# Systematics of the tribe Echiteae and the genus *Prestonia* (Apocynaceae, Apocynoideae)

# Dissertation

zur Erlangung des Doktorgrades

Dr. rer. nat

Eingereicht an der Fakultät für Biologie, Chemie und

Geowissenschaften

J. Francisco Morales

Bayreuth

Die vorliegende Arbeit wurde von Oktober 2013 bis Januar 2016 in Bayreuth am Lehrstuhl

Pflanzensystematik unter Betreuung von Prof. Dr. Sigrid Liede-Schumann und Dr. Mary

Endress (Institute of Systematic and Evolutionary Botany, University of Zurich,

Switzerland) angefertigt.

Vollständiger Abdruck der von der Fakultät für Biologie, Chemie und Geowissenschaften

der Universität Bayreuth genehmigten Dissertation zur Erlangung des akademischen

Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.).

Dissertation eingereicht am: 31.01.2017

Zulassung durch die Promotionskommission: 15.02.2017

Wissenschaftliches Kolloquium: 27.04.2017

Amtierender Dekan: Prof. Dr. Stefan Schuster

Prüfungsausschuss:

Prof. Dr. Sigrid Liede-Schumann

(Erstgutachterin)

Prof. Dr. Carl Beierkuhnlein

(Zweitgutachter)

Prof. Dr. Bettina Engelbrecht

(Vorsitz)

PD. Dr. Ulrich Meve

This dissertation is submitted as a "Cumulative Thesis" that includes four publications: one published, two accepted, and one in preparation for publication.

# **List of Publications**

- 1. Morales, J.F. & S. Liede-Schumann. 2016. The genus *Prestonia* (Apocynaceae) in Colombia. Phytotaxa 265: 204–224.
- 2. Morales, J.F., M. Endress & S. Liede-Schumann. Sex, drugs and pupusas: Disentangling relationships in Echiteae (Apocynaceae). Accepted, Taxon.
- 3. Morales, J.F., M. Endress & S. Liede-Schumann. A phylogenetic study of the genus *Prestonia* (Apocynaceae). Accepted, Annals of the Missouri Botanical Garden.
- 4. Morales, J.F. & M. Endress. A monograph of the genus *Prestonia* (Apocynaceae, Echiteae). To be submitted to Annals of the Missouri Botanical Garden or Phytotaxa.

# 4. Declaration of contribution to publications

The thesis contains three research articles for which most parts were carried out by myself, under the supervision of Dr. Mary Endress, University of Zürich and Prof. Dr. Sigrid Liede-Schumann, University of Bayreuth. Field work for the DNA samples was conducted in Brazil, Colombia, Costa Rica, Panama and Peru from 2010 to 2015, supported by a private donor, the Instituto para la Investigación científica para la Amazonia de Colombia (SINCHI), the Graduate School of Bayreuth University and the DeutscheAkademische Austauschdienst (DAAD). Molecular work was done at the University of Bayreuth, under the supervision of Angelika Täuber and Margit Gebauer. Herbarium work was supported partially by the Missouri Botanical Garden, St. Louis, Missouri and the University of South Florida, Florida. Prof. Dr. Sigrid Liede-Schumann and J. Francisco Morales chose the DNA markers used in the phylogenetic studies. Papers were prepared under consideration of the comments and suggestions of all coauthors.

# 1st publication

Morales, J.F. & S. Liede-Schumann. 2016. **The genus** *Prestonia* (**Apocynaceae**) in **Colombia**. Phytotaxa 265: 204–224.

#### Authors' contribution:

Fieldwork in several Colombian departments (Antioquia, Cundinamarca, Guaviare, Guainia, and Tolima), the visit of different herbaria in Colombia and United States, and the morphological analysis of the herbarium samples were done by J. Francisco Morales, as well as the idea and structure of the manuscript, including distribution maps and line drawings. Photographs for this paper were taken in Colombia during 2013. J. Francisco Morales drafted the paper, Dr. Mary Endress reviewed a preliminary version and Prof. Dr. Sigrid Liede-Schumann added some suggestions and comments, which were incorporated in the final version.

# 2nd publication

Morales, J.F., M. Endress & S. Liede-Schumann. Sex, drugs and pupusas: Disentangling relationships in Echiteae (Apocynaceae) (Accepted: Taxon)

#### Authors' contribution:

Fieldwork for collecting the DNA samples in Latin America, as well as the visit to different herbaria with the same purpose was carried out by J. Francisco Morales from 2010 to 2015. J. Francisco Morales did the molecular work alone under the assistance of Angelika Täuber and Margit Gebauer at the Department of Plant Systematics, University of Bayreuth. Sequence alignments, matrices, and data analysis were carried out under the supervision of Prof. Dr. Sigrid Liede-Schumann. J. Francisco Morales wrote the paper, conducted the final data analysis, and drew the figures. Dr. Mary Endress corrected and reviewed the draft. Prof. Dr. Sigrid Liede-Schumann reviewed the final version of the manuscript before sending it for publication.

### 3rd publication

Morales, J.F., M. Endress & S. Liede-Schumann. A phylogenetic study of the genus *Prestonia* (Apocynaceae) (Accepted: Annals of the Missouri Botanical Garden).

#### Authors' contribution:

The DNA material was obtained by J. Francisco Morales from 2010 to 2015 through fieldwork in Latin America or the visit to different herbaria. Molecular laboratory work, sequence alignments, and matrices assembling were done by J. Francisco Morales. Dr. Sigrid Liede-Schumann reviewed the final versions of the assembled DNA sequence matrices. The manuscript was prepared by J. Francisco Morales with the support of Dr. Mary Endress, who also reviewed the paper and made several comments and suggestions. The final version was reviewed by Prof. Dr. Sigrid Liede-Schumann and all comments were incorporated in the final version of the manuscript.

4th publication

Morales, J.F. & M. Endress. A monograph of the genus *Prestonia* (Apocynaceae, Echiteae, Prestoniinae) (In preparation, to be submitted March 2017)

# Authors' contribution:

The first author conducted the study of herbarium specimens and field work in several neotropical countries, drafted the paper, descriptions, illustrations, maps, and took most of the pictures included in the paper. Dr. Mary Endress improved the English style and the structure of the paper and made several comments on the original manuscript, included in the final version to be submitted. The paper is almost ready to be sent for publishing and only minor formatting issues are still lacking.

# **CONTENT**

Summary  Zusammenfassung		1
		3
1.	General Introduction	5
2.	Aims of Research	9
3.	Synopsis	10
	3.1 Materials and Methods	10
	3.2 Results and Discussion	13
	3.3 Conclusion and emerging research challenges	18
	3.4 References	20
Pu	blications	
	1. The genus <i>Prestonia</i> (Apocynaceae) in Colombia.	27
	2. Sex, drugs and pupusas: Disentangling relationships in Echiteae	75
	(Apocynaceae).	
	3. A phylogenetic study of the genus <i>Prestonia</i> (Apocynaceae).	132
	4. A monograph of the genus <i>Prestonia</i> (Apocynaceae, Echiteae,	183
	Prestoniinae)	
Ac	knowledgements	494
(Eidesstattliche) Versicherungen und Erklärungen		495

# **Summary**

Of the 9 tribes in Apocynaceae-Apocynoideae, the Echiteae is a group of lianas (rarely erect herbs) and comprises 19 genera and about 200 species, of which 16 genera are restricted to the Neotropics. The tribe Echiteae was proposed more than 120 years ago, but its composition has varied through time. The results of some phylogenetic studies have suggested that the tribe is non-monophyletic, a condition also applying to of its genera in the present circumscription. In this work, we provide the first phylogenetic study of the Echiteae, using nuclear (ITS) and chloroplast markers, in order to test the monophyly of the tribe and its subtribes, analyzing the largest dataset ever compiled.

The results show that Echiteae and four of its subtribes (Echitinae, Parsonsiinae, Peltastinae and Prestoniinae) as previously circumscribed are non-monophyletic. The fifth subtribe, Pentalinoninae, though monophyletic, does not belong to Echiteae; *Prestonia* and *Temnadenia* are resolved as polyphyletic, whereas *Fernaldia* is nested within *Echites* and *Peltastes* is nested in *Macropharynx*, and therefore, these two genera are reduced to synonymy. Fourteen genera are maintained and a new subtribe Laubertinae is proposed. In the ancestors of Echiteae, we hypothesize that an evolutionary shift took place in which steroidal alkaloids and/or cardenolides, characteristic for apocynoids, were replaced by parsonsine type pyrrolizidine alkaloids as the henceforth predominant chemical defense compounds.

*Prestonia* is the second largest genus of Echiteae, with ca. 56 species distributed in Tropical America and the West Indies. The last monograph was published in 1936, but it is out of date due the number of species described since then. Only synopsis for some areas and flora treatments are available. Preliminary phylogenetic studies have suggested that the genus is not monophyletic. At the same time, four infrageneric classifications proposals have been published, but never have been tested with molecular data. Therefore, the circumscription of *Prestonia* and the relationships between the species remained unresolved.

Two phylogenetic analyses using chloroplast (trnL intron and trnL-trnF intergenic spacer, rpl16 intron, rps16 intron, matK and 3'/5' trnK intron) and nuclear data (ITS) were

conducted for *Prestonia* with three aims: 1) to determine if the genus is monophyletic and to establish its relationships with the others genera in the tribe Echiteae, 2) to evaluate the current infrageneric classification proposals, as well as to determine the interspecific relationship in *Prestonia*, 3) to provide the necessary nomenclatural and / or taxonomic changes. The results of the present thesis show that *Prestonia* in the previous circumscription was polyphyletic, because *P. riedelii* is sister to *Rhodocalyx* and *Temnadenia ornata* is nested inside *Prestonia*. In consequence, the first species was transferred to *Rhodocalyx* and the second species to *Prestonia*. In the second part of the study and with a larger sampling, *Prestonia* could be shown to be monophyletic, but the sections proposed by Schumann, Woodson or Pichon are non-monophyletic. A new infrageneric classification is proposed, recognizing six sections: *Coalitae, Denticulata, Exsertae, Haemadictyon, Mollis*, and *Prestonia*.

As result of this study, the first synopsis of *Prestonia* for Colombia (the second most diverse country in South America) recognizing 25 species was published. And finally, this thesis is proposing a new monograph for *Prestonia*, with 56 species currently accepted. Descriptions, illustrations, distribution maps and IUCN conservation criteria are provided for every species. A key to the species is presented and the 6500 herbarium specimens examined were assigned to species and annotated.

# Zusammenfassung

Unter den 9 Triben in den Apocynaceae-Apocynoideae repräsentieren die Echiteae eine Gruppe von ca. 19 Gattungen und 200 Arten. Es sind Lianen, selten aufrechte Kräuter, die mit allein 16 Gattungen auf die Neotropis beschränkt sind. Die Tribus Echiteae wurde vor 120 Jahren eingerichtet, aber ihre Zusammensetzung variierte immer wieder. Die Resultate einiger Untersuchungen legten aber nahe, dass die Tribus nicht monophyletisch sei, ebenso wie einige ihrer Gattungen in der gegenwärtigen Umschreibung. In dieser Arbeit wird nun die erste phylogenetische Analyse der Echiteae vorgelegt. Es wurden Kern- (ITS) und Chloroplasten-Marker verwendet, um die Monophylie der Echiteae und ihrer Subtriben zu testen. Insgesamt ist dies umfassendste Bearbeitung dieser Taxa die jemals vorgelegt wurde.

Echiteae mit ihren vier Subtriben (Echitinae, Parsonsiinae, Peltastinae and Prestoniinae), so konnte hier gezeigt werden, sind in ihrer gegenwärtigen Umschreibung nicht monophyletisch. Die fünfte Subtribus, Pentalinoninae, obwohl monophyletisch, gehört dagegen nicht in die Tribus Echiteae. *Prestonia* und *Temnadenia* erwiesen sich als polyphyletisch, wohingegen *Fernaldia* in *Echites* eingenistet ist und *Peltastes* in *Macropharynx*, und somit in die Synonmie verschoben wurden. Vierzehn Gattungen werden aufrechterhalten, und eine neue Subtribus, Laubertinae, wird vorgeschlagen. Unter den Vorfahren der Echiteae gab es, so kann vermutet werden, einen evolutionären Wechsel von steroidalen Alkaloiden und/oder Cardenoliden – Substanzen die sehr charakteristisch sind für Apocynoideae – hin zu Pyrrolizidinalkaloiden vom Parsonsia-Typ, die nunmehr vorherrschende Komponente der chemischen Verteidigung.

Prestonia ist mit ca. 56 Arten die zweitgrößte Gattung innerhalb der Echiteae, die im tropischen America und auf den Westindischen Inseln verbreitet ist. Die letzte Monographie, 1936 veröffentlicht, ist jedoch veraltet, da seitdem viele neue Arten beschrieben wurden. Für einige Gebiete sind aber Synopsen und Flora-Bearbeitungen vorhanden. Einige Untersuchungen ergaben, dass die Gattung nicht monophyletisch sei. Drei zeitgleich publizierten infragenerischen Klassifikationsvorschläge blieben aber ohne molekular-phylogenetische Überprüfung, so daß die Umschreibung der Gattung und ihre

infragenerische Gliederung bislang unverstanden blieben. Die zwei nun durchgeführten phylogenetischen Analysen, basierend auf insgesamt sieben verschiedenen molekularen Markern, hatten vor allem drei Ziele: 1) Überprüfung der Monophylie von *Prestonia* und Aufklärung der Verwandtschaftverhältnisse innerhalb der Echiteae, 2) Evaluation der bestehenden infragenerischen Klassifikation von *Prestonia* sowie der interspezifischen Verwandtschaftsbeziehungen, 3) Taxonomische und nomenklatorische Umsetzung der Ergebnisse.

Es konnte gezeigt werden, dass *Prestonia* in ihrer bisherigen Umschreibung polyphyletisch ist, da *P. riedelii* in *Rhodocalyx* gruppiert und *Temnadenia ornata* in *Prestonia* eingenistet ist. Folglich wurde die erste Art zu *Rhodocalyx* und die zweite zu *Prestonia* transferiert. In der zweiten Teiluntersuchung und auf Basis eines erweiterten Probenumfangs ist *Prestonia* nunmehr monophyletisch, aber die Sektionen wie sie von Schumann, Woodson oder Pichon vorgeschlagen wurden, sind nicht monophyletisch. Die neue, hier vorgeschlagene infragenerische Klassifikation anerkennt nunmehr die sechs Sektionen: *Coalitae, Denticulata, Exsertae, Haemadictyon, Mollis* und *Prestonia*.

Für Kolombien, das Land mit der zweithöchsten Biodiversität in Süd Amerika, wurde als Ergebnis dieser Arbeit die erste Synopsis für *Prestonia* publiziert. Es werden 25 Arten anerkannt. Darüber hinaus wird eine Monographie von *Prestonia* vorgelegt, in der aktuell 56 Arten akzeptiert werden. Beschreibungen, Abbildungen, Verbreitungskarten und die IUCN-Schutzkriterien für jede Art werden bereitgestellt. Ein Bestimmungschlüssel wurde erstellt und die 6500 untersuchten Herbarbelege wurden zugeordnet und annotiert..

#### 1. General Introduction

Apocynaceae comprises about 366 genera and 3700 species distributed throughout the tropics, subtropics, and temperate regions (Endress & al., 2014; Morales & Liede-Schumann, 2016). Some are widespread ornamentals, especially in tropical regions, where they have sometimes become naturalized (e.g., Allamanda cathartica L., Asclepias curassavica L., Catharanthus roseus (L.) G. Don, Kopsia fruticosa (Roxb.) A. DC., Nerium oleander L., Plumeria rubra L., Tabernaemontana divaricata R.Br. ex Roem. & Schult., Thevetia peruviana (Pers.) K. Schum.).

As many groups of plants, in Apocynaceae the classification of genera has been based on morphological characters. Although sometimes the generic limits traditionally used in some groups are more or less well defined and supported by synapomorphic characters, in other groups the limits are confusing and the generic concepts have been in dispute for several decades. Even more, the acceptance of some genera has been based more on the tradition than upon strong evidence. The use of molecular data (nuclear and chloroplast) has provided a new tool and new evidence to understand and to study the relationships of plants families and their members.

The family Apocynaceae was traditionally recognized as two separate families – Apocynaceae s. str. and Asclepiadaceae – until Endress & Bruyns (2000) united the two and proposed five subfamilies: Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadaceae, which were further divided into several tribes. The first two subfamilies included the genera traditionally treated as Apocynaceae s. str., whereas the last three included those usually treated in Asclepiadaceae. Since then, numerous phylogenetic studies (e.g., Endress & al., 2007a, Livshultz & al., 2007, 2010, Liede & al., 2002, Liede-Schumann & al., 2005, Meve & Liede 2004a, 2004b, Rapini & al., 2004, 2006, Simões & al., 2004, 2007, 2010, 2016) have proposed new realignments or improvements to this classification. In addition, results based on non-molecular data have added significantly towards improving relationships at higher taxonomic levels within the family (e.g., Van der Weide & Van der Ham, 2012, Lens & al., 2008, 2009, Wanntorp &

Kunze, 2009). Monographs and floristic treatments published over the past 20 years have provided additional information contributing to a more accurate circumscription of genera and a more realistic idea of the morphological variation present in some genera (e.g., Middleton, 2011, 2014; Morales, 1997 a, 1999a, 2003, 2005 a,b, 2006a, 2010, 2013).

Since the reamalgamation of Apocynaceae and Asclepiadaceae by Endress & Bruyns (2000), two subsequent updates with several changes and improvements to the original classification have been made (Endress & al., 2007b, 2014). Studies based on molecular and morphological data in some tribes of Apocynaceae have led to clarification of groups with a long history of taxonomic conflicts, such as *Mandevilla* Lindl. and *Tabernaemontana* L. (e.g., Simões & al., 2004, 2006, 2007). In several parts of the classification, however, intertribal relationships and composition of tribes and subtribes are still uncertain. This is because the molecular data available for some groups are scarce, fragmented or absent. Thus, in various parts of the phylogeny resolution is still too low to propose formal classification changes. In a number of tribes and subtribes, some genera are recognized on weak morphological differences, and have been maintained based more on tradition than anything else. As a consequence, delimitation of several taxa at the genus level and above is still in dispute. (e.g., Simões & al., 2007, Liede-Schumann & al., 2014, Rapini, 2002, Silva & al., 2012).

#### 1.1. The tribe Echiteae

The tribe Echiteae was proposed by Bentham (1876) (as "Echitideae"). Since then, several classification proposals have been made (e.g., Schumann, 1895; Pichon, 1950; Leeuwenberg, 1994; Endress et al. 2007b) and the number of genera included in the tribe has varied. The first phylogenetic study to include a more extensive sampling of Echiteae, was the molecular phylogenetic study of the apocynoids and the APSA clade (comprising apocynoids, Periplocoideae, Secamonoideae and Asclepiadoideae) by Livshultz & al. (2007), based only on plastid data. It showed that Echiteae is paraphyletic, with the members distributed in several clades. However, it included only a partial sampling of the species and genera of the tribe. Based on this study, Endress & al. (2007b) excluded five genera from the Echiteae, reducing the number of genera to 20.

The great majority of molecular studies in the subfamilies Apocynoideae and Rauvolfioideae have been based on plastid sequences alone and only two analyses have been conducted using nuclear data (*phytochrome* A): Livshultz & al. (2010) and Middleton & Livshultz (2012). Endress & al. (2014) published the most recent classification proposal for Apocynaceae, in which Echiteae was divided into five subtribes.

We present the first molecular phylogeny focusing on Echiteae based on sequence data from the internal transcribed spacer (ITS) from the nuclear ribosomal DNA and three plastid DNA regions (*trnL* intron and *trnL-trnF* intergenic spacer, *rpl16* intron, *matK* and 3' /5' *trnK* intron), including almost all genera currently accepted in the tribe.

## 1.2. The genus *Prestonia*

Prestonia is distributed from Mexico and the West Indies to northern Argentina, from sea level up to 2800 m. It is characterized by a scandent habit, opposite leaves, dichasial or monochasial cymose inflorescences, an annular corona around the corolla mouth, free corona lobes within the corolla tube, and truncate seeds (Morales, 1997). The genus has been involved in disputes regarding its generic circumscription for many decades. Woodson (1931, 1936, 1960) included two species in *Prestonia (Echites agglutinatus* and *P. caudata* Woodson), despite their lack of the annular corona around the mouth or the free coronal lobes within the tube. Echites woodsonianus Monac., a species similar to the precedent was transferred by Gentry (1983) to Prestonia. Morales (1997b) transferred these species back to Echites. Morales & Williams (2004) proposed Allotoonia J.F. Morales & J.K. Williams based on the results of a cladistic analysis based on morphology (Williams, 2004). The results of Livshultz et al., 2007, showed that at least two species of Allotoonia were nested in a clade with the included species of *Echites* and *Fernaldia*, which was corroborated by Morales et al. (2017, submitted). Rhodocalyx Müll. Arg., which also has an annular corona around the mouth, was reduced to the synonymy of Prestonia by Morales (1999b), but it was retrieved together with Prestonia riedelii (Müll. Arg.) Markgr. in Livshultz et al. (2007), suggesting the paraphyly of *Prestonia*. Morales et al. (2017) obtained the same relationship and transferred *P. riedelii* to *Rhodocalyx*.

Four infrageneric classifications have been proposed for *Prestonia*. The first was that of Baillon (1891), who recognized three sections (*Euprestonia*, *Prestonianthe*, and *Haemadictyon*), but he did not cite the species included in each section. Schumann (1895), recognized two sections: *Euprestonia* (seven species) and *Haemadictyon* (three species), based on pubescence of stems, inflorescence type, and sepal shape. Woodson (1936), recognized four sections: *Acutifoliae*, *Annulares*, *Coalitae*, and *Tomentosae*, which were differentiated based on degree of corolla tube pubescence, shape and texture of the sepals, and characteristics of the annular corona, free corona lobes, and anthers. Annulares, included 33 species, Tomentosae 14, Acutifoliae nine, and Coalitae only four species. Pichon (1950) recognized five sections based on length of the corolla lobes, type of suprastaminal indumentum within the corolla tube, and features of the gynoecium and androecium.

He recognized Haemadictyon (50 species), Euprestonia (11 species), Rhaptocarpus (three species) and Trichopharynx (one species), whereas the type of Pichon's fifth section, Trichopharynx, was transferred to Echites by Morales (1997b). These classifications have never been tested using molecular data. Few species of Prestonia have been included in molecular-based studies. Livshultz et al. (2007) included only eight species, whereas Morales et al. (2017), included 16 taxa. However, a larger sample is needed to test the monophyly of the genus and to evaluate the infrageneric classification proposals (Schumann, 1895; Woodson, 1936; Pichon, 1950).

We present the first molecular phylogeny of Prestonia, comprising ca. 86% of the total of currently accepted species, based on nuclear (ITS) and plastid data (matK and 3' / 5' trnK intron, rpl16 intron, rps16 intron, trnL intron and trnL-trnF intergenic spacer). The last monograph of Prestonia was published more than 80 years ago (Woodson, 1936) and considering the new circumscription of the genus, novelties and synonyms published since then, the necessity of a new monograph is evident. A synopsis of the genus in Colombia was published recently (Morales & Liede-Schumann, 2016), as a precursor study of the new monograph provided here.

#### 2. Aims of Research

This study is the first to investigate in detail the molecular phylogeny and relationships of the tribe Echiteae and the genus *Prestonia*, based on sequence data from the internal transcribed spacer (ITS) from the nuclear ribosomal DNA and three/four plastid DNA regions (*trnL intron and trnL-trnF* intergenic spacer, *rpl16* intron, *mat*K and 3' / 5' *trn*K intron for Echiteae and the precedent three plus *rps16* intron for *Prestonia*). The three available, different intrageneric classifications proposals of *Prestonia* (Apocynaceae, Echiteae) needs to be tested for monophyly with molecular methods. A treatment of the Colombian species of *Prestonia* has never been done and the last monograph of the genus was published more than 70 years ago, suggesting the necessity of a new monograph.

### The aims of the study are:

- 1. To test the monophyly of the tribe Echiteae and its subtribes sensu Endress & al. (2014)
- 2. To assess the monophyly of the Echiteae genera as currently delimited
- 3. To provide a more accurate hypothesis of the relationships among the Echiteae genera
- 4. To compare reports of pyrrholizinid alkaloids (PAs) to our phylogeny to determine if there is a meaningful pattern in their distribution.
- 5. To test the monophyly of *Prestonia* with a larger sample than in previous studies
- 6. To determine the relationship between the different species of *Prestonia*
- 7. To evaluate the infrageneric classifications of Schumann (1895), Woodson (1936) and Pichon (1950)
- 8. To provide a new infrageneric classification
- 9. To provide a treatment of the Colombian species of *Prestonia*.
- 10. To provide taxonomic and nomenclatural changes as needed derived from the three studies.

# 3. Synopsis

#### 3.1 Materials and Methods

### 3.1.1. Taxon sampling (publication 2 and 3)

A total of 70 species, including representatives of 17 of the 19 genera (except *Ecua* and *Bahiella*) and from the five subtribes currently recognized in Echiteae by Endress & al. (2014) were defined as the ingroup. Ten species of seven genera from two different tribes were selected as the outgroup, based on the results of previous analyses (Livshultz & al., 2007, 2010) and two species of *Rhabdadenia* (Rhabdadenieae) were used to root the tree. For the third paper, 50 species of *Prestonia* were sampled, including at least two members each from the all the sections of Schumann (1895), Woodson (1936) and Pichon (1950). The outgroup taxa included thirteen species from six genera of Echiteae and two species of *Odontadenia* (Odontadeniae) were used as rooting taxa.

# 3.1.2. DNA extraction, amplification and sequencing (publication 2 and 3)

Total genomic DNA was extracted from silica gel-dried leaf material using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). The three cpDNA regions were sequenced using published primers: trnL intron and trnL-trnF intergenic spacer (Taberlet & al., 1991), rpl16 intron (Baum & al., 1998) and matK and 5'/3' trnK intron (Endress & al., 1996); Bafeel & al., 2011). The primers ITS4 (White & al., 1990) and ITS5m (Sang & al., 1995) were used to amplify ITS. For rps16 intron (used in Prestonia) the protocol given in Simões et al. (2004) was used. The PCR amplifications were performed in a Biometra T-Personal Thermocycler and PCR products were visualized with electrophoresis on 2% agarose gels.

#### 3.1.3. Phylogenetic analysis (publication 2 and 3)

Sequence contigs were built with Codon Aligner v. 3.7.1 and v. 6.0.2 (CodonCode Corp., Centerville, Massachusetts, U.S.A.). Sequences were prealigned in MAFFT v.7 (Katoh, 2013), followed by manual adjustments in Mesquite v. 2.71 (Maddison & Maddison, 2011).

Several data matrices were analyzed: the individual chloroplast data sets, combined plastid data set, nuclear data set and combined molecular data set (plastid + nuclear). No strongly supported incongruent clades were found between three individual partitions of the plastid data, and thus they were combined (combined plastid matrix), nor between combined plastid matrix and ITS matrix, and therefore they were combined in a single matrix (combined molecular matrix). In all analyses, ITS was divided in 5 partitions. Matrices were analyzed using maximum likelihood (ML); for the combined plastid, ITS and combined molecular matrices Bayesian inference (BI) was also analyzed.

Maximum-likelihood (ML) analyses were calculated using RAxML version 8.2.8 (Stamatakis, 2006, Stamatakis et al., 2008), as implemented in CIPRES version 3.3 (Miller et al., 2010), setting the non-bootstrap values and tree search to 1000 replicates. The output tree files were generated with Figtree (Rambaut, 2014). Bootstrap support value was interpreted as follows: 50%-74% as weak, 76%-89% as moderate, and  $\geq 90\%$  as strongly supported. Bayesian inference was calculated using MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), applying separate models to each data partition, with unlinked partitions, and parameters estimated independently. Models of sequence evolution were selected using the Bayesian information criterion (BIC) in jModelTest v.2.1.1 (Darriba et al., 2012). MrBayes was run using two parallel runs for 10 million generations, each using one cold and three heated MCMC chains, sampling every 10,000 generations, until an average standard deviation of split frequencies  $\leq 0.01$  was reached. The first 25% of the trees was discarded (sump function) and the remaining 75% used to calculate a majority-rule consensus and posterior probabilities (PP, sumt function). Burn-in values, mixing of the MCMC chains, and independent tree sampling were determined through inspection of the MCMC samples employing Tracer v.1.5 (Rambaut & Drummond, 2007). The 50% majority-rule consensus tree was edited in Figtree v.1.4.2. (Rambaut, 2014). Posterior probability values  $\geq 0.95$  were considered as strongly supported.

# 3.1.2. Taxonomic treatment (publication 1, 4)

The taxonomic descriptions were based in more than 6500 specimens from the following 158 herbaria: A, AAU, ALCB, AS, ASE, ASU, B, BAB, BEREA, BHCB, BIGU, BM, BOLV, BR, C, CAS, CAUP, CAY, CEN, CEPEC, CGE, CH, CHAPA, CICY, CIIDIR, CIMI, CM, COAH, COL, CR, CVRD, CUVC, CUZ, DPU, DS, DUKE, E, EAP, ECON, ENCB, ESA, ESAL, F, FCME, FCQ, FDG, FI (including FI-W), FUEL, G (including G-BOIS, G-DC), GB, GFJP, GH, HAL, HB, HBG, HERZU, HOXA, HRB, HRCB, HSB, HST, HUA, HUEFS, HUFU, HUQ, IAN, IBGE, INB (\*\*), INPA, IPA, JAUM, JE, JEPS, JPB, K, L, LAGU, LD, LE, LIL, LP, LPB, LZ, M, MA, MBM, MBML, MEDEL, MEXU, MHES, MICH, MIRR, MG, MO, MOL, MVFA, MVJB, NA, NY, O, OXF, P (including P-BA, P-HB, P-JU, P-L), PEL, PH, PMA, PORT, PR, PSO, Q, QAME, QAP, QCA, QCNE, QPLS, R, RB, S, SCZ SI, SP, SPF, SPFR, TEFH, TEX, TRIN, TULV, U, UB, UBT, UC, UCAM, UCOB, UDCB, UEC, UFMT, UFP, UPS, US, USF, USJ, USM, USZ, UVAL, VALLE, VEN, VIC, W, WU, WAG, WIS, XAL, Z, and ZT (herbarium acronyms according to Thiers (2012)). The herbarium INB (\*\*) was incorporated in CR. All type collections available were examined. Field work was carried out in El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Peru, Bolivia, and Brazil. Common names and uses cited for some species, as well as phenology, and habitat data, were taken from labels from herbarium specimens. The descriptions of the morphological structures follow Font Quer (1953), Radford et al. (1974), and Harris & Harris (1994). In species with infundibuliform corollas, the terminology for regions of the tube follows Morales & Fuentes (2004b). Distribution maps were generated with ArcGIS 10.3 (ESRI, Redlands, California), using geographical coordinated from the specimens database.

### **3.1.3.** Conservation assessment (publication 4)

The conservation status of the species of *Prestonia* was assessed by calculating the extent of occurrence (EOO) and the area of occupancy (AOO) using GeoCAT (Geospatial Conservation Assessment tool; Bachman et al. 2011) and applying the IUCN Red List Categories and Criteria, version 3.1 (IUCN 2012; IUCN 2013). The AOO was calculated based on a user defined grid cell of 2 km.

#### 3.2 Results and Discussion

# 3.2.1. The genus *Prestonia* (Apocynaceae) in Colombia. Phytotaxa 265: 204–224 (Publication 1)

A synopsis of the species of *Prestonia* in Colombia was performed, recognizing 25 species. This is the first treatment of that genus ever compiled for the country, with an estimated diversity of ca. 24,500 species of vascular plants (Bernal et al. 2015). Previous studies (Morales et al. 2010, Bernal et al. 2015) are just annotated checklists, which don't include keys, maps or comprehensive descriptions. *Prestonia megagros* (Vell.) Woodson, a poorly collected Amazonian species, is reported for the first time based on a collection from Leticia, Department of Amazonas. Although *P. surinamensis* has been reported for Colombia (Morales *et al.* 2011), the study of the collections cited has revealed that was a misidentification of the widespread *P. tomentosa*. At the same time, *Prestonia antioquiana*, an endemic new species, was described and illustrated. This species has been identified as *P. trifida*, but differs by its verrucose petioles and winged fruits. A key to the taxa is included, as well as descriptions, distribution maps, a checklist of representative specimens examined and taxonomic notes for every taxon, including the discussion of its possible taxonomic affinities.

# 3.2.2. Sex, drugs and pupusas: Disentangling relationships in Echiteae (Apocynaceae) (Publication 2)

This study represents the first one to evaluate the monophyly of the tribe Echiteae with a comprehensive sampling, using the nuclear internal transcribed spacer (ITS) and three plastid markers (matK and 3' / 5' trnK intron, rpl16 intron, trnL intron and trnL-trnF intergenic spacer). In the analysis, almost all the currently accepted genera of the tribe were included, except Artia and Bahiella, from which it was impossible to obtain positive PCR reactions. A total of 408 sequences were used, of which 344 were newly generated.

Our results showed that as currently circumscribed Echiteae and four of its subtribes (Echitinae, Parsonsiinae, Peltastinae and Prestoniinae) are non-monophyletic and the last subtribe proposed by Endress et al. (2014), the Pentalinoninae, should be excluded from Echiteae, because it is nested within the outgroup.

Seven genera were found to be monophyletic (*Angadenia*, *Artia*, *Asketanthera*, *Laubertia*, *Parsonsia*, *Thenardia* and *Thoreauea*). With regard to the other genera, *Temnadenia* is polyphyletic, with two species as sister to *Macropharynx/Peltastes/Prestonia riedelii* (Müll. Arg.) Markgr./*Rhodocalyx*, and one species as sister to two species of *Prestonia*. *Peltastes* is nested within *Macropharynx*, rendering both genera non-monophyletic. *Fernaldia* is nested within *Echites* and *Prestonia* is polyphyletic because one species, *Prestonia riedelii*, is resolved as sister to the monospecific *Rhodocalyx*. Within Echiteae, three major clades are recognized: the Peltastinae clade, the Echitinae clade and the Parsonsiinae-Prestoniinae clade.

The Peltastinae clade is divided into two subclades: the Laubertia subclade and the Peltastes subclade. The first includes three species of *Laubertia* resolved as sister of *Hylaea*, whereas the second clade includes *Macropharynx*, *Peltastes*, *Rhodocalyx* and *Temnadenia*. We propose the recognize the first clade as a new subtribe, Laubertinae and the second subclade as the subtribe Peltastinae, already recognized (Endress et al. 2014) but here proposed with a new circumscription and excluding *Asketanthera*, included by Endress et al.(2014) in this tribe. *Peltastes* should be reduced to the synonymy of *Macropharynx*, *Rhodocalyx* should include *Prestonia riedelii* and *Temnadenia* is reduced to only two species.

The Echitinae clade includes three subclades: (1) the Thenardia clade (*Thenardia* and *Thoreauea*), (2) Asketanthera subclade (*Asketanthera*) and (3) Echites subclade (*Echites* and *Fernaldia*). All genera in the Echitinae clade are resolved as monophyletic, with the exception of *Echites*, which includes *Fernaldia*, a result which was also obtained by Livshultz et al. (2007). Therefore, it should be included in *Echites*. This clade is proposed as the subtribe Echitinae, but with a different circumscription compared to Endress et al. (2014).

The last clade comprises two subclades: the Parsonsiinae subclade (*Parsonsia* and *Artia*) and the Prestoniinae subclade (*Prestonia*). These subclades are also proposed as subtribes, but comprising only the genera cited before. The combinations resulting from the merging of *Fernaldia* and *Peltastes* and the transfer of *P. riedelii* and *T. ornata* to *Rhodocalyx* and *Prestonia*, respectively, are proposed.

In the ancestors of Echiteae, we hypothesize that an evolutionary shift took place in which steroidal alkaloids and/or cardenolides, characteristic for apocynoids, were replaced by parsonsine type pyrrolizidine alkaloids as the predominant defense compounds.

### 3.2.3. A phylogenetic study of the genus *Prestonia* (Apocynaceae) (Publication 3)

The aim of this study was to test the monophyly of *Prestonia* with a larger sample compared to Morales et al. (2017), as well as to test the monophyly of the three infrageneric classifications proposed for the genus. A total of 62 nuclear (ITS) and 258 chloroplast sequences (*matK* and 3' / 5' trnK intron, rpl16 intron, rps16 intron, trnL intron and trnL-trnF intergenic spacer) from 65 species (including 50 species of *Prestonia*) were analyzed, including representatives of all sections ever proposed, with a larger sample compared to previous studies.

Prestonia as circumscribed by Morales et al. (2017) is resolved as monophyletic. Almost all sections of the infrageneric sections proposed by Schumann (1895), Woodson (1936) and Pichon (1950) are para- or polyphyletic. Schumann's sect. Euprestonia is resolved as monophyletic. In Woodson's and Pichon's systems, only sect. Coalitae and sect. Rhaptocarpus are monophyletic, respectively. The most extreme example of polyphyly is found in Schumann's sect. Haemadictyon, Woodson 's sect. Annulares and Pichon's sect. Haemadictyon, the constituent species of which are scattered among three, five and six clades, respectively. In Woodson's classification, sect. Acutifoliae is also polyphyletic, with species in two different clades, and sect. Tomentosae is paraphyletic, because here P. cordifolia grouped in the Mollis clade. In Pichon's classification, the sole species of sect. Tetraceras, P. parviflora, is nested among species of his sect. Euprestonia, and sect. Rhaptocarpus is polyphyletic, with its members grouped with two species of sect. Haemadyction.

Five clades were retrieved: the Haemadictyon clade, Mollis clade, Coalita clade, Denticulata clade and Prestonia clade. The Haemadictyon clade is retrieved as sister to all other clades in *Prestonia* and is divided into two clades. The first clade includes two species, *P. marginata* and *P. quinquangularis* and the second nine taxa. They have in common sepals without longitudinal veins, a glabrous corolla with conspicuous annular

corona, free corona lobes with the apices exserted or included, and follicles that are free or that remain longitudinally fused together up to maturity

The Mollis clade comprises only two species (*P. cordifolia* and *P. mollis*). They are characterized by membranaceous, glabrous to minutely puberulent leaf blades, membranaceous sepals with conspicuous longitudinal veins, glabrous or minutely puberulent corollas, well-developed annular corona, free corona lobes with the apices conspicuously exserted and follicles that remain longitudinally fused together up to maturity.

The Coalita clade comprises two clades: one comprising *P. coalita* and related species and the second with five species. *Prestonia pickelii* described by Markgraf in 1938, was retrieved in this clade, far away from *P. quinquangularis*, showing that they are not even closely related as was suggested by Morales (2008). The second clade is characterized by a conspicuous annular corona and free corona lobes versus an inconspicuous annular corona and absent free corona lobes in the first clade.

The last two clades are the Denticulata clade and the Prestonia clade (1/98), with 11 and 17 species, respectively. The plants of the Denticulata clade tend to be robust, woody lianas. They have coriaceous, glabrous leaf blades, glabrous or minutely puberulent corollas, conspicuous annular corona, free corona lobes with the apices exserted or included, and follicles that are free or that remain longitudinally fused together up to maturity. Finally, the species of the Prestonia clade are characterized by membranaceous leaves, with pubescent blades, membranaceous sepals, conspicuously pubescent corollas, conspicuous annular corona, sometimes deeply lobed or reduced to five conical projections, free corona lobes with the apices exserted or included or absent, and free follicles.

We propose a new infrageneric classification for *Prestonia*, recognizing six sections: *Coalitae, Denticulata, Exsertae, Haemadictyon, Mollis*, and *Prestonia. Prestonia pickelii* is removed from the synonymy of *P. quinquangularis* and resurrected as an accepted species.

# **3.2.4.** A monograph of the genus *Prestonia* (Apocynaceae, Echiteae) (publication 4)

The last monograph of *Prestonia* was published by Woodson (1936), who recognized 61 species and four sections. A taxonomic revision was carried out based on more than 6000 herbarium specimens and field work in seven countries, recognizing 58 species classified in six sections following the infrageneric classification proposed by Morales et al. (2017). *Prestonia* is widely distributed from northern Mexico and the West Indies to northern Argentina, ranging from sea level up to 2200 m, although most species occur below 1100 m. The genus has been reported almost in all the neotropical countries, with the exception of Chile. In Uruguay it is represented only by *P. lagoensis*, based on single specimen collected by Fruchard with a vague locality ("Montevideo, Asunción"). Since this species has not been reported in adjacent areas and the nearest locality from which it is known with certainty is located much farther north, the locality of this specimen may be erroneous, something that is known to occur in some other genera and species for Uruguay (Morales, 2010).

Only six species are relatively widely distributed, whereas about 39% of the taxa are endemic to a single country. Only one species (*P. quinquangularis*) is known from the Caribbean and another one is also reported from Trinidad (*P. exserta*). Brazil has the highest number of endemic species with eight taxa, followed by Colombia with four taxa, Ecuador with three species, and Bolivia, Costa Rica, and Panama with two taxa each. However, the center of diversity of the genus is located between Colombia, Ecuador and Peru, where 34 species are known.

Several species are very variable with regards to the color of the corolla lobes and many taxa whose distinction is based only on this character have been reduced to the synonymy in the last decade, which is confirmed by our results. Although some species are widespread and well collected (e.g, *P. portobellensis*, *P. tomentosa*, *P. trifida*), several others (e.g., *P. amazonica*, *P. macroneura*, *P. cogolloi*) are only known from a few specimens. In general, little is known about the pollination of these plants and besides personal records of the authors based on field work, no studies about the pollinaton biology in *Prestonia* have been carried out. Nomenclature, descriptions, detailed illustrations, photographs and distribution maps are provided for each species.

### 3.3 Conclusion and emerging research challenges

This thesis comprises a group of studies in order to understand the systematics of the Apocynaceae, subfamily Apocynoideae, subtribe Echiteae, providing a new circumscription, as well as a new infrageneric classification and monograph for *Prestonia*.

Phylogenetic analyses showed that a new circumscription was necessary in order to resolve Echiteae as monophyletic, as well as its four subtribes. Some genera were retrieved as non-monophyletic and several taxonomic implications were proposed, including the reduction to the synonymy of two genera (*Fernaldia* and *Peltastes*) and the recircumscription of others (*Prestonia*, *Rhodocalyx*, *Temnadenia*). Although the phylogeny of Echiteae is now well resolved with highly supported clades, more studies are necessary including material from *Bahiella* and *Ecua*, in order to define its relationships. The subtribe Pentalinoninae was removed from the Echiteae, but its taxonomic affinities are still uncertain. In our study, Pentalinoninae was retrieved as sister of Odontadeniae, but further studies (including the remaining genera of that tribe and a larger sampling) are necessary to determinate if this subtribe should be included in Odontadeniae or another tribe. In *Prestonia* we could show that all the infrageneric classifications were non-monophyletic and thus, a new classification was proposed. Additional studies including more nuclear markers and the remaining missing taxa could help to improve our understanding of the relationships between some species.

So far, few studies have been made to test the monophyly of tribes, subtribes or the currently generic circumscription of many groups in the Apocynoideae and the few available are based mostly on plastid markers. The incongruence between the classifications based on morphology and the evidence provide by molecular analysis has been reported in apocynoids and rauvolfioids (e.g., Simões et al. 2004, 2006, 2010; Livshultz et al. 2007, Morales et al. 2017), showing the necessity to evaluate other classifications still not tested.

The inclusion of nrDNA (ITS) in our studies provided a significantly increased phylogenetic signal, compared to the results based only on cpDNA markers. Similar results have been found in others studies in neotropical apocynoids (e.g., Livshultz, 2010).

The ITS dataset proved to be the most informative, on which ca. 17 % of the aligned characters are parsimony informative. The enhanced variability of nuclear loci compared to other markers provides great potential in phylogenetic studies, however, the design and identification of universal primers are somewhat difficult due to the polyploidy present in plants. Future studies in the apocynoids should mandatorily include nuclear markers.

In *Prestonia* the number of names available before this monograph surpassed the numbers of currently accepted taxa. The genus now has a clarified taxonomy and this study can be used for future studies in biogeography, delimitation of priority areas for conservation, character evolution and others. Monographic studies should be carried out in several groups because many genera only have old and outdated monographs available and a clear taxonomy is the base for many studies. In *Prestonia* and other genera of the Echiteae, the information about pollination is poor and basically inexistent, therefore, future studies in this area should be proposed.

Finally, Apocynaceae is well known to be rich in toxic bioactive secondary metabolites, which are restricted mostly to genera of the Rauvolfioideae, whereas the pyrrolizidine alkaloids (PAs) are restricted to Apocynoideae and reported to four tribes, one of them the Echiteae. Although several studies have been made in Apocynaceae, there are many gaps of information to confirm the presence of PAs in several genera in the Echiteae, as well other groups in Apocynoideae. Future studies could help to confirm the presence of PAs in untested genera, therefore providing an additional tool to elucidate relationships in the family.

#### 3.4 References

- Bafeel, S.O., Arif, I., Bakir, M., Khan, H., Al Farhan, A, Al Homaidan, A., Ahamed, A. & Thomas, J. 2011. Comparative evaluation of PCR success with universal primers of maturase K (matK) and ribulose-1,5-bisphosphate carboxylase oxygenase large subunit (rbcL) for barcoding of some arid plants. *Plant Omics* 4: 195–198.
- **Baillon, H.E.** 1891. Histoire des Plantes 10. Librairie Hachete & Co, Paris.
- **Baum, D.A., Small, R.L. & Wendel, J.F.** 1998. Biogeography and floral evolution of baobabs (*Adansonia*, Bombacaceae) as inferred from multiple data sets. *Syst. Biol.* 47: 181–207.
- **Bentham, G.** 1876. Apocynaceae, Asclepiadaceae. Pp. 680–785 in: Bentham, G & J. D. Hooker (eds.), *Genera Plantarum*, Vol. 2. London: Williams & Norgate.
- Bernal, R., Gradstein, S.R. & Celis, M. (eds.). 2015. Catálogo de plantas y líquenes de Colombia. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia. Available from:

  <a href="http://catalogoplantascolombia.unal.edu.co">http://catalogoplantascolombia.unal.edu.co</a> (accessed: 17 February 2016).
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. 2012. jModelTest 2: More models, new heuristics and parallel computing. *Nature Meth.* 9: 772. http://dx.doi.org/10.1038/nmeth.2109
- **Endress, M. E. & Bruyns, P**. 2000. A revised classification of the Apocynaceae s.l. Bot. Rev. (Lancaster) 66: 1–56.
- Endress, M.E., Sennblad, B., Nilsson, S., Civeyrel, L., Chase, M., Huysmans, S., Grafström, E. & Bremer, B. 1996. A phylogenetic analysis of Apocynaceae s. str. and some related taxa in Gentianales: a multidisciplinary approach. *Opera Bot. Belg.*7: 59–102.
- Endress, M.E., van der Ham, R.W.J.M., Nilsson, S, Civeyrel, L., Chase, M.W., Sennblad, B., Potgieter, K., Joseph, J., Powell, M., Lorence, D., Zimmerman, Y.-M., & Albert, V.A. 2007a. A phylogenetic analysis of Alyxieae (Apocynaceae) based on rbcL, matK, trnL intron, trnL-F spacer sequences, and morphological characters. *Ann. Missouri Bot. Gard.* 94: 1–35.

- Endress, M.E., Liede-Schumann, S. & Meve, U. 2007b. Advances in *Apocynaceae*: The enlightenment, an introduction. *Ann. Missouri Bot. Gard.* 94: 259–267.
- Endress, M.E., Liede-Schumann, S. & Meve, U. 2014. An updated classification for Apocynaceae. *Phytotaxa* 159: 175–194.
- Font Quer, P. 1953. Diccionario de botánica. Labor S.A, Barcelona, 1244 pp.
- **Gentry, A.H.** 1983. A new combination for a problematic Central American Apocynaceae. Ann. Missouri Bot. Gard.70: 205–206.
- Harris, J.G. & Harris, M.W. 1994. Plant identification terminology: an illustrated glossary. Spring Utah, Lake, 198 pp.
- **Huelsenbeck, J.P. & Ronquist, F.R.** 2001. MrBayes: Bayesian inference of phylogeny. *Biometrics* 17: 754–755.
- **Katoh, K.** 2013. Multiple Alignment using Fast Fourier Transform (MAFFT), version 7 http://mafft.cbrc.jp/alignment/server/
- Lens, F., Endress, M.E., Baas, P., Jansen, S. & Smets, E. 2008. Wood anatomy of Rauvolfioideae (Apocynaceae): A search for meaningful non-DNA characters at the tribal level. *Amer. J. Bot.* 95: 1199–1215.
- Lens, F., Endress, M.E., Baas, P., Jansen, S. & Smets, E. 2009. Vessel grouping patterns in subfamilies Apocynoideae and Periplocoideae confirm phylogenetic value of wood structure within Apocynaceae. *Amer. J. Bot.* 96: 2168–2183.
- **Leeuwenberg, A.J.M.** 1994. Series of Apocynaceae XXXVIII. Taxa of Apocynaceae above the genus level. *Agric. Univ. Wageningen Pap.* 94: 45–60.
- **Liede, S. & Kunze, H.** 2002. *Cynanchum* and the Cynanchinae (Apocynaceae Asclepiadoideae) a molecular, anatomical and latex triterpenoid study. *Org. Divers. Evol.* 2: 239–269.
- **Liede-Schumann, S., Rapini, A., Goyder, D.J. & Chase, M.W.** 2005. Phylogenetics of the New World subtribes of Asclepiadeae (Apocynaceae -Asclepiadoideae): Metastelmatinae, Oxypetalinae, and Gonolobinae. *Syst. Bot.* 30: 184–195.
- **Liede-Schumann, S., Nikolaus, M.,Silva, U.C.S., Rapini, A., Mangelsdorff, R.D. & Meve, U.** 2014. Phylogenetics and Biogeography of the Genus Metastelma (Apocynaceae-Asclepiadoideae-Asclepiadeae: Metastelmatinae). *Syst. Bot.* 39: 594–612. 2014.

- **Livshultz, T**. 2010. The phylogenetic position of milkweeds (Apocynaceae subfamilies Secamonoideae and Asclepiadoideae): evidence from the nucleus and chloroplast. Taxon 59: 1016–1030.
- **Livshultz, T., Middleton, D.J., Endress, M.E. & Williams, J.K**. 2007. Phylogeny of Apocynoideae and the APSA clade (Apocynaceae s.l.). Ann. Missouri Bot. Gard. 94: 324–359.
- **Maddison, W.P. & D.R. Maddison.** 2011. Mesquite: A modular system for evolutionary analysis, version 2.75 <a href="http://mesquiteproject.org">http://mesquiteproject.org</a>.
- **Meve, U. & Liede, S.** 2004a. Generic delimitations in tuberous Periplocoideae (Apocynaceae) from Africa and Madagascar. *Ann. Bot. (Oxford)* 93: 407–414.
- **Meve, U. & Liede, S.** 2004b. Subtribal division of Ceropegieae (Apocynaceae–Asclepiadoideae). *Taxon* 53: 61–72.
- Middleton, D.J. 2011. Apocynaceae. Pp. 1–235 in: Kiew, R., Chung, R.C.K., Saw, L.G., Soepadmo, E. & Boyce, P.C. (eds.), *Flora of Peninsular Malaysia*, *ser.* 2, *Seed plants*, *vol.* 2. Kepong: Forest Research Institute Malaysia.
- **Middleton, D.J.** 2014. Apocynaceae, subfamilies Rauvolfioideae and Apocynoideae. *Flora of Cambodia, Laos and Vietnam, vol. 33.* Paris: Muséum National d'Histoire Naturelle and Edinburgh: Royal Botanic Garden Edinburgh.
- **Middleton, D.J. & Livshultz, T.** 2012. *Streptoechites* gen. nov., a new genus of Asian Apocynaceae. *Adansonia*, sér. 3, 34: 365–375.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 in: *Proceedings of the Gateway computing environments workshop (GCE)*, 14 Nov 2010, New Orleans: Institute of Electrical and Electronics Engineers.
- **Morales, J.F.** 1997a. A synopsis of the genus *Prestonia* (Apocynaceae) section *Tomentosae* in Mesoamerica. *Novon* 7: 59–66.
- **Morales, J.F**. 1997b. A re-evaluation of the genera *Echites* and *Prestonia* section *Coalitae* (Apocynaceae). Brittonia 49: 328–336.
- **Morales, J.F.** 1999a. A synopsis of the genus *Odontadenia*. Series of revisions of Apocynaceae XLV. *Bull. Jard. Bot. Natl. Belg.* 67: 381–477.

- **Morales, J.F.** 1999b. *Rhodocalyx* (Apocynaceae), a new synonym of *Prestonia. Novon* 9: 89–91.
- **Morales, J.F.** 2002. Studies in Neotropical Apocynaceae I: A revision of the genus *Laubertia. Rhodora* 104: 170–186.
- **Morales, J.F**. 2003. Studies in Neotropical Apocynaceae III: A revision of the genus *Secondatia*, with discussion of generic classification. *Candollea* 58: 305–319.
- **Morales, J.F.** 2005a. Estudios en las Apocynaceae Neotropicales XVII: Una revision del genero *Galactophora* Woodson (Apocynaceae, Apocynoideae). *Sida* 22: 2053–2079.
- Morales, J.F. 2005b. Estudios en las Apocynaceae Neotropicales XIX: la familia Apocynaceae s. s.tr. (Apocynoideae y Rauvolfioideae) de Costa Rica. *Darwiniana* 43: 90–191.
- **Morales, J.F.** 2006a. Estudios en las Apocynaceae Neotropicales XXVI: Una monografia del genero *Mesechites* (Apocynoideae, Mesechiteae. *Candollea* 61: 215–277.
- **Morales, J. F.** 2008. Estudios en las Apocynaceae Neotropicales XXXV: Novedades nomenclaturales en el género *Prestonia* para Brasil (Apocynoideae, Echiteae). Darwiniana 45: 213–217.
- **Morales, J.F.** 2010. La familia Apocynaceae s. str. (Apocynoideae, Rauvolfioideae) en Uruguay. *Darwiniana* 48: 68–86.
- **Morales, J.F.** 2013. Estudios en las Apocynaceae Neotropicales XLIX: sinopsis de las Apocynaceae (Apocynoideae, Rauvolfioideae) de Chile. *Darwiniana* 1: 39–45.
- **Morales, J.F. & Fuentes, A.** 2004. Estudios en las Apocynaceae Neotropicales VIII: nuevas especies de *Mandevilla* para Peru y Bolivia, con notas sobre la morfologia floral en corolas infundibuliformes. *Candollea* 59: 167–174.
- **Morales, J.F. & Williams, J.K**. 2004. *Allotoonia*, a new neotropical genus of Apocynaceae based on a subgeneric segregated of *Echites*. Sida 21: 133–158.
- **Morales, J.F. & Liede-Schumann, S.** 2016. The genus *Prestonia* (Apocynaceae) in Colombia. Phytotaxa 265: 204–224.
- Morales, J.F, Merello, M. & Stevens, W.D. 2011. Apocynaceae. *In*: Idárraga-Piedrahita, A., Ortiz, R., Callejas Posada, R. & Merello, M. (Eds.) *Flora de*

- Antioquia: Catálogo de las Plantas Vasculares, Vol. 2. Universidad de Antioquia, Medellín, , pp. 257–268.
- **Morales, J. F., M. E. Endress & S. Liede-Schumann.** 2017. Sex, drugs and pupusas: Disentangling relationships in Echiteae (Apocynaceae). Taxon 00: 000–000.
- **Pichon, M**. 1950. Classification des Apocynacées XXV, Echitoideés. Mem. Mus. Natl. Hist. Nat. sér. B, Bot.1: 1–142.
- Radford, A.E., Dickison, W.C., Massey, J.R. & Bell, C.R. 1974. Vascular plant systematics. Harper & Row, New York, 891 pp.
- Rambaut, A. 2014. FigTree, version 1.4.2. <a href="http://tree.bio.ed.ac.uk/software/figtree/">http://tree.bio.ed.ac.uk/software/figtree/</a>
- **Rambaut, A. & Drummond, A.J.,** 2007. Tracer. Version 1.5. http://beast.bio.ed.ac.uk/Tracer/
- **Rapini, A.** 2012. Taxonomy "under construction": advances in the systematics of Apocynaceae, with emphasis on the Brazilian Asclepiadoideae. *Rodriguésia* 63: 75–88.
- Rapini, A., Fontella-Pereira, J., Lamare, E. & Liede-Schumann, S. 2004. Taxonomy of *Peplonia* (including *Gonioanthela*) and a reinterpretation of Orthosieae (Asclepiadoideae, Apocynaceae). *Kew Bull.* 59: 531–539.
- **Rapini, A., Chase, M.W. & Konno, T.U.P.** 2006. Phylogenetics of South American Asclepiadeae (Apocynaceae). *Taxon* 55: 119–124.
- **Ronquist, F. & Huelsenbeck, J.P.** 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Sang, T., Crawford, D.J. & Stuessy, T. 1995. Documentation of reticulate evolution in peonies (*Paeonia*) using internal transcribed spacer sequences of nuclear ribosomal DNA: implication for biogeography and concerted evolution. *Proc. Natl. Acad. Sci. U.S.A.* 92: 6813–6817.
- **Schumann, K. M**. 1895. Apocynaceae. Pp. *109–189 in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien IV(2). Engelmann, Leipzig.
- **Schumann, K.M.** 1895. Apocynaceae. Pp. 109–189 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien* IV(2). Leipzig: Engelmann, 1897.

- Silva, U.C.S., Rapini, A., Liede-Schumann, S., Ribeiro, P.L., & van den Berg, C. 2012. Taxonomic considerations on Metastelmatinae (Apocynaceae) based on plastid and nuclear DNA datasets. *Syst. Bot.* 37: 795–806.
- Simões, A.O., Endress, M.E., van der Niet, T., Conti, E. & Kinoshita, L.S. 2004.

  Tribal and intergeneric relationships of Mesechiteae (Apocynoideae, Apocynaceae): evidence from three noncoding plastid DNA regions and morphology. *Amer. J. Bot.* 91: 1409–1418.
- Simões, A.O., Endress, M.E., van der Niet, T., Kinoshita, L.S. & Conti, E. 2006. Is *Mandevilla* (Apocynaceae, Mesechiteae) monophyletic? Evidence from five plastid DNA loci and morphology. *Amer. J. Bot.* 94: 1409–1418.
- Simões, A.O., Livshultz, T., Conti, E. & Endress, M.E. 2007. Phylogeny and systematics of the Rauvolfioideae (Apocynaceae) based on molecular and morphological evidence. *Ann. Missouri Bot. Gard.* 94: 268–297.
- **Simões, A.O., Endress, M.E. & Conti, E.** 2010. Systematics and character evolution of Tabernaemontaneae (Apocynaceae, Rauvolfioideae) based on molecular and morphological evidence. *Taxon* 59: 772–790.
- Simões, A.O., Kinoshita, L.S., Koch, I., Silva. M.J. & Endress, M.E. 2016. Systematics and character evolution of Vinceae (Apocynaceae). *Taxon* 65: 99–122.
- **Stamatakis**, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- **Stamatakis, A., Hoover, P. & Rougemont, J.** 2008. A rapid bootstrap algorithm for the RAxML Web servers. *Syst. Biol.* 57: 758–771.
- **Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J.** 1991. Universal primers for amplification of three noncoding regions of chloroplast DNA. *Annual Rev. Pl. Physiol. Pl. Molec. Biol.* 17: 1105–1109.
- Van der Weide, J.C. & Van der Ham, R.W.J.M. 2012. Pollen morphology and phylogeny of the tribe Tabernaemontaneae (Apocynaceae, subfamily Rauvolfioideae). *Taxon* 61: 131–145.

- **Wanntorp, L. & Kunze, H.** 2009. Identifying synapomorphies in the flowers of *Hoya* and *Dischidia* Towards phylogenetic understanding. *Int. J. Pl. Sci.* 170: 331–342.
- White, T.J., Bruns T, Leem S. & Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, & J.J., White, T.J. (eds.). *PCR Protocols: A Guide to Methods and Applications*. San Diego, CA: Academic Press.
- **Woodson, R.E., Jr.** 1936. Studies in the Apocynaceae. IV. The American genera of Echitoideae. *Ann. Missouri Bot. Gard.* 23: 169–438.
- Woodson, R. E., Jr. 1960. Miscellanea taxonomica II. Ann. Missouri Bot. Gard. 47: 73–80. Woodson, R. E. & R.W. Schery. 1940. Contributions toward a Flora of Panama IV. Miscellaneous collections, chiefly by Paul H. Allen. Ann. Missouri Bot. Gard. 27: 265–365.

# **Publication 1**

Morales, J.F. & S. Liede-Schumann. 2016.

The genus Prestonia (Apocynaceae) in Colombia. Phytotaxa 265: 204–224.

The genus Prestonia (Apocynaceae) in Colombia

J. FRANCISCO MORALES $^1$  & SIGRID LIEDE-SCHUMANN $^2$ 

Department of Plant Systematics, University of Bayreuth, Universitätsstr. 30, 95440

Bayreuth, Germany;

email: drifranciscomorales@gmail.com

email: sigrid.liede@uni-bayreuth.de

**Abstract** 

A treatment of *Prestonia* in Colombia is presented, including a key to the 25 species,

descriptions, distribution data, and selected specimens examined. Prestonia megagros is

reported for the country for first time, and conversely, P. surinamensis is excluded.

Prestonia antioquiana is newly described and ilustrated. A lectotype is designated for

Echites megagros.

**Key words**: Apocynoideae, Echiteae, South America

Resumen

Un tratamiento de Prestonia en Colombia es presentado, incluyendo una clave a las 25

especies, descripciones, datos de distribution, and especímenes seleccionados examinados.

Prestonia megagros se reporta por primera vez y P. surinamensis es excluida para ese pais.

Prestonia antioquiana es descrita como una novedad e ilustrada. Un lectotipo es designado

para Echites megagros.

27

#### Introduction

Colombia is one of the countries with the highest biodiversity in South America. Some regions have been widely highlighted in terms of floristic diversity (e.g., Galindo *et al.* 2003; García *et al.* 2004; Cárdenas, 2007, Cárdenas *et al.* 2008; Cardona *et al.* 2011; Idárraga-Piedrahita *et al.* 2011), which is likely correlated with the high diversity of climatic and geographic conditions, and major geological events (e.g., Gentry, 1982, 1988; Mosquera *et al.* 2007). Thus far, more than 24500 species of vascular plants have been reported for Colombia (Bernal *et al.* 2015), a number surpassed only by that of Brazil (ca. 32500 taxa) (Forzza *et al.* 2010). However, several areas are poorly collected and more information for several biogeographic regions is still needed.

Apocynaceae with more than 3700 species and ca. 355 genera, is especially diverse in the New world, although it is also well represented in the Old world (Endress *et al.* 2014). The classification of the family has undergone major changes over the last 15 years, beginning with inclusion of the traditional Asclepiadaceae (Endress & Bruyns, 2000). As the result of several phylogenetic studies, tribal and subtribal circumscriptions have changed, some genera have been placed into synonymy and new genera have been described (e.g., Meve & Liede-Schumann, 2004, Simões *et al.* 2006, 2007, Endress & Hansen, 2007; Livshultz *et al.* 2007). However, the infra- or intergeneric delimitation for some groups is still in dispute.

In Colombia, Apocynaceae is represented by 73 genera and 294 species, of which ca. 45 genera and 256 species belong to the Apocynaceae s.s. (Bernal *et al.* 2015). One of the most speciose genera is *Prestonia* R. Brown (1810: 58) (Apocynoideae, Echiteae), which comprises ca. 56 species, with a center of diversity in South America, although it ranges from Mexico and the Caribbean to northern Argentina and Paraguay (Morales, 2010). *Prestonia* plants can be found in primary and secondary forest, but are most common around the margins of forest or along streams. They are more commonly found in secondary bushland or open areas. The genus has been reported from the coastal lowlands (sea level) up to ca. 3000 m (Morales, 1997, 2010; Morales & Morillo, 2015). Woodson (1936) recognized four sections in *Prestonia* defined by leaves pubescence, inflorescence structure, corolla pubescence, corona features, and fruits characters (e.g., pubescence).

Although an alternative classification was proposed by Pichon (1951), it has not taken up by subsequent researchers.

Even though some synopses or revisions have been published for Venezuela and Ecuador (Morillo, 1978; Morales, 2010), the only publication dealing in part with the genus in Colombia is the Woodson monograph (1936), which is severely outdated. Although some species have been described in recent years (Morales, 2004, 2010), a comprehensive treatment of the genus is still lacking. The aim of this study, therefore, is to evaluate and define the species diversity of *Prestonia* in Colombia. A total of 25 species are recognized, four of them endemic: (*P. antioquiana* (described here), *P. cogolloi*, *P. haughtii*, *P. papillosa*). This revision is part of a Ph.D. thesis submitted by the first author to the University of Bayreuth, Germany.

## Materials and methods

The type collections of all taxa described or reported in Colombia have been examined, as well as specimens from the following herbaria: A, B, BM, BR, C, CAUP, CGE, COAH, COL, CR, CUVC, F, FCME, G, GH, HUA, HUQ, IBGE, INB (incorporated in CR), JAUM, K, M, MA, MEDEL, MO, NY, O, P, PSO, S, TULV, UCAM, UCOB, UDCB, US, USF, VALLE, W, WAG, Z, and ZT. Field work has been conducted by the first author between 2003 and 2014 to several Departments (Antioquia, Atlántico, Cundinamarca, El Valle, Guainia, Guaviare, Quindio).

A key to the identification of all known species in Colombia is provided. Each species entry is followed by a diagnostic morphological description (based mostly on Colombian material), distribution data, diagnostic notes, and representative specimens examined. Information obtained from herbarium labels was used to define the habitat and elevation range of each species. Biogeographic areas follow Bernal *et al.* (2015) and only one representative specimen is cited for each Department. For a full synonymy, see Morales *et al.* (2011) and Morales & Morillo (2015). Herbarium acronyms follow Thiers (2015).

## **Taxonomic treatment**

**Prestonia** R. Brown (1811: 58), nom. cons. Type:—*Prestonia tomentosa* R. Brown (1811: 70).

Lianas or vines. Branchlets terete or somewhat flattened, with milky or clear latex, glabrous to variously pubescent, with intrapetiolar colleters. Leaves opposite, leaf blades glabrous or variously pubescent, membranaceous to coriaceous. Inflorescence a monochasial or dichasial cyme, axillary to terminal, few- to many-flowered, glabrous, glabrescent to variously pubescent, bracts scarious to foliaceous. Sepals 5, free, rarely connate at the base and forming a campanulate cup, each sepal with a single entire to variously lacerated colleter centered at the base within. Corolla salverform, rarely infundibuliform, glabrous to pubescent, lobes 5, aestivaton dextrorse, annular corona present around the mouth, usually with 5 free corona lobes within the staminal sectors of the tube, sometimes free corona lobes absent. Stamens 5, anthers connivent and agglutinated to the style-head. Carpels two, apocarpous but united at the apex, style-head spool-shaped; ovules many, several-seriate; nectary annular, variously lobed, or divided into 5 free lobes. Follicles 2, apocarpous, usually free, sometimes united longitudinally until mature, glabrous or variously pubescent, rarely winged. Seeds numerous, dry, truncate, comose at the micropylar end.

## Key to the species of *Prestonia* in Colombia

- 1. Corolla tube, abaxial surfaces of the corolla lobes and follicles pubescent to varying degrees, the indument ferrugineous, brown, or yellow... 2.
- Corolla tube, abaxial surfaces of the corolla lobes and follicles glabrous, glabrescent, or puberulent (*P. megagros*), the indument green or colorless ... 8.
- 2. Corolla tube without free corona lobes within ... P. mexicana
- Corolla tube with free corona lobes within ... 3.
- 3. Apices of the free corona lobes deeply included within the corolla tube, and conspicuously below the apices of the anthers; inflorescence terminal, subterminal or axillary ... 4.
- Apices of the free corona lobes exserted or slightly included, equaling or above the apices of the anthers; inflorescence axillary ... 5.

- 4. Sepals  $8-11 \times 2-3$  mm; anthers 7-9(-11) mm long; pedicels 11-14 mm long; inflorescence axillary to subterminal ... *P. mucronata*
- Sepals 2.5–4 × 1–1.5 mm; anthers 3.5–4 mm long; pedicels 5–7 mm long; inflorescence terminal or subterminal ... *P. parviflora*
- 5. Rachis and peduncle of the inflorescence tomentose, tomentulose, or velutinous, the indument more or less adpressed ... 6.
- Rachis and peduncle of the inflorescence hirsute to hispid, the indument more or less erect ... 7.
- 6. Leaf blades sparsely and irregularly hirsute to hirsutulous abaxially, the indument irregularly distributed; sepals 3–4.5 mm wide; nectary as tall as the ovary ... *P. cogolloi*
- Leaf blades densely velutinous-tomentose abaxially, the indument uniformly distributed; nectary taller than the ovary ... *P. tomentosa*
- 7. Leaf blades densely velutinous to velutinous-tomentose abaxially; follicles 8–14 mm diam. ... *P. seemannii*
- Leaf blades moderately to sparsely hirsute abaxially; follicles 20–22 mm diam. ... *P. ipomaeifolia*
- 8. Corolla tube without free corona lobes within ... P. coalita
- Corolla tube with free corona lobes within ... 9.
- 9. Sepal apices reflexed; inflorescence a monochasial cyme ... P. quinquangularis
- Sepal apices not reflexed; inflorescence a monochasial or dichasial cyme ... 10.
- 10. Free corona lobes less than 1.5 mm long, their apices conspicuously below the anther apices, deeply included... 11.
- Free corona lobes 2–5.5 mm long, their apices equalling to conspicuously above the anther apices, exserted or barely included ... 15
- 11. Sepals basally connate for 1/3–1/2 of their length, forming a campanulate cup ... *P. haughtii*
- Sepals free, not forming a campanulate cup ... 12.
- 12. Inflorescence a monochasial cyme, unbranched ... 13.
- Inflorescence a dichasial cyme, branched ... 14.
- 13. Sepals 2.5–5 mm long; free corona lobes 1–1.5 mm long; anthers 4–4.6 mm long; follicles 13–24 cm long; seeds 10–15 mm long ... *P. cayennensis*

- Sepals 6.5–8 mm long; free corona lobes 1.5–2 mm long; anthers 5.3–5.5 mm long; follicles 29–32 cm long; seeds 17–19 mm long ... *P. vaupesana*
- 14. Corolla tube  $6-9 \times 2-2.1$  mm, the lobes 5-6 mm long ... *P. papillosa*
- Corolla tube  $13-18 \times 3-5$  mm, the lobes 9-15 mm long ... P. annularis
- 15. Leaf blades membranaceous, the tertiary veins scarcely impressed abaxially, inconspicuous (or nearly so) adaxially ... 16.
- Leaf blades coriaceous to subcoriaceous, the tertiary veins conspicuously impressed on both surfaces ... 18.
- 16 Inflorescence conspicuously longer than the adjacent leaves; sepals falcate ... P. falcatosepala
- Inflorescence shorter than or equaling adjacent leaves; sepals not falcate ... 17.
- 17. Free corona lobes almost totally exserted; inflorescence a dichasial cyme, usually 1-2-branched. ... *P. exserta*
- Free corona lobes with the apices slightly exserted or barely included; inflorescence a monochasial cyme, unbranched ... *P. folsomii*
- 18. Sepals  $3-8 \times 2-3(-4)$  mm ... P. longifolia
- Sepals  $(9-)10-20 \times 3-8 \text{ mm} \dots 19$ .
- 19. Leaf blades densely to moderately puberulent abaxially; follicles puberulent ... *P. megagros*
- Leaf blades glabrous or glabrescent with indument restricted to the midrib abaxially; follicles glabrous, glabrescent or papillate... 20.
- 20. Inflorescence a monochasial cyme; sepals with the base drying darker than the rest of the surface ... *P. lindleyana*
- Inflorescence a dichasial cyme; sepals drying with a more or less uniform color ... 21.
- 21. Floral bracts  $8-18 \times 2.8-4$  mm, narrowly elliptic, narrowly ovate-elliptic or narrowly ovate, conspicuously foliaceous ... *P. rotundifolia*
- Floral bracts  $1-6 \times 0.5-1.5$  mm, linear, linear-elliptic or linear-ovate, not foliaceous ... 22.
- 22. Corolla tube sparsely puberulent; follicles divaricate... P. vana
- Corolla tube glabrous; follicles not divaricate... 23.

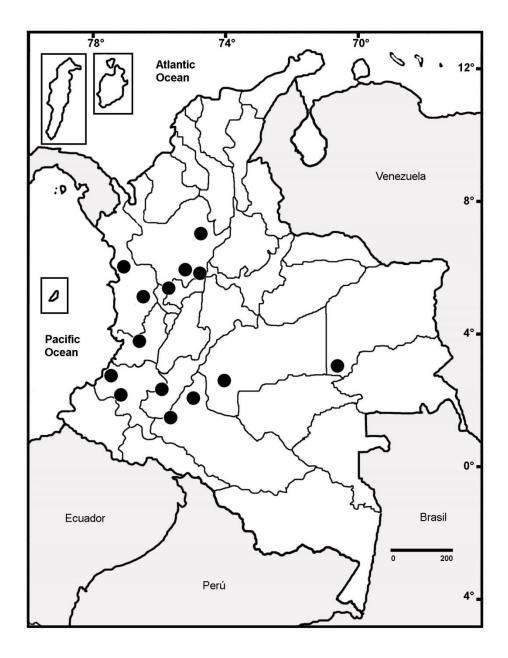
- 23. Stems papillate-puberulent; nectary completely covering the ovary; follicles 6–8 mm diam., firmly membranaceous when old ... *P. portobellensis*
- Stems glabrous; nectary not covering the ovary; follicles 8–11 mm diam., somewhat woody when old ... 24.
- 24. Petioles not verrucose; corolla lobes 8.5–15 mm long; seeds 18–21 mm long ... *P. trifida*
- Petioles conspicuously and irregularly verrucose; corolla lobes 17–21 mm long; seeds 15–17 mm long ... *P. antioquiana*

Prestonia annularis (L.f.) G. Don (1837: 84). Echites annularis Linnaeus f. (1781: 166). Haemadictyon (?) annulare (Linnaeus f.) Candolle (1844: 428). Temnadenia annularis (Linnaeus f.) Miers (1878: 216). Type:—SURINAME. Without data. Herb. Alstroemerii s.n. (lectotype, designated by Morales (2007b) S-LINN 09–34535!) Fig. 1.

**Stem** glabrous to glabrescent at maturity. **Petioles** 0.9–2.7 cm; leaf blade 9–35 × 5–21 cm, elliptic, ovate-elliptic to broadly ovate, apex acuminate or acute, base obtuse to rounded, coriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, minutely puberulent to glabrescent, peduncle 2–7 cm, pedicels 1.1–2.1 cm long, floral bracts 1–5 × 0.5–1 mm, linear. **Sepals** 10–17 × 2.5–4.5 mm, free, narrowly ovate to narrowly elliptic, not reflexed, glabrous, foliaceous, drying with a more or less uniform color. **Corolla** yellow (with purple stripes) or greenish white, glabrous outside, tube 13–18 × 3–5 mm, lobes 9–15 × 6–12 mm, obliquely obovate, free corona lobes 1–1.5 mm long, deeply included, their apices conspicuously surpassed by the anther apices, annular corona entire to subentire. **Anthers** 5–6 mm, the apices slightly exserted or barely included. **Ovary** 1–2 mm tall, nectary 1.2–2.3 mm, surpassing the ovary, irregularly 5-lobed. **Follicles** 32–44 × 0.6–0.8 cm, free, but usually united at the tips (at least when young), glabrous; seeds 14–20 mm, coma 2–3.5 cm, tan.

**Distribution**:—Colombia to Peru, Bolivia, northeastern Brazil, Guyanas, and Trinidad and Tobago. Pacific, Magdalena Valley, Andes, Guyana and Sierra de la Macarena, from 0 to 1550 m.

**Taxonomic notes**:—*Prestonia annularis* shows an overall resemblance to *P. portobellensis* (Beurling) Woodson (1931: 553), from which it differs by its shorter free corona lobes (1–1.5 mm vs. 4–5 mm), that are deeply included within the corolla tube (vs. exserted).



**FIGURE 1**. Distribution of *Prestonia annularis*.

Representative specimens examined:—COLOMBIA. Antioquia: Río Segovia, Segovia, 21 July 1979, Renteria et al. 1728 (COL, HUA). Boyacá: Puerto Boyacá, Dos Quebradas, 25 November 1997, Méndez 69 (COL). Caquetá: Florencia, corregimiento de Santo Domingo, vereda Santander, finca Mónaco, 16 March 2012, Restrepo & Aguilar 776 (CAUP). Cauca: Timbiqui, Quebrada Yucal, tributario del Río Bubuey, comunidad Indígena Almorzadero, 24 September 2000, Reina et al. 937 (CAUP). Chocó: Bahía Solano, Puerto Mutis, 4 January 1973, Gentry & Forero 7162 (COL, MO, Z). Meta: Parque Nacional Natural Tinigua, Río Duda, Serranía Chamusa, Centro de Investigaciones Ecológicas La Macarena, April 1997, Stevenson 2040 (COAH, COL, HUA, NY).

## Prestonia antioquiana J. F. Morales & S. Liede-Schumann, sp. nov. Figs. 2–5.

*Prestonia antioquiana* resembles *P. trífida*, but differs by its petioles conspicuously and irregularly verrucose, and follicles with 3-4 longitudinal wings.

Type:—COLOMBIA. Antioquia: San Luis, Río Claro, 26 December 1983, A. Cogollo 1133 (holotype JAUM!, isotypes COL!, HUA!, MO!).

Stem glabrous. Petioles 1.5–3 cm, conspicuously and irregularly verrucose; leaf blade  $19-35 \times 7-14$  cm, broadly elliptic, elliptic to obovate-elliptic, apex obtuse and shortly acute, base obtuse, coriaceous, glabrous; tertiary veins impressed on both surfaces. Inflorescence a dichasial cyme, axillary, shorter than the adjacent leaves, densely and minutely puberulent, peduncle 7-14 cm, pedicels 0.8-2 cm long, floral bracts  $1.5-2 \times 0.5-1.5$  mm, linear. Sepals  $11-16 \times 4-6.5$  mm, free, narrowly ovate to narrowly ovate-elliptic, not reflexed, inconspicuously puberulent, foliaceous, drying with a more or less uniform color. Corolla cream to greenish cream, usually glabrous outside, tube  $17-18 \times 4-5$  mm, lobes  $17-21 \times 7-9$  mm, obliquely obovate; free corona lobes 3-3.5 mm long, the apices exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire. Anthers 5.1-5.8 mm, the apices slightly exserted. Ovary 1-1.5 mm tall, nectary divided into 5 lobes 1-1.7 mm, equaling or barely surpassing the ovary. Follicles  $14-28 \times 0.9-1.1$  cm, free, but usually united at the tips (at least when young), with 3-4 longitudinal wings, glabrous; seeds 15-17 mm, coma 2.8-3.4 cm, tan.



**FIGURE 2**. Petioles of *P. antioquiana* and *P. trifida*.



**FIGURE 3**. *Prestonia antioquiana* A. Flowers. B. Dissected calyx, with one sepal removed, showing the colleter (arrow).

**Distribution**:—Endemic to the Department of Antioquia, Colombia, in tropical wet forest at 150–800 m of elevation.

**Etimology**:—The species is named after the Antioquia Department, one of the most diverse departments in the country.

**Taxonomic notes**:—*Prestonia antioquiana* resembles *P. trifida* (Poeppig) Woodson (in Gleason & Smith 1933: 392), but can be differentiated by its verrucose petioles (vs. not verrucose), longer corolla lobes (17–21 mm vs. 8.5–15 mm), follicles with 3-4 longitudinal wings, and shorter seeds (15–17 mm vs.18–21 mm).

Representative specimens examined:—COLOMBIA. Antioquia: NE de Cáceres, Troncal de La Paz, 6 November 1987, *Callejas et al. 5406* (CR, HUA, MO, NY, US, WAG); San Luis, vereda Las Confusas, 20 May 1990, *Cogollo et al. 4503* (COL, JAUM, MO); San Luis, Quebrada La Cristalina, 4 December 1986, *Ramírez & Cárdenas 233* (CR, HUA, JAUM, MO).

*Prestonia cayennensis* (Candolle) Pichon (1951: 25). *Haemadictyon cayennense* Candolle (1844: 427). Type:—FRENCH GUIANA. Cayenne: Cayenne, s.d., *J. Vargas s.n.* (holotype G-DC!) Fig. 5.

**Stem** glabrous or minutely papillate-puberulent. **Petioles** 0.3–1 cm; leaf blade 4.5– $16 \times 1.8$ –5 cm, elliptic to narrowly elliptic, apex acute to caudate, base cuneate to obtuse, subcoriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a monochasial cyme, axillary, shorter or longer than the adjacent leaves, glabrous to sparsely puberulent, peduncle 2.5–5.7 cm, pedicels 0.8–1.5 cm long, floral bracts 0.5– $2 \times 0.5$ –1 mm, linear. **Sepals** 2.5– $5 \times 1$ –1.5 mm, free, narrowly ovate to narrowly elliptic, not reflexed, glabrous, very small, drying with a more or less uniform color. **Corolla** yellowish green to pinkish green, glabrous outside, tube 12– $17 \times 2.5$ –4 mm, lobes 7– $11 \times 4$ –6 mm, obliquely obovate, free corona lobes 1–1.5 mm long, deeply

included, their apices conspicuously surpassed by the anther apices, annular corona entire. **anthers** 4–4.6 mm, the apices slightly exserted. **Ovary** 1.5–2 mm tall, nectary 1.1–1.7 mm, usually shorter than the ovary, divided into 5 lobes, free or connate basally. **Follicles** 13–24  $\times$  0.3–0.4 cm, free, but sometimes united at the tips (at least when young), glabrous; seeds 10–15 mm, coma 1.5–3.8 cm, cream.

**Distribution**:—Colombia to Bolivia, Guyanas, and Brazil. In Colombia in the Pacific, Amazon, and Guyana, 0–450 m.

**Taxonomic notes:**—This species is vegetatively similar to *P. vaupesana* Woodson (in Schultes 1957: 178), but can be recognized by its smaller sepals (2.5–5 mm vs. 6.5–8 mm), free corona lobes deeply included within the tube, and shorter follicles.

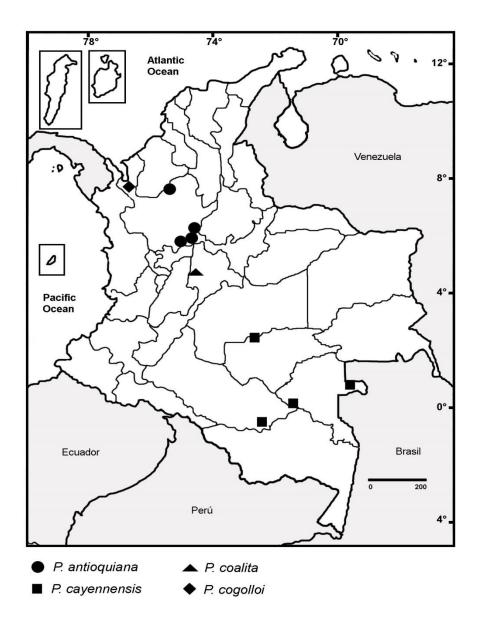
Representative specimens examined:—COLOMBIA. Caquetá: cima del Cerro Chiribiquete, January 1944, *Gutiérrez et al. 565* (MO). Guainia: Río Negro, Piedras del Cocuy, 24 February 1965, *Fernández et al. 6991* (COL). Guaviare: San José del Guaviare, serranía de la Lindosa, camino entre ciudad de Piedra y filo de Piedra, 22 March 2008, *Cárdenas et al. 21467* (COAH). Vaupés: Río Papurí, entre Santa Teresita y Piracuara, 4 July 2002, *Castaño & Betancur 1553* (COL).

Prestonia coalita (Vellozo) Woodson (1931: 552). Echites coalitus Vellozo (1825: 112). Rhaptocarpus coalitus (Vellozo) Miers (1878: 152). Type:—BRAZIL. Fl. Flumin., Icon 3: pl. 40. 1827 (1831) [lectotype, designated by Morales (2006)] Fig. 5.

**Stem** glabrous to inconspicuously puberulent. **Petioles** 0.51 cm; leaf blade 4.5– $12.4(-17) \times 3-6$  cm, elliptic to ovate-elliptic, apex acute and shortly apiculate, base obtuse, membranaceous, glabrous or glabrescent, tertiary veins impressed abaxially, and barely visible adaxially. **Inflorescence** a usually a dichasial cyme, axillary, shorter than the adjacent leaves, puberulent to glabrous, peduncle 0.4–1.1 cm, pedicels 0.4–1 cm long, floral bracts  $1.7-3 \times 1-1.5$  mm, linear. **Sepals**  $3-7 \times 2-3.3$  mm, free, linear, usually

reflexed, glabrous, drying with a more or less uniform color. **Corolla** cream to creamish green, glabrous outside, tube  $10-16 \times 1.5-1.9$  mm, without free corona lobes within, lobes

 $5-8.5 \times 4-4.5$  mm, obliquely obovate, annular corona entire. Anthers 4.5-5.5 mm, included. **Ovary** 0.9-1.1 mm tall, nectary 0.9-1.1 mm, equaling the ovary, 5-lobed. **Follicles**  $18-36 \times 0.4-0.7$  cm, connate longitudinally or free and united only at the tips, glabrous; seeds 8-10 mm, coma 2.7-3.8 cm, cream.



**FIGURE 5**. Distribution of *P. antioquiana*, *P. cayennensis*, *P. coalita*, and *P. cogolloi*.

**Distribution**:—Colombia to Bolivia and Argentina. Magdalena Valley, 200–800 m.

**Taxonomic notes**:—*Prestonia coalita* is characterized by the following combination of characters: leaf blades glabrous or glabrescent, inflorescence a dichasial cyme, with flowers densely congested, and corollas without free corona lobes within.

**Representative specimen examined**:—COLOMBIA. Cundinamarca: San Juan de Río Seco, entre Cambao y San Juan de Río Seco, 23 September 1981, *Rangel & Salamanca* 3292 (COL, CR).

*Prestonia cogolloi* J.F. Morales (2007a: 148). Type:—COLOMBIA. Antioquia: Turbo, road to Tapón del Darién, Río León, 16 January 1985, *J. Brand, E. Renteria & A. Cogollo* 1329 (holotype JAUM!, isotype CR!) Fig. 5.

Stem sparsely to moderately hirsutulous, glabrescent at maturity. **Petioles** 1.1–2 cm; leaf blade  $24-33.5 \times 15.4-20$  cm, broadly elliptic to broadly obovate, apex cuspidate, base slightly subcordate, membranaceous, sparsely puberulent adaxially (but the indument more dense along the midrib), sparsely and irregularly hirsute to hirsutulous abaxially, the pubescence irregularly distributed, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the subtending leaves, tomentose, peduncle 4.8-5.5 cm, pedicels 0.8-1 cm long, floral bracts  $5-14 \times 2-4$  mm, elliptic to ovate-elliptic. **Sepals**  $11-13 \times 3-4.5$  mm, free, narrowly elliptic, not reflexed, tomentulose, foliaceous, drying with a more or less uniform color. **Corolla** yellow, densely hispid outside, tube  $11-14 \times 3.5-4.5$  mm, lobes  $8-9 \times 6-8$  mm, obliquely obovate, free corona lobes 3-4 mm long, the apices exserted, their height equaling that of the anther apices, annular corona entire. **Anthers** ca. 6 mm, the apices exserted. **Ovary** 2–2.5 mm tall, nectary 2-2.5 mm, equalling the ovary, irregularly lobed. **Follicles** unknown.

**Distribution**:—Endemic, grows in the Pacific area, 50–100 m.

**Taxonomic notes**:—*Prestonia cogolloi* resembles *P. ipomaeifolia* Candolle (1844: 429), but differs by its inflorescences with the rachis and peduncle tomentulose (vs. hirsute) and corona lobes 3–4 mm long (vs. 2–2.3 mm).

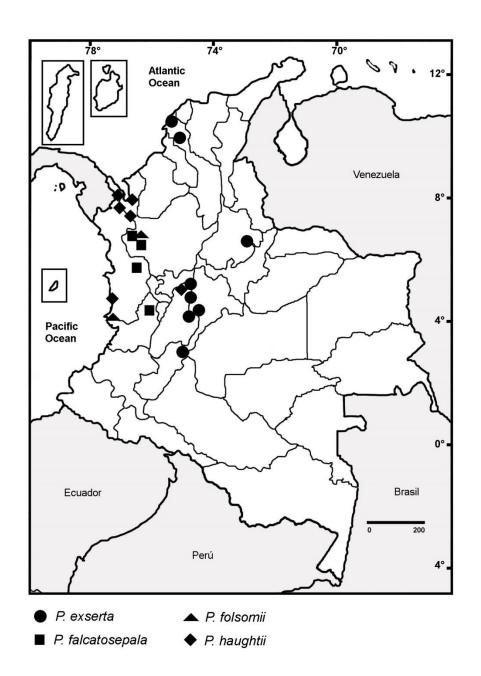
**Representative specimen examined:**—COLOMBIA. Antioquia: cerca de Río León, 15 km al O de Chigorodó, 19 March 1962, *Feddema 1953* (US)

*Prestonia exserta* (Candolle) Standley (1925: 460). *Haemadictyon exsertum* Candolle (1844: 426). Type:—VENEZUELA. Distrito Federal: Caracas, 1830, *J. Vargas 54* (holotype G-DC!) Fig. 6.

**Stem** puberulent to glabrescent. **Petioles** 0.6-1.2 cm; leaf blade  $4.9-11.2 \times 2.4-5.1$  cm, elliptic to broadly ovate, apex acute to short-acuminate, base obtuse or rounded, membranaceous, glabrous or puberulent adaxially, tomentulose to glabrescent abaxially, tertiary veins scarcely impressed abaxially, inconspicuous adaxially. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, puberulent, peduncle 0.6-2.2 cm, pedicels 0.9-1.3 cm long, floral bracts  $2-6 \times 1-1.6$  mm, linear or linear-elliptic. **Sepals**  $7-8 \times 2-4$  mm, free, linear to narrowly ovate or narrowly obovate, the apices not reflexed, puberulent, subfoliaceous, drying with a more or less uniform color. **Corolla** yellowish green, glabrous outside, tube  $13-17 \times 3-3.8$  mm, lobes  $9-12 \times 4-5$  mm, obliquely obovate, free corona lobes 4-5 mm long, almost completely exserted, their apices conspicuously surpassing the anther apices, annular corona entire. **Anthers** 4-5 mm, the apices exserted. **Ovary** 2-2.5 mm tall, nectary 1-1.5 mm, shorter than the ovary, divided into 5 lobes. **Follicles**  $23-28.5 \times 0.3-0.4$  cm, free and united at the tips or connate longitudinally, glabrous; seeds 11-15 mm, coma 2.1-2.6 cm, creamish.

**Distribution**:—Central Panama to Venezuela, and Trinidad y Tobago. Caribbean plains and Magdalena Valley, 0–750 m.

**Taxonomic notes**:—*Prestonia exserta* resembles *P. folsomii* J. F. Morales (1996: 285), but it is easily separated by its conspicuously exserted free corona lobes.



**FIGURE 6**. Distribution of *P. exserta*, *P. falcatosepala*, *P. folsomii*, and *P. haughtii* 

Representative specimens examined:—COLOMBIA. Bolivar: entre Cartagena y Turbaco, 16 January 1941, *Dugand & Jaramillo 2839* (COL, US). Cesar: Poponte, valle del Magdalena, 19 Octuber 1924, *Allen 777* (MO). Chocó: Loma de los Colorados, cerca a San Juan de Nepomuceno, 31 December 1992, *Gentry et al. 78449* (MO). Cundinamarca: camino a Puerto Bogotá, entre Río Magdalena a Puerto Salgar, 5 March 1977, *Gentry et al.* 

18083 (COL, MO). Huila: Villavieja, resguardo Indígena Tatacoa, 31 Octuber 2003, Figueroa & Galeano 450 (COL, CR). Magdalena: Cienaga Río Frío, January 1949, Romero-Castañeda 1362 (COL). Santander: 40 km al S de Bucaramanga, 16 December 1948 Araque & Barkley 328 (COL, FMB, MEDEL, MO, US, VALLE). Tolima: Chicoral, 13 May 1949, Haught 6437 (COL, MO, US).

*Prestonia falcatosepala* J.F. Morales (2004: 162). Type:—ECUADOR. Carchí: border between Carchí and Esmeraldas, road from Lita to Alto Tambo, 27 June 1991, *H. van den Werff, B. Gray & G.A. Tipaz 12076* (holotype MO!, isotype CR!) Fig. 6.

**Stem** puberulent to glabrescent. **Petioles** 1–1.6 cm; leaf blade  $3.5-6.7 \times 2.4-3.2$  cm, elliptic to ovate, apex acuminate, base obtuse to rounded, membranaceous, glabrescent or minutely puberulent abaxially, tertiary veins scarcely impressed abaxially, and inconspicuous adaxially. **Inflorescence** a monochasial cyme, axillary, longer than the adjacent leaves, puberulent to glabrescent, peduncle 5–9.5 cm, pedicels 2.2-2.8 cm long, floral bracts  $4-5 \times 0.5-1$  mm, linear. **Sepals**  $7.5-9 \times 2.3-3.3$  mm, free, narrowly elliptic, falcate, not reflexed, puberulent to glabrous, very small. **Corolla** lobes yellow, with purple lines basally, glabrous, tube  $15-17 \times 3-3.8$  mm, lobes  $10-11 \times 8-9$  mm, obliquely obovate, free corona lobes 3-4 mm long, exserted, their apices conspicuously surpassing the anther apices, annular corona entire. **Anthers** 5-6 mm, the apices slightly exserted. **Ovary** 1.6-2 mm tall, nectary 1-1.4 mm, shorter than the ovary, variously 5-lobed. **Follicles**  $25.5-29 \times 0.2-0.3$  cm, connate longitudinally, glabrous; seeds 7-8 mm, coma 1.7-2.8 cm, cream.

**Distribution**:—Colombia to Peru. Pacific, Andes, and Cauca Valley, at 550–1300 m.

**Taxonomic notes**:—*Prestonia falcatosepala* is morphologically similar to *P. exserta*, but it is distinguished by its elongated inflorescences, scarious floral bracts, and falcate sepals.

**Representative specimens examined:**—COLOMBIA. Antioquia: Urrao, Vereda Cruces, Vereda Cruces, camino al Río Penderisco desde la escuela La Esperanza,

alrededores del puente sobre el Río Penderisco, Parque Nacional Natural Las Orquídeas, 6 May 2013, *Hoyos-Gómez et al. 2313* (COL). Chocó: 31 km E de Quibdó, ca. 14 km E de Tutunendo, cerca a la villa Chocoana El Veintiuno, 14 June 1982, *Gentry & Brand 36932* (COL, JAUM, MO, USF). Risaralda: Mistrató, San Antonio de Chamí, carretera a La Mesenia, 27 April 1992, *Betancur et al. 3485* (COL).

*Prestonia folsomii* J. F. Morales (1996: 285). Type:—COLOMBIA. Valle del Cauca: Buenaventura, Bajo Calima region, between Buenaventura and Málaga, km 51.3, 8 February 1990, *T. Croat & J. Watt 70348* (holotype CR!, isotypes MO!, USF!) Fig. 6.

**Stem** puberulent to glabrescent. **Petioles** 0.4–1 cm; leaf blades  $4.2-10.8 \times 2.6-5.1$  cm, elliptic to narrowly obovate, apex acuminate, base obtuse, membranaceous, sparsely puberulent to glabrescent, tertiary veins scarcely impressed abaxially, inconspicuous adaxially. **Inflorescence** a monochasial cyme, axillary, shorter than the adjacent leaves, puberulent, peduncle 2.4-3.8 cm, pedicels 0.9-2.2 cm long, floral bracts  $2.8-3.8 \times 1-1.2$  mm, linear. **Sepals**  $10-13 \times 3-4$  mm, free, narrowly ovate to elliptic, not reflexed, sparsely puberulent, foliaceous to subfoliaceous, drying with a more or less uniform color. **Corolla** yellow, glabrous outside, tube  $11-13 \times 3-4$  mm, lobes  $12-13 \times 8-9$  mm, obliquely obovate, free corona lobes 2-2.8 mm long, the apices slightly exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire. **Anthers** 4-4.5 mm, the apices exserted. **Ovary** 1-1.5 mm tall, nectary ca. 1.5 mm, conspicuously longer than the ovary, moderately 5-lobed. **Follicles** unknown.

**Distribution**:—Panama and Colombia. Pacific, 100–600 m..

**Taxonomic notes:**—*Prestonia folsomii* shows some resemblance to *P. exserta*, but the latter species can be differentiated by the free corona lobes 4–5 mm long, with their apices almost completely exserted and conspicuously surpassing the anthers apices, and shorter corolla tube (vs. free corona lobes 2–2.8 mm long, with their apices equaling or slightly surpassing the anther apices).

**Representative specimens examined**:—COLOMBIA. Antioquia: Frontino, Encarnación, Parque Nacional natural Las Orquídeas, sector Venados, 11 April 2011, *Betancur et al. 15159* (COL).

*Prestonia haughtii* Woodson (1948: 235). Type:—COLOMBIA. Antioquia: Necoclí, 25 June 1946, *O. Haught 4911* (holotype MO!, isotypes COL!, US!). Fig. 6.

**Stem** glabrous. **Petioles** 0.8–1.8 cm; leaf blade  $19-23 \times 7.9-12$  cm, obovate or elliptic, apex rounded and mucronulate, base obtuse, coriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** usually a dichasial cyme, axillary, shorter than the adjacent leaves, glabrous, peduncle 3.5-7 cm, pedicels 1.2-2 cm long, floral bracts  $1-1.5 \times 1$  mm, linear. **Sepals**  $7-9 \times 5-6$  mm, connate at the base for 1/3-1/2 of their length, forming a campanulate cup, ovate, not reflexed, glabrous foliaceous, drying with a more or less uniform color. **Corolla** yellow, glabrous outside, tube  $15-20 \times 5-6.5$  mm, lobes  $13-16 \times 6-7$  mm, obliquely obovate, free corona lobes 1-1.5 mm long, included, their apices conspicuously surpassed by the anther apices, annular corona entire to inconspicuously lobed. **Anthers** 4.5-5 mm, included. **Ovary** ca. 1 mm tall, nectary ca. 2 mm, conspicuously surpassing the ovary, variously 5-lobed. **Follicles** 33-38 cm  $\times 1.1-1.4$  cm, free or connate longitudinally, glabrous; seeds unknown.

**Distribution**:—Endemic. Pacific and Magdalena Valley, 50–450 m.

**Taxonomic notes:**—*Prestonia haughtii* is distinguished by its glabrous leaves, sepals connate for 1/3–1/2 of their length, forming a conspicuous campanulate cup, and free corona lobes less than 2 mm long.

Representative specimens examined:—COLOMBIA. Antioquia: Turbo, carretera Currulao-Nueva Antioquia, 11 km de Currulao, 3 August 1987, *Callejas et al. 5008* (COL, HUA, NY, WAG). Chocó: Turbo, carretera al Tapón del Darién, 28 January 1984, *Brand & Lozano 816* (COL, CR, JAUM, MO). Tolima: Mariquita, 1851–1852, *Triana 1958* (P).

*Prestonia ipomaeifolia* Candolle (1844: 429). Type:—FRENCH GUIANA. Cayenne: Cayenne, s.d., *J. Le Blond s.n.* (holotype G-DC!) Fig. 7

**Stem** sparsely hirsute. **Petioles** 1.2–2.2 cm; leaf blade  $16-29 \times 9.5-19$  cm, elliptic, apex acuminate, base obtuse to rounded, membranaceous, sparsely hirsute on both surfaces, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the subtending leaves, hirsute, peduncle 1.9-2.8 cm, pedicels 0.3-0.7 cm long, floral bracts  $7-15 \times 3-4$  mm, narrowly elliptic, subfoliaceous. **Sepals**  $7-11 \times 3.5-6$  mm, free, ovate to narrowly elliptic, not reflexed, sparsely hirsute, foliaceous to subfoliaceous, drying with a more or less uniform color. **Corolla** yellow, hirsute outside, tube  $12-14 \times 4-5$  mm, lobes  $8-11 \times 6-8$  mm, obliquely obovate, free corona lobes 2-2.2 mm long, the apices exserted, their height surpassing that of the anther apices, annular corona entire. **Anthers** 5.8-6 mm, included. **Ovary** ca. 1 mm, glabrous, nectary 2-2.8 mm tall, conspicuously surpassing the ovary, entire to slightly 5-lobed. **Follicles**  $9-11 \times 2-2.2$  cm, divaricate, free, the tips divergent, hirsute or pilose; seeds not seen.

Distribution:—Panama to Peru, Guyana, and French Guiana. Pacific, below 200 m.

**Taxonomic notes**:—*Prestonia ipomaeifolia* can be confused with *P. cogolloi*, but differs by its sparsely to moderately hirsute dichasial inflorescences and corona lobes 2–2.3 mm.

Representative specimens examined:—COLOMBIA. Antioquia: Turbo, Caracolí, vía Turbo-San Pedro de Urabá, 23 km ENE de Turbo, 1 August 1987, *Callejas et al. 4893* (HUA). Chocó: Bojayá, Río Atrato, 14 April 1982, *Forero et al. 9248* (COL, CR, MO).

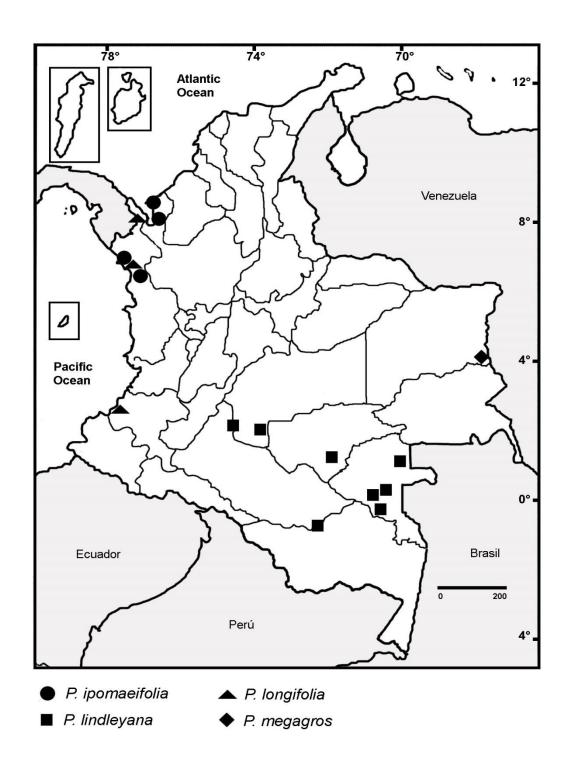


FIGURE 7. Distribution of P. ipomaeifolia, P. lindleyana, P. longifolia, and P. megagros

*Prestonia lindleyana* Woodson in Gleason & Smith (1933: 392). *Haemadictyon calycinum* Lindley ex Miers (1878: 259), nom. illeg. Type:—BRAZIL. Amazonas: near Manaus, Río Negro, October 1851, *R. Spruce 1882* (holotype CGE!, isotypes K!, NY!) Fig. 7.

Stem inconspicuously puberulent to glabrescent. **Petioles** 0.6–1 cm; leaf blade 8.9–17  $\times$  3–8.5 cm, elliptic to obovate-elliptic, apex acute or acuminate, base obtuse, subcoriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a monochasial cyme, axillary, shorter or longer than the adjacent leaves, puberulent to glabrescent, peduncle 5–8.5 cm, pedicels 0.6–1.1 cm long, floral bracts 1–2  $\times$  0.5–1 mm, linear. **Sepals** 10–12  $\times$  3–4.5 mm, free, narrowly ovate, not reflexed, glabrous, foliaceous, the base drying clearly darker than the rest of the sepal. **Corolla** yellow, glabrous outside, tube 10–15  $\times$  3–4 mm, lobes 6–9  $\times$  5–6 mm, obliquely obovate, free corona lobes ca. 2 mm long, the apices barely exserted, their height equaling or slightly surpassing that of the anther apices, annular corona subentire **Anthers** 4.2–5.3 mm, the apices exserted. **Ovary** 1.5–1.9 mm tall, nectary 1.5–2 mm, equaling the ovary, divided into 5 separate lobes. **Follicles** 13–24  $\times$  0.5–0.6 cm, free, but sometimes united at the tips, glabrous; seeds 18–20 mm, coma 2–3.1 cm, tannish cream.

**Distribution**:—Colombia, Venezuela, and northern Brasil. Amazon, 200–550 m.

**Taxonomic notes**:—*Prestonia lindleyana* can be recognized by its unbranched inflorescence, scarious bracts, and sepals with the base drying darker than the rest of the sepal.

Representative specimens examined:—COLOMBIA. Amazonas: Río Caqueta, alrededores de Araracuara, 10 November 1982, *Idrobo et al. 11427* (COL). Guaviare: Miraflores, entre El Caño y Maloca de El Capitán, 7 January 1993, *Gamboa & Pedreros 206* (CUVC). Meta: San Juan del Lozada, via Villa Rica-El Coclí, 12 August 2008, *Castro & Navarrete 5877* (COAH). Vaupés: riberas del Río Inirida, sitio Raudal Alto o Mariapiri, 3 February 1953, *Fernández 2054* (COL, US).

Prestonia longifolia (Sessé & Moçiño) J. F. Morales (1996: 286). Echites longifolius Sessé & Moçiño (1887 [1893]: 45). Type:—MEXICO. Veracruz: San Andrés Tuxtla, s.d., M. Sessé & J. Moçiño 5007 (lectotype MA! designated by Morales (1996); isolectotype, F!) Fig. 7.

**Stem** glabrous to glabrescent. **Petioles** 0.7–1.8 cm; leaf blade 8.5– $17.5 \times 3.5$ –8.5 cm, elliptic, apex short-acuminate, base obtuse, subcoriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than or equaling the adjacent leaves, glabrous or glabrescent, peduncle 2.6–5.5 cm, pedicels 0.1–1.6 cm long, floral bracts ca.  $1 \times 0.5$  mm, linear. **Sepals** 3– $8 \times 2$ –3 (–4) mm, free, narrowly ovate, not reflexed, glabrous, very small, drying with a more or less uniform color, the veins inconspicuous. **Corolla** cream to yellowish green, glabrous outside, tube 14– $18 \times 3.5$ –4 mm, lobes 7– $11 \times 6$ –8 mm, obliquely obovate, free corona lobes 2–2.8 mm long, slightly exserted, their apices equaling the anther apices, annular corona entire. **Anthers** 5–5.4 mm, the apices slightly exserted. **Ovary** 1.5–2 mm tall, nectary 2–2. mm, surpassing the ovary, 5-lobed. **Follicles** 29– $45 \times 0.3$ –0.4 cm, free, but sometimes united at the tips (at least when young), glabrous; seeds 9–11 mm, coma 1.7–2.7 cm, cream.

**Distribution**:—Southern Mexico to Colombia, Pacific, below 300 m.

**Taxonomic notes**:—*Prestonia longifolia* can be confused with *P. portobellensis*, but differs by its smaller sepals 3–8 mm and free corona lobes apices 2–2.8 mm long (vs. sepals 11–18 mm and free corona lobes 4–5 mm).

**Representative specimens examined:**—COLOMBIA. Chocó: Acandí, Unguia, 3 July 1976, *Forero 552* (COL, MO). Cauca: Guapi, Parque Nacional Gorgona, entre playa Blanca y Gorgonilla, 5 September 1987, *Lozano et al. 5634* (COL).

Prestonia megagros (Vellozo) Woodson (1934: 623). Echites megagros Vellozo (1825: 110) Haemadictyon megalagrion Müller Argoviensis (1860a: 170), nom. illeg. Prestonia megalagrion Miers (1878: 149). Type:—BRAZIL. Without data, Fl. Flumin., Icon. 3: pl. 33. 1827 (lectotype designated here) Fig. 7.

Stem papillate-puberulent, glabrescent at maturity. Petioles 2–1.4 cm; leaf blade 10.5– $19 \times 6.5$ –10.5 cm, elliptic to obovate, apex abruptly short-acuminate, base obtuse to rounded, coriaceous to subcoriaceous, densely to moderately papillate-puberulent on both surfaces, tertiary veins conspicuously impressed on both surfaces. Inflorescence a dichasial cyme, axillary, shorter than or equaling adjacent leaves, minutely papillate-tomentulose, peduncle 5.5–7.5 cm, pedicels 1.1–1.4 cm long, floral bracts 4– $8 \times 1.5$ –2 mm, linear-ovate. Sepals 10– $15 \times 3$ –4 mm, free, narrowly elliptic, not reflexed, densely papillate-tomentulose, foliaceous, drying with a more or less uniform color, the veins not impressed. Corolla yellow, glabrous outside, tube 11– $14 \times 4$ –4.5 mm, lobes 9– $12 \times 7$ –8 mm, obliquely obovate, free corona lobes 3–3.5 mm long, the apices barely exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire. Anthers 5–6 mm, the apices barely exserted. Ovary 1.5–1.9 mm tall, nectary 1.9–2 mm, surpassing the ovary, variously 5-lobed. Follicles 12– $15 \times 1$ –1.2 cm, divaricate, free, the tips divergent, puberulent; seeds 15–18 mm, coma 2.9–4 cm, tannish.

**Distribution**:—Colombia, Peru, Venezuela, and Brazil. Amazon, below 200 m.

**Taxonomic notes**:—*Prestonia megagros* is a distinctive species characterized by its densely to moderately papillate-puberulent leaf blades, dichasial inflorescence, free corona lobes with apices barely exserted, and divaricate follicles.

The original plate published by Vellozo (1827) is selected as the lectotype of *Echites megagros*.

**Representative specimens examined**:—COLOMBIA. Amazonas: Leticia, estación biológica El Zafire, October 2006, *Álvarez et al. 3829* (JAUM).

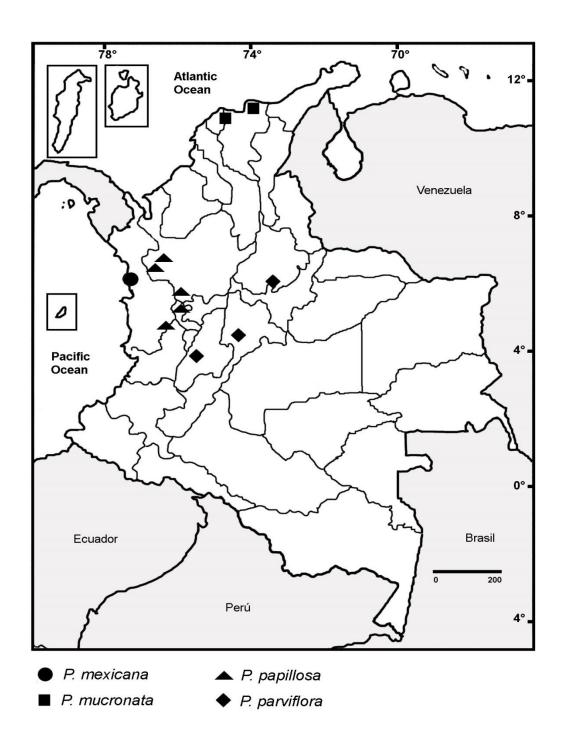


FIGURE 8. Distribution of P. mexicana, P. mucronata, P. papillosa, and P. parviflora

*Prestonia mexicana* Candolle (1844: 429). *Mitozus mexicanus* (Candolle) Miers (1878: 225). Type:—MEXICO. Oaxaca: San Bartolo, August 1834, *G. Andrieux 251* (holotype G-DC!, isotypes, K!) Fig. 8.

Stem variously pubescent. Petioles 0.8-2 cm; leaf blade  $10-22 \times 7-13.5$  cm, elliptic to obovate-elliptic, apex acute or acuminate, base obtuse or rounded, membranaceous, puberulent adaxially, tomentose or tomentulose abaxially, tertiary veins impressed on both surfaces. Inflorescence a dichasial cyme (but resembling an umbel), axillary, usually shorter than the adjacent leaves, moderately tomentose or tomentulose, peduncle 1.3-3.4 cm, pedicels 0.9-2.8 cm long, floral bracts  $5-10 \times 3.5-4.5$  mm, elliptic to narrowly ovate. Sepals  $16-28 \times 5-10$  mm, free, ovate, not reflexed, tomentose or tomentulose, foliaceous to subfoliaceous, drying with a more or less uniform color. Corolla cream to yellowish green, tomentose or tomentulose outside, tube  $25-34 \times 4-5$  mm, lobes  $12-15 \times 9-10$  mm, obliquely obovate, free corona lobes absent, annular corona entire to lobed. Anthers 6-6.9 mm, included or the apices exserted. Ovary 1-1.5 mm tall, nectary 1.5-2.7 mm, surpassing the ovary, entire, 5-lobed or divided into 5 nectaries. Follicles  $6.5-10 \times 1-2$  cm, divaricate, free, the tips divergent, densely hirsute or hirsutulous; seeds 11-14 mm, coma 2.5-3.9 cm, cream.

**Distribution**:—Mexico to northern Colombia. Pacific, 0–350 m.

**Taxonomic notes**:—*Prestonia mexicana* resembles *P. tomentosa* R. Brown (1811: 70) and *P. seemannii* Miers (1878: 146), but differs by its corolla tube without free corona lobes.

**Representative specimens examined**:—COLOMBIA. Chocó: El Carmen, alrededores de Bahía Solano Norte, 7 May 1992, *Barbosa 7001* (HUA).

*Prestonia mucronata* Rusby (1920: 90). Type:—COLOMBIA. Magdalena: Las Nubes, 18 December 1898, *H.H. Smith 1656* (holotype NY!, isotypes G!, K!, MO!, P!, US!, Z!) Fig. 8.

Stem densely ferrugineous-tomentose. Petioles 0.9–1.4 cm; leaf blade  $4.3-7.3 \times 3-$ 5 cm, elliptic to broadly ovate, apex acute to short-acuminate, base obtuse, membranaceous, ferrugineous-hirsutulous adaxially, ferrugineous-hirsutulous ferrugineous-sericeous abaxially, tertiary veins rather inconspicuous. Inflorescence a dichasial cyme (but resembling an umbel), axillary to subterminal, shorter than or equaling adjacent leaves, ferrugineous-tomentulose, peduncle 2–3.2 cm, pedicels 1.1–1.4 cm long, floral bracts  $2-4 \times 0.5-1.5$  mm, linear-ovate. Sepals  $8-11 \times 2-3$  mm, free, elliptic, not reflexed, ferrugineous-tomentulose, subfoliaceous, drying with a more or less uniform color. Corolla yellowish green, ferrugineous-tomentulose outside, tube  $9-12 \times 3-4$  mm, lobes 9–11 × 5–7 mm, obliquely obovate, free corona lobes ca. 1 mm long, deeply included, their apices conspicuously below the anther apices, annular corona subentire to irregularly lobed. Anthers 7–9 mm, included. Ovary 1.5–2 mm tall, nectary ca. 1.5 mm, shorther than the ovary, divided into 5 nectaries. Follicles  $16-20 \times 0.4-0.7$  cm, free, usually united at the tips, ferrugineous-tomentose; seeds unknown.

**Distribution**:—Colombia and Venezuela. Sierra Nevada de Santa Marta, 1900–2200 m.

**Taxonomic notes**:—*Prestonia mucronata* morphological resembles *P. parviflora* (Bentham) Bentham (1876: 709), but it is distinguished by its longer anthers and larger sepals.

**Representative specimens examined**:—COLOMBIA. Magdalena: San Sebastián de Rábago, 8 March 1948, *Romero-Castañeda* 897 (COL).

Prestonia papillosa (Müller Argoviensis) J.F. Morales (2004: 161). Haemadictyon papillosum Müller Argoviensis (1860b: 432). Type:—COLOMBIA. Antioquia: s.d., J. Triana 157 (holotype P!) Fig. 8.

**Stem** papillate-puberulent, glabrescent at maturity. **Petioles** 0.5–0.7 cm; leaf blade 9.5– $16 \times 3.9$ –8.5 cm, elliptic to obovate-elliptic, apex obtuse and abruptly acute, base obtuse, coriaceous to subcoriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, longer than the adjacent leaves, minutely puberulent, peduncle 5.5–8.8 cm, pedicels 0.7–2 cm long, floral bracts 1– $2 \times 0.5$ –1 mm, linear. **Sepals** 3.5– $4.5 \times 1$ –1.5 mm, free, very narrowly ovate, slightly reflexed or not reflexed, glabrescent, very small, drying with a more or less uniform color. **Corolla** yellowish green to yellowish pink, glabrous to glabrescent outside, tube 6– $9 \times 2$ –2.1 mm; lobes 5– $6 \times 3$ –4 mm, ovate, free corona lobes less than 1 mm long, included, their apices conspicuously below the anther apices, annular corona entire, inconspicuous. **Anthers** 4.5–5 mm, the apices conspicuously exserted. **Ovary** ca. 1.5 mm tall, nectary ca. 2 mm, surpassing the ovary, composed of 5 lobes. **Follicles** 15– $20 \times 0.4$ –0.5 cm, free, but usually united at the tips, glabrous; seeds 16–18 mm, coma 2–2.3 cm, cream.

**Distribution**:—Endemic. Andes, 1000–2000 m.

**Taxonomic notes**:—*Prestonia papillosa* shows an overall resemblance to *P. cayennensis*, but it can be differentiated by the papillate-puberulent stems, inflorescence structure, and smaller corollas.

Representative specimens examined:—COLOMBIA. Antioquia: Jardín, carretera Jardín-Río Sucio, 7 km de Jardín, 7 June 1987, *Callejas et al. 3750* (HUA, MO, NY, USF). Chocó: San José del Palmar, vereda San Antonio, finca San Vicente, 20 April 1998, *López et al. 1802* (HUA). Risaralda: Mistrato, 17 March 1991, *Galeano et al. 2481* (COL).

*Prestonia parviflora* (Bentham) Bentham (1876: 709). *Haemadictyon parviflorum* Bentham (1857: 355). *Temnadenia parviflora* (Bentham) Miers (1878: 215). Type:— COLOMBIA. Cundinamarca: Pandi, s.d., *K. Hartweg 1053* (holotype K!, isotype CGE!) Fig. 8.

Stem minutely ferrugineous-tomentulose to sparsely puberulent. Petioles 1.5-2.8 cm; leaf blade  $9-21 \times 3.8-10.5$  cm, elliptic to broadly elliptic, apex short-acuminate, base obtuse, membranaceous, sparsely puberulent adaxially, tomentulose abaxially, tertiary veins rather obscure. Inflorescence a dichasial cyme, terminal or subterminal, rarely axillary, shorter than the adjacent leaves, ferrugineous-tomentulose, peduncle 1.4-2.4 cm, pedicels 0.5-0.7 cm long, floral bracts  $1-3 \times 0.5-1$  mm, linear. Sepals  $2.5-4 \times 1-1.5$  mm, free, very narrowly elliptic, not reflexed, tomentulose, small and inconspicuous. Corolla yellow, ferrugineous-tomentulose outside, tube  $4-6 \times 1.5-2.5$  mm, lobes  $4-7 \times 3-4$  mm, obliquely obovate, free corona lobes ca. 1 mm long, deeply included, their apices conspicuously below the anther apices, annular corona inconspicuous. Anthers 3.5-4 mm, the apices barely exserted. Ovary 1.4-1.5 mm tall, nectary ca. 1 mm, slightly shorter than the ovary, irregularly 5-lobed. Follicles  $31-35 \times 0.4-0.7$  cm, united at the tips, ferrugineous-tomentose; seeds 14-14.5 mm, coma 2-3 cm, tannish cream.

**Distribution**:—Colombia, Venezuela, Ecuador, and Peru. Andes, 1400–2100 m.

**Taxonomic notes**:—*Prestonia parviflora* is distinguished by its tomentulose leaves, terminal or subterminal inflorescences, sepals 2.5–4 mm, free corona lobes ca. 1 mm long, and anthers 3.5–4 mm long.

Representative specimens examined:—COLOMBIA. Cundinamarca: Tena, cerca del Salto de Tequendama, 5 January 1999, *Díaz & Gómez 3* (CR). Quindio: Pijas, El Sinabrio, finca Las Pavas, 14 October 1999, *Macías et al. 1334* (HUQ). Santander: Suaita, Finca Marbella, sector Flandes, 30 March 2004, *Fernández-Alonso et al. 21310* (COL). Tolima: El Fresno, 7 May 1940, *Cuatrecasas 9396* (COL, VALLE, US).

*Prestonia portobellensis* (Beurling) Woodson (1931: 553). *Echites portobellensis* Beurling (1854: 137). Type:—PANAMA. Colón: Portobello, April 1826, *J. Billberg s.*n. (holotype S!) Fig. 9.

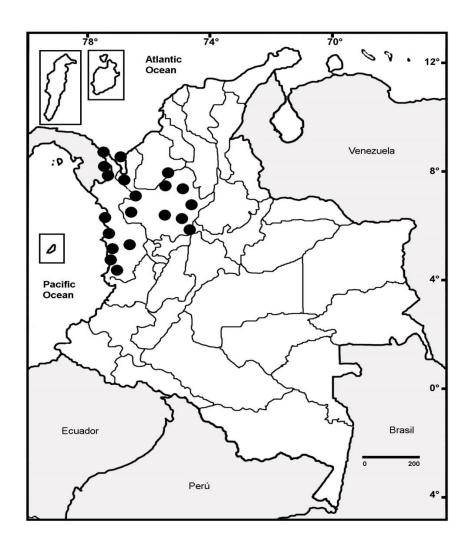
**Stem** papillate-puberulent. **Petioles** 1–2.9 cm; leaf blade  $11-31.5 \times 7.5-16$  cm, elliptic to obovate, apex obtuse to short-acuminate, base obtuse, coriaceous to subcoriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, densely to sparsely puberulent, peduncle 3.5–5.8 cm, pedicels 0.9–2.2 cm long, floral bracts  $1-3 \times 10^{-2}$ 0.9-1.3 mm, linear. **Sepals**  $11-18\times4-7$  mm, free, rarely connate at the base for 1/6 of their length and forming an inconspicuous campanulate base, narrowly elliptic to narrowly ovate, not reflexed, glabrous, foliaceous to subfoliaceous, drying with a more or less uniform color. Corolla yellowish green, with the lobes with red and purple stripes, glabrous outside, tube  $14-18 \times 6-7$  mm, lobes  $10-16 \times 10-13$  mm, obliquely obovate, free corona lobes 4–5 mm long, the apices exserted, their height surpassing that of the anther apices, annular corona entire to scarcely 5-lobed. Anthers 5-6 mm, the apices barely exserted. Ovary ca. 2 mm tall, nectary ca. 2 mm, surpassing and completely covering the ovary, entire to slightly 5-lobed. Follicles  $33-61 \times 0.6-0.8$  cm, free, but usually united at the tips (at least when young), papillate to glabrescent; seeds 11-18 mm, coma 2.6-3 cm, tan.

**Distribution**:—Mexico to Venezuela and Ecuador. Pacific, Magdalena Valley, 0–650 m.

**Taxonomic notes:**—This species resembles *P. annularis* and *P. longifolia*; this trio is characterized by glabrous leaves, similar inflorescence structure, scarious floral bracts, conspicuous annular corona, and slender follicles. *Prestonia portobellensis* differs by its corona lobes apices conspicuously surpassing the anther apices (vs. corona lobes apices equaling or conspicuously surpassed by the anthers apices).

Representative specimens examined:—COLOMBIA. Antioquia: Turbo, cerca a Tapón del Darién, sector Río León-Lomas Aisladas, km 37, 27 February 1984, *Brand 940* (COL, HUA, JAUM, MO). Chocó: Parque Nacional Los Katios, 16 July 1979, *Barbosa* 

1043 (MO, USF); Bahía Solano, corregimiento El Valle, carretera El Valle-Almejal, 15 April 1989, Espina et al. 2462 (CHOCO, CR, HUA). Magdalena: camino a San Pedro de la Sierra, Quebrada Botella, 29 September 1972, Kirkbride 2269 (COL, NY). Nariño: Monte Alto, S de Tumaco, 16 October 1955, Romero-Castañeda 5390 (COL). Putumayo: Río Putumayo, puerto Porvenir, 22 November 1940, Cuatrecasas 10762 (COL, US). Quindió: Circasia, vereda Barcelona Alta, 23 March 1991, Agudelo et al. 1056 (HUQ). Valle del Cauca: Río Nayo, debajo de Puerto Merizalde, 1 March 1943, Cuatrecasas 14323 (VALLE).



**FIGURE 9**. Distribution of *P. portobellensis* 

Prestonia quinquangularis (Jacquin) Sprengel (1825: 637). Echites quinquangularis Jacquin (1760: 13). Temnadenia quinquangularis (Jacquin) Miers (1878: 212). Type:—COLOMBIA. Atlántico: Cartagena, Cerro La Popa, without data, Jacq., Select. Stirp. Amer. Hist. t. 25. 1763. (lectotype designated by Morales (2004)) Fig. 10.

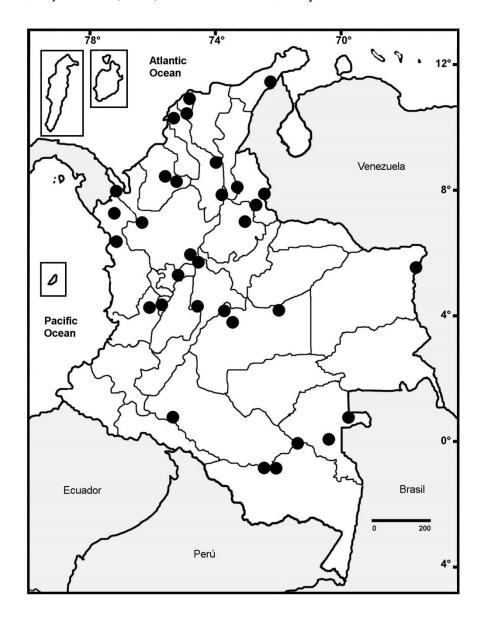
Stem glabrous to glabrescent. Petioles 0.5-1.9 cm; leaf blade  $6-10.5 \times 2-5$  cm, elliptic to broadly ovate, apex acute, short-acuminate or obtuse, base obtuse to rounded, membranaceous to firmly membranaceous, glabrous, rarely minutely puberulent abaxially, tertiary veins slightly impressed on both surfaces, sometimes inconspicuous. Inflorescence a monochasial cyme, axillary, longer than the adjacent leaves, glabrous to glabrescent, peduncle 3-11 cm, pedicels 0.6-1.1 cm long, floral bracts  $1-2 \times 0.5-1$  mm, scarious, linear. Sepals  $1-3 \times 1-1.5$  mm, free, very narrowly ovate, normally reflexed, glabrous, very small, drying with a more or less uniform color. Corolla yellowish green to cream, glabrous outside, tube  $15-20 \times 3-4.5$  mm, lobes  $10-13 \times 6-9$  mm, obliquely obovate, free corona lobes 1-1.5 mm long, included, their apices conspicuously below the anther apices, annular corona entire. Anthers 4-5 mm, the apices slightly exserted. Ovary ca. 1.5 mm tall, nectary ca. 1.5 mm, equalling the ovary, deeply and irregularly 5-lobed. Follicles  $25.5-38 \times 0.3-0.5$  cm, usually connate longitudinally (rarely free and united only at the tips), glabrous; seeds 8-12 mm, coma 2-3.4 cm, cream to white.

**Distribution**:—Widespread. Nicaragua and the Antilles to northern Argentina. Pacific, Magdalena Valley, Cauca Valley, Caribbean plains, Andes, Orinoquia, Guyana and Sierra de la Macarena, and Amazon, 0–1000 m

**Taxonomic notes**:—*Prestonia quinquangularis* is distinguished by its unbranched inflorescence, reflexed sepal apices, and free corona lobes deeply included within the tube.

Representative specimens examined:—COLOMBIA. Amazonas: Puerto Santander, Monochoa-Ciudad Perdida-Araracuara, 26 March 1994, *Cárdenas et al. 4511* (COAH, MO). Antioquia: San Luis, Quebrada La Cristalina, 1 September 1994, *Acevedo-Rodríguez & Callejas 6765* (MO, NY, US). Arauca: Arauca, Caño Limón, 16 Octuber 1997, *Betancur & Uribe 7534* (COL). Atlántico: Santa Rosa, finca La Peluza, 3 February

2000, López 4973 (HUA). Chocó: Riosucio, Parque Nacional Natural Los Katios, camino a



**FIGURE 10**. Distribution of *P. quinquangularis* 

los saltos El Tendal y La Tigra, 28 March 1999, *Fonnegra et al. 6883* (COL, HUA, MO). Córdoba: Ayapel, Monte Líbano, 21 May 1949, *Romero-Castañeda 1715* (COL, CR, MEDEL, MO). Guajira: Maicao, Tabaco, 17 May 1981, *Arboleda et al. 597* (HUA); entre Cuestecita y Carraipia, márgenes de Río Cesar, 30 November 1959, *Cuatrecasas et al.* 

25516 (COL, US). Guaviare: El Retorno, camino de Cerritos a Cerro Piedra Gorda, 19 Octuber 1995, Cárdenas et al. 6700 (COAH). Magdalena: Río Cesar y Río Azucarbuena, El Callao, 29 Octuber 1959, Cuatrecasas et al. 24923 (COL, US); Puerto Ocaña, September 1852, Holton s.n. (NY). Meta: O de Puerto Gaitán, camino a Puerto López, Río Yucao, 31 December 1973, Davidse & Llanos 5442 (COL, MO). Norte de Santander: entre Chinácota y La Esmeralda, 19 May 1927, Killip & Smith 20923 (NY, US). Quindió: Montenegro, vereda El Gigante, Hacienda Santa Cecilia, Río Banvieja, 24 September 1985, Arbeláez et al. 1075 (HUA, HUQ). Risaralda: La Virginia, 20 March 1989, Ramos & Silverstone-Sopkin 1909 (CUVC, MBM, MO). Santander: valle del Río Surata, entre Bucaramanga y El Jaboncillo, 2 January 1927, Killip & Smith 16305 (F, NY, US). Tolima: Ibagué, Melgar, 6 December 2000, Diana & Henry 430 (TOLI). Valle del Cauca: Valle, Zarzal, Cartago, 16 November 1986, Silverstone-Sopkin et al. 2563 (CR, CUCV, MO). Vaupés: Río Vaupés, Raudal Macucu, 14 November 1952, Romero-Castañeda 3488 (COL).

*Prestonia rotundifolia* K. Schumann ex Woodson (1936: 318). Type:—ECUADOR. Manabi: El Recreo, August 1893, *B. Eggers 15078* (holotype M!, isotypes, NY!, P!, US!) Fig. 11.

**Stem** glabrous to glabrescent. **Petioles** 0.8-2 cm; leaf blade  $11-17 \times 6.5-10$  cm, obovate, elliptic to broadly ovate, apex acute to obtuse, base obtuse to rounded, coriaceous to subcoriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, minutely puberulent, peduncle 2.1-7.8 cm, pedicels 0.9-1.3 cm long, floral bracts  $8-18 \times 2.8-4$  mm, elliptic to narrowly ovate, conspicuously foliaceous. **Sepals**  $10-15 \times 3-4.5$  mm, usually connate at the base for 1/3 of their length, forming a campanulate cup, rarely completely free, narrowly ovate to narrowly elliptic, not reflexed, sparsely puberulent to glabrescent, foliaceous, drying with a more or less uniform color. **Corolla** cream, glabrescent outside, tube  $13-16 \times 3.5-5$  mm, lobes  $10-13 \times 6-8$  mm, obliquely obovate, free corona lobes 2-3 mm long, the apices slightly exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire. **Anthers** 4.5-5 mm, the apices barely exserted. **Ovary** 

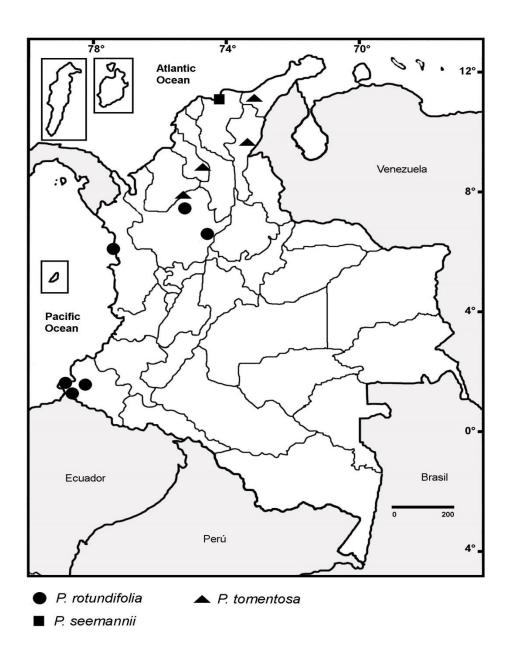


FIGURE 11. Distribution of P. rotundifolia, P seemannii, and P. tomentosa

1.5-2 mm tall, nectary 1.5-2.1 mm, equaling or scarcely surpassing the ovary, divided into 5 nectaries. **Follicles**  $21-35 \times 0.4-0.8$  cm, free, but united at the tips, glabrescent; seeds 14-16 mm, coma 2.5-3.5 cm, tannish cream.

**Distribution**:—Colombia, Ecuador, and Peru. Pacific, Magdalena Valley, Amazon, 0–700 m.

**Taxonomic notes**:—*Prestonia rotundifolia* resembles *P. trifida* and *P. antioquiana*, but is differentiated by its foliaceous floral bracts.

Representative specimens examined:—COLOMBIA. Amazonas: Leticia, corregimiento de la Pedrera, Río Cahuinarí, bocas del Río Pamá, rebalse Medio de Dique Natural, 26 November 1990, *Fundación Botánica Pedro Rastrojo 3399* (HUA). Antioquia: Puerto Berrío, vereda Alicante, 1 km S de finca Penjame, carretera San Juan de Bedout-La Cabaña, 2 March 1990, *Callejas et al. 9285* (HUA, MO, NY, USF). Chocó: Bahía Solano, Puerto Mutis, 4 January 1973, *Gentry & Forero 7161* (COL, MO) Nariño: Barbacoas, entre Barbacoas y Payán, 4 November 1989, *Ramírez 1789* (PSO).

*Prestonia seemannii* Miers (1878: 146). Type:—PANAMA. Panama: near Panama City, s.d., *B. Seemann 159* (holotipo BM! Fig. 11.

**Stem** moderately hispid or glabrescent. **Petioles** 0.5–1 cm; leaf blade 7.6–17.2  $\times$  5.3–10 cm, elliptic to obovate, apex acute or acuminate, base obtuse, membranaceous, hispid-velutinous adaxially, densely velutinous to velutinous-tomentose abaxially, tertiary veins impressed on both surfaces. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the adjacent leaves, ferrugineous-hispid, peduncle 1.7–2.6 cm, pedicels 0.5–1 cm long, floral bracts 5–8  $\times$  2.5–4 mm, narrowly elliptic to narrowly ovate-elliptic, subfoliaceous. **Sepals** 9–11  $\times$  3–4 mm, free, ovate to narrowly elliptic, not reflexed, hispid-velutinous, foliaceous, drying with a more or less uniform color. **Corolla** yellow to cream, hirsute outside, tube 12.5–15  $\times$  3–4 mm, lobes 10–15  $\times$  4–6 mm, obliquely obovate, free corona lobes 1.5–2.2 mm long, the apices barely exserted or included, their height equaling or slightly surpassing that of the anther apices, annular corona entire to subentire. **Anthers** 5–6 mm, the apices exserted. **Ovary** ca. 1 mm tall, nectary 1.5–2 mm, surpassing the ovary, entire to irregularly 3- or 5-lobed. **Follicles** 10–13  $\times$  8–1.4 cm, divaricate, free, the tips divergent, hispid; seeds 11–14 mm, coma 2.6–3.2 cm, cream.

**Distribution**:—Panama and Colombia. Caribbean plains, below 500 m.

**Taxonomic notes**:—*Prestonia seemannii* can be recognized by its sparsely velutinous to velutinous-tomentose leaf blade, free corona lobe apices exserted, and hispid follicles.

**Representative specimen examined:**—COLOMBIA. Magdalena: Santa Marta, s.d., *Purdie s.n.* (K).

*Prestonia tomentosa* R. Brown (1811: 70). Type:—BRAZIL. Rio de Janeiro: Rio de Janeiro, s.d., *J. Banks 684* (holotype BM!) Fig. 11.

Stem densely ferrugineous-tomentose. Petioles 0.5-1.3 cm; leaf blade  $8.5-21 \times 6-13.5$  cm, elliptic to broadly ovate, apex short-acuminate, base obtuse or rounded, membranaceous, sparsely puberulent adaxially, densely and uniformly velutinous-tomentose abaxially, tertiary veins impressed on both surfaces. Inflorescence a dichasial cyme (but resembling an umbel), axillary, shorter than the adjacent leaves, ferrugineous-tomentose or ferrugineous-tomentulose, peduncle 0.8-2.5 cm, pedicels 0.5-1.2 cm long, floral bracts  $8-19 \times 2-5$  mm, elliptic to narrowly ovate-elliptic, foliaceous. Sepals  $11-17 \times 5.5-7$  mm, free, ovate to narrowly obovate, not reflexed, tomentulose to hispid-tomentulose, foliaceous to subfoliaceous, drying with a more or less uniform color. Corolla yellow, densely sericeous outside, tube  $11-18 \times 3.5-5$  mm, lobes  $9.5-12 \times 5-7$  mm, obliquely obovate, free corona lobes 2.5-3.4 mm long, the apices exserted and conspicuously surpassing the anther apices, annular corona entire. Anthers 5-6 mm, the apices barely exserted. Ovary ca. 1.5 mm tall, nectary 1.5-2 mm, surpassing the ovary, 5-10 lobed. Follicles  $5-10 \times 1.6-2.2$  cm, divaricate, free, the tips divergent, hispid or hispidulous; seeds 8-10 mm, coma 3-4.2 cm, tannish cream.

**Distribution**:—Colombia to Bolivia, Paraguay and Brazil. Caribbean plains, Sierra Nevada de Santa Marta, Sierra de la Macarena, 300–1000 m.

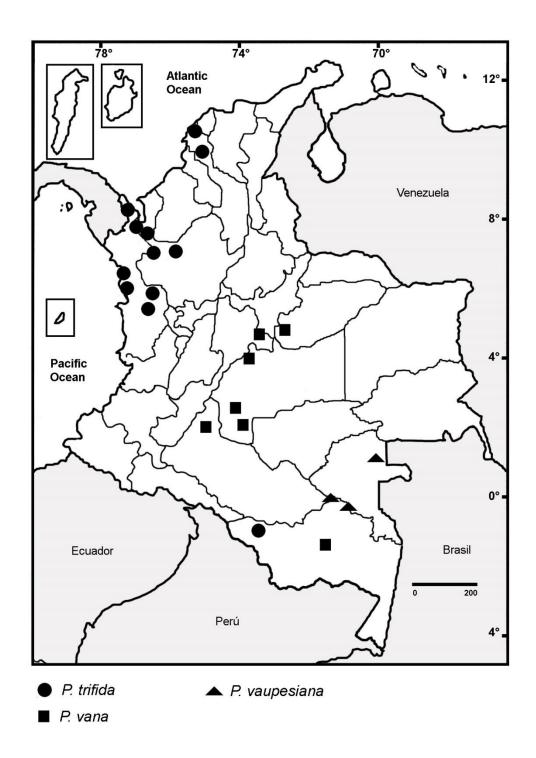
**Taxonomic notes:**—*Prestonia tomentosa* shows an overall resemblance to *P. seemannii* and *P. mexicana*; from the former it differs by its densely velutinous-tomentose

leaf blades (vs. tomentose or tomentulose), and from *P. mexicana* by its corolla tube with conspicuous corona lobes (vs. corona lobes absent). The specimens cited in Bernal *et al.* (2015) as *P. surinamensis* Müller Argoviensis (1860b: 433), actually corresponds to *P. tomentosa*. So far, *P. surinamensis* has not been collected in Colombia.

Representative specimens examined:—COLOMBIA. Antioquia: Cáceres, El Doce, Bajo Cauca, entre Quebradas Puri y Corrales, 26 March 1978, *Callejas 509* (COL, HUA, NY). Bolivar: San Pedro, 29 May 1949, *Romero-Castañeda 1770* (COL, IAN, MEDEL). Cesar: La Jagua de Ibirico, La Victoria de San Isidro, vereda el Zumbador, vía La Jagua-El Zumbador, 17 March 1996, *Fernández-Alonso et al. 13843* (COL). Guajira: Sierra Nevada de Santa Marta, Río Cañas, 19 August 1986, *Cuadros & Gentry 2948* (K, MEXU, MO, NY, USF). Meta: El Porvenir, 120 m, May 1978, *Eberhard s.n.* (USJ).

Prestonia trifida (Poeppig) Woodson (in Gleason & Smith 1933: 392). Haemadictyon trifidum Poeppig (1845: 67). Type:—PERU. Loreto: Maynas, February 1831, E. Poeppig 2161 (holotype W!, isotypes F!, NY!) Figs. 2, 12.

Stem glabrous. Petioles 1–2 cm; leaf blade  $11-25 \times 6.5-13.5$  cm, obovate to broadly elliptic, apex obtuse, retuse to acuminate, base obtuse to rounded, coriaceous to subcoriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. Inflorescence a dichasial cyme, axillary, shorter than the adjacent leaves, puberulent to glabrescent, peduncle 4-12 cm, pedicels 0.9-2.2 cm long, floral bracts  $1-3 \times 0.5-1.5$  mm, linear to linear-ovate. Sepals  $11-15 \times 3-5$  mm, free, narrowly ovate to very narrowly elliptic, not reflexed, puberulent to glabrescent, foliaceous, drying with a more or less uniform color. Corolla cream to yellowish green, glabrous, tube  $11-18 \times 3-4$  mm, lobes  $8.5-15 \times 6-9$  mm, obliquely obovate, free corona lobes 2.5-4 mm long, the apices exserted, their height slightly surpassing that of the anther apices, annular corona entire. Anthers 5-6 mm, the apices slightly exserted. Ovary ca. 1.5 mm tall, nectary 1-1.5 mm, equaling the ovary, sometimes divided into 5 lobes. Follicles  $24-40 \times 0.8-1$  cm, connate longitudinally or free but united at the tips, glabrescent; seeds 18-21 mm, coma 2.5-3.3 cm, tannish cream.



**FIGURE 12**. Distribution of *P. trifida*, *P. vana*, and *P. vaupesiana* 

**Distribution**:—Costa Rica to Peru and northwestern Brazil. Pacific, Caribbean plains, and Magdalena Valley, 0–800 m.

**Taxonomic notes**:—*Prestonia trifida* resembles *P. antioquiana*, but is distinguished by its non-verrucose petioles (vs. conspicuously verrucose) and smooth follicles (vs. 3-4-winged).

Representative specimens examined:—COLOMBIA. Antioquia: entre Villa Areteaga y Chigorodó, Lomitas, 1 October 1961, *Cuatrecasas & Willard 26110* (COL, US). Bolivar: San Juan Nepomuceno, Loma de Los Colorados, 2 September 1986, *Cuadros 3158* (COL, MO, NY, USF). Chocó: Quibdó, carretera Quibdó-Guayabal, 25 June 1985, *García 108* (CHOCO, COL, MO). Córdoba: Valencia, Alto Sinú, 3 January 1985, *Cogollo 2016* (JAUM, MO). Cundinamarca: Puerto Bogota, vereda Acapal, Línea San Carlos-Purnio, 13 December 1999, *Jiménez et al. 416* (JAUM). Santander: Andes, carretera a Puerto Nuevo y Barranca, después de La Estrella, 1 February 2000, *Vélez & Suárez 3674* (JAUM).

*Prestonia vana* Woodson (1936: 323). Type:—PERU. Loreto: Alto Amazonas, Balsapuerto, May 1933, *G. Klug 3066* (holotype MO!, isotypes F!, G!, US!) Fig. 12.

**Stem** puberulent to glabrescent. **Petioles** 1.7–2.3 cm; leaf blade 14– $21 \times 9.5$ –15 cm, elliptic to broadly elliptic, the apex obtuse and shortly acuminate, base obtuse to rounded, coriaceous to subcoriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, minutely puberulent to glabrescent, peduncle 3.2–9.5 cm, pedicels 1.3–2.4 cm long, floral bracts 3– $5 \times 1$ –1.5 mm, linear to linear-ovate. **Sepals** 10– $12 \times 3$ –4.5 mm, free, narrowly ovate to narrowly elliptic, not reflexed, puberulent to glabrescent, foliaceous, drying with a more or less uniform color. **Corolla** yellowish cream, sparsely puberulent outside, tube 15– $16 \times 3$ –4 mm, lobes 9– $10 \times 6$ –7 mm, obliquely obovate, free corona lobes 3.5–4 mm long, the apices exserted, their height surpassing that of the anther apices, annular corona entire to variously 5-lobed. **Anthers** ca. 5 mm, the apices barely exserted. **Ovary** 1.5–2 mm tall, nectary 1.7–2.1 mm, equaling or barely surpassing the ovary, 5-lobed. **Follicles** 8– $10 \times 10$ 

0.8–1.3 cm, divaricate, free, the tips divergent, conspicuously winged longitudinally, glabrescent; seeds 11–12 mm, coma 1.2–2 cm, tannish cream.

**Distribution**:—Colombia, Ecuador, and Peru. Amazon, Guyana, and Sierra de la Macarena, 150–700 m.

**Taxonomic notes**:—*Prestonia vana* can be confused with *P. trifida*, but is easily recognized by its puberulent corolla tube, and conspicuously winged follicles.

Representative specimens examined:—COLOMBIA. Amazonas: Río Caquetá, frente a Isla Yarumal, 17 May 1997, *Sánchez et al. 3065* (COAH). Boyacá: Santa María, vereda Culima, carretera Santa María-Mambita, antes del Río Chivor, 1 April 2006, *Betancur et al. 12181* (COL). Caquetá: Arbolitos, Río Caguán, 12 April 1953, *Romero-Castañeda 3972* (COL, MO). Casanare: entre Monterrey y Aguazul, 28 October 1997, *Pinto et al. 42* (COL). Meta: Cordillera La Macarena, entre Río Guejar y Caño Guayapita, 20 December 1950, *Idrobo & Schultes 824* (COL, F, MO, U, US).

*Prestonia vaupesana* Woodson (in Schultes 1957: 178). Type:—COLOMBIA. Vaupés: Apaporis river, around Cachivera de Jirijirimo, 16 September 1951, *R. Schultes & I. Cabrera 14039* (holotype MO!, isotypes COL!, US!) Fig. 12.

**Stem** glabrous to glabrescent. **Petioles** 0.5–0.7 cm; leaf blade 7.5– $12.5 \times 3.2$ –6 cm, elliptic to ovate-elliptic, acuminate to short-acuminate, base obtuse to rounded, subcoriaceous, glabrous, tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a monochasial cyme, axillary, shorter than or equaling adjacent leaves, glabrous, peduncle 7.5–15 cm, pedicels 1.4–1.6 cm long, floral bracts 1– $2 \times 0.5$ –1 mm, linear. **Sepals** 6.5– $8 \times 1$ –1.8 mm, free, narrowly elliptic, not reflexed, glabrous, scarious, drying with a more or less uniform color. **Corolla** yellowish green, glabrous outside, tube 14– $16 \times 2.5$ –3 mm, lobes 9– $10 \times 6$ –7 cm, obliquely obovate, free corona lobes 1–1.5 mm, barely included, their height conspicuously surpassed by that of the anther apices, annular corona entire. **Anthers** 5.3–5.5 mm, the apices barely exserted. **Ovary** ca. 1.5 mm tall, nectary 1.2–1.4 mm, equaling or barely shorter than the ovary, deeply 5-lobe. **Follicles** 29–10

 $32 \times 0.2$ –0.3 cm, free, but usually united at the tips, glabrous; seeds 17–19 mm, minutely and densely papillate, coma 3.5–5 cm, cream.

**Distribution**:—Colombia, Venezuela, and northern Brazil. Amazon, 150–400 m.

**Taxonomic notes**:—*Prestonia vaupesana* is vegetatively similar to *P. cayennensis*, sharing several morphological features such as glabrous leaves, inflorescence structure, and scarious bracts, but can be distinguished by its sepals 6.5–8 mm long and free corona lobes included within the tube.

Representative specimens examined:—COLOMBIA. Amazonas: La Victoria, Río Apaporis, sector cueva de Guacamaya, 18 March 2009, *Cárdenas et al.* 22007 (COAH). Vaupés: Mitú, aguas arriba del Río Vaupes, 12 November 2009, *Cárdenas & Aguirre* 24552 (COAH).

## **Excluded species**

Prestonia surinamensis Müller Argoviensis (1860b: 433) has been reported for Colombia (Morales *et al.* 2011, Morales & Morillo, 2015), but that was a misidentification of *P. tomentosa*.

### Acknowledgements

J. Francisco Morales holds a PhD research grant (Forschungsstipendien für Doktoranden und Nachwuchswissenschaftler für mehr als 6 Monate) from the Deutscher Akademischer Austauschdienst (DAAD) and their support is highly appreciated. The staff of the cited herbaria are thanked for their assistance and support. Visits to some Colombian herbaria (e.g., CAUP, COAH, COL, FMB, HUA, HUCO, HUQ, JAUM, MEDEL, TOLI, VALLE) and MO by the first author were partially financed by the University of Bayreuth Graduate School (Germany), the Deutscher Akademischer Austauschdienst (DAAD), and the Missouri Botanical Garden (MO only). The first author would like to thank Mary Endress (Z) for her valuable comments on the manuscript, and revision and improvement of the English, as well as personal support. Alvaro Idárraga (HUA), Dayron Cárdenas (COAH), Felipe Cardona (HUA), Fernando Alzate (HUA), Julio Betancur (COL), Mario Alberto

Quijano (HUCO), and Ricardo Callejas (HUA) are sincerely thanked for their assistance during field work in Colombia.

#### References

- Bentham, G. (1839-1857) Plantas hartwegianas imprimis mexicanas adjectis nonnullis grahamianus enumerat novasque describit. W. Pamplin, London, 393 pp.
- Bentham G. (1876) Apocynaceae. *In:* Bentham, G. & Hooker, J.D. (Eds.), *Genera Plantarum*, Vol. 2. Lovell Reeve & Co., Williams & Norgate, London, pp. 681–728.
- Bernal, R., Gradstein, S.R. & Celis, M. (Eds.) (2015) *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia. Available from: <a href="http://catalogoplantascolombia.unal.edu.co">http://catalogoplantascolombia.unal.edu.co</a> (accessed: 17 February 2016).
- Beurling, P.J. (1854) Primitiae Florae Portobellensis. *Kongliga Vetenskaps Academiens Handlingar* 40: 107–148.
- Brown, R. (1811) On the Asclepiadeae, a natural order of plants separated from the Apocineae of Jussieu. *Memoirs of the Wernerian Natural History Society* 1: 12–78.
- Candolle, A.P. de (1844) Apocynaceae. *In*: Candolle, A.P. de (Ed.), *Prodromus systematis naturalis regni vegetabilis*, Vol. 8. Paris, Treuttel & Würtz, pp. 317–489.
- Cárdenas, D. (2007) Vegetación y flora iniridense. *In*: Cárdenas, D. (Ed.), *Flora del escudo guayanés en Inírida (Guainía, Colombia)*. Instituto Amazónico de Investigaciones Científicas Sinchi, Bogotá, , pp. 13–118.
- Cárdenas, D., Castaño, N., Zubieta, M. & Jaramillo, M. (2008) Flora de las formaciones rocosas de la serranía de La Lindosa. Instituto Amazónico de Investigaciones Científicas Sinchi, Bogotá, 162 pp.
- Cardona, F., David, H., Gómez, H.S. & Roldán, F. (2011) Flora de Embalses, Centrales Hidroeléctricas de ISAGEN en el Oriente Antioqueño San Carlos, Jaguas y Calderas. Guía Ilustrada. ISAGEN, Universidad de Antioquia, Herbario Universidad de Antioquia, Medellín, 230 pp.
- Don, G. (1837) A general history of the dichlamydeous plants 4, J.G. & F. Rivington, London, 908 pp.

- Endress, M.E. & Bruyns P. (2000) A revised classification of the Apocynaceae s.l. *The Botanical Review (Lancaster)* 66: 1–56.
- Endress, M.E. & Hansen, B.F. (2007) *Pinochia*, a new genus of Apocynaceae, Apocynoideae from the Greater Antilles, Mexico and Central America. *Edinburgh Journal of Botany* 64: 269–274.
- Endress, M.E., Liede-Schumann, S. & Meve, U. (2014) An updated classification for Apocynaceae. *Phytotaxa* 159: 175–194.
- Forzza, R.C., Baumgratz, J.F.A., Costa, A., Hopkins, M., Leitman, P.M., Lohmann, L.G., Martinelli, G., Morin, M.P., Coelho, M.A.N., Peixoto, A.L., Pirani, J.R., Queiroz, L.P., Stehmann, J.R., Walter, B.M.T. & Zappi, D.C. (2010) *Catálogo de plantas e fungos do Brasil*. Vol. 1. Instituto de Pesquisas Jardim Botânico, Rio de Janeiro, 871 pp.
- Galindo, T., Betancur, J. & Cadena, J. (2003) Estructura y composición florística de cuatro bosque Andinos del Santuario de Flora y Fauna Guanentá-Alto río Fonce, cordillera Oriental, Colombia. *Caldasia* 25: 313–335.
- García, F., Moreno, M., Robledo, D., Mosquera, L. & Palacios, L. (2004) Composición y diversidad florística de los bosques de la cuenca hidrográfica del rió Cabí, Quibdó, Chocó. Revista Institucional Universidad Tecnológica del Chocó 20: 13–23.
- Gentry, A. (1982) Neotropical floristic diversity. *Annals of Missouri Botanical Garden* 69: 557–593.
- Gentry, A. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of Missouri Botanical Garden* 75: 1–74.
- Gleason, H.A. & Smith, A.C. (1933) Plantae Krukovianae (Concluded). *Bulletin of the Torrey Botanical Club* 60: 379–396.
- Idárraga-Piedrahita, A, Ortiz, R.D.C, Callejas, R. & Merello, M. (2011) Flora de Antioquia: Catalogo de las plantas vasculares del departamento de Antioquia. Universidad de Antioquia, Medellín, 939 pp.
- Jacquin, N.J. (1760) Enumeratio Systematica Plantarum, quas in infulis Caribaeis vicinaque Americes continente detexit novas, aut jam cognitas emendavit. T. Haak, Leiden, 41 pp.

- Linnaeus, C.f. (1781 [1782]) Supplementum Plantarum Systematis Vegetabilium Editionis Decimae Tertiae, Generum Plantarum Editionis Sextae, et Specierum Plantarum Editionis Secundae. Braunschweig, 468 pp.
- Livshultz, T., Middleton, D.J., Endress, M.E. & Williams, J.K. (2007) Phylogeny of Apocynoideae and the APSA clade (Apocynaceae s.l.). *Annals of the Missouri Botanical Garden* 94: 324–359.
- Meve, U. & Liede. S. (2004) Generic delimitations in tuberous periplocoideae (Apocynaceae) from Africa. *Annals of Botany* 93: 407–414.
- Miers, J. (1878) *On the Apocynaceae of South America*. Williams & Norgate, London, Edinburgh, 291 pp.
- Morales, J.F. (1996) Novelties in *Prestonia* (Apocynaceae). Novon 6: 285–287.
- Morales, J.F. (1997) A synopsis of the genus *Prestonia* (Apocynaceae) section Tomentosae in Mesoamerica. *Novon* 7: 59–66.
- Morales, J.F. (2004) Estudios en las Apocynaceae Neotropicales VII: Novedades taxonómicas en *Prestonia* (Apocynaceae, Apocynoideae) para Colombia y Ecuador, con comentarios sobre el grado de lobulación del nectario. *Candollea* 59: 159–165.
- Morales, J.F. (2006) Estudios en las Apocynaceae Neotropicales XXVII: lectotipificaciones misceláneas en el género *Prestonia* (Apocynoideae, Echiteae). *Brenesia* 66: 75–78.
- Morales, J.F. (2007a) Estudios en las Apocynaceae Neotropicales XXXII: tres nuevas especies de *Prestonia* (Apocynoideae, Echiteae) para Sur America. *Anales del Jardín Botánico de Madrid* 64: 147–154.
- Morales, J.F. (2007b) Estudios en las Apocynaceae Neotropicales XXXV: novedades nomenclaturales en el genero Prestonia para Brasil (Apocynoideae, Echiteae). *Darwiniana* 45: 213–217.
- Morales, J.F. (2010) Estudios en las Apocynaceae Neotropicales XL: sinopsis del género *Prestonia* (Apocynoideae, Echiteae) en Ecuador. *Anales del Jardín Botánico de Madrid* 67: 13–21.
- Morales, J.F, Merello, M. & Stevens, W.D. (2011) Apocynaceae. *In*: Idárraga-Piedrahita, A., Ortiz, R., Callejas Posada, R. & Merello, M. (Eds.) *Flora de Antioquia: Catálogo de las Plantas Vasculares*, Vol. 2. Universidad de Antioquia, Medellín, , pp. 257–268.

- Morales, J.F. & Morillo, G. (2015) Apocynaceae. *In:* Bernal, R., Gradstein, S.R. & Celis,
   M. (Eds.). *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias
   Naturales, Universidad Nacional de Colombia, Bogotá. Available from:
   <a href="http://catalogoplantascolombia.unal.edu.co">http://catalogoplantascolombia.unal.edu.co</a> (accessed: 17 February 2016)
- Morillo, G. (1978) Estudio preliminar de las especies venezolanas de *Prestonia* (Apocynaceae). *Memoria de la Sociedad de Ciencias Naturales La Salle* 110: 195–226.
- Mosquera, L.J., Robledo, D. & Asprilla, A. (2007) Diversidad florística de dos zonas de bosque tropical húmedo en el Municipio de Alto baudó, Chocó, Colombia. *Acta Biológica Colombiana* 12: 75–90.
- Müller Argoviensis, J. (1860a) Apocynaceae. *In*: Martius, C.F.P. von (Ed.), *Flora Brasiliensis* 6(1). J.G. Cottae, München, Wien, Leipzig, pp. 1–180.
- Müller Argoviensis, J. (1860b) Species novae nonnullae americanae ex Ordine Apocynearum et observations quaedam in species generis Echitis Auctorum earumque distributio in genera emendata et nova. *Linnaea* 30: 387–454.
- Pichon, M. (1951) Classification des Apocynacées XXV Echitoideés. *Mémoires du Muséum National d'Histoire Naturelle. Nouvelle Série. Série B, Botanique* 1: 1–142.
- Poeppig, E.F. (1840–1845) Nova genera ac species plantarum quas in regno chilensi peruviano et in terra amazonica annis mdcccxxvii ad mdcccxxxii legit Eduardus Poeppig et cum Stephano Endlicher descripsit iconibusque illustravit.Vol. 3. Friderici Hofmeister, Leipzig. 91 pp.
- Rusby, H.H. (1920) Descriptions of three hundred new species of South American plants, with an index to previously published South American species by the same author. H.H. Rusby. New York, 170 pp.
- Schultes, R.E. (1957) Plantae austro-americanae X: Americae Australis Plantae Novae vel Alia ratione significantes. *Botanical Museum Leaflets* 18: 113–180.
- Sessé y Lacasta, M. & Mociño, J.M. (1887 [1893]) Flora mexicana. Naturaleza (Mexico City) ser. 2, 2(App.): 25–48.
- Simões, A.O., Endress, M.E., van der Niet, T., Kinoshita, L.S. & Conti, E. (2006) Is *Mandevilla* (Apocynaceae, Mesechiteae) monophyletic? Evidence from five plastid

- DNA loci and morphology. *Annals of the Missouri Botanical Garden* 93(4): 565–591.
- Simões, A.O, Livschultz, T., Conti, E. & Endress, M.E. (2007) Phylogeny and systematics of the Rauvolfioideae (Apocynaceae) based on molecular and morphological evidence *Annals of the Missouri Botanical Garden* 97: 268–297.
- Sprengel, C.P.J. (1825) *Systema vegetabilium*, ed. 16. Librariae Dietrichianae, Göttingen, 992 pp.
- Standley, P.C. (1925) New plants from Central America IV. *Journal of the Washington Academy of Sciences* 15: 457–462.
- Thiers, B. [continuously updated]. *Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium.*Available from: http://sweetgum.nybg.org/ih (accessed: November 2015).
- Vellozo, J.M.C. (1825 [1829]) *Echites. In*: Vellozo, J.M.C. (Ed.), *Florae Fluminensis* Vol. 1. Typographia Nationali. Rio de Janeiro, pp. 109–115.
- Vellozo, J.M.C. (1827 [1831]) In Vellozo, J.M.C. (Ed.), Florae Fluminensis Icones. Senefelder. Paris. T. 25–49.
- Woodson, R.E. (1931) New or otherwise noteworthy Apocynaceae of Tropical America. Annals of the Missouri Botanical Garden 18: 541–557.
- Woodson, R.E. (1934) New or otherwise noteworthy Apocynaceae of Tropical America IV. *Annals of the Missouri Botanical Garden* 21: 613–623.
- Woodson, R.E. (1936) Studies in the Apocynaceae. IV. The American genera of Echitoideae. *Annals of the Missouri Botanical Garden* 23: 169–438.
- Woodson, R.E. (1948) Miscellaneous new Apocynaceae and Asclepiadaceae. *Annals of the Missouri Botanical Garden* 35: 233–238.

# **Publication 2**

Morales, J.F., M. Endress & S. Liede-Schumann. Sex, drugs and pupusas: Disentangling relationships in Echiteae (Apocynaceae)

(accepted: Taxon, reference number D-16-00180R2)

## Sex, drugs and pupusas: Disentangling relationships in Echiteae (Apocynaceae)

- J. Francisco Morales, <sup>1</sup> Mary Endress <sup>2</sup> & Sigrid Liede-Schumann <sup>1</sup>
- 1 Department of Plant Systematics, University of Bayreuth, Universitätstrasse 30, 95440 Bayreuth, Germany
- 2 Institute of Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, 8008 Zürich, Switzerland

Author for correspondence: J. Francisco Morales, drjfranciscomorales@gmail.com

### **Abstract**

Echiteae (Apocynaceae) comprises about 200 species divided among 19 genera, 16 of which are restricted to the Neotropics, the other three to the Paleotropics. There are two large genera, *Prestonia* and *Parsonsia* in the Neotropics and Paleotropics, respectively, whereas three-fourths of the genera contain only 1–4 species. In this study DNA of 82 species was extracted and amplified for four molecular markers: three plastid (*trnL* intron and *trnL-trnF* intergenic spacer, *rpl16* intron, *matK* and 3'/5' *trnK* intron) and the nuclear ribosomal region ITS. The ingroup comprised 70 species from 17 genera in the tribe, and included representatives of all subtribes; the outgroup included five species each from the two putatively most closely related tribes, Odontadenieae and Mesechiteae, as well as two rooting species. Phylogenetic analyses were conducted using Bayesian inference and maximum likelihood approaches. Echiteae and four of its subtribes (Echitinae, Parsonsiinae, Peltastinae and Prestoniinae) as currently circumscribed were shown to be non-monophyletic. The fifth subtribe, Pentalinoninae, though monophyletic, does not belong to Echiteae; it was resolved as sister to a clade of Odontadenieae, where it fits better, since in both the characteristic secondary compounds are cardenolides. *Prestonia* 

75

and *Temnadenia* were resolved as polyphyletic, with *P. riedelii* grouped with *Rhodocalyx* and *T. ornata* nested within *Prestonia*. *Fernaldia* is nested within *Echites* and *Peltastes* is nested in *Macropharynx*. Fourteen genera are maintained. The new subtribe Laubertinae is proposed, as are the combinations resulting from the merging of *Fernaldia* and *Peltastes* and the transfer of *P. riedelii* and *T. ornata* to *Rhodocalyx* and *Prestonia*, respectively. In the ancestors of Echiteae, we hypothesize that an evolutionary shift took place in which steroidal alkaloids and/or cardenolides, characteristic for apocynoids, were replaced by parsonsine type pyrrolizidine alkaloids as the predominant defense compounds.

**Keywords** apocynoids; molecular phylogeny; *Parsonsia*; *Prestonia*; pyrrolizidine alkaloids; systematics

## **Supplementary material**

### **INTRODUCTION**

Apocynaceae is one of the ten largest plant families (Rapini, 2012), with about 366 genera and 3700 species distributed throughout the tropics, subtropics, and temperate regions (Endress & al., 2014; Morales & Liede-Schumann, 2016). The family is well known to be rich in toxic bioactive secondary metabolites. Probably the best known are the complex indole alkaloids, found in several tribes of the rauvolfioids, which have diversified into a vast array of types (Bisset, 1958, 1961; Hegnauer, 1989; Kisakürek & al., 1983), and are widely used in traditional medicine around the world (Schultes, 1979; van Beck & al., 1984; Bisset, 1989; Hutchings, 1989; Wong & al., 2013). In the rest of the family, in contrast, indole alkaloids are absent, having been replaced mainly by steroidal alkaloids and cardenolides (Hegnauer, 1970; Endress & al., 1990, Endress & Bruyns, 2000). A much rarer type of secondary compound are the pyrrolizidine alkaloids (PAs), which have evolved independently in twelve angiosperm families (Burzynski & al., 2015). More than 95% of all PA-containing species are found in four families: Asteraceae, Boraginaceae, Fabaceae and Orchidaceae (Ober & Hartmann, 2000). In Apocynaceae, PAs are known only from apocynoids, where they have been indicated in eleven genera from four tribes: Nerieae (one genus), Malouetieae (one genus), Apocyneae (two genera) and Echiteae (seven genera) (Brown, 1987; Hernández-Baz & al., 2013; Burzynski & al., 2015). In all but two genera, they are in the form of 1,2-dehydropyrrolizidine alkaloids (dehydroPAs in the terminology of Colegate & al., 2016).

Toxic secondary metabolites in plants have arisen as a means of phytochemical protection for the plant against herbivores (e.g., Reimann & al., 2004). However, certain groups of insects have a close association with poisonous plants, and in an evolutionary arms race have become adapted to the toxins, allowing insects to sequester and utilize them to their own advantage against predators (e.g., Orr & al., 1996; Trigo, 2000; Nishida, 2002; Despres & al., 2007). A well known example is that of the iconic monarch butterfly, *Danaus plexippus* L. (Nyphalidae-Danainae), the larvae of which feed on various species of *Asclepias* L. (Asclepiadoideae-Asclepiadeae) and sequester cardenolides, which causes the adults to be unpalatable (Malcolm & Brower, 1989). Similarly, insects adapted to PAs belong to such diverse groups as beetles, grasshoppers and butterflies and moths. In Apocynaceae PA-containing plants have evolved complex associations with two groups of Lepidoptera: danaid butterflies and arctiid moths (Brown, 1984; Edgar, 1984; Nishida, 2002; Bowers, 2009).

PA-containing plants also figure prominently as contaminants causing disease in both grazing animals and humans (Edgar & al., 2015). In non-adapted vertebrates, PAs are slow-acting toxins that over time can lead to debilitating chronic medical conditions. In tropical countries, where Apocynaceae often figure prominently in traditional medicine, human ingestion most likely occurs when a PA-containing plant is used in herbal medicines, as reported by Colegate & al. (2016) for *Alafia* Thouars and *Amphineurion* (A. DC.) Pichon, two PA-containing apocynoids that are used to treat a wide range of ailments.

Since the reamalgamation of Apocynaceae and Asclepiadaceae by Endress & Bruyns (2000), two subsequent updates with several changes and improvements to the original classification have been made (Endress & al., 2007b, 2014). However, intertribal relationships and composition of several tribes and subtribes are still uncertain. Endress & Bruyns (2000) proposed five subfamilies (Rauvolfioideae, Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadaceae), of which Apocynoideae and Rauvolfioideae remain paraphyletic. In order to avoid the stigmatism of non-monophyly, Simões & al. (2016)

proposed treating the two subfamilies informally as the apocynoid and rauvolfioid grade, respectively. In this paper we refer to them simply as apocynoids and rauvolfioids.

Bentham (1876) was the first to propose the tribe "Echitideae", which, however, corresponded to the whole of the apocynoids. He recognized five subtribes: Parsonsieae, Nerieae, Ecdysanthereae, Ichnocarpeae, and Euchitideae. Schumann (1895) followed almost the same classification, but named the group "Echitoideae-Echitideae". During that time and in subsequent decades, the taxonomy of neotropical genera, in particular, was confused, in large part due to the work of Miers (1878). Woodson (e.g., 1933, 1935, 1936) clarified the prevailing confusion in the Echitoideae (= apocynoids), publishing monographs for almost all neotropical genera and proposing many synonyms. However, his work focused mainly on taxonomy at the species level, and only superficially addressed intergeneric classification. Pichon (1950a) proposed an expanded Echitoideae, dividing it into four tribes (Ecdysanthereae, Ichnocarpeae, Nerieae, Parsonsieae). His circumscription, however, was paraphyletic (e.g., Livshultz & al., 2007; Endress & al., 2014), with genera included in other tribes of the current apocynoids (e.g., Apocyneae, Malouetieae). The classification of Leeuwenberg (1994) followed that of Pichon very closely in some parts, except that genera that had since been put into synonymy were absent and newly described genera were added. Furthermore, Leeuwenberg (1994) applied the priority rule to suprageneric ranks, thereby changing a number of names. Thus Echitoideae became Apocynoideae. In Apocynoideae Leeuwenberg accepted three tribes: Echiteae, Wrightieae, and Apocyneae. Echiteae was further divided into three subtribes: Echitinae (which was very similar in composition to Pichon's Parsonsieae (Pichon, 1950a), but excluding subtribes Parsonsiinae and Pachypodiinae), Parsoniinae (which corresponded for the most part with Pichon's Parsonsieae-Parsonsiinae and Nerieae-Amphineuriinae) Pachypodiinae (which in both Pichon's and Leewenberg's classifications included only Pachypodium Lindl.). Thus in the 1990's, several classification proposals for the Echiteae were available (Table 1), but genera were delimited only by morphological characters, some of which are almost impossible to determine accurately (i.e., Pichon's "retinacle" (Pichon, 1948)), but none were supported by molecular data. In the classification by Endress & Bruyns (2000) Apocynoideae was divided into five tribes: Wrightieae, Malouetieae, Apocyneae, Mesechiteae, and Echiteae, without any further divisions into subtribes; Echiteae included 22 genera (Table 1).

Table 1. Genera of Echiteae their tribal and subtribal position in five major classifications

	Pichon	Leeuwenberg (1994)	Endress & Bryuns (2000)	Endress & al. (2007)	Endress & al. (2014)	
	(1950a)	(1))+)	Bryuns (2000)	(2007)		
Angadenia Miers	Parsonsieae , Urechitinae	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Pentalinoninae	
Artia Guillaumin	Parsonsieae , Parsonsiinae	Echiteae, Parsoniinae	Echiteae	Echiteae	Echiteae, Parsonsiinae	
Asketanthera Woodson	Parsonsieae , Prestoniinae	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Peltastinae	
Bahiella J. F. Morales	-	-	-	Echiteae	Echiteae, Echitinae	
Echites P. Browne	Parsonsieae , Chonemorphinae	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Echitinae	
Ecua Middleton	-	-	Echiteae	Echiteae	Echiteae, Parsonsiinae	
Fernaldia Woodson	Parsonsieae , Prestoniinae ,	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Echitinae	
Hylaea J.F. Morales	-	-	Echiteae	Echiteae	Echiteae, Prestoninae	
Laubertia A. DC.	Parsonsieae , Prestoniinae	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Prestoninae	
Macropharynx Rusby	Parsonsieae , Prestoniinae	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Peltastinae	
Parsonsia R. Br.	Parsonsieae , Parsonsiinae	Echiteae, Parsoniinae	Echiteae	Echiteae	Echiteae, Parsonsiinae	
Peltastes Woodson	Parsonsieae , Peltastinae	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Peltastinae	
Pentalinon Voigt	Parsonsieae , Urechitinae	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Pentalinoninae	
Prestonia R. Br.	Parsonsieae , Prestoniinae	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Prestoninae	
Rhodocalyx Müll. Arg.	Parsonsieae , Prestoniinae	Echiteae, Echitinae		Echiteae	Echiteae, Prestoninae	
Salpinctes Woodson		Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Pentalinoninae	
Temnadenia Miers	Parsonsieae , Prestoniinae	Echiteae, Echitinae	Echiteae	Echiteae	Echiteae, Peltastinae	
Thenardia Kunth	Parsonsieae , Parsonsiinae	Echiteae, Parsoniinae	Echiteae	Echiteae	Echiteae, Parsonsiinae	
Thoreauea J.K. Williams	-	-	-	Echiteae	Echiteae, Parsonsiinae	

Blank space = not recognized or studied by author; – = not described at the time of the study.

One of the earliest molecular-based studies to include genera of Echiteae sensu Endress & Bruyns (2000) was the family-wide analysis of Potgieter & Albert (2001) based on *trn*L intron and *trn*L-F spacer sequences. This phylogeny included five representatives

of Echiteae, which formed a well-supported, but unresolved clade. A year later Sennblad & Bremer (2002) published a broadscale study of the family based on *rbc*L, which included three genera of Echiteae grouped in a weakly supported polytomy together with all included species of Periplocoideae.

The first phylogenetic study to include a more extensive sampling of Echiteae, which were evaluated in a broad context, was the molecular-based analysis of apocynoids and the APSA clade (comprising apocynoids, Periplocoideae, Secamonoideae and Asclepiadoideae) by Livshultz & al. (2007), which was based on four plastid regions (trnL intron and trnL-trnF spacer, rps16 intron, rpl16 intron and matK and 3' trnK intron) and included at least one species each of 17 of the 22 genera included in Echiteae by Endress & Bruyns (2000). Missing were Asketanthera Woodson, Ecua Middleton, Hylaea J.F. Morales, Macropharynx Rusby and Thenardia Kunth. Three additional genera were included to determine whether they deserved generic recognition: Allotoonia J.F. Morales & J.K. Williams, Rhodocalyx Müll. Arg. and Salpinctes Woodson. The first had been described to accommodate a group of species previously treated in Echites P. Brown (Morales & Williams, 2004), whereas Rhodocalyx had been reduced to the synonymy of Prestonia R. Br. by Morales (1999a). Finally, the rare, monotypic Salpinctes had been reduced to the synonymy of Mandevilla Lindl. by Morales (1998).

The phylogenetic study by Livshultz & al. (2007) showed that Echiteae sensu Endress & Bruyns (2000) was paraphyletic, with the members distributed in several clades, some of them quite disparate. Most of the species were grouped in the New World clade, with the exception of the three included species of *Rhabdadenia* Müll. Arg., which formed a strongly supported clade sister to the New World clade, but this without support. The New World clade was split into two main clades. One was optimally supported and represented the core Echiteae; the other was not supported and consisted of three clades, all without support. Overall, this study suggested that some of the taxonomic proposals of Endress & Bruyns (2000) should be studied further and additional molecular data would be necessary to properly define the limits of some tribes (e.g., Echiteae), since larger samplings have been shown to improve phylogenetic resolution (e.g., Graybeal, 1998; Rannala & al., 1998). The most important results for Echiteae were the implied exclusion of five genera (*Amalocalyx* Pierre, *Cycladenia* Benth., *Neobracea* Britton, *Pottsia* Hook. &

Arn. and *Stipecoma* Müll. Arg.), recognition of *Rhodocalyx* and *Salpinctes*, and the reduction of *Allotoonia* into the synonymy of *Echites*. Furthermore, there were implications that *Prestonia* as currently delimited is most likely not monophyletic, and that *Fernaldia* Woodson could be part of *Echites*. However, given the need for a more comprehensive sampling, no further changes were proposed at the time.

Based primarily on the results of Livshultz & al. (2007), the classification by Endress & al. (2007) recognized three new tribes in their Apocynoideae: Nerieae, Odontadenieae and Baisseeae, bringing the total number of tribes in the subfamily to eight. In addition, five genera were excluded from the Echiteae and transferred to other tribes. Furthermore, *Rhodocalyx* was again recognized as a valid genus, and the recently described genera *Thoreauea* J.K. Williams (Williams, 2002) and *Bahiella* J.F. Morales (Morales, 2006a) were added. Echiteae was thus reduced to a group of 20 genera, of which at least one (*Prestonia*) was implied to be paraphyletic.

Although great strides have been made in clarifying relationships within the apocynoids, the great majority of molecular studies to date have been based on plastid sequences alone. Two molecular analyses have been published using *phytochrome* A: Livshultz & al. (2010) and Middleton & Livshultz (2012), both of which combined sequences of *phytochrome* A with those from the same four plastid regions as in Livshultz & al., 2007. Only the first, which attempted to pinpoint the position of the milkweeds (Secamonoideae + Asclepiadoideae) in the APSA clade, and which included ten genera of Echiteae, mainly to orient the phylogeny, is pertinent to our study. The included species of Echiteae formed an unsupported clade, comprised of two maximally supported clades: one comprising *Pentalinon* Voigt and *Angadenia* Miers, and the other the remaining eight genera of the core Echiteae. The results supported those of Livshultz & al. (2007); but, the small number of Echiteae included precluded any further elucidation within the tribe. Since then, no phylogenetic studies involving Echiteae have been published.

Endress & al. (2014) published the most recent classification proposal for Apocynaceae. In it Apocynoideae were divided into nine tribes, four of which (Nerieae, Malouetieae, Echiteae, Apocyneae) were further divided into subtribes. The composition of Echiteae was the same as in Endress & al., 2007, except that *Rhabdadenia* was included in a tribe of its own. The remaining 19 genera were divided into five subtribes (Table 1).

In this paper we present the first molecular phylogeny focusing on Echiteae based on sequence data from the internal transcribed spacer (ITS) from the nuclear ribosomal DNA (nrDNA) and three plastid DNA (cpDNA) regions (*trnL* intron and *trnL-trnF* intergenic spacer, *rpl16* intron, *matK* and 3'/5' *trnK* intron). The main objectives of the study are: (1) to test the monophyly of the tribe Echiteae and its subtribes sensu Endress & al. (2014), (2) to assess the monophyly of its genera as currently delimited, (3) to provide a more accurate hypothesis of the relationships among its genera, (4) to provide taxonomic and nomenclatural changes as needed, and (5) to compare reports of PAs to our phylogeny to determine if there is a meaningful pattern in their distribution.

#### MATERIALS AND METHODS

**Taxon sampling.** — Seventy species, including representatives of 17 of the 19 genera and from the five subtribes currently recognized in Echiteae by Endress & al. (2014) were defined as the ingroup. Five genera (Asketanthera, Hylaea, Macropharynx, Thenardia and Thoreauea) were included in a molecular analysis here for the first time. The two missing genera are Ecua and Bahiella. The first is monospecific and endemic to eastern Indonesia. It is known from only two older collections (Middleton, 1996), and although we tried several times to extract DNA from one of the herbarium specimens, we were never able to get a positive PCR reaction. Bahiella comprises two species and is endemic to northeastern Brazil (Morales, 2006a). As in Ecua, due to its rarity, we had to resort to extracting DNA from herbarium material. Only partial sequences were obtained for the cpDNA regions, and ITS sequences were incomplete and with many gaps, which led to incongruence among the datasets. Therefore, we chose to exclude these two genera from the study. The number of included species compared to the total number of species currently recognized in each genus is as follows: Angadenia (2/3), Artia Guillaumin (2/4), Asketanthera (2/4), Echites (9/10), Fernaldia (3/3), Hylaea (1/2), Laubertia A. DC.(3/4), Macropharynx (4/5), Parsonsia R. Br. (8/ca. 82), Peltastes Woodson (8/10), Pentalinon (2/2), Prestonia (16/ca. 58), Rhodocalyx (1/1), Salpinctes (1/1), Temnadenia Miers (3/4), Thenardia Kunth (3/3) and Thoreauea (2/3) (Table 2). Ten species of seven genera from two different tribes were selected as the outgroup, based on the results of previous analyses (Livshultz & al., 2007, 2010): Odontadenia Benth., Pinochia B.F. Hansen & M.E. Endress, Secondatia A. DC., and Thyrsanthella (Baill.) Pichon (Odontadenieae), and Allomarkgrafia Woodson, Elytropus Müll. Arg. and Mandevilla (Mesechiteae). Finally, two species of Rhabdadenia (Rhabdadenieae) were used to root the tree. Specimens for this study were collected mainly by the first author; others were provided by colleagues (see Acknowledgments). Leaf tissue was preserved using silica gel and then refrigerated at -20 °C. In species for which fresh material was not available, DNA was extracted from leaf fragments from dried herbarium specimens deposited at CR (formerly INB) or Z. For Hylaea arborescens (Monach.) J.F. Morales, instead of leaf fragments from herbarium specimens, flower buds were used. We found when using samples from herbarium specimens that addition of a small amount of alcohol for preservation at the time of collection or the high heat during drying tended to affect leaves more strongly than buds and flowers. When it was not possible to get usable DNA out of leaves, it sometimes worked with flowers and buds. We assume this is because the inflorescence is a more compact (thicker) mass than the leaves, so that the alcohol/heat was less likely to penetrate to all buds and flowers. In general, all new sequences for each species were obtained from the same specimen. However, for several of the sequences available from GenBank a different specimen was used (mostly to obtain ITS). We were unable to get positive PCR reactions from Temnadenia stenantha Woodson and T. meyeri C. Ezcurra, although we made extractions of all available specimens. Taxa sampled, voucher information and GenBank accession numbers are given in Appendix 1.

DNA extraction, amplification, sequencing and alignment. — Total genomic DNA was extracted from silica gel-dried leaf material, from herbarium specimens or from flower buds using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany), following the manufacturer's instructions. In order to improve the extraction of DNA, 5 µL of maturase K was included in every sample during the lysis process. Additional modifications for samples from herbarium specimens included incubation for 60 min during lyses (mixing every 10 min) and incubation for 20 min on ice after adding the AP3 buffer to the lysate mix.

**Table 2**. Genera and species of Echiteae sampled in three phylogenetic studies

Genera	Species	Livshultz et al. 2007	Livshultz 2010	This study
Angadenia	3	2	2	2
Artia	4	1	1	2
Asketanthera	4	-	-	2
Bahiella	2	-	-	-
Есиа	1	-	-	-
Echites	10	4	2	9
Fernaldia	3	1	-	3
Hylaea	2	-	-	1
Laubertia	4	1	1	3
Macropharynx	5	-	-	4
Parsonsia	ca. 82	8	1	8
Peltastes	10	-	2	8
Pentalinon	2	1	1	2
Prestonia	ca. 56	8	2	16
Rhodocalyx	1	1	1	1
Salpinctes	1	1	-	1
Temnadenia	4	2	2	3
Thenardia	3	-	-	3
Thoreauea	3	-	-	2

The three cpDNA regions were sequenced using published primers: trnL intron and trnL-trnF intergenic spacer (trnL c, trnF f [Taberlet & al., 1991]), rpl16 intron (rpl16 F71, rpl16 R1516 [Baum & al., 1998]) and matK and 5'/3' trnK intron (matK 503F, 503R, 681F, trnk 3914F, trnk 2R [Endress & al., 1996]; matK 390F [Bafeel & al., 2011]). The primers ITS4 (White & al., 1990) and ITS5m (Sang & al., 1995) were used to amplify ITS. The amplification of the complete sequence of matK and trnK intron was made in two parts, through the combination of one trnK primer (F or R) with one matK primer (R or F), respectively.

Amplification of the cpDNA regions was conducted in a volume of 25  $\mu$ L containing 2.5 mM MgCl<sub>2</sub>, 0.2 mM dNTPs, 0.25  $\mu$ M of each primer (forward and reverse), 10 mM Tris-HCL (pH 8.6 at 25°C), 50 mM KCl, 5  $\mu$ g/mL BSA, 0.15 U Taq polymerase, and 1  $\mu$ L of unquantified DNA, sometimes diluted up to 10-fold or 100-fold. In samples of *Peltastes* and *Macropharynx*, the DNA was diluted up to 200-fold, because 10-fold or 100-

fold dilutions yielded negative results. In DNA extracts from herbarium specimens or with weak PCR products, the concentration of the components was modified as follows: 3 mM MgCl<sub>2</sub>, 1 mM dNTPs, 0.5 μM of each primer, 8 μg/mL BSA, and 0.3 U Taq polymerase. The thermocycler protocol used consisted of 3 min at 94°C (4 min for *matK-trnK* intron), followed by 30 cycles of 1 min at 93°C (35 cycles for *matK-trnK* intron), 1 min at 58°C (*trnL* intron and *trnL-trnF*, *rpl* 16) or 55°C (*matK-trnK* intron), 2 min at 72°C, and 7 min at 72°C (*matK-trnK* intron).

Amplification of ITS was carried out in a volume of 25 μL containing 0.2 mM dNTPs, 0.18 μM of each primer (forward and reverse), 10mM Tris-HCL, 50 nM KCl, 5 μl Q-solution, 0.15 U Taq polymerase, and 1 μL of unquantified DNA (undiluted). For weak PCR products, the concentration was modified as follows: 0.25 mM dNTPs, 0.2 μM of each primer (forward and reverse), 10 μl Q-solution, and 0.3 U Taq polymerase. The cycling program included an initial denaturing cycle at 94°C for 3 min, followed by 30 cycles of 94°C for 1 min, 55°C for 1 min, 72°C for 3 min, and a final extension of 72°C for 5 min.

PCR amplifications were performed in a Biometra T-Personal Thermocycler and PCR products were visualized with electrophoresis on 2% agarose gels. Sequence contigs were built with Codon Aligner v. 3.7.1 and v. 6.0.2 (CodonCode Corp., Centerville, Massachusetts, U.S.A.).

Sequences were prealigned in MAFFT v.7 (Katoh, 2013), followed by manual adjustments in Mesquite v. 2.71 (Maddison & Maddison, 2011). Alignment of the *matK* and 5'/3' trnK intron, trnL intron and trnL-trnF intergenic spacer was relatively easy and straightforward, whereas for the rpl16 intron it was more difficult, due the presence of homopolymers and gaps in several sections. Alignment of ITS proved to be the most difficult, due to the irregular sequences and gaps in the ITS1 and ITS2 regions. Terminal regions in the alignment that appeared ambiguous were excluded from the analyses.

**Phylogenetic analyses.** — Six data matrices were analyzed: (1) *trnL* intron and *trnL-trnF* intergenic spacer; (2) *rpl16* intron; (3) *matK* and 5'/3' *trnK* intron; (4) combined plastid (matrices 1—3 combined); (5) ITS; (6) combined molecular (matrices 4 and 5 combined). Because simultaneous analysis of combined data has been proposed as the best approach to phylogenetic inference (Nixon & Carpenter, 1996), we tested the combinability

of all partitions by searching for incongruence between individual data sets. For this, we compared the results on a node-to-node basis of all individual data sets with respect to levels of resolution and bootstrap support, as applied by other authors (e.g., Wiens, 1998; Sheahan & Chase, 2000; Whitten & al., 2000; Reeves & al., 2001). Serious conflict was assumed when deviant tree topologies were supported by ≥70% bootstrap (BS) values and ≥95% posterior probabilities (PP). No strongly supported incongruent clades were found between three individual partitions of the plastid data, and thus they were combined (combined plastid matrix). Incongruence was also not found between the combined plastid matrix and ITS matrix, and therefore they were combined in a single matrix (combined molecular matrix). In all analyses, ITS was divided into 5 partitions. Individual as well as combined matrices were analyzed using maximum likelihood (ML); for the combined plastid, ITS and combined molecular matrices Bayesian inference (BI) was also utilized. All individual and combined data matrices and generated trees are deposited in TreeBASE (accession number 19847).

Maximum-likelihood analyses were performed using RAxML version 8.2.8 (Stamatakis, 2006, Stamatakis & al., 2008), as implemented in CIPRES version 3.3 (Miller & al., 2010). The non-bootstrap analysis and tree search was set to 1000 replicates. The output tree files in graphic format with the bootstrap values were generated using Figtree (Rambaut, 2014). Bootstrap support value was interpreted as follows: 50%-74% as weak, 76%-89% as moderate, and  $\geq$  90% as strongly supported. BI analyses were conducted using MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), applying separate models to each data partition, with unlinked partitions, and parameters estimated independently. The optimal model of sequence evolution was selected using Modeltest v.2.1.1 (Darriba & al., 2012) applying the Bayesian information criterion (BIC). The analysis was allowed to run for 100 million generations, sampling every 10,000 generations, until an average standard deviation of split frequencies  $\leq 0.01$  was reached. Two independent runs starting from different random trees were performed in order to test convergence of the same result. The first 25% of the trees were considered as burn-in and discarded from subsequent analyses, before calculating a majority-rule consensus of the remaining 7500 posterior distribution trees using the sumt function. Burn-in values, adequate mixing of the MCMC chains, and independent tree sampling were determined through inspections of the MCMC samples employing Tracer v.1.5 (Rambaut & Drummond, 2007a). The 50% majority-rule consensus tree was reconstructed from the post burn-in trees with Tree Annotator v.1.5.4 (Rambaut & Drummond, 2007b) and edited in Figtree v.1.4.2. (Rambaut, 2014). Posterior probability values  $\geq 0.95$  were considered as strongly supported.

### **RESULTS**

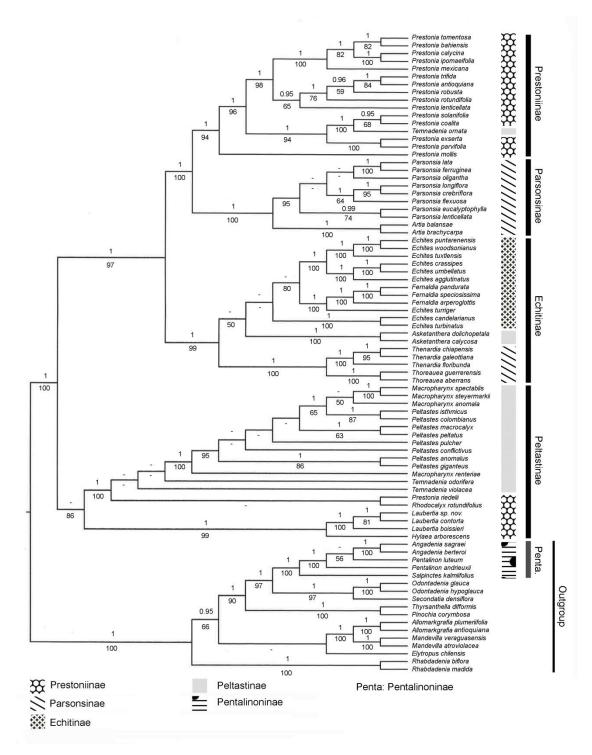
Sequence characteristics and tree statistics are given in Table 3. For all species, the complete set of partial or complete sequences studied was obtained, with the following exceptions: ITS was not obtained for *Parsonsia flexuosa* Baill. and *P. lata* Markgr. This was not expected to affect the results of the combined analysis (Wiens, 2003). A total of 408 sequences were used in this study, of which 344 were newly generated; another 64 were obtained from GenBank. Some sequences already available in Genbank were sequenced again in order to confirm some discrepancies or complete missing sections near the ends. Taxa sampled, voucher information and GenBank accession numbers are given in Appendix 1.

The model TVM+g was selected for *matK* and model GTR + g was selected for ITS, *rpl16* intron, *trnL* intron and *trnL-trnF* intergenic spacer and 5'/3' *trnK* intronF. The main clades resolved in the combined plastid dataset (Fig. 1) were recovered in the nuclear data set (Fig. 2), but there were three minor incongruences in terminal clades. The first concerns two species of *Parsonsia* (*P. eucalyptophylla* F. Muell. and *P. lenticellata* C.T. White). In the cpDNA tree they are resolved as sisters in a weakly supported clade, whereas the other species in the genus are grouped in an unsupported clade; in the nrDNA tree, however, *P. eucalyptophylla* and *P. lenticellata* are in different clades. We were unable to obtain the complete set of ITS sequences for *Parsonsia*, and assume that this is probably affecting the resolution between the trees. The second concerns *Macropharynx* and *Peltastes*. Although the clade is strongly supported in both the cpDNA and nrDNA trees, the position of both genera vary within the clade, but with only weak or no support. In the cpDNA tree three species of *Macropharynx* are nested in a clade within *Peltastes*, whereas the fourth species, *M. renteriae*, is resolved as sister to the rest of the clade. In the nrDNA

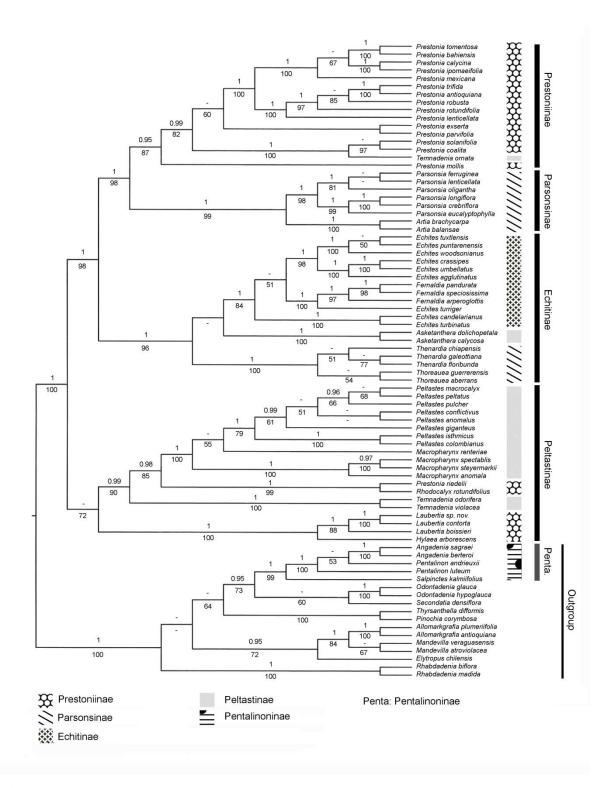
tree the same three species of *Macropharynx* are retrieved in a clade that is sister to a clade in which *M. renteriae* is sister to all species of *Peltastes*. The sequences of all the species in this clade show little variation in all the markers. The last minor incongruence refers to the clade containing *Prestonia coalita* (Vell.) Woodson and the clade containing *P. exserta* (A. DC.) Standl. In the cpDNA tree both clades are grouped in one highly supported clade, but in the nrDNA tree, *P. exserta* is resolved as sister to the clade containing *P. coalita*, but this position is only weakly supported. With the exception of these three minor incongruences, no strongly supported incongruent clades were found between the nrDNA and cpDNA data matrices; therefore, all partitions were combined in a single matrix (combined molecular). The ML tree from the combined molecular dataset was congruent with the BI topology. All further discussion will be based on the majority rule consensus cladogram resulting from the BI analysis of the combined molecular dataset (Fig. 3).

Table 3. Summary statistics of data sets

Locus	Number of taxa	Total length (bp)	Variant characters (n)	Parsimony- informative characters (n)	CI	RI
trnL intron and trnL-trnF intergenic spacer	82	1055	213	106 (10.04%)	0.670	0.882
rpl16 intron	82	1272	401	232 (18.23%)	0.658	0.879
<i>matK</i> /5'/ 3' <i>trnK</i> intron	82	2580	651	367 (14.22%)	0.654	0.883
chloroplast combined	82	4907	1265	705 (14.36%)	0.647	0.876
ITS	80	853	521	454 (53.22%)	0.430	0.751
ITS and chloroplast combined	82	5760	1786	1159 (20.12%)	0.511	0.804



**Fig. 1**. Maximum likelihood consensus tree based on the cpDNA dataset (*trnLF*; *rpl16*; *matK-trnK* intron). Posterior probabilities are indicated above each branch and maximum likelihood bootstrap support below. Bootstrap values < 50% are indicated by a dash (-).



**Fig. 2.** Maximum likelihood consensus tree based on nrDNA (ITS) dataset. Posterior probabilities are indicated above each branch and maximum likelihood bootstrap support below. Bootstrap values < 50% are indicated by a dash (-).

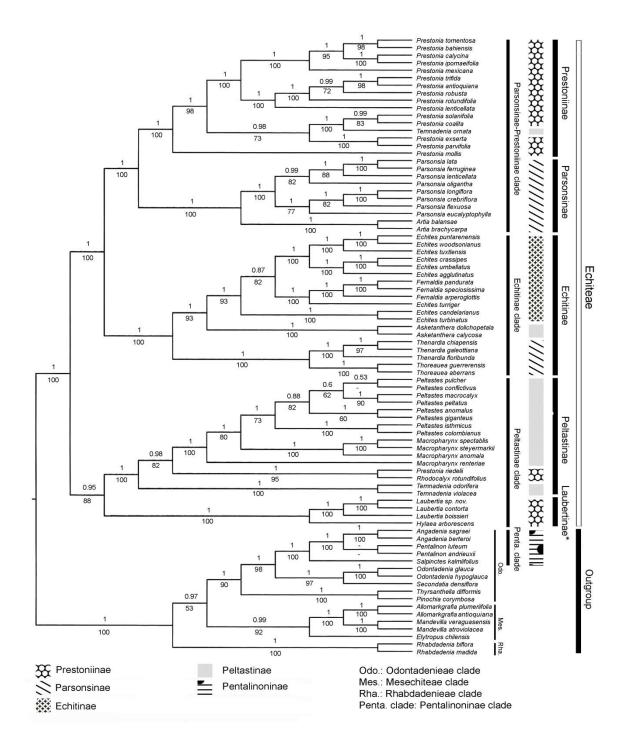


Fig 3. Maximum likelihood consensus tree based on the cpDNA (trnLF; rpl16; matK-trnK intron) and nrDNA (ITS) dataset. Beginning from inside and moving outwards, clade names within the outgroup are indicated by thin black lines in the innermost column, and clade names within the ingroup are in the second column, subtribes in the Endress & al. (2014) classification are shown by patterns in the third column, the new subtribal classification proposed here is indicated by thicker black bars in the fourth column and the delimitation of the tribe Echiteae and the outgroup in the outermost column. Posterior probabilities are indicated above each branch and maximum likelihood bootstrap support (> 50%) below. Bootstrap values < 50% are indicated by a dash (-).

Echiteae (sensu Endress & al. (2014)) was shown to be non-monophyletic, since the clade of the three genera comprising their subtribe Pentalinoninae (*Angadenia*, *Pentalinon* and *Salpinctes*), although strongly supported (1/100), is nested within the outgroup, in a clade (1/90) comprising four genera (*Odontadenia*, *Pinochia*, *Secondatia*, *Thyrsanthella*) of the tribe Odontadeniae (Endress & al., 2014). The other four subtribes of Echiteae defined by Endress & al. (2014) – Echitinae, Parsonsiinae, Peltastinae, Prestoniinae – were all found to be polyphyletic.

Of the seventeen genera included in this study that were recognized in the tribe by Endress & al. (2014), monophyly could not be assessed for three either because they are monospecific (Rhodocalyx, Salpinctes) or because we were only able to obtain PCR products from one species (Hylaea). Of the remaining 14 genera, seven were found to be monophyletic with high (1/97-100) support (Angadenia, Artia, Asketanthera, Laubertia, Parsonsia, Thenardia and Thoreauea). Pentalinon was retrieved as monophyletic in the combined tree but without support. In the cpDNA and nrDNA trees it was resolved as paraphyletic, with one species in a sister relationship with the two species of Angadenia and the other as sister to this. The other six genera were resolved as para- or polyphyletic. Temnadenia is polyphyletic, with species sister two as Macropharynx/Peltastes/Prestonia riedelii (Müll. Arg.) Markgr./Rhodocalyx, and one strongly supported (1/100) as sister to two species of *Prestonia*. *Peltastes* is nested within Macropharynx in a clade with strong support (1/100), rendering both genera nonmonophyletic. Fernaldia is nested within Echites and resolved as sister to E. turriger Woodson with strong support (1/100), and, as a consequence, is not monophyletic. Finally, Prestonia is polyphyletic because one species, Prestonia riedelii, is positioned far removed from the other species, as sister to the monospecific Rhodocalyx, with strong support (1/95).

After exclusion of the Pentalinoninae, three major clades are recognized within the core Echiteae, all strongly supported: the Peltastinae clade (0.95/88), resolved as sister to the remaining clades (1/100); the Echitinae clade (1/100) and the Parsonsiinae-Prestoniinae clade (1/100, respectively).

The Peltastinae clade is divided into two clades: the Laubertia clade (1/100) and the Peltastes clade (1/100). The first includes three species of *Laubertia*, which are resolved as sister of *Hylaea* (1/100). The second clade includes three of the genera in subtribe Peltastinae sensu Endress & al. (2014): *Macropharynx*, *Peltastes*, and *Temnadenia*. *Temnadenia* is polyphyletic, with two species resolved as sister (1/100) to all other species in this clade, and one, *T. ornata* (Hoehne) Woodson, strongly supported (1/100) as sister to two species of *Prestonia*, far removed in the Parsonsiinae-Prestoniinae clade. *Rhodocalyx* and one species of *Prestonia*, *P. riedelii* are positioned in Peltastinae with strong support (1/95). The *Macropharynx-Peltastes* group is resolved with high support (1/100). *Macropharynx renteriae* A.H. Gentry is resolved as sister to the remaining species of *Macropharynx* and *Peltastes*, whereas the other three included species of *Macropharynx* form a strongly supported clade (1/100) that is sister to all included species of *Peltastes* (1/80). Thus, neither genus is monophyletic.

Next is the Echitinae clade (1/100), where three clades can be differentiated: the Thenardia clade (1/100), Asketanthera clade (1/100) and Echites clade (1/93). All genera in the Echitinae clade are resolved as monophyletic, with the exception of *Echites*, which includes *Fernaldia*. The Thenardia clade includes *Thoreauea* and *Thenardia*, both resolved as monophyletic with strong support (1/100). Next is a strongly supported clade (1/100) with two species of *Asketanthera* resolved as sister of *Echites*. *Echites* is strongly supported (1/93). However, the three included species of *Fernaldia* are nested within it, in a strongly supported clade (1/100) that is strongly supported (1/100) as sister to *E. turriger*, rendering *Echites* paraphyletic.

The last clade is the Parsonsiinae-Prestoniinae core clade, which contains the bulk of the species in the tribe, and can be broken down into two clades: the Parsonsiinae clade (1/100), and Prestoniinae clade (1/100). The Parsonsiinae clade comprises all included species of *Artia* and *Parsonsia*, both resolved as monophyletic with strong support (both 1/100). This clade is resolved as sister (1/100) to the Prestoniinae clade, which includes the bulk of the included species of *Prestonia*, together with *Temnadenia ornata*, which is maximally supported as sister to *Prestonia coalita* and *P. solanifolia* (Müll. Arg.) Woodson, further underscoring the polyphyly of Prestoniinae.

#### **DISCUSSION**

Nuclear markers, particularly ITS, have been used in phylogenetic studies in Asclepiadoideae for the past 15 years or longer (Meve & Liede, 2001; Wanntorp & al., 2006, 2014; Goyder & al., 2007; Surveswaran & al., 2009; Bruyns & al., 2010; Silva & al., 2012; Liede-Schumann & al., 2016), and *phytochrome* A has been used in broadscale studies of the APSA clade to improve resolution of relationships among tribal or subtribal lineages (Livshultz, 2010). In phylogenetic analyses focused on the traditional Apocynaceae (apocynoids and rauvolfoids), however, the use of nuclear markers has been quite limited. The first use of nrDNA in an analysis of non-Asclepiadoid Apocynaceae that we are aware of was the unpublished doctoral thesis of Kurt Potgieter (1999) on *Aspidosperma* Mart. & Zucc. based on ITS. Hendrian & Kondo (2007a, b, c) used ITS in an attempt to resolve the controversy as to whether *Neisosperma* Raf. should be recognized as a genus distinct from *Ochrosia* Juss, and Middleton & Livshultz (2012) included *phytochrome* A in a study of Old World Apocyneae.

Several phylogenetic studies have shown that ITS is especially useful because it is relatively easily amplified from herbarium material and is informative at the species level (Baldwin & al., 1995) as well as in resolving intergeneric relationships (Trovo & al., 2013), although in some groups it has been problematic because it was incongruent with the plastid data, mainly due to divergent paralogs, multiple copies, and hybridization (e.g., Álvarez & Wendel, 2003; Silva & al., 2012; Spalik & al., 2009; Weitmier & al., 2015). In Apocynaceae, this sort of incongruence has been reported in Malouetieae, subtr. Pachypodiinae (Burge & al., 2013), as has the presence of incomplete and non-alignable sequences in Vinceae (Simões & al., 2016). In Asclepiadeae subtr. Metastelmatinae the presence of paralogs in ITS has been reported (Rapini & al., 2006), but studies in other tribes and subtribes of the same subfamily (Asclepiadeae subtr. Cynanchinae and Ceropegieae, subtr. Stapeliinae) have suggested the absence of paralogs (e.g., Liede & Kunze, 2002; Meve & Liede, 2002). But, for this study several preliminary PCR tests conducted with ITS on different samples from the same set of species (*Echites candelarianus* J.F. Morales, *Parsonsia lenticellata*, *Peltastes isthmicus* Woodson,

*Prestonia portobellensis* (Beurl.) Woodson, *Thenardia floribunda* Kunth), revealed sequences without overlapping peaks and with no major incongruences between them.

This is the first densely sampled study of Echiteae as circumscribed by Endress & al., 2014. An overview of the circumscription of Echiteae in five selected classifications over the past 65 years (Pichon, 1950a; Leeuwenberg, 1994; Endress & Bruyns, 2000, Endress & al., 2007b, 2014) (Table 1) reveals that in all of them the tribe is paraphyletic. However, with the exception of the three genera of Pentalinoninae, all genera included by Endress & al. (2014) are supported as part of Echiteae. Pentalinoninae (comprising Angadenia, Pentalinon and Salpinctes), though monophyletic, is resolved outside of the tribe, supporting the earlier results of Livshultz & al. (2007) and Livshultz (2010).

Pentalinoninae clade. — The name of the subtribe was proposed by Pichon (1950a) (although without a Latin description), who included it within the Echiteae. The first molecular study to include a genus of Pentalinoninae was that of Potgieter & Albert (2001), in which one species of *Pentalinon* was part of a large polytomy comprising the bulk of the apocynoids. Six years later, in a study based on plastid DNA by Livshultz & al. (2007), all three genera of Pentalinoninae were included. The subtribe was maximally supported as part of her "New World clade" but was positioned outside of Echiteae sensu Endress & al. (2014), grouping instead in a clade together with three genera included in the tribe Odontadenieae (*Odontadenia*, *Secondatia* and *Stipecoma*) by Endress & al. (2014), although as part of an unsupported complex polytomy also involving a clade with Mesechiteae and a clade comprised of two other genera of Odontadenieae. In a subsequent study using nuclear DNA but based on a reduced sampling (Livshultz, 2010), the two included genera of this group (*Pentalinon* and *Angadenia*) were strongly supported (100% BS) as sisters and came out as sister to the core Echiteae, but again without support.

The molecular evidence presented here agrees with the results of the cpDNA-based phylogeny of Livshultz & al. (2007). In addition to the rooting taxon, *Rhabdadenia*, we retrieved two other clades outside of the Echiteae clade: one comprising all included genera of Mesechiteae (*Allomarkgrafia*, *Elytropus* and *Mandevilla*), but without support, and one composed of Pentalinoninae together with the included genera of Odontadenieae (*Odontadenia*, *Secondatia*, *Thyrsanthella* and *Pinochia*), which is highly supported (1/90). Pentalinoninae is resolved as sister (1/98) to the clade formed by the two genera,

*Odontadenia* and *Secondatia* (Fig. 3). Thus, in order to achieve a monophyletic Echiteae, Pentalinoninae must be excluded. Further studies with a larger sampling and including the remaining genera of Odontadenieae are necessary to determine if Pentalinoninae is nested therein or if it deserves its own tribal rank.

Pentalinon has traditionally been separated from Angadenia based on the presence of elongated and spirally intertwined linear apical anther appendages (Woodson, 1933). Otherwise, floral structure of the two genera is very similar. In Livshultz & al. (2007) and Livshultz (2010), the two included species of Angadenia formed a strongly supported (99% BS) clade and were in turn strongly supported as sister (100% BS) to the one included species of Pentalinon sampled. In the present study, both recognized species of Pentalinon and two of the three currently accepted species of Angadenia were sampled. In the BI analysis of the combined molecular dataset Pentalinon was retrieved in a polytomy with Angadenia. Although Angadenia is maximally supported as monophyletic and it is nested within Pentalinon in both the combined cpDNA tree and nrDNA tree, it has a meaningful feature (elongated and spirally intertwined linear apical anther appendages) to distinguish it from Pentalinon. Therefore, we keep Angadenia as distinct from Pentalinon.

Salpinctes is a rarely collected and poorly known monospecific genus of small erect shrubs with thick, coriaceous leaves and solitary flowers. It has a restricted distribution in dry savanna scrub and swampy tepui meadows in British Guyana and Amazonian Brazil and Venezuela. Its affinities have been in dispute from the beginning. When Woodson (1931a) described the genus, he hypothesized that its closest relatives were *Echites*, *Macropharynx* and *Stipecoma*, the last included in Odontadenieae in Endress & al. (2014). Five years later, in his big treatment of the American genera of Echitoideae (=apocynoids), Woodson (1936) remarked that the genus was no better understood than when he first published it and placed it between *Peltastes* and *Galactophora* Woodson. He suggested that its closest relative was most likely *Galactophora*, another small shrub with thick, coriaceous leaves with similar distribution and found in similar habitats, which he had described four years earlier, stating that it was "... a genus apparently without any direct affinity among the genera of its subfamily."(Woodson, 1932a). Although his idea about a close relationship between *Salpinctes* and *Galactophora* was shown to be incorrect, his hypothesis about the isolated position of *Galactophora* was borne out, when it came out as

sister to the other genera of the distant Malouetia clade in Livshultz & al. (2007), and was later placed as the sole member of Malouetieae subtr. Galactophorinae by Endress & al., 2014.

The other two genera of subtribe Pentalinoninae (*Angadenia* and *Pentalinon*) have a center of distribution in the Caribbean Basin, and each includes two recognized species. *Angadenia* is found mainly in the Greater Antilles and Bahamas, with one species reaching Florida. Of the two species of *Pentalinon*, one is centered in the Antilles and Bahamas and Florida; the other in Mexico and Central America as far south as Nicaragua. The two genera have traditionally been included in the Echiteae (e.g., Schumann, 1895; Woodson, 1935; Leeuwenberg, 1994; Endress & Bruyns, 2000), whereas *Salpinctes* was added more recently (Endress & al., 2007; Livshultz & al., 2007).

**Peltastinae clade**. — This clade is resolved as strongly supported. Within the Peltastinae clade two clades are recognized: Laubertia and Peltastes.

Laubertia clade. — In the plastid-based study by Livshultz & al. (2007) *Laubertia* came out as sister to the sampled members of Echiteae, but without support. Due to the limited sampling no more detailed relationships of *Laubertia* could be discussed. Livshultz (2010) obtained the same relationship in the ML tree of the nuclear dataset and the MP tree of the combined dataset, but in the ML tree for the combined data set *Laubertia* was resolved as sister to genera treated here in the Peltastinae clade (but only weakly supported), which is congruent with its position in our results. In this study, *Laubertia* is strongly supported as sister to *Hylaea* (1/100). In Endress & al. (2014) these two genera were included, together with *Prestonia* and *Rhodocalyx*, in their subtribe Prestoniinae, rendering it polyphyletic.

Laubertia is a genus of four species with a disjunct distribution in Mexico, Guatemala and Belize in Mesoamerica, and in Colombia, Ecuador, Peru, Bolivia and Brazil in South America (Morales, 2002a), which has to date been considered to be closely related to *Prestonia*, based on the presence of an annular corona around the corolla mouth (Woodson, 1936; Pichon, 1950a; Endress & al., 2014). The rarely collected and poorly known *Hylaea* contains two species confined to the Venezuelan and Brazilian Amazon, respectively (Morales, 1999b). An annular corona and/or free corona lobes are present in a few genera in the Echiteae (e.g., *Hylaea*, *Laubertia*, *Prestonia*, *Rhodocalyx*, *Thoreauea*),

although sometimes one or the other is absent. These structures have played an important role in differentiating genera within Echiteae. For example, *Laubertia* flowers have an annular corona, included anthers, but lack free corona lobes, whereas in *Hylaea* flowers lack an annular corona, have completely exserted anthers and free corona lobes (Morales, 1999b). We sampled one of the two species of *Hylaea* (both known only from the type) and three species of *Laubertia* (including an uncertain species) of four accepted species. In our phylogeny, genera with corona structures in Echiteae (*Hylaea*, *Laubertia*, *Prestonia*, *Rhodocalyx* and *Thoreauea*) are placed in four different clades. In Endress & al. (2014), the first four of these genera were included in subtribe Prestoniinae. *Thoreauea*, in contrast, was placed in subtribe Parsonsiinae because of its syncarpous ovary.

Peltastes clade. —The Peltastinae as currently circumscribed (Endress & al., 2014), including *Asketanthera*, *Macropharynx*, *Peltastes* and *Temnadenia* (Table 1), is resolved here as polyphyletic. *Rhodocalyx* and *Prestonia riedelii* (placed in Prestoniinae in the classification of Endress & al., 2014) are nested within this clade, whereas *Asketanthera* is nested in the subtribe Echitiinae. The Peltastinae clade can be divided into three clades: *Temnadenia*, *Rhodocalyx* and *Prestonia riedelii*, and *Macropharynx* and *Peltastes*.

Temnadenia currently comprises four species, two of them endemic to Brazil and the other two also extending to adjacent Colombia, Peru or Bolivia. The genus was described by Miers (1878), who is infamous among specialists of Neotropical Apocynaceae for his undiscerning eye and poor judgement, thus wreaking nomenclatural havoc in the group for decades to come. Miers described 22 species of Temnadenia, four of which have since been treated as synonyms of other species in the genus, and the remainder put into synonymy of existing species of Echites, Prestonia or Mandevilla. Woodson (1936) reduced the genus to four species: T. ornata, T. stellaris (Lindl.) Miers (T. odorifera (Vell). J.F. Morales), T. stenantha, and T. violacea (Vell.) Miers. Ezcurra (1981) added an additional species, T. meyeri which was later treated in Macropharynx (Xifreda, 1984) and whose closer affinities remain unknown (Morales, 2005a). In our study, Temnadenia is resolved as polyphyletic, with two species nested in the Peltastinae clade (T. odorifera and T. violacea) and one (T. ornata) deeply nested within Prestonia. Temnadenia should be considered a genus of two species endemic to Brazil. Temnadenia meyeri is morphologically very similar to P. riedelii, but lacks the annular corona around the corolla

mouth. The affinities of *T. meyeri* and *T. stenantha* are uncertain. The inclusion of these species in future analyses is essential in order to determine the appropriate placement and to test the monophyly of *Temnadenia*.

Rhodocalyx, described by Müller Argoviensis (1860), is a monospecific genus restricted to cerrados in Brazil, Bolivia and Paraguay. The genus has a convoluted taxonomic history, first being expanded by the inimitable Miers (1878) with an additional 11 species, almost all of which are currently placed in *Mandevilla*. Based on the overall similarity of *Rhodocalyx* to *Prestonia riedelii* pointed out by Ezcurra & al. (1992), Rhodocalyx was put into the synonymy of Prestonia by Morales (1999a). In our study Rhodocalyx grouped with Prestonia riedelii, with strong support (1/95). The relationship between R. rotundifolius-P.riedelii to genera here included in the Peltastinae clade was also recovered with 100% BS in Livshultz & al. (2007). However, in that study the position of the bulk of the included species of *Prestonia* was not supported and the sister relationship of R. rotundifolius and P. riedelii only poorly supported. Most importantly, sampling was inadequate to address these issues. For these reasons Endress & al. (2014) deemed it most prudent to include Rhodocalyx in Prestoniinae until an adequate sampling of the pertinent genera was available. The R. rotundifolius-P.riedelii clade is strongly supported as sister to the clade comprising the included species of *Peltastes* and *Macropharynx*, and clearly distinguished from the Temnadenia clade below. Based on the strong support combined with the morphological similarity of the two genera, we transfer *P. riedelii* to *Rhodocalyx*.

Macropharynx currently includes five recognized species and has a wide distribution from Honduras and Costa Rica in Central America all the way south to northern Argentina. Peltastes has ten species and has nearly the same distribution as Macropharynx. Both are large, robust lianas, with conspicuous ferrugineous-tomentose to hispid indument, often climbing high into the canopy, and festooning large expanses at forest edges or other disturbed areas. Macropharynx and Peltastes are grouped in a strongly supported clade (1/100). Peltastes has previously been included in four phylogenetic studies, all of them broadscale and focused on resolving higher level relationships: Potgieter & Albert (2001) and Sennblad & Bremer (2002) (each of which contained just one species – Peltastes peltatus (Vell.) Woodson)), and Livshultz & al. (2007) and Livshultz (2010) (both of which included two species: P. peltatus and P. isthmicus

Woodson). *Macropharynx*, in contrast, has previously never been studied molecularly. Traditionally, *Peltastes* has been differentiated mainly by its peltate leaves. A further difference is that there are conspicuous bracteoles on the pedicel in *Macropharynx*, whereas these are absent in *Peltastes*. Otherwise, the overall appearance of the two genera is very similar. Considering the position of *M. renteriae* and the possibility of cross lab contamination, we made three extractions from different populations in Costa Rica and Panama and the results were always the same. Based on the strongly supported position (1/100) of *M. renteriae* as sister to the remaining members of the *Macropharynx-Peltastes* clade and their close resemblance, we propose inclusion of *Peltastes* in *Macropharynx*.

**Echitinae clade.** — This clade is strongly supported (1/100) and can conveniently be broken into three clades: *Thernardia/Thoreauea*, *Asketanthera*, and *Echites/Fernaldia*.

The Thernardia/Thoreauea clade includes all currently recognized species of Thenardia and all but one of the described Thoreauea species. The monophyly of both is strongly supported: Thenardia (1/100) and Thoreauea (1/100). Both genera have a center of distribution in Mexico, with one species of *Thenardia* also reaching northern Central America (Morales, 2009a). Hypotheses of the possible closest relatives of *Thenardia* have varied, though usually these were members of Echiteae as delimited here. Although Woodson (1936) did not make a clear statement as to relationships, in his natural key to Neotropical apocynoids, Thenardia, Echites and Prestonia came out together, based on features such as clear latex and sepals with a solitary episepalous colleter inside. Pichon (1950b) suggested a close relationship with *Parsonsia* and *Artia*, based primarily on the exserted stamens and ovary with fused carpels. Leeuwenberg (1994) followed Pichon (1950b) for the most part, but also included *Delphyodon* K. Schum. and *Grisseeae* Bakh.f. (both now included in the synonymy of *Parsonsia* (Middleton, 1997)), and – presumably based on their conspicuously exserted anthers, also Pottsia and Isonema R. Br., two unrelated genera currently included in tribes Apocyneae and Nerieae, respectively (Endress & al., 2014). Williams (1995, 1998) suggested that *Thenardia* is probably most closely related to Echites and Fernaldia, based on the solitary calycine colleter and New World distribution common to all three, rather than to the Old World genera Parsonsia and Artia, which concurs with our phylogeny.

Thoreauea was described by Williams (2002) from a single specimen from Mexico, based on its isolated position in the morphological cladistic analysis of potential relatives (*Echites, Forsteronia* G. Mey., *Laubertia, Parsonsia, Prestonia* and *Thenardia*). It was characterized by its urceolate corolla with a dissected corona around the mouth. The circumscription of the genus was complemented by the description of two additional species shortly thereafter (Morales, 2005c; Diego & Lozada-Pérez, 2006). Morales (2005c), suggested a possible relationship with *Hylaea*, *Laubertia* and *Prestonia* based on the presence of a corona around the corolla mouth. In the morphology-based analysis of Williams (2002) *Thoreauea* was placed as sister to a clade comprised of two clades: one containing the four included species of *Parsonsia* and one species of *Forsteronia*, and the other the two included species of *Thenardia*. Of these, only the clade of *Thenardia* species received strong support; the other clades received either weak or no support.

The next clade, comprising the two included species of *Asketanthera*, is strongly supported, both as monophyletic and as sister to *Echites* and *Fernaldia*. *Asketanthera* was included in Peltastinae by Endress & al. (2014) because of its foliaceous bracts; this further adds to the polyphyly of that subtribe and at the same time renders Echitinae non-monophyletic. *Asketanthera* and its four constituent species were described by Woodson (1932a). It is restricted to the Greater Antilles, with one species endemic to Cuba and the other three endemic to Hispaniola. It is one of the most rarely collected and poorly known genera in Neotropical Echiteae, and little more is known about it than when it was first published.

The final clade of the Echitinae clade includes *Echites*, which is resolved as paraphyletic, with *Fernaldia* nested deeply within it. This supports the findings of a cladistic analysis based on morphological characters (Williams, 2004), in which the single species of *Fernaldia* included came out as sister to three representatives of *Echites* subgen. *Echites* (although without support). The author remarked that the main difference between the two genera was the corolla shape (infundibuliform in *Fernaldia* versus salverform in *Echites*). Our results are also congruent with those of Livshultz & al. (2007), in which the single included species of *Fernaldia* was strongly supported as sister to *Echites turriger*, a species with a salverform corolla with glabrous lobes, and this clade was in turn strongly supported as sister to the remaining included species of *Echites*. The authors commented on

the weakness of the morphological features that distinguish the two genera, and suggested the inclusion of *Fernaldia* in *Echites*. Here, *Fernaldia* also groups in a clade (1/100) with *E. turriger*, and this clade is deeply nested within *Echites*. Our results are based on a denser sampling, including all species of *Fernaldia* and eight of the nine species of *Echites*, which allows us to say with confidence that *Fernaldia* should be included in *Echites* in order to make the latter monophyletic.

Fernaldia, another genus described by Woodson (1932a), ranges from Mexico to Costa Rica. Traditionally, it has been distinguished from other Neotropical apocynoids by its infundibuliform corolla with long hairs on the inner surface of the lobes (Morales, 2002b, 2009a), although sometimes the hairs are so sparse that the lobes are glabrescent. The flower buds of one species, *F. pandurata* (A. DC.) Woodson (commonly called *loroco*), are popular as a condiment to flavor rice and *pupusas* (thick, handmade tortillas) in El Salvador and Guatemala, and has been introduced to southern Florida, where it is grown in some Hispanic communities (Morton & al., 1990). To the best of our knowledge, *loroco* is the only member of Echiteae that is used for human consumption.

In the early days of plant systematics, the name *Echites* was given to just about any lactiferous liana in the New World. The generic concept remained vague and inclusive for more than 150 years, until Woodson (e.g., 1931b, 1932a, 1932b, 1936) courageously tackled the problem, describing a number of new genera to accommodate some, and transferring many others to existing genera, thereby reducing *Echites* to just six species distributed in Mesoamerica and the Caribbean. In his revision of New World apocynoids, Woodson (1936) published an elaborate classification for the six accepted species in Echites, including two subgenera, based on rather minor differences: Euechites (with corollas up to 8 cm long with spreading obovate lobes) and *Pseudechites* (with shorter corollas with reflexed very narrow to filiform lobes). Echites subgen. Euechites was further subdivided into two sections: Umbellatae (with twisted corolla tube and restricted to northern Mesoamerica) and Yucatanenses (with non-twisted corolla tube and widely distributed from Florida, the Caribbean and Mesoamerica). In section Umbellatae, Echites umbellatus Jacq. was further split into two varieties (typica and crassipes). Woodson himself, speaking about var. crassipes, noted in a comment at the end, "These plants appear to be no more than microphyllous, depauperate individuals of var. typica, and it is doubtful

whether they should even be recognized as a variety." A few species still remained incorrectly placed in other genera and were transferred to *Echites* (Morales, 1997). The first molecular-based study to include *Echites* was the broadscale analysis based on *trnL* intron and *trnL-F* spacer by Potgieter & Albert (2001); only one species was included and it came out in a strongly supported polytomy including all other representatives of the core Echiteae as defined here. Three years later, Williams (2004) published a morphological cladistic analysis of 42 species of 22 apocynoid genera, in which the representatives of *Echites* subgen. *Pseudechites* (Woodson, 1936) were retrieved in a moderately supported clade far removed from those of *E.* subgen. *Echites*, which grouped together, but without support. Based on the results of Williams (2004), a new genus was erected to accommodate the species of *Echites* subgen. *Pseudechites* Woodson (Morales & Williams, 2004), which, however, was not supported by molecular evidence obtained by Livshultz & al. (2007) and in this study. Finally, 260 years after it was first described, the generic limits of *Echites* are stable at last. From a nebulous catch-all, *Echites*, as currently defined, comprises 11 species, distributed from Florida through the West Indies and in Mesoamerica.

**Parsonsiinae-Prestoniinae clade**. — This clade is resolved with strong support (1/100). It contains the only Old World members of the tribe, and represents the by far most species-rich group in Echiteae, with an estimated 140 species, the overwhelming majority of them concentrated in the two genera *Parsonsia* and *Prestonia*. This clade is divided into two well supported clades, and includes three genera: *Artia* and *Parsonsia* (Parsonsiinae), and *Prestonia* (Prestoniinae).

Both Parsonsiinae and Prestoniinae, as proposed in the classification of Endress & al. (2014), are polyphyletic: Parsonsiinae because, in addition to *Artia*, *Ecua* and *Parsonsia*, it also included *Thenardia* and *Thoreauea* (resolved here as part of the Echitinae), and Prestoniinae because of the four included genera (*Prestonia*, *Hylaea*, *Laubertia*, and *Rhodocalyx*), the last three are included in the Peltastinae clade here. As resolved here, Parsonsiinae comprises *Artia* and *Parsonsia* (and presumably *Ecua*), and Prestoniinae only *Prestonia* (Fig. 3). The close relationship between *Parsonsia* and *Prestonia* has been suggested in earlier studies (e.g., Sennblad & al., 1998, Sennblad & Bremer, 2002).

In the study by Livshultz & al. (2007), which was based on four cpDNA markers, Parsonsia and Artia were resolved as nested within Prestonia, but without statistical support. In Livshultz (2010), using nuclear and plastid data, *Prestonia* was resolved as sister to the *Artia-Parsonsia* clade, but with only moderate support. Also, because of the reduced sampling (only two species of *Prestonia* and one each of *Artia* and *Parsonsia*), the relationships of this group could not be addressed. Here, the increased taxon sampling together with nuclear data resolved the relationships between these groups with high support, resolving the *Artia-Parsonsia* clade as sister to the *Prestonia* clade.

Parsonsiinae clade. — The monophyly of *Artia* is tested and confirmed here for the first time. It is resolved as sister to *Parsonsia*, which is congruent with the results of Livshultz & al. (2007) and Livshultz (2010). The close relationship between the two genera was also suggested by Pichon (1950c). *Artia* was described by Guillaumin (1941), currently encompasses four species, and is restricted to New Caledonia. It bears a strong resemblance to *Parsonsia*, and it would be interesting to see where it would come out with a larger sampling of *Parsonsia*, and with *Ecua*.

Parsonsia is strongly supported as monophyletic (1/100). The genus was described by Robert Brown in his landmark treatise on Apocynaceae (Brown, 1810) and has a broad distribution in tropical and subtropical regions of Asia and the southwestern Pacific, including New Caledonia (with 16 recognized species, all endemic), New Zealand and Australia (where the genus has radiated extensively, with 33 of the 35 accepted species being endemic). Estimates for the number of species vary: Pichon (1950c) and Middleton (1997) suggested somewhat more than 80, Leeuwenberg (1994) 50, and Williams (1996) 130 species.

Prestoniinae clade. — This clade is strongly supported (1/100) and includes only the New World genus *Prestonia*. The circumscription of *Prestonia* has been problematic since Woodson (1936) monographed the genus. Woodson accepted 61 species, but included *P. agglutinata* (Jacq.) Woodson, currently placed in *Echites* (Morales, 1997). Later, Monachino (1957, 1961) described two additional species in *Prestonia*, *P. arborescens* Monach. and *P. leptoloba* Monach., which were removed and treated as a new genus (*Hylaea*) by Morales (1999b). Previous phylogenetic studies have suggested that *Prestonia* is polyphyletic (e.g., Livshultz & al. 2007; Livshultz, 2010), with at least one species (*P. riedelii*) grouped with *Rhodocalyx* (Peltastinae), which is congruent with our results here (based on an enlarged sampling including 15 species of *Prestonia*). Here we propose

exclusion of *P. riedelii* from the Prestoniinae and its inclusion in the Peltastinae, to make both subtribes monophyletic. The infrageneric relationships in *Prestonia* are mainly unresolved and more species need to be sampled in order to evaluate the classifications of Woodson (1936) and Pichon (1950a).

Sex, drugs and pupusas: Pyrrolizidine alkaloids in Echiteae. — Still relatively little is known about the distribution of PAs in Apocynaceae. The impetus to check for the presence of PAs in the lab has almost always come from field observations of specialized danaid butterflies and arctiid moths showing a strong association with a particular species (Brown, 1984; Edgar, 1984; Nishida, 2002; Bowers, 2009). To date, not many species of Apocynaceae have been tested for PAs in the lab, and with the exception of Parsonsia and *Prestonia*, where a number of species have tested positive, presence of PAs is mostly based on a single species (Burzynski & al., 2015). Nonetheless, one can make some deductions by comparing the available data to our phylogeny. (1) Test results for PAs were negative for Pentalinon (Burzynski & al., 2015), which provides independent support for its exclusion from Echiteae as proposed here; (2) Low molecular weight PA derivatives have been reported in Anodendron A. DC. (Apocyneae) and Holarrhena R. Br. (Malouetieae), and Colegate & al. (2016) confirmed the presence of two different types of low molecular weight dehydroPAs (neither one of the parsonsine type) in Alafia (Nerieae) and Amphineurion (Apocyneae); (3) DehydroPAs of the parsonsine type have been reported and/or confirmed only in Echiteae and in all three main clades: Temnadenia and Peltastes (Peltastinae clade), Echites/Fernaldia and Thenardia (Echitinae clade) and Parsonsia and Prestonia (Parsonsiinae-Prestoniinae clade) (Brown, 1987; Brehm & al., 2007; Hernández-Baz & al., 2013; Burzynski & al., 2015 and references therein; Colegate & al., 2016). This is reminiscent of the situation in complex indole alkaloids, in which biogenetic pathways diversify and have led to structurally ever more derived types, which may be characteristic for a particular clade (Kisakürek & al., 1983; Endress & al., 1990). For example, the rauvolfioid tribe Tabernaemontaneae contains a number of different indole alkaloids, many of them of a relatively less evolved structure that are also found elsewhere in rauvolfioids. But ibogan type indole alkaloids, the structurally most derived 'J type' in the evolutionary system described in Kisakürek & al.(1983), are found exclusively in Tabernaemontaneae

and thus characterize that tribe (Van Beck & al., 1984; Van Beck & Van Gessel, 1988; Zhu & al., 1990). One can surmise from this that in the ancestors of Echiteae, there has been an evolutionary shift in the chemical defense compounds, from the usual steroidal alkaloids and cardenolides in apocynoids to dehydroPAs of the parsonsine type.

Although PAs evolved as a defense against herbivores (Thoden & Boppré, 2010; Trigo, 2011), certain insect groups have evolved a tolerance to these toxins, which the larvae ingest with plant material (Trigo & al., 1996; Hartmann & Ober, 2000). In a more specialized behavior known as pharmacophagy (Boppré, 1984), adults imbibe PAs from injured or withered plant parts. The insects then put the sequestered toxic compounds to their own use against predators (Boppré, 1984, 1986; Nishida, 2002; Brehm & al., 2007). Two groups of Lepidoptera – arctiid moths and danaid butterflies – have evolved an even more derived use of PAs. Males use them as the basis for male-mating pheromones (Boppré, 1990, 1995; Schulz, 1998; Schulz & al., 2004). Males of the arctiid moth Creatonotos Hübner have expandable scent-producing organs (coremata), which are covered with long pheromone-exuding hair-pencils (Pliske, 1975; Honda & al., 2006), the size and pheromone content of which depend on the moth's ingestion of PAs. Experiments have shown that coremata of males with no PAs in their diet were merely two stalks with very few hair-pencils, but the coremata of those that were fed PAs developed four tubes longer than the insect's body length, densely covered with long hair-pencils (Boppré & Schneider, 1985), demonstrating that the moths have evolved a dependence on the toxic PAs in their host plants to produce pheromones. At dusk males expand their long, feathery hair-pencils, emitting pheromones that attract females as well as other males. The result is the formation of a lek, a mating arena in which group sex takes place (Boppré, 1995). A number of specialists working on various aspects of PA-containing plants and their associated lepidoptera, have hypothesized that PA-containing Apocynaceae are the most likely ancestral host plants, which led to the evolution of pharmacophagy because lepidopteran species considered to be less specialized in both the Old and New World feed on Apocynaceae as caterpillars, whereas more derived species are able to take up PAs from various plant sources as adults (Edgar, 1984; Trigo & al., 1996; Brehm & al., 2007).

It has long been known that PA-containing plants are a leading cause of poisoning in grazing animals, and have resulted in significant loss of livestock. In a number of countries PAs are also the most common plant toxins causing disease in humans due to contamination of staple foods such as grain, meat, milk and honey (Edgar & al., 2002, 2015; Chen & al., 2010; Wiedenfeld & Edgar, 2011). Herbal teas, dietary supplements and traditional medicines made from plants containing PAs similarly pose a potential health threat to the patients who consume them (Chen & al. 2009 and references therein). Considering that the plant known as *loroco* (*Fernaldia pandurata*) is nested within *Echites* – one of the PA-containing genera – one wonders what effect it might have on those gourmets who consider *pupusas* –thick hand-made tortillas (Morales, 2006b) – filled with loroco flowers a delicacy. Although in the analysis by Burzynski & al. (2015) PAs were found to be absent in *F. pandurata*, Colegate & al. (2016) reported their presence in the same species, confirming an earlier finding by del Castillo & al. (1970). There are indications that PA levels may vary among plants of the same species, or depend on what part of the plant was tested (Burzynski & al. (2015). A great deal more work remains to be done and new discoveries made in this fascinating interface between entomology, plant systematics and chemical ecology.

#### TAXONOMIC IMPLICATIONS

**Echiteae** Bartl., Ord. Nat. Pl.: 204. 1830 – Type: *Echites* P.Browne, Civ. Nat. Hist. Jamaica 182. 1756. 14 genera.

Lianas, rarely trees; latex white or translucent; old stems sometimes with suberose bark. Leaves opposite, rarely verticillate, without colleters on the midrib, membranaceous to coriaceous, rarely revolute. Inflorescences axillary to terminal, panicles, thyrsiform, umbelliform, subumbelliform, helicoid, dichasial or monochasial cymes, bracts foliaceous or scarious, bracteoles on pedicels sometimes present, sepals foliaceous or not, with one episepalous colleter at the base inside, sometimes more numerous and arranged in a ring, rarely colleters absent; corolla salverform or infundibuliform, rarely rotate or urceolate, the tube sometimes spirally contorted, sometimes with longitudinal grooves, usually with suprastaminal and infrastaminal ribs, the lobes obliquely obovate, narrowly elliptic to ovate or oblong ovate, commonly spreading during anthesis, rarely erect, suberect, or totally

reflexed; aestivation dextrorse, rarely valvate or subvalvate; an annular corona sometimes present at the mouth and free corona lobes in the staminal sectors above the insertion of the stamens, stamens included, with apices exserted, or completely exserted, with geniculate filaments, sometimes closely surrounding the style; style-head with a basal collar; ovary apocarpous or syncarpous; nectary annular and irregularly lobed or divided into five separate nectaries. Follicles free or fused longitudinally, rarely divaricate, usually continuous, rarely moniliform, rarely with ribs; seeds truncate, subtruncate to rostrate. Southeastern United States to northern Argentina, West Indies, New Caledonia, tropical and subtropical Asia, and southwestern Pacific.

Subtr. Echitinae Kitt., Taschenb. Fl. Deutschl., ed. 2, 1: 449. 1843 – Type: *Echites* P.Browne, Civ. Nat. Hist. Jamaica 182. 1756.

Asketanthera Woodson in Ann. Missouri Bot. Gard. 19(1): 46. 1932.

Echites P.Browne, Civ. Nat. Hist. Jamaica 182. 1756.

Thenardia Kunth, Nov. Gen. Sp. (quarto ed.) 3: 209, t. 240. 1818 [1819].

Thoreauea J.K. Williams in Lundellia 5: 47, f. 1-2. 2002.

**Subtr. Laubertinae** J.F.Morales, M.E.Endress & Liede, **subtrib. nov.** – Type: *Laubertia boissieri* A.DC., Prodr. 8: 487. 1844.

This subtribe can be recognized by its salverform corolla, with the tube sometimes spirally contorted, corolla lobes completely reflexed during anthesis, annular corona and free corona lobes present or absent, moniliform follicles, and truncate seeds.

Lianas or trees; latex mostly translucent, rarely white. Leaves opposite, membranaceous, glabrous, margins not revolute. Inflorescence a helicoid cyme, axillary; sepals with a single episepalous colleter at the base inside or colleters absent; corolla salverform, the tube sometimes spirally contorted, the lobes completely reflexed; with or without an annular corona, free corona lobes present or absent, stamens included or

completely exserted, not closely encircling the style; ovary apocarpous; nectary annular and lobed. Follicles moniliform, without ribs; seeds truncate.

Hylaea J.F.Morales in Novon 9(1): 83. 1999.

Laubertia A.DC., Prodr. 8: 486. 1844.

**Subtr. Parsonsiinae** Benth. & Hook.f., Gen. Pl. 2: 687. 1876 – Type: *Parsonsia* R.Br., Mem. Wern. Nat. Hist. Soc. 1: 64. 1811, *nom. cons*.

Artia Guillaumin in Bull. Soc. Bot. France 88(2-6): 380. 1941.

Ecua Middleton in Blumea 41(1): 33. 1996

Parsonsia R.Br. in Mem. Wern. Nat. Hist. Soc. 1: 64. 1811, nom. cons.

**Subtr. Peltastinae** Pichon ex M.E. Endress in Phyotaxa 159: 182. 2014 – Type: *Peltastes* Woodson in Ann. Missouri Bot. Gard. 19(4): 375. 1932.

Macropharynx Rusby in Mem. New York Bot. Gard. 7: 327, t. 6. 1927.

Rhodocalyx Müll. Arg., Müll. Arg. Fl. Bras. 6(1): 172. 1860.

Temnadenia Miers, Apocyn. S. Am.: 207. 1878.

**Subtr. Prestoniinae** Pichon ex M.E.Endress in Phyotaxa 159: 183. 2014 – Type: *Prestonia* R.Br., Asclepiadeae: 58. 1810.

Prestonia R.Br., Asclepiadeae: 58. 1810, nom. cons.

#### Incertae sedis

Bahiella J.F.Morales in Sida 22(1): 342, f. 2-3. 2006.

The relationships and affinities of *Bahiella* cannot be determined at this time. It was included in Echitinae by Endress et al. (2014). We obtained only incomplete and partial cpDNA sequences (*trnLF*, *rpl16*). The results suggest that it could be related to

Parsonsiinae or Prestoniinae; but until complete sequences can be analyzed, we prefer to maintain it as "incertae sedis".

# **New synonymies**

- Echites P.Browne, Civ. Nat. Hist. Jamaica 182. 1756 Type: Echites umbellatus Jacq., Enum. Syst. Pl. 13. 1760
- = Fernaldia Woodson in Ann. Missouri Bot. Gard. 19: 48(1). 1932 Type: Fernaldia pandurata (A.DC.) Woodson in Ann. Missouri Bot. Gard. 48(1). 1932.
- Macropharynx Rusby in Mem. New York Bot. Gard. 7: 327, t. 6. 1927 Type:Macropharynx fistulosa Rusby, Mem. New York Bot. Gard. 7: 329, t. 6. 1927
- = *Peltastes* Woodson in Ann. Missouri Bot. Gard. 19(4): 375. 1932 Type: *Peltastes* peltatus (Vell.) Woodson in Ann. Missouri Bot. Gard. 19: 376(4). 1932.

#### **New combinations**

In some several cases, the type specimen has been misplaced, and it was therefore not possible to determine the barcode. We have indicated these by an asterisk (\*) preceding the herbarium acronym.

- Echites asperoglottis (Woodson) J.F.Morales & M.E.Endress, comb. nov. ≡ Fernaldia asperoglottis Woodson in Ann. Missouri Bot. Gard. 26(2): 96. 1939 − Holotype: Mexico, Guerrero, Sierra Madre del Sur, N of río Balsas, 5 Nov 1937 (fl), Y. Mexia 8751 (MO barcode MO022157; isotypes: ARIZ barcode ARIZ5149, CAS barcode CAS2736, F barcode F48200 (photo F neg. 56468), G barcode G169390, GH barcode GH57724, K barcodeK582730, NY barcode NY73866, S barcode S2694, UC barcode UC645092, U barcode U112843, US barcode US112015).
- Echites speciosissimus (Woodson) J.F.Morales & M.E.Endress, comb. nov. ≡ Fernaldia speciosissima Woodson in Ann. Missouri Bot. Gard. 26(4): 300. 1939 Holotype: Panama. Chiriquí, río Chiriquí to Remedios, 11 Jul 1938 (fl), R.E. Woodson, P. Allen & R. Seibert 1179 (MO barcode MO022158).

- Macropharynx abnorma J.F.Morales & M.E.Endress, nom. nov. ≡ Peltastes anomalus J.
  F.Morales in Candollea 60(2): 295, f. 4–5. 2005, non Macropharynx anomala
  Woodson in Ann. Missouri Bot. Gard. 21(4): 614(4). 1934 Holotype: Peru,
  Cajamarca, San Ignacio, San José de Lourdes, Laurel, 17 May 1997 (fl), J. Campos
  & W. Vargas 3883 (MO barcode MO1809930; isotypes: \*CR, K barcode K898019).
- Macropharynx colombiana (Woodson) J.F. Morales & M.E. Endress, comb. nov. ≡
  Peltastes colombianus Woodson in Ann. Missouri Bot. Gard. 19(4): 378(4). 1932 –
  Holotype: Colombia, Magdalena, Santa Marta, 27 Jun 1899 (fl), H. Smith 2412 (MO barcode MO100293; isotypes: BM barcode BM85118, CM barcode CM1727, F barcode F48318, G barcode G169755, GH barcode GH57763, K barcode K582817, NY barcode NY318261, P barcode P3874171, PH barcode PH20940, US barcode US112010).
- Macropharynx conflictiva (J.F.Morales) J.F.Morales & M.E.Endress, comb. nov. ≡
   Peltastes conflictivus J.F.Morales in Candollea 60(2): 297, f. 8. 2005. Holotype:
   Peru, San Martín, San Martín, Cataratas de Ahuashiyacu, road from Tarapoto to Yurimaguas, 29 Jul 1986 (fl), S. Knapp 7852 (\*USF; isotypes: F barcode F48319, MEXU barcode MEXU488077, \*MO, \*NY, USM barcode USM47).
- Macropharynx gigantea (Woodson) J.F.Morales & M.E. Endress, comb. nov. ≡ Peltastes giganteus Woodson in Ann. Missouri Bot. Gard. 19(4): 378. 1932 Holotype: Bolivia, without data (fl), M. Bang 2804 (MO barcode MO149066; isotypes: C barcode C10005859, \*F, K barcode K582818, NY barcode NY318260, US barcode US112011).
- Macropharynx isthmica (Woodson) J.F.Morales & M.E.Endress, comb. nov. ≡ Peltastes isthmicus Woodson in Ann. Missouri Bot. Gard. 23(2): 187. 1936 Holotype: Panama, Chiriqui, vicinity of San Félix, Dec 1911 (fl), H. Pittier 5125 (US barcode US433095).

- Macropharynx macrocalyx (Müll.Arg.) J.F.Morales & M.E.Endress, comb. nov. ≡
  Peltastes macrocalyx (Müll.Arg.) Woodson in Ann. Missouri Bot. Garden 19(4):
  376. 1932. Echites macrocalyx Müll. Arg., Fl. Bras. 6(1): 160. 1860. Stipecoma macrocalyx (Müll. Arg.) Miers, Apocyn. S. Am.: 136. 1878 Lectotype (designated by Morales 2005b: 301): Brazil, Bahia, Santa Anna, 1850 (fl), M. Blanchet s.n., (G barcode G169753).
- Macropharynx peltata (Vell.) J.F.Morales & M.E. Endress, comb. nov. ≡ Peltastes peltatus (Vell.) Woodson in Ann. Missouri Bot. Gard. 19(4): 376. 1932 = Echites peltatus Vell., Fl. Flumin. 110. 1829 (1825) ≡ Stipecoma peltata (Vell.) Miers, Apocyn. S. Am. 134. 1878 Lectotype (designated by Morales 2005b: 302): Brazil, without data, Fl. Flumin., Icon 3: t. 32. 1831 (1827).
- Macropharynx peruviana (Woodson) J.F.Morales & M.E.Endress, comb. nov. ≡Peltastes peruvianus Woodson in Ann. Missouri Bot. Gard. 47(1): 77. 1960 Holotype: Peru, Huanuco, Fila Divisoria, 6 Sep 1946 (fl), F. Woytkowski 34492 (MO barcode MO100290-; isotypes: \*CR, F barcode F48320, G barcode G169745, \*USM).
- Macropharynx pulchra (Miers) J.F.Morales & M.E.Endress, comb. nov. ≡ Peltastes pulcher (Miers) J.F.Morales in Candollea 60(2): 306, f. 15. 2005. Stipecoma pulchra Miers, Apocyn. S. Am.: 135, t. XVIII. 1878 Holotype: Brazil, Rio de Janeiro, Morro Flamengo, without date (fl), J. Miers 3877 (BM barcode BM952731).
- Macropharynx venusta (J.F.Morales) J.F.Morales & M.E.Endress, comb. nov. ≡Peltastes venustus J.F.Morales in Candollea 60(2): 307, f. 16. 2005 Holotype: Ecuador, Napo, Archidona canton, Napo-Galeras national park, Cordillera de Galeras, trail to Santa Rosa de Arapino, 18 Mar 1997 (fl, fr), A. Álvarez, A. Pohla, P. Cerda & B. Shiguando 1681 (QCNE barcode QCNE15; isotype: \*CR).

Prestonia ornata (Hoehne) J.F.Morales & M.E.Endress, comb. nov. ≡ Echites ornatus Hoehne, Comm. Lin. Telegr., Bot. 6: 82, pls. 120, 131, f. 1. 1915. Temnadenia ornata (Hoehne) Woodson in Ann. Missouri Bot. Gard. 19(4): 383. 1932. Lectotype (lectotype, designated by Morales 2005a: 214): Brazil, Mato Grosso, Piruena, May 1909 (fl), F.C. Hoehne 1965 (R barcode R210956).

Rhodocalyx riedelii (Müll.Arg.) J.F.Morales & M.E.Endress, comb. nov. ≡ Prestonia riedelii (Müll. Arg.) Markgr. in Repert. Spec. Nov. Regni Veg. 20: 26. 1924.
Haemadictyon riedelii Müll. Arg., Fl. Bras. 6: 170. 1860. Temnadenia riedelii (Müll. Arg.) Miers, Apocyn. S. Am. 216. 1878. Echites riedelii (Müll. Arg.) Malme in Bull. Herb. Boissier, sér. 2, 4: 196. 1904. – Holotype: Brazil, Without data (fl), L. Riedel 1973 (P barcode P00646723 (photo F neg. 38795); isotype: LE).

## **ACKNOWLEDGEMENTS**

Plant material was kindly provided in part by the following persons: Xavier Cornejo (GUAY), Paul Forster (BRI), Alfredo Fuentes (USZ), Barry, and Isa Hammel (MO), Bruce Hansen (USF), Alejandro Rapini (HUEFS), Andre Simões (UEC), and Victor Steinmann (RSA-POM). We thank Paul Forster (BRI) for generously sending leaf samples of several species of Parsonsia. The collection and export permit for Pentalinon andrieuxii (Müll. Arg.) B.F. Hansen & Wunderlin) was obtained through Ivón Ramírez and the Centro de Investigaciones Científicas de la Península de Yucatán, México (CICY). We are also very grateful to the former Herbarium (INB, now incorporated in CR) of the Instituto Nacional de Biodiversidad (INBio) in Costa Rica for allowing the first author to collect samples from the herbarium and for the collecting permit in Costa Rica. This collection holds one of the most extensive collections of neotropical Apocynaceae, including poorly collected taxa, and many herbarium specimens not preserved using alcohol, which allowed us to obtain positive PCR reactions for critical species. Angelika Täuber and Margit Gebauer (Bayreuth University, Germany) provided advice, and important suggestions during the lab work and DNA extraction and amplification, their help is greatly acknowledged. Michael Grayum (MO) has provided literature references over the past several years, and his continued

support is appreciated. We gratefully thank Andre Simões (University of Campinas, Brazil) and Rafael Acuña (University of Bonn, Germany) for kindly sharing their original and modified matK amplification protocols. J. Francisco Morales holds a PhD research grant (Forschungsstipendien für Doktoranden und Nachwuchswissenschaftler für mehr als 6 Monate) from the Deutscher Akademischer Austauschdienst (DAAD). Financial support was provided by the University of Bayreuth Graduate School (Germany) and the Deutscher Akademischer Austauschdienst (Germany). The first author wishes to express his gratitude to the Missouri Botanical Garden and Olga Martha Montiel, who have supported several visits to their herbarium in the last decade. The following herbaria allowed the study of their collections: B, C, CEPEC, CICY, CR (including INB), E, F, G, GUAY, M, MBML, MO, O, P, USF, USJ. Field assistance for the first author was provided by Alev Oder and Daniel Soto (Bolivia), Marccus Alves, Diogo Araujo, Andre Fontana, Ludovic Kollmann, Isa de Morais, Ricardo Perdiz, and Alessandro Rapini (Brazil), Ronald Abarca, Isler Chinchilla, and Luis Fonseca (Costa Rica), Julio Betancur, Ricardo Callejas, Dayron Cárdenas, Felipe Cardona, Álvaro Idárraga, and Mario Alberto Quijano (Colombia), Gabriel Cerén, Eunice Echeverría, and Jenny Menjivar (El Salvador), Cármen Galdámez (Panama), Carlos Amasifuen, Aniceto Daza, Carlos Reynel, Rocio Rojas, and Roberto Vásquez (Perú), and Oscar Muñoz (Venezuela). Barcode information of the type of Peltastes venustus was kindly provided by Efrain Freire and Diana Fernández (QCNE).

## LITERATURE CITED

- **Álvarez**, **I. & Wendel**, **J.F.** 2003. Ribosomal ITS sequences and plant phylogenetic inference. *Molec. Phylogenet. Evol.* 29: 417–434.
- **Bafeel, S.O., Arif, I., Bakir, M., Khan, H., Al Farhan, A, Al Homaidan, A., Ahamed, A. & Thomas, J.** 2011. Comparative evaluation of PCR success with universal primers of maturase K (matK) and ribulose-1,5-bisphosphate carboxylase oxygenase large subunit (rbcL) for barcoding of some arid plants. *Plant Omics* 4: 195–198.
- Baldwin, B.G., Sanderson, M.J., Porter, J.M., Wojciechowski, M.F., Campbell, C.S. & Donoghue, M.J. 1995. The ITS region of nuclear ribosomal DNA: A valuable

- source of evidence on angiosperm phylogeny. *Ann. Missouri Bot. Gard.* 82: 247–277.
- **Baum, D.A., Small, R.L. & Wendel, J.F.** 1998. Biogeography and floral evolution of baobabs (*Adansonia*, Bombacaceae) as inferred from multiple data sets. *Syst. Biol.* 47: 181–207.
- **Bentham, G.** 1876. Apocynaceae, Asclepiadaceae. Pp. 680–785 in: Bentham, G & J. D. Hooker (eds.), *Genera Plantarum*, Vol. 2. London: Williams & Norgate.
- **Bisset, N.G.** 1958. The occurrence of alkaloids in the Apocynaceae. *Ann. Bogoriensis* 3: 105–236.
- **Bisset, N.G.** 1961. The occurrence of alkaloids in the Apocynaceae. Part II. A review of recent developments. *Ann. Bogoriensis* 4: 65–144.
- **Bisset, N.G.** 1989. *Tabernanthe*: uses, phytochemistry, and pharmacology. Pp. 19–26 in: Leeuwenberg, A.J.M. (ed.), Series of revisions of Apocynaceae XXIX. *Wageningen Agric. Univ. Pap.*89: 19–26.
- Boppré, M. 1984. Redefining "Pharmacophagy". J. Chem. Ecol. 10: 1151–1154.
- **Boppré, M.** 1986. Insects pharmacophagously utilizing defensive plant chemicals (pyrrolizidine alkaloids). *Naturwissenschaften* 73: 17–26.
- **Boppré, M. & Schneider, D.** 1985. Pyrrolizidine alkaloids quantitatively regulate both scent organ morphogenesis and pheromone bio-synthesis in *Creatonotos* moths (Lep.: Arctiidae). *J. Comp. Physiol.* 157: 569–577.
- **Boppré, M.** 1990. Lepidoptera and pyrrolizidine alkaloids: exemplification of complexity in chemical ecology. *J. Chem. Ecol.* 16: 165–185.
- **Boppré, M.** 1995. Pharmakophagie: Drogen, sex und Schmetterlinge. *Biol. Unserer Zeit* 25: 8–17.
- **Bowers, M.D.** 2009. Chemical defenses in woolly bears: Sequestration and efficacy against predators and parasitoids. Pp. 83–114 in: Conner, W.E. (ed.), *Tiger moths and woolly bears. Behavior, ecology, and evolution of the arctiidae*. New York: Oxford University Press.
- **Brehm, G.** 2007. Pyrrolizidine alkaloids and pharmacophagous Lepidoptera visitors of (Apocynaceae) in a montane forest in Ecuador. *Ann. Missouri Bot. Gard.* 94: 463–473.

- **Brown, R.** 1810. On the Asclepiadeae, a natural order of plants separated from the Apocineae of Jussieu. [Pre-print of: *Mem. Wern. Nat. Hist. Soc.* 1: 12–78 (1811)].
- **Brown, Jr., K.S.** 1984. Adult-obtained pyrrolizidine alkaloids defend Ithomiine butterflies against a spider predator. *Nature* 309: 707–709.
- **Brown, Jr., K.S.** 1987. Chemistry at the Solanaceae/Ithomiinae Interface. *Ann. Missouri Bot. Gard.* 74: 359–397
- **Bruyns, P. V., al Farsi, A., & Hedderson, T.** 2010. Phylogenetic relationships of *Caralluma* R. Br. (Apocynaceae). *Taxon* 59: 1031–1043.
- **Burge, D.O., Mugford, K., Hastings, A. & Agrawal, A.** 2013. Phylogeny of the plant genus *Pachypodium* (Apocynaceae). *Peer J.* 1: 1–20.
- **Burzynski, E.A., Minbiole, K.P.C. & Livshultz, T.** 2015. New sources of lycopsamine-type pyrrolizidine alkaloids and their distribution in Apocynaceae. *Biochem. Syst. Ecol.* 59: 331–339.
- Chen, T., Mei, N. & Fu, P.P. 2010. Genotoxicity of pyrrolizidine alkaloids. *J. Appl. Toxicol.* 30: 183–196.
- Colegate, S. M., Gardner, D. R., Betz, J. M., Fischer, O. W., Liede-Schumann, S. & Boppré, M. 2016. Pro-toxic 1, 2-Dehydropyrrolizidine Alkaloid Esters, Including Unprecedented 10-Membered Macrocyclic Diesters, in the Medicinally-used *Alafia* cf. *caudata* and *Amphineurion marginatum* (Apocynaceae: Apocynoideae: Nerieae and Apocyneae). *Phytochem. Anal.* 27: 257–276. DOI 10.1002/pca.2624
- Candolle, A.P. de 1844. *Prodromus systematis naturalis regni vegetabilis*, vol. 8. Parisis [Paris]: Sumptibus Fortin, etc. http://dx.doi.org/10.5962/bhl.title.286
- Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. 2012. jModelTest 2 : More models, new heuristics and parallel computing. *Nature Meth.* 9: 772. http://dx.doi.org/10.1038/nmeth.2109
- del Castillo, B., de Aguirre, A.E., Bretón, J.L., Gonzalez, A.G. & Trujillo, J. 1970. Loroquin, a new necine isolated from *Urechites karwinsky* Mueller (1-hydroxymethylene-7-keto-dihydropyrrolizine). *Tetrahedron letters* 11:1219–1220.
- **Despres, L., David, J. P. & Gallet, C.** 2007. The evolutionary ecology of insect resistance to plant chemicals. *Trends Ecol. Evol.* 22: 298–307. doi:10.1016/j.tree.2007.02.010

- **Diego, N. & Pérez, L.L.** 2006. *Thoreauea guerrerensis* (Apocynaceae, Apocynoideae), una nueva especie de Guerrero, México. *Novon* 16: 332–335.
- **Edgar, J.A.** 1984. Parsonsieae: Ancestral larval foodplants of the Danainae and Ithomiinae. Pp. 91–93 in: Ackery, P.R. & Vane-Wright, R.I. (eds.), *The biology of butterflies*. London: the Royal Entomological Society.
- **Edgar, J.A., Roeder, E. & Molyneux, R.J.** 2002. Honey from plants containing pyrrolizidine alkaloids: a potential threat to health. *J. Agric. Food Chem.* 50: 2719–2730.
- **Edgar, J.A., Molyneux, R.J. & Colegate, S.M.** 2015. Pyrrolizidine alkaloids: Potential role in the etiology of cancers, pulmonary hypetension, congential anomalies, and liver disease. *Chem. Res. Toxicol.* 28: 4–20.
- **Endress, M.E. & Bruyns P.** 2000. A revised classification of the Apocynaceae s.l. *Bot. Rev.* (*Lancaster*) 66: 1–56.
- Endress, .E., Hesse, M., Nilsson, S. Guggisberg, A. & Zhu, J.-P. 1990. The systematic position of the Holarrheninae (Apocynaceae). *Pl. Syst. Evol.* 171: 157–185.
- Endress, M.E., Sennblad, B., Nilsson, S., Civeyrel, L., Chase, M., Huysmans, S., Grafström, E. & Bremer, B. 1996. A phylogenetic analysis of Apocynaceae s. str. and some related taxa in Gentianales: a multidisciplinary approach. *Opera Bot. Belg.*7: 59–102.
- Endress, M.E., van der Ham, R.W.J.M., Nilsson, S, Civeyrel, L., Chase, M.W., Sennblad, B., Potgieter, K., Joseph, J., Powell, M., Lorence, D., Zimmerman, Y.-M., & Albert, V.A. 2007a. A phylogenetic analysis of Alyxieae (Apocynaceae) based on rbcL, matK, trnL intron, trnL-F spacer sequences, and morphological characters. *Ann. Missouri Bot. Gard.* 94: 1–35.
- Endress, M.E., Liede-Schumann, S. & Meve, U. 2007b. Advances in *Apocynaceae*: The enlightenment, an introduction. *Ann. Missouri Bot. Gard.* 94: 259–267.
- Endress, M.E., Liede-Schumann, S. & Meve, U. 2014. An updated classification for Apocynaceae. *Phytotaxa* 159: 175–194.
- **Ezcurra, C.** 1981. Novedades en los géneros *Temnadenia* y *Macrosiphonia* (Apocynaceae). *Hickenia* 1: 241–245.

- Ezcurra, C., Endress, M.E. & Leeuwenberg, A.J.M. 1992. Apocynaceae. Pp. 1–121 in: Spichiger, R & Ramella, L. (eds.), *Flora del Paraguay*, *Vol. 17*. Conservatoire et Genève: Conservatoire et Jardin botaniques de la Ville de Genève, and St. Louis: Missouri Botanical Garden, St. Louis.
- **Goyder, D, Nicholas, A & Liede-Schumann, S**. 2007. Phylogenetic relationships in subtribe Asclepiadinae (Apocynaceae: Asclepiadoideae). *Ann. Missouri Bot. Gard*. 94: 423–434. DOI: 10.3417/0026-6493(2007)94[423:PRISAA]2.0.CO;2.
- **Guillaumin, A.** 1941 Matériaux pour la flore de la Nouvelle-Calédonie. LIX. Révision des Apocynacées. *Bull. Soc. Bot. Fr.* 88: 358–359.
- **Graybeal, A.** 1998. Is it better to add taxa or characters to a difficult phylogenetic problem? *Syst. Biol.* 47: 9–17.
- Hartman, T. & Ober, D. 2000. Biosynthesis and metabolism of pyrrolizidine alkaloids in plants and specialized insect herbivores. Pp. 207–224 in: Leeper, F.J. & Vederas, J.C. (eds.), Topics in current chemistry: Biosynthesis. Aromatic polyketides, isoprenoids, alkaloids. Berlin: Springer.
- **Hegnauer, R.** 1970. Cardenolide und Bufadienolida (= Cardenolide): Verbreitung und systematische Bedeutung. *Pl. Med. (Stuttgart)* 19: 137–153.
- Hegnauer, R. 1989. Chemotaxonomie der Pflanzen 8. Birkhäuser: Basel.
- **Hendrian & Kondo, K**. 2007a. Molecular phylogeny of *Ochrosia sensu lato* (Apocynaceae) based on ITS sequence data: an evidence for the inclusion of *Neisosperma. Chromosome Bot.* 2: 127–132.
- **Hendrian & Kondo, K**. 2007b. Molecular phylogeny of *Ochrosia sensu lato* (Apocynaceae) based on rps16 intron and ITS sequence data: supporting the inclusion of *Neisosperma*. *Chromosome Bot*. 2: 133–140.
- **Hendrian & Kondo, K**. 2007c. Monophyly of *Ochrosia sensu lato* (Apocynaceae): evidence from ITS, rps16 intron and morphological characters. *Chromosome Bot.* 2: 141–149.
- Hernández-Baz, F., Coates, R., Teston, J.A. & González, J.M. 2013. Scena propylea (Druce) (Lepidoptera: Erebidae) an endemic species of Mexico. Neotrop. Entomol. doi:10.1007/s13744-013-0119-3

- **Honda, Y., Honda, K. & Ômura, H.** 2006. Major components in the hairpencil secretion of a butterfly, Euploea mulciber (Lepidoptera, Danaidae): Their origins and male behavioral responses to pyrrolizidine alkaloids. *J. Insect Physiol.* 52: 1043–1053.
- **Huelsenbeck, J.P. & Ronquist, F.R.** 2001. MrBayes: Bayesian inference of phylogeny. *Biometrics* 17: 754–755.
- **Hutchings, A.A.** 1989. A survey and analysis of traditional medicinal plants as used by the Zulu, Xhosa and Sotho. *Bothalia* 19: 111–123.
- **Katoh, K.** 2013. Multiple Alignment using Fast Fourier Transform (MAFFT), version 7 http://mafft.cbrc.jp/alignment/server/
- **Kisakürek, M. V., A. J. M. Leeuwenberg & M. Hesse.** 1983. A chemotaxonomic investigation of the plant families of Apocynaceae, Loganiaceae, and Rubiaceae by their indole alkaloid content, Pp. 211–376 in: Pelletier, W.W. (ed.), *Alkaloids: Chemical and biological perspectives*, vol. 1. New York: Wiley.
- **Leeuwenberg, A.J.M.** 1994. Series of Apocynaceae XXXVIII. Taxa of Apocynaceae above the genus level. *Agric. Univ. Wageningen Pap.* 94: 45–60.
- **Liede, S. & Kunze, H.** 2002. *Cynanchum* and the Cynanchinae (Apocynaceae Asclepiadoideae) a molecular, anatomical and latex triterpenoid study. *Org. Divers. Evol.* 2: 239–269.
- Liede-Schumann, S., Khanum, R., Mumtaz, A.S., Gherghel, I. & Pahlevani, A. 2016. Going west – A subtropical lineage (*Vincetoxicum*, Apocynaceae: Asclepiadoideae) expanding into Europe. *Molec. Phylogenet. Evol.* 94: 463–46.
- **Livshultz, T.** 2010. The phylogenetic position of milkweeds (Apocynaceae subfamilies Secamonoideae and Asclepiadoideae): evidence from the nucleus and chloroplast. *Taxon* 59: 1016–1030.
- **Livshultz, T., Middleton, D.J., Endress, M.E. & Williams, J.K.** 2007. Phylogeny of Apocynoideae and the APSA clade (Apocynaceae s.l.). *Ann. Missouri Bot. Gard.* 94: 324–359.
- **Maddison, W.P. & D.R. Maddison.** 2011. Mesquite: A modular system for evolutionary analysis, version 2.75 <a href="http://mesquiteproject.org">http://mesquiteproject.org</a>.

- **Malcolm, S.B. & Brower, L.P.** 1989. Evolutionary and ecological implications of cardenolide sequestration in the monarch butterfly. *Experientia* 45: 284–295. doi:10.1007/BF01951814
- Meve, U. & Liede, S. 2001. Inclusion of *Tenaris* and *Macropetalum* in *Brachystelma* (Apocynaceae-Asclepiadoideae-Ceropegieae) inferred from non-coding nuclear and chloroplast DNA sequences. *Plant Syst. Evol.* 228: 89–105
- **Meve, U. & Liede, S.** 2002. A molecular phylogeny and generic rearrangement of the stapelioid Ceropegieae (Apocynaceae- Asclepiadoideae). *Pl. Syst. Evol.* 234: 171–209.
- **Middleton, D.J**. 1996. *Ecua*, a new genus of Apocynaceae from Malesia. *Blumea* 41: 33–35.
- **Middleton, D J.** 1997. A revision of *Parsonsia* R. Br. (Apocynaceae) in Malesia. *Blumea* 42: 191–248.
- **Middleton, D.J. & Livshultz, T.** 2012. *Streptoechites* gen. nov., a new genus of Asian Apocynaceae. *Adansonia*, sér. 3, 34: 365–375.
- Miers, J. 1878. On the Apocynaceae of South America. London: Williams & Norgate.
- Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 in: *Proceedings of the Gateway computing environments workshop (GCE)*, 14 Nov 2010, New Orleans: Institute of Electrical and Electronics Engineers.
- **Monachino, J.** 1957. A new species of *Prestonia* from Brazil. *Phytologia* 6: 12–13.
- **Monachino, J.** 1961. Apocynaceae, in: Maguire, B., Wurdack, J.J., and collaborators. The Botany of the Guayana Highland Part IV. *Mem. New York Bot. Gard.* 10: 59–65.
- **Morales, J.F.** 1997. A reevaluation of *Echites* and *Prestonia* section *Coalitae* (Apocynaceae). *Brittonia* 49: 328–336.
- Morales, J.F. 1998. Salpinctes (Apocynaceae) is a synonym of Mandevilla. Novon 8: 429.
- **Morales, J.F.** 1999a. *Rhodocalyx* (Apocynaceae), a new synonym of *Prestonia. Novon* 9: 89–91.
- **Morales, J.F.** 1999b. *Hylaea* (Apocynaceae-Apocynoideae), a new genus from South America. *Novon* 9: 83–85.

- **Morales, J.F.** 2002a. Studies in Neotropical Apocynaceae I: A revision of the genus *Laubertia. Rhodora* 104: 170–186.
- **Morales, J.F.** 2002b. Studies in Neotropical Apocynaceae II: A revision of the genus *Fernaldia. Rhodora* 104: 186–200.
- **Morales, J.F.** 2005a. Estudios en las Apocynaceae Neotropicales XIII: revisión del género *Temnadenia* (Apocynoideae, Echiteae). *Candollea* 60: 207–231.
- **Morales, J.F.** 2005b. Estudios en las Apocynaceae Neotropicales XX: Monografia del generos *Peltastes* (Apocynoideae, Echiteae), con una sinopsis de *Stipecoma* (Apocynoideae, Echiteae). *Candollea* 60: 289–334.
- **Morales, J.F.** 2005c. Estudios en las Apocynaceae Neotropicales XV: sinopsis del género *Thoreauea* (Apocynoideae, Echiteae), con una nueva especie de Veracruz, México. *Brittonia* 53: 258–263.
- **Morales, J.F.** 2006a. Estudios en las Apocynaceae Neotropicales XXIV: *Bahiella* (Apocynoideae: Echiteae) un desapercibido género endémico de Bahia, Brasil. *Sida* 22: 333–353.
- **Morales, J.F.** 2006b. Estudios en las Apocynaceae Neotropicales XXVIII: la familia Apocynaceae (Apocynoideae, Rauvolfioideae) de El Salvador, Centroamérica. *Darwiniana* 44: 453–489.
- **Morales, J.F.** 2009a. Estudios en las Apocynaceae Neotropicales XXXIX: revision de las Apocynoideae y Rauvolfioideae de Honduras. *Anales Jard. Bot. Madrid* 66: 217–262.
- **Morales, J.F.** 2009b. Estudios en las Apocynaceae neotropicales XXXVII: monografía del género *Rhabdadenia* (Apocynoideae: Echiteae). *J. Bot. Res. Inst. Texas* 3: 541–564.
- **Morales, J.F. & Liede-Schumann, S**. 2016. The genus *Prestonia* (Apocynaceae) in Colombia. *Phytotaxa* 265: 204–224.
- **Morales, J.F. & Williams, J.K.** 2004. *Allotoonia*, a new neotropical genus of Apocynaceae based on a subgeneric segregated of *Echites*. *Sida* 21: 133–158.
- Morton, J. F., Alvarez, E. & Quiñonez, C. 1990. Loroco, *Fernaldia pandurata* (A. DC.) Woodson (Apocynaceae): A popular edible flower of Central America. *Econ. Bot.* 44: 301–310.

- Müller Argoviensis. J. 1860. Apocynaceae. Pp. 1–1955 in: Martius, C.F.P. (ed.), *Flora Brasiliensis* 6(1). Leipzig: Fleischer.
- **Nishida, R.** 2002. Sequestration of defensive substances from plants by Lepidoptera. *Ann. Rev. Entomol.* 47: 57–92.
- Nixon, K.C. & Carpenter, J.M. 1996. On simultaneous analysis. *Cladistics* 12: 221–241.
- **Ober, D. & Hartmann, T.** 2000. Phylogenetic origin of a secondary pathway: The case of pyrrolizidine alkaloids. *Pl. Molec. Biol.* 44: 445–450.
- Orr, A.G., Trigo, J.R., Witte, L. & Hartmann, T. 1996. Sequestration of pyrrolizidine alkaloids by larvae of *Tellervo zoilus* (Lepidoptera: Ithomiinae) and their role in the chemical protection of adults against the spider *Nephila maculata* (Araneidae). *Chemoecol.* 7: 68–73.
- **Pichon, M**. 1948. Classification des Apocynacées XIX, Le rétinacle des Echitoideés. *Bull. Soc. Bot. France* 95: 211–216.
- **Pichon, M.** 1950a. Classification des Apocynacées XXV, Echitoideés. *Mem. Mus. Natl. Hist. Nat. sér. B, Bot.*1: 1–142.
- **Pichon, M.** 1950b. Classification des Apocynacées: XXVIII, Supplémente aux Plumerioïdées, *Mem. Mus. Natl. Hist. Nat. sér. B, Bot.* 1: 1–74.
- **Pichon, M.** 1950c. Classification des Apocynacées: XII, Les *Parsonsia* et les *Artia* de l'herbier du Muséum. *Notul. Syst. (Paris)* 14: 4–21.
- **Pliske, T.E.** 1975. Attraction of Lepidoptera to plants containing pyrrolizidine alkaloids. *Environ. Entomol.*4: 455–473.
- **Potgieter, K.** 1999. Phylogenetic study of Apocynaceae Juss. and *Aspidosperma* Mart. and Zucc. Unpublished PhD thesis from the University of Illinois at Urbana-Champaign.
- **Potgieter, K. & Albert, V.A.** 2001. Phylognetic relationhips within Apocynaceae s.l. based on *trnL* intron and *trnL-F* spacer sequences and propagule characters. *Ann. Missouri Bot. Gard.* 88: 523–549.
- Rambaut, A. 2014. FigTree, version 1.4.2. http://tree.bio.ed.ac.uk/software/figtree/
- Rambaut, A. & Drummond, A.J., 2007a. Tracer. Version 1.5. http://beast.bio.ed.ac.uk/Tracer/

- Rambaut, A. & Drummond, A.J. 2007b. TreeAnnotator, version 1.5.4. http://beast.bio.ed.ac.uk/
- Rannala, B., Huelsenbeck, J.P., Yang, Z. & Nielsen, R. 1998. Taxon sampling and the accuracy of large phylogenies. *Syst. Biol.* 47: 702–710.
- **Rapini, A.** 2012. Taxonomy "under construction": advances in the systematics of Apocynaceae, with emphasis on the Brazilian Asclepiadoideae. *Rodriguésia* 63: 75–88.
- **Rapini, A., Chase, M.W. & Konno, T.U.P.** 2006. Phylogenetics of South American Asclepiadeae (Apocynaceae). *Taxon* 55: 119–124.
- Reeves, G., Chase, M.W., Goldblatt, P., Rudall, P.J., Fay, M.F., Cox, A.V., Lejeune, B. & Souza-Chies, T. 2001. Molecular systematics of Iridaceae: evidence from four plastid DNA regions. *Amer. J. Bot.* 88: 2074–2087.
- **Reimann, A., Nurhayati, N., Backenköhler, A. & Ober, D.** 2004. Repeated evolution of the pyrrolizidine alkaloid–mediated defense system in separate angiosperm lineages. *Pl. Cell* 16: 2772–2784.
- **Ribeiro, P.L., Rapini, A., Damascena, L.S. & van den Berg, C.** 2014. Plant diversification in the Espinhaço Range: Insights from the biogeography of *Minaria* (Apocynaceae). *Taxon* 63: 1253–1264.
- **Ronquist, F. & Huelsenbeck, J.P.** 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
- Sang, T., Crawford, D.J. & Stuessy, T. 1995. Documentation of reticulate evolution in peonies (*Paeonia*) using internal transcribed spacer sequences of nuclear ribosomal DNA: implication for biogeography and concerted evolution. *Proc. Natl. Acad. Sci. U.S.A.* 92: 6813–6817.
- **Schultes, R.E.** 1979. De plantis toxicariis e mundo novo tropicale commentationes. XIX. Biodynamic apocynaceous plants of the northeast Amazon. *J. Ethnopharmacol.* 1: 165–192.
- **Schulz, S.** 1998. Insect-plant interactions-metabolism of plant compounds to pheromones and allomones by Lepidoptera and leaf beetles. *Eur. J. Org. Chem.* 1998: 13–20.
- Schulz, S., Beccaloni, G., Brown, Jr., K. S., Boppré, M., Freitas, A. V. L., Ockenfels, P. & Trigo, J. R. 2004. Semiochemicals derived from pyrrolizidine alkaloids in male

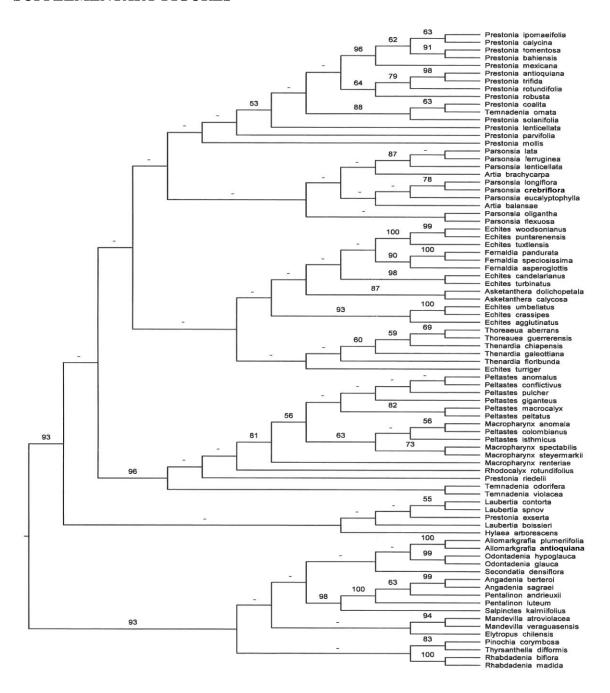
- ithomiine butterflies (Lepidoptera: Nymphalidae: Ithomiinae). *Biochem. Syst. Ecol.* 32: 699–7713.
- **Schumann, K.M.** 1895. Apocynaceae. Pp. 109–189 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien* IV(2). Leipzig: Engelmann, 1897.
- **Sennblad, B. & Bremer, B.** 2002. Classification of Apocynaceae s.l. according to a new approach combining Linnaean and phylogenetic taxonomy. *Syst. Biol.* 5: 389–409.
- **Sennblad, B., Endress, M.E. & Bremer, B.** 1998. Morphology and molecular data in phylogenetic fraternity: the tribe Wrightieae (Apocynaceae) revisited. *Amer. J. Bot.* 85: 1143–1158.
- **Sheahan, M.C. & Chase, M.W.** 2000. Phylogenetic relationships within Zygophyllaceae based on DNA sequences of three plastid regions with special emphasis on Zygophylloideae. *Syst. Bot.* 25: 371–384.
- Silva, U.C.S., Rapini, A., Liede-Schumann, S., Ribeiro, P.L. & van den Berg, C. 2012. Taxonomic considerations on Metastelmatinae (Apocynaceae) based on plastid and nuclear DNA datasets. *Syst. Bot.* 37: 795–806.
- Simões, A.O., Kinoshita, L.S., Koch, I., Silva. M.J. & Endress, M.E. 2016. Systematics and character evolution of Vinceae (Apocynaceae). *Taxon* 65: 99–122.
- **Spalik, K., Downie, S.R. & Watson, M.F.** 2009. Generic delimitations within the *Sium* alliance (Apiaceae tribe Oenantheae) inferred from cpDNA rps16-50trnK (UUU) and nrDNA ITS sequences. *Taxon* 58: 735–748.
- **Stamatakis**, **A**. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
- **Stamatakis, A., Hoover, P. & Rougemont, J.** 2008. A rapid bootstrap algorithm for the RAxML Web servers. *Syst. Biol.* 57: 758–771.
- Surveswaran, S., Kamble, M.Y., Vadav, S.R. & Sun, M. 2009. Molecular phylogeny of *Ceropegia* (Asclepiadoideae, Apocynaceae) from Indian Western Ghats. *Pl. Syst. Evol.* 281: 51–63.
- **Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J.** 1991. Universal primers for amplification of three noncoding regions of chloroplast DNA. *Annual Rev. Pl. Physiol. Pl. Molec. Biol.* 17: 1105–1109.

- **Thoden, T.C. & Boppré, M.** 2010. Plants producing pyrrolizidine alkaloids: sustainable tools for nematode management? *Nematology* 12: 1–24.
- **Trigo, J.R.** 2000. The chemistry of antipredator defense by secondary compounds in neotropical Lepidoptera: Facts, perspectives and caveats. *J. Braz. Chem. Soc.* 11: 551–561.
- **Trigo, J.R.** 2011. Effects of pyrrolizidine alkaloids through different trophic levels. *Phytochem. Rev.* 10: 83–98.
- Trigo, J.R., Brown, K.S., Jr., Witte, L., Hartmann, T., Ernst, L. & Barata, L.E.S. 1996. Pyrrolilzidine alkaloids: Different acquisition and use patterns in Apocynaceae and Solanaceae feeding ithomiine butterflies (Lepidoptera: Nymphalidae): *Biol. J. Linn. Soc.* 58: 99–123.
- **Trovo, M., Andrade, M.J., Sano, P.T., Ribeiro, P.L. & van den Berg, C.** 2013. Molecular phylogenetics and biogeography of Neotropical Paepalanthoideae with emphasis on Brazilian *Paepalanthus* (Eriocaulaceae). *Bot. J. Linn. Soc.* 171: 225–243.
- Van Beck, T.A. & Van Gessel, M.A.J.T. 1988. Alkaloids of *Tabernaemontana* species.
  Pp. 76–226 in: S.W. Pelletier (ed.), *Alkaloids: Chemical and biological perspectives*, Vol. 6. New York: Wiley.
- Van Beck, T.A., Verpoorte, R., Baerheim-Svendsen, A., Leeuwenberg, A.J.M. & Bisset, N.G. 1984. *Tabernaemontana* L. (Apocynaceae): A review of its taxonomy, phytochemistry, ethnobotany and pharmacology. *J. Ethnopharmacol.* 10: 1–156
- Wanntorp, L., Kocyan, A. & Renner, S.S. 2006. Wax plants disentangled: A phylogeny of *Hoya* (Apocynaceae) using molecular markers. *Molec. Phylogenet. Evol.* 39: 722–733.
- Wanntorp, L., Grudinski, M., Forster, P.I. Muellner-Riehl, A.N. & Grimm, G.W. 2014. Wax plants (*Hoya*, Apocynaceae) evolution: Epiphytism drives successful radiation. *Taxon* 63: 89–102.
- **Wiedenfeld, H. & Edgar, J.A.** 2011. Toxicity of pyrrolizidine alkaloids to humans and ruminants. *Phytochem. Rev.* 20: 137–151.

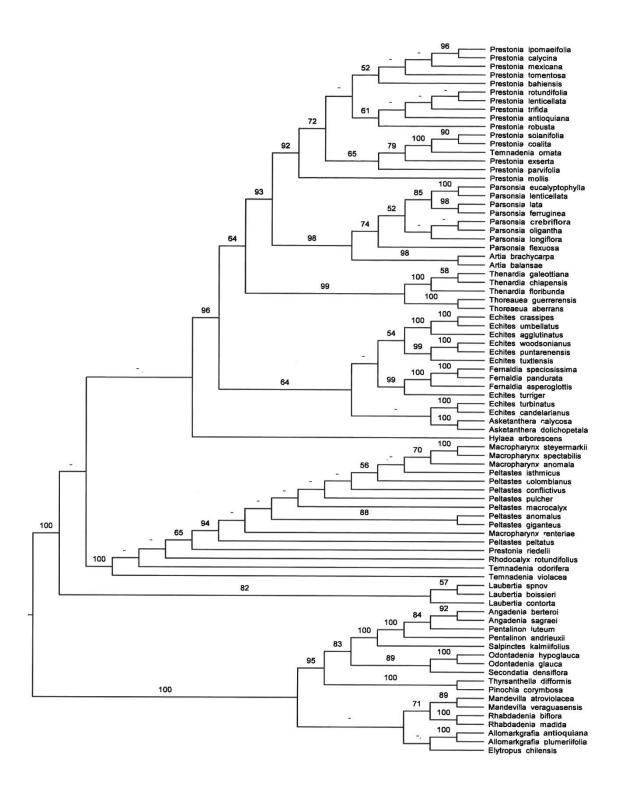
- Weitemier, K., Straub, S.C.K., Fishbein, M. & Liston, A. 2015. Intragenomic polymorphisms among high-copy loci: a genus-wide study of nuclear ribosomal DNA in *Asclepias* (Apocynaceae) *PeerJ* 3:e718. doi.org/10.7717/peerj.718.
- White, T.J., Bruns T, Leem S. & Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M.A., Gelfand, D.H., Sninsky, & J.J., White, T.J. (eds.). PCR Protocols: A Guide to Methods and Applications. San Diego, CA: Academic Press.
- Whitten, W.M., Williams, N.H. & Chase, M.W. 2000. Subtribal and generic relationships of Maxillarieae (Orchidaceae) with emphasis on Stanhopeinae: combined molecular evidence. *Amer. J. Bot.* 87: 1842–1856.
- **Wiens, J.J.** 1998. Combining data sets with different phylogenetic stories. *Syst. Biol.* 47: 568–581.
- **Wiens, J. J.** 2003. Missing data, incomplete taxa, and phylogenetic accuracy. *Syst. Biol.* 52: 528–538.
- Williams, J.B. 1996. *Parsonsia. In*, Foster, P.I. & Williams, J.B. (eds.). *Fl. Australia* 28: 54–189.
- **Williams, J.K.** 1995. A new species of *Thenardia* (Apocynaceae, Apocynoideae) from Chiapas, Mexico, with notes on the genus. *Brittonia* 47: 403–407.
- Williams, J.K. 1998. A revision of *Thenardia* (Apocynaceae, Apocynoideae). *Lundellia* 78: 78–94.
- Williams, J.K. 2002. *Thoreauea* (Apocynaceae: Apocynoideae), a new genus from Oaxaca, Mexico. *Lundellia* 5: 47–58.
- **Williams, J.K.** 2004. Polyphyly of the genus *Echites* (Apocynaceae: Apocynoideae: Echiteae): Evidence based on a morphological cladistic analysis. *Sida* 21: 117–131.
- **Wong, S.K., Lim, Y.Y. & Chan, E.W.C.** 2013. Botany, uses, phytochemistry and pharmacology of selected Apocynaceae species: A review. *Pharmacogn. Commun.* 3: 2–11.
- **Woodson, R.E., Jr.** 1931a. Apocynaceae, p. 453 in: Gleason, H.A. (ed.), Botanical results of the Tyler-Duida Expedition. *Bull. Torrey Bot. Club* 58: 277–506.
- **Woodson, R.E., Jr.** 1931b. New or otherwise noteworthy Apocynaceae of Tropical America. *Ann. Missouri Bot. Gard.* 18: 541–557.

- **Woodson, R.E., Jr.** 1932a. New or otherwise noteworthy Apocynaceae of Tropical America II. *Ann. Missouri Bot. Gard.* 19: 45–76.
- **Woodson, R.E., Jr.** 1932b. New or otherwise noteworthy Apocynaceae of Tropical America III. *Ann. Missouri Bot. Gard.* 19: 375–387.
- **Woodson, R.E., Jr.** 1933. Studies in the Apocynaceae IV. The American genera of Echitoideae. *Ann. Missouri Bot. Gard.* 20: 605–790.
- **Woodson, R.E., Jr.** 1935. Studies in the Apocynaceae. IV. The American genera of Echitoideae. *Ann. Missouri Bot. Gard.* 22: 153–306.
- **Woodson, R.E., Jr.** 1936. Studies in the Apocynaceae. IV. The American genera of Echitoideae. *Ann. Missouri Bot. Gard.* 23: 169–438.
- **Xifreda, C.C.** 1984. Estudios sobre Apocynaceae Argentinas IV. El género *Macropharynx* y una nueva combinación. *Kurtziana* 17: 163–167.
- **Zhu, J.-P., Guggisberg A., Kalt-Hadamowsky, M. & Hesse, M.** 1990. Chemotaxonomic study of the genus *Tabernaemontana* (Apocynaceae) based on their indole alkaloid content. *Pl. Syst. Evol.* 172: 13–34.

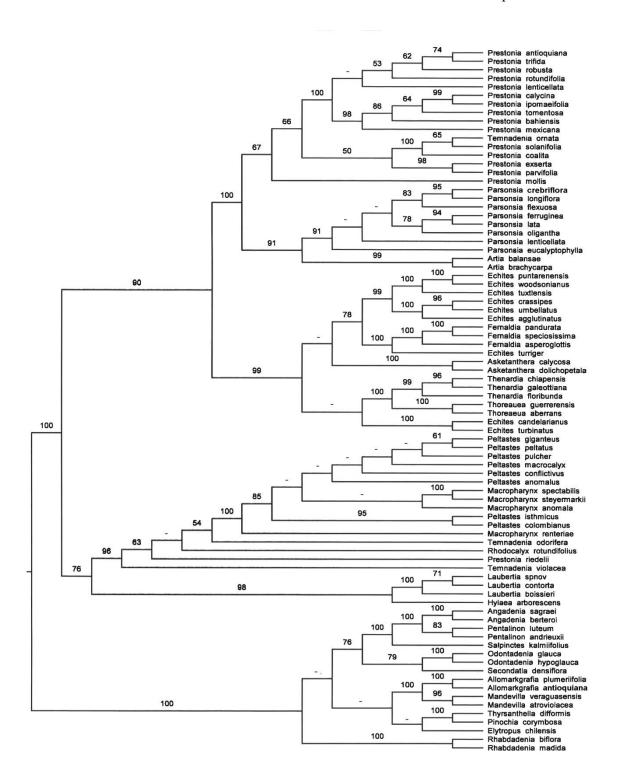
## SUPPLEMENTARY FIGURES



**Fig. S1**. Maximum likelihood consensus tree based on *trnLF* dataset. Bootstrap values < 50% are indicated by a dash (-).



**Fig. S2**. Maximum likelihood consensus tree based on *rpl16* dataset. Bootstrap values < 50% are indicated by a dash (-).



**Fig. S3**. Maximum likelihood consensus tree based on *matK-trnK* dataset. Bootstrap values < 50% are indicated by a dash (-).

# **Publication 3**

Morales, J.F., M. Endress & S. Liede-Schumann. A phylogenetic study of the genus *Prestonia* (Apocynaceae) (accepted: Annals of the Missouri Botanical Garden, reference number: ambg-D-17-00002) SYSTEMATICS OF PRESTONIA (APOCYNACEAE: APOCYNOIDS: ECHITEAE) EIGHTY YEARS AFTER WOODSON<sup>1,2</sup>

J. Francisco Morales, Mary E. Endress and Sigrid Liede-Schumann

## ABSTRACT

Prestonia (Apocynoideae, Echiteae) comprises ca. 58 species, which are lianas with eglandular leaves, axillary or terminal cymose inflorescences, sepals with a single colleter, flowers with an annular corona around the mouth and free corona lobes, follicular fruits and truncate seeds that are comose at the micropylar end. Three infrageneric classifications have been proposed in the last 110 years, all of them based only on morphological characters and none of which have been tested with molecular data. In the present study, 62 nuclear and 258 chloroplast sequences from 65 species were analyzed in order to test the infrageneric classifications proposed for *Prestonia*, including representatives of all sections ever proposed, as well as to test the monophyly of the genus with a larger sample compared to previous studies. *Prestonia* was shown to be monophyletic, but the infrageneric sections proposed by Schumann, Woodson and Pichon are all non-monophyletic. We propose a new infrageneric classification for *Prestonia*, recognizing six sections: *Coalitae*, *Denticulata*, *Exsertae*, *Haemadictyon*, *Mollis* and *Prestonia*. A key to the sections is provided. *Prestonia pickelii* is removed from the synonymy of *P. quinquangularis* and resurrected as an accepted species.

Keywords: apocynoids, classification, ITS, molecular phylogeny, Prestoniinae, systematics

<sup>1</sup>We dedicate this work to the memory of Robert E. Woodson, Jr. to commemorate the 80<sup>th</sup> anniversary of his landmark monograph of the Neotropical apocynoids published in the Annals in 1936.

<sup>2</sup>Xavier Cornejo (GUAY) and Alessandro Rapini (HUESF) sent preserved material of *P. amabilis* and *P. bahiensis* respectively; Xavier also provided several photos and notes of species of *Prestonia* from Ecuador; their help is gratefully acknowledged. We thank Paul Forster (BRI) for generously sending leaf samples of several species of *Parsonsia*. Barry and Isa Hammel (MO) provided several DNA samples of species from Costa Rica; their support in the last four years is greatly appreciated. Bruce Hansen (USF) generously supported the visit of the first author to the University of South Florida. We extend our thanks to the following herbaria, which allowed the study of their collections: B, C, CEPEC, CICY, COAH, COL, CR (including INB), E, F, G, GUAY, HUA, HUQ, JAR, JAUM, L, M, MBML, MEDEL, MHES, MO, NY, O, P, PMA, RB, S, U, UBT, US, USF, USJ, WAG, and Z. Angelika Täuber and Margit Gebauer from Plant Systematics Molecular Laboratory, Universität Bayreuth, Germany assisted and helped during the DNA extraction and amplification processes. The first author thanks Michael Grayum (MO) his continued support in many ways, providing critical references and the proper interpretation of the International Code of Botanical Nomenclature. We gratefully thank Andre Simões (University of Campinas, Brazil) and Rafael Acuña (University of Costa Rica, Costa Rica) for kindly sharing their original and modified *matK* amplification protocols. This study was supported by a PhD research grant (Forschungsstipendien für Doktoranden und Nachwuchswissenschaftler für mehr als 6 Monate) from the Deutscher Akademischer Austauschdienst (DAAD) to J. Francisco Morales, which is gratefully acknowledged. Financial support was provided by the University of Bayreuth Graduate School (Germany) and the Deutscher Akademischer Austauschdienst (Germany). The first author wishes to express his gratitude to the Missouri Botanical Garden, in particular, Olga Martha Montiel, who have supported several visits to their herbarium over the last decade. The first author thanks the following persons for field assistance: Alfredo Fuentes, Alev Oder, and Daniel Soto (Bolivia), Marccus Alves, Diogo Araujo, Andre Fontana, Ludovic Kollmann, Isa Lucia de Morais, Ricardo Perdiz, and Alessandro Rapini (Brazil), Fernando Alzate, Julio Betancur, Ricardo Callejas, Dayron Cárdenas, Felipe Cardona, Álvaro Idárraga, and Mario

Alberto Quijano (Colombia), Ronald Abarca, Isler Chinchilla, Frank González, and Luis Fonseca (Costa Rica), Gabriel Cerén, Eunice Echeverría, and Jenny Menjivar (El Salvador), Carlos Rocha (Nicaragua), Cármen Galdámez (Panama), Carlos Amasifuen, Aniceto Daza and Carlos Reynel (Perú), and Ronald Abarca and Carlos González (Venezuela).

Apocynaceae includes more than 366 genera and 5000 species (Rapini, 2012) and is distributed throughout the tropics, subtropics and temperate regions. The classification by Endress & Bruyns (2000) reunited Apocynaceae and Asclepiadaceae and divided it into five subfamilies: Rauvolfioideae and Apocynoideae from the traditional Apocynaceae, and Periplocoideae, Secamonoideae and Asclepiadoideae from the traditional Asclepiadaceae. Since then a number of phylogenetic studies have contributed to the resolution of relationships at the tribal, subtribal or generic level, which has led to the reorganization or description of tribes and subtribes and the synonymization of several genera (e.g. Meve & Liede, 2004; Simões et al., 2004, 2006, 2010; Liede-Schumann et al., 2005; Rapini et al., 2006, 2011; Endress & Hansen, 2007, Endress et al., 2007a, b; Livshultz et al., 2007; Silva et al. 2012; Khanum et al. 2016; Meve et al., 2017; Morales et al. (2017). Despite these advances, many groups are still unresolved or the resolution is too low to accurately define their relationships. Apocynoideae and Rauvolfioideae remained paraphyletic, and thus informal ranks were proposed for these two subfamilies by Simões et al. (2016). The family thus currently comprises three formal subfamilies (Periplocoideae, Secamonoideae, and Asclepiadaceae) and two informal groups (apocynoids and rauvolfioids), the classification followed in Morales et al. (2017) and here.

<sup>&</sup>lt;sup>3</sup> Department of Plant Systematics, University of Bayreuth, Universitätstrasse 30, 95440 Bayreuth, Germany. <u>drjfranciscomorales@gmail.com</u> (J.F. Morales); <u>sigrid.liede@unibayreuth.de</u> (S. Liede-Schumann).

<sup>&</sup>lt;sup>4</sup> Institute of Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, 8008 Zürich, Switzerland. mendress@systbot.uzh.ch (M.E. Endress).

In the apocynoids, nine tribes were proposed by Endress et al. (2014): Apocyneae, Baisseeae, Echiteae, Malouetieae, Mesechiteae, Nerieae, Odontadenieae, Rhabdadenieae and Wrightieae, of which only Echiteae, Mesechiteae and Rhabdadeniae (the last comprising only one genus) have been resolved as monophyletic (Simões et al. 2004; Livshultz et al. 2007, 2010; Morales et al. 2017). Echiteae included 19 genera divided among five subtribes: Echitinae, Parsonsiinae, Peltastinae, Pentalinoninae and Prestoniinae. A molecular phylogenetic evaluation by Morales et al. (2017) found that the tribe and all its subtribes, as circumscribed by Endress et al. (2014), were paraphyletic. One subtribe (Pentalinoninae) was excluded because it came out with the outgroup, and the remaining four subtribes were recircumscribed, and a new tribe (Laubertinae) was described; in addition, two genera (Fernaldia Woodson and Peltastes Woodson) were found to be paraphyletic and were reduced to synonyms. In the classification of Morales et al., 2017), Echiteae comprises 15 genera and ca. 200 species, distributed among five subtribes: Echitinae, Laubertinae, Parsonsiinae, Peltastinae and Prestoniinae. Parsonsia R. Br. (Parsonsiinae, 80-90 species) and *Prestonia R. Br.* (Prestoniinae, ca. 58 species) are by far the largest genera in the tribe, whereas the remaining genera all contain less than 15 species.

Prestonia is distributed in the Neotropics, ranging from Mexico and the West Indies to northern Argentina in a wide variety of habitats, from sea level up to 2800 m. The genus has a complex taxonomic history. It was described by Brown (1810) based a single species (P. tomentosa Brown), characterized by having corollas with an annular corona around the mouth and five free corona lobes within the tube. Lindley (1826) proposed Haemadictyon Lindl., which he distinguished from Prestonia by its nectary composed of five individual lobes (vs. an annular disc nectary). Miers (1878) was the first to reduce Haemadictyon to a synonym of Prestonia, but at the same time, he described other new genera such as Mitozus Miers, Rhaptocarpus Miers, and Temnadenia Miers, to which he transferred several species of Prestonia together with species of unrelated "good genera", creating taxonomic havoc that prevailed for more than 50 years. Baillon (1891) and Schumann (1895) also considered Haemadictyon to be a synonym of Prestonia. Schumann made some additional combinations but he did not evaluate the genera proposed by Miers (1878), and thus, the taxonomy of the Prestonia remained confused. The monotypic Belandra Blake was

described based on a single specimen from Belize and assumed to be related to *Echites* P. Browne and *Odontadenia* Benth., but without discussion of its relationships with *Prestonia* (Blake, 1917). Woodson (1931, 1936) made a significant contribution to clarifying the taxonomy of *Prestonia* by sorting out the nomenclatural mess created by Miers (1878), thereby including *Rhaptocarpus* wholly, and *Mitozus* and *Temnadenia* in part, as synonyms. He also reduced *Belandra* to a synonym, described many new species. His circumscription of *Prestonia* recognized 60 species distributed in four sections (Woodson, 1936). Pichon (1950a) recognized five sections and accepted 66 species, including some species described after the publication of Woodson's classification in 1936 (e.g., *P. dentigera* Woodson, *P. macrophylla* Woodson, *P. pickelii* Markgr.) and proposed a new combination for *Haemadictyon cayennensis* A.DC. (*P. cayennensis* (A. DC.) Pichon),

which was overlooked by Woodson (1936).

Prestonia has continued to be embroiled in disputes regarding its generic circumscription for the last 80 years. Woodson (1931, 1936) included Echites agglutinatus Jacq. in *Prestonia* sect. *Coalitae*, despite its lack of an annular corona around the mouth or free coronal lobes within the tube. Woodson (1960) described P. caudata Woodson, a species with some shared morphological characters with P. agglutinata (Jacq.) Woodson, including lack of an annular corona and free corona lobes, which he thus also included in sect. Coalitae. Gentry (1983) transferred Echites woodsonianus Monac. to Prestonia, based on the acceptance of P. agglutinata. Morales (1997b) evaluated Prestonia sect. Coalitae, and based on floral morphological characters, determined that P. agglutinata, P. caudata, and P. woodsonianus (Monac.) A.H. Gentry were inappropriately placed in Prestonia, and transferred them to *Echites*. In a cladistic analysis based on morphology alone, these three species grouped together in a clade separate from the included species of *Echites* (Williams, 2004), and were thus treated as a separate genus, Allotoonia J.F. Morales & J.K. Williams (Morales & Williams, 2004). In the study by Livshultz et al., 2007, the two included species of Allotoonia were nested in a clade with the included species of Echites and Fernaldia. This relationship was corroborated by Morales et al. (2017), who treated both Allotoonia and Fernaldia as synonyms of Echites.

Rhodocalyx Müll. Arg., a genus of erect herbs from the cerrados of southern South America, was reduced to the synonymy of *Prestonia* by Morales (1999) based on the presence of an annular corona around the corolla mouth. In a molecular phylogenetic study of tribe Mesechiteae by Simões et al. (2004), *Rhodocalyx* was included as part of the outgroup and was retrieved together with *Prestonia riedelii* (Müll. Arg.) Markgr., a relationship that was confirmed by Livshultz et al. (2007), suggesting the paraphyly of *Prestonia. Rhodocalyx* was therefore, reinstated as a valid genus by Livshultz et al. (2007). In the study by Morales et al. (2017), *P. riedelii* was again resolved as sister to *Rhodocalyx* and this clade was far removed from the other included species of *Prestonia* and *P. riedelii* was thus transferred to *Rhodocalyx*.

Temnadenia, as originally circumscribed by Miers (1878), included 22 species, the great majority of which were transferred to other genera of neotropical apocynoids such as *Echites, Prestonia* or *Mandevilla* Lindl. by Woodson is his landmark monograph of American apocynoids (Woodson, 1936), who in the end recognized only four species. An additional species (*T. meyeri* C. Ezcurra) was described by Ezcurra in 1981, but was later treated in *Macropharynx* Rusby (Xifreda, 1984); its closer affinities remain unknown (Morales, 2005b). Three species of *Temnadenia* were included in the study by Morales et al. (2017), one of which, *T. ornata* (Hoehne) Woodson, was deeply nested among species of *Prestonia*, and was therefore transferred to *Prestonia*, in order to make the latter monophyletic. The affinities of both *T. meyeri* and *T. stenantha* Woodson could not be tested, as all PCR reactions for these two species failed (Morales et al., 2017).

Four infrageneric classifications have been proposed for *Prestonia*. The first was that of Baillon (1891), who recognized three sections (*Euprestonia*, *Prestonianthe*, and *Haemadictyon*). But since he did not cite the species included in each section, his proposal is impossible to evaluate. Of the remaining three classifications (Table 1), the first, by Schumann (1895), recognized two sections: *Euprestonia* (seven species) and *Haemadictyon* (three species), based on pubescence of stems, inflorescence type, and sepal shape. The second, by Woodson (1936), recognized four sections: *Acutifoliae*, *Annulares*, *Coalitae* and *Tomentosae*, which were differentiated based on degree of corolla tube pubescence, shape and texture of the sepals, and characteristics of the annular corona, free corona lobes, and

**Table 1**. Sections of *Prestonia* in three infrageneric classifications.

	Total accepted species	Section	Number of species
Schumann (1895)	10	Euprestonia	7
		Haemadictyon	3
Woodson (1936)	60	Acutifoliae	9
		Annulares	33
		Coalitae	4
		Tomentosae	14
Pichon (1950)	66	Euprestonia	11
		Haemadictyon	50
		Rhaptocarpus	3
		Tetraceras	1
		Trichopharynx	1

anthers. The largest section, *Annulares*, included 33 species, *Tomentosae* 14, *Acutifoliae* nine, and *Coalitae*, the smallest, with only four species. The section names *Acutifoliae* and *Tomentosae* were illegitimate, because they included the types of Schumann's sections *Haemadictyon* and *Euprestonia*, respectively. The most recent infrageneric classification of *Prestonia* was proposed by Pichon (1950a), who recognized five sections, based on length of the corolla lobes, type of suprastaminal indumentum within the corolla tube, and features of the gynoecium and androecium. He accepted Schumann's sections *Haemadictyon* (with 50 species, including in the synonymy Woodson's sections *Annulares* and *Acutifoliae*) and *Euprestonia* (with 11 species), but not Woodson's sect. *Coalitae*, the members of which he placed in two different sections: *Rhaptocarpus* (three species) and *Trichopharynx* (one species). *Rhaptocarpus* is an illegitimate name, because it includes the type of Woodon's sect. *Coalitae* (Woodson, 1936), whereas the type of Pichon's fifth section, *Trichopharynx*, was transferred to *Echites* by Morales (1997b). These three infrageneric classification systems differ as to the composition of each section, have nomenclatural problems, were based only on morphological characters, and have never been evaluated using molecular

data. New species have been described by several authors over the years, and many others have been reduced to synonymy (e.g., Woodson, 1939, 1948; Woodson & Schery, 1940, 1942; Gentry, 1974; Markgraf, 1975; Morales, 1996, 1997a, 2004a,b,c, 2006, 2007a,b, 2010, 2011; Morales & Liede-Schumann, 2016), adding to the current infrageneric confusion.

The use of markers from nuclear ribosomal DNA (nrDNA) has been shown to be informative and has helped resolve relationships between species and genera (e.g, Baldwin et al., 1995; Trovo et al., 2013), even species complexes that have been particularly difficult to resolve with chloroplast DNA (cpDNA), due to a rapid or recent radiation (Bell et al., 2015). In Apocynaceae, the use of nuclear markers has helped to resolve or elucidate some problematic groups in Periplocoideae and Asclepiadoideae (e.g., Meve & Liede, 2001; Goyder et al., 2007; Ionta & Judd, 2007; Surveswaran et al., 2009; Bruyns et al., 2010; Wanntorp et al., 2014; Joubert et al., 2016; Khanum et al., 2016). But in apocynoids and rauvolfoids, the use of nuclear markers has been limited and mostly restricted to Old World groups (e.g., Hendrian & Kondo 2007a, b, c; Middleton & Livshultz, 2012; Uemachi & Shimomura, 2013). Only three studies (utilizing either phytochrome A and ITS) have been published that included more than a handful of Neotropical genera of apocynoids and/or rauvolfioids: Potgieter (1999), Livshultz (2010) and Morales et al. (2017. The infrageneric relationships of larger genera often remain unclear or are totally unresolved, and the monophyly of several earlier infrageneric classifications based only on morphological characters has not been tested.

Although significant progress has been made in our understanding of relationships within Echiteae in the past decade, rarely have more than one or two species of *Prestonia* been included in molecular-based studies. Eight species were included by Livshultz et al. (2007) in a study using cpDNA. In a phylogenetic study of tribe based on nrDNA and cpDNA markers by Morales et al. (2017), 16 of the 56 currently recognized species of *Prestonia* were included. In that paper, the monophyly of *Prestonia* was hypothesized, after inclusion of *Temnadenia ornata* as a new combination and transfer of *P. riedelii* to *Rhodocalyx*. But a larger sample is needed to accurately test monophyly of the genus and to

evaluate the current infrageneric classification proposals (Schumann, 1895; Woodson, 1936; Pichon, 1950a).

Here we present a phylogenetic analysis of *Prestonia* based on sequences from four cpDNA regions (*matK* and 3' / 5' trnK intron, rpl16 intron, rps16 intron, trnL intron and trnL-trnF intergenic spacer) and one nrDNA region, the internal transcribed spacer (ITS). The sampling includes ca. 86 % of the currently accepted species (50/ca. 58 species, Morales & Liede-Schumann, 2016). Our aims are four-fold: (1) to test the monophyly of *Prestonia* with a larger sample than in previous studies; (2) to determine the relationship between the different species of *Prestonia*; (3) to evaluate the infrageneric classifications of Schumann (1895), Woodson (1936) and Pichon (1950a); and (4) to provide a new infrageneric classification, including taxonomic realignments and nomenclatural changes as needed.

## MATERIALS AND METHODS

TAXON SAMPLING

Fifty of the 58 currently recognized species of *Prestonia* were sampled, including at least two members each from the all sections of Schumann (1895), Woodson (1936) and Pichon (1950a) (Table 2). The classification of Schumann (1895) included ten species, of which nowadays only three are accepted, the other seven being treated as synonyms. The outgroup taxa included thirteen species from six genera of Echiteae (*Artia* Guillaumin, *Asketanthera* Woodson, *Echites*, *Laubertia* A. DC., *Parsonsia*, and *Temnadenia*) representing subtribes Echitineae, Parsonsiinae, and Peltastinae, which were shown to be the groups most closely related to *Prestonia* (Morales et al., 2017). In addition, two species of *Odontadenia* (Odontadeniae) were used as rooting taxa.

 Table 2. Species of Prestonia and their sectional placement in three previous infrageneric classifications and this study.

	Schumann (1895)	Woodson (1936)	Pichon (1950a)	This study
Prestonia acrensis J.F.Morales			-	Prestonia
Prestonia acutifolia (Benth. ex Müll. Arg.) K. Schum.	Haemadictyon	Acutifoliae	Haemadictyon	*
Prestonia agglutinata (Jacq.) Woodson	3.5	Coalitae	Trichopharynx	米米
Prestonia amabilis J.F. Morales	74			Denticulatae
Prestonia amanuensis Woodson	12	Tomentosae	Euprestonia	*
Prestonia amazonica (Benth. ex Müll. Arg.) J.F. Macbr.	-	Annulares	Haemadictyon	Denticulatae
Prestonia annularis (L.f.) G. Don	:•	Annulares	Haemadictyon	Haemadictyon
Prestonia antioquiana J.F. Morales & Liede	급설	(A)	2	Denticulatae
Prestonia bahiensis Müll. Arg.		Tomentosae	Euprestonia	Prestonia
Prestonia boliviana J.F. Morales & A. Fuentes	1.6	9621	)	Haemadictyon
Prestonia brachypoda S.F. Blake	12	Tomentosae	Euprestonia	*
Prestonia brittonii N.E. Br.	1.	Annulares	Haemadictyon	*
Prestonia calycina Müll. Arg.	Euprestonia		=	Prestonia
Prestonia cayennensis (A. DC.) Pichon	-	5 <b>-</b>	Haemadictyon	Haemadictyon
Prestonia clandestina J.F. Morales	(+)	-	-	Prestonia
Prestonia coalita (Vell.) Woodson	<u>B</u> 1	Coalitae	Rhaptocarpus	Coalitae
Prestonia cogolloi J.F. Morales	-			Prestonia
Prestonia concolor (S.F. Blake) Woodson	: *	Annulares	Haemadictyon	*
Prestonia cordifolia Woodson	3.5	Tomentosae	Euprestonia	Mollis
Prestonia cyaniphylla (Rusby) Woodson		Acutifoliae	Haemadictyon	Haemadictyon
Prestonia denticulata (Vell.) Woodson	12	Annulares	Haemadictyon	Haemadictyon
Prestonia dentigera Woodson	12	717771111111111111111111111111111111111	Haemadictyon	*
Prestonia didyma (Vell.) Woodson		Annulares	Haemadictyon	Exsertae
Prestonia discolor Woodson	-	Annulares	Haemadictyon	*
Prestonia dusenii (Malme) Woodson	-	Coalitae	Rhaptocarpus	Coalitae
Prestonia ecuadorensis K. Schum.	Haemadictyon	*	Haemadictyon	*
Prestonia exserta (A. DC.) Standl.	-	Annulares	Haemadictyon	Exsertae
Prestoria falcatosepala J.F. Morales		Ammures	Tuemaaiciyon	Exsertae
and the second s	-			Exsertae
Prestonia folsomii J.F. Morales	Hanna di atuan	*	II = ous a di atsoci	*
Prestonia gaudichaudii (A. DC.) K. Schum.	Haemadictyon -	Annulares	Haemadictyon	*
Prestonia guatemalensis Woodson	13		Haemadictyon	*
Prestonia guianensis Gleason		Annulares	Haemadictyon	*
Prestonia finitima Woodson	-	Annulares	Haemadictyon	Prestonia
Prestonia hammelii J.F. Morales		- 4 4:6 T:	- T:	*
Prestonia hassleri Woodson	8.5	Acutifoliae	Haemadictyon	Denticulatae
Prestonia haughtii Woodson	-	*	Haemadictyon *	Demiculatae *
Prestonia hirsuta Müll. Arg.	Euprestonia			
Prestonia ipomaeifolia A. DC.		Tomentosae	Euprestonia	Prestonia *
Prestonia isthmica Woodson	-	Tomentosae	Euprestonia	552
Prestonia lacerata Woodson		Annulares	Haemadictyon	-
Prestonia lagoensis (Müll. Arg.) Woodson		Acutifoliae	Haemadictyon	Haemadictyon *
Prestonia lanata Müll. Arg.	Euprestonia	*	*	*
Prestonia latifolia Benth.	Euprestonia		*	*
Prestonia laxa Rusby ex Woodson		Annulares	Haemadictyon	
Prestonia leco A. Fuentes & J.F. Morales	72		@	Denticulatae
Prestonia lenticellata A.H. Gentry	32		<u>=</u>	Denticulatae
Prestonia lindleyana Woodson	5.T.	Annulares	Haemadictyon	Denticulatae
Prestonia lindmanii (Malme) Hoehne	12	Acutifoliae	Haemadictyon	*
Prestonia longifolia (Sesse & Moc.) J.F. Morales		12	-	Haemadictyor
Prestonia longituba K. Schum.	Euprestonia	*	*	*
Prestonia lutescens Müll. Arg.	Euprestonia	*	*	*

Table 2. Species of Prestonia and their sectional placement in three previous infrageneric classifications and this study.

	Schumann (1895)	Woodson (1936)	Pichon (1950a)	This study
Prestonia macroneura Woodson	14	Annulares	Haemadictyon	Denticulatae
Prestonia macrophylla Woodson	: <del>*</del> :	<u>=</u>	Haemadictyon	
Prestonia marginata Markgr.	-	Acutifoliae	Haemadictyon	Haemadictyon
Prestonia megagros (Vell.) Woodson		Annulares	Haemadictyon	Denticulatae
Prestonia mexicana A. DC.	Euprestonia	Tomentosae	Euprestonia	Prestonia
Prestonia mollis Kunth	9 <del>4</del> 9	Annulares	Haemadictyon	Mollis
Prestonia mucronata Rusby	87.0	Tomentosae	Haemadictyon	Prestonia
Prestonia obovata Standl.		Annulares	Haemadictyon	*
Prestonia ornata (Hoehne) J.F. Morales & M.E. Endress	14	-	<u>.</u>	Coalitae
Prestonia pachyphylla Woodson		Acutifoliae	*	*
Prestonia papillosa (Müll. Arg.) Woodson	-	-	=	Haemadictyon
Prestonia parviflora (Benth,) Benth. & Hook. f.	120	Tomentosae	Tetraceras	Prestonia
Prestonia parvifolia K. Schum. ex Woodson	0-0	Annulares	Haemadictyon	Exsertae
Prestonia peregrina Woodson	121	Annulares	Haemadictyon	*
Prestonia perplexa Woodson	-	Annulares	Haemadictyon	*
Prestonia phenax Woodson		Annulares	Haemadictyon	-
Prestonia pickelii Markgr.		-	Haemadictyon	Coalitae
Prestonia plumierifolia Markgr.	-	Annulares	Haemadictyon	Denticulatae
Prestonia portobellensis (Beurl.) Woodson	-	Annulares	Haemadictyon	Haemadictyor
Prestonia premontana J.F. Morales	120	=	-	Prestonia
Prestonia purpurissata Woodson		Annulares	Haemadictyon	*
Prestonia quinquangularis (Jacq.) Spreng.	191	Acutifoliae	Haemadictyon	Haemadictyor
Prestonia racemosa J.F. Morales	121	-	=	Prestonia
Prestonia riedelii (Müll. Arg.) Margr	9 <del>4</del> 8	Tomentosae	Haemadictyon	李楽宗
Prestonia riverae J.F. Morales	121			Prestonia
Prestonia robusta Rusby	-	Annulares	Haemadictyon	Denticulatae
Prestonia rotundifolia K. Schum. ex Woodson		Annulares	Haemadictyon	Denticulatae
Prestonia schippii Woodson	-	Annulares	Haemadictyon	*
Prestonia schumanniana Woodson	-	Tomentosae	Euprestonia	Prestonia
Prestonia seemannii Miers	(-)			Prestonia
Prestonia simulans Woodson	~	Acutifoliae	Haemadictyon	*
Prestonia solanifolia (Müll. Arg.)Woodson	5 <del>-</del> 5	Coalitae	Rhaptocarpus	Coalitae
Prestonia speciosa Donn. Sm.	-	Tomentosae	Euprestonia	Prestonia
Prestonia succo J.F. Morales	-	2	* 2	?
Prestonia surinamensis Müll. Arg.	.5	Tomentosae	Euprestonia	Prestonia
Prestonia tomentosa R. Br.	-	Tomentosae	Euprestonia	Prestonia
Prestonia trifida (Poepp.) Woodson	(5)	Annulares	Haemadictyon	Denticulatae
Prestonia tysonii A.H. Gentry	-			Prestonia
Prestonia vallis Woodson	151	Annulares	Haemadictyon	*
Prestonia vana Woodson	(2)	Annulares	Haemadictyon	Denticulatae
Prestonia vaupesana Woodson			-	Haemadictyon
Prestonia velutina Woodson	120	Annulares	Haemadictyon	*
Prestonia versicolor Woodson	-	Annulares	Haemadictyon	*

<sup>\*</sup> Treated as a synonym; \*\* = Included in Echites; \*\*\* = Included in Rhodocalyx; -= not treated; ? = incertae sedis

*Prestonia mollis* Kunth and *P. quinquangularis* (Jacq.) Spreng. exhibit a high degree of morphological variation, in vegetative as well as floral parts, which has led to the description of a number of species over the years. Woodson (1936) described *P. cordifolia* Woodson, which he included in sect. *Tomentosae* based on its pubescent corolla and leaves and purple flowers. However, the type is similar to some extreme morphotypes of *P. mollis* 

observed by the first author in the Peruvian Andes. In the same work, Woodson accepted several species (P. acutifolia (Benth. ex Müll. Arg.) K. Schum., P. marginata (Benth.) Woodson, P. pachyphylla Woodson and P. simulans), which are morphologically similar to P. quinquangularis, and which he differentiated from the last only by their coriaceous leaf blades, a character sometimes present in specimens from the Amazon Basin or the Guiana Shield. All these taxa have been reduced to the synonymy of P. quinquangularis duringr the past decade (e.g., Morales, 2006, 2007b, 2010). However, the name *P. marginata* has been involved in a confused nomenclatural situation. Bentham (1841) proposed Haemadictyon marginatum, a species from southwestern Guyana (Upper Takutu-Essequibo, Pirara). Markgraf (1924), described P. marginata based on a Ule specimen from the Roraima state, Brazil. Both type collections are conspecific and were collected in the Guiana Shield. Woodson (1936) considered *Haemadictyon* a synonym of *Prestonia* and made the combination P. marginata (Benth.) Woodson based on Bentham's name. At the same time, he erroneously considered Markgraf's name (1924) to be illegitimate and proposed a new name, P. pachyphylla for that species. However, the name by Markgraf (1924) has priority according to Article 11.4 of the International Code of Nomenclature (McNeill et al., 2012), and thus, Woodson's names P. marginata (Benth.) Woodson and P. pachyphylla are illegitimate. The placement of P. marginata Markgr has been in dispute. Morales (2007b) reduced it into the synonymy of P. quinquangularis, but in some checklists and floristic treatments for South America (e.g., Zarucchi et al., 1995; Funk et al., 2007) it has been placed under the synonymy of P. cayennensis (A. DC.) Pichon. In order to determine the relationship of this group of species (P. mollis-P. cordifolia and P. quinquangularis-P. marginata), two samples each of P. mollis and P. quinquangularis were included: one of the typical morphotype of both species and the second from a morphotype that matches the type of P. cordifolia (cordate and pubescent leaves, and purple corollas) and one that matches the type of P. marginata (coriaceous leaves from the Guiana Shield). The list of taxa, vouchers and Genbank accession numbers are given in Appendix 1. Eight species of *Prestonia (P. amazonica* (Benth. ex Müll. Arg.) J.F. Macbr., P. cogolloi J. F. Morales, P. folsomii J. F. Morales, P. haughtii Woodson, P. macroneura Woodson, P. megagros (Vell.) Woodson, P. racemosa J. F. Morales and P. succo J. F. Morales) were not included in this study. These species are poorly collected and few

specimens for DNA extraction are available. We tried to obtain positive PCR products from several specimens without success.

# DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

DNA extraction, amplification, primers and sequencing procedures for the matK and 3' / 5' trnK intron, rpl16 intron, rps16 intron, trnL intron and trnL-trnF intergenic spacer and ITS are described in Morales et al. (2017). For the rps16 intron the protocol was given in Simões al. (2004)used. The primer 825R (5'et GATAGCATAGTGCGATAGAGTC-3') was designed for use in sequencing the 5' trnK intron in combination with the primer trnK-3914F. For sequences already available in GenBank, sometimes a different voucher specimen was used to obtain ITS. Alignment of the matK and 5'/3' trnK intron, trnL intron, trnL-trnF intergenic spacer and rps16 intron was relatively easy and straightforward, whereas alignment of ITS was the most difficult due to the large number of gaps, followed by the rpl16 intron, which presented large mononucleotide repeats. Regions of ambiguous alignments were excluded. Sequences were manually assembled using CodonCode Aligner version 3.7.1 (CodonCode Corp., Centerville, Massachusetts, U.S.A.).

#### PHYLOGENETIC ANALYSES

We analyzed seven matrices: the individual datasets (1) *matK* and 5'/3' *trnK* intron; (2) *rpl16* intron; (3) *rps16* intron; (4) *trnL* intron and *trnL-trnF* intergenic spacer; (5) ITS, (6) combined cpDNA dataset (matrices 1–4) and (7) combined molecular dataset (matrices 5–6). All matrices were deposited in TreeBASE (accession number 19980). First we checked for hard incongruence among the individual plastid matrices, and then between the combined cpDNA matrix and the nrDNA matrix, testing the combinability of the partitions

by searching for incongruences between them, in order to combine the data following the procedures given in Morales et al. (2017). Incongruence was also not found between the combined cpDNA matrix and nrDNA matrix, so they were combined in a single matrix (combined molecular matrix). The individual cpDNA matrices were analyzed using maximum likelihood (ML), whereas the combined cpDNA matrix, the nrDNA matrix and the combined molecular matrix were analyzed using ML and Bayesian inference (BI). For the two analyses involving ITS, the nrDNA matrix was divided into five partitions.

Maximum-likelihood (ML) analyses were calculated using RAxML version 8.2.8 (Stamatakis, 2006, Stamatakis et al., 2008), as implemented in CIPRES version 3.3 (Miller et al., 2010), setting the non-bootstrap analysis and tree search to 1000 replicates. The output tree files were generated with Figtree (Rambaut, 2014). Bootstrap support value was interpreted as follows: 50%-74% as weak, 75%-89% as moderate, and  $\geq 90\%$  as strongly supported.

Bayesian inference was calculated using MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), applying separate models to each data partition, with unlinked partitions, and parameters estimated independently. Models of sequence evolution were selected using the Bayesian information criterion (BIC) in jModelTest version 2.1.1 (Darriba et al., 2012). MrBayes was run using two parallel runs for 10 million generations, each using one cold and three heated MCMC chains, sampling every 10,000 generations, until an average standard deviation of split frequencies ≤ 0.01 was reached. The first 25% of the trees was discarded (sump function) and the remaining 75% used to calculate a majority-rule consensus and posterior probabilities (PP, sumt function). Burn-in values, mixing of the MCMC chains, and independent tree sampling were determined through inspection of the MCMC samples employing Tracer v.1.5 (Rambaut & Drummond, 2007). The 50% majority-rule consensus tree was edited in Figtree version1.4.2. (Rambaut, 2014). Posterior probability values ≥ 0.95 were considered as strongly supported.

### **RESULTS**

# **SEQUENCES**

The markers chosen for this investigation were successfully sequenced for all species, with the following exceptions. For the two outgroup species *Asketanthera calycosa* (A. Rich.) Woodson and *Parsonsia lenticellata* T. C. White we were unable to amplify the *rps16* intron. For *P. mollis*, *P. cordifolia* and *P. marginata*, despite several amplifications from two different specimens, ITS sequences always exhibited double overlapping peaks, a problem already reported with this marker (Rapini et al., 2006; Spalik et al., 2009; Burge et al., 2013; Weitmier et al., 2015; Simões et al., 2016). Therefore, for these three species ITS was not included, which was not expected to affect the results of the combined analysis (Wiens, 2003). In total, 62 nrDNA and 258 cpDNA sequences were analyzed, of which 46 and 205, respectively, were newly generated; the remaining sequences were obtained from GenBank. Species sampled, vouchers and GenBank accession numbers are given in Appendix 1. Alignment characteristics statistics are summarized in Table 3. The most informative of the regions studied was ITS, with 47.17% parsimony informative characters (Table 3). In contrast, the most informative cpDNA markers (*rps16* intron, *rpl16* intron) barely reached 10 % (10.04 % and 9.03 %, respectively).

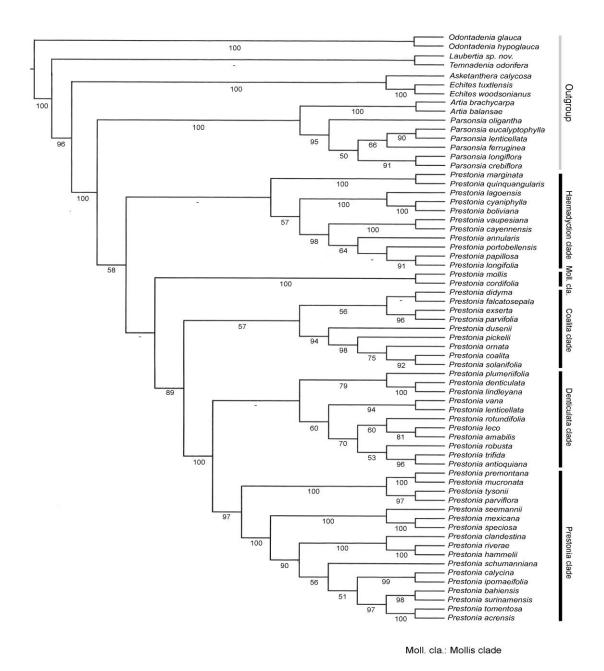
## DNA ANALYSES

The most complex model GTR +  $\Gamma$  + I was implemented for each partition (Huelsenbeck & Rannala, 2004). No strongly supported incongruent clades were found between the *rpl16* intron (Fig. S2) *rps16* intron (Fig. S3) and *trnL* intron and *trnL-trnF* intergenic spacer (Fig. S4) trees. In the *matK* and 5'/3' *trnK* intron tree (Fig. S1), *Artia* and *Parsonsia* were retrieved in an unsupported clade with a group of species of *Prestonia*. In the combined cpDNA tree (Fig. 1) and the nrDNA tree (Fig. 2), only minor discrepancies were found. In the combined cpDNA tree, the maximally supported (BS=100%) Mollis clade (comprising *P. mollis* and *P. cordifolia*) was retrieved as sister to the Coalita,

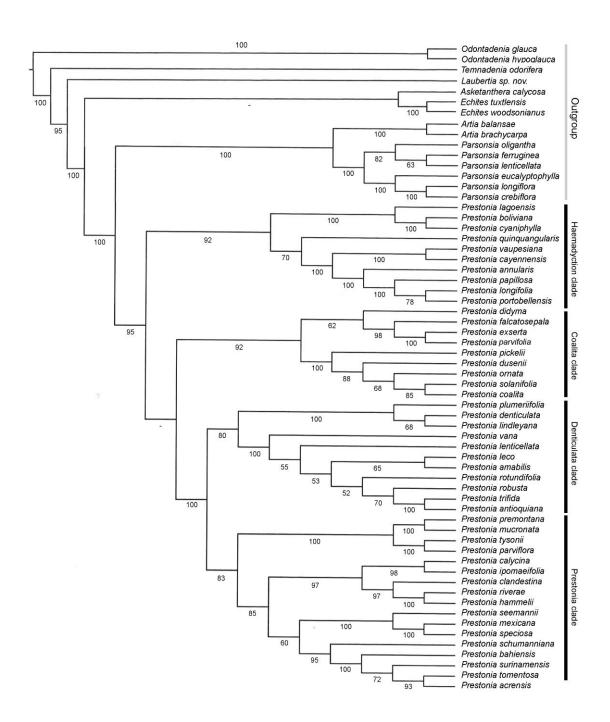
Denticulata and Prestonia clades, whereas in the nrDNA tree *P. mollis* and *P. cordifolia* were not included and therefore, the Mollis clade is missing. In the combined cpDNA tree, the sisters *P. quinquangularis* and *P. marginata* (BS=100%) are retrieved within the Haemadictyon clade, in an unresolved relationship with the weakly supported (BS=57%) clade with the remaining species of the clades of the ingroup. In the nrDNA tree, *P. marginata* is missing, *and P. quinquangularis* is positioned within the Haemadictyon clade on a branch by itself, and between a clade formed by three species (*P. boliviana J.F. Morales & A. Fuentes, P. cyaniphylla* (Rusby) Woodson, *P. lagoensis* (Müll. Arg.) Woodson) and weakly supported (BS=70%) as sister to a clade, which includes the other species of the clade (Fig. 2). Although, the topologies do not match completely, the clades, which form the heart of this study, were resolved in both the combined cpDNA tree and the nrDNA tree (Figs. 1, 2, respectively). Therefore, the two datasets were combined into a single matrix (combined molecular matrix). All further discussion is based on the majority rule consensus cladogram resulting from the BI analysis of the combined molecular matrix (Fig. 3).

Table 3. Summary statistics of data sets

Locus	Number of taxa	Total length (bp)	Variant characters (n)	Parsimony- informative characters (n)	CI	RI
trnL intron and	65	991	109	65 (6.6 %)	0.780	0.912
trnL- $trnF$						
intergenic spacer						
rpl16 intron	65	1229	210	111 (9.03 %)	0.734	0.890
matK /5'/ 3' trnK	65	2585	395	224 (8.66 %)	0.623	0.841
intron						
rps16 intron	63	956	149	96 (10.04 %)	0.710	0.889
ITS	62	812	490	383 (47.17 %)	0.536	0.763
Chloroplast	65	5761	863	496 (8.61 %)	0.645	0.846
combined						
ITS and chloroplast	65	6573	1353	879 (13.37 %)	0.574	0.795
combined						



**Fig. 1**. Maximum likelihood consensus tree based on the combined cpDNA dataset (*matK* and 3' / 5' trnK intron, rpl16 intron, rps16 intron, trnL intron and trnL-trnF intergenic spacer). Clades from the consensus tree based on the combined molecular dataset (combined cpDNA and nrDNA datasets) (Fig. 3) are indicated by black bars. Bootstrap values ≥ 50 are indicated above branches.



**Fig. 2**. Maximum likelihood consensus tree based on the nrDNA (ITS) dataset. Clades from the consensus tree based on the combined molecular dataset (Fig. 3) are indicated by black bars. Bootstrap values values ≥ 50 are indicated above branches.



Fig 3. Maximum likelihood consensus tree based on the combined molecular dataset. Clades are indicated by thin black bars in the innermost column. Sections in the classifications of Schumann (1895), Woodson (1936) and Pichon (1950a) are shown by patterns in the three middle columns labeled as S, W and P, respectively. The new sectional classification proposed here is indicated by thin black bars in the outermost column with section names in bold. Bayesian posterior probabilities (≥ 0.95) are indicated above each branch and maximum likelihood bootstrap support (> 50%), below.

## PHYLOGENETIC RELATIONSHIPS

Prestonia as circumscribed by Morales et al. (2017) is optimally resolved as monophyletic (1/98). Five clades can be recognized: the Haemadictyon clade, Mollis clade, Coalita clade, Denticulata clade and Prestonia clade (Fig. 3). The first clade to diverge within the ingroup, the Haemadictyon clade is strongly supported by PP (1), but only moderately so by ML (85). It is retrieved as sister to all other clades in *Prestonia* and is divided into two clades. The first clade (1/100) includes two species, P. marginata and P. quinquangularis and the second, which is unsupported, nine species; it is further divided into two clades, both optimally supported (1/100), comprising three and six species, respectively. Next in branching order is the strongly supported Mollis clade (1/100), which comprises only two species (P. cordifolia and P. mollis). The relationship between the Mollis clade and the Haemadictyon clade is strongly supported by PP (0.95), but only moderately so by ML (80). This clade is resolved as sister (1/100) to the large clade comprising the Coalita, Denticulata and Prestonia clades, of which the Coalita clade branches off first. It is strongly supported (1/95), and comprises two clades: one strongly supported by PP (0.99), but only weakly so by ML (65) with four species, and the second optimally supported (1/100) with five species. Next in branching sequence is the a large clade (1/100), which includes the bulk of the species in the genus and is divided into two clades: the Denticulata clade (0.99/85) and the Prestonia clade (1/98), with 11 and 17 species, respectively.

## **DISCUSSION**

The present study presents the first densely sampled phylogeny of the Neotropical lianoid genus *Prestonia*, using a combined cpDNA (*matK* and 3' / 5' trnK intron, rpl16 intron, rps16 intron, trnL intron and trnL-trnF intergenic spacer) and nrDNA (ITS). The inclusion of nrDNA in this study provided a significantly increased phylogenetic signal, compared to the results based only on cpDNA markers. Similar results have been found in others studies in neotropical apocynoids (e.g., Livshultz, 2010; Morales et al. 2017). The ITS dataset proved to be the most informative, with ca. 17 % of the aligned characters being parsimony

informative. The enhanced variability of nuclear loci compared to other markers, provides great potential in phylogenetic studies. However, the design and identification of universal primers is somewhat difficult due to the polyploidy present in plants (Naumann et al., 2011). Our results based on nrDNA data are congruent with the results based on cpDNA data, with some minor discrepancies, although incongruence between nuclear and plastid data is not an uncommon result (e.g., Fan et al., 2009; Pelser et al., 2010; Silva et al., 2012).

# ROBERT E. WOODSON, JR. AND MARCEL PICHON

Robert E. Woodson, Jr., at the Missouri Botanical Garden in St. Louis, and Marcel Pichon, at the Muséum National d'Histoire Naturelle in Paris, were two of the most important specialists of Apocynaceae in the first half of the 20<sup>th</sup> century. Both published a large number of key papers and monographic works that greatly furthered knowledge on Apocynaceae, particularly the rauvolfioids and apocynoids (Humbert & Léandri, 1955; Allen & al, 1965; Nevling, Jr., 1965). They both possessed a keen eye and an innate feel for "good" characters. Thus, despite their work being based only on morphological characters, which are notoriously prone to repeated evolutionary trends in distant clades, their great knowledge of the plants allowed them to reach often surprisingly accurate hypotheses of relationship in difficult groups. Until the advent of molecular phylogenetics, their treatments provided the framework for our understanding of the family and into which new species were continually being intercalated. The two were also good friends. For example, Woodson said about his new species Aspidosperma pichonianum Woods., "The species commemorates my friend M. Marcel Pichon, of the Muséum National d'Histoire Naturelle" (Woodson, 1951: 176). And, both died suddenly and tragically young in the midst of their careers: Woodson was 59, and Pichon only 33 years old, leaving a huge gap in the research of one of ten largest plant families (Rapini, 2012).

As a curator at the Missouri Botanical Garden (Mathias, 1965), with its intensive collecting in Latin America, Woodson was in an ideal position to study the many specimens of Apocynaceae pouring in from collectors in the Neotropics. In order to put names on them, he first had to come to terms with *Echites*. One must keep in mind that in

the 19<sup>th</sup> century, more or less all Neotropical apocynoid lianas were described in the genus *Echites*. It was Woodson who is responsible for the seemingly Herculean task of painstakingly sorting through the descriptions and scrutinizing the types of all Neotropical plants described as *Echites*, describing new genera as needed, resolutely bringing order out of chaos. He also tackled the confusion brought about by John Miers, who was not only a consummate splitter, but at the same time combined unrelated taxa (Simões et al., 2010; Morales et al, 2007), teasing apart the conglomerate "genera", gathering like with like and redefining them. Many of the current generic circumscriptions used in Neotropical taxonomy are those proposed by Woodson's (e.g., Woodson, 1931, 1932a, b) and especially his large monograph of Neotropical apocynoids (Woodson, 1933, 1934, 1935, 1936). Woodson published the last monograph of *Prestonia* (Woodson, 1936). In that work and subsequent publications, he described 30 species and transferred another 14 from other genera, making him the author of 44 species, and thus the most prolific systematist who ever worked in *Prestonia*.

Pichon, as head of phanerogams at the Museum National d'Histoire Naturelle in Paris focused mainly on the big picture: classification at the genus level and above and on a global scale. He was amazingly productive in his short life, publishing a prodigious number of large, broad-based worldwide classifications down to subtribal level, incorporating detailed morphological descriptions of floral organs (e.g., Pichon, 1948b), as well as a number of smaller papers, especially to improve the infrageneric classification of several larger genera in both rauvolfioids and apocynoids (e.g., Pichon1947a, b,1948a, c, 1950a, b, c). For his outstanding monograph of Landolphieae in Africa (Pichon, 1953), he was awarded the Prix De Candolle in 1953 (Humbert & Léandri, 1955). He provided the last infrageneric classification of *Prestonia* Pichon (1950a), placing a few species overlooked by Woodson and intercalating species described after publication of Woodson's monograph (Woodson, 1936).

# PHYLOGENY COMPARED TO PREVIOUS CLASSIFICATIONS

The broader taxon sampling allowed us to corroborate the hypothesis of monophyly for the genus after the taxonomic changes proposed by Morales et al. (2017), and to evaluate the sections of three previous infrageneric classification systems: Schumann (1895), Woodson (1936) and Pichon (1950a). Almost all sections of these are para- or polyphyletic. Schumann's sect. *Euprestonia* is resolved as monophyletic. In Woodson's and Pichon's systems, only sect. *Coalitae* and sect. *Rhaptocarpus* are monophyletic, respectively. The most extreme example of polyphyly is found in Schumann's sect. *Haemadictyon*, Woodson 's sect. *Annulares* and Pichon's sect. *Haemadictyon*, the constituent species of which are scattered among three, five and six clades, respectively. In Woodson's classification, sect. *Acutifoliae* is also polyphyletic, with species in two different clades, and sect. *Tomentosae* is paraphyletic, because here *P. cordifolia* grouped in the Mollis clade. In Pichon's classification, the sole species of sect. *Tetraceras*, *P. parviflora*, is nested among species of his sect. *Euprestonia*, and sect. *Rhaptocarpus* is polyphyletic, with its members grouped with two species of sect. *Haemadyction*.

Below, we discuss each of the five main clades recovered in *Prestonia* and their constituent species compared to the three previous infrageneric classifications by Schumann (1895), Woodson (1936) and Pichon (1950a). For the remainder of the discussion, we refrain from citing these three references. Many of the species included by

Schumann are nowadays treated as synonyms; therefore, in Figure 3 we used the currently accepted names, but the complete list is given in the Table 2.

# HAEMADICTYON CLADE

Of the eleven species in this clade, four were described or accepted after 1950 (*P. boliviana*, *P. longifolia* (Sessé & Moc.) J.F. Morales, *P. papillosa* (Müll. Arg.) J.F. Morales, *P. vaupesana* Woodson) and thus not treated by Schumann, Woodson or Pichon. Of the remaining seven, four (*P. cyaniphylla*, *P. lagoensis*, *P. marginata* and *P. quinquangularis* (as *P. acutifolia* (Benth. ex Müll. Arg. K. Schum.)) were included by Woodson in sect. *Acutifoliae* and another two (*P. annularis* (L.f.) G. Don and *P. portobellensis* (Beurl.) Woodson) in sect. *Annulares*. The basionym of *P. cayennensis* (A.

DC.) Pichon, *Haemadictyon cayennense* A. DC., was not treated in Woodson's monograph. Schumann's sect. *Haemadictyon* is polyphyletic, since its three species were retrieved in three different clades (*Haemadictyon*, *Mollis* and *Denticulata*). Woodson's sect. *Acutifoliae* originally included nine species, five of which have been reduced to synonymy in recent years (Morales, 2004 b, 2005a, 2008) and it is monophyletic, but was retrieved in a close relationship with a group of species included by him in sect. *Annulares*. Fifteen of the 33 species accepted by Woodson in his original circumscription of sect. *Annulares* (Table 1) have been reduced to synonymy and its remaining representatives are divided among three clades, confirming that section as polyphyletic as well.

Section *Haemadictyon* as defined by Pichon was resolved as grossly polyphyletic here, with its members distributed within all major clades. We propose to recognize the Haemadictyon clade as a section. Since the type of sect. *Haemadictyon* is included here, Schumann's section name is maintained, but with a different species circumscription.

Species from this clade are distributed from Mexico and some Caribbean Islands to Bolivia and northern Argentina from 0 to 1600 m, but are mostly confined to South America, with only three species (*P. longifolia*, *P. portobellensis* and *P. quinquangularis*) reaching Central America and Mexico. They have in common sepals without longitudinal veins, a glabrous corolla with conspicuous annular corona, free corona lobes with the apices exserted or included, and follicles that are free or that remain longitudinally fused together up to maturity. The species are gouped into three clades. The five species of the first and second clade are characterized by membranaceous, glabrous to minutely puberulent leaf blades and membranaceous sepals, and are found in cerrados, dry forest, gallery forest and open areas from southern Nicaragua and Caribbean Islands to northern Argentina. The six species of the third clade have subcoriaceous, glabrous leaf blades and firmly membranaceous sepals and typically grow in wet forest or tropical wet forest from Mexico to Bolivia and northern Brazil.

*Prestonia quinquangularis* is one of the most variable species in the genus regarding shape, texture, and indument of the leaves. Specimens from dry forest have small, completely glabrous leaves, whereas specimens from the tropical wet forest from the Amazonian basin and the Guianas tend to have larger leaves, which may be sparsely

puberulent. The relationships of *P. marginata* have been disputed in some more recent floras and checklists. For example, Zarucchi et al. (1995), Funk et al. (2007) and Hokche et al. (2008) all included this species in the synonymy of *P. cayennensis*, whereas Morales (2008) considered it to be a synonym of *P. quinquangularis*. We included a specimen of *P. marginata* here in order to determine its taxonomic affinities. It is closely related to *P. quinquangularis*, supporting the proposal of Morales (2008). The status of *P. marginata* will be addressed in the upcoming monograph of *Prestonia* (Morales & Endress, unpub. data). Pichon's sect. *Haemadictyon* (based on Schumann's sect. *Haemadictyon*) and Woodson's sect. *Acutifoliae* have the same type (*Prestonia acutifolia* (nowadays = *P. quinquangularis*), rendering Woodson's name a *nom. illeg*. Baillon (1891) proposed sect. *Haemadictyon*, but without citing any species, preventing it from being lectotypified and thus, turning it in a *nom. nud*. We therefore maintain Schumann's name *Haemadictyon* for this section, but with a different species circumscription.

### **MOLLIS CLADE**

Schumann included *Prestonia ecuadorensis* K. Schum. (reduced to the synonymy of *P. mollis* by Woodson (1936)) in his sect. *Haemadictyon*. In Woodson's key to *Prestonia*, *P. mollis* came out in the same group with *P. exserta* (A. DC.) Standl. (including *P. tobagensis* Urb. and *P. velutina* Woodson (Morales 2004b, 2006)), *P. parvifolia* Woodson and *P didyma* (Vell.) Woodson (including *P. perplexa* Woodson (Morales, 2007b)). However, *P. exserta*, *P. parvifolia* and *P. didyma* are nested in the Coalita clade. Woodson included *P. cordifolia* in sect. *Tomentosae*, based on its tomentulose leaves and puberulent corollas, and hypothesized that is closest was *P. calycina* Müll. Arg. (Woodson, 1936: 354), a species here included in the distant Prestonia clade. Pichon included both species of the Mollis clade in his sect. *Haemadictyon* (which included 50 species in total). Although we were not able to include nrDNA data in our analysis for *P. mollis* and *P. cordifolia*, we propose to recognize this clade as a section, based on its high support (1/100).

Species of the Mollis clade are distributed in Ecuador and northern Peru, with a disjunct population in Central Panama, where they are found mainly in disturbed areas or

dry forest from sea level up to 2500 m. They are characterized by membranaceous, glabrous to minutely puberulent leaf blades, membranaceous sepals with conspicuous longitudinal veins, glabrous or minutely puberulent corollas, well-developed annular corona, free corona lobes with the apices conspicuously exserted and follicles that remain longitudinally fused together up to maturity. At higher elevations, the plants tend to be more pubescent, with a uniform indument on stems, leaves, and inflorescences. Corolla color ranges from purple, yellowish purple to yellow. Plants from high elevations were described by Woodson as *P. cordifolia*, which is possibly an extreme morphotype of the variable *P. mollis*, with purple corollas and larger leaves. Following Woodson (1936), *P. cordifolia* has been accepted in some floristic works focusing on Peru (e.g. Macbride, 1959; León et al. 2006), without questioning its validity. Whether or not both species should be accepted is a question that will be addressed in the upcoming monograph of *Prestonia*.

## COALITA CLADE

The strongly supported Coalita clade (1/95) is divided into two clades. The first (0.99/65) comprises four species: *P. didyma*, *P. parvifolia*, *P. exserta* and *P. falcatosepala* J.F. Morales. The last was described only in 2004, and consequently was not included in previous infrageneric proposals. The first three species were considered by Woodson to be related to *P. annularis* and *P. mollis* (which are placed in different, distant clades here) and thus he included them as part of his sect. *Annulares*, whereas they were included in sect. *Haemadictyon* in Pichon's classification, The second clade (1/100) includes all species of Woodson's sect. *Coalitae* as well as Pichon's sect. *Rhaptocarpus*. None of the species of the Coalita clade were treated by Schumann, because some were not yet described or were placed under a different genus (e.g., *Echites*).

Although the first clade is only weakly supported by ML, it is strongly supported by PP (1). Furthermore, species of the first clade are characterized by a conspicuous annular corona and free corona lobes versus inconspicuous annular corona and absent free corona lobes in the second clade,. Therefore, we propose to recognize the first clade as a new section, *Exsertae*.

Representatives of the this clade grow in dry, moist, or tropical wet forest and bordering zones in Central Panama, Colombia, Ecuador, Peru and southeastern Brazil, from 0 up to 1100 m. All species have membranaceous leaf blades that are glabrous (or sparsely puberulent on the abaxial surface), membranaceous sepals, glabrous corollas, conspicuous annular corona, free corona lobes with the apices exserted (sometimes almost totally exserted), and follicles that are free or that remain longitudinally fused together up to maturity.

Two of the included species in the second clade, P. ornata (Hoehne) J.F. Morales & M.E. Endress and P. pickelii Markgr., have a complex taxonomic history. Prestonia ornata was originally described in *Echites* (Hoehne, 1915) and was transferred to *Temnadenia* by Woodson (1932b), which was accepted by Morales (2005b). However, in a recent molecular-based study of the tribe Echiteae, the included sample of T. ornata grouped within *Prestonia*, thus the formal transfer was made (Morales et al. (2017), an action that is supported with the larger sampling here. Prestonia pickelii was described by Markgraf in1938, too late to be treated in Woodson's monograph; Pichon placed it in sect. Haemadictyon, thus, causing his sect. Rhaptocarpus to be paraphyletic. Prestonia pickelii is known from only two collections from Pernambuco state, Brazil. It was reduced to the synonymy of P. quinquangularis (Morales, 2008), based on certain morphological similarities (e.g, leaf shape, inflorescence type, small flowers, inconspicuous annular corona). According to our phylogeny, however, the two are not even closely related; therefore, P. pickelii is re-instated here as a valid species. We propose to recognize this second clade as a section, with Woodson's name Coalitae maintained, but with a different species circumscription.

Species of this clade are typically found in dry forest and cerrados, in Colombia to Bolivia and Paraguay from 0 up to 1000 m, although *P. ornata* grow in tropical wet forest. Representatives of this clade are characterized by membranaceous leaf blades that are glabrous (or sparsely puberulent on the abaxial surface), membranaceous sepals, with or without longitudinal veins, glabrous or minutely puberulent corollas, inconspicuous annular corona, free corona lobes usually absent, and follicles that are free or that remain longitudinally fused together up to maturity. Species without a free corona are uncommon,

and outside of the species in this clade, has been reported in only a few species of the Prestonia clade.

#### DENTICULATA CLADE

Of the 11 currently recognized species in this clade, seven were treated in Woodson's sect. *Annulares* or Pichon's sect. *Haemadictyon*, whereas Schumann included only *P. denticulata* (Vell.) Woodson (as *P. gaudichaudii* A. DC.) in his sect. *Haemadictyon*. The other four species (*P. amabilis* J.F. Morales, *P. antioquiana* J.F. Morales & Liede, *P. lenticellata* A.H. Gentry, *P. leco* A. Fuentes & J.F. Morales) were all described after 1950, and thus were not treated in any previous classification. Three species resolved here in the Denticulata clade (*P. robusta*, *P. rotundifolia*, *P. trifida*) were included in the study by Morales et al. (2017), where they also formed a strongly supported clade. Other phylogenetic studies dealing with relationships in the apocynoids (Livshultz et al. 2007, Livshultz, 2010) did not include any species of this clade. Although the support in the ML analysis was only moderate (85), the clade is highly supported by PP (0.99); accordingly, it is proposed as a new section, *Denticulatae*.

Members of this clade are restricted to tropical wet forest regions from southern Costa Rica to Bolivia and Brazil, from 0 to 1000 m. Several of them are poorly collected because they grow in isolated areas of the Amazonian basin. The plants tend to be robust, woody lianas. They have coriaceous, glabrous leaf blades, glabrous or minutely puberulent corollas, conspicuous annular corona, free corona lobes with the apices exserted or included, and follicles that are free or that remain longitudinally fused together up to maturity.

#### PRESTONIA CLADE

The Prestonia clade is divided into two main clades. The smaller of the two includes four species, all of them characterized by terminal inflorescences, small corollas, and elongated linear, free follicles, whereas the larger comprises thirteen species, which have axillary inflorescences, longer corollas and stouter follicles.

All species of the Prestonia clade that were known at the time, were included by Schumann in sect. *Euprestonia* and by Woodson in sect. *Tomentosae*, whereas they were placed in three different sections in Pichon's classification. The smaller clade includes *P. mucronata* Rusby from Pichon's sect. *Haemadictyon* and *P. parviflora* (Benth.) Benth. & Hook. f., the sole species of his sect. *Tetraceras*, which he separated from his sect. *Euprestonia* based on the short corolla tube, ovules 6-seriate and linear follicles (vs. longer corolla tube, ovules 8-12-seriate and stouter follicles). Although *P. mucronata* has the same diagnostic features as *P. parviflora*, because its fruits were unknown at the time, Pichon erroneously placed it in sect. *Haemadictyon*; thus, both sections are paraphyletic. All the species in the larger clade that were known at the time were included by Pichon in his sect. *Euprestonia*. We propose to recognize the Prestonia clade as a section.

Species of the Prestonia clade are found from Mexico to Bolivia and northern Argentina, growing in a wide range of environments, including forest and open areas from sea level up to 2500 m. Species of *Prestonia* from montane or premontane forest are found only in this clade. The species are characterized by membranaceous leaves, with pubescent blades, membranaceous sepals, conspicuously pubescent corollas, conspicuous annular corona, sometimes deeply lobed or reduced to five conical projections, free corona lobes with the apices exserted or included or absent, and free follicles.

# PLACEMENT OF SPECIES NOT SAMPLED

Based on their morphological features, we suggest possible placement of the eight species not sampled in the proposed infrageneric classification as follows: *P. amazonica*, *P. haughtii*, *P. macroneura* and *P. megagros* are placed in sect. Denticulatae based on the coriaceous and glabrous leaf blades, coriaceous sepals without visible veins, corolla with conspicuous annular corona and free corona lobes and follicles somewhat woody at maturity, *P. cogolloi* and *P. racemosa* are placed in sect. Prestonia based on thecorolla tube, abaxial surfaces of the corolla lobes and follicles variously pubescent, with the

indument ferrugineous or brown, and *P. folsomii* is placed in sect. Exsertae due to membranaceous leaf blades and sepals, sepals with conspicuous longitudinal veins, corolla tube 11–14 mm long, with a conspicuous annular corona and free corona lobes). The affinities of *P. succo* cannot be determined at this time, because its features (e.g., small membranaceous leaves, small corollas, an inconspicuous annular corona and absence of free corona lobes) do not match any other known species. Based on its vegetative characters it resembles the members of the section Coalitae, but without molecular evidence no further discussion is possible.

#### TAXONOMIC IMPLICATIONS

**Prestonia** R. Brown, Asclepiadaceae 58. 1810, nom. cons. – Type: *Prestonia tomentosa* R. Br., (Pre-print of: Mem. Wern. Nat. Hist. Soc. 1: 70. 1811). Ca. 58 species.

Lianas or vines; bark conspicuously suberose; latex white or translucent; stems with intrapetiolar colleters. Leaves opposite, without colleters, glabrous or variously pubescent, membranaceous to coriaceous or subcoriaceous, sometimes revolute at the margin. Inflorescence a monochasial or dichasial cyme, axillary, terminal or subterminal, few- to many-flowered, glabrous to variously pubescent, bracts scarious to foliaceous. Sepals 5, free, diminutive to foliaceous, with one episepalous colleter at the base inside. Corolla salverform, rarely infundibuliform, glabrous to variously pubescent, lobes dextrorsely contort; annular corona usually present around the mouth, entire to variously lobed, 5 free corona lobes usually within the staminal sectors of the tube, with the apices exserted or deeply included, sometimes free corona lobes absent. Stamens included or with the apices exserted, anthers connivent and agglutinated to the style-head, filaments short, densely hirsute. Style-head spool-shaped; ovules many, several-seriate; nectary annular, variously lobed, sometimes divided into 5 individual nectaries. Follicles 2, apocarpous, usually free but united just at their apices, sometimes completely longitudinally united through maturity, rarely winged, glabrous or variously pubescent. Seeds numerous, dry, truncate, glabrous, comose at the microphylar end.

The key to the sections in the new classification is based on the morphological descriptions in the new monograph for the genus (Morales & Endress, unpublished data).

# KEY TO THE SECTIONS OF PRESTONIA

- 1. Intrapetiolar colleters usually conspicuous; corolla tube, abaxial surfaces of the corolla lobes and follicles variously pubescent, the indument ferrugineous, brown, or yellow... sect. *Prestonia*
- Intrapetiolar colleters inconspicuous; corolla tube, abaxial surfaces of the lobes and follicles glabrous, glabrescent, or sparsely puberulent, the indument green or colorless ... 2
- 2. Leaf blades and sepals coriaceous to subcoriaceous; follicles somewhat woody... sect.

  \*Denticulatae\*
- 2. Leaf blades sepals and follicles membranaceous;... 3
- 3. Annular corona inconspicuous, sometimes absent; corolla tube usually without free corona lobes within (except *P. pickelii*) ... sect. *Coalitae*
- 3. Annular corona conspicuous; corolla tube with free corona lobes within ... 4
- 4. Sepals without visible veins, the apices reflexed or not reflexed; follicles free, but usually united at the tips (at least when young), rarely connate (*P. quinquangularis*) . . . sect. *Haemadictyon*
- 4. Sepals with the veins conspicuously impressed, the apices not reflexed; follicles usually connate longitudinally ...5
- 5. Corolla lobes 18–34 mm long, the tube 20–36 mm long... sect. *Mollis*
- 5. Corolla lobes 6–14 mm long, the tube 9–17 mm long... sect. Exsertae
- Sect. Coalitae Woodson, Ann. Missouri Bot. Gard. 23: 278-1936. Sect. Rhaptocarpus Pichon, Mém. Mus. Natl. Hist. Nat., B, Bot. 1: 27. 1951, nom. illeg. Type: Prestonia coalita (Vell.) Woodson, Ann. Missouri Bot. Gard. 18: 552. 1931. Echites coalitus Vell., Fl. Flumin. 112. 1825[1829].

Prestonia coalita (Vell.) Woodson, Ann. Missouri Bot. Gard. 18: 552. 1931. Prestonia dusenii (Malme) Woodson, Ann. Missouri Bot. Gard. 18: 552. 1931. Prestonia ornata (Hoehne) J. F. Morales & M.E. Endress, Taxon 000: 000. 2017.

Prestonia pickelii Markgr., Notizbl. Bot. Gart. Berlin-Dahlem 14: 129 1938.

Prestonia solanifolia (Müll. Arg.) Woodson, Ann. Missouri Bot. Gard. 23: 282 1936.

Sect. Denticulatae J. F. Morales, M. Endress & Liede, sect. nov. – Type: Prestonia denticulata (Vell.) Woodson, Ann. Missouri Bot. Gard. 23: 284. 1936. Echites denticulatus Vell., Fl. Flumin. 110. 1829.

Prestonia amabilis J. F. Morales, Sida 21: 161, f. 1. 2004.

Prestonia amazonica (Benth. ex Müll. Arg.) J. F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 34. 1931.

Prestonia antioquiana J. F. Morales & Liede, Phytotaxa 265: 207, f.2A, 3A; f. 4. 2016.

Prestonia denticulata (Vell.) Woodson, Ann. Missouri Bot. Gard. 23: 284. 1936.

Prestonia haughtii Woodson, Ann. Missouri Bot. Gard. 35: 235. 1948.

Prestonia leco A. Fuentes & J. F. Morales, Novon 20: 278, f. 1. 2010.

Prestonia lenticellata A. H. Gentry, Ann. Missouri Bot. Gard. 61: 896. 1974.

Prestonia lindleyana Woodson, Bull. Torrey Bot. Club 60: 392. 1933.

Prestonia macroneura Woodson, Ann. Missouri Bot. Gard. 23: 321. 1936.

Prestonia megagros (Vell.) Woodson, Ann. Missouri Bot. Gard. 21: 623. 1934.

Prestonia plumierifolia Markgr., Notizbl. Bot. Gart. Berlin-Dahlem 10: 1038. 1930.

Prestonia robusta Rusby, Descr. S. Amer. Pl. 91. 1920.

Prestonia rotundifolia K. Schum. ex Woodson, Ann. Missouri Bot. Gard. 23: 318. 1936.

Prestonia trifida (Poepp.) Woodson, Bull. Torrey Bot. Club 60: 392. 1933.

Prestonia vana Woodson, Ann. Missouri Bot. Gard. 23: 323. 1936.

Sect. Exsertae J. F. Morales, M. Endress & Liede, sect. nov. Type: Prestonia exserta (A. DC.) Standl., J. Wash. Acad. Sci. 15: 460. 1925. Haemadictyon exsertum A. DC., Prodr. 8: 426.1844.

Prestonia didyma (Vell.) Woodson, Ann. Missouri Bot. Gard. 23: 308. 1936.

Prestonia exserta (A. DC.) Standl., J. Wash. Acad. Sci. 15: 460. 1925.

Prestonia falcatosepala J. F. Morales, Candollea 59: 162, f. 3. 2004.

Prestonia folsomii J. F. Morales, Novon 6: 285, f. 1. 1996.

Prestonia parvifolia K. Schum. ex Woodson, Ann. Missouri Bot. Gard. 23: 302. 1936.

Sect. Haemadictyon K. Schum., Nat. Pflanzenfam. 4: 188. 1895. Sect. Acutifoliae Woodson, Ann. Missouri Bot. Gard. 23: 284. 1936, nom. illeg. Type: Prestonia acutifolia (Benth. ex Müll. Arg.) K. Schum. Nat. Pflanzenfam. 4: 188. 1895. Haemadictyon acutifolium Benth. ex Müll. Arg. Fl. Bras. 6: 167. 1860.

Sect. Annulares Woodson, Ann. Missouri Bot. Gard. 23: 296. 1936. Type: *Prestonia annularis* (L.f.) G. Don, Gen. Hist. 4: 84. 1837. *Echites annularis* L.f., Suppl. Pl. 166. 1781[1782].

Prestonia annularis (L. f.) G. Don, Gen. Hist. 4: 84. 1837.

Prestonia boliviana J. F. Morales & A. Fuentes, Sida 21: 166, f. 1. 2004.

Prestonia cayennensis (A. DC.) Pichon, Mém. Mus. Natl. Hist. Nat., B, Bot. 1: 25. 1951.

Prestonia cyaniphylla (Rusby) Woodson, Ann. Missouri Bot. Gard. 23: 284. 1936.

Prestonia lagoensis (Müll. Arg.) Woodson, Ann. Missouri Bot. Gard. 23: 293. 1936.

Prestonia longifolia (Sessé & Moc.) J. F. Morales, Novon 6: 287. 1996.

Prestonia marginata Markgr., Notizbl. Bot. Gart. Berlin-Dahlem 9: 88. 1924.

Prestonia papillosa (Müll. Arg.) J. F. Morales, Candollea 59: 161. 2004.

Prestonia portobellensis (Beurl.) Woodson, Ann. Missouri Bot. Gard. 18: 553. 1931.

Prestonia quinquangularis (Jacq.) Spreng., Syst. Veg. [Sprengel] 1: 637. 1825[1824].

Prestonia vaupesana Woodson, Bot. Mus. Leafl.18: 178. 1958.

**Sect. Mollis** J. F. Morales, M. Endress & Liede, **sect. nov.** – Type: *Prestonia mollis* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 221, t. 242. 1818[1819].

Prestonia mollis Kunth, Nov. Gen. Sp. (quarto ed.) 3: 221, t. 242. 1818[1819].

Prestonia cordifolia Woodson, Ann. Missouri Bot. Gard. 23: 352. 1936.

Sect. Prestonia. Sect. Tomentosae Woodson, Ann. Missouri Bot. Gard. 23: 344. 1936, nom. illeg. Type: Prestonia tomentosa R. Br., Mem. Wern. Nat. Hist. Soc. 1: 70. 1811.

Sect. Tetraceras Pichon, Mém. Mus. Natl. Hist. Nat., B, Bot. 1: 26. Type: *Prestonia parviflora* (Benth.) Benth. & Hook. f., Gen. Pl. 2: 709. 1876.

Prestonia acrensis J. F. Morales, Acta Amazon. 34: 669. 2004.

Prestonia bahiensis Müll. Arg., Fl. Bras. 6: 164. 1860.

Prestonia calycina Müll. Arg., Fl. Bras. 6: 162. 1860.

Prestonia clandestina J. F. Morales, Novon 7: 60 1997.

Prestonia cogolloi J. F. Morales, Anales Jard. Bot. Madrid 64: 148, f. 1. 2007.

Prestonia hammelii J. F. Morales, Novon 7: 60. 1997.

Prestonia ipomaeifolia A. DC., Prodr. 8: 429. 1844.

Prestonia megagros (Vell.) Woodson, Ann. Missouri Bot. Gard. 21: 623 1934.

Prestonia mexicana A. DC., Prodr. 8: 429. 1844.

Prestonia mucronata Rusby, Descr. S. Amer. Pl. 90.1920.

Prestonia parviflora (Benth.) Benth. & Hook. f., Gen. Pl. 2: 709. 1876.

Prestonia premontana J. F. Morales, Anales Jard. Bot. Madrid 64: 150, f. 2. 2007.

Prestonia racemosa J. F. Morales, Anales Jard. Bot. Madrid 64: 153, f. 3. 2007.

Prestonia riverae J. F. Morales, Novon 7: 63, f. 1. 1997.

Prestonia schumanniana Woodson, Ann. Missouri Bot. Gard. 23: 364. 1936.

Prestonia seemannii Miers, Apocyn. S. Am. 146. 1878.

Prestonia speciosa Donn. Sm., Bot. Gaz. 27: 435. 1899.

Prestonia surinamensis Müll. Arg., Linnaea 30: 433. 1860.

Prestonia tomentosa R. Br., Mem. Wern. Nat. Hist. Soc. 1: 70. 1811.

Prestonia tysonii A. H. Gentry, Ann. Missouri Bot. Gard. 61: 895. 1974.

## **Literature Cited**

- Allen, C.K., D.J. Rogers & L.I. Nevling, Jr. 1965. Robert Everard Woodson, Jr. (1904—1963). Brittonia 17: 1–11.
- Baillon, H. E. 1891. Histoire des Plantes 10. Librairie Hachete & Co, Paris.
- Baldwin, B. G., M. J. Sanderson, J. M. Porter, M. F. Wojciechowski, C. S. Campbell & M.J. Donoghue. 1995. The *ITS* region of nuclear ribosomal DNA: A valuable source of evidence on angiosperm phylogeny. Ann. Missouri Bot. Gard. 82: 247–277.
- Bell, C., G. Calderon, L. González, A. Scholz & S. Liede-Schumann. 2015. Resolving relationships within Valerianaceae (Dipsacales): New Insights and Hypotheses from Low-Copy Nuclear Regions. Syst. Bot. 40: 327–335.
- Bentham, G. 1841. Contributions towards a Flora of South America–Enumeration of Plants collected by Mr. Schomburgk in British Guiana, J. Bot. (Hooker) 3: 212–250.
- Blake, S. F. 1917. Descriptions of new spermatophytes, chiefly from the collections of Professor M.E. Peck in British Honduras. Contr. Gray Herb. 52: 78–79.
- Brown, R. 1810. On the Asclepiadeae, a natural order of plants separated from the Apocineae of Jussieu. (Pre-print of: Mem. Wern. Nat. Hist. Soc. 1: 12–78 [1811].)
- Bruyns, P. V., A. al Farsi & T. Hedderson. 2010. Phylogenetic relationships of *Caralluma* R. Br. (Apocynaceae). Taxon 59: 1031–1043.
- Burge, D. O., K. Mugford, A. Hastings & A. Agrawal. 2013. Phylogeny of the plant genus *Pachypodium* (Apocynaceae). Peer J. 1: 1–20.
- Darriba, D., G. L. Taboada, R. Doallo & D. Posada. 2012. jModelTest 2: More models, new heuristics and parallel computing. Nature Meth. 9: 772.

- Endress, M. E. & P.V. Bruyns 2000. A revised classification of the Apocynaceae s.l. Bot. Rev. (Lancaster) 66: 1–56.
- Endress, M. E. & B. F. Hansen. 2007. *Pinochia*, a new genus of Apocynaceae, Apocynoideae from the Greater Antilles, Mexico and Central America. Edinburgh J. Bot. 64: 269–274.
- Endress, M. E., R. W. J. M. van der Ham, S. Nilsson, L. Civeyrel, M. W. Chase, B. Sennblad, K. Potgieter, J. Joseph, M. Powell, D. Lorence, Y. M. Zimmerman & V. A. Albert. 2007a. A phylogenetic analysis of Alyxieae (Apocynaceae) based on *rbcL*, *matK*, *trnL* intron, *trnL-F* spacer sequences, and morphological characters. Ann. Missouri Bot. Gard. 94: 1–35.
- Endress, M. E., S. Liede-Schumann & U. Meve. 2007b. Advances in Apocynaceae: The enlightenment, an introduction. Ann. Missouri Bot. Gard. 94: 259–267.
- Endress, M. E., S. Liede-Schumann, & U. Meve. 2014. An updated classification for Apocynaceae. Phytotaxa 159: 175–194.
- Ezcurra, C. 1981 Novedades en los generos *Temnadenia* y *Macrosiphonia* (Apocynaceae). Hickenia 1: 241-246
- Fan, J., H.N. Qin, D. Z. Li & X. H. Jin. 2009. Molecular phylogeny and biogeography of *Holcoglossum* (Orchidaceae: Aeridinae) based on nuclear *ITS*, and chloroplast *trnL*-*F* and *matK*. Taxon 58: 849–861.
- Funk, V. A., P. E. Berry, S. Alexander, T. H. Hollowell & C. L. Kelloff. 2007. Checklist of the plants of the Guiana Shield (Venezuela: Amazonas, Bolivar, Delta Amacuro; Guyana, Surinam, French Guiana). Contr. U.S. Natl. Herb. 55: 1–584.
- Gentry, A. H. 1974. Notes on Panamian Apocynaceae. Ann. Missouri Bot. Gard. 61: 891–900.
- Gentry, A. H. 1983. A new combination for a problematic Central American Apocynaceae. Ann. Missouri Bot. Gard.70: 205–206.

- Goyder, D, A. Nicholas & S. Liede-Schumann. 2007. Phylogenetic relationships in subtribe Asclepiadinae (Apocynaceae: Asclepiadoideae). Ann. Missouri Bot. Gard. 94: 423–434.
- Hendrian & K. Kondo. 2007a. Molecular phylogeny of *Ochrosia* sensu lato (Apocynaceae) based on *ITS* sequence data: An evidence for the inclusion of *Neisosperma*. Chromosome Bot. 2: 127–132.
- Hendrian & K. Kondo. 2007b. Molecular phylogeny of *Ochrosia* sensu lato (Apocynaceae) based on *rps16* intron and *ITS* sequence data: Supporting the inclusion of *Neisosperma*. Chromosome Bot. 2: 133–140.
- Hendrian & K. Kondo. 2007c. Monophyly of *Ochrosia* sensu lato (Apocynaceae): Evidence from *ITS*, *rps16* intron and morphological characters. Chromosome Bot. 2: 141–149.
- Hoehne, F. C. 1915. Historia Natural. Botanica. Parte 6. Comm. Lin. Telegr., Bot. 5: 1–96, pl. 113–131.
- Hokche, O., P. E. Berry & O. Huber. 2008. Nuevo Catálogo de la Flora Vascular de Venezuela. Fundación Instituto Botánico de Venezuela, Caracas.
- Huelsenbeck, J. P. & F. R. Ronquist. 2001. MrBayes: Bayesian inference of phylogeny. Biometrics 17: 754–755.
- Huelsenbeck, J. P. & B. Rannala. 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. Syst. Biol. 53: 904–913.
- Humbert, H. & J. Léandri. 1955. Marcel Pichon (1921–1954). Bull. Soc. Bot. France 102, Suppl. 1: 95–98. http://dx.doi.org/10.1080/00378941.1955.10835055
- Ionta, G. M. & W. S. Judd. 2007. Phylogenetic relationships in Periplocoideae (Apocynaceae s.l.) and insights into the origin of pollinia in the subfamily. Ann. Missouri Bot. Gard. 94: 360–375.

- Joubert, L., C. Klak, A. M. Venter, H. J. T. Venter & P. V. Bruyns. 2016. A widespread radiation in the Periplocoideae (Apocynaceae): The case of *Cryptolepis*. Taxon 65: 487–501.
- Khanum, R., S. Surveswaran, U. Meve & S. Liede-Schumann. 2016. *Cynanchum* (Apocynaceae: Asclepiadoideae): A pantropical Asclepiadoid genus revisited. Taxon 65: 467–486.
- León, B., J. Roque, C. Ulloa Ulloa, N. Pitman, P. Jørgensen & A. Cano. 2006. El Libro Rojo de las Plantas Endémicas del Perú. Revista Peruana Biol. 13(2): 1–971.
- Liede-Schumann, S., A. Rapini, D. J. Goyder & M. W. Chase. 2005. Phylogenetics of the New World subtribes of Asclepiadeae (Apocynaceae-Asclepiadoideae): Metastelmatinae, Oxypetalinae, and Gonolobinae. Syst. Bot. 30: 184–195.
- Lindley, J. 1826. Report upon the new or rare plants which have flowered in the Garden of the Horticultural Society at Chiswick, from its first formation to March 1824, to March 1825. Trans. Hort. Soc. London 6: 62–100.
- Livshultz, T. 2010. The phylogenetic position of milkweeds (Apocynaceae subfamilies Secamonoideae and Asclepiadoideae): Evidence from the nucleus and chloroplast. Taxon 59: 1016–1030.
- Livshultz, T., D. J. Middleton, M. E. Endress & J. K. Williams. 2007. Phylogeny of Apocynoideae and the APSA clade (Apocynaceae s.l.). Ann. Missouri Bot. Gard. 94: 324–359.
- Macbride, J. F. 1959. Apocynaceae, Flora of Peru. Publ. Field Mus. Nat. Hist., Bot. Ser. 13: 363–455.
- Markgraf, F. 1924. Neue Apocynaceen aus Südamerika. <u>Notizbl. Bot. Gart. Berlin–Dahlem</u> 9: 77–90.
- Markgraf, F. 1938. Neue Apocynaceen aus Südamerika VII. Notizbl. Bot. Gart. Berlin-Dahlem 14: 128–132.

- Markgraf, F. 1975. Novedades Venezolanas en las Apocynaceae. Acta Bot. Venez. 10: 247–250.
- Mathias, M.E. 1965. Robert E. Woodson, Jr. (1904–1963). Ann. Missouri Bot. Gard. 52: 225–228.
- McNeill, J., F.R.Barrie, W.R., Buck, V. Demoulin, W. Greuter, D.L. Hawksworth, P.S.Herendeen, S. Knapp, K. Marhold, J. Prado, W.F. Prud'homme van Reine, G.F.Smith, J.H.Wiersema, & N.J. Turland (editors) 2012. International Code of Nomenclature for algae, fungi, and plants (Melbourne Code): Adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Regnun Vegetabile 154. Koeltz Scientific Books. Königstein [online ed.: http://www.iapt-taxon.org/nomen/main.php].
- Meve, U. & S. Liede. 2001. Inclusion of *Tenaris* and *Macropetalum* in *Brachystelma* (Apocynaceae-Asclepiadoideae-Ceropegieae) inferred from non-coding nuclear and chloroplast DNA sequences. Plant Syst. Evol. 228: 89–105.
- Meve, U. & S. Liede. 2004. Subtribal division of Ceropegieae (Apocynaceae–Asclepiadoideae). Taxon 53: 61–72.
- Meve, U., A. Heiduk & S. Liede-Schumann. 2017. Origin and early evolution of Ceropegieae (Apocynaceae-Asclepiadoideae). Syst. Biodiv. 15(2): 143–153.
- Middleton, D. J. & T. Livshultz. 2012. *Streptoechites* gen. nov., a new genus of Asian Apocynaceae. Adansonia, sér. 3, 34: 365–375.
- Miers, J. 1878. On the Apocynaceae of South America. Williams & Norgate, London.
- Miller, M.A., W. Pfeiffer & T. Schwartz. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Pp. 1–8 *in* Proceedings of the Gateway computing environments workshop (GCE), 14 Nov 2010, Institute of Electrical and Electronics Engineers, New Orleans.
- Morales, J. F. 1996. Novelties in *Prestonia* (Apocynaceae). Novon 6: 285–287.

- Morales, J. F. 1997a. A synopsis of the genus *Prestonia* (Apocynaceae) section *Tomentosae* in Mesoamerica. Novon 7: 59–66.
- Morales, J. F. 1997b. A reevaluation of *Echites* and *Prestonia* section *Coalitae* (Apocynaceae). Brittonia 49: 328–336.
- Morales, J. F. 1999. *Rhodocalyx* (Apocynaceae), a new synonym of *Prestonia*. Novon 9: 89–91.
- Morales, J. F. 2004a. Estudios en las Apocynaceae Neotropicales IV: Notas taxonómicas en *Prestonia*, con una nueva especie de Ecuador. Sida 21: 159–163.
- Morales, J. F. 2004b. Estudios en las Apocynaceae Neotropicales VII: Novedades taxonómicas en *Prestonia* (Apocynaceae, Apocynoideae) para Colombia y Ecuador, con comentarios sobre el grado de lobulación del nectario. Candollea 59: 159–165.
- Morales, J. F. 2004c. Estudios en las Apocynaceae Neotropicales VI: Una nueva especie de *Prestonia* (Apocynaceae, Apocynoideae) para Brasil. Acta Amazonica 34: 669–670.
- Morales, J. F. 2005a. Estudios en las Apocynaceae Neotropicales XIX: La familia Apocynaceae s. str. (Apocynoideae y Rauvolfioideae) de Costa Rica. Darwiniana 43: 90–191.
- Morales, J. F. 2005b. Estudios en las Apocynaceae Neotropicales XIII: Revisión del género *Temnadenia* (Apocynoideae, Echiteae). Candollea 60: 207–231
- Morales, J. F. 2006. Estudios en las Apocynaceae Neotropicales XXVII: Lectotipificaciones misceláneas en el género *Prestonia* (Apocynoideae, Echiteae). Brenesia 66: 75–78.
- Morales, J. F. 2007a. Estudios en las Apocynaceae Neotropicales XXXII: Tres nuevas especies de *Prestonia* (Apocynoideae, Echiteae) para Sur America. Anales Jard. Bot. Madrid 64: 147–154.

- Morales, J. F. 2007b. Estudios en las Apocynaceae Neotropicales XXXV: Novedades nomenclaturales en el género *Prestonia* para Brasil (Apocynoideae, Echiteae). Darwiniana 45: 213–217.
- Morales, J. F. 2008. Estudios en las Apocynaceae Neotropicales XXXV: Novedades nomenclaturales en el género *Prestonia* para Brasil (Apocynoideae, Echiteae). Darwiniana 45: 213–217.
- Morales, J. F. 2010. Estudios en las Apocynaceae Neotropicales XL: Sinopsis del género *Prestonia* (Apocynoideae, Echiteae) en Ecuador. Anales Jard. Bot. Madrid 67: 13–21.
- Morales, J. F. 2011. Studies in the Neotropical Apocynaceae XLI: A new species of *Prestonia* (Apocynoideae, Echiteae) from Peru and a key to the Peruvian species. Phytotaxa 29: 28–32.
- Morales, J. F. & J. K. Williams. 2004. *Allotoonia*, a new neotropical genus of Apocynaceae based on a subgeneric segregate of *Echites*. Sida 21: 133–158.
- Morales, J. F. & S. Liede-Schumann, S. 2016. The genus *Prestonia* (Apocynaceae) in Colombia. Phytotaxa 265: 204–224.
- Morales, J. F., M. E. Endress & S. Liede-Schumann. 2017. Sex, drugs and pupusas: Disentangling relationships in Echiteae (Apocynaceae). Taxon 00: 000–000 (accepted).
- Naumann, J., L. Symmank, M.-S. Samain, K. F. Müller, C. Neinhuis, C. W. dePamphilis & S. Wanke. 2011. Chasing the hare Evaluating the phylogenetic utility of a nuclear single copy gene region at and below species level within the species rich group *Peperomia* (Piperaceae). BMC Evol. Biol. 2011: 357.
- Nevling, Jr., L.I. 1965. A catalogue of the published works of Robert E. Woodson, Jr. Ann. Missouri Bot. Gard. 52: 229–233.

- Pelser, P. B., A. H. Kennedy, E. J. Tepe, J. B. Schidler, B. Nordenstam, J. W. Kadereit & L. F. Watson. 2010. Patterns and causes of incongruence between plastid and nuclear Senecioneae (Asteraceae) phylogenies. Amer. J. Bot. 97: 856–873.
- Pichon, M. 1947a. Classification des Apocynacées II, genre *Rauvolfia*. Bull. Soc. France 94: 3–39.
- Pichon, M. 1947b. Classification des Apocynacées: IV, genre *Alstonia* et genres voisins. Bull. Mus. Hist. Nat., sér. 2, 19: 294–301.
- Pichon, M. 1948a. Classification des Apocynacées: X. Genre *Mandevilla*. Bull. Mus. Hist. Nat. (Paris), sér. 2, 20: 201–108.
- Pichon, M. 1948b. Classification des Apocynacées XIX, Le rétinacle des Echitoïdeés. Bull. Soc. Bot. France 95: 211–216.
- Pichon, M. 1948c. Classification des Apocynacées: VI, Genre *Tabernaemontana*. Not. Syst. 13: 230–253.
- Pichon, M. 1950a. Classification des Apocynacées XXV, Echitoïdeés. Mém. Mus. Natl. Hist. Nat., sér. B, Bot.1: 1–142.
- Pichon, M. 1950b. Classification des Apocynacées: XXVIII, Supplément aux Plumerioïdées, Mém. Mus. Natl. Hist. Nat., sér. B, Bot. 1: 145–166.
- Pichon, M. 1950c. Classification des Apocynacées: XII, Les *Parsonsia* et les *Artia* de l'herbier du Muséum. Notul. Syst. (Paris) 14: 4–21.
- Pichon, M. 1953. Classification des Apocynacées: XXXV, Monographie des Landolphiées. Mém. Inst. Franç. Afrique Noire 35: 1–437.
- Potgieter, K. 1999. Phylogenetic study of Apocynaceae Juss. and *Aspidosperma* Mart. and Zucc. Unpublished PhD thesis from the University of Illinois at Urbana-Champaign.
- Rambaut, A. 2014. FigTree, version 1.4.2. <a href="http://tree.bio.ed.ac.uk/software/figtree/">http://tree.bio.ed.ac.uk/software/figtree/</a>

- Rambaut, A. & A. J. Drummond. 2007. Tracer. Version 1.5. http://beast.bio.ed.ac.uk/Tracer/
- Rapini, A. 2012. Taxonomy "under construction": Advances in the systematics of Apocynaceae, with emphasis on the Brazilian Asclepiadoideae. Rodriguésia 63: 75–88.
- Rapini, A., M. W. Chase & T. U. P. Konno. 2006. Phylogenetics of South American Asclepiadeae (Apocynaceae). Taxon 55: 119–124.
- Rapini, A., J. Fontella & D. Goyder. 2011. Towards a stable generic circumscription in Oxypetalinae (Apocynaceae). Phytotaxa 26: 9–16.
- Ronquist, F. & J. P. Huelsenbeck. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574.
- Schumann, K. M. 1895. Apocynaceae. Pp. 109–189 *in* A. Engler & K. Prantl (editors), Die natürlichen Pflanzenfamilien IV(2). Engelmann, Leipzig.
- Silva, U. C. S., A. Rapini, S. Liede-Schumann, P. L. Ribeiro & C. van den Berg. 2012. Taxonomic considerations on Metastelmatinae (Apocynaceae) based on plastid and nuclear DNA. Syst. Bot. 37: 795–806.
- Simões, A. O., M. E. Endress, T. van der Niet, E. Conti & L. S. Kinoshita. 2004. Tribal and intergeneric relationships of Mesechiteae (Apocynoideae, Apocynaceae): evidence from three noncoding plastid DNA regions and morphology. Amer. J. Bot. 91: 1409–1418.
- Simões, A. O., M. E. Endress, T. van der Niet, L. S. Kinoshita & E. Conti. 2006. Is *Mandevilla* (Apocynaceae, Mesechiteae) monophyletic? Evidence from five plastid DNA loci and morphology. Amer. J. Bot. 93: 565—591.
- Simões, A. O., M. E. Endress & E. Conti. 2010. Systematics and character evolution of Tabernaemontaneae (Apocynaceae, Rauvolfioideae) based on molecular and morphological evidence. Taxon 59: 772–790.

- Simões, A. O., L. S. Kinoshita, I. Koch, M. J. Silva & M. E. Endress. 2016. Systematics and character evolution of Vinceae (Apocynaceae). Taxon 65: 99–122.
- Spalik, K., S. R. Downie & M. F. Watson. 2009. Generic delimitations within the *Sium* alliance (Apiaceae tribe Oenantheae) inferred from cpDNA *rps16-5'trnK* (UUU) and nrDNA ITS sequences. Taxon 58: 735–748.
- Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22: 2688–2690.
- Stamatakis, A., P. Hoover & J. Rougemont. 2008. A rapid bootstrap algorithm for the RAxML web servers. Syst. Biol. 57: 758–771.
- Surveswaran, S., M. Y. Kamble, S. R. Yadav & M. Sun. 2009. Molecular phylogeny of *Ceropegia* (Asclepiadoideae, Apocynaceae) from Indian Western Ghats. Pl. Syst. Evol. 281: 51–63.
- Trovo, M., M. J. Andrade, T. P. Sano, P. L. Ribeiro & C. van den Berg. 2013. Molecular phylogenetics and biogeography of Neotropical Paepalanthoideae with emphasis on Brazilian *Paepalanthus* (Eriocaulaceae). Bot. J. Linn. Soc. 171: 225–243.
- Uemachi, A. & T. Shimomura. 2013. Molecular phylogeny of *Trachelospermum* (Apocynaceae) in Japan based on cpDNA and nrDNA nucleotide sequences. Acta Phytotax. Geobot. 64: 1–13.
- Wanntorp, L., M. Grudinski, P. I. Forster, A. N. Muellner-Riehl, & G. W. Grimm. 2014. Wax plants (*Hoya*, Apocynaceae) evolution: Epiphytism drives successful radiation. Taxon 63: 89–102. http://dx.doi.org/10.12705/631.3
- Weitemier, K., S.C. Straub, M. Fishbein & A. Liston. 2015. Intragenomic polymorphisms among high-copy loci: A genus-wide study of nuclear ribosomal DNA in *Asclepias* (Apocynaceae) PeerJ 3:e718.
- Wiens, J. J. 2003. Missing data, incomplete taxa, and phylogenetic accuracy. Syst. Biol. 52: 528–538.

- Williams, J.K. 2004. Polyphyly of the genus *Echites* (Apocynaceae: Apocynoideae: Echiteae): Evidence based on a morphological cladistic analysis. Sida 21: 117–131.
- Woodson, R. E., Jr. 1931. New or otherwise noteworthy Apocynaceae of Tropical America. Ann. Missouri Bot. Gard. 18: 541–556. http://dx.doi.org/10.2307/2394193
- Woodson, R.E., Jr. 1932a. New or otherwise noteworthy Apocynaceae of Tropical America II. Ann. Missouri Bot. Gard. 19: 45–76.
- Woodson, R. E., Jr. 1932b, New or otherwise noteworthy Apocynaceae of Tropical America III. Ann. Missouri Bot. Gard.19: 375–387.
- Woodson, R. E., Jr. 1933. Studies in the Apocynaceae IV. The American genera of Echitoideae. Ann. Missouri Bot. Gard. 20: 605–790.
- Woodson, R. E., Jr. 1934. New or otherwise noteworthy Apocynaceae of Tropical America IV. Ann. Missouri Bot. Gard. 21: 613–623.
- Woodson, R. E., Jr. 1935. Studies in the Apocynaceae. IV. The American genera of Echitoideae. Ann. Missouri Bot. Gard.22: 153–306.
- Woodson, R. E., Jr. 1936. Studies in the Apocynaceae. IV. The American genera of Echitoideae. Ann. Missouri Bot. Gard. 23: 169–439.
- Woodson, R.E., Jr. 1939. New or otherwise noteworthy Apocynaceae of Tropical America VII. Ann. Missouri Bot. Gard. 26: 257–259. http://dx.doi.org/10.2307/2394294
- Woodson, R. E., Jr. 1948. Miscellaneous new Apocynaceae and Asclepiadaceae. Ann. Missouri Bot. Gard. 35: 233–238.
- Woodson, R. E., Jr. 1951. Studies in the Apocynaceae VIII. An interim revision of the genus *Aspidosperma* Mart. & Zucc. Ann. Missouri Bot. Gard. 38: 119–206.
- Woodson, R. E., Jr. 1960. Loganiaceae, Apocynaceae and Asclepiadaceae. *in* Miscellanea taxonomica II. Ann. Missouri Bot. Gard. 47: 73–80.

- Woodson, R.E. & R.E. Schery. 1940. Contributions toward a Flora of Panama IV. Miscellaneous collections, chiefly by Paul H. Allen. Ann. Missouri Bot. Gard. 29 27: 265–365
- Woodson, R. E. & R.W. Schery. 1942. Contributions toward a Flora of Panama VI. Collections chiefly by H. von Wedel in Bocas del Toro. Ann. Missouri Bot. Gard. 29: 317–379.
- Xifreda, C.C. 1984. Estudios sobre Apocynaceae Argentinas IV. El género *Macropharynx* y una nueva combinación. Kurtziana 17: 163–167.
- Zarucchi, J. L., G. Morillo, M. E. Endress, B. F. Hansen & A. J. M. Leeuwenberg. 1995. Apocynaceae. Pp. 471–571 *in* P. E. Berry, B. K. Holst & K. Yatskievych (editors), Flora of the Venezuelan Guayana, Vol. 2. Timber Press, Portland, Oregon and Missouri Botanical Garden, St. Louis.

## SUPPLEMENTARY FIGURE LEGENDS

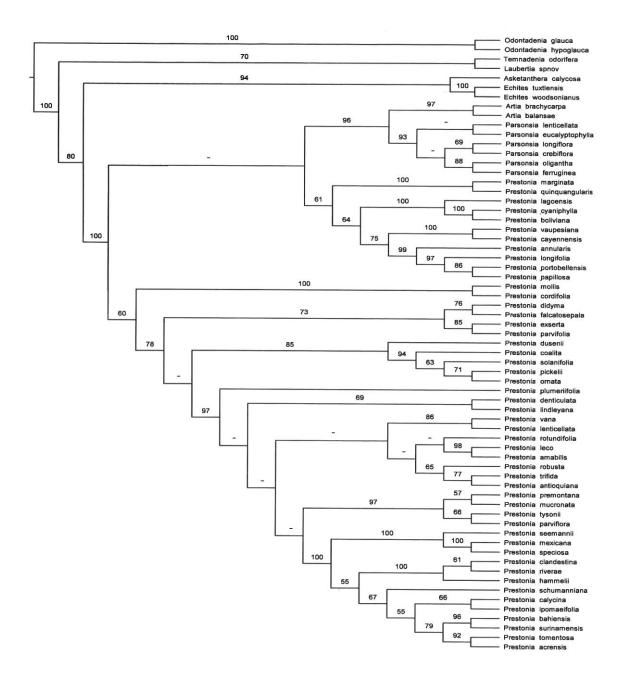


Fig. S1. Maximum likelihood consensus tree based on the matK and 3' / 5' trnK intron dataset. Bootstrap values values  $\geq 50$  are indicated above branches.

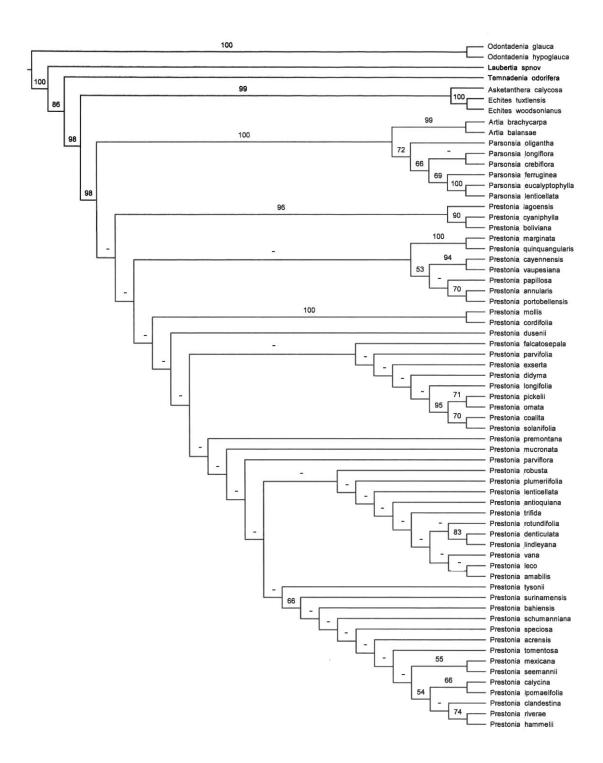


Fig. S2. Maximum likelihood consensus tree based on the rpl16 intron dataset. Bootstrap values values  $\geq 50$  are indicated above branches.

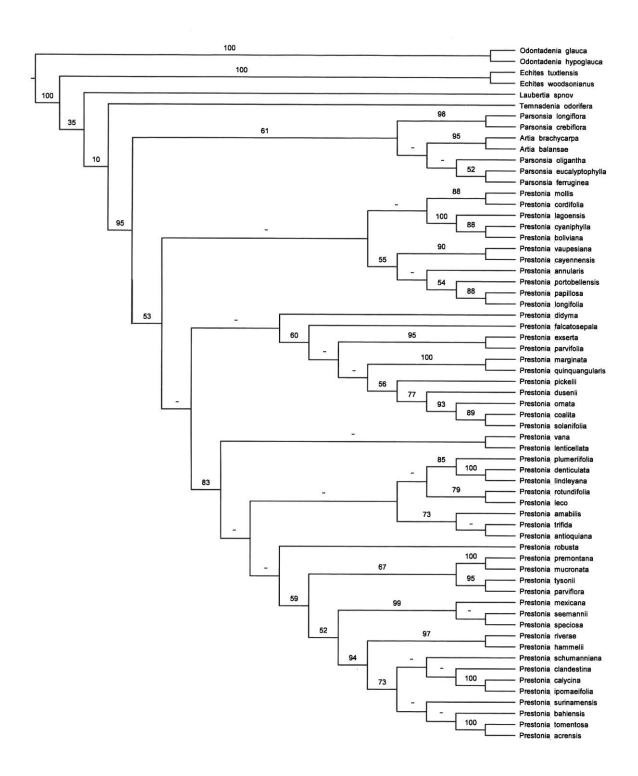
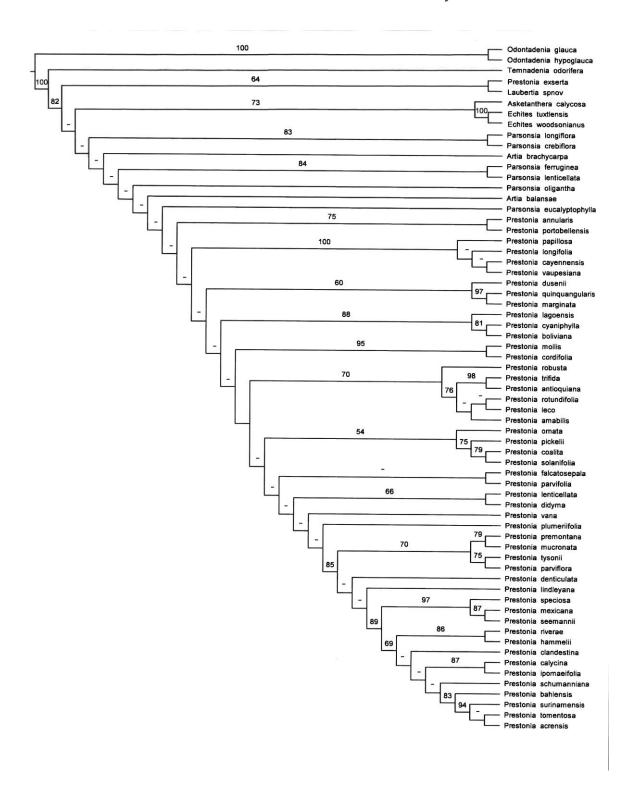


Fig. S3. Maximum likelihood consensus tree based on the rps16 intron dataset. Bootstrap values values  $\geq 50$  are indicated above branches.



**Fig. S4.** Maximum likelihood consensus tree based on the trnL intron and trnL-trnF intergenic spacer dataset. Bootstrap values values  $\geq 50$  are indicated above branches.

# **Publication 4**

Morales, J.F. & M. Endress. A monograph of the genus *Prestonia* (Apocynaceae, Echiteae, Prestoninae) (In preparation, to be submitted March 2017)

A monograph of *Prestonia* (Apocynaceae, Echiteae, Prestoninae)

J. FRANCISCO MORALES<sup>1</sup> & MARY ENDRESS<sup>2</sup>

Department of Plant Systematics, University of Bayreuth, Universitätsstr. 30, 95440

Bayreuth, Germany;

email: drifranciscomorales@gmail.com

Institute of Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107,

8008 Zürich, Switzerland

email: mendress@systbot.uzh.ch

**Abstract** 

A taxonomic revision of *Prestonia* (Echiteae, Prestoninae) was carried out based on more

than 6000 herbarium specimens and field work in seven countries, recognizing 58 species

classified in six sections. Prestonia is widely distributed from northern Mexico and the

West Indies to northern Argentina, ranging from sea level up to 2200 m, although most

species occur below 1100 m. The genus has been reported almost in all the neotropical

countries, with the exception of Chile. A key to the species, descriptions, illustrations and

distribution maps for all the species are included.

Key words: Apocynoideae, Echiteae, Gentianales, Neotropics

183

### Introduction

Prestonia Brown (1810: 58) (Apocynaceae, Apocynoideae) comprises 56 species, distributed from Mexico and the West Indies to northern Argentina, with a center of diversity in South America, where 49 species are reported. The genus is easily recognized by the following combination of characters: leaf blades without colleters, cymose inflorescences, sepals with an episepalous colleter, corolla tube with an annular corona around the mouth, usually with five free coronal lobes within, and truncate seeds (Woodson 1936; Morales 1997a, 2010). Prestonia is similar to Laubertia Candolle (1844: 486), but differs by its sepals lacking calycine colleters (Morales, 2002). Other genera of the tribe Echiteae with coronal structures are Hylaea Morales (1999: 83) and Thoreauea Williams (2002: 47), but the former is distinguished by its anthers, totally exserted outside the tube, and corollas lacking the annular corona, while the latter has stamens fused below the anthers and lacks free coronal lobes within the tube.

The last monograph of the genus was published by Woodson (1936), who recognized 61 species and four sections. Since then, many novelties have been published (including new species or synonyms), rendering this treatment outdated. A monograph of *Prestonia* is presented here. More than 6600 herbarium specimens were examined, including all the type collections available.

### **Historical Survey**

*Prestonia*, described by Brown (1810) with a single species (*P. tomentosa* Brown), was the first taxonomic proposal to break up *Echites* P. Browne (1756: 182). The prologue of the latter genus was diffuse and vague, which resulted in every species from the New World with opposite leaves and scandent habit being described in that genus in the next XX decades. *Prestonia* was characterized by Brown by having corollas with an annular corona around the mouth and five free coronal lobes within the tube.

Lindley proposed the genus *Haemadictyon* Lindley (1825: 70), which he distinguished from *Prestonia* by its nectary composed of five individual nectaries (vs. an annular disc necgtary). Alphonse de Candolle (1844) and Müller Argoviensis (1860a) followed Brown's and Lindley's proposals, describing several species and transferring other species previously described in *Echites*. Müller also proposed *Rhodocalyx* Müller

Argoviensis (1860a: 172), which he recognized as distinct from the two genera above by its erect habit, corollas lacking free coronal lobes within, and fusiform fruits.

The Apocynaceae of South America by Miers (1878) was probably the worst treatment ever published on neotropical Apocynaceae. Miers confused the generic realignments proposed by previous authors, describing many new genera and species, mostly based on weak morphological differences (Hansen, 1985; Morales 1999 b), and some species were even treated under two different genera (e.g., *Amblyanthera andrieuxii* Müller Argoviensis (1860b: 422), in *Echites* and *Mesechites* Müller Argoviensis (1860a: 150)). Although Miers was the first to reduce *Haemadictyon* to a synonym of *Prestonia*, at the same time, he described other new generas such as *Mitozus* Miers (1878: 217), *Rhaptocarpus* Miers (1878: 151), and *Temnadenia* Miers (1878: 207), to which he transferred several species of *Prestonia*, creating taxonomic uncertainty in the genus and family.

Schumman (1895) also considered *Haemadictyon* to be a synonym of *Prestonia*, made some additional combinations and proposed two sections: *Euprestonia* (seven species) and *Haemadictyon* (three species). However, he did not evaluate the genera proposed by Miers (1878), and thus, the taxonomy of the genus remained confused.

The monotypic *Belandra* S.F. Blake (1917: 78) was described based on a single specimen from Belize. The genus was assumed to be related to *Echites* and *Odontadenia* Bentham (1841: 242), but without discussion of its relationships with *Prestonia*.

In papers or monographs, Woodson (1931, 1932, 1933, 1935, 1936) clarified the taxonomy of the Neotropical "Echitoideae": in *Prestonia* he recognized four sections (*Acutifoliae*, *Annulares*, *Coalitae*, and *Tomentosae*) and 61 species (eight of them new combinations and 19 newly described); *Belandra* and *Haemadictyon* were treated as synonyms. The four sections were differentiated based on degree of corolla tube pubescence, shape and texture of the sepals, and characters of the free coronal lobes, annular corona, and anthers. After Woodson's monograph, the taxonomy of the genus remained stable for several decades and just new species or synopsis or revisions for specific geographical areas or countries have been published (e.g., Morillo 1978, Morales 1997a, 2010).

Later, Woodson described *P. caudata* Woodson (1960: 79), a species related to *P. agglutinata* (Jacquin) Woodson, which shared similar morphological characters, including lack of coronal structures. Following Woodson's inclusion of these species in section *Coalitae*, Gentry (1983) transferred *Echites woodsonianus* Monachino (1959: 245) to *Prestonia*. Morales (1997b) evaluated this section and determinated that *P. agglutinata*, *P. caudata*, and *P. woodsonianus* (Monachino) A.H. Gentry were inappropriately placed in Prestonia, and transferred them to *Echites*.

Morales (1999c) described the genus *Hylaea* (1999: 83), based on two species previously described in *Prestonia* (*P. arborescens* (Monachino) J.F. Morales (1961: 63) and *P. leptoloba* (Monachino) J.F. Morales (1957: 12)), in which the anthers and free corona lobes are completely exserted and which lack an annular corona around the mouth. *Rhodocalyx* was reduced to the synonymy of *Prestonia* by Morales (1999a). Later, a molecular analysis by Livshultz et al. (2007) suggested that should be treated as a valid genus, although sampling was too sparse to make a prudent decision on this at the time.

### Materials and methods

The taxonomic descriptions provided in this monograph were based in more than 6500 specimens from the following 159 herbaria: A, AAU, ALCB, AS, ASE, ASU, B, BAB, BEREA, BHCB, BIGU, BM, BOLV, BR, C, CAS, CAUP, CAY, CEN, CEPEC, CGE, CH, CHAPA, CICY, CIIDIR, CIMI, CM, COAH, COL, CR, CVRD, CUVC, CUZ, DPU, DS, DUKE, E, EAP, ECON, ENCB, ESA, ESAL, F, FCME, FCQ, FDG, FI (including FI-W), FUEL, G (including G-BOIS, G-DC), GB, GFJP, GH, HAL, HB, HBG, HERZU, HOXA, HRB, HRCB, HSB, HST (\*), HUA, HUEFS, HUFU, HUQ, IAN, IBGE, INB (\*\*), INPA, IPA, JAR (\*), JAUM, JE, JEPS, JPB, K, L, LAGU, LD, LE, LIL, LP, LPB, LZ, M, MA, MBM, MBML, MEDEL, MEXU, MHES, MICH, MIRR, MG, MO, MOL, MVFA, MVJB, NA, NY, O, OXF, P (including P-BA, P-HB, P-JU, P-L), PEL, PH, PMA, PORT, PR, PSO, Q, QAME, QAP, QCA, QCNE, QPLS, R, RB, S, SCZ SI, SP, SPF, SPFR, TEFH, TEX, TRIN, TULV, U, UB, UBT, UC, UCAM, UCOB, UDCB, UEC, UFMT, UFP, UPS, US, USF, USJ, USM, USZ, UVAL, VALLE, VEN, VIC, W, WU, WAG, WIS, XAL, Z, and ZT. The herbarium marked with an asterisk (\*) is not registred in

Index Herbariorum (Thiers, continuously updated). The herbarium INB (\*\*) was incorporated in CR.

Field work was carried out in El Salvador, Nicaragua, Costa Rica, Panama, Colombia, Peru, Bolivia, and Brazil, in many trips to different departments, states or provinces, between 2002 and 2015. Different populations of several species were studied, in order to understand the intraspecific variation within the genus and to photograph floral anatomical structures. In addition, flowers in spirit were preserved in a mix of pure ethanol (80%) and glycerin (20%) for further study in the laboratory. The descriptions of the morphological structures follow Font Quer (1953), Radford et al. (1974), and Harris & Harris (1994). In species with infundibuliform corollas, the terminology for regions of the tube follows Morales & Fuentes (2004b).

All type collections available were examined and most of the necessary lectotypes or neotypes have been validated in previously published papers s (e.g., Morales 2006b, 2007b, 2010).

Common names and uses cited for some species, as well as phenology, and habitat data, were taken from labels from herbarium specimens. Geographical coordinates (when available) were used to prepare distribution maps with ArcView GIS 3.2 software (ESRI 1999)

## Morphology

**Habit:**— All the species of the genus are lianas or herbaceous vines, usually terrestrial, rarely reported as epiphytic.

**Stems:**—Branchlets are terete or subterete, sometimes somewhat flattened in young stems. Sometimes lenticels are present and have relative taxonomic value at lower leves to distinguish some species (e.g., *Prestonia lenticellata* A.H. Gentry). Stems of various species usually become suberose with age

Like most Apocynaceae, *Prestonia* is characterized by the presence of latex. Latex color varies from watery to milky, depending on the species and in some species both types have been reported (e.g., *P. quinquangularis* (Jacquin) Sprengel), *P. mollis* Kunth), and is unknown for *P. mucronata* Rusby.

Intrapetiolars colleters are present at the nodes, these are typically narrowly conical to fusiform or linear filiform, and mostly inconspicuous (less than 1 mm long), excepting section *Prestonia*, in which intrapetiolar colleters are relatively long and conspicuous (usually around 2 mm long or more). Intrapetiolar colleters are useful to distinguish some sections within the genus, but of little use at the species level. Woodson (1930) referred to these as stipular remains (modified structures), Rio et al. (2002) conducted an anatomical study and characterization of intrapetiolar colleters in *P. coalita*, that confirmed that they have a secretory function. I found nothing in the literature about the ecological relationships between intrapetiolar colleters in the subfamily Apocynoideae and insects, I have observed ants visiting the colleters in young shoots of *Prestonia bahiensis* Müller Argoviensis and *P. mexicana* A. DC., where small drops of secretions were visible at the tips.

Stem indument is a useful character to distinguish sections and some species, but need to be used in conjunction with others morphological characters (e.g., inflorescence structure, flowers, fruit shape), since the density and color is highly variable in some species (e.g., *P. mexicana*, *P. tomentosa*). In section *Prestonia*, stems and branchlets have long conspicuous hairs, which vary from green to yellow or ferrugineous, whereas in the others sections, they are usually glabrous, glabrate or papillate-puberulent, with indument (if present) short and inconspicuous, green or colorless.

**Leaves:**—Petioles are subterete, without colleters along the adaxial surface. Leaves are always opposite, petiolate, and without colleters on the midrib. Blade is green, with the exception of a few species (e.g., *P. quinquangularis*, in which the abaxial surface of young leaves is sometimes purple, greenish purple or reddish green. Shape and size of the blade is more or less consistent, but not diagnostic for any species. Within a complex of related species (e.g., *P. annularis* (L.f.) G. Don and *P. portobellensis* (Beurling) Woodson, *P. lagoensis* (Müller Argoviensis) Woodson, and *P. cyaniphylla* (Rusby) Woodson) sterile material is virtually identical and it's not possible to separate them without inflorescences or flowers. Bullate laminas are uncommon in the genus and are found only in *P. lenticellata P. macroneura* Woodson, and *P. vana* Woodson. Margin is entire and usually flat, only a few species of section Denticulatae have revolute margins.

Texture varies from membranaceous to coriaceous or subcoriaceous. Although this character is relatively uniform in most species, in *P. quinquangularis* it is highly variable,

and several species have been described based solely on extreme variations of the blade texture.

Venation type is brochidodomous, with the secondary veins usually impressed (at least on the abaxial surface). Tertiary veins vary from conspicuously impressed and irregularly reticulated to inconspicuous or not impressed, without any noticeable correlation to section.

Indument (if present) is composed by simple unicelular hairs. In section *Prestonia* pubescence of leaf blade varies from tomentose or tomentulose to velutinous, hirsute, hirsutulous, or puberulent. Pubescence is usually more dense on the abaxial surface, on the adaxial surface, it is more sparse or the surface can be glabrate. In some species (e.g., *P. calycina* Müller Argoviensis, *P. ipomaeifolia* A. DC), the indument pattern is relatively uniform, but in others (e.g., *P. mexicana*, *P. tomentosa*) indument varies across the distributional range, sometimes becoming very variable in different populations from the same locality. In others sections leaves are usually glabrous or glabrate, with a few exceptions (e.g., *P. megagros* (Vellozo) Woodson), which have leaves papillate and moderately to densely puberulent on the abaxial surface.

**Inflorescence:**—Inflorescences in *Prestonia* are cymes, either monochasial (unbranched) or dichasial (branched), usually with the pedicels spirally arranged. Monochasial inflorescences can be short or elongated, with the flowers laxly distributed or more or less agglomerate, the latter being more common in sections Exsertae and Hamedictyon. Dichasial inflorescences are predominant in the genus, and display a wide range of variations, and can be branched one to four times. The last is uncommon and only occasionally found in a few species of section Denticulatae (e.g., *P. amabilis* J.F. Morales, *P. antioquiana* J.F. Morales). Sometimes twice branched inflorescences, have small and reduced rachises, with the flowers densely clustered, thus appearing umbelliform or subumbelliform. These have been described as umbeliform in several treatments: however, these inflorescences are true cymes (classified as aggregate dichasia).

Inflorescences are almost always axillary, just four species in section *Prestonia* have terminal or subterminal inflorescences, sometimes alternating with axillary inflorescences at the same branch: i.e., *P mucronata*, *P. parviflora* (Bentham) Bentham, *P. premontana* J.F. Morales, *P. tysonii* A.H. Gentry.

In section *Prestonia* (and few members of section Haemadictyon), the inflorescences have the same type of indumentum as the stems and leaves. In the other sections, the inflorescences are usually glabrous or glabrate, rarely minutely pubescent in some species (e.g., *P. megagros*, *P. vana*).

Floral bracts are always present, partially surrounding the base of the pedicels. They are persistent or early deciduous, membranaceous, and vary from scarious to foliaceous or subfoliaceous. The shape is variable and is correlated directly with the texture. In general, the consistency of the floral bracts is taxonomically significant to identify and separate some groups of species. The greatest variability is found in section *Prestonia*, where in some species (e.g., *Prestonia mexicana*) bracts of different sizes and shapes are found in the same inflorescence. Bracts veins are usually inconspicuous, although in a few species (e.g., *P. exserta* (A. DC.) Standley), the veins are conspicuously reticulate. Bracteoles are absent in the genus.

Peduncles are relatively short, slender or thickened, sometimes woody in fruiting material. Pedicels are slender, or slightly thickened, sometimes dextrorsely spirally twisted in spiral (e.g., *P. lindleyana* Woodson, *P. portobellensis*). In fresh material pedicels are commonly green, although a wide range of variation is found in section *Hamedictyon*, where in some species (e.g., *P. annularis*, *P. portobellensis*) can vary from purplish green, reddish green or maroonish green to greenish white or almost pure white.

**Calyx:**—The calyx is glabrous, glabrate, or variously pubescent. Pubescence is characteristic for the section *Prestonia*, whereas in section Denticulatae only a few species have pubescent calyx. In species of section *Prestonia*, the indumentum is more dense on the abaxial surface than on the adaxial surface, sometimes the adaxial surface has only a few sparse hairs, and eventually becomes glabrate.

The calyx has 5 sepals (diminute or foliaceous), which are united at the base, and more or less equal in size. The shape varies from ovate, elliptic to obovate, with several intermediate forms present. The texture is typically membranaceous, with exception of section Denticulatae, in which coriaceous or subcoriaceous sepals are predominant. Although Woodson (1936), sometimes gave significant emphasis to the texture of the sepals to separate some groups of taxa, here it is not considered reliable to distinguish species based only on this character

Sepals exhibit a wide range of colors, and may be green, reddish green, purplish green, to greenish white or almost white. Furthermore, several combinations between green, red, purple, or lilac occur in some species, even in the same inflorescence (e.g., *P. portobellensis*). The sepals are usually free along their entire length, but in a few rare instances (e.g., *P. amabilis*, *P. haugthii* Woodson, *P. rotundifolia* K. Schumann ex Woodson) they are fused basally for ½-1/3 of their length, forming a cup shaped base.

Veins of the sepals are usually conspicuous and irregularly reticulate in sections Exsertae and Mollis. In section *Prestonia*, the veins are sometimes conspicuous, although in some species the veins are hidden by pubescence (e.g., *P. mucronata*) or not evident at all (e.g., *P. hammelii* J.F. Morales). In the remaining sections, the veins are usually inconspicuous or not evident. The presence or absence of discernable veins on the sepals may be used (in combination with other morphological characters) to identify some species, but in general, their taxonomic use is very limited.

Without exception, the sepals have a single colleter located at the base on the adaxial surface, these vary from entire or subtentire to variously and irregularly lacerated. A single colleter per sepal is characteristic for genera of the Echiteae, with exception of *Laubertia*, in which the sepals lacks the colleters (Morales 2002). Colleters in section *Prestonia* are delicately membranaceous, usually erect or suberect, and variously pubescent toward the apex (sometimes the indumentum surpassing the apices), while in others sections, the colleters are more or less adnate to the sepals, and glabrous.

The shape and degree of laceration of the colleters has been used as an important diagnostic character for separation and recognition of species within the genus. These characters were widely used by Woodson (1936), who distinguished several species of section *Prestonia*, based largely on those characteristics. However, in that section the degree of laceration is correlated with the stage of floral development: in immature flowers (before anthesis), the colleter is usually entire or subentire, whereas in old flowers (when the corolla falls), the colleter is irregularly lacerated. Furthermore, deeply lacerated colleters have been erroneously described as numerous and indefinite. The use of this feature for differentiation of species is thus of little value.

**Corolla:**—The corolla is almost always salverform, only two species have an infundibuliform corolla: *P. clandestina* J.F. Morales and *P. speciosa* Donnell Smith. In a

few taxa, the tube is slightly expanded just below the mouth (e.g., *P. cyaniphylla*), and sometimes has five longitudinal grooves, usually most conspicuous near the stamens. The tube is more or less straight, except in *P. amazonica*, where it's spirally twisted around the stamens. Spital twisting around the stamens is found in few genera of the tribe Echiteae (e.g., *Laubertia*). Intraspecific variation in the corolla length can be significant in few species (e.g., *P. coalita*, *P. mexicana*, *P. portobellensis*). This range of morphological variation was responsible for the description of numerous superfluous taxa, which have been reduced to synonymy over the last twenty years.

Corolla color (particularly the lobes) can be quite variable in several species, are one of the most variable. The annular corona vary from white, green to yellow, sometimes with dark yellow, green, or red spots. In section *Prestonia*, corollas are yellow, green or cream, with several intermediate colors, but always without purple veins or stripes. In section Haemadictyon, the lobes are yellow, creamish green, greenish white, or purplish green, but with the veins deep yellow, purple or redish purple (and several irregular combinations in between). In *Prestonia mollis*, one of the most variable species in the genus, plants from lower elevations (below 1000 m) tend to have lobes yellow or greenish yellow, whereas in populations from higher elevations (usually more than 1500 m) the lobes are greenish lilac, or lilac. Some of these variations have been proposed as separate species (*P. cordifolia* Woodson); however, the degree of intergradation of this feature observed in the populations and specimens studied, makes recognition of these ecological variations untenable. In other species (e.g., *P. longifolia* (Sessé & Mociño) J.F. Morales, *P. portobellensis*) the variation shows no correlation with elevation and many forms are found within the same altitudinal range.

Aestivation of the corolla lobes is dextrorse. The lobes are commonly obliquely obovate, more or less extended at anthesis, but soon after the apices become reflexed towards the apices

A diagnosis character for delimiting sections within the genus is the type of external pubescence of the corolla tube, especially its length and color. In section *Prestonia* corollas are pubescent (but never minutely puberulent), with conspicuous indumentum on the tube and abaxial surface of the lobes, drying ferrugineous, yellow or tannish yellow (or something intermediate). The exception is *P. hammelii* with corollas only sparsely

pubescent externally. In contrast, species from others sections usually have glabrous or glabrate corollas. In a few species of section Denticulatae the corolla tube is minutely puberulent (e.g., *P. lenticellata*, *P. vana*), with colorless (even in dried specimens), diminutive, and inconspicuous indumentum, but the abaxial surface of the lobes glabrous or glabrate. In general, the inner surface of the corolla tube is glabrous, with pubescence restricted to the region where the filaments are adnate.

The presence of well-developed coronal structures is one of the most important characters in the genus. These structures are common and highly variable in the Asclepiadoideae and Periplocoideae (Liede & Kunze 1993, Fishbein 2001). They are less common in the Apocynoideae and Rauvolfioideae. In *Prestonia*, the corolla tube has an annular corona around the mouth, which can be entire, subentire to 5-lobed or irregularly lobed. In some species, the annular corona is very thin and sometimes inconspicuous (e.g., *P. coalita*, *P. solanifolia* (Müller Argoviensis) Woodson, whereas in others (e.g., *P. mexicana*, *P. riverae* J.F. Morales) is reduced to 5 conical callous ridges. In addition, there are usually five 5 free coronal lobes, opposite and behind the stamens, but in a few species (e.g., *P. coalita*, *P. mexicana*) these are absent or rarely reduced to callous ridges. The point of insertion of the free coronal lobes is a useful character to distinguish in some species complexes. The free coronal lobes may be deeply included within the tube (e.g., *P. quinquangularis*), with only the tips barely exserted (e.g., *P. portobellensis*) or almost totally exserted (e.g., *P. falcatosepala* J.F. Morales).

Androecium:—Stamens are inserted in the upper part of the corolla tube (from abouth the middle to near the mouth). Anthers may be wholly included or with the apices exserted, but are never completely exserted. Anthers are bilocular, equal in length, usually very narrowly elliptic, and strongly attached to the style-head by a dense group of hairs. Dorsally they may be glabrous, glabrescent, or variously pubescent.

The anthers are highly specialized, with conspicuous sclerenchymatic guide-rails, with long-acuminate or narrowly acute apices, and sterile, conspicuously sagittate basal part (Woodson's "peltate connective") (Fallen, 1986). The basal lobes usually vary from acuminate to acute, ranging length from 0.5 to about 2 mm. Anthers are tetrasporangiate, and the pollen grains are spherical to subspherical, and triporate with smooth or minutely pitted or perforated surface. Endress et al. (1996) reported sizes of  $(49)53(56) \times (48)52(55)$ 

 $\mu$ m for the pollen grains in *P. mollis*, with pores of 4  $\mu$ m in diameter and with an external and internal annular thickening.

Filaments are free, short, very thin, and variously pubescent (rarely glabrescent and then the indumentum composed of unicellular hairs.) At their junction with the anthers, the filaments are conspicuously and abruptly bent inwards and rest against the style and the basal part of the style-head.

**Gynoeceum:**—The gynoecium is apocarpous or syncarpous, bicarpellate, and usually glabrous to glabrescent. The carpels are united apically by a common style, with the style-head located at the apex. Style length is of little use as a taxonomic character, since it is very similar in many species. The style-head is more or less fusiform, spool-shaped, and with a basal collar, which varies from entire to slightly lobed. Ovules are numerous and several-seriate.

A disc nectary encircles the base of the ovary. The disc varies from entire or subentire to variously lobed at the apex, sometimes totally divided into five individual nectary lobes. Woodson (1936) gave an considerable emphasis to the degree of lobation and the length of the nectary to distinguish certain species. However, the intergradation of this character observed in different plants of the same species (even in the same population) as well as in herbarium specimens, makes it unreliable to differentiate species.

**Fruits:**—Fruits of *Prestonia* are apocarpous two free divaricate follicles (but often remaining just at the tips), or syncarpous and completely connate longitudinally. Follicles are usually continuous, less commonly obscurely articulated; moniliform follicles are rare and restricted and found in only two species (*P. denticulata* (Vellozo) Woodson and *P. leco* A. Fuentes & J.F. Morales). In section Haemadictyon fruits are virtually identical in many species and thus, the identification of fruiting specimens can be difficult or even impossible in some cases.

Follicles texture varies from firmly membranaceous to woody and coriaceous. In general, the fruits are smooth externally, with the exception of *P. antioquiana* and *P. vana*, which have prominent longitudinal ribs or wings respectively.

Several characters such as pubescence, shape, and size of the follicles can provide an excellent tool for the distinguishing of some species and even sections. In section *Prestonia* follicles are conspicuously pubescent, whereas in other sections, they are usually

glabrous, glabrescent, or minutely puberulent, with the exception of *P. megagros*, with minutely tomentulose fruits.

Seeds are numerous, truncate, subfusiform or narrowly elliptic, with the seed coat rugose to varying degrees, and have a tuft of hairs (coma) at the micropilar end.

**Roots:**—Geophytic growth is known for some genera in the Apocynaceae (e.g., Meve & Liede, 2004; Appezzato da Glória & Estelita, 1999). In *Prestonia* root tubers are reported for first time in seedlings (sometimes) as well as in mature plants from *P. mollis* 

## Cytology and secondary chemistry

Few studies have been published on cytology in *Prestonia*: the only reference found is the work of Laan & Arends (1985), who reported 2 n = 18 in *P. quinquangularis*.

Probably the most characteristic secondary compounds found in *Prestonia* (and in *Parsonsia*, another Old World member of the Echiteae) are pyrrolizidine alkaloids (PAs). Some studies suggest that in Apocynaceae, PAs are restricted to the tribe Echiteae (e.g., Brehm et al. 2007). These compounds are imbibed and sequestered by insects – especially certain lepidoptera – which incorporate them into their own systems for the production of pheromones (Boppré 1986) or for defense (Hartmann et al. 2001, 2003)

In *Prestonia*, PAs have been reported in *P. amabilis*, *P. longifolia* (as. *P. guatemalensis* Woodson), *P. portobellensis*, and *P. quinquangularis* (as *P. acutifolia* (Bentham ex Müller Argoviensis) K. Schumann) and in *P. coalita* (Edgar 1984, Trigo & Brown 1990, Pasteels et al. 2003, Brehm et al. 2007).

The dominant PA in *P. portobellensis* is the triester parsonsine, which was originally extracted from *Parsonsia heterophylla* A. Cunn (Eggers & Gainsford, 1979). It has been reported that *P. portobellensis* is the host for beetles of the genus *Platyphora* (Escarideae, *Platyphora boucardi*). These beetles transform the PAs contained in the leaves into specialized protection glands (Hartmann et al., 2003). In addition, it has been reported by one collector that unidentified beetles also feed from the leaves of *P. mollis* (*D. Janzen T-10*, MO)

In addition, saponins have been reported in *P. portobellensis*. Smith (1977) reported the presence of N-Dimethyltryptamine and N-Methyltryptamina in *P. amazonica*, but without citing any specific voucher. The misidentification of this species has been widely

used in the chemical and pharmacological literature for many years, based on the incorrect interpretation of the type, as was proven by Schultes and Raffauf (1960). Therefore, the report is uncertain.

At anthesis, flowers of certain species (e.g. *P. mexicana*, *P. tomentosa*) are visited by large numbers of ants, which are agglomerated around the anthers or the corolla mouth, around the colleters of the sepals or internally around the nectaries. Similar ants have been seen around the colleters of young shoots.

No publications were found about pollinators and pollination mechanisms in *Prestonia*. Some collectors reported that Euglossine bees and hummingbirds have been seen visiting flowers of *P. lindleyana* (*Zent 2184*, MO), *P. longifolia* (*Aguilar 13891*, CR), and *P. megagros* (*Barcelar-Lima 36*, INPA).

### **Distribution**

Prestonia is widely distributed from northern Mexico and the West Indies to northern Argentina, ranging from sea level up to 2200 m, although most species occur below 1100 m. The genus has been reported almost in all the neotropical countries, with the exception of Chile. In Uruguay it is represented only by P. lagoensis, based on single specimen collected by Fruchard with a vague locality ("Montevideo, Asunción"). Since this species has not been reported in adjacent areas and the nearest locality from which it is known with certainty is located much farther north, the locality of this specimen may be erroneous, something that is known to occur in some other genera and species for Uruguay (Morales, 2010 b).

# **Habitat and Ecology**

*Prestonia* is found in tropical wet forests, cloud forests, seasonally flooded forests, moist forest, dry forest, savannas, rocky outcrops, and coastal vegetation associations. However, the genus is most common in tropical wet forests, below 1000 m, with very few species reported in dry forest (e.g., *P. coalita*, *P. parvifolia*). A few species (i.e., *P. mucronata* and *P. premontana*) are restricted to pre-montane or montane cloud forests, sometimes even up to 2300 m.

Commonly plants grow in sunny areas, whether at forest edges, the canopy, or secondary disturbed vegetation in open areas. Although most species are found in specific vegetation habitats, some species (e.g., *P. mexicana*, *P. mollis*) show a wide range of ecological tolerance, growing from sea level up to 2500 m, in dry forest, moist forest, tropical wet forest, or even in cloud forest.

#### Uses

A few uses for *Prestonia* have been reported, all of them exclusively in field notes of various collectors. Most of these relate to the use of *Prestonia* folk medicine in specific geographic regions. These uses (briefly described) are given here and collectors numbers and last names are cited in parentheses as a reference.

Flowers of *P. mollis* have been used as an infusion or tea for the treatment of hepatitis in Peru (*Shonle 30*) and macerated young shoots are used in conjunction with a mixture of food to kill foxes (*Woytkowski 6766*). Inhalation of the infusion of the leaves of the same species is used as an abortive (*Bonifaz & Cornejo 2899*).

Rubbing leaves of *P. portobellensis* and *P. rotundifolia* (previously cooked) directly on the mother's chest several times a day (*Barford 41052*, *Kvist and Asanza 40831*) supposedly help stimulate the production of breast milk.

Prestonia trifida is the only species in which it is reported that the fruit is edible, both for some animals (e.g., birds, monkeys) as well as for humans (Aulestia et al. 1333). This is the only report of edible fruits in the members of the tribe Echiteae. Other uses reported for this species include treatment of inflamed eyes by wiping with cotton soaked in a mixture of macerated fruit (Aulestia et al. 1333).

At the beginning of Nineteenth century, Reinberg (1921) mentioned that *Prestonia amazonica* was used in the lower Amazon basin to prepare Yaje, an hallucinogenic drink similar to Ayahuasca, a reference that has been widely perpetuated in the ethnobotany, chemistry and pharmacology literature. However, Schultes and Raffauf (1960) refuted this and showed that it was a misidentification due to a misinterpretation of the original field notes of Richard Spruce, who extensively studied various ethnobotanical uses of plants during his excursion in the Amazon (Schultes & Raffauf 1992). Since then, there has been further report which lends support to this.

# **Terminology**

Terminology of infundibuliform corollas follows Morales and Fuentes (2004 b). All measurements are based on mature parts (e.g, leaves, inflorescences, flowers, fruits), from herbarium specimens or fresh material. Peduncle length is measured from the base (where it originates in the axil of the leaf) up the first bifurcation (in dichasial inflorescences) or up the point where the first pedicel born (in monochasial inflorescences). Measurements of anthers, ovary, and nectaries are based on rehydrated or fresh flowers.

The coronal structures in *Prestonia* (annular corona and free coronal lobes) are shown in the figure 1. In the last monograph of the genus (Woodson 1936), a different terminology was used for various characters in the key and descriptions. Their respective analogy is cited as follows: here stipular appendages are called intrapetiolar colleters, the squamellae are replaced by colleters, and finally the epiestaminals appendages and faucal ring are described as free coronal lobes and annular corona respectively.

#### KEY TO THE SECTIONS OF PRESTONIA

- 1. Intrapetiolar colleters usually conspicuous; corolla tube, abaxial surfaces of the corolla lobes and follicles variously pubescent, the indument ferrugineous, brown, or yellow... sect. *Prestonia*
- 1. Intrapetiolar colleters inconspicuous; corolla tube, abaxial surfaces of the lobes and follicles glabrous, glabrescent, or sparsely puberulent, the indument green or colorless ... 2
- 2. Leaf blades and sepals coriaceous to subcoriaceous; follicles somewhat woody... sect. \*Denticulatae\*
- 2. Leaf blades sepals and follicles membranaceous;... 3
- 3. Annular corona inconspicuous, sometimes absent; corolla tube usually without free corona lobes within (except *P. pickelii*) ... sect. *Coalitae*
- 3. Annular corona conspicuous; corolla tube with free corona lobes within ... 4

- 4. Sepals without visible veins, the apices reflexed or not reflexed; follicles free, but usually united at the tips (at least when young), rarely connate (*P. quinquangularis*) . . . sect. *Haemadictyon*
- 4. Sepals with the veins conspicuously impressed, the apices not reflexed; follicles usually connate longitudinally ...5
- 5. Corolla lobes 18–34 mm long, the tube 20–36 mm long... sect. Mollis
- 5. Corolla lobes 6–14 mm long, the tube 9–17 mm long... sect. Exsertae

#### GENERAL KEY TO THE SPECIES OF *PRESTONIA*

- 1. Intrapetiolar colleters usually conspicuous, more than 1.5 mm long; corolla tube, abaxial surfaces of the corolla lobes and follicles variously pubescent, the indument ferrugineous, brown, or yellow... 2.
- Intrapetiolar colleters inconspicuous, less than 1 mm long; corolla tube, abaxial surfaces of the lobes and follicles glabrous, glabrescent, or sparsely puberulent, the indument green or colorless
   ... 20
- 2. Corolla infundibuliform ...3.
- Corolla salverform ... 4.
- 3. Pedicels 1–5 mm; lower part of the corolla tube 3–4 mm long; free coronal lobes 1.5–2 mm ... *P. clandestina*
- Pedicels 9–17 mm; lower part of the corolla tube 12–19 mm long; free coronal lobes absent ... *P. speciosa*
- 4. Corolla tube without free corona lobes within ... 5.
- Corolla tube with free corona lobes within ... 8.
- 5. Corolla tube  $9-13 \times 2-2.5$  mm long; Ecuador ... P. schumanniana
- Corolla tube  $(18-)20-36 \times 3-5$  mm long; Mexico to northern Colombia ... 6.
- 6. Leaf blades and inflorescences sparsely hirsutulous to glabrescent; sepals and corolla very sparsely hirsutulous; sepals 9–15 mm long ... *P. hammelii*
- Leaf blades and inflorescences densely to moderately pilose, tomentose or tomentulose; sepals 14–30 mm long ... 7.
- 7. Corolla tube 24–36 mm long; anthers 6–7.1 mm long ... P. mexicana
- Corolla tube (18–)20-23 mm long; anthers 10–12 mm long ... P. riverae

- 8. Free coronal lobes with the apices deeply included within the corolla tube, their apices conspicuously surpassed by the apices of the anthers; inflorescence terminal, subterminal or axillary ... 9.
- Free coronal lobes with the apices exserted or slightly included, their apices equaling or surpassing the apices of the anthers; inflorescence axillary ... 12.
- 9. Sepals  $8-12 \times 2-3$  mm; anthers 6.5-9(-11) mm long; pedicels 9-15 mm long; inflorescence axillary to subterminal ... *P. mucronata*
- Sepals  $2.5-6(-7) \times 1-1.5$  mm; anthers 3.5-6 mm long; pedicels 2-10 mm long; inflorescence terminal or subterminal ... 10.
- 10. Free corona lobes 2.5–3.5 mm long; corolla tube 10–12 mm long, the lobes 10–12 mm long ... *P. premontana*
- Free corona lobes 1-2.1 mm long; corolla tube 4–6 mm long, the lobes 4–6 mm long ... 11.
- 11. Petiole 1.2–3 cm long; sepals 1–1.5 mm wide; free coronal lobes ca. 1 mm long; ovary glabrescent to sparsely hirsutulous ... *P. parviflora*
- Petiole 0.4–1.1 cm long; sepals 2–3.5 mm wide; free coronal lobes 1.9–2.1 mm long; ovary glabrous ... *P. tysonii*
- 12. Inflorescence a monochasial cyme, elongated and resembling a raceme ... 13.
- Inflorescence a dichasial cyme, congested and resembling an umbel ... 14.
- 13. Branchlets moderate to sparsely hirsute; pedicels 3–6 mm long; corolla lobes 4–5 mm long; anthers 4.5–5 mm long ... *P. acrensis*
- Branchlets densely ferrugineous-tomentose; pedicels 12–17 mm long; corolla lobes 11–13 mm long; anthers 6–7 mm long... *P. racemosa*
- 14. Rachis and peduncle of the inflorescence tomentose, tomentulose, or velutinous, the indument more or less adpressed ... 15.
- Rachis and peduncle of the inflorescence hirsute, hispid, the indument more or less erect ... 17.
- 15. Leaf blades sparsely and irregularly hirsute to hirsutulous on the abaxial surface, the indument irregularly distributed; sepals 3–4.5 mm wide; nectary as tall as the ovary ... *P. cogolloi*
- Leaf blades densely velutinous or velutinous-tomentose on the abaxial surface, the indument uniformly distributed; nectary taller than the ovary ... 16.
- 16. Mature inflorescences usually branched at the base; follicles minutely ferrugineous-sericeous to glabrescent; sepals 3.5-7 mm wide; seeds 15–22 mm long; tropical wet forest ... *P. surinamensis*
- Mature inflorescences usually not branched at all; follicles hispid or hispidulous, seeds 8–10 mm long; moist forest, dry forest, cerrados or savannas in dry areas... *P. tomentosa*

- 17. Leaf blades densely velutinous to velutinous-tomentose on the abaxial surface; follicles 8–14 mm wide ... 18.
- Leaf blades moderately to sparsely hirsute on the abaxial surface; follicles 13–23 mm wide ... 19.
- 18. Corolla lobes 7–9 mm; bracts 1–2 mm wide; follicles 5.5–7 cm; Brazil ... P. bahiensis
- Corolla lobes 9–15 mm; bracts 2–4.5 mm wide; follicles 10–13 cm; Panama and Colombia ... *P. seemannii*
- 19. Tertiary veins conspicuously reticulate on the abaxial surface; leaf blade with the apex caudate-acuminate to long-acuminate; sepals  $7-12(-17) \times 2.5-6$  mm; free coronal lobes 2-2.5 mm ... P. *ipomaeifolia*
- Tertiary veins not reticulate on the abaxial surface; leaf blade with the apex abruptly short-acuminate to acute; sepals  $12-21 \times 7-10$  mm; free coronal lobes 3-4 mm ... *P. calycina*
- 20. Corolla tube without free coronal lobes within ... 21.
- Corolla tube with free coronal lobes within ... 25.
- 21. Inflorescence longer than the adjacent leaves ... 22.
- Inflorescence shorter than the adjacent leaves ... 23.
- 22. Corolla tube 5.5–8.5 mm long, the lobes 5–6 mm long; leaf blades (0.5–)0.8–1.6 cm wide ... *P. succo*
- Corolla tube 14–20 mm long, the lobes 24–40 mm long; leaf blades 2–6.5(–7.5) cm wide ... *P. ornata*
- 23. Leaf blades densely and minutely puberulent on the abaxial surface; anthers ca. 3 mm long ... *P. solanifolia*
- Leaf blades glabrous, glabrescent, or minutely papillate—puberulent on the abaxial surface; anthers 3.1–6 mm long ... 24.
- 24. Sepals obovate to narrowly obovate, the apices rounded to broadly obtuse; coma 2–2.5 cm long ... *P. duseniii*
- Sepals linear to very narrowly elliptic, the apices acute to acuminate; coma 2.5–4(–4.5) cm long ... *P. coalita*
- 25. Sepal apices reflexed; inflorescence a monochasial cyme ... 26.
- Sepal apices not reflexed; inflorescence a monochasial or dichasial cyme ... 30
- 26. Free corona lobes 2.5–4 mm long, the apices height slightly surpassing that of the anther apices, exserted ... 27.
- Free corona lobes 0.8–1.5 mm long, the apices height conspicuously surpassed by that of the anther apices, deeply included within the corolla tube ... 28.

- 27. Corolla tube 8–9 mm long; pedicels 20–30 mm long; sepals 2.5– $3 \times 1$ –1.2 mm; anthers 3.8–4.1 mm long ... *P. boliviana*
- Corolla tube 13–20 mm long; pedicels 8–14(–18) mm long; sepals 3–6  $\times$  1.5–2 mm; anthers 5–6 mm long ... *P. lagoensis*
- 28. Sepals 1.5–2.5 mm wide, broadly elliptic to ovate, apices acute to abruptly acuminate; stamens inserted about midway within the corolla tube; ... *P. cyaniphylla*
- Sepals 0.8–1.2 mm wide, very narrowly ovate, apices acuminate; stamens inserted near the corolla mouth; ... 29.
- 29. Corolla tube 5.7–6.8 × 1.2–1.8 mm; anthers 2.4–2.6 mm long ... P. pickelii
- Corolla tube  $(11-)14-20 \times 3-5$  mm; anthers 4-5.5 mm long ... P. quinquangularis
- 30. Free corona lobes less than 2 mm long, the apices height conspicuously surpassed by that of the anther apices, included... 31.
- Free corona lobes 2–5.5 mm long, the apices height equalling to slightly surpassing that of the anther apices, exserted or barely included ... 37.
- 31. Sepals connate at the base for 1/3–1/2 of their length, forming a campanulate base ... 32
- Sepals free, not forming a campanulate base ... 33.
- 32. Branchlets and inflorescences minutely and densely puberulent; sepals (10–)12–19 mm long; tube 14–15 mm long; follicles 18–27.5 cm long ... *P. amabilis*
- Branchlets and inflorescences glabrous; sepals 7–10 mm long; tube 15–21 mm long; follicles 32–40 cm long ... *P. haughtii*
- 33. Inflorescence a monochasial cyme, unbranched ... 34.
- Inflorescence a dichasial cyme, branched ... 35.
- 34. Sepals 2.5–5 mm long; free coronal lobes 1–1.5 mm long; anthers 4–4.6 mm long; follicles 11–26 cm long; seeds 10–16 mm long ... *P. cayennensis*
- Sepals 6.5–8 mm long; free coronal lobes 1.5–2 mm long; anthers 5.3–5.5 mm long; follicles 29–33 cm long; seeds 17–19 mm long ... *P. vaupesana*
- 35. Corolla tube  $6-9 \times 1.9-2.1$  mm, the lobes 5-6 mm ... P. papillosa
- Corolla tube  $13-22 \times 3-6$  mm, the lobes 7-22 mm long ... 36.
- 36. Corolla lobes 7–15(–17) mm long; anthers with the apices slightly exserted or barely included; follicles 0.5–0.8 cm diam., continuous to inconspicuously articulated ... *P. annularis*
- Corolla lobes 19–22 mm long; anthers deeply included; follicles 1.2–1.6 cm diam., moniliform ... *P. leco*
- 37. Leaf blades membranaceous, the tertiary veins scarcely impressed abaxially, inconspicuous (or nearly so) adaxially ... 38.

- Leaf blades coriaceous to subcoriaceous, the tertiary veins conspicuously impressed on both surfaces ... 43.
- 38. Corolla tube 19–36 mm long, the lobes  $17-26(-34) \times 6-13(-17)$  mm ... P. mollis
- Corolla tube 9–18 mm long, the lobes 6– $14 \times 3$ –9 mm ... 39.
- 39 Inflorescence conspicuously longer than the adjacent leaves; sepals falcate ... P. falcatosepala
- Inflorescence shorter than or equaling adjacent leaves; sepals not falcate ... 40.
- 40. Floral bracts foliaceous to subfoliaceous, 2.5–4 mm wide... P. parvifolia
- Floral bracts scarious, 0.5–1.8 mm wide ... 41.
- 41. Free coronal lobes almost totally exserted; inflorescence a dichasial cyme, usually 1-2-branched. ... *P. exserta*
- Free coronal lobes with the apices slightly exserted or barely included; inflorescence a monochasial cyme, unbranched ... 42.
- 42. Leaf blades very sparsely puberulent to glabrescent on the adaxial surface, usually puberulent on the abaxial surface; floral bracts 2.5–4 mm long; sepals sparsely puberulent; Panama and Colombia... *P. folsomii*
- Leaf blades glabrous on both surfaces; floral bracts 5–14 mm long; sepals glabrous; Brazil ... *P. didyma*
- 43. Sepals  $3-8 \times 1-3(-4)$  mm ... 44.
- Sepals  $(9-)10-20 \times 3-8 \text{ mm} \dots 47$ .
- 44. Leaf blade apices obtuse to rounded and mucronulate ... P. plumierifolia
- Leaf blade apices short-acuminate or cuspidate ... 45.
- 45. Inflorescence a dichasial cyme, conspicuously branched; petioles 0.6–2 cm long; corolla tube 14–19 mm long ... *P. longifolia*
- Inflorescence a monochasial cyme, unbranched or rarely branched and with just an inconspicuous basal branch; petioles 0.2–1.1 cm long; corolla tube 9–15 mm long ... 46.
- 46. Peduncle 2–3.2 cm long; corolla tube straight around the stamens; follicles 18–60 cm long, moniliform ... *P. denticulata*
- Peduncle 5–7.5 cm long; corolla tube spirally twisted around the stamens; follicles 8.5–11.5 cm, continuous ... *P. amazonica*
- 47. Leaf blades densely to moderately puberulent on the abaxial surface; follicles densely and minutely tomentulose ... P. megagros
- Leaf blades glabrous or glabrescent with indument restricted to the midrib on the abaxial surface; follicles glabrous or glabrescent ... 48.
- 48. Branchlets with many lenticels, these conspicuously suberose at maturity ... P. lenticellata

- Branchlets with few lenticels, these not suberose ... 49.
- 49. Inflorescence a monochasial cyme; sepals with the base drying darker than the rest of the surface ... *P. lindleyana*
- Inflorescence a dichasial cyme; sepals drying with a more or less uniform color ... 50.
- 50. Floral bracts  $5-25 \times 2.5-3.5$  mm, narrowly elliptic, narrowly ovate-elliptic or narrowly ovate ... 51
- Floral bracts  $1-6 \times 0.5-1.5$  mm, linear, linear-elliptic or linear-ovate ... 53.
- 51. Leaf blade bullate; corolla tube inconspicuously puberulent externally; free corona lobes 3.5–4 mm long ... *P. macroneura*
- Leaf blade not bullate; corolla tube glabrous externally; free corona lobes 2–3 mm long... 52.
- 52. Floral bracts 6–18(–25) mm long; follicles 4–9 mm diam.; seeds 14–16 mm long (without the coma) ... *P. rotundifolia*
- Floral bracts 3–8 mm long; follicles 11–13 mm diam.; seeds (16–)18–21 mm long (without the coma) ... *P. robusta*
- 53. Corolla tube minutely and conspicuously puberulent; follicles divaricate, winged... P. vana
- Corolla tube glabrous; follicles not divaricate, wingless ... 54.
- 54. Stems papillate-puberulent; nectary completely covering the ovary; follicles 6–8 mm diam., firmly membranaceous when old ... *P. portobellensis*
- Stems inconspicuously puberulent to glabrous or glabrate; nectary not covering the ovary; follicles 8–11 mm diam., somewhat woody when old ... 55.
- 55. Petioles conspicuously and irregularly verrucose; corolla lobes 7–15 mm long; seeds 18–23 mm long ... *P. trifida*
- Petioles not verrucose; corolla lobes 17–21 mm long; seeds 15–17 mm long ... P. antioquiana

- I. Prestonia sect. Coalitae Woodson, Ann. Missouri Bot. Gard. 23: 278 1936. Sect. Rhaptocarpus Pichon, Mém. Mus. Natl. Hist. Nat., B, Bot. 1: 27. 1951, nom. illeg. Type: Prestonia coalita (Vell.) Woodson, Ann. Missouri Bot. Gard. 18: 552. 1931. Echites coalitus Vell., Fl. Flumin. 112. 1825[1829].
- Prestonia coalita (Vellozo) Woodson (1931: 552). Echites coalitus Vellozo (1825: 112).
  Rhaptocarpus coalitus (Vellozo) Miers (1878: 152). Type:—BRAZIL. Fl. Flumin., Icon 3: pl. 40. 1827 (1831) [lectotype, designated by Morales (2006 b)]. Fig. 1.
- Echites sulphureus Vellozo (1825: 109). Mesechites sulphurea (Vellozo) Müller Argoviensis (1860: 151). Type:—BRAZIL. Fl. Flumin., Icon 3: pl. 26. 1827 (1831) [lectotype, designated by Morales (2006 a)].
- Echites vauthieri Candolle (1844: 457). Type:—BRAZIL. Rio de Janeiro: Serra de Orgâos, 1833, M. Vauthier 78 (holotype G-DC! [photo F neg. 7562!], isotypes P! [2 sheets]).
- Echites martii Müller Argoviensis (1860: 155). Rhaptocarpus martii (Müll. Arg.) Miers (1878: 153). Type:—BRAZIL. Rio de Janeiro: Rio de Janeiro, s.d., M. Martius s.n. (lectotype M! [photo F neg. 20148!], designated by Morales (2006b)).
- Rhaptocarpus apiculatus Miers (1878: 153). Type:—BRAZIL. Ceará: without exact locality, 1839, C. Gardner 1754 (holotype BM! [photo MO!], isotypes CGE! [2 sheets], K! [2 sheets], NY!, P!).
- Mitozus concinnus Miers (1878: 223). Type:—BRAZIL. Ceará: Penedo, Río San Francisco, March 1838, C. Gardner 1353 (holotype BM!, isotype K!).

**Stem** glabrous, glabrescent to inconspicuously puberulent, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, less than 1 mm long. **Petioles** 0.4-1.1 cm; leaf blade  $4.5-14.5(-17) \times 2-6.5(-9)$  cm, narrowly elliptic, elliptic, ovate-elliptic to ovate, apex acute, shortly apiculate, mucronate to abruptly acuminate, base obtuse to rounded, membranaceous, sometimes conspicuously revolute, glabrous adaxially, glabrous, glabrescent to minutely puberulent abaxially, secondary veins impressed on both surfaces, tertiary veins impressed abaxially, somewhat inconspicuous adaxially. **Inflorescence** a usually a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, minutely and densely papillate-puberulent to glabrous or glabrescent, peduncle 0.3-1.3 cm, pedicels 0.4-1.1 cm long, floral bracts  $1.5-3 \times 1-1.5$  mm, linear, scarious and inconspicuous, green. **Sepals**  $3-8 \times 2-3.5(-4)$  mm, free, membranaceous, linear to very narrowly elliptic, the apices acute to acuminate, usually reflexed, glabrous, glabrescent to inconspicuously puberulent, very small, drying with a more or less uniform

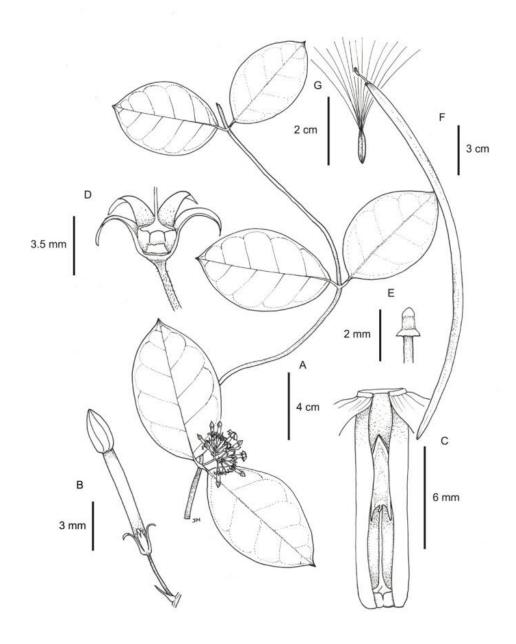


Fig. 1 *Prestonia coalita* (A-E from *Folli 1803*, INB; F-G from *Duarte 10419*, INB). A. Stem with inflorescence. B. Calyx, pedicel, and bract. C. Open corolla tube, showing the anthers, ovary, and nectary. D. Calyx with one sepal removed, showing the colleter, nectary, and ovary. E. Style-head. F. Follicle. G. Seed.

color, the veins not impressed, colleters less than 1 mm long, minutely lacerate to subentire at the apex. **Corolla** salverform, cream, creamish green to green, glabrous outside, tube  $10-17 \times 1.5-2$  mm, sometimes somewhat inflated at the base, without free corona lobes within, annular corona entire, delicate and inconspicuous, corolla lobes  $5-9 \times 4-5$  mm, obliquely obovate. **Stamens** inserted about midway within the corolla tube, anthers 4.5-6 mm, dorsally glabrous, included. **Ovary** 0.9-1.1 mm tall, glabrous, style-head ca. 1 mm, nectary 0.9-1.1 mm, slightly shorter than or equaling the ovary, 5-lobed or completely divided into 5 separate nectaries, each one entire to subentire. **Follicles**  $18-38(-45) \times 0.3-0.8$  cm, continuous to inconspicuously articulated, connate longitudinally or free but united at the tips (at least when young), glabrous or glabrescent, sometimes conspicuously lenticellate or the lenticels inconspicuous or almost absent, firmly membranaceous to very slightly woody when old, sometimes somewhat verrucose; seeds 8-11 mm, coma 2.5-4(-4.5) cm, cream.

**Distribution and habitat**:—Gallery forest, dry forest, moist forest, caatingas, and savannas in Colombia, northern Venezuela, Guyana, Brazil, Peru, Bolivia, Paraguay, and northern Argentina, 0–1200 m of elevation.

**Phenology:**—Flowering October through May. Fruiting February through July.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local names:—Áurea (Espirito Santo, Linhares, Brazil); cipó capa homen (Santa Catarina, Brazil); cipó capador (Santa Catarina, Brazil); cipó de cainama (Bahia, Cruz das Almas, Brasil); cipó de leite (Santa Catarina, Espirito Santo, Brazil); cipó de paina (Santa Catarina, Brazil); cipó de porco (Minas Gerais, Brazil); cipózhino de leite (São Paulo, Brazil); cipó para tudo (Pernambuco, Brazil); guiné (Minas Gerais, Mato Grosso, Brazil).

**Taxonomic notes**:—*Prestonia coalita* has a wide ecological tolerance and several highly variable morphological characters. These include size, shape, and texture of the blades, sepal length, and follicles texture, and many intermediate states in all these characters were found in the different populations studied.

Prestonia coalita resembles P. dusenii and P. solanifolia, a trio characterized by scarious floral bracts, lack of free corona lobes, and thin and inconspicuous annular corona; these three species also have a similar geographic distribution. Prestonia coalita differs of P. dusenii by the linear to very narrowly elliptic sepals with acute to acuminate apices (vs. obovate to narrowly obovate with rounded to broadly obtuse apices). From Prestonia solanifolia it differs by its anthers (4.5–6 mm vs. 3 mm) and glabrous to inconspicuously puberulent stems (vs. minutely puberulent).

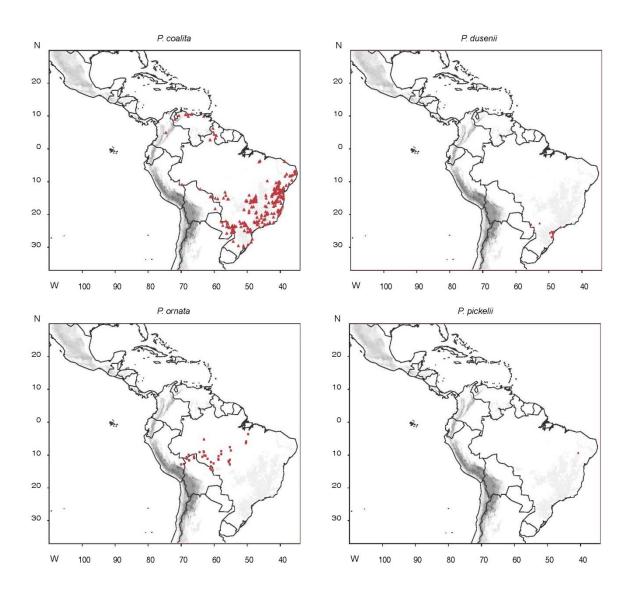


Fig. 2 Distribution maps of *Prestonia coalita*, *P. dusenii*, *P. ornata* and *P. pickelii*.

**Additional specimens examined**:—COLOMBIA. Cundinamarca: San Juan de Río Seco, entre Cambao y San Juan de Río Seco, 23 September 1981, *Rangel & Salamanca 3292* (COL, CR).

VENEZUELA. Barinas: SO de Río Capitanejo, August 1966, *Steyermark et al. 96539* (F, US, VEN). Bolivar: Las Trincheras, cuenca superior del Río Caura, 11 June 1984, *Carabot & Rosquete 4649* (NY). Carabobo: Maturín, cerca de Las Trincheras, 23 December 1938, *Alston 5990* (BM, NY, S); Valencia, Las Tricheras, Quebrada María Teresa, 6 August 1982, *Benitez de Rojas & Rojas 3050* (MY, VEN). Distrito Federal: fila Corozo, N de fila Naiguatá, 2 August 1980, *Manara s.n.* (VEN); vertiente norte, entre Osma y los Caracas, excursión Osma-lado N de la fila San José-Fila Guarataro-Río Chiquito-Las Caracas, 10-11 March 1992, *Meier & Paredes 1888* (B); entre Las

Delicias y Toma de Mata de Plátano, Cerro Naiguatá, 31 March 1972, *Morillo & Manara* 2077 (VEN, Z), *Morillo & Manara* 2083 (VEN, Z); Cerro Naiguatá, cerca a Quebrada Basenilla, 3 November 1963, *Steyermark* 91878 (K, NY, US, VEN). Lara: S de Cerro Verde, entre Palmarito y Cerro Verde, 1976, *Morillo et al.* 6561 (VEN). Miranda: Quebrada de las Comadres, cerca de Las Mostazas, November 1924, *Allart* 246 (US, VEN); Carrizalito, camino viejo a Los Teques, 14 November 1976, *Carreño* 6 (VEN); cabeceras del Río Guarita, 10 August 1975, *Steyermark* & *Berry* 111979 (VEN, Z). Portuguesa: entre La Estación y La Laguna, al NNO de Ospino, 1 November 1982, *Steyermark* et al. 127018 (MO, VEN). Yaracuy: San Felipe, Veroes, S de Bella Vista, 11 July 1973, *Agostini et al.* 1733 (NY, U, US, VEN, Z). Zulia: Bolívar, entre las Tres Marías y el Río Chiquito, February 1980, *Bunting* & *Stoddart* 8911 (NY).

GUYANA. Cuyuni-Mazaruni: fila S de las Montañas Pakaraima, Montaña Ureisha, 5 January 1982, *Knapp & Mallet 2846* (MO). Upper Takutu-Upper Essequibo: Río Rupununi, Quebrada Sand, September 1948, *Forest Department 64* (K, NY, U); Wubuwak, Kanuku, Octuber 1948, *Forest Department 5768* (K, NY, U); Iramaipang, Kanuku, November 1948, *Forest Department 5905* (K, NY, U); Río Rupununi, 1948, *Forest Department 5941* (NY, U).

PERÚ. Loreto: Maynas, 1831, *Poeppig 20* (F, NY, P). San Martín: Chazuta, Río Huallaga, April 1935, *Klug 4091* (F, MO, NY, P, S, US).

BRAZIL. Alagoas: Arapiraca, Morro do Porco y Morro de Microondas, 9 June 1981, Andrade-Lima et al. 26 (IPA); Taquarana, Agreste, 21 May 1994, Barros & Bayma 200 (HST, MAC, NY). Amazonas: Alzilândia, Río Purus, parte superior del Río Acre, 26 March 1998, Daly et al. 9799 (CR, MO, NY, U, WAG). Bahia: Itacaré, carretera Itacaré-Taboquinhas, ca. 6 km de Itacaré, 14 December 1992, Amorin et al. 922 (CEPEC, NY, USF); Jacobina, carretera Jacobina-Itaitu, ca. 22 km, 21 February 1983, Amorin et al. 983 (CEPEC, NY, USF), Amorin et al. 984 (CEPEC, NY, USF); Itacaré, carretera Ihleus-Itacaré, ca. 6 km de Itacaré, 6 January 2000, Amorin et al. 3230 (CEPEC, NY, USF); Boa Nova, Parque Nacional de Boa Nova, sector Oeste, 3 March 2013, Aona et al. 2171 (HURB, RB); 2 km al N de Cruz das Almas, 14 January 1997, Arbo et al. 7209 (CEPEC); Feira de Santana, Tanquinho, 15 January 1997, Arbo et al. 7226 (CEPEC, CTES, NY); rodovia BR-4, camino a Jequié, 28 January 1965, Belém & Mendes 331 (IAN, U, UB); Jacobina, 1842, Blanchet 3513 (BM, F, FI, G, K, MICH, W); Feira de Santana, Ipuaçu, 19 May 2005, Couto et al. 72 (HUEFS); Rui Barbosa, Serra do Orobó, 7 February 2005, Cardoso 231 (HUEFS, NY); Rui Barbosa, Serra do Orobó, Fazenda Bom Jardim, 26 March 2005, Cardoso et al. 378 (HUEFS); Castro Alves, 4 November 1995, C. de Carvalho 95 (HUEFS); Encruzilhada, ca. 2.5 km de la ciudad para Riberão do Largo, 15 August 2001, Carvalho et al. 6929 (CEPEC, HUEFS, NY); Senhor do Bonfim, Fazenda Campo Verde, 20 January 1979, Dobereiner & Tokarnia 1478 (CEPEC, P); Vila de Peixe Cruz, cerca a córrego Catinguinha, 2 May 1991, Carvalho & Silva 305 (BHCB, MO); Vitória da Conquista, 26 December 1989, Carvalho et al. 2595 (CEPEC, G); Vitória da Conquista, ramal a 15 km de carretera a Illhéus, 19 February 1992, Carvalho et al. 3800 (CEPEC, NY, USF); Itacaré, Marambaia, 15 July 1995, Carvalho et al. 6046 (CEPEC, NY, USF); Río de Contas, Ponte do Coronel, 13 km carretera a Mato Grosso, 29 December 1997, Carvalho et al. 6415 (CEPEC, NY, USF); Feira de Santana, Ipuacu, 5 May 2005, Couto et al. 52 (HUEFS); NE de Planalto, 30 March 1976, Davidse et al. 11642 (MO, Z); Utinga, 9 January 1996, Félix s.n. (HST 5051, INPA, IPA); Andaraí, camino a Olho D'Água do Praião, 26 January 1995, Félix & Guerra 6855 (HST); Morro do Chapéu, Capoeiras, s.d., Félix 7249 (HST); Almadina, carretera a Ibitupã, ca. 20 km, Fazenda São Roque, 12 March 2005, Fiaschi et al. 2751 (CEPEC, HUEFS); Itatim, Morro do Agenor, 28 January 1996, França et al. 1547 (HUEFS); Itatim, Morro das Tocas, 20 April 1996, França et al. 1610 (HUEFS); Anguera, Morro da Fazenda Retiro, 29 April 1999, França et al. 2708 (CEN); Andaraí, camino viejo a Lençóis, 4 February 1999, França et al. 2633 (HUEFS); Nova Itarana, ca. 4 km al O de Nova Itarana, carretera a Planaltino, 14 May 2001, Franca et al. 3498 (CEPEC, HUEFS, MBM); Abaíra, Povoado da Tromba, Serra da Tromba, 9 July 1992, Ganev 625 (HUEFS, K, NY); Abaíra, Mendonça de Daniel Abreu, 12 January 1994, Ganev 2817 (HUEFS); Abaíra, entre Zuelgo-Samabaia, 5 February 1994, Ganev 2967 (HUEFS, K, NY); Abaíra, camino Catolés-Guarda, 5 April 1994, Ganev 3057 (HUEFS, K, NY); Jequié, Maracás, carretera a Contendas do Sincorá, 23 March 1988, Ginzbarg et al. 832 (CEPEC, MO, TEX-LL); Rio de Contas, Estrada Real, 1 January 2000, Giuletti & Harley 1620 (HUEFS); Piemonte da Diamantina, Miguel Calmon, Parque Sète Passagens, 22 December 2006, Guedes et al. 13116 (ALCB, R), Guedes et al. 13272 (ALCB, R); Taperoá, rodovia Taperoá-Valença, km 13, estrada a Serapeí, 10 December 1980, Hage et al. 413 (CEPEC); Serra do Río de Contas, carretera a Abaira, 18 January 1972, Harley et al. 15230 (CEPEC, IPA, K, MO, NY, P, U, US, Z); 9 km SO de Mucugé, carretera a Cascavel, Río Paraguaçú, February 1974, Harley et al. 16107 (CEPEC, K, MO, NY, P, U, US, Z); Serra do Jacobina, O de Estiva, ca. 12 km al N de Senhor do Bonfim, autopista BA-130 camino a Juazeiro, 1 March 1974, Harley et al. 16611 (CEPEC, K, Z); Serra do Curral Feio, NO de Lagoinha, carretera de Minas do Mimoso, 5 March 1974, Harley et al. 16754 (CEPEC, K, NY, P, U, US, Z [2 sheets]); Rio de Contas, camino a Jussiape, 20 March 1999, Harley et al. 53540 (HUEFS); Brejo de Cima, Mucugê, 22 January 1984 Hatschbach 48173 (C, CEPEC, HBG, MBM, US, WAG, Z); Nova Viçosa, 8 December 1984, Hatschbach & Silva 48721 (CEPEC, HBG, MBM, MO, Z); Brotas de Macaúbas, camino a Briti, 12 March 1998, Hastchbach et al. 67689 (MBM, WAG); Itacaré, trilha entre a Praia da Ribeira e Reserva Particular do Patrimônio Natural da Prainha, 23 January 2005, Heiden et al. 955 (RB); Serra da Água de Rega, N de Seabra, carretera

a Água de Rega, 23 February 1971, Irwin et al. 30765 (F, K, NY, UB, US, Z [2 sheets]); Serra da Água de Rega, carretera a Cafarnaum, N de Água de Rega, 28 February 1971, Irwin et al. 31242 (C, F, K, MO, NY, UB, US, Z [2 sheets]); Ilhéus, Mara de Esperança, carretera Ilhéus-Itabuna, 30 January 2000, Jardim et al. 2597 (CEPEC); São Miguel das Matas, Fazenda Engenho da lama, 4.5 km al S de la cidade, 24 February 2000, Jardim et al. 2885 (CEPEC); Feira da Mata, autopista Cocos-Feira da Mata, a 23 km de Cocos, 17 April 2001, Jardim et al. 3619 (CEPEC, HUEFS); Itiruçu-Maracás, 21 May 1969, Jesus & Santos 395 (CEPEC, IPA [2 sheets], P, Z), Jesus & Santos 444 (CEPEC, P); Maracás, Fazenda Vale Aprazivel, 22 April 2002, Leite et al. 249 (HUEFS, UFP); Feira de Santana, Ipuaçu, Monte Alto, 25 November 2005, Lima et al. 9 (HUEFS); Ipuaçu, Inselberg Monte Alto, 30 September 2003, Lucca et al. 13 (HUEFS, MBM); Morro do Chapéu, Río Ferro Doido, 3 March 1997, Lughandha et al. 5990 (ALCB, CEPEC, HUEFS, K); Mucugê, 10 February 2006, Machado 12 (HUEFS); Mucugê, faxenda Casquilho, Serra do Bastião, 28feb 2007, Machado et al. 45 (HUEFS); Maracás, carretera Maracás-Contendas do Sincorá, 14 February 1979, Mattos-Silva et al. 244 (CEPEC, NY, USM, Z); Marcás, Fazenda Gameleira, rodovia BA-250, trecho Itiruçu y Maracás, 1 March 1988, Mattos-Silva et al. 2277 (CEPEC); Itatim, Morro da Pedra Grande, 8 April 2005, Melo et al. 447 (HUEFS); Itatim, Morro das Tocas, 91 km de Feira de Santana, 14 April 1995, Melo & França 1168 (HUEFS); Itaberaba, Morro do Itiberaba, 4 June 2005, Melo et al. 3887 (HUEFS); Caetité, Brejinho das Ametistas, August 2008, Mendes et al. 250 (BHCB); Lençóis, BR-242, 27 January 2001, Miranda 47a (HUEFS, MBML); Rio da Contas, 17 January 2003, Miranda et al. 4042 (BHCB, HUEFS, HST); Ibicaraí, rodovia BR-415, 40 km O de Itabuna, 2 March 1978, Mori et al. 9360 (CEPEC, NY, Z); Vitória da Conquista, km 2 de rodovia BA-265, Barra do Choça, 4 March 1978, Mori et al. 9415 (CEPEC, K, NY, Z); Livramento do Brumado, carretera entre Brumado y Río de Contas, July 1979, Mori et al. 12274 (CEPEC, NY, US, WAG, Z); Mucugê, camino para Capão do Correio, 15 February 2002, Nunes et al. 868 (CEPEC, HUEFS, MBML); Mundo Novo Aliança, estrada do Feijão para Morro do Chapéu, 14 May 2002, Nunes et al. 940 (CR, HUEFS, UFP); Licinio de Almeida, 2 km antes de la ciudad, 10 January 2006, Nunes et al. 636 (HUEFS); Morro do Chapéu, cachoeira Domingos Lopes, 5 April 2002, Oliveira et al. 153 (HUEFS, HST, MBM, NY, UB, UFP); Maracás, Fazenda Lava-pées, Oliveira et al. 417 (CEN, HUEFS); Pindobaçú, 10 March 1981, Orlandi 346 (CEPEC, HRB, MG, UB); Mucugê, Guiné, 15 February 1997, Passos et al. 5714 (ALCB, CEPEC, CR); Bahia, Itabuna, 14 June 1971, Pinheiro 1335 (CEPEC, Z); Guaratinga a São Paulinho, Bahia, 29 March 1973, Pinheiro 2048 (CEPEC, Z); Cruz das Almas, 15 February 1981, Pinto 54 (CEPEC, HUEFS, IPA); Ibicaraí, a 3 km de la ciudad, carretera Itabuna-Vitoria da Conquista, 16 February 1988, Pirani et al. 2329 (USF); SE de Ituaçú, 22 June 1987, Queiroz 1655 (CEPEC, HUEFS, VIC); Valente, Santa Bárbara, 29 December 1992, Queiroz et al. 3013 (HUEFS, NY, UB, WAG); Caetité, 3 km al N, camino a Maniaçu, 28 Octuber 1993, Queiroz & Nascimento 3626 (HUEFS); Umburanas, Serra do Curral Feio (serra da Empreltada), ca. 10 km al NO de Delfino, 12 April 1999, Queiroz et al. 5439 (CEPEC, HUEFS); Lençóis, ca. 2.4 km al N, camino a BR-242, 18 February 2000, Queiroz et al. 6130 (CEPEC, HUEFS, INPA); Rui Barbosa, Serra do Orobó, Fazenda Bom Jardin, 26 May 2005, Oueiroz et al. 10689 (HUEFS); Itabuna, carretera Coaraci a Almadina, 8 March 1971, Raimundo 1066 (CEPEC, Z); Rio de Contas, Estrada Real, 20 April 2003, Rapini 1069 (HUEFS); Rio de Contas, Marion, 21 February 2004, Rapini et al. 1128 (HUEFS); Itapicurú, 1890, Schrciuer s.n. (R); Utinga, camino a Serra Atalaia, 1 March 2003, Senna et al. 103 (HUEFS); Ilhéus, entre Olivença y Vila Brasil, 16 February 1982, Silva et al. 1535 (CEPEC, HUEFS, WAG); Itatim, Pedra Grande, 9 April 2005, Silva et al. 25 (HUEFS); Maracás, camino a Sincora, 25 February 2000, Silva et al. 277 (HUEFS); Catolés, camino a Catolés, ca. 9 km del entrocamiento con Abaira, BA-146, 21 January 2002, Simões et al. 1150 (BHCB, UEC); Carnaiba, June 1994, Sobral & Ganev 7643 (HUEFS); Seabra, 7 km al O, 12 April 2005, Souza et al. 1117 (HUEFS); Andaraí, January de Lençóis, 13 February 1994, Souza et al. 5210 (K, SP); Caetité, Café Baiano, carretera a Brumado, 7 ar 1994, Souza et al. 5341 (K, SP); Jaguararí, camino do Engenho, estrada para Grotas, 24 May 2005, Souza-Silva & Rapini 26 (HUEFS); Pindobaçu, base de Serra da Fumaça, 12 April 2006, Sousa-Silva & Santos 153 (HUEFS); Licinio de Almeida, camino de tierra a Caetité, dirección a Serra do Jambreiro, 4 November 2006, Souza-Silva et al. 247 (HUEFS); Caetité, São Francisco, carretera a Lagoa Real, 8 February 1997, Stannard et al. 5238 (ALCB, CEPEC, HUEFS, K); Mucugê, Fazenda Pedra Grande, carretera a Boninal, 17 February 1997, Stannard et al. 5812 (ALCB, K); Abaíra, Mendonça de Daniel Abreu, 25 February 1992, Standard et al. 51587 (CEPEC, CR, HUEFS, K, MO, NY, SPF); Almadina, 5.3 km from Almadina on road to Ibatupã, then left 7.9 km on road to Serra dos Sete Paus, 4 April 1997, Thomas et al. 11445 (CEPEC); Poçoes, Fazenda Bôa Esperança, 7.5 km al S de Morrinhos, 7 February 2004, Thomas et al. 13960 (CEPEC, USF); Jequié, 14.7 km al S de Mandacaru, camino a Serra dos Brejos, 6 February 2004, Thomas et al. 13894 (CEPEC, NY). Brasilía: Pires do Rio-Luziânia, 23 April 1979, Heringer et al. 1226 (IBGE, Z); Bacia do Río São Bartolomeu, 29 September 1979, Heringer et al. 2824 (IBGE, K, MO, US); São Bartolomeu, 5 June 1979, Heringer et al. 1512 (IBGE, NY, US, Z), 29 November 1979, Heringer et al. 2024 (IBGE, MG); Río São Bartolomeu, 6 February 1980, Heringer et al. 3253 (IBGE, K, MO, NY, US, Z); Bacia do Río São Bartolomeu, cerca a Riberão Taboca, 10 February 1981, Heringer et al. 6164 (K, UB); Taboca, 25 March 1982, Heringer et al. 6578 (IBGE, K, MG, MO, US), 9 June 1981, Heringer et al. 7040 (K, MG, MO, UB, US); Bacia do Río São Bartolomeu, 4 August 1981, Heringer et al. 7310 (IBGE, K, MO); Lagoa Feia, E de Sobradinho, 26 February 1966, Irwin et al.

13182 (IAN, K, MG, MO, NY, UB, US, Z); Parque Municipal Gama, 21 March 1966, Irwin et al. 14163 (F, MO, NY, UB, Z); córrego Landim, NE de Brasília, 7 May 1966, Irwin et al. 15678 (MO, NY, UB, Z); Capão da Onça, 35 km al S de Planaltina, 22 February 1970, Irwin et al. 26514 (UB); Río São Bartolomeu, Quebrada Neri, 1 March 1992, Melo & França 603 (CEN, CR, UB); Río São Bartolomeu, cerca a Barra do Río Paranoá, 19 March 1987, Mendonca et al. 790 (IBGE); Río São Bartolomeu, Quebrada Neri, 1 March 1992, Neri et al. 603 (CR, UB); carretera Brasília-Goiânia, BR-060, cerca de Samambaia, 12 March 1996, Oliveira et al. 505 (IBGE, Z); Jacarépagua, 7 May 1958, Pereira 3744 (MO, RB); Parque Olhos d'Agua, 26 March 1997, Pires 319 (CEN); Brasília, zona do Calcáreo, 24 April 1983, Pires et al. 9306 (U, UB); área de Preservação Ambiental do Carifunga, 3 February 1994, Proença 1080 (CR, UB); Río Corumbá, 23 March 1993, Pereira da Silva et al. 1267 (CEN, CR, UFP). Ceará: 2 km al O de Maranguape, 1 August 1944, Cutler 8133 (MO), 9 March 1945, Cutler 8294 (MO); Serra do Maranguape, 17 February 1956, Ducke 2629 (IAN, NY); without exact locality, s.d., Allemão 983 (P, R); s.d., Gardner 1755 (W); Fortaleza, Serra do Maranguape, April 1957, Guedes 461 (IAN, Z); Serra de Pacatuba, sítio Pataguari, 17 February 1968, Andrade-Lima 68–5291 (IPA); exact locality lacking, 20 April 1910, Löfgren 620 (S); Estação Maramguape, 17 February 2006, Oliveira & Galileu 2163 (UFP). Espirito Santo: Cariacica, Reserva Biológica Duas Bocas, 16 February 2008, Amorin et al. 7126 (MBML, RB); autopista S-080, división donde nace el camino a Governador Lindemberg y Bananal, 29 January 1997, Arbo et al. 7816 (CEPEC); Santa Teresa, Várzea Alegre, Río Santa María Río Doce, cerca cachoeira do Carlini, 16 July 2003, Assis et al. 967 (MBMB); Reserva Natural Vale, Linhares, 18 Feb 2014, Biral 953 (CVRD); Águia Branca, Assentamento 16 de April 2006, Demuner et al. 2006 (CR, MBML); Águia Branca, Rochedo, 7 June 2006, Demuner et al. 2425 (CR, MBML), Demuner et al. 2433 (MBML); Marilândia, Liberdade, Agua Viva, Pedra do Cruzeiro, 21 March 2007, Demuner et al. 3365 (MBML); Rio Bananal, Alto Bananal, 25 April 2007, Demuner et al. 3773 (CR, MBML); Águia Branca, San Luzia, 21 December 2007, Demuner et al. 4858 (CR, MBML); Santa Leopoldina, Morro agudo, 28 January 2008, Demuner et al. 4887 (CR, MBML); entre Linhares y Vitória, 20 February 1965, Duarte 8833 (CR, RB [2 sheets]); Linhares, Reserva Florestal da Linhares, estrada Gávea, 27 January 1993, Folli 1803 (CR, CVRD, WAG); Reserva Florestal da Linhares, próximo Marca de Ferro, 8 January 1997, Folli 2897 (CR, CVRD, USF); Reserva Florestal da Linhares, Orelha de Onça, 23 February 2000, Folli 3580 (CR, CVRD); Reserva Natural da CVRD, Linhares, estrada Gávea, 22 April 2002, Folli 4249 (CVRD); Reserva Natural da CVRD, Linhares, 21 March 2008, Folli 5977 (CVRD); Nova Venécia, Área de Proteção Ambiental da Pedra do Elefante, fazenda Santa Rita, 16 July 2008, Forzza et al. 5150 (CEPEC, RB); Linhares, Reserva Florestal da Sooretama, 8 April 1984, Hatschbach 47729 (SI); Itaúnas, Conceição da Barra, 20 May 1999, Hastchbach et al. 69216 (MBM, U, WAG); Santa Tereza, Várzea Alegre, carretera a Patrimônio, 7 February 2002, Kollmann et al. 5540 (CR, HUFU, MBML, UEC); Reserva Natural Vale, Linhares, 29 April 2008, Lopes 1586 (CVRD), 30 April 2008, Lopes 1600 (CVRD); Águia Branca, Águas Claras, 2 February 2006, Magnago et al. 669 (MBML); Colatina, Alto Moaciz, Pedra do Cruzeiro, 22 February 2006, Magnago et al. 758 (CR, MBML); Águia Branca, 25 July 2006, Magnago et al. 1075 (CR, MBML); São Mateus, Reserva Biológica de Sooretama, Lagoa do Macaco, 1982, Martinelli et al. 2167 (MO, B); Linhares, Barro Novo, 10 February 1993, Pirani & Kallunki 2767 (NY, SPF, WAG); Reserva Natural Vale, Linhares, 21 March 2008, Siqueira 393 (CVRD); Águia Branca, 6 July 2007, Vervloet et al. 2834 (CR, MBML). Goiás: Serra Geral do Paraná, NE de São João da Aliança, 22 March 1973, Anderson 7724 (MO, NY, UB, US); Serra Dourada, S de Goiás Velho, NE de Mossâmedes, 12 May 1973, Anderson 10160 (MO, NY, R, UB); Caldas Novas, 11 February 1993, Cordovil et al. 235 (CEN); 31 km al N de la intersección de las autopistas BR-153 y GO-54, 10 April 1976, Davidse et al. 12243 (INPA, MO, Z); Pirenópolis, Serra dos Pirineus, estrada subiendo a Serra desde Pirenópolis, 26 March 2006, *Delprete 9697* (NY); Gioanápolis, Parque Estadual Altamiro de Moura Pacheco, trilha do Tamanduà, 31 March 2005, Fonseca et al. 3753 (HST, IBGE); Lageado, Cristalina, 12 April 198, Hatschbach 43836 (MBM, Z); carretera Pires do Rio-Luziânia, km 30, 23 April 1979, Heringer et al. 1233 (IBGE, NY, Z); Serra Dourada, E de Goiás Velho, 29 January 1966, Irwin et al. 11865 (IAN, NY, UB, Z); Río Paraná, N de Formosa, 30 March 1966, Irwin et al. 14277 (NY, UB, Z); Serra do Morcego, NE de Formosa, 21 April 1966, Irwin et al. 15226 (F, IAN, K, MO, NY, UB, Z [2 sheets]); Serra Geral do Paraná, São João da Aliança, 15 March 1971, Irwin et al. 31843 (F, MO, NY, UB, Z); NE de Goiás Velho, NA Fazienda das Esmeraldas, 12 February 1980, Kirkbride et al. 3415 (CR, G, UB, US); Cachoeira Alta, 10 km al O de Goiás, 20 February 1982, Oliveira & Anderson 396 (Z); Formosa, Salto do Itiquirá, 5 June 1991, Pereira & Lopes 1663 (CR, IBGE, MO, WAG); Alexânia, Fazenda Cafundo, 19 February 2003, Pereira-Santos et al. 7250 (CEN); Río Corumbá, Ipameri, 28 April 1994, dos Santos et al. 296 (CEN); córrego Mato Grande, Luziânia, 13 March 2003, Silva et al. 7415 (CEN, HUEFS). Maranhão: Alzilândia, Río Pindaré, 29 May 1979, Jangoux & Bahia 957 (MG); Santa Luzia, Fazenda Agripec, 7 km al O de Buriticupu, BR-322, 3 April 1983, Taylor et al. 1128 (MG, NY). Mato Grosso: Chapada dos Guimarães, 22 March 1983, Carreira et al. 393 (INPA, MG, USF); Chapada dos Guimarães, São Vicente, 22 March 1983, Carreira et al. 598 (MG, NY, USF); carretera de Pontes e Lacerda a Vila Velha, 4 May 1983, Carreira et al. 697 (MG, NY); Vila Bela, 5 May 1983, Carreira et al. 815 (NY); Jauru, 7 May 1995, Hatschbach et al. 62377 (BR, K, MBM, NY, WAG); Arinos, São José do Río Claro, cerca a Río Arinos, 26 April 1997, Ivanauskas et al. 1955 (CR, ESA); Santa Cruz da Barra, Río Paraguay, 25 March 1894, Lindman 3163 (S); Santa Anna da Chapada, 12 March 1894, Malme 1472 (S); Chapada dos Guimarães, São Vicente, Cachoeirina, 22 March 1983, Silva & Lima 598 (USF); Parecis, NNO de Diamantino, Fazenda Camargo, 22 May 1997, Souza et al. 16920 (CR, ESA). Mato Grosso do Sul: Iguatemi, MS-295, 5 km O de Iguatemi, 10 March 2004, Hatschbach et al. 76893 (MBM). Minas Gerais: Galheiro, Perdizes, 30 April 2004, Amorin et al. 860 (HUFU, UB); Jardim Botânico do Belo Horizonte, 7 April 1933, Barreto 479 (BHCB), 14 March 1934, Barreto 481 (BHCB); Morro das Pedras, Belo Horizonte, 23 April 1933, Barreto 963 (BHCB); Tombos, Fazenda das Sète Voltas, 18 January 1936, Barreto 4016 (BHCB); Estação Experimental, 8 May 1935, Barreto 4030 (BHCB), 18 August 1938, Barreto 8787 (BHCB); Sujo, 3 January 1940, Barreto 10568 (BHCB, CR); Rio Grande, 1997, Brina s.n. (BHCB); Dionísio, 7 February 1986, Campos 49 (BHCB); without exact locality, s.d., Claussen s.n. (K); without exact locality, 1838, Claussen 359 (P [2 sheets], UPS); Pedra Azul, N de Medina, 30 March 1976, Davidse et al. 11530 (MO, NY, SP, Z), Davidse et al. 11575 (MO, SP, Z); Pedra Azul, entre Itaobim y Teophilo Ottoni, 24 November 1964, *Duarte 8596* (CR, RB); Pedra Azul, Itaobim, 25 May 1967, *Duarte 10419* (CR, RB, Z [3 sheets]); Carmópolis de Minas, Estação Ecológica da Mata do Cedro, 25 January 2004, Echtermacht & Domas 205 (BHCB), 17 May 2004, Echtermacht & Domas 436 (BHCB); Paraopebas, 25 August 1957, Fróes 33316 (IAN); São Thomé das Letras, 20 February 1991, Gavilanes et al. 4854 (CR, ESAL); Minas Gerais, 17 January 1985, Gentry et al. 49653 (MO, WAG, Z); Vicosa, Estação Experimental Coronel Pacheco, 28 February 1956, Gómes 2489 (CR, VIC); Campus da Universidade Federal de Minas Gerais, 13 April 1981, Grandi 2667 (BHCB); Itinga, Morais, 18 February 1989, Hatschbach & Cordeiro 52692 (C, CR, HBG, MBM, WAG); Araçuaí, Fazenda Bom Sucesso, Eneas, 17 February 1991, Hatschbach et al. 55218 (BHCB, C, MBM, WAG); Tejuco, Uberlândia, 6 February 1994, Hatschbach & Silva 59822 (BHCB, C, FLOR, M, MBM, NY, WAG); Paraopeba, 30 Octuber 1959, Heringer 7250 (HB, UB, Z); Serra do Cabral, N de Joaquim Felício, 10 March 1979, Irwin et al. 27356 (F, K, MO, NY, UB, Z); Serra do Espinhaco, faldas de Serra do Piedade, 16 January 1971, Irwin et al. 30519 (C, F, K, NY, UB, US, Z); Serra do Espinhaço, carretera a Roças Novas, E de Belo Horizonte, 17 January 1971, Irwin et al. 30615 (MO, NY, UB, Z); Pindaré, 11 December 1978, Jangoux & Bahia 337 (MG, Z); Salinas, cerca del aeropuerto, 7 April 2002, Jost et al. 461 (HUEFS); Carrancas, camino Carrancas-Itutinga, 15 February 2000, Kinoshita et al. 2000-10 (BHCB, UEC); Belo Horizonte, Estação Ecológica de Universidade Federal de Minas Gerais, 8 March 1994, 29 March 1994, Lombardi 549 (BHCB, WAG); Januária, Fabião, Rio Peruaçu, 25 May 1997, Lombardi & Salino 1786 (BHCB); Salto da Divisa, Fazenda Santana, 19 February 2003, Lombardi et al. 5045 (BHCB); Jaraguá, Campo Verde, 4 February 1944, Macedo 262 (NY); Villa Progresso, 10 January 1940, Magalhães 4 (BHCB); Serra do Curral, Belo Horizonte, 25 July 1942, Magalhães 3214 (K, NY); Coronel Murta, NE de Minas, 7 April 1959, Magalhães 15216 (CR, MO, RB); Coronel Duarte, 5 April 1959, Magalhães 15493 (IAN); 20 km al N de Itaobim, 30 March 1959, Magalhães 15534 (IAN); Itaobim, May 1961, Magalhães 18857 (HB, Z); Montes Claros, Serra do Cattoni.10 November 1938, Markgraf 3316 (RB); Barbacena, 15 November 1907, Maura 541 (K); Arcos, Río São Miguel, 31 December 2002, Mello & Mello 295 (BHCB, RB); Fazenda Amargoso, MG-439, km 15, 29 July 2004, Mello 1231 (BHCB, RB); Caratinga, Fazenda Montes Claros, 20 February 1994, Mendonça & Lemos Filho s.n. (BHCB); Francisco Sá, Lavras, 3 January 1991, Neto & Gavilanes 5032 (CR, ESAL); Fazenda Baleia, Belo Horizonte, 26 February 1940, Oliveira 16 (IAN); Brumadinho, Inhotim, 11 February 2009, Oliveira & Rodrigues 437 (BHCB); Joaquim Felício, entre Várzea da Palma y Joaquim Felício, 31 km al E do Rio das Velhas, 10 February 1988, Pirani et al. 2140 (NY, USF); entre Felixlândia y Brasília, 19 June 1964, Pires 57952 (MG, NY, US, Z); Caldas, 1857, Regnell 358 (C, LD, O [2 sheets], S [3 sheets], U, UPS [3 sheets], US); without exact locality, 4 December 1862, Regnell 358a (LD); Januária, Vale do Peruaçu, 14 February 1998, Salino & Gotschalg 4028 (BHCB); Medina, Reservatório do córrego Riberão, 26 May 1999, Salino & Morais 4678 (BHCB, CR); Cabeceira Grande, entre Palmital y BR-251, 16 May 2002, Santos et al. 1211 (CEN), 27 June 2002, Santos et al. 1339 (CEN); Carrancas, camino para Minduri-Cruzilia, 9 January 1998, Simões et al. 81 (UEC, Z), Simões et al. 84 (BHCB, UEC); Carrancas, Serra de Carrancas, 28 March 1998, Simões et al. 149 (BHCB, UEC); Itajubá, Pedra acute, February 2000, Simões & Ouast 1041 (BHCB, UEC); Padre Paraiso, a 1 km de la ciudad, cerca a BR-116, 26 March 2002, Simões & Singer 1278 (BHCB, UEC); entre Araxá y Uberaba, 22 February 1978, Shepherd et al. 7231 (MG, UEC, US); Pedra Azul, 14 February 1994, Souza et al. 5189 (CR, ESA); Fazenda Montes Claros, Caratinga, 8 January 1996, Stehmann & Mendonça s.n. (BHCB, WAG); Novo Cruzeiro, Fazenda Araras, 2 Octuber 2004, Stehmann et al. 3627 (BHCB, CEPEC); Novo Cruzeiro, carretera Palmeiras-fazenda Araras, 2 December 2004, Stehmann et al. 3703 (BHCB); without exact locality, 1816–1821, St. Hilaire 31 (P [2 sheets]), St. Hilaire 179 (P [p.p.]), St. Hilaire 530 (P [3 sheets]), St. Hilaire 2207 (P); Perdizes, 27 Octuber 1994, Tameirao-Neto & Werneck 1176 (BHCB); Araxá, Perdizes, 17 December 1994, Tameirão-Neto & Werneck 1177 (BHCB, CR), 30 July 1994, Tameirão-Neto & Werneck 1182 (BHCB, CR); Nova Ponte, 23 February 1997, Tameirão-Neto 2305 (BHCB, WAG); Almenara, carretera a Rubim, 15 February 1988, Thomas et al. 5983 (NY, WAG); São Sebastião do Paraiso, Pontilhão do Moggana, March 1945, Vidal 553 (R); Cabeceira Grande, Río Preto, 14 February 2002, Walter et al. 4996 (CEN, HUEFS); Belo Horizonte, Lagoa Santa, 1865, Warming s.n. (C, O, S); without exact locality, 1845, Widgren s.n. (FI-W, K, LD, P, S, U, UPS, WU); Serra do Curral, Riberão do Mutuca, 29 April 1945, Williams 6759 (GH, MO).

Paraíba: Maturéia, Serra do Teixeira, Pico do Jabre, 20 December 1997, Agra et al. 4419 (MO); Areia, Lava-Pés, 19 April 1993, Félix 5716 (EAN, HST); Itapororoca, Fazenda Macacos, 11 March 1995, Félix 7105 (HST); Areia, 12 February 1947, Xavier s.n. (JPB # 1374, IPA). Paraná: Paiqueré, Londrina, 4 March 2004, Carneiro 19 (MBM); Vila Alta, Fazenda Santa Mônica, 5 December 1996, Carneiro 87 (MBM); Jundiaí do Sul, Fazenda Monte Verde, 5 January 1997, Carneiro 283 (MBM); Turmeiras do Oeste, 25 January 2004, Caxambú 287 (MBM); BR-269, km 74, Ortigueira, Serra do Cadeado, 1 March 1986, Chagas et al. 1008 (MBM); Capa Grande, 23 January 1903, Dusén 2939 (BM, S); Porto de Cima, 23 December 1908, Dusén 7442 (S); Río Tibagy, Ponta Grossa, 7 January 1904, *Dusén s.n.* (S, UPS), 17 March 1909, *Dusén 8038* (BM, G, S), 13 February 1911, Dusén s.n. (SI); Mata Laranjinha, Bandeirantes, 13 March 1995, Ferrari-Tomé 287 (MBM); Cerro Azul, Morro Grande, 5 February 1950, Hatschbach 1802 (FI, S); Cerro Azul, Morro Grande, 8 February 1960, Hatschbach 6728 (MBM, MO, Z); Cerro Azul, Lageado Grande, February 1961, Hatschbach 7713 (MBM); Arapoti, Fazenda do Tigre, 26 February 1961, Hatschbach 7829 (MBM, Z [2 sheets]); Candido Rondon, 13 December 1965, Hatschbach 13358 (B, MBM, U, US, Z [2 sheets]); Serra Dourada, Umuarama, 19 January 1967, Hatschbach 15738 (B, C, F, L, MBM, NY, P, US, Z); Pérola, Xambre, 23 January 1967, Hatschbach et al. 15847 (L, MBM, US, Z); Missal, Medianeira, 9 February 1969, Hatschbach 21005 (MBM); Porecatú, 13 February 1970, Hatschbach 23477 (MBM, NY, Z); Quero-Quero, Palmeira, 6 May 1973, Hatschbach 31852 (MBM, Z); Serra do Canha, Cerro Azul, 20 March 1974 (fl Hatschbach 33836 (MBM, Z); Barra Río Pardo, Adrianópolis, 5 April 1976, Hatschbach 38541 (MBM, Z); Riberão do Tigre, Cerro Azul, 8 December 1983, Hatschbach 47556 (MBM); Ribera do Tigre, Cerro Azul, 8 December 1983, Hatschbach & Silva 50870 (C, HBG, MBM, MU, SI, US); Indiavaí, cerca a Río Jauru, 8 May 1995, Hatschbach et al. 62508 (C, HUA, MBM, MEXU, WAG); Jundiaí do Sul, Fazenda Monte Verde, 14 January 2000, Hatschbach et al. 69946 (MBM); Colonia Militar del Brasil, Río Paraná, cerca de desembocadura en el Río Igazú, 16 February 1900, Hicken 25 (SI [2 sheets]); Jaguariaíva, 8 May 1914, Jonsson 286 (S); Ribera do Tigre, Cerro Azul, 19 January 198, Kummrow 1664 (HBG, MBM); cerca de Porto Byington, 23 January 1967, Lindeman & de Haas 4401 (K, MBM, NY, U); cerca a Umuarama, 19 January 1967, Lindeman & Haas 4248 (C, MO, P, RB, U, UC, WIS); Reserva Biológica Santa Helena, Itaipú, 18 February 1987, Motta 694 (MBM); Santa Helena, 1975, Pedersen 11009 (C, K, L, MBM, MO, NY, UC, Z); Parque Nacional Iguaçú, 14 February 1960, Pereira 5326 (B, HB, K, M, RB, U, Z [3 sheets]); Itaipu, Foz de Iguaçu, 26 January 1998, Ponciano 941 (MBM); São Pedro do Ivaí, Fazenda Barbacena, 18 December 2003, Ribas et al. 5670 (MBM); Sengés, 5 km de Sengés, camino a Itararé, 13 February 1995, Souza et al. 19 (ESA, MBM); Ivahy, 1 February 1937, Tessmann 6040 (BR, G, K, MBM, RB, U); Fazenda Rio Vermelho, 24 February 1949, Tessmann s.n. (MBM). Pernambuco: Vicência, Jundiá, 29 November 1957, Andrade-Lima 57-2823 (IPA); Floresta, encosta da Serrra Do Aripuá, 8 January 1961, Andreda-Lima 61-3633 (IPA); Triunfo, divisa dos Municipios Triunfo-Princesa Isabel, 26 February 1986, Lima & Gallindo 121 (IPA); Brejo da Madre de Deus, subida para Fazenda Bituri, 13 November 1993, Miranda et al. 1098 (HST, IPA); Arcoverde, Serra do Mimoso, 11 December 1997, Miranda & Gomes 2890 (HST); Triunfo, Lagoa do Mariano, 18 June 1999, Miranda & Silva 3525 (HST); Arcoverde, Serrra das Varas, 21 February 2006, Pereira et al. 2506 (HUEFS, IPA); Vicência, Engenho Canavieiras, 17 February 1966, Teixeira 2605 (US); Surubim, 30 November 1941, Xavier s.n. (JPB # 440, IPA). Rio de Janeiro: Paraty, camino a Fazenda Olaria, 18 December 2007, Bovini 2693 (CR, RB); Rio de Janeiro, s.d., Bowie & Cunningham s.n. (BM, MO); Rio das Ostras, Praia Virgem, 15 Octuber 2001, Braga 2723 (R); Rio das Ostras, Restinga de Praia Virgem, 1 May 1999, Damasceno 980 (RB); Saquarema, Ipitangas, 7 March 1989, Fanney et al. 2232 (HUEFS, RB); cerca a Rio de Janeiro, s.d., Gaudichaud s.n. (P); Gavea, 12 February 1870, Glaziou 4090 (C, P); Cosmevelho, 20 January 1870, Glaziou 4091 (C [2 sheets], P [3 sheets]); Copacabana, s.d., Glaziou 4092 (P); Marica, 11 January 1879, Glaziou 11177 (C, K, P); entre Jacarepaguas y Tijuca, 28 December 1878, Glaziou 11191 (C, K, P [2 sheets]); Rio de Janeiro, s.d., Glaziou 12940 (C, K [2 sheets], P [2 sheets]); Río Preto, 7 June 1898, Glaziou 21719 (K, P); Petrópolis, Carangola, February 1944, Góes & Constantino s.n. (CR, RB); Rio de Janeiro, 1821, Langsdorff s.n. (P [2 sheets]); Guanabara, Reserva Florestal do Jardim Botânico, 19 January 1949, Lucre & Braga 1343 (RB); Paraty, Apa-Cairucu, Morro da Fazenda Olaria, 20 Octuber 1993, Marquete 1261 (RB); Parati, Paratimirim, Ilha da Cotia, 8 January 1989, Martinelli et al. 13292 (CR, RB, UB); Búzios, reserva Tauá, 6 March 2004, Machado 66 (RB); exact locality lacking, s.d., Pohl 5168 (W); Cantagalo, 1839, Pohl 5397 (BM, L, M, NY, W); Paratí, 1 January 2006, Proença & Harris 3077 (RB, UB); Cantagllo, s.d., Schott s.n. (BR); Rio de Janeiro, 1816-1821, St. Hilaire 13 (F, P), St. Hilaire 123 (P); Ihla Hurtada, 24 December 1967, Sucre 1999 (RB); Petrópolis, Vila Bom Sucesso, 26 January 1968, Sucre & Braga 2187 (K, RB); Petrópolis, Vila Bom Sucesso, 27 January 1968, Sucre et al. 2216 (CR, RB); Vale Bonsucesso, Petrópolis, 24 January 1969, Sucre & Braga 4484 (MO, RB); Rio de Janeiro, 1861-1862, Weir 214 (F, K, P). Rio Grande do Sul: Colonia San Pedro, Torres, 29 January 1977, Hagelund 10874 (Z); Torres, Lageadinho, 6 January 1992, Jarenkow & Záchia 2028 (MBM, PEL); Vale do Sol, Linha XV de Novembro, 23 January 1993, Jarenkow & Falkenberg 2279 (MBM, PEL); São Francisco de Paula, carretera a Taguara, 29 January 1994, Krapovickas & Cristóbal 44708 (CTES, MICH); Santo Angelo, 14 February 1893, Lindmann 957 (S, UPS); Santo Angelo, 16 January 1893, Malme 502 (LD, S, UPS), 14 January 1893, Malme 957 (S); Porto Alegre, 16 December 1901, Malme 827 (S); monte Ferrabraz, 12 January 1949, Rambo 39946 (B), 16 May

1949, Rambo 41612 (B); monte Ferrabraz, Nova Hamburgo, 5 July 1949, Rambo 42370 (L). Rondônia: Guajará-Mirim, ca. 5 km NO de Costa Marques, 29 March 1987, Nee 34537 (INPA, MG, NY, USF). Roraima: Ilha de Maracá, 5 January 1988, Milliken & Miller 776 (K [2 sheets], MIRR, NY); São Leopoldo, 20 December 1948, Rambo 39008 (B); Monte Ferrabras, Novo Hamburgo, 16 May 1949, Rambo 41612 (B); Novo Hamburgo, 25 May 1949, Rambo 41698 (B); Serra do Maturuca, Urucá, 19 November 1954, Rodríguez 571 (INPA, MO). Santa Catarina: Morro da Lagoa, Florianópolis, 22 February 1992, Falkenberg 5610 (MBM); Laguna, Morro Nossa Senhora da Gloria, 24 January 1984, Krapovickas & Cristobal 39384 (CTES, MBM); without exact locality, s.d., Barle s.n. (G-DC); Ibirama, 5 February 1956, Reitz & Klein 2628 (HBR, MO, NY, S, SI, US, Z); Pilões, Palhoca, 23 February 1956, Reitz & Klein 2842 (HBR, Z); Matador, Río do Sul, 31 December 1958, Reitz 6159 (HBR, Z); Floresta, 25 January 1962, Reitz & Klein 12019 (HBR, Z). São Paulo: Bariri, 28 November 1976, Aquilante 5 (MBM, Z); Piracicaba, Tamandupa, 6 January 1994, Barreto et al. 1729 (CR, ESA, UEC); Itirapina, Itaquari, Salto de Itaquari, 15 February 1993, Barros 2712 (HST, SP); Moaco, 23 February 1913, Brade 5696 (S); Paraguaçu Paulista, Fazenda São José, 1 km al O de Rio São Mateus, 8 February 1965, Eiten et al. 5896 (US); Itaquaquecetuba, 1 March 1939, Gehrt s.n. (SP, US); cerca de Atabaia, 29 January 1978, Gentry 21479 (MO, Z); lago de la represa Atabainha, 5 January 1985, Gentry & Zardini 49226 (MO); Jundiaí, Serra do Japi, 21 January 1976, Leitão Filho et al. 1596 (L); 25 km al NO de Mogi-Guaçú, Fazenda Campininha, 4 February 1977, Gibbs & Leitão Filho 4356 (NY); Vinhedo, 17 December 2001, Guillaumon s.n. (MBM, SPSF); al NO de Mogi-Guaçu, Fazenda Campininha, 4 April 1977, Gibbs & Leitão 4326 (F, INPA, UEC, UB); carretera entre Bauru y Marilia, 7 June 1976, Leitão et al. 2019 (CR, RB, UEC); Limeira, 15 January 1949, Lima s.n. (RB); without exact locality, Martius 2261 (M), Martius 2262 (M); Santos, 31 January 1875, Mosén 3433 (S); Serra do Caracol, 25 December 1875, Mosén 4269 (S [2 sheets]); Campinas, s.d., Novaes 390 (WU); Santa Lúcia, 15 December 1943, Pickel 1112 (K); Teodoro Sampaio, 15 February 1996, Souza & Souza 342 (CR, ESA); Restinga, entre Batatais y França, 8 January 1996, Souza et al. 9756 (CR, ESA); between Rio Grande and Alto da Serra, 1902, Wacket s.n. (WU). Sergipe: Poço Redondo, Serra da Guia, trilha para o topo da Serra, 17 December 2010, Farinaccio & Machado 796 (ASE); Poço Redondo, Serra da Guia, 21 November 2009, Machado et al. 50 (ASE); Poço Redondo, Serra da Guia, 9 February 2010, Machado et al. 201 (ASE). Data lacking: 1814-1817, Bowie & Cunningham 97 (BM); January 1827, Burchell 4080 (K); s.d., Burchell 4284 (K, P); s.d., Burchell 4731 (K); 1815–1818, Freyreiss s.n. (HAL); 1839, Guillemin 493 (P [2 sheets]); s.d., Lund s.n. (C); s.d., Martius s.n. [M]; s.d., Regel s.n. (CGE); s.d., Regnell 1358 (P); s.d., Riedel s.n. (K, P, S, UPS, Z); s.d., Riedel s.n. (FI, LE, P [2 sheets], W); s.d., Schott 2452 (NY, W); s.d., Schott 5396 (NY); s.d., Sello s.n. (B, U, UPS); s.d., Sello 21 (CGE, P); s.d., Sello 52 (P); s.d., Sello 152 (K); April 1897, Ule 4284 (HBG); s.d., Warming s.n. (NY, O, S); 1845, Widgren 378 (UPS).

BOLIVIA. Beni: Vaca Diez, Villa Chácobo, Alto Ivón, 19 March 1984, *Boom 4548* (LPB, NY, WAG, Z). Santa Cruz: Chiquitos, SE de Roboré, 4 February 1995, *Abbott & Mostacedo 16067* (BEREA, CR, SI, USZ, WU); Reserva Ecológica El Refugio, O de Toledo, 16 May 1995, *Guillén & Chore 3686* (CR, MO, USF, USZ); Los Fierros, 3 March 1997, *Jiménez et al. 1118* (LPB, MO [2 sheets], USF, USZ); Ñuflo de Chávez, Concepción, 30 April 1977, *Krapovickas & Schinini 32034* (CTES, MO, WIS, Z); Ñuflo de Chávez, entre San Javier y Concepción, 27 March 2004, *Morrone & Belgrano 4950* (SI); El Encanto, 28 June 1993, *Saldias et al. 2771* (LPB, MO, NY, USZ); Velasco, 4 April 1986, *Seidel 170* (LPB, MO, M, P).

PARAGUAY. Alto Paraná: Reserva Biológica Limoy de Itaipú, 18 April 1986, Brunner & Caballero 1854 (G, MO, PY, USF); cerca a Hernandarias, 31 January 1982, Fernández-Casas & Molero 5712 (G, MA, MO, NY); N de Hernandarias, 10 January 1974, Schinini 8100 (CTES, G); Estancia Río Bonito, 28 November 1995, Zardini et al. 43868 (MO), 28 February 1996, Zardini & Silva 44692 (AS, MO, USF); Itaipu Binacional Paraguay-Brasil, refugio biológico Tati Yupi, 18 July 200, Zardini et al. 60182 (CR, MO), 19 July 200, Zardini & Mallorquin 60204 (CR, MO). Amambay: Parque Nacional Cerro Corá, Cerro Muralla, 17 May 1995, Ezcurra et al. 1879 (SI); Parque Nacional Cerro Corá, 1982, Fernández-Casas & Molero 6088 (COL, G, MA, MO, NY); Paso Ñande Jara, 19 March 1983, Hahn et al. 1250 (MO); SO de Pedro Juan Caballero, 16 February 1978, Pedersen 12267 (C, CTES, L, SI, Z); Parque Nacional Cerro Corá, cerca a Cerro Muralla, 7 February 1982, Solomon et al. 6796 (CM, G, MO, SI, USF); Parque Nacional Cerro Corá, Cerro Muralla, 6 January 1988, Soria 2012 (G [2 sheets], MO); Parque Nacional Cerro Corá, January 1994, Soria 6396 (FCQ, MO), 15 May 1995, Soria 6998 (FCQ, MO); Parque Nacional Cerro Corá, carretera a Colonia Naranja Hai, 10 January 1997, Soria 7670 (FCQ, MO); Cerro Apua, O de Cruce Bella Vista, 20 February 1997, Soria 7802 (FCQ, MO); Estancia Don Juancito, Cerro Ysau, 12 June 1996, Zardini & Cardozo 44945 (AS, MO), Zardini & Cardozo 44945 (MO); cerca de Lorito Picada, 14 June 1996, Zardini & Cardozo 45146 (AS, CR, MO, USF); Parque Nacional Cerro Corá, 26 February 1997, Zardini & Guerrero 46539 (AS, CR, MO, USF); Parque Nacional Mbaracayú, 27 May 1999, Zardini & Chaparro 50779 (AS, CR, MO); sendero a Arroyo Estrell, 8 May 2000, Zardini & Guerrero 54103 (CR, MO); Cerro Corá, 27 February 2001, Zardini & Acosta 56199 (CR, MO). Caaguazú: Vaquería Capibary, 1898–1899, Hassler 5944 (BM, G, NY); E de Ygatimí, 13 March 1997, Jiménez et al. 1798 (BM, CTES, G, MO, PY). Canindeyú: Colonia Fortuna, cerca de Kuruguaty, 7 May 1974, Arenas 687 (SI); Arroyo Guazú, cerca de Colonia Residenta, 4 February 1982, Fernández-Casas & Molero 5956 (COL, G, HUA, MA, MO, NY); Guadalupe, carretera a Puerto Adela, 16 December 1982, Hahn et al. 963 (CR, G, MO, SI, USF); Ñandurokai, 15 March 1997, Jiménez et al. 1855 (BM, CTES, G, MO, PY); Reserva Natural Mbaracayú, Ñandurokai, 15 January 1998, Zardini & Guerrero 48023 (AS, CR, MO, USF), 11 June 1998, Zardini & Chaparro 48697 (LPB, USF), 25 May 1999, Zardini & Chaparro 50503 (AS, CR, MO), 27 May 1999, Zardini & Chaparro 50704 (AS, MO). Concepción: Viña, February 1896, Anisits s.n. (S); entre Río Apa y Río Aquidabam, 1908–1909, Fiebrig 4601 (BM, G, K, L, P, SI); Estancia San Fernando, 17 March 1994, Zardini & Guerrero 38967 (AS, MO); Valle del Río Mi-apa, 27 June 2002, Zardini & Gómez 58972 (CR, MO). San Pedro: Estancia Alegría, March 1994, Soria 6586 (FCQ, MO); Primavera, 11 April 1955, Woolston 500 (C, K, MO, NY, S, SI [2 sheets], U, UC); Primavera, 15 March 1957, Woolston 1449 (K); Bosque Yaguareté, 19 January 1996, Zardini & Guerrero 44465 (AS, CR, MO, USF), 30 July 1996, Zardini & Guerrero 45324 (AS, CR, MO, USF), 27 May 1997, Zardini & Zavala 46759 (AS, CR, MO, USF), Zardini & Zavala 46760 (AS, CR, MO, USF), Zardini & Zavala 46761 (AS, CR, MO, USF), 13 March 1998, Zardini & Guerrero 48453 (USF); Antequera, 23 June 2001, Zardini & Guerrero 56531 (FACEN, CR, MO). Data lacking: s.d., Fiebrig 17 (G).

ARGENTINA. Misiones: Ayo Uruguay, cerca de Puerto Bemberg, 31 January 1951, *Capurro 734* (SI); Iguazú, Pedro Bossetti, 21 May 1999, *Keller 57* (CTES, SI); Iguazú, Puerto Península, cerca a Puerto Iguazú, 2 March 1996, *Vanni et al. 3594* (CTES, K).

Prestonia dusenii (Malme) Woodson (1931: 552). Echites dusenii Malme (1928: 9). Type:—BRAZIL. Paraná: Paranaguá, Alexandra, Serra da Prata, 5 March 1911, P. Dusén 11486 (holotype S! [photo F neg. 26881!], isotypes BM!, G!, K!, S! [2 sheets], UPS!, US!). Fig. 2, 3.

Stem glabrous to glabrescent, latex white, the lenticels inconspicuous or absent, (if present) not suberose, intrapetiolar colleters minute, 0.2–0.4 mm long. Petioles 0.4–1.3 cm; leaf blade 2– $12(-15) \times 2$ –7 cm, elliptic to narrowly elliptic, apex acute, short-acuminate or caudate, base obtuse to rounded, membranaceous, glabrescent to minutely puberulent along the midrib adaxially, glabrescent to minutely papillate-puberulent abaxially, secondary veins slightly impressed abaxially, inconspicuous adaxially, tertiary veins usually inconspicuous. Inflorescence a dichasial cyme, axillary, shorter than the adjacent leaves, few-flowered, the flowers more or less clustered, glabrescent to minutely puberulent, peduncle less than 0.7 cm, pedicels 0.5–0.9 cm long, floral bracts 1– $2 \times 0.5$ –1 mm, linear, scarious, minute, green. Sepals 4– $7 \times 1.5$ –3 mm, free, membranaceous, obovate to narrowly obovate, the apices rounded to broadly obtuse, inconspicuously mucronulate, slightly reflexed, glabrous to glabrescent, usually very small, drying

with a more or less uniform color, the veins conspicuously impressed, colleters less than 1 mm long, minutely lacerate at the apex. **Corolla** salverform, yellow, glabrous, glabrescent or inconspicuously puberulent outside, tube  $9-13 \times 2-3.5$  mm, usually inflated at the base, without free corona lobes within, annular corona entire, delicate and inconspicuous, corolla lobes  $5-9 \times 4-5$  mm, obliquely obovate. **Stamens** inserted about midway within the corolla tube, anthers 4-5 mm, dorsally glabrous, included. **Ovary** 1-1.5 mm tall, glabrous, style-head 1-1.3 mm, nectary 1-1.5 mm, equaling the ovary, variously 5-lobed, each lobe entire. **Follicles**  $14-24 \times 0.2-0.4$  cm, contínuos, free, but sometimes united at the tips (at least when young), minutely puberulent to glabrescent, without lenticels, firmly membranaceous when old; seeds 9-12 mm, coma 2-2.5 cm, cream.

**Distribution and habitat:**—Endemic to southern Brazil, where it grows in moist forest, gallery forest, and similar disturbed from 0 to 900 m.

**Phenology**:—Specimens with flowers have been collected from November through June. Fruiting December through March.

Conservation Assessment:—Endangered (EN) (IUCN 2001).

Local name:—Cipó de leite (Santa Catarina, Brazil).

**Taxonomic notes:**—This species is related to *P. coalita* and *P. solanifolia*, but differs by its leaf blades that are glabrescent to minutely puberulent along the midrib abaxially, shortly branched inflorescences, scarious bracts, obovate to narrowly obovate sepals, and lack of free corona lobes.

Additional specimens examined:—BRAZIL. Mato Grosso do Sul: Dourados, O de Amambaí, 11 December 1982, *Hatschbach 45877* (CR, MBM, US, Z). Paraná: Paranaguá, Ihla do Mel, Morro Bento Alves, 7 March 1987, *Britez 384* (MBM); Morretes, Picada Mamona, 31 December 1949, *Hatschbach 1731* (MBM, S, Z); Paranaguá, Sertão, 14 February 1951, *Hatschbach 2130* (MBM, US); Campina Grande do Sul, rodovia BR–2, Ribeirão do Cedro, 18 February 1962, *Hatschbach 8945* (MBM); Campina Grande do Sul, Río Trinidade, 10 February 1964, *Hatschbach 10956* (HB, MBM, Z [2 sheets]); Morretes, Marumbi, 5 January 1966, *Hatschbach et al. 13458* (CR, MBM, NY, RB, U, US, Z); Serrinha, Guaraqueçaba, 8 August 1968, *Hatschbach 18497* (C, L,

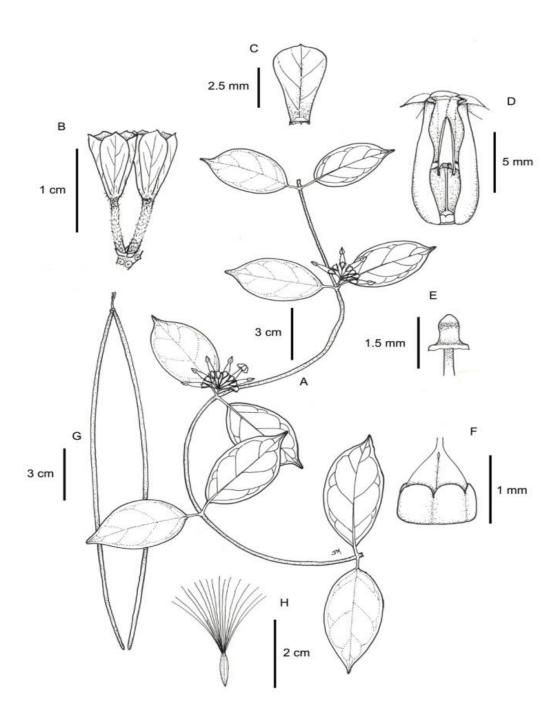


Fig. 3 *Prestonia dusenii* (A-F from *Hatschbach 45877*, INB; G-H from *Hatschbach 1731*, Z). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of one sepal, showing the basal colleter. D. Open corolla tube, showing the insertion point of the anthers. E. Style-head. F. Nectary and ovary. G. Follicles. H. Seed.

MBM, UC, Z); Morretes, Floresta, 23 January 1969, *Hatschbach & Koczicki 20389* (C, MBM, MICH, NY); Guaraqueçaba, Rio da Costa, 9 February 1972, *Hatschbach 29128* (MBM); Río Pequenho, Antonina, 10 January 1974, *Hatschbach 33660* (LP, MBM, UC, Z); Guaraqueçaba, Río Pederneiras, 15 March 1984, *Kuniyoshi & Pizani 4750* (CM, MBM); Morro de Quitumbê, Guaraqueçaba, 9 February 1994, *Lima 234* (NY, UPCB); Guaraqueçaba, Morro do Rio das Pacas, 20 January 1993, *Prado et al. 453* (MBM); Paranaguá, Colônia Pereira, 6 February 2002, *Ribas & Silva 4311* (CR, MBM). Santa Catarina: Bom Retiro, Blumenau, 10 March 1960, *Klein 2385* (HBR, Z); Santa Catarina, June 1868, *Mueller 131* (K); Luis Alves, Itajaí, 9 January 1956, *Reitz & Klein 2401* (HBR, MO, US); Tres Barras, Garuva, San Francisco do Sul, 19 December 1957, *Reitz & Klein 5730* (HBR, MO, Z), 26 March 1958, *Reitz & Klein 6609* (HBR); without exact locality, 1888, *Ule 807* (HBG, US). São Paulo: Santos, 20 January 1875, *Mosén 3433b* (S). Data lacking: s.d., *Burchell 3520* (K); January 1875, *Glaziou 3433* (P).

Prestonia ornata (Hoehne) J. F. Morales & M. Endress, Taxon 00: 000-000. Echites ornatus
Hoehne (1915: 82). Temnadenia ornata (Hoehne) Woodson (1932b: 383). Type:—
BRAZIL. Mato Grosso: Piruena, May 1909, F. Hoehne 1965 (lectotype, R! [2 sheets] designated by Morales (2005b)). Fig. 2, 4.

**Stem** glabrous to glabrescent, usually with milky latex, with few lenticels, the lenticels not suberose, intrapetiolar colleters minute, less than 1.5 mm long. Petioles 0.3-1.5 cm; leaf blade láminas  $4.5-15(-18) \times 2-6.5(-7.5)$  cm, narrowly elliptic, elliptic, to ovate-elliptic, apex acute to short-acuminate, base obtuse, rounded to broadly acute, membranaceous, sometimes revolute, glabrous, secondary veins slightly impressed on both surfaces, tertiary veins usually not impressed or inconspicuous. **Inflorescence** a dichasial cyme, axillary, longer than the adjacent leaves, manyflowered, the flowers more or less clustered, glabrous to inconspicuously puberulent, peduncle 1.3-9.1 cm, pedicels 0.9–1.4 cm long, floral bracts  $1-3.5 \times 1-1.5$  mm, scarious, linear, inconspicuous, green. Sepals  $3.5-5 \times 1-1.5$  mm, free, membranaceous, very narrowly ovate to narrowly ovate, the apices acuminate, commonly reflexed, glabrous, very small, drying with a more or less uniform color, the veins not impressed, colleters less than 1 mm long, slightly to deeply erose at the apex. Corolla salverform, yellow, glabrous outside, tube 14–20 × 2–2.8 mm, straight, without free corona lobes within, annular corona reduced to inconspicuous calloused ridges, delicate and inconspicuous, corolla lobes  $24-40 \times 10-22$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 4.2–5 mm, glabrous dorsally, included. Ovary 1–1.5 mm tall, glabrous, style-head 1.1–1.5 mm, nectary 0.6-0.8 mm, usually shorter than the ovary, completely divided into 5 separate nectaries, each one entire to subentire. Follicles  $70-110 \times 0.15-0.3$  cm, inconspicuously articulated, usually connate longitudinally, glabrous, without lenticels, membranaceous when old; seeds 13–15 mm, coma 1.9–4.3 cm, cream.

**Distribution and habitat:**—From northwestern Brazil to southeastern Peru and northeastern Bolivia, where it grows in wet forests and savannas, from 100-550 m.

**Phenology**:—Flowering April through August, fruiting in July.

Conservation Assessment:—Vulnerable (VU) (IUCN 2001).

**Taxonomic notes:**—This species is related with *P. succo* and the *P. coalita* complex, but differs by its inflorescence much longer than the adjacent leaves and bigger corolla lobes.

**Additional specimens examined**:—PERU. Madre de Dios: Reserva Natural Tambopata, 1 June 1987, *Gentry & Jaramillo 58014* (CR, MO, USM).

BRAZIL. Acre: Río Branco, camino de Xapuri, 6 May 1980, Coêlho et al. 1670 (INPA, U); Xapurí, Seringal Cachoeira, BR-317, ramal Cachoeira, 16 ao longo do ramal, 30 May 2010, Medeiros et al. 599 (USF); camino a Rio Branco, 8 July 1965, Pires & Martin 10039 (IAN, NY, UB); Rio Branco, Campus Universitario, 8 June 1983, Rosas & Werner 16 (INPA). Amazonas: Rio Curuquetê, Cachoeira Republic, 24 July 1971 (fl, fr), Prance et al. 14538 (F, INPA, K, MO, NY, S, U, US, Z); Aripuanã, 28 May 1979, Silva & Rosario 4675 (NY, USF); Porto Velho, camino a Rodagem, 31 May 1952, Black et al. 14656 (IAN). Mato Grosso: Cuiabá-Porto Velho, Patronal, 9 June 1984, Cid et al. 4402 (INPA, K, NY, RB, USF); Piruena, May 1909, Hoehne 1964 (R); Nova Bandeirantes, camino a Rolândia, 4 June 1997, Ivanauskas et al. 2038 (CR, ESA); Juína, Horto Municipal da Juína. Sinop, 3 July 1985, Macedo 1860 (INPA); Apiacás, Estrada da represa, próxima a 2ª Cachoeira Salto Apiacás, Joara, 24 May 1988, Macedo 1906 (INPA); Próximo ao Posto Fiscal do Celeste, Sinop, 31 May 1995, Macedo et al. 4186 (INPA); Nova Ubiratâ, 28 April 1997, Nave et al. 1344 (CR, ESA); Claúdia, camino de fazenda Inês Maria a Rio Renato, 13 July 1997, Nave et al. 1550 (CR, ESA); Sinop, 19 July 1997, Nave et al. 1661 (CR, ESA). Pará: Itaituba, carretera Santarém-Cuiabá, 4 May 1983, Amaral et al. 1146 (INPA, K, MG, NY, WAG), 15 May 1983, Amaral et al. 1264 (INPA, NY, RB, WAG); Parque Botânico de Carajás, 8 June 1987, Araújo 123 (IAN, RB); Tucuruí, márgenes da PA-149 até o km 50, 22 August 1983, Revilla et al. 8309 (INPA, NY); Marabá, 17 May 1982, Secco et al. 247 (MG, NY, US, USF); Marabá, Carajás, Serra Norte, Mina de Manganês, 1 June 1983, Silva et al 1421 (HRB, MG); Serra dos Carajás, NO del campamento AMZA, 10 June 1982, Sperling et al. 6074 (CR, INPA, K, MG, NY). Rondônia: Jaru, carretera Cuiabá-Porto Velho, 2 July 1984, Cid et al. 4963 (INPA, MO); S of Nova Vida, 15 August 1968, Forero & Wrigley 7088 (NY); Rio Madeira, cerrado between Jaciparaná y Rio Madeira, 25 June 1968, Prance et al. 5196 (F, INPA, MO, NY, P, R, S, U, US), 26 June 1968,

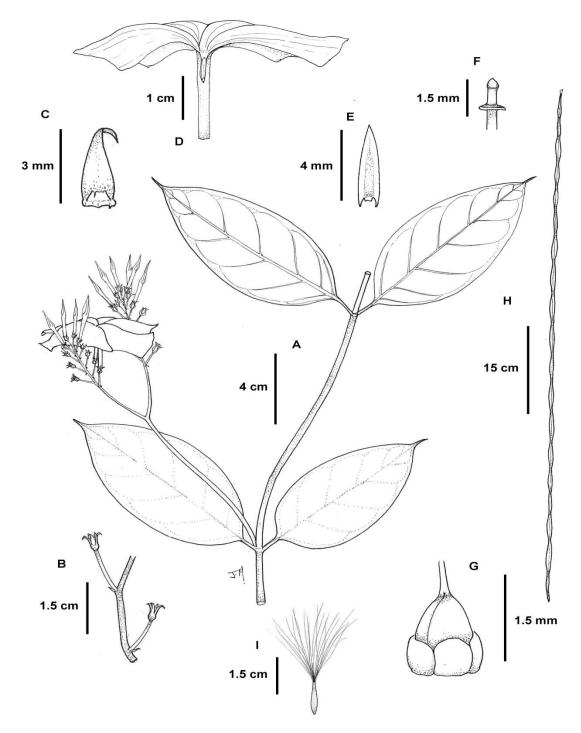


Fig. 4 *Prestonia ornata* (*Araujo 123*, IAN). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of the sepal, showing the colleter. D. Open corolla mouth, showing the anthers. D. Style-head. E. Anther, dorsal view. F. Style-head. G. Nectaries and ovary. H. Follicles. I. Seed.

Prance et al. 5234 (A, COL, G, INPA, K, M, MICH, MG, NY, R, S, US); Subbase Sao Luiz, projecto RADAM, 23 June 1976, Rosa 818 (IAN); Vilhena, estrada nova que va para Colorado do Oeste, 17 km de Vilhena, 27 May 1984, Rosário et al. 603 (MG); rodovia Alvorada-Presidente Médici, km 15, 20 June 1983, Silva 6290 (INPA); Ariquemes, Mineração Mibrasa, Setor Alto Candeias, km 128, Sudoeste de Ariquemes, 16 May 1982, Teixeira et al. 507 (NY); Santa Barbara, carretera BR-364, 23 May 1982, Teixeira et al. 642 (F, INPA, MO, MG, NY, US, USF), 24 May 1982, Teixeira et al. 722 (CR, F, INPA, K, MG, MO, NY, US, USF); Porto Velho, Represa Samuel, 7 June 1986, Thomas et al. 4965 (INPA, K, NY, USF).

BOLIVIA. Beni: Vaca Diez, Riberalto, 29 June 1992, *Gentry et al.* 77560 (CR, MO); E de Riberalta, camino a Guayaramerín, 19 May 1982, *Solomon* 7679 (LPB, MO, NY, USF, WAG); Vaca Diez, Riberalta, 22 May 1987, *Solomon* 16731 (LPB, MO, USF). Pando: Manupiri, N de Puerto América, 19 May 1994, *Jardim* 761 (CR, MO, USF, USZ); Moreno, S del río Madre de Dios, 26-28 May 1992, *Killeen* 3955 (LPB, MO, NY, USZ); Madre de Dios, 27 July 1992, *Rueda* 964 (CR, MO); Federico Román, río Negro, 17 June 1987, *Solomon* 17087 (LPB, MO, USF, USZ); Nicolás Suarez, E de Porvenir, camino a Puerto Rico, 15 August 1982, *Sperling & King* 6642 (CR, INPA, LPB, MG, NY). Santa Cruz: Velasco, Aserradero El Chore, Parque Nacional Noel Kempff, 24 August 1995, *Guillén et al.* 4115 (CR, MO, USZ); Velasco, Estancia Flor de Oro, 27 June 1991, *Nee* 41451 (LPB, NY, USF); Velasco, 29 June 1997, *Thomson et al.* 23 (MO).

*Prestonia pickelii* Markgraf (1938: 129). Type:—BRAZIL. Pernambuco: Tapera, 13 September 1934, *B. Pickel 3690* (holotype IPA!). **Fig. 2, 5.** 

Stem glabrous, the latex unknown, the lenticels not evident, intrapetiolar colleters minute, less than 0.5 mm long. Petioles 0.3–1 cm; leaf blade 5-10.5  $\times$  2.2–3.5 cm, elliptic to obovate-elliptic, apex short-acuminate, base acute, membranaceous, glabrous on both surfaces, secondary veins slightly impressed on both surfaces, tertiary veins inconspicuous. Inflorescence a monochasial cyme, axillary, longer than the adjacent leaves, many-flowered, the flowers laxly disposed to more or less clustered, minutely and sparsely puberulent, peduncle 2.4–2.8 cm, pedicels 0.6–0.9 cm long, floral bracts 0.5– $1.3 \times 0.4$ –0.7 mm, scarious, linear, inconspicuous, green. Sepals 1– $1.4 \times 0.8$ –1.2 mm, free, membranaceous, very narrowly ovate, the apices acuminate, reflexed, very sparsely puberulent to glabrous, very small, drying with a more or less uniform color, the veins not impressed, colleters less than 0.3 mm long, subentire to irregularly erose at the apex. Corolla salverform, yellow, glabrous outside, tube 5.7– $6.8 \times 1.2$ –1.8 mm, slightly expanded toward the mouth, free corona lobes 0.8–1.2 mm long, included, slightly shorter than the apices of the anthers, their height slightly shorter that of the anthers apices, annular corona subentire, delicate and

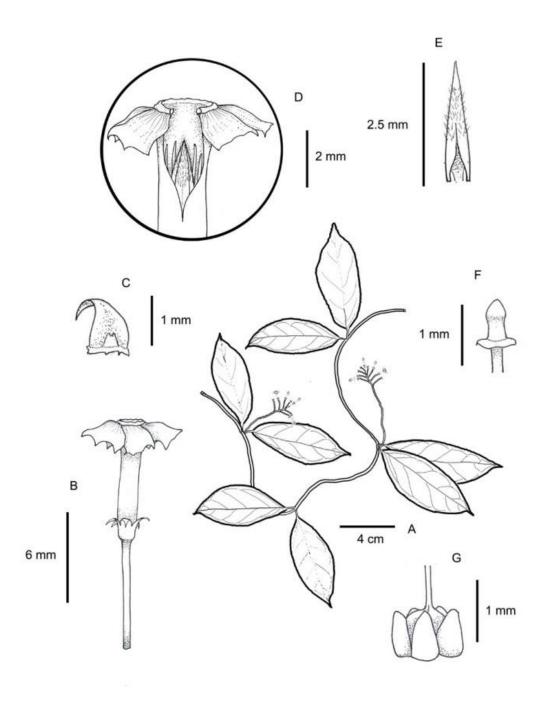


Fig. 5 *Prestonia pickelii* (*B. Silva s.n.*, INB). A. Flowering branch. B. Corolla. C. Sepal, adaxial view. D. Partially open corolla mouth, showing the free coronal lobes and anthers. E. Anther, dorsal view. F. Style-head. G. Nectaries and ovary.

inconspicuous, corolla lobes  $2.8-3.5 \times 1.5-1.9$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 2.4-2.6 mm, minutely puberulent dorsally, included. **Ovary** 0.7-0.8 mm tall, glabrous, style-head 0.6-0.8 mm, nectary 0.6-0.8 mm, usually equaling or slightly shorter than the ovary, divided into 5 individual glands, each one entire. **Follicles** unknown.

**Distribution and habitat**:—Endemic to Brasil, in dry forest in northeastern Brazil, at 250–400 m of elevation.

**Phenology**:—Flowering September.

Conservation Assessment:—Data deficient (DD) (IUCN 2001).

**Taxonomic notes:**—*Prestonia pickelii* is a poorly known species, similar to the variable *P. quinquangularis* and was reduced to the synonymy of the latter by Morales (2010a). However, after detailed study of the type and one additional specimen, it is here restated as a valid species, which can be separated by its smaller flowers.

**Additional specimens examined**:—BRAZIL. Pernambuco: cerca de Petrolina, 1 October 2000, *Silva s.n.* (CR, MO).

Prestonia solanifolia (Müller Argoviensis) Woodson (1936: 282). Haemadictyon solanifolium Müller Argoviensis (1860: 171). Temnadenia solanifolia (Müller Argoviensis) Miers (1878: 214). Type:—BRAZIL. Rio de Janeiro: without data, G. Schüch s.n. (lectotype W! designated by Woodson (1936). Fig. 6, 7.

Temnadenia corrugulata Miers (1878: 215). Type:—BRAZIL. Rio de Janeiro: without data, J. Bowie & A. Cunningham s.n. (holotype BM!).

*Temnadenia tenuicula* Miers (1878: 216). Type:—BRAZIL. Rio de Janeiro: Río Paquequer, Serra de Orgãos, January 1838, *J. Miers* 4050 (holotype BM!).

**Stem** minutely puberulent, glabrescent at maturity, color of latex unknown, the lenticels inconspicuous or absent, (if present) not suberose, intrapetiolar colleters minute, less than 1 mm long. **Petioles** 0.9-1.3 cm; leaf blade  $5-12(-13.5) \times 2.3-7$  cm, elliptic, ovate to narrowly obovate, apex short-acuminate to abruptly acuminate, base obtuse to rounded, membranaceous, sparsely and minutely puberulent to glabrescent adaxially, densely and minutely puberulent abaxially, indument drying tan, secondary veins slightly impressed on both surfaces, tertiary veins rather inconspicuous. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, minutely puberulent, peduncle 0.6-1.1 cm, pedicels 0.4-1 cm long, floral bracts  $2-3 \times 1-1.3$  mm, linear, scarious, minute, green. **Sepals**  $3-4 \times 1-1.5$  mm, free, membranaceous, very narrowly elliptic, the apices acuminate, slightly reflexed, minutely puberulent, very small, drying with a more or less uniform color, the veins conspicuously

impressed, colleters less than 1 mm long, deeply lacerate at the apex. **Corolla** salverform, yellow, glabrous outside, tube  $6-8\times 2$  mm, straight, without free corona lobes within, annular corona entire, delicate and inconspicuous, corolla lobes  $5-7\times 4-6$  mm, obliquely obovate. **Stamens** inserted about midway within the corolla tube, anthers ca. 3 mm, dorsally glabrous, included. **Ovary** 1–1.5 mm tall, glabrous, style-head 0.5-0.75 mm, nectary 0.5-7.5 mm, conspicuously shorter than the ovary, divided into 5 lobes, each one entire to subentire. **Follicles** (inmature)  $15-18\times 0.2-0.3$  cm, continuous, connate longitudinally united at the tis, densely and minutely puberulent or papillate-puberulent, without lenticels, firmly membranaceous; seeds unknown.

**Distribution and habitat**:—Moist forest and disturbed vegetation in southeastern Brazil (Minas Gerais and Rio de Janeiro states), from 450 to 950 m.

**Phenology**:—Flowering October and December. A collection with inmature fruits was collected in November.

Conservation Assessment:—Endangered (EN) (IUCN 2001).

Taxonomic notes:—This species is related to *P. coalita*, but differs by its anthers ca. 3 mm long (vs. 4.5–6 mm), minutely puberulent stems (vs. glabrous, glabrescent to inconspicuously puberulent), and densely and minutely puberulent follicles (vs. glabrous or glabrescent). Woodson (1936) argued that *P. coalita* is glabrous overall, with only the abaxial surface of the leaf blade sometimes inconspicuously papillate-puberulent, whereas in *P. solanifolia* plant is densely puberulent. In general, the stems and leaves of *P. coalita* are glabrous, but sometimes the leaf blades are minutely puberulent, and thus, very similar to those of *P. solanifolia*. *Prestonia solanifolia* needs further study because the collections available are few and incomplete. Since Woodson's (1936) monograph, only one additional specimen has been collected ever since (although major herbaria in Brazil were visited in order to find more collections). Only one specimen with inmature fruits is known. At least in the collections available, the characters used here to separate *P. solanifolia* from *P. coalita* are consistent. However, future field studies in the localities where this species has been reported, may show that *P. solanifolia* needs to be relegated to the synonymy of *P. coalita*.

Additional specimens examined:—BRAZIL. Minas Gerais: without exact locality, s.d., *Claussen s.n.* (P); Viçosa, Mato Virgen, 21 November 1930, *Mexia 5337* (A, CAS, CR, F, G, GH, K, MICH, MO, NY, S, VIC, U, UC, US, WIS, VIC, Z); Viçosa, Centro de Pesquisa de Florestas Naturais, 10 Octuber 1989, *Vieira 640* (CR, VIC); without exact locality, *1831*, *Ackermann s.n.* (M). Data lacking:, *Claussen s.n.* (P).

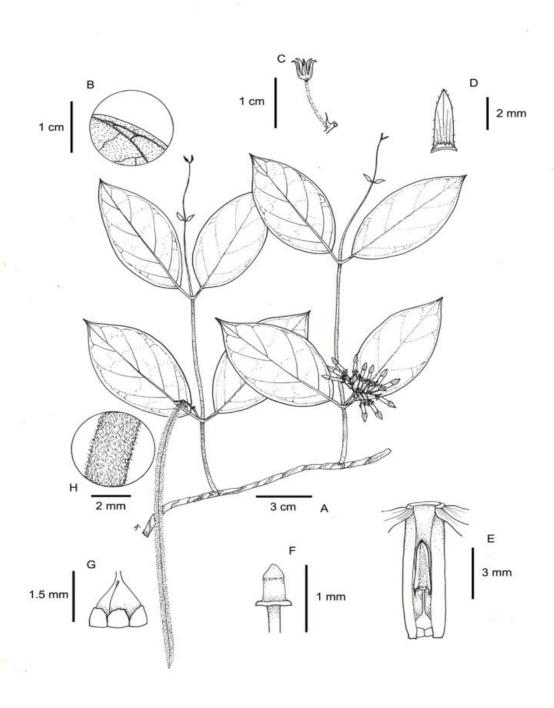


Fig. 6 *Prestonia solanifolia* (A-f from *Mexia 5337*, UC; E from *Vieira* 640, INB). A. Stem with inflorescence and follicles. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and bract. D. Single sepal, adaxial view. E. Open corolla tube, showing the point of insertion of the anthers. F. Style-head. G. Nectaries and ovary.

II. Prestonia sect. Denticulatae J. F. Morales, M. Endress & Liede, sect. nov. – Type: Prestonia denticulata (Vell.) Woodson, Ann. Missouri Bot. Gard. 23: 284. 1936. Echites denticulatus Vell., Fl. Flumin. 110. 1829.

Prestonia amabilis J.F. Morales (2004: 161). Type:—ECUADOR. Pastaza: Hacienda San Antonio de Baron von Humboldt, 2 km NE of Mera, 27 February-19 March 1985, D. Neill, M.A Baker, W.A. Palacios & J. Zaruma 5975 (holotype MO!, isotypes CR!, NY!, QCNE!, USF!). Fig. 7, 8

Stem minutely ferrugineous-puberulent when young, very sparsely puberulent to glabrescent at maturity, with milky látex (rarely yellow), sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 0.5-1 mm long. **Petioles** 1–2 cm; leaf blade  $13-23 \times 6.5-13.5$  cm, elliptic to broadly elliptic, apex obtuse and abruptly short-acuminate or apiculate, base obtuse to rounded, coriaceous to subcoriaceous, sometimes somewhat revolute, glabrous adaxially, inconspicuously papillate-puberulent to glabrous abaxially, secondary and tertiary veins conspicuously impressed on both surfaces. Inflorescence dichasial cyme, axillary, usually longer than the adjacent leaves, many-flowered, the flowers laxly disposed or somewhat clustered, minutely and densely to sparsely ferrugineous-puberulent, peduncle 6.5–22 cm, pedicels (1–)1.7– 2.8 cm long, floral bracts  $1-2 \times 0.5-1$  mm, linear, scarious, minute, green. Sepals  $(10-)12-19 \times (3-)12-19 \times (3$ )4–6 mm, connate at the base for 1/3–1/2 of their length, forming a campanulate-cup, coriaceous to subcoriaceous, narrowly ovate to narrowly ovate-elliptic, the apices acuminate to shortly acuminate, not reflexed, minutely and densely ferrugineous-puberulent, rarely glabrescent, foliaceous, drying with a more or less uniform color, the veins usually not impressed, colleters 1–1.5 mm long, entire, subentire to minutely erose at the apex. Corolla salverform, the lobes yellow, with purple or red lines, glabrous outside, tube  $14-15 \times 3-4$  mm, straight, free corona lobes 1.5-2 mm long, included or the apices barely exserted, their height conspicuously surpassed by that of the anther apices, annular corona entire, thickened, corolla lobes 9–11 × 7–9 mm, obliquely obovate. Stamens inserted near the corolla mouth, anthers 4.8–5.2 mm, dorsally glabrous, the apices conspicuously exserted. Ovary 1-1.5 mm tall, glabrous, style-head 1-1.1 mm, nectary 1.5-2.4 mm, conspicuously surpassing the ovary, usually deeply and irregularly 5-lobed, each lobe somewhat erose or lacerated. **Follicles**  $18-27.5 \times 0.8-1.2$  cm, continuous to inconspicuously articulated, free, the tips divergent, glabrescent, sparsely lenticellate, somewhat woody when old; seeds 16–19 mm, coma 3.5–4.8 cm, dark brown.

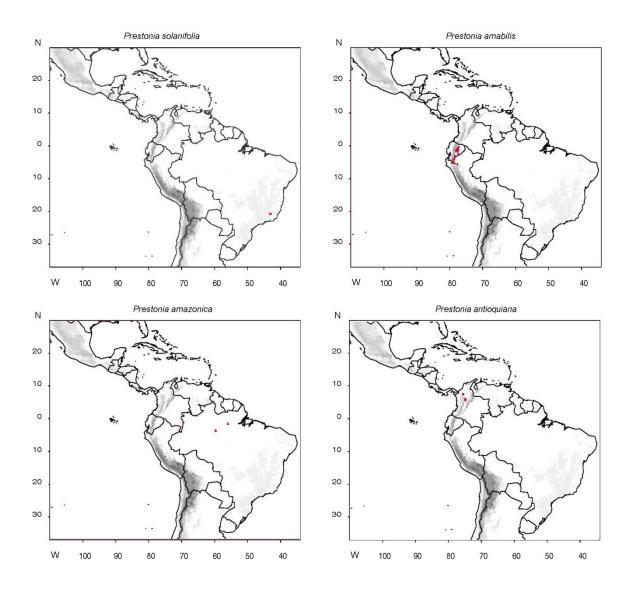


Fig. 7 Distribution maps of Prestonia solanifolia, P. amabilis, P. amazônica and P. antioquiana

**Distribution and habitat:**—Premontane, montane, and cloud forest (including disturbed areas) from (400)1100 to 1800 m in southern and southeastern Ecuador and northern of Peru. This species has also been reported in tropical wet forest, but seems to be more common in montane forest

**Phenology**:—Flowering specimens have been collected from February through December, fruiting specimens have been collected in February, March, and November.

Conservation Assessment:—Vulnerable (VU) (IUCN 2001).

Local name:—Guaguap (Morona-Santiago, Morona, Ecuador).

**Taxonomic notes:**—*Prestonia amabilis* shows some resemblance to *P. haughtii* by having sepals connate basally, forming a cup, but differs by its conspicuously branched

inflorescence, sepals minutely ferrugineous—puberulent on the abaxial surface (vs. glabrous or glabrescent), and anthers with the apices conspicuously exserted (vs. included). *Prestonia amabilis* resembles *P. annularis*, but differs by its larger inflorescence, sepals connate basally (vs. free) and ferrugineous—puberulent on the abaxial surface (vs. glabrous, glabrescent, or very sparsely puberulent), and thicker follicles.

Additional specimens examined:—ECUADOR. Morona-Santiago: Taisha, 8 February 1962, Cazalet & Pennington 7729 (B); cuenca Río Coango, entre Río Tsuirim y Numpatkain, 27 October 1999, Fuentes et al. 1232 (MO, QCNE); Limón Indanza, cuenca del Río Coangos, Río Tsuirin, October 1999, Ronquillo et al. 1018 (MO); Morona, cordillera del Cutucú, parte alta del Río Shacham Entza, 14 April 2002, Suin et al. 1628 (MO). Napo: carretera entre Coca y Loreto, cerca a Río Pinguillo, 20 October 1988, Cerón et al. 5331 (MO, USF); Loreto, faldas volcán Sumaco, O de Ávila Viejo, 13 February 1996, Freire & Cerda 18 (MO, QCNE); faldas del Volcán Sumaco, O de Ávila Viejo, 15 February 1996, Freire & Cerda 114 (QCNE); Shinguipino, entre ríos Napo y Tena, 30 September 1960, Grubb et al. 1688 (K, NY); Tena, carretera Campococha-Chontapunta, 23 August 1997, Núñez & Tapuy 616 (MO, QCNE); NNO de Coca, Río Huashito, 27 October 1982, Pennington 10637 (K, NY, QCA, QCNE, U). Napo-Pastaza: Veracruz, 18 February 1956, Asplund 19472 (S); Mera, 25 March 1940, Lugo 112 (S). Pastaza: 18 km E Puyo, finca Ursula, near house, 9 January 2016, Cornejo & Kai 8760 (GUAY, NY); Arajuno, parroquia Villano, 3-7 July 1998, Freire & Innunda 3189 (MO, QCNE); Arajuno, campamentos 11-12, 15-20 September 1998, Freire et al. 3433 (MO, Z); Puyo-Arajuno road, 1-5 km al SO de Diez de Agosto, 4 March 1980, Harling & Andersson 16860 (GB, USF); 1-4 km al N de Puyopungu, 24 September 1976, Lugo 4991 (USF); 3-4 km al E de Puyopungu, 28 September 1976, Lugo 5017 (USF); Río Putuime, in the vicinity of Puyopungu, 4 October 1976, Lugo 5118 (GB, USF); sendero Puyopungu-Pomona, ca. 3 km E de Puyopungu, 6 October 1976, Lugo 5128 (USF); Puyo, Santa

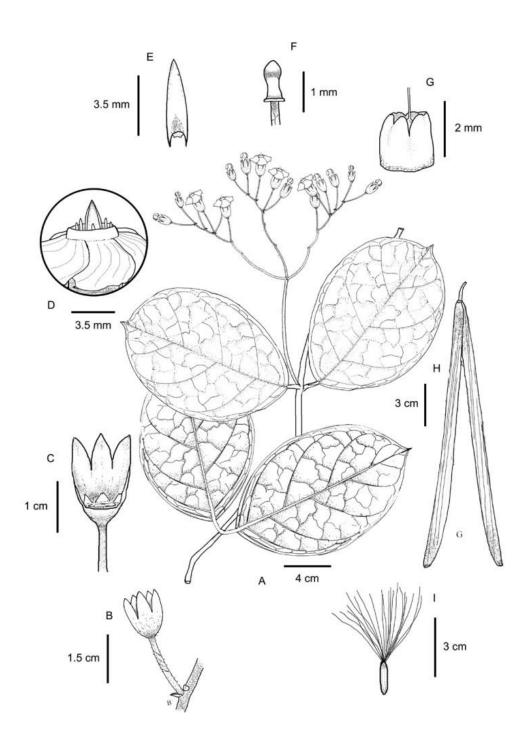


Fig. 8 *Prestonia amabilis* (A-G from *Palacios 10102*, USF; H-I from *Brehm s.n.*, INB). A. Stem with inflorescence. B. Calyx, pedicel, and floral bract. C. Calyx with two sepals removed, showing the colleters at the base of the sepals. D. Corolla mouth, showing the tips of the anthers and free coronal lobes. E. Anther, dorsal view. F. Style-head. G. Nectary. H. Follicles. I. Seed.

Cecilia, Villano, 1 May 1992, *Palacios 10102* (MO, QCNE, USF); Cantón Puyo, Los Vencedores, km 32 carretera Puyo-Macas, Estación Experimental ESPOCH, 8 June 1996, *Soejarto et al. 9651* (F); Pozo Villano, 3 December 1991, *Tipaz et al. 426* (MO, QCNE). Zamora-Chinchipe: Parque Nacional Podocarpus, 4 km S de Zamora, 30 November 2000, *Brehm s.n.* (CR); Nangaritza, Miazi, Río Nangaritza, 28 July 1993, *Gentry 80568* (MO); El Pangui, Cordillera del Cóndor, cuenca del Río Wawaime, tributario del Río Quimi, 24 October 2006, *van der Werff et al. 21669* (CR, MO).

PERÚ. Amazonas: Bagua, Aramango, entre Nueva Esperanza y la Catarata, 17 December 2001, *Vásquez et al.* 27422 (NY, USM). Cajamarca: San José de Lourdes, base del Cerro Picorana, 25 August 1999, *Díaz et al.* 10726 (CR, MO); Jaén, Santa Rosa, 3 km al N de Santa Rosa, 24 March 2006, *Ortiz & Mateo 1199* (CR, MO); San Ignacio, Tabaconas, caserío La Bermeja, entre camino Bermeja-Huanquillo, 19 November 1997, *Rodríguez & Cruz 2033* (CR, MO). San Martín: Rioja, Pardo Miguel, Aguas Verdes, 19 June 1997, *Sánchez & Dillon 8948* (CPUN, USF).

Prestonia amazonica (Bentham ex Müller Argoviensis) J. F. Macbride (1931: 34). Haemadictyon amazonicum Bentham ex Müller Argoviensis (1860: 166). Type:—BRAZIL. Pará: Trombetas, lago Quiriquiry, December 1849, R. Spruce 239 (holotype M!, isotypes CGE!, FI-W!, K!, W! [photo F neg. 31797!]). Fig. 7, 9.

Stem inconspicuously puberulent when young, glabrous to glabrescent at maturity, with milky latex, the lenticels more or less common and slightly suberose, intrapetiolar colleters minute, 0.5-1.3 mm long. **Petioles** 0.4-1.1 cm; leaf blade  $7-22.5 \times (3-)4.5-11.5$  cm, elliptic, apex shortacuminate, base broadly cuneate, obtuse to rounded, coriaceous to subcoriaceous, sometimes slightly revolute, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a monochasial cyme, rarely branched and with just an very short basal branch, axillary, usually longer than the adjacent leaves, many-flowered, the flowers somewhat clustered, densely and minutely puberulent, peduncle 5–7.5 cm, pedicels (0.7–)1.1–2.1 cm long, floral bracts  $1-3 \times 1-1.5$  mm, linear, scarious, minute, green. **Sepals**  $5-8 \times 2-3$  mm, free, coriaceous to subcoriaceous, narrowly ovate, the apices acuminate, not reflexed, very sparsely puberulent to glabrescent, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins slightly impressed or not impressed, colleters less than 1 mm long, subentire to irregularly lacerate at the apex. Corolla salverform, yellow cream, glabrous outside, tube  $13-15 \times 3-4$  mm, spirally contorted around the attachment of the stamens, free corona lobes 2–4 mm long, slightly exserted or barely included, their height equaling or slightly shorter that of the anther apices, annular corona thickened, corolla lobes  $7-9 \times 5-6$  mm, obliquely obovate. **Stamens** inserted near the corolla

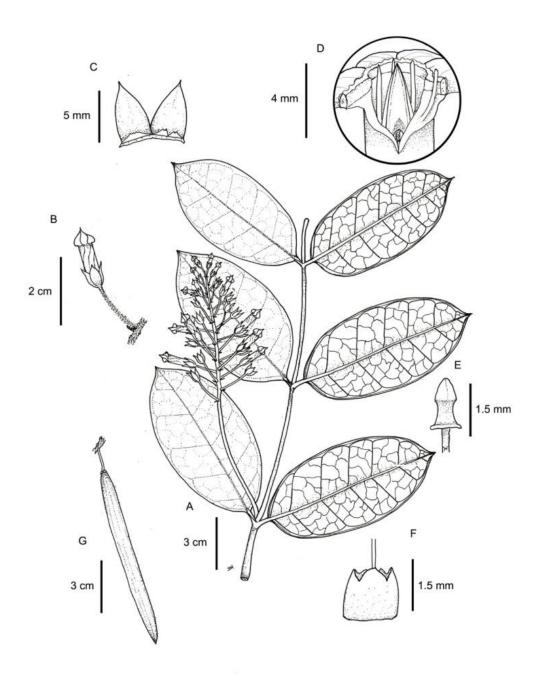


Fig. 9 *Prestonia amazonica* (A-F from *Spruce 239*, CGE; G from *Tokarnia 1167*, INPA). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of two sepals, showing the colleters. D. Corolla tube partially open, showing the annular corona, free coronal lobes, and the anthers. E. Style-head. F. Nectary. G. Follicle.

mouth, anthers 4.5–5 mm, dorsally glabrous, the apices slightly exserted or barely included. **Ovary** 1–1.5 mm tall, glabrous to glabrescent, style-head 1.2–1.5 mm, nectary 1.1–1.7 mm, equaling or surpassing the ovary, slightly 5-lobed, each lobe entire to subentire. **Follicles**  $8.5–11.5 \times 0.7–0.8$  cm, continuous, free, the tips divergent, glabrous, without lenticels, somewhat woody when old; seeds unknown.

**Distribution and habitat:**—Seasonal blackwater-flooded forest (igapó) and tropical wet forest in the states of Amazonas and Para, Brazil, 0 to 300 m.

**Phenology**:—*Prestonia amazonica* has been collected with flowers in November, December, and April and with fruits in June and July.

**Conservation Assessment**:—Critically endangered (CR)

**Taxonomic notes:**—*Prestonia amazonica* can be confused with *P. denticulata*, a species endemic to the state of Rio de Janeiro, Brazil. Both species have in common branchlets and leaves usually minutely puberulent when young, unbranched inflorescences, and sepals usually less than 8 mm long. *Prestonia amazonica* is distinguished by the following combination of characters: corolla tube twisted around stamens (vs. straight and not twisted), free corona lobe apices below those of the anthers in the corolla tube (vs. slightly surpassing the apices of the anthers), and follicles continuous (vs. moniliform) and 7-8 mm diam. (vs. 2-3 mm).

Additional specimens examined:—BRAZIL. Amazonas: Manaus, Igarapé do Franco, 21 December 1955, *Chagas s.n.* (INPA # 3158, MG, NY); frontera de Brasil y Colombia, Novo Japurá, Vila Bittencourt, Río Apapóris, igarapé Preguiça, 21 November 1982, *Cid & Lima 3784* (CR, INPA, MG, NY, USF); cerca de Manaus, 21 April 1905, *Labray 81* (P); Autazes, Fazenda Taboquinha, 25 July 1976, *Tokarnia 1167* (CR, INPA). Pará: Trombetas, lago Quiriquiry, December 1849, *Spruce 535* (CGE, K [2 sheets], P [2 sheets]).

*Prestonia antioquiana* J. F. Morales & Liede (2016: 207). Type:—COLOMBIA. Antioquia: San Luis, Río Claro, 26 December 1983, *A. Cogollo 1133* (holotype JAUM!, isotypes COL!, HUA!, MO!). **Fig. 7, 10.** 

**Stem** inconspicuously puberulent when young, glabrous to glabrescent at maturity, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters usually inconspicuos, less than 1.2 mm long. **Petioles** 1.5-3(-3.5) cm, conspicuously and irregularly verrucose; leaf blade  $19-35 \times 7-14(-21)$  cm, broadly elliptic, elliptic to obovate-elliptic, apex obtuse and shortly acute, base obtuse, coriaceous to subcoriaceous, sometimes slightly revolute, glabrous; secondary and tertiary veins impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, densely and minutely puberulent,

peduncle 6.6–14.2 cm, pedicels 0.8–2 cm long, floral bracts  $1.5-2 \times 0.5-1.5$  mm, linear, scarious, minute, green. **Sepals**  $11-16 \times 4-6.5$  mm, free, coriaceous to subcoriaceous, narrowly ovate to narrowly ovate-elliptic, the apices acute to very shortly acuminate, not reflexed, very sparsely and inconspicuously puberulent, foliaceous, drying with a more or less uniform color, the veins inconspicuous, not impressed, colleters ca. 1 mm long, minutely and irregularly erose or lacerate at the apex. **Corolla** salverform, cream to greenish cream, usually glabrous outside, rarely the lobes very sparsely and inconspicuously puberulent outside, tube  $17-18 \times 4-5$  mm, straight, free corona lobes 3-3.5 mm long, the apices exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire, thickened, corolla lobes  $17-21 \times 7-9$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5.1-5.8(-6.1) mm, dorsally glabrous, the apices slightly exserted. **Ovary** 1-1.5 mm tall, glabrous, style-head 1.2-1.5 mm, nectary 1-1.7 mm, equaling or barely surpassing the ovary, divided into 5 nectaries, each one lacerate to subentire. **Follicles**  $14-28 \times 0.9-1.1$  cm, continuous, free, but usually united at the tips (at least when young), wingless but with 3-4 longitudinal ribs, glabrous or glabrescent, without lenticels, woody when old, conspicuously verrucose; seeds 15-17 mm, coma 2.8-3.4 cm, tan to tannish cream.

**Distribution and habitat:**—Endemic to the Department of Antioquia, Colombia, in tropical wet forest, and disturbed areas, at 150–800 m of elevation.

**Phenology**:—*Prestonia antioquiana* has been collected with flowers from November through January and with fruits in May, September, and December.

**Conservation Assessment**:—Endangered (EN) (IUCN 2001).

**Taxonomic notes**:—*Prestonia antioquiana* resembles *P. trifida*, but can be differentiated by its verrucose petioles, longer corolla lobes (17–21 mm vs. 7–15 mm), follicles with 3-4 longitudinal ribs, and shorter seeds (15–17 mm vs.18–23 mm).

Additional specimens examined:—COLOMBIA. Antioquia: NE de Cáceres, Troncal de La Paz, 6 November 1987, *Callejas et al. 5406* (CR, HUA, MO, NY, US, WAG); El Prodigio, 23 September 1990, *Cárdenas et al. 2938* (COL, JAUM, MEDEL, MO); entre Río Claro y Río Samaná, San Luis, 14 January 1983, *Cogollo & Brand 390* (JAUM, MO); San Luis, vereda Las Confusas, 20 May 1990, *Cogollo et al. 4503* (COL, JAUM, MO); Puente Nare, Vereda Caño Seco, Hacienda La Brasilia, Quebrada La Soná, 28 September 2001, *David et al. 29* (HUA); San Luis, Quebrada La Cristalina, 4 December 1986, *Ramírez & Cárdenas 233* (CR, HUA, JAUM, MO); Río Claro, carretera Antioquia-El Cairo, 18 September 1982, *Renteria et al. 2771* (JAUM, MO).

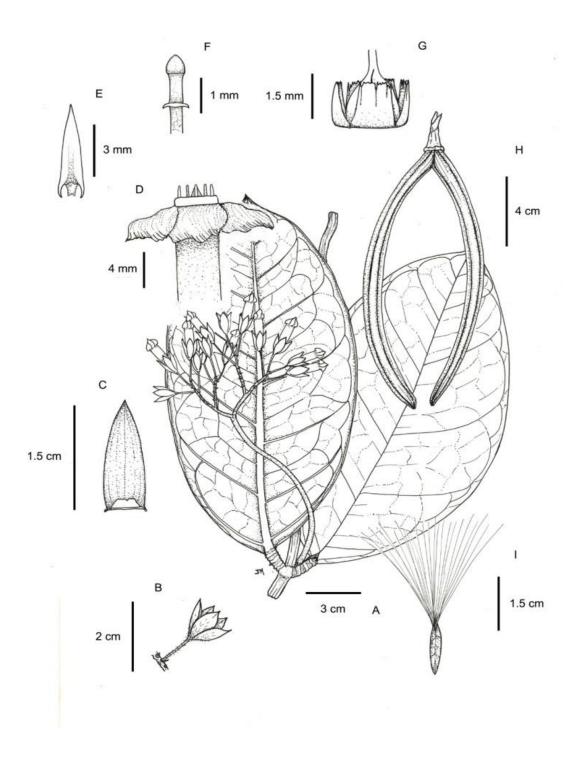


Fig. 10 Prestonia antioquiana (A-G from Cogollo 1133, HUA; H-I from Cárdenas et al. 2938, MEDEL). A. Stem with inflorescence. B. Calyx, pedicel, and bract. C. Adaxial view of one sepal, showing the colleter at the base. D. Upper part of the corolla tube, showing the tips of the anthers, free coronal lobes, and annular corona. E. Anther, dorsal view. F. Style-head. G. Nectaries and ovary. H. Follicles. I. Seed.

- Prestonia denticulata (Vellozo) Woodson (1936: 328). Echites denticulatus Vellozo (1825: 110).
  Haemadictyon macroneuron Müller Argoviensis (1860: 169), nom. illeg. Haemadictyon denticulatum (Vellozo) Miers (1878: 257). Type:—BRAZIL. Rio de Janeiro. Without data, Fl. Flumin., Icon 3: pl. 30. 1827 (1831) [lectotype designated by Morales (2007)]. Fig. 11, 12
- Echites suberosus Vellozo (1825: 111). Type:—BRAZIL. Without data, Fl. Flumin., Icon. 3: pl. 34. 1827 (1831) [lectotype designated by Morales (2007b)].
- Haemadictyon gaudichaudii Candolle (1844 : 426). Prestonia gaudichaudii (A. DC.) K. Schumann (1895: 188). Type:—BRAZIL. Rio de Janeiro: near Rio de Janeiro, 1834, C. Gaudichaud 533 (lectotype G-DC! designated by Morales (2007b), isolectotypes B [destroyed, photo F neg. 4544!], FI-W!, P!, US!).
- Haemadictyon ovatum Miers (1878: 258). Type:—BRAZIL. Rio de Janeiro: Monte Corcovado, s.d., *J. Miers* 4628 (lectotype BM!, designated by Morales (2007b).

Stem inconspicuously puberulent when young, glabrescent at maturity, color of latex unknown, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 0.5–1 mm long. **Petioles** 0.2-0.6(-1) cm; leaf blade  $5-12(-13.5) \times 2.2-5$  cm, elliptic to narrowly obovate, apex short-acuminate, base obtuse to rounded, coriaceous to subcoriaceous, glabrous adaxially, minutely puberulent along the midrib to glabrous abaxially, secondary and tertiary veins conspicuously impressed on both surfaces. Inflorescence a monochasial cyme, axillary, equaling or longer than the adjacent leaves, usually many-flowered, the flowers somewhat clustered, minutely puberulent, peduncle 2–3.2 cm, pedicels (0.4-)0.7-1.4 cm long, floral bracts  $1-3 \times 1-1.5$  mm, linear, scarious, minute, green. Sepals  $4-6 \times 2-3$  mm, free, coriaceous to subcoriaceous, narrowly ovate, narrowly elliptic to very narrowly obovate, the apices acute to shortly acuminate, not reflexed, minutely and very sparsely puberulent, sometimes glabrescent, scarious, drying with a more or less uniform color, the veins not impressed, colleters ca. 1 mm long, entire to minutely erose at the apex. Corolla salverform, cream, glabrous outside (but the annular corona minutely papillate-puberulent), tube 9–  $13 \times 3-4$  mm, straight, free corona lobes 2.5–3.5 mm long, the apices exserted, their height slightly surpassing that of the anther apices, annular corona entire, thickened, corolla lobes  $5-7 \times 5-6$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 3.9–5.5 mm, dorsally glabrous, the apices exserted. Ovary 1.5–2 mm tall, glabrous, style-head 1–1.3 mm, nectary 1.5–2.1 mm, equaling or barely surpassing the ovary, 5-lobed, sometimes completely divided into 5 lobes, each lobe subentire. Follicles 18–60 × 0.2–0.3 cm, conspicuously moniliform, free, but sometimes united at the tips when young, glabrous to minutely puberulent, without lenticels, slightly woody when old; seeds 12–14 mm, coma 1.5–2.2 cm, tannish cream.

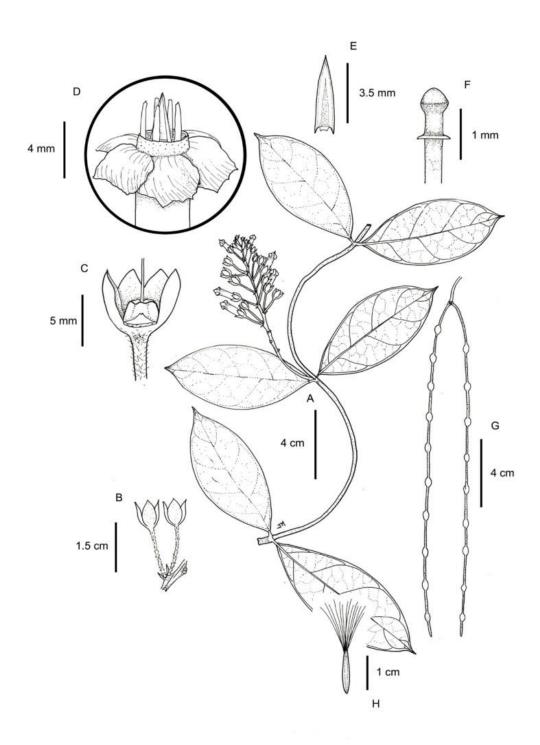


Fig. 11 *Prestonia denticulata* (A-F from *Constantino 7787*, RB; G-H from *Evandro & Knowles 533*, INPA). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Calyx with a sepal removed, showing the colleter and nectary. D. Corolla mouth, showing the apices of the anthers and the free coronal lobes. E. Anther, dorsal view. F. Style-head. G. Follicles. H. Seed.

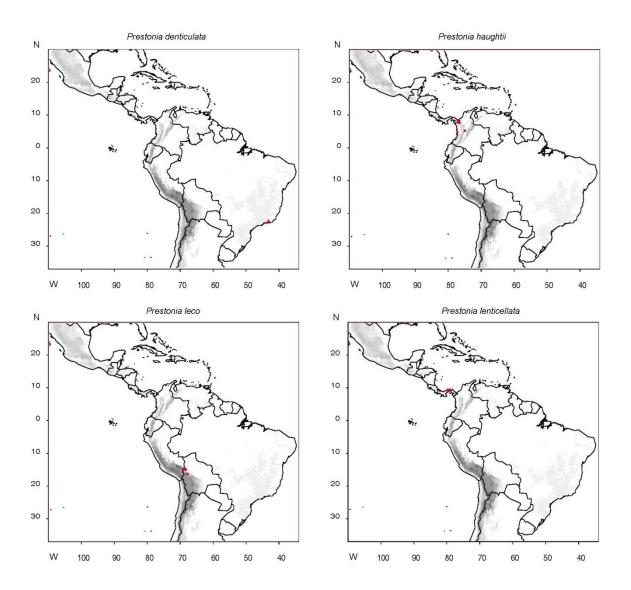


Fig. 12 Distribution maps of Prestonia denticulata, , P. haughtii, P. leco and P. lenticellata

**Distribution and habitat**:—Endemic to tropical wet forest (Mata Atlantica) and related disturbed areas in the Rio de Janeiro state, Brazil, from 100–400 m.

**Phenology**:—*Prestonia denticulata* has been collected with flowers in February, March, and May, fruiting specimens from February through April and in June.

## **Conservation Assessment**:—Critically endangered (CR)

**Taxonomic notes:**—*Prestonia denticulata* is characterized by its unbranched inflorescence, pedicels minutely puberulent, sepals 4–6 mm long, corolla tube glabrous outside, free corona lobes with the apices exserted, and follicles conspicuously moniliform. Although moniliform follicles are somewhat common in other genera of Mesechiteae (e.g., *Mandevilla*,

*Mesechites*), it is a rare character in *Prestonia* and other members of Echiteae. Moniliform follicles are otherwise known only from *P. leco*, endemic to Bolivia.

Prestonia denticulata shows an overall resemblance to *P. amazonica* and *P. vaupesana*, which also have an unbranched inflorescence and small sepals, but is readily identified by its moniliform follicles. Furthermore, *P. denticulata* is restricted for southeastern Brazil (state of Rio de Janeiro), whereas the other two species are founf only in the Amazonian basin. This species was reported to the state of Para by Rio & Kinoshita (2005), based on *Spruce 1882* (NY). However, this collection is the type of *P. lindleyana*, a different species. For more detailed discussion see Morales (2007).

Additional specimens examined:—BRAZIL. Rio de Janeiro: Santa Teresa, 11 February 1815, Bowie & Cunningham s.n. (BM, MO); exact locality lacking, 27 January 1935, Brade 14162 (RB, S); Recreio dos Banderaintes, Prainha, subida para topo do morro da Bôa Vista, 4 May 2004, Braga et al. 7365 (CR, MBM, NY, RB); São Domingo, s.d., Burchell 2849 (K); without exact locality, s.d., Boog s.n. (K); without exact locality, s.d., Comitis 21 (C); Jardín Botânico do Rio de Janeiro, 13 February 1916, Constantino 7787 (CR, RB, US); without exact locality, June 1832, Drake s.n. (P); Rio de Janeiro, Jardim Botânico, 13 February 1976, Fontella et al. 522 (CR, MO, RB); without exact locality, 1829, Forrest s.n. (CGE); cerca a Rio de Janeiro, 1834, Gaudichaud 532 (B [destroyed], FI-W, G-DC, P [2 sheets, photo F neg. 4544], US); Rio de Janeiro, 5 May 1879, Glaziou 374 (P); Rio de Janeiro, s.d., Glaziou 3728 (BR); Praia Grande, 18 March 1871, Glaziou 4881 (C, K, P); Lagoa Rodrigo de Freitas, 2 February 1881, Glaziou 12954 (K, P [3 sheets]); Petrópolis, March 1944, Góes 426 (RB); Barra do Pirahy, 13 April 1926, Hoehne & Gehrt 17319 (NY); without exact locality, 1835, *Hooker s.n.* (K); Jardin Botânico do Rio de Janeiro, 8 April 1999, Marquete et al. 2973 (RB), 8 January 2003, Marquete 3450 (RB); without exact locality, s.d., Mikan s.n. (NY, W [photo F neg. 31798]); Jacarepaguá, Serra do Pau da Fome, Sitio da Boiuna. 14 January 1962, Pabst 6800 (B); Jardim Botânico, 15 July 1958, Pereira 4015 (MO, RB), 5 January 1959, Pereira 4234 (MO, RB); Guanabara, Rio de Janeiro, 20 March 1942, Pereira 79 (B, HB); Rio de Janeiro, 1835, Raben s.n. (C [2 sheets]); without exact locality, s.d., Regnell s.n. (CGE); without exact locality, s.d., Richard s.n. (P); without exact locality, s.d., Riedel s.n. (G-DC, GH, LE, P, U, W); Rio de Janeiro, s.d., Riedel 589 (BR, C, P); Barra do Maricá, s.d., Souza s.n. (R); without exact locality, 1837, Tweedie 1266 (K [2 sheets]); Serra do Bica, February 1897, Ule 4285 (CR, HBG, R), 15 April 1897, Ule 4286 (HBG); without exact locality, 1843, Weddell 505 (P). Data lacking: s.d., Glaziou 3725 (C); s.d., Miers 1567 (BM); s.d., Motta s.n. (R).

Prestonia haughtii Woodson (1948: 235). Type:—COLOMBIA. Antioquia: Necoclí, 25 June 1946,O. Haught 4911 (holotype MO!, isotypes COL!, US!). Fig. 12, 13

Prestonia macrophylla Woodson (1948: 235). Type:—COLOMBIA. Antioquia: Río Turbo, boca de Quebrada Los Indios, 15 July 1946, O. Haught 4377 (holotype MO!, isotypes COL!, K!, US!).

Stem glabrous, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, ca. 1 mm long. **Petioles** 0.8-2 cm; leaf blade  $17-24(-30) \times 7-13$  cm, obovate, elliptic, or broadly elliptic, apex rounded and mucronulate to emarginate, base obtuse to broadly acute, coriaceous to subcoriaceous, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** usually a dichasial cyme, rarely a monochasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers laxly disposed to somewhat clustered, glabrous or glabrescent, peduncle 3–7.5(–10) cm, pedicels 1.1–2.2 cm long, floral bracts  $1-2 \times 0.5$ – 1 mm, linear, scarious, minute, green. **Sepals**  $7-10 \times 5-6$  mm, connate at the base for 1/3-1/2 of their length, forming a campanulate-cup, coriaceous to subcoriaceous, ovate to narrowly ovate, the apices shortly acuminate, not reflexed, glabrous to glabrescent, foliaceous, drying with a more or less uniform color, the veins usually inconspicuous, colleters 1–2 mm long, subentire to minutely erose at the apex. Corolla salverform, yellow, glabrous outside, tube  $15-21 \times 5-7$  mm, straight, free corona lobes 1-1.5 mm long, included, their height conspicuously surpassed by that of the anther apices, annular corona entire to inconspicuously and irregularly lobed, thickened, corolla lobes (10-)13-16(-25) × 6-8 mm, obliquely obovate. Stamens inserted near the corolla mouth, anthers 4.5-5.5(-6) mm, dorsally glabrous, included. Ovary ca. 1 mm tall, glabrous, style-head 1.2–1.6 mm, nectary 2–2.5 mm, conspicuously surpassing the ovary, variously 5-lobed, sometimes almost divided into 5 lobes, each lobe subentire to irregularly lacerate. Follicles  $32-40 \text{ cm} \times 1-1.5$ cm, continuous, free or connate longitudinally, glabrous, lenticels inconspicuous or not evident, woody when old, rugous; seeds unknown.

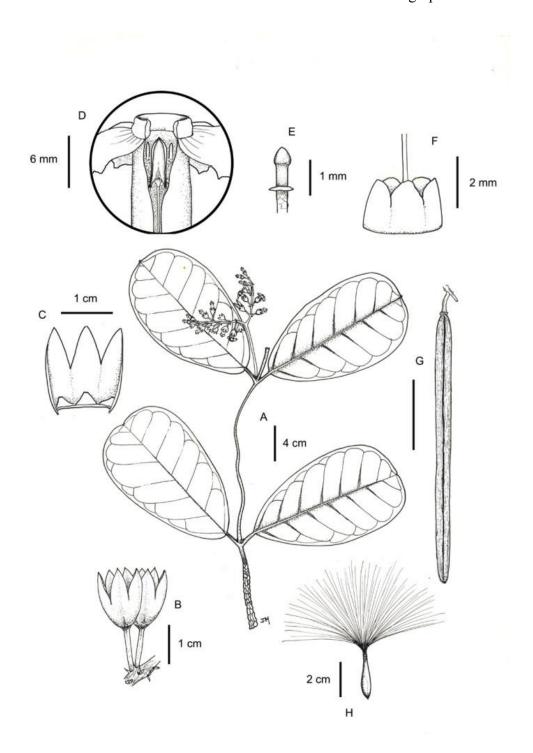


Fig. 13 *Prestonia haughtii* (*Callejas et al. 5008*, HUA). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of three sepals, showing the colleters at the base. D. Open corolla tube, showing the included anthers and free coronal lobes. E. Stylehead. F. Nectary. G. Follicles. H. Seed.

**Distribution and habitat**:—Endemic to Colombia, where it grows in tropical wet forest, moist forest, gallery forest, and disturbed areas, from 0 to 450 m.

**Phenology**:—*Prestonia haughtii* has been collected with flowers in January and from June through August and with fruits in January and August.

Conservation Assessment:—Endangered (EN) (IUCN 2001).

**Taxonomic notes:**— $Prestonia\ haughtii$  is very distinctive in the genus by its sepals, which are connate for 1/3-1/2 of their length, forming a conspicuous campanulate base. Others species with this feature include P. amabilis and P. rotundifolia, which can be separated easily by the characters given in the key.

Analysis of the types and the differences given by Woodson (1948) to distinguish *Prestonia haughtii* from *P. macrophylla* (larger leaves, shorter corolla tube, and larger nectary) revealed that the two are indistinguishable. Furthermore, size and shape of nectaries in the genus can be very variable in some species (Morales, 2004b) and recognition of two separate species based on this character alone is untenable.

Additional specimens examined:—COLOMBIA. Antioquia: Turbo, carretera Currulao-Nueva Antioquia, 11 km de Currulao, 3 August 1987, *Callejas et al. 5008* (COL, HUA, NY, WAG). Chocó: Turbo, carretera al Tapón del Darién, 28 January 1984, *Brand & Lozano 816* (COL, CR, JAUM, MO); cerca a Río León, O de Chirogodó, 18 March 1962, *Feddema 1951* (NY, S, US); Acandí, Unguia, 6 June 1976, *Forero et al. 1908* (COL); Río Baudo, E de Pizarro, cerca a La Porquera, 11 June 1967, *Fuchs et al. 21775* (COL); vereda Bohios, carretera a los Bajos, 6 August 1985, *Renteria & Cárdenas 4371* (JAUM); Chigorodó, vereda Malagón, El Cocuelo, 11 January 1986, *Renteria et al. 4568* (JAUM, MO). Tolima: Mariquita, 1851–1852, *Triana 1958* (P).

Prestonia leco A. Fuentes & J.F. Morales (2010: 278) Type:—BOLIVIA. La Paz: Franz Tamayo, Santo Domingo, cabeceras del arroyo Tintaya, 25 October 2006, A. Fuentes, M. Cornejo, E. Ticona & S. Sompero 11225 (holotype LPB!; isotypes BOLV!, CR!, LPB!, MO!, NY!, USZ!). Fig. 12, 14.

**Stem** very minutely puberulent when young, glabrescent at maturity, latex white, sparsely lenticellate, these not subcrose, intrapetiolar colleters minute, 0.7-1.3 mm long. **Petioles** 0.4-0.6(-1.2) cm; leaf blade  $7-15.2(-18) \times 2.8-7.7$  cm, elliptic to obovate, apex acuminate, acute to rounded, base acute, rarely obtuse, coriaceous to subcoriaceous, slightly revolute, sparsely and inconspicuously puberulent adaxially, glabrescent at maturity, minutely and sparsely puberulent abaxially, secondary veins conspicuously impressed on both surfaces, the tertiary veins somewhat inconspicuous adaxially. **Inflorescence** a dichasial cyme, axillary to subterminal, shorter or slightly

longer than the adjacent leaves, usually many-flowered, the flowers somewhat clustered, minutely puberulent, peduncle 1.5–7(–10.5) cm, pedicels 0.8–2 cm long, floral bracts 2.5–6  $\times$  0.8–1.7 mm, narrowly ovate to narrowly ovate-elliptic, scarious, minute, green. Sepals  $11-16.5 \times 4-7$  mm, usually free, coriaceous to subcoriaceous, elliptic to ovate-elliptic, the apices acute, not reflexed, minutely and very sparsely puberulent, sometimes glabrescent, foliaceous, drying with a more or less uniform color, the veins not impressed, colleters up to 3 mm long, entire to minutely erose at the apex. Corolla salverform, yellow, the annular corona pink, the base of the lobes tinged with red, glabrous outside, tube  $18-22 \times 4-6$  mm, somewhat inflated at the base and around the position of the stamens, free corona lobes ca. 1 mm long, included, their height conspicuously surpassed by that of the anther apices, annular corona slightly 5-lobed, thickened, corolla lobes  $19-22 \times 8-11$ mm, obliquely obovate to obliquely elliptic-obovate. Stamens inserted near the corolla mouth, anthers 5-7 mm, dorsally glabrous, deeply included. Ovary 2.1-2.5 mm tall, glabrous, glabrous, style-head 1.3-1.5 mm, nectary 2.1-2.6 mm, equaling or barely surpassing the ovary, deeply and variously 5-lobed, each lobe irregularly lacerate. Follicles  $18-38 \times 1.2-1.6$  cm, conspicuously moniliform, free, but sometimes united at the tips (at least when young), minutely puberulent when young, glabrescent at maturity, conspicuously lenticellate, somewhat woody when old, slightly verrucose; seeds 14–18 mm, coma 2–4.5 cm, yellowish brown.

**Distribution and habitat**:—Endemic to humid montane forest or moist forest (Yunga forest) in La Paz department, Bolivia, growing mainly in primary forest, from 1400–2000 m.

**Phenology**:—*Prestonia leco* has been collected with flowers in October and November and fruits in June and October.

**Conservation Assessment:**—Vulnerable (VU), the area of occurrence of less than 20,000 km2 and fewer than 10 known localities.

**Local name**:—Chillima (La Paz, Bolivia).

**Taxonomic notes:**—*Prestonia leco* was collected for first time more than 30 years ago but mature flowers were only collected recently. Due to the lack of herbarium specimens with mature flowers or fruits, the first collections were identified as *P. annularis*. Flowering plants and mature flowers are difficult to collect since this species grows in primary forest and blooms only in larger trees from the canopy, once young shoots reach full sun.

Prestonia leco resembles P. denticulata, but differs by its branched inflorescence, longer corolla tube, and thicker follicles. In addition, the two species have different

geographical distributions. For a further discussion of the relationships with some other species, see Fuentes & Morales (2010).

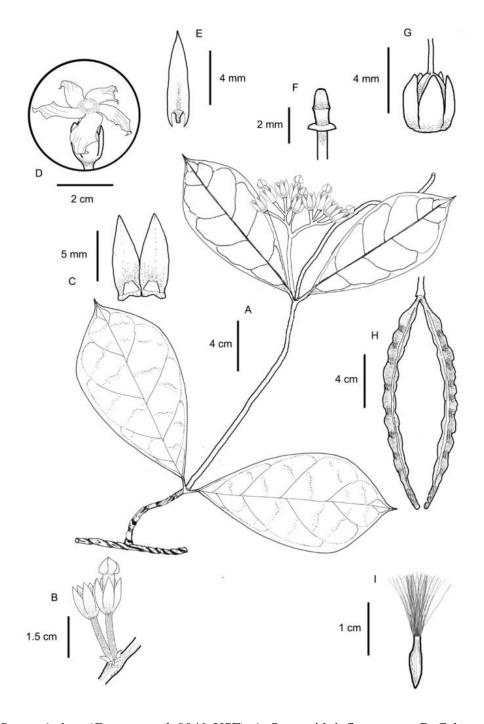


Fig. 14 *Prestonia leco* (*Fuentes et al. 9046*, USF). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of two sepals. D. Corolla and lobes. E. Anther, dorsal view. F. Style-head. G. Nectary and ovary. H. Follicles. I. Seed.

Additional specimens examined:—BOLIVIA. La Paz: Sud Yungas, Chulumani, entrando a Apa Apa, 27 October 2006, *Beck et al. 29543* (LPB); Franz Tamayo, Área Natural de Manejo Integrado Apolobamba, comunidad Mojos, Fuertecillo, entre la senda Keara-Sumpulo, 3 mar 2012, *Boza et al. 2686* (LPB); Parque Nacional Madidi, Mojos, campamento Fuertecillo, sobre la senda a Queara, 25 April 2007, *Cayola et al. 2596* (LPB, MO); Franz Tamayo, Parque Nacional Madidi, Fuertecillo, entre Tokoake y Carjata, 29 June 2005, *Fuentes et al. 9046* (CR, LPB, MO, USF); Franz Tamayo, Santo Domingo, Tintaya, 16 October 2006, *Fuentes et al. 11052* (LPB, MO, USF); Área natural de manejo integrado Madidi, entre Moima y Pata, 20 August 2008, *Fuentes et al. 13303* (LPB); Franz Tamayo, Parque Nacional Madidi, sector Chamala, por el antiguo camino Pelechuco-Apolo, 20 June 1999, *Fuentes et al. 14612* (MO); Franz Tamayo, Calabatea, 44 km al SO de Apolo, ca. 10 km al S de Correo, 4 June 1990, *Gentry & Beck 70925* (LPB, MO); Nor Yungas, Senda de Fuertecillo a Tokuaque, 11 November 2001, *Orellana & Quispe 2004* (LPB); Nor Yungas, entre Yolosa y Río Huarinilla, 12 November 1982, *Solomon 8760* (CR, INPA, LPB, MO, USF, WAG); Nor Yungas, SO de Yolosa, carretera a Chuspidata, 23 March 1984, *Solomon et al. 12077* (LPB, MO).

Prestonia lenticellata A.H. Gentry (1974: 896). Type:—PANAMA. Panamá: El Llano-Cartí road, 16 km N of El Llano, 23 March 1973, R. Dressler 4303 (holotype MO!, isotypes F! [photo F neg. 56495!], MO!, PMA!, TEX-LL!). Fig. 12, 15.

**Stem** densely and minutely puberulent when young, usually conspicuously glabrescent at maturity, with many lenticels, the lenticels conspicuously suberose at maturity, with milky latex, intrapetiolar colleters usually inconspicuos, 1-1.5 mm long. **Petioles** 0.5-1.2 cm; leaf blade  $(8-)11-24 \times (4-)5.5-16(-17.9)$  cm, elliptic to broadly elliptic, mucronate to obtuse, base rounded or slightly subcordate, coriaceous to subcoriaceous, somewhat revolute, usually conspicuously bullate, glabrescent adaxially, sparsely puberulent along the midrib abaxially, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a monochasial cyme, rarely a dichasial cyme (but with just one basal branching), axillary, shorter than the adjacent leaves, many-flowered, the flowers more or less clustered, minutely puberulent, peduncle 4.5-9.7 cm, pedicels 0.7-3.2 cm long, floral bracts  $2-8 \times 1-1.5$  mm, linear, scarious and inconspicuous, green. **Sepals**  $10-16 \times 4-5$  mm, free, coriaceous to subcoriaceous, narrowly ovate, the apices acute to acuminate, not reflexed, glabrous or glabrescent, foliaceous, drying with a more or less uniform color, the veins usually inconspicuous, colleters 2-2.5 mm long, entire, subentire, to variously lacerate at the apex. **Corolla** salverform, yellowish green, minutely and densely to sparsely puberulent outside, tube  $13-18 \times 3.3-5$  mm, straight, free corona lobes 3.5-4.5 mm long, the apices conspicuously exserted, their

height conspicuously surpassing that of the anther apices, annular corona entire, thickened, corolla lobes  $11-14 \times 6-8$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 4–5 mm, glabrous, glabrescent to minutely puberulent dorsally, included or the apices barely exserted. **Ovary** 1.5–2 mm tall, minutely puberulent, rarely glabrescent, style-head 1.8–2.1 mm, nectary 1.5–2 mm, equaling the ovary, moderately to deeply 5-lobed, each lobe entire to subentire. **Follicles** 21–35  $\times$  0.5–1 cm, continuous, free, but usually united at the tips (at least when young), glabrous, conspicuously lenticellate, somewhat woody when old; seeds unknown.

**Distribution and habitat:**—Endemic to tropical wet forest, premontane wet forest, cloud forest, and related secondary vegetation, in central Panama, from 0–500 m.

**Phenology**:—*Prestonia lenticellata* has been collected with flowers from February through October and with fruits in February through April.

Conservation Assessment:—Endangered (EN) (IUCN 2001).

**Taxonomic notes:**—*Prestonia lenticellata* is characterized by its densely lenticellate stems, with conspicuously suberose lenticels, coriaceous to subcoriaceous leaf blades, scarcely branched inflorescences, scarious floral bracts, corolla tube puberulent outside, and free corona lobe with the apices conspicuously exserted. This species shows an overall resemblance to *P. antioquiana*, *P. portobellensis*, and *P. trifida*, having in common the structure of the inflorescence, scarious floral bracts, and free corona lobe apices exserted, but differs by the conspicuous suberose lenticels, bullate leaf blades, and minutely puberulent corolla tube.

Additional specimens examined:—PANAMÁ. Colón: Santa Rita, 3 April 2013, Acevedo-Rodríguez et al. 15273 (PMA); fila Santa Rita, 1 March 1971, Croat 13876 (MO, PMA); Santa Rita lumber road, ca. 15 km E of Colón 5 October 1969, Dressler & Lewis 3715 (F, GH, MO, PMA); Santa Rita, 18 March 1969, Lucre & Dressler 4825 (CR, RB [3 sheets]); fila Santa Rita, 17 February 1986, McPherson 8460 (CR, MO). Panamá: carretera El Llano-Cartí, cerca a El Llano, 28 March 1976, Croat 33814 (MO); La Eneida, ca 16 km, east of Cerro Azul (Goofy Lake), 5 April 1973, Dressler 4314 (MO, PMA); Isla Barro Colorado, 20 March 1929, Frost 214 (F); km 16 de la carretera a Cartí, 23 March 1973, Kennedy & Dressler 2907 (CR, MO, PMA, SCZ); cerca de Gatúncillo, 26 February 1923, Piper 5609 (US). San Blas: Nusagandí, 12 August 1984, Nevers & Pérez 3703 (CR, MO, PMA, USF); San Blas, El Llano-Cartí, km 18.5, 20 November 1984, Nevers & Herrera 4371 (CR, MO, PMA).

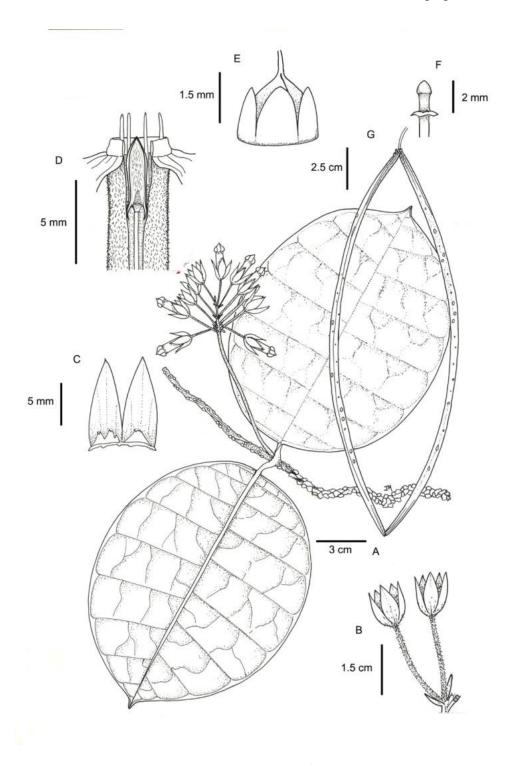


Fig. 15 *Prestonia lenticellata* (A-F from *McPherson 8460*, INB; G from *Lucre & Dressler 4825*, RB). A. Stem with inflorescence. B. Calyces, sepals, and pedicels. C. Adaxial view of two sepals. D. Open corolla tube, showing the anthers and the free coronal lobes. E. Nectaries and ovary. F. Style-head. G. Follicles.

Prestonia lindleyana Woodson in Gleason & Smith (1933: 392). Haemadictyon calycinum Lindley ex Miers (1878: 259), nom. illeg. Type:—BRAZIL. Amazonas: cerca de Manaus, Río Negro, October 1851, R. Spruce 1882 (holotype CGE!, isotypes B [destroyed], BR!, CGE! [2 sheets], K! [2 sheets], NY!, P!, W! [photo F neg. 31800!]). Fig. 16, 17.

**Stem** inconspicuously puberulent when young, glabrescent at maturity, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 0.5–1 mm long. **Petioles** 0.4– 1.1 cm; leaf blade  $(7-)8.5-18(-22) \times 3-10.5(-12.4)$  cm, elliptic, obovate-elliptic, to ovate-elliptic, apex acute, acuminate to short-acuminate, base obtuse to rounded, rarely subcordate, coriaceous to subcoriaceous, glabrous adaxially, the abaxial surface glabrous or glabrescent and inconspicuously puberulent along the midrib, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a monochasial cyme, axillary, shorter or longer than the adjacent leaves, few- to many-flowered, the flowers somewhat clustered, inconspicuously puberulent to glabrescent, peduncle (3.5-)4.5-9 cm, pedicels 0.5-1.2(-1.7) cm long, floral bracts  $1-2 \times 0.5-1$  mm, linear, scarious, minute, green. Sepals  $(9-)10-12 \times 3-5$  mm, free, coriaceous to subcoriaceous, narrowly ovate to narrowly elliptic, the apices acute to acuminate, not reflexed, glabrous to glabrescent, foliaceous, the veins not evident, the base drying clearly darker than the rest of the sepal, colleters 1-1.5 mm long, entire, subentire, to minutely erose at the apex. Corolla salverform, yellow to yellowish green, glabrous outside, tube  $9-16 \times 3-4$  mm, straight, free corona lobes 2-2.5 mm long, the apices barely exserted, their height equaling or slightly surpassing that of the anther apices, annular corona subentire to slightly 5-lobed, thickened, corolla lobes  $6-10 \times 5-6$  mm, obliquely obovate. Stamens inserted near the corolla mouth, anthers 4.1–5.5 mm, dorsally glabrous, the apices exserted. Ovary 1.5-2 mm tall, glabrous, style-head 1.1-1.5 mm, nectary 1.5-2.1 mm, equaling or barely surpassing the ovary, divided into 5 nectaries, each one minutely and irregularly erose to subentire. Follicles  $12-25(-51) \times 0.5-0.6$  cm, continuous, sometimes inconspicuously articulated, free, but sometimes united at the tips (at least when young), glabrous to glabrescent, lenticels inconspicuous or not evident, slightly woody when old; inmature seeds 18–22 mm, coma 2–4 cm, tannish cream.

**Distribution and habitat:**—Tropical wet forest and moist forest, where it grows in primary or secondary forest, savannas and vegetation along river banks in southern Colombia, Venezuela and northern Brasil, from 50 to 550 m.

**Phenology**:—Flowering specimens have been collected almost year round Fruiting specimens have been collected from September through March.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local name:—Bejuco de Sapo (T.F. Amazonas, Venezuela)

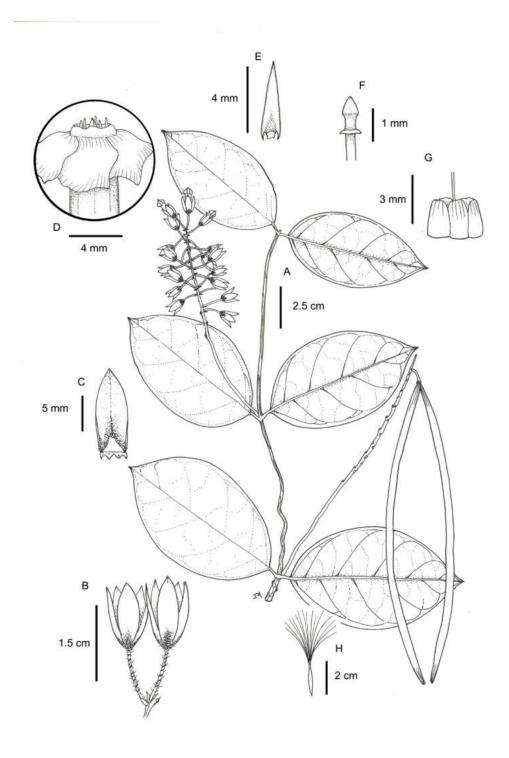


Fig. 16 *Prestonia lindleyana* (*Perez & Sosa 920*, INB). A. Stem with inflorescence and follicles. B. Calyces, pedicels, and floral bracts. C. Adaxial view of one sepal, showing the colleter at the base. D. Corolla mouth, showing the anthers and the free coronal lobes. E. Anther, dorsal view. F. Style-head. G. Nectaries. H. Seed.

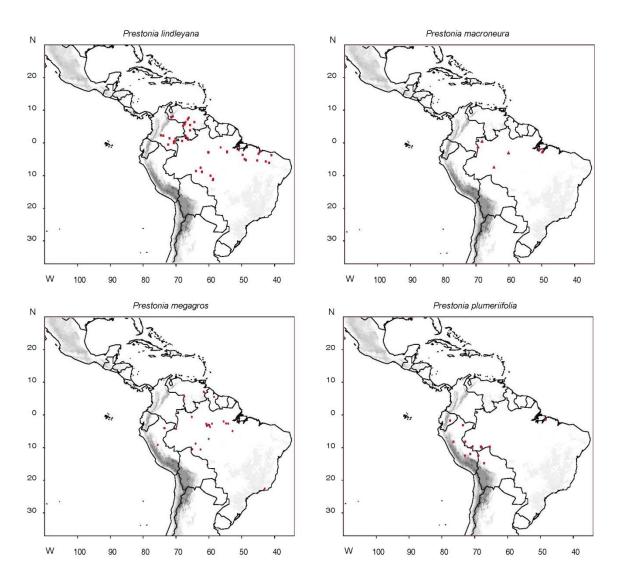


Fig. 17 Distribution maps of *Prestonia lindleyana*, *P. macroneura*, *P. megagros* and *P. plumeriifolia* 

**Taxonomic notes:**—*Prestonia lindleyana* is a distinctive species characterized by its unbranched inflorescence, scarious bracts, sepals with the base drying darker than the rest of the sepal, free corona lobes with apices exserted, and continuous follicles. This species is similar to *P. amazonica*, but *P. lindleyana* differs by its longer sepals ((9–)10–12 mm vs. 5–8 mm), and longer follicles (12–25(–51) mm vs. 8.5–11.5 mm).

Additional specimens examined:—COLOMBIA. Amazonas: Río Caqueta, alrededores de Araracuara, 10 November 1982, *Idrobo et al. 11427* (COL). Amazonas-Vaupes: Soratama, sobre la boca del Río Kananarí, January 1952, *Schultes & Cabrera 19578* (US), *Schultes & Cabrera 19858* (US). Guaviare: Miraflores, entre El Caño y Maloca de El Capitán, 7 January 1993, *Gamboa &* 

Pedreros 206 (CUVC). Meta: San Juan del Lozada, via Villa Rica-El Coclí, 12 August 2008, Castro & Navarrete 5877 (COAH); zona norte de La Macarena, Quebrada La Cristalina, 10 August 1972, Echeverry & Jaramillo 2288 (COL). Vaupés: riberas del Río Inirida, sitio Raudal Alto o Mariapiri, 3 February 1953, Fernández 2054 (COL, US); Soratama, Río Apaporis, entre el Río Pacoa y el Río Kananarí December 1951, García-Barriga 13999 (COL, US); Río Vaupés, Mitú, June 1958, García-Barriga et al. 16077 (COL); Río Paca, December 1, 52, Romero-Castañeda 3927 (COL, NY).

VENEZUELA. T.F. Amazonas: Río Orinoco, Isla del Ratón, 18 November 1965, Breteler 4719 (U, WAG [2 sheets], VEN); Atures, Río Cataniapo, vía Gavilán, 12 October 2000, Carabot et al. 2690 (MERF, VEN); Río Orinoco, s.d., Chaffanjo 537 (P); Atures, Alto Carinagua, 30 August 1995, Contreras 20 (VEN); Atures, alrededor de Puerto Ayacucho, Isla Ratón, 20 July 1977, Huber & Tillett 942 (NY, VEN); al SO de San Carlos de Rio Negro, 17 April 1979, Liesner 6737 (MO, VEN); Amazonas, 31 March 1984, Liesner 17048 (MO, NY); Atabapo, falda del Duida, cerca de Culebra en el Río Cunucunuma, 23 February 1985, Liesner 17856 (MO); Río Yatua, 6 December 1953, Maguire et al. 36684 (MO, NY, US, VEN); Atures, Río Ventuari, 30 April 1986, Melgueiro & Velásquez 647 (MO); Río Orinoco, 27 September 1973, Morillo & Ishikawa 3591 (VEN); N de Puerto Ayacucho, 1977, Morillo 6736 (VEN); Carinagua, E de Puerto Ayacucho, 1977, Morillo 6823 (VEN), Morillo 6827 (MO, MY); Isla Ratón, Río Orinoco, 1978, Morillo et al. 7351 (MY, VEN); Orinoco, 1957, Pannier et al. 985 (MO, VEN); Atabapo, Río Cunucunuma, Culebra Conuco, 8 February 1993, Pérez & Sosa 787 (CR), Pérez & Sosa 789 (MO), 6 March 1993, Pérez & Sosa 920 (CR); Alto Orinoco, s.d., Ranser-Schwabe 985 (VEN), Ranser-Schwabe 986 (VEN); Estación INOS-Gavilán, 15 October 1988, Romero 1736 (VEN); Atures, raudales de Atures, al S de Puerto Ayacucho, 6 September 1985, Steyermark et al. 131451 MO); Isla Ratón, 2 June 1940, Williams 13246 (VEN); Hani Waeiló Ibuhu, 12 April 1998, Zent & Zent 2184 (MO). Barinas: entre Esmeralda y El Curito, SO de Capitanejo, 25 August 1966, Steyermark & Rabe 96568 (MO, VEN). Bolivar: Cedeño, entre Puerto Ayacucho y Caicara, entre Caño Aguamena y Caño Garzón, 23 March 1986, Guánchez et al. 4215 (VEN); Cedeño, S de Los Pijiguaos, 4 November 1985, Holst & van der Werff 2593 (CR, MA, MO, U, VEN); Cedeño, al N de Puerto Ayacucho, 10 August 1985, Melgueiro & Sánchez 251 (VEN); Río Caura, Salto Pará, 12 May 1982, Morillo & Liesner 9175 (MO, VEN); Río Caura, cerca a Salto Pará, 14 January 1977, Steyermark et al. 112935 (K, MO, VEN); camino a Salto Chavaripo, 88.7 km al SO de Caicar de Orinoco, 4 September 1985, Steyermark et al. 131336 (MO), 4 September 1985, Steyermark et al. 131337 (MO). Mérida: Libertador, Santa María de Caparo, 23 October 1979, Burandt 855 (VEN); Río Caparo, al ESE de Santa Bárbara, 11 March 1980, Liesner & A. González 9359 (MO, VEN).

BRAZIL. Amazonas: Porto Brito, Río Negro, 22 November 1984, Bilby & Webber 219 (WAG); Manaus, Igarapé do Franco, 21 December 1955, Chagas s.n. (INPA, MO); manaus, Igarapé do Buião, 26 April 1955, Coêlho 993 (INPA); São Gabriel da Cachoeira, Río Negro, 27 October 1932, Ducke s.n. (K, RB # 23947, S, U, US); Manaus, s.d., Kuhlmann 8 (RB); Humaitá, cerca a Livramento, 12 October 1934, Krukoff 6763 (NY); carretera Manaus-Humaitá, 19 September 1980, Lowrie et al. 117 (INPA, MG, MO, NY); carretera Manaus-Rio Branco, 27 March 1961, Rodriguez & Lima 2297 (INPA); Manaus, Ponta Negra, 12 November 1962, Rodrigues et al. 4781 (INPA); entre Manaus y Porto Velho, 22 September 1979, Vieira et al. 76 (INPA, NY, RB, WAG). Ceará: Capoeira, Serra da Ibiapaba, 8 March 1981, Fernandes & Nunes 9913 (MO). Maranhão: Vitoria do Mearim, 16 May 2005, Carneiro 31 (IAN); exact locality lacking, 17 June 1907, Ducke s.n. (MG # 597); Rio Anil, 14 May 1949, Fróes 24285 (IAN); Barra do Corda, 6 April 1983, Miranda et al. 411 (CR, HRB). Mato Grosso: Dardanelos, Río Aripuanã, 13 June 1974, Cordeiro 19 (RB); Juima, linha meia quatro, 19 April 1985, Costa 691 (CR, R); Río Juruena, 23 June 1977, Rosa et al. 2165 (CR, F, IAN, INPA, MG, MO, NY, WAG). Pará: Mineração Río do Norte, Porto Trombetas, 1991, Evandro & Knowles 533 (INPA); Santarém, Jatobá, 1998–2005, Knowles 1437 (CR, MG); Belterra, Maguari, 1998–2005, Knowles 1510 (CR, MG); Pau Seco, 25 May 1996, Mitja 3582 (INPA); Tucuruí, Río Tocantins, cerca a Represa Tucuruí, 22 March 1980, Plowman et al. 9887 (HRB, INPA, MG, MO, NY, US, WAG); Ilha do Marajó, Río Pracuubamirím, Sitio Campina, ca. 1 hour upstream from São Sebastião de Boa Vista, 20 October 1984, Sobel et al. 4733 (CR, INPA, K, MG, NY, US, USF); AMZA, campamento azul, 30 May 1982, Sperling et al. 5874 (CR, INPA, NY); NO del campamento AMZA, 10 June 1984, Sperling et al. 6074 (F, INPA, K, MG, NY, US, USF). Piaui: Pimenteiras, 28 km al S, camino Pimenteiras-Valença do Piauí, 19 May 1988, Bianchetti et al. 702 (CR); Agricolândia, Tamboril, 23 July 1979, Chagas & Silva 41 (IBGE, US). Rondônia: Porto Velho, Cuiabá, 20 September 1962, Duarte 7014 (CR, RB); cerca a Tabajará, región superior del Río Machado, November 1931, Krukoff 1427 (K, MICH, MO, NY, S, U, UC). Tocantins: Rio Araguaia, 29 March 1961, Oliveira 1548 (CR, IAN, UB).

*Prestonia macroneura* Woodson (1936: 321). Type:—BRAZIL. **Amazonas**: Porto dos Juris, near Cataract, s.d., *M. Martius 3029* (holotype M!, isotype W!). **Fig. 17, 18.** 

**Stem** glabrous to glabrescent, with milky latex, sparsely lenticellate, these not subcrose, intrapetiolar colleters minute, 0.5-1 mm long. **Petioles** 0.5-1 cm; leaf blade  $10-16 \times 5-8$  cm, obovate to elliptic, apex short-acuminate, base obtuse to cuneate, coriaceous to subcoriaceous, bullate, sometimes slightly revolute, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary,

shorter than the adjacent leaves, few- to many-flowered, the flowers densely clustered, glabrous, glabrescent, or minutely puberulent, peduncle 2–3 cm, pedicels 0.9–2.2 cm long, floral bracts 5– $15 \times 2.5$ –3.5 mm, narrowly elliptic, narrowly ovate-elliptic to narrowly ovate, foliaceous, green to purplish green. **Sepals** 10– $20 \times 4$ –8 mm, free, coriaceous to subcoriaceous, narrowly elliptic to narrowly ovate, the apices acuminate, not reflexed, minutely puberulent to glabrescent, foliaceous, drying with a more or less uniform color, the veins inconspicuous or not impressed, colleters less than 1 mm long, deeply erose at the apex. **Corolla** salverform, cream, inconspicuously puberulent outside, tube 13– $15 \times 3$ –4 mm, straight, free corona lobes 3.5–4 mm long, the apices exserted, their height surpassing that of the anther apices, annular corona usually 5-lobed, thickened, corolla lobes 7– $11 \times 6$ –9 mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers ca. 5 mm, glabrous, glabrescent, or minutely puberulent dorsally, the apices barely exserted. **Ovary** 1.4–1.7 mm tall, glabrous, style-head 1.4–1.7 mm, nectary 1.4–1.8 mm, equaling or barely surpassing the ovary, 5-lobed, each lobe entire to subentire. **Follicles** 13.5– $16 \times 0.4$ –0.9 cm, continuous, divaricate free, inconspicuously puberulent, without lenticels, somewhat woody when old; seeds unknown.

**Distribution and habitat:**—Seasonal blackwater-flooded forest (igapó) and tropical wet forest, including margins of small creeks from 0–300 m in Amazonas state, Brazil.

**Phenology**:—*Prestonia macroneura* has been collected with flowers in November and December, fruiting specimens in May.

Conservation Assessment:—Endangered (EN) (IUCN 2001).

**Taxonomic notes:**—When Müller Argoviensis (1860) described Haemadictyon macroneuron he included Echites denticulata Vellozo in the synonymy (basionym of P. denticulata), and thus, rendering illegitimate the name. According the article 58.1 of the Code of Nomenclatural Botany (2011), the name proposed by Woodson (1936) should be considered as a new name (not a combination).

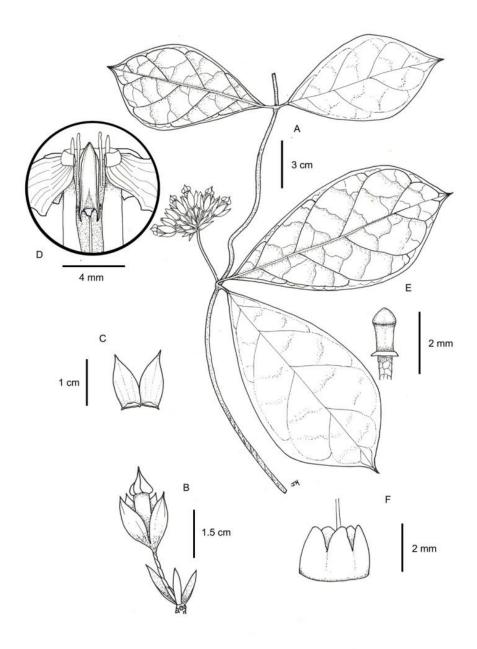


Fig. 18 *Prestonia macroneura* (A-F from *Amaral et al. 601*, INPA; G from *Amaral 302*, MG). A. Stem with inflorescence. B. Calyx, pedicel, and floral bracts. C. Adaxial view of two sepals. D. Open corolla tube, showing the anthers and free coronal lobes. E. Style-head. F. Nectary. G. Follicles

Prestonia macroneura is often confused with P. robusta and P. rotundifolia, since these three species have foliaceous bracts. Prestonia macroneura differs of P. rotundifolia by its inflorescence, with the flowers densely agglomerated (resembling an umbelliform inflorescence), longer free corona lobes (3.5–4.5 mm vs. 2-3 mm), and bullate leaves. Prestonia robusta is

distinguished from *P. macroneura* by its longer petioles (1.2–1.6 cm vs. 0.5–1 cm), non bullate leaf blades (vs. bullate), and shorter corona lobes (2 –3 mm vs. 3.5–4.5 mm).

Additional specimens examined:—BRAZIL. Amazonas: Vila Bittencourt, Río Japurá, 20 November 1982, *Amaral et al. 601* (CR, F, INPA, MG, MO, NY, RB, US, USF); Río Negro, s.d., *Martius 664* (M); Esperança, 7 December 1945, *Pires & Black 908* (IAN); Río Negro, São Gabriel do Cachoeira, 25 November 1987, *Stevenson et al. 1047* (INPA, MO, NY). Pará: Melgaço, Caxiuanã, 18 May 2002, *Amaral et al. 302* (MG); Rio São Manoel abaixo do Igarapé Preto, 4 December 1951, *Pires 3773* (IAN, US).

Prestonia megagros (Vellozo) Woodson (1934: 623). Echites megagros Vellozo (1825: 110)
Haemadictyon megalagrion Müller Argoviensis (1860: 170), nom. illeg. Prestonia megalagrion Miers (1878: 149), nom. illeg. Type:—BRAZIL. Without data, Fl. Flumin.,
Icon. 3: pl. 33. 1827 (lectotype designated here). Fig. 17, 19

Haemadictyon asperum Müller Argoviensis (1860: 169). Type:—BRAZIL. Rio de Janeiro: cerca a Rio de Janeiro, s.d., L. Riedel s.n. (holotype LE, n.v.).

Prestonia laeta Miers (1878: 149). Type:—BRAZIL. Rio de Janeiro: Monte Corcovado, s.d., J. Miers s.n. (holotype BM!).

Stem densely papillate-puberulent or minutely papillate-tomentulose when young, usually glabrescent at maturity, with milky latex, with few lenticels (in old stems), the lenticels not suberose, intrapetiolar colleters usually inconspicuos, 1–1.5 mm long. **Petioles** 0.9–1.5 cm; leaf blade (7.5-)9.5-21 × (5-)6-12.5 cm, broadly ovate, elliptic, broadly elliptic to obovate, apex abruptly short-acuminate to obtuse-apiculate, base obtuse to rounded, coriaceous to subcoriaceous, usually revolute, papillate and moderately to densely puberulent adaxially, indument green in fresh material, sometimes drying ferrugineous, sometimes glabrescent, the abaxial surface densely to moderately papillate-puberulent, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than or equaling adjacent leaves, manyflowered, the flowers more or less clustered, minutely and densely papillate-puberulent or papillatetomentulose, pedurcle 5–8.5 cm, pedicels (0.6-)0.9-1.5 cm long, floral bracts  $4-9 \times 1.5-2.5$  mm, linear-ovate to narrowly ovate or narrowly elliptic, scarious and inconspicuous, green. Sepals 10- $16 \times 3-4$  mm, free, coriaceous to subcoriaceous, narrowly elliptic, the apices acute to acuminate, not reflexed, usually densely and minutely papillate-tomentulose, foliaceous, drying with a more or less uniform color, the veins not impressed, colleters ca. 1.5 mm long, minutely erose or lacerate at the apex. Corolla salverform, yellow, glabrous outside, sometimes very sparsely papillatepuberulent abaxially of the lobes (but soon glabrescent), tube 10–14 × 4–5 mm, straight, free corona lobes 3–4 mm long, the apices barely exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire, thickened, corolla lobes  $9-13 \times 7-8$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5–6 mm, dorsally glabrous, the apices barely exserted. **Ovary** 1.5–2 mm tall, glabrous, style-head 1.5–1.8 mm, nectary 1.9–2.5 mm, conspicuously surpassing the ovary, variously 5-lobed, each lobe entire. **Follicles**  $12-16 \times 1-1.3$  cm, continuous, divaricate, free, the tips divergent, densely and minutely tomentulose, the indument green in fresh material, without lenticels, somewhat woody when old; seeds (11-)14-18 mm, coma 2.7–4.1 cm, tannish brown to creamish brown.

**Distribution and habitat:**—Tropical wet forest, where it grows in primary forest, secondary disturbed vegetation, and along river margins in Colombia, southeastern Venezuela, northeastern Peru, northern Brazil and disjunct in southeastern Brazil (state of Rio de Janeiro) from 0 to 500 m.

**Phenology**:—Flowering specimens have been collected from February through September and December, fruiting specimens in June and July.

**Conservation Assessment:**—Vulnerable (VU), the area of occurrence of less than 20,000 km2 and fewer than 10 known localities.

**Taxonomic notes:**—*Prestonia megagros* is easily recognized by the following combination of characters: stems densely puberulent or minutely tomentulose when young, leaves usually revolute, with the blade densely to moderately puberulent on the abaxial surface, inflorescence a dichasial cyme, glabrous corolla, free coronal lobes with the apices barely exserted, and divaricate follicles.

**Additional specimens examined**:—COLOMBIA. Amazonas: Leticia, estación biológica El Zafire, October 2006, *Álvarez et al. 3829* (JAUM).

VENEZUELA. T.F. Amazonas: Atures, Río Cataniapo, San Pedro de Cataniapo, 4 August 1981, *Guánchez 1426* (VEN). Bolivar: Tumeremo a Anacoco, 18 March 1974, *Gentry et al. 10654* (MEXU, MO, US VEN, Z); Guama, Río Sopapo, 24 September 1973, *Morillo & Ishikawa 3421* (VEN); vía Anacoco, cerca a la carretera Tumeremo-El Dorado, 1978, *Morillo et al. 7672* (MO, MY, VEN); vía Anacoco, 1978, *Morillo et al. 7692* (MY, VEN).

GUYANA. Upper Demerara-Berbice: Río Demerara, Quebrada Sibaruni, 3 September 1950, *Forest Department 6328* (K [2 sheets], NY, U).

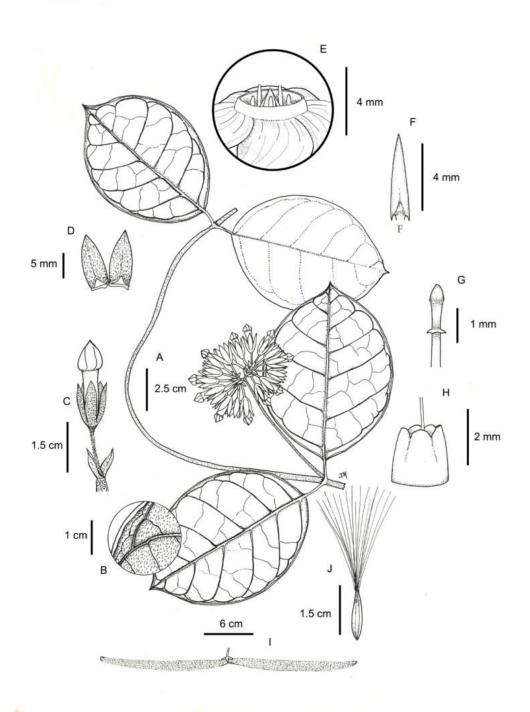


Fig. 19 *Prestonia megagros* (A-H from *Vásquez et al. 5419*, INB; I-J from *Coêlho et al. s.n.*, INPA). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts. D. Adaxial view of the sepals, showing the colleters at the base. E. Corolla mouth, showing the annular corona, free coronal lobes, and apices of the anthers. F. Anther, dorsal view. G. Style-head. H. Nectary. I. Follicles. J. Seed.

PERÚ. Loreto: Maynas, Mishana, Río Nanay, 25 July 1984, *Vásquez et al. 5419* (AMAZ, CR [2 sheets], MO, USF, WAG). Ucayali: Padre Abad, fundo Yacu Mama, carretera Agaytia-Boqueron Padre Abad, 19 June 2004, *Schunke-Vigo & Graham 15655* (USF).

BRAZIL. Amazonas: Autazes, comunidade indígena de Murutinga, 30 September 2004, Bacelar-Lima 36 (INPA); Manáus, km 10 de BR-17, 31 January 1955, Chagas s.n. (INPA #727, MG, NY); Río Negro, afluente do Río Negro, Río Canaburi, 16 June 1976, Côelho 475 (INPA, MG); BR-319, entre km 165-200, June 1980, Coêlho et al. s.n. (CR, INPA [4 sheets]); Novo Aripuanã, cerca a Corujá, 2 May 1985, Cid 5984 (INPA, MO, NY); Igarapé do Passarinho, Manaus, 20 September 1957, Ferreira 85–57 (INPA, MO); Manaus, 2 July 1892, Glaziou s.n. (P); Manacapuru, Sitio Santana-Ramal Bela Vista, Manaus-Manacapuru road, km 58, 24 January 2002, Kinupp & Colleto 2126 (INPA); carretera Manaús-Humaitá, km 180, 16 September 1980, Lowrie et al. 13 (NY); Rio Tea, afluente del Rio Negro, punto 09, 10 June 1976, Marinho 492 (IAN, Z); Manaus, Igarapé do Passarinho, 20 September 1957, Pereira 85/57 (INPA); Reserva Florestal Ducke, Manaus-Itacoatiara, 28 March 1995, Sothers et al. 378 (CR, INPA, K, MG, MO, NY, SP, SPF, UB, WAG). Pará: Óbidos, 11 May 1905, Ducke s.n. (MG #7227), 23 July 1927, Ducke s.n. (RB # 21602, S, US), 11 May 1905, Ducke s.n. (RB # 21634 [3 sheets], US); Santarém, Alter do Chão, 1998-2005, Knowles 1456 (MG); Santarém, Jatobá, 1988-2005, Knowles 1545 (MG), Knowles 1546 (MG); Santarém, Río Caruauna, reserve da SUDAM, Barreirinha, 2 September 1988, Rosario et al. 1130 (MG). Rio de Janeiro: Teresópolis, 12 December 1869, Glaziou 4082 (P). Rondônia: Río Jarú, Seringal 71, 3 April 1973, Pena 293 (IAN); estrada Guajrá-Mrim-Abunã, km 45-60, 1 February 1983, Silva & Rosario 477 (INPA, MG [2 sheets], NY); Porto Velho, Ramal Teotônio, 5 Abril 2010, Silveira 326 (RB, RON).

Prestonia plumierifolia Markgraf (1930: 1038). Type:—BRAZIL. Amazonas: Río Purus, cultivated in the Jardím Botânico de Belém (Pará), 9 August 1905, J. Huber 7030 (holotype B [destroyed, photo F neg. 4550!], lectotype US! designated by Morales (2006b), isolectotypes MG!, RB!, US!). Fig. 17, 20

**Stem** inconspicuously puberulent when young, glabrous to glabrescent at maturity, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, ca. 1 mm long. **Petioles** 0.5-1.5 cm; leaf blade  $8-20 \times (3-)4.5-11$  cm, obovate to broadly obovate, apex obtuse to rounded and mucronulate, base obtuse to cuneate, coriaceous to subcoriaceous, sometimes slightly revolute, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers laxly disposed, minutely puberulent to glabrescent, peduncle 1.8-4 cm, pedicels 0.4-1.1 cm

long, floral bracts  $1-2 \times 0.5-1$  mm, linear, scarious, minute, green. **Sepals**  $6-8 \times 2-3(-4)$  mm, free, coriaceous to subcoriaceous, narrowly elliptic, the apices acute to acuminate, not reflexed, minutely puberulent to glabrescent, foliaceous, drying with a more or less uniform color, the veins not evident, colleters hasta 1.5 mm long, subentire to minutely erose at the apex. **Corolla** salverform, cream, glabrous to glabrescent outside, tube  $(11-)12-17(-19) \times 3.5-5$  mm, more or less straight, rarely somewhat inflated near the base, free corona lobes 2.5-4 mm long, barely included or the apices barely exserted, their height equaling or slightly surpassing that of the anther apices, annular corona usually entire or subentire, thickened, corolla lobes  $7-10 \times 7-9$  mm, narrowly and obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 4.9-5.3 mm, dorsally glabrous, the apices slightly exserted o barely included. **Ovary** 1.5-2.5 mm tall, glabrous, style-head 1-1.5 mm, nectary 1.5-2.4 mm, equaling the ovary, variously 5-lobed, sometimes almost divided into 5 free lobes, each lobe subentire. **Follicles**  $29-35(-40) \times 0.6-1$  cm, continuous, usually connate longitudinally, glabrous to glabrescent, moderately lenticellate, woody when old; seeds 12-14 mm, coma 2.7-3.8 cm, tannish yellow.

**Distribution and habitat**:—Tropical wet forest in eastern Ecuador, Peru, Bolivia and northwestern Brazil, from 100 to 550(-700) m.

**Phenology**:—*Prestonia plumierifolia* has been collected with flowers in April, August and from October through February. Fruiting specimens have been collected in April, May, and November.

Conservation Assessment:—Vulnerable (VU) (IUCN 2001).

**Taxonomic notes**:—*Prestonia plumierifolia* shows an overall resemblance to *P. amazonica*, *P. denticulata*, and *P. vaupesana*, but can be distinguished from these by the obovate or narrowly obovate leaves, dichasial inflorescence, and usually connate longitudinally woody follicles. *Prestonia trifida* sometimes has conspicuously obovate leaves, but *P. plumierifolia* differs by its shorter sepals.

**Additional specimens examined**:—ECUADOR. Pastaza: Pastaza, Pozo Petrolero Villano, December 1991, *Hurtado 3023* (CR, MO, QCNE).

PERÚ. Cusco: La Convención, Echarate, Ivochote, comunidad nativa Monte Carmelo, 14 November 2005, *Huamantupa et al. 7108* (CR, MO). Loreto: Maynas, cerca de Iquitos, 1977, *Revilla 2614* (CR, MO, USF). Madre de Dios: Río Manú, Estación Cocha Cashu, 26 November 1980, *Foster 5913* (F); Tambopata, Las Piedras, Quebrada Gamitana, 15 August 2004, *Suclli et al. 1896* (MO). San Martín: Mariscal Cáceres, Puerto Pizana, Río Huallaga, 4 January 1971, *Schunke 4615* (F, MO, NY, US); Tocache Nuevo, cerca de Tocache, 25 May 1975, *Schunke 8613* (CR, MO, USF); Quebrada Ishichimi, Mariscal Cáceres, Tocache Nuevo, 6 November 1980, *Schunke 12402* 

(AMAZ, CR, F, MO, RB, USM, Z). Ucayali: Purús, cuenca del Río Purús, Río Curanja, cerca de Colombiana, 21 February 2000, *Graham & Schunke-Vigo 1035* (USF).

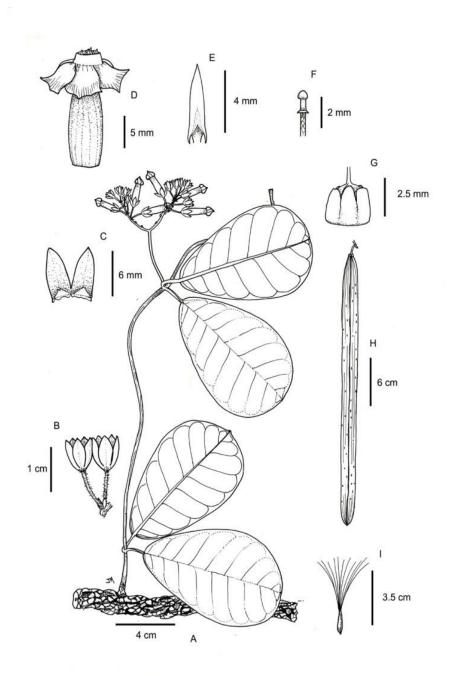


Fig. 20 *Prestonia plumierifolia* (A-E from *Killeen & Krudenky 3606*, INB; H-I from *Schunke 8613*, MO). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of two sepals. D. Corolla. E. Anther, dorsal view. F. Style-head. G. Nectary and ovary. H. Follicles. G. Seed.

BRAZIL. Acre: Río Branco, Sena Madureira, 23 October 1980, *Cid & Souza 3013* (INPA, MG, MO, NY, RB, US); Marechal Taumaturgo, Río Jurú, N de São João do Breu, 2 April 1993, *Daly et al. 7711* (CR, INPA, MO, NY, WAG); without exact locality, 9 August 1908, *Huber s.n.* (MG [photo F neg. 45949]); Bujarí, Riozinho do Andirá, 21 December 2008, *Medeiros et al. 104* (NY, USF); Río Branco, Sena Madureira, km 5, atrás de Fogas, 21 October 1980, *Nelson 761* (HST, INPA, MICH, MG, MO, NY, R, RB, US, USF, WIS).

BOLIVIA. Beni: Ballivian, Arroyo San Bernardino, 13 February 1992, *Killeen & Krudenky 3606* (CR, LPB, MO, USZ). Pando: Río Madeira, Abuna, 19 November 1968, *Prance et al. 8653* (INPA, K, MG, MO, NY, P, R, S, U, US, WAG, VEN).

Prestonia robusta Rusby (1920: 91). Type:—BOLIVIA. La Paz: Tumupasa, 15 December 1901, L. Williams 57 (holotype NY!). Fig. 21, 22.

Stem minutely puberulent when young, glabrous to glabrescent at maturity, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 0.5-1 mm long. **Petioles** 1.2–1.6 cm; leaf blade  $(8.5-)10.5-22.5(-28) \times (5.5-)7-16$  cm, broadly elliptic to broadly obovate, apex obtuse to rounded and apiculate, base obtuse to rounded, coriaceous to subcoriaceous, sometimes slightly revolute, glabrous, rarely inconspicuously puberulent along the midrib abaxially, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, minutely puberulent, peduncle 3-6.5 cm, pedicels 0.4–1.4 cm long, floral bracts  $3-8 \times 2.5-3.5$  mm, narrowly elliptic to narrowly ovate, scarious and inconspicuous to subfoliaceous, green. Sepals  $(11-)13-17 \times (4-)5-7$  mm, free, coriaceous to subcoriaceous, narrowly ovate to narrowly elliptic, the apices acute to shortly acuminate, not reflexed, glabrous, rarely minutely and sparsely puberulent, foliaceous, drying with a more or less uniform color, the veins not impressed, colleters 1–1.5 mm long, minutely erose at the apex. Corolla salverform, yellowish white, glabrous to glabrescent outside, tube  $13-17 \times (3.5-1.00)$ )4-6 mm, straight, free corona lobes 2-3 mm long, barely included or the apices exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire to subentire, thickened, corolla lobes  $8-10 \times 7-9$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5-6 mm, dorsally glabrous, the apices barely exserted. Ovary 1.5-2 mm tall, glabrous, style-head 1.5–1.9 mm, nectary 1.5–2.1 mm, equaling or barely surpassing the ovary, variously 5-lobed, each lobe entire to subentire. Follicles 16–19.5 × 1.1–1.3 cm, continuous, divaricate, free, the tips divergent, becoming conspicuously narrower towards the apices, glabrous, sometimes sparsely lenticellate, somewhat woody when old, longitudinally striate; seeds (16–)18–21 mm, coma 1.5–2.8(–3.1) cm, tannish cream.

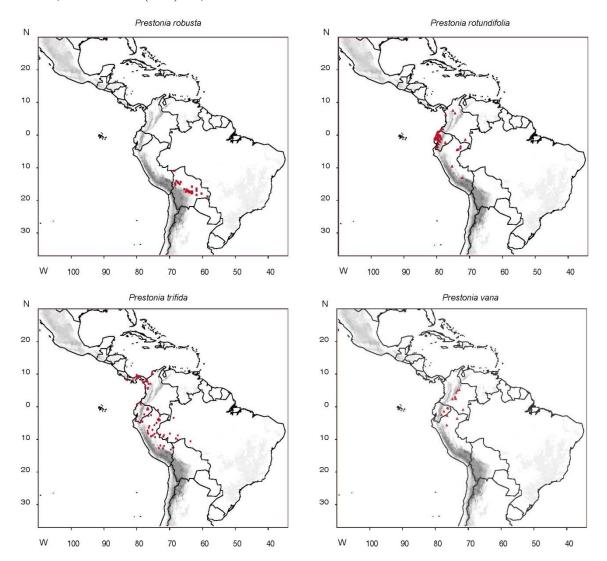


Fig. 21 Distribution maps of Prestonia robusta, P. rotundifolia, P. trifida, and P. vana

**Distribution and habitat:**—This species occurs in Bolivia and Peru (where it is known by a single collection) in moist forest, gallery forest, savanna woodland, Chaco forest, and disturbed vegetation from 200–600 m.

**Phenology**:—*Prestonia robusta* has been collected with flowers throughout the year and with fruits from March through August.

Conservation Assessment:—Vulnerable (VU) (IUCN 2001).

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

km2 and fewer than 10 known localities.

**Local names**:—Bejuco de leche (Santa Cruz, Bolivia); bejuco leche leche (Cochabamba, Bolivia); chochos (Beni, Bolivia)

**Uses:**—In Bolivia, a specimen reports the local use of this species (Guareco 264, CR, LPB), but without any specific use detailed.

**Taxonomic notes:**—*Prestonia robusta* is distinguished by the following combination of characters: coriaceous to subcoriaceous leaf blades, secondary and tertiary veins conspicuously impressed, dichasial inflorescence (resembling an umbelliform inflorescence), foliaceous bracts, 3–8 mm long, sepals (11–)13–17 mm, glabrous or glabrescent corolla, free corona lobes barely included or the apices exserted, and woody follicles. *Prestonia robusta* has been confused with *P. rotundifolia*, but differs by the inflorescence, with more agglomerate flowers, somewhat smaller floral bracts, and thicker follicles. *Prestonia trífida* is somewhat related, but it is easily separated by the inconspicuous and scarious bracts, and thinner follicles.

**Additional specimens examined**:—PERÚ. Ucayali: Boquerón Padre Abad, 22 August 1946, *Woytkowski 34418* (F, MO, UC).

BOLIVIA. Beni: Ballivián, Rurrenabaque, 11 March 1982, *Beck 8286* (RB); Ballivian, Río Beni, San Borja, 8 March 1987, *Beck 13240* (CR, LPB, MO, M, SI, USF); Ballivian, Río Beni, Rurrenabaque, encañada Suse, 18 May 1990, *Daly et al. 6501* (LPB, MO, NY, USF); Ballivian, Río Beni, confluencia con Río Quiquibey, 23 May 1990, *Daly et al. 6597* (NY); Ballivian y Yacuma, Estación Biológica del Beni, 27 January 1995, *Guareco 264* (CR, LPB, M). Cochabamba: Carrasco, Estación Experimental Sacta, 23 April 2002, *Churchill & Arroyo 21601* (MO); José Carrasco Torrico, Río Blanco, 1 June 2000, *Paz et al. 628* (LPB); José Carrasco Torrico, Puerto Villarroel, 10 June 2000, *Paz et al. 791* (LPB); Capinota, Sindicato, Villa Mercedez, 27 January 2007, *Peñaranda 398* (HSB, MO); José Carrasco Torrico, Río Blanco, 30 May 2000, *Seidel 3511* (LPB), 4 June 2000, *Seidel 3605* (LPB). La Paz: Franz Tamayo, Calabatea, SO de Apolo, Río Yuyo, 4 June 1990, *Gentry & Beck 70295* (LPB, MO); Franz Tamayo, Hacienda Ubito, valle del Río Ubito, 12 July 1993, *Kessler 3834* (LPB); Sud Yungas, Alto Beni, Colonia Buena Vista, 4 August 1994, *Seidel &* 

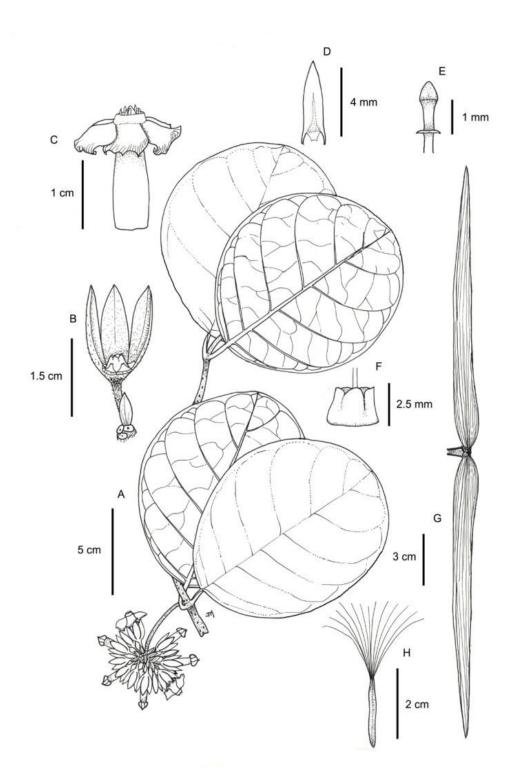


Fig. 22 *Prestonia robusta* (A-F from *Nee 39682*, INB; G-H from *Beck 13240*, INB). A. Stem with inflorescence. B. Calyx with two sepals removed, showing the nectary and colleters. C. Corolla. D. Anther, dorsal view. E. Style-head. F. Nectary. G. Follicles. H. Seed.

Vaquiata 7610 (CR, LPB, MO); Sud Yungas, Colonia Tupiza, 27 December 1994, Seidel & Vaquiata 7706 (LPB). Pando: Nicolás Suárez, zona de Campoana, junto a barra San José, riberas del Nareuda, 15 January 1983, Fernández-Casas 8294 (NY). Santa Cruz: Andrés Ibáñez, La Guardia, 9 January 1998, Beck 23463 (LPB); Ñuflo de Chávez, Estancia San Miguelito, 2 December 1995, Fuentes 1354 (MEXU, USZ); Germán Busch, El Carmén, Estancia Campo En Medio, 3 May 1997, Gutiérrez et al. 2143 (LPB, MEXU); Ñuflo de Chávez, Las Trancas, 22 November 1994, Jardim & Mamani 1288 (USZ); Warnes, Pampa de Viru-Viru, 13 August 1994, Menacho & Gutiérrez 621 (NY, USZ); Cotoca, Jardin Botánico de Santa Cruz, 24 Decmber 2010, Morales 19322 (CR); Cordillera, Bañados del Izozog, Estancia Cachari, 13 March 1991, Navarro & Vargas 375 (USZ); Andrés Ibáñez, Jardín Botánico de Santa Cruz, carretera a Cotoca, 15 July 1987, Nee 35184 (LPB, MO, NY, USF); Ichilo, Parque Nacional Amboró, a lo largo de Río Saguayo, 18 December 1988, Nee 37237 (CR, LPB, MO, NY, USF); Ichilo, N de Buena Vista, cerca a Laguna Madrejón, 1 November 1990, Nee 39682 (CR, LPB, MO, NY, USF, USZ); 13 km al NE de Warnes, carretera a La Esperanza, 11 July 1994, Nee 45172 (MO, NY, SI, USF, USZ); Ichilo, January del Río Ichilo, entre Villa Tunari y Buena Vista, 22 December 1995, Nee 46446 (NY); Ichilo, carretera a Puerto Grether, 20 October 1999, Nee 50211 (MO, NY, USZ); Ichilo, SO del Condor, 19 November 2000, Nee & Chávez 51515 (CR, NY, USF); Guarayos, Ascensión de Guarayos, Parque Botánico Guarayú, 3 March 1993, Ramos et al. 81 (LPB, USZ); Sara, Buenavista, 29 September 1916, Steinbach 2863 (NY, SI); Bosques de Buena Vista, Sara, 13 May 1921, Steinbach 5671 (G); Buenavista, Sara, 30 December 1925, Steinbach 7376 (G, K, NY); Chiquitos, NO de Chochís, entre Ipias y Taperas, 28 December 1999, Wood & Goyder 15679 (K, LPB). Data lacking: January 1865, Pearce s.n. (K).

Prestonia rotundifolia K. Schumann ex Woodson (1936: 318). Type:—ECUADOR. Manabi: El Recreo, August 1893, B. Eggers 15078 (holotype M!, isotypes B [destroyed, photo F neg. 4551!], K!, L!, LD!, NY!, O!, P! [2 sheets], PR!, S!, US!). Fig. 21, 23.

**Stem** inconspicuously puberulent when young, glabrous to glabrescent at maturity, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 0.5-1 mm long. **Petioles** 0.6-2(-3) cm; leaf blade  $(9-)10-18 \times (4.5-)6-11$  cm, obovate, broadly elliptic to broadly ovate, apex acute, obtuse to rounded and mucronulate, base obtuse to rounded, coriaceous to subcoriaceous, sometimes slightly revolute, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers usually clustered, minutely puberulent, peduncle 2-8 cm, pedicels 0.7-1.5 cm long, floral bracts  $6-18(-25) \times 2.5-4(-6)$  mm, elliptic, narrowly elliptic to

narrowly ovate, conspicuously foliaceous, green, rarely purplish green. **Sepals** 9–15  $\times$  3–5 mm, usually connate at the base for 1/3 of their length, forming a campanulate-cup, rarely completely free (mostly in old flowers), coriaceous to subcoriaceous, narrowly ovate to narrowly elliptic, the apices acute to shortly acuminate, not reflexed, minutely and sparsely puberulent to glabrescent, foliaceous, drying with a more or less uniform color, the veins not impressed, colleters 1–1.5 mm long, subentire o minutely erose at the apex. **Corolla** salverform, cream, glabrescent outside, tube  $13-17 \times 3.5-5$  mm, straight, free corona lobes 2–3 mm long, the apices slightly exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire, thickened, corolla lobes 9–13  $\times$  6–8 mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 4.5–5 mm, dorsally glabrous, the apices barely exserted. **Ovary** 1–2 mm tall, glabrous, style-head 1–1.5 mm, nectary 1–2.1 mm, equaling or scarcely surpassing the ovary, divided into 5 nectaries, each one subentire to minutely erose. **Follicles** 19–37  $\times$  0.4–0.9 cm, continuous, sometimes inconspicuously articulated, free, but usually united at the tips, glabrescent, moderately lenticellate, somewhat woody when old; seeds 14–16 mm, coma 2.5–4 cm, tannish cream.

**Distribution and habitat**:—Tropical wet forest, premontane wet forest, and disturbed areas in northern and southwestern Colombia, Ecuador, and Peru, from 0–700 m.

**Phenology:**—Specimens with flowers or fruits have been collected throughout the year.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Local names**:—Asusu Sili (Pichincha, Ecuador); Chu chu maceranu tape (Esmeraldas, Ecuador); pachón (Guayaquil, Ecuador).

**Uses:**—In Ecuador, the leaves are boiled and rubbed on the chest, to stimulate breast milk production (*Kvist & Asanza 40831*). The leaves are boiled and the decoction is cooled and used for the treatment of pains in general (*Kvist 40674*).

**Taxonomic notes:**—*Prestonia rotundifolia* is recognized by the following combination of characters: inflorescence branched, with the flowers densely clustered, floral bracts foliaceous, free corona lobes with the apices exserted, and fruits usually continuous. It is related to *P. robusta* and *P. macroneura*, having in common the leaf shape, similar inflorescences, and foliaceous bracts, but *P. rotundifolia* can be distinguished by its longer floral bracts and thinner follicles.

Additional specimens examined:—COLOMBIA. Amazonas: Leticia, corregimiento de la Pedrera, Río Cahuinarí, bocas del Río Pamá, rebalse Medio de Dique Natural, 26 November 1990, *Fundación Botánica Pedro Rastrojo 3399* (HUA). Antioquia: Puerto Berrío, vereda Alicante, 1 km S de finca Penjame, carretera San Juan de Bedout-La Cabaña, 2 March 1990, *Callejas et al. 9285* (HUA, MO, NY, USF); Cáceres, corregimiento el Tigre, vereda El Tamaná, Quebrada La Reversa, 21 February 1997, *Ramírez et al. 5979* (JAUM). Chocó: Bahía de Solano, 13 June 1950, *Fernández* 

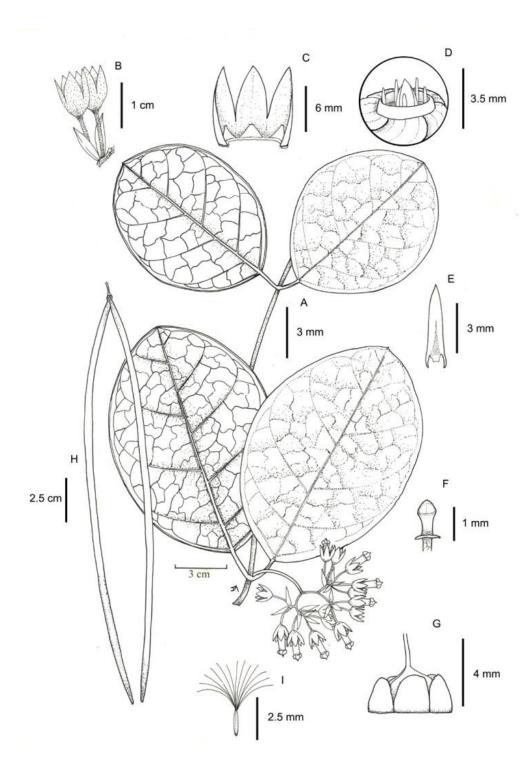


Fig. 23 *Prestonia rotundifolia* (A-G from Bass & Pitman 346, INB; H-I from *Dodson 5176*, QCNE). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of three sepals, showing the colleters at the base. D. Corolla mouth showing the anthers and free coronal lobes. E. Anther, dorsal view. F. Style-head. G. Nectaries and ovary. H. Follicles. I. Seed.

333 (US); Bahía Solano, Puerto Mutis, 4 January 1973, *Gentry & Forero 7161* (COL, MO) Nariño: Barbacoas, entre Barbacoas y Payán, 4 November 1989, *Ramírez 1789* (PSO); Tumaco, 19 September 1950, *Romero-Castañeda 2204* (COL [2 sheets]).

ECUADOR. Bolivar: Hacienda Changuil, Río San Antonio, 12 August 1995, Cornejo & Bonifaz 4263 (GUAY, USF). El Oro: 7.3 millas al E de Saracay, 23 November-15 December 1978, Escobar 881 (MO). Esmeraldas: Estación Biológica Bilsa, Montañas de Mache, O de Quinindé, 1 December 1994, Bass & Pitman 330 (MO); Quinindé, Montañas de Mache, 13 December 1994, Bass et Pitman 346 (CR, QCNE); reserva Mache-Chindul, Río Ene, propiedad Luis Cabrera, 3 May 2003, Bonifaz & Cornejo 5048b (GUAY); Quinindé, Estación Biológica Bilsa, 5 km O de Santa Isabel, 18 October 1994, Clark & Adnepos 209 (CR, QCNE); Quinindé, Estación Biológica Bilsa, Montañas de Mache, March 1995, Clark & Troya 507 (QCNE); Quinindé, Estación Biológica Bilsa, Montañas de Maché, O de Santa Isabela, 4 May 1995, Clark & Watt 737 (QCNE); Muisne, San Salvador, E de puerto Nuevo, 13 July 1996, Clark et al. 2854 (CR, QCNE); San Lorenzo, 25 May 1994, Cornejo & Bonifaz 2700 (GUAY, USF); Fila de Bilsa, E de San José de Bilsa, SO de Esmeraldas, 12 km al SO de El Salto, carretera Atacames-Muisne, 28 January 1991, Gentry & Josse 72783 (MO), 29 January 1991, Gentry & Josse 72840 (F, MO, QCNE); reserva forestal de Jardín Tropical, Universidad Técnica Luis Vargas Torres, 4 February 1991, Gentry & Lajones 73078 (MO); El Timbre, cerca a Esmeraldas, 6 August 1962, Játiva & Epling 430 (NY, S, UC); cerca a San Lorenzo, 31 July 1963, Játiva & Epling 602 (S, UC); San Lorenzo, 10 July 1964, Játiva & Epling 691 (S, UC); Río Cayapa, Zapallo Grande, 1 August 1982, Kvist & Asanza 40786 (AAU, MO, QCA), 3 August 1982, Kvist & Asanza 40831 (QCA); Quinindé, Estación Biológica Bilsa, Montañas de Mache, 6 December 1994, Pitman & Bass 1025 (CR, MO, QCNE); San Lorenzo, 21 August 1967, Sparre 18296 (NY, S); San Miguel, sector Río Grande, comunidad Corriente Grande, 24 November 1992, Tipaz et al. 2324 (QCNE). Guayas: Río Daule, Pichincha, Hacienda Santa Barbarita, 18–26 April 1959, Harling 4746 (S), Harling 4778 (S); carretera Naranjal-Machala, ca. 13 km S de Naranjal, 22 May 1980, Harling & Anderson 19288 (GB, USF); Guayaquil, 1806, Tafalla s.n. (distributed as "Ruiz & Pavón 17/56", BM, G, MA [2 sheets]); Guayas, El Naranjito, September 1908, Sodiro s.n. (P [2 sheets], QPLS). Loja: km 20 entre Alamor y Puyango, 2 April 1980, Harling & Anderson 17770 (GB, USF). Los Ríos: Rio Palenque field station, 2 km S Patricia Pilar, 14 April 1995, Bremer et al. 3379 (UPS, USF); Hacienda Clementina, Cerro Guineales, 23 March 1996, Cornejo & Bonifaz 4911 (GUAY); Estación Biológica Río Palenque, 19 September 1972, Dodson 5176 (AAU, F, MO, QCA [2 sheets], QCNE, SEL); bosque Jauneche, Vinces, 19 August 1978, Dodson et al. 7164 (AAU, F, MO, SEL); Vinces, Jauneche, 23 March 1980, Dodson & Gentry 9773 (GUAY, MO, SEL); Centro Río Palenque, 22 February 1974, Gentry 10120 (MO, SEL); Río Palenque, entre Santo Domingo de Los Colorados y Quevedo, 29 September 1979, Gentry et al. 26663 (AAU, MO, SEL); Jauneche, Carlos Vinces, entre Mocachi y Palenque, estero Peñafiel, 24 January 1981, Gentry et al. 30727 (MO, SEL); without exact locality, 2 August 1962, Játiva & Epling 294 (S, UC); Hacienda Clementina, Cerro Samaná, 25 October 1995, Knudsen et al. 507 (OCA); Hacienda Clementina, entre Babahoyo y Montalve, 15 February 1967, Sparre 14569 (RB, S, US); Río Palenque Science center, km 56 on the Quevedo-Santo Domingo road, 3 February 1980, Watson 266 (NY, USF, WAG). Manabí: Pedernales, Cerro Pata de Pájaro, June 1996, Clark et al. 2623 (QCNE); Jama, Hacienda Camerones, S de Pedernales, 9 April 1997, Clark et al. 4355 (CR, MO, QCNE); Jipijapa, Cerro Montecristi, 29 January 2001, Clark et al. 6201 (QCNE, US); 15 km E de San Plácido, 70 km E de Protoviejo, 6 August 1980, Hansen et al. 7955 (CR, MO [2 sheets], NY, USF [2 sheets]); entre Junín y Alhajuela, 12 km SSO de Junín, 10 May 1980, Harling et al. 18986 (GB, USF); Camarones, al S de Pedernales, 15 December 1998, Neill et al. 11517 (MO, QCNE); Pedernales, Cerro Pata de Pájaro, 12 March 1997, Vargas et al. 1344 (MO, QCNE). Pichincha: cooperativa Santa Marta, SE de Santo Domingo de los Colorados, 5 February 1979, Dodson et al. 7615 (QCNE, SEL); carretera Santo Domingo-Rosa Zárate, Río Blanco, 9 May 1968, Harling et al. 9326 (GB, USF); Río Toachí, cerca a Santo Domingo, 3 August 1962, Játiva & Epling 331 (S, UC); Santo Domingo, 18 July 1963, Játiva & Epling 540 (NY, S, UC); carretera Santo Domingo-Puerto Limón, Icongoma Grande, 21 July 1982, Kvist et al. 40674 (AAU, MO, QCA); ríos Toachí y Pilatón, December 1883, Sodiro s.n. (QPLS); Río Toachí, Pichincha, s.d., Verleysen s.n. (QPLS). Zamora-Chinchipe: Taisha, 8 February 1962, Wash et al. 7729 (B, UC). Data lacking: s.d., Schott s.n. (BM).

PERÚ. Cusco: Urubamba, Ollantaytambo, Huaytampo, 8 November 2002, *Huamantupa* 2443 (MO); Huanuco: Pachitea, Codo de Pozuzo, cerca a Río Pozuzo, Pachitea, 23 October 1982, *Foster 9402* (F, MO, NY, USF, USM); Pachitea, Picallpa, montañas Sira, 4 November 1988, *Wallnöfer 11–41188* (W, WAG, Z). Loreto: Nauta, Quebrada Saragoza, 10 January 1988, *Vásquez & Jaramillo 10332* (MO, USF); Maynas, Indiana, Yanamono, Explorama Lodge, 4 December 1988, *Vásquez et al. 11337* (MO, USF, USM); Maynas, Sargento Lores, Constancia Norte, Shapajillal, 13 April 1997, *Vásquez et al. 23070* (MO, USF).

Prestonia trifida (Poeppig) Woodson in Gleason & Smith (1933: 392). Haemadictyon trifidum Poeppig (1845: 67). Type:—PERU. Loreto: Maynas, February 1831, E. Poeppig 2161 (holotype W! [photo F neg. 31801!], isotypes F! [2 sheets, photo F neg. 56500!], NY!).
Fig. 21, 24.

- Prestonia evansii S. Moore (1895: 395). Type:—BRAZIL. Mato Grosso: entre Santa Cruz y Villa María, December 1891, *S. Moore 819* (lectotype K! designated by Morales (2006 b), isolectotypes BM!, NY!, R!, WU!).
- Prestonia glabrata K. Schumann (1905: 189). Type:—PERU. San Martín: Tarapoto, December 1902, E. Ule 6604 (lectotype G-DC! designated by Morales (2006 b), isolectotypes HBG!, MG!).
- Prestonia obovata Standley (1925: 459). Type:—PANAMA. Panamá: Canal Zone, between Gamboa and Cruces, 2 July 1911, H. Pittier 3767 (holotype US!, isotypes GH!, K!).

**Stem** inconspicuously puberulent when young, glabrous to glabrescent at maturity, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters usually inconspicuos, less than 1.2 mm long. **Petioles** 0.8-2.1(-3.5) cm; leaf blade  $(8-)10-27(-31.5) \times (4.5-)6-16.5$  cm, obovate, broadly ovate to broadly elliptic, apex obtuse, retuse, abruptly short-acuminate to acuminate, base obtuse, rounded to broadly acute, coriaceous to subcoriaceous, sometimes slightly revolute, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers usually densely clustered, minutely puberulent to glabrescent, peduncle 3-13(-25) cm, pedicels (0.6-)0.8-2.5(-3.5) cm long, floral bracts  $1-3 \times 0.5-1.5$  mm, linear to linear-ovate, scarious, minute, green. Sepals  $(9-)10-15 \times 3-6$  mm, free, coriaceous to subcoriaceous, narrowly ovate to very narrowly elliptic, the apices acute to shortly acuminate, not reflexed, minutely puberulent to glabrescent, foliaceous, drying with a more or less uniform color, the veins not impressed, colleters ca. 1 mm long, minutely erose to somewhat lacerate at the apex. Corolla salverform, cream to yellowish green, usually glabrous, rarely sparsely and inconspicuously papillate outside, tube 11–19 × 3–4 mm, straight, free corona lobes 2–4 mm long, the apices exserted, their height slightly surpassing that of the anther apices, annular corona entire to subentire, thickened, corolla lobes  $7-15 \times 6-9$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 4.5-6 mm, glabrous to inconspicuously puberulent dorsally, the apices slightly exserted. Ovary 1–1.5 mm tall, glabrous to glabrescent, style-head 1.1–1.5 mm, nectary 1–1.6 mm, equaling or barely surpassing the ovary, sometimes divided into 5 nectaries, each one subentire to irregularly lacerate. Follicles  $22-41(-45) \times 0.8-1.1$  cm, continuous, connate longitudinally or free but united at the tips, minutely and moderately puberulent when young, but soon glabrescent, lenticels inconspicuously lenticellate, usually somewhat woody when old; seeds 18–23 mm, coma 2.5–3.5 cm, tannish cream.

**Distribution and habitat:**—Widely distributed from southwestern Costa Rica and Panama throughout Colombia, Ecuador, Peru to northwestern Brazil in tropical wet forest

(including floodplain forest), moist forest, premontane forest, cloud forest, swamp areas, and disturbed areas, from 0 to 850(-1000) m.

**Phenology**:—Specimens with flowers or fruits have been collected throughout the year.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local names:—Quenegapoca (Napo, Ecuador); rimí (Loreto, Pampa Hermosa, Perú).

**Uses:**—In Ecuador the macerated fruits are used for treating inflamed eyes. It has also been reported that the fruits are edible, and eaten by several animals and humans (*Aulestia et al.* 1333). In Colombia the fruits are used by the Kuna Indians as na anticoagulant (*Forero 571*).

**Taxonomic notes:**—*Prestonia trifida* resembles *P. antioquiana*, sharing several morphological features such as leaf shape, inflorescence structure, scarious floral bracts, and glabrous corolla. The former species is distinguished by its non verrucose petioles (vs. conspicuously verrucose) and continuous follicles (vs. 3-4-ribbed). Other species morphologically somewhat similar are *P. macroneura*, *P. robusta*, and *P. rotundifolia*, but all these species have foliaceous floral bracts, whereas in *P. trifida* floral bracts are always scarious.

The follicles of this species are usually free and united just at the tips, but some collections from Panama and Colombia have follicles completely connate longitudinally. These population were described as P. obovata. However, they agree with the specimens from South America in all other morphological characteristics.

Additional specimens examined:—COSTA RICA. Puntarenas: Clarita, Quebrada León, Península de Burica, 29 November 1972, *Lent 3093* (CR, F, MO); Punta Burica, Punta Banco, entre Quebrada Pita y Quebrada Nicaragua, 20 December 1998, *Morales & Abarca 6900* (CR, F, K, MO).

PANAMÁ. Chiriquí: a lo largo de carretera a Puerto Armuelles a San Bartola, 19 May 1976, *Croat 35029* (MO); cerca de San Bartolomé, Península de Burica, 28 July-1 August 1940, *Woodson & Schery 869* (MO, US). Coclé: La Mesa above El Valle, with road to Cerro Pilón, 21 July 1974, *Croat 25365* (PMA). Colón: Cerro Santa Rita, 13 September 1979, *Antonio 1776* (MO); camino maderero Santa Rita, 6 February 1968, *Correa & Dressler 681* (MO); al E de la fila Santa Rita, 14 February 1968, *Correa & Dressler 697* (MO, PMA); camino a la Zona maderera de Santa Rita, 16 January 1969, *Correa & Dressler 1110* (MO, PMA); zona maderera de Santa Rita, 6 January 1969, *Correa & Dressler 1110* (MO, PMA); zona maderera de Santa Rita, 8 April 1971, *Croat 14141* (MO); Altos de Pacora, La Eneida, ca. 16 km NE de Cerro Azul, 29 April 1973, *Dressler 4367* (PMA); Achiote, 2 June 1973, *Dressler 4402* (MO, PMA); Santa Rita, fila del Este, 23 February 1968, *Duke 15248* (MO); fila Santa Rita, 23 January 1968, *Dwyer 8426* (MO); Sardinilla, Salamanca, 8 March 1998, *Florpan & Guerra 2994* (PMA); fila Santa Rita,

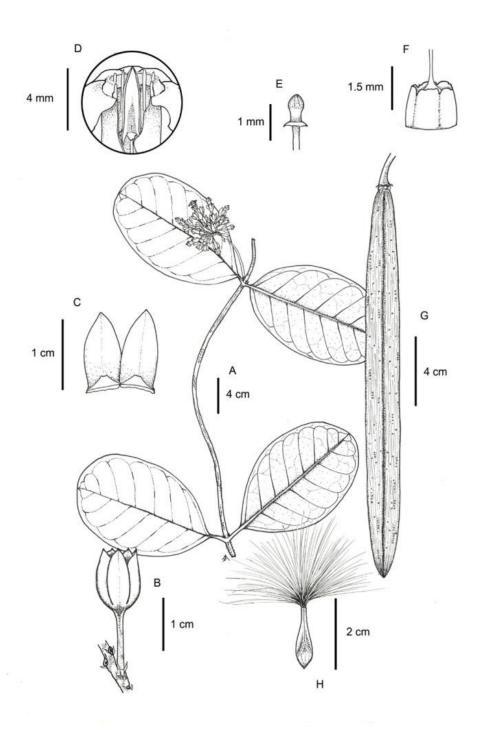


Fig. 24 *Prestonia trifida* (A-F from *Dik 580*, INB; G-H from *Rentería et al. 10638*, HUA). A. Stem with inflorescence. B. Calyx, pedicel, and floral bracts. C. Adaxial view of two sepals, showing the colleters at the base. D. Open corolla mouth, showing the anthers and free coronal lobes. E. Style-head. F. Nectary. G. Follicles. H. Seed.

cerca a Agua Clara, 12 March 1971, Foster & Morton 2244 (DUKE, MO, PMA); Altos de Pacora, 31 January 1996, Galdames et al. 2449 (PMA); Santa Rita, February 1968, Gómez-Pompa et al. 3309 (MEXU, MO); carretera El Llano-Cartí, 13 January 1978, Hammel 861 (MO, WAG, Z); Cerro Jefe, carretera a Santa Rita, E de Agua Clara, 4 March 1973, Kennedy 2755 (F, GH, MO); SO de Portobelo, 24 March 1973, Liesner 1043 (CR, F, MO); Cerro Jefe, 15 June 2008, Martínez et al. 305 (PMA); Colón, 13 January 1987, McPherson 10269 (MO); Teck Cominco Petaquilla mining concession, 19 June 2008, McPherson 20535 (MO, PMA); Santa Rita ridge, 7 Km by road from Transisthmian highway, 3 Km SE of Puerto Pilon, 13 February 1974, Nee & Hale 9678 (MO, PMA); Sierra Llorona, Santa Rita, 23 February 2011, Pérez et al. 2434 (PMA). Darién: cerca de Pinogana, 6 October 1938, Allen 915 (GH, MO); Río Pirre, 14 July 1971, Croat & Porter 15533 (MO); S de El Real, 22 June 1962, Duke 5054 (GH, MO, UC); N de Pucro, 22 June 1967, Duke 13006 (MO); Río Balsa, entre Manene y Tusijuanda, 26 July 1967, Duke 13580 (MO); Chepigana, SE de Jaqué, 29 April 1980, Garwood 985 (MEXU, MO, PMA); SO del Cerro Tacarcuna, 6 February 1975, Gentry & Mori 14178 (MO); E de Santa Fé, 16 July 1966, Tyson et al. 4656 (MO [2 sheets]); entre Garachine y Sambu, Garachine, 29 November 1990, Herrera 824 (CR, PMA); 10 NE de Jaqué, Río Tabuelitas, cerca de Biroqueirá, debajo de la boca del Río Pavarandó, 29 January 1981, Sytsma & D'Arcy 3270 (MO, USF, WAG). Panamá: Cerro Jefe, along road below Summit into Chagres Valley, 21 February 1988, Almeda et al. 5848 (PMA); parque nacional Chagres, reserva forestal de Madden, 25 September 2000, Araúz & Flores 2417 (PMA); Isla Barro Colorado, 1931, Aviles 1 (MO); carretera a Cartí, 13 March 1973, Busey 912 (MO); carretera Pipeline, cerca a Gamboa, 26 June 972, Clewell & Tyson 3281 (EAP, MO [2 sheets], TEFH); Cerro Jefe, 3 October 1969, Correa et al. 1613 (MEXU, MO, PMA); área que está entre la región de Cerro Jefe y la Eneida, 12 February 1971, Correa et al. 1729 (GH, MO, PMA); parque nacional Altos de Campana, sendero de interpretación, 29 November 1990, Correa & Montenegro 7499 (PMA), 19 December 1993, Correa et al. 8353 (PMA), 1 April 1993, Correa & Montenegro 9426 (PMA), 28 April 1994, Correa & Montenegro 10450 (PMA); Isla Barro Colorado, 1 April 1970, Croat 9252 (MO [2 sheets]); carretera Pipeline, 26 June 1972, Croat 17408 (MO, USF); cerca a Madden Dam, cerca a Alahuela, 27 November 1934, Dodge 16590 (G, K, MO, U); Sabanas a lo largo de del Río Azote Caballo, 7 December 1934, Dodge et al. 16865 (K, MO, UC); E de Cañitas, 16 May 1973, Dressler 4390 (MO, PMA); El Llano-Cartí, ca. 20 km al N de El Llano, 19 January 1974, Dressler 4549 (MO, PMA); Cerro Campana, 13 April 1967, Duke 10733 (MO); Cerro Jefe, 12 March 1967, Dwyer et al. 7255 (MO); Cerro Jefe, 5 January 1972, Dwyer 9432 (MO), Dwyer & Gentry 9481 (PMA); Chepo, El Llano-Cartí road, 14 Km from Panamerican highway, 22 January 1977, Folsom & Kauke 1422 (MEXU, MO, PMA); Parque Nacional Campana, Serranía del Llorón, Cerro de los Monos, 9 May 1997, Galdames et al. 3893 (CR, MO, PMA, SCZ); Cerro Jefe, 1 January 1972, Gentry et al. 3507 (MO); Cima de Cerro Jefe, 1 April 1972, Gentry 4872 (MO); Cerro Jefe cloud forest, along road past, Escuela Altos de Pacora, 16-20 Km E of Cerro Azul village, 5 January 1975, Gentry & Mori 13443 (AAU, GH, MO, PMA); carretera El Llano-Cartí, 18 km de la carretera Panamericana, 14 February 1975 Gentry & Mori 14204 (AAU, MO, PMA); Cerro Jefe, February 1968, Gómez-Pompa et al. 3074 (MEXU, MO); carretera El Llano-Cartí, 28 August 1982, Hamilton & Stockwell 1099 (MO, PMA, USF, WAG); El Llano a Cartí-Tupile, 23 March 1973, Kennedy & Dressler 2941 (MO); a lo largo de El Llano-Cartí, 9 January 1975, Luteyn & Wilbur 4663 (CR, DUKE); cerca de Cerro Jefe, carretera a Alto Pacora, 10 February 1988, McPherson 12096 (MO, USF); El Llano-Cartí road, 10.8 Km from Interamerican Highway, 27 December 1974, Mori & Kallunki 4136 (AAU, MO, PMA), 13 April 1975, Mori & Kallunki 5580 (AAU, MO); N de El Llano, 12 December 1973, Nee et al. 8731 (MO, US); Chepo, along El Llano-Cartí road 8 Km N of Panamerican highway at El Llano, 5 March 1974, Nee & Warmbrodt 10338 (MO, PMA, US, VEN); Tocumen, 23 November 1975, Restrepo 20 (MO, PMA); Isla Barro Colorado, July 1982, Schmalzel 768 (MEXU, MO); Isla Barro Colorado, 12 October 1931, Shattuck 129a (MO [2 sheets]); Cerro Jefe, 5 millas de Cerro Azul, camino a Altos de Pacora, 18 March 1981, Sytsma & Antonio 3834 (MO); Cerro Jefe, 27 January 1966, Tyson et al. 3337 (MO [2 sheets]); 4 millas al O de Chepo, 21 September 1972, Tyson 3739 (MO [2 sheets], PMA); Isla Barro Colorado, 24 July 1929, Wetmore & Woodworth 865 (A, MO). San Blás: carretera El Llano-Cartí, 7 March 1985, Nevers et al. 5003 (MO, WAG), 2 March 1986, Nevers 7219 (BM, COL, CR, MO, PMA, USF).

COLOMBIA. Antioquia: entre Villa Areteaga y Chigorodó, Lomitas, 1 October 1961, Cuatrecasas & Willard 26110 (COL [2 sheets], US); Urabá-Chigorodó-Malagón, Caño Malagón, 22 March 1986, Renteria 4711 (MO); Puerto Bélgica, carretera a Río Man, 8 April 1951, Romero-Castañeda 2330 (MEDEL [2 sheets]); entre Río Guapá y León, 18 March 1948, Yepes et al. 18c345 (MEDEL). Bolivar: San Juan Nepomuceno, Loma de Los Colorados, 2 September 1986, Cuadros 3158 (COL, MO, NY, USF); Bolivar, 11 January 1988, Gentry et al. 60852 (MO); Santa Catalina, Hacienda El Ceibal, 2 March 2000, Rodríguez & Olivares 31 (COL). Chocó: entre La Oveja y Quibdó, 1 April 1931, Archer 1749 (US); parque natural nacional Los Katios, vía de Sautata a cabaña Cristales, s.d., Barbosa 1427 (MO); playa Blanca, 12 May 1990, Barboza 6581 (CHOCO, MO); Medellín, Urabá, Cerro del Cuchillo, sector La Eugenia, camino de Nova a la Cumbre, 14 April 1988, Cárdenas 1639 (JAUM, MO); Riosucio, Urabá, Cerros del Cuchillo, sector La Eugenia, 19 May 1988, Cárdenas 1988 (JAUM [2 sheets], MO); Río Chintado, cerca de La Nueva, 6 February 1967, Duke 9847 (GH, MO); Lloró, 2.5 km de Yutó hacia Lloró, 7 August 1982, Escobar

et al. 2147 (HUA); Río Sucio, carretera a Sautatá, Salto El Tendal, 12 July 1996, Fonnegra 6113 (HUA); Acandí, Unguia, reserva indígena Cuna de Arquía, 5 July 1976, Forero 571 (COL, MO); Río Serrano, afluente del Río Atrato, 4-6 km arriba de Guayabal, 29 April 1975, Forero et al. 1333 (COL, NY); Quibdó, carretera Quibdó-Guayabal, 25 June 1985, García 108 (CHOCO, COL, MO); Parque Nacional Utría, bocas del Río Pichí, 10 June 1990, García 462 (CHOCO, MO, USF); Río El Valle, entre El Valle y villa indígena del Choco, 10 August 1976, Gentry et al. 17496 (COL, MO); nueva calle construida entre el S de Uyuto y Lloro, 17 August 1976, Gentry & Fallen 17849 (COL, CR, MO, Z); Quibdó-Tutunendo road, ca. 4 km W of Tutunendo, 6 January 1981, Gentry et al. 30272 (MO); carretera (en construcción) del km 27 (2 km S de Yuto) a Lloró, carretera Quibdó-Istmina, 15 June 1982, Gentry & Brand 36942 (COL, JAUM, MO); Río Sucio, Parque Nacional Los Katios, camino Peye-antiguo puerto de Peye, 13 June 1976, León 39 (COL, MO, NY); Río Bohios, cerca a Don Eladio, 29 June 1985, Renteria et. al. 4274 (JAUM, MO); Sautatá, Parque Natural Nacional Los Katios, camino de la estación al Salto de Tilupo, 11 October 1994, Rentería et al. 10638 (HUA), 22 March 1995, Rentería et al. 10911 (HUA [2 sheets]); Quibdó, Río Atrato, June 1954, Romero-Castañeda 4655 (COL). Córdoba: Valencia, Alto Sinú, 3 January 1985, Cogollo 2016 (JAUM, MO); unión del Río Tigre y Río Manso, Parque Nacional Paramillo, 27 July 1988, Gentry & Cuadros 63815 (MO). Cundinamarca: Puerto Bogota, vereda Acapal, Línea San Carlos-Purnio, 13 December 1999, Jiménez et al. 416 (JAUM). Santander: Andes, carretera a Puerto Nuevo y Barranca, después de La Estrella, 1 February 2000, Vélez & Suárez 3674 (JAUM); Cimitarra, vereda La Traviata, camino viejo Puerto Berrío-Puerto Boyaca, 1 December 1998, Rodríguez et al. 1219 (JAUM).

ECUADOR. Esmeraldas: San Lorenzo, Reserva Etnica Awá, Centro Guadalito, July 1992, Aulestia et al. 276 (MO, QCNE). Morona-Santiago: El Centro Shuar Kankaim, Río Kankaim, 19 September 1985, Shiki 124 (NY). Napo: Orellana, Parque Nacional Yasuní, carretera y oleducto Maxus en construcción, km 46-52, September 1993, Aulestia & Andi 579 (MO, QCNE, USF); Aguarico, Reserva Étnica Huaorani, December 1993, Aulestia et al. 1333 (CR, MO, QCNE); Orellana, Parque Nacional Yasuní, 6 October 1993, Dik 580 (CR, MO, QCNE, USF); Estación Biológica Jatum Sacha, 30 December 1987, Gentry et al. 60124 (MO, QCNE, USF); La Joya de los Sachas, Pompeya, lado S del Río Napo, campamento Maxus, Río Jivino, carretera de Maxus, km 1-5, October 1992, Grijal1va et al. 179 (MO, QCNE, USF). Pastaza: Lorocachi, Lagartococha, 1 June 1980, Brandbyge & E. Asanza 31452 (AAU, QCA); Río Ishpingo, tributario del Río Pastaza, 22 July 1980, Øllgaard et al. 35025 (AAU, QCA). Zamora-Chinchipe: Nangaritza, Shaime, 27 October 1991, Palacios et al. 8676 (MO, QCNE, USZ).

PERÚ. Amazonas: Condorcaqui, Río Santiago, 5 December 1979, Huashikat 1441 (MO); Condorcanqui, El Cenepa, Mamayaque, 14 February 1997, Vásquez et al. 22578 (MO, MOL, USF, USM). Huánuco: Honoria, Parque Nacional Iparia, Río Pachitea, 8 December 1966, Schunke 1329 (COL, F. G. NY, US); Bosque Nacional Iparia, a lo largo de Río Pachitea, 7 March 1967, Schunke 1723 (F, NY, US), 9 March 1967, Schunke 1736 (F, US); Bosque Nacional Iparia, Isla de Pacanas, 5 km arriba del campamento de Iparia, 14 November 1967, Schunke 2318 (F). Cusco: La Convención, Río Manguriari, Alto Urubamba, 2 February 1991, Nüñez & Ortiz 12762 (MO); Cusco, Camisea, Armihuari, 28 January 1997, Acevedo-Rodríguez et al. 9254 (CR, MO, NY, US [2] sheets], USM, WAG); O de Quincemil, 6 October 1976, Wasshausen & Encarnación 720 (K, MO, NY, US, USM); La Convención, Echarate, Kepashiato, Puguientimari-Pomoreni, 22 March 2007, Valenzuela et al. 9353 (CR, MO). Loreto: Tigre, Río Corriente, Caserío Jíbaros, 26 November 1979, Ayala et al. 2445 (AMAZ, MO, USF); Maynas, 18 August 1978, Díaz et al. 461 (MO); Coronel Portillo, carretera Federico Basadre, km 99, arboretum Von Humbolt, 2 December 1978, Díaz & H. Osores 667 (AMAZ, F, MO, NY); Río Nanay, cerca a Morona Cocha, al N de Iquitos, 21 March 1977, Gentry et al. 18540 (AMAZ, F, MO, USM); Bosque Nacional Humboldt, km 86 de la vía Pucallpa-Tingo María, 27 March 1977, Gentry et al. 18750 (MO); Río Nanay, Santa Clara, 7 April 1977, Gentry et al. 19102 (F, MO); Maynas, Alto Río Nanay, between Santa María de Nanay y Diamante Azul, 25 March 1978, Gentry et al. 26223 (AMAZ, F, MO, USF, USM); Alto Amazonas, Andoas, Río Pastaza, near Ecuador border, 16 August 1980, Gentry et al. 29847 (AMAZ, F, MO, NY, USM); Explorama Lodge, 29 August 1983, Gentry et al. 43843 (MO); Loreto, Rio Samiria, trocha Tacshacocha, 1 November 1984, Grández 13 (AMAZ); Pacaya, Reserva Nacional Samiria, 18 November 1986, Grández & Jaramillo 727 (MO, WAG); Maynas, Río Tigre-Río Corrientes, Cocha Belem, 20 May 1987, Grández & Chiquispama 727a (MO), 20 May 1987, Grández & Chuquispama 1004 (WAG); Putumayo, Maijuna, territorio de área propuesta, al N de Iquitos, entre Río Napo y Río Algodón, 24 oct 2009 (fl), Huamantupa et al. 13320 (AMAZ); Mishuyacu, cerca a Iquitos, January 1930, Klug 774 (F, NY, US), Klug 915 (F, NY, US); Alto Amazonas, Río Huallaga, Yurimaguas, 11 February 1924, Kuhlmann 1364 (RB [2 sheets]); parte baja del Río Ucayali, Jenaro Herrera, 1993, Kvist & Freitas 890 (AMAZ, K); Pampa Hermosa, Río Corrientes, December 1985, Lewis et al. 10076 (MO, USM); Requena, Río Tepiche, Santa Elena, 16 October 1968, McDaniel & Marcos 11299 (MO); Maynas, Santa María de Nanay, 10 km al O del caserío Mishana, reserva Cocha Yaramá, 13 March 1991, Pipoly et al. 14902 (AMAZ, MEXU, MO [2 sheets], USF); Maynas, Iquitos, Río Nanay, 22 March 1976, Revilla 381 (AMAZ, MO, USM, Z); Río Nanay, 12 November 1976, Revilla 1788 (MO, WAG); Maynas, cerca de Iquitos, 1977, Revilla 2689 (MO); Alto Amazonas, Yurimaguas, carretera del caserío de Munich, 12 May 1977, Rimachi 3030 (MO); Maynas, Iquitos, Río Momón, 1 February 1985, Rimachi 7727 (MO, US); Maynas, Fernando Lores, Río Amazonas, caserío de Samaria, 8 September 1988, Rimachi 8808 (IBE, US, USM); Maynas, Punchana, Río Momón, 9 September 1993, Rimachi 10728 (IBE, MBM, MO, US); Maynas, Iquitos, Río Itaya, Puerto Venezia, 21 September 1994, Rimachi 11117 (IBE, MO, NY, US); Maynas, 6 September 1967, Torres 355 (AMAZ, BM, ECON); Maynas, San Antonio, Río Itaya, 14 December 1982, Vásquez et al. 3603 (F, K, MO, NY, USF, USM); Maynas, Quebrada Tamshiyacu, 26 August 1983, Vásquez & Jaramillo 4378 (MO, USF); Ucayali, Canchahuayo, Isla Baños, 29 November 1985, Vásquez et al. 7005 (MO). Madre de Dios: Tambopata, Río Tambopata, Infierno, 17 January 1991, Alexiades & Pesha 1105 (NY, USM, WAG); Tambopata, Puerto Maldonado, 25 January 1976, Gentry & Revilla 16325 (MO, NY, Z); Manú, Río Salvación, 7 May 1987, Núñez et al. 8070 (MO, USF, USM); Parque Nacional Manú, Río Manú, s.d., Núñez et al. 14574 (MO); Tambopata, Puerto Maldonado, Cusco Amazónico, 23 November 2002, Valenzuela & Huamantupa 988 (CR, MO, NY); Tambopata, Concepción a Lago Sandoval, 15 January 1967, Vargas 18595 (MO, US). San Martín: Rioja, Venceremos, cerca al límite con Amazonas, carretera Rioja-Pomacocha, 13 February 1984, Gentry et al. 45522 (MO); Mariscal Cáceres, Juan Jui, Alto Río Huallaga, October 1931, Klug 3921 (CAS, GH, K, MO, NY, S, US, WIS); Nuevo Tocache, Instituto Agropecuario de Tocache, 10 November 1969, Schunke 3600 (COL, F, G, MO, NY, US); Tocache, Tocache Nuevo, Pueblo Viejo de Tocache, 10 February 1970, Schunke 3796 (F, K, MO, NY); Mariscal Cáceres, Tocache, Tocache Nuevo, Quebrada Ishichimi, 16 April 1970, Schunke 3931 (COL, F, G, NY, US); Tocache, Río Chonta Yaca (Uchiza), 23 January 1962, Schunke 5776 (F, MO, UC, US, USM); Puerto Pizana, Río Huallaga, Tocache Nuevo, 22 June 1974, Schunke 6988 (F, MEXU, MO, US, Z); Tocache Nuevo, March 1975, Schunke 8256 (CR, MO, USF); Mariscal Cáceres, Tocache Nuevo, Quebrada de Pucayacu, 4 October 1980, Schunke 12313 (MO); Tarapoto, December 1929, Williams 6049 (F, NY); Tarapoto, 26 December 1929, Williams 6726 (F); Huinguillo, 10 March 1962, Woytkowski 7178 (F, MO, NY, USF). Tumbes: Zarumilla, Bosque Nacional de Tumbes, cerca de Campo Verde, 19 December 1967, Simpson et al. 415 (COL, F, US, USM). Ucayali: Reserva Pacaya-Samiria, 3 December 1978, Díaz et al. 667a (MO), 12 December 1978, Díaz et al. 797 (MO); Coronel Portillo, Calleria, Río Utiquinia, cabecera de la Quebrada Maronillo, afluente de la Quebrada Manuela, 8 October 2003, Graham 2665 (USF); Purús, camino al Río de la novia, al E del aeropuerto de Puerto Esperanza, 22 March 2002, Schunke 15150 (USF, USM); Padre Abad, Quebrada Chesman, cerca al Boquerón de Padre Abad, Río Yurac, 7 March 2004, Schunke & Graham 15839 (USF); Padre Abad, carretera a la Quebrada Alto San Pedro, al O de Aguaytía, 18 October 2004, Schunke & Graham 16469 (USF); Coronel Portillo, Leoncio Prado, Yarinococha, 15 May 1984, *Vásquez 4998* (COAH, MO). Data lacking: 1829, *Poeppig s.n.* (NY, W).

BRAZIL. Acre: Jordão, 7 February 2009, *Acevedo-Rodríguez et al. 14862* (NY, RB); carretera Río Branco-Porto Velho, 13 February 1979, *Albuquerque et al. 1373* (INPA, NY, WAG, US); Feijó, Río Jurupari, colocação Novo Oriente, 13 February 2010, *Brasil et al. 591* (MO, NY); Rio Branco, Río Purus, Riozinho do Rola, 14 March 1997, *Daly et al. 9531* (NY, WAG); Senador Guiomard, Rio Iquiri, upstream from km 37, departing from Rio Branco, 20 May 2009, *Daly et al. 13785* (NY); Porto Walker, Río Juruan Mirim, comunidade Porongaba, 16 November 2001, *Delprete et al. 7854* (NY); Antimary, 31 March 1094, *Huber s.n.* (MG # 4269); Bujarí, Riozinho do Andirá, BR-364, km 52, 23-25 April 2010, *Medeiros et al. 510* (NY); Jordão, Río Tarauaca, downstream from Foz de Jordão, 11 February 2009, *Michelangeli et al. 1406* (RB, USF); Río Acre, 25 jul 1988 (fr), *Nünez et al. 9482* (AMAZ); Mâncio Lima, Bacia do Alto Juruá, Río Moa, entre igarapé São Pedro e Río Azul, 4 May 1996, *Silveira et al. 1198* (NY). Amazonas: São Paulo de Olivença, cerca a Palmares, 11 September-26 October 1936, *Krukoff 8319* (K, MO, NY, S, U). Rondônia: Río Jatuarana, región del Río Machado, December 1931, *Krukoff 1545* (K, NY, U); Mineração Campo Novo BR–421, 2 km W, 120 km de Ariquemes, 16 October 1979, *Vieira et al. 478* (NY, USF), *Vieira et al. 479* (INPA, MO, NY, USF).

Prestonia vana Woodson (1936: 323). Type:—PERU. Loreto: Alto Amazonas, Balsapuerto, May 1933, G. Klug 3066 (holotype MO!, isotypes F! [photo F neg. 56501!], G!, K!, NY!, S!, US!). Fig. 21, 25.

Stem minutely puberulent when young, glabrescent at maturity, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 1–1.5 mm long. Petioles 1.5–2.5 cm; leaf blade  $12-22 \times 8.5-16$  cm, elliptic to broadly elliptic, obtuse and shortly caudate to rounded or rarely emarginate, base obtuse to rounded, coriaceous to subcoriaceous, sometimes somewhat bullate, somewhat revolute, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. Inflorescence a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, minutely puberulent to glabrescent, peduncle (0.8-)3-10.5 cm, pedicels 1.2-2.5 cm long, floral bracts  $3-6 \times 1-1.5$  mm, linear to linear-elliptic or linear-ovate, scarious, minute, green. Sepals  $10-12 \times 3-4.5$  mm, free, coriaceous to subcoriaceous, narrowly ovate to narrowly elliptic, the apices shortly acuminate, not reflexed, minutely puberulent to glabrescent, foliaceous, drying with a more or less uniform color, the veins not impressed, colleters 1-1.5 mm long, minutely erose to variously lacerate at the apex. Corolla salverform, yellowish cream, minutely and conspicuously puberulent outside, tube  $15-16 \times 3-4$  mm, straight, free corona

lobes 3.5–4 mm long, the apices exserted, their height surpassing that of the anther apices, annular corona entire, subentire to variously 5-lobed, thickened, corolla lobes  $9-11 \times 6-7$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5-5.5 mm, minutely puberulent dorsally, the apices barely exserted. **Ovary** 1.5–2 mm tall, glabrous to glabrescent, style-head 1.2–1.5 mm, nectary 1.5–2.1 mm, equaling or barely surpassing the ovary, 5-lobed and divided into 5 lobes, sometimes some of them connate basally, each one entire to subentire. **Follicles** 8–10.5  $\times$  0.8–1.5 cm, continuous, divaricate, free, the tips divergent, conspicuously winged longitudinally, minutely puberulent, without lenticels, somewhat woody when old; seeds 11–13 mm, coma 1.2–2.2 cm, tannish cream.

**Distribution and habitat:**—Tropical wet forest, moist forest, seasonally inundated forest, and forest over quartzite formations in Colombia, Ecuador, and northern Peru, from 150–1050 m.

**Phenology**:—*Prestonia vana* has been collected with flowers in October through May and with fruits in April, August, October, and November.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Taxonomic notes**:—*Prestonia vana* is easy to recognize by its coriaceous to subcoriaceous and somewhat bullate leaf blades, conspicuously branched inflorescences, scarious floral bracts, puberulent corolla tube, and winged follicles. Morphologically, it resembles *P. trifida*, *but P. vana* can be separated by its puberulent corolla tube and winged fruits. Winged fruits are an unusual character in the tribe Echiteae and in *Prestonia* are known only in this species.

Additional specimens examined:—COLOMBIA. Amazonas: Río Caquetá, frente a Isla Yarumal, 17 May 1997, Sánchez et al. 3065 (COAH). Boyacá: Santa María, vereda Culima, carretera Santa María-Mambita, antes del Río Chivor, 1 April 2006, Betancur et al. 12181 (COL). Caquetá: Arbolitos, Río Caguán, 12 April 1953, Romero-Castañeda 3972 (COL, MO). Casanare: entre Monterrey y Aguazul, 28 October 1997, Pinto et al. 42 (COL). Meta: Sierra La Macarena, 14 January 1984, González et al. 6377 (COL); Cordillera La Macarena, entre Río Guejar y Caño Guayapita, 20 December 1950, Idrobo & Schultes 824 (COL, F, MO, U, US); Sierra La Macarena, 3 March 1962, Idrobo 4889 (COAH, COL [2 sheets], CR); Villavicencio, Reserva Bavaria, 15 November 1995, Lozano et al. 7357 (COL, MA); Sierra de La Macarena, Río Guayapa, 29 November 1950, Philipson et al. 1595 (BM, COL, US); Parque Nacional Natural Tinigua, Río Duda, Serranía Chamosa, centro de investigaciones ecológicas La Macarena, trocha V, April 1997, Stevenson 2058 (COAH, COL, HUA, NY).

ECUADOR. Morona-Santiago: Limón, Cordillera Occidental, 19 October 1943, *Acosta* 6440 (F, QCNE). Napo: Estación de Biodiversidad Tiputini, Río Tiputini, 25 October 1998, *Burnham & Loor 1767* (CR, MICH [2 sheets], MO, QCA); Añango, Río Napo, 9 March 1983,

Lawesson et al. 39366 (AAU, QCA, WAG). Pastaza: Río Landayacu, 25 November 1990, Gudiño 1147 (MO, NY, QCA, QCNE, USF).

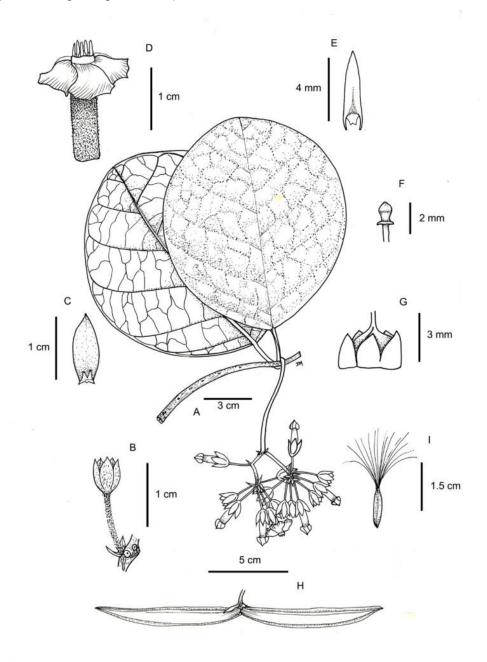


Fig. 25 *Prestonia vana* (A-E from *Stevenson 2058*, HUA; H-I from *Idrobo 4889*, INB). A. Stem with inflorescence. B. Calyx, pedicel, and floral bracts. C. Adaxial view of one sepal. D. Corolla. E. Anther, dorsal view. F. Style-head. G. Nectary and ovary. H. Follicle. I. Seed.

PERÚ. Loreto: Andoas, 11 January 1976, *Gentry et al. 15848* (CR, MO, Z); Alto Amazonas, Andoas, Río Pastaza, near Ecuador border, 14 August 1980, *Gentry et al. 29659* (AMAZ, MO, USM); Alto Amazonas, Andoas, Río Pastaza, al N de Iquitos, 21 November 1980, *Vásquez & Jaramillo 841* (AMAZ, MEXU, MO, NY, USF, USM).

- III. Prestonia Sect. Exsertae J. F. Morales, M. Endress & Liede, sect. nov. Type: Prestonia exserta (A. DC.) Standl., J. Wash. Acad. Sci. 15: 460. 1925. Haemadictyon exsertum A. DC., Prodr. 8: 426.1844.
- Prestonia didyma (Vellozo) Woodson (1936: 308). Echites didymus Vellozo (1825: 109).
  Rhaptocarpus didymus (Vellozo) Miers (1878: 152). Type:—BRAZIL. Rio de Janeiro: Fl. Flumin., Icon 3: t. 27. 1827 (1831) [lectotype, designated by Morales (2007b)]. Fig. 26, 27
- Haemadictyon membranaceum Müller Argoviensis (1860: 167). Type:—BRAZIL. Rio de Janeiro, Itaipú, s.d., A. Schott 5389 (holotype W! [photo F neg. 31799!]).
- Prestonia perplexa Woodson (1936: 304). Type:—BRAZIL. Without data, C. Lund s.n. (holotype C! [2 sheets]).

**Stem** sparsely puberulent when young, glabrescent at maturity, with clear latex, the lenticels inconspicuous or absent, (if present) not suberose, intrapetiolar colleters minute, 2–4 mm long. **Petioles** 0.9–2 cm; leaf blade  $(4.5–)5.5–14.5(-17)\times3–7.5(-10)$  cm, elliptic to ovate-elliptic, apex acuminate to short-acuminate, base cuneate to obtuse, membranaceous, glabrous, secondary veins impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. **Inflorescence** usually a monochasial cyme, axillary, shorter than the adjacent leaves, few- to many-flowered, the flowers somewhat clustered, minutely and densely puberulent, peduncle 2–5(-6) cm, pedicels 1–2.1 cm long, floral bracts  $5–14\times1–1.8$  mm, linear to linear-ovate, scarious and inconspicuous, green. **Sepals**  $8–15(-18)\times3–5$  mm, free, membranaceous, ovate, narrowly ovate to narrowly elliptic, the apices acuminate, not reflexed, glabrous, subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed, colleters 1–1.5 mm long, subentire to minutely erose, or minutely lacerate at the apex. **Corolla** salverform, the lobes with the base white, yellowish white to yellowish green, purple

toward the apex, glabrous outside, tube  $9-16 \times 3-5$  mm, straight, free corona lobes 2-4 mm long, slightly exserted or barely included, their height slightly shorter that of the anther apices, annular corona thickened, entire to subentire, corolla lobes  $(6-)8-12 \times 5-7$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5-6 mm, dorsally glabrous, the apices exserted. **Ovary** 1-2 mm tall, glabrous, style-head 1.5-2.1 mm, nectary 1.2-2.2 mm, equaling or surpassing the ovary, irregularly 5-lobed, each lobe subentire to irregular and minutely lacerate. **Follicles**  $(16-)18-26.5 \times 0.4-0.7$  cm, continuous, connate longitudinally or free and united at the tips (at least when young), glabrous, without lenticels, membranaceous when old; seeds 10-15 mm, coma (2.7-)3-4 cm, tannish cream.

**Distribution and habitat**:—Endemic to Brazil, where it grows in tropical wet forest, resting vegetation, and similar secondary vegetation in southeastern Bahia, Espirito Santo, Minas Gerais, and Rio de Janeiro, from 0–250 m.

**Phenology**:—Specimens with flowers have been collected en January, August, September, and December and with fruits in May.

Conservation Assessment:—Endangered (EN) (IUCN 2001).

**Taxonomic notes:**—*Prestonia didyma* is characterized by the membranaceous leaves, unbranched or slightly branched inflorescences, scarious or inconspicuously subfoliaceous bracts, free corona lobes slightly exserted or barely included, and anthers with the apices exserted. The follicles can be completely connate or free and just fused at the tips, a feature present in others species in the genus (e.g., *P. trifida*). It resembles *P. parvifolia* and *P. folsomii*, but can be separated by the glabrous leaves (vs. puberulent), and its different geographic distribution. For more details about the synonymy of P. perplexa under this species, see Morales (2007).

Additional specimens examined:—BRAZIL. Bahia: Canabrava, 3–5 km O de Olivença, 14 June 2003, *Hatschbach et al. 75104* (MBM); Itabuna, Porto Seguro, ramal de São José do Panorama, 18 January 1972, *Pinheiro 1724* (CEPEC, Z). Espirito Santo: Águia Branca, Assentamento 16 de Abril, 16 March 2006, *Demuner et al. 2021* (CR, MBML); Barra de São Francisco, parque municipal Sombra da Tarde, 12 December 2000, *Kollmann et al. 3502* (MBML). Minas Gerais: Jequeri, represa hidroeléctrica Providência, 27 November 1997, *Salino 3806* (BHCB, CR, WAG). Rio de Janeiro: Mata de Restinga, 11

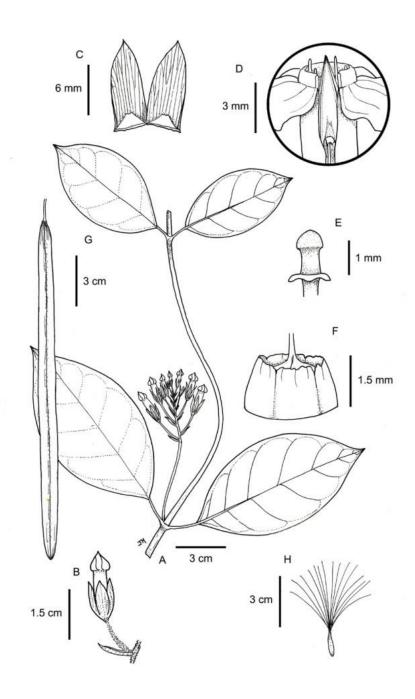


Fig. 26 *Prestonia didyma* (A-F from *Pinheiro 1724*, Z; G-H from *Sucre & Plowman 5110*, INB). A. Stem with inflorescence. B. Calyx, pedicel, and bract. C. Adaxial view of two sepals, showing the colleters at the base. D. Distal part of the corolla tube partially open, showing the anthers and free coronal lobes. E. Style-head. F. Nectary and ovary. G. Follicles. H. Seed.

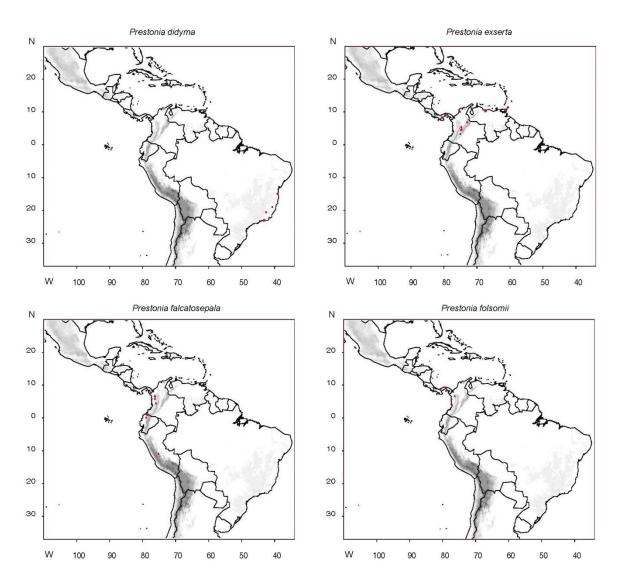


Fig. 27 Distribution maps of Prestonia didyma, P. exserta, P. falcatosepala and P. folsomii

January 1985, *Gentry et al. 49479* (MO, Z); Guanabara, Jacarepaguá, Serra do Pau da Fome, Sitio da Boiuna, 14 January 1962, *Pabst* s.n. (B, HB); Jacarepagua, Sitio São Jose, 4 Octuber 1954, *Pereira 736* (RB); carretera a Boiuna, 23 September 1958, *Pereira et al. 4310* (HB, MO, RB); Jacarepaguá, 4 August 1958, *Pereira 4103* (F, HB, MBM, MO, RB); Jacarepaguá, Boiuna, Sitio San Jose, 14 December 1958, *Pereira et al. 4857* (CR, MO, RB); Restinga da Praia de Itaipú, 27 May 1969, *Sucre & Plowman 5110* (CR, RB [2 sheets]). Data lacking:, *Lund s.n.* (C).

- Prestonia exserta (Candolle) Standley (1925: 460). Haemadictyon exsertum Candolle (1844: 426). Type:—VENEZUELA. Distrito Federal: Caracas, 1830, J. Vargas 54 (holotype G-DC! [photo F neg. 7545!], isotype FI-W!). Fig. 27, 28.
- Prestonia tobagensis Urban (1908: 467). Type:—TRINIDAD AND TOBAGO: near Frechfield, 23 Octuber 1889, *B. Eggers 5568* (lectotype HBG! designated by Morales (2006 b), isolectotypes K!, P!).
- Prestonia gracilis Rusby (1920: 91). Type:—COLOMBIA. Magdalena: cerca a Masinga, 18 November 1898, H.H. Smith 1644 (holotype NY!, isotypes CM!, K!, MICH!).
- Prestonia fendleri N. E. Brown (1923: 53), syn. nov. Type:—TRINIDAD AND TOBAGO. Without locality, 1877–1880, A. Fendler 628 (holotype NY, lost; lectotype (designated here) BM!, isolectotype K!).
- *Prestonia velutina* Woodson (1931: 554). Type:—COLOMBIA. Tolima: Honda, August 1919, *B. Ariste-Joseph s.n.* (holotype NY, lost; lectotype (designated here) US!).

Prestonia dumeticola Pittier ex V. M. Badillo (1947: 302), nom. nud.

Prestonia fraternorum Pittier ex V. M. Badillo (1947: 302), nom. nud.

**Stem** sparsely and minutely puberulent to glabrescent, with clear latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, less than 1 mm long. **Petioles** 0.4-1.4(-1.6) cm; leaf blade  $(3-)4.5-11.8 \times (1.3-)2.1-5.5$  cm, elliptic to broadly ovate, apex acute to short-acuminate, base obtuse, rounded to broadly acute, membranaceous, glabrous, glabrescent, or puberulent adaxially, densely puberulent, tomentulose to glabrescent abaxially, rarely glabrous, secondary veins impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. Inflorescence a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers somewhat clustered, minutely puberulent to glabrescent, peduncle 0.3-2.5 cm, pedicels 0.7-1.6 cm long, floral bracts  $1-6(-10) \times 1-1.8$  mm, linear, linear-elliptic to linear-ovate, scarious and inconspicuous, green. Sepals  $6.5-8(-11) \times 1.5-4$  mm, free, membranaceous, linear, linear-elliptic, narrowly elliptic, narrowly ovate to narrowly obovate, the apices acuminate, not reflexed, densely to sparsely puberulent, sometimes glabrescent, subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed, colleters 1-1.5 mm long, minutely lacerate or erose at the apex. Corolla salverform, yellowish green to cream, glabrous outside, tube 13–18 × 3–4 mm, straight, free corona lobes 4–5.5 mm long, almost completely exserted, their height conspicuously surpassing that of the anther apices, annular corona thickened, entire, corolla lobes 8–14  $\times$  4–6 mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 4–5.1 mm, dorsally glabrous, the apices exserted. **Ovary** 2–2.5 mm tall, glabrous, style-head 1–1.3 mm, nectary 1–1.5 mm, shorter than the ovary, divided into 5 lobes, sometimes somewhat connate at the base, each one entire to subentire. **Follicles** 21.5–30.5  $\times$  0.3–0.5 cm, continuous, free and united at the tips (at least when young) or connate longitudinally, glabrous, without lenticels, membranaceous when old; seeds 11–16 mm, coma 2.1–2.9 cm, creamish white to cream.

**Distribution and habitat**:—From central Panama, Colombia to Venezuela, and Trinidad y Tobago, where it grows in dry forest (including xerophytic vegetation), moist forest, disturbed forest edge, and similar secondary vegetation, from 0 to 750(–1000) m.

**Phenology**:—Flowering October through June. Fruiting October through January.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local name:—Bejuco de mecate (Aragua, Venezuela).

**Taxonomic notes:**—*Prestonia exserta* is morphologically related to *P. falcatosepala*, but differs by its shorter inflorescences, with the flowers somewhat clustered, pedicels 7–16 mm, and sepals not falcate. Other similar species includes *P. folsomii* and *P. parvifolia*, which, however, have free corona lobes completely included within the tube (vs. corona lobes with the apices conspicuously exserted in P. exserta).

Woodson (1936) distinguished *Prestonia exserta* from *P. velutina* mainly by the shape and length of the floral bracts. However, study of the types and additional collections, shows an intergradation of these characters, with many intermediate states; thus, *P. velutina* is reduced to the synonymy of the former. The flowers on the two types are indistinguishable and some other slight differences in shape and pubescence of the leaves intergrade. The pubescence is more dense in specimens from dry areas (compared to those from moist forest), but even in collections from the same locality, density of the indumento is highly variable. In general, pubescence is very variable in many genera of Apocynaceae (e.g., Morales, 1999) and therefore, this character should be used with caution and only in conjunction with other morphological features.

Prestonia fendleri (overlooked by Woodson (1936)), is reduced to the synonymy of *P. exserta* here. The types of *P. fendleri* and *P. velutina* were sent to Venezuela in 1978, but the loan was lost in the mail. Two lectotypes are selected, choosing the best preserved specimens among the remaining isotypes.

Additional specimens examined:—PANAMÁ. Coclé: Aguadulce, 14 November 1976, Calderón 16 (CR, MO, PMA); a lo largo de la carretera Panamericana, 178 W of Panama city, 12 December 1977, Folsom 6899 (MO, PMA). Darién: cerca de Veracruz, 15 Octuber 1962, Duke 6068 (MO). Herrera: vía a Potuga, 24 Octuber 1978, Hammel 5272 (MO). Panamá: Arraiján Loma del Río, 10 November 2002, Aiello 1624 (PMA), Aiello 1658 (PMA); Isla Taboga, 16 December 1938, Allen 1289 (EAP, GH, MO); Palo Seco, 17 November 1940, Allen 2248 (MO, US); Panamá, parque Metropolitano, 4 December 1995, Galdames & Oedegaard 2400 (PMA); playa Farfan, 2 January 1972, Gentry 3555 (MO); Bella Vista, 16 Octuber 1922, Killip 12009 (US); Isla Taboga, February 1923, Macbride 2785 (F); Matías Hernández, 25 December 1914, Pittier 6904 (US); cerca de Culebra, February 1912, Pittier 5723 (US); ½ km SE of Summit Gardens, 2 February 1974, Nee 9522 (CR, MO, PMA, VEN); Panamá, parque Metropolitano, 29 October 2000, Sakai 646 (PMA); Isla Taboga, December 1923, Standley 27046 (US); Balboa, November 1923-January 1924, Standley 32155 (US); Penonome, 23 February-March 1908, Williams 362 (NY, US). Veraguas: Río Santa María, SO de Aguadulce, 11 February 1982, Knapp et al. 3321 (CR, MO).

COLOMBIA. Bolivar: Santa Rosa, Bayunca, Finca Canalete, 14 February 2000, Correa & Gómez 1748 (HUA); entre Cartagena y Turbaco, 16 January 1941, Dugand & Jaramillo 2839 (COL, US). Cesar: Poponte, valle del Magdalena, 19 Octuber 1924, Allen

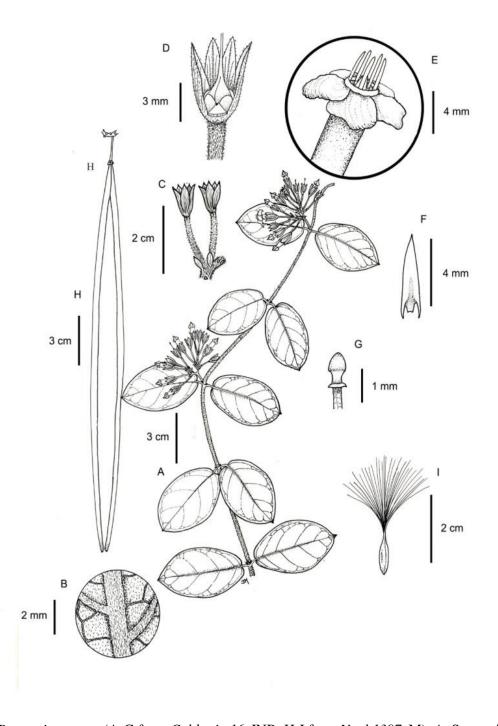


Fig. 28 Prestonia exserta (A-G from Calderón 16, INB; H-I from Vogl 1397, M). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyces, pedicels, and floral bracts. D. Mouth of the corolla tube, showing the exserted free coronal lobes. E. Anther, dorsal view. F. Style-head. F. Calyx with a sepal removed, showing the colleter, nectaries, and ovary. H. Follicles. I. Seed.

777 (MO). Chocó: Loma de los Colorados, cerca a San Juan de Nepomuceno, 31 December 1992, Gentry et al. 78449 (MO). Cundinamarca: Nariño, camino a Los Mangos, 15 February 1986, Fernández-Alonso & Jaramillo 5311 (COL); camino a Puerto Bogotá, entre Río Magdalena a Puerto Salgar, 5 March 1977, Gentry et al. 18083 (COL, MO); vicinity of Apulo, 5 May 1944, Killip et al. 38269 (COL); Girardot, 15 September 1929, Toro 59 (NY). Huila: Villavieja, desierto de la Tatacoa, Doche, 8 January 2003, Figueroa & Calderón 45 (COL); Villavieja, desierto de La Tatacoa, vereda cabuyal, Quebrada Los Hoyos, 22 April 2003, Figueroa et al. 219 (COL); Villavieja, desierto de la Tatacoa, San Nicolás, 29 Octuber 2003, Figueroa et al. 383 (COL), Figueroa et al. 390 (COL); Villavieja, desierto de La Tatacoa, El Cardón, 30 Octuber 2003, Figueroa et al. 409 (COL); Villavieja, resguardo Indígena Tatacoa, 31 Octuber 2003, Figueroa & Galeano 450 (COL, CR). Magdalena: Magdalena, February 1876, André 1538 (K); Cienaga Río Frío, January 1949, Romero-Castañeda 1362 (COL); Tucurinca, 1 March 1950, Romero-Castañeda 2135 (COL). Santander: Cepitá, 16 December 1998, Albesiano & Buenahora 633 B (COL, CR); 40 km al S de Bucaramanga, 16 December 1948 Araque & Barkley 328 (COL, FMB, MEDEL, MO, US, VALLE); entre el Cañón del Chicamocha y Valle de Rupala, 14 June 1962, Saravia 853 (COL). Tolima: Valle del Río Magdalena, Armero, 6 Octuber 1940, Cuatrecasas 10536 (COL); Carmen de Apicalá, entre Girardot y Carmen de Apicalá, 30 April 1973, Escobar 206 (HUA); Chicoral, 13 May 1949, Haught 6437 (COL, MO, US); Flandes, 18 December 1946, Schneider 202 (COL), 26 July 1950, Schneider 987 (S); Valle del Alto Magdalena, La Chamba, 1 November 1962, Uribe 4129 (COL, US); Beltran 19 May 1926, Woronow & Juzepczuk 4878 (LE [2 sheets]). Data lacking: s.d., Goudot s.n. (K).

VENEZUELA. Aragua: Parque Nacional Henry Pittier, al S de Cata, 14 April 1981, Carnevali et al. 554 (VEN); Maracay, 9 June 1968, Ferrari 412 (VEN); carretera La Victoria-Guacamaya, S de La Victoria, 1976, Morillo et al. 6591 (MER); Quebrada Seca, al N de Las Tejerías, 16 September 1978, Morillo 7738 (MO, VEN); Parque Nacional Henry Pittier, al S de Cata, 12 April 1981, Morillo et al. 8456 (VEN); entre Cagua y Villa de Cura, 5 February 1935, Pittier 13561 (MO, US); Trinidad de Maracay, 18 April 1913, Pittier 6047 (US); Cata, 20 Octuber 1975, Trujillo 13375 (VEN); Maracay y Valencia, 20

December 1938, Williams & Alston 330 (BM, EAP, F, MICH, NY, S, U, US, VEN); entre El Consejo y La Victoria, 19 February 1928, Williams 11057 (F, US, VEN); Maracay, 1934, Vogl 1397 (M [3 sheets]). Bolivar: Cedeño, cercanías de Panare, 7 Octuber 1985, Boom & Grillo 6284 (VEN); Cedeño, villa Panare de Corozal, 27 September 1985, Boom & Grillo 6155 (NY); Distrito Piar, base SE del Auyan-tepuí, a lo largo del Río Uruyén, 23 November 1982, Davidse & Huber 22533 (MO, NY, VEN); N de El Dorado, 15 March 1974, Gentry et al. 10457 (MO, VEN); Caño Pablo, tributario del Río Caura, 10 May 1982, Liesner & Morillo 14005 (MO, VEN); entre El Dorado y Santa Elena de Uairén, 21 September 1980, Maas & Steyermark 5331 (VEN); Río Caura, Río arriba del Campamento Las Pavas, May 1982, Morillo & Liesner 8894 (MO, VEN); Río Caura, Salto Para, 12 May 1982, Morillo & Liesner 9164 a (VEN); Altiplanicie de Nuria, al E de Miamo, 8 January 1961, Steyermark 88185 (MO, NY, VEN). Carabobo: Puerto Cabello, 3 January 1955, Asplund 15119 (S, UPS). Distrito Federal: Caracas, September 1971, Aristeguieta 7961 (VEN); La Guaira, April 1854, Birschit s.n. (K); camino El Rincón-Las Tunitas, al SE de Maiquetía, 4 June 1971, Morillo & Manara 1102 (VEN); Cordillera de la Costa, desde El Humboldt hasta Boca del Tigre y bajando a Punta de Mulatos, 12 March 1972, Morillo & Manara 1916 (VEN); Vargas, entre Macuto y Caraballeda, 11 June 1972, Morillo 2375 (VEN); cerca a Mamo, 1923, Pittier 11092 (G, US, VEN); Puerto Escondido, 2 March 1930, Pittier 13412 (G, NY, US, VEN); Parque Nacional El Ávila, Quebrada del Río Anare, 11 June 1984, Rutkis 860 (VEN). Falcón: Parque Nacional Morrocoy, Cerro de Chichiriviche, s.d., Guariglia & Rodríguez 1335 (VEN); S de Punta Faustina, SE de Chichiriviche, 29 August 1974, Steyermark & Manara 110403 (VEN). Guarico: entre Altagracia de Orituco y Taguay, September 1966, Aristeguieta & Agostini 6440 (MO, US, VEN); carretera Ipare-San Francisco de Maicara, al NE de Ipare, December 1976, Morillo 4886 (VEN); Camatagua, November 1975, Restan 33 (VEN). Lara: Palavecino, desde La Mata hacia el Parque Nacional Terepaima, 23 Octuber 1981, Burandt & Decaer 991 (VEN); Palavecino, La Miel, 28 December 1966, Smith 411 (VEN); cerca de Caballito, carretera Barquisimeto-Acarigua, 13 January 1976, Tillett et al. 761-4 (VEN). Mérida: La Victoria, 21 November 1856, Fendler 2111 (BM, GH, K, MO). Miranda: Hacienda El Volcán, cerca a Santa Lucía, 10-16 May 1918, Pittier 8272 (US); Cuá, Hacienda Buenavista, 18 Octuber 1980, Ramírez 288 (VEN); S de Los Teque, 10 December 1943,

Steyermark 54980 (F, MO). Data lacking: September año perdido, Moritz 1900 (HBG); 16 December 1901, Warming 308 (C).

TRINIDAD AND TOBAGO. Eastern Tobago: Welbeck, 23 November 1912, Broadway 4350 (M, NY); cerca de Charlotteville, 16 Octuber 1937, Sandwith 1799 (K). Port de Spain: Port de Spain, 20 November 1921, Williams 10966 (NY). San Juan Laventille: camino a Spring, Scarborough, 13 November 1911, Broadway 4150 (L, NY, S, U, Z); Cascade, St. Anna, 4 December 1923, Broadway s.n. (F, NY). Siparia: Erin, March 1908, Broadway 2730 (NY). Western Tobago: Estación Botánica Tobago, 6 December 1909, Broadway 3373 (NY, C, SI); Whim, Tobago, 2 April 1940, Cheesman 297 (MO); Bacolet, 13 Octuber 1937, Sandwith 1753 (K). Without exact locality, 1877–1880, Fendler 623 (K, NY, P).

Prestonia falcatosepala J.F. Morales (2004: 162). Type:—ECUADOR. Carchí: border between Carchí and Esmeraldas, road from Lita to Alto Tambo, 27 June 1991, H. van den Werff, B. Gray & G.A. Tipaz 12076 (holotype MO!, isotype CR!). Fig. 27, 29

Stem minutely and sparsely puberulent when young, glabrous to glabrescent at maturity, with clear latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, ca. 1 mm long. Petioles 1–1.8 cm; leaf blade  $3.2-7 \times 1.9-3.5$  cm, elliptic, ovate-elliptic to ovate, apex acuminate to caudate, base obtuse to rounded or truncate, membranaceous, glabrescent to very sparsely and inconspicuously puberulent adaxially, glabrescent to minutely puberulent abaxially, secondary veins impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. Inflorescence a monochasial cyme, axillary, longer than the adjacent leaves, many-flowered, the flowers laxly disposed, very sparsely puberulent to glabrescent peduncle 4–11 cm, pedicels 1.8-3 cm long, floral bracts  $4-5 \times 0.5-1$  mm, linear, scarious, minute, green. Sepals  $7-10(-11) \times 2-3.5(-4)$  mm, free, membranaceous, narrowly elliptic, falcate, the apices acuminate, not reflexed, inconspicuously puberulent to glabrous or glabrescent, very small, rarely slightly subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed, colleters ca. 1 mm long, subentire to irregular and minutely erose at the apex. Corolla salverform, the tube reddish green, the lobes yellow, with purple lines basally,

glabrous or glabrescent outside, tube  $15-18 \times 3-4$  mm, more or less straight, free corona lobes 3–4 mm long, almost completely exserted, their height conspicuously surpassing that of the anther apices, annular corona entire, thickened, corolla lobes  $10-11 \times 8-10$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5–6 mm, dorsally glabrous, the apices slightly exserted. **Ovary** 1.5–2 mm tall, glabrous, style-head 1.1–1.4 mm, nectary 1–1.5 mm, conspicuously shorter than the ovary, variously 5-lobed, sometimes almost completely divided into 5 lobes, each one entire. **Follicles** 22.5–29  $\times$  0.2–0.3 cm, continuous, completely connate longitudinally, glabrous, without lenticels, membranaceous when old; seeds 7–8 mm, coma 1.5–3 cm, cream.

**Distribution and habitat**:—Premontane forest and montane forest (including forest edges) in Colombia, northwestern Ecuador, and northern Peru, from 550 to 1400 m.

**Phenology**:—Specimens with flowers have been collected from February to June, and November and with fruits in June and July.

Conservation Assessment:—Vulnerable (VU).

**Taxonomic notes**:—*Prestonia falcatosepala* is somewhat similar to *P. exserta* can be recognized by its glabrescent to inconspicuously puberulent leaf blades, elongated and unbranched inflorescences, with peduncles 4–11 cm, flowers laxly disposed, scarious floral bracts, pedicels 1.8–3 cm, falcate sepals, free corona lobes, anthers with the apices exserted, and follicles longitudinally completely connate.

Additional specimens examined:—COLOMBIA. Antioquia: Urrao, vereda Calles, Parque Nacional Natural Las Orquídeas, Río Calles, 30 November 1993, *Cogollo et al.* 7608 (JAUM, MO); Urrao, Vereda Cruces, Vereda Cruces, camino al Río Penderisco desde la escuela La Esperanza, alrededores del puente sobre el Río Penderisco, Parque Nacional Natural Las Orquídeas, 6 May 2013, *Hoyos-Gómez et al.* 2313 (COL); Frontino, carretera de Nutibara a La Blanquita, 5 November 1988, *Zarucchi et al.* 7175 (HUA, MO). Chocó: carretera Tutunendo a El Carmen, Alto Río Atrato, alrededores del campamento El Doce, 28 April 1979, *Forero et al.* 6030 (COL, MO); 31 km E de Quibdó, ca. 14 km E de Tutunendo, cerca a la villa Chocoana El Veintiuno, 14 June 1982, *Gentry & Brand* 36932 (COL, JAUM, MO, USF). Risaralda: Mistrató, San Antonio de Chamí, carretera a La Mesenia, 27 April 1992, *Betancur et al.* 3485 (COL).

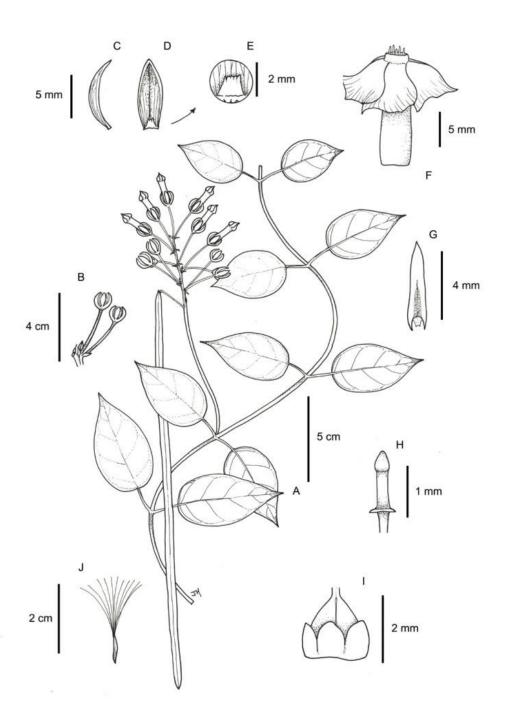


Fig. 29 Prestonia falcatosepala (Werff et al. 12076, INB). A. Stem with inflorescence and follicles.
B. Calyx, pedicels, and bracts. C. Sepal, lateral view. D. Adaxial view of the sepal. E. Colleter. F. Corolla. G. Anther, dorsal view. H. Style-head. I. Nectary and ovary. J. Seed.

ECUADOR. Carchí: Tulcán, parroquia Tobar Donoso, Sector Sabalera, June 1992, *Tipaz et al. 1234* (QCNE). Esmeraldas: Esmeraldas, Lita-San Lorenzo road, 10 km NW of Lita, 11 May 1990, *Gentry et al. 70178* (CR, MO, QCNE); without exact locality, 1881, *Lehmann 729* (G). Pichincha: Reserva ENDESA, Río Silanche, km 113 de la carretera Quito-Puerto Quito, 10 km al N de la carretera principal, 22 February 1984, *Jaramillo 6393* (AAU, MO, QCA), 21 March 1985, *Jaramillo 7572* (AAU, MO, QCA).

PERÚ. Junín: Chanchamayo, Río Colorado, 22 March 1984, *Smith et al.* 6479 (CR, MO, USM).

Prestonia folsomii J. F. Morales (1996: 285). Type:—COLOMBIA. Valle del Cauca: Buenaventura, Bajo Calima region, between Buenaventura and Málaga, km 51.3, 8
February 1990, T. Croat & J. Watt 70348 (holotype CR!, isotypes MO!, USF!). Fig. 27, 30

**Stem** densely and minutely puberulent when young, glabrescent at maturity, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 0.5–1 mm long. **Petioles** 0.4–1.2 cm; leaf blade  $(2.5-)4-12 \times (1.8-)2.5-5.5$  cm, elliptic, obovateelliptic to narrowly oboyate, apex acuminate or abruptly apiculate, base cuneate to obtuse, membranaceous, very sparsely puberulent to glabrescent adaxially, usually puberulent abaxially, secondary veins impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. Inflorescence a monochasial cyme, rarely a dichasial cyme (but with just one basal branching), axillary, shorter than the adjacent leaves, few- to many-flowered, the flowers somewhat clustered, minutely puberulent, peduncle 2.2–4 cm, pedicels 0.7–2.4 cm long, floral bracts  $2.5-4 \times 1-1.3$  mm, linear to linear-ovate, scarious, minute, green. Sepals 8-13 × 3-4 mm, free, membranaceous, narrowly ovate, narrowly elliptic to elliptic, the apices acute, not reflexed, sparsely puberulent, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed or the veins slightly impressed and rather inconspicuousl, colleters ca. 1 mm long, entire to inconspicuously erose at the apex. Corolla salverform, yellow to yellowish green, glabrous to glabrescent outside, tube  $11-14 \times 3-4$  mm, straight, free corona lobes 2–3 mm long, the apices slightly exserted, their height equaling or slightly surpassing that of the anther apices, annular corona thickened, entire, corolla lobes

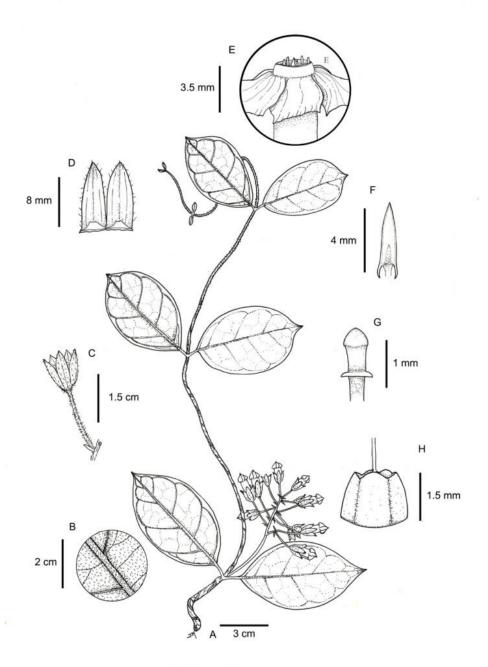


Fig. 30 *Prestonia folsomii* (*Croat & Watt 70348*, INB). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bract. D. Adaxial view of two sepals, showing the basal colleters. E. Corolla mouth, showing the annular corona, and the apices of the free coronal lob. F. Anther, dorsal view. G. Style-head. H. Nectary.

 $12-14 \times 8-9$  mm, obliquely obovate to obliquely narrowly obovate. **Stamens** inserted near the corolla mouth, anthers 4-4.5(-5) mm, glabrous to glabrescent dorsally, the apices exserted. **Ovary** 1–1.5 mm tall, glabrous, style-head 1–1.3 mm, nectary 1.5–2 mm, conspicuously longer than the ovary, slightly to moderately 5-lobed, each lobe entire to subentire. **Follicles** unknown.

**Distribution and habitat**:—Southeastern Panama and southeastern Colombia in tropical wet forest and premontane rainforest, from 100 to 800 m.

**Phenology**:—It flowers sporadically from March-August.

Conservation Assessment:—Endangered (EN) (IUCN 2001).

**Taxonomic notes:**—This rarely collected species resembles *P. exserta*, sharing membranaceous leaves, scarious bracts, inflorescences with flowers somewhat clustered, and stamen apices exserted. *Prestonia folsomii* is recognized by the free corona lobes with apices exserted, but conspicuously surpassed by the apices of the anthers, and the somewhat shorter corolla tube. In addition, this species is restricted to tropical wet forest and premontane rainforest, whereas *P. exserta* is more common in dry forest (including xerophytic vegetation) and moist forest.

Additional specimens examined:—PANAMÁ. Coclé: 7 km N de El Copé, 18 August 1977, Folsom 4954 (MO). Panamá: carretera El Llano-Cartí, km 19.1, 6 May 1985, Nevers et al. 5620 (MO), 11 March 1986, Nevers et al. 7346 (MO, USF).

COLOMBIA. Antioquia: Frontino, Encarnación, Parque Nacional natural Las Orquídeas, sector Venados, 11 April 2011, *Betancur et al. 15159* (COL).

*Prestonia parvifolia* K. Schumann ex Woodson (1936: 302). Type:—ECUADOR. Manabí: cerca a Hacienda El Recreo, 6 May 1895, *B. Eggers 15430* (lectotype K! designated by Morales (2006 b), isolectotypes P! [2 sheets], US!). **Fig. 31, 32.** 

**Stem** sparsely puberulent when young, glabrescent at maturity, with milky latex, sparsely lenticellate, these not subcrose, intrapetiolar colleters minute, less than 1 mm long. **Petioles** 0.4–0.7(-0.9) cm; leaf blade 3.5–7(14.5) × 1.6–4.2(9) cm, elliptic, obovate-elliptic to obovate, apex short-acuminate, base obtuse to cuneate, membranaceous, sparsely puberulent to glabrescent adaxially, densely to sparsely puberulent abaxially, rarely

glabrescent, secondary veins impressed on both surfaces, tertiary veins rather inconspicuous. Inflorescence a dichasial cyme, axillary, shoter or equaling adjacent leaves, few- to many-flowered, the flowers somewhat clustered, the flowers usually clustered, minutely puberulent to hirsutulous, peduncle 0.5–1 cm, pedicels 0.7–1.3 cm long, floral bracts 7-11 × 3-4 mm, narrowly elliptic to narrowly ovate-elliptic, conspicuously foliaceous, green. Sepals  $10-15 \times 2.5-4(-5)$  mm, free, membranaceous, very narrowly elliptic to very narrowly obovate, the apices shortly acuminate, not reflexed, minutely and sparsely puberulent, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins usually conspicuous and impressed, colleters 1–1.5 mm long, subentire to minutely lacerate or erose at the apex. Corolla salverform, the lobes cream or pinkish cream, glabrous, glabrescent or inconspicuously puberulent outside, tube 15–18 × 4–4.5 mm, straight, free corona lobes 3-4 mm long, the apices exserted, their height surpassing that of the anther apices, annular corona thickened, entire, corolla lobes  $8-10 \times 5-7$  mm, obliquely obovate. Stamens inserted near the corolla mouth, anthers 5-6 mm, dorsally glabrous, included or the apices barely exserted. Ovary 1.5–2 mm tall, glabrous, style-head 1.3–1.8 mm, nectary 0.8–1.1 mm, shorter than the ovary, variously 5-lobed, each lobe entire, subentire to irregularly lacerate. Follicles unknown.

**Distribution and habitat:**—Dry forest in Ecuador (and doubtful in Peru), where it grows in primary forest, disturbed forest edge, vegetation on rocky outcrops, cliffs and secondary vegetation along roadsides, at 0–500 m. This species is known in Peru from a single specimen (collected by *Ruiz & Pavon*), but without any data of locality.

**Phenology**:—Specimens with flowers have been collected in January, February, July, September, and October.

**Conservation Assessment**:—Critically endangered (CR)

Local name:—Vetilla (Guayas, Ecuador).

**Taxonomic notes:**—This species is morphologically related to *P. folsomii* and *P. didyma*, but can be distinguished by the following combination of characters: free corona lobes with the apices exserted, their height surpassing that of the anther apices, leaf blades minutely puberulent on the abaxial surface, peduncle less than 1 cm long, floral bracts 7–11 mm, and anthers 5–6 mm. One additional character is that *P. parvifolia* grows in dry forest in Ecuador and Peru, whereas *P. folsomii* grows in tropical wet forest and premontane

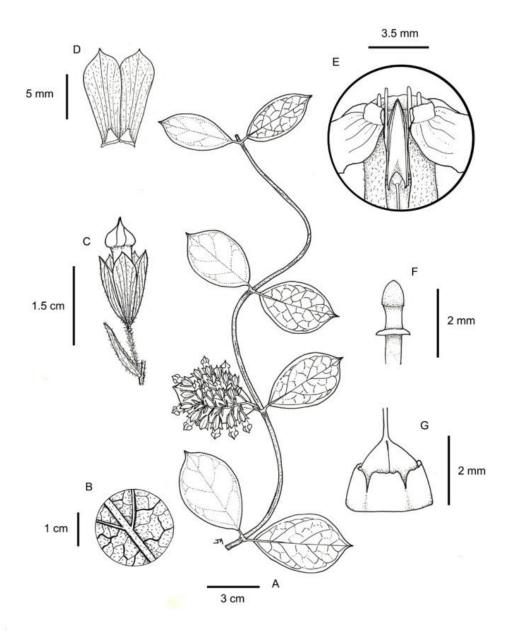


Fig. 31 *Prestonia parvifolia* (*Eggers 15078b*, O). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Sepals, pedicel, and bract. D. Adaxial view of two sepals, showing the basal colleters. E. Open corolla mouth, showing the <u>anthers</u> and free coronal lobes. F. Stylehead. G. Nectary and ovary.

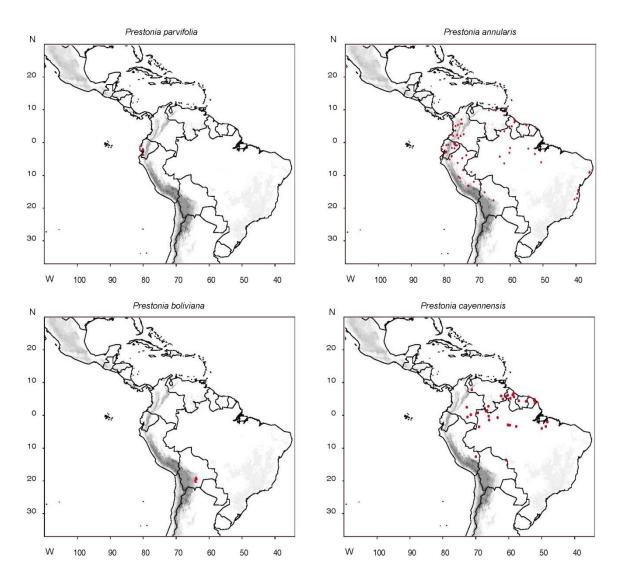


Fig. 32 Distribution maps of Prestonia parvifolia, P. annularis, P. boliviana and P. cayennensis

rainforest in southeastern Panama and southeastern Colombia, and *P. didyma* is endemic to tropical wet forest and coastal vegetation in southeastern of Brazil.

The collection *Tafalla s.n.* was distributed under the name of *Pavón s.n.*, but Ruiz & Pavón never collected in Ecuador. Also, probably the collection from Peru, is a Tafalla specimen from Ecuador, wrongly distributed under the Pavón name. For further information see Tafalla (1989).

**Additional specimens examined**:—ECUADOR. El Oro: camino entre Arenillas y El Toro, 23 nov-15 December 1978, *Escobar et al. 926* (MO). Guayas: Guayaquil, 16

February 1939, Asplund 5010 (CR, S); cercanías de Guayaquil, Cerro Azul, 13 June 1955, Asplund 16626 (S); Guayaquil, 22 February 1991, Cerón 13354 (MO); Bosque Protector Cerro Blanco, September 1994, Cornejo 180 (GUAY); Cerro Azul, 26 June 1994, Cornejo & Bonifaz 2932 (GUAY); Botadero San Eduardo, 28 Octuber 1996, Cornejo & Bonifaz 5339 (GUAY); Capeira, entre Guayaquil a Daule, 15 January 1983, Dodson et al. 13375 (MO, SEL); Cerro Azul, cerca a Casa Viejas, carretera a Salinas, 25 September 1981, Dodson & Dodson 11529 (CR, MO, Q, SEL, USF); Guayaquil, s.d., Tafalla s.n. (distributed as Pavón) (BR, G [2 sheets], OXF, US). Manabí: El Recreo, July 1893, Eggers 15078b (LD [2 sheets], O, PR, US); 12 km de Guayaquil a Playa Salina, 21 April 1962, Gilmartin 677 (NY); Guayaquil, Bosque Protector Cerro Blanco, Cerro Mirador de Monos, 26 February 1992, Rubio & Palacios 2467 (CR, MO, QCNE); Guayaquil, s.d., Spruce s.n. (K).

PERÚ. Data lacking: 1799, Ruiz & Pavón 17/51 (G, MA).

- IV. Prestonia sect. Haemadictyon K. Schum., Nat. Pflanzenfam. 4: 188. 1895. Sect. Acutifoliae Woodson, Ann. Missouri Bot. Gard. 23: 284. 1936, nom. illeg. Type: Prestonia acutifolia (Benth. ex Müll. Arg.) K. Schum. Nat. Pflanzenfam. 4: 188. 1895. Haemadictyon acutifolium Benth. ex Müll. Arg. Fl. Bras. 6: 167. 1860.
- Sect. Annulares Woodson, Ann. Missouri Bot. Gard. 23: 296. 1936. Type: *Prestonia annularis* (L.f.) G. Don, Gen. Hist. 4: 84. 1837. *Echites annularis* L.f., Suppl. Pl. 166. 1781[1782].
- Prestonia annularis (L.f.) G. Don (1837: 84). Echites annularis L.f. (1781: 166).
  Haemadictyon (?) annulare (L. f.) Candolle (1844: 428). Temnadenia annularis (L. f.) Miers (1878: 216). Type:—SURINAME. Without data. Herb. Alstroemerii s.n. (lectotype, designated by Morales (2007b) S-LINN 09–34535!). Fig. 32, 33.
- Prestonia brittonii N. E. Brown (1924: 5) syn. nov. Type:—TRINIDAD AND TOBAGO. Heights of Aripo, 10–26 January 1922, W. Broadway 10009 (holotype NY!).
- Prestonia guianensis Gleason (1926: 299) syn. nov. Type:—GUYANA. Pomeroon-Supenaam: Pomeroon river, 17–24 December 1922, *J. Cruz 3097* (holotype NY, lost; lectotype (designated here) US!, isolectotypes GH!, MO!, US!).

- Prestonia purpurissata Woodson (1936: 311) Type:—COLOMBIA. Valle del Cauca: La Cumbre, 14–19 May 1922, F. Pennell 5719 (holotype US!, isotypes GH, n.v., MO!, NY!).
- Prestonia finitima Woodson (1936: 312). Type:—BRAZIL. Amazonas: Humayta, near Tres Casas, 14 September–11 October 1934, *B. Krukoff 6190* (lectotype NY! designated by Morales (2007b), isolectotypes A! [2 sheets], B!, F!, GH, n.v., K!, MICH!, MO!, S!, U!, US!).
- Prestonia phenax Woodson (1936: 314) Type:—PERU. Loreto: Urwald, Ucayali, 26 July 1923, G. Tessmann 3046 (lectotype NY! designated by Morales (2010a)).
- Prestonia peregrina Woodson (1936 : 334) Type:—ECUADOR. Pichincha: Tanpadi, July 1920, O. Heilborn 771 (holotype S!, isotypes G!, G-DC!, GH!, S!).
- Prestonia vallis Woodson (1936: 335) Type:—COLOMBIA. Valle del Cauca: Bravo river, 27 July 1962, *J. Robinson 133* (neotype, CR!, designated by Morales (2010a); isoneotypes, COL!, K!, MO!, US!).
- Prestonia discolor Woodson (1936: 386) syn. nov. Type:—GUYANA. Cuyuni-Mazaruni: Karau creek, Mazaruni river, 25 May 1933, T. Tutin 141 (holotype BM!, isotype CGE!).
- Prestonia morilloi Markgraf (1975: 249) Type:—VENEZUELA. Distrito Federal: El Avila National Park, between Topo Macanillal and Pico Izcaragua, 15 July 1973, *G. Morillo*, *B de Morillo* & *B. Manara 3248* (holotype Z!, isotypes CAR, n.v., MY!, VEN!).

**Stem** minutely puberulent when young, glabrous to glabrescent at maturity, with clear latex, the lenticels more or less common, but not suberose, intrapetiolar colleters minute, 0.5-1 mm long. **Petioles** (0.5-)0.7-3(-3.5) cm; leaf blade  $(5.5-)8-39(-42)\times(3.5-)4.5-22$  cm, narrowly elliptic, elliptic, ovate-elliptic to broadly ovate, apex acuminate, caudate or acute, base obtuse to rounded, membranaceous, sometimes slightly revolute, glabrous, rarely inconspicuously papillate-puberulent along the midrib abaxially, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers more or less clustered, minutely puberulent to glabrous or glabrescent, peduncle 1.5-8 cm, pedicels (0.8-)1-2.2(-2.8) cm long, floral bracts  $1-5\times0.5-1$  mm, linear, scarious, minute, green.

**Sepals**  $(6-)9.5-18 \times (1.5-)3-5$  mm, free, coriaceous to subcoriaceous, narrowly ovate, ovate-elliptic, elliptic to narrowly elliptic, the apices acute to shortly acuminate, not reflexed, glabrous to glabrescent, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins inconspicuous, not impressed, colleters 0.5–2 mm long, minutely erose at the apex. Corolla salverform, the tube pink or cream, the lobes yellow (with purple stripes), greenish white, white or reddish white, glabrous to glabrescent outside, tube 13–18  $\times$  3–5 mm, sometimes somewhat inflated at the base, free corona lobes 1–1.5(–2) mm long, deeply included, their height conspicuously surpassed by that of the anther apices, annular corona entire to subentire, thickened, corolla lobes 7-15(-17) × 6-12 mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5–6 mm, minutely puberulent to glabrescent dorsally, the apices slightly exserted or barely included. Ovary 1–2 mm tall, glabrous, style-head 1-2 mm, nectary 1.2-2.3 mm, surpassing the ovary, irregularly 5lobed, rarely completely divided into 5 separate nectaries, each one irregularly lacerate, minutely puberulent to glabrous or glabrescent. Follicles  $31-46 \times 0.5-0.8$  cm, continuous to inconspicuously articulated, free, but usually united at the tips (at least when young), glabrous, without lenticels, membranaceous when old; seeds 14–20 mm, coma 2–4 cm, tan to brown.

**Distribution and habitat:**—Tropical wet forest, wet savannas, flooded forest, premontane and montane forest, and disturbed areas in Colombia, Ecuador, Venezuela, Trinidad and Tobago, Guyana, Suriname, Peru, Bolivia, and northeastern Brazil, from 0 to 2000(2300) m.

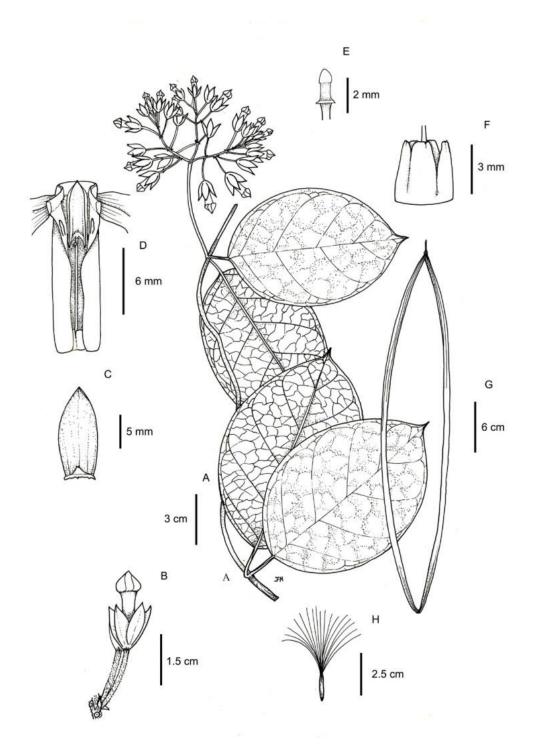


Fig. 33 *Prestonia annularis* (A-F from *Jaramillo et al. 632*, INB; G-H from *Henkel et al. 1753*, US). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of the sepal, showing the colleter at the base. D. Open corolla tube, showing the free coronal lobes deeply included, anthers, and anular corona. E. Style-head. F. Nectary. G. Follicles. H. Seed.

**Phenology**:—Flowering from June through March. Fruiting September through March.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local name:—Bejuco lecho blanco (Cauca, Colombia).

**Taxonomic notes:**—*Prestonia annularis* can be confused with *P. portobellensis* and *P. robusta*, a group of species that shares features such as similar leaf shape, inflorescence structure, and firmly membranaceous follicles (except *P. robusta*). *Prestonia annularis* is easily separated by its shorter free corona lobes (1-1.5(-2) mm vs. (2.5-)4-5 mm), that are deeply included within the corolla tube (vs. exserted). *Prestonia robusta* differs by its free corona lobes with apices deeply included (vs. barely included or exserted), and smaller and thicker follicles  $(16-19.5 \times (0.7-)1.1-1.3 \text{ cm vs. } 31-46 \times 0.5-0.8 \text{ cm})$ .

The types of *Prestonia brittonii P. discolor*, and *P. guianensis* matches the type of *P. annularis*, and thus, relegated to its synonymy. At the time of Woodson's monograph, *P. annularis* was known from only five collections, and these species only from the type. The study of the many specimens available since them, shows that the characters used by Woodson (1936) to recognize them (leaf blade apices and sepals color) can vary even on the same specimen.

In 1978, a loan (with several types) sent from the New York Botanical Garden (NY) to the Herbario Nacional de Venezuela (VEN) was lost, which included the holotype of *P. guianensis*. Therefore, a lectotype is selected here from among the remaining isotypes.

Ruiz & Pavón never collected in Ecuador and the collection from Guayaquil probably is a Tafalla specimen with a wrong locality (Guayaquil). For further information see Tafalla (1989).

Additional specimens examined:—COLOMBIA. Antioquia: Jardín, vereda Las Manguitas, Finca La Margarita, borde del Río Docató, 19 September 1986, *Marulanda et al. 166* (HUA); Río Segovia, Segovia, 21 July 1979, *Renteria et al. 1728* (COL, HUA); San Luis, La Loma, antes de llegar al Río Claro, s.d., *Renteria et al. 5062* (HUA); Inza, corregimiento de Turminá, parte baja de microcuenca Quebrada La Chorrera, 8 July 2011, *Restrepo & Salazar 577* (CAUP). Boyacá: Puerto Boyacá, Dos Quebradas, 25 November 1997, *Méndez 69* (COL). Caquetá: San Vicente del Caguán, Los Monos, Cordillera

Oriental, 24 November 1990, *Betancur & Churchill 2090* (HUA); Florencia, corregimiento de Santo Domingo, vereda Santander, finca Mónaco, 16 March 2012, *Restrepo & Aguilar 776* (CAUP); Florencia, corregimiento de Santo Domingo, vereda Santander, finca Mónaco, 28 March 2012, *Restrepo & Aguilar 900* (CAUP). Cauca: Quebrada La Laguna, 15 October 1944, *Core 1260* (US); cabeceras del rìo Pinche, al NO de Argelia, 27 September 1944, *Core 1373* (US); Timbiqui, Quebrada Yucal, tributario del Río Bubuey, comunidad Indígena Almorzadero, 24 September 2000, *Reina et al. 937* (CAUP). Chocó: Bahía Solano, Puerto Mutis, 4 January 1973, *Gentry & Forero 7162* (COL, MO, Z); Río Taparí, San Juan, 20 August 1962, *Hugh-Jones 290* (CGE, K). Meta: Parque Nacional Natural Tinigua, Río Duda, Serranía Chamusa, Centro de Investigaciones Ecológicas La Macarena, April 1997, *Stevenson 2040* (COAH, COL, HUA, NY).

VENEZUELA. Anzoátegui: a lo largo de Río Cangrejo, Río Zumbador, NE de Bergantín, 24 February 1945, *Steyermark 61175* (F [2 sheets], MO, VEN). Carabobo: a lo largo de Río San Guían, S de Borburata, 2 April 1966, *Steyermark et al. 95446* (MO, US, VEN, Z). Delta Amacuro: Winikina river, N of the Yaruara confluence, May 1997, *Werner et al. 285* (NY). Distrito Federal: Cerro Naiguatá, Parque Nacional El Ávila, August 1979, *Manara 1007* (VEN); *Morillo et al. 3248* (CAR, MY, VEN, Z). Lara: NE de El Altar, vía Buria, 12 February 1978, *Smith & Junior 9000* (UCOB, VEN). Miranda: Parque Nacional Guatopo, Sitio Agua Blanca, March 1966, *Aristeguieta 6031* (MO, NY, VEN); Guatopo, Santa Crucita, 1974, *Delascio et al. 2201* (MO). Portuguesa: Guanare, entre Biscucuy y Tocuyo, 22 January 1982, *Rutkis 424* (VEN).

GUYANA. Cuyuni-Mazaruni: villa Chinoweing, 21 February 1987, *Pipoly 10411* (NY). Demerara-Mahaica: finca Ramsaroop, 25 January 1992, *Hoffmann & Capellaro 847* (P, US). Potaro-Siparuni: Parque Nacional Kaieteur, 26 January 1987, *Pipoly et al. 10019* (CR, FDG, MO, NY, P, US). Upper Demerara-Berbice: s.l., 31 March 1993, *Henkel et al. 1753* (P, US); Río Essequibo, Isla Lau Lau, 14 June 1993, *Henkel & Williams 2142* (CR, MO, NY, P, US); Demerara, s.d., *Parker s.n.* (K). Upper Takutu-Upper Essequibo: parte superior del Río Rupununi, cerca a Dadanawa, 30 May 1922, *Cruz 1420* (F, NY, MO, US); Quebradas White y Groete, Río Essequibo, 23 March 1944, *Forest Department 4505* (K, NY).

SURINAME. Brokopondo: Río Surinam, 1912, *Angremond s.n.* (U, Z). Pará: Río Surinam, 26 June 1913, *Alprato 40* (U). Paramaribo: Paramaribo, s.d., *Focke 1056* (U); cerca de la ciudad de Paramaribo, Zorg, 17 November 1960, *Kramer & Hekking 2087* (U); Paramaribo, 25 June 1850, *Wullschlägel 1028* (BR, U, W). Data lacking: s.d., *Hohenacker 629* (S); s.d., *Hostmann et al s.n.* (S).

FRENCH GUIANA. St. Laurent Du Maroni: Haut Tampock, s.d., *Moretti* 67 (CAY), 1977, *Moretti* 671 (CAY [2 sheets]). Locality lacking: 7 March 1874, *Mélinon* 169 (P).

ECUADOR. Azuay: 20-25 km al E de Jesús María, 12 April 1980, Gentry et al. 28508 (MO). Guayas: Comuna Loma Alta, al E de El Suspiro, 1 February 1997, Cornejo & Bonifaz 5559 (GUAY, USF); Cordillera Chongón-Colonche, Cerro La Cruz, 27 September 1997, Cornejo & Bonifaz 5810 (GUAY, USF); Balao, May 1892, Eggers 14527 (L, M); "Guayaquil", 1799, Tafalla s.n. (distributed as "Ruiz & Pavón" F, MA). Los Ríos: Estación Biológica Río Palenque, 1 September 1972, Dodson & McMahon 5029 (QCA). Morona-Santiago: Gualaquiza, Misión Bomboiza, 1967, Sparre 19066 (NY, S). Napo: Orellana, Río Tiputini, 20 September 1998, Burnham & Kline 1719 (MO, QCNE); Río Tiputini, ca. 20 km al E de la confluencia con el Río Tivacuno, 6-8 km aguas arriba de la estación, 9 November 1998, Burnham & Rodríguez 1814 (F. MICH, MO, OCA, OCNE); Dureno, Comunidad Cofán, S de Río Aguarico, 27 December 1988, Cerón et al. 5835 (MO, QCNE); Nueva Loja, s.d., Lugo 3304 (GB, USF); Las Sachas, carretera Coca-Lago Agrio, 13 February 1973, Lugo 3350 (GB, USF); Santa Cecilia, carretera Lago Agrio-Baeza, ca. 16 km al O de lago Agrio, 27 February 1973, Lugo 3537 (GB, USF); estación INIAP-San Carlos, 5 km al S de las Sanchas, 8 October 1987, Neill et al. 7866 (MO); Orellana, Parque Nacional Yasuní, sobre camino Maxus, 25 June 1995, Neill & Aulestia 10418 (QCNE). Pastaza: Arajuno, campos 11–12, 15–20 September 1998, Freire et al. 3474 (QCNE); Pozo Petrolero Ramírez, 20 km al S de Curaray, 21–28 February 1991, Zak & Espinoza 4916 (MEXU, MO, NY, QCNE, USF).

PERÚ. Amazonas: Condorcanqui, Monte Virgen, Río Santiago, 21 August 1979, Huashikat 113 (MO); Bagua Imaza, región del Marañón, Nueva Samiria, 17 March 1995, Jaramillo et al. 632 (MO). Cusco: La Convención, Santa Ana, Localidad Idma Santi, 17 October 2007, Farfán et al. 1763 (CR, MO); La Convención, Vilcabamba, Paltaybamba, Mesacancha, 9 June 2002, Valenzuela et al. 180 (MO); La Convención, Maranura, Río Blanco, 29 November 2006, Valenzuela et al. 8253 (CR, MO). Loreto: Alto Amazonas, al O de Shucushayacu, Rio Huallaga above Yurimaguas,11 October 1985, Gentry et al. 52228 (MO, USF); Huambisa, Valle del Río Santiago, N de Pinglo, 5 March 1980, Huashikat 2204 (MO, UC, Z); Maynas, Irío Momón, del caserío de Sargento Lores al caserío de Punta Alegre, 5 April 1988, Rimachi 8546 (F, NY); Iquitos, Loreto, San José de Parinari, Río Marañón, 10 August 1981, Vásquez et al. 2286 (CR, MO, USF). Madre de Dios: Manú, Cocha Cashu, 13 September 1986, Núñez 6113 (MO, USF); Cusco Amazónico, 18 October 1991, Timana & Jaramillo 2676 (MO). Pasco: Oxapampa, Pozuzo, Parque Nacional Yanachaga Chemillen, sector Pan de Azucar, 10 April 2003, Montegudo et al. 4924 (HOXA); Oxapampa, Villa Rica, bosque de protección San Matías-San Carlos, Cerro El Ascensor, 6 July 2003, Perea & Mateo 200 (HOXA); Oxapampa, Villa Rica, Centro Bocaz, trocha a Pampa Bocaz, 19 September 2003, Perea et al. 393 (CR, HOXA). Ucayali: entre Quebrada Shesha y base de Cerro Las Cachoeiras, NE de Pucallpa, 24 June 1987, Gentry & Díaz 58493 (MO); Coronel Portillo, Calleria, Río Utiquinia, Quebrada Agua Blanca, afluente de la Quebrada Maquisapay, 6 October 2003, Graham 2283 (USF); Coronel Portillo, Calleria, Quebrada Pumayacu, Rio Utiquinia, 13 March 2003, Schunke-Vigo & Graham 15336 (USF). Data lacking: 1799, Ruiz & Pavón 7/58a (MA [2 sheets]).

BRAZIL. Acre: Jordão, along Tarauacá river, 11 February 2009, Acevedo et al. 14921 (NY). Alagoas: Ibateguara, Coimbra, 12 December 2001, Oliveira & Grilo 666 (UFP). Amazonas: Igarapé de Flores, 1 July 1955, Chagas s.n. (INPA, MO, NY); Manaus, Igarapé do Buião, 26 April 1955, Coêlho s.n. (INPA 993); without exact locality, s.d., Downville s.n. (G [2 sheets], G-DC); Coari, Rio Solimôes, Rio Uruçu, 11 October 2001, Ferreira et al. 12257 (INPA); without exact locality, s.d., Moricand s.n. (G [2 sheets]); Manaus, margen do Igarapé do Beirão, 21 November 1955, Rodrigues 2943 (INPA, NY); BR-174, km 139, Ramal Canoas, Presidente Figueiredo, 10 February 1999, Silva et al. 897 (INPA). Bahia: Itanhém, camino entre Itanhém y Batinga, ca. 16 km, 29 December 2004, Amorin et al. 4669 (CEPEC, HUEFS); Ilhéus, CEPEC, km 22 da rodovia Ihléus-Itabuna, BR 415, 5 June 1986, Hage & Brito 2052 (CEPEC); Canavieiras, estrada para Una, 7 January 2002, Nunes et al. 747 (HUEFS); km 25 de la autopista Guaratinga-Sao Paulinho, 2 April 1973, Pinheiro 2082 (CEPEC); Camacã, camino a Jacaraci, 26 January 1971,

Santos 1414 (CEPEC); trecho de la autiopista BR–101 entre Ubaitaba y Posto Santo Antônio do Sul, 22 June 1972, Santos 2331 (CEPEC); Ilhéus, área do CEPEC, 5 December 1978, Santos 3414 (CEPEC, HUEFS, WAG); Ilhéus, CEPEC, km 22 da rodovia Ihléus-Itabuna, BR 415, 24 August 1981, Santos 3646 (CEPEC), 18 November 1981, Santos & Mattos 3696 (CEPEC, WAG); reserva do CEPEC, cuadra D, Ihhéus, March 1987, Sovral & dos Santos 5493 (CEPEC). Pará: Altamira, Estación Experimental EMBRAPA, carretera Altamira-Itaituba, 17 August 1978, Bahia 68 (CR, F, MG, MO, NY); ríos Pacaja y Muirapiranga, Ilha de Breu, 17 September 1965, Prance et al. 1321 (IAN, NY, U, WAG); Igarapú, 6 February 1903, Rodrigues s.n. (MG # 3326). Pernambuco: Cabo, Gurjaú, estação de tratamento d'agua COMPESA, 20 December 1983, Gallindo et al. 867 (IPA); Maraial, Lagoa dos Gatos, Serra do Urubu, 13 March 1994, Miranda et al. 1441 (HST).

BOLIVIA. La Paz: Franz Tamayo, Parque Nacional Madidi, Río Quendeque, 25 January 2002, *Fuentes et al. 3617* (LPB, MO); Sud Yungas, colonia Tupiza, 27 December 1994, *Seidel & Vaquiata 7708* (CR, LPB). Santa Cruz: Río Surutu, 8 October 1925, *Steinbach 7272* (NY).

Prestonia boliviana J.F. Morales & A. Fuentes (2004a: 166). Type:—BOLIVIA.
Chuquisaca: valle del Río Limón, entre Padilla y Monteagudo, 13 February 1994, J.
Wood 7970 (holotype LPB!, isotypes CR!, K!). Fig. 32, 34

**Stem** glabrous, with clear latex, the lenticels inconspicuous or absent, (if present) not suberose, intrapetiolar colleters minute, less than 0.5 mm long. **Petioles** 1.5–2.5 cm; leaf blade  $8-9 \times 4-5$  cm, broadly ovate, apex acuminate, base obtuse to rounded or cordate, membranaceous, glabrous, secondary veins slightly impressed on both surfaces, tertiary veins rather inconspicuous or inconspicuous. **Inflorescence** usually a monochasial cyme, rarely a dichasial cyme (but with just one basal branching), axillary, the flowers laxly disposed, longer than the adjacent leaves, many-flowered, glabrous to glabrescent, peduncle 5-6.5 cm, pedicels 2-3 cm long, floral bracts  $1.5-2 \times 0.5-1$  mm, linear, scarious, minute, green. **Sepals**  $2.5-3 \times 1-1.2$  mm, free, membranaceous, very narrowly ovate, the apices acuminate, somewhat reflexed, glabrous to glabrescent, very small, drying with a more or less uniform color, the veins not impressed, colleters 0.5-1 mm long, inconspicuously lacerate at the apex. **Corolla** salverform, cream, glabrous outside, tube  $8-9 \times 2.5$  mm,

straight, free corona lobes 2.5-3 mm long, the apices exserted, their height slightly surpassing that of the anther apices, annular corona entire, thickened, corolla lobes  $8-10 \times 5$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 3.8-4.1 mm, dorsally glabrous, the apices exserted. **Ovary** 1.3-1.5 mm tall, glabrous, style-head 0.7-0.9 mm, nectary 1-1.2 mm, conspicuously shorter than the ovary, usually deeply and irregularly 5-lobed, each one entire to subentire. **Follicles** unknown.

**Distribution and habitat:**—Endemic to moist forest, remnant forests, and similar secondary vegetation in Bolivia, from 1300 to 1750 m.

**Phenology**:—Flowering specimens have been collected in February, May, and December.

**Conservation Assessment**:—Vulnerable (VU), the area of occurrence of less than 20,000 km2 and fewer than 10 known localities.

**Taxonomic notes:**—*Prestonia boliviana* morphologically resembles *P. lagoensis*, having in common the leaf shape, inflorescence structure, and free corona lobes with the apices exserted, but *P. boliviana* can be differentiated by the following combination of characters: smaller sepals  $(2.5-3 \times 1-1.2 \text{ mm vs. } 3-6 \times 1.5-2 \text{ mm})$ , shorter corolla tube (8-9 mm vs. 13-20 mm), and longer pedicels (20-30 mm vs. 8-14(18) mm).

Additional specimens examined:—BOLIVIA. Chuquisaca: Luis Calvo, Entierillos, serranía del Lña, 17 December 2003, *Carretero et al. 944* (HSB, MO), 18 December 2003, *Carretero et al. 994* (HSB, MO); Luis Calvo, Las Frías, subiendo a la cima de la serranía de Yahuañanca, 22 December 2003, *Carretero et al. 1039* (HSB, MO), 23 December 2003, *Carretero et al. 1037* (HSB, MO); Tomina, Llantoj, al E de la Serranía de Kaska Orcko, 20 December 2004, *Gutiérrez et al. 1129* (HSB, MO); Hernando Siles, Monteagudo, Comunidad San Lorenzo, 26 December 2007, *Nina et al. 10* (CR, HSB, MO); entre Padilla y Monteagudo, Río Marcani, 1 June 2003, *Morales 9326* (LPB); Hernando Siles, Huacareta, Serranía Los Milagros, cañón Lacayotal, 27 December 2005, *Serrano et al. 7023* (USF); Hernando Siles, Huacareta, Serranía Los Milagros, sendero a la Laguna, 29 December 2006, *Serrano et al. 7088* (USF).

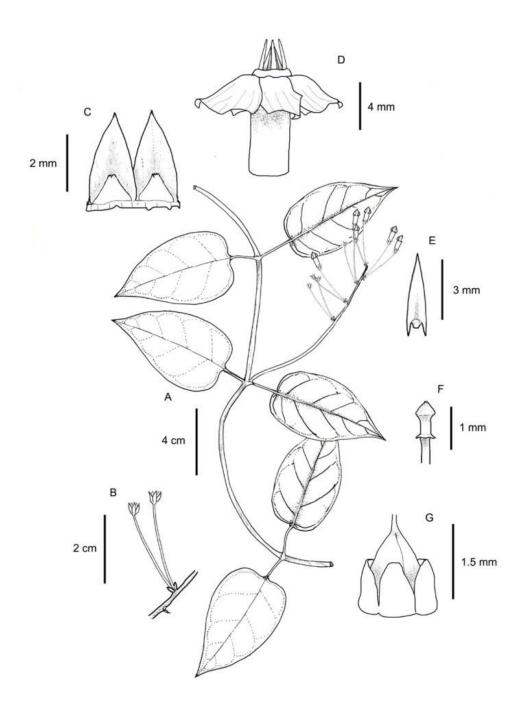


Fig. 34 *Prestonia boliviana* (*Wood 7970*, LPB). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of two sepals, showing the colleters. D. Corolla, showing the free coronal lobes and the apices of the anthers. E. Anther, dorsal view. F. Style-head. G. Nectaries and ovary.

Prestonia cayennensis (Candolle) Pichon (1951: 25). Haemadictyon cayennense Candolle (1844: 427). Type:—FRENCH GUIANA. Cayenne: Cayenne, s.d., J. Vargas s.n. (holotype G-DC! [photo F neg. 7544!]). Fig. 32, 35

**Stem** glabrous, glabrescent or minutely papillate-puberulent, with milky latex, with few lenticels, the lenticels not suberose, intrapetiolar colleters minute, less than 1 mm long. **Petioles** 0.3–1 cm; leaf blade  $4.5-16 \times 1.8-5$  cm, elliptic to narrowly elliptic, apex acute, acuminate to caudate, base cuneate to obtuse, membranaceous, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. Inflorescence a monochasial cyme, axillary, shorter or longer than the adjacent leaves, many-flowered, the flowers more or less clustered, glabrous, glabrescent to minutely and sparsely puberulent, peduncle 2–7 cm, pedicels (0.5-)0.8-1.6 cm long, floral bracts  $0.5-2 \times 0.5-1$  mm, linear, scarious, minute, green. Sepals  $2.5-5 \times 1-1.5$  mm, free, coriaceous to subcoriaceous, narrowly ovate, narrowly ovate-elliptic to narrowly elliptic, the apices acuminate, not reflexed, glabrous, very small, drying with a more or less uniform color, the veins not evident or slightly impressed, colleters 0.5–1.5 mm long, entire, subentire, or minutely lacerate at the apex. Corolla salverform, yellowish green to pinkish green, glabrous outside, tube 12–18 × 2.5-4 mm, more or less straight, free corona lobes 1-1.5 mm long, deeply included, their height conspicuously surpassed by that of the anther apices, annular corona entire, thickened, corolla lobes  $7-12 \times 4-6$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 4–4.6 mm, glabrous or minutely puberulent dorsally, the apices slightly exserted. Ovary (1.3–)1.5–2 mm tall, glabrous, style-head 1.40–1.55 mm, nectary 1.1–1.7 mm, usually shorter than the ovary, divided into 5 lobes, free or connate basally, each one entire, subentire to irregularly erose. Follicles  $11-26 \times 0.3-0.4$  cm, more or less continuous to inconspicuously articulated, free, but sometimes united at the tips (at least when young), glabrous to glabrescent, without lenticels, membranaceous when old; seeds 10-16 mm, coma 1.5-4 cm, cream.

**Distribution and habitat:**—Tropical wet forest, seasonal blackwater-flooded forest, forest over quartzite formations, and disturbed areas from 0 to 500 m in Colombia, Venezuela, Guyanas, Brazil, Peru, and Bolivia.

**Phenology**:—Flowering specimens have been collected throughout the year, fruiting specimens from August through March.

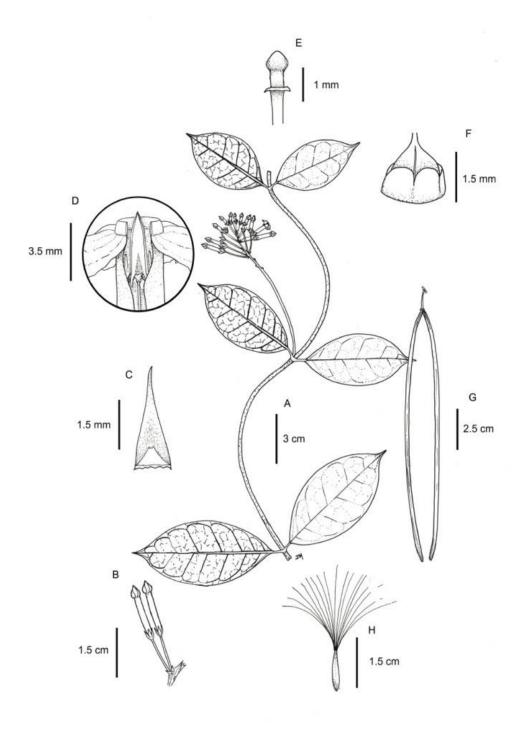


Fig. 35 *Prestonia cayennensis* (A-F from *Grainville et al. 10145*, INB; G-H from *Mexia 6029*, CAS). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view

of one sepal, showing the colleter. D. Open corolla tube (distal part), showing the anthers and the deeply included coronal lobes. E. Nectaries and ovary. F. Style-head. G. Follicles. H. Seed.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Taxonomic notes:**—*Prestonia cayennensis* shows an overall resemblance to *P. vaupesana*, since both species have usually unbranched inflorescences, and small sepals. However, the former has smaller sepals (2.5–5 mm vs. 6.5–8 mm), free corona lobes deeply included (vs. barely included), shorter follicles (11–26 cm vs. 29–33 cm), and shorter seeds (10–16 mm vs. 17–19 mm). *Prestonia quinquangularis* has been confused with this species, but it can separated by the tertiary veins slightly impressed on both surfaces and sepals with reflexed apices.

Additional specimens examined:—COLOMBIA. Caquetá: cima del Cerro Chiribiquete, January 1944, *Gutiérrez et al. 565* (MO). Guainia: Río Negro, Piedras del Cocuy, 24 February 1965, *Fernández et al. 6991* (COL). Guaviare: San José del Guaviare, serranía de la Lindosa, camino entre ciudad de Piedra y filo de Piedra, 22 March 2008, *Cárdenas et al. 21467* (COAH). Vaupés: Río Inirida, 7 February 1953, *Fernández 2196* (COL); Río Papurí, entre Santa Teresita y Piracuara, 4 July 2002, *Castaño & Betancur 1553* (COL); Río Apaporis, entre Río Pacoa y Río Kananari, 17 June 1951, *Schultes et al. 12953* (COL).

VENEZUELA. T.F. Amazonas: Casiquiare, al SE de San Fernando de Atabapo, sector El Pozo, 10–16 January 1988, *Aymard et al. 6337* (PORT, VEN); a lo largo de Río Yatua, cerca a Piedra Catipan, 6 February 1954, *Maguire et al. 37530* (NY, VEN); Río Casiquiare, boca del Pasimoni y El Porvenir, February 1989, *Stergios et al. 13143* (CR, HBG [2 sheets], PORT, Z). Barinas: 7 km al N de Santa Bárbara, 1 April 1974, *Gentry et al. 11128* (MO). Bolivar: Piar, al O del Amaruay-tepui, 4 May 1986, *Liesner & Holst 20584* (VEN); Caño Makampai, Río Carona, cerca de Wonken, 11 September 1983, *Morillo et al. 9444* (VEN).

GUYANA. Berbice-Courantyne, sabana Digitama, 29 October 1989, *Gillespie et al.* 2564 (P, NY, US). Cuyuni-Mazaruni: Río Mazaruni, Essequibo, s.d., *Abraham 412* (K); Iramaipang, December 1948, *Forest Department 611* (K, NY); Río Mazaruni, Quebrada Takutu, 4 December 1944, *Forest Department 4874* (K [2 sheets], NY); Río Mazaruni,

September 1880, Jenman 795 (K, NY); Mazaruni, November 1886, Jenman 2465 (K, NY); región superior del Río Mazaruni, 20 December 1922, Leng 415a (NY); Waramaden, 9 June 1990, McDowell & Gopaul 3179 (NY, P, U, US); a lo largo del Río Eping, 13 November 1990, McDowell & Gopaul 3759 (NY, US, WAG). Potaro-Siparuni: Río Potaro, 9 March 1962, Cowan & Soderstrom 2098 (NY, US); Parque Nacional Kaieteur, 8 May 1989, Gillespie et al. 1382 (P, US); Parque Nacional Kaieteur, río Potaro above falls, 16 November 1991, Gillespie 4285 (U, US); Río Potaro, Tumatumari, July 1921, Gleason 336 (K, NY, US); Río Potaro, 21 July 1993, Henkel & Williams 2313 (CR, MO, US); Cataratas Kaieteur, 100-700 m upstream from the falls, 7 October 1987, Kvist et al. 38 (BRG, CAY, NY, O, P, U, US, VEN); Río Potaro, cerca de Cataratas Kaieteur, 10 May 1944, Maguire & Fanshawe 23351 (F, K, MO, NY, U, US [2 sheets]); Sabana Haieka, E de Villa Chinoweing, 21 August 1960, Tillett & Tillett 45223 (NY). Upper Demerara-Berbice: Malali, Río Demerara, October 1922, Cruz 2631 (GH, MO, NY, US). Data lacking: s.d. Richard s.n. (P); s.d., Schomburgk s.n. (K).

FRENCH GUIANA. Cayenne: Kaw mountains, Tresor Reserve, Kaw, 30 January 2003, *Ek et al. 1423* (U); Crique Angélique, montañas Kaw, 14 November 1987, *Grainville 10145* (CAY, CR, P, VEN); Oyapock, Maripa, 13 September 1977, *Jacquemin 2108* (CAY [2 sheets], P); montañas Kaw, Trésor, crique Favard, 10 February 1996, *Jansen-Jacobs et al. 5243* (CAY, U); Portal, s.d., *Sagot s.n.* (P). St. Laurent Du Maroni: Charvein, 14 November 1913, *Benoist 240* (P). Data lacking: s.d., *Richard s.n.* (P).

SURINAME. Marowijne: Lely mountains, 25 November 2004, *Jansen-Jacobs et al.* 6767 (NY). Sipaliwini: Mountains Bakhuis, concession BMS, zone 9, 11 December 2006, *Bordenave et al.* 8615 (P).

PERÚ. Madre de Dios: Tambopata, puerto Maldonado, Aguajal Huitoto, 10 October 2004, *Chocce et al. 384* (BRIT).

BRAZIL. Amapá: Río Oiapoque, cerca a Pedra Alice, 18 August 1960, *Irwin et al.* 47599 (IAN, MG, NY, Z). Amazonas: Igarapé de Flores, carretera BR–17, 1 July 1955, *Chagas 1296* (INPA, MO, NY); Manaus, parque 10, 12 August 1955, *Coêlho, s.n.* (INPA # 1648); Manaus, Igarapé do Buião, 21 November 1955, *Dionisio s.n.* (INPA, MO); São Paulo de Olivença, near Palmares, 11 September-26 October 1936, *Krukoff 8168* (F); Manaus, Igarapé do Buião, 26 April 1955, *Luís s.n.* (INPA, MO); Manaus, Cachoeira

Grande dos Bilhares, 17 March 1958, *Pessoal do C.P.F. s.n.* (INPA # 6201); Maués, 30 November 1946, *Pires 100* (IAN); Baixo, Río Negro, Igarapé do Arara, 22 November 1962, *Rodrigues & Coêlho 4852* (INPA); Rio Aiuanã, Santa Izabel, 16 August 1999, *van Roosmalen et al. 1447* (INPA); Barcelos, Río Jauari, 5 July 1985, *Silva 298* (MG, MO, NY); Manaus, Igarapé do Buião, 21 November 1955, *Williams s.n.* (MG, INPA # 2943). Pará: Approaga, Río Capim, 22 June 1897, *Huber 847* (MG, RB # 21632); Río Thome Assú, Acará, 1 August 1935, *Mexia 6029* (CAS, K, MO, NY, UC, US); autopista BR–10, Belém-Brasília, Fazenda Maravilha, Río Ipixuna, 9 February 1973, *Oliveira 6060* (IAN). Data lacking: s.d., *Glaziou 3058* (C), *Glaziou 3059* (C).

BOLIVIA. Santa Cruz: Velasco, Parque Nacional Noel Kempff, campamento La Torre, 24 November 1993, *Arroyo et al. 418* (CR, MO, USZ)

Prestonia cyaniphylla (Rusby) Woodson (1936: 284). Echites cyaniphyllus Rusby (1907: 409). Type:—BOLIVIA. La Paz: s.d., M. Bang 2267 (holotype NY, n.v., isotypes K!, MO!, US!). Fig. 36, 37

Prestonia hassleri Hassler 12527 Woodson (1936: 285). Type:—PARAGUAY. Central: lake Ypacaray, March 1913, C. Hassler 12527 (holotype MO! [photo F neg. 12527!], isotypes B [destroyed], BAF n.v., BM!, C!, G! [3 sheets], K!, L!, NY!, SI!, US!, Z!).

**Stem** glabrous to glabrescent, with clear latex, the lenticels inconspicuous or absent, (if present) not suberose, intrapetiolar colleters minute, less than 1 mm long. **Petioles** 0.5–3.2 cm; leaf blade  $3-13.5 \times 2-6.5(-8.1)$  cm, elliptic, broadly elliptic, ovate-elliptic to ovate, apex short-acuminate, acute or acute-mucronulate, base obtuse, rounded to slightly cordate, membranaceous, glabrous, secondary veins impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. **Inflorescence** a monochasial cyme, rarely a dichasial cyme (but with just one basal branching), axillary, longer or equaling adjacent leaves, many-flowered, the flowers laxly disposed to somewhat clustered, glabrous, peduncle 2-6.5(-8) cm, pedicels 0.5-1.1 cm long, floral bracts  $1-3 \times 0.5-1$  mm, linear, scarious, minute, green. **Sepals**  $3-5.5 \times 1.5-2.5$  mm, free, membranaceous, broadly elliptic to ovate, the apices acute to abruptly acuminate, slightly reflexed or not reflexed, glabrous, very small, drying with a more or less uniform color, the veins slightly impressed

Corolla salverform, yellowish green, glabrous or glabrescent outside, rarely inconspicuously and sparsely puberulent, tube  $10-15 \times 3-4$  mm, somewhat inflated at the base; free corona lobes 0.6-1 mm long, deeply included, their height conspicuously surpassed by that of the anther apices, annular corona entire, thickened, corolla lobes  $4-9 \times 4-5$  mm, obliquely obovate. **Stamens** inserted about midway within the corolla tube, anthers 4.5-5 mm, dorsally glabrous, included. **Ovary** 1.5-2 mm tall, glabrous, style-head 1-1.25 mm, nectary 0.8-1.3 mm, conspicuously shorter than the ovary, divided into 5 lobes, each one entire to subentire. **Follicles**  $12.5-28 \times 0.2-0.3$  cm, continuous to inconspicuously articulated, connate longitudinally, more rarely free, but united at the tips, glabrous, without lenticels, membranaceous when old; seeds 5-8 mm, coma (1.7-)2-3 cm, cream.

**Distribution and habitat:**—Moist forest, gallery forest, remnant forest, and along roadsides in Bolivia, southern Brazil, Paraguay, and northern Argentina, from 100 to 1300 m.

**Phenology**:—Flowering October through May. Fruiting January through August.. Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Taxonomic notes:**—*Prestonia cyaniphylla* can be confused with *P. boliviana*, *P. lagoensis*, and *P. quinquangularis*, but it is easily distinguished by its membranaceous leaves, scarious floral bracts, broadly elliptic to ovate sepals, included anthers, and free corona lobes deeply included, inserted about midway within the corolla tube. For further discussion on its synonymy with *P. hassleri*, see Morales (2007b).

Additional specimens examined:—BRAZIL. Mato Grosso do Sul: Parque Nacional Iguaçú, 5 May 1949, *Falcão 142* (RB); Ponto Alto, Ponta Pora, 12 February 1983, *Hatschbach 46157* (HBG, MBM, MO, US, Z); al O de Iguatemi, 7 February 1993, *Hastchbach et al. 58600* (MBM, WAG); Bonito, alrededor de Proyecto Guaicurus, 14 March 2003, *Hatschbach et al. 74736* (CR, MBM). Paraná: Liponópolis, 24 September 2005, *Carneiro et al. 487* (HUFU); Loanda, Marilena, 6 April 1959, *Hatschbach 5645* (B, C, L, MBM, MO, U, Z); Icaraima, Porto Camargo, 20 January 1967, *Hatschbach 15767* (L, MBM, Z); Santa Helena, Porto Verde, 9 December 1977, *Hastchbach 40537* (C, MBM, NY, WAG); Nostra Senhora das Graças, 7 November 1987, *Hatschbach & Silva 51675* 

(MBM, WAG); Salto do Iguaçú, Río Paraná, February 1918, *Lutz 1444* (R); Terra Rica, Três Morrinhos, 9 February 2008, *Ribas et al. 799* (MBM). Santa Catarina: s.d., *Allemão 199* (R).

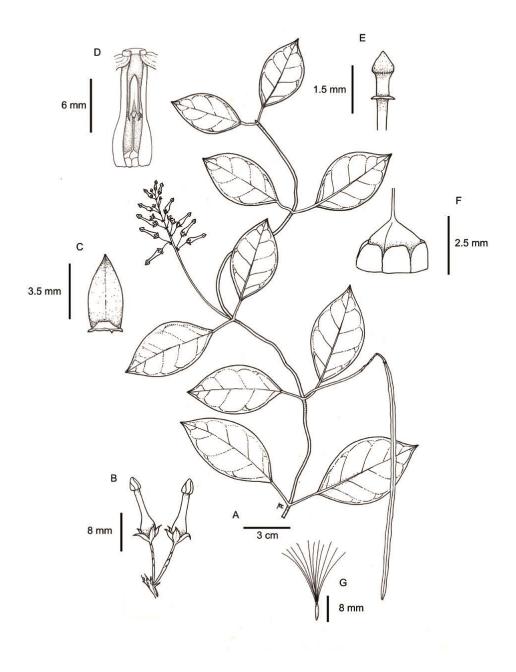


Fig. 36 *Prestonia cyaniphylla* (A-E from *Biganzoli et al. s.n.*, INB; F-G from *Zardini 4590*, INB). A. Stem with inflorescence and follicles. B. Calyces, pedicels, and floral bracts. C. Adaxial

view of the sepal, showing the colleter. D. Open corolla tube, showing the anthers, ovary, and nectary. E. Style-head. F. Nectaries and ovary. G. Seed.

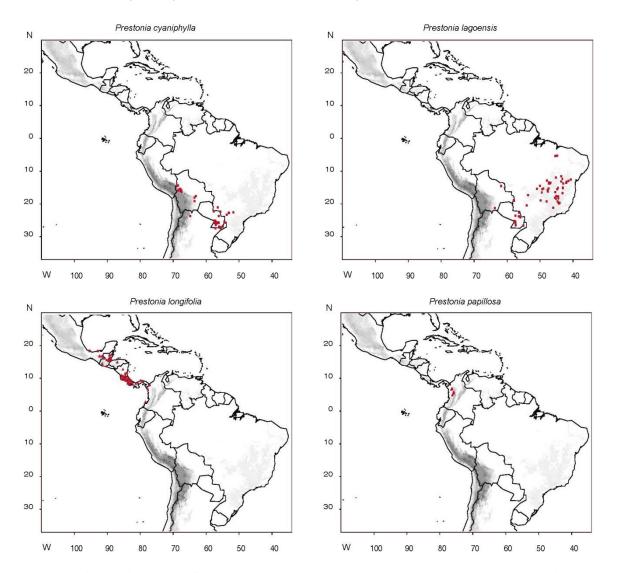


Fig. 37 Distribution maps of Prestonia cyaniphylla, P. lagoensis, P. longifólia and P. papillosa

BOLIVIA. La Paz: Larecaja, Caranavi, hacia Guanay, 28 November 1980, *Beck* 3795 (LPB, M, Z); Sud Yungas, Río Tamanpaya, 2 January 1990, *Beck et al.* 17306 (LPB, MO, SI, USF); Sud Yungas, Chicaloma, 6 February 1996, *Beck* 22636 (CR, LPB, M, NY); Nor Yungas, Coroico-Caranavi, 23 January 1983, *Besse et al.* 1764 (MO, SEL); Milluhuaya, Nor Yungas, December 1917, *Buchtien* 4372 (HBG [2 sheets], G, NY, US); Franz Tamayo, Parque Nacional Maididi, camino de Apolo-Azariamas, arroyo Pintata, 24 February 2003, *Paniagua et al.* 5591 (CR, LPB, MO); Nor Yungas, Yoloso, carretera a Caranavi, 13 November 1982, *Solomon* 8868 (MO); Nor Yungas, NE de Yoloso, 9 March

1984, Solomon & Stein 11710 (LPB, MO, USF); Larecaja, al SO de Tipuani, camino a Unutuluni, 24 January 1988, Solomon 17689 (LPB, MO); Nor Yungas, entre Caranavi y Bolinda, 20 February 1999, Wood & Mondaca 14543 (LPB, USZ); Sud Yungas, entre Chulumani y La Asunta, 16 December 1999, Wood & Goyder 15475 (K, LPB). Santa Cruz: Ñuflo de Chávez, Estancia San Miguelito, campamento La Pascana, 4 March 1996, Fuentes 1557 (USZ); Andres Ibáñez, Jardín Botánico de Santa Cruz, 9 May 1991, Gentry et al. 73627 (MO); Cordillera, N de Yatarenda, 17 April 1977, Krapovickas & Schinini 31462 (CTES, Z); Andrés Ibáñez, entre Santa Cruz y Samaipata, 13 January 1987, Nee 33500 (CR, LPB, MO, NY); Vallegrande, SSE de Los Gitanos, 27 December 1989, Nee & Vargas 38476 (LPB, NY); Andrés Ibáñez, valle del Río Salado, entre Santa Cruz y Samaipata, 22 January 1998, Nee 48086 (NY, USZ); Ichilo, Buena Vista, 26 April 2001, Schönenberger & von Balthazar 418 (LPB, Z).

PARAGUAY. Amambay: Sierra de Amambay, 1907–1908, Rojas 10341 (G); Parque Nacional Cerro Corá, 5 January 1988, Zardini et al. 5684 (FCQ, MO). Caaguazú: without exact locality, February 1905, Hassler 8867 (G, NY, UC); Colonia Dr. Juan Ramón Chávez, Santa Rosa, 16 March 1983, Simonis et al. 45 (CR, G [3 sheets], K, MO, NY, RB, S [2 sheets], U [2 sheets], WAG [2 sheets], VEN). Caazapa: Estancia Tapytá, Río Tebicuary, 16 December 1999, Zardini & Brítez 53121 (AS, MO). Canendiyú: Guarani, 3 February 1982, Fernández et al. 5852 (G, NY). Central: Asunción, 1876-1878, Balansa 1373 (G [2 sheets], K, P); Asunción, 1920, Collector unknown s.n. (LP); Villa Elisa, 10 December 1965, Pedersen 7519 (C, K [2 sheets], Z); Tarumandy, 2 April 1973, Schinini 6202 (CTES, G [2 sheets], Z); Central y Tororo, a lo largo de tributario del Río Paraguay, 13 January 1990, Zardini & Velásquez 18133 (MO); Estero del Ypoá, al SO de Nueva Italia, frente a Isla Guazú, 10 February 1990, Zardini & Velásquez 18785 (SI); Tavarory-Acosta Ñu, 4 March 1992, Zardini & Tilleria 30956 (SI). Cordillera: Tobaty, s.d., Hassler 669 (G); San Bernardino, s.d., Hassler 3061 (G, NY); San Bernardino, s.d., Hassler 3583 (BM, BR, G [2 sheets], K, NY, P, S, UC, W); Cerro Tobatí, 16 December 1987, Zardini & Degen 4011 (MO, SI); Cerro Zanja Jhœ, antes de Atyra, 30 July 1988, Zardini 6179 (MO, PY); región este de la cuenca del Río Piribebuy, al O de Arroyos y Esteros, 3 March 1990, Zardini & Velásquez 19651 (MO). Guairá: Tororo, 10 December 1988, Degen 1082 (MO, Z); Tororo, Cerro Mymy, 16 December 1988, Degen 1213 (FCQ, MO); Colonia Independencia, 30 March 1972, Pedersen 10116 (C, L, Z); Colonia Independencia, May 1967, Schinini 1623 (CTES, G); Colonia Independencia, 22 December 1986, Schinini & Bordas 25086 (CR, CTES, G [2 sheets], MO); Cerro Nelville, E de Mbocayaty, 24 March 1993, Schinini et al. 27899 (CTES, G, SI); camino al Cerro Acatí, 14 December 1988, Soria 2890 (G [2 sheets], MO, Z); Cerro Mumuy, 16 December 1988, Soria 2965 (MO); Cordillera de Ybytyruzú, carretera a Cerro Polilla, 19 January 1988, Zardini et al. 4243 (G, MO, SI); Cordillera de Ybytyruzú, Cerro Peró, 17 February 1989, Zardini & Velásquez 10903 (MO); Cordillera de Ybytyruzú, carretera Melgarejo-Antena, 13 March 1989, Zardini & Velásquez 11423 (SI); Cordillera de Ybytyruzú, E de Melgarejo, 28 May 1989, Zardini et al. 12218 (MO); Cordillera de Ybytyruzú, carretera a Polilla, Cerro Acatí, 23 July 1989, Zardini & Velásquez 13655 (FCQ, MO); Cordillera de Ybytyruzú, carretera de Melgarejo a Antena, 13 March 1989, Zardini & Velásquez 11475 (FCQ, MO), Zardini & Velásquez 11519 (MO), Zardini & Velásquez 11561 FCQ, MO); O de Melgarejo, 14 July 1989, Zardini & Velásquez 13347 (MO), Zardini & Velásquez 13368 (MO); Cordillera de Ybytyruzú, case de Cerro Mymy, camino a Cerro Polilla, 23 July 1989, Zardini 13739 (RB); General Bernardino Caballero, 9 July 1993, Zardini & Tilleria 36554 (USF). Paraguarí: Parque Nacional Ybycuí, 14 January 1989, Aguayo 14 (CR, MO, PY, SI); Acahay, 11 June 1992, Degen 2590 (MO); Cordillera de Altos, Octuber 1902, Fiebrig 64a (G, G-DC, GH, HBG, K, L, M, PR); Cordillera de Villa Rica, 5 Octuber 1905, Hassler 8765 (K); Acahay, 6 May 1987, Mereles 919 (MO); Piraju, 9 February 1982, Pérez & Duré 129 (BAB); Cerro Mbatoví, 26 November 1987, Soria & Zardini 1884 (G, MO, SI); Lago Ypoa, 26 November 1988, Soria & Mereles 2736 (FCQ, MO); Cerro Mbatoví, 10 December 1987, Zardini & Soria 3949 (MO, SI), 26 January 1989, Zardini & Velásquez 9916 (MO), 26 January 1989, Zardini & Velásquez 10021 (MO, SI); Compañia Costa Segunda, Cerro Palacios, 8 June 1988, Zardini 4590 (CR, G, MO, SI); Macizo Acahay, 11 June 1988, Zardini 4761 (MO); Cerro Palacios, 9 July 1988, Zardini 5635 (MO); Cerro Mbatoví, 26 January 1989, Zardini & Velásquez 9890 (CR, FCQ, G, MO, SI); Cerro Mbatoví, 26 January 1989, Zardini & Velásquez 10018 (FCQ, MO, SI); Parque Nacional Ybycu'i, entre Arroyo Minas y Arroyo Corrientes, 27 January 1989, Zardini & Aguayo 10098 (MO); Parque Nacional Ubycu'i, 18 March 1989, Zardini 11937 (SI); Parque Nacional Ybycu'i, Arroyo corrientes, 18 March 1989, Zardini & Velásquez 12077 (SI),

Zardini & Velásquez 12088 (SI); Macizo Acahay, 11 June 1989, Zardini et al. 12709 (SI); Acahay Massif, NE peak, 11 June 1989, Zardini et al. 12842 (B); Montaña Mbatoví, 24 June 1989, Zardini & Velásquez 13100 (NY, SI); Montaña Palacios, 24 June 1989, Zardini & Velázquez 13244 (MO); Estero del Ypoá, O de Carapeguá, 7 January 1990, Zardini & Velázquez 17701 (MO); Parque Nacional Ybycu'i, S de la esquina NO del parque, 22 June 1991, Zardini & Velázquez 27711 (MO, PY); Acahay Massif, Easternmost Peak, Western Part, 13 January 1992, Zardini & Tilleria 29804 (MO, NY, SI); Macizo Acahay, 13 January 1992, Zardini & Franco 29867 (SI), Zardini & Aquino 29688 (SI); Parque Nacional Ybycu'i, La Rosada, 3 February 1992, Zardini & Tilleria 30313 (MO, NY, PY); Macizo Acahay, 17 February 1992, Zardini & Aquino 30464 (MO); Macizo Acahay, Eastern most peak, 26 February 1992, Zardini & Tilleria 30800 (SI, USF); Estero del Ypoá, Trinchera Cué, 5 August 1993, Zardini & Tilleria 36799 (AS, MO). San Pedro: Primavera, 28 December 1959, Woolston 1156 (C, K, LIL, NY, S, SI, U, UC): Alto Paraguay, Primavera, 1953–1961, Woolston 1276 (C, K, MO, NY, S); Bosque Yaguareté, 19 January 1996, Zardini et al. 44461 (AS, CR, MO, USF). Data lacking: 1885–1895, Hassler 1465 (G [2] sheets], K, NY, P); March 1929, Jørgensen 4182 (DS, LP, MO, NY, S, SI, US); s.d., Ortega 1189 (G [2 sheets]); s.d., Ortega 1231 (G [2 sheets]).

ARGENTINA. Corrientes: Ituzaingo, Santa Rita, 15 February 1991, *Tressens et al.* 3913 (CTES, MO). Jujuy: Ledesma, camino a Valle Grande, 22 February 1972, *Cabrera et al.* 22355 (LP); Ledesma, Calilegua, Río Zora, 21 March 1979, *Cabrera et al.* 30397 (SI); Ledesma, Caimancito, 9 February 1980, *Cabrera* 31381 (CR, MO, SI); Ledesma, camino a Valle Grande, cerca de Arroyo Aguas Negras, 6 March 1983, *Hunziker et al.* 10636 (SI); Ledesma, cerca a Río San Lorenzo, 11 February 1992, *Hunziker et al.* 12270 (CR, SI); Ledesma, camino al Arroyo Aguas Negras, 24 February 1985, *Kiesling et al.* 5635 (SI); Río Agua Negra, 8 April 1970, *Legname et al.* 7404 (LIL, W); Ledesma, camino a Vinalito, 21 February 1998, *Morrore et al.* 2891 (SI); Ledezma, 24 January 1906, *Spegazzini s.n.* (BAB 15750, CR); Ledesma, entre Ruta 34 y Aguas Calientes, 19 January 1988, *Zuloaga & Deginani* 3641 (SI). Misiones: Candelaria, 9 December 1997, *Biganzoli et al.* 1686 (CR, SI); Cueva de Girolanco, January 1907, *Collector unknown s.n.* (LP); Layado Bonito, February 1907, *Collector unknown s.n.* (LP); Posadas, Loreto, 30 January 1908, *Ekman* 1593 (LD, S); Candelaria, Bompland, 1 February 1910, *Jørgensen s.n.* (BAB 34632);

Leandro, 10 February 2000, Maruñak 996 (COL, CTES, LPB, SI); Candelaria, Loreto, 30 August 1946, Montes 2184 (SI); Puerto Rico, Cainiguás, 16 May 1949, Montes 3887 (LP); Candelaria, Loreto, 16 February 1951, Montes 12289 (LP); Cainiguás, Capioví, 12 April 1951, Montes 15183 (MO, SI); San Pedro, Laharrague, 25 July 1951, Montes 15419 (LD, LIL, S); Vistoria, 13 August 1951, Montes 15465 (C. G. LIL); Candelaria, 27 February 1952, Montes 15482 (LD [2 sheets], LIL, UPS); Cainguás, carretera de Aristobulo del Valle a Jardín América, 11 February 1996, Morrone et al. 650 (CR, SI); General Manuel Belgrano, entre Wanda y Deseado, Río Uruzú, 21 April 1997, Morrone et al. 1935 (MO, SI); Cerro Corá, Candelaria, 20 February 1992, Petersen 15800 (C); Oberá, 26 December 1973, Pire et al. 176 (CTES, Z); San Ignacio, desvío a Teyú-Cuaré, 27 January 1976, Romanczuk et al. 528 (SI); Apóstoles, Parque Provincial de la Sierra, 5 March 2002, Romero et al. 2946 (SI); San Ignacio, Puerto Viejo, 21 March 1946, Schwartz 2287 (LIL, MO); Capital, Posadas, 16 January 1907, Spegazzini s.n. (BAB 20521); Iguazú, Puerto Esperanza, 8 March 1907, Spegazzini s.n. (BAB 17663); Capital, Posadas, 16 January 1907, Spegazzini s.n. (BAB 20519), Spegazzini s.n. (BAB 20787); Candelaria, Santa Ana, 30 January 1907, Spegazzini s.n. (BAB 17661), Spegazzini s.n. (BAB 17671); San Ignacio, Teyœ Cuaró, S de Gendarmería, 10 December 1987, Vanni & Radovancich 1059 (CTES, K); San Ignacio, parque provincial Teyucuaré, peñón del Teyucuaré, 6 March 1995, Zuloaga et al. 5310 (SI). Salta: José de San Martín, entre Dique Itiyuro y ruta 34, 8 February 1992, Hunziker et al. 12194 (SI); Río Pescado, 3 March 1943, Meyer 5073 (BAB, BM, LIL, MO, NY, UC); Iquira, Aguaray, 6 January 1940, Schreiter 10828 (F, LIL, NY, SI, US [2 sheets]); Quebrada Capiazuti, 6 August 1944, Schulz 5390 (LIL, NY).

- Prestonia lagoensis (Müller Argoviensis) Woodson (1936: 296). Haemadictyon lagoense Müller Argoviensis (1869: 115). Type:—BRAZIL. Minas Gerais: Belo Horizonte, Lagoa Santa, 21 January 1864, C. Warming s.n. (lectotype (designated here) C! [photo F neg. 22245!], isolectotypes K!, P!, S!). Fig. 37, 38
- Haemadictyon acutifolium Bentham ex Müller Argoviensis var. latifolium Müller Argoviensis (1860: 167). Type:—BRAZIL. Mato Grosso: near Cuiabá, February 1832, M. Manso 33 (lectotype M! designated by Morales (2006b), isolectotypes G!, G-DC!).

Haemadictyon warmingii Müller Argoviensis 116: (1869: 116). Type:—BRAZIL. Minas Gerais: without data, *C. Warming s.n.* (lectotype (designated here) C! [photo F neg. 22246!], isotype K!).

Haemadictyon lindmanii Malme (1899: 31). Prestonia lindmanii (Malme) Hoehne (1915: 88). Type:—BRAZIL. Mato Grosso: Santa Cruz da Barra, 25 March 1894, C.
Lindmann 3161 (holotype S!, isotypes LD!, UPS!).

**Stem** glabrous, rarely glabrescent, with clear latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 0.5–1(–1.5) mm long. **Petioles** 0.5–2.2 cm; leaf blade  $4-11.5(-13) \times 2-6$  cm, elliptic, broadly elliptic to ovate, rarely suborbicular, apex acuminate, acute to obtuse, base cuneate to obtuse or rounded, membranaceous, glabrous, secondary veins impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. Inflorescence a monochasial cyme, axillary, equaling or longer than the adjacent leaves, many-flowered, the flowers laxly disposed, glabrous, peduncle 2–7.5 cm, pedicels 0.8-1.4(-1.8) cm long, floral bracts  $1-2 \times 0.5-1$  mm, linear, scarious, minute, green. Sepals  $3-6 \times 1.5-2$  mm, free, membranaceous, very narrowly ovate, the apices acute to acuminate, slightly reflexed, glabrous, very small to slightly subfoliaceous, drying with a more or less uniform color, the veins not impressed, colleters 0.5-1 mm long, variously lacerate at the apex. Corolla salverform, yellowish green, glabrous outside, tube  $13-20 \times 3-4$  mm, more or less straight, free corona lobes 2.5-4 mm long, the apices barely exserted, their height slightly surpassing that of the anther apices, annular corona entire, thickened, corolla lobes 6-11 × 4-7 mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5–6 mm, dorsally glabrous, the apices barely exserted. Ovary 1.5–2 mm tall, glabrous, style-head 1.1–1.4 mm, nectary 1.5–2 mm, equaling the ovary, deeply 5-lobed or completely divided into 5 nectaries, each entire to subentire. Follicles  $27.5-40 \times 0.2-0.3$  cm, more or less continuous to inconspicuously articulated, usually connate longitudinally, rarely free and united at the tips, glabrous, without lenticels, membranaceous when old; seeds 9–14 mm, coma 2–3 cm, cream.

**Distribution and habitat**:—Bolivia, southwestern Brazil, northeastern Paraguay, Uruguay, and northern Argentina, growing in dry forest, moist forest, gallery forest, mesophytic forest, cerrados, caatingas, forest on granitic outcrops, and disturbed vegetation, from 150–950 m.

**Phenology**:—Flowering and fruiting occurs from October through May.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local name:—Cipózhino de leite (São Paulo, Brazil).

**Taxonomic notes:**—*Prestonia lagoensis* resembles *P. quinquangularis* and the two are confused. *Prestonia lagoensis* can be recognized by its longer free corona lobes, (2.5–4 mm vs. 1–1.5 mm), usually with the apices barely exserted (vs. deeply included), and longer sepals (3–6 mm vs. 1–3 mm). Further, *P. lagoensis* tends to have delicately membranaceous leaf blades compared to those of *P. quinquangularis*, but since this character is unreliable, it is not included in the key. Another morphologically related species is *P. cyaniphylla*, which has similar leaf shape, unbranched inflorescence, and corolla shape, but differs by its free corona lobes than are shorter than those in *P. lagoensis* (ca. 1 mm vs. 2.5–4 mm), deeply included within the tube, and broadly elliptic to obovate sepals (vs. very narrowly ovate). Although fruiting collections are difficult to separate, *P. cyaniphylla* has pedicels more densely clustered. For a full discussion of the reduction of *P. lindmanii* as a synonym of *P. lagoensis*, see Morales (2007)

Additional specimens examined:—BRAZIL. Bahia: Itaberaba, cerca de Tanque Verdadeiro, Fazenda Serra da Monta-Pasto, 10 March 1982, *Bastos 219* (HRB, HST, IBGE, IPA, U); Bahia, 1840, *Blanchet 3223* (G, P); Bom Jesus da Lapa, carretera de Lapa a Ibotirama, 17 April 1983, *Carvalho et al. 1803* (B, CEPEC, CR, WAG); Bom Jesus da Lapa, ca. 8 km de la carretera entre Lapa y Ibotirama, 17 April 1983, *Carvalho et al. 1814* (B, CEPEC, HUEFS, NY, WAG); Riachão das Neves, cerca de Serra do Brejinho, 1 February 2000, *Fonseca et al. 1253* (CEN, HUEFS, RB); Morpará, Mucambo do Alto,

Serra do Piripiri, 21 January 2001, *Guedes & Filho 7776* (CEPEC, HUEFS, RB); Rio de Contas, 5 km camino a Livramento, 8 March 2004, *Harley et al. 55074* (HUEFS); Igaproâ, 14 February 1991, *Hatschbach et al. 55123* (MBM); Oliveira dos Brejinhos, Canabrava, 16 March 1998, *Hatschbach et al. 67780* (C, CEPEC, MBM, WAG); Iguassú, 28 December 1922, *Porto 841* (RB); Bom Jesus da Lapa, Morrão, ca. 12.5 km al NE del camino Bom Jesus da Lapa-Ibotirama, 9 February 2000, *Queiroz et al. 5783* (CEPEC, HUEFS); Seabra, Abaíra, camino viejoAbaíra-São José, 1 km de Abaíra, 28 February 1992, *Standard et al. 51655* (CEPEC, CR, HUEFS, K, MO, NY, SPF). Brasília: Córrego do Ouro, 28 November

2001, Santos 1003 (CEN); Formosa, 28 November 2002, Santos et al. 1745 (CEN). Goiás: Serra da Atalaia, Chapada dos Veadeiros, SO de Monte Alegre de Goiás, 12 March 1973, Anderson 6936 (MBM, MG, MO, NY, R, UB); Chapada dos Veadeiros, 4 km al S de Terezinha, 18 March 1973, Anderson 7387 (MO, NY, UB); Niquelândia, Fazenda Limoeiro, 22 November 1992, Cordovil et al. 181 (CEN); Goiás Velho, camino a Serra Dourada, 18 December 1968, Grazielae et al. 753 (UB, Z); Formosa, 9 January 1977, Hatschbach 39361 (MBM, UC); Niquelândia, km 17 de rodovia para Caldas, 19 January 1992, Hatschbach et al. 56259 (C, MBM, WAG); Serra do Morcego, NO de Formosa, 18 April 1966, Irwin et al. 14970 (NY, UB USF); Serra dos Pirineus, Porangatu, carretera a Niquelândia, 23 January 1968, Irwin et al. 19040 (IAN, NY, UB, US, Z); cerca a Goiás Velha, January 1957, Magalhães s.n. (HB, Z); Nova Roma, Fazenda Cachoeira, 1 March 2000, Mendonça et al. 4112 (CEN, IBGE, US); Bom Jesus da Lapa, 12.5 km NE from Bom Jesus da Lapa-Ibotirama road, 9 February 2000, *Queiroz et al.* 5785 (INPA); Quirinópolis, near the city, 2 Nov 2016, Resende et al. 4652 (JAR); São Domingos, Fazenda São Vicente, 9 March 2004, Santos et al. 2207 (CEN); estrada de Goiânia a Anápolis, km 15, 26 November 1976, Shepherd et al. 3583 (NY, UEC). Maranhão: 2 km al N de Presidente Dutra, Fazenda São Paulo, 24 February 1983, Schatz et al. 757 (INPA, MG, NY, USF [2] sheets]); Barra do Corda, Cocal Grande, 34 km NE of Barra do Corda, Rio Mearim, 7 March 1983, Schatz et al. 872 (INPA, L, MG, NY, US, USF [2 sheets]). Mato Grosso: Río Araguaia, Alto Araguaia, 16 November 1973, Hatschbach & Koczicki 33280 (MBM, Z); Corumbá, February 1911, Hoehne 3677 (R); campus da Universidade Federal do Mato Grosso, 19 January 1979, Maciel 45 (INPA). Mato Grosso do Sul: E de Ribas do Río

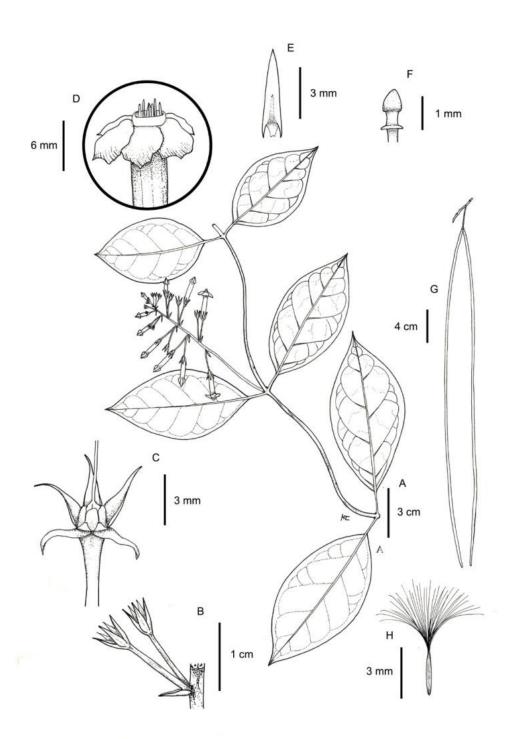


Fig. 38 *Prestonia lagoensis* (A-F from *Lombardi & Temponi 2189*, INB; G-H from *Silveira 67*, VIC). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Open calyx, showing the colleters, nectary, and ovary. D. Corolla mouth, showing the annular corona and free coronal lobes. E. Anther, dorsal view. F. Style-head. G. Follicles. H. Seed.

Pardo, 25 January 1979, Krapovickas & Cristóbal 34371 (C, CTES, MO, Z); Corumbá, 7 April 1903, Malme s.n. (S, UPS); Corumbá, Pedreira de Xavier, 29 January 1991, Ratter et al. 6520 (K). Minas Gerais: E de Río Pandeiros, carretera a Januária, 18 April 1973, Anderson 9130 (NY, UB, US, Z); Jardim Botânico de Belo Horizonte, 16 December 1932, Barreto 477 (BHCB); Caerste de Lagoa Santa, Octuber 1995, Brina & Costa s.n. (BHCB); Vespasiano, Santa Luzia, 17 December 1937, Burret et al. 10160 (BHCB); Pirapora, Várzea da Palma, 18 November 1962, Duarte 7406 (CR, HB, NY, RB, Z); São Romao, Sudeste, 16 December 2000, Gomes et al. 131 (BHCB, UB); Belo Horizonte, Pedro Leopoldo, 12 February 1973, Hatschbach & Ahumada 31486 (CR, MBM, Z); Várzea de Palma, Córrego Bebedouro, 15 January 1996, Hatschbach et al. 64104 (MBM, WAG); Serra do Espinhaço, Monte Azul, vía a Montevidiu, 14 January 1997, Hastchbach et al. 65705 (CR, MBM, U, WAG); Horto Florestal de Paraopeba, 30 November 1954, Heringer 3315 (B, HB, RB, UB, 20 December 1953 Heringer 3329 (RB, UB), 26 January 1956, Heringer 5078 (UB); Horto Florestal de Paraopeba, 22 March 1956, Heringer 18158 (B), 20 October 1959, Heringer 18175 (B); Séte Lagoas, Paraopeba, 30 Octuber 1959, Heringer 7247 (HB, UB, Z); Curvelo, Río Bicudo, 20 km W of Corinto, 3 March 1970, Irwin et al. 26806 (IAN, NY, UB, Z); Serra do Cabral, N de Joaquim Felício, 11 March 1970, Irwin et al. 27378 (F, K, NY, UB, US, Z); Belo Horizonte, 8 March 1994, Lombardi & Toledo 512 (BHCB); Januária, Fabiâo, antes de Cerrado do Judas, 16 February 1998, Lombardi & Temponi 2189 (BHCB, CR, WAG); Cabo Verde, 22 December 1943, Macedo 148 ((NY); Ituiutaba, 6 April 1944, *Macedo 319* (NY), 5 January 1956, *Macedo 4104* (IAN, K); Santana de Pirapama, Serra do Cipó, Fazenda Toucan Cipó, 19 November 2009, Milliken et al. 4132 (RB, SPF); Monjolo, camino Corinto-Diamantina, 14 November 2010, Mota et al. 1785 (BHCB); Campus de la Universidade Federal de Minas Gerais, 12 February 1981, Oliveira 707 (BHCB); Francisco Sá, 5 March 1990, Tameirão-Neto 97 (ESAL); campus de Física, Universidade Federal de Minas Gerais, 12 February 1981, Oliveira 2526 (BHCB, WAG); Cabeceira Grande, Río Preto, 27 March 2002, Pereira-Santos et al. 6321 (CEN); NO de Minas Gerais, Projeto Integrado de Colonização, 19 November 1989, Ratter et al. 6432 (IBGE, K, NY, US); Paraopeba, 5 February 1987, Silveira 67 (CR, VIC); camino para Cristália, 14 km de Grão-Mogol, 24 January 2002, Simões et al. 1179 (UEC, Z); Monte Azul, 7 km E of Monte Azul towards and beyond Vila Angical, 29 January 1991, Taylor et al. 1482 (E, K [2 sheets], VEN, Z); Nova Ponte, 4 December 1996, Tameirão-Neto 2227 (BHCB); cerca de Três Marias, 28 January 1960, Trinta & Fromm 25 (R); Lagoa Santa, 22 February 1865, Warming s.n. (C ([photo F neg. 22260!]); Lagoa Santa, s.d., Warming 658 (C); exact locality lacking, s.d., Glaziou 20412 (C). Mato Grosso: Corumba, 1903, Malme s.n. (S). Rio de Janeiro: Rio de Janiero, 1882, Glaziou 12940a (K), without exact locality, s.d., Glaziou 12943 (C, P), Glaziou 14072 (C, K, P). Tocantins: Palmeirópolis, Serra de Palmeirópolis, 23 January 1992, Hastchbach & Kummrow 56337 (MBM, WAG); Parana, Fazenda São João, 26 March 2004, Sevilla et al. 3815 (CEN).

BOLIVIA. Santa Cruz: Velasco, carretera a Las Mechitas, Cerro Pelao, 22 January 1997, *Guillén et al. 238* (MO, USF, USZ); Velasco, Cerro Pelao, 7 April 1994, *Guillén & Surubi 1251* (MO, USZ); Velasco, Cerro Pelao, N de El Empalme, 26 March 1994, *Saldias et al. 3588 b* (BRIT, CR, MO, USZ); Acero, Lomas de Tijuipa, 20 February 1916, *Steinbach 1774* (SI). Tarija: Gran Chaco, 3 km E del centro de Villa Montes, en el camino a Paraguay, 9 February 2006, *Nee & Linneo 54002* (MO, NY, USF, USZ).

PARAGUAY. Alto Paraguay: Chaco, s.d., Fiebrig 1207a (G [5 sheets]). Amambay: Cerro Corá, Cerro Lorito II, 11 December 1978, Bernardi 19138 (G); Parque Nacional Cerro Corá, 8 November 1982, Fernández-Casas & Molero 6097 (G, MO, NY); Río Apa, 1901–1902, Hassler 8065 (BM, BR, C, G, K, LIL, MICH, MO, P, UC, RB, S, US, W), Hassler 8065a (G, P); Parque Nacional Cerro Corá, 9 February 1982, Solomon et al. 6844 (MO); Parque Nacional Cerro Corá, 26 February 1997, Zardini & Guerrero 46523 (AS, CR, MO, USF). Canendiyú: cerca a Igatymí, 4 February 1982, Fernández-Casas & Molero 5941 (G, HUA, MA, MBM, MO, NY). Central: SE de Limpio, 9 May 1974, Schinini 8785 (CR, G, MO); Lagos Ypoá y Yabeby, 3 August 1991, Zardini & Velásquez 28340 (MO, NY, SI). Concepción: Río Apa y Río Aquidabán, s.d., Fiebrig 4344 (BM, G [2 sheets], K, SI). Misiones: San Miguel, Estancia Cardoso, 25 May 1993, Zardini & Tilleria 35801 (AS, CR, MO, USF). Paraguarí: Macizo Acahay, 17 February 1992, Zardini & Tilleria 30565 (CR, MO, PY, USF); Macizo Acahay, 17 February 1992, Zardini & Aquino 30416 (CR, MO, PY). San Pedro: Bosque Yaguareté, 23 August 1995, Zardini & Garcete 43433 (AS, CR, MO), 18 January 1996, Zardini & Guerrero 44405 (AS, CR, MO, USF), 19 January 1996, Zardini & Guerrero 44456 (CR, MO, USF), Zardini & Guerrero 44464 (AS, CR, MO, USF); cerca de Ybapobo, 2 March 2001, Zardini & Guerrero 56503 (FACEN, CR, MO).

ARGENTINA. Misiones: San Pedro, Caraguatay, 10 May 1949, *Montes 1700* (CR, K, LIL, RB).

URUGUAY. State unknonw: "Montevideo, Asunción", January 1873, Fruchard 1020 (K, P).

- Prestonia longifolia (Sessé & Moçiño) J. F. Morales (1996: 286). Echites longifolius Sessé & Moçiño (1887 [1893]: 45). Type:—MEXICO. Veracruz: San Andrés Tuxtla, s.d., M. Sessé & J. Moçiño 5007 (lectotype MA! designated by Morales (1996); isolectotype, F!). Fig. 37, 39.
- Belandra concolor S.F. Blake (1917: 78). Prestonia concolor (S.F. Blake) Woodson in Standley & Record (1936: 327). Type:—BELIZE. Toledo: Río Grande riverbanks, 25 March 1907, M. Peck 953 (holotype GH!).
- Prestonia dentigera Woodson (1939: 258). Type:—COSTA RICA. San José: near El General, January 1939, A. Skutch 3864 (holotype US!).

**Stem** glabrous to glabrescent, with clear or milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 0.5-1 mm long. **Petioles** 0.6-2 cm; leaf blade  $(6-)7.5-19.5(-25) \times 2.5-9.5(-11)$  cm, elliptic to narrowly elliptic, rarely obovate, apex short-acuminate to cuspidate, base obtuse to rounded, membranaceous, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than or equaling the adjacent leaves, many-flowered, the flowers somewhat clustered, glabrous, glabrescent, or inconspicuously puberulent, peduncle 2.4-6.5 cm, pedicels 0.8-1.7(-2.4) cm long, floral bracts  $1-1.3 \times 0.5-1$  mm, linear, scarious, minute, green. **Sepals**  $3-8 \times 2-3$  mm, free, coriaceous to subcoriaceous, narrowly ovate to very narrowly ovate, the apices acute to long-acuminate, not reflexed, glabrous, very small, drying with a more or less uniform color, the veins inconspicuous, colleters ca. 1 mm long, entire at the apex. **Corolla** salverform, cream to yellowish green, glabrous outside, tube  $14-19 \times 3.5-5$  mm, straight, free corona lobes 2-3 mm long, barely included or slightly exserted, their height equaling the anther apices, annular corona entire, thickened, corolla lobes  $7-12 \times 6-8$  mm, obliquely obovate to narrowly and obliquely obovate. **Stamens** 

inserted near the corolla mouth, anthers 5–5.5 mm, minutely puberulent to glabrescent dorsally, the apices slightly exserted. **Ovary** 1.5–2 mm tall, glabrous, style-head 1–1.5 mm, nectary 2–3 mm, surpassing the ovary, 5-lobed, each lobe irregularly and minutely lacerate. **Follicles** 29–53  $\times$  0.3–0.4 cm, continuous, free, but sometimes united at the tips (at least when young), glabrous, without lenticels, membranaceous when old; seeds 9–12 mm, coma 1.5–3 cm, cream.

**Distribution and habitat**:—Southern Mexico throughout northern Colombia, in tropical wet forest, moist forest, and gallery forest (rarely in margins of flooded forest or mangroves) at 0–1600.

**Phenology**:—Flowering and fruiting specimens have been collected throughout the year.

**Conservation Assessment**:—Least Concern (LC), not endangered (IUCN 2001).

Local name:—Loroco de venado (Ahuachapán, El Salvador).

**Taxonomic notes**:—*Prestonia longifolia* resembles *P. portobellensis*: both species have similar leaf blades, dichasial inflorescences, scarious bracts, continuous and slender follicles, and grow sympatrically in some areas. The former is easily separated by its sepals  $3-8 \times 2-3$  mm (vs.  $(9-)10-18(-21) \times (3-)4-7$ ) mm) and free corona lobe apices barely included (rarely slightly exserted), surpassed by those of the anthers (vs. free corona lobe apices exserted and conspicuously surpassing those of the anthers). *Prestonia annularis* is also very vegetatively similar, but has very small free corona lobes that are deeply included within the corolla tube.

Additional specimens examined:—MEXICO. Chiapas: Ocosingo, a S de Nuevo Guerrero, 29 May 2002, *Aguilar 887* (MEXU, MO); Ocosingo, 8.1 km SE from Lacanjá, Chansayab, 19 April 2003, *Aguilar & Chancayum 6447* (MEXU); Ocosingo, Dos Arroyos, 2 km N of Nuevo Guerrero, 24 May 2002, *Aguilar & Álvarez 1043* (MO); Ocosingo, 6.5 km S of Nuevo Guerrero, road to Santo Domingo, 6 May 2002, *Álvarez et al. 919* (MEXU); Ocosingo, 8 km NO de Bonampak, Lacanja-Changayab, Río Lacanja, 14 May 1982, *Davidse et al. 20474* (MEXU, MO, USF); Ocosingo, 7 km SE from Bonampak, 17 May 1984, *Martínez 6383* (MEXU); Ocosingo, 4 km E from Nuevo Guerrero, 5 May 2002, *Soto et al. 23170* (MEXU). Guerrero: carretera Palenque-Boca Lancantum, 14 April 1986, *Martínez 18174* (CR [2 sheets], MEXU). Tabasco: Arroyo Polo, puente El Coco, Centla, 29

July 1998, Guadarrama et al. 6575 (MEXU). Veracruz: Ounta de Chuniapan, Río Chuniapan, laguna de Sontecomapán, Catemaco, 22 May 1985, Calzada 11596 (MEXU, XAL); Sontecomapán, al N de Catumaco, 14 August 1998, Campos & León 5355 (BIGU, MEXU); Río Texcaltita, 4 km al S de San Andrés Tuxtla, camino a Santiago Tuxtla, 10 August 1983, Cedillo 2454 (MEXU); Sontecomapán, 23 May 1981, Gentry et al. 32279 (BM, COL, MEXU, MO, USF); Laguna Escondida, San Andres Tuxtla, 4 May 1983, Ibarra 613 (MEXU); San Andrés Tuxtla, Estación de Biología Tropical Las Tuxtlas, 4 June 1985, Ibarra & Sinaca 2481 (MEXU); Río Coscoapan, Catemaco, 26 March 1973, Menéndez 129 (MEXU). Data lacking: s.d., Sessé & Mociño 5077 (MA).

GUATEMALA. Alta Verapaz: entre Semococh y La Laguna, 10 May 1942, Steyermark 46371 (F, MO). Izabal: Selempin El Estor, río Oscuro, 8 December 2006, Cajas 13 (USCG); Livingston, s.d., Cazali et al. s.n. (USCG); Cadenas, Puerto Méndez, Río Gracias, 3 June 1970, Contreras 9941 (MEXU, MO, NY); Quebrada Lagarto, Ensenada de Los Lagartos, 16 June 1988, Martínez et al. 22838 (MEXU, MO, USCG); Río Dulce, 27 June 1988, Martínez et al. 23100 (MEXU, USCG); Río Dulce, biotopo Chocón, 20 June 1996, Pöll s.n. (UVAL); Río Dulce, entre Livingston y 6 millas Río arriba, 14 April 1940, Steyermark 39434 (F, MO). Petén: La Cumbre, Río Pusila, 10 August 1969, Contreras 8894 (MEXU, MO, TEX); N de Modesto Méndez, 6 September 1970, Harmon 2500 (MO). Suchitepéquez: Chicacao, La Corona, 30 March 2003, MacVean 676 (UVAL).

BELIZE. Belize: carretera a Rich Woods, 30 May 1974, *Dwyer 12528* (MO). Toledo: Río Sarstoon, frontera Belize-Guatemala, 28 July 1979, *Dwyer 14876* (MO); Golden stream, 16 May 1944, *Gentle 4613* (EAP, MEXU, MO, TEX); Río Grande, 10 March 1933, *Schipp 465* (F); Quebrada Jacinto, 26 May 1933, *Schipp 564* (BM, F, GH, K, MO, NY, S, UC, Z).

HONDURAS. Olancho: refugio de vida silvestre La Muralla, sendero El Pizote, 29 April 1993, *Nelson & Andino 15942* (TEFH).

EL SALVADOR. Ahuachapán: San Francisco Menéndez, Río Cuayapa, 24 February 1992, *Sandoval & Chinchilla 283* (B, LAGU, MO).

NICARAGUA. Zelaya: El Escobillo, entre Colonia Serrano y Yolaina, 29 July 1982, *Sandino 3327* (MO, WAG); entre Río Blanco y Río Copular, 14 February 1979, *Stevens 12257* (MO); SO de Bluefields, 2 April 1981, *Stevens 19764* (MO).

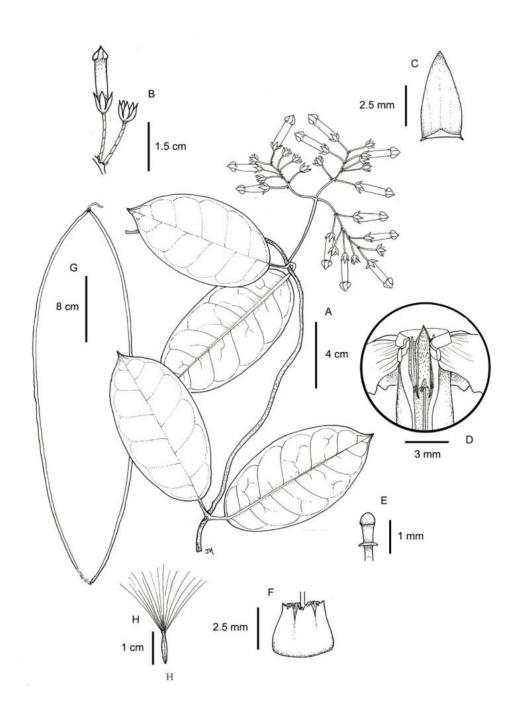


Fig. 39 *Prestonia longifolia* (A-F from *Morales 2073*, INB; G-H from *Angulo 133*, INB). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of the sepal, showing the colleter. D. Open corolla tube, showing the anthers and the free coronal lobes. E. Style-head. F. Nectary. G. Follicles. H. Seed.

COSTA RICA. Alajuela: San Ramón, La Palma, 27 July 1925, Brenes 4086 (CR, NY), Brenes 4399 (CR); Piedades, 24 April 1927, Brenes 5488 (F), La Palma de San Ramón, 26 August 1928, Brenes 6297 (F), 7 July 1927, Brenes 5594 (F); San Carlos, Cerro Las Crucitas, 25 July 1996, González et al. 1120 (CR); Reserva Nubosa Monteverde, Valle Peñas Blancas, 13 June 1986, Haber et al. 5100 (MO); Reserva Biológica Bosque Eterno de los Niños, 20 June 1996, Krings 1 (CR); Área protegida Tenorio, Bijagua, 20 April 1995, Penneys et al. 480 (CR, MO); San Ramón, Cerro Chato, 8 June 1999, Rodríguez & Ramírez 5041 (CR); Zarcero, s.d., Smith 591 (MO); Guadalupe, Alfaro Ruiz, 31 May 1940, Smith 2675 (F, MO [2 sheets]); Parque Nacional Volcan Tenorio, Upala, Río Zapote, sendero hacia laguna Danta, 28 December 2007, Solano et al. 4946 (CR). Cartago: Guayacán, ca. 20 km al NNE de Turrialba, 3 August 1974, Maas 1106 (U). Guanacaste: La Cruz de Abangares, 10 September 1985, Haber & Bello 2687 (MO, USF); Cerro Frío, Tilarán, 30 June 1987, Haber & Bello 7330 (MO); Parque Nacional Guanacaste, Estación Pitilla, 12 November 1990, Ríos 183 (CR); Rincón de la Vieja, Colonia Blanca, 14 April 1991, Rivera 1250 (CR); Península de Nicoya, Bejuco, 25 August 1994, Rodríguez & Estrada 236 (CR); carretera a Tilarán, 5 May 1984, Taylor 3025 (DUKE). Heredia: Finca La Selva, 22 August 1979, Grayum & Bien 2505 (DUKE, MO); Sarapiquí, Puerto Viejo, 24 March 1980, Hammel 8262 (DUKE), Hammel 8736 (DUKE); La Selva, Río Puerto Viejo, 19 May 1982, *Hammel 12339* (DUKE); Sarapiquí, 28 November 1981, *Smith 599* (DUKE). Limón: Reserva Biológica Hitoy Cerere, 20 October 1992, Carballo 445 (CR); Talamanca, 5 July 1983, Gómez-L. 9499 (CR, F); cuenca del Bananito, Finca Selva bananito lodge, Río Carbón, 13 April 2008, Hammel et al. 24687 (CR); Parque Nacional Barbilla, Colonia Puriscaleña, 25 June 2000, Mora 1207 (CR, MO); Cerro Muchila, fila Matama, 14 April 1989, Robles & Chacón 2791 (CR); Río Blanco, Las Brisas de Veragua, road to Veragua rainforest, 26 May 2011, Sánchez et al. 2360 (CR). Puntarenas: Golfo Dulce, Aguabuena, 12 September 1991, Aguilar 413 (CR, MO), Aguilar 418 (CR, MO); Península de Osa, Los Patos, 21 December 1993, Aguilar & Guzmán 2802 (CR); Golfo Dulce, Cerro de Oro, 15 November 1994, Aguilar 3678 (CR); Península de Osa, Aguabuena, 13 March 1996, Aguilar 4523 (CR); Península de Osa, Los Charcos, 8 September 2012, Aguilar 13891 (CR); Golfo Dulce, Cerro de Oro, 15 March 1995, Angulo 133 (CR); Península de Osa, Cerro de Oro, 11 February 1996, Angulo 538 (CR); Monteverde, 9 February 1976, Dryer 713 (CR, NY); Golfito, Piedras Blancas, Río Bonito, 14 April 1997, Fletes 467 (CR, MO); Cordillera de Tilarán, San Luis, 12 November 1993, Fuentes 567 (CR); Puntarenas, Boscosa, Aguabuena, 11 September 1996, Croat et al. 79220 (CR, MO); Monteverde, 3 August 1978, *Haber 580* (MO); Monteverde, 16 January 1985, *Haber 1225* (MO); Santa Elena, Monteverde, 3 July 1991, Haber & Zuchowski 10715 (CR); Golfito, Parque Nacional Esquinas, 20 August 2000, Huber & Weissenhofer 1987 (WU); Rincón de Osa, 11 February 1974, Liesner 2049 (MO, USF); Reserva Forestal Golfo Dulce, Agujas, sendero Ajo, 4 October 1997, Lobo 109 (CR); NO de La Palma, Osa, 7 March 2001, Mayfield & Roberts 314 (CR); Golfito, fila Gamba, 27 February 1995, Morales 3565 (CR, MO); Aguirre, Cerritos, carretera entre Tarrazú y Quepos, 20 February 2006, Morales 13764 (CR); Rancho Quemado, Península de Osa, 15 May 1991, Quesada 511 (CR); Parque Nacional Corcovado, Esquinas, 22 January 1994, Segura & Quesada 269 (CR); O de Rincón, 31 October 1992, Thomsen 156 (C, CR, K); N de Villa Neily, 3 August 1981, Wilbur 32602 (DUKE). San José: Tarrazú, San Lorenzo, SE of Cerro Toro, 1 April 1987, Estrada et al. 689 (CR); Puriscal, San Martín de Puriscal, 5 January 1994, Jiménez et al. 1423 (CR); Parque Nacional La Cangreja, Puriscal, 20 November 1993, Morales 2073 (CR); Valle del Candelaria, San Jerónimo, camino al bajo, 28 December 2013, Morales & Zemog 21414 (USJ); Parque Nacional Carara, Bijagualito, 25 November 1991, Zúñiga 546 (CR, K).

PANAMÁ. Bocas del Toro: al SE y NE del campamento Changuinola 1 del IRHE, 19 January 1980, *Correa et al. 3426* (PMA); entre Represa Fortuna y Chiriquí, 10 March 1985, *Croat & Grayum 60240* (MO); cerca de Almirante, 20 November 1971, *Gentry 2804* (MO, Z); Changuinola, Cerro Frío, headwater of Rio Tskui, 22 October 2008, *Monro et al. 6268* (BM, PMA). Chiriquí: Punta Burica, El Chorogo, cabecera del Río San Bartolo, 15 may 2007 (fl), *Hernández et al. 329* (PMA); Península de Burica, unnamed Quebrada opposite Quebrada Macho of Panama; 11 mi. (18 km) south of Puerto Armuelles, 22 February 1973, *Liesner 177a* (MO). Coclé: camino a Coclesito, 20 April 1978, *Hammel 2521* (MO). Colón: 1-2 km del camino a Portobelo, Río Guanche, 17 February 1982, *Knapp & Schmalzel 3588* (MO, USF). Panamá: 4 millas al O de Tortí, 1 March 1982, *Knapp & Mallet 3931* (MO, USF). San Blas: Dubaganalla, 14 February 1967, *Duke 10198* (MO [2 sheets]); carretera El Llano-Cartí, 4 November 1984, *Nevers & Herrera 4157* 

(MO). Veraguas: NO de Santa Fé, camino a Calovebora, 16 May 1975, *Mori & Kallunki* 6153 (MO).

COLOMBIA. Chocó: Acandí, Unguia, 3 July 1976, Forero 552 (COL, MO); Río Sucio, Truando, 24 October 1956, Romero-Castañeda 6112 (COL). Cauca: Guapi, Parque Nacional Gorgona, entre playa Blanca y Gorgonilla, 5 September 1987, Lozano et al. 5634 (COL), 7 September 1987, Lozano et al. 5686 (COL).

Prestonia papillosa (Müller Argoviensis) J.F. Morales (2004: 161). Haemadictyon papillosum Müll. Argoviensis (1860: 432). Type:—COLOMBIA. Antioquia: s.d., J. Triana 157 (holotype P!). Fig. 37, 40

**Stem** conspicuously papillate-puberulent when young, glabrescent at maturity, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, less than 1 mm long. **Petioles** 0.5–0.7 cm, minutely papillate; leaf blade  $(6-)8.5-17 \times 3-8.5$  cm, elliptic to obovate-elliptic, apex obtuse and abruptly acute, base obtuse to rounded, membranaceous, sometimes slightly revolute, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. Inflorescence a dichasial cyme, axillary, longer than the adjacent leaves, usually many-flowered, the flowers usually clustered, minutely puberulent, peduncle 4.5–9 cm, pedicels 0.6-2.1(-2.8) cm long, floral bracts  $1-2\times0.5-1$ mm, linear, scarious, minute, green. Sepals  $3-4.5(-6) \times 1-1.5$  mm, free, coriaceous to subcoriaceous, very narrowly ovate, the apices acuminate, the apices slightly reflexed or not reflexed, glabrous to glabrescent, very small, drying with a more or less uniform color, the veins not impressed, colleters ca. 1 mm long, entire at the apex. Corolla salverform, yellowish green to yellowish pink, glabrous to glabrescent outside, tube  $6-9 \times 1.9-2.1$  mm, usually somewhat inflated at the base; free corona lobes less than 1 mm long, included, their height conspicuously surpassed by that of the anther apices, annular corona entire, delicate and inconspicuous, corolla lobes  $5-6 \times 3-4$  mm, ovate. **Stamens** inserted near the corolla mouth, anthers 4.5–5.3 mm, dorsally glabrous, the apices conspicuously exserted. Ovary ca. 1.5 mm tall, glabrous, style-head 1.1–1.3 mm, nectary 2–2.5 mm, conspicuously surpassing the ovary, composed of 5 lobes, rarely connate basally, each lobe somewhat lacerate to subentire. Follicles  $15-21 \times 0.4-0.5$  cm, continuous to inconspicuously articulated, free, but usually united at the tips (at least when young), glabrous, lenticels inconspicuous or not evident, membranaceous when old; seeds 16–19 mm, coma 2–2.5 cm, cream.

**Distribution and habitat:**—Endemic to Colombia, where it grows in premontane and montane forest (cloud forest), including disturbed vegetation along roadsides, and creeks from 1000–2000 m.

**Phenology**:—Flowering specimens have been collected in March, June, and September and fruits in September and December.

**Conservation Assessment:**—Vulnerable (VU), the area of occurrence of less than 20,000 km2 and fewer than 10 known localities.

**Taxonomic notes**:— $Prestonia\ papillosa$  was included in the synonymy of P.  $marginata\ (=P.\ quinquangularis)$  by Woodson (1936), a species with some similar morphological features, but not closely related.  $Prestonia\ papillosa$  resembles P. cayennensis: the two species have small sepals and corolla with free corona lobes deeply included within the tube, conspicuously exceeded by the apices of the anthers.  $Prestonia\ papillosa$  can be differentiated by the stems papillate-puberulent when young, inflorescence a dichasial cyme, sepals 3-4(-6) mm, and corolla tube 6-9 mm long.

Additional specimens examined:—COLOMBIA. Antioquia: Frontino, Parque Natural Nacional Las Orquídeas, camino de la Finca Guadulala al Alto de Carauta, 2 December 1986, *Callejas et al. 3009* (HUA); Jardín, carretera Jardín-Río Sucio, 7 km de Jardín, 7 June 1987, *Callejas et al. 3750* (HUA, MO, NY, USF); Frontino, Nutibara, cuenca alta del Río Cuevas, 24 September 1987, *Sánchez et al. 1640* (HUA, MEDEL); Jericó, December 1940, *Thomas 3495* (US); without exact locality, 1851–1857, *Triana 1915* (P); Frontino, carretera Nutibara-Murrí, 24 September 1987, *Zarucchi et al. 5762* (B, COL, HUA, MO, USF). Chocó: San José del Palmar, vereda San Antonio, finca San Vicente, 20 April 1998, *López et al. 1802* (HUA). Risaralda: Mistrato, 17 March 1991, *Galeano et al. 2481* (COL).

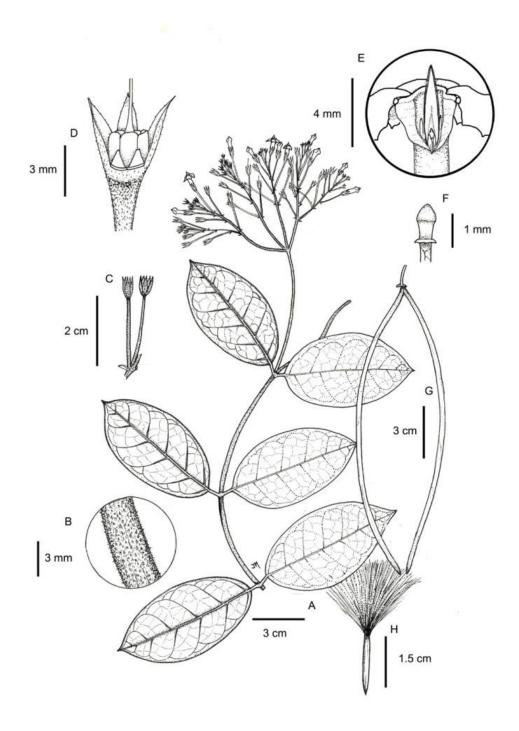


Fig. 40 *Prestonia papillosa* (*Zarucchi et al. 5762*, HUA). A. Stem with inflorescence. B. Branchlet, showing the indument. C. Calyx, pedicel, and bracts. D. Calyx with two sepals removed,

showing the colleters and nectaries. E. Corolla mouth and tube partially open, showing the free coronal lobes and anthers. F. Style-head. G. Follicles. H. Seed.

- Prestonia portobellensis (Beurling) Woodson (1931: 553). Echites portobellensis Beurling (1854: 137). Type:—PANAMA. Colón: Portobello, April 1826, J. Billberg s.n. (holotype S!, isotype S!). Fig. 41, 42.
- Haemadictyon schizadenium Müller Argoviensis (1860: 431). Prestonia schizadenia (Müller Argoviensis) Hemsley (1881: 312). Type:—MEXICO. Veracruz: Papantla, s.d., W. Karwinsky s.n. (holotype LE n.v.; isotype M!).
- Prestonia macrocarpa Hemsley (1881: 311). Type:—PANAMA. Colón: Chagres, January—March 1850, A. Fendler 250 (lectotype BM! designated by Morales (2006b), isolectotypes GH!, K! [3 sheets], MO!, P!, W!).
- Prestonia guatemalensis Woodson (1936: 339). Type:—GUATEMALA. Alta Verapaz: Sepacuitle, October 1901, P. Owen 1 (holotype US!).
- Prestonia laxa Rusby ex Woodson (1936: 317). Type:—COLOMBIA. Magdalena: Valparaiso, 26 March 1899, H. Smith 1647 (holotype NY! [2 sheets], isotypes CM!, GH!, K!).
- *Prestonia schippii* Woodson (1936: 337). Type:—BELIZE Toledo: El Dorado, September 1922, *W. Schipp S-388* (holotype F! [photo F neg. 522873!]).
- Prestonia versicolor Woodson (1936: 332). Type:—PANAMA. Darién: near Cana, 17 April-8 June 1908, L. Williams 940 (holotype NY (lost). Neotype (designated here):—PANAMA. Darién: 10 km NE de Jaque, headwaters of Pavarandó river, 31 January 1981, W. D'Arcy & K. Sytsma 14526 (neotype MO!; isoneotypes, USF!, WAG!).

**Stem** minutely papillate-puberulent, rarely glabrescent at maturity, with clear or milky latex (rarely yellow), sparsely lenticellate, these not suberose, intrapetiolar colleters minute, less than 1.1 mm long. **Petioles** 0.9-3(-8) cm, sometimes papillate; leaf blade  $(8-10-34.5 \times (3-)5.5-18$  cm, elliptic, narrowly elliptic to obovate, apex obtuse to short-acuminate, base obtuse, rounded to broadly cuneate, membranaceous, sometimes slightly revolute, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, many-flowered,

the flowers usually densely clustered, minutely and densely to sparsely puberulent, rarely glabrescent, peduncle 2.5–6 cm, pedicels 0.7–2.4 cm long, floral bracts  $1-3 \times 0.9-1.3$  mm, linear, scarious, minute, green. **Sepals**  $(9-)10-18(-21) \times (3-)4-7$  mm, free, rarely connate at the base for 1/6 of their length and forming an inconspicuous campanulate base, coriaceous to subcoriaceous, narrowly elliptic to narrowly ovate, obtuse, the apices acute to acuminate, not reflexed, glabrous, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins not impressed, colleters 1–2 mm long, usually entire to inconspicuously and variously erose at the apex. Corolla salverform, yellowish green, the lobes with red and purple stripes, rarely the lobes creamish white and without stripes, glabrous outside, tube  $13-19(-23) \times 6-7$  mm, straight, free corona lobes (2.5-)4-5 mm long, the apices exserted, their height surpassing that of the anther apices, annular corona entire, subentire to scarcely 5-lobed, thickened, corolla lobes  $9-16 \times 10-13$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5–6 mm, minutely puberulent to glabrescent dorsally, the apices barely exserted. Ovary 1.5–2 mm tall, glabrous, style-head 1.5-2 mm, nectary 1.5-2 mm, conspicuously surpassing and covering completely the ovary, entire to slightly 5-lobed, each lobe entire to subentire. Follicles  $30-65 \times 0.6-0.8$ cm, continuous, free, but usually united at the tips (at least when young), inconspicuously papillate to glabrescent, lenticels inconspicuous or not evident, membranaceous when old; seeds 10–20 mm, coma 2.4–3.1 cm, tan or cream.

**Distribution and habitat:**—From Mexico throughout Central America and Colombia to northeastern Venezuela, and Ecuador, where it grows in tropical wet forest (including disturbed vegetation and secondary growth), moist forest, margins of flooded forest, savannas, and swamp areas from 0–1350 m.

**Phenology**:—Flowering specimens have been collected from February through November, fruiting specimens from April through December.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local names:—Bejuco berba (Herrera, Panamá); bejuco loroco de venado (Ahuachapán, San Francisco Menéndez, El Salvador); bejuco papalguapa (Ahuachapán, San Benito, El Salvador); granadilla de montaña (Izabal, Guatemala); guagig tupa (San Blas, Cangandí, Panamá); loroco de venado de bajillo (Ahuachapán, San Benito, El

Salvador); loroquillo (Ahuachapán, San Francisco Menéndez, El Salvador); tchomiserano-tapé (Esmeraldas, Ecuador).

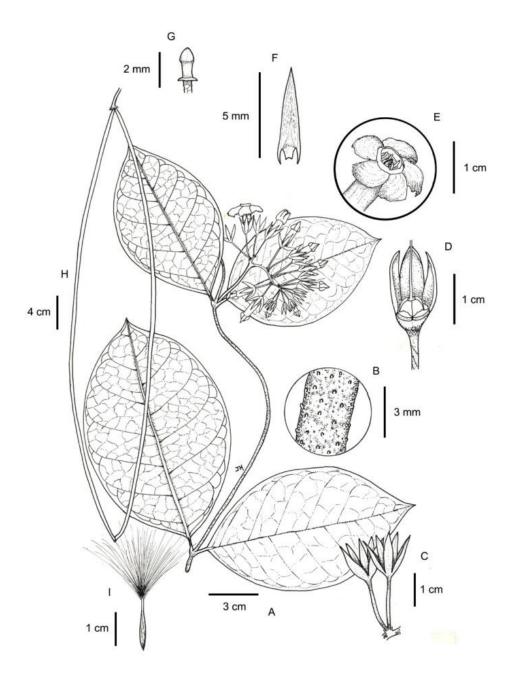


Fig. 41 Prestonia portobellensis (A-C from Morales & Ureña 2838, INB; D-G from Morales & Abarca 5555, INB; H-I from Callejas et al. 4753, HUA). A. Flowering branch. B.

Branchlet, showing the indument. C. Calyces, pedicels, and floral bracts. D. Calyx with two sepals removed, showing the colleters and nectary. E. Corolla mouth. F. Anther, dorsal view. G. Style-head. H. Follicles. I. Seed.

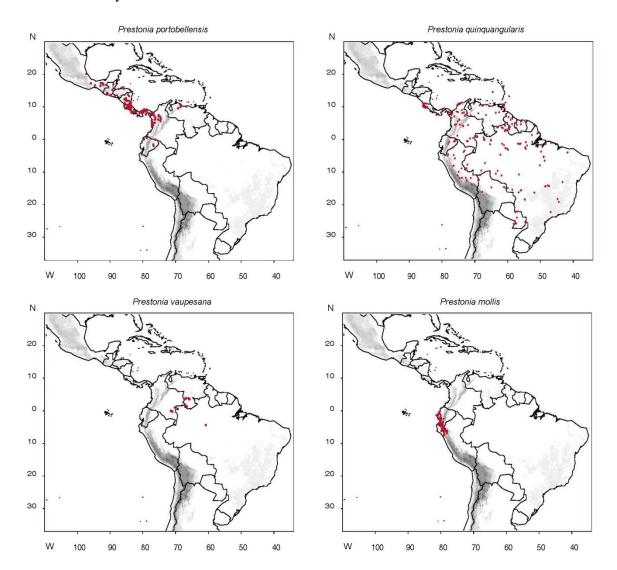


Fig. 42 Distribution maps of *Prestonia portobellensis*, *P. quinquangularis*, *P. vaupesana* and *P. mollis* 

**Uses:**—In Ecuador a decoction of the leaves is rubbed on the chest of pregnant women to stimulate the production of milk (*Barford 41052*).

**Taxonomic notes:**—*Prestonia portobellensis* and some related species (e.g., *P. annularis*, *P. longifolia*) show a wide range of variation in certain features (e.g., size and shape of the leaf blade, size and number of flowers in the inflorescence), which led to the description of numerous species over the years. The most important differences are found in the flowers. *Prestonia annularis* resembles *P. portobellensis*, but differs by the free

corona lobes deeply included within the tube, 1-1.5(-2) mm (vs. free corona lobes with apices exserted, (2.5-)4-5 mm). *Prestonia longifolia* has sometimes been confused with *P. portobellensis*, but the two species can be separated by the differences in sepals and the insertion of the free corona lobes (see discussion under *P. longifolia*).

The type of *Prestonia laxa* has a more open cyme, compared to the type of *Echites portobellensis*, which has a more agglomerate inflorescence. The remaining morphological characteristics are similar, with no noticeable discontinuous differences. This degree of variation in the inflorescence is also found among the individual populations studied, therefore, *P. laxa* is here relegated to the synonymy of *P. portobellensis*.

The holotype of *Prestonia versicolor* was lost in 1978, during the shipment of a loan to Venezuela. This species is known only from the holotype and an additional paratype cited in the original prologue (Cooper 237, NY). Apparently, both collections were shipped in the lost loan. Due to the lack of additional duplicates, W. D'Arcy & K. Sytsma 14526 is selected as neotype because this collection most closely fits the original protologue and it was collected near the type locality.

Additional specimens examined:—MÉXICO. Chiapas: Ocosingo, 8.2 km de Nuevo Guerrero, 6 March 2003, Aguilar 5966 (MEXU); Ocosingo, 45 km despúes de la desviación a Palenque, entre Lacanjá-Chansayab, 20 May 1991, Gónzalez-Espinoza et al. 1469 (MEXU); 2 km E of Teapa, on road to Puyacatenco, 12 November 1984, Martínez et al. 8551 (MEXU); Escuintla, 20 December 1936, Matuda 2159 (A, K, MEXU, MO, UC); Acacoyagua, Escuintla, 11 June 1947, Matuda 16460 (EAP, MEXU); Yajalón, Cerro Tz'iz Ton, 30 August 1983, Méndez 6550 (CR, MEXU); Trinitaria, Cuauhtemoc, carretera Monte Bello-Santa Elena, 15 May 1985, Méndez 8224 (CR, MEXU); Yajalón, Chi, June 1983, Shilom 6191 (MEXU). Oaxaca: Santa María Chimalapa, Arroyo Piedra de Cal, 8 June 1984, Hernández 98 (CHAPA, MO); Santa María Chimalapa, Río Milagro, 23 March 1985, Hernández 1026 (CHAPA, MO); Concordia, April 1933, Morton & Makrinius 2348 (US); Monte Negro, 3 May 1939, Schultes et al. 747 (ECON). Queretaro: NO de Zimapan, 22 August 1957, Waterfall & Wallis 14263 (MO). Tabasco: Tacotalpa, antes de Tapijulapa, 27 May 1982, Cowan et al. 3443 (MO); Macuspana, 8 July 1981, Ramamoorthy 2556 (MEXU); Tenosique, June 1939, Matuda 3405 (F, K, MEXU); Río Puyacatego, cerca del cruce Teapa-Tacotalpa, 23 August 1996, Ortiz et al. 2239 (MEXU); Puyacatengo, Teapa,

25 September 1983, *Ventura 20648* (CR, MEXU). Veracruz: Laguna Tisatal, NE de Tapalapan, 19 June 1972, *Beaman 6204* (BR, MEXU); Sontecomapán, 15 July 1972, *Beaman et al. 1740* (MEXU); Fortuño, Río Coatzacoalcos, February 1937, *Williams 8861* (MO). Data lacking: (fl), *Galeotti 1583* (BR).

GUATEMALA. Alta Verapaz: cerca a Finca Sepacuite, 4 April 1902, *Cook & Griggs 405* (US); Pansamalá, August 1897, *Tuerckheim 1225* (US). Chimaltenango: falda SO del Volcán Fuego, 20 September 1942, *Steyermark 52066* (F, MO). Izabal: Quirigua Vieja, May 1919, *Pittier 8544* (US). Santa Rosa: Volcán Tecuamburro, February 1893, *Heyde & Lux 4539* (BM, GH, K, US). Sacatepequez: entre Río Jute y Río Pantaleón, Escuintla y Santa Lucía Cotz, 24 January 1939, *Standley 63607* (F, MO); a lo largo de Río Guacalate, NO de Escuintla, 14 March 1941, *Standley 89279* (F, MO). Suchitepéquez: Mazatenango, 13 February 1906, *Kellerman 5885* (US).

BELIZE. Belice: finca de Richards Woods, 6 July 1972, *Dwyer 10103* (MO). Cayo: Cayo, 21 June 1973, *Gentry 8437* (MO, NY). Toledo: cerca a Columbia, 12 October 1946, *Gentle 6073* (MEXU [2 sheets], MO, NY); Quebrada Blue, 17 June 1981, *Whitefoord 3291* (BM, MEXU, MO). Data lacking: 27 November 1929, *Schipp 64* (F).

HONDURAS. Atlántida: E de Tela, a lo largo de Río Piedras Gordas, 15 August 1981, *Escobar 24* (MO, TEFH); Río Juana Leandra, Corozal, al E de La Ceiba, 1–3 May 1980, *Nelson 5538* (TEFH); Tela, Río Piedras Gordas, 15 August 1981, *Nelson 7757* (TEFH, US). Colón: Trujillo, Río Negro, 7 September 1980, *Saunders 600* (MO, NY). Comayagua: Barranco Trincheras, al N de Siguatepeque, 28 July 1962, *Molina 10839* (EAP). Cortes: entre Agua Azul y Pito Solo, 26 August 1955, *Molina 5565* (EAP, US). Olancho: Río Catacamas, 17 May 1987, *Ortega 366* (TEFH).

EL SALVADOR. Achuachapán: San Benito, S de Pilitas, 13 February 1994, *Chinchilla s.n.* (B, LAGU, MO); San Francisco Menéndez, 24 February 1994, *Martínez s.n.* (B, LAGU, MO); El Imposible, 30 May 1976, *Muyshondt s.n.* (MO); San Francisco Menéndez, El Corozo, 12 May 2000, *Rosales 118* (B, LAGU, MO), 1 February 2000, *Rosales 295* (B, LAGU, MO), 11 April 2000, *Rosales 556* (B, LAGU, MO); San Francisco Menéndez, Quebrada de la Tere, 21 February 1996, *Sandoval & Sandoval 309* (B, CR, LAGU); San Benito, Cooperativa Los Laureles, 23 March 1997, *Sandoval 378* (B, EAP, LAGU, MO); San Benito, 18 April 1995, *Sandoval & Sandoval 894* (B, CR, EAP, LAGU,

MO); San Benito, Río Guayapa, al O de Piedrona, 17 February 1993, *Sandoval & Sandoval 1013* (B, LAGU, MO). San Vicente: Las Galeras, entre San Miguel y San Vicente, 9 February 1998, *Davidse et al. 37486* (B, BM, ITIC, LAGU, MEXU, MO). Sonsonate: Izalco, 25 February 1907, *Pittier 2012* (US); cerca de Sonsonate, March 1922, *Standley 22349* (GH, NY, US).

NICARAGUA. Atlántico Norte: Comarca de El Cabo, El Puente, Río Leicus, cerca de Waspan, 24 August 1965, Molina 15148 (EAP). Boaco: Boaco, 11 February 1983, Moreno 20143 (MO, WAG), Moreno 20179 (MO). Chontales: 0,6 km from Sanyo Domingo-EL Ayote road, at 3,5 km NE of Santo Domingo Parque, Río Sucio, 11 December 2012, Stevens 33402 (MO); Matagalpa: Río Blanco, Reserva Natural Cerro Musún, 15 July 2000, Rueda & Caballero 14327 (MO). Río San Juan: Indio-Maíz, San Juan del Norte, a lo largo de Río Indio, 3 August 1996, Rueda et al. 4887 (MO); Reserva Indio-Maíz, a lo largo de Caño Chontaleño, 22 February 1997, Rueda et al. 6265 (MO). Rivas: cerca a Rivas, 15 September 1983, Moreno 22187 (MO). Zelaya: monkey Point, Caño El Pato, 25 October 1981, Moreno 12409 (MO); cerca a Las Benitas, 4 February 1982, Moreno et al. 14691 (MO); Caño Montecristi, cerca a Las Benitas, 6 February 1982, Moreno & Sandino 14871 (MO); Zelaya, 6 February 1982, Moreno & Sandino 14880 (MO); Bil Tingnia, NO de Bonanza, 13 May 1978, Neill 4003 (MO); a lo largo de Río Maíz, 8 January 1995, Rueda et al. 2634 (MO); Zelaya, 16 February 1994, Rueda et al. 3086 (MO); Estación Experimental El Recreo, 13 February 1985, Soza et al. 452 (MO); entre El Empalme y Limbaika, 7 March 1981, Stevens & Moreno 19447 (MO); Monkey Point, 7 April 1981, Stevens 20000 (MO); Bahía Monkey Point, 29 September 1981, Stevens 20698 (MO).

COSTA RICA. Alajuela: Monteverde, 15 July 1984, Acevedo-Rodríguez 419 (US); Río Peñas Blancas, 18 December 1988, Bello 612 (CR, MO); San Ramón, Pata de Gallo, 19 December 1929, Brenes 11521 (A, CR, F, NY) Brenes 11521a (F); San Carlos, Aguas Zarcas, 23 May 2000, Estrada 2353 (CR); Upala, 13 February 1982, Gómez-L. 7672a (CR); Monteverde, Río Peñas Blancas, 23 October 1987, Haber & Bello 7641 (CR), 14 December 1987, Haber & Bello 7901 (CR); Zona Protectora Arenal-Monteverde, Valle Peñas Blancas, 30 April 1995, Haber & Bello 11963 (CR, MO); Upala, Laguna Las Camelias, 19 April 1988, Herrera 1845 (CR, F, MO, PMA, WAG); Volcán Arenal, 19

April 1973, Lent et al. 3309 (CR, F, MO); Caño Negro, 16 March 1993, Martínez et al. 74 (CR); San Ramón, San Lorenzo, 5 June 1994, Morales & Carnevali 2904 (CR, MO); San Carlos, Coopesanjuan, entre Quebrada Danta y Río Aguas Zarquitas, 4 July 2003, Morales 9393 (CR); Rincón de la Vieja, Colonia Libertad, 26 July 1991, Rivera 1462 (F, MO); San Carlos, Fortuna, 5 March 2004, Rodríguez 8502 (CR); San Ramón, Peñas Blancas, Chachagua, 24 November 2007, Rodríguez 11712 (CR); Volcán Arenal, O de Fortuna, 19 July 1988, Russell et al. 533 (MO, US). Cartago: Turrialba, 19 November 1952, Córdoba 266 (CR, EAP); Quebrada Casa Blanca, Tapantí, 6 August 1984, Grayum & Sleeper 3705 (CR, MEXU, MO, USF); Turrialba, Florencia Norte, August 1982, Hazlett et al. 7345 (CR); Turrialba, 28 September 1950, León 2772 (USJ), León 2777 (EAP), 20 July 1955, León 4615 (CR, EAP); Las Vueltas de Tucurrique, 27 February 1955, León 4463 (USJ); Parque Nacional Barbilla, Matina, 22 November 2000, Mora & Rojas 1743 (CR, MO); Pejibaye, 31 October 2010, Morales 19055 (CR); Tuís, November 1897, Tonduz 11552 (US). Guanacaste: 5 km al NO de Bagaces, 27 April 1978, Haber 89 (MO, USF); Volcán Arenal, 21 April 1973, Lent 3393 (F); Parque Nacional Guanacaste, Estación Pitilla, 3 March 1991, Moraga 297 (U). Heredia: Finca La Selva, 5 July 1983, Chacón 1042 (DUKE); Río Sarapiquí, 14 May 1981, Folsom 10098 (DUKE); ríos Hondura y Sucio, 24 April 1981, Gómez-L. 6564 (CR); Parque Nacional Braulio Carrillo, Fila Carrillo, 4 April 1984, Gómez et al. 21152 (CR, DUKE, MO, NY, US, USF), May 1984, Gómez et al. 22782 (MEXU, MO [2 sheets], NY, USF); Finca La Selva, Río Puerto Viejo, 9 March 1980, Hammel 7973 (CR, DUKE, F, MO), Hammel 8338 (DUKE), Hammel 8456 (DUKE, F), Quebrada El Sura, 1 June 1980, Hammel 8918 (DUKE), Hammel 9442 (DUKE), Hammel et al. 12770 (DUKE); Sarapiquí, Zona Protectora La Selva, 21 June 1984, Jacobs 2497 (DUKE); Puerto Viejo, Río Sarapiquí, 12 September 1981, Smith 213 (DUKE), Smith 286 (DUKE), Smith 305 (DUKE, MO), Smith 421 (DUKE); Zona Protectora La Selva, Río Puerto Viejo, 9 May 1984, Wilbur & Jacobs 34133 (CR, DUKE); Parque Nacional Braulio Carrillo, Magsasay, 8 November 1990, Zumbado 84 (CR). Limón: La Estrella, Quebrada Barrera, 27 June 2000, Acosta 1896 (CR); Parque Nacional Cahita, Puerto Viejo, 5 July 2000, Acosta et al. 2180 (CR); Barra del Colorado, Sardinas, 25 November 1992, Araya 53 (CR); Barra del Colorado, Puerto Lindo, 24 July 1995, Araya & Corrales 798 (CR, K, MO); entre Cahuita y Limón, 30 November 1975, Baker et al. 27 (F); Parque Nacional Tortuguero, 19 March 1982, Barringer et al. 1941 (F); entre Canaan y Chimirol, Valle del General, 30 December 1969, Burger et al. 7154 (F); Talamanca, Sixaola, Playa Gandoca, 14 November 2000, Estrada & Solano 2504 (CR); Talamanca, entre San Miguel y Gandoca, 22 January 1997, González et al. 1727 (CR, MO); Puerto Vargas, Parque Nacional Cahuita, 16 April 1978, Gómez-L. 3661 (USJ); Lagunas Tortuguero, 19 March 1982, Gómez-L. 7833 (CR); entre Home Creek y Cahuita, 5 May 1983, Gómez et al. 20506 (MO); Parque Nacional Tortuguero, a lo largo de Río Suerte, 21 January 1997, Grayum et al. 11118 (CR, MO); Río Santa Clara, Guápiles, Holm et al. 428 (A, WIS, USJ); Talamanca, Sukut, 7 July 1989, Herrera 3199 (CR, MO); Pococí, Palmitas, 18 April 1997, Jiménez et al. 2288 (CR, MO); Río Parismina, 31 March 1972, Lent 2440 (F, MEXU); Fila Matama, Cerro Muchilla, falda NO, 24 March 2001, Morales 7680 (CR); Gandoca Manzanillo, cerca de Quebrada Hone Wark, 4 May 2001, Morales 7960 (CR, MO); Puerto Viejo, playa Negra, 5 May 2001, Morales 7986 (CR); Delta Río San Juan, June 1890, Pittier 2574 (CR); Moín, Limón, June 1898, Pittier 12401 (GH, US); Limón, September 1899, Pittier 16016 (A, US); Parque Nacional Tortuguero, 3 December 1987, Robles 1442 (CR), Lomas de Sierpe, 10 June 1988, Robles 1910 (CR, MO); Tortuguero, 7 July 1988, Robles 1926 (CR); Pococí, Parque Nacional Tortuguero, Caño Chiquero, 26 November 1994, Rodríguez 366 (CR); Puerto Vargas a Cahuita, 4 October 1983, Sánchez & Zamora 143 (F, TEFH); Finca Los Diamantes, 29 February 1956, Schubert 1114 (A); Parque Nacional Tortuguero, 11 November 1989, Solano 27 (CR), Solano 184 (CR); Cerro Coronel, E de Laguna Danto, 20 September 1986, Stevens 24604 (CR, MEXU, MO, USF); NNE de Barra del Colorado, 18 March 1987, Stevens et al. 25000 (CR, MEXU, MO); Río Sucio, cerca a Corinto, 26 April 1949, Williams 16549 (EAP, USJ). Puntarenas: Parque Nacional Piedras Blancas, serranìas de Golfito, Río Bonito, 10 June 2000, Acosta et al. 1686 (CR); Golfo Dulce, Drake, 24 April 1992, Aguilar 1184 (CR); Península de Osa, Aguabuena, 10 August 1993, Aguilar 2104 (CR, MO); Parque Nacional Corcovado, 2 September 1993, Aguilar 2157 (CR, MO); Buenos Aires, Potrero grande, sabanas Helechales, 5 March 2000, Aguilar 6053 (COL); Parque Nacional Corcovado, Sirena, 19 February 2001, Aguilar 6395 (CR); Zona Protectora Las Tablas, Finca Cafrosa, 21 May 1999, Alfaro 2290 (CR); Parque Nacional Manuel Antonio, 28 February 1982, Barringer et al. 1711 (F); Golfito de Golfo Dulce, 12 April 1930, Brenes 12284 (F); Jiménez, 29

September 1896, Cooper 10205 (CR, US); Monteverde, 18 June 1977, Dryer 1492 (CR, F); Parque Nacional Piedras Blancas, La Nicuesa, 1 November 1997, Fletes 514 (CR, MO); Parque Nacional Manuel Antonio, 28 February 1982, Gómez-L. 7764 (CR); Jardín Botánico Wilson, 8 February 1990, Gómez-L. et al. 11912 (CR, F, MO, USJ); Río Peñas Blancas, 20 October 1987, Haber & Cruz 7513 (MO); Monteverde, 12 July 1991, Haber et al. 10842 (CR); Golfo Dulce, entre Rancho Quemado y Drake, 12 April 1992, Hammel et al. 18491 (CR [2 sheets], MO); Aguabuena, fila Casa Loma, 3 October 1990, Herrera 4464 (CR, F, MO); Osa, Sierpe, fila Casaloma, 27 January 1991, Herrera 4882 (CR, MO); Golfito, Cerro Las Torres, 31 January 1992, Herrera 5043 (CR, F, MO); Golfito, Río Esquinas, 10 February 1991, Induni 210 (CR, MO); Parque Nacional Corcovado, Sirena, 5 February 1988, Kernan 92 (CR, MO), 30, March 1988, Kernan 343 (CR, MO), 31 December 1988, Kernan et al. 849 (CR, MO); Coto Brus, a lo largo de Río Java, 29 June 1994, Kress & Flores 94-4253 (MO, US); Ballena, Playa Hermosa, Dominical, 28 June 2002, Kriebel 334 (CR); Golfito, El Ñeque, Puerto Jiménez, 30 December 2004, Kriebel et al. 5052 (CR); Golfo Dulce, Bahía Rincón, 25 November 1993, Morales et al. 2086 (CR, MO, NY, USF); parque internacional La Amistad, sendero los Gigantes, 22 February 2006, Morales et al. 13751 (CR); Potrero Grande, La Lucha, Río Guineal, 3 November 2010, Morales et al. 19116 (CR); Parque Nacional Corcovado, SO de Esquinas, 25 June 1993, Quesada & Segura 671 (CR); Parque Nacional Corcovado, Esquinas, 10 April 1994, Quesada 865 (CR); Coto Brus, Altamira, 15 September 1997, Quesada 2022 (CR); Parque Nacional Manuel Antonio, 7 August 2001, Rodríguez et al. 7390 (CR); Golfo Dulce y Río Térraba, December 1947, Skutch 5368 (EAP, US); Santo Domingo, Golfo Dulce, March 1896, Tonduz 9889 (BR [2 sheets], US), Tonduz 9935 (BR [2 sheets], CR, NY, US); SE de Buenos Aires, 8 July 1977, Webster et al. 21908 (F, UC); Reserva Biológica Carara, 9 May 1990, Zúñiga 198 (CR, F, MO, USJ). San José: Tarrazú, Llanos de Santa María, 9 July 1997, Estrada et al. 971 (CR); Parque Nacional Carara, cerca a Río Carara, 2 April 1993, Gentry et al. 79315 (CR, MO); Santiago de Puriscal, carretera a Cerbatana, 1 May 1997, Jiménez et al. 2297 (CR, F, MO); Zona Protectora La Cangreja, Puriscal, 3 March 1994, Morales et al. 2413 (CR, K, MO); Acosta, fila San Jerónimo, 29 May 1994, Morales & Ureña 2838 (CR, MEXU, MO, NY, UB); Reserva Biológica Carara, 19 April 1995, Morales & Zamora 4017 (CR, MO); Acosta, fila Bustamante, entre Sabanillas y Sabanas,

28 July 1996, *Morales & Abarca 5555* (CR, K, MO, NY); Cerros de Turrubares, cabeceras Río Caite, 26 April 2002, *Morales & Hammel 8535* (CR); Parque Nacional La Cangreja, Alto Concepción, Quebrada Grande, sendero a Río Negro, 14 September 2003, *Morales & González 9849* (CR); Acosta, Aserrí, Aguabuena, cabeceras Quebrada Laja, 24 September 2003, *Morales et al. 992* (CR); Acosta, Quebrada Carate, Falda S de Alto Mostazal, 2 May 2004, *Morales 10545* (CR); Acosta, entre Caspirola y Colorado, 1 October 2004, *Morales 11639* (CR); Acosta, entre Zoncuano y Las Vegas Río Parrita, 7 April 2005, *Morales & Santamaría 12684* (CR); Acosta, San Jerónimo, Soledad, 9 March 2014, *Morales 21445* (CR); Parque Nacional Carara, Río Carara, 5 May 1999, *Rodríguez et al. 4830* (CR).

PANAMÁ. Bocas del Toro: Río Changuinola, cerca a Changuinola, 10 September 1963, Dwyer s.n. (MO); Water Valle, 16 September 1940, von Wedel 799 (GH, MO); Water Valle, 18 September 1940, von Wedel 852 (GH, MO); cerca del Lago Chiriquí, 19 October 1940, von Wedel 1262 (MO), 14 November 1940, von Wedel 1622 (MO), 20 November 1940, von Wedel 1702 (GH, MO); Isla Old Bank, 8 February 1941, von Wedel 2022 (GH, MO), von Wedel 2076 (GH, MO); Isla Colón, cerca del Lago Chiriquí, 3 June 1941, von Wedel 2471 (GH, MO); Nances Cay, cerca del Lago Chiriquí, 21 October 1941, von Wedel 2859 (GH, MO). Chiriquí: camino hacia Soledad, SO del campamento Fortuna, hasta la región de finca Pitti, 8 June 1976, Correa et al. 2093 (PMA); Camino hacia la finca Landau, NE del campamento de Fortuna (Hornito), 13 August 1976, Correa et al. 2349 (PMA); camino hacia Soledad, SO del campamento Fortuna, hasta la región de finca Pitti, 14 August 1976, Correa et al. 2391 (PMA); NO del Campamento Fortuna. 23 September 1976, Correa et al. 2617 (PMA); Represa Fortuna, 20 June 1987, Croat 66510 (MEXU, MO, PMA, USF); Boquete, 20 May 1938, Davidson 684 (A, F, MO); cerca a Questa Piedra, camino a Río Monte, 7 June 1977, Folsom 3988 (MO); Represa Fortuna, 15 September 1977, Folsom et al. 5554 (MEXU, MO, PMA); Guanaca, Valle La Mina, Hornitos, 15 March 1998, Galdames et al. 4187 (F, MO, PMA, SCZ); cercanías de la presa Fortuna, sendero al Río Hornito, 11 August 1985, McPherson 9935 (MO, USF); Represa Fortuna, cerca de Río Hornito, 1 July 1987, McPherson 11163 (MO); cerca a Fortuna, 6 May 1976, Mendoza 313 (MO, PMA); Sendero Cordillera, cerca de la división Continental, 7 July 1997, Montenegro 1698 (PMA); NE de San Félix, carretera a Cerro Colorado, 18 March 1974, Nee 10706 (MO). Coclé: cerca de El Valle, 14 May 1939, Allen 1800 (EAP,

MO [2 sheets]); El Valle de Antón, 29 June 1946, Allen 3552 (EAP, MO); camino a Coclesito, 12 millas de Llano Grande, 17 December 1983, Churchill et al. 4157 (MO, PMA, USF); La Mesa cerca de el Valle, carretera a Cerro Pilón, 21 July 1974, Croat 25392 (MO); El Petroso, 9 April 1977, D'Arcy 11333 (MO); La Mesa cerca de El Valle, 13 August 1972, Gentry 5642 (MO); El Valle de Antón, a lo largo de Río Antón, 2 February 1935, Hunter & Allen 372 (MO, NY, P, S); La Pintada, El Copé, parque nacional general de División Omar Torrijos Herrera, camino hacia el Calvario, 3 September 2010, Vergara et al. 285 (PMA). Colón: cerca del campamento Piña, 11 July 1946, Allen 3588 (EAP, K, MO, USF); a lo largo de Río Guanche, 5 July 1979, Antonio 1229 (MO, Z); Donoso, proyecto minero de Petaquilla, 12 December 2007, Araúz & Moreno 1476 (PMA); Camino maderero Santa Rita, 30 July 968, Correa & Dressler 908 (F, MO, PMA); Santa Rita, al E de la zona montañosa, 16 August 1968, Correa & Dressler 988 (PMA); Santa Rita, 25 March 1999, Correa et. al. 11495 (MO, PMA); cerca de San Miguel de la Borda, 21 April 1970, Croat 9875 (MO); cerca de Río Indio, entre Portobelo y Nombre de Dios, 23 March 1976, Croat 33614 (MO, NY); fila Santa Rita, 28 July 1972, D'Arcy 6136 (MO); Colón, 27 June 1984, D'Arcy et al. 15555 (MO); N de Río Guanche, 16 November 1975, Davidse & D'Arcy 10069 (MO); Río Guanche, 22 May 2001, Florpan et al. 5185 (PMA); Santa Rita, camino a Sierra Llorona, 18 May 2005, Florpan et al. 6686 (PMA); O de Portobelo, 24 April 197, Gentry 5142 (MO); Gatún, 28 January 1860, Hayes 450 (GH [2 sheets], NY); camino de la fila Santa Rita, 22 May 1982, Knapp & Schmalzel 5235 (MO); fila Santa Rita, 9 April 1969, Lewis et al. 5398 (MO); cerca de la Torre de Radio, en el final del camino a Santa Rita, 1 August 1983, Miller & Miller 919 (MO, NY, PMA, USF, WAG); cerca a Río Boquerón, 11 October 1974, Mori & Kallunki 2434 (MO); Quebrada Santa Marta, SO de Pina, 17 May 1974, Nee 11700 (MO); fila Santa Rita, NE de Colón, 6 January 1983, Schmalzel 2067 (MO); Achiote, 12 July 1966, Tyson et al. 4527 (MO). Darién: NE de Jaque, Río Pavarandó, 31 January 1981, D'Arcy & Sytsma 14513 (MO); entre Río Membrillo y Río Subcuti, 21 August 1966, Duke 8605 (MO); Ensenada del Guayabo, SE de Jaqué, 14 January 1983, Garwood et al. 293 (BM, MO, PMA); Ensenada del Guayabo, SE de Jaqué, 29 April 1980, Garwood 992 (MO, PMA, TEFH, VEN); colinas Periaque, cerca a Río Sabana y Lara, 16 julio 1966, Tyson et al. 4721 (MO [2 sheets]); cerca a Mamey, 11 March 1982, Whitefoord & Eddy 476 (BM [2 sheets]). Herrera: cerca de Las Minas, entre Río Las Trancas y Las Minas, 22 February 1963, Stern et al. 1808 (MO). Los Santos: Loma Prieta, Cerro Grande, 8 June 1967, Lewis et al. 2207 (MO, UC). Panamá: Península de Bohío, 26 January 1999, Aizprúa & Flores 1445 (PMA); Isla Taboga, 16 December 1938, Allen 1269 (MO); cerca de Campana, 1 July 1939, Allen 1887 (MO); faldas de Cerro Jefe, 20 January 1980, Antonio et al. 3433 (MO); Isla Barro Colorado, 1931, Aviles 101 (MO); Isla Barro Colorado, 28 August 1929, Bangham 467 (A), 6 September 1929, Bangham 569 (A, F); Barro Colorado, January 1939, Brown 18 (EAP), Brown 119 (F); Cerro Campana, 11 March 1973, Busey 862 (MO); cerca a La Eneida, Cerro Jefe, 8 August 1968, Correa & Dressler 945 (MO, PMA), 12 February 1971, Correa et al. 1722 (MO, PMA); Cerro Jefe, 3 October 1969, Correa et al. 1588 (PMA); Gamboa navy Pipeline, 5 February 1971, Correa et al. 1709 (PMA); parque nacional Altos de Campana, sendero Zamora, 7 April 1994, Correa & Montenegro 10417 (PMA); parque nacional Altos de Campana, sendero al Cerro de la Cruz, 13 October 1994, Correa & Montenegro 10848 (PMA); parque nacional Altos de Campana, sendero al Cerro Campana, 20 April 1995, Correa & Montenegro 11073 (PMA); Isla Barro Colorado, Península Groos Point, 25 April 1968, Croat 5084 (F, MO); Isla Barro Colorado, Fuertes Cove, 1 May 1968, Croat 5272 (MO); Isla Barro Colorado, 7 June 1971, Croat s.n. (MO), 12 December 1967, Croat 4256 (MO), 1 May 1968, Croat 5283 (MO), 18 May 1968, Croat 5639 (MO), 15 September 1968, Croat 6096 (MO), 1 October 1968, Croat 6606 (MO), 15 January 1969, Croat 7260 (MO), 20 January 1969, Croat 7358 (MO), 5 February 1969, Croat 7707 (MO), 15 February 1971, Croat 13497 (MO); Zona del Canal, 4 April 1970, Croat 9328 (MO), 1 January 1971, Croat 12989 (MO); Zona del Canal, entre Fuerte Sherman y Fuerte San Lorenzo, 10 July 1971, Croat 15433 (MO); Cerro Azul, 23 June 1972, Croat 17326 (C, F, MO); Zona del Canal, 21 April 1970, D'Arcy 4294 (MO); carretera El Llano-Cartí, 12 September 1976, D'Arcy 10658 (MO); Cerro Jefe, 11 April 1977, D'Arcy 11371 (MO); Cerro Campana, 19 April 1971, Dressler & Williams 3961 (MO); Isla San José, Archipiélago de Las Perlas, 20 May 1973, Dressler 4399 (F, MO, PMA); Isla San José, 18 July 1967, Duke 12566 (MO); Cerro Azul, 17 July 1967, Dwyer 2067 (MO), 14 July 1963, Dwyer 5038 (MO); entre Cerro Jefe y La Eneida, 17 January 1968, Dwyer et al. 8198 (MO), Dwyer 8226 (MO); Cerro Jefe, 5 January 1972, Dwyer 9440 (MO, NY); Río Manoni, cerca a Chepo, 11 September 1962, Duke 5588 (MO); Río Pacora, cerca a Río

Corso, 9 June 1967, Duke 11988 (MO); Isla San José, 14 May 1945, Erlanson 117 (GH, US), 26 June 1945, Erlanson 367 (GH, US); Chorrera, hacia La Arenosa, 21 April 2004, Florpan et al. 6511 (PMA); Parque Nacional Soberanía, camino de Plantación, 2 July 1991, Florpan et al. 855 (PMA); N del lago Goofy, 11 March 1977, Folsom et al. 1955 (MO); Cerro Jefe, 11 April 1977, Folsom et al. 2523 (MO, PMA); Barro Colorado Island, E side of Pena Blanca Peninsula, 8 June 1969, Foster 962 (F, PMA), 29 June 1969, Foster 1053 (PMA), 6 July 1969, Foster 1086 (MO, PMA); O de Balboa, 24 July 1978, Garber 143 (MO); Cerro Azul, January 1972, Gentry et al. 3400 (MO); cerca a Río Espavel, 23 January 1972, Gentry 3788 (BM, MO, PMA); camino Pipeline, 22 March 1972, Gentry 4799 (MO); Cerro Jefe, 21 December 1972, Gentry 6750 (MO, NY, Z); carretera El Llano-Cartí, 15 February 1975, Gentry & Mori 14207 (F, MO, PMA); Antigua Camaronera, 5 August 2000, Guerra & Guardia 1151 (PMA); Panamá, s.d., Hayes 375 (K); Isla San José, Golfo de Panamá, Johnston 347 (GH, L, MO, P, U), Johnston 686 (GH), Johnston 767 (GH, MO), Johnston 1096 (GH); cerca a Gamboa, 14 February 1973, Kennedy & Steiner 2463 (MO); carretera a Cerro Campana, 19 August 1967, Kirkbride 244 (MO, NY); valle del Río Terable, 9 June 1982, Knapp & Schlmalzel 5475 (MO); cerca a Bohio, Zona del Canal, 12 February 1911, Maxon 4775 (BM, C, US); Cerro Jefe, a lo largo de Río Pacora, 23 January 1986, McPherson & Merello 8122 (MO); NO de Cerro Azul, 18 December 1974, Mori & Kallunki 3785 (MO); Cerro Campana, 8 August 1975, Mori & Bolten 7678 (MO); Río Mendosa, 8 km NO de Gamboa, 9 February 1974, Nee 9578 (F, MO, PMA); Zona del Canal, 1911, Pittier 2220 (BM, US); cerca de Frijoles, Zona del Canal, 1 July 1911, Pittier 3756 (GH, NY, US); Isla Barro Colorado, 28 January 1982, Schmalzel & Herrera 335 (MO), 3 February 1982, Schmalzel & Herrera 363 (MO, WAG), 12 March 1982, Schmalzel 463 (MO, WAG), 10 August 1982, Schmalzel 789 (MO); Isla Taboga, 1 January 1867, Thiebauh 1274 (P); Fuerte Sherman, 13 October 1965, Tyson & Chu 1683 (MO); falda O del Cerro Campana, 21 May 1966, Tyson 4030 (MO); Isla Barro Colorado, 16 January 1932, Wetmore & Abbe 219 (A, GH, F, MO), 3 February 1932, Woodworth et al. 377 (F). San Blas: entre Puerto Obaldía y Puerto Armila, 29 April 1980, D'Arcy 13687 (MO); tierra firme frente a las Isla Miria Ubigandup, camino Digole, 19 July 1987, Herrera 267 (MO, PMA); sendero Kuna, O de la carretera Llano-Cartí, 16 December 1987, McPherson 11874 (MO); El Llano a Cartí, 19 November 1984, Nevers et al. 4373 (MO, PMA); El Llano, 26 January 1985, Nevers 4653 (MO, PMA, WAG); El Llano-Cartí, 31 January 1985, Nevers 4776 (MO, PMA); Cangandí, 16 May 1985, Nevers 5675 (MO); sendero de la boca del Río Irgandi al tributario del Río Cartí Senni, 20 December 1985, Nevers & Herrera 6604 (MO, PMA, USF). Veraguas: Isla de Coiba, carretera a playa Hermosa, 25 October 1979, Antonio 2386 (MO, PMA, USF [2 sheets]), Antonio 2388 (MO, USF, WAG); Isla Coiba, entre Barco Quebrado y campamento Playa Blanca, 3 September 1995, Aranda et al. 2337 (MA, PMA); Isla de Coiba, camino a El Catival, 22 January 1994, Castroviejo et al. 7125 (COL, MA, MBM, PMA); Isla de Coiba, campamento Manila, Río Manila, 16 March 1996, Castroviejo et al. 13504 (MA); 2 km al O de Santa Fé, 18 March 1973, Croat 23030 (C, MO, NY, USF, WAG); Isla de Coiba, siguiendo la Quebrada del Río Escondido, 19 November 1994, Espinosa et al. 518 (PMA); Parque Nacional Isla de Coiba, Montijo, entre Juncal y Producción, 12 March 1996, Galdames et al. 2711 (MA, PMA); Isla Coiba, Montijo, Río Manila, extremo S de Coiba, frente a la Isla de Jicarón, 16 March 1996, Galdames et al. 2816 (PMA); Concepción, 17 October 1978, Hammel 5241 (MO); Azuero, fila El Pavo, SE de El Cortezo, 28 October 1978, Hammel 5433 (MO); Río Santa María, puente cerca a Santa Fé, 19 March 1982, Knapp & Kress 4327 (MO, USF); Isla de Coiba, Quebrada del Río Escondido, 19 November 1994, Martín-Ballesteros et al. 518 (MA); Isla de Coiba, entre el Campamento de Playa Blanca y el de Barco Quebrado, 26 November 1994, Martín-Ballesteros et al. 740 (MA), Martín-Ballesteros et al. 759 (MA); Santa Fé, cerca de la base del Cerro San Antonio, s.d., *Polanco 3661* (PMA); Finca Colonia Ponuga, 21 December 1986, Rodríguez 74 (CR, F, MO, PMA). Data lacking: 11 July 1936, *Lindsay 445* (F).

COLOMBIA. Antioquia: Turbo, carretera a Tapón del Darién, 29 January 1984, Brand & González 841 (JAUM, MO); Turbo, cerca a Tapón del Darién, sector Río León-Lomas Aisladas, km 37, 27 February 1984, Brand 940 (COL [2 sheets], HUA, JAUM [2 sheets], MO); El Doce, 215 km de Medellín, 23 April 1977, Callejas 146 (HUA); carretera Dabeiba-Chigorodó, 30 July 1987, Callejas et al. 4753 (HUA, NY); Puerto Berrío, Finca Penjamo, 6 March 1990, Callejas et al. 9389 (HUA); Necoclí, Reserva Indígena Caimán New, August 1992, Castaño et al. 39, 42, 80 (all HUA), June 1992, Castaño et al. 116 (HUA); San Luis, Río Claro, sector Nor occidental, 30 April 1984, Cogollo 1537 (HUA, JAUM, MO); San Luis, Río Claro, sector Sur oriental, 4 September 1984, Cogollo 1951

(JAUM, MO); Lomas Aisladas, cerca a carretera Panamericana, 23 January 1985, Cuadros 2047 (COL, MO, US); Jericó, December 1945, Daniel 3495 (MEDEL); Guatapé, vereda Santa Rita, 19 April 1985, Escobar et al. 5052 (HUA); Ituango, 5 April 2000, Estudiantes B. T. M. 71 (MEDEL); Cáceres, Jardín, Hacienda Catatumbo, 21 February 1988, Fonnegra & Roldán 2373 (HUA [2 sheets], MO [2 sheets], USF); Frontino, sector Venados Abajo, predio La Esperanza, parque nacional natural Las Orquídeas, 12 July 2013, Hoyos-Gómez et al. 2429 (JAUM); San Luis, Quebrada La Cristalina, sector SO, 30 July 1987, Ramírez & Ramírez 1404 (COL, HUA, JAUM, MO); Chigorodó, vereda Malagón, vía Cocuelo, 13 January 1986, Renteria et al. 4594 (JAUM, MO); Chigorodó, carretera Chigorodó-Malagón, 16 January 1986, Renteria et al. 4648 (JAUM, MO); Angelópolis, 27 July 1927, Toro 269 (MEDEL, NY); Triganá, Capurganá, alrededores del Jardín Botánico, 14 June 2010, Tuberquía et al. 3181 (HUA); Urabá, Dabeida, El Pital, 15 January 1947, Uribe 1486 (JAUM). Chocó: Bahia Solano, playita de Cuesta, 14 April 2003, Arias 280 (HUA); Parque Nacional Los Katios, 16 July 1979, Barbosa 1043 (MO, USF); Alto Río Jurubidí, cerca a Quebrada Munduquera, 6 May 1990, Barbosa 6478 (MO); Balboa, reserva Las Palmeras, 3 April 2000, Correa et al. 111 (HUA); Río San Juan, Quebrada del Taporal, 30 May 1946, Cuatrecasas 21495 (VALLE); Río Neguá, tributario del Río Atrato, 3 April 1958, Cuatrecasas et al. 24184 (COL, US); Bahía Solano, corregimiento El Valle, carretera El Valle-Almejal, 15 April 1989, Espina et al. 2462 (CHOCO, CR, HUA), Espina et al. 2494 (CHOCO, HUA); Bahia Solano, corregimiento el Valle, entre El Valle y Boroboro, 16 April 1989, Espina et al. 2548 (CHOCO, HUA); Parque Nacional Ensenada de Utria, playa Piedra Rancho a caída Cocalito, 18 April 1990, Espina et al. 3654 (CHOCO, MO, USF); Bahía de Solano, cerca a Mutis, 9 June 1950, Fernández 287 (COL, US); Acandí, vereda Coquital, 23 May 1989, Fonnegra et al. 2807 (CAS, HUA, MEXU, NY, USF); Río Mutatá, 7 January 1973, Forero & Gentry 696 (COL), Forero & Gentry 698 (COL, MO); entre Quibdó y Guayabal, 20 April 1975, Forero et al. 1240 (COL [2 sheets], MO, NY, VEN); Riosucio, Parque Nacional natural Los Katios, campamento de Tilupo, s.d., Forero et al. 1570 (COL, NY); Río Sucio, entre Tilupo y Peye, 2 June 1976, Forero et al. 1758 (COL); cerca a San Pedro de Ingara, 2 September 1976, Forero et al. 2502 (COL); Río Ingara, 30 August 1976, Forero et al. 2356 (COL); Hoya del Río San Juan, Río Bicordó, 5 April 1979, Forero et al. 4657 (COL, MO); Hoya del Río San Juan, 7 April 1979, Forero et al.

4841 (COL, MO); Río Atrato, entre Loma del Sapo y Bocas de Guayabal, 23 June 1983, Forero et al. 9452 (COL, MO); Región del Río Baudó, 6 February 1967, Fuchs & Zanella 21780 (MO, U), 1967, Fuchs et al. 22186 (COL); E de Tutunendo, carretera Quibdó-Medellín, 12 August 1976, Gentry & Fallen 17538 (COL, MO); Río San Juan, entre Dipurdu y San Miguel, 14 August 1976, Gentry & Fallen 17684 (COL, MO); Jurubida, playa Peñas Blancas, Quebrada Aguas Frías, 25 December 1991, Gómez et al. 346 (HUA, MO, USF); Acandí, bahía de Sapzurro, 19 March 2005, Hoyos-Gómes & Upegui 123 (CR, MO); sendero Bagado-Certegui, 9 December 1983, Juncosa 1573 (F, JAUM, MO, USF); Mecana, N de Bahia Solano, Quebrada La Platanilla, al N del Río Mecana, 10 January 1984, Juncosa 1858 (JAUM, MO, USF); Río Sucio, Parque Nacional Los Katios, 26 November 1976, León 559 (COL); Acandí, entre Goleta y Playona, 11 April 1990, López 253 (HUA); Istmina, Río San Juan, 11 September 1983, Murillo 3 (COL, CHOCO); Río San Juan, tributario del Río Taparal, 15 November-6 December 1979, Rooden et al. 658 (U); Riosucio, Parque Nacional Los Katios, sector Tilupo, 12 July 1983, Sánchez & Hoyos 562 (MEDEL); Nuquí, Alto de Buey, 12 June 1940, von Sneidern s.n. (S), 1 July 1940, von Sneidern s.n. (S); Parque Nacional Los Katios, 26 April 1982, Zuluaga 810 (COL). Magdalena: entre La Gran Vía y San Pedro de la Sierra, 10 May 1983, Escobar & Santa 3487 (HUA); camino a San Pedro de la Sierra, Quebrada Botella, 29 September 1972, Kirkbride 2269 (COL, NY). Nariño: Monte Alto, S de Tumaco, 16 October 1955, Romero-Castañeda 5390 (COL). Putumayo: Río Putumayo, puerto Porvenir, 22 November 1940, Cuatrecasas 10762 (COL, US). Quindió: Circasia, vereda Barcelona Alta, 23 March 1991, Agudelo et al. 1056 (HUQ). Valle del Cauca: Río Nayo, debajo de Puerto Merizalde, 1 March 1943, Cuatrecasas 14323 (VALLE); Río Calima, La Trojita, 19 February-10 March 1944, Cuatrecasas 16237a (VALLE [in part]); Río Cajambre, Quebrada del Corozal, 17 May 1944, Cuatrecasas 17741 (VALLE); bahía Málaga, 2 March 1987, Millán 45 (CUVC).

ECUADOR. Esmeraldas: Río Zapallo Grande, tributario de Río Cayapa, 25 October 1982, *Barford 41052* (AAU, QCA); Reserva Ecológica Mache Chindul, Estación Bilsa, 2 October 1996, *Clark 2996* (CR, MO); Garrapata, cerca a Borbón, 14 July 1964, *Játiva & Epling 768* (S, SEL, UC); La Guayacana, Isla Pichangal, 24 July 1967, *Játiva & Epling 2004* (S, UC). Pastaza: Pastaza, pozo petrolero Corrientes, 35 km SE de Curaray, 1–13

September 1990, *Gudiño 769* (COL, MEXU, MO, NY, QCNE, USF); Vía Auca, S de Coca, cerca al límite Napo-Pastaza, 7 January 1989, *Hurtado et al. 1357* (MO).

VENEZUELA. Apure: Paéz, E de El Nula, 2 July 1983, van der Werff & González 4755 (MO, VEN), van der Werff & González 4768 (VEN). Aragua: entre El Paujil y El Socorro, al S de El Consejo, 15 July 1979, Steyermark & Stoddart 118114 (VEN). Bolivar: Tierra Alta, Río Sinú, 7–10 March 1918, Pennell 4569 (NY). Distrito Federal: Cerro Avila, entre Papelón y Quebrada Chacaito, 25 September 1977, Manara s.n. (MICH, VEN); entre Portachuelo y Peñita, sin fecha precisa, Rojas 1549 (MY). Falcón: Sierra de San Luis, al S de la Tabla, 16 July 1967, Steyermark 98902 (VEN, Z). Lara: cerca a Laguna Negra, Loma de Los Naranjos, Montaña de Macanillal y fila de San Esteban, March 1975, Steyermark et al. 111612 (MO, VEN, Z). Miranda: NE de Los Teques, colinas de Carrizal, 12 November 1973, Morillo & Morillo 3690 (VEN); Colinas de Carrizal, 13 August 1977, Morillo et al. 6615 (VEN); ecabeceras Río Guarita, 10 August 1975, Steyermark et al. 111898 (MO, NY, VEN, Z). Yaracuy: Cerro La Chapa, N de Nirgua, 21 October 1982, Davidse et al. 20856 (MO, VEN); Sierra de Aroa, Cerro Negro, cerca a San Felipe, 1967, Steyermark & Wessels-Boer 100418 (MO, NY, VEN).

- Prestonia quinquangularis (Jacquin) Sprengel (1825: 637). Echites quinquangularis Jacquin (1760: 13). Temnadenia quinquangularis (Jacquin) Miers (1878: 212). Type:—COLOMBIA. Atlántico: Cartagena, Cerro La Popa, without data, Jacq., Select. Stirp. Amer. Hist. t. 25. 1763. (lectotype designated by Morales (2004 b)). Fig. 42, 43
- Echites nutans Anderson, Trans. Soc. London Encour. Arts 25: 203. 1807. Haemadictyon nutans (Anderson) Candolle (1844: 426). Prestonia nutans (Anderson) Voss in Siebert & Voss (1894: 658). Type:—DOMINICAN REPUBLIC. Santiago: Santo Domingo, s.d. S. Linnsey s.n. (holotype K!).
- Haemadictyon venosum Lindley (1825: 70). Prestonia venosa (Lindley) Nicholson (1886: 216). Type:—SAINT VINCENT AND THE GRENADINES, 1849, G. Calley s.n. (holotype K!, isotype CGE!).

- Echites leptolobus Stadelmeyer (1841: 15). Temnadenia leptoloba (Stadelmeyer) Miers (1878: 211). Type:—BRAZIL. Amazonas: Río Japurá, s.d., *M. Martius s.n.* (holotype M! [photo F neg. 20146!]).
- Haemadictyon marginatum Bentham (1841: 250). Prestonia marginata (Bentham) Woodson (1936: 291), nom. illeg. Type:—GUYANA. Upper Takutu-Essequibo: Pirara, s.d., R. Schomburgk 713 (holotype K! [2 sheets]; isotype L!).
- Haemadictyon acutifolium Bentham ex Müller Argoviensis (1860: 167). Prestonia acutifolia (Bentham ex Müller Argoviensis) K. Schumann (1895: 188). Type:—
  BRAZIL. Amazonas: near Manaus, Río Negro, December 1850–March 1851, R. Spruce 1002 (holotype M!, isotypes B [destroyed, photo F neg. 4547!], CGE!, FIW!, K!, NY, n.v., W!).
- Haemadictyon caliginosum Miers (1878: 260). Type:—PERU. San Martín: San Martín, Tarapoto, s.d., R. Spruce 4924 (holotype BM!, isotypes BR!, K! [2 sheets]).
- Echites bangii Rusby (1907: 409). Type:—BOLIVIA. Without data, *M. Bang 2053* (lectotype NY! designated by Morales (2006 b), isolectotypes B (destroyed), BM!, F! [photo F neg. 51102!], G! [3 sheets], K! [2 sheets], MO!, NY!, US!).
- Echites hulkianus Pulle (1912: 160). Type:—SURINAME. Sipaliwini: Río Lucie, 26 November 1910, *J. Hulk 383* (holotype U!).
- Echites laurentiae-disca Rusby (1920: 85). Type:—VENEZUELA. Delta Amacuro: Santa Catalina, Bajo Orinoco, May 1896, H. Rusby & R. Squires 302 (holotype NY!, isotypes BM!, COL!, F!, G!, K!, M!, MICH!, MO!, UC!, US!, VEN!, WU!, Z! [2 sheets]).
- Prestonia marginata Markgraf (1924: 88). Prestonia pachyphylla Woodson (1936: 292) nom. illeg. Type:—BRAZIL. Roraima: Serra do Mairary, Surumu, Río Branco, November 1909, E. Ule 8451 (lectotype NY! designated by Morales (2007 b), isolectotypes K!, M!, U!, US!).
- Prestonia acutifolia (Bentham ex Müller Argoviensis) K. Schumann var. latissima Markgraf (1926: 982). Type:—PERU. Loreto: cerca a Amaqueria, Ucayali, 24 November 1923, G. Tessmann 3368 (lectotype G! designated by Morales (2006 b), isolectotypes NY!, S!).

Prestonia simulans Woodson (1936: 293). Type:—COLOMBIA. Cundinamarca: Tocaima, December 1932, M. Arbeláez 2140 (holotype US!, isotype COL!).

**Stem** glabrous to glabrescent, usually with clear latex, rarely with milky latex, with few to several lenticels, the lenticels not suberose, intrapetiolar colleters minute, less than 1 mm long. **Petioles** 0.3-2(-3.2) cm; leaf blade  $(4-)5.5-12.5(-20) \times 1.8-5.5(-10.5)$  cm, narrowly elliptic, elliptic, ovate-elliptic to broadly ovate, rarely obovate-elliptic, apex acute, short-acuminate, obtuse to rounded and abruptly mucronulate, base obtuse, rounded to broadly acute, rarely subcordate, membranaceous to firmly membranaceous, sometimes revolute, glabrous, rarely glabrescent or minutely puberulent abaxially, secondary veins impressed on both surfaces, tertiary veins slightly impressed on both surfaces, sometimes inconspicuous. Inflorescence a monochasial cyme, axillary, longer than the adjacent leaves, many-flowered, the flowers laxly disposed to more or less clustered, glabrous to glabrescent, peduncle 2–15 cm, pedicels 0.4-1.2(-1.6) cm long, floral bracts  $1-2 \times 0.5-1$ mm, scarious, linear, inconspicuous, green. Sepals  $1-3(-4) \times 1-1.5$  mm, free, membranaceous, very narrowly ovate, the apices acuminate, commonly reflexed, glabrous, very small, drying with a more or less uniform color, the veins not impressed, colleters less than 1 mm long, entire to slightly erose at the apex. Corolla salverform, yellowish green to cream, glabrous outside, rarely minutely puberulent, tube  $(11-)14-20 \times 3-5$  mm, straight, free corona lobes 1–1.5 mm long, included, their height conspicuously surpassed by that of the anther apices, annular corona entire, thickened, corolla lobes  $8-13 \times 6-10$  mm, obliquely obovate. Stamens inserted near the corolla mouth, anthers 4-5.5 mm, minutely and sparsely puberulent dorsally, rarely glabrous or glabrescent, the apices slightly exserted. Ovary 1.5–2 mm tall, glabrous, style-head 1.25–1.55 mm, nectary 1.3–1.8 mm, usually shorter than the ovary, usually deeply and irregularly 5-lobed, each lobe lobe entire. **Follicles**  $23.5-40 \times 0.3-0.5$  cm, continuous to inconspicuously articulated, usually connate longitudinally (rarely free and united only at the tips), glabrous, without lenticels, membranaceous when old; seeds 7–14 mm, coma 2–3.5(–4) cm, cream to white.

**Distribution and habitat:**—From southern Nicaragua and the Antilles to northern Argentina, where it grows in dry forest, moist forest, tropical wet forest, savannas, gallery forest, white sand formations, amazonian seasonal flooded forest (Varzea), and vegetation

over quartzite formation from 0–700(–1000) m. *Prestonia quinquangularis* was reported by Urban (1908) for St. Vincent, but I have not seen specimens from that island.

**Phenology**:—Flowering and fruiting throughout the year.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Local names**:—Bejuco de sapo (T.F. Amazonas, Venezuela); bejuco de uña (Bolivar, Colombia); colorado (Bolivar, Venezuela); copita de monte (El Valle, Colombia).

**Taxonomic notes:**—*Prestonia quinquangularis* is characterized by its usually glabrous (rarely puberulent) leaves, unbranched inflorescence, scarious bracts, reflexed sepal apices, usually glabrous (rarely puberulent) corolla tube, free corona lobes deeply included, and follicles usually connate longitudinally. This species is commonly confused with *P. lagoensis* (see discusion under that species).

A number of names (*P. marginata*, *P. pachyphylla*, *P. simulans*) have been proposed over the years to describe several populations of this species, based mainly on variation in the texture and venation of leaves. Variation in the length and size of leaf blades is extreme in some specimens (e.g., Ancuash 530). Furthermore, secondary and tertiary venation varies from slightly impressed (dry forest: e.g., *Morales 2377*) up to conspicuously impressed (tropical wet forest, e.g., *Morales 21372*). Despite this variation, floral characters are remarkably similar throughout its range. Thus, recognition of several species or varieties based on these weak (and not continuous) differences is not justified.

The characters of the nectary and fruits proposed by Woodson (1936) to separate *Prestonia acutifolia* from *P. quinquangularis* vary within the geographical range of the species, with no real discontinuities. The degree of lobulation of the nectary is a variable character in *Prestonia*, in general as has been discussed previously for other species in the genus (Morales 2004b). It was this same variability that prompted Monachino (1958) to suggest the reducing *P. acutifolia* to the synonymy of *P. quinquangularis*. Morphologically, the type of *P. simulans* fits within the concept of *P. quinquangularis*, making necessary its reduction to a synonym of the latter.

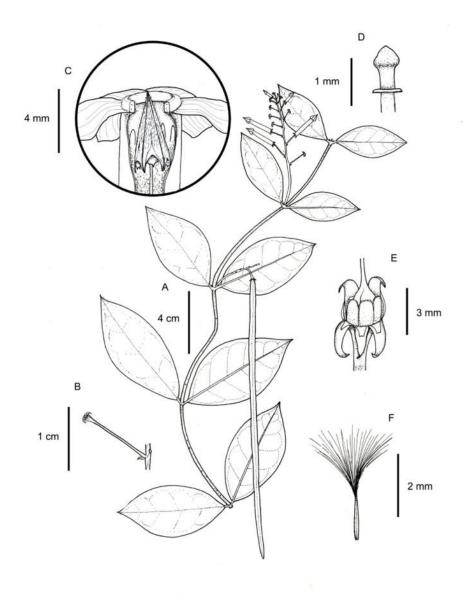


Fig. 43 *Prestonia quinquangularis* (*Morales & González 3293*, INB). A. Stem with inflorescence and follicles. B. Calyx, pedicel, and bract. C. Open corolla mouth, showing the annular corona, free coronal lobes, and the anthers. D. Style-head. E. Open calyx. F. Seed.

**Additional specimens examined:**—NICARAGUA. Rivas: Cerros de Potrero Largo, cerca a Bahía Salinas, February 1997, *Morales 6759* (CR).

COSTA RICA. Guanacaste: Palo Verde Field Station, 1 January 1979, Anderson 4838 (ASU); playa Garza, Nicoya, 25 November 1988, M. Chavarría 326 (CR); Parque Nacional Barra Honda, 12 September 1995, Chavarría 1280 (CR); Cañas, 6 December 1969, Daubenmire 347 (F); Santa Rosa, 30 Octuber 1982, Gómez-L. 8989 (CR); O de Bagaces, 2 December 1971, Heithaus 468 (CR, MO); Finca La Pacífica, N de Cañas, December 1976, Janzen T-10 (MO); Parque Nacional Santa Rosa, 8 December 1977, Janzen 10721 (MO), 3 November 1984, Janzen 12415 (MO); Santa Rosa, 21 January 1978, Liesner 4307 (MO); Parque Nacional Guanacaste, Los Almendros, 19 December 1992, López 30 (CR); Parque Nacional Barra Honda, Los Mesones, 7 September 1993, Morales et al. 1657 (CR, MO); Parque Nacional Santa Rosa, Cerros Murciélago, 16 February 1994, Morales 2377 (CR, K, MO); Cerros Raspado El Burro, Sardinal, 14 December 1994, Morales & González 3293 (CR, K); Murciélago, fila Hacha, bahía Coquito, 2 April 2001, Morales 7900 (CR); Parque Nacional Santa Rosa, sector Murciélago-Santa Elena, ríos Quebrada Grande y Cachimbo, los Llanos, 11 April 2005, Morales 12770 (CR, MO); Península de Santa Elena, Parque Nacional Guanacaste, Fila El Hachal, 27 January 2012, Morales 21007 (CR); Playa Ostional, cerca de la playa, 31 December 2013, Morales & Fonseca 21419 (USJ); NO de Bagaces, 7 November 1973, Opler 1967 (MO); Parque Nacional Guanacaste, Cerro El Hacha, 28 December 1989, Taylor et al. 9767 (CR, MO). Puntarenas: Reserva Natural Absoluta Cabo Blanco, 1 December 1969, Burger & Liesner 6533 (CR, F, MO); Hojancha, Puerto Carrillo, 26 December 1989, Flores & Hammel 47 (CR, MO); Península de Nicoya, playa Órganos, 19 February 1993, Hammel & Garita 18825 (CR, MO); Península de Nicoya, Curú, 5 September 1995, Sanders et al. 17772 (USJ). San José: Turrubares, San Juan de Mata, 28 November 2001, Estrada et al. 3122 (CR); Parque Nacional La Cangreja, Alto Limón, 31 dic 2011, Morales & Quesada 19976 (CR).

PANAMÁ. Darién: Río Morti, 15 March 1968, *Duke 15419* (MO); El Real, 1-3 km al S de la ciudad, 7 January 1975, *Gentry 13460* (COL, MO, PMA). Panamá: Arraiján, Loma del Río, 21 September 1997, *Aiello 1514* (PMA); parque nacional Altos de Campana, 12 January 1995, *Correa & Montenegro 10900* (PMA); Lighthouse clearing, 18 December 1967, *Croat 4401* (MO); cerca de El Llano, 14–19 Octuber 1962, *Duke 5802* (MO); carretera a Pipeline, N de Gamboa, 7 December 1981, *Knapp 2285* (MO, USF, WAG); Isla

Barro Colorado, 25 March 1982, *Knapp 4442* (MO); cerca de Gamboa, November 1911, *Pittier 4784* (US); Isla Barro Colorado, 12 Octuber 1931, *Shattuck 129* (A, MO); playa Farfan, 26 January 1966, *Tyson et al. 3180* (MO); Isla Barro Colorado, 3 January 1932, *Wetmore & Abbe 119* (F, GH [2 sheets], MO); Isla Barro Colorado, Barbour trail, 12 February 1932, *Woodworth & Vestal 498* (A, F, MO). Veraguas: Isla de Coiba, Playa de la Salina, 27 January 1994, *Castroviejo et al. 7190* (PMA); Isla de Coiba, campamento de los Pozos, 22 November 1994, *Cuadras et al. 7913* (PMA); Isla de Coiba, Quebrada del Río Escondido, 19 November 1994, *Espinoza & Luque 498* (MA); Soná, Bahía Honda, del Playa del Sol a Lerén, 4 February 2002, *Ibáñez et al. 1668* (MA); Barra Honda, Playa del Sol, 12 March 2002, *Ibáñez et al. 1775* (PMA); Isla de Coiba, campamento de Los Pozos, 22 November 1994, *Velayos et al. 7913* (MA).

CUBA. Santa Clara: Soledad, Cien Fuegos, 28 August 1931, *Jack* 8371 (NY, US).

JAMAICA. Datos de localidad perdidos, 1925, van den Brink 3604 (U).

DOMINICA. St John Parish, 7 June 1996, Hill 28239 (US, USF).

MARTINIQUE. Without exact locality, 1846, Garnier 216 (BM); 1820, Pleé s.n. (P).

GUADELOUPE. Capesterra, 28 Octuber 1895, Duss 3713 (NY).

COLOMBIA. Amazonas: Puerto Santander, Monochoa-Ciudad Perdida-Araracuara, 26 March 1994, *Cárdenas et al. 4511* (COAH [2 sheets], MO); Araracuara, Río Caquetá, cerca a Isla Sumeta, 11 June 1990, *Álvarez et al. 815* (COAH, JAUM, NY); Río Caquetá, Monochoa, 1 January 1977, *Sastre & Raichel 5094* (CR, MO, P). Amazonas-Vaupés: Río Apaporis, entre el Río Pacoa y el Río Kananari, 17 June 1951, *Schultes & Cabrera 12593* (US), Antioquia: San Luis, Quebrada La Cristalina, 1 September 1994, *Acevedo-Rodríguez & Callejas 6765* (MO, NY, US); San Luis, Río Claro, sector sur-occidental, 30 May 1984, *Cogollo 1699* (JAUM); Sonsón, cementos Argos, vía Vivero-La Arpía, 30 March 2012, *David et al. 4182* (HUA); San Carlos, Juanes, 16 November 1999, *Jiménez et al. 210* (JAUM); Sabanalarga, Quebrada Niquia, Colequerre, 4 July 2002, *Marrugo et al. 808* (MEDEL); San Luis, Quebrada La Cristalina, sector SE, 28 September 1987, *Ramírez & Cárdenas 1757* (JAUM); Puerto Berrío, 20 June 1928, *Toro 1105* (MEDEL, NY); Urabá, Dabeida, 13 January 1947, *Uribe 1457* (JAUM). Arauca: Arauca, Caño Limón, 16 Octuber 1997, *Betancur & Uribe 7534* (COL); Arauca-Arauquita, campo petrolero de Caño Limón, 22 May 2008, *Betancur & Uribe 12883* (COL); carretera a Caño Limón, vereda Todos Los

Santos, 8 August 1996, *Quiñones 2787* (COL). Atlántico: Sabanalarga, finca Loma de los Indios, 10 February 2000, Correa 2014 (HUA); entre Sabanagrande y Santo Tomás, 3 August 1959, Dugand 5170 (US); Barranquilla, May 1927, Elías 181 (US), August 1929, Elias 292 (US). Bolivar: San Martín de Loba, April-May 1916, Currán 35 (S, US); Torrecilla, cerca de Turbaco, 7–19 November 1926, Killip & Smith 14643 (US); Santa Rosa, finca La Peluza, 3 February 2000, López 4973 (HUA); Monte Líbano, 23 May 1949, Romero-Castañeda 1744 (COL); cerca a Carmen de Bolívar, 19 September 1963, Romero-Castañeda 10004 (COL). Chocó: Acandí, bahía El Aguacate, 6 November 2006, Cardona et al. 1696 (HUA); Río Truando, between Río Sucio and La Nueva, 5 February 1967, Duke 9819 (NY); Riosucio, Parque Nacional Natural Los Katios, camino a los saltos El Tendal y La Tigra, 28 March 1999, Fonnegra et al. 6883 (COL, HUA, MO); hoya del Río Atrato, Bojayá, Quebrada del Fuerte, arriba de Bellavista, 15 April 1982, Forero et al. 9278 (COL, NY); Parque Nacional Natural Los Katios, 18 April 1982, Zuluaga 1147 (COL). Córdoba: Planeta Rica, Marañonal, Cerro Queresa, 26 Octuber 1990, Roldan et al. 1498 (HUA [p.p.], MO); Ayapel, Monte Líbano, 21 May 1949, Romero-Castañeda 1715 (COL, CR, MEDEL, MO). Guajira: Maicao, Tabaco, 17 May 1981, Arboleda et al. 597 (HUA); entre Cuestecita y Carraipia, márgenes de Río Cesar, 30 November 1959, Cuatrecasas et al. 25516 (COL, US). Guaviare: El Retorno, camino de Cerritos a Cerro Piedra Gorda, 19 Octuber 1995, Cárdenas et al. 6700 (COAH). Magdalena: Río Cesar y Río Azucarbuena, El Callao, 29 Octuber 1959, Cuatrecasas et al. 24923 (COL, US); Puerto Ocaña, September 1852, Holton s.n. (NY); Cienaga, entre La Gran Vía y El Mico, 30 December 1966, Romero-Castañeda 10802 (COL); Santa Marta, July 1903, Smith 1645 (K, NY, US). Meta: O de Puerto Gaitán, camino a Puerto López, Río Yucao, 31 December 1973, Davidse & Llanos 5442 (COL, MO); 20 km al SE de Villavicencio, 17 March 1939, Killip 34294 (US); Villavicencio, Quebrada Cañabrava 18 March 1939, Killip 34468 (COL, MO, US); Río Manacacias, cerca a Puerto Gaitan, 26 March 1971, Pinto & Bernal 1576 (COL, CR). Norte de Santander: entre Chinácota y La Esmeralda, 19 May 1927, Killip & Smith 20923 (NY, US). Quindió: Quimbayá, vereda La Española, finca El Ocaso, 31 July 1997, Agudelo et al. 3555 (HUQ); Montenegro, vereda El Gigante, Hacienda Santa Cecilia, Río Banvieja, 24 September 1985, Arbeláez et al. 1075 (HUA, HUQ); Calarca, La Moravita, hacienda Las Acacias, 21 April 1987, Arbeláez et al. 2024 (HUQ); Quimbaya, El Laurel, hacienda El

Ocasol, Playa Azul, 22 July 199, Villa & Flores 417 (HUQ [2 sheets]). Risaralda: La Virginia, 20 March 1989, Ramos & Silverstone-Sopkin 1909 (CUVC, MBM, MO); Pereira, Hacienda La Carmelita, Valle del Río Cauca, 12 August 1991, Silverstone-Sopkin & Arroyo 6316 (CUVC, MO). Santander: valle del Río Surata, entre Bucaramanga y El Jaboncillo, 2 January 1927, Killip & Smith 16305 (F, NY, US); región superior del Valle del Río Lebrija, al NO de Bucaramanga, 29 December 1926, Killip & Smith 16308 (F, MO, NY, US); Río Suratá valley, between Bucaramanga and El Jaboncillo, 2 jan 1927, Killip & Smith 16385 (NY); al O de la Quebrada Mensuli, cerca a Floridablanca, 11 July 1953, Langenheim 3286 (COL, UC, US); Badillo, Río Magdalena, 18 January 1918, Pennell 3912 (NY); Cimitarra, vereda Los Ranchos, Hacienda Monterrey, 1 Octuber 1998, Rodríguez et al. 1085 (JAUM); Cimitarra, Puerto Araujo, Zoocriadero Zoocarare, 24 January 2000, Rodríguez et al. 3074 (JAUM). Tolima: Ortega, vereda San Francisco, 2 April 1996, Calle et al. 27 (COL [2 sheets]); Ibagué, Melgar, 6 December 2000, Diana & Henry 430 (TOLI); Ortega, Resguardo de Aico, 26 January 2000, Suárez & Santos 114 (COL); Mariquita, 7 June 1958, Uribe 3164 (COL). Valle del Cauca: Cartago, December 1946, Duque 4082a (COL [2 sheets]); Zarzal, 6 April 1986, Gentry et al. s.n. (CUVC); cerca a Buenaventura, entre Buga y Madronal, 29 September 1961, Idrobo 4676 (COL); Zarzal, 21 July 1922, Pennell et al. 8426 (NY, US); Cuchilla, al E de Zarzal, 22 July 1922, Pennell et al. 8536 (NY); Valle, Zarzal, 7 December 1986, Silverstone-Sopkin et al. 2617 (CUCV, MO); Cartago, 16 November 1986, Silverstone-Sopkin et al. 2563 (CR, CUCV, MO); Valle, 19 September 1987, Silverstone-Sopkin & González 3267 (CUCV, MO); Zarzal, entre La Paila y Zarzal, Hacienda El Medio 20 September 1987, Silverstone-Sopkin & González 3278 (CUVC), 24 Octuber 1987, Silverstone-Sopkin & Paz 3295 (CUVC), 24 Octuber 1987, Silverstone-Sopkin & Paz 3323 (CUVC), 19 March 1988, Silverstone-Sopkin & Paz 3698 (CUVC), 28 May 1988, Silverstone-Sopkin et al. 4008 (CUVC), 11 June 1988, Silverstone-Sopkin & Paz 4058 (CUVC), 11 June 1988, Silverstone-Sopkin & Paz 4059 (MO), 1 February 1992, Silverstone-Sopkin 6495 (CUVC); vereda El Guácimo, finca El Porvenir, entre Toro y San Francisco, 3 July 1989, Silverstone-Sopkin et al. 5392 (CUVC). Vaupés: Río Inirida, a medio camino entre Raudal Alto y Morichal, 7 February 1953, Fernández 2196 (US); Río Vaupés, Raudal Macucu, 14 November 1952, Romero-Castañeda 3488 (COL).

VENEZUELA. T.F. Amazonas: Atures, Río Sopapo, 25 March 1993, Castillo 3422 (VEN); Río Orinoco, s.d., Chaffanjon s.n. (P [2 sheets]); exact locality lacking exacta, 26 July 1984, Davidse 27933 (MO, U, US, VEN); al N de San Carlos de Rio Negro, al S de la confluencia del Río Negro y el Brazo Casiquiare, 11 April 1979, Liesner 6523 (MO, VEN), 26 April 1979, Liesner 7002 (MO, VEN), 2 May 1979, Liesner 7161 (VEN); SE de San Carlos de Río Negro, 25 January 1980, Liesner 8695 (MO, VEN); Río Negro, entre Piedra Cocuy y Santa Rosa, April 1953, Maguire & Wurdack 34991 (NY, US, VEN); near Palomal, 15 km S of Puerto Ayacucho, 9 November 1953, Maguire et al. 36101 (NY); Río Yatua, cerca a Laja Catipan, 6 February 1954, Maguire et al. 37529 (MO, NY, S, VEN); Atabapo, Caño Yegua, November 1989, Marín 491 (MO, PORT); Río Negro, entre la desembocadura del Río Casiquiare y San Carlos de Río Negro, 26 April 1974, Morillo et al. 4050 (VEN, Z); Río Negro, entre Isla Paleta y el Caño de la División O y S de Santa Lucía, 28 April 1974, Morillo 4112 (VEN, Z); Río Guainia, desde el Raudal del Lombriz hasta la boca del Casiquiare, 5 February 1977, Morillo 5260 (VEN), Morillo 5265 (VEN); cerca de la boca del Casiquiare, 5 February 1977, Morillo 5321 (VEN); Río Guainia, desde el raudal de Lombriz, 5 February 1977, Morillo 5352 (VEN); vía a Gavilán, E del cruce con la carretera a Puerto Ayacucho-Sanariapo, 17 November 1977, Morillo 6726 (VEN); San Vicente, Río Orinoco, 8 April 1978, Morillo et al. 7375 (VEN); Río Casiquiare, 1853-1854, Spruce 3430 (K [2 sheets], P [2 sheets]); Río Casiquiare, entre la boca y la piedra de Guachapita, Río Negro, 27 November 1984, Stergios & Aymard 7375 (MO); Río Yatúa, entre la boca y la piedra Catipán, Río Negro, 1–2 December 1984, Stergios & Aymard 7456 (MO, PORT); Río Negro, Bajo Casiquiare, entre la Boca del Pasimoni y Porvenir, 4 December 1984, Stergios & Aymard 7613 (VEN); Río Negro, Río Casiquiare, entre Guachapita y El Porvenir, 15 April 1985, Stergios et al. 8124 (MO, PORT); Río Casiquiare, entre la piedra Corocoro y boca del Siapa, 1986, Stergios & Aymard 9192 (NY, PORT, VEN); Río Casiquiare, entre Buena Vista y Duruquene, 20-30 Octuber 1986, Stergios et al. 9618 (MO); Río Yatua, Cerro Arauicaua, 13 April 1970, Steyermark & Bunting 102642 (VEN, Z); raudales de Atures, al S de Puerto Ayacucho, 1 February 1984, Steyermark & Berry 129860 (VEN); Río Guainia, Maroa, 12 February 1942, Williams 14308 (G). Apure: unión de los ríos Capanaparo y Orinoco, 1977, Davidse & González 12650 (F, MO, NY, VEN); San Fernando, boca de los ríos Arauca y Orinoco, 14 May

1977, Davidse & González 13237 (MEXU, MO, VEN, Z); bancos del Río Arauca, SO de El Faro, May 1977, Davidse & González 13425 (MO, VEN); Reserva San Camilo, S de El Nula, 27 March 1968, Steyermark et al. 101401 (VEN, Z). Aragua: Maracay, 1934, Vogl 1410 (M [2 sheets]). Bolivar: Laguna Los Icacos, cerca de ciudad Bolivar, June 1961, Aristeguieta 4665 (MO, VEN); Distrito Piar, La Camilera, O de El Manteco, July 1978, Delascio & Liesner 6996 (MO, NY, VEN); San Martín de Turumban, Río Cuyuni, al SO de Tumeremo, February 1980, Delascio & López 8870 (VEN); entre Guasipati y Santa Rosa, 19 March 1974, Gentry et al. 10749 (MO, VEN); Ciudad Bolivar, 4–25 November 1929, Holt & Gehriger 164 (US); Río Paragua, entre Guaiquinima y Río Torono, 16 April 1943, Killip 37513 (MO, NY, US); E de La Paragua, 23 July 1978, Liesner & González 5452 (MO, NY, VEN); Las Trincheras, Caura arriba, 11 June 1984, López-Palacios et al. 4672 (NY); Tumeremo, 9 August 1979, Morillo 8054 (VEN); carretera Ciudad Bolivar-Maripa, 26 February 1980, Morillo & Carnevali 8264 (VEN); Río Caura, margen del Salto Para, 12 May 1982, Morillo & Liesner 9164 (MO, U, VEN); represa Hurí, al NE de Ciudad Piar, 4-5 April 1981, Liesner & González 11191 (MO, VEN); Río Venamo, entre Río Cuyuní y Caño Apanao, 18 July 1983, Stergios et al. 6123 (MO, PORT); Río Caura, May 1988, Stergios & Delgado 12838 (CR, MO, NY, PORT); Río Caura, Caño La Ceiba, May 1988, Stergios & Delgado 12923 (MO, NY, PORT, VEN); E de Miamo, altiplanicie Nuría, 8 January 1961, Steyermark 88222a (NY, VEN); Isla Santa Elena, opposite mouth of Rio Pargueni, 13 December 1955, Wurdack & Monachino 39870 (NY); Laja Caruto, Raudal Marimare, December 1955, Wurdack & Monachino 39976 (NY, VEN). Carabobo: cerca de la Alcabala de El Limón, Parque Nacional Henry Pittier, 22 December 1981, Manara s.n. (VEN). Delta Amacuro: entre Tucupita y Los Güires, 17 April 1973, Agostini & Agostini 1619 (NY, U, VEN, Z); Casacoima, Los Cocos, Río Orinoco, 4 June 2003, Delascio & Chacón 18971 (VEN); Tucupita, entre Tucupita y aeropuerto, Caño Manamo, camino a San Rafael, 23 Octuber 1977, Stevermark et al. 115223 (MO, VEN). Falcón: Democracia, alrededores de Buruica, Quebrada Araguato, entre Cerro Pozo Azul y Cerro Moporal, 1 March 1972, Agostini & Agostini 1026 (VEN); via a Chichiriviche, 21 November 1975, Smith 7916 (VEN); Silva, Cerro Chichiriviche, entre Lizardo y Mallorquines, 4 September 1974, Steyermark & Manara 110703 (NY, VEN). Guarico: Altagracia de Orituco-Taguay, September 1966, Aristeguieta et al. 6432 (MO, NY, US, VEN). Lara: near Colonia Tovar,

1854–1855, Fendler s.n. (MO); Pico Pico, finca de Tovar, al N de Bargusimeto, 20 September 1968, Smith 4471 (VEN); cerca de Barquisimeto, al E del Valle de El Cuji, 20 September 1968, Smith 4496 (VEN); La Bahitra, al NE de Barquisimeto, 29 September 1967, Tillett 6710 (VEN). Mérida: cerca a Barinitas, 15 Octuber 1963, Breteler 3159 (U, WAG [2 sheets], VEN). Miranda: 7 km E de Cúpira, new road 1 km S of main road, starting at Río Chupaquire S of El Guacuco, 16 May 1981, Liesner & González 11907 (CR, F, MO, VEN); al N de Golfeados Arichuna y al N de Charallave, 12 December 1973, Morillo et al. 3820 (VEN); Parque Nacional El Ávila, hacienda La Siria, al N de Guatire, 15 September 1979, Morillo & Bustamante 8084 (VEN). Monagas: entre Caicara y Guanaguana, 16 July 1972, Dumont et al. 7719 (NY, VEN); Río Huarapicha, al O de Jusepin, 28 April 1979, Seigler 11130 (MEXU). Nueva Esparta: Cerro Copey, Isla Margarita, 7 April 1983, Sudgen 1139 (K, VEN). Portuguesa: Guanare, 18 February 1982, Aymard 1015 (PORT, VEN); Guanare, 20 Octuber 1983, Stergios & Aymard 6497 (PORT, VEN); entre Paraiso de Chabausquen y Peña Blanca, 5 September 1966, Stevermark & Rabe 97428 (NY, US, VEN). Sucre: hacia Chaguaramas y playa Medina, 13 June 1995, Manara s.n. (VEN); Península de Paría, Maturincito, 14 May 1997, Silva 1172 (VEN); Sucre, Quebrada Zurita, Paso Hondo, al S de Limonal y Santa Fé, 18 August 1973, Stevermark et al. 107811 (MO, NY, VEN); Río Manzanares, al O de Tataracual, 15–17 September 1973, Steyermark et al. 108479 (VEN). Táchira: Capacho, Páramo Tres Esquinas, El Valle, 18 November 1984, Bono 4356 (FI); Sierra El Casadero, entre Las Dantas y Las Adjuntas, 12 November 1979, Steyermark et al. 120167 (MO); S de La Mulata, cerca a la frontera Colombia-Venezuela, 13 November 1979, Steyermark et al. 120245 (MO, VEN). Vargas: Carrasquel, Caruao, 7 November 1925, Pittier 11951 (US, VEN). Yaracuy: San Felipe, Veroes, entre Guabina y La Yuca, 10 July 1973, Agostini et al. 1705 (G, K, MY, U, VEN, Z). Zulia: vicinity of Cristobal Colón, 5 January-22 February 1923, Broadway 298 (NY); Bolivar, carretera Maracaibo-Carora, al SE de la Sabana de la Plata, 27 Octuber 1977, Bunting 5768 (VEN); Miranda, carretera El Mecocal-El Consejo, 22 December 1977, Bunting & Chacón 5992 (VEN); entre la carretera Lara-Zulia y El Zamuro, 27 November 1979, Bunting 8252 (NY, VEN); Colón, carretera Casigua-Palmira, 18 November 1980, Bunting & Fucci 9834 (NY, P, VEN), Bunting & Fucci 9839 (P, VEN); Cerro Socopo, Burro Negro, 5 August 1980, Bunting 9484 (MO, NY, P, VEN);

Mene Grande, Baralt, 4 May 1968, Ferrari 378 (F, VEN); cerca de Mene Grande, 2 November 1992, Pittier 10655 (G, NY, US, VEN); Distrito Miranda, Socopo, 24 November 1986, Zambrano 1414 (HERZU, VEN). Data lacking: 1881, Chaper s.n. (P); 1893, Geay s.n. (P); 1891–1892, Warming 256 (C).

TRINIDAD AND TOBAGO. San Juan Laventille: Cerca a Río Caroni, S de Arima, 11 April 1921, *Britton & Britton 2894* (K, NY). Data lacking: s.d., *Bergler s.n.* (W); s.d., *Rohr s.n.* (C), *Rohr 22* (C), *Rohr 23* (C); s.d., *Vahl s.n.* (B-W 5177). Estación Experimental St. Clair, 22 May 1907, *Broadway 2582* (C, M, Z); Caparo, April 1908, *Broadway 2707* (NY); Sabana O'Meara, Arima, 16 April 1908, *Broadway 2799* (L, NY, Z); Moruga, La Lune road, 8 February 1916, *Broadway 7593* (NY); without exact locality, 22 November 1932, *Broadway 9100* (BM, K, NY); without exact locality, 4 April 1940, *Cheesman 310* (MO); without exact locality, 9 August 1940, *Cheesman 349* (MO); without exact locality, 1877–1880, *Fendler 625* (BM, K, NY, P); without exact locality, June 1846, *Grisebach s.n.* (K); finca St. Joseph Stock, 13 February 1958, *Purseglove 6085* (K); without exact locality, 1786–1791, *Rohr 94* (BM, C [2 sheets]).

GUYANA. Cuyuni-Mazaruni: Río Mazaruni, 28 Octuber 1952, Forest Department 7139 (MICH, NY, U); Río Cuyuni, cerca a Aurora, 10 Octuber 1989, Gillespie et al. 2236 (U, US); Río Cuyuni, between Aurora and Takar-opati Island, 13 Octuber 1989, Gillespie & Tiwari 2340 (NY, U, US); Río Mazaruni, 20 December 1922, Leng 415 (NY); Río Cuyuni, Cataratas Akaio, 25 November 1929, Sandwith 688 (NY). East Berbice-Corentine: Río Courantyne, Octuber 1879, Glaziou s.n. (P); Río Courantyne, November 1879, Jenmann 314 (P); bancos del Río Courantyne, cerca de Baba Grant Sawmill, 17 April 1989, McDowell & Gopaul 2285 (MO, U, US). Potaro-Siparuni: Reserva Iwokama, 30 September 1995, Clarke 306 (CR, P, US). Upper Takutu-Upper Essequibo: Rupununi, Karanambo, 17 February 1990, Acevedo-Rodríguez & Tiwari 3284 (CR, MO, NY, U, US); Rupununi, Villa Karasabai, 6 March 1990, Acevedo-Rodríguez et al. 3470 (U, US, VEN); Río Rupununi, April 1968, Daris 808 (BRG, K, NY); villa Sand Creek, 22 June 1989, Gillespie et al. 1769 (MO, US); sabanas Rupununi, 20 February 1992, Hoffman & Capellaro 1013 (NY, US); Rapunini, Lethen, Río Takutu, 18 April 1956, Irwin 766 (US); Río Takutu, al S de Lethen, 19 April 1956, Irwin 820 (US); Montañas Kanuku, 9 February 1985, Jansen-Jacobs et al. 98 (B, CAY, MO, NY, U, US, WAG, WIS); Rupununi, Karanambo, 26 July 1995, JansenJacobs et al. 4645 (P, U, WAG); Río Rupununi, Karanambo, 5 September 1988, Maas et al. 7301 (U); NE de Surama, 22 February 1990, McDowell et al. 1965 (P, US); entre Río Takutu y montañas Kanuku, March 1938, Smith 3362 (NY). Upper Demerara-Berbice: Río Essequibo, Rockstone, 31 July 1921, Gleason 886 (NY); Río Essequibo, 22 May 1993, Henkel & Williams 2105 (CR, MO, NY, P, US); Mabura Hill, 180 km SSE of Gerogetown, Essequibo river, Waraputa Falls, 6 April 1988, Steege & de Jager 312 (U).

SURINAME. Pará: Tibiti and Brand savanne, 6 January 1949, *Lanjouw & Lindeman 1673* (U). Sipaliwini: Monte Bakhuis, entre rios Kabalebo y Coppename, 20 km del aeropuerto de Kabalebo, 30 December 1964, *Florschütz & Maas 2591* (U). Saramacca: Río Saramaca, Brokolonka, June 1944, *Maguire et al. 23790* (G, MO, NY, P, RB, U, UC, US); Río Coppename, 1954, *Mennega 510* (U); Río Kabalebo, 5 September 1920, *Pulle 441* (NY, U, Z).

ECUADOR. Los Ríos: Estación Biológica Río Palenque, entre Santo Domingo de los Colorados y Quevedo, 11 January 1987, Buitrán 124 (QCA). Napo: Reserva forestal Yasuni, Río Tiputini, 21 June 1995, Acevedo-Rodríguez & Cedeño 7441 (MO, NY, QCNE, QCA, US); Chiro Isla, Rivademeira, Río Napo, 22 April 1996, Bensman 234 (MO, WIS); lagunas Cuyabeno, 21 August 1981, Brandbyge et al. 33869 (AAU, QCA, WAG); Estación de Biodiversidad Tiputini, Río Tiputini, ca. 25 km E of confluence with Río Tivacuno, 18 March 1998, Burnham 1667 (F, MICH, MO, QCA, QCNE); Estación de Biodiversidad Tiputini, Río Tiputini, ca. 25 km E of confluence with Río Tivacuno, 11 November 1998, Burnham 1822 (CR, F, MICH, MO, QCA, QCNE); Río Cuyabeno, 10 km upstream from Río Aguas Negras, 15 February 1980, Holm-Nielsen et al. 21156 (AAU), Holm-Nielsen et al. 21159 (AAU, F, K, MO, QCA, U, WAG); Misahuallí, cerca al Río Napo, 28 March 1969, Lugo 903 (GB, USF); Cotundo, N de Tena, 18 May 1972, Lugo 2356 (GB, USF). Pastaza: Mera, 22 April 1969, Lugo 1168 (GB, USF); Río Pastaza, entre Río Bobonaza y Río Ishpingo, 22 July 1980, Øllgaard et al. 34986 (AAU, K, MO, NY, QCA, WAG); Río Ishpingo, tributario del Río Pastaza, 22 July 1980, Øllgaard et al. 35037 (AAU, K, MO, NY, QCA, WAG). Pichincha: E faldas de Cerro Pichincha, Quebrada Los Condores, 28 April 1971, *Macbride 208* (QCA).

PERÚ. Amazonas: Condorcanqui, Quebrada Sasa, Río Cenepa, 2 June 1973, Ancuash 530 (MO, USM, Z); Yamayakat, 31 January 1996, Jaramillo et al. 1029 (MO, USM, WAG); Quebrada de Apipkagentsa, Río Cenepa, 9 April 1973, Kayap 604 (MO, Z); Condorcanqui, cerca de Pongo de Manseriche, Río Santiago, 3 January 1932, Mexia 6370 (CAS, G, K, MICH, MO, NY, S, U, UC, US, WIS, Z); Huambisa, Río Santiago, 7 February 1980, Tunqui 758 (MO, SI, UC, USF); Imaza, Yamayakat, Río Marañón, 14 July 1997, Vásquez et al. 24296 (CR, MO, MOL, USM). Ayacucho: valle del Río Apurimac, cerca de Kimpitiriki, 10-11 May 1929, Killip & Smith 23026 (US). Cusco: Cusco, Armihuari, 28 January 1997, Acevedo-Rodríguez et al. 9258 (CR, MO, NY, P, US, USM, WAG); Convención, Quempiri, Río Ene, 24 July 1965, Ferreyra 16376 (MO, USM); La Convención, Echarate, Chahuares, 9 April 2007, Huamatupa & Carrión 8930 (CR, MO); Convención, entre Palma Real y Chahuanes, 17 April 1966, Vargas 17353 (US). Huancavelica: Tayacaja, Quintabamba, al SE de Huachocolpa, 15 April 1964, Tovar 4660 (US). Huánuco: Pachitea, Honoria, Bosque Nacional Iparia, 10 Octuber 1967, Schunke 2202 (F, NY); entre Monzón y Huallaga, 28 August 1903, Weberbauer 3605 (G); Locro, Río Huallaga, 7 August 1954, Woytkoski 1321 (MO); Tingo María, Río Huallaga, 7 August 1954, Woytkowski 1326 (MO). Junín: Tarma, La Merced, valle de Chanchamayo, 18 January 1946, Ferreyra 374 (MO, USM); La Merded, Chanchamayo, 25 January 1946, Ferreyra 488 (USM); cerca de La Merced, valle de Chanchamayo, 7 June 1963, Ferreyra 14944 (CR, USM); La Merced, 26 June 1976, Gentry & Prance 16412 (F, K, MO, Z); La Merced, 29 May-4 June 1929, Killip & Smith 23387 (F, MO, NY, US); Cahuapanas, Río Pichis, 20-21 July 1929, Killip & Smith 26817 (NY, US); La Merced, August 1923, Macbride 5245 (F, K); La Merced, August 1947, Soukup 3515 (F); Hacienda Génova, 4 July 1962, Woytkowski 7375 (MO [2 sheets], NY, UC); hacienda Génova, 14 July 1962, Woytkowski 7390 (MO [2 sheets]). Loreto: cercanías de Iquiutos, Hacienda Soledad, Río Itaya, 16 November 1940, Asplund 14559 (S); Río Mazám, just above La Libertad, ca. 35 km above Mazán, 10 July 1976, Gentry & Revilla 16646 (AMAZ, F, MO, USF, USM, Z); Bosque Nacional von Humboldt, carretera Upcallpa-Tingo María, 26 March 1977, Gentry et al. 18669 (AMAZ, MO, USF, USM); Río Trapiche, 8 December 1977, Gentry et al. 21265 (F, MO, NY, USF, USM); Mariscal Cáceres, Tocache Nuevo, trail up Río Huallaga valley toward Limón, 11 Mar 1979, Gentry et al. 25525 (AMAZ, MO); Quebrada Yanomono, Río Amazonas cerca de la boca del Río Napo, 5 November 1979, Gentry et al. 27525 (F, MO, NY); Puerto Arturo, Río Huallaga, bajo de Yurimaguas, 24–25 August

1929, Killip & Smith 27840 (F, MO, NY, US); Yurimaguas, Río Huallaga, 22 August-9 September 1929, Killip & Smith 28212 (NY, US); valle del Río Marañón, 20 August-3 September 1929, Killip & Smith 29204 (US); Mishuyacu, cerca a Iquitos, February 1930, Klug 1075 (F, US); Mishuyacu, cerca a Iquitos, April 1930, Klug 1119 (MO, NY, US); Florida, Río Putumayo, March-April 1931, Klug 2105 (COL, F, K, MICH, MO, NY, S, US); Maynas, Río Yaguasyacu, afluente del Río Ampiyacu, alrededores de Brillo Nuevo, 5 May 1977, Plowman et al. 7261 (F, K, MO, US, USM); Gamitanacocha, Río Mazán, 10 March 1935, Schunke 356 (F, MO [2 sheets], NY, UC, USM). Madre de Dios: Parque Nacional Manú, Río Manú, Pakitsa station, 16 December 1988, Foster & Baldeón 12579 (F, US). Pasco: Oxapampa, Palcazú, comunidad nativa Nueva Aldea-sector Santa María, 20 March 2009, Rojas & Rivera 6553 (CR, MO). San Martín: Mariscal Cáceres, tail along Río Huallaga, N of Tocache Nuevo, 15 March 1979, Gentry & Aronson 25777 (AMAZ, F, MO, USF, USM); Tocache Nuevo, Río Huallaga, 2 January 1971, Schunke 4612 (COL, F, G [2] sheets], MO, NY, US); Tocache, Quebrada Paraiso, cerca a Tocache nuevo, 25 November 1974, Schunke 8128 (F, MO, PMA, Z); Mariscal Cáceres, Tocache Nuevo, Quebrada Cachiyacu, 9 May 1975, Schunke 8443 (F, MO, Z), Schunke 8447 (F, MO, Z); Mariscal Cáceres, Tocache Nuevo, desembocadura del Río Tocache, 6 August 1980, Schunke 12077 (MO); Tambopata, Las Piedras, a lo largo de la Quebrada Gamitana, 26 January 1991, Timaná et al. 1380 (CR, MO); Tarapoto, December 1929, Williams 5550 (F, MO); Alto Río Huallaga, December 1929, Williams 6287 (F), Williams 6645 (F); Huinguillo, 10 March 1962, Woytkowski 7194 (MO); Juanji, 22 March 1962, Woytkowski 7117 (K, MO, UC); San Martín, Tarapoto, 26 February 1947, Woytkowski 35188 (F, G, MO, UC); Vaca Pozo, Río Cumbazo, SE de Tarapoto, February 1947, Woytkowski s.n.(USM).

BRAZIL. Acre: Río Branco, Bujari, Río Purus, Seringal Andirá, 23 March 1995, Daly et al. 8444 (MO, NY, WAG). Amapá: Río Flechal, 13 August 1962, Pires & Cavalcante 52510 (IAN, MG, NY, S, US, Z); Serra do Navio, slopes of Observatorio Ore Body, 12 November 1964, Cowan 38279 (NY); Río Jarí, Monte Dourado and São Melitão, 10 December 1967, Oliveira 3771 (IAN, NY); Jarí, Río Jarí, entre Monte Dourado y São Militão, 28 April 1969, Silva 1929 (IAN, INPA, MG, NY, WAG). Amazonas: Alto Rio Negro, al N de Barcelos, 6 August 1996, Acevedo-Rodríguez et al. 7987 (INPA, MO, US); Río Preto, tributario de Río Negro, 17 August 1966, Acevedo-Rodríguez et al. 8421 (INPA,

US); Rio Içara, near Malacacheta, 8 May 1948, Black 48–2567 (IAN, MO); Territorio do Guaporé, Porto Velho, 28 May 1952, Black & Cordeiro 52–14587a (IAN, MO, NY); cerca del Roraima y Bôa Vista, s.d., Carnevali 106 (VEN); Manaus, km 9 de BR-17, February 1955, Chagas s.n. (INPA # 832, MG); Río Samaúna, Río Negro, 6 April 1959, Coêlho s.n. (INPA, MO); Río Negro, Camanaus, São Gabriel do Cachoeira, 2 December 1978, Damião 2951 (COL, INPA); Taperinha cerca de Santarem, 7 July 1927, Ginzberger 344 (WU), 30 July 1927, Ginzberger 345 (WU); Madeira, Borba, 9 May 1985, Henderson et al. 423 (INPA, MG, NY, USF); Manaus, Tarumã Grande, 24 Octuber 1977, Keel et al. 183 (NY); Rio Negro, near Paraná do Maçuera, 6 July 1999, Lohmann 335 (INPA, SPF); Río Negro, boca del Río Marié, igapó, 12 Octuber 1987, Maas & Lima 6708 (INPA, NY, RB), Maas & Lima 6735 (INPA, NY, USF); Río Negro, Ilha Tamanduá (Ilha Marajó), 20 Octuber 1987, Maas et al. 6814 (INPA, MG, NY, RB, U, USF); Río Negro, Paraná de Jutaí, 14 June 1990, Mori et al. 21316 (INPA, NY, WAG); Río Negro, Ponta do Pagodão, 20 June 1992, Mori & Gracie 22408 (INPA, NY, US); Caracaraí, 27 April 1974, Pires et al. s.n. (IAN # 14307, RB); Río Curuquetê, cerca de Cachoeira Santo Antônio, 16 July 1971, Prance et al. 14271 (C, F, INPA, K, MG, NY, P, R, S, U, US, VEN, Z); cuenca del Río Negro, Tapuruquara, 21 Octuber 1971, Prance et al. 15767 (INPA, MG, NY, U, Z [2 sheets]); baixo Rio Negro, cerca a Lago Tupí, 17 December 1958, Rodrigues 725 (INPA, MO, UB); Manaus, Carretera Manuas-Itacoatiara, 9 November 1960, Rodrigues & Chagas 1895 (INPA); Cacau Pirêra, 20 March 1961, Rodrigues & Lima 2242 (INPA), Rodrigues & Lima 2268 (INPA); Manaus, Lago de Janauarí, Río Negro, 5 May 1961, Rodrigues & Coêlho 2503 (INPA); Santa Isabel do Rio Negro, Río Negro, cerca de Ilha Tamaquaré, 25 September 2000, Silva et al. 988 (INPA, MG); Boca do Rio Içana, near Jauaçanã, 10 May 1973, Silva et al. 1458 (INPA); Manaus, 1854, Spruce 1130 (K); Santarem, 1850, Spruce 1854 (K); without data, Schultes 9895 (IAN); São Gabriel da Cachoeira, near Tapajós, 5 km from São Gabriel, Rio Negro, 15 June 2008, Zartman 7852 (INPA). Brasilía: Perto do Rio das Salinas, 26 February 1981, Kirkbride 3947 (INPA, UB, US). Goiás: Chapada dos Veadeiros, São João da Aliança, Serra Geral do Paraná, 24 March 1973, Anderson 7862 (NY, UB); Chapada dos Veadeiros, O de Alto de Paraiso, 24 March 1969, Irwin et al. 24986 (IAN, MO, NY, RB, UB, Z); Piranhas, Río Araguaia, 23 June 1966, Irwin et al. 17679 (IAN, UB, US, Z); entre Niquelândia y Uruaçu, morro na Fazenda Traíras, 13 April 1996, Marquete et al. 2469 (IBGE, MO, RB). Mato Grosso: km 23 km de Vila Bela, 5 May 1983, Carreira et al. 810 (MG); Cuiabá, 22 March 1894, Malme 1478 (G-DC, LD, S, US, UPS [2 sheets], Z); Cuiabá, 2 July 1903, *Malme 3122* (LD [2 sheets], S, UPS [2 sheets], US); Cuiabá, 14 June 1902, Malme s.n. (S); Cuiabá, 14 April 1979, C.J. Silva et al. 103 (RB, UFMT); Poconé, rodovia Transpantaneira, despúes de la portería de IBDF, 23 March 1983, Silva & Lima 3354 (MG). Mato Grosso do Sul: Campo Grande, Água Rica, Sidrolândia, 12 April 1972, Hatschbach 29438 (C, MBM, NY, UC, US, Z); Coxim, Rio Coxim, 15 May 1973, Hatschbach 31971 (MBM, Z); Aquidauana, 21 February 1932, Reiss s.n. (WIS). Minas Gerais: Curvelo, O de Corinto, 4 March 1970, Irwin et al. 26884 (IAN, NY, UB, Z); Paraopeba, 2 April 1963, Pereira 7519 (CR, HB, RB, Z [2 sheets]); without exact locality, 1816–1821, St. Hilaire s.n. (P), St. Hilaire 154 (P). Pará: Rio Ituqui, São Sebastião, 20 June 1947, Black 892 (IAN); Cacaul Grande, Santarém, 30 Octuber 1950, Black & Ledoux 10415 (IAN); Oriximiná, 12 June 1957, Black et al. 57–19995 (IAN); Rio Negro, Nova Vida, 5 February 1959, Cavalcante 514 (MG); Oriximiná, Río Paru do Oeste, cerca de Raimunda, 4 September 1980, Cid et al. 2005 (INPA, MG, NY, RB, WAG); Oriximiná, Río Trombetas, 17 June 1980, Davidson & Martinelli 10327 (INPA [2 sheets], MG, MO, NY, RB, US, USF); Vila Nova, Campos, 4 November 1900, Ducke 1994 (MG); Belém, Jardín Botânico Emilio Goeldi, 4 March 1960, Egler 896 (K); Porto Trombeta, Mineração Rio do Norte, 1991, Evandro & Knowles 477 (INPA); Lagoa do Maripá, Monte Alegre, 11 September 1953, Fróes 30188 (MG); Río Acre, Antimary, 30 March 1904, Huber 4243 (MG); Vila Caraña, Porto Trombetas, 14 April 1988, Knowles 1172 (INPA); Santarém, Alter do Chão, 1998-2005, Knowles 1458 (MG); Cachoeira Porteira, Rio Trombetas, 15 jan 1991, Knowles 1678 (INPA); Tucurui, Rio Tocantins, 31 January 1980, Lisboa et al. 1327 (MG); Oriximiná, Río Trombetas, 17 June 1980, Martinelli et al. 7003 (CR, INPA, MG, NY, RB [3 sheets], USF); Alter do Chão, 24 September 1987, Miranda 37 (INPA); Belém, 6 Octuber 1945, Pires & Black 373 (IAN); Conceição do Araguaia, ca. 20 km O de Redenção, cerca de Córrego São João y Trocamento Santa Teresa, 11 February 1980, Plowman et al. 8719 (F, INPA, MG, MO, NY, US, WAG); Oriximiná, 24 Octuber 1928, Sampaio 5346 (R); Santarém, Alter do Chão, 15 Octuber 1989, Sanaiotti 104 (E, INPA); Marabá, Serra Norte, km 134, 14 May 1982, Secco et al. 164 (NY), Secco et al. 165 (MG); Belém, Museo Emilio Goeldi, 25 June 1963, Silva s.n. (MG # 30588); Jarí, carretera

entre Planalto y Tinguelin, km 12, 20 September 1969, Silva 2780 (IAN); Tucuruí. Río Tocantins, 29 May 1980, Silva & Rosário 5256 (INPA, MG); Porto Trombetas, Mineração Rio do Norte, 30 December 1994, Soares & Knowles 1230 (INPA); Lageira, aeropuerto de Río Maicuru, 20 July 1981, Strudwick et al. 3295 (INPA, K, NY, US, USF), Strudwick et al. 3296 (MG); Lageira, Río Maicuru, 21 July 1981, Strudwick et al. 3358 (HBG, INPA, K, MG, NY, US, USF). Paraiba: Piauí, camino a Sète Cidades, 27 May 1997, Félix & Pires 7895 (HST). Paraná: Fóz de Iguaçú, Parque Nacional Fóz de Iguaçú, 15 April 1965, Hatschbach 12577 (MBM, Z); Parque Nacional do Iguaçu, Foz do Iguaçu, December 1990, Sobral et al. 6557 (MBM). Rondônia: Porto Velho, 28 May 1950, Black et al. 52 (IAN, Z); Río Jamari, entre São João y Santa Cruz, 28 June 1965, Pires 9930 (UB, Z); Pires & Martin 9940 (C, IAN, K, UB, Z [2 sheets]); Porto Velho-Cuiabá road, BR–364, km 159, 9 February 1983, Teixeira et al. 1430 (INPA, MG); Río Pacáas Novos, 21 March 1978, Ubitaran et al 220 (MG, MICH, MO, NY, US, WAG, WIS). Roraima: Rio Branco, Rio Ucajaí, 9 September 1951, Black & Magalhaes 51–13240 (IAN, NY); Campus Cauamé, near Rio Cauamé, 20 April 2007, Flores e tal. 1488 (MIRR); Cantá, camino para Serra da Lua, 17 August 2007, Flores et al. 1568 (CR, MIRR); Campus Cauamé, 24 January 2008, Flores et al. 1728 (MIRR); Reserva Biológica Maracá, Río Urariquera, 8 March 1987, Harley 24748 (CR, INPA, K, MIRR, NY); Ilha de Maracá, Alto Alegre, 12 June 1986, Hopkins et al. 684 (INPA, K, MG, MIRR, NY, US, USF); Bôa Vista, Río Branco, July 1913, Kuhlmann 578 (RB, US); Reserva Ecológica SEMA, Ilha de Maracá, 23 May 1987, Milliken & Bowles 265 (INPA, K, MIRR, NY); Río Uraricoeira, 22 May 1987, Nelson & Mera 1550 (CR, INPA, K, NY); Serra do Mairary, Surumu, Río Branco, November 1909, Ule 8452 (MG, U). São Paulo: Mogi-Mirim, Itapira, 11 January 1994, Barreto et al. 1763 (CR, ESA); Morro das Pedras, 1924, Brade 9120 (R). Data lacking: s.d., Martius s.n. (M); 1877–1878, Robert 674 (P).

BOLIVIA. Beni: Ballivian, Espíritu, valle del Río Yacuma, 5 September 1986, *Beck* 5839 (LPB, MO, M, P); Ballivian, Rurrenabaque, 1921, *Cárdenas 1748* (K, MICH, NY); Ballivian, Cercado, Trinidad, 28 March 1992, *Chonono & Saavedra 214* (CR, LPB); Trinidad, 10 April 1979, *Krapovickas & Schinini 34737* (C, CTES, MO, Z). La Paz: La Paz, parque natural y area natural de manejo integrado Madidi, Norte de Apolo, 10 June 2005, *Araujo et al. 1879* (MO, NY); Nor Yungas, cerca a Coroico, carretera a Caranaví, 30

April 1983, Beck 8304 (CR, HBG, LPB, M, NY, SI, USF); Mapirí, San Carlos, Larampinni, 4 April 1927, Buchtien 1208 (HBG, LPB, MO, US); Nor Yungas, NE de Yocosa, 9 March 1984, Solomon & Stein 11721 (LPB, MO, USF). Pando: Nicolas Suarez, Cobija, 19 Octuber 1988, Beck 17156 (CR, LPB); Nicolás Suárez, cerca a Cobija, 8 January 1983, Fernández-Casas 8092 (CTES, G, LPB, MA, MO, NY); Manupiri, entre Conquista y Río Madre de Dios, 29 January 1983, Fernández-Casas 8547 (CTES, G); Madre de Dios, Bolivar, Río Manupare, 2 June 1987, Solomon 16852 (LPB, MO, USF). Santa Cruz: Andrés Ibáñez, Ciudad, Equipetrol Norte, 22 April 1997, Coimbra 4632 (NY); Velasco, Campamento Toledo, 28 May 1984, Guillén & Coria 1598 (MO, USZ), 9 June 1984, Guillén & Choré 1767 (F, K, MO, NY, USZ); Reserva Ecológica El Refugio, 27 April 1995, Guillén & Roca 3339 (MO, USZ); Velasco, Reserva Ecológica El Refugio, 27 April 1995, Guillén & Roca 3370 (CR, MO, USZ), 2 May 1995, Guillén & Chore 3426 (CR, MO, USZ), 3 May 1995, Guillén et al. 3477 (CR, USZ); Santa Cruz, El Pari, 14 April 1946, Peredo s.n. (LIL, MO, NY, WIS [2 sheets]); Angel Sandoval, San Fernando, Río San Fernando, 7 May 1997, Saldias et al. 5205 (MO, NY); Sara, Buenavista, 22 April 1917, Steinbach 3331 (SI). Data lacking: May 1886, Rusby 2383 (BM, F, K, NY, WIS); December 1901, Williams 444 (BM, K, NY).

PARAGUAY. Alto Parana: Puerto Stroessner, 7 December 1984, *Stutz 2013* (CR, G, K, NY). Amambay: Paso Nandéjara, 19 March 1987, *Hahn et al. 1234* (MO, USF); Río Estrella, cerca a Río Apa, 1901–1902, *Hassler 7916* (G); Río Apa, 1901–1902, *Hassler 7993* (BM, G [2 sheets], NY); Río Apa, 1901–1902, *Hassler 8172* (G, K, LIL, MO, NY, S, UC); Sierra de Amambay, cerca a Esperanza, 1907–1908, *Hassler 10270* (G, NY). Caaguazú: Ruta 2, 8 February 1989, *Zardini & Aguayo 10578* (SI). Central: Río Paraguay, cerca a Asunción, 1874, *Balansa 1372* (BR, G [2 sheets]); Arroyo Mboiy, 2 March 1975, *Schinini 10937* (CTES, Z); Estero del Ypoá, al SO de Nueva Italia, Isla Guazú, 10 February 1990, *Zardini & Velásquez 18730* (SI); Laho Ypoá, Pindoty, 27 June 1991, *Zardini & Velásquez 28002* (NY, SI); Estero del Ypoá Pindoty, 17 June 1992, *Zardini & Tilleria 32012* (NY, SI); Estero del Ypoá, Puerto Guyrati-Villa Oliva, 14 January 1993, *Zardini & Aquino 34676* (NY, WAG). Chaco: Bermejo, puerto Bermejo, 8 March 1901, *Kermes s.n.* (BAB); Puerto Casado, December 1916, *Rojas 2095* (SI). Concepción: Villa Sara, entre Río Apa y Aquidabán, 1908–1909, *Fiebrig 5009* (BM, G [2 sheets], K, L, LIL, SI), *Fiebrig* 

4601a (K); Alto Paraguay, Primavera, 1955, Woolston 502 (C, K, NY, P, S, SI, U, UC); Primavera, Alto Paraguay, 5 May 1957, Woolston 1446 (K), Woolston 1447 (K), Woolston 1448 (K). Cordillera: Villa Río Piribebuy, O de Arroyos, 3 March 1990, Zardini & Velásquez 19664 (MO). Paraguarí: Lago Ypoa, 26 November 1988, Soria et al. 2736 (CR, FCQ, G); entre Nueva Italia y Carapeguá, 14 December 1989, Zardini & Velásquez 16794 (SI); Parque Nacional Ybycu´i, cerca de La Rosada, 3 February 1992, Zardini & Franco 30361 (SI); Estero Ypoá, arroyo Cañabe, 18 March 1992, Zardini & Guerrero 31176 (LPB, MO, NY, SI). Presidente Hayes: Río Negro, O de Puerto Galileo, 16 February 1994, Zardini & Bertoni 38269 (CR, MO, PY), Zardini & Bertoni 38288 (CR, MO, PY). San Pedro: cerca a San Estanislao, s.d., Hassler 6001 (BM, C, G [2 sheets], K, LIL, MICH, MO, NY, S, UC); Antequera, 23 June 2001, Zardini & Guerrero 56551 (CR, MO).

ARGENTINA. Formosa: Pilcomayo, El Porteño, 10 January 1980, *Guaglianone et al. 537* (CR, SI); El Monte, January 1919, *Jørgensen 3119* (B, BA, SI, US); Puesto Porteño, Pilcomayo, 11 January 1947, *Morel 2093* (C, LIL). Misiones: Cataratas del Iguazú, 20 March 1944, *Meyer 6506* (F, GH, LIL, SI, U); El Dorado, 6 March 1944, *Meyer 6818* (F, LIL, U); San Pedro, Isla Caraguatay, 27 November 1943, *Porta 165* (SI).

Prestonia vaupesana Woodson in Schultes (1957: 178). Type:—COLOMBIA. Vaupés: Apaporis river, around Cachivera de Jirijirimo, 16 September 1951, R. Schultes & I. Cabrera 14039 (holotype MO!, isotypes COL!, GH!, NY! [fragment], US!). Fig. 42, 44.

**Stem** glabrous to glabrescent, with milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, less than 0.5 mm long. **Petioles** 0.5–0.8(–1) cm; leaf blade 6.5–12.5(–14)  $\times$  2.8–6 cm, elliptic to ovate-elliptic, acuminate to short-acuminate, base obtuse to rounded, membranaceous, glabrous, secondary and tertiary veins conspicuously impressed on both surfaces. **Inflorescence** a monochasial cyme, axillary, shorter than or equaling adjacent leaves, many-flowered, the flowers somewhat clustered, glabrous, peduncle 6.5–16 cm, pedicels 1.3–1.6 cm long, floral bracts 1–2  $\times$  0.5–1 mm, linear, scarious, minute, green. **Sepals** 6.5–8  $\times$  1–1.8 mm, free, coriaceous to subcoriaceous, narrowly elliptic, the apices acuminate, not reflexed, glabrous, scarious, drying with a more or less uniform color, the veins not impressed, colleters ca. 1 mm long,

subentire at the apex. **Corolla** salverform, yellowish green, glabrous outside, tube  $14-16 \times 2.5-3$  mm, straight, free corona lobes 1-1.5 mm, barely included, their height conspicuously surpassed by that of the anther apices, annular corona entire, thickened, corolla lobes  $9-10 \times 6-7$  cm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5.3-5.5 mm, very sparsely puberulent to glabrescent dorsally, the apices barely exserted. **Ovary** 1-1.5 mm tall, glabrous, style-head 1.1-1.5 mm, nectary 0.9-1.4 mm, equaling or barely shorter than the ovary, deeply 5-lobed or completely divided into 5 nectaries, each one entire to subentire. **Follicles**  $29-33 \times 0.2-0.3$  cm, continuous, rarely inconspicuously articulated, free, but usually united at the tips (at least when young), glabrous, without lenticels, membranaceous when old; seeds 17-19 mm, very minutely and densely papillate, coma (1.5-)4-5 cm, cream.

**Distribution and habitat:**—Forest over quartzite formations, tropical wet forest and disturbed vegetation in Amazonas from southeastern Colombia to Venezuela and northern Brazil from 150 to 400 m.

**Phenology**:—*Prestonia vaupesana* has been collected with flowers in February through July and October, fruiting specimens from March through August.

**Conservation Assessment**:—Vulnerable (VU)

**Taxonomic notes:**—*Prestonia vaupesana* resembles *P. amazonica* and *P. denticulata*, sharing similar inflorescences, scarious floral bracts, and small sepals. However, *Prestonia vaupesana* is easily separated by its glabrous inflorescences, and thinner follicles. *Prestonia lindleyana* is also superficially similar to *P. vaupesana* by its unbranched inflorescences, but the sepals of the former are longer and with the base drying darker than the rest of the sepal.

Additional specimens examined:—COLOMBIA. Amazonas: La Victoria, Río Apaporis, sector cueva de Guacamaya, 18 March 2009, *Cárdenas et al.* 22007 (COAH). Vaupés: Mitú, aguas arriba del Río Vaupes, 12 November 2009, *Cárdenas & Aguirre* 24552 (COAH); Mitú, Río Vaupés, 12 November 1939, *Pérez & Cuatrecasas* 6753 (COL);

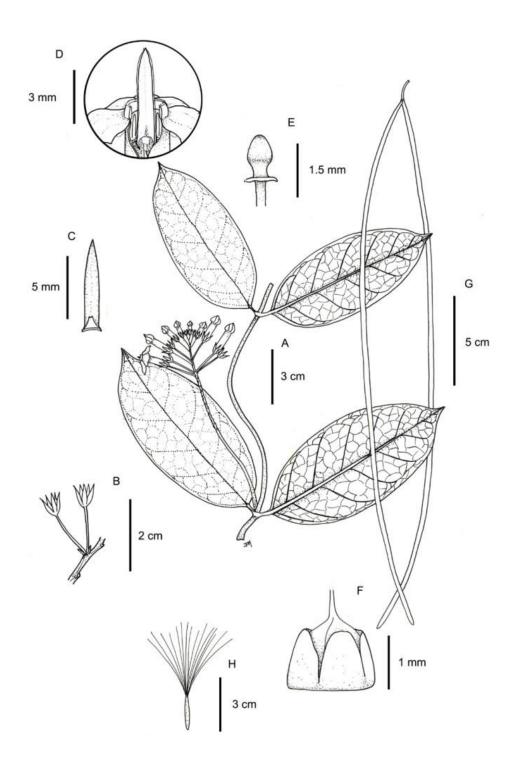


Fig. 44 *Prestonia vaupesana* (A-F from *Zarucchi et al. 1155*, COL; G-H from *Liesner 18653*, INB). A. Stem with inflorescence. B. Calyces, pedicels, and floral bracts. C. Adaxial view of one sepal, showing the colleter at the base. D. Open corolla mouth, showing the anthers and the free coronal lobes. E. Style-head. F. Nectaries and ovary. G. Follicles. H. Seed.

Río Apaporis, Raudal Yayacopi, La Playa, 18 August 1952, *Schultes & Cabrera 16974* (US); Mitú, a lo largo de Río Kubiyú, 1 April 1975, *Zarucchi et al. 1155* (COL, GH, MO, USF), 10 July 1975, *Zarucchi 1430* (COL [2 sheets], GH, MO); Mitú and vicinity; along Río Vaupes just below Urania, 7 August 1976, *Zarucchi 1872* (COAH, MO); Mitú, Urania, 7 August 1976, *Zarucchi et al. 1976* (COL, GH, MO).

VENEZUELA. T.F. Amazonas: Atabapo, salto Yureba, Bajo Ventuari, 24 October-4 November 1981, *Delascio & Guánchez 10864* (VEN); Atabapo, Salto del Caño Yureba, Bajo Ventuari, 22 March 1982, *Guanchez 1577a* (VEN, Z); Atabapo, 3 April 1984, *Liesner 17195* (MO, VEN); Atabapo, 7 March 1985, *Liesner 18407* (MO, MY); Atabapo, Salto Yureba, Cerro Yureba, 14 March 1985, *Liesner 18653* (CR, MO, NY, MY, WIS); carretera San Carlos-Solano, S de Caño Chola, 2 February 1977, *Morillo & Hasegawa 5076* (VEN); Río Cunucunuma, entre las comunidades de Culebra y Huachamacari, entre el Cerro Duida y Huachamacari, 1982, *Steyermark et al. 126176* (VEN); Atabapo, Culebra, Río Cunucunuma, March 1983, *Steyermark & Delascio 129028* (VEN, Z).

BRAZIL. Amazonas: carretera Manaus-Porto Velho, km 124, 25 March 1974, *Campbell et al.* 20906 (GH, INPA, MG, MO, NY, S, U, UFMG, US).

- V. *Prestonia* sect. Mollis J. F. Morales, M. Endress & Liede, sect. nov. Type: *Prestonia mollis* Kunth, Nov. Gen. Sp. (quarto ed.) 3: 221, t. 242. 1818[1819].
- Prestonia mollis Kunth (1818: 221). Haemadictyon molle (Kunth) Candolle (1844: 427). Type:—PERU. Loreto: Marañón, s.d., A. Humboldt & A. Bonpland 3608 (holotype P-HB! (photo F neg. 38794!), isotype F!). Fig. 42, 45
- Prestonia glabrata Kunth (1818: 222). Haemadictyon glabratum (Kunth) Candolle (1844: 427). Type:—ECUADOR. Guayas: Guayaquil: s.d., A. Humboldt & A. Bonpland 3835 (holotype P-HB! [photo F neg. 38792!]).
- Haemadictyon pallidum Candolle (1844: 428). Haemadictyon pallidum Candolle var. genuinum Van Heurck & Müller Argoviensis (1871: 163), nom. illeg. Type:—

- PERÚ. Without data, *H. Ruiz & J. Pavón 7/58* (holotype G-DC!, isotype MA! (photo F neg. 29218!)).
- Haemadictyon pallidum Candolle var. velutinum Van Heurck & Müller Argoviensis (1871: 162). Type:—ECUADOR. Without exact locality, 1857–1859, R. Spruce 6019 (holotype G [2 sheets], isotypes AWH, CGE!, K! [3 sheets], NY! [2 sheets], OXF!, P!, W!).
- Haemadictyon pallidum Candolle var. glabrum Van Heurck & Müller Argoviensis (1871: 163). Type:—ECUADOR. Guayas: river Daule, near Guayaquil, 1855, R. Spruce 6484 (holotype AWH, isotypes CGE!, G!, K!, OXF!, P!, W!).
- Haemadictyon tomentellum Bentham in Hinds (1845: 126). Type:—ECUADOR. Guayas: Guayaquil, 1836–1839, G. Barclay & R. Hinds 503 (holotype BM!, isotype K!).
- Echites pallidus Miers (1878: 195). Type:—ECUADOR. Guayas: Guayaquil, 1842, K. Hartweg 670 (holotype BM!, isotypes CGE!, FI-W!, G!, K! [2 sheets], LD!, OXF!, P!).
- Prestonia ecuadorensis K. Schumann (1895: 188). Type:—ECUADOR. Guayas: Isla Puná, May 1892, Eggers 14722 (lectotype (designated here) M!, isolectotypes B [destroyed, photo F neg. 4547!], O!, US!).
- Prestonia weberbaueri Markgraf (1924: 89) Type:—PERU. Cajamarca: Marañón a Bellavista, 2 May 1912, A. Weberbauer 6231 (lectotype G!, designated by Morales (2006 b), isolectotypes F! [photo F neg. 56497!], MOL!).
- Prestonia cordifolia Woodson (1936: 352) syn. nov. Type:—PERU. Cajamarca: Catache, Contumazá, 27 May 1875, A. Raimondi 8228 (holotype B destroyed). Neotype (designated here):—PERU. Cajamarca: Contumazá, Andaloy, San Benito-Yetón, 17 May 1979, Sagástegui et al. 9249, (neotype F!; isoneotypes F!, HUT [destroyed], MO!, Z!).

**Stem** densely and minutely tomentulose to minutely puberulent when young, sometimes glabrescent at maturity, with clear or milky latex, sparsely lenticellate, these not suberose, intrapetiolar colleters minute, 0.5-0.8 mm long. **Petioles** 0.5-4(-5) cm; leaf blade  $3.5-16.5 \times 2-10(-12)$  cm, elliptic, ovate, broadly ovate to ovate-elliptic, apex acuminate to short-acuminate, base truncate, obtuse, rounded, subcordate to conspicuously cordate, membranaceous, minutely puberulent to glabrescent or glabrous adaxially, densely and

minutely tomentulose, puberulent to glabrescent or glabrous abaxially, indument drying tan, secondary veins impressed on both surfaces, tertiary veins impressed abaxially, somewhat inconspicuous adaxially. Inflorescence a dichasial cyme, rarely a monochasial cyme, axillary, shorter or longer than the adjacent leaves, many-flowered, the flowers densely to more or less clustered, minutely tomentulose, minutely puberulent to glabrescent, peduncle 0.5-6 cm, pedicels 0.6-2.7 cm long, floral bracts 5-20(-26) × 2.5-3.5 mm, narrowly elliptic, narrowly ovate-elliptic to narrowly ovate, usually foliaceous to subfoliaceous, sometimes a few ones scarious and inconspicuous, green. Sepals 8-22 × 1.5-6(-8) mm, usually free, rarely connate at the base along 1/6 of their length, forming and forming an inconspicuous campanulate base, membranaceous, linear, narrowly elliptic to narrowly ovate, the apices acute to acuminate, not reflexed, minutely puberulent, glabrescent or glabrous, very small to subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed, colleters ca. 1 mm long or less, entire to inconspicuously lacerate at the apex. Corolla salverform, yellow, yellowish green, green lilac to green purple, puberulent, glabrescent or glabrous outside, tube  $19-36 \times 3-6$  mm, the base somewhat inflated and gradually expanding toward the mouth, free corona lobes 2–5 mm long, the apices exserted, their height surpassing that of the anther apices, annular corona entire, thickened, corolla lobes  $17-26(-34) \times 6-13(-17)$  mm, obliquely obovate. Stamens inserted near the corolla mouth, anthers 6–8 mm, minutely puberulent dorsally, rarely glabrescent, the apices usually exserted. **Ovary** 1.5–2.5 mm tall, glabrous, style-head 1.9-2.3 mm, nectary 1-2 mm, equaling, surpassing or shorter than the ovary, entire, subentire to variously 5-lobed or completely divided into 5 nectaries, each entire, subentire or slightly lacerate. **Follicles**  $14-26(-30.5) \times 0.7-0.9$  cm, continuous, connate longitudinally, glabrous to glabrescent, without lenticels, firmly membranaceous to slightly woody when old; seeds 8–11 mm, coma 3–4 cm, cream.

**Distribution and habitat**:—Southern Panama, Ecuador to northern Peru, in dry forest, premontane dry forest, montane dry forest, and moist forest, from 0–1800(–2500) m.

**Phenology**:—Flowering throughout the year. Fruiting February-October.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Local names**:—Arrachillas (El Oro, Ecuador); bejuco lechoso yellow (Manabí, Ecuador); coneco (Loja, Ecuador); contra de culebra (Guayas, Ecuador); guia-guia

(Cajamarca, Perú); hierba del cogimiento (Cajamarca, Coén, Perú); platanillo (Piura, Perú); sanalotodo (Guayas, Ecuador); vela-vela (Cajamarca, Contumazá, Perú).

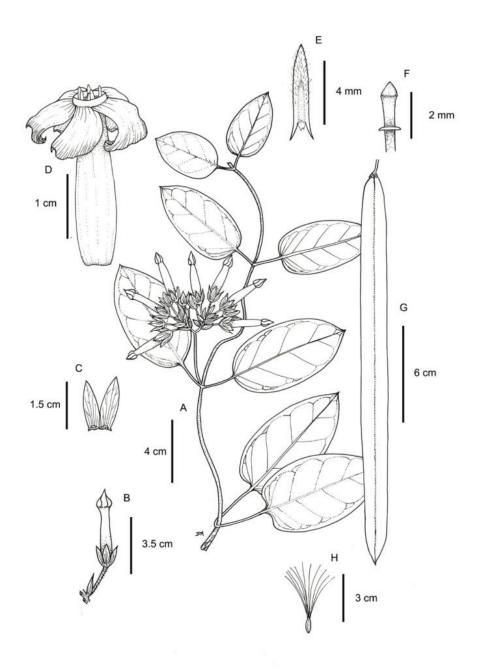


Fig. 45 *Prestonia mollis* (A-F from *Neill et al. 10671*, INB; G-H from *Palacios & Cerón 13868*, QCNE). A. Flowering stem. B. Calyx, pedicel, and bract. C. Adaxial view of two sepals. D. Corolla. E. Anther, dorsal view. F. Style-head. G. Follicles. H. Seed.

**Uses:**—In Peru an infusion flowers has been used to treat for hepatitis (*Shonle 30*). Macerate young shoots and floral buds are mixed with food and used to kill foxes (*Woytkowsky 6766*). In Ecuador an infusion of the leaves has been used as a natural abortive (*Cornejo & Bonifaz 2899*) or for the treatment of infections (*Escobar & Berry 718*).

**Taxonomic notes**:—*Prestonia mollis* displays a great deal of variation in shape, indument, and length of leaf blades, shape and length of the sepals, and color of the corolla lobes; it is probably the most variable species in the genus. There are numerous local populations throughout its geographical range, sometimes with little variation in a few characters, but with a broad range of intergradations between them, which make specific recognition, even at varietal level untenable. Variation in size and shape of the leaf blades, as well as sepal size is extensive (Fig. 46). The nectary shows an equally high degree of variation, ranging from entire to subentire, conspicuously lobed or almost completely divided into five separated nectaries (Morales, 2004 b).

Prestonia cordifolia has been characterized by its puberulent and purplish corolla, exserted corona lobes, dorsally pubescent anthers, and leaf blade with cordate base, characters supposedly restricted to plants above 1500 m in northern Peru. However, specimens from lowland elevations (e.g., Palacios 3306, MO) also have cordate leaves, similar to those from highlands (Woytkowsky 6897, F, MO, Z). The only "real" difference is the corolla colour, however, there are some populations with intermediate flowers, in which the corolla is greenish white or greenish yellow, slightly infused with purplish brown or maroon. However, since the same variation is found in other species of the genus (e.g., P. portobellensis) and there are no real discontinuities, P. cordifolia is reduced to synonymy of P. mollis.

Prestonia cordifolia was included in section "Tomentosae" (section Prestonia) by Woodson (1936), mainly because of its puberulent corolla. External pubescence of the corolla is a common character for many species of section *Prestonia* but sometimes specimens from section Mollis have puberulent corollas. The type of *P*. cordifolia lacks the conspicuously developed intrapetiolar colleters, typical for members of section Prestonia.

The type of *Prestonia cordifolia* was destroyed in 1943. Thus, a neotype is selected here, which matches with the original description and is from the same type locality.

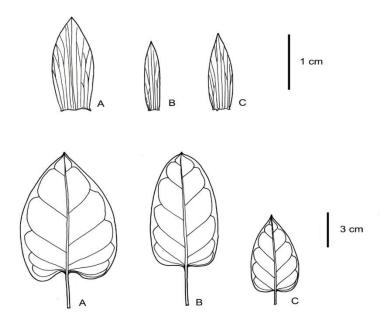


Fig. 46 Variation of the leaf shape and sepals shape in *P. mollis*. A. *Díaz & Peña 4036*, INB. B. *Campos & Díaz 2027*, MO. C. *Neill et al. 10671*, INB.

Prestonia ecuadorensis has been reported as a nomen nudum in various papers (e.g., Woodson, (1936), Morales (2010a)), but the name was validly published by Schumann (1895). The type deposited at Berlin (B) was destroyed during World War II. The lectotype selected here, is the best preserved specimen from the known duplicates. However, as was pointed out by Morales (2010a), there are two specimens of Eggers with the same date and collection number, but with different localities and both are the types of two different species (P. ecuadorensis (= P. mollis), and P. schumanniana). For a full explanation, see Morales (2010a).

**Additional specimens examined:**— PANAMÁ. Darién: without exact locality, 1966, *Bristan 4* (MO). Data lacking: *Neé s.n.* (MA).

ECUADOR. Azuay: Río León, 2 Octuber 1944, Camp 548 (NY); entre Machala y Santa Isabel, Río San Francisco, 11 June 1971, MacBryde 437 (MO); cerca de Santa Isabel, camino de Cuenca a Pasaje, 1 December 1974, Plowman, et al. 4591 (S). Chimborazo: cañón del Río Chanchan cerca Huigra, 7-14 May 1945, Camp 3221 (NY); cañón del Río Chanchan, entre Naranjapata y Huigra, 19 June 1943, Camp 3855 (NY, S); Pallatanga, September 1891, Sodiro s.n. (P, QPLS). El Oro: al E de Pinas, 30 September 1981, Besse et al. 729 (CR, MO, SEL); Bosque petrificado Puyango, 1 June 1995, Cornejo et al. 4010 (GUAY, USF); Puyango y cerca, August 1978, Daly 31 (CR, MO, NY, QCA, WAG); Santa Rosa, 9 July 1986, *D'Arcy 16438* (MO); Quebrada Seca, 23 Nov-16 December 1978, Escobar & Berry 718 (HUA, QCA, TEX), 23 Nov-15 December 1979, Escobar 900 (QCA); Zaruma, 28 July 1959, Harling 6139 (S); Huaquillas, línea fronteriza, 5 September 1978, Jaramillo & Narváez 764 (QCA, QCNE [2 sheets]); bosque petrificado Puyango, 23 August 1996, Klitgaard et al. 321 (AAU, MO, QCNE); Chilla, entre Cune y Chilla, 4 August 1996, Palacios & Cerón 13868 (QCNE); cerca de la unión del Río Luis y Río Asbocas, 10 km al S de Portobelo, 6 Octuber 1944, Wiggins 10903 (US), Wiggins 10905 (US). Esmeraldas: Esmeraldas, 31 May 1955, Asplund 16542 (NY, S); Esmeraldas, 16 January 1996, Billiet & Jadin 6572 (BR, MO); vía Sua-Atacames, 23 June 1991, Blasco 1676 (AAU, OCNE); 10 km S de Muisne, entre Esmeraldas y Santo Domingo, 16 km al N de Atacames, 31 July 1980, Hansen et al. 7908 (MO [2 sheets], USF, WAG); 23 SE de Esmeraldas, carretera a Río Mate, 1 August 1980, Hansen et al. 7940 (USF, WAG); Esmeraldas, 28 August 1947, Harling 1720 (S); cerca de Esmeraldas, 12 September 1974, Hudson 749 (CR, MO, QCA, Z); Esmeraldas-Atacamis, 7 August 1962, Játiva & Epling 449 (NY, S, SEL, UC); Esmeraldas, 14 July 1881, Lehmann 730 (BM); Bahía de Caraquez, s.d., Lehmann 731 (L); entre Esmeraldas y Tablazo, 14 September 1977, Maas et al. 2909 (U, WAG); Playa E de Súa, 4 July 1971, MacBryde & Duellmann 537 (MO); San Lorenzo, 22 August 1977, *Quinto de Biología s.n.* (Q); Bahía de Caraquez, 14 September 1990, Weigend 995 (M). Guayas: Guayaquil, Puná, 1852, Andersson 79 (S [2 sheets]); Guayas, July 1876, André 4216 (K); Guayaquil, 4 km al O de la ciudad, 16 February 1939, Asplund 5001 (S); Guayaquil, 15 August 1939, Asplund 7701 (LD, R, S, UPS, US); Guayaquil, Cerro Santa Ana, 16 January 1955, Asplund 15194 (S); entre Daule y Santa Lucía, 4 March 1955, Asplund 15610 (B, NY, R, S, UPS, US, USF, Z); Guayaquil, 21 June 1955, Asplund 16680 (G, K, LD, NY, S, UPS [2 sheets], US, Z); Isla de Puná, August 1836, Barclay 354 (BM); Isla de Puná, September 1836, Barclay 344 (BM [2 sheets]), September 1838, Barclay 2435 (BM); El Progreso, entre Salinas y Guayaquil, 3 November 1983, Barfod et al. 48481 (AAU, QCA, QCNE, WAG); Río Boliche, E de Durán, 30 September 1955, Böcher et al. 211 (C, S); Isla Salando, Parque Nacional Machahilla, 28 September 1991, Cerón 16652 (CR, MO, QAP); Naranjal, Reserva Ecológica manglares Churote, parroquia Taura, 27 December 1991, Cerón et al. 17778 (CR, MO, QAP); Guayaquil, campus politécnico, July 1993, Cornejo 270 (QCNE); Guayas, urbanización Capeira, 18 June 1994, Cornejo & Bonifaz 2899 (GUAY, QCNE); Botadero San Eduardo, 28 October 1996, Cornejo & Bonifaz 5337 (GUAY, USF); entre Guayaquil y Daule, 24 September 1961, Dodson & Thien 701 (MO, QCA); Capeira, Dodson et al. 11055 (GUAY, MO, Q, SEL); entre Guayaquil y Daule, 16 February 1982, Dodson & Gentry 12552 (MO); Isla Puná, May 1892, Eggers 14722 (B [destroyed, photo F neg. 4547], L, M, O, US); Guayaquil, 29 July 1966, Eliasson & Eliasson 18 (S); Guayaquil, August 1836, Gaudichaud 44 (P [4 sheets]); O de Guayaquil, camino a Salinas, 17 February 1974, Gentry 9996 (MO, QCA); E de Recinto Olón, cerca a Manglaralto, 19 February 1974, Gentry 10038 (MO, QCA, Z); carretera de Guayaquil a Salinas, 30 Octuber 1974, Gentry 12247 (MO, Z); Valle de Río Ayampe, 18 January 1991, Gentry & Josse 72379 (F, MO, OCNE); Guayaquil, 21 Octuber 1958, *Harling 3021* (S); Guayaquil, 20 km al O de la ciudad, 8 May 1959, Harling 5021 (S); Guayaquil, April 1968, Harling et al. 8796 (GB, USF); Chongón, Hacienda Cerro Azul, 15 January 1974, Harling & Andersson 11508 (GB); carretera de Guayaquil a Salinas, km 15 al 23 desde Guayaquil, 13 March 1974, Harling & Anderson 12558 (GB, USF); road Guayaquil-Nobol, Piedrahita, 1-5 km S of Nobol, 29 November 1980, Harling & Andersson 16791 (GB); alrededor de Guayaquil, 16 January 1943, Haught 3515 (US); Guayaquil, 18–20 June 1923, Hitchcock 19937 a (US); entre Guayaquil y Salinas, 21–24 June 1923, Hitchcock 20069 (NY, US); 8 millas al S de Milagro, 11-13 July 1923, Hitchcock 20593 (NY, US); aeropuerto de Guayaquil, 19 January 1963, Iltis & Iltis 1633 (K, WIS); La Frutilla, cerca a julio Moreno, 21 July 1962, Játiva & Epling 129 (NY, S, UC, US); Cerro de Isera, cerca a julio Moreno, 28 August 1965, Játiva & Epling 952 (NY, UC); E de Buenos Aires, 28 March 1973, Holm-Nielsen et al. 2549 (AAU, MO, NY, S); Isla Puna, cerca de Bellavista, 13 May 1987, Madsen 63398 (AAU, QCA, QCNE); entre Guayaquil y Salinas, 10 December 1934, Mexia 6759 (CAS, MO, NY, US); Guayaquil, September 1924, Mille 24 (US), July 1925, Mille 39 (QCA), Mille 44 (QCA), Mille 57 (NY, QCA); Guayaquil, September 1927, Mille 75 (QCA); Bosque Protector Cerro Blanco, 29 February 1996, Neill & Núñez 10485 (QCNE); base de Cerro Blanco, 8 August 1996, Neill et al. 10671 (CR, OCNE); Bosque Protector Cerro Blanco, entre Guayaquil y Salinas, 30 September 1996, Núñez 277 (CR, MO, QCNE); Cerro Blanco, 5 April-20 May 1996, Núñez & Yogual 486 (QCNE); San Antonio, 22 March 1967, Pineda 73 (S); Guayaquil, July 1836, Remy s.n. (P [2 sheets]); Guayaquil, Bosque Protector Cerro Blanco, carretera a Salinas, 15 August 1991, Rubio et al. 1904 (MO, QCNE), 17 August 1991, Rubio et al. 1931 (CR, MO, QCNE); Isla de Puná, 16 June 1934, Schimpff 1192 (M, Z); Isla de Puna, December 1890, Sodiro s.n. (QPLS); Guayaquil, s.d., Sodiro 307 (QPLS); Guayaquil, 23 May 1967, Sparre 16713 (MO, S); Guayaquil, 27 Octuber 1924, Stevens 40 (US); N de Guayaquil, 29 August 1939, Stork et al. 8971 (G, K, UC, US); Guayaquil, carretera a Salinas, 2 September 1963, Valverde 11 (COL); Salinas, sin fecha, Valverde 483 (COL). Loja: Cangonamá, al O de Catacocha, 1 January 1981, Balslev 1336 (NY); parroquia vilcabamba, Yamburara, 4 September 1990, Cerón & Ocampo 11870 (QAP, QCNE); San Sebastián de Yulua, 3 March 1991, *Chacón 15* (QCNE); km 5 vía San Vicente-Catamayo, 18 May 1997, Cornejo & Bonifaz 5269 (GUAY, USF); entre La Toma y San Pedro, 11 July 1947, Espinoza 1595 (MO, P); Malacatos, 19 March 1972, Harling 11304 (GB, USF); Vilcabamba-Yangana, 15 April 1974, Harling & Anderson 13581 (GB, USF); Catacocha-Macara, ca. 12 km al SO de Catacocha, 8 February 1977, Harling et al. 15225 (GB, USF); entre Empalme y Celica, ca. 5 km al O del El Empalme, 12 November 1977, Harling et al. 15402 (GB, USF); entre Loja y Zaruma, km 86 desde Loja, 13 February 1977, Harling et al. 15454 (GB, USF); entre Alamor y Cazaderos, 5 km al O de El Limo, 3 April 1980, Harling & Anderson 17809 (GB, USF); entre Celica y El Empalme, carretera Catacocha-Macará, 1-2 km de El Empalme, 11 April 1980, Harling & Anderson 18140 (GB, USF); Lucarqui, entre Catacocha y Macará, ca. 7 km al N del cruce a Celica, 12 April 1980, Harling & Anderson 18193 (GB, USF); camino viejo entre Macará y Cariamanga, 3-6 km al E de Macará, 18 April 1980, Harling & Anderson 18419 (GB, USF); entre Malacatos y Vilcabomba, 3 February 1985, Harling & Anderson 21481 (AAU, QCA); entre Celica y El Empalme, a 12 km de Celica, 24 February 1985, Harling et al. 22486 (GB, MO, QCA);

camino Macará-Cariamanga, km 15, 26 February 1985, Harling & Anderson 22566 (QCA, USF); carretera Caraimanga-Yambaca-El Toldo-Chaco, 17 February 1993, Harling et al. 24466 (GB, S); al E de Vilcabamba, 10 May 1978, Hart 1312 (US); camino Macará-Sozoranga, O de Tambo Negro, 27 January 1991, Kessler 2254 (GOET, QCA); Pupacos, W of Catacocha, km 26 on road Catacocha-Macará, 30 April 1996, Klitgaard et al. 154 (AAU); O de Catamayo, camino a Catacocha, 6 February 1984, Knapp & Mallet 6255 (QCA, QCNE, US [2 sheets]); Catamayo, 3 km along track via hosteria Bella Vista, 12 January 1998, Lewis & Hughes 3751 (AAU, K, MO, QCNE); entre Empalme y Macará, Tangula, 20 September 2000, Madsen et al. 7360 (AAU, QCNE); entre la Toma y Loja, km 12, 2 September 1988, Madsen & Ellemann 75180 (AAU, QCA, QCNE); bosque petrificado de Puyango, 6 January 1990, Mena et al. 2548 (QCA); N de Sozoranga, camino a Tumbunuma, 18 September 1989, Munday & Maldonado 11 (QCA); Río Sabianga, cerca de Quebrada Hueco Hondo, 26 September 1989, Munday & Maldonado 72 (QCA, QCNE); entre Loja y Catamayo, valle Catamayo, 25 February 1989, Øllgaard et al. 90665 (AAU, QCA, QCNE); Macará, carretera a Papayal, Quebrada Papayal, 2 January 1989, Palacios 3306 (MO); entre Loja y Portovelo, 3-6 Octuber 1915, Rose et al. 23324 (US); Río Comunidades, entre Vilcabamba y Yangana, 14 March 1967, Sparre 16153 (S); Guayachuma, km 85 de la carretera Loja-Machala, 23 September 1967, Sparre 18869 (S); Río Macará, 27 March 1910, Townsend 74 (US). Los Ríos: N de Palestina, 30 July 1962, Játiva & Epling 290 (NY, UC); Vinces, 9 January 1949, Scolnik 1515 (SI). Manabí: entre Montecristi y La Pila, January 1979, Besse et al. 127 (QCA, SEL); Bahía de Caráquez, carretera a Chone, 4 June 1989, Cerón et al. 6712 (MO); entre Puerto Cayo y Machalilla, 6 June 1989, Cerón et al. 6753 (MO, QCNE, USF); camino San Sebastián-Agua Blanca, 20 September 1991, Cerón 16614 (QAP, QCNE); Sucre, Punta Los Frailes, La Chorerra, SO de Pedernales, 29 June 1999, Delinks & Robles 344 (MO, QCNE); entre Colima de Pajan y Jijijapa, 23 December 1961, Dodson & Thien 1689 (MO, QCA); El Recreo, 4 April 1897, Eggers 14956 (C, K, L, LD, O, P, PR, US); Manta, 10 Octuber 1952, Fagerlind & Wibom 554 (LD, NY, R, S, UPS); O de Puerto Viejo, 1974, Gentry et al. 12202 (MO, QCA, S, Z); Estero Manta Blanca, Parque Nacional Machalilla, S de Agua Blanca, 24 January 1991, Gentry & Josse 72720 (F, MO, QCNE); 4 km NE de Portoviejo, 6 August 1980, Hansen et al. 7963 (MO, NY, USF, WAG); 3 km NE de Montichristi, 21 km al S de Portoviejo, 7

August 1980, Hansen et al. 7968 (MO, NY, USF); carretera Montecristi-Jipijapa, 13 May 1968, Harling et al. 9486 (USF); Bahia de Caráques, 15 June 1973, Holm-Nielsen et al. 7202 (AAU, NY, S); carretera Santa Elena-Jipijapa, Río Pital, Puerto López, 26 Octuber 1980, Holm-Nielsen et al. 27862 (AAU, CR, QCA), Holm-Nielsen et al. 27868 (AAU), Holm-Nielsen et al. 27869 (AAU); carretera Montecristi-Porto Viejo, 27 Octuber 1980, Holm-Nielsen et al. 27897 (AAU, CR, QCA); bahía del Río Chone, SSE de bahía de Caraquez, 8 July 1977, *Iltis & Iltis E–170* (L, MO, QCA, S); Tosagua, cerca a Portoviejo, 1 September 1965, Játiva 988 (UC); Manta, E de Tarqui, 2-3 km from Río Manta, 25 Octuber 1988, Madsen 84373 (AAU, QCA), Madsen 84374 (AAU, QCA); Jama, Cerro del Matal, 17 December 1998, Neill et al. 11612 (CR, MO, QCNE, Z [2 sheets]); entre San Mateo y El Aromo, 23 July 2001, Neill & Asanza 13315 (MO); Jaramijó, Reserva de bosque seco Lalo Loor, 22 km S de Pedernales, 6 January 2006, Neill et al. 15110 (CR, MO); Jijijapa, Parque Nacional Machalilla, Isla de la Plata, 18 August 1993, Núñez 123 (QCNE); Sucre, 16 September 1993, Webster et al. 30630 (MO, QCNE, UC); Parque Nacional Machalilla, Isla de la Plata, NO de Puerto López, 21 November 1993, Woodruff & Núñez 586 (MO, QCNE). Data lacking: 1903, Lehmann 193 (K [2 sheets]); s.d., Lehmann 1062 (K); s.d., Jameson s.n. (K, W); 27 Octuber 1933, Schimpff 315 (G, Z).

PERÚ. Apurimac: Abancay, Jaén, 15 May 1975, Hooking 21 (USM). Amazonas: entre La Peca y Bagua Chica, 24 Octuber 1978, Barbour 4272 (MO); Luya, Camporredondo, 29 March 1997, Campos et al. 3719 (CR); entre Bagua e Imazita, 3 August 1997, Castro et al. 17408 (MO); Chachapoyas, Balsas, Río Marañón, 7 August 1958, Ferreyra 13352 (MO, USM) Suyobamba, 3 km NE de Pedro Ruíz Gallo, 6 February 1988, Gentry et al. 61297 (MO, NY, USF, USM); Bagua, Churuja, 1 September 1974, Gutte et al. 3453 (LZ); Chachapoyas, Río Marañón, Balsas, 28 May 1964, Hutchison & Wright 5415 (F, K, G, GH, LE, M, MICH, MO, NY, P, UC, US, USM); Bagua, entre Bagua Grande y Río Marañón, Octuber 1964, Hutchison & Wright 6766 (F, MO, NY, UC, US, USM); Bongora, valle de Utcubamba, entre Chachapoyas y Pedro Ruiz, Octuber 1990, Kahn & Moussa 2803 (CR, USM), Kahn & Moussa 2808 (IAN, USM), Kahn & Moussa 2814 (CR, IAN, USM); Bongora, Pedro Ruiz, Chachapoyas, Octuber 1990, Kahn & Moussa 2846 (IAN), Kahn & Moussa 2859 (CR, USM [2 sheets]); Puerto Huacabamba, Río Marañón, 26 May 1960, López & Sagastegui 3158 (NY); Chachapoyas, 1862, Mathews

s.n. (BM, G [2 sheets], K, NY); Chachapoyas, Balsas-Chachapoyas, camino a Leimebamba, 7 May 1970, Sagastegui 7489 (HUT [destroyed], NY, US); Chachapoyas, carretera Celendín-Chachapoyas, 24 May 1984, Smith & Cabanillas 7049 (CR, MO, USM); Pongo de Rentema, 9 March 1998, van der Werff et al. 14584 (CR, MO, USF, USM); Bongara, Jasán, 21 March 2000, Vásquez & Rojas 26495 (MO, USM); along road Pedro Ruiz-Chachapoyas, 11 March 1998, van der Werff et al. 14703 (MO); Utcubamba, Bagua Grande, 26 March 2001, van der Werff et al. 16415 (MO); Cumba, 7 December 2001, Vásquez et al. 27144 (CR, MO). Cajamarca: Jaén, entre Herradura y San Felipe, 31 January 1954, Angulo 2138 (HUT, NY, SI); Jaén, s.d., Benson 20 (MO); Huarango, Nueva Esperanza, 19 January 1996, Campos & Díaz 2027 (MO, USM); San Ignacio, Faical, 18 April 1996, Campos & Díaz 2628 (MO, USF, USM); San Ignacio, Huarango, Puerto Ciruelo, 26 April 1996, Campos & Díaz 2672 (CR, MO, USF, USM); San Ignacio, San José de Lourdes, Puerto Chinchipe-Lambacasa, 27 April 1996, Campos & Díaz 2691 (CR, MO, USF); San Ignacio, Namballe, caserío Las Abejas, 7 July 1997, Campos & Pezantes 4091 (CR, MO, USF); San Ignacio, Huarango, San Martín del Chinchipe, 14 September 1999, Campos et al. 6216 (CR, MO, NY, USM); San Ignacio, San José de Lourdes, 29 Octuber 1999, Campos & Vargas 6342 (CR, MO, USM); Jaen, Pucar, 21 Octuber 1998, Castro et al. 19681 (MO); a lo largo de la carretera entre Bagua y Olmos, valle del Río Chamaya, 43,7 km E de Pucará, 62.3 km O del puente sobre el Río Marañón cerca de Bagua, 18 April 1984, Croat 58365a (MO, USM); Jaén, entre la Unión y Piquijaca, 29 July 1998, Díaz et al. 9933 (CR, MO); Contumazá, La Cueva, entre Cascas y San Benito, 21 Octuber 1990, Dillon & Sagástegui 6057 (F, HAO, MO, NY, QCA, US, USF); 200 km al E de Olmos, 25 December 1970, Ellenberg 3652 (NY); Arnocolpa, cerca de San Miguel de Asunción, 10 April 1950, Ferreyra 7078 (MO, US, USM); Chota, cerca de Llama, 13 August 1952, Ferreyra 8398 (MO, USM); Jaén, entre puente 24 de julio y Chamaya, 27 June 1959, Ferreyra 13695 (MO, USM); Jaén, cerca de Cochalan, 13 July 1982, Ferreyra & Sánchez 19591 (USM); Jaén, Río Marañón, Bellavista, 14 July 1982, Ferreyra & Sánchez 19600 (USM); Contumazá, cerca de Santa Ana, 11 July 1983, Ferreyra 19948 (US, USM); Contumazá, cerca de Chilete, 15 May 1984, Ferreyra & Chanco 20185 (USM); E de Pucará, carretera a Bagua, 11 June 1978, Gentry et al. 22733 (CR, MO, USM, Z); valle del Río Chamaya, E de Pucará, 27 September 1957, Hutchison 1406 (F, MO, NY, UC [2 sheets], US, USM); Jaén, Pucará, Río Huancabamba, 11 January 1964, Hutchison & Wrigth 3526 (UC, USM); Hualgayoc, cerca a Casa Hacienda, 29 August 1964, Hutchison & Bismarck 6333 (UC, US); Celendín, entre Celendín y Balsas, 20 September 2001, McHahon et al. 626 (USM, WS); Contumaza, carretera Cascas-El Chorrillo, 22 August 1994, Merello et al. 1061 (MO, M); Jaén, entre Pucará y Chamaya, ca. 5 km al E de Pucará, Río Huancabamba, 12 July 1980, Plowman et al. 14234 (F, HUT, MO, USF, WAG); San Ignacio, entre Puerto Naranja y Puerto Huaquillo, 29 July 1997, Rodríguez & Campos 1852 (CR, MO, USF); Jaén, Chamaya, 8 June 2000, Rojas et al. 919 (CR, MO); Contumazá, entre San Benito y Santiago, 30 May 1959, Sagástegui & Saname 2925 (NY); Contumazá, San Benito-Guzmango, Andaloy, 1 May 1981, Sagástegui 9730 (HUT, JAUM, MEXU, MO) Santa Cruz, 19 December 1984, Sagástegui et al. 12374 (HUT, MO, USF); Contumazá, alrededores de San Benito, 3 February 1985, Sagástegui et al. 12482 (F, HUT, MO, USF, WIS); Contumazá, 23 March 1988, Sagástegui et al. 13055 (F, HUT, MO); Contumazá, El Rupe, km 13, carretera de Chilete a Contumazá, 3 May 1980, Sánchez 2244 (CPUN, F, SI); entre Santa Cruz y San Ignacio, 9 June 1966, Schunke & Edwin 3733 (F, IAN, NY, US); Celendin, Río Marañón valley, Celendin-Balsas road, 25 km onward from Celendin, 16 July 1983, Smith & Sánchez 4331 (AMAZ, B, MEXU, MO, SI, USF); Fundo Los Arrascue, O de Pucará, a lo largo de la Ouebrada Chaupe, 19 June 1993, Shonle 30 (MO); Jaén, August 1962, Soukup 4892 (US); Celendín, valle del Marañón, al frente de Balsas, s.d., Weberbauer 4265 (MOL); Pucará, 11 March 1950, Woytkowski 5662 (G, MO, US); Colasay, 11 Octuber 1961, Woytkowski 6897 (F, MO, NZ), 30 Octuber 1961, Woytkowski 7036 (F, K, MO, NY, US); Río Chamaya, 1 Octuber 1961, Woytkowski 6799 (MO, US, Z); Colasay, 5 Octuber 1961, Woytkowski 6849 (MO), 11 Octuber 1961, Woytkowski 6932 (MO); Jaén, entre el Río Huancabamba y Jaén, 21-24 Octuber 1952, Vargas 10428 (MO); San Ignacio, entre Huarango y San Martín, 13 May 1996, Vásquez et al. 20831 (CR, MO); San Ignacio, Namballe, Río Namballe, 8 December 1997, Vásquez & Rojas 25203 (MO, MOL, USF); San Ignacio, San José de Lourdes, Crucero, 19 April 1999, Vásquez & Campos 26118 (MO, USF). Cusco: Convención, Echarate, 3 February 1939, Stork et al. 10499 (K, UC). La Libertad: Trujillo, carretera entre Chongogape y Carhuaquero, km 29, 15 April 1988, Díaz & Baldeón 2786 (MO); Ascope, Trujillo, 7 August 1948, López 826 (NY); Trujillo, Chicame, June 1943, Sandeman 4045 (K); Trujillo,

Huancabamba, August 1943, Sandeman 4266 (K); valle de Chicame, hacienda Chiclín, 27 November 1948, Scolnik 1366 (SI, US). Lambayeque: Lambayeque, cerca Pampa de Olsmos, subida a Porculla, 4 March 1961, Ferreyra 14229 (USM); E de Olmos, carretera a Pucará, 10 June 1978, Gentry et al. 22564 (MO); carretera Mesones a Muro, entre Olmos y Jaén, 5 January 1964, Hutchison & Wright 3418 (F. K. M. MICH, MO, NY, P. UC [2] sheets], US, USM); Lambayeque, E de Olomos, carretera a Jaén, 1964, Hutchison & Wright 6707 (UC, US); Zapotal, Notupe, Chiclayo, 9 May 1981, Llatas 655 (HUT, MO, USF); Salas, s.d., Ochoa 1617 (F); Olmos, Beatita de Humay, 29 August 1993, Sagástegui et al. 15061 (F, HAO, MO, NY); Purculla, 28 September 1961, Woytkowski 6766 (K, MO, NY, UC, USM), Woytkowski 6785 (MO, US); Mandanguia, 1 November 1961, Woytkowski 7045 (MO). Piura: Jaén, Huancabamba, 31 dec 1953, Angulo 2119 (NY); Huancabamba, caserío El Pasaje, Cerro El Jardín, 23 September 1989, Arakaki 80 (USM); ca. 3 km E de Canchaque, carretera a Huancabamba, 19 July 1991, Dillon & Sánchez 6223 (F, NY); Piura, December 1955, Ferreyra & Wille s.n. (USM); Huancabamba, entre Palambla y Faique, cerca de Canchaque, 2 May 1955, Ferreyra 10873 (MO, USM); Piura, Serrán, 17 September 1985, Ferreyra & Chanco 20474 (USM); Huancabamba, Quebrada Shumaya, afluente del Río Huancabamba, 14 June 1947, Fosberg 27888 (USF, USM); E de Olmos, carretera a Pucará, 10 June 1978, Gentry et al. 22647 (F. MO, USM); Palambia, Canchaque-Turmalina, Huancabamba, 2 September 1976, Sagástegui 8550 (NY); Ayabaca, Curilca, 6 April 1976, Sagástegui & Cabanillas 8664 (HUT, MO, Z); Palamble, 1954, Soukup 4275 (F). Tumbes: Zarumilla, entre el Caucho y Condor Flores, 20 Octuber 1988, Díaz & Vásquez 3045 (USM); Contra Almirante Villar, Casitas, Parque Nacional Cerros de Amotape, 2 May 1990, Díaz & Peña 4036 (CR, MO, USM); Matapalo, entre El Caucho y Campo Verde, 25 Octuber 1992, Díaz et al. 5156 (MO); Matapalo, entre El Caucho y Quebrada Naranjal, 25 January 1995, Díaz et al. 7505 (MO, USM); Villar, El Ciénego, al SE de Zorritos, 28 May 1957, Ferreyra 12250 (MO, USM); Río Zarumilla, Tumbes, 25 November 1955, Herrera 2162 (NY); Bosque Nacional de Tumbes, cerca a Cerro Tres Picos, 17 December 1967, Simpson et al. 401 (COL, F, US, USM); Matapalo, Bosque Nacional de Tumbes, cerca a Campo Verde, 19 December 1967, Simpson et al. 432 (F, USM); Pampas de Hospital, Bosque Nacional de Tumbes, 27 December 1967, Simpson et al. 496 (COL, F, US, USM). Data lacking: 1840, Mathews 3027 (BM); Neé s.n. (MA).

- VI. *Prestonia* Sect. Prestonia. Sect. Tomentosae Woodson, Ann. Missouri Bot. Gard. 23: 344. 1936, nom. illeg. Type: *Prestonia tomentosa* R. Br., *Mem. Wern. Nat. Hist. Soc.* 1: 70. 1811.
- Sect. Tetraceras Pichon, Mém. Mus. Natl. Hist. Nat., B, Bot. 1: 26. Type: *Prestonia parviflora* (Benth.) Benth. & Hook. f., Gen. Pl. 2: 709. 1876.
- Prestonia acrensis J.F. Morales (2004: 669). Type:—BRAZIL. Acre: Cruzeiro do Sul, RADAM/Brasil Project base camp, 3 March 1976, J. Ramos & Mota 249 (holotype INPA!). Fig. 47, 48

**Stem** moderately to sparsely hirsute, color of latex unknown, sparsely to moderately lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2–3.5 mm long. **Petioles** 0.4–0.6 cm; leaf blade  $10-12 \times 7-8.5$  cm, elliptic, apex caudate-acuminate, base rounded to slightly cordate, membranaceous, sparsely to moderately hirsute adaxially, densely to moderately hirsute abaxially, indument drying yellow, secondary veins impressed on both surfaces, tertiary veins impressed abaxially, somewhat inconspicuous adaxially. **Inflorescence** a monochasial cyme, axillary, shorter than the subtending leaves, many-flowered, the flowers densely clustered, densely to moderately hirsute, peduncle less than 1.1 cm, pedicels 0.3–0.6 cm long, floral bracts  $3-13 \times 3-6$  mm, narrowly elliptic, foliaceous to subfoliaceous, green. Sepals 10–13 × 3–4 mm, free, membranaceous, narrowly elliptic to narrowly ovate-elliptic, the apices acute to shortly acuminate, not reflexed, densely hirsute, foliaceous, drying with a more or less uniform color, the veins slightly impressed, colleters 1.9–2.2 mm long, entire to scarcely erose at the apex. Corolla salverform, yellow to yellowish green, densely hirsute outside, tube 9–14 × 3–4 mm, straight, free corona lobes 2–3 mm long, the apices barely exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire to subentire, delicate and inconspicuous, corolla lobes  $4-5 \times 2-3$  mm, ovate. **Stamens** inserted near the corolla mouth, anthers 4.5–5 mm, inconspicuously puberulent to glabrescent dorsally, the apices barely exserted. Ovary ca. 1 mm tall, densely hirsute, style-head 1.2–1.5 mm, nectary 2–3 mm, conspicuously surpassing the ovary, slightly and irregularly 5-lobed, each lobe subentire. Follicles unknown.

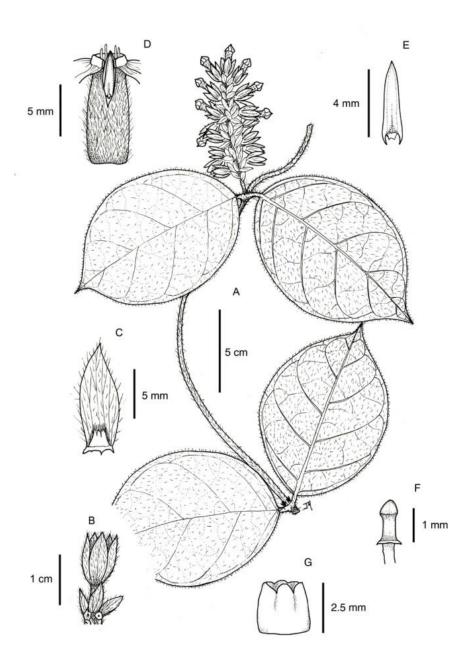


Fig. 47 *Prestonia acrensis* (*Ramos & Mota 249*, INPA). A. Stem with inflorescence. B. Calyx, pedicel, and floral bracts. C. Adaxial view of the sepal, showing the colleter at the base. D. Corolla tube partially open, showing the annular corona, free coronal lobes, and anthers. E. Anther, dorsal view. F. Style-head. G. Nectary.

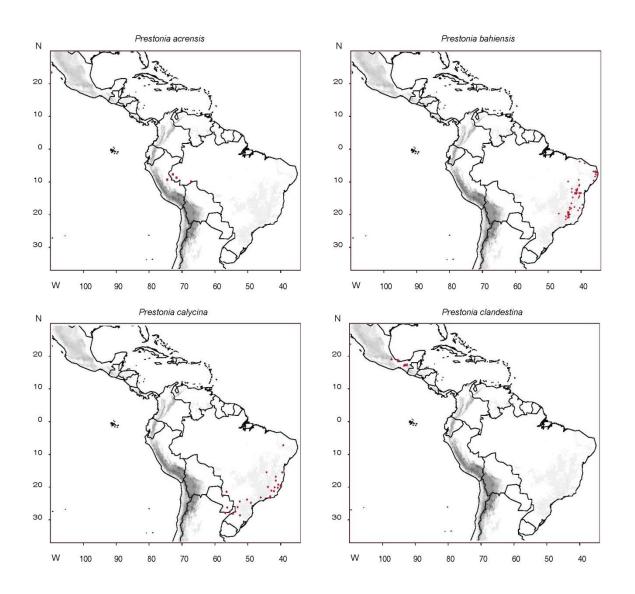


Fig. 48 Distribution maps of Prestonia acrensis, P. bahiensisk, P. calycina and P. clandestina

**Distribution and habitat:**—Moist forest and dry forest in northeastern Brazil and Peru, from 100–400 m.

**Conservation Assessment**:—Endangered (EN)

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Phenology**:—Flowering April and May.

**Taxonomic notes:**—*Prestonia acrensis* is closely related with *P. tomentosa*, but differs by the indument of stems and leaves (hirsute vs. tomentose or velutinous-tomentose) and their inflorescence (monochasial vs. dichasial). This species shows an overall resemblance to *P. calycina*, *P. cogolloi*, and *P. ipomaeifolia*, but is recognized by its corollas with ovate lobes  $4-5 \times 2-3$  mm and elongated inflorescences. Additional characters to separate this species from *P. cogolloi* and *P. ipomaeifolia* include smaller leaves and from *P. calycina*, shorter corolla tube (9–14 mm vs. 15–21 mm) and shorter anthers (4.5–5 mm vs. 5.5–7 mm).

Additional specimens examined:—PERÚ. Huanuco: Pachitea, Honorea, Bosque Nacional de Iparia, Río Pachitea, cerca del campamento Miel de Abeja, 5 January 1967, *Schunke 1470* (NY, US).

BRAZIL. Acre: Jordão, Taraucá river, 11 February 2009, *Acevedo-Rodríguez et al.* 14951 (NY); Acrelândia, a lo largo de la autopista BR–364, de Rio Branco a Porto Velho, km 88, 2 December 2001, *Croat 85856* (NY, RB, USF). Amazonas: Igarapé de Flores, May 1955, *Chagas s.n.* (NY).

Prestonia bahiensis Müller Argoviensis (1860: 164). Type:—BRAZIL. Bahia: St. Thome, June 1844, J. Blanchet 3776 (lectotype BR!, designated by Woodson (1936), isolectotypes G-DC!, MG!, P!, W!). Fig. 48, 49

**Stem** densely ferrugineous-hispidulous, with clear or milky latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2–3 mm long. **Petioles** 0.3–0.8(–1) cm; leaf blade 5–13.5(–15.5) × 2.2–8.5 cm, elliptic, ovate-elliptic to ovate, apex obtuse to short-acuminate, base obtuse to rounded, rarely subcordate, membranaceous, sparsely ferrugineous-hispid adaxially, densely velutinous to velutinous-tomentose abaxially, indument drying drying brown to reddish brown, secondary veins impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the subtending leaves, many-flowered, the flowers densely clustered, ferrugineous-hirsute, peduncle 1.3–2.5 cm, pedicels 0.3–1.5 cm long, floral bracts 5–12 × 1–2 mm, narrowly elliptic, narrowly ovate-elliptic to narrowly ovate, inconspicuous to subfoliaceous, green. **Sepals** 10–13 × 2–6 mm, free, membranaceous, narrowly ovate to

ovate-elliptic, the apices acute to acuminate, not reflexed, densely to moderately hirsute, foliaceous, drying with a more or less uniform color, the veins usually conspicuously impressed, colleters 1.5-2 mm long, subentire to irregularly erose at the apex. **Corolla** salverform, yellow to yellowish green, densely hirsute outside, tube  $12-18 \times 4-5$  mm, straight, free corona lobes 2-3 mm long, the apices barely exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire, subentire, or slightly 5-lobed, thickened, corolla lobes  $7-9 \times 5-6$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 6-6.5 mm, dorsally glabrous, the apices exserted. **Ovary** ca. 1.5 mm tall, glabrous, style-head 2-2.5 mm, nectary 2-2.5 mm, conspicuously surpassing the ovary, irregularly 5-lobed, each lobe slightly erose. **Follicles**  $5.5-7 \times 0.8-1.3$  cm, continuous, divaricate, free, the tips divergent, densely ferrugineous-hirsute, without lenticels, somewhat woody when old; seeds 12-14 mm, coma 2-3.5(-4) cm, cream to tannish cream.

**Distribution and habitat**:—Endemic to Brazil, where it grows in moist forest, gallery forest, cerrados, disturbed cloud forest, and in roadside thickets, from 500–1500 m.

**Phenology**:—Specimens with flowers have been collected from November through May and with fruits in March, April, and June.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Local names**:—Cipo cabeludo (Minas Gerais, Brazil); gitirana páo darco (Paraíba, Brazil).

**Uses:**—In Brazil (Minas Gerais) the flowers are used to treat kidney problems, back pains, and as a tranquilizer (*Rodriguez s.n.*, BHCB).

**Taxonomic notes**:—*Prestonia bahiensis* is related to *P. tomentosa* and commonly misidentified in herbaria, since both species grow sympatrically in some regions of Brazil and they are vegetatively similar. However, it can be distinguished by the hirsute corollas and follicles 8–13 mm diam. (vs. corollas densely sericeous and follicles 16–25 mm in *P. tomentosa*).

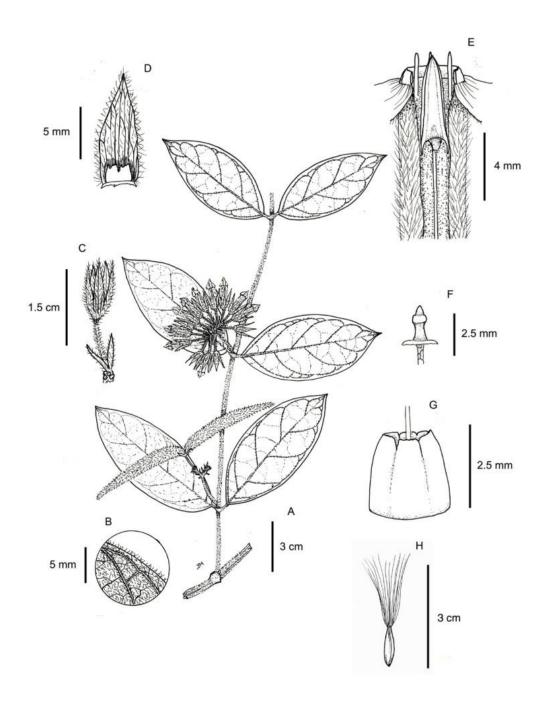


Fig. 49 *Prestonia bahiensis* (*Cesar 160*, INB). A. Stem with inflorescence and follicles. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts. D. Adaxial view of the sepal, showing the colleter at the base. E. Open corolla tube, showing the anthers and free coronal lobes. F. Style-head. G. Nectary. H. Seed.

Additional specimens examined:—BRAZIL. Alagoas: Atalaia, serra da Nacéia, 24 March 1983, Esteves 1689 (MAC, NY). Bahia: Abaíra, camino a Catoles, 19 km de la carretera Abaíra-Piatã, 13 April 1999, Amorin et al. 2841 (CEPEC, MO, NY, USF); BR-242, 26 km al E de Lençóis, 20 January 1997, Arbo et al. 7533 (CEPEC, CTES, MO, NY, WAG); St. Thome, s.d., Blanchet 24 (G, M, P); autopista BR-4, 60 km al N de la frontera con Minas Gerais, 25 June 1965, Belém 1197 (CEPEC, IAN, U, UB); Vitória da Conquista, ramal a 15 km de la carretera Vitória da Conquista-Ilheus, 19 February 1992, Carvalho et al. 3808 (CEPEC, NY, WAG); without exact locality, 1843, Claussen s.n. (W); Santa Cruz Cabrália, reserva biológica do Pau-Brasil, 5 January 1972, Eupunino 103 (CEPEC); Utinga, 9 January 1996, Félix s.n. (HST # 5034, INPA, MG); Ibicoara, 17 January 1996, Félix s.n. (HST # 5119, IPA, MG); Andaraí, 26 May 2001, Félix et al. 6856 (HST); Maracás, trevo de Itiruçu, 3 November 2007, Ferreira et al. 1779 (CEPEC, HUEFS); Andaraí, camino viejo a Lençóis, 4 February 1999, França et al. 2631 (HST, HUEFS); Rio de Contas, Riacho da Pedra de Amolar, 24 January 1994, Ganev 2859 (HUEFS); Abaíra, Jaqueira, Rio de Água, 12 May 1994, Ganev 3248 (HUEFS); Lençóis, Paí Ínacio, 12 March 1997, Gasson & Natalino 6211 (HUEFS); Saúde, camino a Cachoeira Paiaió, 7 April 1996, Guedes et al. 2908 (HUEFS); Rio de Contas, camino a Fazenda Marion, 1.2 km de cruce con Jussiape, 7 February 2004, Harley et al. 54821 (HUEFS); Macaúbas, camino a Canatiba, Serra Poçoês, 18 January 1997, Hatschbach et al. 65905 (C, CEPEC, MBM); Brotas de Macaúbas, camino a Buriti, 12 March 1998, Hastchbach et al. 67687 (MBM, WAG); Abaíra, Brejo do Engenho, 27 December 1992, Hind et al. 50470 (CEPEC, HUEFS, K, NY); Jacobina, Itaitú, carretera a 2 km de la carretera Jacobina-Capim Grosso, 27 October 1995, Jardim et al. 710 (CEPEC, NY, USF); Licinio de Almeida, camino a Urandi, 3.8 km antes de la ciudad, 31 March 2001, Jardim et al. 3311 (CEPEC, NY); Lençóis, BR-242, 27 January 2001, Miranda 50 (HUEFS); Maracás, autopista BA-250, 13-25 km al E de Maracás, 18 November 1978, Mori et al. 11173 (CEPEC); Maracás, Fazenda Nova Esperança, 27 February 2000, Oliveira et al. 379 (HUEFS); Maracás, Fazenda Lava-pés, 29 February 2000, Oliveira et al. 422 (HUEFS); Maracás, 16 February 2004, Oliveira et al. 1043 (HUEFS, P), cerca a Planalto Bahiano, 17 January 1965, Pereira & Pabst 9538 (CR, HB, M, R, Z); Itiruçu, Maracás, km 32, 7 July 1971, Pinheiro 1433 (CEPEC); Rio de Contas, Marion, 21 February 2004, Rapini et al. 1130 (HUEFS); km 19 de la carretera de Conquista a Barra do Choça, 22 November 1972, Santos 2502 (CEPEC, Z); Maracás, 18 km al S de Maracás, camino antiguo a Jequié, 15 February 1979, Santos et al. 3469 (CEPEC, NY); Itiruçu, autopista BA–250, en la unión a Jaguaquara y Maracás, 29 February 1988, Mattos-Silva et al. 2222 (CEPEC); autopista BR-116, km 1112, entre Vitoria da Conquista y Jequié, 10 September 1977, Shepherd et al. 4466 (MBM, UEC); Licinio de Almeida, camino de tierra para Urandir, 2 November 2006, Silva et al. 211 (HUEFS); Andaraí, entre Itaberaba y Lençóis, 13 February 1994, Souza et al. 5206 (K [2 sheets], SP); Abaíra, Barra, 27 February 1992, Stannard et al. 51643 (CEPEC, HUEFS, K, MO, NY [2 sheets]). Ceará: Cratéus, Serra das Almas, 25 February 2002, Araújo 1230 (HUEFS), Araújo 1290 (HUEFS); Baturité, Caridade, 11 January 1938, Eugenio 961 (RB). Espirito Santo: camino a Nanuque, 7 November 1953, Duarte 3890 (RB); Barra de São Francisco, parque municipal Sombra da Tarde, 21 December 2000, Kollmann et al. 3457 (CR, MBML, RB, UEC). Minas Gerais: Fazenda da Chicaca, Santa Luzia, 25 October 1945, Assis 31 (MO); Vila São Geraldo, Belo Horizonte, 5 January 1940, Barreto 60 (IAN); Fazenda do Cipó, Santa Luzia, 13 January 1933, Barreto 482 (BHCB); Villa Independencia, 10 November 1932, Barreto 533 (BHCB); Cardoso, Belo Horizonte, 17 January 1933, Barreto 534 (CR, F, PAMG); Jardim Botânico, 6 April 1933, Barreto 536 (RB), 10 June 1934, Barreto 582 (BHCB); Caeté, 30 November 1933, Barreto 537 (R); Santa Luzia, 21 April 1934, Barreto 580 (BHCB); Penha de França, Itamaranoiba, 24 November 1937, Barreto 10006 (BHCB); Estação Experimental, 7 December 1939, Barreto 10284 (BHCB); Lagoa Santa, s.d., Engler s.n. (C); Campus de la Universidade Federal de Minas Gerais, 7 December 1981, Fernandes 48 (BHCB); Campus de la Universidade Federal de Minas Gerais, December 1977, Ferrari s.n. (BHCB); Senador Mourão, Diamantina, 24 January 1978, Hatschbach 40873 (MBM); Vespasianao, November 1915, Hoehne 6245 (R); Caeté, January 1916, Hoehne 6624 (R); Serra do Itabirito, SE de Belo Horizonte, 10 February 1968, Irwin et al. 19735 (CR, IAN, NY, UB, US, Z); Serra do Espinhaço, Lapinha, 20 km N of Serro, on road (MG-2) to Diamantina, 25 February 1968, Irwin et al. 20837 (NY); Grão Mogol, 3 km del puente camino a Cristália, 12 January 2006, Jardim et al. 4943 (CEPEC, HUEFS); Carrancas, camino Carrancas-Itutinga, a 5 km de la ciudad, 15 February 2000, Kinoshita et al. 2000/11 (BHCB, UEC); Jequitibá, 31 July 1962, Lanna 245 (RB); Santana do Riacho, Serra do Cipó, 27 April 1993,

Lombardi & Toledo 191 (BHCB, WAG); Santa Terezinha, Ituiataba, 20 September 1946, Macedo 755 (MBM, MO); Estação Experimental, 2 January 1940, Magalhães 97 (R); Belo Horizonte, Reserva Forestal de UFMB, 2 April 1984, Mattos-Silva et al. 1652 (CR, RB); Campus de la Universidade Federal de Minas Gerais, November 1977, Oliveira s.n. (BHCB); Grão-Mogol, trilha da Tropa, Alto da Serra, 11 December 1989, Pirani et al. 12487 (NY); alrededores de Belo Horizonte, 22 February 1932, Porto & Fagundes 2188 (RB); entre Ponte do Sapueahy y Retero, 23 January 1868, Regnell III 1600 (F, LD, O, S [3] sheets], UPS [2 sheets], US); Carmópolis de Minas, April 1985, Rodriguez s.n. (BHCB); Lagoa Dourada, 31 April 1956, Roth s.n. (RB); Estação Ecológica da Universidade Federal de Minas Gerais, Belo Horizonte, 6 June 1990, Santos et al. 49 (BHCB, WAG); Montezuma, carretera a Montugaba, Bahia, 14 March 1994, Souza et al. 5493 (K, SP); São Gonçalo do Rio Abaixo, 30 November 1987, Stehmann et al. 532 (RB); Novo Cruzeiro, carretera Palmeiras-fazenda Araras, 2 October 2004, Stehmann et al. 3573 (BHCB), 2 December 2004, Stehmann et al. 3609 (BHCB); Novo Cruzeiro, caminho Palmeiras para Fazenda Araras, 2 December 2004, Stehmann et al. 3698 (BHCB, CEPEC); Estação Ecológica de la Universidade Federal de Minas Gerais, 14 November 1990, Tameirão-Neto E. 244 (BHCB); Serra do Curral, May 1955, Vidal 177 (R); Passa Quatro, Mantiqueira, October 1948, Vidal s.n. (R); Belo Horizonte, Lagoa Santa, s.d., Warming s.n. (C, G, G-DC [photo F neg. 22259]), 24 November 1963, Warming s.n. (C); Morro das Pedras, S de Belo Horizonte, 12 February 1945, Williams 5533 (A, GH, MO, US); Morro das Pedras, cerca de Belo Horizonte, 4 March 1945, Williams & Assis 5972 (MO). Paraíba: Natuba, Sítio Paquevira de Natuba, 27 November 1971, Andrade-Lima et al. 1046 (IPA); Sapé, Fazenda Pacatuba, 27 April 2001, César 160 (CR, JPB); Sapé, Sema II, 24 May 1990, Félix & Santana 3074 (CR, IPA, JPB); Bananeira, 19 January 1993, Félix et al. s.n. (EAC #6977, HST); Areia, 20 November 1939, Vasconcelos 411 (R); Escola de Agronomia de Nordeste, Areia, 10 May 1953, Moraes 713 (IAN, UB, US); Areia, Fernando Leal, 2 February 1947, Xavier s.n. (JPB #1379, IPA). Pernambuco: Bonito, 1 km hacia Camocim de São Félix, 10 February 1967, Andrade-Lima 67-4939 (IPA); São Lourenço da Mata, Estação Ecológica de Tapacurá, 5 June 1998, Lopes s.n. (UFP 21991); Capoeira de Atapú, s.d., Mariz 498 (UFP); Tapera, São Bento, Sitio de Soares, 9 July 1934, Pickel 3576 (IPA [2 sheets]). São

Paulo: Mogy-Mirim, 20 March 1874, *Mosén 1461* (S). Data lacking: s.d., *Claussen s.n.* (W); s.d., *Schwacke s.n.* (R).

*Prestonia calycina* Müller Argoviensis (1860: 162). Type:—BRAZIL. Minas Gerais: without locality, 1816–1821, *A. St. Hilaire s.n.* (holotype P! [photo F neg. 38791!], isotype F!). **Fig. 48, 50.** 

Prestonia hirsuta Müller Argoviensis (1860: 164), nom. illeg. Type:—BRAZIL. Minas Gerais: without data, *J. Pohl 5167* (lectotype (designated here) W!, isolectotypes, F, NY!, P!).

**Stem** dense to sparsely ferrugineous-hirsute, with clear latex, moderately lenticellate, these slightly to moderately suberose, intrapetiolar colleters conspicuous, 2.5-3.5 mm long. **Petioles** 0.5–1.1 cm; leaf blade  $(9-)10.5-19.5(-21) \times 6-13.5$  cm, elliptic to broadly ovate, apex abruptly short-acuminate to acute, base obtuse, rounded to subcordate, membranaceous, sparsely hirsute to hirsutulous adaxially, sparsely to moderately hirsute abaxially, the indument drying yellow to somewhat ferrugineous, secondary and tertiary veins impressed on both surfaces. Inflorescence a dichasial cyme (but resembling an umbel), axillary, shorter than the subtending leaves, many-flowered, the flowers densely clustered, hirsute, rarely glabrescent, peduncle 1–3(–5) cm, pedicels 0.3–1.1 cm long, floral bracts 5–14 × 2.5–5 mm, narrowly elliptic to narrowly ovate-elliptic, foliaceous to subfoliaceous, green. Sepals  $12-21 \times 7-10$  mm, free, membranaceous, narrowly ovate to elliptic, the apices acuminate, not reflexed, hirsute, foliaceous, drying with a more or less uniform color, the veins conspicuous to inconspicuous, colleters 4–5 mm long, entire, subentire to minutely and irregularly lacerate at the apex. Corolla salverform, yellow to yellowish green, sparsely hirsute to hirsutulous outside, rarely minutely tomentulose, tube 15–21 × 4–5 mm, inflated basally, straight, free corona lobes 3–4 mm long, the apices barely exserted, their height equaling that of the anther apices, annular corona entire to subentire, thickened, corolla lobes  $10-16 \times 7-10$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5.5–7 mm, dorsally puberulent, the apices exserted. **Ovary** 1.5–2 mm tall, glabrous, style-head 1.6–2.1 mm, nectary 2–3 mm, surpassing the ovary, moderately to deeply 5-lobed, each lobe subentire. Follicles 5.5-12 × 1.3-2 cm, continuous, divaricate, free, the tips divergent, densely to sparsely hirsute, rarely hirsutulous, without lenticels, somewhat woody when old; seeds 10–14 mm, coma 2.5–4.3 cm, cream to tannish cream.

**Distribution and habitat:**—Moist forest, disturbed forest edge, and along roadside thickets in southern Brazil, Paraguay, and northern Argentina, from 100 to 800 m.

**Phenology**:—Flowering September-March. Fruiting March-August.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local names:—Baba de boi preto, peludinha amarela (Espirito Santo, Brazil)

**Taxonomic notes:**—*Prestonia calycina* is vegetatively similar to *P. ipomaeifolia*, but differs by the larger leaves, with the tertiary veins not reticulated, anthers dorsally glabrous, and by its different geographical range. *Prestonia calycina* is related to *P. tomentosa*, but *P. calycina* can be recognized by its hirsute indument, which is conspicuous in almost all the vegetative structures (vs. velutinousNKE-tomentose or tomentose in the latter).

Pohl 5167 is selected as the lectotype of Prestonia hirsuta: this collection is better preserved and it is known from at least two more duplicates, while the other syntype (Gaudichaud 51) is only known for a single collection at the Natural History Museum of Paris (P).

Additional specimens examined:—BRAZIL. Bahia: Itaberaba, Serra de Orobó, Fazenda Monte Verde, 23 April 2006, *Cardoso et al. 1293* (HUEFS, NY); Jussari, entrada a 7.5 km de la autopista Jussari-Palmira, Fazenda Teimoso, Reserva Particular do Patrimonio Natural Serra do Teimoso, 17 January 2000, *Jardim et al. 2486* (CEPEC, NY); Itamarajú, km 3 de caminho que une BR-101 con el Pueblo de Pirajá, 23 January 1974, *Santos 2752* (CEPEC, RB). Ceara: Granjeiro, 21 August 1913, *Lützelburg 25813* (M). Espírito Santo: Santa Teresa, Pedra Alegre, 10 November 2000, *Demuner 1577* (HUSU, MBML, RB); Águia Branca, Assentamento 16 de Abril, 15 March 2006, *Demuner et al. 2004* (MBML); entre Serra da Cima y Pancas, 19 November 1953, *Duarte 3718* (RB); Reserva Forestal de Linhares, Municipal Canto Grande, 6 January 1999, *Folli 3326* (CVRD, USF); Vargem Alta, 15 September 1947, *Nascimento s.n.* (RB # 60981); km 9 de la autopista de Linhares a Regencia, 28 November 1973, *Pinheiro & Santos 2318* (CEPEC); carretera de Linhares a Barro Novo, 30 November 1973, *Pinheiro & Santos 2339* (MBML); Reserva de Linhares, Caingá, 4 November 1999, *Scatolin 12* (CVRD);

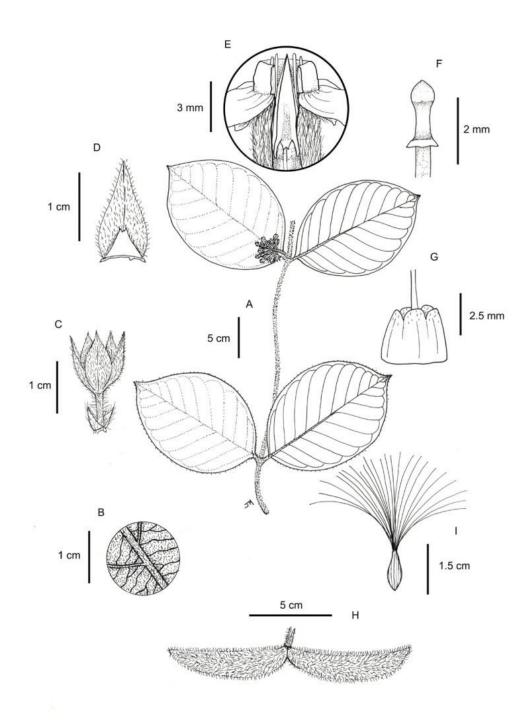


Fig. 50 *Prestonia calycina* (*Barreto 1506*, INB). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts. D. Adaxial view of one sepal, showing the colleter. E. Distal part of corolla tube partially open, showing the anthers, annular corona, and free coronal lobes. F. Style-head. G.Nectary. H. Follicles. I. Seed.

Reserva Natural Vale, Linhares, estrada Aceiro Bobbio, 11 January 2008 (fl), Siqueira 383 (CVRD); Reserva Natural Vale, aceiro Caliman, 4 December 2010, Siqueira 593 (CVRD). Mato Grosso do Sul: proyecto Guaicurus, Bonito, 9 November 2002, Hatschbach et al. 73980 (MBM), 14 March 2003, *Hatschbach et al.* 74737 (C, INPA, MBM). Minas Gerais: Muriaé, Tombos, Fazenda da Cachoeira, 9 July 1935, Barreto 1506 (BHMH, CR, F, PAMG, R); Monte Verde, PHC Santa Barbara, 12 January 2010, Costa & Sanglard 841 (BHCB); Governador Valadares, 25 November 1964, Duarte 8602 (RB); Pedra Azul, Itaobim, 18 January 1965, Duarte 8752 (CEPEC, CR, HB, RB); Lagoa Santa, November 1865, Engler s.n. (C); Vicosa, Estação Coronel Pacheco, 15 November 1940, Heringer 445 (CR, RB [2 sheets], SP, US); Viçosa, 4 December 1958, Irwin 2209 (NY, UC, US); Viçosa, escuela de Agricultura, 15 January 1935, Kuhlmann s.n. (NY, VIC); N de Teófilo Otôni, 19 April 1959, Magalhães 15730 (HB, MO); carretera a San Miguel, Viçosa, 4 April 1930, Mexia 4561 (BM, CAS, F, K, NY, MO, S, U, UC, US, WIS); Universidade Federal de Viçosa, 25 November 1988, Oliveira s.n. (VIC); Januária, Vale do Rio Peruaçu, 24 May 1997, Salino 3085 (BHCB); Caratinga, 7 January 1991, Stehmann & Mendonça s.n. (BHCB); Lagoa Santa, November 1865, Warming s.n. (C). Paraná: Jundiai do Sul, 31 October 2002, Carneiro 1392 (MBM); Río Chopim, cerca a Barra, Adrianópolis, 11 June 1968, Hatschbach & Guimarães 19372 (C, CR, MBM, NY, UC, Z); Rio Azul, Barra, Adrianópolis, 17 December 1975, Hatschbach 37885 (C, HB, HBG, MBM, MO, WAG). Rio de Janeiro: Gavea, 18 September 1874, Glaziou 7761 (C, P); without exact locality, 1876, Glaziou 8173 (C [2 sheets], K, P [3 sheets]); Petrópolis, 1881, Glaziou 12077 (C, K, P, R); without exact locality, February 1882, Glaziou 12944 (C, K, MG, P [2 sheets]); Guanabara, mata da Pedra do Marinheiro, 18 January 1969, Lucre & Braga 4431 (CR, RB [3 sheets]); Petrópolis, December 1943, Góes & Constantino s.n. (RB # 49408). Rio Grande do Sul: Iraí, Carretera RS-5, 18-25 March 1964, Brescia & Borsani 3334 (MFVA); Santa Rosa, Poca Picada, 1 May 1966, Hagelund 4388 (HBR, Z); Santa Rosa, Giruá, 16 December 1966, Hagelund 4952 (CR, HBR, Z). Santa Catarina: Morro das Piedras, Florianópolis, 1924, Brade 9128 (R); Itapiranga, near Uruguay, 6 February 1951, Rambo 49951 (B, L, S). São Paulo: without exact locality, 1833, Gaudichaud 51 (P). Data lacking: s.d., Baillon s.n. (P-BA); October 1838, Gardner 1760 (K); s.d., Glaziou 18363 (C, K); s.d., Lund s.n. (C); s.d., Sello 550 (UC).

PARAGUAY. Caaguazú: cerca a Caaguazú, 1905, *Hassler 9059* (BM, G [2 sheets], NY). Guaira: Cordillera de Ybytyruzú, 5 km al S de Melgarejo, 28 May 1989, *Zardini & Velásquez 12298* (MO, NY, SI). Paraguarí: Chololó, 1900, *Hassler 6776* (BM, G [3 sheets], K [2 sheets], LIL, MICH, MO, P, S, SI, UC). San Pedro: Alto Paraguay, 10 May 1957, *Woolston 819* (C, K, NY, S, SI, U, UC); Alto Paraguay, Primavera, 16 February 1958, *Woolston 942* (C, K, NY, S, U, UC).

ARGENTINA. Corrientes: Ituzaingó, Río Aguapey, *Cristóbal et al. 2062* (CR, CTES, G); Ituzaingó, 6 March 1985, *Tressens et al. 3176* (CR, CTES, K, MBM, MO, UC). Misiones: San Ignacio, Finca Osonunú, 19 September 2000, *Biganzoli et al. 2114* (LPB, MO, SI); parque Iguazú, 25–30 June 1963, *Del Puerto & Brescia 2565* (MVFA [3 sheets]) El Dorado, 8 March 1944, *Meyer 6748* (BR, U); cerca a Santa Ana, 1910, *Rodríguez 300* (B, BA, BAF, LP, SI [3 sheets]).

Prestonia clandestina J.F. Morales (1997: 60). Type:—MEXICO. Veracruz: San Andrés Tuxtla, Las Tuxtlas Biological Station, 13 July 1984, G. Ibarra & S. Sinaca 1893 (holotype CR!, isotypes MEXU!, MO!, NY!). Fig. 48, 51

**Stem** shortly pilose, tomentulose to glabrescent, with clear latex, sparsely to moderately lenticellate, these slightly to moderately suberose, intrapetiolar colleters conspicuous, 3.5–6(-8) mm long. **Petioles** 0.5–1.5 cm; leaf blade 12– $24 \times 5.5$ –14 cm, obovate, elliptic to broadly elliptic, apex acute, caudate or long-acuminate, base broadly cuneate to obtuse, membranaceous, usually glabrescent to sparsely puberulent adaxially, densely tomentose to velutinous-tomentose abaxially, indument drying yellowish brown, secondary and tertiary veins impressed on both surfaces. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the subtending leaves, many-flowered, the flowers densely clustered, densely tomentulose to velutinous, peduncle 1.4–2.6 cm, pedicels 0.1–0.5 cm long, floral bracts 4– $14 \times 2$ –5 mm, narrowly elliptic, narrowly ovate-elliptic to narrowly ovate, foliaceous, green. **Sepals** 16– $23 \times 3$ –7 mm, free, membranaceous, narrowly ovate, the apices acute to acuminate, not reflexed, sericeous, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed, colleters 2–3 mm long, slightly erose or lacerate at the apex. **Corolla** infundibuliform, yellow to cream, densely tomentulose outside, lower part of the

corolla tube  $3-4 \times 4-5$  mm, the upper part 4-6 mm, 6-10 mm diam. at the orifice, conical, free corona lobes 1.5-2 mm long, deeply included within the tube, their height conspicuously surpassed by that of the anther apices, annular corona entire, delicate and inconspicuous, corolla lobes  $29-36 \times 14-17$  mm, obliquely obovate to obliquely narrowly obovate. **Stamens** inserted at the base of the upper part of the corolla tube, anthers 7.1-8.2(-8.7) mm, dorsally glabrous, the apices barely exserted, rarely included. **Ovary** ca. 1 mm tall, glabrous, style-head 1.8-2.2 mm, nectary 1.5-2 mm, surpassing conspicuously the ovary, subentire, slightly 5-lobed to irregularly lacerate. **Follicles**  $9.5-12 \times 1.8-2.2$  cm, continuous, divaricate, free, with the tips divergent or falcate and the tips sometimes united (at least when young), tomentose to tomentulose, without lenticels, somewhat woody when old; seeds 11-16 mm, coma 3.5-4 cm, cream.

**Distribution and habitat:**—Endemic to southern Mexico, where it grows in moist forest, gallery forest, and secondary vegetation, from 0–1000 m.

**Phenology**:—Flowering specimens have been collected from February through May and August and with fruits from July through November

**Conservation Assessment**:—Vulnerable (VU), the area of occurrence of less than 20,000 km2 and fewer than 10 known localities.

**Taxonomic notes:**—*Prestonia clandestina* is characterized by the following combination of characters: leaf blades densely tomentose to velutinous—tomentose abaxially, inflorescences with sessile or subsessile flowers, densely congested and resembling an umbel, and infundibuliform corollas, with free corona lobes within. This species resembles *P. speciosa*, but differs by their flowers, with longer lobes and free corona lobes within. In *Prestonia*, infundibuliform corollas are reported only in *P. clandestina* and *P. speciosa*, both restricted to Mesoamerica. Although in the description of *P. pickelii*, Markgraf (1938) reported that the corolla was infundibuliform, the corolla is salverform, just very slightly expanded before the mouth.

When Morales (1997a) published *P. clandestina* flowers were originally described as lacking free corona lobes, but study of additional material, has shown that small free corona lobes are present.

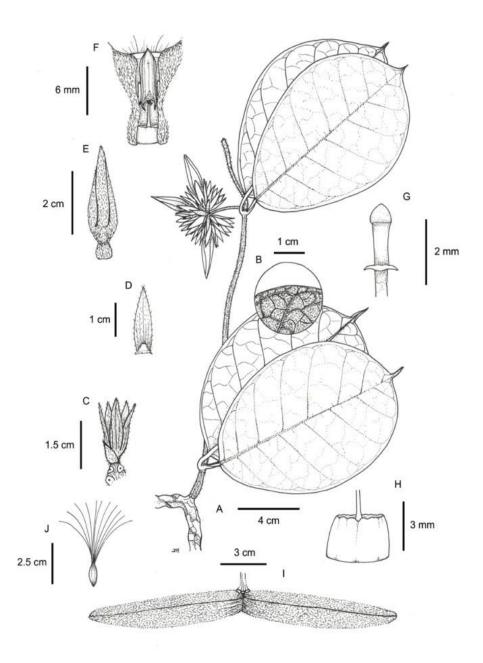


Fig. 51 *Prestonia clandestina* (*Ibarra & Sinaca 1893*, INB). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and bract. D. Adaxial view of one sepal, showing the colleter. E. Floral bud. F. Open corolla tube, showing the anthers, free coronal lobes, and annular corona. G. Style-head. H. Nectary. I. Follicles. J. Seed.

Additional specimens examined:—MÉXICO Chiapas: Ocosingo, al SO de Frontera Corozal, 8 November 2004, Aguilar & Arcos 12252 (MEXU); Selva Negra, 10 km above Rayón Mezcalapa, along road to Jitotol, Rayón, 13 July 1972, Breedlove 26119 (MEXU); Ocosingo, Lacandona, 26 June 1994, Levy & Durán 52 (MEXU); Ocosingo, Ejido Nueva Palestina, 28 February 1996, Luna-Gómez 110 (MEXU); Ocosingo, Chitallin, Yajalón, 10 February 1984, Méndez 7230 (MEXU, MO, NY); Barranca Zarahuatos, al E de Ocote, 30 March 1950, Miranda 6334 (MEXU). Oaxaca: Tuxtepec, Chiltepec y alrededores, July 1940, Martinez 57 (A, US). Veracruz: Cerro Cintepec, E de Zapoapan, Catemaco, 8 February 1972, Beaman 5614 (F, US); Sapoapan, carretera a La Magdalena, 8 November 1972, Calzada 665 (BM, F, GH, K [2 sheets], MEXU, MO); Estación Biológica Las Tuxtlas, San Andrés de Tuxtla, 7 May 1972, Calzada 834 (BR, F, MEXU, MO), camino a Laguna Escondida, San Andrés Tuxtla, 7 November 1973, Calzada 1049 (MEXU [2 sheets]); Las Tuxtlas, 1 June 1998, Campos 5340 (MEXU); SO de Ejido La Palma, Catemaco, 1 August 1986, Cedillo 3656 (MEXU, MO); Las Tuxtlas, 13 February 1984, Ibarra et al. 2530 (MEXU); Estación Biológica Las Tuxtlas, 12 June 1985, Ibarra & Sinaca 1893 San Andrés Tuxtla, entre Montepío y Balzapote, 4 August 1982, Ramamoorthy 3931 (MEXU); Laguna Escondida, 3 km NO de las Tuxtlas, 28 November 1985, Sinaca 345 (MEXU), 14 May 1986, Sinaca & Chigo 722 (MEXU); Laguna Escondida, Estación Las Tuxtlas, 26 September 1986, Sinaca 994 (MEXU); Cochinitos, Coyame, Las Tuxtlas, 25 May 1967, Sousa 3079 (MEXU [2 sheets], MO).

Prestonia cogolloi J.F. Morales (2007: 148). Type:—COLOMBIA. Antioquia: Turbo, road to Tapón del Darién, Río León, 16 January 1985, J. Brand, E. Renteria & A. Cogollo 1329 (holotype JAUM! [2 sheets], isotype CR!). Fig. 52, 53.

**Stem** sparsely to moderately hirsutulous, glabrescent at maturity, with milky latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2-3 mm long. **Petioles** 1-2.2 cm; leaf blade  $23-35 \times 14-22$  cm, broadly elliptic to broadly obovate, apex cuspidate to caudate-acuminate, base slightly subcordate, membranaceous, very sparsely puberulent adaxially (but the indument more dense along the midrib), sparsely and

irregularly hirsute to hirsutulous abaxially, the pubescence irregularly distributed, eventually glabrescent, indument drying yellow, secondary and tertiary veins impressed on

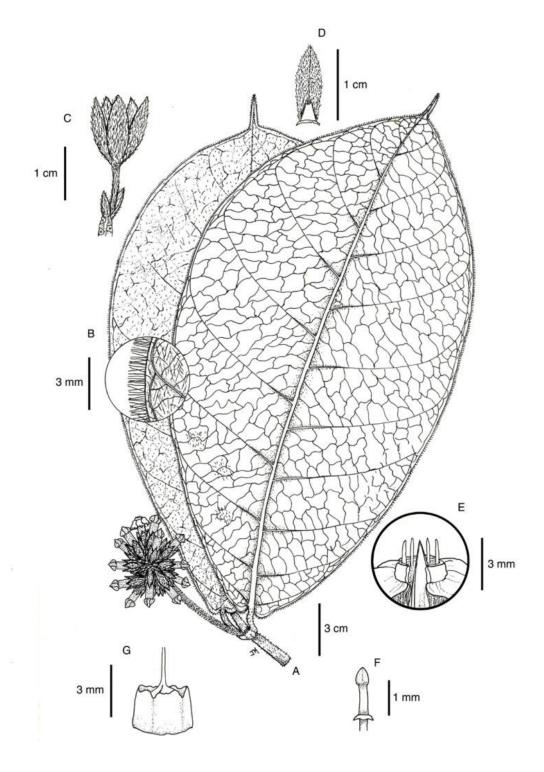


Fig. 52 *Prestonia cogolloi (Brand et al. 1329*, JAUM). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts. D. Adaxial view of the sepal,

showing the colleter. E. Open corolla mouth, showing the anthers and free coronal lobes. F. Style-head. G. Nectary and ovary.

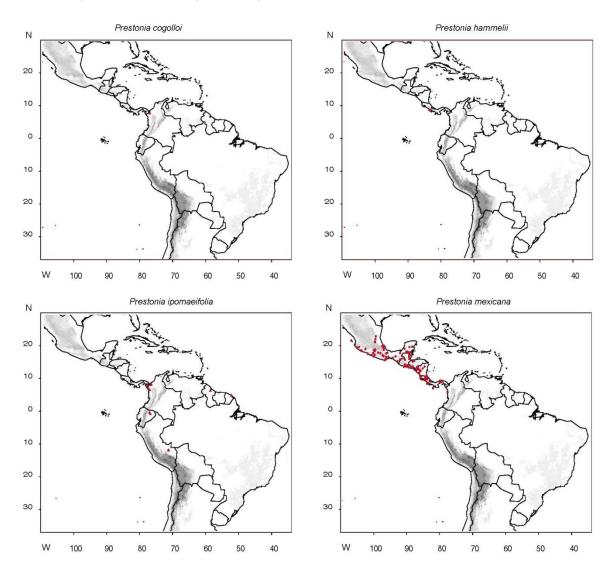


Fig. 53 Distribution maps of Prestonia cogolloi, P. hammeli, P. ipomaeifolia and P. mexicana

both surfaces. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the subtending leaves, many-flowered, the flowers densely clustered, ferrugineous-tomentose, peduncle 4.8-5.5 cm, pedicels 0.8-1 cm long, floral bracts  $5-14 \times 2-4$  mm, elliptic, narrowly elliptic to ovate-elliptic, foliaceous, green. **Sepals**  $11-13 \times 3-4.5$  mm, free, membranaceous, narrowly elliptic to elliptic, the apices acute, not reflexed, tomentulose, foliaceous, drying with a more or less uniform color, the veins conspicuously impressed or sometimes delicate and inconspicuous, colleters 2-2.5 mm long, entire at the

apex. **Corolla** salverform, yellow, densely hispid outside, tube  $11-14 \times 3-4.5$  mm, straight, free corona lobes 3–4 mm long, the apices exserted, their height equaling that of the anther apices, annular corona entire, thickened, corolla lobes  $8-9 \times 6-8$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5.9-6.1 mm, dorsally glabrous, the apices exserted. **Ovary** 2–2.5 mm tall, glabrous, style-head ca. 1.4–1.9 mm, nectary 2–2.5 mm, equalling the ovary, variously and irregularly lobed. **Follicles** unknown.

**Distribution and habitat:**—Endemic to Colombia, where it grows in tropical wet forest, from 50–100 m.

**Phenology**:—Flowering specimens have been collected in January and March.

Conservation Assessment:—Data deficient (DD) (IUCN 2001).

**Taxonomic notes**:—*Prestonia cogolloi* could be confused with *P. ipomaeifolia*, but differs by some characters of the leaf blades (e.g., shape, indument), inflorescence pubescence, and length of the free corona lobes.

**Additional specimens examined**:—Colombia. Antioquia: cerca de Río León, 15 km al O de Chigorodó, 19 March 1962, *Feddema 1953* (US)

Prestonia hammelii J.F. Morales (1997: 60). Type:—COSTA RICA. Puntarenas: Reserva Forestal Golfo Dulce, Península de Osa, Rancho Quemado, ca. 15 km W of Rincón, 31 May 1988, B. Hammel, G. Herrera, M. Chavarria & A. Solís 16918 (holotype CR!, isotypes MO!, WAG!). Fig. 53, 54

**Stem** sparsely puberulent, sparsely hirsutulous to glabrescent, with clear latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 3–5 mm long. **Petioles** 0.7-2 cm; leaf blade  $11-24 \times 4.8-13.5$  cm, elliptic to narrowly elliptic, apex cuspidate to caudate, base obtuse to rounded, membranaceous, very sparsely hirsutulous or glabrescent on both surfaces (moderately hirsute or pilose in young leaves) indument drying tan, secondary and tertiary veins impressed on both surfaces. **Inflorescence** a monochasial cyme, axillary, shorter than or equaling adjacent leaves, few- to manyflowered, the flowers laxly disposed to somewhat clustered, sparsely hirsutulous, peduncle 3.5-9 cm, pedicels 0.6-1 cm long, floral bracts  $2-8 \times 1-2$  mm, linear to linear-ovate, scarious, minute, green. **Sepals**  $0.9-15 \times 2.5-3$  mm, free, membranaceous, very narrowly ovate to very narrowly elliptic, the apices acute to acuminate, not reflexed, very sparsely

hirsutulous, rarely glabrescent, subfoliaceous, drying with a more or less uniform color, the veins inconspicuous or not evident, colleters 2–3 mm long, subentire to variously erose at the apex. **Corolla** salverform, yellow, very sparsely hirsutulous outside, tube  $21-24 \times 3-4$  mm, straight, free corona lobes absent, annular corona entire, delicate and inconspicuous, corolla lobes  $14-16 \times 8-9$  mm, obliquely obovate. **Stamens** inserted ca. in the middle of the tube, anthers 8.8-10 mm, glabrous dorsally, included. **Ovary** ca. 0.9-1 mm tall, glabrous, style-head 2.2-3(-3.5) mm, nectary 1-1.1 mm, equaling or barely surpassing the ovary, slightly 5-lobed, each lobe entire or subentire. **Follicles** unknown.

**Distribution and habitat:**—Tropical wet forest, vegetation along riverbanks, and secondary vegetation in southern Costa Rica, from 100 to 600 m.

**Phenology**:—Specimens with flowers have been collected in March, April, and June.

## **Conservation Assessment**:—Endangered (EN)

**Taxonomic notes**:—*Prestonia hammelii* is unique in section *Prestonia*, as it lack most of the indument on stems and leaves. It is recognized by its sparsely hirsutulous to glabrescent leaf blades, sparsely hirsutulous corolla, with inconspicuous indumentum, and free corona absent. Immature leaves are more pubescent than are mature leaves, which are nearly glabrous or glabrescent

Additional specimens examined:—COSTA RICA. Puntarenas: camino a Bahía Drake, 18 July 2001, *Mayfield & Roberts 878* (CR); Victorino's farm, Osa, 25 July 2001, *Mayfield & Roberts 1384* (CR); Parque Nacional Corcovado, Esquinas, 15 April 1993, *Quesada & Segura 619* (CR, MO); fila Costeña, S de San Isidro del General, 6 March 1985, *Taylor et al. 4871* (DUKE).

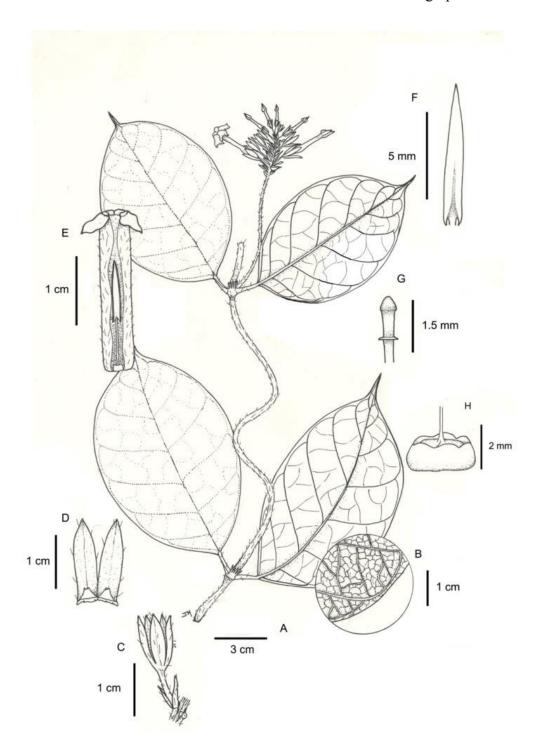


Fig. 54 *Prestonia hammelii* (A-E from *Hammel et al. 16918*, INB; F-H from *Quesada & Segura 619*, INB). A. Stem with inflorescence. B. Abaxial surface of the leaf blade, showing reticulated tertary veins. C. Calyx, pedicel, and floral bracts. D. Adaxial view of two sepals, showing the colleters at the base. E. Open corolla tube, showing the insertion of the stamens. F. Anther, dorsal view. G. Style-head. H. Nectary and ovary.

Prestonia ipomaeifolia Candolle (1844: 429). Type:—FRENCH GUIANA. Cayenne: Cayenne, s.d., J. Le Blond s.n. (holotype G-DC! [2 sheets, photo F neg. 7543!]). Fig. 53, 55

**Stem** sparsely a moderately hirsute, with clear or milky latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2–4.5 mm long. **Petioles** 1–2.5 cm; leaf blade  $14-35 \times 8.5-24$  cm, elliptic to narrowly elliptic, apex caudate-acuminate to long-acuminate, base obtuse to rounded, membranaceous, sparsely hirsute on both surfaces, sometimes glabrescent adaxially, indument drying yellowish brown, seconday and tertiary veins conspicuously impressed on both surfaces. Inflorescence a dichasial cyme (but resembling an umbel), axillary, shorter than the subtending leaves, many-flowered, the flowers densely clustered, sparsely to moderately hirsute, peduncle 1.5-3(-4.5) cm, pedicels 0.3-0.8(-1.4) cm long, floral bracts  $6-17 \times 2.5-4$  mm, narrowly elliptic to narrowly ovate-elliptic, subfoliaceous, green. Sepals  $7-12(-17) \times 2.5-6$  mm, free, membranaceous, ovate to narrowly elliptic, the apices acute to shortly acuminate, not reflexed, sparsely hirsute, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed or inconspicuous, colleters 2.5–3.5 mm long, irregularly and variously lacerate at the apex. Corolla salverform, yellow to cream, hirsute outside, tube  $12-15 \times 4-5$  mm, straight, free corona lobes 2-2.5 mm long, the apices exserted, their height surpassing that of the anther apices, annular corona entire to subentire, delicate and inconspicuous, corolla lobes  $8-12(-15) \times 6-9$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5.8–6.1 mm, dorsally glabrous, included. Ovary ca. 1 mm, glabrous, style-head 1.5–1.8 mm, nectary 2–3 mm tall, conspicuously surpassing the ovary, entire to slightly 5-lobed, each lobe entire. Follicles 9–  $12.5 \times 2-2.3$  cm, continuous, divaricate, free, the tips divergent, hirsute or pilose, without lenticels, somewhat woody when old; seeds not seen.

**Distribution and habitat:**—From southern Panama, northeastern Colombia, Ecuador, Peru, Guyana, and French Guiana, where it grows in tropical wet forest, vegetation along riverbanks and secondary thickets from 0 to 500 m.

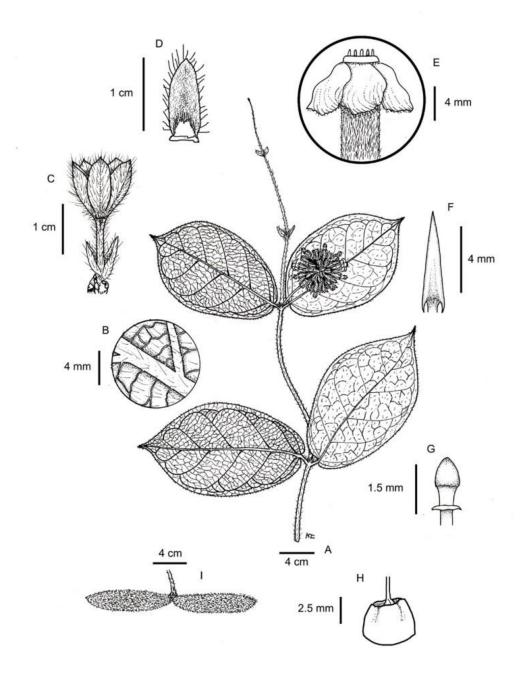


Fig. 55 *Prestonia ipomaeifolia* (A-G from *Callejas et al. 4903*, HUA; H-I from *Bernal 92*, COL). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts. D. Sepal, adaxial view. E. Mouth of the corolla tube, showing the apices of the free coronal lobes. F. Anther, dorsal view. G. Style-head. H. Nectary. I. Follicles.

**Phenology**:—Flowering specimens have been collected from October through January and March through August, fruiting specimens in March.

**Conservation Assessment**:—Least Concern (LC), not endangered (IUCN 2001).

**Taxonomic notes**:—*Prestonia ipomaeifolia* is very distinctive dur to the hirsute indument, on stems, leaves, inflorescences, and fruits. This type of indument is also present in others species of section *Prestonia* (e.g., *P. acrensis*, *P. calycina*, *P. cogolloi*). However, *Prestonia ipomaeifolia* is distinguished from the above species by the following combination of characters: sparsely to moderately hirsute dichasial inflorescences, with flowers densely clustered and resembling an umbel, corolla lobes 8–12(–15) mm long, and free corona lobes 3–4 mm long. The name *P. ipomaeifolia* has been misapplied to specimens from central Panama, which actually correspond to *P. seemannii*.

Additional specimens examined:—PANAMÁ. Darién: cerca a la boca del Río Yape, 12 July 1937, *Allen 366* (MO); carretera de El Real a Pinigana, 20 June 1962, *Duke 4885* (MO); cerca de El Real, Río Tuira, 1 July 1959, *Stern et al. 778* (G, GH, MO, US); without exact locality, May 1862, *Hayes s.n.* (BM).

COLOMBIA. Antioquia: Turbo, Caracolí, vía Turbo-San Pedro de Urabá, 23 km ENE de Turbo, 1 August 1987, *Callejas et al. 4893* (HUA); Necoclí, Caribia, reserva natural regional La Pradera, December 2009, *Londoño et al. 1203* (HUA). Chocó: Río Trunado, 25 March 1958, *Bernal 92* (COL [2 sheets]); Río Nercua, cerca Quebrada Barrial, 22 May 1967, *Duke 11422* (NY); Bojayá, Río Atrato, 14 April 1982, *Forero et al. 9240* (COL, MO), *Forero et al. 9248* (COL, CR, MO), *Forero et al. 9240* (MO).

GUYANA. Cuyuni-Mazaruni: Río Mazaruni, 1 October 1944, *Forest Department* 4746 (K [2 sheets], NY).

FRENCH GUIANA. Cayenne: Cayenne, s.d., L'Hérisier 718 (G).

ECUADOR. Napo: Orellana, Huashito, N de Coca, November 1989, *Gudiño 207* (MO, QCNE). Pastaza: Pozo petrolero Masaramu, 40 km al NE de Montalvo, 1–16 May 1990, *Gudiño 398* (MO, QCNE, USF).

PERÚ. Huánuco: Pachitea, Honoria, Bosque Nacional Iparia, Río Pachitea, 25 January 1967, *Schunke 1554* (F [2 sheets]), 29 March 1967, *Schunke 1807* (F, NY, US). Madre de Dios: reserva de Tambopata, 10 July 1994, *Cornejo & Zumarán 2444* (MOL); Parque Nacional Manú, Río Manú, Pakitsa station, Tachigali trail to 8 km N of camp, 25

- December 1988, *Foster et al. 12783* (F, US); Parque Nacional Manú, Estación Biológica Cocha Cashu, August 1989, *Núñez et al. 11524* (CR, MO, USF).
- Prestonia mexicana Candolle (1844: 429). Mitozus mexicanus (A. DC.) Miers (1878: 225).

  Type:—MEXICO. Oaxaca: San Bartolo, August 1834, G. Andrieux 251 (holotype G-DC! [photo F neg. 7542!], isotypes FI-W!, K! [2 sheets], M!, P!). Fig. 53, 56
- Haemadictyon mexicanum Candolle (1844: 428). Type:—MEXICO. Without data, *Icone M. Sessé & J. Moçiño s.n.* (lectotype (designated here) G! (photo F neg. 30759!)).
- Prestonia sericea M. Martens & Galeotti (1844: 360). Exothostemon sericeum (M. Martens & Galeotti) Miers (1878: 241). Type:—MEXICO. Oaxaca: without data, H. Galeotti 1586 (holotype BR!).
- Echites conglobatus Sessé & Moçiño (1893: 45). Lectotype:—MEXICO. Without data, Sessé & Mociño 5082 (lectotype MA!, designated by Morales (1997a), [photo F neg. 41268!]; isolectotype, F!).
- Prestonia longituba K. Schumann (1895: 188). Type:—COSTA RICA. Without data, B.
  Hoffmann 522 (B (destroyed, photo F neg. 4545!). Neotype (designated here):—
  COSTA RICA. San José: Cerros de Escazú, Aserrí, Río Saurez, 22 January 1994,
  J.F. Morales, M. Barrantes & J. Chinchilla 2278 (neotype MO!, isoneotypes, B!,
  CR!, F!, NY!, U!).
- Prestonia isthmica Woodson (1931: 555). Type:—COSTA RICA. San José: between Aserrí and Tarbaca, 6 December 1925, P. Standley 41332 (holotype US!).
- Prestonia amanuensis Woodson (1936: 359). Type:—BELIZE. Stann Creek: 6 miles from Stan Creek, August 1929, W. Schipp S-7 (lectotype NY! designated by Morales (1997a), isolectotypes F! [photo F neg. 56492!], GH!, Z!).
- Prestonia remediorum Woodson (1939: 299). Type:—PANAMA. Chiriquí: Río Chiriquí a Remedios, 11 July 1938, R. Woodson, P. Allen & R. Seibert 1180 (holotype MO!, isotype MO!).
- Prestonia allenii Woodson (1940: 332). Type:—PANAMA. Coclé: N of El Valle, 4 June 1939, P. Allen & A. Alston 1855 (holotype MO! [photo MEXU!], isotypes EAP!, F! [photo F neg. 56491!], GH!, MO!, NY!, US!).

Prestonia wedelii Woodson (1942: 365). Type:—PANAMA. Bocas del Toro: valle del Agua, 26 October 1940, H. von Wedel 1353 (holotype MO!, isotypes GH!, MO!, US!).

**Stem** variously pubescent, sometimes glabrescent at maturity, with clear latex, sparsely to moderately lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 1.5-4(-5) mm long. **Petioles** 0.5-2.2 cm; leaf blade  $8-27 \times 5-16$  cm, orbicular, elliptic, narrowly elliptic to obovate-elliptic, apex acute, acuminate, caudate, or obtuse, base cuneate, obtuse, rounded, or slightly cordate, membranaceous, variously puberulent adaxially, variously tomentose or tomentulose abaxially, indument green or somewhat ferrugineous or yellow when fresh, drying yellowish brown or ferrugineous, secondary and tertiary veins impressed on both surfaces. Inflorescence a dichasial cyme (but resembling an umbel), axillary, usually shorter than the adjacent leaves, few- to manyflowered, the flowers densely clustered, densely to moderately pilose, tomentose or tomentulose, peduncle 0.9–4.4 cm, pedicels 0.5–3.2 cm long, floral bracts  $3-12 \times 2.5-5$ mm, elliptic, narrowly elliptic, narrowly ovate-elliptic to narrowly ovate, foliaceous to subfoliaceous, green. Sepals  $14-30 \times 4-12$  mm, free, membranaceous, ovate to very narrowly ovate, the apices acute to acuminate, not reflexed, tomentose or tomentulose, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed, colleters 1–3 mm long, entire to variously erose or lacerate at the apex. Corolla salverform, cream to yellowish green, tomentose, tomentulose, or variously pubescent outside, tube  $24-36 \times 4-5$  mm, usually straight, sometimes gradually expanding toward the mouth, free corona lobes absent, annular corona entire, subentire to deeply 5lobed, rarely irregularly lobed, thickened, corolla lobes 12–16 × 9–11 mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 6–7.1 mm, dorsally glabrous, included or the apices exserted. Ovary 1–1.5 mm tall, glabrescent to puberulent, style–head 2.1–2.5 mm, nectary 1.5–3.5(–4) mm, surpassing the ovary, entire, subentire, 5-lobed or completely divided into 5 nectaries, each irregularly lacerate. Follicles  $5.5-11 \times 1-2$  cm, continuous, divaricate, free, the tips divergent, densely hirsute or hirsutulous, without lenticels, somewhat woody when old; seeds 11–15 mm, coma 2.5–4.2 cm, cream.

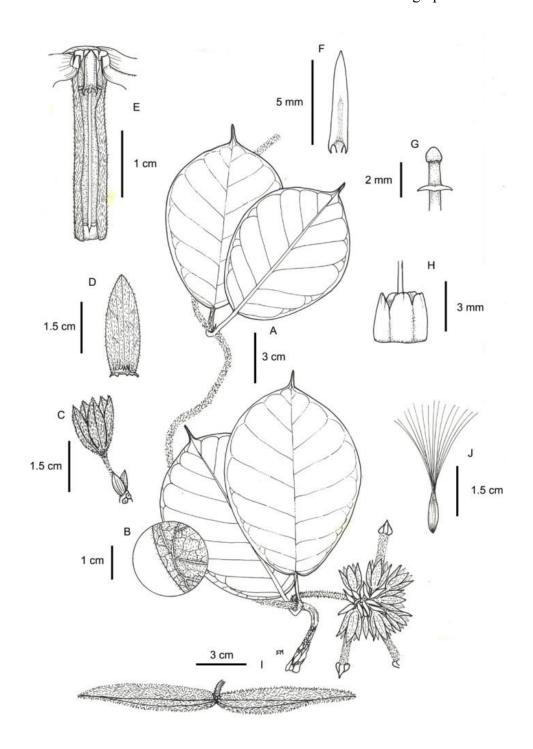


Fig. 56 *Prestonia mexicana* (A-H from *Aguilar 2507*, INB; I-J from *Morales et al. 2278*, INB). A.
Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and bracts.
D. Sepal, adaxial view. E. Open corolla tube, showing the annular corona and anthers. F.
Anther, dorsal view. G. Style-head. H. Nectary. I. Follicles. J. Seed.

**Distribution and habitat**:—Dry forest, moist forest, premontane forest, montane forest, gallery forest, thickets along roadsides, and coastal vegetation, from Mexico to northern Colombia (Choco department), from 0 to 1800 m.

**Phenology**:—Flowering and fruiting throughout the year.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local names:—bejuco hocico de pezote (Ahuachapán, El Salvador); cacho de chivo (Costa Rica; El Salvador; Guatemala); cacho de venado lechoso (Zelaya, Nicaragua); cuchamper, cuchamper de zope (Ahuachapán, El Salvador); cuerno de venado (Michoacan, Mexico); cuna de amor (Colima, Mexico); el pica-pica (Queretaro, Mexico); hocico de pezote (Ahuachapán, El Salvador); huevo de gato (Guerrero, Mexico); lengua de oso (Ahuachapán, El Salvador); ocico de hormiguero (Ahuachapán, El Salvador).

**Taxonomic notes**:—*Prestonia mexicana* resembles *P. riverae* and *P. schumanniana*, but differs from the first by its pedicellate flowers, shorter anthers, and divaricate follicles and from the second by its larger flowers.

Prestonia mexicana is the most variable species in section Prestonia, as to type and density of pubescence, inflorescence size, shape of the colleters, and lobulation of the annular corona and nectary. Several species proposed by Woodson (1936, 1939) were reduced to the synonymy of P. mexicana by Morales (1997a), since the types exhitib only morphological variation, that fits within the broad range of intraspecific variation of P. mexicana. Woodson (1933, 1935, 1936) used the degree of laceration of colleters to separate species, not only in Prestonia, but also in other genera. However, this character varies even in different flowers of the same inflorescence. Another variable character is the lobation or laceration of the nectary, which varies from annular disc to completely divided into five separate nectaries, with many intermediate states.

The type of *Prestonia longituba* was destroyed during War World II. Since no additional duplicates are known, a neotype is selected here. *Haemadictyon mexicanum* was described based on a plate from the Sessé & Mociño expedition and deposited at Geneve (G). This plate (without a specific number) is selected as the lectotype. While the collections of Mociño were at Geneva, several copies of the original illustrations were made. For a full reference, see Maldonado (1996).

Additional specimens examined:—MÉXICO. Campeche: Calakmul, Ejido Narciso Mendoza, 25 August 1997, Álvarez 307 (CR, MEXU); Calakmul, 51.6 km N of Xpujil, 22 August 2002, Álvarez et al. 2000 (MEXU); Calakmul, 7.7 km SE from Ejido dos naciones, 4 February 2003, Álvarez, & Jiménez, 3659 (MEXU, USCG); Calakmul, 1.6 km NO from Dos Naciones, 12 August 2003, Álvarez 6181 (MEXU); Calakmul, 1 km from Eugenio Echeverría, 3 jan 2004, Álvarez & Jiménez 7750 (MEXU); Ejido Dos Lagunas, 45 km al N de Xpujil, camino a Dzibalchén, 30 July 1996, Alvaro & Alvaro 443 (MEXU); 5 km E de Santa Maria, Xcabacab, 7 March 1982, Cabrera et al. 2075 (MEXU, MO); Chicana archeological área, 15 February 1988, Cabrera & Cabrera 15528 (MEXU); Pustunich, carretera a Yacasay, Champotón, 14 January 1985, Chan 4653 (CICY, CR); Catazajá, 24 November 1999, Gutiérrez 6725 (MEXU, UCAM); Calakmul, 9 August 1997, Martínez et al. 28332 (EAP, MEXU, MO), 19 October 1997, Martínez et al. 29120 (BIGU, MEXU); Calakmul, al O de la Mancolona, 25 October 1997, Martínez et al. 29350 (BIGU, MEXU); Calakmul, al SE de dos Naciones, 27 October 1997, Martínez et al. 29413 (BIGU, MEXU). Chiapas: Ocosingo, 2 km al S de Nuevo Francisco León, 6 September 2002, Aguilar 2628 (MEXU); Ocosingo, Ojo de Agua de San Javier, 2 December 2002, Aguilar & Cortés 4491 (MEXU); Ocosingo, 2.87 km al SE de Francisco León, 7 November 2003, Aguilar 8418 (MEXU); Ocosingo, 5.35 km from Nuevo Guerrero, 6 December 2003, Aguilar & López 8696 (MEXU, MO); Ocosingo, 2.74 km al SSO de Frontera Corozal, 19 August 2004, Aguilar & Arcos 11366 (MEXU); Ocosingo, 1.15 km W of Frontera Corozal, 5 November 2004, Aguilar & Arcos 12204 (MEXU); Arriaga, carretera México 190, puente Toronjal, 10 August 1992, Alvarado et al. 500 (CR, MEXU); 32 km NO de Ocozonoautla, 27 August 1972, Breedlove 27485 (DS, MO); S de La Trinitaria, 21 November 1980, Breedlove & Almeda 47632 (MO); O de Las Cruces, a lo largo de carretera a La Mina, 19 September 1981, Breedlove 52929 (DS, MEXU, NY); Tzimol, S de Comitán, carretera a Tzimol y Tuxtla Gutiérrez, 20 October 1981, Breedlove 53738 (MO, NY); San Fernando Chiapas, Cerro a 500 m camino a cañada Juan Crispin, 25 February 2010, Domínguez 162 (MO); Ocosingo, 3 km al SE de Maya de Lacanjá-Chansayab, 2 October 1994, Flores 4617 (MEXU); Ocosingo, Crucero Corozal, road Palenque-Boca Lacantum, 5 April 1985, Martínez 11559 (MEXU); Ocosingo, Arroyo Agua Azul, 3 km W of Frontera Corozal road to Palengue, 1 November 1986, Martínez 14605 (MEXU); Ocosingo, 16 km NW of Boca Lacantum, road to Palenque, October 1985, Martínez 14536 (MEXU), November 1985, Martínez 14842 (MEXU); Ococingo, O de Frontera Corozal, Arroyo Agua Azul, 15 January 1986, Martínez 16229 (MEXU, MO); Ocosingo, 15 km NW of Boca Lacantum, roda to Palenque, 12 June 1986, Martínez & Soto 18606 (MEXU); Nuevo Guerrero, 100 km SE of Palenque, road to Boca Lacantum, 27 June 1986, Martínez 19054 (MEXU); 15 km W of Tzimol, on road to Pujiltic, 14 February 1987, Martínez 20062 (MEXU); Escuintla, 2 November 1936, Matuda 581 (MEXU, MO); Miramar, 11 August 1937, Matuda 1621 (MEXU, MO); Escuintla, July 1938, Matuda 2623 (GH, K, MEXU, MO, NY); Las Garzas, 1958, Matuda 2812 (MEXU); Aguacate, Palenque, July 1939, Matuda 3803 (A, MEXU); Soconusco, 26 May 1947, Matuda 16526 (F); Tonalá, 27 August 1949, Matuda 18780 (F, MEXU); Colonia Cuauhtémoc, San Fernando, 5 September 1988, Palacios 707 (CHIP, MEXU); Berriozabal, 1 km W from junction Airport-Ocozocoautla-México, 3 March 1988, Reyes et al. 398 (MEXU); Ocozocoautla, 1 km NW from junction Airport-Ocozocoautla-México, 17 September 1988, Reves 961 (MEXU); Tuxtla Gutiérrez, Cañón del Sumidero, 27 January 1990, Reyes et al. 1442 (BM, MEXU); Ocosingo, Colonia Benito Juárez, Miramar, 23 August 1993, Reyes & Sousa 2181 (MEXU). Colima: cerca de Manzanillo, 2 December 1925, Ferris 6232 (US); Manzanillo, 1 December 1890, Palmer 1028 (BM, G, GH, K, NY, US); Cerro de Manzanillo, September 1922, Reko 4496 (NY, US); Escuintla, ca. 10,6 miles from Escuintla on road to El Triunfo, base of mountain Obando, 16 July 1976, Stevens et al. 2452 (MO); playa Santiago, E de Manzanillo, 8 September 1935, West 3506 (MO, UC). Guanajato: Atarjea, El Nacimiento, 10 January 1991, Ventura & López 9093 (CIIDIR, IEB). Guerrero: Cañón de la Mano Negra, 4–8 km N de Iguala, 15 February 1970, Anderson et al. 5779 (DUKE); Iguala y Buenavista, Cañón de la Mano, entre Los Amates y El Naranjo, N de Iguala, 20 July 1986, Catalán 11 (CHAPA, MEXU, MO), 19 October 1986, Catalán 330 (CHAPA, MO); El Limoncillo, General Heliodoro Castillo, 19 July 1999, Cruz 4240 (FCME, MEXU); Acapulco, La Estación, Laguna Tres Palos, 4 September 1987, Diego 4366 (FCME, MEXU); La Unión, road to La Majaguita and Las Trancas, Costa Grande, 6 October 1986, Goreti 2200 (MEXU); Luvianos, Temascaltepec, 10 August 1933, *Hinton 4508* (BM, K, MA, MO, US); Plaza de Gallos, Temascaltepec, 26 October 1933, *Hinton 5051* (A, BM, GH, K, MO, US); Anonas, Temascaltepec, 15 November 1933, Hinton 5214 (A, BM, GH, K, MO);

Vallecitos, Montes de Oca, 9 June 1937, Hinton 11365 (F, GH, K, MO, NY, US); Campo Morado, Otatlán, 25 July 1939, Hinton 14492 (GH, MEXU, NY, US); Teniente José Azueta, Ixtapa Zihuatanejo, El Candil, 5 August 2004, Juárez & Ortiz 715 (MEXU); E de Guayameo, Zirándaro, 21 March 1983, Martínez et al. 4946 (MEXU, MO); NO de Petatlán, carretera a El Camalote, 23 October 1983, Martínez & Soto 5111 (MEXU, MO, NY); cañada Tecoapano, NE side of Cerro Xilotzin, 17 September 1995, Moreno-Gutiérrez 1048 (FCME, MEXU); Atoyac de Álvarez, Nueva Dehli, 21 km al NE de Paraiso, 19 August 1985, Soto & Román 10153 (MBM, MEXU); Petatlán, near El Parotal, 23 km E from Coyuquilla, 24 October 1985, Soto et al. 11408 (MEXU); Chapultepec, General Helidoro Castillo, 30 September 1999, Soto 17267 (FCME, MEXU). Jalisco: Chamela, La Huerta, 29 July 1985, Ayala 93 (MEXU); Chamela, carretera vieja a Nacastillo, 5 August 1985, Ayala & Magallanes 106 (MEXU, NY), 9 September 1985, Ayala & Ayala 215 (MEXU); La Huerta, playa Careyitos, 5 October 1985, Ayala & Lott 276 (MEXU); Chamela, 26 September 1985, Bullock 1678 (MEXU, NY); Estación de Biología Chamela, 24 September 1997, Domínguez 503 (MEXU); N de Barra de Navidad, 2 January 1973, Jonson 2973 (MO); Estación Biológica La Chamela, La Huerta, 24 September 1981, Lott 567 (MEXU, MO, USF); La Huerta, N de La Chamela, 25 September 1981, Lott 585 (MEXU, NY); La Huerta, Estación Biológica La Chamela, 9 October 982, Lott & Hernández 1410 (MEXU, MO), 21 November 1984, Lott & Bullock 2307 (MEXU); Rancho Cuixmala, al SO de Laguna de Corte, camino a casa Jeannette, 24 October 1990, Lott et al. 2877 (MEXU); camino a Nacastillo, Universidad de Guadalajara, 3 February 1977, Magallanes 487 (MEXU [2 sheets]), 11 August 1977, Magallanes 769 (MEXU); km 50 of the Navidad-Puerto Vallarta highway, La Huerta, 4 km from El Faro, 20 September 1986, Pérez 2016 (MEXU); Autlán, 1-2 km al NO de La Yerbabuena, 9 March 1990, Santana et al. 4759 (MEXU); camino a Nacastillo, Chamela, 3 February 1977, Solís 487 (MEXU); camino a Nacastillo, 11 August 1977, Solís 769 (MEXU). México: Palmar Chico, Cerro de los Capulines, 26 August 1954, Matuda 31351 (MO). Michoacán: Bahia de San Telmo, Coahuayana, 29 August 1979, Guerrero 244 (MEXU, XAL); 5 km on the road Aquila-La Placita, Aquila, 9 December 1979, Guerrero et al. 527 (MEXU); 3 km W from Cruz de Cachan, Aquila, 29 September 1980, Guerrero 983 (MEXU); Aquila, 2 km al E de Cruz de Campos, camino a Aquila, 24 September 1983, Martínez et al. 4454 (MEXU); 4

km SE from San Juan de Lima, on the road to Tecoman, Playa Azul, Coahuayana, 24 September 1983, Martínez et al. 4509 (MEXU); Cruz de Campos, 2 September 1980, Soto & Cortés 2614 (MEXU, MO); NE de Coahuayana de Hidalgo, 7 March 1981, Soto & Torres 2793 (MEXU, MO); 2 km NE from Coahuayana de Hidalgo, 27 March 1981, Soto & Torres 2794 (MEXU); Chinicuila, Villa Victoria, 15 July 1985, Soto 9444 (MEXU); Coahuayanam 13 km SE from Palos Marías, 18 October 1988, Soto et al. 11149 (MEXU); Aquila, 3 km E from Maroate, road to Pómaro, 21 October 1985, Soto et al. 11227 (MEXU). Morelos: Cuernavaca, 14 November 1865, Bourgeau 1392 (P [3 sheets]); Barranca cerca a Cuernavaca, June 1896, Pringle 6341 (BM, BR, F, G, G-DC, HBG, JE, K, L, MEXU [2 sheets], MO, M, NY, P [2 sheets], UC, US, W, WU, Z), November 1896, Pringle 6224 (BM, BR, G, G-DC, GH, HBG, JE, K, MEXU [2 sheets], MO, M, NY, P [2 sheets], UC, US, W, WU, Z [2 sheets]). Nayarit: Tepic El Arco, al NO de La Escondida, 21 March 1989, Flores et al. 964 (MEXU); Tepic, al O de La Yerba, carretera Tepic-Miramar, 19 September 1994, Flores et al. 3929 (MEXU); 15 MW from Campamento Balleto, María Madre Island, 9 January 1981, Téllez 4129 (MEXU). Oaxaca: without exact locality, 1833, Andrieux 398 (G); 2 km before Alta de la Virgen de Guadalupe, road between Martín Chino and Plan Juan Martínez, Santa María Jacatepec, 26 October 1989, Calzada 15080 (MEXU); Santo Domingo Tehuantepec, Cerro El Arenal, W of Buenos Aires, road to San Miguel Tenango, 31 August 1991, Campos 3961 (MEXU); Río El Aguacate, 25 July 1982, Cedillo et al. 1685 (MEXU, MO); San Carlos Yautepec, San Miguel Chongo, 4 March 1999, Elorsa & Scheidegger 1812 (EAP, MEXU); Pochutla, NE de Chacalapa, carretera a Finca Monte Cristo, 1 July 1984, Hernández & Torres 417 (MO); al S de Matías Romero, Cerro El Timbón, al E de carretera 185, 28 October 1998, Ishiki & Koch 2371 (BAB); Temascal, 16 November 1963, Janzen s.n. (UC), 30 October 1963, Janzen s.n. (UC); Santa Gertrudis, August 1872, Liebmann 11942 (C); Oaxaca, s.d., MacDougal 50 (NY, US); Tehuantepec, El Zacatal, Rancho Limón, 17 km W of Tehuantepec, 18 February 1986, Martínez-C. 416 (MEXU); San Bartolo Yautepec, entre San Bartolo y La Ciénaga, 13 November 1988, Martínez-C. 2062 (MEXU); San Miguel Chimalapa, camino de Benito Juárez a Coralilla, cañón del Río Escondido, 21 February 1985, Maya 1249 (CHAPA, MEXU), 27 February 1985, Maya 1267 (CHAPA, MEXU); cabecera de arroyo La Ciénaga, al S de la División, ca. 8-9 km al ESE de Benito Juárez, 21 May 1985, Maya 1653

(CHAPA, MEXU); Tuxtepec, 4 August 1961, Schwabe s.n. (B); 25 km N of Puerto Escondido, 20 April 1976, Sousa et al. 5570 (MEXU); Chichihua, 16.5 km NE fo Santiago Ixtaltepec, trail to Santa María Chimalapa, Juchitan, 17 January 1984, Tenorio & Torres 5192 (MEXU); Tehuantepec, 11 km NW from Lachiviza, trail to Lachiquiri, Santa María Guienagati, 15 March 1986, Tenorio et al. 11126 (MEXU); San Miguel Suchixtepec, Carrizal, N of San Miguel Suchixtepec, Miahuatlan, 21 September 1992, Tenorio et al. 18376 (MEXU); El Limón, 11.1 km al SO de la entrada a Buenos Aires, Tehuantepec, 9 December 1983, Torres 4246 (MEXU); N de Matías Romero, carretera a Palomares, 16 January 1984, Torres & Tenorio 4388 (MEXU, MO); Juchitán, NE de Santiago Ixtaltepec, Chichihua, 17 January 1984, Torres & Tenorio 4430 (MEXU, MO); Juchitñan, arroyo Palomares, al N de Santa María, camino al Río del Corte, 29 August 1984, Torres 6008 (MEXU); Yautepec, 1.5 km from La Torre, San Cristóbal, 22 October 1988, Torres & Tenorio 12887 (MEXU). Puebla: San Diego, March 1951, Bravo 452 (MEXU). Queretaro: 2 km al S de Matzacintla, camino al Río Moctezuma, Landa, 28 July 1988, Carranza 909 (MEXU); cañada Las Víboras, al N de Landa, 30 July 1988, Carranza 933 (MEXU); Jalpan, 2–3 km from Tanchanaquito, Río Santa Marta, 27 July 1996, Carranza & Pérez 4918 (MEXU); Cañada Posa del Hualul, al E de Tilazo, Landa, 4 September 1989, González 950 (MEXU); Carrizal, al SO del Embocadero, Jalpan, 11 March 1988, Herrera 88 (MEXU); al S de Tanchanaquito, Los Sarros, s.d., López 543 (IEB, MEXU); NE of Tanchanaquito, between La Barranquita y la Barranca Grande, Jalpan, 25 August 1993, López 715 (MEXU); Río Santa Marta, between La Isla and Tanchanaquito, Jalpan, 24 November 1990, Servín 685 (MEXU). Quintana Roo: José María Morelos, 6.76 km January from Hoton P. Blanco, 18 March 2004, Álvarez & Ramírez 8353 (MEXU); 4 km N of Estero Franco, road to Tomás Garrido, 30 ul 1984, Cabrera & Cabrera 6880 (MEXU); Coba, June-July 1938, Lundell & Lundell 7768 (MEXU); NO de Puerto Felipe, Carrillo, 4 August 1972, Webster & Lynch 17666 (MEXU, MO). San Luis Potosí: San Luis Potosí, August 1910, Purpus 5390 (NY, UC, US); Cerro Plateado, Ciudad Valles, 6 July 1985, Tenorio & Ramamoorthy 9185 (CR, MEXU [2 sheets]). Sinaloa: Concodia, 5 km al NE de Concordia, 9 August 1985, Vega 1743 (MEXU). Tabasco: Tenosique, 11 March 1976, Calzada et al. 2224 (MEXU, MO); Boca Cerro, Tenosique, 1-5 July 1939, Matuda 3582 (MEXU). Tamaulipas: cerca a Ciudad Victoria, 1 August 1948, Meyer & Rogers 2859

(BM, BR, G, MO, U); 3.2 km from Las Salinas, road to cabecera Municipal, Altamira, 19 July 1994, Mora-López & Mora 548 (MEXU); Gómez Farias, Reserva de la Biósfera Rancho del Cielo, 27 June 1988, Vásquez et al. 4897 (USF, WIS). Veracruz: 5 km S of Caballo Blanco, Atoyar, 23 August 1985, Acevedo & Vásquez 462 (MEXU); Pizapán, S de San Andrés Tuxtla, 25 December 1972, Calzada 903 (BR, MEXU); El Salto de Evipantla, cerca a Comoapán, 12 January 1973, Calzada 937 (BR, MEXU); Estación Biológica Morro de la Mancha, 29 September 1977, Calzada 3659 (CR, F, MEXU); Rancho El Callejón, km 24 between Alvarado and Mosquitero, 29 March 1992, Calzada 17565 (MEXU); carretera a Palmar, 10 June 1979, Castillo & Tapia 752 (F, MEXU, XAL); Jalcomulco, 26 August 1983, Castillo & Medina 2877 (UC, XAL); Veracruz, 1731, Collector unknown s.n. (BM # 81925); 10 km E of Xalapa, 10 May 1972, Dorantes 591 (MEXU); 3 km from El Raudal, roat to Vega de Alatorre, 3 February 1965, Gómez-Pompa & Riba 82 (MEXU); Veracruz, 18 July 1865, Govin s.n. (P); Coatzacoalcos, zona de Salvaguarda-Pemex-La Cangrejera, 14 July 1999, Hanan et al. 1391 (EAP, MEXU); Cuitláhuac, 3 km al NO de Cuitláhuac, 3 July 1980, Hansen & Nee 7571 (F, USF); Rinconada, 13 January 1973, Hernández & Dorantes 1805 (F, MEXU [2 sheets]); 3 km NE of Boca del Río, Alvarado, 11 February 1995, Ibarra et al. 3935 (MEXU); Laguna Tamiahua, 3 May 1939, LeSuer 355 (F, TEX); 2 km SW from Cantarranas, Paso de Ovejas, 27 August 1985, Medina & Vásquez 456 (MEXU); 2 km from Barranca de Pachuquilla, Puente Nacional, 9 December 1985, Medina & Ortiz 697 (MEXU); Naolinco, 3 km al O de San Antonio Paso del Toro, 14 January 1984, Nee & Taylor 28771 (F, NY, XAL); Antigua, August 1912, Purpus 6021 (BM, GH, MO, UC); Zacuapan, June 1916, *Purpus 7665* (GH, MO, NY, UC [2 sheets], US, Z [2 sheets]); Zacuapan, September 1917, Purpus 8034 (UC); without exact locality, 1916, Purpus 8093 (UC); Hacienda del Mirador, October 1920, Purpus 8900 (RB, UC); Zacuapan, June 1926, Purpus 10737 (R, US); Zainapan, September 1928, Purpus 10857 (GH, US); Zacuapan, 1929, Purpus 11134 (K, MO, NY); 8 km SSE of Coatzacoalcos, 14 July 1999, Sinaca et al. 1391 (MEXU); La Laja, between Corral Falso and Pinoltepec, 16 km SE of Jalapa, Zapata, 20 March 1975, Souza & Delgado 4559 (MEXU), 16 August 1975, Sousa & Ramos 4704 (MEXU); La Laja, 2 km W between Corral Falso and Pinoltepec, 8 January 1986, Torres & Hernández 6426 (MEXU); Totutla, El Encinal, 12 December 1970, Ventura 2988 (MEXU, NY); Dos Ríos Pinoltepec, 17 June 1971, Ventura

3718 (CR, MEXU); Dos Ríos, Lucero, 13 June 1974, Ventura 10156 (EAP); Miradores, Dos Ríos, 9 May 1975, Ventura 11301 (ENCB, MEXU); Tlapacoyan, Arroyo de Piedra, 3 August 1976, Ventura 13136 (EAP, MEXU); Ixtacuacuo, Tlapacoyan, 25 March 1977, Ventura 13485 (ENCB, MEXU); Martínez de la Torre, Coapa, 20 October 1983, Ventura 20728 (CR, MEXU). Yucatán: Chichen Itzá, July 1938, Lundell & Lundell 7460 (MO). Data lacking: 1858, Ervendberg 127 (G, GH); 1841–1842, Karwinsky 1096 (LE); s.d., Pavón s.n. (FI-W, G); s.d., Sessé & Moçiño 1427 (MA, photo F neg. 41267).

GUATEMALA. Alta Verapaz: Cubilquitz, August 1903, Tuerckheim 8539 (US). Baja Verapaz: San Jerónimo, 24 July 1988, Tenorio et al. 14791 (MEXU, MO, USCG). Huehuetenango: Río Azul, Nentón, 5 December 2006, García et al. 2167 (USCG); Nentón, Aldea Nentón, road to Gracias a Dios, 5 March 2009, Maareten et al. 5552 (MO); entre Santa Ana y Nentón, Sierra de los Cuchumatanes, 27 August 1942, Steyermark 51420 (F). Izabal: al O de El Estor, 31 August 1988, Martínez & Stevens 23370 (MEXU). Jutiapa: cerca de Jutiapa, 24 October 1940, Standley 75305 (F, MO); entre Jutiapa y La Burrera, 1 November 1940, Standley 75976 (F). Petén: Aguada el Charco, 25 January 1961, Contreras 1870 (MO); Uaxactun, Bajo La Juventud, 26 December 1963, Contreras 3673 (MEXU); Parque Nacional Tikal, bajo Santa Fé, 16 February 1959, Lundell 15573 (F, MO, NY, TEX). Quezaltenango: Montaña Chicharro, S de Santa María de Jesús, Stevermark 34310 (F, MO). Santa Rosa: Santa Rosa, May 1892, Heyde & Lux 3161 (US); Naranjo, March 1893, Heyde & Lux 4496 (BM, G, GH, K, MO, M, NY, US); Santa Rosa, November 1940, Standley 78816 (F, MO); La Sepultura, 5 December 1940, Standley 79365 (F, MO). Solola: Santo Tomás, camino Madre Vieja, 28 May 1998, MacVean et al. s.n. (UVAL). Data lacking: July 1860, Hayes s.n. (GH).

BELIZE. Cayo: Vaca Plateau, cataratas Vaca, 9 August 1989, *Balick et al.* 2074 (MO, NY); Benque Viejo, Río Mopan, 22 October 1967, *Contreras 7175* (G, TEX); N de Blancameaux Lodge, Mountain Pine ridge, 12 July 1973, *Dwyer 11632* (F, NY); Waterhole, cerca a Vaca, 10 April 1938, *Gentle 2470* (A, MICH); S de El Millionario, 29 May 1973, *Gentry 7660* (F, MICH, MO); Cohune Ridge, August 1936, *Lundell 6462* (MICH, MO, NY, S, US); Belmopan, 27 July 1970, *Spellman & Newey 1906* (MO), 28 July 1970, *Spellman & Newey 1920* (MO [2 sheets]). Stan Creek: Reserva Quebrada Sick Grass, 20 September 1939, *Gentle 3004* (A, MEXU, MICH, NY). Toledo: Punta Gorda, 29

July 1979, *Dwyer 14896* (MO); Río Grande, 4 September 1944, *Gentle 4796* (MEXU); cerca a Crique Queva, 8 July 1946, *Gentle 6000* (MO); Acahual, cerca a Orange Point, 29 September 1951, *Gentle 7452* (F, G, MO, NY). Data lacking: s.d., *Gentle 1505* (F, MICH).

HONDURAS. Comayagua: Río Tepanguare, al O de Lejamaní, 12 December 1983, Holst 1471 (EAP). Cortéz: Potrerillos, Aldea El Olivo, 13 April 1975, Erazo 65 (MO). La Paz: Cerro La Cueva del León, al SO de La Paz, 13 June 1983, Holst 1171 (EAP). Francisco Morazán: Quebrada El Naranjo, tributario del Río La Orilla, al SO de Zamorano, 10 March 1995, Linares et al. 2276 (EAP), 3 July 1996, Linares & Hubbard 3453 (EAP); Quebrada Suyapa, Suyapa, 7 October 1948, Molina 1213 (EAP, GH, MO); Quebrada Suyapa, NE de Tegucigalpa, 10 August 1949, Molina 2569 (BM, EAP, GH, US); Zamorano, 27 March 1999, Montes 4 (TEFH); cercanías de El Zamorano, 3-17 August 1947, Standley 11595 (EAP); Quebrada de Suyapa, cercanías de Suyapa, Sep-Dic 1948, Standley 12942 (EAP); El Zamorano, carretera a San Antonio de Oriente, 7 July 1949, Standley 20895 (EAP, GH); cercanías de El Zamorano, 31 July 1949, Standley 22041a (EAP); Río Yeguare, 20 March 1947, Williams & Molina 12207 (EAP); faldas del Cerro Majicoran, Río de la Orilla, drenaje del Río Yeguare, 16 October 1949, Williams 16932 (EAP); Chagüite, 20 August 1943, Valerio 400 (EAP); camino San Antonio, 21 October 1943, Valerio 1344 (EAP). Yoró: Cordillera Nombre de Dios, colinas al S de San José de Texiguat, 17 May 1991, Davidse et al. 34506 (CR, EAP, MO, TEFH); El Progreso, 8 April 1970, *Harmon & Dwyer 3470* (MO).

EL SALVADOR. Ahuachapán: San Francisco Menéndez, El Corozo, 19 August 2000, Rosales 765 (B, BM, LAGU, MEXU, MO), Rosales 766 (B, LAGU, MO), Rosales 885 (B, BM, EAP, LAGU, MO); Ahuachapán, Área Protegida Santa Rita, 5 May 2004, Rosales 2464 (CR, LAGU); Parque Nacional El Imposible, San Benito, 25 September 1991, Morales et al. 1270 (B, LAGU, MEXU, MO), 12 December 1989, Sermeño 30 (B, LAGU, MO), 1 October 1991, Villacorta et al. 861 (LAGU, MO), Villacorta et al. 886 (B, LAGU, MO); San Benito, N de Cerro Piedra del Filo, 21 May 1993, Sandoval & Pérez 1259 (B, LAGU, MO); Parque Nacional El Imposible, San Benito, mirador el Mulo, 16 April 1997, Sandoval 1535 (B, LAGU); cerca de Ahuachapán, 9 January 1922, Standley 19913 (GH, NY, US). Chalatenango: Ojos de Agua, Las Vueltas, 16 June 1997, Villacorta 2393 (LAGU, MO). La Libertad: San Diego, El Amatal, 28 December 1996, Aparicio &

Rivera 104 (B, CR, LAGU); km 14 de la carretera a La Libertad, 8 July 1957, Lagos 836 (USF). La Unión: Volcan de Conchagua, 1 December 2006, Estrada 3847 (CR, MHES); El Aguacatalón, Conchagua, 2 December 2006, Menjivar et al. 823 (MHES). San Miguel: NO de San Miguel, 23 February 1976, Croat 32798 (MO, Z). Sonsonate: Cuisnahuat, área natural protegida El Balsamar, 12 April 2011, Rodríguez et al. 2288 (LAGU, MO). Data lacking: June 1937, Calderón 32 (F); 22 June 1958, Weberling 843 (WAG).

NICARAGUA. Boaco: Piedra Sembrada al N de Camoapa, 29 August 1991, Moreno 10596 (MO). Chinandega: Chichigalpa, volcan Casita, bajando sobre la Olma de las Antés hacia la Hacienda Versalle, 7 February 2004, Coronado 530 (MO); Volcán San Cristóbal, 3 August 1984, Hernández et al. 584 (MO). Estelí: Río Isiqui, 20 February 1982, Moreno 15237 (MO); Kukamonga, 1 August 1983, Moreno 21831 (MO); La Concepción, 19 December 1993, Moreno 22600 (MO); cerca a la entrada de Estelí, 30 December 1977, Stevens 5780 (MO); cerca a Estanzuela, 11 August 1978, Stevens 9942 (MEXU, MO); N de estela, 13 January 1981, Stevens et al. 18917 (MBM, MEXU, MO, VEN). Granada: Volcán Mombacho, 25 July 1980, Moreno 1440 (MEXU, MO), 16 September 1980, Moreno 2600 (MO); Volcán Mombacho, 19 September 1976, Neill 776 (MO). Matagalpa: El Barro, 18 November 1984, Moreno 25056b (MEXU, MO, WAG). Nueva Segovia: Valle de Córdoba, 15 December 1865, Bourgeau 1510 (G [2 sheets], GH, K, M, P [10 sheets], US); Quebrada El Nancital, 7 August 1977, Stevens 3007 (MEXU, MO, VEN). Zelaya: Zelaya, March 1982, Moreno 23821 (MO); cerca a Zelaya, 6 January 1982, Ortiz 553 (MO).

COSTA RICA. Alajuela: colinas de Santiago, 31 May 1901, *Brenes* 14276 (GH); San Carlos, NE de Boca Tapada, 27 July 1996, *Hammel 20324* (CR); Los Ángeles de San Ramón, 21 December 1936, *Solís 478* (MO). Cartago: CATIE, Turrialba, August 1981, *Hazlett & Artavia 7123* (MO, NY); March 1982, *Hazlett & Artavia 7447* (CR, MO); Turrialba, s.d., *Lankaster 127* (K, P); Quebrada Cascajal, S de Guatuso, 23 July 1967, *Lent 1111* (MO); Tuís, November 1897, *Tonduz 11553* (US). Guanacaste: Rincón de la Vieja, 4 November 1993, *Espinoza 632* (CR, MO); Rincón de la Vieja, Las Pailas, 11 January 1994, *García & Morales 288* (CR); entre Santa Cruz y Vista de Mar, July 1985, *Gómez et al. 23669* (MO); Parque Nacional Santa Rosa, 17 June 1979, *Janzen 11694* (MO); Santa Rosa, 13 May 1980, *Janzen 11892* (MO); Hojancha, Río Nosara, 25 June 2002, *Morales 8716* (CR); entre Cartago y Candelaria, 1845–1848, *Øersted 15538* (C); Nicoya, without data,

Pittier s.n. (US); colinas de Nicoya, May 1900, Tonduz 13945 (US). Heredia: Estación Biológica La Selva, 16 August 1979, Grayum 2390 (CR, MO); Finca La Selva, Río Puerto Viejo, 7 May 1980, Hammel 8616 (CR, MO), 18 July 1982, Hammel & Trainer 13250 (CR, DUKE); Santo Domingo, 31 October 1993, Hammel & Hammel 19106 (CR, MO, USF); Santo Domingo, Río Tures, ca. 1 km al S de San Francisco de San Isidro de Heredia, 8 September 2003, Hammel & Pérez 22867 (CR, MO). Limón: Talamanca, Río Barbilla y Quebrada Cañabral, 20 October 1988, Herrera & Martínez 2224 (CR, F, MO, WAG); Pococi, Río Corinto, 11 January 1996, Morales & Saborío 5076 (CR). Puntarenas: Península de Osa, Chocuaco, 4 September 1991, Aguilar 325 (CR, MO); Reserva Forestal Golfo Dulce, Rancho Quemado, 17 August 1992, Aguilar & Fernández 1249 (CR); Península de Osa, Sirena, 13 October 1993, Aguilar 2507 (CR, MO); Península de Osa, Los Mogos, 6 January 1994, Aguilar et al. 2972 (CR); Península de Osa, Estación Los Patos, 2 June 1994, Aguilar 3306 (CR); Golfo Dulce, Bahía Chal, 13 December 1996, Aguilar 4748 (CR); Golfo Dulce, cerca a Chocuaco, 26 May 1997, Aguilar 5141 (CR); Parque Nacional Corcovado, Estación San Pedrillo, 28 October 1997, Aguilar 5309 (CR); Golfito, Parque Nacional Corcovado, Estación Sirena, 4 July 2000, Aguilar 6268 (CR); península de Nicoya, Río Blanco, Quebrada Negra, 14 May 2003, Alfaro & González 4405 (CR); Delta del Río Esquinas, 28–29 August 1950, Allen 5623 (EAP); O de Rincón de Osa, June 1968, Burger et al. 5486 (F [2 sheets]); Osa, Los Mogos, 11 January 1991, Castro 50 (CR, MO); Esquinas, Golfito, 1983, Gómez 19668 (CR, MEXU, MO, NY, USF, WAG); Punta Leona, 27 December 1995, Hammel 20042 (CR); Golfito, Parque Nacional Esquinas, Golfo Dulce, 14 February 2000, Huber 1753 (WU); San Vito de Java, Coto Brus, 29 August 1996, Krings 139 (USJ); Parque Nacional Corcovado, Sirena, 6 July 1977, Liesner 2962 (MO, USF); Península de Osa, San Pedrillo, 13 March 1993, Marín 40 (CR, MO); Isla Violines, Sierpe, 23 September 1991, Marín 191 (CR, MO); Punta Burica, Punta Banco, 20 December 1998, Morales & Abarca 6899 (CR); Península de Osa, playa San Josecito, 15 November 1993, Quesada et al. 831 (CR); Península de Nicoya, Curú, 9 September 1995, Sanders et al. 17825 (USJ); Corcovado, Esquinas, 25 August 1993, Segura & Quesada 140 (CR); Río Ceibo, cerca a Buenos Aires, February 1892, Tonduz 6652 (BR [2 sheets], G [2 sheets], US). San José: Aserrí. Río Saurez, barrio Lourdes, 9 May 2001, Acosta et al. 3060 (CR); San José, s.d., Hoffmann 522 (B (destroyed, photo F neg. 4545)); Mora, camino al Río Jaris, 15 February 2004, Kriebel 4339 (CR); fila Bustamante, Naranjal, 5 February 1995, Morales et al. 3473 (CR); Cerros de Caraigres, fila Aguabuena, entre Quebradas Pilas y Ceniza, 26 December 1996, Morales 5937 (CR); Cerros de Caraigres, Quebrada Salvaje, cerca a La Legua, 8 December 1996, Morales 6252 (CR); Acosta, Ceiba Este, 1 December 2002, Morales & Abarca 8807 (CR); Aserrí, Saurez, 15 October, Morales 10102 (CR); Acosta, Tiquites, Fila Aguabuena, cabeceras Río Tiquires, 25 April 2005, Morales 12864 (CR); cerca a Río María Aguilar, 1893, Pittier 8441 (G [2 sheets]); Santa Ana, San Rafael de Escazú, 24 July 2004, Santamaría 90 (CR); Desamparados, Finca Los Ortuño, 5 August 2009, Santamaría et al. 7964 (CR); cerca de San José, February 1924, Standley 34797 (US); Altos del Tablazo, 15 July 1981, Taylor 45 (DUKE, MO); San José, August 1896, Tonduz 7278 (K, US); Río Virilla, cerca a San Juan, October 1898, Tonduz 7441 (BM, BR [3 sheets], G [3 sheets], GH, K, M, US); Río Torres, San Francisco de Guadalupe, May 1893, Tonduz 8004 (Z); La Verbena, cerca a Alajuelita, April 1894, Tonduz 8904 (BR, NY, US, Z); San Francisco de Guadalupe, 21 September 1913, Tonduz 17741 (BM, K, P); Aserrí, Río Saurez, 15 June 1999, Vargas & Ramírez 256 (CR, MO). Data lacking: 1877, Endres 191 (BM, K); 1919–1920, Lankester s.n. (K, G); s.d. Lankaster 125 (K [2 sheets]).

PANAMÁ. Bocas del Toro: valle Water, 31 October 1940, von Wedel 1452 (MO). Chiriquí: cerca del Lago Chiriquí, 13 November 1941, von Wedel 1611 (GH, US). Coclé: El Valle de Antón, 4 June 1939, Alston 8717 (BM, MO); El Valle de Antón, July 1935, Siebert 493 (MO). Colón: fila Santa Rita, January 1968, Dwyer et al. 9025 (MO); fila Santa Rita, 8-12 miles from Trans-istmican highway, 17 April 1988, McPherson 12450 (MO, PMA, USF); fila Santa Rita, 2 March 1975, Mori & Kallunki 4924 (MO). Panamá: Finca Indio, Cerro Jefe, 3 May 1971, D'Arcy 5237 (MO, PMA); Cerro Jefe, 10 December 1966, Dwyer 287 (MO); N de El Llano, 25 July 1972, Gentry 5575 (MO, Z); carretera El Llano-Cartí, 28 March 1974, Nee & Tyson 10963 (MO); Isla de Barro Colorado, 3 July 2008, Pérez 2052 (PMA); Isla Barro Colorado, Barbour point, 10 ene 1932, Shattuck 706 (F, MO); Santa Rita, 18 March 1969, Sucre & Dressler 4817 (RB); Cerro Jefe, 10 July 1976, Sullivan 205 (B, MO, PMA); carretera El Llano-Cartí, 12 September 1980, Sytsma 1044 (BM, MO, PMA, USF); Isla Barro Colorado, E of Barbour point, 10 January 1932, Wetmore & Abbe 179 (A [2 sheets], F, MO). San Blas: Río Acla, 10 February 1979, Sudgen

423 (MO). Veraguas: Parque Nacional Isla de Coiba, Isla Jicarón, Quebrada de los Puercos, 10 September 1997, *Galdames et al.* 4027 (MA, PMA).

COLOMBIA. Chocó: El Carmen, alrededores de Bahía Solano Norte, 7 May 1992, *Barbosa 7001* (HUA [2 sheets]).

Prestonia mucronata Rusby (1920: 90). Type:—COLOMBIA. Magdalena: Las Nubes, 18 December 1898, H.H. Smith 1656 (holotype NY!, isotypes A n.v., BR!, CM!, G! [2 sheets], GH n.v., K!, MICH!, MO!, P!, S! [2 sheets], TEX-LL!, U!, UC!, US! [2 sheets], W!, WIS!, Z!). Fig. 57, 58

Stem densely ferrugineous-tomentose, color of latex unknown, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous or somewhat inconspicuous, 1– 1.5 mm long. **Petioles** 0.7–1.5 cm; leaf blade  $4-7.5(-8.5) \times 3-5$  cm, elliptic, ovate-elliptic to broadly ovate, apex acute to abruptly short-acuminate, base obtuse to rounded, membranaceous, sparsely and minutely ferrugineous-hirsutulous adaxially, minutely ferrugineous-hirsutulous to ferrugineous-sericeous abaxially, indument drying ferrugineous, secondary veins impressed on both surfaces, tertiary veins rather inconspicuous. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary to subterminal, shorter than or equaling adjacent leaves, few-flowered, the flowers more or less clustered, ferrugineous-tomentulose, peduncle 1.8–3.4 cm, pedicels 0.9–1.5 cm long, floral bracts 2–5  $\times$  0.5–1.5 mm, linear-ovate, scarious and inconspicuous, green. Sepals 8–12  $\times$  2–3 mm, free, membranaceous, elliptic, the apices acute to acuminate, not reflexed, minutely ferrugineous-tomentulose, subfoliaceous, drying with a more or less uniform color, the veins usually inconspicuous and not impressed, colleters ca. 1 mm long, inconspicuously erose at the apex. Corolla salverform, yellowish green, dense to sparsely ferrugineoustomentulose outside, tube  $9-13 \times 3-4$  mm, gradually expanding toward the mouth, free corona lobes ca. 1 mm long, included, their height conspicuously surpassed by that of the anther apices, annular corona subentire to irregularly lobed, thickened, corolla lobes 9–11 × 5–7 mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 6.5–9(–11) mm, dorsally glabrous, included. Ovary 1.5–2 mm tall, glabrous, style-head 1.6–2 mm, nectary 1–1.5 mm, conspicuously shorther than the ovary, divided into 5 nectaries, each irregularly erose or lacerate. Follicles  $15-20 \times 0.4-0.7$  cm, continuous, free, usually united at the tips (at least when young), densely ferrugineous-tomentose, without lenticels, firmly membranaceous when old; seeds unknown.

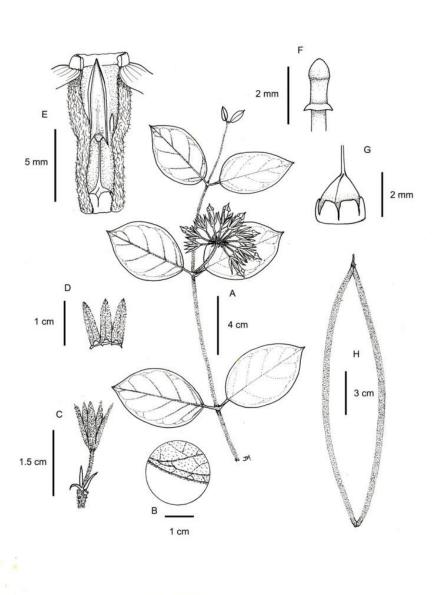


Fig. 57 *Prestonia mucronata* (A-G from *Smith 1656*, NY; H from *Davidse & Miller 28065*, USF). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts. D. Adaxial view of three sepals. E. Open corolla tube, showing the anthers and the deeply included free coronal lobes. F. Style-head. G. Nectaries and ovary. H. Follicles.

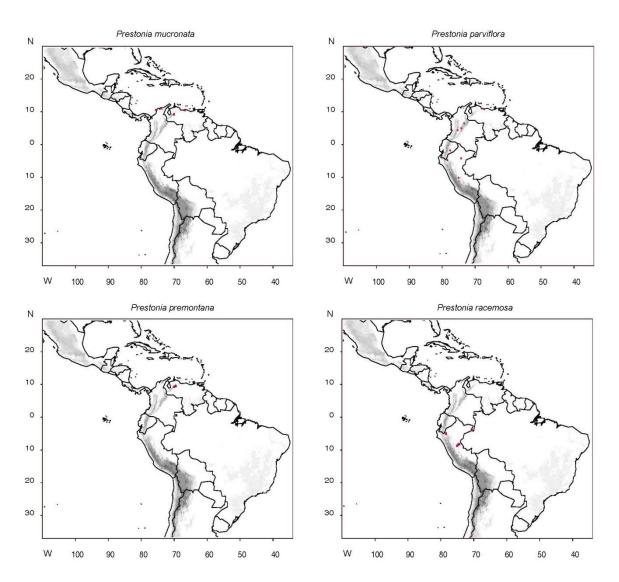


Fig. 58 Distribution maps of Prestonia mucronata, P. parviflora, P. premontana and P. racemosa

**Distribution and habitat**:—Montane forest, cloud forest, and premontane forest in northern Colombia and northwestern Venezuela, from 1900 to 2200 m.

**Phenology**:—Flowering April, June, and December. A single specimen with old fruits was collected in June.

## Conservation Assessment:—Endangered (CR)

**Taxonomic notes:**—*Prestonia mucronata* is a poorly collected species, closely related to *P. parviflora* and *P. premontana*. All three species have terminal inflorescences and small flowers, with free corona lobes deeply included and are restricted to the Andes of northern South America. *Prestonia mucronata* is distinguished from the other two species by its longer anthers and larger sepals.

Prestonia mucronata was relegated to the synonymy of *P. parviflora* by Morillo (1978), who argued that the differences cited by Woodson (1936) between the two species overlap. After analyzing all specimens cited by Morillo, I conclude that he mixed collections of two different species: *P. parviflora* and *P. premontana*, but did not examine any collection of *P. mucronata* (including the type).

Additional specimens examined:—COLOMBIA. Magdalena: San Sebastián de Rábago, 8 March 1948, *Romero-Castañeda 897* (COL); Santa Marta, Cerro Quemao y Cerro San Lorenzo, 24 April 1959, *Romero-Castañeda 7892* (COL).

VENEZUELA. Distrito Federal: Vargas, Serranía de la Costa, entre La Victoria y Colonia Tovar, carretera a Costa de la Maya, ca. 8-12 km al O de Colonia Tovar, 16 June 1984, *Davidse & Miller 28065* (MO, NY, USF, WAG, VEN); E de Junquillo, July 1944, *Steyermark 57000* (MO, NY, US, VEN). Trujillo: Boconó, Parque Nacional Guaramacal, February 1997, *Stergios et al. 17036* (CR, PORT, US).

Prestonia parviflora (Bentham) Bentham (1876: 709). Haemadictyon parviflorum Bentham (1857: 355). Temnadenia parviflora (Bentham) Miers (1878: 215). Type:—COLOMBIA. Cundinamarca: Pandi, s.d., K. Hartweg 1053 (holotype K! [2 sheets], isotypes CGE!, LD!). Fig. 58, 59

**Stem** minutely ferrugineous-tomentulose to sparsely puberulent, with clear latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters usually conspicuous, 1.5-2.5(-3) mm long. **Petioles** 1.2-3 cm; leaf blade  $(6-)8-23 \times (3-)4-11.5(-13)$  cm, elliptic to broadly elliptic, apex apiculate to short-acuminate, base usually obtuse, rarely rounded, membranaceous, very sparsely puberulent adaxially, dense to sparsely tomentulose abaxially, indument drying yellow or somewhat ferrugineous, secondary veins usually impressed on both surfaces, tertiary veins rather inconspicuous. **Inflorescence** a dichasial cyme, terminal or subterminal, rarely axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, minutely and densely ferrugineous-tomentulose, peduncle 1.1-2.7 cm, pedicels 0.5-0.7 cm long, floral bracts  $1-3 \times 0.5-1$  mm, linear to linear-ovate, scarious, minute, green. **Sepals**  $2.5-4 \times 1-1.5$  mm, free, membranaceous, very narrowly elliptic, the apices acuminate, not reflexed, densely tomentulose, small and inconspicuous, drying with a more or less uniform color, the veins

not impressed, colleters 0.75-1 mm long, variously lacerate at the apex. **Corolla** salverform, yellow, densely ferrugineous-tomentulose outside, tube  $4-6 \times 1.5-2.5$  mm, usually straight, but somewhat inflated around the stamens, free corona lobes ca. 1 mm long, deeply included, their height conspicuously surpassed by that of the anther apices, annular corona inconspicuous, subentire to inconspicuously 5-lobed or irregularly lobed, corolla lobes  $4-8 \times 3-4$  mm, obliquely obovate. **Stamens** inserted near the corolla moutdh, anthers 3.5-4 mm, dorsally glabrous, the apices barely exserted. **Ovary** 1.25-1.5 mm tall, glabrescent to sparsely hirsutulous apically, style-head 1.5-1.75 mm, nectary ca. 1 mm, slightly shorter than the ovary, irregularly 5-lobed, each lobe subentire. **Follicles**  $31-37 \times 0.4-0.7$  cm, somewhat articulated, free, united at the tips, densely ferrugineous-tomentose, without lenticels, firmly membranaceous when old; seeds 14-15.5 mm, coma 2-3 cm, tannish cream.

**Distribution and habitat**:—Moist forest, premontane forest, montane forest, and thickets along roadsides in northern Colombia, northeastern Venezuela, Ecuador, and Peru, from (300–)1300–2150 m.

**Phenology**:—Flowering January-October, and December. Fruiting March-April.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Taxonomic notes**:—*Prestonia parviflora* morphologically resembles *P. mucronata* and *P. premontana*, but it is distinguished from *P. mucronata* by its shorter sepals (2.5-4 mm vs. 8-12 mm) and shorter anthers (3.5-4 mm vs. 6.5-9(-11)) mm and from *P. premontana* by its larger leaves  $[(8-)10-23 \times (3-)4-11.5(-13) \text{ cm vs. } 2.5-10 \times 1.5-4.3 \text{ cm})$ , shorter corona lobes (1 mm vs. 2.5-3.5 mm), and corolla tube 4-6 mm long (vs. 10-12 mm).

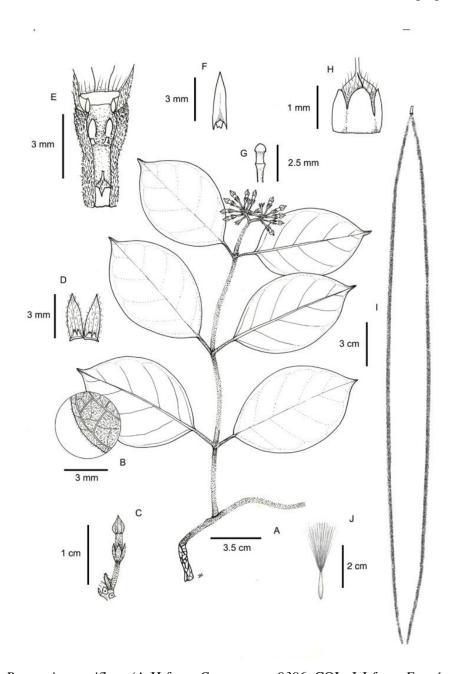


Fig. 59 *Prestonia parviflora* (A-H from *Cuatrecasas 9396*, COL; I-J from *Fernández-Alonso et al. 21310*, COL). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Bud, calyx, pedicel, and bract. D. Adaxial view of two sepals, showing the colleters at the base. E. Corolla tube partially open (anthers removed), showing the free coronal lobes, annular corona, ovary, and nectary. F. Anther, dorsal view. G. Style-head. H. Nectary and ovary. I. Follicles. J. Seed.

**Additional specimens examined**:—COLOMBIA. Cundinamarca: Tocaima, 19 February 1876, *André 1485* (K [3 sheets]); Tena, cerca del Salto de Tequendama, 5 January

1999, Díaz & Gómez 3 (CR); Bogotá, 1844, Goudot s.n. (K, P); Bogotá, cerca a Granada, 1892, Triana 1919 (B [destroyed, photo F neg. 4549], BM, FI, RB, US); cerca a Tena, January 1854, Triana 3815 (COL, P); Tena, 1851–1857, Triana s.n. (BR, COL). Quindio: Filandia, reserva forestal de Bremen, 12 April 1988, Arbeláez et al. 2526 (HUQ); Calarcá, Peñas Blancas, finca Buenavista, 24 September 1999, Macías et al. 1308 (HUQ); Pijas, El Sinabrio, finca Las Pavas, 14 October 1999, Macías et al. 1334 (HUQ); Calarcá, La Virginia, vereda Peñas Blancas, 19 July 1991, Vélez et al. 2656 (HUQ). Santander: Suaita, Finca Marbella, sector Flandes, 30 March 2004, Fernández-Alonso et al. 21310 (COL). Tolima: El Fresno, 7 May 1940, Cuatrecasas 9396 (COL, VALLE, US). Data lacking: 1783–1808, Mutis 465 (MA, US), Mutis 1995 (MA), Mutis 4094 (MA); s.d., Triana 1979 (COL).

VENEZUELA. Distrito Federal: El Junquito, June 1944, *Lasser 57108* (VEN); Libertador, NE de Colonia Tovar, camino a Costa Maya, 8 December 1982, *Steyermark et al.* 127767 (MO, NY, VEN, WAG).

ECUADOR. Morona-Santiago: Macuma, 27 January 1981, *Gentry et al. 30892* (MO); Macuma, ca. 50 km NE de Macas, 21 March 1973, *Lugo 3640* (GB, USF); Achuntza, asentamiento Jibaro en las cercanías de Macuma, ca. 50 km al N de cerca de Macas, 23 March 1973, *Lugo 3687* (GB, USF).

PERÚ. Cajamarca: San Ignacio, Huarango, Nuevo Mundo, Caserío Piraguas, Quebrada Santa Rosa, 12 November 1997, *Rodríguez & Núñez 1932* (CR, MO). Cusco: La Convención, Echarati, Cashiriari, 28 August 1998, *Beltrán et al. 3075* (US, USM). Loreto: Ucayali, Cesar Bela Chacra, SE de Aguaytia, 1 November 1972, *Schunke 5486* (CM, CR, F, NY, WAG [2 sheets]). Pasco: Oxapampa, Villa Rica, Puellas-Yuncullmas, 24 April 2009, *Valenzuela et al. 12636* (CR, MO).

Prestonia premontana J.F. Morales (2007: 150). Type:—VENEZUELA. Lara: Morán, cabeceras Río Tocuyo, Guaitó, 13 October 1974, J. Steyermark & Carreño 111114 (holotype Z!, isotypes F!, VEN!). Fig. 58, 60

**Stem** densely ferrugineous-tomentose, with clear latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters somewhat inconspicuous 1–2(–2.5) mm long. **Petioles** 0.4–1.2 cm; leaf blade  $2.5-10 \times 1.5-4.3$  cm, elliptic, narrowly elliptic, narrowly ovate-elliptic or narrowly ovate, apex acuminate to abruptly short-acuminate, base obtuse, membranaceous, sparsely sericeous adaxially, velutinous-tomentose abaxially, indument drying ferrugineous, secondary veins usually impressed on both surfaces, tertiary veins rather inconspicuous. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, terminal, or subterminal, shorter than or equaling adjacent leaves, few-flowered, the flowers densely clustered, ferrugineous-tomentulose, peduncle 1-3 cm, pedicels 0.5-1 cm long, floral bracts  $1.5-3 \times 0.5-1$  mm, filiform, scarious, minute, green. Sepals  $4.5-6(-7) \times$ 1–1.5 mm, free, membranaceous, narrowly ovate to narrowly elliptic, the apices acute to short-acuminate, not reflexed, densely ferrugineous-tomentose, very small, drying with a more or less uniform color, the veins not impressed, colleters less than 1 mm long, subentire at the apex. Corolla salverform, yellowish green, densely ferrugineous-tomentose outside, tube  $10-12 \times 2-2.5$  mm, straight, free corona lobes 2.5-3.5 mm long, included, their height surpassed by that of the anther apices, annular corona deeply 5-lobed, thickened, corolla lobes  $(12.5-)14-16 \times 2.5-3.5$  mm, obliquely narrowly obovate. **Stamens** inserted ca. in the middle of the tube, anthers 5–6 mm, dorsally glabrous, included. **Ovary** 1.5–2 mm tall, glabrous, style-head 1.7–2 mm, nectary 1.4–1.6 mm, conspicuously shorter than the ovary, deeply 5-lobed, each lobe irregularly lacerate. **Follicles** unknown.

**Distribution and habitat**:—Endemic to Venezuela, where it grows in montane forest and premontane forest, from 1800 to 2300 m.

**Phenology**:—Flowering April, July and from August-October.

**Conservation Assessment**:—Endangered (CR)

**Taxonomic notes:**—*Prestonia premontana* can be recognized by the following combination of characters: terminal inflorescences, sepals 4.5–6(–7) mm long, corolla lobes (12.5–)14–16 mm, free corona lobes 2.5–3.5 mm, and anthers 5–6 mm. This species is related to *P. mucronata* and *P. parviflora*, sharing characters such as terminal

inflorescences and small flowers (see discussion for these taxa). For a further discussion about the taxonomic history of *P. premontana* see Morales (2007a)

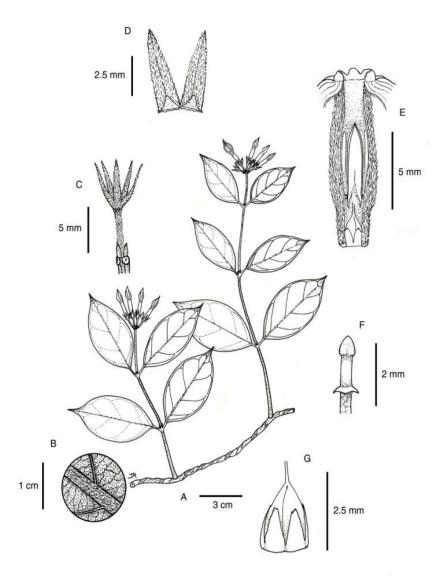


Fig. 60 *Prestonia premontana* (*Steyermark & Carreño 111114*, F). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts. D. Adaxial view of two sepals. E. Open corolla tube, showing the anthers, free coronal lobes and the anular corona. F. Style-head. G. Nectary and ovary.

**Taxonomic notes:**—*Prestonia premontana* can be recognized by the following combination of characters: terminal inflorescences, sepals 4.5–6(–7) mm long, corolla lobes (12.5–)14–16 mm, free corona lobes 2.5–3.5 mm, and anthers 5–6 mm. This species is related to *P. mucronata* and *P. parviflora*, sharing characters such as terminal inflorescences and small flowers (see discussion for these taxa). For a further discussion about the taxonomic history of *P. premontana* see Morales (2007a)

Additional specimens examined:—VENEZUELA. Barinas: Bolivar, entre Altamira y Santo Domingo, 5 August 1983, van der Werff & Ortiz 5895 (VEN). Lara: Distrito Jiménez, Parque Nacional Yacambú, SE de Sanare, 23 October 1982, Davidse & González 21235 (MO, WAG, VEN); Parque Nacional Yacambú, cerca a El Blanquito, S de Sanare, April 1978, Morillo & Laboureau 7264 (VEN); S de Agua Negra, 23 Km E de Cubiro, cerca a Nuezal, 6 July 1974, Steyermark et al. 110163 (NY, VEN, Z).

Prestonia racemosa J.F. Morales (2007: 153). Type:—PERU. Amazonas: Bagua, Imaza, Yamayakat, 8 November 1996, R. Vásquez, P. Stern, R. Rojas & R. Aguilar 21615 (holotype CR!, isotypes MO!, USM!). Fig. 58, 61

Stem densely ferrugineous-tomentose, with milky latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2–2.5 mm long. Petioles 0.8–1.4 cm; leaf blade 12– $17 \times 6$ –10 cm, elliptic to obovate, apex caudate-acuminate, base obtuse to rounded, membranaceous, sparsely puberulent adaxially, densely velutinous-tomentose abaxially, indument drying ferrugineous to brown, secondary and tertiary veins impressed on both surfaces. Inflorescence a monochasial cyme, axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, ferrugineous-tomentose, peduncle 5–1.5 cm, pedicels 1.2–1.9 cm long, floral bracts 1.2–1.9 cm long, floral bracts 1.2–1.9 cm, narrowly elliptic to narrowly ovate-elliptic, foliaceous to subfoliaceous, green. Sepals 11– $12 \times 5$ –1.2 cm, free, membranaceous, ovate to ovate-elliptic, the apices mucronulate, not reflexed, hispid-tomentulose, foliaceous, drying with a more or less uniform color, the veins usually inconspicuous, rarely conspicuously impressed, colleters 1.2–1.2 cm long, irregularly lacerate and hispid at the apex. Corolla salverform, yellow to yellowish green, densely hispid o hispid-tomentose outside, tube 14–16 120.5 mm, straight, free corona lobes 120.5 mm long, the apices exserted, their height equaling or slightly surpassing that of the

anther apices, annular corona entire to subentire, thickened, corolla lobes  $11-13 \times 6-8$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 6–7 mm, dorsally glabrous, the apices barely exserted. **Ovary** ca. 1.5 mm tall, glabrous, style-head 1.8–2.5 mm, nectary 2.5–3 mm, conspicuously surpassing the ovary, irregularly lacerate, not lobed. **Follicles** 15–18  $\times$  1.2–1.3 cm, continuous, divaricate, free, the tips divergent, hispid-tomentulose, without lenticels, somewhat woody when old; seeds 12–15 mm, coma 1.5–3 cm, cream.

**Distribution and habitat**:—Endemic to Peru (departments of Amazonas and Loreto ) in moist forest, dry forest, and thickets, from 300–500 m.

**Phenology**:—Specimens with flowers have been collected from June to August and November and fruits have been collected in March, June, and July.

**Conservation Assessment:**—Vulnerable (VU), the area of occurrence of less than 20,000 km2 and fewer than 10 known localities.

**Taxonomic notes**:—*Prestonia racemosa* resembles *P. tomentosa*, having in common leaf blades, inflorescences, and follicles with similar indument, but it is separate by its ferrugineous pubescence, elongated and unbranched inflorescences, anthers 6–7 mm, and longer follicles.

Additional specimens examined:—PERÚ. Amazonas: Bagua, Imaza, Yamayakat, 19 March 2001, *Rojas et al. 997* (MO); Bagua, Imaza, Yamayakat, Río Marañón, 18 July 1994, *Vásquez et al. 18775* (MO). Loreto: Pucallpa, 3 June 1960, *Woytkowski 5758* (MO, UC, US); Mariscal Castilla, Caballococha, 11 July 1987, *Vásquez & Jaramillo 9223* (MO, USF, USM); Amazonas, Caballococha, cerca al aeropuerto, 14 August 1989, *Vásquez & Jaramillo 12718* (MO, USF, USM). Ucayali: km 1 de carretera Marginal, al S del km 86, de la carretera Pucallpa-Tingo María, 1 June 1983, *Gentry & Jaramillo 41392* (MO); Coronel Portillo, Calleria, Río Utiquinia, cerca de la Quebrada Pumayacu, 6 September 2003, *Graham 2260* (USF); Coronel Portillo, Yarinococha, 26 March 1981, *Vásquez & Jaramillo 1457* (MO).

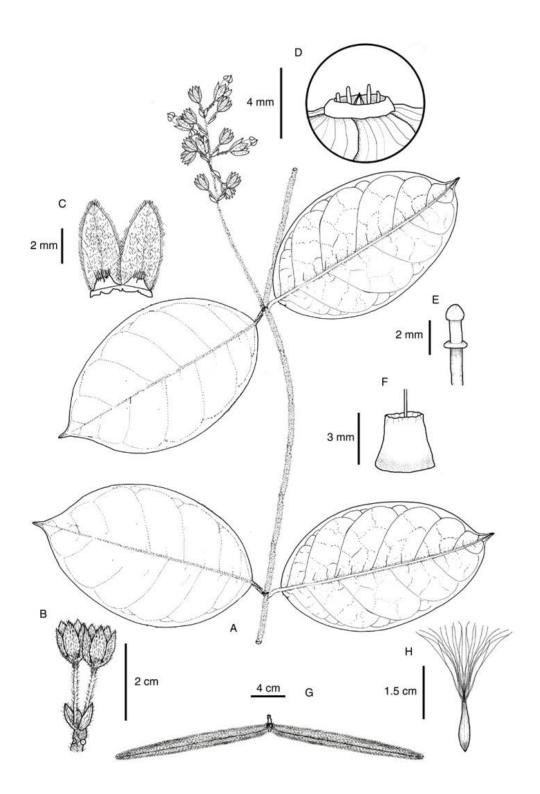


Fig. 61 *Prestonia racemosa* (A-F from *Vásquez et al. 21615*, MO; G-H from *Vásquez et al. 18775*, MO). A. Stem with inflorescence. B. Calyx, pedicel, and floral bracts. C. Adaxial view of the sepal, showing the colleter. D. Corolla mouth, showing the apices of the anthers and the free coronal lobes. E. Style-head. F. Nectary. G. Follicles. H. Seed.

*Prestonia riverae* J.F. Morales (1997: 63). Type:—COSTA RICA. Guanacaste: Parque Nacional Rincón de la Vieja, El Canal, 2 April 1991, *G. Rivera 1211* (holotype CR!, isotypes CR!, MO!). **Fig. 62, 63.** 

**Stem** densely to moderately sericeous, sparsely puberulent at maturity, with clear latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2–5 mm long. **Petioles** 0.6–1.8 cm; leaf blade  $9-23 \times 5.5-13$  cm, elliptic, narrowly elliptic to orbicular, apex acute to short-acuminate, base obtuse to rounded, membranaceous, sparsely puberulent adaxially, densely tomentose or tomentulose abaxially, indument drying ferrugineous, secondary veins impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. Inflorescence a dichasial cyme (but resembling an umbel), axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, tomentose to tomentulose, peduncle 0.8–2.3 cm, pedicels less than 0.3 cm long, floral bracts 6–8 × 2–3.5 mm, elliptic, narrowly elliptic, to narrowly ovate-elliptic, subfoliaceous, green. Sepals  $15-24 \times 3-7$  mm, free, membranaceous, narrowly ovate to narrowly elliptic, the apices acute to acuminate, not reflexed, tomentose to tomentulose, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed or inconspicuous, colleters 2.5–4 mm long, entire to somewhat lacerate at the apex. Corolla salverform, yellow, tomentose to tomentulose outside, tube  $(18-)20-23 \times 3-5$  mm, usually straight, slightly constricted below the attachment of the stamens, free corona lobes absent, annular corona reduced to 5 conical calloused ridges, delicate and inconspicuous, corolla lobes 9-12 × 8-9 mm, obliquely obovate. Stamens inserted ca. In the middle of the tube, anthers 10–12 mm, dorsally glabrous, included. Ovary ca. 1 mm tall, glabrous, style-head 2-3 mm, nectary 1.5-2 mm, conspicuously surpassing the ovary, subentire to slightly 5-lobed, each lobe (when lobed) entire to subentire, glabrous to inconspicuously puberulent. Follicles 12–20 × 1.2–2 cm, continuous, free, falcate and usually united at the tips (at least when young) or divaricate with the tips divergent, ferrugineous-hirsutulous, firmly membranaceous to very slightly woody when old; seeds 10–12 mm, coma (2.7–)3–5(–5.3) cm, tannish cream, cream to tannish brown.

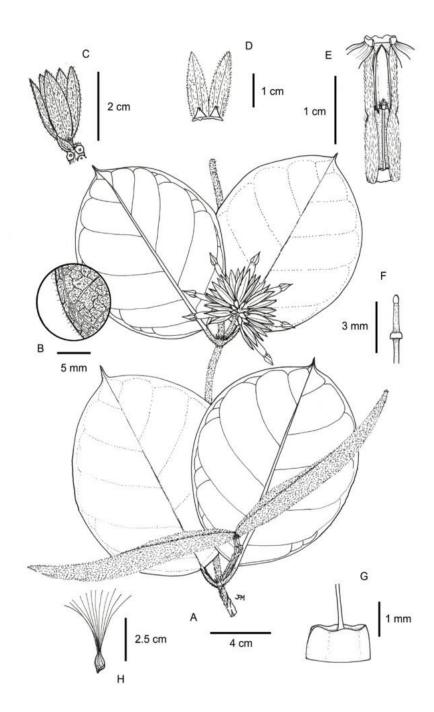


Fig. 62 *Prestonia riverae* (*Hammel 8921*, DUKE). A. Branch with flowers and fruits. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and bract. D. Adaxial view of two sepals. E. Open corolla tube, showing the anthers and anular corona. F. Style-head. G. Nectary. H. Seed.

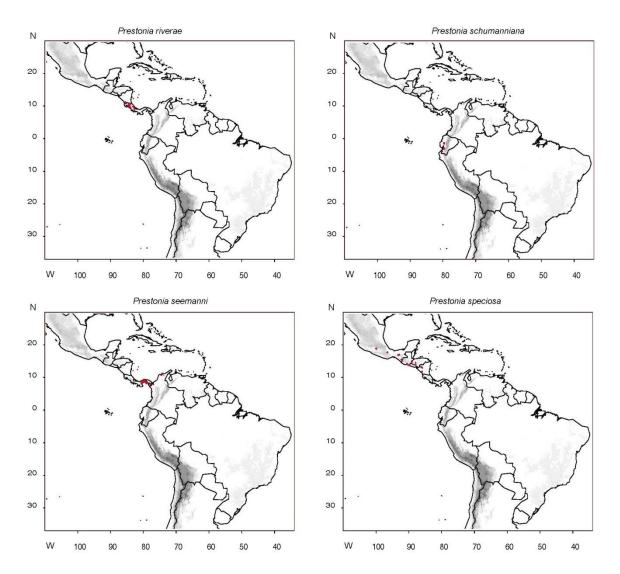


Fig. 63 Distribution maps of Prestonia riverae, P. schumanniana, P. seemannii and P. speciosa

**Distribution and habitat**:—Costa Rica and western Panama, where it grows in tropical wet forest, premontane forest, and secondary vegetation at elevations from 100–900 m.

**Phenology**:—Flowering and fruiting May-September.

Conservation Assessment:—Vulnerable (VU).

**Taxonomic notes:**—*Prestonia riverae* can be separate from *P. mexicana* by its usually sessile or subsessile flowers, longer anthers, and falcate follicles. In *P. riverae* the indument on the abaxial surface of the leaf blades tends to be more dense than in *P.* 

*mexicana*. However, considering the high variability of this character, sterile collections of the two are extremely difficult to separate.

Additional specimens examined:—COSTA RICA. Alajuela: Buena Vista de San Carlos, 2 May 1964, Jiménez 1952 (CR, F, MEXU, MO, NY). Guanacaste: Parque Nacional Guanacaste, San Ramón, 12 November 1994, Espinoza 1190 (CR, K, MO); Parque Nacional Rincón de la Vieja, Hacienda Santa Maria, 17 August 1987, Herrera 736 (CR, F, MEXU, MO, WAG); La Cruz, Parque Nacional Guanacaste, Pitilla, Volcán Orosí, 14 August 1997, Moraga 918 (CR, F, MO); Parque Nacional Guanacaste, San Ramón, 4 April 1995, Quesada 296 (CR, F, K, MO, NY); Rincón de la Vieja, Finca Los Mora, 12 October 1990, Rivera 728 (B, MO). Heredia: Finca La Selva, Puerto Viejo de Sarapiquí, 24 July 1979, Grayum 2027 (DUKE); Sarapiquí, 4 June 1980, Hammel 8921 (CR, MO); Finca La Selva, Sarapiquí, 26 July 1984, *Jacobs* 2977 (DUKE, MO), 28 May 1985, *Jacobs* 3190 (CR, MO); Sarapiqui, reserva biológica La Selva, Río Sarapiquí, 16 April 2010, Morales & Endress 18628 (CR); La Selva, 28 September 1981, Smith 304 (CR, DUKE). Limón: Fila Matama, Cerro Muchila, Río Bananito, 25 January 2001, Morales 7748 (CR); falda N del Cerro Muchila, Fila Matama, 24 May 2009, Morales 17840 (CR). San José: Tarrazú, ca. 15 km al SO de San Marcos, camino a Quepos, 17 February 2006, Hammel et al. 24113 (CR, MO); Acosta, San Jerónimo, fila que baja al Candelaria, 8 March 2014, Morales 21435 (CR).

PANAMA. Bocas del Toro: Caribbean slopes of Cerro Fábrega at foot of Falso Fábrega, Palo Seco Reserve, 27 March 2005, *Monro & Cafferty* 5075 (PMA).

*Prestonia schumanniana* Woodson (1936: 364). Type:—ECUADOR. Guayas: Balao, May 1892, *B. Eggers 14722* (holotype M!). **Fig. 63, 64** 

**Stem** minutely tomentulose to densely puberulent, color of latex unknown, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2–2.5 mm long. **Petioles** 1–1.6 cm; leaf blade 11.5–15.3 × 4.6–7.6 cm, elliptic, apex short-acuminate or caudate, base obtuse, membranaceous, very sparsely puberulent adaxially, minutely tomentulose abaxially, indument drying yellow, secondary veins usually impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the

adjacent leaves, few-flowered, the flowers densely clustered, tomentulose, peduncle 1.8-2 cm, pedicels 1-1.5 cm long, floral bracts  $2-4\times1.5-2$  mm, linear to linear-elliptic, scarious, minute, green. **Sepals**  $9-11\times2.5-3$  mm, free, membranaceous, narrowly elliptic, the apices acute-mucronulate, not reflexed, tomentulose, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins not impressed, colleters 1.5-3 mm long, entire to subentire at the apex. **Corolla** salverform, color unknown, densely tomentulose outside, tube  $9-13\times2-2.5$  mm, straight or slightly expanded toward the mouth, free corona lobes absent, annular corona entire or irregularly 5-lobed, thickened, corolla lobes  $8-11\times4-5$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 6-6.5 mm, dorsally glabrous, the apices exserted. **Ovary** ca. 1.5 mm tall, glabrous, style-head 1.5-2 mm, nectary 1.5-2.5 mm, equaling or surpassing the ovary, slightly 5-lobed, each lobe subentire. **Follicles** unknown.

**Distribution and habitat**:—Endemic to Ecuador, where it grows in dry forest in Ecuador, ca. 100 m.

**Phenology**:—Flowering May.

**Conservation Assessment**:—Endangered (CR)

**Taxonomic notes:**—*Prestonia schumanniana* has been known mostly from the type, which was long misplaced in the Munich herbarium (M). Only one additional specimen is known. This species resembles *P. mexicana*, having similar leaves and inflorescences (shape, structure, and indument), but differs by its smaller flowers. For a full discussion of the taxonomic history of this taxon, see Morales (2010a).

**Additional specimens examined**:—ECUADOR. Los Ríos: Jauneche forest, Jauneche, km 70 Quevedo-Palenque vía Mocachi, Vinces, 27 March 1980, *Dodson & Gentry 9982* (CR, MO, SEL).

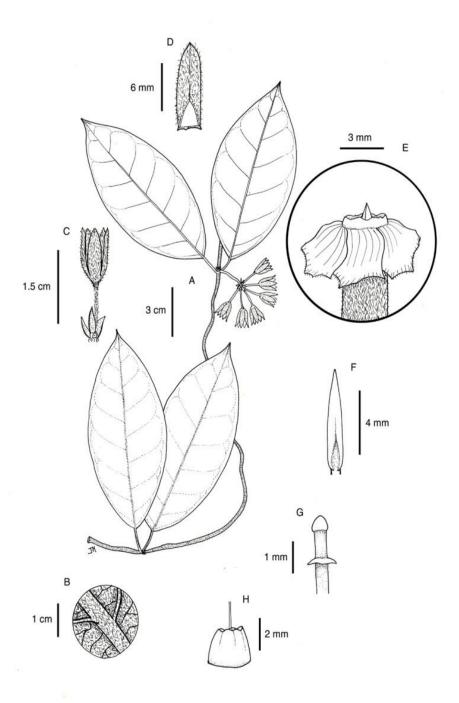


Fig. 64 *Prestonia schumanniana* (*Eggers 14722*, M). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and bract. D. Adaxial view of the sepal, showing the colleter. E. Corolla mouth, showing the annular corona and anthers apices. F. Anther, dorsal view. G. Style-head. H. Nectary.

*Prestonia seemannii* Miers (1878: 146). Type:—PANAMA. Panama: near Panama city, s.d., *B. Seemann 159* (holotipo BM!, isotype K!). **Fig. 63, 65** 

**Stem** moderately to sparsely hispid or glabrescent, with milky latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2.5–3.5 mm long. **Petioles** 0.2–1 cm; leaf blade  $6-21(-26) \times 3-12$  cm, elliptic, narrowly elliptic to obovate, apex acute, caudate, or long-acuminate, base obtuse to rounded, membranaceous, hispidvelutinous adaxially, velutinous to velutinous-tomentose abaxially, indument drying yellow to yellowish brown, secondary and tertiary veins impressed on both surfaces. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the adjacent leaves, fewto many-flowered, the flowers densely clustered, ferrugineous-hispid, peduncle 1–2.6 cm, pedicels 0.3–1 cm long, floral bracts  $5-9 \times 2-4.5$  mm, narrowly elliptic to narrowly ovateelliptic, subfoliaceous, green. Sepals 9–12 × 3–4 mm, free, membranaceous, ovate, narrowly ovate, narrowly ovate-elliptic to narrowly elliptic, the apices acute to shortly acuminate, not reflexed, hispid-velutinos, foliaceous, drying with a more or less uniform color, the veins conspicuously impressed, colleters 2–3 mm long, slightly lacerate at the apex. Corolla salverform, yellow to cream, hirsute outside, tube  $(10-)11.5-16 \times 3-4$  mm, straight, free corona lobes 1–2.5 mm long, the apices barely exserted or included, their height equaling or slightly surpassing that of the anther apices, annular corona entire to subentire, rarely 5-lobed, thickened, corolla lobes 9–15 × 4–6 mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5–6 mm, dorsally glabrous, the apices exserted. Ovary ca. 1 mm tall, puberulent to glabrescent, style-head 1.3–1.6 mm, nectary 1.5–2(–2.5) mm, conspicuously surpassing the ovary, entire, subentire to irregularly tri- or 5-lobed, each lobe (when lobed) irregularly lacerate. Follicles 10–13 × 1–1.4 cm, continuous, divaricate, free, the tips divergent, hispid, without lenticels, slightly woody when old; seeds 11–14 mm, coma (2.3–)2.5–3.2 cm, cream.

**Distribution and habitat:**—Moist forest, tropical wet forest, thickets, and secondary vegetation in Central Panama and with one collection in northern Colombia, from 0 to 500 m.

**Phenology**:—Flowering May-October. Fruiting September-April.

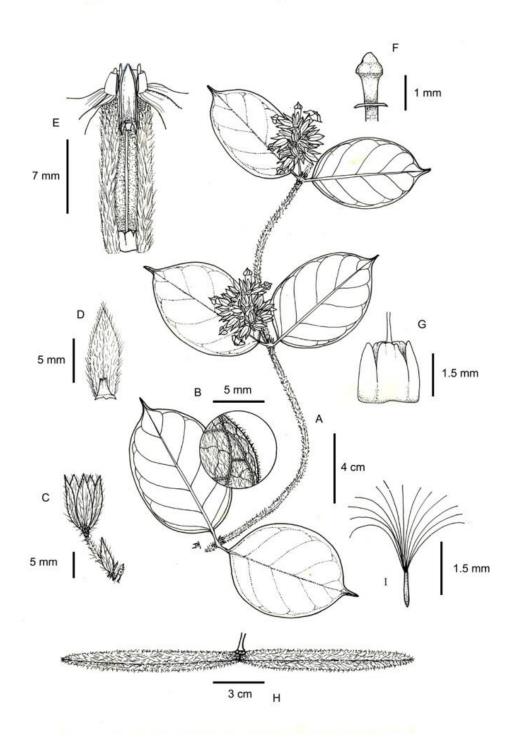


Fig. 65 *Prestonia seemannii* (*Correa et al. 4683*, INB). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and bract. D. Adaxial view of one sepal,. E. Open corolla tube, showing the anthers and free coronal lobes. F. Style-head. G. Nectary. H. Follicles. I. Seed.

## **Conservation Assessment**:—Vulnerable (VU).

**Taxonomic notes**:—*Prestonia seemannii* is characterized by its sparsely hispid or glabrescent stems, with indument drying yellow to yellowish brown, corolla tube 10–13 mm, free corona lobes with the apices exserted, and hispid follicles. This species resembles *P. bahiensis*, but differs by its shorter corona lobes and longer follicles. For a full discussion of the taxomonic history of *P. seemannii* see Morales (1997a).

Additional specimens examined:—PANAMÁ. Coclé: La Pintada, 16 February 1935, Hunter & Allen 520 (G, MO); Nata, cerca a Río Grande, 24 May 1970, Rosario 43 (MO, PMA). Colón: camino maderero de Santa Rita, 10 October 1968, Correa & Dressler 1096 (PMA). Darién: Pigonana de El Real, 15 July 1971, Croat & Porter 15555 (MO); Antón, comunidad del Jobo, camino al Rio La Estancia, 14 July 1996, Montenegro 1377 (PMA); cerca de La Palma, S del Darién, January 1912, Pittier 5494 (US). Los Santos: Managre, 29 July 1963, Dwyer 4171 (GH, MO). Panamá: cerca de Bejuco, 18 October 1938, Allen 980 (MO); Islas Perlas, 5 July 1941, Allen 2590 (MO); Nuevo Arraiján, 9 January 1973, Caicedo 49 (MO, PMA); Bahía Tempolo, 17 November 1974, Cambra 13 (MO, PMA); Cerro Jefe, 6 January 1971, Croat 13060 (MO); Cerro San Francisco, 16 April 1986, Correa et al. 4683 (CR, MO, PMA); Zona del Canal, Madden Dam Bridge, 12 October 1967, Correa 359 (F, MEXU, MO, PMA); s.l., 9 October 1975, Doyen 16 (PMA); Zona del Canal, Ancon Hill, 10 October 1961, Duke 4583 (MO); Paraiso, 29 November 1966, Dwyer 7144 (MO [2 sheets], PMA); Zona del Canal, 27 August 1967, Dwyer 9167 (MO); Isla Taboga, 15 August 1972, Gentry 5727 (CR, MO); Tocumen, 22 September 1975, González 30 (MO, PMA); cerca al aeropuerto, 30 July 2000, González s.n. (CR); cerca a la ciudad de Panamá, 25 September 1869, Hayes s.n. (BM); Bellavista, 25 February 1923, Macbride s.n. (F, US); cerca al Río Tapia, 1 June 1923, Maxon et al. 6735 (US); La Chorrera, 27 November 1975, Medina 32 (MO, PMA); cerca de Bella Vista, 21 February 1923, Piper 5352 (US); Punta Paitilla, 22 February 1923, Piper 5428 (US); camino del Boticario, cerca a Chepo, October 1911, Pittier 4700 (C, BM, GH, US); camino a Tumba Muerto, 6 January 1924, Standley 29757 (US); Punta Paitilla, September 1924, Stevens 340 (US); E de Canita, 30 May 1966, Tyson et al. 4161 (DUKE, MO); cerca a Capira, 12 July

1938, Woodson et al. 1230 (MO). Data lacking: 1850, Duchassaing s.n. (P); 1851, Duchassaing s.n. (P [2 sheets]).

COLOMBIA. Magdalena: Santa Marta, s.d., *Purdie s.n.* (K).

- *Prestonia speciosa* Donnell Smith (1899: 435). Type:—GUATEMALA. Santa Rosa: Buena Vista, April 1893, *N. Heyde & E. Lux 4497* (holotype US!, isotypes BM!, G!, GH!, K! [photo MEXU!], US! [3 sheets]). **Fig. 63, 66.**
- Prestonia grandiflora L.O. Williams (1968: 402). Type:—MEXICO. Chiapas: La Grandeza, 19 May 1945, E. Matuda 15570 (holotype F!, isotypes EAP!, F! [photos F neg. 56493 and 56494], MO! [2 sheets], S!, TEX-LL!).

Stem variously pubescent, sometimes glabrescent at maturity, with clear latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 3.5–5 mm long. **Petioles** 0.4–1.1 cm; leaf blade  $8-26 \times 6-13.5$  cm, obovate, broadly elliptic to orbicular, apex acuminate to caudate, base cuneate, obtuse to rounded, membranaceous, sparsely puberulent to glabrescent adaxially, tomentose or tomentulose abaxially, indument drying brown to somewhat ferrugineous, secondary and tertiary veins impressed on both surfaces. **Inflorescence** a dichasial cyme, axillary, shorter than the adjacent leaves, manyflowered, the flowers densely clustered, tomentulose, peduncle 0.4–2.2 cm, pedicels 0.9– 1.7 cm long, floral bracts  $3-12 \times 2-4$  mm, narrowly elliptic to narrowly ovate-elliptic, foliaceous to subfoliaceous, green. Sepals 9–18 × 4–8 mm, free, membranaceous, ovate, ovate-elliptic to narrowly elliptic, the apices acute to acuminate or mucronulate, not reflexed, tomentulose, foliaceous, drying with a more or less uniform color, the veins conspicuously impressed, colleters 1–2 mm long, slightly erose or lacerate at the apex. **Corolla** infundibuliform, yellow, densely to moderately tomentulose outside, lower part of the corolla tube  $12-19 \times 3-4$  mm, the upper part 10-20 mm, 10-20 mm diam. at the orifice, conical to narrowly campanulate, free corona lobes absent, annular corona entire, subentire or irregularly lobed, thickened, corolla lobes 20–30 × 11–18 mm, obliquely obovate. **Stamens** inserted at the base of the upper part of the corolla tube, anthers 8–9 mm, dorsally glabrous, included. Ovary 1-1.5 mm tall, glabrous, style-head 2-2.5 mm, nectary 3-3.5 mm, conspicuously surpassing the ovary, 5-lobed to irregularly lacerate, each lobe subentire. Follicles 7–9 × 1.8–2.7 cm, continuous, divaricate, free, the tips divergent, densely sericeous or tomentulose, without lenticels, somewhat woody when old; seeds 11.5–14 mm, coma (1.8–)2–3(–3.3) cm, cream.

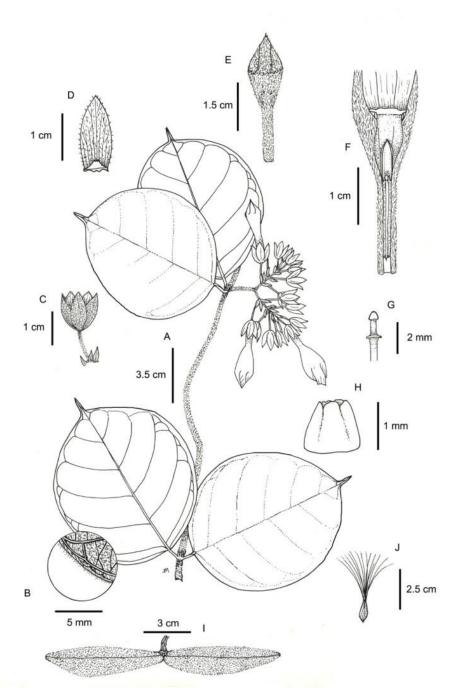


Fig. 66 Prestonia speciosa (A-H from Stevens 21536, MO; I-J from Sandoval 1586, MO). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts.
D. Adaxial view of one sepal, showing the colleter. E. Floral bud. F. Open corolla tube, showing the point of insertion of the anthers. G. Style-head. H. Nectary. I. Follicles. J. Seed.

**Distribution and habitat:**—Cloud forest, premontane forest, moist forest, and secondary vegetation from southern Mexico to northern Nicaragua, from 400 to 1850 m.

**Phenology**:—Flowering February-August. Fruiting February and April.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local name:—Bejuco flores amarilla, bejuco hocico de pezote de altura (Ahuachapán, El Salvador).

**Taxonomic notes**:—*Prestonia speciosa* and *P. clandestina* resemble one another in the infundibuliform corolla, feature found only in these two species. *Prestonia clandestina* is easily differentiated by shorter pedicels (9–17 mm vs. flowers subsessile and with pedicels up to 4 mm) and shorter corolla tube. Fruiting collections of *P. speciosa* are rare (less than three are known), and difficult to separate from *P. mexicana*, since both species have leaf blades with similar pubescence and shape.

Additional specimens examined:—MÉXICO. Chiapas: SE of Cerro Baul, 16 km NW of Rizo de Oro, along road to Colonia Figaroa, Cintalapa, 21 April 1972, *Breedlove 24744* (MEXU); East base of Cerro Tres Picos near Cerro Bola, along a logging road SW of Colonia Agronomos Mexicanos, Villa Corzo, 27 May 1972, *Breedlove 25460* (MEXU); Mapastepec, Reserva El Triunfo, 23 February 1990, *Hampshire et al. 621* (BM [2 sheets], MEXU); Reserva El Triunfo, El Tomatal, Jaltenango, Mapastepec, 21 February 1990, *Heath & Long 698* (MEXU); Siltepec, 23 June 1941, *Matuda 4681* (A, F, MEXU, MICH, MO, NY); a lo largo del Río de Bochil, 27 June 1967, *Shilom 2597* (F [2 sheets], NY). Guerrero: Atoyac de Alvarez, 2 July 1984, *Núñez 1180* (MEXU). Oaxaca: Monte Tierra, 3 km en línea recta al SE de Santa Cruz de Tepetotutla, San Felipe Usial, Tuxtepec, 29 September 1994, *Osorio 270* (MEXU, MO).

GUATEMALA. Quezaltenango: Montaña Chicharro, al S de Santa María de Jesús, *Steyermark 34139* (F). Zacatepequez: faldas del Volcán de Fuego, 1955, *Aguilar 2004* (EAP); Alotenango, *Smith 1448* (US). Data lacking: January 1878, *Bernoulli & Cario 1830* (K).

HONDURAS. Comayagua: Montaña el Cedral, Cordillera Montecillos, 24 May 1956, *Molina 7199* (EAP, F); Comayagua, 1980, *Nelson et al. 6616* (EAP, MO, TEFH).

Copán: O de Copán, 1 August 1977, *Croat 45520* (MO). Yoró: Yoró, January 1981, *Nelson et al.* 7292 (EAP, MO, TEFH).

El SALVADOR. Ahuachapán: San Benito, Cerro Campana, Las Pirámides, 19 February 1994, *Chinchilla et al. s.n.* (B, LAGU, MO); San Francisco Menéndez, El Corozo, Mariposario, 14 April 2000, *Rosales 585* (B, LAGU); El Imposible, San Benito, 16 March 1992, *Sandoval & Chinchilla 311* (B, LAGU, MEXU, MO [2 sheets]); Parque Nacional El Imposible, San Benito, 11 June 1997, *Sandoval 1586* (B, CR, EAP, LAGU, MO); Sierra de Apaneca, Finca Colima, 17 January 1922, *Standley 20091* (US); Apaneca, 2 May 1979, *Witsberger 605* (MO); Cerro Campana, 26 July 1979, *Witsberger 717* (MO). La Libertad: Puerta de La Laguna, 27 April 1922, *Standley 23673* (GH, US). Sonsonate: Laguna de Las Ninfas, 4 March 1991, *Villacorta & Cortez 742* (B, CR, LAGU, MO).

NICARAGUA. Granada: Volcán Mombacho, 19 April 1982, *Moreno 16125* (MO). Jinotega: Santa Lastenia, 5 June 1982, *Stevens 21536* (CR, MEXU, MO, WAG). Matagalpa: Matagalpa, May 1985, *Davidse et al. 30428* (MO, WAG).

Prestonia surinamensis Müller Argoviensis (1860: 433). Type:—SURINAME. Without data, W. Hostmann 981 (lectotype W!, designated by Woodson (1936), isolectotypes B [destroyed, photo F neg. 4552!], K! [2 sheets], MO!, NY!, P!, U!). Fig. 67, 68

Stem minutely ferrugineous-tomentose, usually glabrescent at maturity, with milky latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2.5–3.5 mm long. Petioles 0.3–4 cm; leaf blade 6–29 × 5–18 cm, elliptic, ovate to broadly ovate, apex abruptly short-acuminate, base obtuse to rounded, membranaceous, glabrescent to minutely puberulent adaxially, densely and minutely velutinous abaxially, indument drying brown, secondary veins impressed on both surfaces, tertiary veins scarcely impressed abaxially, rather inconspicuous adaxially. Inflorescence a dichasial cyme (but resembling an umbel), axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, ferrugineous-velutinous, peduncle 1–4 cm, pedicels 0.4–1 cm long, floral bracts 5–18 × 2–5 mm, elliptic, narrowly elliptic to narrowly ovate-elliptic, foliaceous to subfoliaceous, green. Sepals 8–13(–15) × 3.5–7 mm, free, membranaceous, ovate to ovate-elliptic, the apices acute to shortly acuminate, not reflexed, minutely

ferrugineous-sericeous, foliaceous, drying with a more or less uniform color, the veins usually inconspicuous, colleters 2–2.5 mm long, subentire to irregularly erose at the apex. **Corolla** salverform, yellow to yellowish green, densely sericeous outside, tube  $14-18 \times 3-4.5$  mm, straight, free corona lobes 2–4 mm long, slightly exserted, their height equaling or slightly surpassing that of the anther apices, annular corona entire, thickened, corolla lobes  $6-11 \times 5-6$  mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 6-7 mm, dorsally glabrous, the apices barely exserted. **Ovary** ca. 1.5 mm tall, glabrous, stylehead 2–2.2 mm, nectary 2–2.5 mm, conspicuously surpassing the ovary, slightly to deeply 5-lobed, each lobe subentire. **Follicles**  $9-16 \times (1-)1.5-2.3$  cm, continuous, divaricate, free, the tips divergent, minutely ferrugineous-sericeous, sometimes glabrescent when old, without lenticels, woody when old; seeds 15-22 mm, coma (1.7-)3-4 cm, cream.

**Distribution and habitat:**—Tropical wet forest, floodplain forest, vegetation along riverbanks and disturbed forest edges in northern Colombia to Brazil and northern Peru, from 0–1200(1600) m.

**Phenology**:—Flowering occurs sporadically throughout the year. Fruiting specimens have been collected in February and from September-December.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

**Taxonomic notes**:—*Prestonia surinamensis* is closely related to P. *tomentosa*, but differs by its usually more open inflorescences, minutely ferrugineous-sericeous follicles, and seeds 1.5–2.2 cm (vs. 0.8–1 cm). However, specimens with inmature inflorescences can be difficult to identify.

Additional specimens examined:—COLOMBIA. Antioquia: Cáceres, El Doce, Bajo Cauca, entre Quebradas Puri y Corrales, 26 March 1978, *Callejas 509* (COL, HUA, NY); Tarazá, Río Cauca, entre El Doce a Barro Blanco, 13 June 1987, *Daly et al. 5219* (CR, HUA, MO, NY, US, WAG). Bolivar: San Pedro, 29 May 1949, *Romero-Castañeda 1770* (COL, IAN, MEDEL [2 sheets]). Data lacking: 1783–1808, *Mutis 4085* (MA [2 sheets], US).

VENEZUELA. Delta Amacuro: entre La Margarita y Puerto Miranda, 23 November 1960, *Steyermark 87710* (K, NY, U, UB, US, VEN).

GUYANA. Barima-Waini: región superior del Sebai, tributario del Río Kaituma, 17 December 1991, *Hoffmann et al. 644* (P, US). Cuyuni-Mazaruni: Takutu creek, Río

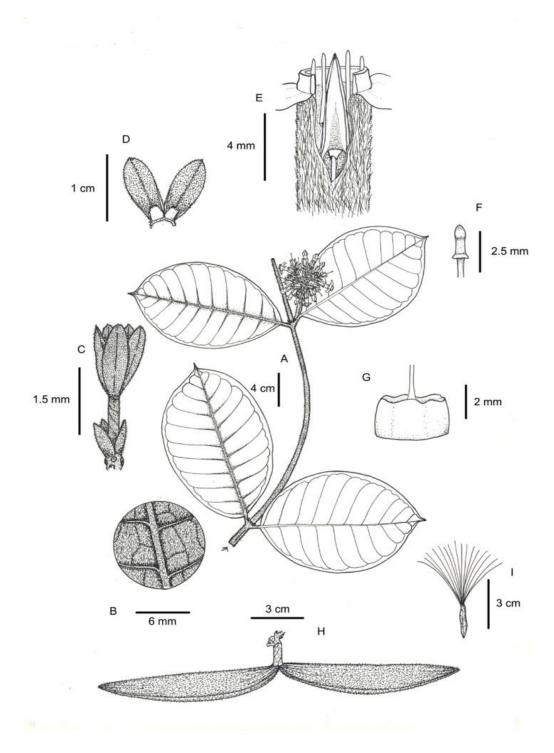


Fig. 67 *Prestonia surinamensis* (A-G from *Callejas 509*, HUA; H-I from *Duarte 6892*, INB). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts. D. Adaxial view of two sepals, showing the colleters at the base. E. Open corolla tube, showing the free coronal lobes and anthers. F. Style-head. G. Nectary. H. Follicles. I. Seed.

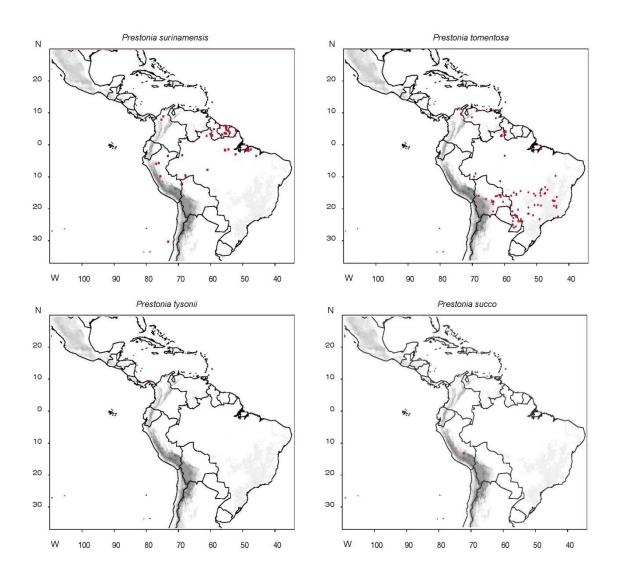


Fig. 68 Distribution maps of Prestonia surinamensis, P. tomentosa, P. tysonii and P. succo

Mazaruni, 10 January 1944, *Fanshawe 2010* (MO). Potaro-Siparuni: Iwokrama, Río Siparuni, cataratas Pakatau, 30 November 1994, *Mutchnick & Allicock 439* (NY, U, US). Upper Demerara-Berbice: región superior del Río Demerara, September 1887, *Jenman 4048* (K, NY); Demerara, s.d., *Parker s.n.* (K [2 sheets]). Upper Takutu-Upper Essequibo: cuenca superior del Río Rupununi, cerca a Dadanawa, 30 May 1922, *Cruz 1419* (CM, F, MO, NY, UC, US), 10 June 1922, *Cruz 1489* (CM, F, MO, NY, RB, UC, US).

SURINAME. Brokopondo: Brownsberg Nature Preserve, Mazaronitop, 23 November 2003, *Andel et al. 4491* (L); Accaribo, Río Surinam, 1912, *Angremond s.n.* (U,

Z [2 sheets]); bank of Sara Creek, S of Koffiekamp, 22 April 1964, *Donselaar 1250* (U); vicinity of Sectio O (railroad Paramaribo-Dam, November 1941, *Krukoff 12303* (MICH, MO, NY, US). Pará: a lo largo de la Quebrada Paulus, región inferior del Río Surinam, 4 October 1954, *Mennega 200* (K [2 sheets], U). Saramacca: Uitkijk, 25 km SO de Paramaribo, 21 nov 1974, *Outer 987* (U). Data lacking: *Wullschlägel 1029* (B [destroyed, photo F neg. 4552], BR, F, M, NY, W). Sipaliwini: Río Zuid, ca. 6 km del aeropuerto de Kayserberg, 10 June 2003, *Evans et al. 3463* (CR, MO); Corantine river, near Apoera, 22 October 1916, *Forest Deparment 2971* (NY, U); cercanías de la villa Kajana, Gran Río, 17 February 1998, *Hoffmann & van Troon 5263* (US); Gonini River, August 1903, *Versteeg 72* (U); Tapanahoni River, August 1904, *Versteeg 753* (U); confluencia de los ríos Palcemeu y Tapanahoni, 13 April 1963, *Wessels Boer 1296* (U, US).

FRENCH GUIANA. St. Laurent Du Maroni: Río Mana, cerca a Saut Ananas, 12 August 1981, *Cremers 7485* (CAY [3 sheets], COL, CR, NY, P, U); Río Inini, Maripasoula, 27 April 1975, *Sastre et al. 3990* (CAY, P, WAG). Cayenne: about 1 km of mouth or River Yaroupi, 26 September 1960, *Irwin et al. 48488* (F, IAN, K, MG, NY, S, U, US, Z); Cayenne, January 1842, *Mélinon 309* (P, WAG); Río Approuague, entre crique Maripa y Saut Machieau, 1 February 1967, *Oldeman 2424* (CAY [3 sheets], MO, NY, P, U).

ECUADOR. Los Ríos: Quevedo-Santo Domingo, O de Los Ángeles, 7 October 1976, *Dodson & Gentry 6506* (MO, SEL). Napo: Sarayacu, Arosemena Tola, carretera de Puyo a Puerto Napo, 8 April 1969, *Lugo 1044* (USF).

PERÚ. Amazonas: Condorcanqui, Río Santiago, Caterpiza, 4 September 1979, *Huashikat 371* (MO). Loreto: Maynas, Río Apayaca, 14 December 1980, *Ayala et al. 2908* (AMAZ, MO, USF); Maynas, Río Nanay, cerca de Santa María de Nanay, 4 January 1976, *Gentry & Ayala 15559* (AMAZ, F, MO, U, USM, Z); Maynas, Iquitos, Río Nanay, Cocha de la Marina, 2 January 1983, *McDaniel & Rimachi 26600* (AMAZ, MO, NY, USM); La Victoria, Río Amazonas, August 1929, *Williams 2942* (F, NY); Maynas, Varadero, Río Amazonas, camino a Mazan (río Napo), 13 November 1980, *Vásquez 743* (AMAZ, F, MO, NY, USF, USM); Alto Amazonas, Yurimaguas, 18 September 1981, *Vásquez & Jaramillo 2563* (MO [2 sheets]). Madre de Dios: Tambopata, 5 km de Puerto Maldonado, cerca de Río Tambopata, 24 January 1976, *Gentry & Revilla 16269* (F, MO, Z). Pasco: Oxapampa,

Pozuzo, carretera Pozuzo-Yanahuanca, 26 May 2009, *Vásquez et al. 35755* (CR, MO). San Martín: Zepelacio, cerca a Moyobamba, January 1934, *Klug 3525* (F, G, K, MO, NY, S, US, WIS); Lamas, Alonso de Alvarado, San Juan de Pacaizapa, 1 June 1977, *Schunke 9579* (MO, U [2 sheets], USM [2 sheets], WAG).

BRAZIL. Acre: Marechal Thaumaturgo, reserva extrativista do Alto Juruá, Bõa Vista do União, 30 apr 2001, Lohmann et al. 400 (NY); Rio Branco, campus Universitario, 29 September 1983, Mota & Santos 68 (INPA). Amazonas: Benjamim Constant, Alto Solimões, cerca a Igarapé, 8 September 1962, Duarte 6892 (CR, RB [3 sheets]). Maranhão: Mineirinho, Río Pindaré, 25 May 1979, Jangoux & Bahia 828 (INPA, MG, RB, Z). Pará: ríos Mojú y Acará, al S de Belém, 1 June 1969, Austin & Cavalcante 4076 (MG, MO), Austin & Cavalcante 4077 (MG, MO); Rio Mucajaí, cerca de Colonia Fernando Costa, 25 August 1951, Black & Magalhães 12901 (IAN); beira do Rio Branco, cerca de Bõa Vista, 26 August 1951, Black & Magalhães 12981 (IAN); Beira do Río Mojú, 1 June 1954, G.A.Black 54–16315 (IAN, MO); without exact locality, 30 December 1829, Burchell 9959 (K), 1 February 1830, Burchell 10093 (K); Altamira, Río Xingu, Transamazonica, km 46, travessão 17, 3 February 1987, Dias et al. 1114 (MG); Óbidos, 11 May 1905, Ducke s.n. (MG # 7277); Río Branco de Óbidos, 28 January 1918, Ducke s.n. (RB #21628, US); São Miguel de Guamá, 16 jan 1945, Fróes 20385 (NY); Igarapé Camatia, 25 January 1949, Fróes 24008 (IAN, MG, NY); Río Mojú, cerca a Mojú, 11 April 1957, Fróes 33168 (IAN); Mexiana, Fazenda Nazareth, 20 September 1901, Guedes s.n. (MG # 2363, RB); Belém, beira do Guamá, 10 May 1949, Guedes 150 (IAN, NY); Belém, 28 November 1945, Pires & Black 754 (IAN); Belém, 8 September 1948, Pires 1274 (IAN); Belém, IPEAN, 18 September 1967, Pires & Silva 10988 (CR, IAN); rodovia BR-401, ente Bôa Vista y Bom Fim, 27 June 1974, Pires & Leite 14688 (IAN); Río Pacaja, Ilha de Breu, 17 September 1965, Prance et al. 1325 (MO, NY, S, U, US, VEN); Río Tocantins, Ilha Jacarecaia, 23 June 1980, Revilla et al. 4475 (INPA); exacl locality lacking, Capoeira, 4 December 1903, Rodrigues s.n. (MG # 4041); camino do Cafezal, 26 November 1947, Silva 89 (IAN); região Garotiro, 28 July 1962, Silva 703 (IAN); Rio Guamá, 4 December 1903, Siqueira s.n. (RB # 21633).

- Prestonia tomentosa Robert Brown (1811: 70). Type:—BRAZIL. Rio de Janeiro: Rio de Janeiro, s.d., J. Banks 684 (holotype BM! [photo BM!, CR!, NY!]). Fig. 68. 69
- Prestonia latifolia Bentham (1841: 250). Type:—GUYANA. Upper Takutu-Essequibo: Pirara, 1839, Schomburgk 755 (lectotype (designated here) K! [2 sheets], isolectotypes B (destroyed), BM!, CAM!, CGE! [2 sheets], F!, FI-W! [2 sheets], G!, G-DC! [2 sheets], L!, NY!, P! [3 sheets], US!, W!).
- Prestonia lutescens Müller Argoviensis (1860: 163). Type:—BRAZIL. Minas Gerais: without data, P. Claussen 1957 (holotype W!).
- *Prestonia lanata* Müller Argoviensis (1860: 164). Type:—BRAZIL. Minas Gerais: without data, *L. Riedel s.n.* (lectotype P!, designated by Morales (2006 b), isolectotype LE n.v.).
- Prestonia cearensis Miers (1878: 148). Type:—BRAZIL. Ceará: without data, C. Gardner s.n. (holotype BM!)
- Prestonia goudotiana Baillon (1889: 792). Type:—COLOMBIA. Cundinamarca: Bogotá, Valle Magdalena, 1844, *J. Goudot s.n.* (lectotype (designated here) P! (photo F neg. 38793!)).
- Prestonia sericocalyx Malme (1899: 29). Type:—BRAZIL. Mato Grosso: Coxipo, near Cuiabá, 27 November 1893, *G. Malme 1276* (holotype S!, isotypes G!, G-DC!, LD! [2 sheets], R!, S!, UPS! [2 sheets], US!, Z!).
- Prestonia brachypoda S.F. Blake (1924: 530). Type:—VENEZUELA. Carabobo: Guaremales, road between Puerto Cabello and San Felipe, May 1920, *H. Pittier* 8832 (holotype US!, isotypes GH!, NY).
- Prestonia cornutisepala Rusby (1927: 329). Prestonia cephalantha Rusby (1927: 330), nom. illeg. Type:—BOLIVIA. La Paz: Ixiamas, 17 December 1921, M. Cardenas 1928 (holotype NY!, isotypes K!, NY!).
- **Stem** densely ferrugineous-tomentose, sometimes glabrescent at maturity, with clear or milky latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 2–3 mm long. **Petioles** 0.3-1.4 cm; leaf blade  $7.5-23(-35) \times 4-15.5(-28)$  cm, elliptic, broadly ovate to suborbicular, apex short-acuminate, base obtuse, rounded, or subcordate, membranaceous, sparsely puberulent adaxially, densely velutinous-tomentose abaxially, indument drying yellow to yellowish brown, secondary and tertiary veins

impressed on both surfaces. **Inflorescence** a dichasial cyme (but resembling an umbel), axillary, shorter than the adjacent leaves, many-flowered, the flowers densely clustered, ferrugineous-tomentose or ferrugineous-tomentulose, peduncle 0.6–2.8 cm, pedicels 0.4– 1.3 cm long, floral bracts 6–20 × 2–6 mm, elliptic, narrowly elliptic to narrowly ovateelliptic, foliaceous, green. Sepals  $10-17(-19) \times 5.5-7.5$  mm, free, membranaceous, ovate, ovate-elliptic to narrowly obovate, acute, the apices acuminate or shortly apiculate, not reflexed, tomentulose to hispid-tomentulose, foliaceous to subfoliaceous, drying with a more or less uniform color, the veins conspicuously impressed, colleters 1.5–2.5 mm long, subentire to minutely and variously lacerate at the apex. Corolla salverform, yellow to yellowish green, densely sericeous outside, tube 11–19 × 3.5–5 mm, straight, free corona lobes 2–4 mm long, the apices exserted, their height conspicuously surpassing that of the anther apices, annular corona entire to subentire, thickened, corolla lobes  $7.5-13 \times 5-8$ mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 5–6 mm, dorsally glabrous, the apices barely exserted. **Ovary** 1–1.5 mm tall, glabrous, style-head 1.5–2 mm, nectary 1.5–2.5 mm, conspicuously surpassing the ovary, variously 5-lobed, each lobe subentire to minutely and irregularly erose. Follicles 5–11 × 1.6–2.5 cm, continuous, divaricate, free, the tips divergent, hispid or hispidulous, without lenticels, woody when old; seeds 8–10 mm, coma 3.1–4.5 cm, tannish cream.

**Distribution and habitat:**—From Colombia to Bolivia, Paraguay and Brazil, where it grows in cerrados, dry forest, moist forest, gallery forest, savannas, and secondary vegetation, from 100 to 1450(–1600) m. *Prestonia tomentosa* was reported for Argentina by Ezcurra (1981), based on a single specimen, without any specific location and deposited in BAF. No additional collections have been found to confirm its presence in that country.

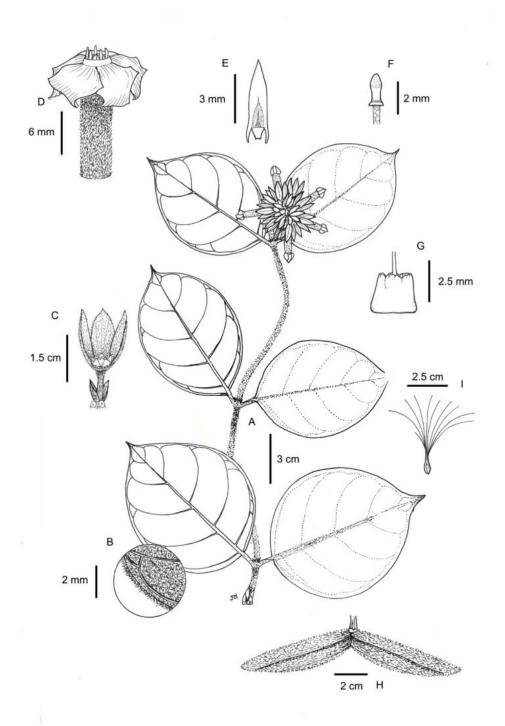


Fig. 69 *Prestonia tomentosa* (A-G from *Zardini & Guerrero 53357*, INB; H-I from *Zardini & Gentry 46975*, INB). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx with two sepals removed. D. Corolla. E. Anther, dorsal view. F. Style-head. G. Nectary. H. Follicles. I. Seed.

**Phenology**:—Flowering throughout the year. Fruiting specimens have been collected April-September.

Conservation Assessment:—Least Concern (LC), not endangered (IUCN 2001).

Local names:—Aguardientico (Guarico, Venezuela); bejuco de sapo, bejuco de seda (Los Llanos, Venezuela); cabeluda (Minas Gerais, Minas Gerais); cipózhino de leite (São Paulo, Brazil); palomitas (Lara, Venezuela).

**Taxonomic notes**:—*Prestonia tomentosa* shows an overall resemblance to *P. surinamensis*, but differs by its ferrugineous-tomentose or ferrugineous-tomentulose inflorescence, with the flowers densely clustered, hispid or hispidulous follicles, and larger seeds (15–22 mm vs. 8–10 mm). However, specimens with inmature inflorescences can be difficult to identify.

Two species are lectotypified here: *P. latifolia* and *P. goudotiana*. The type collection of *P. latifolia* is known for several duplicates, all of them very well preserved: the specimen at K is chosen as the lectotype. *Prestonia goudotiana* is known only from a single collection, which is selected as the lectotype.

Additional specimens examined:—COLOMBIA. Cesar: Chiriguana, 27 July 1924, Allen 178 (MO); La Jagua de Ibirico, La Victoria de San Isidro, vereda el Zumbador, vía La Jagua-El Zumbador, 17 March 1996, Fernández-Alonso et al. 13843 (COL); sabana La Jagua, 7 August 1943, Haught 3596 (COL, US); cerca a Jordán, 5 November 1898, Smith 165 (NY); cerca a Jordán, 5 November 1898, Smith 1657 (CM, F, K, NY, MO). Guajira: Sierra Nevada de Santa Marta, Río Cañas, 19 August 1986, Cuadros & Gentry 2948 (K, MEXU, MO, NY, USF). Meta: El Porvenir, 120 m, May 1978, Eberhard s.n. (USJ).

VENEZUELA. T.F. Amazonas: Orinoco, s.d., *Chaffanjon s.n.* (P); S de Puerto Ayacucho, 6 April 1978, *Morillo & Ocando 7330* (VEN). Anzoátegui: cerca a Río Meia, 10 December 1970, *Morillo 154* (VEN). Barinas: carretera a Pedraza, October 1971, *Aristeguieta 7997* (F, MO, NY, U, VEN); Reserva Ticoporo, 15 July 1964, *Breteler 4013* (WAG [2 sheets]); al NE de Barinas, 1 April 1974, *Gentry et al. 11149* (MEXU, MO, PMA, US, Z). Bolivar: Piar, La Vigía, al O de El Manteco, July 1978, *Delascio & Liesner 6962* (MO, VEN); Piar, vía San Pedro de las Bocas, NO de El Manteco, July 1978, *Delascio & Liesner 7353* (VEN); Río Botanamo, Reserva Imataca, February 1980, *Delascio & Lopes 8780* (VEN), *Delascio & Lopes 8924* (MO, VEN); 18 km al N de Upata,

Grossourdy s.n. (P); al N de Paragua, 28 July 1978, Liesner & González 5759 (VEN); Represa Guri, al E de Ciudad Piar, 7-8 April 1981, Liesner & González 11354 (MO, NY, U, VEN); Heres, Finca El Vapor, Río Carapo, 30 August 1991, Martino et al. 694 (MO, VEN); Río Orinoco, cerca del puente Angostura, 9 August 1979, Morillo & Rutkis 8064 (VEN); al S de ciudad Bolivar, 23 February 1980, Morillo 8233 (VEN); carretera Ciudad Bolivar-Maripa, 26 February 1980, Morillo & Carnevali 8263 (VEN); Cedeño, Río Orinoco, 27 June 1981, Rutkis 363 (US, VEN); Heres, La Mariquita, 4 April 1990, Tillett et al. 728 (VEN); entre El Dorado y Santa Elena, 1957, Trujillo 3716 (MY). Carabobo: cerca a Uramá, Guaremales, 11 November 1920, Pittier 9120 (US, VEN). Cojedes: Las Peonías, September 1975, Delascio & López 3408 (VEN); San Carlos, entre La Culebra y El Laurel, 7 November 1986, Delascio & López 12919 (MO, VEN); Hato Piñero, Cerro Vigiadero, 11 August 1996, Delascio & Gamarra 17218 (VEN); Cerro Mastrantal, Hato Samanote, El Pao, August 1986, Ramia & Ortiz 8588 (K, VEN); O de San Carlos, 24 August 1966, Steyermark et al. 96447 (NY, US, VEN). Falcón: Mauroa, Caracolí-Las Mesas, 19 April 1977, Wingfield 13166 (VEN). Guarico: carretera Ortiz-Galeras del Pao, August 1966, Aristeguieta 6304 (F, MO, NY, U, VEN), Aristeguieta 6255 (MO, NY, VEN); Infante, Espino, Finca San Mateo, 15 February 1991, Martino et al. 1123 (NY, VEN); cerca a Ortiz, Roscio, 8 September 1974, Rodríguez 78 (F, MY). Lara: cerca de Quebrada Arriba, 20 June 1968, Smith 3836 (VEN). Sucre: camino de Río El Medio a Palo de Agua, vía Carúpano-El Pilar, 15 July 1972, Dumont et al. 7693 (VEN); Río Sucre, camino El Río El Medio-Palo de Agua, Cerro al NE de El Rincón, vía Carupano-El Pilar 15 July 1972, Morillo 2693 (US). Yaracuy: San Felipe, carretera El Guayabo-La Hoya, 12 July 1973, Agostini et al. 1830 (CR, RB [2 sheets], U [2 sheets], VEN); entre Marín y Carbonero, 9 April 1925, Pittier 11766 (US, VEN); cerca a Taria, 29 May 1944, Stevermark 56855 (MO, VEN). Zulia: Perijá, carretera Maracaibo-Perijá, al SO de Villa del Rosario, 10 September 1977, Bunting 5418 (NY, VEN); entre El Pensado y Las Mercedes, s.d., Bunting 5615 (F, NY); carretera El Consejo-Palito Blanco-Sabana de la Plata, 22 December 1977, Bunting & Chacón 6012 (NY, VEN); Bolivar, cuenca del Embalse Burro Negro (Pueblo Viejo), entrre Piedras Blancas y Río Chiquito, 2 October 1979, Bunting & Alfaro 8044 (NY, VEN); Mara, cuenca del Río Guasare, 18 November 1982, Bunting

carretera a San Félix, 5 July 1975, Gentry & Berry 14922 (MO, U, VEN, Z); Upata, 1864,

12487 (MO); Acosta, San Gregorio, 19 Ab 1977, Ruiz 1113 (VEN). Data lacking: s.d., Grisol s.n. (P).

GUYANA. Upper Takutu-Essequibo: entre Sand Creek y Villa Shea, 28 May 1996, Clarke & McPherson 1767 (US); Montaña Darukoban, 1 July 1989, Gillespie 1953 (CR, MO, U, US); sabana Rupununi, valle Kumu head, 1962, Goodland & Maycock 437 (NY, U), Goodland 962 (NY, U, US); Rupununi, sendero entre Morris Mines y la villa Karasabai, 7 January 1982, Knapp & Mallet 2879 (BM, MO, USF); al NO de Karasabai, Río Ireng, 8 March 1990, McDowell et al. 2179 (NY, U, US); Pirara, 1841-1842, Schomburgk 374 (CAM, G, K, NY, P, W); Río Rupununi, Karenambo, October 1937, Smith 2210 (F, K, MO, NY, U, US); Iramaipang, Kanuku, November 1948, Wilson 528 (K, NY).

ECUADOR. Guayas: Cerro Blanco, 29 March 1996, Núñez et al. 425 (QCNE).

PERÚ. Pasco: Pasco, Pozuzo, 16 August 1981, *Teppener 81–248* (U). San Martín: San Martín, Tarapoto, December 1902, *Ule 6650* (G-DC, HBG, MG); Alto Río Huallaga, December 1929, *Williams 6825* (F); San Martín, Tarapoto, 25 February 1947, *Woytkowski 35165* (F, MO, UC).

BRAZIL. Acre: Sena Madureira, road to Chico Sales, 2 October 1980, *Cid & Nelson 2686* (INPA); Brasiléia, Xapuri, Reserva Chico Mendes, Seringal Bôa Vista, 9 December 1993, *Figueiredo 202* (NY, USF); Rio Branco, km 45, Rio Branco-Porto Velho road, 18 February 1978, *Santos et al. 18* (MG); Sena Madureira, Bacia do Río Purus, Varação do Cajú, Fazenda Nova Olinda, 25 October 1993, *Silveira et al. 634* (INPA, NY, USF); Río Branco, Surumu, February 1909, *Ule 7939* (G, G-DC, K, L, MG); Serra do Rel, Río Branco, November 1909, *Ule 8266* (G-DC, K, L, MG, UC, US); Río Branco, 17 November 1962, *Vasconcelos s.n.* (CR, INPA). Bahia: Melancias, 20 March 1892, *Glaziou 19621* (P). Goiás: Serra da Atalaia, SO de Monte Alegre de Goiás, 12 March 1973, *Anderson 6919* (K, MO, NY, UB, Z); Serra Dourada, ca. 17 km S de Goiás Velho, 6 km NE de Mossâmedes, 12 May 1973, *Anderson 10155* (C, COL, MO, NY, RB, UB, US, Z); Niquelândia, Macedo Velho Revelo, 14 December 1995, *Fonseca et al. 714* (FAU, IBE, RB); Goiás Velho, camino a Serra Dourada, 10 December 1968, *Grazielae et al. 751* (CR, UB); 47 km al S de Xavantina, camino a Aragarças, 9 November 1968, *Harley et al. 11346* (K); Formosa, UB); Serra Dourada, cerca a Goiás, 18 December 1968, *Harley et al. 11346* (K); Formosa,

9 January 1977, Hatschbach 39358 (MBM, WAG [2 sheets]); entre Anápolis y Brasília, 29 January 1978, Heringer et al. 16761 (IBGE, K, MO, NY, RB, UB, US, USF, WAG, Z); Serra do Morcego, NO de Formosa, córrego Estrema, 18 April 1966, Irwin et al. 14958 (IAN, MO, NY, RB, UB, US, Z); Serra dos Pirineus, N de Corumbá de Goiás, carretera a Niquelândia, 24 January 1968, Irwin et al. 19146 (IAN, K, MO, NY, RB, UB, US, Z); Bocaina, 8 November 1938, Markgraf et al. 3169 (RB); Niquelândia, Codemim, 15 April 1996, Marquete et al. 2536 (IBGE, RB); Goiás Velho, carretera a Serra Dourada, 10 December 1968, Mitzi et al. 751 (IPA, UB, Z); Cristalina, BR-251, Rio Preto, 14 May 2002, Santos et al. 1130 (HUEFS); Corumbá de Goiás, O de Brasília, 23 January 1994, Silva et al. 1858 (IBGE); Colinas do Sul, camino para a Serra da Mesa, 10 February 2002, Simões et al. 1228 (UEC, Z). Mato Grosso: Serra das Araras, Vão Grande, 24 February 2001, Dubs 2767 (E, NY, S, Z); Serra de Santa Bárbara, Porto Esperidião, 12 November 1996, Hatschbach et al. 65533 (MBM); Toscano, Cáceres, January 1909, Hoehne 1199 (R); Cosipó da Ponte, March 1911, Hoehne 3673 (R), Hoehne 3674 (R); Ranchão da Lagoa-Engenho Velho road, 23 November 1976, Macedo et al. 317 (INPA); Salobre, s.d., Santos s.n. (R). Mato Grosso do Sul: Bataguassu, Río Paraná, Río Pardo, Posto Fiscal Quinze Novo, 12 April 1999, Amaral et al. 464 (BOTU, COL); Corumbá, Fazenda María Coelho, 15 January 2006, Brina & Rezende 1235 (BHCB); Piraputanga, Aquidauana, 16 October 1972, Hatschbach 30499 (MBM, Z); Casa Brança, Bataguassu, 10 February 1983, Hatschbach 46106 (HBG, MBM); O de Iguatemi, 8 February 1993, Hatschbach et al. 58646 (CR, HBG, MBM); Porto Murtinho, rodovia Bonito-Campos dos Indios, cerca a Rio Getúlio, 14 November 2002, Hatschbach et al. 74198 (MBM); Aquidauana, rodovia Transpantaneira, cerca de Taboca, 20 March 2003, Hatschbach et al. 74968 (MBM); Bela Vista, Lajeado, 13 March 2004, Hatschbach et al. 77075 (MBM). Minas Gerais: without exact locality, 1840, Claussen s.n. (K [2 sheets]); without exact locality, s.d., Claussen 72 (G [2 sheets], P), Claussen 367 (P), Claussen 1838 (L, P [3 sheets]); Várzea da Palma, 19 November 1962, Duarte 7548 (CR, HB, NY, RB [3 sheets]); Belo Horizonte, Lagoa Santa, 21 January 1864, Engler s.n. (C [2 sheets, photo F neg. 22261], P); without exact locality, 1892, Glaziou 19625 (C, K); Diamantina, cerca a Gruta de Extração, 20 November 1984, Harley et al. 6223 (K, SP); Monte Alegre de Minas, 18 November 1973, Hatschbach & Kocsicki 33390 (HBG, MBM, Z); Barreiro da Vaqueada, Várzea da Palma, 12 March 1995,

Hatschbach et al. 61784 (CUVC, M, MBM, NY, WAG); Serra do Cabral, camino Várzea da Palma a Joaquim Felicio, 5 December 2004, Hatschbach & Barbosa 78883 (MBM, MEXU); Estação Experimental de Café, Coronel Pacheco, 15 November 1940, Heringer s.n. (CR, RB, Z); Paraopeba, Horto Florestal, 22 March 1960, Heringer 5120 (UB), 30 October 1959, Heringer 7244 (F, HB, UB, Z); Serra do Cabral, N de Joaquim Felício, 10 March 1970, Irwin et al. 27367 (NY, Z); Serra do Espinhaço, E de Belo Horizonte, 14 January 1971, Irwin et al. 30355 (F, K, NY, UB, US, Z); Chaveslândia, Santa Victoria, Río Paranaiba, 5 January 1989, Krapovickas & Cristóbal 42805 (C, CTES, F, K, MBM, MICH); Fundão, Ituiataba, 30 January 1948, Macedo 1011 (MO); Santana do Riacho, 24 August 2006, Marquete et al. 3855 (IBGE, RB); Montes Claros, Francisco Sá, 19 December 1989, Neto 12 (CR, ESAL); without exact locality, 1816–1821, St. Hilaire 707 (P), St. Hilaire 2491 (P). Paraná: Guaira, Parque Nacional de Sète Quedas, 18 March 1982, Custodio & Kirizawa 799 (HST, SP); Porto Mendes, 25 March 1977, Hatschbach 39843 (MBM, NY, UC). Rio de Janeiro: Ilha do Governador, 14 December 1876, Glaziou 8800 (BR, C, K, NY, P, UC); Rio de Janeiro, 1910, Lützelburg 1614 (M); Baixada Fluminense, carretera a Friburgo, 25 December 1962, Pabst 7230 (HB, Z [2 sheets]); Morro da Dondoca, 20 February 1966, *Pabst 8870* (HB, M, Z); Palmita, s.d., *Pohl 2214* (BR, F, NY, W). Roraima: Cantá, Serra Grande, 21 apr 2010, Cardoso & Moura 2864 (INPA); 10 km NNW of Bôa Vista, BR-174, 18 October 1977, Coradin & Cordeiro 750 (INPA. NY): Cantá, road to Serra Grande, 15 November 2011, Flores et al. 2488 (MIRR); Bonfim, BR-401, 10 August 2009, Flores et al. 2323 (MIRR); Mucajaí, Vicinal a Tamandare, 3–5 km after the bridge over the Rio Mucajai, 28 May 2011, Jardim et al. 6009 (MIRR); Bôa Vista, Rio Branco, s.d., Kuhlmann581 (RB); Ilha de Maracá, Reserva Ecológica SEMA, 11 June 1987, Milliken 327 (K); Maloca do Maracanã, Normandia, 20 km form Mutum, 13 October 1995, Miranda 1114 (INPA); Surúm, Rio Minapé, Serra Mairari, 28 February 1964, Silva 78 (MG); Bôa Vista, carretera a Confianças, 30 July 1986, Silva et al. 487 (INPA, MO, NY). T.F. Rondonia: road between Pimenta Bueno and Roulin de Moura, 5 km from Jaboti, 7 December 1982, Lisboa et al. 2867 (MG). São Paulo: Ibitinga, 12 January 1941, Grotta 711 (HBG, SP, Z); Rancharia, 14 February 1970, Hatschbach 23500 (MBM, Z); Río São Paulo, Heringer et al. 797 (IBGE, NY, P, USF); Estación Biológica Luiz Antônio Jatai, 4 February 1987, Lêitao et al. 18894 (IBGE, MG, UEC); Reserva Ecológica Morro do Diabo,

Teodoro Sampaio, 27 November 1984, *Pastore et al. s.n.* (F, SPSF). Tocantins: Serra São Roque, entre Posse y Alvorada, 17 April 1966, *Irwin et al. 14952* (MO, NY, UB, Z). Data lacking: 1842, *Claussen 339* (FI-W, G-DC); 1842 *Dupre s.n.* (P); s.d., *Guillermin 72* (G); 1839, *Pohl s.n.* (BR, M); s.d., *Sello s.n.* (FI).

BOLIVIA. Cochabamba: Chapare, El Palmar, km 118, cerca del Río Kachimayu, 22 December 2007, Terán et al. 2029 (BOLV, CR, MO). La Paz: Nor Yungas, Río Yalisa, 4 km N de Coroico, 5 November 1990, Lewis 37908 (CR, L, LPB, MO, NY, SI, USF); Sud Yungas, Alto Beni, Colonia San Pedro, 29 March 1995, Seidel & Vaquiata 7740 (LPB, MO); cerca a La Paz, 30 October 1984, Solomon et al. 12611 (LPB, MO, USF). Santa Cruz: Ñuflo de Chávez, Estancia San Miguelito, Puesto San Ramón, 3 December 1996, Fuentes & Rojas 1363 (USZ); Los Fierros, 7 December 1994, Guillén 2726 (MO, USZ); Ichilo, El Refugio, 25 January 1995, Guillén & Roca 3051 (MEXU, MO, USZ, WAG); Ñuflo de Chávez, entre San Ramón y San Javier, 14 March 2002, Guzman et al. 23 (MO, USZ); Río Blanco, 7 August year lacking, Herzog 950 (L); Río Pirai y Río Cuchí, January 1911, Herzog 1514 (G, S, W, Z); Ñuflo de Chávez, Las Trancas, 14 December 1994, Jardim & Killeen 1430 (CR, MO, USZ); Andrés Ibañez, Santa Cruz de la Sierra, cárcel de Palmasola, 15 January 2006, Mendoza 1998 (NY); Concepción, 4 km al S, 2 January 2009, Morales 18138 (CR); Ichilo, Parque Nacional Amboró, Quebrada Yapoje, upstream from confluence with the Rio Saguayo, 12 December 1989, Nee 38100 (LPB, MO, NY, USF, USZ); Guarayos, Surucusi, 12 July 1991, Nee & Coimbra 41664 (MO, NY, USZ); Andrés Ibáñez, NE de Cotoca, carretera a El Pauro, 18 December 1992, Nee 43149 (MO, NY); Cordillera, 8 February 1946, Peredo s.n. (FI, LIL, NY, P); El Pari, 9 April 1946, Peredo s.n. (LIL, S); Cordillera, Florida, 7 February 1946, Peredo s.n. (LIL, S); Capital, 24 February 1946, Peredo s.n. (LIL, S); La Cuesta, Cabezas, 29 January 1945, Peredo 93 (LIL, NY, S); Velasco, Parque Nacional Noel Kempff Mercado, al NO de Santa Rosa de la Roca, 22 June 1993, Saldias et al. 2665 (MO, USZ); Velasco, Presa Guapomó, 21 January 1986, Seidel 41 (LPB, M, P); Velasco, San Ignacio, Mercedes de las Minas, 29 April 1986, Seidel & Beck 294 (LPB, M, P); Nuflo de Chávez, al E de San Javier, 25 February 1998, Wood et al. 13087 (K); ca. 70 N de San Ignacio de Velasco, carretera a Concepción, 28 February 1998, Wood et al. 13182 (K, LPB, M, USZ); Chiquitos, entre Taperas e Ipias, autopista Santa Cruz-Puerto Suárez, 2 March 2007, Wood et al. 22908 (USZ); Andrés Ibáñez, entre Tierras Nuevas y El Palmar, 13 November 1994, *Vargas & Ortiz 3644* (MEXU, NY, USZ); German Busch, serranía del Mutúm, 9 March 2008, *Villaroel et al. 2045* (USZ). Tarija: Gran Chaco, entre Villamontes y Camiri, 27 September 1985, *Beck et al. 11645* (HBG, LPB, MO, SI, USF).

PARAGUAY. Amambay: cerca a Bella Vista, 16 April 1990, Bernardi 20619 (G. MO); carretera a Bella Vista, 23 February 1994, Krapovickas et al. 44968 (CTES, G, MICH, SI); O de Colonia Yvy-Jhu, 12 June 1996, Zardini & Cardozo 44888 (AS, MO); Estancia Don Juancito, Cerro Ysau, 12 June 1996, Zardini & Cardozo 44964 (AS, CR, MO, USF); Estancia La Serrana, Cerro Lorito, 14 June 1996, Zardini & Cardozo 45090 (AS, CR, MO, USF); cerca de Bella Vista Norte, 11 January 2000, Zardini & Guerrero 53321 (AS, CR, MO), Zardini & Guerrero 53357 (AS, CR, MO); sendero a Arroyo Estrella, 8 May 2000, Zardini & Guerrero 54146 (CR, MO); Cerro Corá, 28 February 2001, Zardini & Acosta 56230 (CR, MO). Caaguazú: Arroyo Yakareíi, 8 February 1989, Zardini & Velásquez, 10758 (MO, NY, SI). Canendiyú: cerca a Saltos de Guairá, 2 February 1982, Fernández-Casas & Molero 5814 (G, MO, NY); cerca a Igatymí, 4 February 1982, Fernández-Casas & Molero 5955 (G, MO, NY); Katueté, 15 February 1984, Hahn 2107 (CR, G, MO, PY, SI, USF); Parque Nacional Mbaracayú, 15 January 1998, Zardini & Guerrero 48030 (AS, CR, MO, USF); Reserva Natural Mbaracarú, 27 May 1999, Zardini & Chaparro 50783 (AS, CR, MO); reserva de la biósfera Mbaracayú, Horqueta Mi-Lagunita, 2 November 2003, Zardini & Chaparro 60818 (CR, MO). Concepción: Río Apa y Río Aquidabán, January 1909, Fiebrig 4462 (G [2 sheets], K); Villa Jana, Río Apa y Río Aquidabán, s.d., Fiebrig 4692 (BM, G [2 sheets], K, LIL, P, SI); Río Apa, 1901–1902, Hassler 7820 (C, F, G [3 sheets], K [2 sheets], LIL, MICH, MO, NY, P, RB, S, SI, UC, US); Arroyo Trementina, E de Paso Barreto, 1 July 1994, Zardini & Guerrero 39945 (AS, CR, MO, USF); Estancia Lapuri, entre Estancia Arrecife y carretera a Valle Mi, 15 January 2000, Zardini & Quintana 53916 (AS, CR, MO). Cordillera: Tobatí, Huguaty Rozado-Itá Espejo, 8 January 1989, Bordas 4382 (G, K); cerca a Piribebuy, 17 September 1988, Ferrucci et al. 753 (CTES, G); cerca a Bernal Cué, 1898-1899, Hassler 3961 (BM, G [2 sheets], K, NY); Río Y-acá, January 1900, Hassler 6776 a (BM, G [2 sheets]); Ypacaray, San Bernardino, February 1913, Hassler 11547 (BAF, BM, C, G, K, L, MO, NY, S, UC, US, Z); Emboscada, 3 August 1984, Mereles et al. 1088 (Z); Ybytu Silla,

23 July 1988, Zardini 5992 (MO), 25 August 1988, Zardini 6697 (CR, MO, SI), 8 February 1991, Zardini & Velásquez 26200 (MO, NY, SI), Zardini & Salina 26072 (MO, SI), 9 March 1991, Zardini et al. 27169 (MO, SI); al O de Arroyos Y Esteros, 18 November 1989, Zardini & Velásquez 16325 (SI); cuenca baja del Río Piribebuy, 25 July 1997, Zardini & Gentry 46975 (AS, CR, MO, USF). Guairá: cerca a Melgarejo, 19 August 1989, Aguayo 592 (CR, MO, SI); Colonia Independencia, 20 December 1986, Schinini et al. 24981 (CTES, G); Naville, 14 July 1989, Zardini et al. 13344 (MO, PY, SI). Paraguarí: entre Cerro Hu y Cerro de Santo Tomás, cerca a Paraguarí, 31 January 1877, Balansa 1376 (G [2 sheets], K, P [2 sheets]); entre Paraguarí y Villa Rica, 2 September 1874, Balansa 1376a (G); Cordillera de Altos, Cerro Chochu, December 1902, Fiebrig 640 (G, LIL); Cordillera de Altos, November 1904, Hassler 2054 (G), April 1916, Hassler 1698 (SI); cerca a Paraguarí, carretera a Peribebuy, 6 February 1966, Krapovickas et al. 12448 (CTES, K, G, SI); Paraguarí, 23 July 1987, Mereles 1090 (SI); Cordillera de Altos, 14 April 1946, Rojas 13313 (K, LIL, S); Cordillera de Altos, 24 April 1981, Soejarto et al. 5162 (F, K); Cerro Paraguarí, March 1983, Stutz 1549 (G [3 sheets]); Parque Nacional Ybycu'í, 27 January 1989, Zardini & Aguayo 10059 (CR, G [2 sheets], MO, PY, SI), 27 January 1989, Zardini et al. 10311 (MO, SI), 24 June 1989, Zardini & R. Velásquez 13233 (MO, SI), 22 June 1991, Zardini & Velásquez 27759 (MO, PY). San Pedro: Alto Paraguay, Primavera, 8 May 1955, Woolston 517a (C, K, MO, NY, UC); Primavera, 6 March 1958, Woolston 958 (K, NY); Antequera, 23 June 2001, Zardini & Guerrero 56533 (CR, MO). Data lacking: s.d., Chodat 201 (G); s.d., Jørgensen 4708 (DS, MO, NY, S, US).

Prestonia tysonii A.H. Gentry (1974: 895). Type:—PANAMA. Panama: Cerro Jefe, Clusia forest, 27 January 1966, E. Tyson, J. Dwyer & K. Blum3214 (holotype MO!, isotypes SCZ!, UC!). Fig. 68, 70

**Stem** densely tomentose or tomentulose, puberulent at maturity, with clear latex, sparsely lenticellate, these slightly suberose, intrapetiolar colleters conspicuous, 1.5-2 mm long. **Petioles** 0.4-1.1 cm; leaf blade  $8-13.5 \times 4-10$  cm, ovate, narrowly ovate to ovate-elliptic, apex acute or acuminate, base obtuse, rounded, or slightly cordate, membranaceous, glabrescent adaxially, densely velutinous-tomentose abaxially, indument drying ferrugineous, secondary veins usually impressed on both surfaces, tertiary veins

rather inconspicuous on both surfaces. Inflorescence a dichasial cyme, terminal or subterminal, shorter than the adjacent leaves, few-flowered, the flowers densely clustered, ferrugineous-tomentose, peduncle 1–2 cm, pedicels 0.2–0.6 cm long, floral bracts 2–3 × 1.5–2 mm, narrowly ovate, scarious, minute, green. **Sepals**  $4-6 \times 2-3.5$  mm, free, membranaceous, ovate-elliptic, the apices acute, not reflexed, tomentose, very small, drying with a more or less uniform color, the veins slightly impressed or not evident, colleters 0.8– 1.1 mm long, entire to minutely erose at the apex. Corolla salverform, cream, tomentose or tomentulose outside, sometimes sparsely puberulent, tube  $5-6 \times 1.5-2$  mm, straight, but somewhat expanded near the mouth, free corona lobes 1.9–2.1 mm long, the apices exserted or barely included, their height conspicuously surpassed by that of the anther apices, annular corona entire, thickened, corolla lobes  $4-5 \times 2.8-3.1$  mm, obliquely obovate. Stamens inserted near the corolla mouth, anthers 3.9–4.1 mm, dorsally glabrous, the apices exserted. Ovary 1.3–1.5 mm tall, glabrous, style-head 1–1.2 mm, nectary 0.9–1 mm, shorter than the ovary, divided into 5 nectaries, each entire to subentire. Follicles 28–  $31 \times 0.4$ –0.5 cm, continuous, free, but united at the tips (at least when young), velutinoustomentose or tomentose, without lenticels, firmly membranaceous when old; inmature seeds 22–24 mm, coma 2.2–2.7 cm, tannish cream.

**Distribution and habitat**:—Cloud forest in Central Panama (cerro Jefe), from 950–1100 m.

**Phenology**:—Flowering January-February and April. A single specimen with fruits has been collected in February.

**Conservation Assessment**:—Critically endangered (CR); area of occurrence estimated to be less than 100 km2, only known from one locality (IUCN 2001)

**Taxonomic notes:**—*Prestonia tysonii* is related to *P. parviflora*, *P. premontana*, and *P. mucronata*, a group of species forming a clade and having in common terminal inflorescences and slender follicles. Terminal inflorescences are rare in the genus and restricted to this group. *Prestonia tysonii* is easily separate from the other species by its corolla tube 5-6 mm long, free corona lobes with the apices exserted, and corolla lobes 4-5 mm long. In addition, this species is endemic to Cerro Jefe, an area in Panama known for its numerous endemic species (De Silk et al., 2009), whereas the other species are restricted to South America.

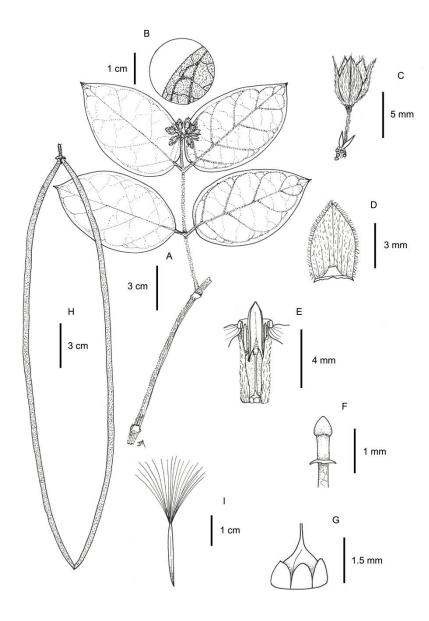


Fig. 70 *Prestonia tysonii* (*Tyson et al. 3214*, MO). A. Stem with inflorescence. B. Abaxial surface of the leaf blade. C. Calyx, pedicel, and floral bracts. D. Adaxial view of one sepal, showing the colleter at the base. E. Open corolla tube, showing the anthers and free coronal lobes. F. Style-head. G. Nectaries and ovary. H. Follicles. I. Inmature seed.

Additional specimens examined:—PANAMÁ. Panamá: summmit of Cerro Jefe, 4 April 1982, *Huft & Knapp 1710* (MO); Cerro Jefe region, along road toward Río San Cristobal, Chagres dranaige, 24 February 1986, *McPherson 8481* (MO); Cerro Jefe, entre Cerro Azul y torre de Radio, 19 February 1981, *Sytsma & D'Arcy 3697* (MO, USF, WAG).

### **INCERTAE SEDIS**

*Prestonia succo* J. F. Morales (2011: 28). Type:—PERU. Cusco: La Convención, Santa Teresa, Yantile, 16 March 2004, *I. Huamantupa*, *M. Ninanzuro & A. Huamantupa* 4079 (holotype CR!, isotypes, CUZ, MO!, MOL!, USM!). **Fig. 68, 71.** 

**Stem** inconspicuously puberulent when young, glabrous to glabrate at maturity, with clear latex, the lenticels not evident, intrapetiolar colleters minute, less than 1 mm long. **Petioles** 2.0–5.5 cm; leaf blade  $1.5-5.3 \times (0.5-)0.8-1.6$  cm, narrowly ovate to narrowly elliptic, apex shortly acuminate, base obtuse to rounded, membranaceous, glabrous on both surfaces, secondary veins impressed abaxially, inconspicuous adaxially, tertary veins not impressed. Inflorescence a monochasial cyme, axillary, longer than the adjacent leaves, few-flowered, the flowers more or less clustered, sparsely puberulent to glabrate, peduncle 2.5–3.6 cm, pedicels 1–1.2 cm long, floral bracts  $0.7-1.1 \times 0.2-0.4$  mm, scarious, linear, inconspicuous, green. **Sepals** 2.9–3.2 × 1.1–1.3 mm, **free**, membranaceous, narrowly ovate, the apices acuminate, not reflexed, very sparsely puberulent to glabrous, the colleter less than 1 mm long, subentire to irregularly erose at the apex. Corolla salverform, bright yellow, minutely and inconspicuously puberulent outside, tube  $5.5-8.5 \times$ 2.3–3.2 mm, slightly expanded toward the base, free corona lobes reduced to callous ridges, annular corona slightly 5-lobed, delicate and inconspicuous, corolla lobes 5-6 × 4-5 mm, obliquely obovate. **Stamens** inserted near the corolla mouth, anthers 3.1–3.3 mm, dorsally glabrous, included or the apices barely exserted. Ovary 1.1–1.3 mm tall, glabrous, stylehead 0.8–1 mm, nectary 1.1–1.3 mm, usually equaling or slightly shorter than the ovary, irregularly 5-lobed, each lobe entire or subentire. **Follicles** unknown.

**Distribution and habitat**:—Endemic to Peru, growing in secondary montane forest, at 1850–3250 m of elevation.

**Phenology:**—Flowering March.

Conservation Assessment:—Data deficient (DD) (IUCN 2001).

**Taxonomic notes**:—*Prestonia succo* shows some resemblance to *P. coalita* and *P. solanifolia*, but differs by its elongated inflorescence and shorter corolla tube.

**Additional specimens examined**:—PERU. Cusco: San Ignacio, La Convención, Santa Teresa, 7 March 2005, *Suclli et al. 2176* (CR, MO).

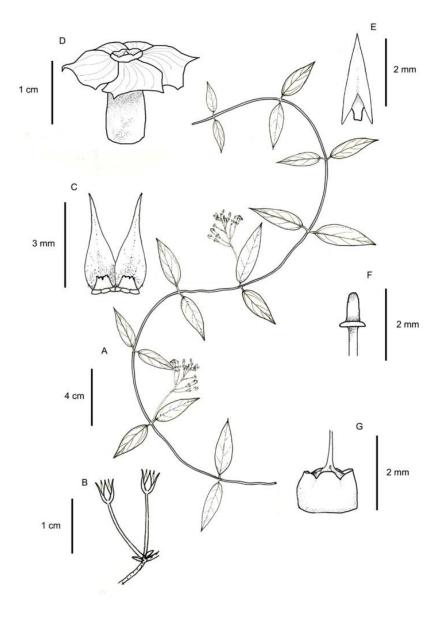


Fig. 71 *Prestonia succo* (*Suclli et al. 2176*, INB). A. Flowering branch. B. Calyces, pedicels, and floral bracts. C. Adaxial view of two sepals. D. Corolla. E. Anther, dorsal view. F. Stylehead. G. Nectary.

# Acknowledgements

I thank the following herbaria, for allow the study of their collections: A, AAU, ALCB, AS, ASE, ASU, B, BAB, BEREA, BHCB, BIGU, BM, BOLV, BR, C, CAS, CAUP, CAY, CEN, CEPEC, CGE, CHAPA, CICY, CIIDIR, CIMI, CM, COAH, COL, CR, CVRD, CUVC, CUZ, DPU, DS, DUKE, E, EAP, EAN, ECON, ENCB, ESA, ESAL, F, FCME, FCQ, FDG, FI, FI-W, FUEL, G, G-BOIS, G-DC, GB, GFJP, GH, HAL, HB, HBG, HERZU, HOXA, HRB, HRCB, HSB, HUA, HUCO, HUQ, HURB, IAN, IBGE, INPA, IPA, JAUM, JE, JEPS, JPB, K, LAGU, LD, LE, LIL, LP, LPB, LZ, M, MA, MBM, MBML, MEDEL, MEXU, MG, MICH, MIRR, MHES, MO, MOL, NY, O, P, P-BA, P-HB, P-JU, P-LA, PEL, PMA, PORT, PR, PSO, Q, QAME, QAP, QCA, QCNE, QPLS, R, RB, RON, S, SI, SP, SPF, SPFR, TEFH, TRIN, TULV, U, UB, UBT, UC, UCAM, UCOB, UDCB, UPS, US, USCG, USF, USJ, USM, USZ, UVAL, W, WU, WAG, WIS, VALLE, VEN, VIC, XAL, Z, and ZT. I wish to express my gratitude to the Missouri Botanical Garden, who have supported several visits to their herbarium. In addition, I want to thank them for the numerous duplicates sent as a gift for identification over the last 20 years.

Field trips were possible in several countries thanks to a group of colleagues and friends, without whose help it would not have been possible to collect and see alive several of the species treated here. The following persons deserve special recognition: in El Salvador, Eunice Echeverría, Gabriel Cerén, and Jenny Menjivar (MHES), in Panama Carmen Galdámez (STRI), in Colombia, Álvaro Idárraga (HUA), Dayron Cárdenas (COAH), Felipe Cardóna (HUA), Fernando Alzate (HUA), Julio Betancur (COL), Mario Alberto Quijano (HUCO), and Ricardo Callejas (HUA), in Peru Carlos Amasifuen Guerra, Carlos Reynel (MOL), Fredy Ramírez, Rocío Rojas (HOXA), and Rodolfo Vásquez (HOXA), in Bolivia Alfredo Fuentes (LPB) and Daniel Soto (USZ), in Brazil Alessandro Rapini (HUESF), Andre Simões (UEC), Andre Paviotti Fontana (MBML), Claudio Nicoletti de Fraga (RB), Ludovic Kollmann (MBML), Marccus Alves (UFP), and Ricardo Perdiz (MIRR) and in Venezuela, Carlos González.

Many people helped with this project over the years: Michael Grayum (MO) provided many critical references and clarified specific doubts about the International Code of Botanical Nomenclature, Barry Hammel and Isabel Pérez (MO) provided information from several specimens at INB and helped in many ways, Bruce Hansen (USF) contributed helpful comments in an early draft of this monograph, provided scanned copies of collections at USF, and also give important clues to resolve the identity of *P. schumanniana*. I also wish to thank Mary Endress (Z) for her critical comments on papers concerning *Prestonia* and related genera, which allowed me to improve the quality of those papers and this monograph. She also provided preserved material for several

species for DNA extraction. Ingrid Koch sent photographs and copies of herbarium specimens on loan to Campinas (UEC), Mary Merello (MO) scanned and sent critical bibliographic references, Gunnar Brehm and Juergen Homeier, provided photographs, flowers in alcohol, and duplicates of *Prestonia amabilis*, Norma Deginani (SI), Laura Iharlegui (LP), and Omaira Hokche (VEN) sent complementary information of material deposited in their herbaria and Rita de Cássia Pereira (IPA), provided scanned images of the type of *Prestonia pickelii*. I would like to thank Ivon Ramírez and the Centro de Investigaciones Científicas de Yucatán, Mexico, for sending a DNA sample of *Pentalinon andrieuxii*. Edgar Mayta Chipana and Alfredo Fuentes (LPB) provided information and images of specimens of *P. annularis*. Pedro Moraes helped to clarify the identity of the type of *E. annularis*. Xavier Cornejo (GUAY) sent information of herbarium specimens at GUAY and provided photos of several species from Ecuador.

Special thanks to the following persons or associations for their support during visits of their herbaria or countries: Walter Berendsohn (Germany), Reneé Fortunato and Norma Deginani (Argentina), Bruno Wallnöfer (Austria), Alfredo Fuentes and Stephan Beck (Bolivia), Alessandro Rapini, Geovane Sigueira, and Marccus Alves (Brazil), Asociación Colombiana de Herbarios, Álvaro Cogollo, Felipe Cardona, Javier Francisco Roldán, José Luis Fernández-Alonso, Mario Alberto Quijano, Philip Silverstone-Sopkin, Ramiro Fonnegra, and Ricardo Callejas (Colombia), Diana Fernández and Homero Vargas (Ecuador), Gabriel Cerén, Eunice Echeverría, Jorge Monterrosa, and Jenny Menjivar (El Salvador), Lucille Allorge (France), Mario Véliz and AnaLu MacVean (Guatemala), Cyril Nelson (Honduras), Leonardo Alvarado and Mario Souza (México), Paul and Hiljte Maas (The Netherlands), Mireya Correa and Carmen Galdámez (Panama), Asunción Cano, Joaquina Alban, Fredy Ramírez, Rodolfo Vásquez, and Rocío Rojas (Peru), Mary and Peter Endress (Switzerland), Bruce Hansen, Fabian Michelangeli, Gerrit Davidse, Michael Grayum, Olga Marta Montiel, Robin Moran, and William Burger (United States), Gabriela Jolochin (Uruguay), Alix Amaya, Eliana Nogueira, Gilberto Morillo, Shingo Nowaza, and Sirly Lheyton (Venezuela). I would like to thank the Anales del Jardín Botánico de Madrid for allowing the reproduction of the images of *P. cogolloi*, *P. premontana*, and *P. schumanniana*.

The following institutions or people authorized the use of photographs: Alfredo Fuentes (*P. leco*), Annette Aiello and the Smithsonian Tropical Research Institute, Panama (*P. exserta*). Edith González (*P. mexicana*), Francisco Castro (*P. lindleyana*, *P. surinamensis*), Geovane Siqueira (*P. calycina*), Gunnar Brehm and Juergen Homeier (*P. amabilis*), Hermes Vega (*P. speciosa*), Julio Betancur and Saúl Hoyos (*P. falcatosepala*), Lázaro Santa Cruz Cervera (*P. mollis*), Luz María Quiñones (*P. vana*), Pablo Roberto Stevenson (*P. annularis*), Reinaldo Aguilar (*P. longifolia*), Rosa Cerros (*P. mexicana*), and Xavier Cornejo (*P. parvifolia* and *P. rotundifolia*). The photographs of *P.* 

*cyaniphylla*, *P. falcatosepala*, and *P. parviflora* were downloaded from the TROPICOS database and they are used with permission (Copyright: Missouri Botanical Garden).

### References

- Appezzato da Glória, B. & Estelita, M.E. (2000) The developmental anatomy of the subterranean system in *Mandevilla illustris* (Vell.) Woodson and *M. velutina* (Mart. ex Stadelm.) Woodson (Apocynaceae). *Revista Brasileira de Botânica* 23: 27–35.
- Baillon, M.H. (1889) Étude des *Prestonia. Bulletin Mensuel de la Société Linnéenne de Paris* 1: 789–792.
- Bentham, G. (1839-1857) Plantas hartwegianas imprimis mexicanas adjectis nonnullis grahamianus enumerat novasque describit. W. Pamplin, London, 393 pp.
- Bentham G. (1876) Apocynaceae. *In:* Bentham, G. & Hooker, J.D. (eds.), *Genera Plantarum*, Vol. 2. Lovell Reeve & Co., Williams & Norgate, London, pp. 681–728.
- Bentham, J. (1841) Contributions towards a Flora of South America.—Enumeration of Plants collected by Mr. Schomburgk in British Guiana. *Journal of Botany* 3: 212–250.
- Beurling, P.J. (1854) Primitiae Florae Portobellensis. *Kongliga Vetenskaps Academiens Handlingar* 40: 107–148.
- Blake, S.F. (1917) Descriptions of new spermatophytes, chiefly from the collections of Professor M.E. Peck in British Honduras. *Contributions from the Gray Herbarium of Harvard University* 52: 78–79.
- Blake, S.F. (1924) New plants from Venezuela. *Contributions from the United States National Herbarium* 20: 519–541.
- Brehm, G., Hartmann, T. & Willmott, K. (2007). Pyrrolizidine alkaloids and pharmacophagous Lepidoptera visitors of *Prestonia amabilis* (Apocynaceae) in a montane rainforest in Ecuador. *Annals of the Missouri Botanical Garden* 94: 463–473.
- Britton, N.L. (1923) Studies of West Indian plants XI. *Bulletin of the Torrey Botanical Club* 50: 35–56.
- Boppré, M. (1986) Insects pharmacophagously utilizing defensive plant chemicals (pyrrolizidine alkaloids). *Naturwissenschaften* 73: 17–26
- Brown, N.E. (1924) Undescribed species from Trinidad. *Bulletin of the Torrey Botanical Club* 51: 4–6.
- Browne, P. (1756) *The Civil and Natural History of Jamaica in Three parts*, Ed. 1. London, P. Browne, 503 pp.

- Brown, R. (1810) On the Asclepiadeae, a natural order of plants separated from the Apocineae of Jussieu. *Memoirs of the Wernerian Natural History Society* 1: 12–78.
- Candolle, A (1844) Apocynaceae. In: Candolle, A. (ed.), *Prodromus systematis naturalis regni* vegetabilis, Vol. 8. Paris, Treuttel & Würtz, pp. 317–489.
- De Sedas, A., Martínez, L., Stapf, M. & Correa, M. (2009) *Guía fotográfica de plantas vasculares del Cerro Jefe, Panamá*. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica, 56 pp.
- Don, G. (1837) A general history of the dichlamydeous plants 4, J.G. & F. Rivington, London, 908 pp.
- Donnell Smith, J. (1899) Undescribed plants from Guatemala and other Central American Republics XXI. *Botanical Gazette* 27: 434–443.
- Edgar, J.A. (1984) Parsonsieae: Ancestral larval food plants of the Danainae and Ithomiinae. *In:* Ackery. P.R. & Vane-Wright, R.I. (eds.), The Biology of Butterflies. The Royal Entomological Society, London, pp. 91–93.
- Eggers, N.J. & Gainsford., G. (1979) Parsonsine (C22H33NO8): a pyrrolizidine alkaloid from Parsonsia heterophylla A. Cunn. Crystal structure communications 8: 597–603
- Endress, M.E., Sennblad, B., Nilsson, S., Civeyrel, L., Chase, M.W., Huysmans, S., Grafström, E., & Bremer, B. (1996) A phylogenetic analysis of Apocynaceae s. str. and some related taxa in Gentianales: a multidisciplinary approach. *Opera Botanica Belgica* 7: 59–102.
- Endress, M.E. & Bruyns P. (2000) A revised classification of the Apocynaceae s.l. *The Botanical Review (Lancaster)* 66: 1–56.
- Endress, M.E., Liede-Schumann, S. & Meve, U. (2014) An updated classification for Apocynaceae. *Phytotaxa* 159: 175–194.
- ESRI (1999) ArcView 3D Analyst. Suface Creation, Visualization in Analysis.
- Ezcurra, C. (1981) Revisión de las Apocynáceas de la Argentina. Darwiniana 23: 367-474.
- Fallen, M.E. (1986) Floral structure in the Apocynaceae: Morphological, functional, and evolutionary aspects. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 106: 245–286.
- Fishbein, M. (2001) Evolutionary innovation and diversification in the flowers of Asclepiadaceae. Annals of the Missouri Botanical Garden 88: 603–623.
- Font Quer, P. (1953) Diccionario de botánica. Labor S.A, Barcelona, 1244 pp.
- Fuentes, A. & Morales, J.F. (2010) *Prestonia leco*, una nueva especie de Apocynaceae de los Bosques montanos húmedos de Bolivia. *Novon* 20: 278–281.

- Gentry, A.H. (1974) Notes on Panamian Apocynaceae. *Annals of the Missouri Botanical Garden* 61: 891–900.
- Gentry, A.H. (1983) A new combination for a problematic Central American Apocynaceae. *Annals of the Missouri Botanical Garden* 70: 205–206.
- Gleason, H.A. (1926) Studies on the flora of northern South America-IX. *Bulletin of the Torrey Botanical Club* 53: 289–301.
- Gleason, H.A. & A.C. Smith (1933) Plantae Krukovianae (Concluded). *Bulletin of the Torrey Botanical Club* 60: 379–396.
- Hansen, B.F. (1985) A monographic revision of *Forsteronia* (Apocynaceae). Ph. D. dissertation, University of South Florida, Tampa, 382 pp.
- Harris, J.G. & Harris, M.W. (1994) *Plant identification terminology: an illustrated glossary*. Spring Utah, Lake, 198 pp.
- Hartmann, T., Theuring, C., Witte, L. & Pasteels, J.M. (2001) Sequestration, metabolism and partial synthesis of tertiary pyrrolizidine alkaloids by the neotropical leaf-beetle *Platyphora boucardi*. *Insect Biochemistry and Molecular Biology* 31: 1041–1056.
- Hartmann, T., Theuring, C., Witte, L., Schulz, S. & Pasteels, J.M. (2003) Biochemical processing of plant acquired pyrrolizidine alkaloids by the neotropical leaf-beetle *Platyphora boucardi*. *Insect Biochemistry and Molecular Biology* 33: 515–523
- Hemsley, W.B. (1881-1882) Botany. In: Godman, F.D. & Salvin. O. (eds.), *Biologia centrali–Americana*. Vol. 2. R.H. Porter, Dulau & Co., London, 621 pp.
- Hinds, R. (1845) The botany of the voyage of H.M.S. Sulphur, under the command of Captain Sir Edward Belcher, R.N., C.B., F.R.G.S. etc. during the years 1836–1842. Smith, Elder & Co., London, 195 pp.
- Hoehne, F.C. (1915) Historia Natural. Botanica. Parte 6. Relatório Commissão de Linhas Telegráphicas Estratégicas de Mato Grosso ao Amazonas 5(41): 1–96, pl. 113–131.
- Humboldt, A., Bonpland, A. & Kunth, C.S. (1818) *Nova Genera et Species Plantarum* (quarto ed.) 3. Graeco-Latino-Germanico, Paris, 456 pp.
- Jacquin, N.J. (1760) Enumeratio Systematica Plantarum, quas in infulis Caribaeis vicinaque Americes continente detexit novas, aut jam cognitas emendavit. T. Haak, Leiden, 41 pp.
- Laan, F.M. van der & Arends, J. (1985) Cytotaxonomy of Apocynaceae. *Genetica* 68: 3–35.
- Liede, S. & Kunze, H. (1993) A descriptive system for corona analysis in Asclepiadaceae and Periplocaceae. *Plant Systematics and Evolution* 185: 275–284.

- Lindley, J. (1825) Report upon the new or nare plants which have flowered in the Garden of the Horticultural Society at Chiswick, from its first formation to March 1824. *Transactions of the Horticultural Society of London* 6: 62–100.
- Linnaeus, C.f. (1771 [1782]) Supplementum Plantarum Systematis Vegetabilium Editionis Decimae Tertiae, Generum Plantarum Editionis Sextae, et Specierum Plantarum Editionis Secundae. Braunschweig, 468 pp.
- Livshultz, T., Middleton, D.J., Endress, M.E. & Williams, J.K. (2007) Phylogeny of Apocynoideae and the APSA clade (Apocynaceae s.l.). *Annals of the Missouri Botanical Garden* 94: 324–359.
- Macbride, J.F. (1931) Spermatophytes, mostly Peruvian-III. *Publications of the Field Museum of Natural History, Botanical Series* 11(1): 1–35.
- Maldonado, J.L. (1996). Flora de Guatemala de José Mociño. Consejo Superior de Investigaciones Científicas, Madrid, 366 pp.
- Malme, G.O. (1904) Apocynaceæ. *In*: Chodat, R & Hassler, E. (eds), Plantæ hasslerianæ soit enumeration des plantes récoltées au Paraguay par le D<sup>r</sup> Émile Hassler, d'Aarau (Suisse) de 1885 à 1902. *Bulletin de l'Herbier Boissier*, sér. 2, 4: 194–196, 257–261.
- Malme, G.O. (1927) Die Apozynazeen der zweiten Regnellschen Reise. *Arkiv för Botanik* 21A: 1–21.
- Malme, G.O. (1928) Gentianaceoe, Apocvnaceoe et Vochysiaeeoe paranenses a Dre. P. Dusen collecta. *Arkiv för Botanik* 22A(2):1–16.
- Markgraf, F. (1924a) Apocynaceae Brasilienses, a cl. F. C. Hoehne communicatae, determinatae. Repertorium Specierum Novarum Regni Vegetabilis 20: 18–26.
- Markgraf, F. (1924b) Neue Apocynaceen aus Südamerika. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 9: 77–90.
- Markgraf, F. (1926) Apocynaceae. *In*: Mildbraed, J. (ed) Plantae Tesmannianae peruvianae III. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 9: 981–982.
- Markgraf. F. (1930) Neue Apocynaceen aus Südamerika III. Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 10: 1033–1039.
- Markgraf, F. (1975) Novedades Venezolanas en las Apocynaceae. *Acta Botánica Venezuelica* 10: 247–250.
- Martens, M. & Galeotti, H. (1844) Enumeratio synoptica plantarum phanerogamicarum ab Henrico Galeotti in regionibus mexicanis collectarum. *Bulletin de l'Academie Royale des Sciences et Belles-lettres de Bruxelles* 11: 355–376.

- Meve, U. & Liede. S. (2004) Generic Delimitations in Tuberous Periplocoideae (Apocynaceae) from Africa. *Annals of Botany* 93: 407–414.
- Miers, J. (1878) On the Apocynaceae of South America. Williams & Norgate, London, Edinburgh, 291 pp.
- Monachino, J. (1957) A new species of *Prestonia* from Brazil. *Phytologia* 6: 12–13.
- Monachino, J. (1959) A new *Echites* from Mexico. *Bulletin of the Torrey Botanical Club* 86: 245–247.
- Monachino, J. (1961) Apocynaceae. *In:* Maguire, B. Wurdack, J.J. and collaborators. The Botany of the Guayana Highland Part IV. *Memoirs of the New York Botanical Garden* 10: 59–65.
- Moore, S.L. (1895) The phamerogamic botany of the Matto Grosso Expedition 1891–92. Transactions of the Linnean Society of London 4: 265–516.
- Morales, J.F. (1996) Novelties in *Prestonia* (Apocynaceae). Novon 6: 285–287.
- Morales, J.F. (1997a) A synopsis of the genus *Prestonia* (Apocynaceae) section Tomentosae in Mesoamerica. *Novon* 7: 59–66.
- Morales, J.F. (1997b) A re-evaluation of the genera *Echites* and *Prestonia* section *Coalitae* (Apocynaceae). *Brittonia* 49: 328–336.
- Morales, J.F. (1999a) *Rhodocalyx* (Apocynaceae), a new synonym of *Prestonia*. *Novon* 9: 89–91.
- Morales, J.F. (1999b) A synopsis of the genus *Odontadenia*. Series of revisions of Apocynaceae XLV. *Bulletin du Jardin Botanique National de Belgique* 67: 381–477.
- Morales, J.F. (199c) *Hylaea* (Apocynaceae-Apocynoideae), a new genus of South America. *Novon* 9: 83–85.
- Morales, J.F. (2002) Studies in Neotropical Apocynaceae I: A revision of the genus *Laubertia*. *Rhodora* 104: 170–186.
- Morales, J.F. (2004a) Estudios en las Apocynaceae Neotropicales IV: Notas taxonómicas en *Prestonia*, con una nueva especie de Ecuador. *Sida* 21: 159–163.
- Morales, J.F. (2004b) Estudios en las Apocynaceae Neotropicales VII: Novedades taxonómicas en *Prestonia* (Apocynaceae, Apocynoideae) para Colombia y Ecuador, con comentarios sobre el grado de lobulación del nectario. *Candollea* 59: 159–165.
- Morales, J.F. (2004c) Estudios en las Apocynaceae Neotropicales VI: Una nueva especie de *Prestonia* (Apocynaceae, Apocynoideae) para Brasil. *Acta Amazonica* 34: 669–670.
- Morales, J.F. (2005) Estudios en las Apocynaceae neotropicales XIV: Nuevas lectotipificaciones en los géneros *Hylaea* J.F. Morales y *Pentalinon* Voigt (Apocynoideae, Echiteae). *Lankesteriana* 5: 159–160.

- Morales, J.F. (2006a) Estudios en las Apocynaceae Neotropicales XXVI: una monografía del género *Mesechites* (Apocynoideae, Mesechiteae). *Candollea* 61: 215–277.
- Morales, J.F. (2006b) Estudios en las Apocynaceae Neotropicales XXVII: lectotipificaciones misceláneas en el género *Prestonia* (Apocynoideae, Echiteae). *Brenesia* 66: 75–78.
- Morales, J.F. (2007a) Estudios en las Apocynaceae Neotropicales XXXII: tres nuevas especies de *Prestonia* (Apocynoideae, Echiteae) para Sur America. *Anales del Jardín Botánico de Madrid* 64: 147–154.
- Morales, J.F. (2007b) Estudios en las Apocynaceae Neotropicales XXXV: novedades nomenclaturales en el genero *Prestonia* para Brasil (Apocynoideae, Echiteae). *Darwiniana* 45: 213–217.
- Morales, J.F. (2010a) Estudios en las Apocynaceae Neotropicales XL: sinopsis del género *Prestonia* (Apocynoideae, Echiteae) en Ecuador. *Anales del Jardín Botánico de Madrid* 67: 13–21.
- Morales, J.F. (2010b) Estudios en las Apocynaceae Neotropicales XLI: La familia Apocynaceae s.str (Apocynoideae, Rauvolfioideae) en Uruguay. *Darwiniana* 48: 68–86.
- Morales, J.F. & Fuentes, A. (2004a) Estudios en las Apocynaceae Neotropicales VI: una nueva especie, nuevos records y nueva sinonimia en las Apocynaceae de Bolivia. *Sida* 21: 165–174.
- Morales, J.F. & Fuentes, A. (2004b) Estudios en las Apocynaceae Neotropicales VIII: nuevas especies de *Mandevilla* para Peru y Bolivia, con notas sobre la morfologia floral en corolas infundibuliformes. *Candollea* 59: 167–174.
- Morales, J.F. & Williams, J.K. (2004) *Allotoonia*, a new neotropical genus of Apocynaceae based on a subgeneric segregate of *Echites*. Sida 21: 133–158.
- Morales, J.F. & Williams, J.K. (2005a) Una nueva combinación en el género *Allotoonia* (Apocynaceae, Apocynoideae, Echiteae). *Lankesteriana* 5: 119–120.
- Morales, J.F. (2005b). Estudios en las Apocynaceae Neotropicales XIII: revisión del género *Temnadenia* (Apocynoideae, Echiteae). *Candollea* 60: 207-231.
- Morales, J.F. (2011) Studies in the Neotropical Apocynaceae XLI: A new species of *Prestonia* (Apocynoideae, Echiteae) from Peru and a key to the Peruvian species. *Phytotaxa* 29: 28–32.
- Morillo, G. (1978) Estudio preliminar de las especies venezolanas de *Prestonia* (Apocynaceae). *Memoria de la Sociedad de Ciencias Naturales La Salle* 110: 195–226.
- Müller Argoviensis, J. (1860a) Apocynaceae. *In*: Martius, C.F.P. von (ed.), *Flora Brasiliensis* 6(1). München, Wien, Leipzig, pp. 1–180.

- Müller Argoviensis, J. (1860b) Species novae nonnullae americanae ex Ordine Apocynearum et observations quaedam in species generis Echitis Auctorum earumque distributio in genera emendata et nova. *Linnaea* 30: 387–454.
- Müller Argoviensis, J. (1869) Apocynaceae. In: Warming, C. (ed.), Symbolae ad floram Brasiliae centralis cognoscendam III. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn, pp 96–116.
- Nicholson, G. (1886) The Illustrated Dictionary of Gardening. Vol III. Upcot Gill, London, 537 pp.
- Pasteel, J.M., Termonia, A., Windsor, D.M., Witte, L., Theuring, C. & Hartmann, T. (2001) Pyrrolizidine alkaloids and pentacyclic triterpene saponins in the defensive secretions of Platyphora leaf beetles. *Chemoecology* 11:113–120.
- Pasteels, J.M., Theuring, C., Witte, L. & T. Hartmann. (2003) Sequestration and metabolism of pyrrolizidine alkaloids by larvae of the leaf beetle *Platyphora boucardi* and their transfer via pupae into defensive secretions of adults. *Journal of Chemical Ecology* 29: 337–355.
- Pichon, M. (1948a) Classification des Apocynacées. I. Carissées et Ambelaniées. *Mémoires du Muséum National d'Histoire Naturelle. Nouvelle Série. Série B, Botanique* 24: 111–181.
- Pichon, M. (1948b) Classification des Apocynacées. XIX. Le rétinacle des Echitoïdées. *Bulletin de la Société Botanique de France* 95: 211–216.
- Pichon, M. (1949) Classification des Apocynacées. IX. Rauvolfiées, Alstoniées, Allamandées et Tabernaémontanoidées. *Mémoires du Muséum National d'Histoire Naturelle* 27: 153–251.
- Pichon, M. (1951) Classification des Apocynacées XXV Echitoideés. *Mémoires du Muséum National d'Histoire Naturelle. Nouvelle Série. Série B, Botanique* 1: 1–142.
- Pittier, H., Lasser, T., Schnee, L., Luces de Febres, Z. & Badillo, V. (1947) *Catálogo de la Flora Venezolana*. Tomo II. Caracas, Litografía y Tipografía Vargas, 577 pp.
- Poeppig, E.F. (1840–1845) Nova genera ac species plantarum quas in regno chilensi peruviano et in terra amazonica annis mdcccxxvii ad mdcccxxxii legit Eduardus Poeppig et cum Stephano Endlicher descripsit iconibusque illustravit.Vol. 3. Friderici Hofmeister, Leipzig. 91 pp.
- Pulle, A. (1926) Neue Beiträge zur Flora Surinams III. mit zwei Tafeln. *Recueil des Travaux Botaniques Néerlandais* 9: 125–169.
- Radford, A.E., Dickison, W.C., Massey, J.R. & Bell, C.R. (1974) *Vascular plant systematics*. Harper & Row, New York, 891 pp.
- Reinberg, P. (1921) Contribution à l'étude des boissons toxiques des indiens du Nord-ouest de l'Amazon, l'ayahuasca, le yagé, le huanto. *Journal de la Societé des Américanistes*, *Paris*. Vol. 4: 49.

- Rio, M.C.S. & Kinoshita, L.S. (2005) *Prestonia* (Apocynaceae) no Sul e Sudeste do Brasil. *Hoehnea* 32(2): 233–258.
- Ruiz, H. & Pavon, J.A. (1799) *Flora Peruviana et Chilensis II*. Typis Gabrielis de Sancha, Madrid, 76 pp.
- Rusby, H.H. (1895) On the collections of Mr. Miguel Bang in Bolivia. Part II. Corrections, additions and notes referring to Part I. *Memoirs of the Torrey Botanical Club* 4: 203–274.
- Rusby, H.H. (1907) An enumeration of the plants collected by Miguel Bang, IV. *Bulletin of the New York Botanical Garden* 4: 309–470.
- Rusby, H.H. (1920) Descriptions of three hundred new species of South American plants, with an index to previously published South American species by the same author. H.H. Rusby: New York, 170 pp.
- Rusby, H.H. (1927) Descriptions of new genera and species of plants collected on the Mulford Biological Exploration of the Amazon valley, 1921–1922. *Memoirs of the New York Botanical Garden* 7: 205–387.
- Schultes, R.E. (1957) Plantae austro-americanae X: Americae Australis Plantae Novae vel Alia ratione significantes. *Botanical Museum Leaflets* 18: 113–180.
- Schultes, R.E. & Raffauf, R. (1960) *Prestonia*: an amazonian narcotic or not? *Botanical Museum Leaflets* 19: 109-122.
- Schumann, K.M. (1895) Apocynaceae. *In*: Engler, A. & Prantl, K. (eds). *Die Natürlichen Pflanzenfamilien* 4: 109–189.
- Schumann, K.M. (1905) Asclepiadaceae, Apocynaceae, Rubiaceae. In: Pilger, R. (ed.), Beiträge zur Flora der Hylaea nach den Sammlungen von E. Ule. Verhandlungen des Botanischen Vereins für die Provinz Brandenburg und die Angrenzenden Länder 47: 100–191.
- Seemann, B. (1857) The botany of the voyage of H.M.S. Herald, under the command of Captain Henry Kellett, R.N., C.B., during the years 1845–51. Lovell Reeve, London, 483 pp.
- Sessé y Lacasta, M. & Mociño, J.M. (1887 [1893]) Flora mexicana. Naturaleza (Mexico City) ser. 2, 2(App.): 25–48.
- Siebert, A. & Voss, A. (1894) Vilmorin's Blumengärtnerei Beschreibung, Kultur und Verwendung des gesamten Pflanzenmaterials für deutsche Gärten. Ed. 3. Vol. 1. Berlin, Paul Parey, 832 pp.
- Smith, T.A. (1977) Review: Tryptamine and related Compounds in plants. *Phytochemistry* 16: 171-175.
- Sprengel, C.P.J. (1825) Systema vegetabilium, ed. 16. Librariae Dietrichianae, Gottingen, 992 pp.

- Stadelmeyer, E. (1841) Echitis nova especies brasilienses descriptae et adumbratae auctore Ernesto Stadelmeyer. *Flora 24(1, Beibl. 1)*: 1–80.
- Standley, P.C. (1924) Trees and shrubs of Mexico. *Contributions from the United States National Herbarium* 23: 1–1721.
- Standley, P.C. (1925) New plants from Central America IV. *Journal of the Washington Academy of Sciences* 15: 457–462.
- Standley, P.C. & Record, S.J. (1936) The forests and flora of British Honduras. *Publications of the Field Museum of Natural History, Botanical Series* 12: 1–432, pl. I–XVI.
- Tafalla, J. (1989) Flora Huayaquilensis sive Descriptiones et icones plantarum huayaquilensium secundum systema linnaeanum digestae. Introductio historica et adnotationes ab Eduardo Estrella confectae et descriptiones. ICONA & Real Jardín Botánico (CSIC), Madrid, 283 pp.
- Thiers, B. [continuously updated]. *Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium.*Available from: http://sweetgum.nybg.org/ih (accessed: August 2014).
- Trigo, J.R. & Brown, K.S. (1990) Variation of pyrrolizidine alkaloids in Ithomiinae: A comparative study between species feeding on Apocynaceae and Solanaceae. *Chemoecology* 1: 22–29.
- Urban, I. (1908) Nova genera et species III. Symbolae Antillanae 5: 287-352.
- Van Heurck, H. & Müller Argöviensis, [J.] (1871) Apocyneae novae. Observationes Botanicae et Descriptiones Plantarum Novarum Herbarii Van Heurckiani. *Recueil d'Observations Botaniques et de Descriptions de Plantes Nouvelles* 2: 138–207.
- Vellozo, J.M.C. (1825 [1829]) *Echites. In*: Vellozo, J.M.C. (ed.), *Florae Fluminensis* Vol. 1. Typographia Nationali. Rio de Janeiro, pp. 109–115.
- Vellozo, J.M.C. (1827 [1831]) In Vellozo, J.M.C. (ed.), Florae Fluminensis Icones. Senefelder. Paris. T. 25–49.
- Williams, L.O. (1968) Tropical American Plants IX. Fieldiana, Botany 31: 401–425.
- Williams, J.K. (2002) *Thoreauea* (Apocynaceae: Apocynoideae), a new genus from Oaxaca, Mexico. *Lundellia* 5: 47–58.
- Woodson, R.E. (1930) Studies in the Apocynaceae I. A critical study of the Apocynoideae, with special reference to the genus *Apocynum*. *Annals of the Missouri Botanical Garden* 17: 1–212.
- Woodson, R.E. (1931) New or otherwise noteworthy Apocynaceae of Tropical America. *Annals of the Missouri Botanical Garden* 18: 541–557.

- Woodson, R.E. (1932a) New or otherwise noteworthy Apocynaceae of Tropical America II. *Annals of the Missouri Botanical Garden* 19: 45–76.
- Woodson, R.E. (1932b) New or otherwise noteworthy Apocynaceae of Tropical America III. Annals of the Missouri Botanical Garden 19: 375-387.
- Woodson, R.E. (1933) Studies in the Apocynaceae IV. The American genera of Echitoideae. *Annals of the Missouri Botanical Garden* 20: 605-790.
- Woodson, R.E. (1934) New or otherwise noteworthy Apocynaceae of Tropical America IV. *Annals of the Missouri Botanical Garden* 21: 613–623.
- Woodson, R.E. (1935) Studies in the Apocynaceae. IV. The American genera of Echitoideae. Annals of the Missouri Botanical Garden 22: 153-306.
- Woodson, R.E. (1936) Studies in the Apocynaceae. IV. The American genera of Echitoideae. Annals of the Missouri Botanical Garden 23: 169–438.
- Woodson, R.E. (1938) Apocynaceae. In: Britton, N.L., Murrill, W.A. & Barnhart, J.H. (eds.), *Flora of North America* 26(2): 103–192.
- Woodson, R.E. (1939) New or otherwise noteworthy Apocynaceae of Tropical America VII. *Annals of the Missouri Botanical Garden* 26: 257–259.
- Woodson, R.E. & Siebert, R.J. (1939) Contributions toward a Flora of Panama III. Collections during the summer of 1938, chiefly by R.E. Woodson, P.A. Allen & R.J. Siebert. *Annals of the Missouri Botanical Garden* 26: 265–325.
- Woodson, R.E. & Schery, R.W. (1940) Contributions toward a Flora of Panama IV. Miscellaneous collections, chiefly by Paul H. Allen. *Annals of the Missouri Botanical Garden* 27: 265–365.
- Woodson, R.E. & Schery, R.W. (1942) Contributions toward a Flora of Panama VI. Collections chiefly by H. von Wedel in Bocas del Toro. *Annals of the Missouri Botanical Garden* 29: 317–379.
- Woodson, R.E. (1948) Miscellaneous new Apocynaceae and Asclepiadaceae. *Annals of the Missouri Botanical Garden* 35: 233–238.
- Woodson, R.E. (1960) Miscellanea taxonomica II. *Annals of the Missouri Botanical Garden* 47(1): 73–80

## Acknowledgements

I want to thanks the Deutscher Akademischer Austauschdienst (DAAD) for the PhD research grant (Forschungsstipendien für Doktoranden und Nachwuchswissenschaftler für mehr als 6 Monate), which allow me to complete my Ph.D. and this thesis, as well as the Missouri Botanical Garden, the Graduate School of the Bayreuth Universität, Dopontoes and Bruce Hansen (University of South Florida) for the economic support to visit their institutions or to make fieldwork in Central or South America.

I am grateful to Prof. Dr. Sigrid Liede-Schumann and PD. Dr. Ulrich Meve for his support, supervision and help during the last years. I am very grateful to Prof. Dr. Sigrid Liede-Schumann who accepts me as her Ph.D student

I thank Dr. Mary Endress, who has been my professor in the last three years: without you, your support, suggestions, comments, and help I will never be able to end this process. Really grateful. "Going to the top is optional, but coming back is compulsory"

Angelika Täuber and Margit Gebauer helped me in the laboratory and encourage me (together with Petra Kraus) in many ways. Priceless!

Many people support me in the last four years: too many to mention their names and the ways they made it: friendship, colleagues, friends, plant material, visit to herbaria, field trips, family, social meetings, love. I just say thank you.

I will never forget when in 1993, Dr. Barry Hammel from the Missouri Botanical Garden, offered me to work with Apocynaceae for the Manual of Plants of Costa Rica. Thank you Barry! For all the trips, for all the fights, for all the help, for all the wine. ... And for you, thank you for be there all the time

# (Eidesstattliche) Versicherungen und Erklärungen

(§ 5Nr. 4 PromO)

Hiermit erkläre ich, dass keine Tatsachen vorliegen, die mich nach den gesetzlichen Bestimmungen über die Führung akademischer Grade zur Führung eines Doktorgrades unwürdig erscheinen lassen.

(§ 8 S. 2 Nr. 5 PromO)

Hermit erkläre ich mich damit einverstanden, dass die eletronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung hinsichtich der eigenständigen Anfertigung der Dissertation unterzogen werden kann.

(§ 8 S. 2 Nr. 7 PromO)

Hermit erkläre ich eidesstattlich, dass ich die Dissertation selbständig verfasst und keine anderen als die vor mir angegebenen Quellen und Hilfsmittel benutzt habe

(§ 8 S. 2 Nr. 8 PromO)

Ich habe die Dissertation nicht bereits zur Erlagung eines akademischen Grades anderweitig eingereicht und habe auch nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden.

(§8 S. 2 Nr. 9 PromO)

Hiermit erkläre ich, dass ich keine hilfe von gewerbliche Promotionsberatern bzw.vermittlen in Anspruch genommen habe und auch künftig nicht nehmen werden

Bayreuth, den 27.04.2017

### J. Francisco Morales