dense ferruginous-hirsute, shorter layer dense ferruginous-tomentose. Flowers with hypanthium 0.2–0.3 cm long, sparse ferruginous-hirsute and dense ferruginous-tomentose; calyx lobes 5, these elliptic to oblong, 0.9–1.1 × 0.2–0.3 cm, externally with pubescence in two layers, longer layer sparsely hirsute, shorter layer densely tomentose, internally yellowish-sericeous; corolla funnelform, 2.0–2.5 cm long, externally yellowish with pubescence in two layers, longer layer villous, shorter layer tomentose, and internally white with red macula in the throat, a ring of yellowish trichomes at apex of the throat, one yellow bearded lobe, corolla lobes 5, 0.7–1.0 cm long, these elliptic, acute, with sinuate margins; stamens 5, filaments 5–7 mm long, anthers 0.4 cm long; ovary with tomentose circular disk at apex, style ca. 1 cm long, stigmatic lobes 2. Fruits capsular, 4.5–5.5 × 3.6–4.9 cm, oblong, with surface verrucose, two layers of trichomes, shorter layer dense ferruginous-tomentose and longer layer isolated ferruginous-hirsute. Seeds not seen.

Illustration. Rogers (1984), picture of holotype.

Phenology. Flowers in October and fruits from October to December.

Distribution and habitat. This species is distributed in Acre and Amazonas states (Brazil) (fig. 7A). It grows in white-sand forest.

Discussion. This is the first time that flowers are described for *P. acreanum* and the abaxial surface of leaves are detailed. Abaxial leaf surface shows a short layer of trichomes

mixed with elongated papillae and a second layer of trichomes that are villous-ferruginous (fig. 7A-C).

This species is similar to *Platycarpum vriesendorpiae*, due to its mostly 3-whorled phyllotaxy, leaves abaxially with dense pubescence, and fruits with similar shape and size. *Platycarpum acreanum* can be differentiated by its lanceolate stipules (vs. triangular in *P. vriesendorpiae*), lamina narrow elliptic to oblong (vs. obovate to elliptic in *P. vriesendorpiae*), lamina abaxially with two layers of pubescence, a shorter layer of tomentose-hispidulous trichomes and a longer layer of tawny-hirsute trichomes (vs. one layer of golden-velutinous trichomes in *P. vriesendorpiae*), and corolla 2.0–2.5 cm (vs. corolla 1.5–2.0 cm in *P. vriesendorpiae*).

Additional specimens examined. BRAZIL. **Acre:** Cruzeiro do Sul: Igarapé Humaitá, afluyente da margem direita do Rio Juruá, atrás da Colocação Dois Portos, 08°19'S, 72°47'W, 27 Oct 1991, *Cid et al. 10407* (INPA, MO, NY); Basin of rio Juruá, vegetation flanking unpaved and unfinished road (BR 307) near intersection with Ramal Pentecostes, 07°24'4.2"S-07°26'8.58"S, 73°01'17.16"- 72°58'9.18"W, 12 Dec 2000, *Daly et al. 10611* (MO); Cruzeiro do Sul, 10 Oct 2014, *Dávila et al. 6321* (UEC, MO); Cruzeiro do Sul, 10 Oct 2014, *Dávila et al. 6334* (UEC, INPA, MO); Porto Walter: Rio Juruá-Mirim, Comunidade San Antonio, 200 m, 12 Nov 2001, *Delprete et al. 7718* (MO, NY); **Amazonas:** Coari, 4°54'07"S, 65°12'14", 13 Jun 2008, Pinto 15 (INPA).

2. *Platycarpum araracuarensense* Dávila *sp. nov.* TYPE: Colombia. Caquetá, Región Araracuara. Alrededores de la pista aérea. 0°25' S 72° 30'W. Meseta de areniscas 200-300 msn. 09 Nov 1991. *Restrepo & Matapi 429* (holotype, COAH!; isotype, MO!, NY!). Fig. 11

Diagnosis: This species is similar to *P. decipiens* due to its glabrescent leaves. However, it differs by its wide elliptic to oblong leaves, abaxially brown when dry, lamina abaxially glabrescent and without papillae (vs. elliptic to narrow-elliptic leaves, abaxially cinereous when dry, lamina abaxially glabrescent with papillate surface in *P. decipiens*).

Trees 20 m tall, 30–50 cm dbh, external bark brown fissured, inner bark yellow; exudate translucent; young stems slightly flattened at top, glabrescent; stipules lanceolate, 1 cm long, caducous, adaxially tomentose, abaxially dense to sparse ferruginous-hirsute. Leaves

decussate; petioles 1.4–1.6 cm long, glabrous or isolated trichomes as in midrib, near abaxial base one narrowly gland U-shaped or inverted triangular, 0.2–0.4 cm long, dark when dry; lamina 14–16 × 6–7 cm, wide elliptic to oblong, brown when dry, retuse at apex, cuneate at base, pubescence adaxially on layer of strigillose trichomes, abaxially one layer of trichomes, sparse white-creamy (< 1 mm) trichomes, surface without papillae abaxially, lamina border with sparse to dense ciliate trichomes, venation eucamptodromous, 16–18 pairs of secondary veins, midrib and secondary veins adaxially plane and abaxially prominent, intersecondary veins absent, reticulum minutely areolate to inconspicuous, reticulate white-tomentose areoles absent, midrib indumentum with sparse to dense trichomes (>1 mm), white to creamy adaxially, midrib indumentum abaxially dense with hirsute or antrorse trichomes. Inflorescences cymose, 6.0–9.0 × 6.6–7.2 cm, pubescence in two layers, shorter layer dense white-adpressed, longer layer dense yellow-to ferruginous-hirsute, with foliar bracts at first or second nodes of inflorescence, linear bracteoles 2–3 mm long. Flowers with hypanthium obconic 1.8–2.0 mm long, pubescence like inflorescence axes; calyx 5 lobes, these deltoid to ovate, 1.5–2.0 × 0.2 cm, externally with pubescence in two layers, shorter layer dense creamy-tomentose, longer layer dense ferruginous-hirsute, internally creamy-sericeous; corolla funnelform, 2.0–2.1 cm long, externally white-yellow with pubescence in two layers, shorter layer dense creamy-tomentose, longer layer dense yellow-tomentose, internally creamy with red macula in the throat, one lobe yellow-bearded and other glabrous, a ring with trichomes at the tube base, corolla lobes 5, 0.7–0.8 × 0.5–0.6 cm, acute; stamens 5, filaments 4.2–5 mm long, anthers ca. 3.5 mm long; ovary inferior in flower, with tomentose circular disk at apex, style 9.8 mm long, stigmatic lobes 2. Fruits capsular, 5.5 × 5 cm, oblong, with surface rugose, sparse ferruginous-tomentose. Seeds not seen.

Phenology. Flower buds in September, flowers in October and fruits in November and February.

Distribution and habitat. This species occurs in Araracuara region, in Caquetá, Colombia. It grows in sandstone plateau at 200–300 m altitude (fig 7A).

Discussion. This species is recognized by its glabrescent and brown leaves when dry. It is morphologically similar to *P. decipiens* because of its glabrescent leaves and oblong fruits, it differs by the brown abaxial leaves when dry and abaxial surface is not papillate (7E) (vs. cinereous and papillae surface in *P. decipiens*), and the intersecondary veins are absent

(vs. present in *P. decipiens*). Moreover, the corolla tube is wide, the lobes are not expanded and measure 0.7–0.8 × 0.5–0.6 cm (vs. corolla tube narrow, lobes expanded and measure 0.9–1.0 × 0.6 cm in *P. decipiens*).

Additional specimens examined. COLOMBIA, Caquetá, Solano, Estación biológica Puerto Abeja, bosque de tierra firme, sector SE PNN serranía de Chiribiquete, 18 oct 1999, *Eusse et al.* 697 (COL); 18 Oct 1999, *Eusse et al.* 707 (COAH); 23 Oct 1999, *Eusse et al.* 721 (COAH); 11 feb 1999, *Rodriguez AME-077* (COAH).

3. *Platycarpum decipiens* Woodson & Steyermark, Amer. J. Bot. 39: 422. 1952; Mem. New York Bot. Gard. 10: 256, Fig. 76, D-H, 1963. TYPE. Venezuela. Amazonas: San Carlos de Rio Negro, en la selva alta, tupida de tierra firme, 3 Feb. 1942 (fr), *Williams 14587* (holotype, F!; isotypes, A!, MO fragments!, NY!, RB!, US!, VEN!).

Platycarpum maguirei Steyermark, Mem. New York Bot. Gard. 10: 255, Fig. 76, I-J. 1963. *syn. nov.* TYPE. Venezuela. Territorio Federal Amazonas: Cerro de la Neblina, slope forest between Camps 2 and 3, 130-700 m, 5 Jan. 1958 (fl), *Maguire et al.* 42597 (holotype, NY!; isotypes, F!, GH!, K not seen, MICH!, MO!, RB!, U not seen, US!, VEN!). *syn. nov.*

Trees 25–30 m tall, ca. 45–60 cm dbh, with external bark fissured and inner bark orange; red exudate; young stems circular and striate, glabrescent; stipules lanceolate, 2.2–5.9 cm long, caducous, adaxially dense creamy-sericeous, abaxially glabrescent to dense ferruginous-hirsute, glaucous surface. Leaves decussate; petioles 1.4–2.0 cm long, glabrescent, near abaxial base one rectangular or U-shaped gland, 3–4 × 1–2 mm long, dark when dry; lamina 13.0–17.5 × 4.0–6.2 cm, elliptic to oblanceolate, abaxially glaucous, acute to retuse at apex, cuneate at base, pubescence adaxially dense white-strigillose, abaxially sparse white-adpressed, all surface cover with papillae and cinereous wax, young leaves with ciliate margins; venation eucamptodromous, 13–22 pairs of secondary veins, midrib and secondary veins adaxially flat or prominent and abaxially prominent, pubescence on veins glabrescent or setulose and hirsute, intersecondary veins present, tertiary veins conspicuous minutely reticulated, reticulate white-tomentose areoles absent. Inflorescences cymose, 9.7–15.0 × 7.5–10.0 cm, pubescence in two layers, shorter layer dense ferruginous-tomentose,

longer layer dense creamy-hirsute, linear bracteoles on distal axes 4.5 mm long, these with same pubescence like axis. Flowers with hypanthium obconic, 1.6–2.7 mm long, ferruginous tomentose-sericeous; calyx lobes 5, these deltoid to oblong, 0.8–1 cm long, externally with pubescence in 2 layers, shorter layer dense adpressed, longer dense hirsute, internally creamy-sericeous; corolla funnelform, 1.7–2.2 cm long, externally white, pubescence in two layers, shorter layer dense creamy-tomentose, longer layer dense creamy-hirsute, internally white with red macula in the throat, one yellow-bearded lobe, a ring of ferruginous trichomes at base of the tube, corolla lobes 5, 0.9–1.0 × 0.6 cm, acute; stamens 5, filaments 7.3–7.6 mm long, anthers 3.5–3.8 mm long; ovary inferior in flower, with tomentose circular disk at apex, style 8 mm long. Fruits capsular, 4.3–5.7 × 4.2–5.0 cm, oblong to ovate in outline, with obcordate apex and cordate base, surface verrucose, ferruginous-hirsute. Seeds 5–5.2 × 2.2 cm, reniform, narrow wing 10 mm wide.

Illustration. Rogers (1984), pictures of habit and inflorescence; Steyermark (1963), flower.

Phenology. Flowers in November, January and June, fruits from January to March.

Distribution and habitat. This species occurs in the Amazonas state in Venezuela and Caquetá department in Colombia (9A). It grows in non-flooded lowland rainforest with sandy soils and in the transition between non-flooded lowland and flooded rainforest.

Discussion. This species is characterized by its glaucous and papillate abaxial leaves, with glabrescent abaxial lamina and fruits oblong to ovate. *Platycarpum decipiens* is morphologically similar to *P. araracuarensense* due to its glabrescent leaves and oblong fruit, see comments in *P. araracuarensense* for differences. Also *Platycarpum decipiens* resembles *P. negrense* because of its glaucous papillate abaxial leaves, but *P. decipiens* has oblong to ovate and larger fruits 4.3–5.7 × 4.2–5 cm (vs. oblate and smaller fruits 3.0–3.6 × 2.0–3.0 in *P. negrense*).

We considered here *Platycarpum maguirei* as a synonymous of *P. decipiens* because it has the same morphology of leaves and flowers. *Platycarpum maguirei* is only known from the type collection from Cerro Neblina (Brazil-Venezuela border), the only difference that we found when compared is that the inflorescence axis pubescence is denser in *P. maguirei* than in *P. decipiens*, which is a weak difference to support *P. maguirei* as a different species.

Additional specimens examined. COLOMBIA. **Caquetá:** Sierra de Chiribiquete, campamento norte, ruta del campamento al límite 50 m de la meseta, 08 Dec 1990, *Castroviejo et al.* 12016 (COL); PNN Serranía de Chiribiquete, Cuenca alta del Río Mesay, 1 Jan 2000, *Prado et al.* 595 (FMB). VENEZUELA. **Amazonas:** Ca. 1 Km al norte de la entrada de la parcela principal del IVIC por la carretera San Carlos de Río Negro-Solano, a uns 4 Km de San Carlos, 23 Mar 2000, *Berry et al.* 7032 (MO, PORT, VEN); Atures, Segundo campamento, unos 110 Km arriba río Guayapo, May 1989, Foldats et al. 9306 (PORT); Fronteira Venezuela e Brazil, caminho à Pedra do Cucuí, 4 Dec 2013, *Dávila et al.* 6482 (UEC); Cerro de la Neblina, slope forest between Camps 2 and 3, 130-700 m, 5 Jan 1958, *Maguire et al.* 42597 (NY, F, GH, K, MICH, MO, RB, U, US, VEN); San Carlos de Río Negro, 2 km E of road to Solano, 7 km above San Carlos, widely scattered in forest, 28 Feb 1978, *Rogers* 16 (MICH); San Carlos de Río Negro, in open area NE of cemetery, 3 Mar 1978, *Rogers* 33 (MICH, NY, U, VEN); Yavita, ca. 1 km W of town, near road to Maroa, scattered in dense forest, on white sand and thick humus, 19 Nov 1979, *Rogers* 98 (MICH, NY, U, VEN); Atabapo, El Almidon, en los límites del Departamento Atabapo y Casiquiare. Río Atacavi. Frente 2, Nov 1989, Velazco 882 (MO, PORT). Río Casiquiare, 15 km from Río Guainia, Caño San Miguel just above Limoncito, 28 Jun 1959, *Wurdack & Adderly* 43226 (F, GH, MICH, MO, NY, R, U, US).

4. *Platycarpum duckei* Steyermark, Amer. J. Bot. 39: 422. 1952. TYPE. Brazil. Amazonas: Río Madeira, Borba, silva paludosa, circa Campo Grande, 25 Aug. 1942 (fl, fr), *Ducke* 1005 (holotype, US!, photo at F!; isotypes, COL!, INPA!, K not seen, MO!, NY!, R!, RB!, US!).

Trees up to 25 m tall, to 50 cm dbh, with external bark striate, and inner bark yellow; exudate red; young stems terete, dense ferruginous-hirsute (1.2–2.2 mm); stipules ovate to deltoid, 2.5–3.0 cm long, caducous, dense tawny indumentum, abaxially dense ferruginous-tomentose (2.0–2.4 mm long). Leaves decussate; petioles 1.2–1.6 cm long, dense ferruginous-hirsute, near abaxial base one narrow rectangular or U-shaped gland, 0.4 cm long, dark when dry; lamina 12.0–17.0 × 4.5–5.8 cm, elliptic, acute to rounded (retuse) at apex, cuneate at base, brown-ferruginous when dry, pubescence adaxially one layer of dense strigose trichomes, abaxially one layer of ferruginous-hirsute trichomes, papillate surface abaxially;

venation eucamptodromous, 14–18 pairs of secondary veins, midrib plane to impressed and secondary veins impressed adaxially, midrib and secondary veins prominent abaxially, with dense hirsute or bent trichomes, intersecondary veins present, tertiary veins alternate percurrent, reticulate white-tomentose areoles absent. Inflorescences cymose, 11–14 × 10 cm, longer layer dense ferruginous-hirsute, shorter layer dense whitish-tomentose, with foliar bracts at first or second node of inflorescence, these 0.6–0.7 cm long, linear bracteoles ca. 4.1 mm long, these with same pubescence of the axis. Flowers with hypanthium obconic, ca. 0.3 cm, pubescence like axis; calyx lobe 5, these oblong to lanceolate, 6–8 × 2–3 mm, pubescence externally in two layers, longer layer dense ferruginous-hirsute, shorter layer dense ferruginous-tomentose, pubescence internally with two layers, longer layer dense ferruginous-hirsute, shorter layer dense ferruginous-tomentose; corolla infundibuliform, 1.2–1.3 cm long, pubescence externally two layers, longer layer dense yellow-to ferruginous-hirsute, shorter layer dense creamy-tomentose, internally white with red macula, one lobe yellow-bearded, a ring of trichomes at base of corolla tube; corolla lobes 5, 0.4–0.5 × 0.3–0.4 cm, acute or rounded at apex; stamens 5, filaments 4–4.8 mm long, anthers 3.4 mm long; ovary inferior in flower, with tomentose circular disk at apex, style ca. 0.7 mm long, stigmatic lobes 2, ca. 1.5 mm long. Fruits capsular, 4.7–4.9 × 3.7–4.4 cm, oblate in outline, emarginate at apex, surface rugose, ferruginous-tomentose. Seeds D-shaped, 2 × 4.5 cm.

Illustration. Roger (1984), flowering branch, flower buds and fruits.

Phenology. Flowers and fruits from July to November.

Distribution and habitat. This species only occurs in Borba, Amazonas state (Brazil) (fig. 9A). It grows in white-sand forest close to flooded areas (*Igapó*).

Discussion. *Platycarpum duckei* is characterized by its elliptic leaves abaxially with dense ferruginous-hirsute indumentum and papillate surface, petioles with dense ferruginous-hirsute trichomes and fruits oblate with emarginate apex. This species is similar to *Platycarpum lorentensis* and *P. orinocense* due to its elliptic leaves and lamina abaxially papillate. See comments in *Platycarpum lorentensis* for differences between all three species.

Additional specimens examined. BRAZIL. Amazonas: Borba, silva paludosa, terris altis, 9 Nov 1935, *Ducke* 237 (MADw, NY, U); Borba, igapó, in terris altis, circa Campo Grande, 1 Sep 1940, *Ducke* 584 (F, MICH, MO, NY, R, US); Borba, estrada Jatuarana,

Igarapé Balneario Lira, 12 Sep 2013, *Dávila & Pereira 6353* (UEC); *Dávila & Pereira 6354* (UEC).

5. *Platycarpum eglandulosum* Steyermark, Mem. New York Bot. Gard. 10:258.1963. TYPE. Guyana. Mazaruni-Potaro District: Pakaraima mountains, frequent in woodland between Chinowieng and Chi-Chi landing, 1000 m, 10 Feb. 1955 (fr), *Maguire et al. 40666* (holotype, NY!; isotypes, GH!, US!, U not seen, VEN!).

Trees 15–20 m tall, dbh unknown, with external bark flaking, inner bark unknown, exudate unknown; young stems terete to slightly triangular, striate, pubescence in two layers, longer layer ferruginous-hirsute, shorter layer cinereous-tomentose; stipules unknown. Leaves 3-whorled; petioles 0.6–1.2 cm long, pubescence as in midrib, gland absent, sometimes not glandular small circular protuberances; lamina 15.0–18.0 × 5.6–8.3 cm, elliptic to oblanceolate, brown when dry, acute to rounded at apex, cuneate at base, pubescence adaxially in two layers, shorter layer minutely dense strigillose, longer layer sparse to dense brownish to whitish-pilose (1.3 mm), denser trichomes in midrib, pubescence abaxially one layer of dense ferruginous-villous (1–1.4 mm) trichomes, midrib and secondary veins with two layers of trichomes, longer layer ferruginous-hirsute, shorter layer dense hispidulous; abaxial surface white papillate; venation eucamptodromous, 16–22 pairs of secondary veins, midrib and secondary veins adaxially impressed and abaxially prominent, intersecondary veins absent, tertiary veins conspicuous alternate percurrent, reticulate white-tomentose areoles absent. Inflorescence unknown. Infrutescences ca. 16 cm long, with 3 axes per node, with 2–3 orders of branching, bracts not seen, pubescence the same as in young stems. Flowers unknown. Fruits capsular, 4.2–4.8 × 5.5–5.8 cm, oblate in outline, with surface verrucose and two layers of trichomes, shorter layer dense ferruginous-tomentose, longer layer sparse hirsute. Seeds 4.2–4.7 × 2.3–2.4 cm, D-shaped, flattened, with marginal wing 0.5–0.7 cm wide.

Phenology: flowers unknown and fruits in October and February.

Distribution and habitat. This species is poorly collected and it is only known from Mazaruni-Potaro district in Guyana (fig. 9A).

Discussion. This species is characterized by its petiole without glands, which is a unique character for *Platycarpum*.

Additional specimens examined. GUYANA. Mazaruni-Potaro District: Probably from a wooded "island" in savanna, midway between Chinowieng and Chi-Chi landing, 900 m, Oct 1979, *Walker s.n.* (MICH).

6. *Platycarpum egleri* G.K.Rogers, Syst. Bot. 6: 87. 1981. TYPE. Brazil. Roraima Territory: Rodovia BR-174 a 60 km de Caracarai (leste-sudeste), campina periodicamente alagável, 29 Jun. 1974 (fl, fr), *Pires & Leite 14758 (235)* (holotype RB!).

Trees or treelets, 1–10 m tall, 1.3–20 cm dbh, external bark with scales and inner bark orange to reddish; exudate red; young stems terete, dense to sparse strigillose; stipules lanceolate, 3–5 cm long, caducous, adaxially dense yellow-sericeous, abaxially dense ferruginous-tomentose. Leaves 3-whorled (rarely decussate); petioles 1.1–2.0 cm long, near abaxial base one narrowly rectangular or lunate gland, 0.2 cm long, dark when dry; lamina 6.0–19.0 × 2.4–8.4 cm, elliptic, rounded to obtuse at apex, cuneate to acute at base, adaxially one layer of sparse or dense strigose trichomes, abaxially glaucous, two layers of trichomes, shorter layer dense adpressed trichomes, longer layer white-tomentose; venation camptodromous, 12–22 pairs of secondary veins, midrib and secondary veins adaxially flat and abaxially prominent, reticulate venation white-tomentose areoles present; Inflorescences cymose, 8–15 × 10 cm, pubescence in two layers, shorter layer dense to sparse ferruginous-tomentose, longer layer dense to sparse ferruginous-hispidulous, with foliar bracts at first node of inflorescence cymose, these 2–3 × 1 cm, linear bracteoles 0.5 cm long, these with pubescence as inflorescence axes. Flowers with hypanthium obconic, ca. 0.2 cm long, pubescence as inflorescence axis; calyx lobes 5, oblong to deltoid, acute at apex, 0.7–1.1 cm long, externally with pubescence in two layers, shorter layer dense cinereous-or creamy-tomentose, longer layer dense white bent trichomes, internally creamy-villous; corolla funnelform, 1.3–2.1 cm long, externally white with pubescence in two layers, longer layer sparse creamy-hirsute, shorter layer dense creamy-tomentose, internally white with red macula in the throat, a ring of creamy trichomes at base, one yellow-bearded corolla lobe, corolla lobes 5, 0.5–0.9 × 0.3–0.5 cm, acute, with crisped margins; stamens 5, filaments ca.

4.5 mm long, anthers 3–4 mm long; ovary inferior in flowers, with tomentose circular disk at apex, style 8–11 mm long, stigmatic lobes 2, ca. 0.8 mm long. Fruits capsular, 2.5–3.0 × 2.0–3.5 cm long, brown to pinkish, oblate with emarginate apex, surface rugose, sparse to dense ferruginous–bent trichomes. Seeds 2.2–2.6 × 1.5–1.7 cm.

Illustration. Rogers (1984), flowering branch, abaxial surface lamina, fruits and seed.

Phenology. Flowers in October and December, fruits from October to March.

Distribution and habitat. *Platycarpum egleri* is endemic to Brazil, occurring in Amazonas and Roraima states (fig. 9A). It is an emergent tree in seasonally flooded shrubby or open areas in white-sand forest.

Discussion. *Platycarpum egleri* is distinguished by its 3-whorled phyllotaxy (rarely decussate) and abaxial leaves with white-tomentose areoles. This species is similar to *Platycarpum schultesii* var. *egleroides* because of its abaxial leaves with white-tomentose areoles, see comments on *P. schultesii* var. *egleroides*. In Roraima state (Brazil) *Platycarpum egleri* occurs in sympatry with *P. froesii*. It is easy to recognize both species because the leaves in *P. egleri* are not revolute and the calyx lobe measures 0.7–1.1 cm, while *P. froesii* has strong revolute leaves and calyx lobe measuring 0.5–0.6 cm long.

Additional specimens examined. BRASIL. Roraima. Caracarái - Parque Nacional Viruá, 6 Oct 2009, *Dávila et al.* 5594 (MO, INPA); 6 Oct 2009, *Dávila et al.* 5595 (MO, INPA); 8 Oct 2009, *Dávila et al.* 5609 (INPA); 8 Oct 2009, *Dávila et al.* 5613 (MO, INPA); 1°28'5"N, 61°0' 29" W, 27 Nov 2009, *Dávila et al.* 5767 (INPA); 1°27'2"N, 61°0'42"W, 2 Dec 2009, *Dávila et al.* 5827 (INPA, MO); 1°26'59"N, 61° 1'25"W, 2 Dec 2009, *Dávila et al.* 5816 (INPA); 1°21'54"N, 60°59'14" W, 4 Dec 2009, *Dávila et al.* 5843 (INPA); 1°28'32" N, 60°57'58"W, 29 Nov 2009, *Dávila et al.* 5788 (INPA); 1°15'47"N, 61°2'19" W, 2010, *Dávila et al.* 5909 (INPA, MO); 1°16'36"N, 60°58'13"W, 2010, *Dávila et al.* 6015 (INPA); 1°16'36"N, 60° 58'13" W, 2010, *Dávila et al.* 6017 (INPA); 1°15'42"N, 60°58'5"W, 1 Mar 2010, *Dávila et al.* 6021 (INPA, MO); 1°26'28"N, 60°58'43"W, 2 Feb 2010, *Dávila et al.* 6032 (INPA); Parque Nacional Viruá. Estrada da perdida, 1°48'57"N, 61°7'40"W, 4 Dec 2009, *Dávila et al.* 5857 (INPA, MO).

7. *Platycarpum froesii* Bremekamp, Acta Bot. Neerl. 6: 374. 1957. TYPE. Brazil. Amazonas: Rio Negro, Preto, Matupiry, campina, open country, 11 Nov. 1947 (flower buds), *Fróes 22812* (holotype, U not seen; isotypes, NY!, US!).

Trees to treelets 2–18 m tall, 5–20 cm dbh, with external bark scales and inner bark orange-reddish; exudate red; young stems terete, sparsely pubescent; stipules lanceolate, 1.0–2.5 cm long, caducous, adaxially dense adpressed trichomes abaxially dense ferruginous-hirsute. Leaves 3-whorled; petioles 0.3–1.0 cm long, indumentum adpressed, near abaxial base one lunate gland, ca. 0.4 cm long, dark when dry; lamina 7.0–15.0 × 3.8–6.5 cm, brown to reddish when dry, oblong to obovate, rounded to obtuse at apex, cuneate at base, margin strongly revolute, pubescence adaxially one layer of sparse to dense tawny-strigose trichomes (fig. 7F), pubescence abaxially with one layer of dense ferruginous-antrorse trichomes (fig. 7G); venation camptodromous, 13–16 pairs of secondary veins, midrib adaxially and abaxially prominent, and secondary veins adaxially plane and abaxially prominent, reticulate white-tomentose areoles absent. Inflorescences cymose 12.6–15.2 × 3.0–5.0 cm, pubescence in two layers, longer layer dense ferruginous-hispid, shorter layer dense tomentose, linear bracteoles ca. 0.2 cm long, ferruginous-tomentose. Flowers with hypanthium obconic, 0.2–0.4 cm, pubescence like inflorescence axes; calyx lobes 5, these 0.5–0.6 × 0.1 cm, deltoid, externally pubescence in two layers, shorter layer dense ferruginous-tomentose, longer layer ferruginous-hispid, internally dense sericeous; corolla funnelform, 1.3–1.5 cm long, externally white-reddish, dense antrorse indumentum externally, and internally white with red macula in the throat, a ring of creamy trichomes at the base, one yellow-bearded lobe, corolla lobes 5, 0.5–0.7 × 0.4 cm, acuminate; stamens 5, filaments 1.1–1.2 mm long, anthers 0.2–0.3 cm long; ovary inferior in flower, with tomentose circular disk at apex, style 0.7–0.8 cm long, stigmatic lobes 2, 0.7–1.0 mm. Fruits capsular, 2.0–6.0 × 2.3–5.7 cm, orbicular in outline, with surface rugose, ferruginous tomentose and hispid. Seeds not seen.

Phenology. Flowers in May, September, November and December, fruits in May, November and December.

Distribution and habitat. *Platycarpum froesii* is endemic to Brazil, this species is recorded in Roraima and Amazonas state (fig. 9A). It occurs in open and shrubby white-sand forest.

Discussion. *Platycarpum froesii* can be distinguished by its strongly revolute leaves, brown to reddish leaves when dry, and lamina oblong to obovate and rounded to retuse at apex. This species has the most revolute lamina in comparison with the other species of the genus. *Platycarpum froessi* could be confused with *P. egleri*, which occurs in sympatry in Roraima state. See comments in *P. egleri* for differences.

Additional specimens examined. BRASIL. **Amazonas.** Rio Negro, Matupiry, 11 Nov 1947, *Fróes* 22812 (NY, US); Barcelos, campinas palmar *Barcella odora* y sabana sobre arena blanca, ubicadas en la ribera izquierda del Río Aracá medio, aprox. 16 km al SE (em línea recta) de la boca del río Juarí, Jul 1885, *Huber* 10769 (K, NY); Parque Nacional do Jaú. Campina do Patauí. Quadrante K6 baia 2 mata baixa de transico. Floresta de Campinarana. Arvore 6m × 5. cm, 4 Sep 1998, *Vicentini* 1382 (INPA, MO). **Roraima:** Caracaraí, Parque Nacional Viruá, 1°29'7"N, 61°2'51"W, 26 Nov 2009, *Dávila et al.* 5758 (MO, INPA); 1°28'53"N, 61°1'14"W, 6 Dec 2009, *Dávila et al.* 5874 (INPA, MO); 1°28'9"N, 61°0'28"W, 31 May 2010; *Dávila et al.* 6192 (INPA, MO); 1°48'57"N, 61°7'40"W, 12 Sep 2010, *Siniscalchi* 52 (INPA); Parque Nacional Viruá. GRID PPBio, 1°48'57"N, 61°7'40"W, 27 Nov 2009, *Dávila et al.* 5771 (INPA, MO).

8. *Platycarpum loretensis* Dávila & L. Kinoshita, *Phytotaxa*: 260(3): 276-282. TYPE. Peru. Loreto: Requena, Jenaro Herrera, Quebrada Sapuena, 13 Sep. 1989 (fl, fr), *Freitas s/n. TB-Cha P 1-II-10* (holotype, AMAZ!; isotypes, F!, MO!).

Trees 15–30 m tall, 10–40 cm dbh; outer bark fissured; exudate red; young stems terete, pubescence in two layers, shorter layer sparsely whitish or translucent strigose, longer layer densely ferruginous-hirsute; stipules lanceolate, 2.7–3.1 cm long, caducous, adaxially densely creamy-villous, abaxially densely ferruginous-hirsute. Leaves decussate; petioles (0.7–)1.8–2.9 cm long, with pubescence in two layers, shorter layer sparsely whitish-strigose, longer layer ferruginous-hirsute, with one gland near abaxial base, inverted U-shaped to slightly rectangular, 0.3–0.4 cm long, dark when dry; lamina (13–)16.3–30.0 × 5.4–10.0 cm, oblanceolate, acute to rounded at apex, cuneate at base; venation broquidodromous, (15–)17–19 pairs of secondary veins, adaxially one layer of strigose trichomes, abaxially papillate with cinereous wax, one layer of ferruginous-tomentose trichomes, midrib and secondary veins

with ferruginous hirsute and antrorse indumentum, intersecondary veins conspicuous and prominulous, tertiary veins prominulous, reticulate white-tomentose areoles absent. Inflorescences cymose, 20.0–23.7 cm long, bracts foliaceous at first and second basal nodes, these 5.0×0.3 cm, linear bracteoles 0.7–1.2 cm long, pubescent in two layers, with longer layer hirsute-ferruginous, shorter layer tomentose-yellowish. Flowers with hypanthium obconic, 0.2–0.3 cm long, ferruginous-tomentose; calyx lobes 5, $1.0\text{--}1.1 \times 0.4\text{--}0.6$ cm, elliptic to oblong, externally with pubescence in two layers, shorter layer villous, longer layer sparsely tomentose, internally yellowish-sericeous; corolla funnelform, 1.9–3.0 cm long, externally pale yellow, pubescence in two layers, shorter layer villous, longer layer tomentose, internally white with red macula in the throat, puberulous, with a ring of trichomes at base, one lobe yellow-bearded, corolla lobes 5, elliptic, 0.7–1.2 cm long, acute, with undulated margins. Stamens 5, filaments 5–8 mm long; anthers 0.3–0.4 cm long, ovary with disk tomentose at apex; style 1.0–1.2 cm long, stigmatic lobes 2, ca. 0.1 cm long. Fruits capsular, $4.7\text{--}5.5 \times 3.6\text{--}4.9$ cm, elliptic in outline, verrucose and tomentose-ferruginous. Seeds 4.9×2.1 cm, elliptic, with marginal wing ca. 0.3 cm wide.

Illustration. Dávila & Kinoshita (2016), line draw of flowering branch, flower and fruit, SEM of leaves and pollen.

Phenology. Flowers in September, fruits in September, November and January.

Distribution and habitat. This species is known only from Loreto department in Peru (fig. 9B). It grows in peatland, swamp forest, and white-sand forest.

Discussion. *Platycarpum loretensis* can be recognized by its oblanceolate leaves, abaxially leaf with conspicuous prominulous intersecondary veins, papillate surface covered by cinereous wax, ferruginous-tomentose indumentum, corollas 1.9–3.0 cm long, and fruits ovate-retuse, $4.7\text{--}5.5 \times 3.6\text{--}4.9$ cm. This species is similar to *Platycarpum orinocense* and *P. duckei* because of its brown-ferruginous indumentum on young stem, stipules and lamina, and abaxial leaves surface papillate (fig. 8B). However, *Platycarpum loretensis* can be differentiated by its oblanceolate leaves (vs. elliptic to ovate to broadly obovate in *P. orinocense* and vs. elliptic leaves in *P. duckei*), and corollas 1.9–3 cm long (vs. 1.2–2(–2.2) cm long in *P. orinocense* and vs. 1.2–1.3 cm long in *P. duckei*).

Additional specimens examined. PERU. **Loreto.** Maynas, Dtto. Fernando Lores, Río Amazonas, Isla de Aguajal, aprox. 2 horas de Tamshiyacu, 6 Sep 1988, *Rimachi* 8767 (MO,

NY, UMS); Vicinity of Iquitos, 1977, *Revilla 4287* (MO); Requena, Dtto. Sapuena, Basin of Rio Ucayali, Jenaro Herrera and vicinity, 4° 55' S, 73° 45' W, at 5 km N of Centro de Investigaciones Jenaro Herrera Requena, 18 Nov 1988, *Daly et al. 5707* (NY); Centro de Investigaciones Jenaro Herrera, 4 Jan 2012, *Dávila et al. 6318* (AMAZ); 21 Nov 1989, *Maytahuari TB P2-2-2 N 184* (AMAZ).

9. *Platycarpum negrense* Ducke, Arq. Inst. Biol. Veg. 1: 212. 1935. TYPE. Brazil. Amazonas: Rio Negro, infra Camanaos in catinga cum palmis "piassaba," 15 Oct. 1932 (fl), *Ducke 23774* (holotype, RB!; isotypes, Knot seen, U not seen, US!, US photo at F!).

Key for the varieties of *Platycarpum negrense*

- 1a. Stipules and young stems with brown appearance, fruits 2.9-3.1 cm.....*P. negrense*
var. *negrense*
- 1b. stipules and young stems with cinereous appearance, fruits 3-3.6 cm.....*P. negrense*
var. *glaucum*

91. *Platycarpum negrense* Ducke var. *negrense*, Fig. 12

Trees 12–30 m tall, ca. 45 cm dbh, with external bark fissured and inner bark light orange; exudate red; young stems circular and angled, glabrous, brown; stipules 1.9–2.2 cm long, brown, caducous, abaxially glabrous to tomentose and yellowish-hirsute, yellow-sericeous adaxially. Leaves decussate; petioles 1–2 cm long, glabrous, near abaxial base one narrowly gland rectangular to ovate depressed, 0.4–0.5 cm long, dark when dry; lamina 11.2–15.2 × 4.1–5.6 cm, oblanceolate to elliptic, acute to retuse at apex, acute and sometimes obtuse at base, adaxially glabrescent (fig. 7H), abaxially glaucous, glabrescent, with surface dense papillate with cinereous wax (fig. 7I), venation eucamptodromous, 15–21 pairs of secondary veins, midrib adaxially and abaxially prominent, secondary veins adaxially and abaxially flat, sparsely white-setulose trichomes along veins, intersecondary veins absent, usually conspicuous minutely reticulated, reticulate white-tomentose areoles absent. Inflorescences cymose, 11.8–12.6 × 9.3–17.5 cm, these axes with pubescence in two layer,

longer layer ferruginous-hirsute, shorter layer dense yellowish-tomentose, with foliaceous bracts at first or second node of inflorescence, these ca. 6.9×2.4 cm, pubescence like leaves, linear bracteoles 2–2.5 mm long, pubescence like inflorescence axes. Flowers with hypanthium obconic, 1–1.3 mm, pubescence in two layers, shorter layer dense creamy-tomentose, longer layer ferruginous-sericeous; calyx lobes 5, deltoid to fusiform, 0.9–1 cm long, externally with pubescence in 2 layers, shorter layer dense creamy-tomentose, longer layer sparsely ferruginous-hirsute, internally creamy-sericeous; corolla infundibuliform, 1.1–2 $\times$ 1.5 cm long, externally shine creamy with pubescence in two layers, longer layer dense sericeous, shorter layer dense tomentose, internally white to pinkish with a red macula in the throat, glabrous except to one yellow bearded lobe, and the ring of ferruginous trichomes at base of the corolla tube, corolla lobes 5, $0.5\text{--}0.6 \times 0.4\text{--}0.5$ cm, acute to acuminate, with slightly crisped margins; stamens 5, filaments 4 mm long, anthers 2.5–2.8 mm long; ovary inferior in flower, with tomentose circular disk at apex, style ca. 8.8 mm long, stigmatic lobes 2, 0.6 mm long. Fruits capsular, $2.9\text{--}3.1 \times 2.2\text{--}2.4$ cm, oblate in outline, with obcordate apex and cordate base, with surface verrucose, with sparse tomentose and hirsute indumentum. Seed not seen.

Phenology. Flowers in September and October, fruits in November and March.

Distribution and habitat. This variety is only known from Rio Negro in Amazonas state (Brazil) and Guainía in Colombia (fig. 9B). It is an emergent tree in forested or shrubby white-sand forest or open savannas.

Discussion. *Platycarpum negrense* is recognized by its elliptic, oblanceolate or obovate leaves with glabrescent abaxial leaves, stipules lanceolate and fruits oblate, sometimes with a glaucousness appearance in young stem, stipules and leaves. In case of glaucousness present, it can be confused with *P. decipiens*, but the shape and size of fruits can be used to separate the two species. *Platycarpum decipiens* has bigger ($4.3\text{--}5.7 \times 4.2\text{--}5$ cm) and oblong fruits, while *P. negrense* has smaller ($3.0\text{--}3.6 \times 2.0\text{--}3.0$ cm) and oblate fruits. *Platycarpum negrense* has two varieties (see key for *Platycarpum negrense* to differentiate). This is the first time that fruits are described for *Platycarpum negrense* var. *negrense*. Fruits are similar to *Platycarpum negrense* var. *glaucum* in shape. *Platycarpum negrense* var. *glaucum* can be differentiated from *P. negrense* var. *negrense* by its stipules and young stems with cinereous appearance, and leaves oblanceolate to elliptic with abaxially leaves glaucous

covered by wax; whereas *P. negrense* var. *negrense* has stipules, leaves and young stem with brown appearance and leaves elliptic or rarely ovate covered with abaxially leaves glaucous covered by wax (fig. 7I).

Additional specimens examined. BRAZIL. **Amazonas**, Lago Jauacaná, rio Içana, 91 msm, 30 Nov 2013, *Dávila et al.* 6436 (INPA, UEC, MO); rio Içana, São Felipe, 21 Sep 1952, *Fróes & Addison* 28672 (UB). COLOMBIA. **Guainía**, Inírida, sector comprendido entre caño Vitina y caño Culebra, 4 Mar 2005, *Cárdenas et al.* 16444 (COAH).

92. *Platycarpum negrense* var. *glaucum* Rogers, Fl. Neotropica. 39: 114. 1984. TYPE: Venezuela. Amazonas: río Atabapo, Santa cruz, frequent in periodically inundated white sand savanna, 17-18 Nov. 1979 (fr), *Roger* 95 (holotype, MICH!; isotype, NY!, U not seen, VEN!)

Trees or treelets 8 m tall, ca. 2 cm dbh. Young stems terete and cinereous colored, glabrous; stipules 1.5–3.0 cm long, glabrous, brown abaxially, adaxially with dense white trichomes. Leaves decussate, petioles 0.4–0.8 cm long, glabrous, glaucous, near abaxial base one narrowly gland U-shaped, ca. 0.4 cm long, dark when dry; lamina 7.4–12.5 × 3.0–5.4 cm elliptic or rarely ovate, acuminate to obtuse at apex, attenuate at base, adaxially with pubescence one layer of strigose trichomes, abaxially glaucous with pubescence one layer of glabrous or minute white adpressed trichomes, venation eucamptodromous, 14–22 pairs of secondary veins, midrib adaxially and abaxially prominent, secondary veins adaxially and abaxially flat, conspicuous minutely reticulated inferior veins, abaxial surface dense papillate with cinereous wax. Inflorescences with pilose ferruginous axes. Flowers unknown. Fruits capsular, 3.0–3.6 × 2.0–3.0 cm, brown, oblate in outline, with obcordate apex and cordate base, with surface rugose, glaucous, sparse ferruginous trichomes. Seeds 1.1–2.5 cm.

Phenology. Flowers unknown, fruits in November.

Distribution and habitat. This variety is only known from Amazonas state in Venezuela (fig. 9B). It grows in inundated white-sand savannas.

Discussion. This variety resembles *Platycarpum decipiens* by its leaves having a characteristic glaucous, but *Platycarpum negrense* var. *glaucum* has oblate and smaller fruits 3.0–3.6 × 2.0–3.0 cm, whereas *P. decipiens* has oblong and larger fruits 4.3–5.7 × 4.2–5

cm. See comments of *P. negrense* var. *negrense* for the differences between the two varieties of *P. negrense*.

Additional specimens examined. VENEZUELA. Amazonas. Santa Cruz, 17-18 Nov 1979, Rogers 91 (MICH).

10. *Platycarpum orinocense* Bonpl., Pl. Aequin. 2: 81, pl. 104. 1811; TYPE (designed by Rogers 1984). Pl. 104 in Humboldt and Bonpland, Pl. Aequin. 2: 81. 1811. *Sickingia orinocensis* (Bonpl.) Sprengel, Syst. Veg. 1: 622. 1825. *Platycarpum orinocense* var. *orinocense*. *syn. nov.*

Henriquezia aturensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 7: 368. 1931. TYPE. *M. Gaillard 204* (holotype, P not seen, fragments at F!, photo at NY!).

Platycarpum orinocense var. *grandiflorum* Steyermark, Mem. New York Bot. Gard. 10: 254. 1963. *syn. nov.* TYPE. Venezuela. Amazonas: Serrania Paru, Rio Paru, Caño Asisi, frequent in savanna, W base of Paru, 200 m, 15 Feb 1951 (fl, fr), *Cowan & Wurdack 31473* (holotype, NY!; isotypes, US!, VEN!). *syn. nov.*

Trees 5–30 m tall, up to 60 cm dbh; young stems terete, striate, pubescence in two layers, shorter layer ferruginous-tomentose, longer layer ferruginous-hirsute; stipules lanceolate, 1.9–5.8 cm long, caducous, oblong, pubescence dense white-villous adaxially, dense ferruginous-hirsute abaxially. Leaves decussate; petioles 0.6–1.8 cm long, at petiole base one narrow gland, ca. 0.5 cm long, dark when dry; lamina (8–)12–20(–25) × 6–10(–15) cm, elliptic to obovate-elliptic, acute, rounded to retuse at apex, cuneate at base, brown-ferruginous when dry, adaxially with one layer of strigose trichomes, abaxially pubescence in two layers abaxially, longer layer ferruginous-to yellow-hirsute, shorter layer dense white-hispidulous; surface abaxially with papillae covered with cinereous wax, 16–20 pairs of secondary veins, midrib flat or prominent and secondary veins prominent adaxially, midrib and secondary veins abaxially prominent, tertiary veins alternate percurrent, pubescence in veins dense hirsute and antrorse trichomes. Inflorescences cymose, 8–16 × 10–20 cm, 3–5 ordering branches, pubescence as young stem, distal axes with bracteoles. Flowers with hypanthium obconic, 0.1–0.2 cm long, dense ferruginous tomentose-hirsute; calyx lobes 5, lanceolate to ovate, 0.5–1 × 0.2–0.3 cm, externally pubescence in two layers, shorter layer

dense whitish-tomentose, longer layer sparse yellow-hirsute, internally sparse yellow-sericeous; corolla funnelform, base flared, 1.2–1.8(–12.2) cm long, externally white to pink, pubescence in two layers, longer layer dense yellow hirsute, shorter layer dense white-tomentose, internally pink with red maculas, one yellow bearded lobe, with a ring of creamy trichomes at base, corolla lobes 5, 0.5–0.9 × 0.4–0.8 cm, oblong; stamens 5, inserted at two different heights in the corolla tube, filaments 4–7 mm long, anthers 2–3 mm long; ovary inferior in flowers; style 6–9 mm long, stigmatic lobes 2, 1–2 mm long. Fruits capsular, 3.0–3.9 × 3–3.8 cm, oblate, with surface verrucose, pubescence in two layers, shorter layer sparse cinereous to ferruginous-tomentose, longer layer hirsute. Seeds 3.6 × 1.8 cm, flattened.

Illustration. Humboldt & Bonpland (1811), flowering branch; Steyermark (1974), flowering branch, flower and fruit, Rogers (1984), line draw of inflorescence.

Phenology. Flowers from November to July and fruits from January to June.

Distribution and habitat. This species occurs in Venezuela and Colombia (fig. 9B), grows in savannas and stunted forest in sandy to rocky soils.

Discussion. This species is recognized by its decussate phyllotaxy, elliptic to ovate to broadly obovate leaves, and with stipules, inflorescence and pubescence abaxial leaves brownish-hirsute. This species is similar to *Platycarpum loretensis* and *P. duckei*, see comments in *P. loretensis* for differences between those species. *Platycarpum orinocense* has a wide variation in morphology, especially in the leaf shape and size. Previously Roger (1984) recognized two varieties based in corolla size and inflorescence pubescence. We do not recognize these varieties because with all the material analyzed these limits disappeared.

Additional specimens examined. COLOMBIA. **Vichada:** Parque Nacional Natural El Tuparro, Centro Administrativo, camino al Bosque de Thomas, 24 Feb 1985, *Barbosa et al.* 3001 (FMB, MO, RB); Puerto carreño Piedras al W del centro administrativo INDERENA. Cerro Peinilla, 3 Apr 1995, *Córdoba et al.* 1166 (COAH, COL); Savannah forest and shrubs in rock crevices on laja outcrop behind Casuarito, across from Puerto Ayacucho, Venezuela, 3 Apr 1984, *Gentry et al.* 46298 (INPA, MO, RB); Rio Orinoco, Casuarito, common on granite outcrops, 4 Nov 1979, Rogers 57 (MICH); Casuarito, afloramiento rocosos alledaños (reductos del Escudo Guayanés), 11 Jan 2004, *Parra* 434 (COL, UDBC). VENEZUELA. **Amazonas:** Puerto Ayacucho, Mar 1950, *Curran* 1789 (VEN); Rio Ventuari, orilla izquierda, aproximadamente en la mitad del camino entre Sta. Barbara y Carmelitas, 21 Apr 1971,

Foldats 57A (US); ca. 15 km al Sur de la desembocadura del Rio Manapiare en el Rio Ventuari, sabana sobre arena blanca, ca. 130 m, 27 Feb 1979, *Huber 3452* (MICH); Serrania del Parú (Aroko), sector Norte, sabanita ubicada en la ribera N del alto Rio Parú, 500 m, 2 Mar 1979, *Huber 3571* (MICH); ca. 30 km al N de Puerto Ayacucho, sabana al E de Rincones de Chacorro, aprox. 80 m, 24 May 1979, *Huber 3807* (MICH); aprox. a unos 10 km al W de la Serrania Asisa, sabana en la ribera derecha del medio rio Asisa, 250 m, 14 Jun 1981, *Huber 6218* (MICH); Distrito Cedenio (Amazonas or Bolivar): savannas of eastern slopes of Cerro Calentura, near headwaters of Caño Parucito, approx. 900 m, 11 Apr 1974, *Jangoux 10109* (VEN); Rio Ventuari, Cerro Moriche, frequent on E slope, 300-800 m, 13 Jan 1951, *Maguire et al. 30850* (NY, U), frequent in montane savanna, 800 m, 14 Jan 1951, *Maguire et al. 30877* (NY, U); Cerro Guanay, savanna hills SW Guanay, sub-D, frequent at base camp, 200 m, 27 Jan 1951, *Maguire et al. 31617* (NY, US, VEN); Cerro Yutaje, dominant tree of savanna, 1 km E of Base Camp, 150 m, 30 Jan 1953, *Maguire & Maguire 35046* (NY, U); Sanariapo, occasional around rock outcrops, 120 m, 24 Apr 1953, *Maguire & Wurdack 35736* (F, NY, U, VEN); Puerto Ayacucho, occasional in scrub forest bordering crystalline laja, 100-120 m, 8 Nov 1953, *Maguire et al. 36063* (NY, RB, U, US, VEN); left bank of Rio Orinoco, 30 km above Santa Barbara, common in Sabana Huachapana, 125 m, 15 Sep 1957, *Maguire et al. 41463* (NY), 18 Jan 1958, *Maguire et al. 42655* (GH, NY, R, RB, US); Rio Orinoco, Sabana de Sta. Barbara, arbol frecuente, 30 Apr 1968, *Medina 474* (VEN); SW de Pto. Ayacucho, Cerro Zamuro, frente a Raudal Zamuro, 140 m, 28 Sep 1973, *Morillo & Ishikawa 3600* (VEN); Puerto Ayacucho, common on granite outcrops, 125 m, 12 Mar 1978, *Rogers 13* (MICH), 25 Feb 1978, *Rogers 15* (MICH, NY, VEN); Sanariapo, 1 km above town on the road to Puerto Ayacucho, rocky meadow near riverbank, 125 m, 13 Mar 1978, *Rogers 43* (MICH); 20 km S of Puerto Ayacucho, on the road to Sanariapo, pasture, 125 m, 13 Mar 1978, *Rogers 44* (MICH); Puerto Ayacucho, abundant on granite outcrops in and around town, 100 m, 1 Nov 1979, *Rogers 54* (MICH); Rio Orinoco, 2 km upstream from Puerto Ayacucho, 100 m, 3 Nov 1979, *Rogers 55* (MICH, NY, VEN); Cerro Yapacana, common on SW face, exposed rocks, 300-900 m, 8 Nov 1979, *Rogers 62* (MICH), 8 Nov 1979, *Rogers 67* (MICH); Puerto Ayacucho, 25 Dec 1964, *Schwabe s.n.* (VEN); San Fernando de Atabapo, along the Rio Orinoco, 100 m, 8 Sep 1944, *Steyermark 58433* (F, MO); Puerto Ayacucho, inmediaciones, 31 Jul 1967, *Terán 4508* (VEN); alrededores de Puerto Ayacucho hacia la desembocadura del Rio

Sanariapo, característico de las lajas graníticas, 23 May 1940, *Williams 13096* (F, VEN); Puerto Ayacucho, común en sabanas, especialmente alrededor de los bloques graníticos, 13 Jan 1942, *Williams 13806* (F, US, VEN); entre Atures y Puerto Ayacucho, característico de los sitios rocosos en las sabanas y a veces en la margen de los morichales, 120 m, 26 Jun 1942, *Williams 15911* (F, US, VEN).

11. *Platycarpum piresii* Dávila *sp. nov.* TYPE: Brazil. Amazonas: Alto Rio Negro, Taracúá, 6 Jun. 1962 (fl), *Pires. J. M. & Silva N.T. 8065* (holotype, MG!; isotype, UB!). Fig. 13

Diagnosis: This species is similar to *Platycarpum negrense* var. *negrense* because of its elliptic to obovate leaves. However, it differs as *P. piresii* by its ferruginous villous abaxial leaves (vs. glabrescent in *P. negrense* var. *negrense*), calyx lobe 0.3–0.5 cm long. (vs. 0.9–1 cm in *P. negrense* var. *negrense*).

Trees 12 m tall; young stems terete, pubescence ferruginous-tomentose; stipules unknown. Leaves decussate; petioles 1.5–2.7 cm long, dense ferruginous-hirsute, near abaxial base one narrowly gland, 0.3 cm long, dark when dry; stipules not seen, caducous; lamina 20.0–21.0 × 7.3–10.0 cm, wide-elliptic to obovate, rounded to retuse at apex, attenuate at base, adaxially one layer of strigose trichomes, abaxially one layer of ferruginous-villous trichomes, surface abaxially with dense papillae, eucamptodromous, 15–17 pairs of secondary veins, midrib and secondary veins adaxially flat with dense adpressed trichomes, midrib and secondary veins abaxially prominent with dense hirsute trichomes, reticulate white-tomentose areoles absent. Inflorescences cymose, 10–19 × 5–6 cm, 3–5 ordering branches, pubescence in two layers, shorter layer dense ferruginous-tomentose, longer layer dense yellow-hirsute, foliar bracts, 5 × 1.5 cm, these with same indumentum like leaves, linear bracteoles, 0.5–1.0 cm long, these with same indumentum as axis. Flowers with hypanthium obconic, ca. 1.5 mm long, dense ferruginous, tomentose-hirsute; calyx lobes 5, deltoid, 0.3–0.5 × 0.2–0.3 cm, externally pubescence in two layers, shorter layer dense cream-tomentose, longer layer sparse yellow-hirsute, internally sparse yellow-sericeous; corolla funnelform, ca. 1.6 cm long, externally creamy, pubescence in two layers, longer layer dense yellow-hirsute, shorter layer dense white-tomentose, internally with red macula, one yellow bearded lobe, with a ring of

creamy trichomes at base, corolla lobes 5, 0.7×0.4 cm, acute; stamens 5, filaments 4–6 mm long, anthers 2–3 mm long; ovary inferior in flowers with tomentose circular disk at apex; style 7 mm long, stigmatic lobes 2. Fruits and seeds unknown.

Phenology. Flowers in June, fruits unknown.

Discussion. This species is recognized by its wide-elliptic to obovate leaves and the abaxial leaf with dense ferruginous-villous trichomes, and surface papillate. It is similar to *Platycarpum negrense* var. *negrense* by its elliptic and obovate leaves, but *P. negrense* var. *negrense* has glabrescent abaxial leaves and the abaxial surface is not papillate.

Distribution and habitat. This species is only known from one collection in Taracuá, rio Negro, Amazonas state (Brazil) (fig. 9B) and it has not habitat type recorded.

12 *Platycarpum rhododactylum* Woodson & Steyermark, Amer. J. Bot. 39: 423. 1952. TYPE. Venezuela. Bolivar: Alto Rio Paragua, cumbre del Cerro Tonoro, 700 m, 2-15 Aug. 1943 (fl, fr), *Cardona 860* (holotype, MO!; isotypes, F!, NY!, US!, VEN!)

Shrubs or treelets, to 5–20 m tall, 60 cm dbh, with external bark scales; young stems triangular or tetrangular, puberulent; stipules deltoid, 1.6–2.3 cm long, caducous, indumentum adaxially with antrorse white trichomes, abaxially glabrous and glaucous. Leaves 3(–4)-whorled; petioles 0.7–1.7 cm long, near abaxial base one narrowly gland, 0.3–0.5 cm long, dark when dry; lamina (8.0–)10.0–18.0 $\times$ (3.5–)4.5–9.0(–12.0) cm, elliptic to broadly elliptic, rounded to retuse at apex, cuneate at base, glabrous to glabrescent adaxially, glabrous or few minutely adpressed trichomes abaxially, all surface abaxially and adaxially glaucous, venation broquidodromous, 13–23 pairs of secondary veins, midrib and secondary veins impressed adaxially and abaxially prominent, tertiary veins alternate percurrent, reticulate white-tomentose areoles absent. Inflorescences congested cymose, 5–16 $\times$ 4–10 cm, condense distal axes with pubescence in two layers, shorter layer dense tomentose-hirsute, longer layer glaucous-to yellow-ferruginous. Flowers with hypanthium obconic, 0.3–0.4 cm, pubescence the same as in inflorescence axes; calyx lobes 4, deltoid (rarely ovate), 0.5–0.7 $\times$ 0.2–0.4 cm, externally indumentum in two layers, longer layer ferruginous-hirsute, shorter layer ferruginous-adpressed, internally dense creamy antrorse trichomes; corolla narrowly tubular, 1.2–2.0 cm long, externally pink, pubescence in two layers, longer layer dense yellow-hirsute,

shorter layer dense creamy-tomentose, internally pink with red macula, one yellow bearded lobe, with a ring of creamy trichomes at base, corolla lobes 4–5, $0.3\text{--}0.5 \times 0.2\text{--}0.3$ cm, oblong; stamens 5, filaments 2–4 mm long, anthers 2–4 mm long; style 0.6–1.3 cm long, stigmatic lobes 2, 1–2 mm long. Fruits capsular, $2.0\text{--}3.0 \times 2.5\text{--}4.5$ cm long, oblate, pinkish to brown, surface rugose, indumentum sparse white. Seeds $2.6\text{--}2.7 \times 1.7\text{--}1.8$ cm, flattened, with marginal wing 0.7 cm wide.

Illustration. Rogers (1984), pictures of habit and inflorescence, fruit, anatomy of seed; Steyermark (1974) flowering branch, flower, fruit and seed.

Phenology. Flowers from February to March and from August to January, fruits from August to May.

Distribution and habitat. This species occurs only in Venezuela, in Bolivar state (fig. 9B). It occurs in quartz sandstone and rocky places with scrubland forest.

Discussion: *Platycarpum rhododactylum* is characterized by the combination of glaucous and glabrescent leaves (fig. 8C-D) and congested cymose inflorescences. *Platycarpum rhododactylum*, *P. decipiens*, and *P. negrense* have leaves abaxially glaucous. But *Platycarpum rhododactylum* differs from those species by its congested cymose inflorescences and flowers with a narrowly tubular corolla, in comparison with cymose inflorescence with infundibuliform corollas in *Platycarpum decipiens* and *P. negrense*.

Additional specimens examined. VENEZUELA. **Bolivar:** Pequeña meseta del norte de Serrania Cararuban, SE de Canaima, 300-600 m, 19 Feb 1964, *Agostini 401* (NY, VEN); Heres, Base central del Guaiquinina-Tepui. 85 Km al S de La Paragua, Aymar abundante al N del Salto Hacha, zona rocosa, 11 May 1987, *Aymard 5722* (PORT); *Aymard 5755* (MO, PORT); A lo largo del rio El Trueno, al N de la base del Guaiquinina-Tepui, 20 May 1987, *Aymard 6145* (PORT); abundante al N del Salto Hacha, zona rocosa, Aug 1957, *Blohm 1* (VEN); Cerro Guaiquinima. Camp 4. Stegolepis savanna with patches of trees, 7 Feb 1990, *Boom et al. 9382* (NY, PORT); Summit of Cerro Tonoro, 700 m, 2-15 Aug 1943, *Cardona 856* (NY, US); Alto Rio Paraqua, cumbre del Cerro Tonoro, 700 m, 15 Aug 1943, *Cardona 860* (F, MO, NY, US, VEN); Alto Caroni, en cumbre de cerro arenisca Cucurital, 24 Feb 1953, *Cardona 2825* (NY, VEN); Alto Caroni, Rio Carrao, Salto Hacha, Mar 1954, *Cardona 2856* (US, VEN); Cerro Guaiquinina, Camp II. Noroeste de la meseta, 11-14 Feb 1990, *Cotton 1065* (PORT); Raúl Leoni, Aza-karon (Castillos de Aza; frente 5). 12 Jun 1992, *Diaz 1035*

(PORT); Gran Sabana, Canaima, ca. 3 km SE Ucaima, dry evergreen forest, ca. 550 m, 10 Oct 1974, *Ehrendorfer 741010-28* (VEN); Raúl Leoni, Macizo Guaiquinina, Cerro Camarón, Oct 1988, *Fernández et al. 4763* (MO, NY); Canaima, on the summit of the hill approx. 1 km at 20? from the AVENSA resort, on sand and sandstone, approx. 500 m, 14 Feb 1978, *Rogers 8* (MICH, NY, U, VEN), *Rogers 17* (MICH); Canaima, on slope approx. 3.2 km at ~260 from the AVENSA resort, on sand and sandstone, 15 Feb 1978, *Rogers 9* (MICH), *Rogers 10* (MICH, NY, U, VEN); Colinas del Rio Cazzao, NW de Ueaima, 500 m, 21 May 1966, *Rutkis & Foldats 505* (VEN); Cumbre del cerro Guaiquinima, a lo largo del río Szczerbanari (rio Canapo), 20 Jan 1977, *Steyermark et al. 113120* (F).

13. *Platycarpum rugosum* Steyermark, Mem. New York Bot. Gard. 10:257. 1963. TYPE. Venezuela. Bolivar: Ueitepui, on summit, dwarf forest, vicinity of km 125 S of El Dorado, between Luepa and Cerro Venamo, 1,100-1,300 m, 7 Mar. 1962 (fl, fr), *Steyermark & Aristeguieta 25* (holotype, VEN!; isotypes F!, NY!, US!)

Trees 11–20 m tall, 30 cm dbh, with external bark rectangular segments; young stems terete to triangular, striate, indumentum in two layers, the longer layer sparse hirsute red, and shorter layer dense strigose white; stipules oblong, ca. 2 cm long, caducous, adaxially dense brown trichomes, abaxially pubescence in two layer, longer layer dense red-hirsute, shorter layer cinereous-strigillose. Leaves 3–whorled; petioles 0.5–1.0 cm long, variable glands near abaxial base, a inverted U–shaped gland and two (or three) stalked rounded on each side of the petiole; lamina (7.0–)11.0–27.0 × 2.4–8.4 cm, elliptic to obovate, revolute, acute to retuse at apex, cuneate to rounded at base, pubescence adaxially in two layers, shorter layer sparse to dense white-strigose, longer layer sparse to dense red-hirsute (fig. 8E), pubescence abaxially in two layers, longer layer dense red-hirsute (ca. 1.9 mm long), shorter layer dense white-strigillose (0.1–0.4 mm long) (fig. 8F), surface not papillate, venation eucamptodromous, 12–17 pairs of secondary veins, midrib and secondary veins adaxially and abaxially prominent, tertiary veins alternate percurrent, midrib and secondary veins covered with both layers of trichomes, reticulate white-tomentose areoles absent, leaf border dense ciliate red trichomes. Inflorescences cymose, 7–11 × 5–6 cm, pubescence with shorter layer whitish-strigose, longer layer dense reddish-hirsute, with foliaceous bracts at first node of inflorescence, 4.0–5.0 ×

1.5–2 cm, with pubescence as leaves, subulate bracteoles 0.3–1 cm long, these axes with same pubescence as inflorescence axis. Flowers with hypanthium obconic, ca. 0.2 cm long., same pubescence as inflorescence axes; calyx 4–5 lobes, oblong, acuminate to rounded at apex, 7.6–10.2 cm, externally with pubescence in two layers, shorter layer dense whitish-tomentose, longer layer dense reddish-hirsute, internally dense cream-to ferruginous-sericeous; corolla funnelform, 1.3–1.4 cm long, externally pink with pubescence in two layers, shorter layer dense yellow-tomentose, longer dense ferruginous-sericeous, internally pink with red macula, with one yellow bearded lobe, corolla lobes 5, 0.4–0.6 × 0.4–0.5 cm, ovate, acute to rounded; stamens 5, filaments 2.7–3.8 mm long, anthers 3–4 mm long; ovary with tomentose circular disk at apex, style 0.6–0.8 mm long, stigmatic lobes 2, 0.8–0.9 mm long. Fruits capsular, 3.1–3.9 × 2.9–4.2 cm, brown, oblate in outline, emarginate at apex and cordate at base, with surface strongly rugose, glabrous or sparse ferruginous-tomentose and sparse hirsute indumentum. Seeds 3.4 × 1.6 cm, flattened, with remaining portion narrowed into marginal wing 3–8 mm wide.

Illustration. Steyermark (1974), terminal branch, glands, calyx, fruit and seed; Roger (1984), pictures of habit, fruits and glands, anatomy of wood.

Phenology. Flowers from February to March, fruits in July and from December to April.

Distribution and habitat. Distributed in the south of Venezuela to the southwest of Guyana (Fig 9B). It occurs in woodland and shrub forest in sandy or rocky soils at 1,100–1,800 m

Discussion. This species is similar to *Platycarpum. eglandulosum* by its 3-whorled leaves and ferruginous leaves. But it can be differentiated from *P. rugosum* by its petioles with 2–3 glands (vs. petioles with absent gland in *P. eglandulosum*), and fruits with surface strongly rugose (vs. verrucose surface in *P. eglandulosum*).

Additional specimens examined. GUYANA. **Cayuni-Mazaruni** Region. Parauima, 15 km W; 0.25 km W of camp near eastern summit of Waukauyentipu. 5°49'57"N 61°12'0"W, 1525 m. *Clarke et al.* 5725 (NY, US). VENEZUELA. **Bolivar:** Gran Sabana, Ilu-tepuí, common in low open wood- land about Camp No. 1, one of the dominant trees, 4500–6000 ft., 13 Mar 1952, *Maguire* 33390 (NY, VEN); 125 km S of El Dorado, on the road to Luepa, dwarf forest on a plateau near the summit of mountain, soil sand and sandstone, approx. 1300

m, 21 Feb 1978, *Rogers 11* (MICH), *Rogers 12* (MICH, NY, U, VEN); 123 km S of El Dorado on the road to Luepa, dwarf forest, approx. 1400 m, 27 Oct 1979, *Rogers 51* (MICH); *Rogers 53* (MICH); vicinity of 131-132 km S of El Dorado, NE of Luepa, dwarf forest in sandstone on summit of plateau, common tree (seen between km 127 and 132) all over summit, 1200 m, 6-11 Mar 1962, *Steyermark & Aristeguieta 92* (NY, VEN); Uei-tepui, between SE slope and summit, dominant in dwarf forest in depressed portions, 1100-1300 m, 19 Apr 1960, *Steyermark & Nilsson 326* (NY, US, VEN); Km 130-131 al S de El Dorado, 19 y 26 Dec 1970, *Steyermark & Dunsterville 104066* (NY, VEN).

14. *Platycarpum schultesii* Steyermark, Bot. Mus. Leaflet. 17: 96. 1955. TYPE. Colombia.

Vaupés: Rio Parana-Pichuna (tributary of Rio Vaupés), 1°10'N, 70°30' W, alt. about 700 ft., Jun. 1953 (fl, fr), *Schultes & Cabrera 19929* (holotype, F!; isotypes, F!, GH!, US!).

Platycarpum schultesii var. *zaruchii* Rogers, Fl. Neotropica. 39:126. TYPE. Venezuela.

Amazonas: Unos 10 km al N del sector NE del Cerro Yapacana, ca. 100 m alt., sabanas de arena blanca, 28 Feb. 1980 (fl, fr), *Huber 4800* (holotype, MICH!; isotype, COL!, MO!, NY!, US!). *syn. nov.*

Key to the varieties of *Platycarpum schultesii*

- 1a. Leaves obovate to rounded, petioles 0.3–0.5 cm long..... *P. schultesii* var. *egleroides*
- 1b. Leaves elliptic, narrow-elliptic (rarely obovate), petioles 1.1–1.2 cm...*P. schultesii* var. *schultesii*

14.1 *Platycarpum schultesii* Steyermark **var. *schultesii***

Shrubs 1–4 m tall; young stems slightly triangular, pubescence dense adpressed; stipules 3.5–7.0 cm long, deltoid, caducous, abaxially dense adpressed. Leaves 3-whorled or decussate; petioles 1.1–1.2 cm long, pubescence same as leaves, near abaxial base one gland, this inverted triangular-shape to slightly rectangular, 0.2–0.5 cm long, dark when dry; lamina 11.0–14.0(–18.0) × 3.6–5.6 cm, elliptic to narrow elliptic, rarely slightly obovate, acute to rounded at apex, cuneate at base, adaxially one layer of dense strigose trichomes, abaxially

glaucous, pubescence in two layers, shorter layer dense whitish-tomentose, longer layer dense whitish bent or erect trichomes (ca. 1 mm long), venation eucamptodromous, 12–20 pairs of secondary veins, midrib and secondary veins adaxially and abaxially prominent, pubescence on veins the same as in lamina, with conspicuous intersecondary, reticulate white-tomentose areoles. Inflorescences cymose, $7.0\text{--}10.0 \times 3.5\text{--}10.0$ cm long, pubescence in two layers, shorter layer dense whitish-adpressed, longer layer dense yellow to ferruginous hirsute, foliaceous bracts at base, 1.8×0.2 cm, pubescence as leaves, on distal axes linear bracts ca. 0.1 cm long, these dense ferruginous. Flowers with hypanthium obconic, 0.8–1.0 mm long, ferruginous; calyx 5 lobes, $0.6\text{--}0.8 \times 0.2\text{--}0.4$ cm, oblong-elliptic, acute at apex, externally pubescence with shorter layer dense white-tomentose, longer layer ferruginous-hirsute, internally white-sericeous; corolla funnelform, 1.0–1.3 cm long, white-cinereous, externally pubescence in two layers, shorter layer dense whitish-tomentose, longer layer dense yellow-adpressed, internally white-pinkish with red macula, one lobe yellow bearded and the others lobes with sparse white trichomes, corolla lobes 5, $0.3\text{--}0.4 \times 0.2\text{--}0.3$ cm, acute at apex; stamens 5, filaments 5.5–8.8 mm long, anthers 2.5–3.2 mm long; ovary with tomentose circular disk at apex, style 0.5–0.7 cm long, stigmatic lobes 2, ca. 0.1 cm long. Fruits capsular, $1.7\text{--}2.3 \times 2.3\text{--}2.8$ cm, ellipsoid with emarginate apex, verrucose, ferruginous-tomentose. Seeds $1.6\text{--}2.1 \times 1.2\text{--}1.3$ cm, reniform, with narrow wing ca. 2.1 mm wide.

Phenology. Flowers from September to february and June, fruits in September and February.

Distribution and habitat. This species occurs in Vaupés area in Colombia and Amazonas state in Venezuela (fig. 9B). It grows in savannas on sandy or sandstones soils.

Discussion. This variety is recognized by its 3-whorled or decussate phyllotaxy and abaxial leaves cinereous with reticulate white-tomentose areolate.

In this treatment we recognized two varieties for *Platycarpum schultesii* (see key for *Platycarpum schultesii*). *Platycarpum schultesii* var. *schultesii*, which has 3-whorled or decussate leaves, elliptic to narrow-elliptic or slightly obovate lamina, acuminate to acute at apex, with venation white-tomentose areoles. And *Platycarpum schultesii* var. *egleroides*, which has decussate leaves, mainly obovate to rounded leaves, round to emarginate apex, and abaxially leaves venation white-tomentose areoles (fig. 8H). We do not recognize the variety *Platycarpum schultesii* var. *zarucchi* because we observed that decussate phyllotaxy is not

enough to differentiate it from *Platycarpum schultesii* var. *schultesii*. For example, the collection *Zarucchi* 2488 has 3-whorled and decussate phyllotaxy.

Additional specimens examined. COLOMBIA. **Vaupés:** Rio Vaupés, Santa Rosa, common in dwarf forest (sabanetta) along Caño Timbó, approx. 10 km N of village, 6 Dec 1979, *Rogers* 103 (MICH, NY, U, VEN); Mitú and vicinity, Rio Paraná-pichuna, on sandstone savanna at major rapids, 25 Jun 1975, *Zarucchi* 1318 (GH, MICH), 6 Sep 1974, *Zarucchi* 1947 (F, GH, MICH, NY, U, VEN), 18 Jul 1979, *Zarucchi* 2488 (GH); Mitú and vicinity, along Rio Vaupés between Rio Ti and Rapids of Mandi, savanna of Caño Timbó, low tree forest, 1 hr. from Rio Vaupés, 23 Sep 1976, *Zarucchi* 2117 (F, GH, MICH).

14.2. *Platycarpum schultesii* var. *egleroides* Dávila var. nov. TYPE: Colombia, Guainía, Puerto Inirida, Carretera Huesito - El Pato Km 5. 3°25'32"N, 67°53'35"W, 116 msnm (fl, fr), 20 Mar. 2005. *Cortés R. & R. López* 2171 (Holotype: COL!, Isotype: COAH!). Fig. 14

Diagnosis: *Platycarpum schultesii* var. *egleroides* is similar to *Platycarpum egleri* because of its leaves with venation white-tomentose areolas in the abaxial surface. However, it differs from *P. egleri* by its obovate to round leaves (vs. elliptic or obovate in *P. egleri*), decussate phyllotaxy (vs. 3-whorled phyllotaxy in *P. egleri*), and fruits 1.3–2.0 cm (vs. 2.5–3 cm in *P. egleri*).

Shrubs 1–5 m tall; young stems flattened and aristae, with dense whitish or translucent strigose trichomes; stipules lanceolate, 1.4–3.3 cm long, calyptrate, caducous, abaxially pubescence in two layers, shorter layer dense tomentose and longer ferruginous-hirsute, adaxially a cream-yellowish indumentum. Leaves decussate; petioles 0.3–0.5 cm long, with dense translucent or brown-reddish strigose indumentum, near abaxial base one gland inverted triangular-shaped to slightly rectangular, 0.3–0.5 cm long, dark when dry; lamina 7.4–13.2 × 3.7–7.6 cm, obovate to rounded (rarely oblong), rounded to retuse at apex, cuneate to rounded at base, with venation eucamptodromous, (8–)10–14 pairs of secondary veins, adaxially on layer of trichomes strigose, abaxially glaucous, two layers of trichomes, shorter layer strigose, longer layer tomentose, with reticulate white-tomentose areoles present. Inflorescences cymose, 5–12 cm long, with 3 orderings of branching, foliaceous bracts at first

or second node of inflorescence, these ca. 5×1 cm, on more distal axes linear bracts 0.5–0.1 cm long, these dense ferruginous-strigose. Flowers with hypanthium obconic, 2.9–3.2 mm, ferruginous-strigose; calyx lobes 5, oblong, $0.5\text{--}0.9 \times 0.2\text{--}0.4$ cm, externally with pubescence in two layers, shorter layer creamy-tomentose, longer layer ferruginous-hirsute, internally shorter layer creamy-sericeous, longer layer creamy-hirsute; corolla funnelform, 1–1.5 cm long, externally yellowish, with pubescence in two layers, longer layer hirsute and shorter layer tomentose, internally white with red macula in the throat, puberulous, one yellow bearded lobe, corolla lobes 5, $0.3\text{--}0.6 \times 0.2\text{--}0.3$ cm, these elliptic, acute at apex; stamens 5, inserted at two different heights in corolla tube, filaments 1.9–2.2 mm long, anthers 2–2.2 mm long, acute at the apex, cordate at the base; ovary inferior in flower, with tomentose circular disk at apex, style 0.4–0.9 cm long, stigmatic lobes 2, ca. 0.1 cm long. Fruits capsular, $1.3\text{--}2.0 \times 2\text{--}3$ cm, elliptic in outline, markedly flattened parallel to woody septum, with surface verrucose, tomentose–ferruginous, dehiscence loculicidal. Seeds 4.9×2.1 cm, elliptic, with surface pitted, with marginal wing ca. 0.3 cm wide.

Phenology. Flowers in March to April and October, fruits in March.

Distribution and habitat. This variety occurs in Guainía department, southeastern of Colombia (fig. 9B). It grows in natural savannas on sandy soils.

Discussion. *Platycarpum schultesii* var. *egleroides* is distinguished by its phyllotaxy decussate, short petioles (0.3–0.5 cm), and leaves with areoles white-tomentose in the abaxial surface. It is similar to *Platycarpum egleri* because it also has white-tomentose areoles in the abaxial surface of the leaves, but *P. schultesii* var. *egleroides* has obovate to rounded leaves (vs. elliptic leaves in *P. egleri*), decussate phyllotaxy (vs. 3-whorled in *P. egleri*), and fruits 1.3–2 cm (vs. 2–3 cm in *P. egleri*).

Additional specimens examined. COLOMBIA. **Guainía.** Inírida. Resguardo La Ceiba - Caranacoa. Sector Huesito, carretera Huesito - El Pato, km. 6 al 10. $3^{\circ}25'24''\text{N}$ $67^{\circ}53'37''\text{E}$, 100–15 m. 25 Apr 2014, *Cárdenas 14774* (COL, COAH); Puerto Colombia, km 52 carretera Huesito (río Inírida-Puerto Caribe-río Guainía), sector caño Pato. $3^{\circ}07'10''\text{N}$ $67^{\circ}47'20''\text{W}$, 4 Oct 2005, *Cárdenas 16836* (COAH); Carretera Huesito-Puerto Caribe (río Inírida-río Guainía) km 53, $3^{\circ}07'10''\text{N}$ $67^{\circ}47'20''\text{W}$, 4 Oct 2005, *Cárdenas 16999* (COAH); Carretera Huesito-El Pato. Km 5, $3^{\circ}00' \text{N}$ $67^{\circ}00' \text{W}$, 20 Mar 2015, *Cortés 2170* (COL); *Cortés 2171* (COL); *Cortés 2172* (COL); Puerto Huesito, sabanas del Alto de La Cruz, entre

el Caiio Chaquita (afluente del Atabapo) y el Caino Gente, 200 m, 18-20 Aug 1975, *Garcia-Barriga 20916* (GH). VENEZUELA. **Amazonas**: Rio Ventuari, frente al caserio de Canaripó, sabana de arena blanca, ca. 100 m, 22 Aug 1978, *Huber 2438* (VEN); Rio Guainía, unos 10 km al W del Cafno Pimichin y unos 5 km al N de Tonina, 100 m, 1 Mar 1980, *Huber 4892* (MICH); 2-3 km al SE del bajo Rio Guasacavi, sabana y caatinga abierta, 90 m, 10 Mar 1980, *Huber 5125* (MICH); 20 km al NW de Yavita, en las cabeceras del Canio Pimichin, extensas sabanas, ca. 120 m, 11 Feb 1981, *Huber & Medina 5951A* (MICH).

15. *Platycarpum vriesendorpiae* Dávila, *sp. nov.* TYPE. Peru. Loreto, Provincia de Requena, Distrito de Soplin, Quebrada Yanayacu-Río Blanco, Campamento Wiswincho, 110-120 msnm, 05°48'33.5"S, 73°51'53.8"W, 10 Oct. 2014 (fr), *Ríos M. 4254* (holotype, AMAZ!, isotypes, F!, MO!, USM!).

Trees 12–25 m tall, 40–45 cm (dbh), with external bark reticulate and inner bark reddish; exudate red; young stem angled, sparsely tomentose; stipules triangular, caducous, 3.3–4.4 cm long, adaxially golden-ferruginous-hirsute, creamy-sericeous abaxially. Leaves ternate or occasionally opposite; lamina 10.0–16.0 × 4.5–7.7 cm, obovate or sometimes elliptic, acute to obtuse at apex, acute at base, golden when dry, with venation eucamptodromous, with 20–24 pairs of secondary veins, with alternate percurrent tertiary veins, the midrib and secondary veins impressed adaxially and prominent abaxially, pubescence adaxially one layer of densely white-strigose trichomes, abaxially with one layer of golden villous trichomes, on midrib and secondary veins densely golden-hirsute, the abaxial lamina surface cinereous papillae. Inflorescence 12–13 × 5–12 cm, with foliaceous bracts present at first or second node of inflorescence, these 5.0 × 0.3 cm, more distal axes with linear bracts 0.7–1.2 cm long and pubescence like inflorescence axes. Flowers with hypanthium obconic, 0.2–0.3 cm, ferruginous-tomentose; calyx lobe 5, these elliptic to oblong, 0.8–1.1 × 0.3–0.4 cm, externally with pubescence in 2 layers, shorter layer yellow-villous, longer layer sparsely ferruginous-tomentose, internally yellowish-sericeous; corolla infundibular, 1.5–2 cm long, externally yellow with pubescence in two layers, longer layer tomentose, shorter layer villous, internally white with a red macula in throat, puberulous and with a ring of yellowish trichomes at the base, lobes 5, ca. 1.6 × 0.5 cm, acute, marginally

crisped, one lower lobe yellow and bearded; stamens 5, filaments 4–6 mm long, anthers 0.3–0.4 cm long; ovary with tomentose circular disk at apex, style 6–7 mm long, stigmatic lobes 2, ca. 2 mm long. Fruits capsular, 4.7–5.5 × 3.6–4.9 cm, elliptic in outline, verrucose, ferruginous-tomentose. Seeds ca. 4.5 × 1.8 cm, elliptic, with marginal wing 0.5 cm wide.

Phenology. Flowers and fruits in October.

Distribution and habitat. This species is known only from northeastern Peru in the southeastern part of Loreto Region, in the Matsés National Reserve and between the Tapiche and Blanco rivers (fig 9B). It grows in white sand forest and in peatlands.

Discussion. This species is similar to *Platycarpum acreanum* due to its mostly 3-whorled phyllotaxy, leaves abaxially with dense pubescence, and fruits with similar shape and size. *Platycarpum vriesendorpiae* differs from *P. acreanum* by its calyptrate stipules that are triangular and 2- or 3-angled (vs. lanceolate in *P. acreanum*), leaf lamina abaxially with one layer of golden velutinous trichomes (vs. two layers of trichomes with a shorter layer tomentose-hispidulous and a longer layer tawny-hirsute in *P. acreanum*), and corolla 1.5–2 cm long (vs. ca. 2.5 cm in *P. acreanum*).

Additional specimens examined. PERU: **Loreto**, Provincia de Requena, margen derecha del río Blanco (tributario del río Tapiche), área de la comunidad indígena MATSES, 124–144 msnm, 05°85'76.83"S, 073°76'03.33"W, 31 Oct 2004, *Dávila et al.* 1114 (AMAZ, F, MO, USM); Provincia de Requena, Distrito de Soplin, Quebrada Yanayacu-Río Blanco, Campamento Wiswincho, 110–120 msnm, 05°48'33.5"S, 73°51'53.8"W, 10 Oct 2014, *Ríos et al.* 4302 (AMAZ).



Figure 6: Morphology of *Platycarpum*. A-F, G-H. *Platycarpum egleri*, D, I. *Platycarpum acreanum*, E. *Platycarpum froesii*. A. Tree habit, B. Terminal branch with cymose inflorescence, C. Young stem showing red exudate, D. Stipule. E. Strong revolute leaves and open capsular fruit, F. Abaxial leaves with white-tomentose areoles, G. Young stem showing petiole base with gland, H. Corolla internally white with red lines and macula and one yellow bearded corolla lobe, I. Capsular fruits, arrow shows perianth scar at base of the fruit.

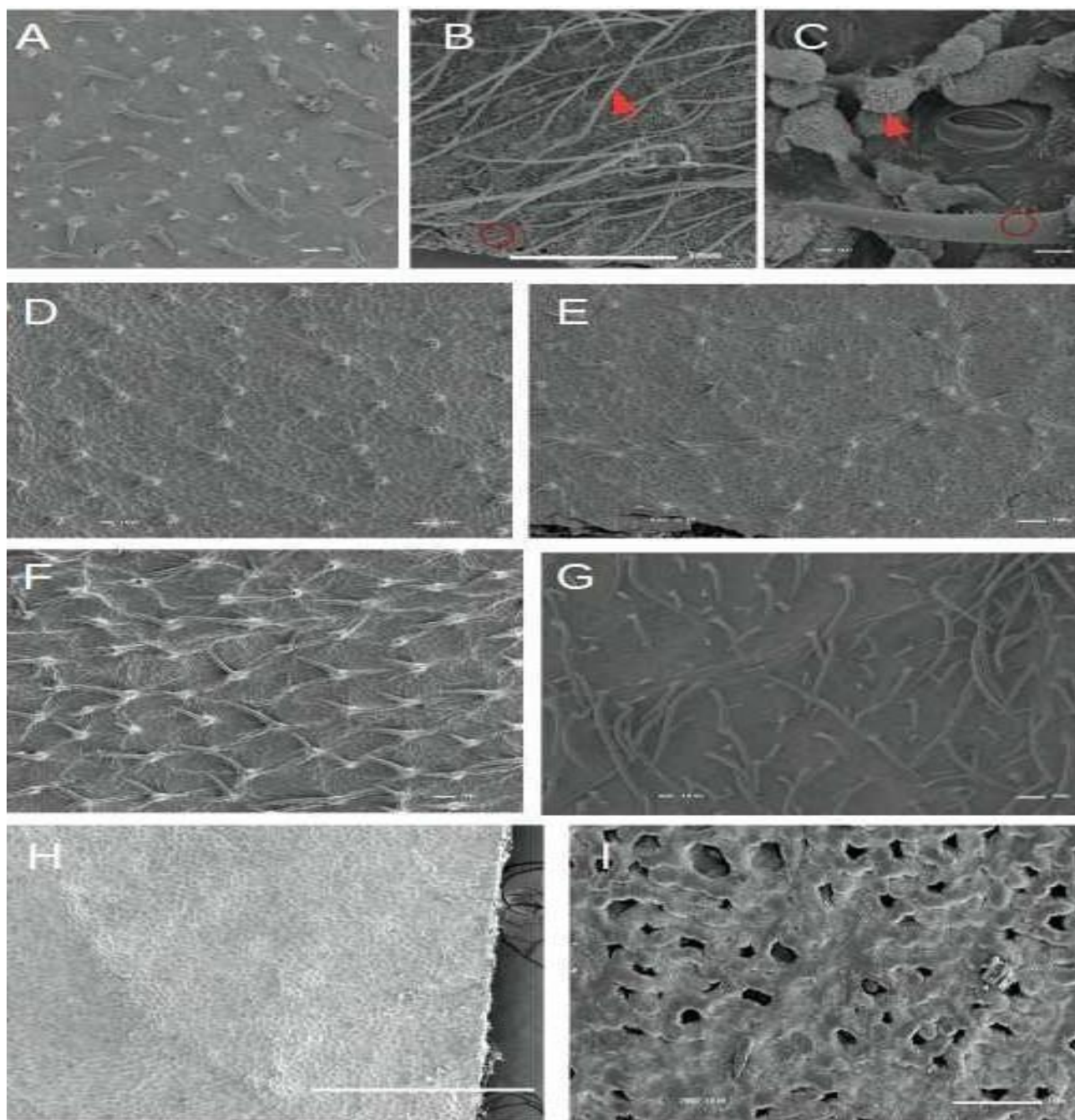


Figure 7: SEM of *Platycarpum* leaves. A-B. *Platycarpum acreanum*. A. Adaxial lamina showing one layer of strigose trichomes, B. Abaxial lamina showing two layer of trichomes, arrow shows longer layer and dot shows shorter layer, C-D. *Platycarpum araracuarensense*, C. Adaxial lamina showing one layer of strigillose trichomes, D. Abaxial lamina with sparse trichomes, E-F. *Platycarpum froesii*, E. Adaxial lamina one layer of dense strigose trichomes, F. Abaxial lamina one layer of antrorse trichomes, G-H. *Platycarpum negrense* var. *negrense*, G. Adaxial lamina glabrous, H. Abaxial lamina glabrescent with surface dense papillate covered with wax.

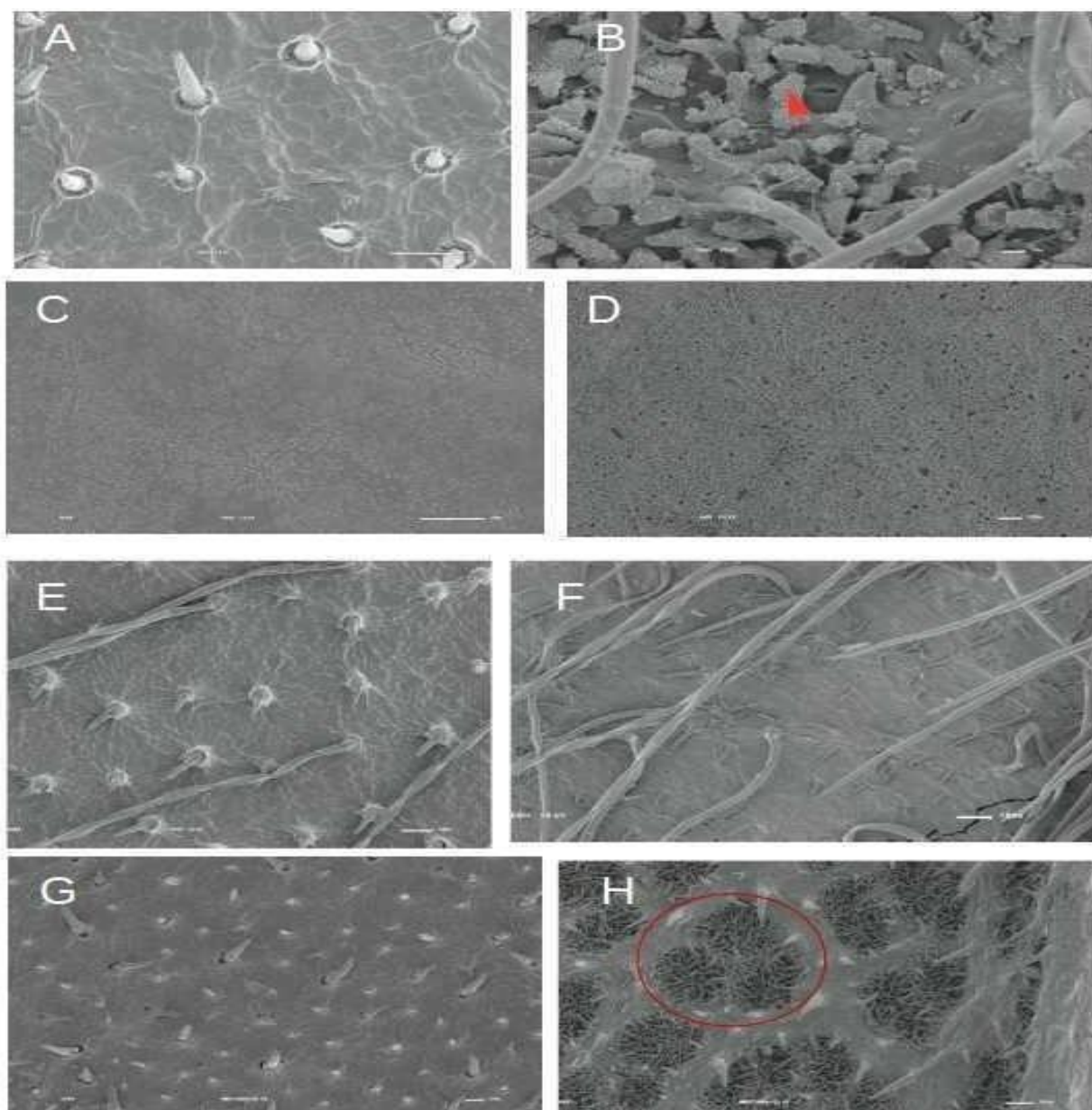


Figure 8: SEM of *Platycarpum* leaves. A-B. *Platycarpum orinocense*, A. Adaxial lamina with one layer of strigose trichomes, B. Abaxial lamina with papillate surface, arrow shows papillae covered with wax, C- D. *Platycarpum rhododactylum*. C. Adaxial lamina showing glabrous surface, D. Abaxial lamina papillate surface with few adpressed trichomes, E-F. *Platycarpum rugosum*, E. Adaxial lamina two layers of trichomes, shorter layer dense strigose and longer layer sparse hirsute, surface not papillate F. Abaxial lamina pubescence in two layers, longer layer dense hirsute and shorter layer dense strigillose. H-I. *Platycarpum schultesii* var. *egleroides*, H. Adaxial lamina on layer of trichomes strigose, I. Abaxial lamina with two layers of trichomes, shorter layer strigose and longer layer tomentose, circle shows areole with white-tomentose trichomes.

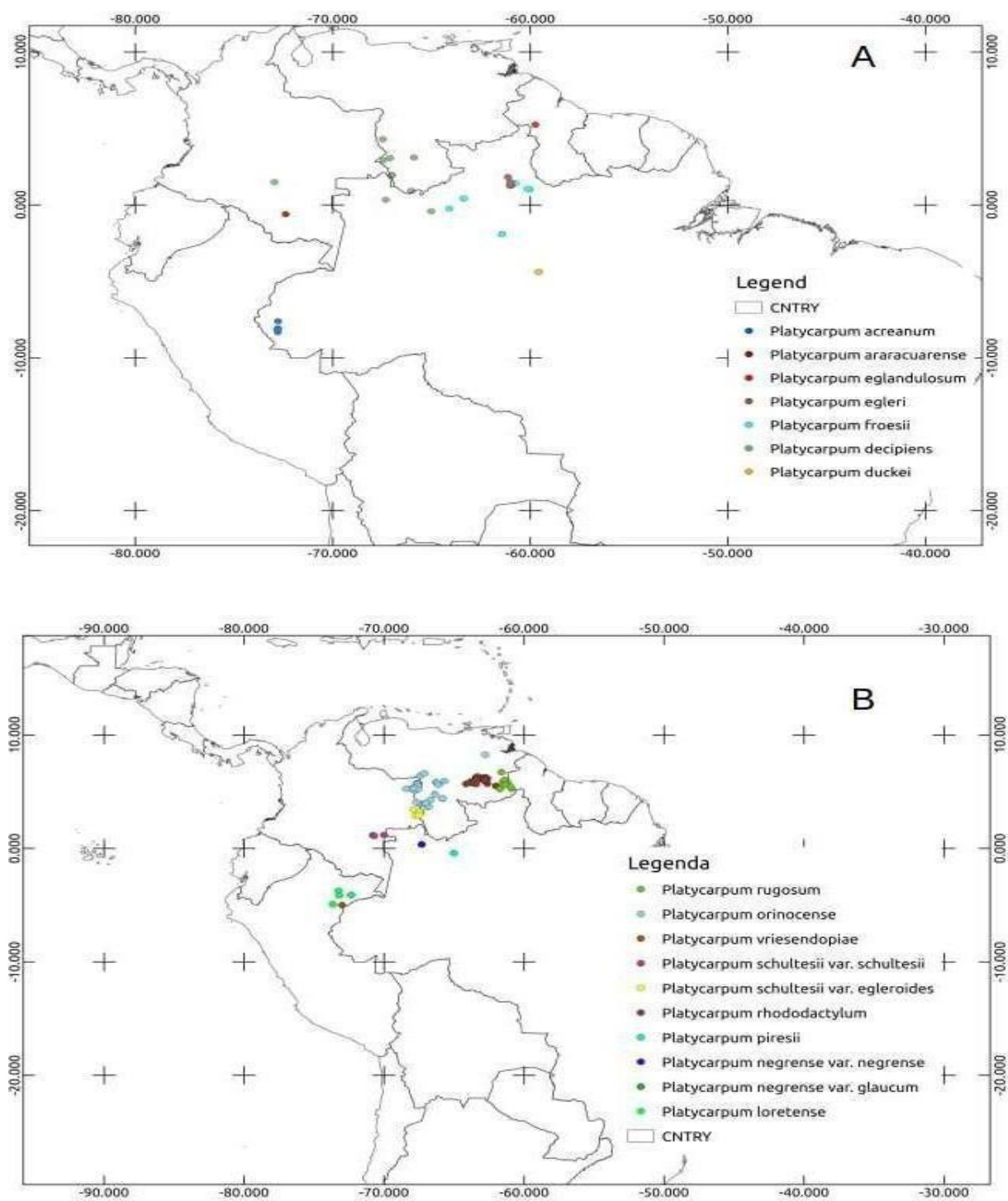


Figure 9: Distribution map of *Platycarpum*

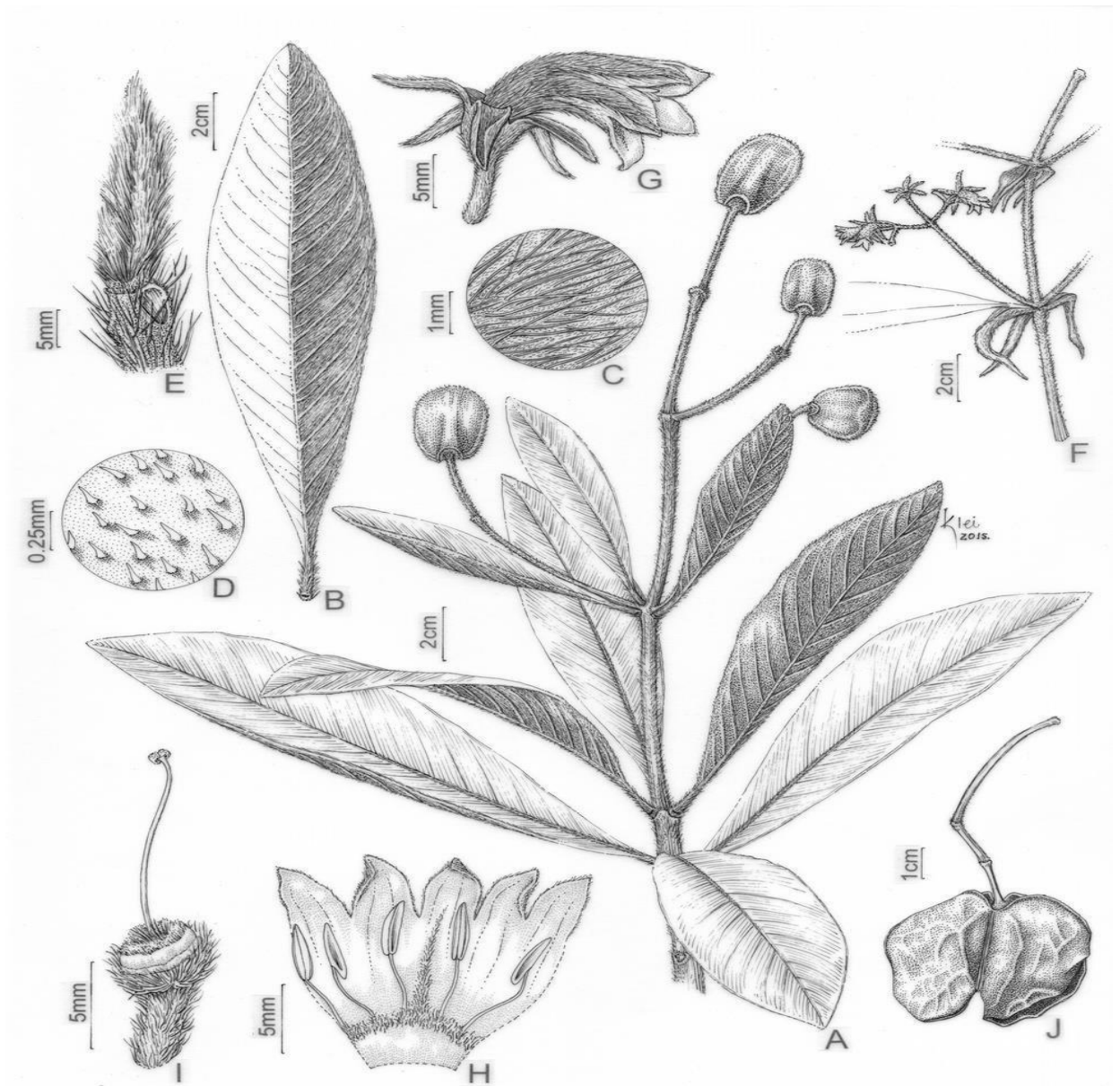


Figure 10: *Platycarpum acreanum*. A. Terminal branch, B. Abaxial leaf, C. Abaxial leaf pubescence, D. Adaxial leaf pubescence, E. Stipule, F. Partial inflorescence, G. Flower, H. Corolla open, I. Flower with corolla removed, J. Open Fruit.

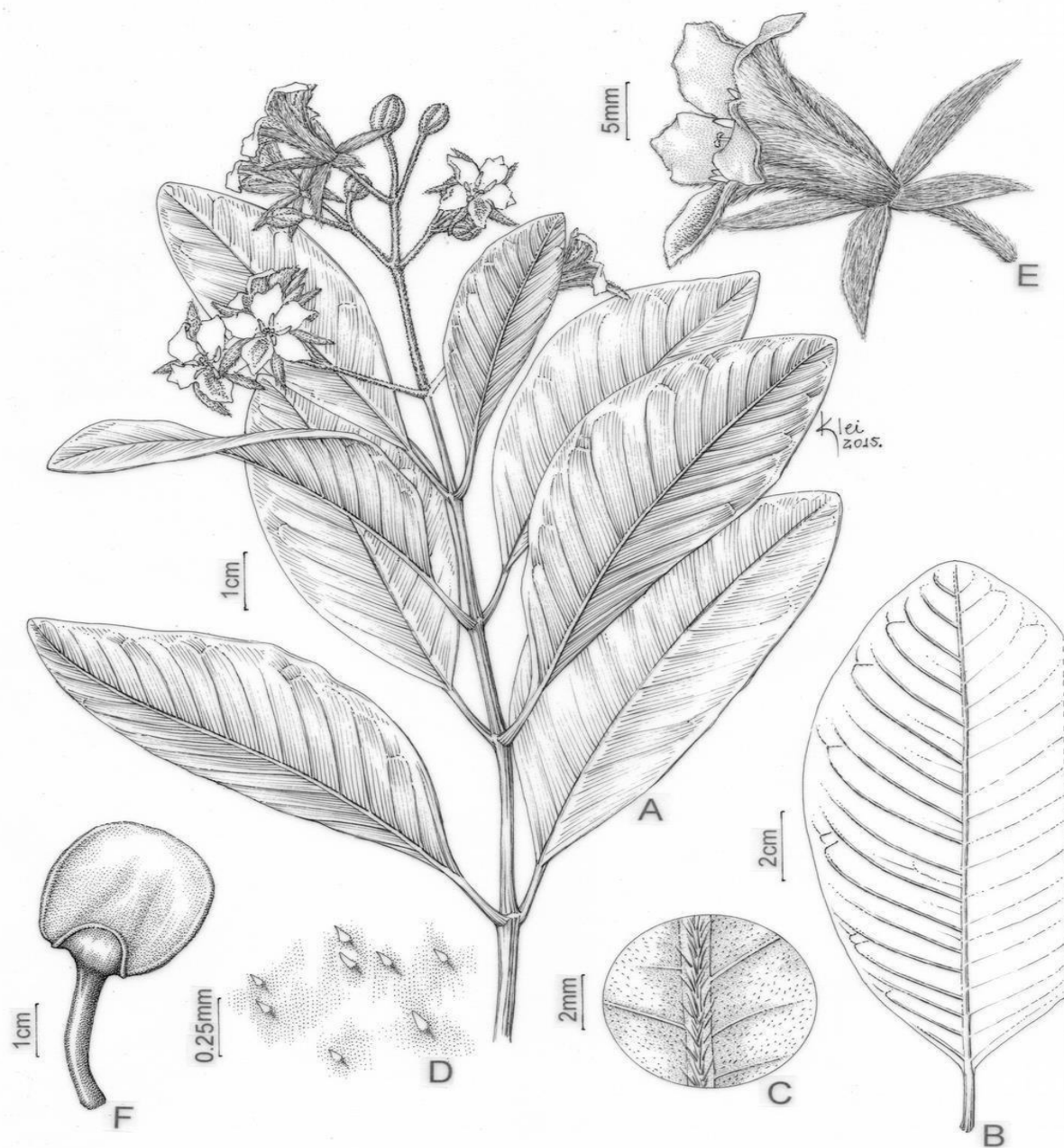


Figure 11: *Platycarpum araracuarens*. A. Terminal shoot, B. Leaf shape, C. Abaxial leaf pubescence, D. Adaxial leaf pubescence, E. Flower, F. Fruit.

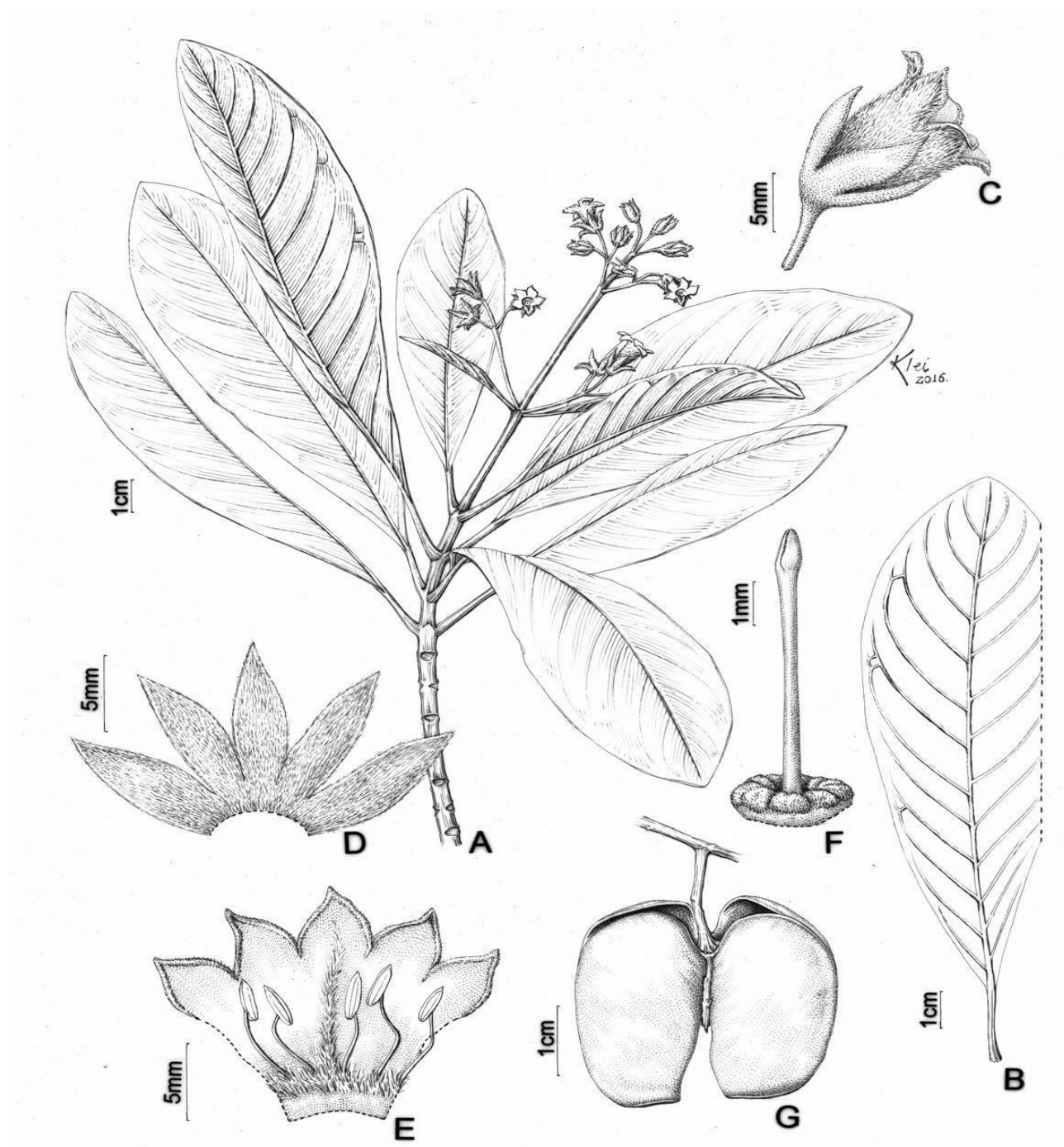


Figure 12: *Platycarpum negrense* var. *negrense*. A. Terminal shoot, B. Leaf shape, C. Flower, D. Open calyx. E. Open corolla. F. Pistil, G. Fruit with open valves.

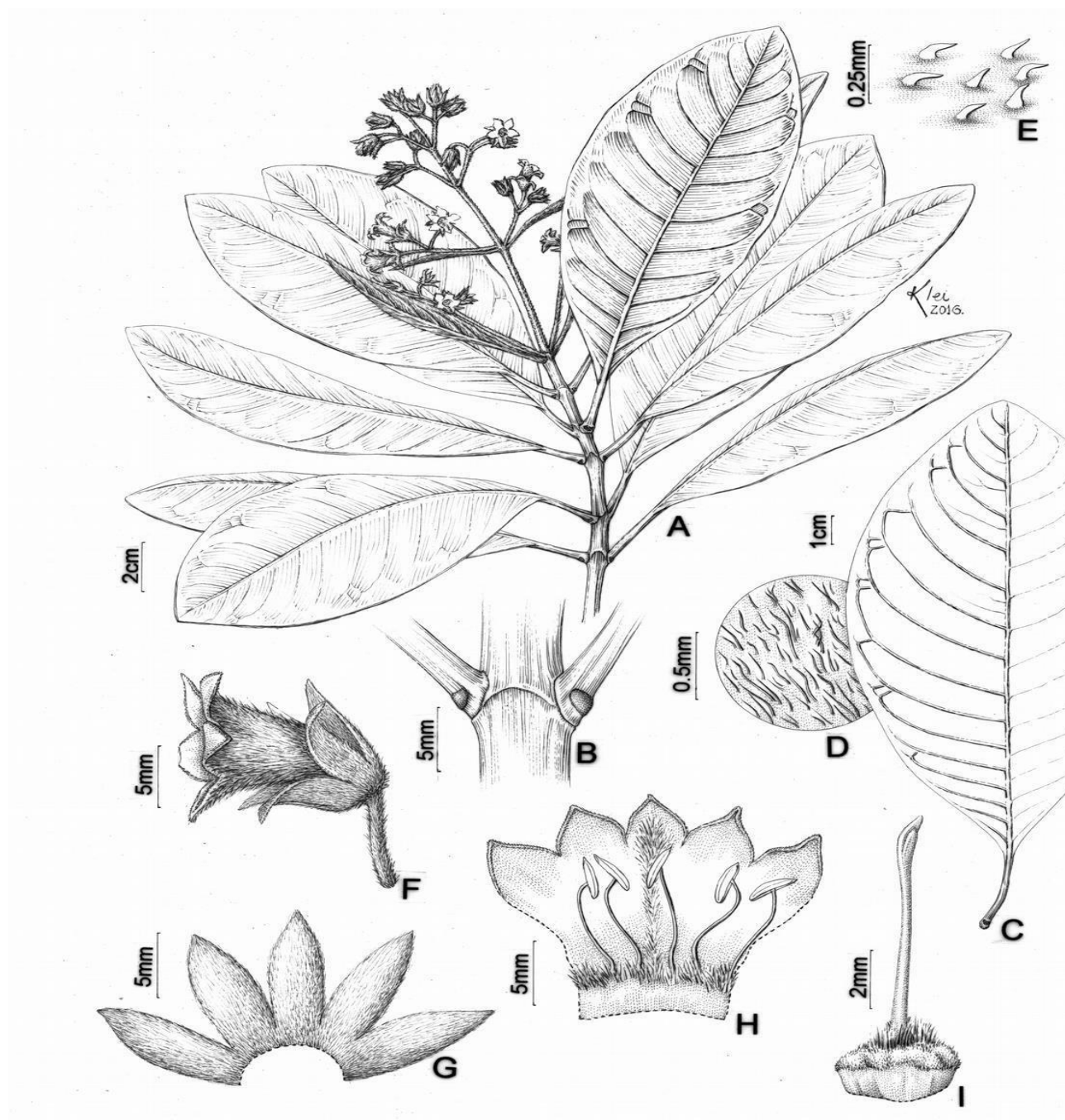


Figure 13: *Platycarpum piresii*. A. Terminal shoot, B. Node with petiole showing a basal petiole gland, C. Adaxial leaf, D. Abaxial leaf with villous trichomes. E. Adaxial leaf showing strigose trichomes, F. Flower, G. Open calyx, H. Open corolla, I. Pistil.

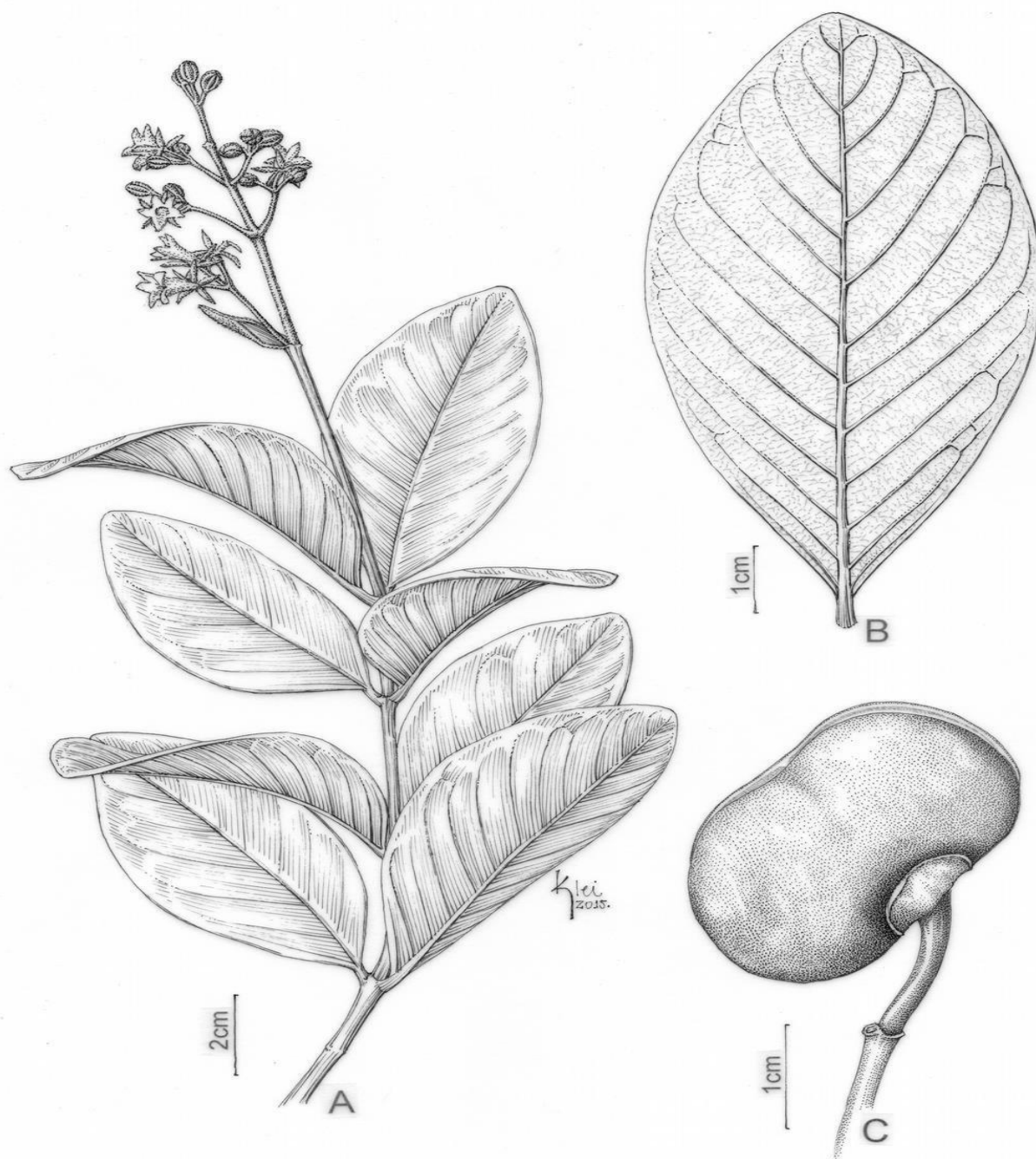


Figure 14: *Platycarpum schultesii* var. *egleroides*. A. Terminal branch with flowers, B. Abaxial leaf, C. Mature fruit.

CONSIDERAÇÕES FINAIS

Henriquezieae tem sido objeto de estudo por quase 200 anos. Esta tribo tem uma atípica morfologia dentro de Rubiaceae, o que tem intrigado muitos taxonomistas. A tribo tem alto endemismo e ocorre em áreas de pouco acesso o que dificulta sua amostragem. O capítulo I desta tese foi focado em avaliar as relações filogenéticas dentro da tribo Henriquezieae com uma ampla amostragem em número de espécies e dados moleculares. Isto nos permitiu inferir que Henriquezieae é um grupo monofilético assim como os três gêneros que a constituem, *Gleasonia*, *Henriquezia* e *Platycarpum*. O gênero *Gleasonia*, que apresenta os caracteres mais típicos de Rubiaceae é o grupo irmão de *Henriquezia* e *Platycarpum*, estes dois últimos gêneros apresentam a maioria dos caracteres considerados atípicos em Henriquezieae. Também postulamos potenciais sinapomorfias para a tribo e para cada um dos gêneros da tribo. Futuros estudos biogeográficos, adicionando as espécies que ocorrem nos “tepui” do escudo da Guianas são necessários, para inferir a área ancestral de Henriquezieae e inferir a irradiação da tribo no Escudo das Guianas e na Amazônia. Estudos biogeográficos também poderiam contribuir para o conhecimento da origem da flora do Escudo das Guianas. Além disso, um mapeamento das características atípicas em Henriquezieae em uma filogenia da família Rubiaceae seria interessante para inferir se a presença de caracteres atípicos em Henriquezieae estão presentes em outros grupos de Rubiaceae e como a presença desses caracteres está relacionada com a diversidade dos grupos.

O capítulo II desta tese foi focado na atualização da taxonomia de Henriquezieae. Depois da revisão taxonômica de Rogers em 1984, foi descoberta uma nova espécie por Boom em 1985, e durante nossa amostragem também foram descobertas quatro novas espécies. *Platycarpum lorentensis* (Dávila & Kinoshita 2016), *Platycarpum vriesendorpiae* (Dávila et al., em processo de revisão) e duas outras novas espécies são descritas neste tratamento taxonômico, *Platycarpum araracuarensense* e *Platycarpum piresii*. Além disso, as coletas realizadas nos últimos anos e as coletas realizadas durante a elaboração desta tese permitiram complementar as descrições de algumas espécies que até agora careciam da descrição de detalhes na sua morfologia. Durante a elaboração do capítulo II percebemos que futuros trabalhos que abordem a delimitação das espécies usando estudos de populações seriam úteis para ampliar a compreensão sobre a circunscrição de *Platycarpum schultesii*.

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ANEXOS

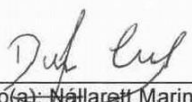


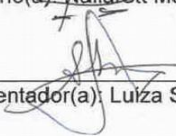
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Em observância ao §5º do Artigo 1º da Informação CCPG-UNICAMP/001/15, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada "*Relações filogenéticas e taxonomia de Henriquezieae Hook. (Ixoroideae, Rubiaceae) no Escudo das Guianas*", 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.

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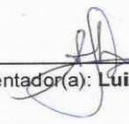
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