UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE BIOLOGÍA
SISTEMÁTICA

SISTEMÁTICA DEL COMPLEJO *RONDELETIA* (RUBIACEAE)

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

M. en C. Jaime Alejandro Torres Montúfar

TUTORA PRINCIPAL DE TESIS: DRA. HELGA OCHOTERENA BOOTH
INSTITUTO DE BIOLOGÍA, UNAM
COMITÉ TUTOR: DRA. MARÍA HILDA FLORES OLVERA
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RANCHO SANTA ANA BOTANIC GARDEN
TUTOR INVITADO: DR. THOMAS BORSCH
BOTANISCHER GARTEN UND BOTANISCHES MUSEUM BERLIN-DAHLEM

CD. MX. MAYO, 2018

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UNAM POSGRADO
Ciencias Biológicas

COORDINACIÓN

OFICIO CPCB/392/2018

Asunto: Oficio de Jurado para Examen de Grado.

Lic. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día 5 de marzo de 2018, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **TORRES MONTÚFAR JAIME ALEJANDRO** con número de cuenta **302118458** con la tesis titulada: **"Sistemática del complejo Rondeletia (Rubiaceae)"**, realizada bajo la dirección de la **DRA. HELGA OCHOTERENA BOOTH:**

Presidente:	DR. ALFONSO OCTAVIO DELGADO SALINAS
Vocal:	DRA. MARÍA VICTORIA SOSA ORTEGA
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Suplente:	DR. DANIEL IGNACIO PIÑERO DALMAU
Suplente	DRA. ROSAURA GRETHER GONZÁLEZ

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx., a 2 de mayo de 2018.

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

c.c.p. Expediente del (la) interesado (a).

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DEDICATORIA PERSONAL

A mis padres, hermano y maple

A María

A ti

ÍNDICE

RESUMEN

Dentro de la familia Rubiaceae varios géneros de la tribu Rondeletieae (Cinchonoideae) han sido considerados cercanamente relacionados con base en su semejanza morfológica y fueron propuestos como el “complejo *Rondeletia*”. Los análisis filogenéticos posteriores han recuperado a este complejo como polifilético, ya que un núcleo importante de sus géneros se mantuvo en Rondeletieae mientras que otros (grupo *Arachnothryx*) se anidaron dentro de la tribu Guettardeae. A pesar de que las filogenias actuales indican que este grupo no es natural, hace falta explorar la propuesta con alguna evidencia morfológica. Además, no se han considerado todos los géneros del complejo cuya ubicación tribal está en duda y se requieren estudios filogenéticos que con un mayor muestreo de especies permitan poner a prueba la monofilia y las relaciones entre los géneros que conforman el complejo y hace falta una propuesta de re-circunscripción de la tribu Rondeletieae acorde a esos resultados. Los objetivos de este estudio son evaluar la evidencia de morfología del polen para explorar si ésta apoya la clasificación del complejo *Rondeletia* en dos tribus; además, poner a prueba la ubicación filogenética y la monofilia de los géneros que conforman el complejo *Rondeletia* y proponer una circunscripción acorde para los géneros monofiléticos representados en su totalidad y para la tribu Rondeletieae. En este trabajo se realizó un estudio sistemático de morfología de polen que apoya la clasificación de los géneros del complejo *Rondeletia* en dos tribus. Nuestros resultados muestran que la discontinuidad de la nexina y las características de la apertura de los granos soportan decisiones taxonómicas sugeridas previamente con datos moleculares. Se presenta un análisis filogenético que contiene el muestreo de especies más amplio a la fecha para la tribu Rondeletieae. En el análisis combinado con evidencia molecular y morfológica se recuperan como monofiléticos tanto el género *Rondeletia* como los géneros que anteriormente se habían anidado en el mismo clado, por lo que se sugiere que *Mazaea*, *Phyllomelia*, *Rachicallis* y *Roigella* deben ser aceptados. Como resultado de esta filogenia, se propone una circunscripción consistente para Rondeletieae; se describe el nuevo género *Tainus*, endémico de la isla La Española, en las Antillas; se aceptan los géneros *Donnellyanthus* y *Rovaeanthus* (considerados por algunos autores como sinónimos de *Arachnothryx* y *Rogiera*, respectivamente, ambos ubicados en la tribu Guettardeae) y se presenta una tratamiento taxonómico de *Rovaeanthus*. Dentro de Guettardeae, se describen dos especies nuevas de *Arachnothryx* endémicas de Oaxaca, México. Se presenta un análisis filogenético que incluye una muestra representativa de los géneros de Guettardeae y un amplio muestreo de las especies del complejo *Rondeletia* que se ubican en esta tribu. Como resultado de esta filogenia, se amplía la circunscripción de *Gonzalagunia* para incluir los géneros *Arachnothryx*, *Javorkaea* y *Renistipula*. Consistentemente con la filogenia, realizamos el tratamiento taxonómico del género *Rogiera*, que se recuperó como monofilético y no contaba con un tratamiento

taxonómico que incluyera a todas sus especies. Concluye la tesis con un planteamiento metodológico iterativo para evaluar la homoplasia en el caso de caracteres complejos. Esta propuesta se vincula empíricamente con la evaluación de la evolución de los tipos de fruto en la subfamilia Cinchonoideae (Rubiaceae). De acuerdo con la interpretación aquí presentada, fue el uso de un estado plesiomórfico de los frutos (caracteres complejos) el que resultó en la propuesta previa del complejo artificial *Rondeletia*.

ABSTRACT

Within Rubiaceae many genera of the tribe Rondeletieae were considered closely related by its morphology and proposed as the "*Rondeletia* complex". Molecular studies are in strong overall agreement in the polyphyly of the "*Rondeletia* complex": some genera are undoubtedly placed at Rondeletieae, while others should be placed within Guettardeae (*Arachnothryx* assemblage). Uncertainties persist in the generic circumscription and placement of some genera of the complex; although the current phylogenies indicate that this group is not natural, it is necessary to explore the proposal with some morphological evidence. Phylogenetic studies are required with a larger species sampling in order to test the monophyly and the relations between the genera, also a proposal of re - circumscription of Rondeletieae according to these results is necessary. The objectives of this study are to evaluate the palynological evidence to explore whether it supports the classification of the *Rondeletia* complex into two tribes; in addition, to test the phylogenetic placement and the monophyly of the genera of the *Rondeletia* complex and to propose a morphological-supported circumscription for the monophyletic genera and for the tribe Rondeletieae.

In this work a study of pollen morphology provides support to the current classification of the *Rondeletia* complex in two tribes. We found that the nexine discontinuities and ednoaperture characteristics support taxonomic decisions previously suggested by molecular data.

We present a phylogenetic analysis that contains the biggest species sampling to date for the Rondeletieae tribe. In the combined analysis based on molecular and morphological evidence, both the genus *Rondeletia* and the genera that had previously been nested in it are recovered as monophyletic, so we suggest that *Mazaea*, *Phyllomelia*, *Rachicallis* and *Roigella* should be accepted. As a result of this phylogeny, we propose a natural circumscription for Rondeletieae; we describe the new genus *Tainus*, endemic to the Hispaniola, in the Antilles; we accept the genera *Donnellyanthus* and *Rovaeanthus* (currently considered by some authors as synonyms for *Arachnothryx* and *Rogiera*, respectively, both located in the tribe Guettardeae) and we present a taxonomic synthesis of *Rovaeanthus*. Within Guettardeae, we describe two new species of *Arachnothryx* endemic to Oaxaca, Mexico. We present a phylogenetic analysis that includes a representative sample of genera of Guettardeae and a wide sampling of the species of the *Rondeletia* complex that are located in this tribe. As a result of this phylogeny, the circumscription of *Gonzalagunia* was expanded to include the genera *Arachnothryx*, *Javorkaea* and *Renistipula*. Consistent with the phylogeny, we performed the taxonomic treatment of the genus *Rogiera*, which recovered as monophyletic and did not have a taxonomic treatment including all of the species. Also, we propose an iterative methodological approach to evaluate homoplasy in the case of complex characters. This proposal is empirically tested using the

evolution of fruit types in the subfamily Cinchonoideae (Rubiaceae). According to our interpretation, the use of a plesiomorphic state of the fruits (complex characters) resulted in the proposal of the *Rondeletia* artificial complex.

PRÓLOGO

Los objetivos de la tesis son abordados en los ocho capítulos que se presentan con formato de artículos de investigación separados, es decir, cada uno con su propia introducción, metodología, resultados y conclusiones. Actualmente, tres capítulos están publicados y cinco en preparación para ser sometidos a publicación.

La tesis inicia con una sección de **antecedentes** en los que se sustenta la investigación, seguida por los **objetivos** y **métodos generales**.

El capítulo I presenta, a manera de introducción, un estudio sistemático sobre la morfología del polen del complejo *Rondeletia* en un contexto filogenético en busca de soporte para la segregación de los géneros en dos tribus: Rondeletieae y Guettardeae. Con un muestreo representativo de géneros de ambas tribus se proponen sinapomorfías que se correlacionan con las filogenias moleculares.

A partir de esta base, la tesis se divide en dos secciones, la primera, con tres capítulos, aborda la problemática del complejo *Rondeletia* relacionada con sus integrantes que se clasifican en la tribu Rondeletieae y la segunda con los de la tribu Guettardeae.

El capítulo II de la tesis corresponde a uno de los objetivos centrales de la misma: la construcción de una hipótesis sobre las relaciones de los géneros del complejo *Rondeletia*. Se enfoca en las relaciones dentro de la tribu Rondeletieae, ya que la tribu está principalmente constituida por géneros del complejo *Rondeletia* (*Mazaea*, *Rachicallis*, *Roigella*, *Rondeletia* y *Phyllomelia*) y pudimos obtener material de especies de casi todos los otros géneros de la tribu. Consecuentemente, este capítulo nos permite evaluar, tanto la monofilia de los géneros, como sus relaciones filogenéticas y la propia circunscripción de la tribu Rondeletieae.

Los capítulos III y IV son consecuencia de la filogenia de la tribu Rondeletieae. El primero aborda la descripción del nuevo género *Tainus* para la República Dominicana, el cual se apoya en evidencia molecular y morfológica. El capítulo IV corresponde al tratamiento taxonómico del género *Rovaeanthus*, el cual había sido considerado como sinónimo de *Arachnothryx*. Aunque se trata de un género pequeño, con sólo dos especies, esta síntesis taxonómica no sólo clarifica su aceptación y clasificación dentro de la tribu Rondeletieae, sino que también aporta nueva evidencia para el reconocimiento de sus especies, acompañada de una clave de identificación, descripciones amplias, datos ecológicos y mapas de distribución producto de la georeferenciación de todo el material que a la fecha se conoce de estas especies.

En la segunda parte de la tesis se aborda la problemática de los géneros del complejo *Rondeletia* ubicados en la tribu Guettardeae.

El capítulo V presenta dos especies nuevas de *Arachnothryx* que se descubrieron durante la revisión de material de herbario y colectas dentro de la zona de la Chinantla, Oaxaca, México.

El capítulo VI aborda la filogenia molecular de los géneros del complejo *Rondeletia* ubicados en la tribu Guettardeae, haciendo particular énfasis en la relación *Arachnothryx-Javorkaea-Gonzalagunia-Renistipula* y sus consecuentes implicaciones taxonómicas.

El capítulo VII corresponde al tratamiento taxonómico del género *Rogiera*, el cual se corroboró como monofilético en los análisis moleculares del capítulo VI. Esta revisión incluye una descripción actualizada del género (sin incluir a las especies de *Rovaeanthus*), una clave dicotómica para la identificación de sus especies, sinonimia que refleja la concepción de las especies a partir de una revisión amplia de material de herbario y colectas en campo, descripciones, datos ecológicos, ilustraciones y mapas de distribución producto de la georeferenciación de todas las colectas examinadas.

Finalmente, el último capítulo de la tesis es un artículo metodológico. **El Capítulo VIII** es una propuesta para el estudio de evolución de caracteres complejos que se recuperan como homoplásicos. Este capítulo permite entender que el complejo Rondeletia haya sido aceptado en el pasado con base en el uso de un carácter simplesiomórfico (los frutos capsulares) y comprender la aparente convergencia entre frutos carnosos en la subfamilia Cinchonoideae, la cual se debe al uso de un carácter complejo (frutos carnosos) que al descomponerse en sus partes permite entender la evolución de este tipo de fruto (carnoso) en la tribu Guettardeae (en particular de *Gonzalagunia*) a partir de frutos capsulares.

Finalmente, el último apartado de la tesis son las **conclusiones generales** de la investigación.

ANTECEDENTES

A. La Familia Rubiaceae

La familia Rubiaceae es una de las más diversas entre las plantas vasculares en el mundo, con entre 500 y 700 géneros y hasta 13 800 especies (Borhidi, 2012; Lorence & Taylor, 2012). Son plantas de distribución cosmopolita con centro diversidad en las zonas tropicales (Robbrecht, 1988). Esta familia se reconoce por la combinación de los siguientes caracteres: hojas simples, opuestas con el margen entero, con estípulas inter o intrapeciolares y ovario ínfero (Standley, 1918; Borhidi, 2012; Lorence & Taylor, 2012).

La clasificación de esta familia a nivel de subfamilias, tribus y géneros ha sido controversial (Bremer *et al*., 1995). La primera división de la familia en subfamilias la propuso Schumann (1891) considerando dos grupos principales basándose en el número de óvulos por lóculo: Cinchonoideae y Coffeoideae. Por su parte, Verdcourt (1958) reconoce tres subfamilias: Cinchonoideae, Rubioideae y Guettardoideae. Más recientemente, después de varias propuestas adicionales, Robbrecht (1988) estableció uno de los esquemas de clasificación para la familia más importantes, el cual se basa en características morfológicas, donde reconoce cuatro subfamilias: Antirrheoideae, Cinchonoideae, Ixoroideae y Rubioideae. Con la evidencia molecular, el esquema de clasificación actual no está libre de controversia: Bremer *et al*. (1995, 1999) reconocen tres subfamilias: Cinchonoideae, Ixoroideae y Rubioideae, mientras que Robbrecht y Manen (2006) reconocen dos: Cinchonoideae (que incluye Ixoroideae) y Rubioideae.

B. El Complejo *Rondeletia*

En la subfamilia Cinchonoideae, una de las tribus que ha presentado mayor controversia en su circunscripción es Rondeletiae, especialmente un conjunto de géneros morfológicamente relacionados con *Rondeletia* (Borhidi *et al*., 2004; Delprete, 1999a). Algunos autores sostienen que existen diferencias morfológicas en flor y fruto suficientes para segregar de *Rondeletia* varios géneros: *Acunaeanthus* Borhidi, J. Komlódi & Moncada, *Arachnothryx* Planch., *Cuatrecasasiodendron* Standl. & Steyerm., *Donnellyanthus* Borhidi, *Javorkaea* Borhidi & Jarai-Koml., *Renistipula* Borhidi, *Rogiera* Planch., *Roigella* Borhidi & Fernández Zeq., *Rovaeanthus* Borhidi y *Suberanthus* Borhidi & Fernández Zeq. (Steyermark, 1964; Borhidi *et al*., 1980; Borhidi & Fernández-Zequeira, 1981a, 1981b; Borhidi 1982; Borhidi & Járai-Komlódi, 1983; Borhidi, 1989, 1994, 2001a, 2001b; Borhidi *et al*., 2004, 2011). Otros autores descartan que estas diferencias sean suficientes para reconocer estos géneros (Standley & Williams, 1975; Lorence, 1991, 1999; Taylor, 2001). Estos taxones constituyen el complejo genérico conocido como el “complejo *Rondeletia*” (Delprete, 1999a).

La evidencia molecular (Rova *et al*., 2002, 2009; Robbrecht & Manen, 2006; Manns & Bremer, 2010) y morfológica (Delprete, 1999a) señala que otros géneros no segregados directamente de *Rondeletia* deben incluirse en el complejo *Rondeletia*: *Cuatrecasasiodendron* Standl. & Steyerm. ex Steyerm., *Gonzalagunia* Ruiz & Pav., *Mazaea* Krug & Urb., *Phyllomelia* Griseb., *Rachicallis* DC. y *Stevensia* Poit.

Este complejo de géneros incluye predominantemente arbustos y árboles de distribución neotropical. Se define por la estivación “imbricada” de los lobos de la corola en combinación con los frutos capsulares. No obstante, dentro del complejo hay considerable variación morfológica, pues las especies pueden tener estípulas deltoides, lineares o lanceoladas, 1-aristadas; flores tetrámeras, pentámeras o hexámeras, la boca de la corola desnuda, con un anillo de tricomas y/o un anillo carnoso; la dehiscencia de la cápsula loculicida o septicida; las semillas rómbicas, triangulares, angulosas o redondeado-angulosas, ocasionalmente alargadas o con los márgenes estrechamente alados y la testa en general profundamente foveolada y rugulosa (Robbrecht, 1988; Delprete, 1999a; Borhidi *et al*., 2004; Lorence, 2012).

El género *Rondeletia* fue originalmente descrito por Charles Plumier (1703), quien se lo dedicó al físico Gulliaume Rondelet de Montpellier, y fue retomado (y validado) por Linneo en 1753 (Kirkbride, 1969; Taylor, 2001). En 1849, Planchon segregó de *Rondeletia* dos géneros: *Arachnothryx* y *Rogiera*. Esta separación se basó en el número de partes florales y la ornamentación de la boca de la corola, considerando que *Rondeletia* posee corola típicamente pentámera, con un anillo carnoso en su boca, mientras que en *Arachnothryx* es tetrámera, con la boca desnuda y en *Rogiera* también es pentámera pero con un anillo de indumento amarillo en su boca.

Joseph D. Hooker (1873) no estuvo de acuerdo con esta propuesta y regresó ambos géneros, *Arachnothryx* y *Rogiera*, como sinónimos de *Rondeletia.* Esta propuesta fue secundada por Schumann (1891) y Standley (1918), argumentando que no existe evidencia contundente para su separación.

En el tratamiento de Rubiaceae de la Flora de Norteamérica, Standley (1918) subdividió a *Rondeletia* en 15 secciones, posteriormente consideradas en parte por Fernández-Zequeira (1994), quien acepta 10 secciones dentro del género *Rondeletia*. Cuatro de estas secciones se encuentran desde México a Centroamérica (*Amoenae*, *Laniflorae*, *Leucophyllae* y *Calycosae*), dos en Centroamérica (*Hondurenses* y *Odoratae*) y el resto en las Antillas. De acuerdo con Standley (1918) el grupo *Amoenae* consta de especies con la corola primordialmente pentámera, con un anillo de indumento amarillo en la boca, características que corresponden al género *Rogiera.* Los grupos *Calycosae*, *Hondurenses*, *Laniflorae*, *Leucophyllae* poseen corolas tetrámeras con la boca desnuda, características de *Arachnothryx.* El resto de las secciones tienen la corola pentámera y presenta un anillo carnoso en la boca y por tanto corresponderían a *Rondeletia* y están restringidas a las Antillas, excepto la sección *Odoratae*, que tiene representantes en tierras continentales.

En la década de los 1960's, Julian A. Steyermark, en sus tratamientos de Rubiaceae para Guyana y Venezuela, resucitó al género *Arachnothryx* para Sudamérica (Steyermark, 1967, 1974). Posteriormente, Attila Borhidi acepta a *Arachnothryx* para México y Centroamérica, con especies no tratadas por Steyermark, y también reconoce a *Rogiera* (Borhidi, 1982). La aceptación de los géneros se basó en la ornamentación de la boca de la corola y la distribución geográfica.

En las últimas décadas, el grupo de trabajo de Borhidi ha propuesto una nueva circunscripción de *Rondeletia*, en la cual reconocen los géneros *Arachnotrhyx* y *Rogiera* además de segregar otros siete géneros de *Rondeletia*: *Acunaeanthus*, *Donnellyanthus*, *Javorkaea*, *Renistipula*, *Roigella*, *Rovaeanthus* y *Suberanthus* (Borhidi & Fernández-Zequeira, 1981a, 1981b; Borhidi 1982, 1989, 1994, 2001a, 2001b; Borhidi & Járai-Komlódi, 1983; Borhidi *et al*., 1980, 2004, 2011). Su delimitación genérica se basa principalmente en el número de partes florales, la ornamentación de la boca de la corola y el número de aperturas y ornamentación de la exina del polen. Sin embargo, los caracteres que ellos usaron son variables, a veces, incluso dentro de una misma especie y se traslapan entre géneros, por lo que diversos autores no reconocen total o parcialmente la segregación de los géneros propuesta por Borhidi y colaboradores, incluso algunos autores llegan al extremo de sólo reconocer a *Rondeletia* (Kirkbride, 1969; Standley & Williams, 1975; Dwyer, 1980; Lorence, 1991, 1999; Taylor, 2001; Lorence, 2012).

Diversos géneros del complejo *Rondeletia* han sido incluidos en algunos análisis filogenéticos basados en secuencias de ADN. En el estudio de Rova *et al*. (2002), empleando el marcador de cloroplasto *trn*L-F, se estudiaron las relaciones entre las tribus Condamineeae, Rondeletieae y Sipaneeae, análisis que resultó en la transferencia de varios géneros de Rondeletieae a la tribu Condamineeae, en la subfamilia Ixoroideae. No obstante, el muestreo del complejo genérico es incompleto, y la falta de resolución y los bajos valores de soporte de sus hipótesis filogenéticas impidieron a los autores tomar decisiones taxonómicas respecto a los géneros del complejo *Rondeletia*. Sin embargo, en ese estudio se resalta que el complejo *Rondeletia* podría ser polifilético, con algunos géneros más cercanamente relacionados a la tribu Guettardeae que a Rondeletieae.

Por su parte, Stranczinger *et al*. (2006) emplearon *ITS* para proponer relaciones de los géneros del complejo *Rondeletia* en México y Centroamérica. En total incluyeron 16 especies, una de *Rondeletia*, dos de *Rogiera* y 13 de *Arachnothryx*. El resultado de este análisis fue el apoyo a la segregación de *Rondeletia* de los géneros *Arachnothryx* y *Rogiera*. No obstante, la falta o pobreza en el muestreo de los otros géneros que conforman el complejo *Rondeletia* impide tomar decisiones taxonómicas contundentes.

Rova *et al*. (2009) realizaron un análisis filogenético para poner a prueba la propuesta de clasificación infragenérica de *Rondeletia.* En ese trabajo incluyeron secuencias de *ITS*, *rps*16 y *trn*L-F de 21 taxones pertenecientes a nueve de las 10 secciones propuestas por Fernández-Zequeira (1994); asimismo, incluyeron 46 taxones de las tribus Rondeletieae y Guettardeae. El análisis apoya la separación de los géneros *Arachnothryx*, *Rogiera*, *Rovaeanthus*, *Suberanthus* y *Rondeletia,* y sugiere que el género *Stevensia* es sinónimo de *Rondeletia* y el género *Cuatrecasasiodendron* de *Arachnotrhyx*. Este estudio apoya además que el complejo *Rondeletia* es polifilético y que los géneros *Arachnothryx*, *Cuatrecasasiodendron*, *Javorkaea*, *Gonzalagunia* y *Rogiera* deben clasificarse en la tribu Guettardeae y no en Rondeletieae, donde tradicionalmente se ubicaban (Rova *et al*., 2002; Robbrecht & Manen, 2006; Rova *et al*., 2009; Manns & Bremer, 2010).

En algunos otros estudios filogenéticos se han incluido representantes del complejo *Rondeletia* (Robbrecht & Manen 2006, Manns & Bremer 2010). No obstante, el muestreo de terminales en la mayoría de los trabajos no fue diseñado para una rigurosa prueba de monofilia y de las relaciones entre los géneros del complejo. Consecuentemente, los resultados, tanto de las filogenias como de sus consecuencias taxonómicas y nomenclaturales, no han sido muy útiles para resolver la problemática del complejo *Rondeletia*.

C. Los géneros del complejo *Rondeletia* en Rondeletieae

Los géneros del complejo *Rondeletia* ubicados en la tribu Rondeletieae se distinguen por las inflorescencias axilares o terminales, la boca de la corola ornamentada con un anillo carnoso (excepto en los géneros monotípicos *Acunaeanthus, Donnellyanthus, Phyllomelia, Rachicallis* y *Roigella* , que tienen la boca de la corola desnuda) y por tener su centro de diversidad en las Antillas.

Acunaeanthus Borhidi, J. Komlódi & Moncada

Género monotípico de Cuba descrito por Borhidi *et al*. (1980), dedicado a Julián Acuña, botánico y agrónomo Cubano. Grisebach (1866) describió la especie *Rondeletia tinifolia* cuestionando su pertenencia al género *Rondeletia* por diferencias morfológicas. Standley (1918) consideró a *R. tinifolia* como la única especie que conforma la sección *Tinifoliae* del género *Rondeletia*; difiere de las otras especies del género por el ovario alargado, 4-angulado y la boca de la corola es desnuda.

La especie fue transferida al género *Mazaea* por Urban (1927) por la forma alargada y la dehiscencia septicida del fruto. Posteriormente, Borhidi *et al*. (1980) describieron el género *Acunaeanthus,* separándolo de *Mazaea* por las semillas aladas, el fruto con el cáliz persistente, la boca de la corola desnuda, las estípulas mayores de 3 mm de largo y la hoja pubescente (Delprete, 1999b).

Donnellyanthus Borhidi

Género monotípico propuesto por Borhidi *et al*. (2011) con base en las flores tetrámeras, con la boca de la corola desnuda y el fruto loculicida. Se distribuye desde México (Oaxaca) hasta Honduras y El Salvador. El nombre está dedicado a J. Donell-Smith y Nelly Diego Pérez.

La especie tipo de este género fue descrita inicialmente como *Bouvardia deamii* Donnell-Smith. Standley (1918) la transfirió a *Rondeletia* debido a los lobos imbricados de la corola y las estípulas enteras. El análisis filogenético de Rova *et al*. (2009) sugiere que es una especie aislada del resto de *Rondeletia*, sin embargo, la mantienen como parte del género *Rondeletia* por los caracteres morfológicos. La clasificación de esta especie había estado en debate: Lorence (1999) la consideraba como *Rondeletia* y Borhidi (2001a) como *Arachnothryx*, hasta que el mismo Borhidi *et al*. (2011) propusieron el género *Donnellyanthus*. Estudios filogenéticos (Manns & Bremer, 2010) corroboran que debe ser aceptado como un género distinto y lo ubican en la tribu Rondeletieae.

***Roigella* Borhidi & M. Fernández Zeq.**

Género monotípico endémico de Cuba que fue segregado de *Rondeletia* por Borhidi & Fernández-Zequeira (1981a) y dedicado al botánico y químico cubano Juan Tomás Roig. Se caracteriza por las estípulas deltoides, la corola pentámera o hexámera, con la boca desnuda, los frutos piriformes, con dehiscencia septicida y el polen 4 a 5 colporado.

Standley (1918) clasificó a la especie tipo en la sección *Correifoliae* del género *Rondeletia*. Estudios filogenéticos reconocen el género *Roigella* como hermano de *Rondeletia* (Manns & Bremer, 2010). No obstante, otros trabajos lo recuperan anidado dentro de *Rondeletia* (Rova *et al*., 2002), sugiriendo que debería considerarse como sinónimo.

***Rondeletia* L.**

Género descrito en 1703 por Plumier (Kirkbride, 1969). Originalmente abarcaba especies distribuidas en México, Centroamérica, Sudamérica y las Antillas. El género *Rondeletia* cuenta con aproximadamente 140 a 160 especies (Fernández-Zequeira, 1994; Lorence, 2012b), que se caracterizan por la corola pentámera con un anillo carnoso en la boca.

Fernández-Zequeira (1994) propuso secciones dentro del género *Rondeletia*, retomando tres de las propuestas por Standley (1918). Las secciones propuestas (*Calophyllae*, *Odoratae*, *Pedicellares*, *Rondeletia*, *Leoninae*, *Rigidae*, *Chamaebuxifoliae*, *Hypoleucae* y *Nipenses*) se distinguen por una combinación de caracteres que incluyen tipo y posición de la inflorescencia, forma de los lobos del cáliz, indumento de la hoja y filotaxia. Sin embargo, Fernández-Zequeira únicamente se enfocó en especies de Cuba, por lo cual no resuelve el problema taxonómico del complejo *Rondeletia* (Rova *et al*., 2009).

Los estudios filogenéticos recuperan a *Rondeletia* en un sentido estricto como parafilético con respecto al clado *Mazaea-Phyllomelia-Rachicallis, Roigella* y *Stevensia* (Rova *et al*., 2002, 2009; Manns & Bremer, 2010), sugiriendo que estos géneros deberían reducirse a la sinonimia de *Rondeletia*. No obstante, en estos trabajos la representación de taxones del género no es muy amplia.

***Rovaeanthus* Borhidi**

Género con dos especies que se distribuyen en México y Centroamérica. Dedicado al botánico sueco Johan Rova (Borhidi *et al*., 2004), quien abordó en estudios filogenéticos la problemática del complejo *Rondeletia*. El género se segregó de *Rondeletia* basándose en sus hojas frecuentemente ternadas (aunque también las tiene opuestas), inflorescencias con hasta tres flores, los lobos calicinos relativamente más grandes que la corola, la boca de la corola con un anillo de indumento amarillo además de un anillo carnoso y las semillas aladas (Borhidi *et al*., 2004).

Para Lorence (2012c), estos caracteres morfológicos representan extremos en la variación de *Rogiera* y por tanto, reduce *Rovaeanthus* a sinonimia de éste. Sin embargo, estudios filogenéticos recuperan *Rovaeanthus* como un género monofilético e incluido en la tribu Rondeletieae (Manns & Bremer, 2010).

***Stevensia* Poit.**

Género endémico de la Isla Hispaniola., descrito por Pierre Poiteau (1804) y dedicado al médico francés Edouard Stevens. Cuenta con once especies que se caracterizan por las flores solitarias, con 2 a 3 lobos calicinos, la corola 5 a 7-lobada y con un anillo carnoso apenas evidente (Borhidi, 2001b).

En el análisis filogenético de la tribu Rondeletieae, Rova *et al.* (2009) señalan que *Stevensia* se anida dentro del género *Rondeletia*, reduciéndolo a la sinonimia de éste. Por su parte, Borhidi (2010) reconoce que las diferencias morfológicas entre *Stevensia* y *Rondeletia* no son suficientes para reconocerlo y también apoya la sinonimia.

***Suberanthus* Borhidi y Fernández-Zeq.**

Género con nueve especies que se distribuyen en Cuba e Hispaniola. Fue separado de *Rondeletia* por Borhidi & Fernández-Zequeira (1981b) con base en el ovario oblongo con paredes lignificadas, exocarpo lenticelado, fruto septicida, semillas aladas y polen tricolporado, reticulado.

Según Borhidi & Fernández-Zequeira (1981b) este género tiene caracteres “afines” a las tribus Cinchoneae y Condaminae, como el polen reticulado y las semillas aladas. La historia taxonómica de *Suberanthus* se relaciona con otros géneros ajenos a Rondeletieae. Sus especies fueron inicialmente descritas por Richard (1850), como *Exostema neriifolium* A. Rich., y por Grisebach (1862, 1863), como *Ferdinandusa stellata* Griseb. y *Ferdinandea brachycarpa* Griseb.. Posteriormente Wright (1873) transfirió estas tres especies a *Rondeletia*, sin embargo Schumann (1897), con base en las características del fruto, las propuso como parte de la sección *Gomphosia* del género *Ferdinandusa*. Urban (1898), retomó la idea de que estas especies pertenecen a *Rondeletia* con base en la morfología floral; esta propuesta fue aceptada por Standley (1918), quien creó la sección *Stellatae* de *Rondeletia* para incluir a estas tres especies. Finalmente, fue considerado como un género nuevo por Borhidi & Fernández-Zequeira (1981b). Estudios filogenéticos recuperan al género *Suberanthus* como monofilético y lo ubican en la tribu Rondeletieae (Manns & Bremer, 2010).

***Mazaea* Krug & Urban**

Mazaea fue descrito por Krug & Urban (1897), dedicándolo a Manuel Gómez de la Maza, director del Jardín Botánico de la Habana. Estos mismos autores (Krug & Urban, 1898) lo renombraron como *Neomazaea* debido a que consideraron que *Mazaea* era un homónimo posterior de un género de algas (*Mazaea* Bornet & Grunow); sin embargo, Mazaea fue declarado inválido por el Código Internacional de Nomenclatura Botánica para el alga (Greuter *et al*., 1994), con lo que el nombre de *Mazaea* como género de Rubiaceae adquirió validez y consecuentemente *Neomazaea* se convirtió en un nombre superfluo (Robbrecht & Bridson, 1993).

Género con dos especies que se distribuyen en Cuba. Se distingue por las inflorescencias axilares, flores 4-lobadas, anillo carnoso en la boca de la corola, de 2 a 6 óvulos por lóculo y cápsulas oblongas (Delprete, 1999b).

Algunos estudios filogenéticos recuperan al género *Mazaea* como monofilético y lo ubican en la tribu Rondeletieae (Manns & Bremer, 2010). No obstante, otros trabajos lo recuperan anidado dentro de *Rondeletia* formando el clado *Mazaea-Phyllomelia-Rachicallis* (Rova *et al*., 2009) y sugieren que debería considerarse como sinónimo de *Rondeletia*.

***Phyllomelia* Gr.**

Género monotípico de Cuba descrito por Grisebach (1866). Postulado como cercanamente relacionado a *Mazea* por la morfología floral, se distingue de éste por el cáliz membranáceo, acrescente y el fruto tipo sámara (Delprete, 1999b).

Algunos estudios filogenéticos concluyen que el género *Phyllomelia* debe ser aceptado (Manns & Bremer, 2010). No obstante, otros trabajos lo recuperan anidado dentro del género *Rondeletia* (Rova *et al*., 2002), sugiriendo que debería considerarse como sinónimo de este último.

***Rachicallis* DC.**

Género monotípico que se distribuye en las Antillas y Estados Unidos de América (Florida) y se caracteriza por ser arbustos que crecen en zonas costeras con caliza; las hojas son muy delgadas y fuertemente revolutas, con márgenes engrosados (Delprete, 1999b).

Algunos estudios filogenéticos concluyen que el género *Rachicallis* debe ser aceptado (Manns & Bremer, 2010). No obstante, otros trabajos lo recuperan anidado dentro del género *Rondeletia* (Rova *et al.*, 2002), sugiriendo que deberían considerarse como sinónimos.

D. Los géneros del complejo *Rondeletia* en la tribu Guettardeae

Los géneros del complejo *Rondeletia* ubicados en Guettardeae se distinguen por las inflorescencias típicamente terminales, la boca de la corola desnuda (excepto *Rogiera*, que tiene un anillo de indumento amarillo) y la distribución geográfica con centro de diversidad en México y Centroamérica.

Arachnothryx Planch.

Género descrito en 1849 por Planchon, cuyo nombre hace alusión a la forma de los tricomas de la corola. Este género tiene su centro de diversidad en México y Centroamérica, con 80 hasta 102 especies (Lorence, 2012a; Borhidi, 2017). Se caracteriza por las flores tetrámeras, con la corola con pubescencia externa aracnoideo-tomentosa y la boca de la corola desnuda, los frutos capsulares loculicidas y las semillas angulosas (Borhidi & Járai-Komlódi, 1983; Lorence, 2012a).

Estudios filogenéticos corroboran la inclusión de *Arachnothryx* en la tribu Guettardeae (Rova *et al.*, 2009; Manns & Bremer, 2010). No obstante, *Arachnothryx* resulta parafilético con respecto a otros géneros (*Cuatrecasasiodendron*, *Javorkaea* y *Gonzalagunia*) de esa tribu.

Cuatrecasasiodendron Standl. & Steyerm.

Género descrito en 1964 por Standley & Steyermark, endémico de Colombia, y dedicado al colector J. Cuatrecasas. Inicialmente fue clasificado en la tribu Rondeletieae por los lobos del cáliz folíaceos, los lobos de la corola imbricados, el ovario con muchos óvulos por lóculo y el fruto capsular (Delprete, 1999a). En la filogenia molecular elaborada por Rova *et al.* (2009) *Cuatrecasasiodendron* se anida dentro de *Arachnothryx*, en la tribu Guettardeae, por tanto en ese trabajo los consideraron como sinónimos.

Javorkaea Borhidi & J. Komlódi

En 1983, Borhidi y Jarai-Komlódi describieron el género *Javorkaea* a partir de *Rondeletia hondurensis*, dedicado a Alexander Jávorka (botánico Húngaro). Es un género con ocho especies que se distribuyen en México y Centroamérica; se caracteriza por el cáliz zigomorfo con 5 a 7-lobos, la corola 4 a 5-lobada, de 2 a 3 cm de largo con la boca desnuda (Borhidi, 2003).

Standley (1918) creó la sección *Hondurenses* para ubicar a *R. hondurensis*, debido a las estípulas largas, la inflorescencia cimoso-corimbosa, con flores pentámeras y la boca de la corola desnuda. Después de la descripción de *Javorkaea* (Borhidi & Jarai-Komlódi, 1983), Borhidi (2001a, 2003) ha transferido varias especies de *Rondeletia* y *Arachnothryx* a *Javorkaea* y ha descrito nuevas especies en el género. A pesar de ello, el mismo Borhidi reconoce que no existe suficiente evidencia para separar *Javorkaea* y lo propone como sinónimo de *Arachnothryx* (Borhidi *et al*., 2004), con base en resultados del estudio de Rova *et al*. (2002) donde una secuencia de "*Javorkaea* sp." se anida en el clado de *Arachnothryx*.

De igual forma, Lorence (2012a) en Flora Mesoamericana, no reconoce a *Javorkaea*, pues considera que todos los caracteres usados para diferenciarlo se encuentran en diversas combinaciones en otras especies de *Arachnothryx*.

***Gonzalagunia* Ruiz & Pav.**

Género descrito por Hipólito Ruiz y José Antonio Pavón (1794). Se caracteriza por las inflorescencias terminales, tirsoides pero con los ejes laterales cortos o reducidos dando apariencia espiciforme, flores 4-meras, ovario típicamente 2-4 locular y frutos tipo drupas (Taylor, 2001; Borhidi, 2012). *Gonzalagunia* posee aproximadamente 35 especies (Taylor, 2012) con centro de diversidad en Centroamérica y Sudamérica. Es el único género del complejo *Rondeletia* ubicado tradicionalmente en la tribu Guettardeae con especies distribuidas en las Antillas.

El género *Gonzalagunia* es morfológicamente similar a *Arachnothryx* por la inflorescencia tirsoidea y las flores 4-meras, pero ambos difieren en el tipo de fruto, ya que en *Gonzalagunia* es carnoso, mientras en *Arachnothryx* es seco. Sin embargo, Ståhl (1999) reporta en Flora de Ecuador individuos de *Gonzalagunia* que presentan frutos secos y carnosos en la misma infrutescencia.

Estudios filogenéticos corroboran la inclusión de *Gonzalagunia* en la tribu Guettardeae (Rova *et al*., 2009; Manns & Bremer, 2010), no obstante *Arachnothryx* es parafilético con respecto a él.

***Renistipula* Borhidi**

Género segregado de *Arachnothryx* por Borhidi *et al*. (2004) y cuyo nombre hace referencia a las estípulas foliáceas, persistentes, más anchas que el tallo y reniformes. *Renistipula* contiene tres especies de México y Centroamérica. Además de las estípulas, *Renistipula* se distingue de *Arachnothryx* por los lobos del cáliz redondeados, la cápsula deprimido-globosa y las semillas aladas. A pesar de estas diferencias, Lorence (2012a) lo considera como sinónimo de *Arachnothryx*.

Un representante de este género fue incluido en el análisis filogenético enfocado a la tribu Hamelieae realizado por Stranczinger *et al*. (2014). En el estudio *Renistipula* se anida dentro de la tribu Hamelieae. Este resultado es cuestionable dado que *Renistipula* carece de los caracteres típicos de Hamelieae tales como los rafidios e inflorescencias ebracteadas (Robbrecht, 1988).

***Rogiera* Planch.**

Descrito en 1849 por Planchon, cuenta actualmente con entre nueve y 18 especies, caracterizadas por la corola típicamente pentámera con un anillo de indumento amarillo (Borhidi, 1982). De acuerdo con el análisis filogenético de Rova *et al*. (2009) se apoya la separación de género *Rogiera* de *Rondeletia* e incluso se debe clasificar en la tribu Guettardeae. Sin embargo, dada la evidencia morfológica y el número limitado de especies incluídas en el análisis filogenético, los autores proponen mantenerlo dentro de Rondeletieae. Otros estudios filogenéticos corroboran la monofilia de *Rogiera* y su inclusión en la tribu Guettardeae (Manns & Bremer, 2010).

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OBJETIVOS

La presente investigación tiene como objetivos: 1) evaluar la evidencia de morfología de polen para explorar si ésta apoya la clasificación del complejo *Rondeletia* en dos tribus. 2) Proponer la ubicación filogenética de todos los géneros del complejo *Rondeletiea*. 3) Poner a prueba la monofilia y circunscripción de los géneros que comprenden el complejo *Rondeletia* y proponer una hipótesis filogenética de relaciones entre ellos. 4) Estudiar la evolución de algunos caracteres morfológicos en el grupo y evaluar en ese contexto su utilidad taxonómica. 5) Explorar nuevas fuentes de evidencia que puedan contribuir en la circunscripción tribal y genérica. 6) Reflejar los resultados de la filogenia en una clasificación consistente. 7) Realizar revisión(es) taxonómica(s) de grupos naturales para los cuales se hayan incluido en la filogenia todas o un número elevado de sus especies.

METODOLOGÍA GENERAL

El método general para abordar el estudio sistemático del complejo *Rondeletia* incluye tres ejes principales que se interconectan y retroalimentan (Figura 3): I) Trabajo en colecciones científicas y revisión bibliográfica, II) Trabajo de campo, III) Trabajo de laboratorio.

I) Colecciones científicas y revisión bibliográfica

A partir de la revisión bibliográfica, la consulta de bases de datos en línea y la consulta de herbarios se generó una base de datos de los géneros y las especies asociados al complejo *Rondeletia*.

La revisión bibliográfica incluye la consulta de literatura especializada (revisiones, floras, artículos), así como la recopilación de protólogos e imágenes de tipos de los taxones examinados.

Se revisaron morfológicamente más de 2000 ejemplares depositados en colecciones científicas consultadas en este trabajo (B, CAS, CHAPA, CHIP, ENCB, F, FCME, HGO, MEXU, MO, NY, US, XAL) además de numerosas imágenes de ejemplares tipo en línea (JSTOR Global Plants). Con la revisión morfológica y la base de datos se direccionó el trabajo de campo y se diseñó el muestreo de terminales para el trabajo de laboratorio posterior.

La revisión de los ejemplares fue fundamental para la toma de decisiones taxonómicas derivadas de los estudios filogenéticos, el reconocimiento de nuevos taxones y, por supuesto, la base para los tratamientos taxonómicos.

La importancia de las colecciones científicas para este trabajo también se resalta con el uso de muestras colectadas recientemente y en buen estado de conservación para extraer ADN.

II) Trabajo de campo

El trabajo de campo tuvo dos propósitos principales, uno, fue el de proveer la materia prima para los estudios filogenéticos (muestras de hojas en silica gel), y, dos, el del reconocimiento de las especies en vivo y su ambiente, fundamental para el entendimiento del grupo. En total se visitaron siete estados de la República Mexicana y República Dominicana, en un promedio de dos salidas por año..

III) Trabajo de laboratorio

En este apartado se conjuntan tanto labores de laboratorio de palinología (técnica de acetólisis y observación del polen), de biología molecular (extracción, amplificación y secuenciación de ADN) así como el de gabinete de herbario (caracterización y medición), cada uno con un método propio y desarrollado en extenso en los respectivos capítulos de esta tesis. El trabajo palinológico se realizó en el Laboratorio de Palinología del Instituto de Geología, UNAM. La secuenciación de ADN se realizó principalmente en Botanischer Garten und Botanisches Museum Berlin-Dahlem y se completó en el Laboratorio de Biología Molecular del Instituto de Biología, UNAM.

CAPÍTULO I. INTRODUCTORIO

What do pollen morphology tell us about the *Rondeletia* complex (Rubiaceae) in the phylogenetic context

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Original Article

What does pollen morphology tell us about the *Rondeletia* complex (Rubiaceae) in a phylogenetic context?

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Running title: Palynology of the *Rondeletia* complex (Rubiaceae)

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ABSTRACT

Background and Aims

Within the tribe Rondeletieae (Rubiaceae) 17 morphologically related genera were considered as the *Rondeletia* complex. Molecular studies agreed that this is a polyphyletic group where a core set of genera remains in Rondeletieae while others share a most recent common ancestor with Guettardeae. Despite molecular evidence no solid morphological characters have been found to corroborate the phylogenetic findings. The aim of this study is to explore whether pollen morphology provides evidence supporting the molecular hypotheses.

Methods

In total, 14 genera and 30 species of Rondeletieae and Guettardeae (including 12 genera of the *Rondeletia* complex) are observed using light microscopy and scanning electron microscopy. Furthermore, we employed a published phylogeny to evaluate pollen phylogenetic signal and its taxonomic relevance.

Key Results

Our results show that the main characters to distinguish genera or groups are polar outline, endoaperture type, and nexine discontinuities. At species level, pollen size, endoaperture type and exine ornamentation are important. The genera included in the *Rondeletia* complex sharing a most recent common ancestor with Guettardeae have nexine discontinuities in the polar areas: endofissures (*Rogiera*) or endocracks (*Arachnothryx* complex: *Arachnothryx-Gonzalagunia*, *Javorkaea* and *Renistipula*), absent in Rondeletiae.

Conclusions

Palynological data: 1) corroborate the exclusion of the *Arachnothryx* complex and *Rogiera* from the *Rondeletia* complex; 2) a close relationship of *Rondeletia* with *Stevensia*, and of *Arachnothryx* with *Gonzalagunia*, *Javorkaea* and *Renistipula*; 2) support the acceptance of *Donnellyanthus, Rachicallis*, *Rogiera*, and *Rovaeanthus*; 3) highlight the need for further pollen research of other genera in these tribes, such as *Blepharidium*, *Machaonia*, *Mazaea* and more species of *Rondeletia*.

INTRODUCTION

Generic limits around *Rondeletia* L. (Rondeletieae) have been re-drawn several times during the past century. The morphological heterogeneity of *Rondeletia* has led to the segregation of many genera: *Acunaeanthus* Borhidi, Jarai-Koml. & Moncada, *Arachnothryx* Planch., *Donnellyanthus* (Donn.Sm.) Borhidi, *Cuatrecasiodendron* Steyerm., *Javorkaea* Borhidi & Jarai-Koml., *Renistipula* Borhidi, *Roigella* Borhidi & Z.M. Fernández, *Rogiera* Planch., *Rovaeanthus* Borhidi, *Suberanthus* Borhidi & Z.M. Fernández and *Tainus* Torr.-Montúfar, H. Ochot. & Borsch (Steyermark, 1964; Borhidi *et al.*, 1980, 2004, 2011; Borhidi and Fernández-Zequeira, 1981*a*, *b*; Borhidi and Jarai-Komlodi, 1983; Torres-Montúfar *et al.*, 2017). These genera form the so called *Rondeletia* complex (Delprete, 1999*a*), which is characterized by quincuncial corolla lobes aestivation, spatulate corolla lobes, many seeded capsular fruits and terminal inflorescences (Robbrecth, 1988; Delprete, 1999*a*; Borhidi *et al.* 2004; Rova *et al.*, 2009, Torres-Montúfar *et al.*, IBUNAM, Mexico, unpubl. res.).

Molecular studies strongly agree that the *Rondeletia* complex is polyphyletic and it has been suggested that the genera *Arachnothryx* (including *Javorkaea*) and *Rogiera* are better classified in the tribe Guettardeae rather than in Rondeletieae (Manns and Bremer, 2010). At the same time, there is strong agreement that *Rondeletia* (including *Stevensia*) shares a more recent common ancestor with *Mazaea*, *Phylomelia*, *Rachicallis*, and *Roigella* (Manns and Bremer, 2010; Torres-Montúfar *et al.*, 2017, 2018), clade that has been called the *Rondeletia* assemblage (Torres-Montúfar *et al.*, 2017). On the other hand, phylogenetic studies (Rova *et al.*, 2002; Robbrecht and Manen, 2006; Rova *et al.*, 2009; Manns and Bremer, 2010; Torres-Montúfar *et al.*, 2017, 2018) have shown that other genera not segregated from *Rondeletia* are closely related to some genera formerly belonging to the *Rondeletia* complex: *Gonzalagunia* Ruiz & Pav., *Mazea* Krug., *Phyllomelia* Griseb., *Rachicallis* DC. and *Stevensia* Poit. Among them, *Gonzalagunia* and *Renistipula* are more closely related to *Arachnothryx* conforming the so called "*Arachnothryx* complex" (Torres-Montúfar *et al.*, IBUNAM, Mexico, unpubl. res.).

Furthermore, some of the genera from the *Rondeletia* complex are controversial and have not universally been accepted (Lorence, 1991; Burger and Taylor, 1993; Lorence, 1999; Taylor, 2001). Even after molecular evidence, some authors have rejected the splitting of some genera until more evidence is included (Lorence and Taylor, 2012).

In total there are 17 genera that at some point have been related directly or indirectly to *Rondeletia*, which despite the fact that it is accepted that they do not form a natural group, still present a challenge in terms of tribal classification and generic circumscription.

Although the phylogenetic relationships within the *Rondeletia* complex have been studied by several researchers, a thorough morphological comparative survey has not been carried out. In particular for Rubiaceae, studies have revealed the importance of pollen morphology in the generic delimitation and infrageneric taxonomy (e.g. Johansson, 1987; Huysmans *et al.*, 1999; Lens *et al.*, 2000; D'hondt *et al.*, 2004; Verellen *et al.*, 2004; Dessein *et al.*, 2005*a*, *b*; Xie and Zhang, 2010). The main antecedent for the *Rondeletia* complex palynology was provided by Igersheim (1993), who described the pollen grains of 20 *Rondeletia* species, including few representatives of *Arachnothryx* and *Rogiera* (treated as subgenera). He concluded that pollen morphology does not support the separation of genera from *Rondeletia* because all taxa have spheroidal, tricolporate to tetracolporate pollen grains with similar ornamentation.

In this study, we further explore the taxonomic value of pollen features of genera in the *Rondeletia* complex using light (LM) and scanning electron (SEM) microscopy using the current phylogenetic framework for comparative purposes (Manns and Bremer, 2010; Torres-Montúfar *et al.*, 2017, and IBUNAM, Mexico, unpubl. res.).

MATERIAL AND METHODS

The present work was undertaken at the Laboratorio de Palinología, Instituto de Geología, at Universidad Nacional Autónoma de México (UNAM). This study was mainly based on samples taken from herbarium material deposited at the Herbario Nacional de Mexico (MEXU) and the herbarium of the Jardín Botánico Nacional Dr. Rafael M. Moscoso (JBSD). For pollen preparation, nearly mature flower buds (just before anthesis) were sampled, including 32 specimens belonging in 14 genera and 30 species (see Appendix A on supplementary material for the list of specimens investigated with scientific names and complete associated data).

The samples were acetolysed in accordance to Erdtman (1960) and mounted in glycerine jelly and deposited in the palynological collection at Instituto de Geología, UNAM. All measurements are in μm. Measurements of polar and equatorial axis's lengths and nexine discontinuities were based LM of at least 25 mature pollen grains per species. Nexine discontinuity measurements were taken at the widest point within a pollen grain. A single representative pollen grain from species within Guettardeae and Rondeletieae was chosen to illustrate polar and equatorial views as well as nexine discontinuities. All other measurements and descriptions were made using SEM micrographs. Representative pollen grains per species within genera of Guettardeae and Rondeletieae were chosen to show general aspects and ornamentation. Descriptive terminology is based on El-Ghazali (1990) and Punt *et al.* (2007), and the descriptions follow the template proposed by Dessein *et al.* (2005*b*) for Rubiaceae pollen.

The observations presented here are contrasted and completed with the observations presented by for Chiococceae by Huysmans *et al.* (1999), for Hillieae by D'Hondt *et al.* (2004) and for Hamelieae by Dessein *et al.* (2005*b*). The main pollen characters at tribal or generic level were manually mapped onto a cladogram based on the results by Manns and Bremer (2010) using CorelDraw X3 v. 13 (2005). Main taxa, at generic level within Guettardeae and Rondeletieae, are summarized from Manns and Bremer (2010) and updated with the current generic circumscriptions according Torres-Montúfar *et al.* (2017, and IBUNAM, Mexico, unpubl. res.). All useful qualitative characters to distinguish genera within Guettardeae and Rondeletieae are schematized to the right of the cladogram (Fig. 1).

RESULTS

We sampled 12 out of the 17 recognized genera in the *Rondeletia* complex; we are missing in our sampling five monotypic genera with limited collections: *Acunaeanthus*, *Cuatrecasiodendron*, *Phyllomelia*, *Roigella*, and *Tainus*.

The pollen grains among the studied genera are heterogeneous in size, aperture number, shape, endoaperture type, exine and nexine ornamentation (Figs. 2–4). Probably the least informative character is the number of apertures because taxa have either the plesiomorphic condition of three apertures, or this character is variable within genera (e.g., *Suberanthus* can have three or four) or even within species (e.g., *Rachicallis americana*, *Rogiera amoena* can have three or four).

We did not find any pollen synapomorphic characteristics for the tribes or main lineages (Guettardeae or Rondeletieae, from our observations; Chiococceae-Hillieae-Hamelieae and the *incertae sedis* genera *Chione* DC. and *Colleteria* David W. Taylor, from literature). Only for Chiococceae the presence of endocracks at polar areas is an important feature, however is not exclusive for this tribe since the endocracks are also present in the *Arachnothryx* complex (Fig. 1). In general the nexine is continuous, although some grains in some species within Rondeletieae have endofissures at mesocolpium. This characteristic contrasts with the genera of the *Rondeletia* complex that share a most recent common ancestor with Guettardeae (*Rogiera* and the *Arachnothryx* complex), which have either endofissures or endocracks.

Groups of genera can be characterized by different combinations of the polar outline, endoaperture type, and exine ornamentation. The pollen heterogeneity does not allow distinguishing genera except for *Rogiera*, which is the only one with nexine discontinuities as endofissures in both poles and *Rachicallis,* which is the only one with divergent endoaperture (Table 1; Fig. 1). The principal differences among species are provided by pollen size, endoaperture type, and exine ornamentation; within each genus specific sets of these characters help differentiating species (Table 2, Plates 2–4). Full pollen grain descriptions for genera and species are presented in Appendix B as supplementary material.

Rondeletieae

The pollen of the clade *Donnellyanthus-Rovaeanthus+Suberanthus-Acuneanthus* (*Acuneanthus* not sampled) is characterized, but not exclusively, by the circular polar outline, convergent endoaperture and the reticulate exine ornamentation (Figs. 1–3). Among the sampled genera, *D. deamii* ranges among the largest pollen grains in Rondeletieae ($\bar{P}$=22.4 µm, $\bar{E}$= 23.9 µm). Within Rondeletieae, but outside this clade, only *Rachicallis* and *Rondeletia belizensis* have circular polar outline and reticulate exine, but the endoaperture type is different in both (parallel in *R. belizensis* and divergent *Rachicallis*). We did not find differences among the pollen in the clade *Rovaeanthus-Donellyanthus*. The genus *Suberanthus* in the sister clade can be distinguished from *Donnellyanthus-Rovaeanthus* by the pollen size ($\bar{P}$=17.9–19.2, $\bar{E}$=17.9–19.2 in *Suberanthus* vs $\bar{P}$=22.4–22.6, $\bar{E}$=23.9–24 in *Donnellyanthus-Rovaeanthus*). Also, for the two *Suberanthus* species examined, the pollen size is the main character to diagnose them; *S. neriifolius* has the biggest pollen grains ($\bar{P}$=19.2, $\bar{E}$=19.2) in contrast with *S. hincheanus* which has small pollen ($\bar{P}$=17.9, $\bar{E}$=17.9).

Most species of the *Rondeletia* assemblage are characterized by the triangular concave polar outline and foveolate exine ornamentation (except for *Rondeletia belizensis* and *Rachicallis*; Fig. 1) and there are no pollen characters that correlate with clades within this lineage.

Within the genus *Rondeletia* there are differences among species mainly in pollen size, but also in endoaperture type and exine ornamentation. The species *R. belizensis* has among the largest pollen size ($\bar{P}$=17.1, $\bar{E}$=17.2 vs. $\bar{P}$=12.3–14.9, $\bar{E}$=13.2–15.6) within the genus, but it is easier to recognize by the qualitative features already mentioned, which contrast with the rest of the species: the reticulate exine ornamentation (vs. foveolate) and by the circular polar outline (vs. triangular concave). The species *R. stereocarpa* is the only one in the genus with colpus equatorialis endoaperture (vs. parallel). The pollen of *R. carnea*, *R. ochracea* and *R. polita* is similar, among these species *R. polita* has the smallest pollen grains ($\bar{P}$=12.3, $\bar{E}$=13.2 vs. $\bar{P}$=14.4–14.9, $\bar{E}$=15.3–15.6), while *R. carnea* and *R. ochracea* are only slightly different in size. The species formerly placed in *Stevensia*, also have foveolate exine ornamentation, triangular concave polar outline and parallel endoaperture; *S. aculeolata* has the largest pollen grains ($\bar{P}$=18.9, $\bar{E}$=18.0) among *Rondeletia*, while the pollen grains of *S. grandiflora* fall within the average for the genus, only being a little more evidently prolate ($\bar{P}$=15.9, $\bar{E}$=15.1).

Guettardeae

The nexine discontinuities in the polar areas allow diagnosing the genera of the *Rondeletia* complex placed in Guettardeae (Figs. 1, 2, 4): *Rogiera* with endofissures (up to 2.2 µm) and the *Arachnothryx* complex with endocracks (bigger than 2.8 µm). This is true even though within the *Rondeletia* assemblage some pollen grains of *Mazaea* and *Rondeletia* have endofissures because they are at mesocolpium.

The pollen in the two sampled species *Rogiera* (out of 9–15), the earlier divergent genus within Guettardeae (Fig. 1) is very similar, although they are morphologically not that similar. The pollen size in *R. amoena* is $\overline{P}$=18.7, $\overline{E}$=18.8 and in *R. gratissima* it is $\overline{P}$=18.2, $\overline{E}$=18.2; they share convergent endopaerture and foveolate exine ornamentation; the endofissure mean width is 1.7 µm in *R. amoena* and 1.6 µm in *R. gratissima*.

The clade formed by *Guettarda* and allies (represented here also with *Chomelia*) is palynologically well defined by the triangular convex polar outline, the closed endoaperture and the subtectate reticulate exine with lumina bigger than 1.4 µm. It differs from the pollen in the sister clade (Fig. 1) with members of the *Arachnothryx* complex (including *Gonzalagunia*, *Javorkaea* and *Renistipula*) by the circular polar outline, equatorialis, convergent, or parallel endoaperture, foveolate exine or, when reticulate, with lumina smaller than 1.10 µm in addition to the endocracks present in one or in both polar areas.

There are differences among the *Arachnothryx* species mainly in pollen size, but in some species also in the endoaperture type, and exine ornamentation. The species *A. buddelioides* has the largest pollen grains ($\overline{P}$= 27.7, $\overline{E}$=26.3 vs. $\overline{P}$=17.5–19.5, $\overline{E}$=17.4–19.5) and is the only one with endocracks at both polar areas (as in *Gonzalagunia*). Also, among the species with foveolate ornamentation, *A. aspera* can be distinguished by the equatorialis endoaperture (vs. parallel) and also by the smallest pollen grain size among the sampled species in the *Arachnothryx* ($\overline{P}$=17.5, $\overline{E}$= 17.4). The pollen grains of *A. calycophylla* and *A. gonzaleoides* are quite similar; the main differences are the foveolae size (0.12–0.14 µm in *A. calycophylla* vs 0.17–0.24 µm in *A. gonzaleoides*) and the endocrack mean width (3.4 µm in *A. calycophylla* vs 3.9 µm in *A. gonzaleoides*). The species *A. capitellata* and *A. guerrerensis* have reticulate exine ornamentation instead of foveolate; they differ between themselves by the parallel endoaperture in the former and convergent in the latter.

All the evaluated species of *Gonzalagunia* overlap the variation within *Arachnothryx*; they have convergent endoaperture, foveolate exine ornamentation and endocracks at both polar areas. They differ among themselves mainly in pollen size: *G. chiapensis* has the biggest pollen grains ($\overline{P}$=30.6,

$\overline{E}$=31.1), *G. hirsuta* is medium size ($\overline{P}$=22.9, $\overline{E}$=22) and *G. osaensis* has the smallest pollen grains ($\overline{P}$=19.9, $\overline{E}$=18.9).

The species formerly placed in *Javorkaea* also overlap the variation with *Arachnothryx*; they have equatorialis endoaperture and endocracks at one polar area. They differ among themselves in pollen size and exine ornamentation: *J. acuminata* has largest pollen grains ($\overline{P}$=21.3, $\overline{E}$=21.3) with reticulate exine while *J. uxpanapensis* has small pollen grains ($\overline{P}$=17.2, $\overline{E}$=17.1) with foveolate exine.

The genus *Renistipula*, like in *Javorkaea*, overlaps the variation with *Arachnothryx* and both species share the equatorialis endoaperture and endocracks at one polar area. Pollen size and exine ornamentation are the main characters to differentiate between species: *R. costaricensis* has bigger pollen grains ($\overline{P}$=17.2, $\overline{E}$=17.3) with foveolate exine, while *R. galeottii* has smaller pollen grains ($\overline{P}$=16.2, $\overline{E}$=16.2) and reticulate exine ornamentation.

DISCUSSION

The main characters to distinguish genera or phylogenetic groups are: polar outline, endoaperture type, and nexine discontinuities. It was already mention that endoaperture type and nexine discontinuities can have phylogenetic signal (e.g., Dessein *et al*., 2005*b*), but polar outline shows to be relevant as a potential synapomorphy for the *Rondeletia* assemblage (triangular concave) and for *Guettarda* and allies (triangular convex). At species level, pollen size, endoaperture type and exine ornamentation are important. The two last ones are often believed to be more constant at supraspecific hierarchies, hence believed to have potential phylogenetic signal (e.g., Dessein *et al*., 2005*b*).

In contrast to the palynological study by Igersheim (1993), our results show that pollen morphology, such as the endoaperture type, exine ornamentation and particularly the size and position of nexine discontinuities, provides evidence for the separation of the genera belonging in the *Rondeletia* complex: the genera *Arachnothryx*, *Gonzalagunia*, *Javorkaea* and *Rogiera* (Guettardeae) are characterized by the presence of nexine discontinuities, in contrast to the genera that remains within Rondeletieae in which the nexine discontinuities are absent or rarely present, in which case they are at the mesocolpium instead of at the polar areas.

The nexine discontinuities were described by Huysmans *et al.* (1998) for the tribe Isertieae as "star-shaped nexine thinnings in which the three arms of the star ran between the ectocolpi and may be fused with the endocingulum in the centre of the mesocolpium". For the tribes Catesbeaeae and Chiococceae (now both considered as Chiococceae) these were described as three endocolpi perpendicular to the ectocolpi, with diverging ends often branching were described (Huysmans *et al.*, 1999). In Dessein *et al.* (2005*b*) these observations were re-interpreted as irregular grooves in the inner nexine surface, and the later authors mentioned that this is a widespread character within Rubiaceae in different lineages among the three subfamilies (e.g. Rubioideae: Anthospermaeae, Gaertnereae, Spermacoceae; Ixoroideae: Ixoreae, Sabiceeae; Cinchonoideae: Chiococceae, Isertieae).

Ochoterena (2000) reported that transmition electron microscopy (TEM) showed that the pollen discontinuities in some genera of now Chiococceae correspond to complete absence of nexine (Fig. 5). For the genera of Guettardeae, it would be important to have observations using TEM to know if in this tribe the endocracks/endofissures correspond to complete absence of the nexine or if they are just reductions in nexine thickness (nexine thinnings). Irrespectively of these cases, we decided to use the terms endocracks or endofissures for the pollen in the taxa that we studied since this term was used for Chiococceae, which is phylogenetically close to Guettardeae-Rondeletieae (Robbrecht and Manen, 2006; Rova *et al.*, 2009; Manns and Bremer, 2010; Torres-Montúfar *et al.*, 2017, 2018).

Rondeletieae

Pollen characteristics do not provide insights for the circumscription of Rondeletieae vs Guettardeae. Whether they are maintained as two tribes (as suggested by Robbrecht and Manen, 2006; Manns and Bremer, 2010) or merged into a single tribe (as suggested by Rova *et al*. 2009) cannot be assess by pollen morphology.

Within the tribe, there are trends in pollen morphology that correlate with the two main clades: one clade (*Donnellyanthus*, *Rovaeanthus* and *Suberanthus*) with circular polar outline and reticulate exine while the other (the *Rondeletia* assemblage) with triangular concave polar outline and foveolate exine. If these trends are confirmed when more genera are pallynologically studied (i.e., *Acrosynanthus*, *Acunenathus*, *Blepharidium* and *Tainus*), pollen could resolve the controversial placement of *Blepharidium* as sister to either clade in phylogenetic studies (Manns and Bremer, 2010 vs. Torres-Montúfar *et al*., IBUNAM, Mexico, unpubl. res.).

The genera *Donnellyanthus* and *Rovaeanthus* are currently treated in the Flora of Mesoamerica as synonyms of *Arachnothryx* and *Rogiera* respectively (Lorence & Taylor, 2012). Pollen morphology show some differences among these genera, such as the absence of the endocracks/endofissures in *Donnellyanthus* and *Rovaeanthus*; for that reason, we believe that the pollen morphology provides evidence for the separation of these genera as in molecular studies (Rova *et al.*, 2002, 2009; Manns and Bremer, 2010).

Contrary to Igersheim (1993), pollen evidence confirms that the *Rondeletia* complex is not monophyletic, as molecular phylogenetic analyses suggest (Rova *et al.*, 2002; Robbrecht and Manen, 2006; Rova *et al.*, 2009; Manns and Bremer, 2010; Torres-Montúfar *et al.*, 2017, 2018 and IBUNAM, Mexico, unpubl. res.).The presence of endocracks in the *Arachnothryx* complex and endofisures in *Rogiera* supports the exclusion of these genera from the generic complex. These characteristics are more easily observable with LM, we recommend therefore that both technics continue to be used in a complementary way.

Within the *Rondeletia* assemblage only *Rachicallis* can be easily distinguished by the divergent endoaperture. For the rest, the other genera overlap with the variation within *Rondeletia*. The pollen morphology of *Mazaea* and *Stevensia* reflects the close relationship with *Rondeletia*, recovered in molecular phylogenetic analyses (Manns and Bremer, 2010) or even the lack of resolution or intermingling among them (Rova *et al.*, 2002; Rova *et al*., 2009; Torres-Montúfar *et al*, 2017). The genus *Rondeletia* is the most diverse within the tribe (with around 120 spp; Fernández-Zequeira, 1994; Borhidi *et al.*, 2004), and as such, it is not surprising that the pollen morphology is also very variable within it. Palynological evidence shows similarities between some species of *Rondeletia* (*R. ochracea*, *R. polita* and *R. stereocarpa*) and *Stevensia* in characters which are variable within the genus. The fact that the pollen morphology of *Stevensia* overlaps with respect to that in *Rondeletia*, therefore, is of little contribution to support or reject the treatment of *Stevensia* as a synonym of *Rondeletia* (Rova *et al.*, 2002, 2009; Manns and Bremer, 2010).

To further evaluate the potential contribution of pollen morphology to the infrageneric classification of *Rondeletia* proposed by Fernández-Zequeira (1994) more species of the genus need to be palinologically studied. At least the continental species of *Rondeletia* sampled in this study (*R. belizensis*) is quite different from the others by having circular polar outline and reticulate exine ornamentation. There are not too many species in the genus that are not present in the Antilles and it would be interested to know if they all share the pollen characteristics of *R. bellizensis* or are more similar to those in the rest of the sampled species of *Rondeletia*.

Guettardeae

The presence of similar endocracks in *Arachnothryx, Gonzalagunia, Javorkaea* and *Renistipula* supports the exclusion of these genera from the *Rondeletia* complex, as molecular phylogenetic analyses suggests (Rova *et al.*, 2002; Robbrecht and Manen, 2006; Rova *et al.,* 2009; Manns and Bremer, 2010; Torres-Montúfar *et al.*, 2017, 2018 and IBUNAM, Mexico, unpubl. res.). Nevertheless, the pollen characters do not provide evidence for the inclusion within Guettardeae. The nexine discontinuities are unique for each specific lineage: endocracks in on one or both polar areas for the

Arachnothryx complex (*Arachnothryx, Gonzalagunia, Javorkaea* and *Renistipula*) and endofissures in one of the polar areas for *Rogiera*.

The genera of Guettardeae (other than those of the *Arachnothryx* complex) examined here and from literature (Roubik and Moreno, 1991; Molina *et al.*, 2002) differ with respect to those in the *Arachnothryx* complex by the triangular convex polar outline and the closed endoaperture. Hence, in contrast to Rondeletieae, each studied clade is palynologically well differentiated within Guettardeae. It would be important to characterize the pollen of *Machaonia* Bonpl. to see if it supports another well differentiated lineage within the tribe.

The genus *Gonzalagunia* was traditionally classified in Isertieae (Robbrecht, 1988), however, molecular phylogenies placed it sharing a most recent ancestor with Guettardeae and closely related to *Arachnothryx*, *Javorkaea* and *Renistipula* (Rova *et al.*, 2002; Robbrecht and Manen, 2006; Rova *et al.*, 2009; Torres-Montúfar *et al.*, 2017, 2018). Indeed, pollen characters exhibit high overlapping among these four genera (Fig. 2), supporting the need for a possible synonymy, as suggest by the molecular phylogenetic studies (Torres-Montúfar *et al.* IBUNAM, Mexico, unpubl. res.). The species evaluated of *Gonzalagunia* have endocracks at both polar areas as in *A. buddleioides*.

CONCLUSIONS

Our results suggest that pollen morphology can be important in systematic studies of Rondeletieae-Guettardeae since it correlates to some degree with the current phylogenetic hypotheses and in several cases provides insight for taxonomic decisions. Despite this, there is no palynological support at tribal level.

Pollen morphology does not evolve in the same way even among closely related phylogenetic lineages; while there are important features supporting each of the main clades within Guettardeae, within Rondeletieae there is a lack of palynological support for most clades.

In general, at supraspecific level, polar outline, endoaperture type and nexine discontinuities provide the most information while at species level pollen size, endoaperture type and exine ornamentation are relevant.

We pointed that the nexine continuity, better observable using LM, is an important pollen morphological character correlated to phylogenetic lineages. The endocracks (*Arachnothryx* complex) and endofissures (*Rogiera*) are characteristic of the taxa previously believed to belong in the *Rondeletia* complex that in fact share a most recent common ancestor with Guettardeae. They are also useful to distinguish them from other genera in Guettardeae.

The pollen of the genus *Stevensia* falls within the variation of the pollen in *Rondeletia*. Most of the *Rondeletia* species have pollen with foveolate exine ornamentation and parallel endoaperture as *Stevensia*. Nevertheless, those features are also present outside Rondeletia (i.e., *Mazaea*) and hence, there is no conclusive evidence provided by pollen morphology to synonymize both genera.

In other cases, palynological data corroborates the findings in phylogenetic studies and also provides morphological evidence for the derived taxonomic decisions:

1) The genera *Donnellyanthus* and *Rovaeanthus* (currently recognized as synonymous of *Arachnothryx* and *Rogiera*, respectively) should be accepted and placed within Rondeletieae, because they do not have pollen discontinuities.

2) The genus *Javorkaea* is supported as synonym of *Arachnothryx*; like in many *Arachnothryx* species, *Javorkaea* has endocracks at both poles and equatorialis endoaperture. Pollen of *Gonzalagunia* and *Renistipula* also falls within the variation of *Arachnothryx*.

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SUPPLEMENTARY DATA

Supplementary data are available at https://(link) and consist of the following. Appendix A: voucher specimens corresponding to the evaluated species in our study, including full scientific names, locality, collection date, collector and collection number, herbarium, and number of pollen preparation deposited at Laboratorio de Palinología of the Instituto de Geología. Appendix B: Full pollen description of the taxa evaluated, following the template suggested by Dessein *et al.* (2005*b*) for Rubiaceae pollen.

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TABLE 1. Principal characters of pollen grains of the evaluated genera of the *Rondeletia* complex

Tribe	**Genera**	**Number of Apertures**	**Endoaperture type**	**Exine ornamentation**	**Nexine discontinuities**	**Endocrack/ Endofissure width (µm)**
Rondeletieae	*Donnellyanthus*	3	Convergent	Reticulate	Absent	-
	Mazaea	3	Parallel	Foveolate	Absent or rarely endofissures at mesocolpium	2.2
	Rachicallis	3-4	Divergent	Reticulate	Absent	-
	Rondeletia	3	Parallel Equatorialis	Foveolate Reticulate	Absent or rarely endofissures at mesocolpium	0.8–0.9
	Rovaeanthus	3	Convergent	Reticulate	Absent	-
	Stevensia	4-3	Parallel	Foveolate	Absent or rarely endofissures at mesocolpium	-
	Suberanthus	3-4	Convergent	Reticulate	Absent	-
Guettardeae	*Arachnothryx*	3	Equatorialis Parallel Convergent	Foveolate Reticulate	Endocracks at one pole or both poles	2.8–4.0
	Chomelia	3	Closed	Reticulate	Absent	-
	Javorkaea	3	Equatorialis	Foveolate Reticulate	Endocracks at one pole	3.5–3.8
	Gonzalagunia	3	Convergent	Foveolate	Endocracks at both poles	3.7–4.2
	Guettarda	3	Closed	Reticulate	Absent	-
	Renistipula	3	Equatorialis	Foveolate Reticulate	Endocracks at one pole	2.8–2.9
	Rogiera	3-4	Convergent	Foveolate	Endofissures at both poles.	1.6–1.7

TABLE 2. Principal characters of pollen grains of the evaluated species of the *Rondeletia* complex.

	$\bar{P}$ (µm)	**$\bar{E}$ (µm)**	**Polar outline**	**Equatorial outline**	**Endoaperture type**	**Ornamentation**	**Figure**
RONDELETIEAE							
Donnellyanthus deamii	22.4	23.9	Circular	Circular	Convergent	Reticulate	2.A 3.A
Mazaea phialanthoides	15.4	15.9	Triangular concave	Ellipsoidal	Parallel	Foveolate	2.B 3.B
Rachicallis americana	15.5	15.6	Circular	Circular	Divergent	Reticulate	2.C 3.C
Rondeletia							
R. belizensis	17.1	17.2	Circular to subtriangular	Circular	Parallel	Reticulate	2.D 3.D
R. carnea	14.9	15.6	Triangular concave	Ellipsoidal	Parallel	Foveolate	2.E 3.E
R. ochracea	14.4	15.3	Triangular concave	Ellipsoidal	Parallel	Foveolate	3.F
R. polita	12.3	13.2	Triangular concave	Ellipsoidal	Parallel	Foveolate	2.F
R. stereocarpa	12.9	13.7	Triangular concave	Ellipsoidal	Equatorialis	Foveolate	-
Rovaeanthus strigosus	22.6	24.0	Circular	Circular	Convergent	Reticulate	2.G 3.G–H
Stevensia							
S. aculeolata	18.9	18.0	Triangular concave	Ellipsoidal	Parallel	Foveolate	2.H 3.I–J
S. grandiflora	15.9	15.1	Triangular concave	Ellipsoidal	Parallel	Foveolate	-
Suberanthus							
S. hincheanus	17.9	17.9	Circular	Circular	Convergent	Reticulate	3.K–L
S. neriifolius	19.2	19.2	Circular to subtriangular	Circular	Convergent	Reticulate	2.I
GUETTARDEAE							
Arachnothryx							
A. aspera	17.5	17.4	Circular	Circular	Equatorialis	Foveolate	4.A–B
A. buddleioides	27.7	26.3	Circular	Circular	Parallel	Foveolate	2.J–K
A. calycophylla	19.0	19.0	Circular	Circular	Parallel	Foveolate to microreticulate	2.L–M 4.C–D
A. capitellata	19.3	19.2	Circular	Circular	Convergent	Reticulate	4.E–F
A. gonzaleoides	18.9	19.0	Circular	Circular	Parallel	Foveolate	2.N–O 4.G–H
A. guerrerensis	19.5	19.5	Circular	Circular	Parallel	Reticulate	-
Chomelia protracta	29.8	31.5	Triangular convex	Ellipsoidal	Closed	Reticulate	-
Gonzalagunia							
G. chiapasensis	30.6	31.1	Circular	Circular	Convergent	Foveolate	2.P
G. hirsuta	22.9	22.0	Circular	Circular	Convergent	Foveolate	4.I

G. osaensis	19.9	18.9	Circular	Circular	Convergent	Foveolate	2.Q–R 4.J
Guettarda tikalana	29.0	31.5	Triangular convex	Ellipsoidal	Closed	Reticulate	2.S
Javorkaea							
J. acuminata	21.3	21.3	Circular	Circular	Equatorialis	Reticulate	2.T–U
J. uxpanapensis	17.2	17.1	Circular	Circular	Equatorialis	Foveolate	4.K–L
Renistipula							
R. costaricensis	17.2	17.3	Circular	Circular	Equatorialis	Foveolate	4.M–N
R. galeottii	16.2	16.2	Circular	Circular	Equatorialis	Reticulate	2.V
Rogiera							
R. amoena	18.7	18.8	Circular	Circular	Convergent	Foveolate	4.O–P
R. gratissima	18.2	18.3	Circular	Circular	Convergent	Foveolate	2.W–X

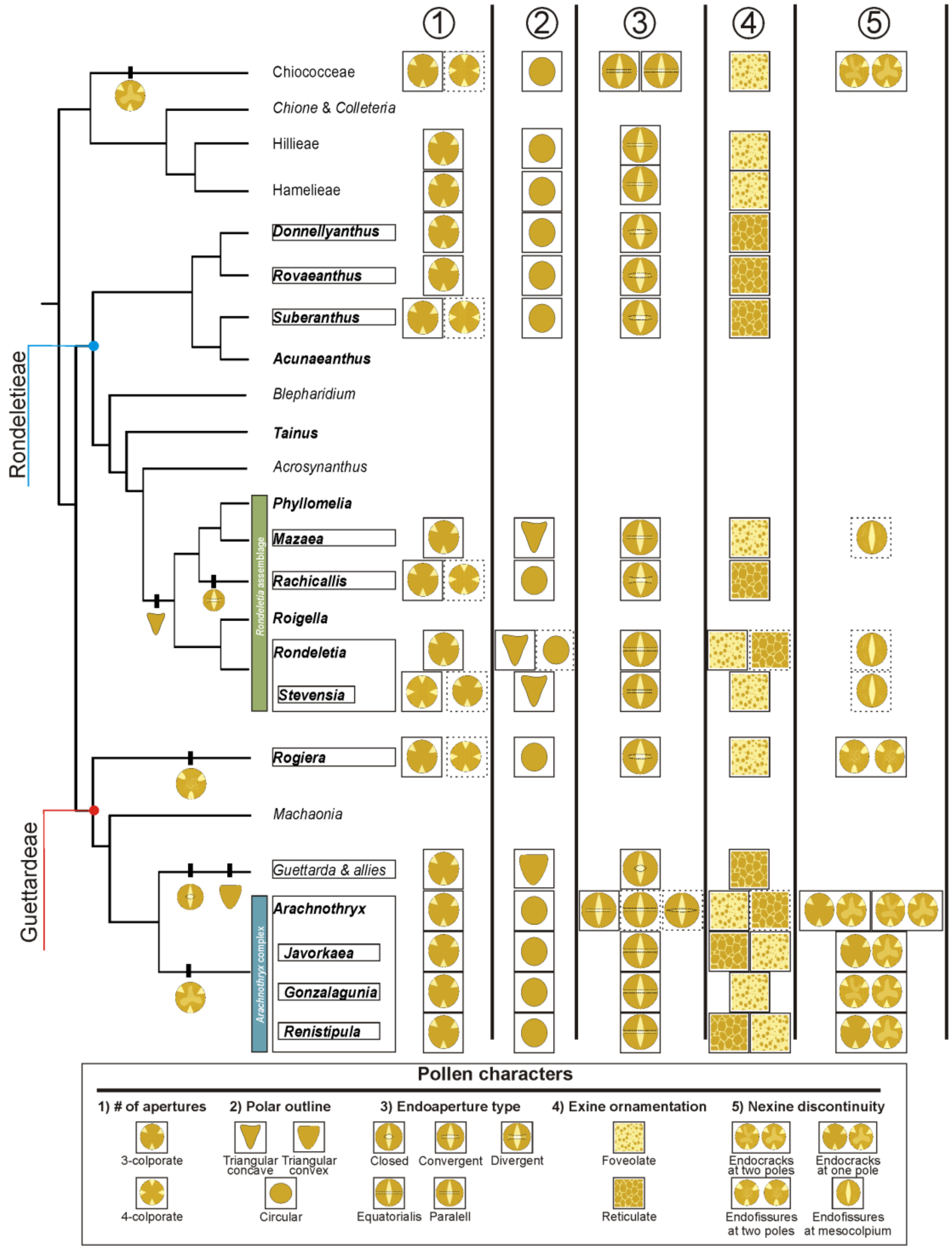

FIG. 1. Pollen characters and their phylogenetic signal. Cladrogram summarized from Manns and Bremer (2010) and complemented with Torres-Montúfar and collaborators (2017a and unpublished results). The number of apertures, endoaperture morphology, polar outline, exine ornamentation and nexine continuity are schematized on the right columns. Pollen characters with strong phylogenetic signal are mapped on the corresponding internodes: triangular concave polar outline defines the *Rondeletia* assemblage, although some of its members have reversals to circular polar outline; triangular convex polar outline and closed endoaperture are synapomorphies for the clade *Guettarda*-allies; divergent endoaperture is unique to *Rachicallis*; endocracks evolved independently in two of the sampled lineages (Chiococceae and the *Arachnothryx* complex), while endofissures (*Rogiera*) appeared only once. Within Rondeletieae the clade represented by *Donnellyanthus-Rovaeanthus-Suberanthus* is characterized by the combination of convergent endoaperture and reticulate exine. Bold names indicate genera belonging in the *Rondeletia* complex; the names enclosed inboxes correspond to those studied here. Dotted boxes for the schematized characters indicate character states rarely present.

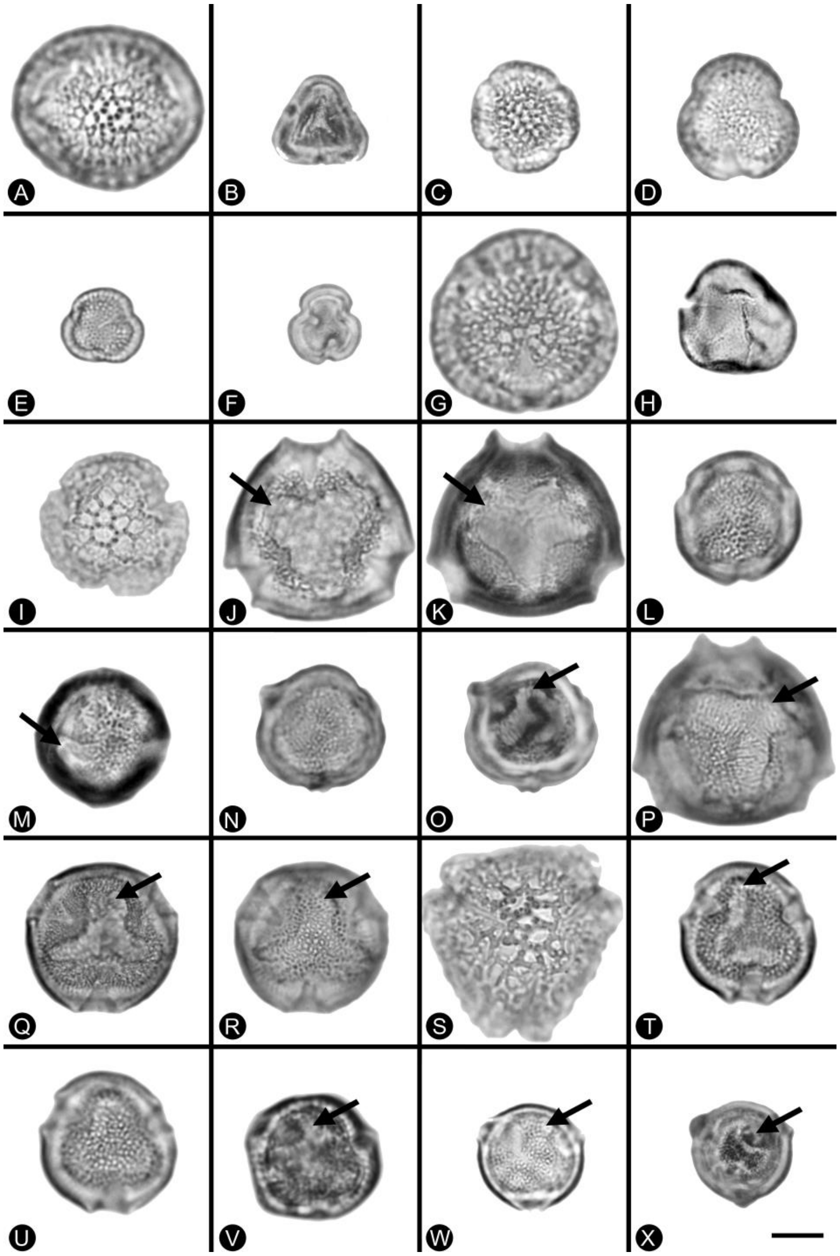

FIG. 2. LM polar views of pollen grains for all studied species. Rondeletieae. A. *Donnellyanthus deamii*. **B.** *Mazaea phialantoides*. **C.** *Rachicallis americana*. **D.** *Rondeletia belizensis*. **E.** *Rondeletia carnea*. **F.** *Rondeletia polita*. **G.** *Rovaeanthus strigosus*. **H.** *Stevensia aculeolata*. **I.** *Suberanthus neriifolius*. **Guettardeae. J–K.** *Arachnothryx buddleioides*. **L–M.** *Arachnothryx calycophylla*. **N–O.** *Arachnothryx gonzaleoides*. **P**. *Gonzalagunia chiapasensis*. **Q–R.** *Gonzalagunia osaensis*. **S.** *Guettarda tikalana*. **T–U.** *Javorkaea acuminata*. **V.** *Renistipula galeottii*. **W–X.** *Rogiera gratissima*. Scale bar: 5 µm. Nexine discontinuities are signaled with arrows.

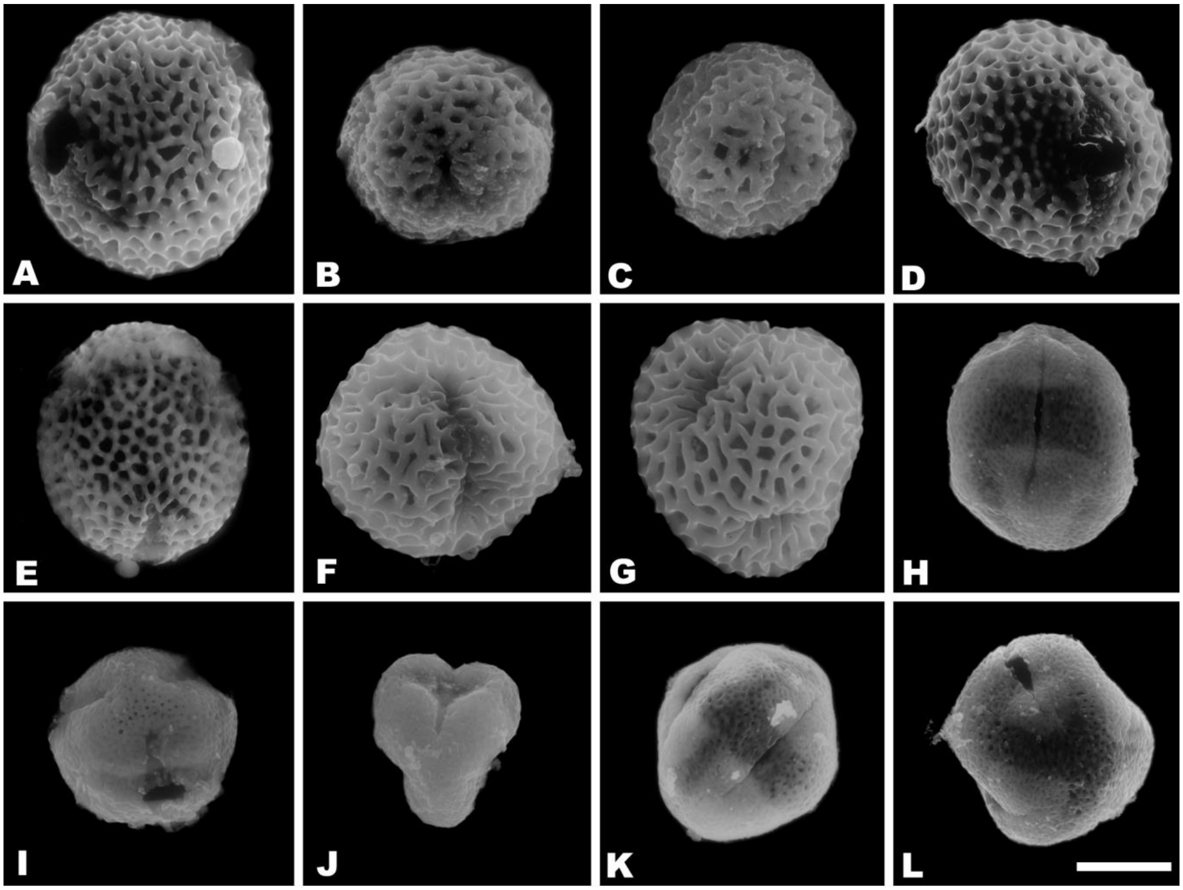

FIG. 3. SEM views of pollen grains of the sampled genera from Rondeletieae. A. *Donnellyanthus deamii*, oblique view. **B.** *Mazaea phialantoides*, equatorial view. **C.** *Rachicallis americana,* equatorial view. **D.** *Rondeletia belizensis,* oblique view. **E.** *Rondeletia carnea*, oblique view. **F.** *Rondeletia ochracea*, oblique view. **G-H.** *Rovaeanthus strigosus*, equatorial view (**G**), polar view (**H**). **I–J.** *Stevensia aculeolata*, equatorial view (**I**), oblique view (**J**). **K–L.** *Suberanthus hincheanus*, equatorial view (**K**), oblique view (**L**) Scale bar: 5 µm.

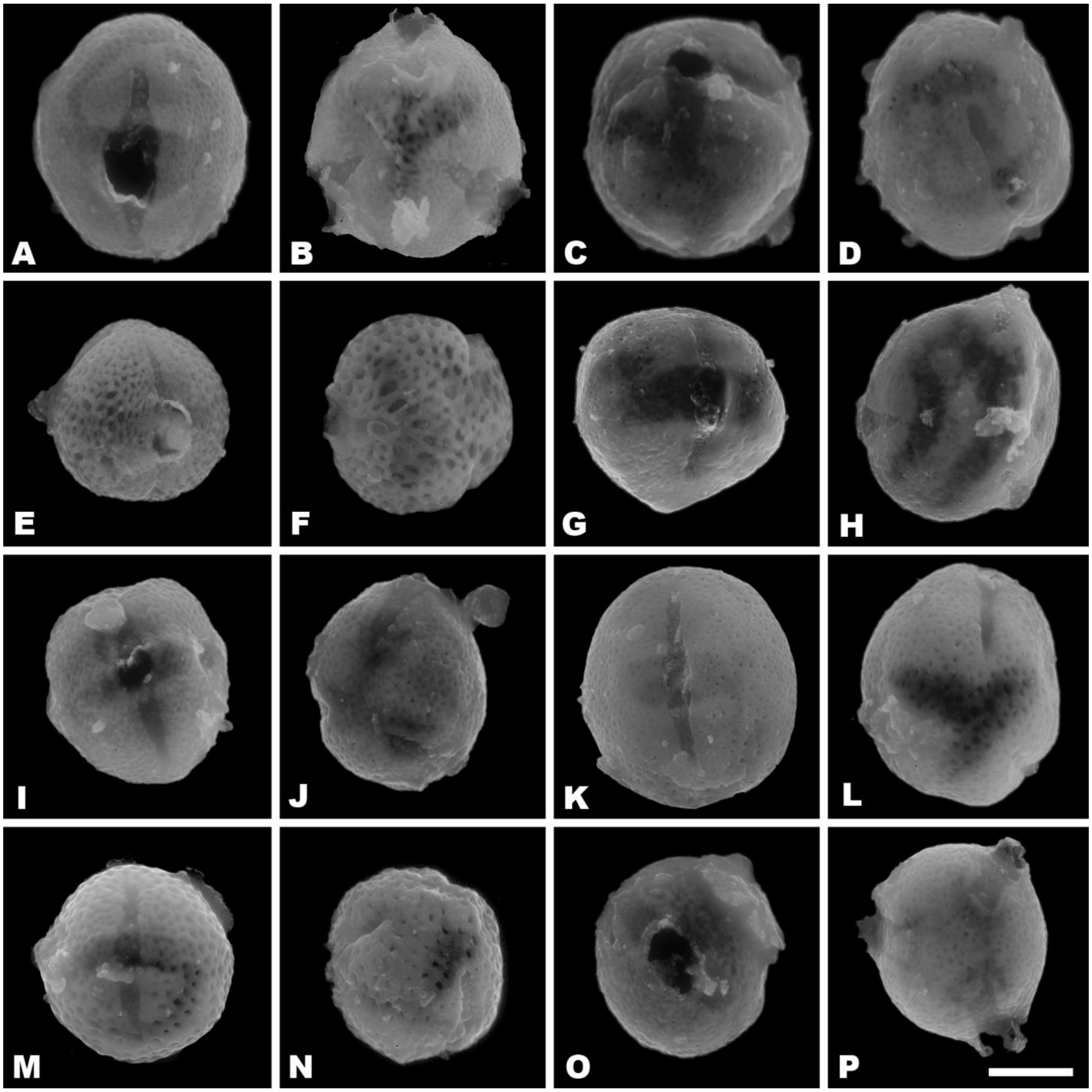

Fig. 4. SEM views of pollen grains of the sampled genera from Guettardeae. A–B. *Arachnothryx aspera*, equatorial view (**A**), polar view (**B**). **C–D.** *Arachnothryx calycophylla,* equatorial view (**C**), oblique view (**D**). **E–F.** *Arachnothryx capitellata*, equatorial view (**E**), polar view (**F**). **G–H.** *Arachnothryx gonzaleoides*, equatorial view (**G**), polar view (**H**). **I.** *Gonzalagunia hirsuta*, equatorial view. **J.** *Gonzalagunia osaensis*, polar view. **K-L.** *Javorkaea uxpanapensis*, equatorial view (**K**), oblique view (**L**). **M–N.** *Renistipula costaricensis*, equatorial view (**M**), oblique view (**N**). **O–P.** *Rogiera amoena*, equatorial view (**O**), polar view (**P**). Scale bar: 5 µm.

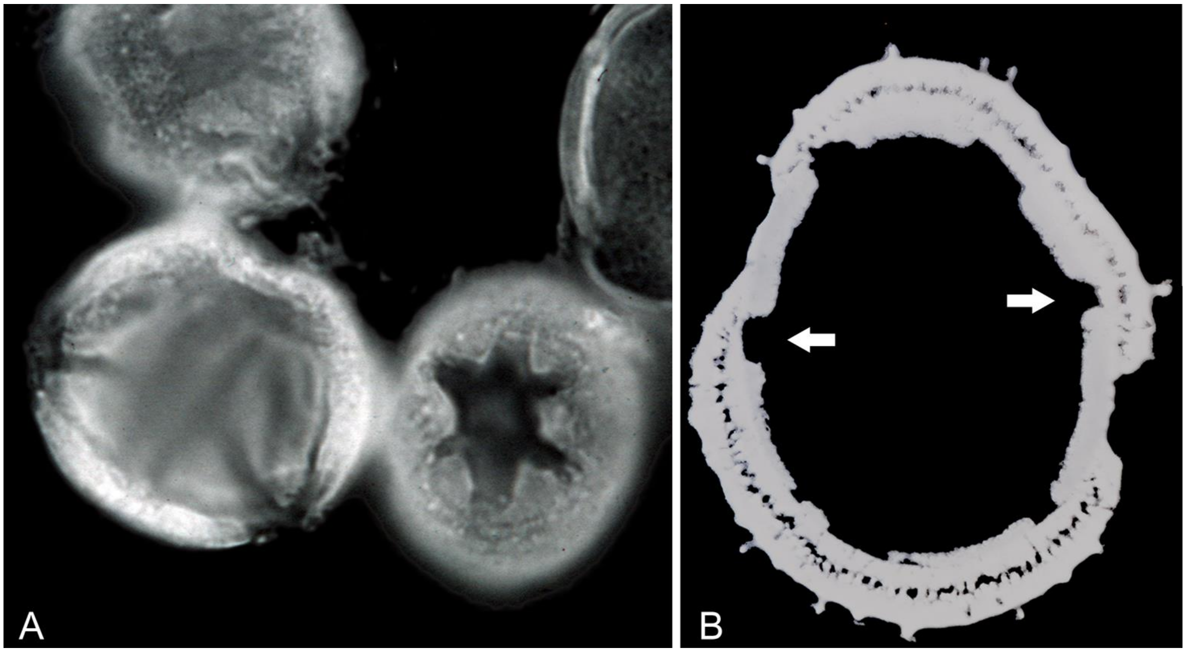

FIG. 5. Endocracks in the pollen grains of Badusa (Chiococceae). 1) LM polar views; endocracks are pointed by the arrow. 2) TEM image polar view; two endocrack arms are pointed by arrows. Reproduced from Ochoterena (2000).

APPENDIX A. Voucher specimens corresponding to the evaluated species

Arachnothryx aspera (Standl.) Borhidi. Costa Rica, Puntarenas. Monteverde, pacific slope, Río Guacimal valley. 13/01/1985. W. A. Haber *1218*, MEXU (IG: H-1183).

Arachnothryx buddleioides (Benth.) Planch. México. Oaxaca, Dto. Ixtlán, La Esperanza. 29/11/1987. R. Lopez Luna *548*, MEXU (IG: H-1533).

Arachnothryx calycophylla Steyerm. Venezuela, Tachira, between junction of Rio Qunimari and Río Frio, 8 km upstream to La Laguna. 30/07/1979. J. Steyermark *119100*, MEXU (IG: H-1535).

Arachnothryx capitellata (Hemsl.) Borhidi. México, Oaxaca, Dto. Mixe, Totontepec. 08/10/1990. J. Rivera Reyes *1661*, MEXU (IG: H-1540).

Arachnothryx gonzaleoides (Standl.) Borhidi. México. Veracruz, Lomas al S del poblado 11, ca. 27 km al E de La Laguna, cerca del arroyo. 20/07/1980. T. Wendt *2638*, MEXU (IG: H-1539).

Arachnothryx guerrerensis (Lorence) Borhidi. México. Guerrero, between Puerto El Gallo and Atoyac. 20/10/1984. D.E. Breedlove *61973*, MEXU (IG: H-1542).

Chomelia protracta (Bartl. ex DC.) Standl. México, Oaxaca, Totontepec Villa de Morelos. 23/05/1991. J. Rivera Reyes *1865*, MEXU (IG- H-1910).

Gonzalagunia chiapasensis (Standl.) Standl. & Steyerm. México. Chiapas, On the south-east side of Volcán Tacaná above Talquian. 05/03/1972. D. E. Breedlove *24382*, MEXU (IG: H-1200).

Gonzalagunia hirsuta Schum. República Dominicana. Cordillera Septentrional: Moca: lado N de la Loma "El Mogote". 05/10/2003. R. G. García *1493*, JBSD (IG: H-1531).

Gonzalagunia osaensis C.M. Taylor. Costa Rica. Puntarenas, Cantón de Golfito P.N. Corcovado; Península de Osa. Estación Sirena. 13/08/1994. R. Aguilar *3539*, MEXU (IG: H-1544).

Guettarda tikalana Lundell. México. Chiapas, A 1 km de Nuevo México, Ocosingo. 24/05/2002. G. Aguilar M. *1767*, MEXU (IG: H-1199).

Javorkaea acuminata (Oerst. ex Standl.) Borhidi. México. Oaxaca, Dto. Ixtlán, La Esperanza, km 75 de la carr. Valle Nacional a Ixtlán. 08/03/1981. R. Cedillo T. *924*, MEXU (IG: H-1180).

Javorkaea uxpanapensis (Lorence & Cast.-Campos) Borhidi. México. Veracruz, Por el Río Márquez a 25 km al Sureste. 07/05/1975. M. Avendaño *115*, MEXU (IG: H-1534).

Renistipula costaricensis (Standl.) Borhidi. Honduras, Atlántida, confluence of Río Bonito and large quebrada flowing from the SW. 20/04/1996. R. Evans *2523*, MEXU (IG: H-1541).

Renistipula galeottii (Standl.) Borhidi. México. Veracruz, 10 km al E de Lago Catemaco. 09/06/1972. J. H. Beaman *6097*, MEXU (IG: H-1186).

Rogiera amoena Planch. México. Oaxaca, Dto. Tlaxiaco, 10 km al S de San Isidro Chicahuaxta carr. Tlaxiaco-Putla. 13/04/1987. R. Torres C. *9603*, MEXU (IG: H-1911).

Rogiera gratissima Planch. & Linden. México. Chiapas, La Trinitaria, 100 m al Norte de mirador de Lago Tziscao. 19/04/1995. H. Mejia *254*, MEXU (IG: H-1187).

Donnellyanthus deamii (Donn.Sm.) Borhidi. Honduras, El Paraíso, Alrededores de Tolobre ca. 15 km al S de San Lucas. 07/08/2002. J. L. Linares *6232*, MEXU (IG: H-1911).

Mazaea phialanthoides (Griseb.) Krug & Urb. República Dominicana, 60 km East of Vinales, south of La Mulata on road to San Juan de Sagua. 14/06/1953. R. L. Dressler *1232*, JBSD (IG: H-1528).

Rachicallis americana (Jacq.) Hitchc. México. Quintana Roo, Cozumel, A 1 km al N de la zona urbana de San Miguel de Cozumel. 08/07/1985. E. Cabrera C. *8867*, MEXU (IG: H-1537).

Rondeletia belizensis Standl. México. Chiapas, Crucero Corozal sobre el camino Palenque-Boca Lacantum, 18/06/1986. E. Martínez S. *18845*, MEXU (IG: H-1536).

Rondeletia carnea Urb. & Ekman. República Dominicana, Sierra de Bahoruco, 23.5 km al "Sur" de Puerto Escondido en el camino sobre la sierra Aceitillar. 18/03/1988. T. Zanoni *33822*, JBSD (IG: H-1538).

Rondeletia ochracea Urb. República Dominicana, Cordillera Central, arriba la Loma Arroyo Hondo; entre Sabana de Miguel Martín y El Cercado. 29/07/1982. T. Zanoni *22205*, JBSD (IG: H-1532).

Rondeletia polita Griseb. Jamaica. Along Reynold Jamaica Mines bucket lines from mine area at Golden to Ocho Ríos. 23/04/1954. G. Proctor *8363*, MEXU (IG: H-1188).

Rondeletia stereocarpa Griseb. República Dominicana. Jeepable trail on the south slopes of Morne Macaque (Micotrin) between Laudat and Fresh Water Lake in montane thicket. 03/08/1964. R.L. Wilbur *8221*, MEXU (IG: H-1201).

Rovaeanthus strigosus (Benth.) Borhidi. México. Chiapas, Mirador El Caminero, 5 km al NW de Rincón Chamula. 03/10/1975. J. Rzedowski *33643*, MEXU (IG: H-1189).

Stevensia aculeolata Alain. República Dominicana. Sierra de Bahoruco, 20 km S de Puerto Escondido en el camino sobre la sierra Aceitillar. 18/04/1991. T. Zanoni *35958*, JBSD (IG: H-1543).

Stevensia grandiflora Alain. República Dominicana. San Francisco de Macoris, en la parte Sur de la Loma Quita Espuela. 15/09/1986. M. Mejía *1789*, JBSD (IG: H-1527).

Suberanthus hincheanus (Urb. & Ekman) Borhidi. República Dominicana. Cordillera Septentrional, "El Mogote". 01/06/2003. A. Veloz *3945*, JBSD (IG: H-1530).

Suberanthus neriifolius (A. Rich.) Borhidi & M. Fernández Zeq. Cuba. Santa Clara, 10 km west of Santa Clara. 15/06/1941. R. A. Howard *5096*, MEXU (IG: H-1202).

APPENDIX B. Full pollen description of the taxa evaluated.

Rondeletieae tribe

1. *Donnellyanthus deamii* (Donn. Sm.) Borhidi

Pollen grains isopolar, radiosymmetric, tricolporate, oblate-spheroidal, polar outline circular, equatorial outline circular. Polar axis (P): 22.4 µm (17.2–24.9 µm), equatorial axis (E): 23.9 µm (17.7–25.3 µm). Polar area big (0.53). Ectocolpus without margo. Endoapertures lalongate, convergent costae. Exine subtectate, reticulate, heterobrocate, columellate, some columellae bigger than 0.5 µm in diameter. Lumina of 0.93–1.2 µm diameter, muri of 0.38–0.41 µm. Exine 2.6 µm (2.3–2.9 µm) thick. Sexine:nexine ratio 3:1. Endocracks or endofissures absent.

2. *Mazaea phialanthoides* (Griseb.) Krug & Urb.

Pollen grains isopolar or rarely heteropolar, radiosymmetric, tricolporate; oblate-spheroidal; polar outline triangular concave, equatorial outline ellipsoidal. Polar axis (P): 15.4 µm (14.1–16.1 µm); equatorial axis (E): 15.9 µm (15.7–17.9 µm). Polar area small (0.18). Interangulate apertures. Ectocolpus with margo; endoapertures lalongate, parallel costae with meridional edges indistinct. Exine tectate, foveolate. Foveolae 0.66–0.73 µm, distance among foveolae of 0.57–0.62 µm. Exine 1.9 µm (1.7–2.2 µm) thick, columellae less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Rarely with endofissures at mesocolpium, 2.2 µm in width.

3. *Rachicallis americana* (Jacq.) Hitchc.

Pollen grains isopolar, radiosymmetric, tricolporate or rarely tetracolporate; spheroidal; polar outline circular, equatorial outline circular. Polar axis (P): 15.5 µm (15.0–16.3 µm), equatorial axis (E): 15.6 µm (14.7–16.1 µm). Polar area small (0.22). Ectocolpus without margo; endoapertures lalongate, divergent costae with closed meridional edges. Exine subtectate, reticulate, homobrocate, columellate, some columellae bigger than 0.5 µm in diameter. Lumina of 0.50–0.59 µm in diameter, muri of 0.55–0.62 µm. Exine 2.3 µm (1.9–2.6 µm) thick. Sexine:nexine ratio 3:1. Endocracks or endofissures absent.

4. *Rondeletia*

Pollen grains isopolar radiosymmetric, tricolporate; spheroidal to oblate-spheroidal; polar outline triangular concave or circular to subtriangular, equatorial outline circular or ellipsoidal. Polar area medium or small. Interangulate apertures. Ectocolpus with margo and acute colpus apex; endoapertures lalongate, colpus equatorialis or parallel costae with meridional edges closed or indistinct. Exine tectate, foveolate to subtectate reticulate, heterobrocate, columellate, columellae equal or less than 0.5 µm in diameter. Sexine:nexine ratio 2:1 or 3:1. Endofissures absent or occasionally mesocolpium, 0.8–0.9 µm width.

4.1 *Rondeletia belizensis* Standl.

Pollen grains tricolporate, spheroidal, polar outline circular, equatorial outline circular. Polar axis (P): 17.1 µm (15.2–18.9 µm), equatorial axis (E): 17.2 µm (15.0–18.6 µm). Polar area medium (0.26). Ectocolpus with margo; endoapertures parallel costae with closed meridional edges. Exine subtectate, reticulate, heterobrocate, lumina diminish towards colpus, columellate, some columellae up to 0.5 µm in diameter. Lumina of 0.6–0.7 µm diameter, muri of 0.58–0.62 µm. Exine 2.3 µm (1.9–2.4 µm) thick. Sexine:nexine ratio 2:1. Endocracks or endofissures absent.

4.2 *Rondeletia carnea* Urb. & Ekman

Pollen grains isopolar, tricolporate; oblate-spheroidal. Polar outline triangular concave, equatorial outline ellipsoidal. Polar axis (P): 14.9 µm (14.1–16.3 µm); equatorial axis (E): 15.6 µm (14.2–15.9 µm). Polar area small (0.23). Ectocolpus with margo; endoapertures parallel costae with meridional edges indistinct. Exine foveolate, Foveolae 0.16–0.22 µm, distance among foveolae 0.72–0.81 µm. Exine 2.0 µm (1.7–2.2 µm) thick, columellae less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Rarely with fine endofisures at mesocolpium, 0.8 µm in width.

4.3 *Rondeletia ochracea* Urb.

Pollen grains isopolar, tricolporate; oblate-spheroidal. Polar outline triangular concave, equatorial outline ellipsoidal. Polar axis (P): 14.4 µm (14.0–16.0 µm); equatorial axis (E): 15.3 µm (14.0–15.9 µm). Polar area small (0.19). Ectocolpus without margo; endoapertures parallel costae with meridional edges indistinct. Exine foveolate, Foveolae 0.22–0.30 µm, distance among foveolae of 0.77–0.84 µm. Exine 2.1 µm (1.7–2.2 µm) thick, columellae less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Rarely with fine endofisures at mesocolpium, 0.9 µm in width.

4.4 *Rondeletia polita* Griseb.

Pollen grains isopolar, tricolporate, oblate-spheroidal. Polar outline triangular concave, equatorial outline ellipsoidal. Polar axis (P): 12.3 µm (10.9–13.5 µm; equatorial axis (E): 13.2 µm (11.2–14.1 µm). Polar area small (0.17). Ectocolpus with margo. Endoapertures parallel costae with closed meridional edges. Exine foveolate, Foveolae of 0.16–0.20 µm diameter, distance among foveolae 0.75–0.80 µm. Exine 2.1 µm (1.6–2.3 µm) thick, columellae less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Endocracks or endofissures absent.

4.5 *Rondeletia stereocarpa* Griseb.

Pollen grains isopolar, tricolporate, oblate-spheroidal. Polar outline triangular concave, equatorial outline ellipsoidal. Polar axis (P): 12.9 µm (11.0–13.5 µm); equatorial axis (E): 13.7 µm (11.2–14.0 µm). Polar area small (0.16). Ectocolpus without margo; endoapertures colpus equatorialis. Exine foveolate, Foveolae 0.32–0.37 µm, distance among foveolae 0.46–0.76 µm, diminish towards colpus. Exine 1.9 µm (1.7–2.2 µm) thick, columellae equal or less than 0.5 µm in diameter. Sexine:nexine ratio 3:1. Endocracks or endofissures absent.

5. *Rovaeanthus strigosus* (Benth.) Borhidi

Pollen grains isopolar, radiosymmetric, tricolporate, oblate-spheroidal, polar outline circular, equatorial outline circular. Polar axis (P): 22.6 µm (17.4–24.9 µm), equatorial axis (E): 24.0 µm (17.8–25.1 µm). Polar area big (0.53). Ectocolpus without margo. Endoapertures lalongate, convergent costae. Exine subtectate, reticulate, heterobrocate, lumina diminish towards the ectoapertures, columellate, some columellae bigger than 0.5 µm in diameter. Lumina of 0.96–1.34 µm diameter, muri of 0.46–0.51 µm. Exine 2.4 µm (1.9–3.0 µm) thick. Sexine:nexine ratio 3:1. Endocracks or endofissures absent.

6. *Stevensia*

Pollen grains isopolar or rarely heteropolar, radiosymmetric, tetracolporate or tricolporate; prolate-spheroidal; polar outline triangular concave, equatorial outline ellipsoidal. Polar area medium. Interangulate apertures, ectocolpus with margo and acute colpus apex; endoapertures parallel costae with meridional edges indistinct. Exine tectate, foveolate, columellate, columellae equal or less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Endocracks absent or endofissures rarely present at mesocolpium, 0.8–2.2 µm in width.

6.1 *Stevensia aculeolata* Alain

Pollen grains isopolar or rarely heteropolar, tetracolporate or tricolporate. Polar axis (P): 18.9 µm (16.6–19.8 µm); equatorial axis (E): 18.0 µm (16.2–19.0 µm). Endoapertures parallel costae with meridional edges indistinct. Foveolae 0.37–0.46 µm, distance among foveolae 0.70–0.75 µm, diminish towards colpus. Exine 2.0 µm (1.9–2.2 µm) thick, columellae equal or less than 0.5 µm in diameter. Rarely with endofisures at mesocolpium, 1.8 µm in width.

6.2 *Stevensia grandiflora* Alain

Pollen grains isopolar, tetracolporate or tricolporate. Polar axis (P): 15.9 µm (14.8–16.4 µm); equatorial axis (E): 15.1 µm (14.2–16.2 µm). Polar area medium (0.38). Endoapertures parallel costae with meridional edges indistinct. Foveolae 0.34–0.37 µm, distance among foveolae 0.48–0.89 µm. Exine 2.3 µm (1.6–2.5 µm) thick, columellae equal or less than 0.5 µm in diameter. Endocracks or endofissures absent.

7. *Suberanthus*

Pollen grains isopolar, radiosymmetric, tricolporate or rarely tetracolporate; spheroidal; polar outline circular, equatorial outline circular. Polar area big. Ectocolpus without margo and acute apex; endoapertures lalongate, convergent costae with meridional edges indistinct. Exine subtectate reticulate, heterobrochate or homobrochate, columellate, some columellae bigger than 0.5 µm in diameter. Sexine:nexine ratio 2:1 or 3:1. Endocracks or endofissures absent.

7.1 *Suberanthus hincheanus* (Urb. & Ekman) Borhidi

Pollen grains tricolporate; spheroidal; polar outline circular, equatorial outline circular. Polar axis (P): 17.9 µm (16.0–19.2 µm), equatorial axis (E): 17.9 µm (16.1–19.9 µm). Exine homobrocate. Lumina of 0.94–1.07 µm in diameter, muri of 0.46–0.51 µm. Exine 2.8 µm (2.5–3.3 µm) thick. Sexine:nexine ratio 3:1.

7.2 *Suberanthus neriifolius* (A. Rich.) Borhidi & M. Fernández

Pollen grains tricolporate or rarely tetracolporate; spheroidal; polar outline circular, equatorial outline circular. Polar axis (P): 19.2 µm (18.7–20.4 µm); equatorial axis (E): 19.2 µm (18.7–20.0 µm). Exine heterobrocate. Lumina of 0.95–1.12 µm diameter, muri of 0.48–0.54 µm. Exine 2.8 µm (2.4–3.2 µm) thick. Sexine:nexine ratio 2:1.

Guettardeae tribe

8. *Arachnothryx*

Pollen grains heteropolar, radiosymmetric, tricolporate; spheroidal, oblate-spheroidal to prolate-spheroidal; polar outline circular, equatorial outline circular. Polar area medium or small. Ectocolpus with margo, acute colpus apex; endoapertures lalongate, colpus equatorialis or parallel costae with indistinct meridional edges or convergent with closed meridional edges. Exine tectate foveolate or subtectate reticulate, columellate, columellae less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Endocracks at one pole or both poles (*A. buddleioides*), 2.8–4.0 µm in width.

8.1. *Arachnothryx aspera* (Standl.) Borhidi

Spheroidal pollen grains. Polar axis (P): 17.5 µm (16.6–20.8 µm); equatorial axis (E): 17.4 µm (16.6–21.0 µm); polar area medium (0.33 µm). Endoapertures colpus equatorialis, thinned at mesocolpium area. Exine 1.82 µm (1.75–2.15 µm) thick, tectate, foveolate with microreticulated pattern, foveolae 0.28–0.36 µm, distance among foveolae 0.68–0.73 µm. Endocracks with irregular shape at one pole, trifurcate or tetrafurcate, 3.9 µm in width.

8.2. *Arachnothryx buddleioides* (Benth.) Planch.

Spheroidal pollen grains. Polar axis (P): 27.7 µm (25.1–30.1 µm); equatorial axis (E): 26.3 µm (23.2–30.0 µm). Polar area big (0.55). Endoapertures parallel costae and meridional edges indistinct. Exine tectate, foveolate, with striate pattern, foveolae 0.25–0.32 µm, distance among foveolae 0.30–0.40 µm. Exine 1.9 µm (1.7–2.3 µm) thick. Endocracks with irregular or trifurcate shape at both poles and at the mesocolpium area, 4.0 µm in width.

8.3. *Arachnothryx calycophylla* Steyerm.

Prolate-spheroidal pollen grains. Polar axis (P): 19.0 µm (17.9–20.0 µm); equatorial axis (E): 19.0 µm (17.6–19.1 µm). Polar area medium (0.27). Endoapertures parallel costae with meridional edges indistinct. Exine tectate, foveolate to microreticulate, lumina diminish towards colpus edges and towards one pole, becoming foveolate, lumina 0.23–0.26 µm and muri 0.20–0.23 µm wide; foveolae 0.12–0.14 µm, distance among foveolae 0.28–0.30 µm. Exine 1.85 µm (1.8–2.2 µm) thick. Endocracks with irregular shape at one pole and at the mesocolpium area, 3.4 µm in width.

8.4 *Arachnothryx capitellata* (Hemsl.) Borhidi

Spheroidal pollen grains. Polar axis (P): 19.3 µm (16.3–23.3 µm); equatorial axis (E): 19.2 µm (16.0–23.4 µm). Polar area medium (0.30). Endoapertures convergent costae with closed meridional edges. Exine subtectate, reticulate, heterobrochate, lumina diminish towards colpus edges and towards one pole. Lumina 0.91–1.07 µm, muri 0.44–0.46 µm wide. Exine 1.95 µm (1.7–2.4 µm) thick. Endocracks with irregular shape at one polar area, 3.2 µm in width, coinciding with bigger lumina.

8.5 *Arachnothryx gonzaleoides* (Standl.) Borhidi

Oblate-spheroidal pollen grains. Polar axis (P): 18.9 µm (17.6–21.2 µm); equatorial axis (E): 19.0 µm (17.3–20.3 µm). Polar area medium (0.32). Endoapertures parallel costae with closed meridional edges. Exine tectate, foveolate, pole with endocracks has bigger foveola and striate pattern, foveolae 0.17–0.24 µm, distance among foveolae 0.39–0.43 µm wide. Exine 1.88 µm (1.8–2.0 µm) thick. Endocracks with irregular or trifurcate shape at one polar area, sometimes extended to the mesocolpium, 3.9 µm in width.

8.6 *Arachnothryx guerrerensis* (Lorence) Borhidi

Spheroidal pollen grains. Polar axis (P): 19.5 µm (16.6–21.5 µm); equatorial axis (E): 19.5 µm (15.8–22.3 µm). Polar area medium (0.37). Endoapertures parallel costae with closed meridional edges. Exine subtectate, reticulate, heterobrochate, the pole with endocracks has bigger lumina, lumina 0.22–0.60 µm, muri 0.19–0.61 µm wide. Exine 2.15 µm (1.9–2.3 µm) thick. Endocracks with irregular or trifurcate shape at one polar area, 3.7 µm in width.

9. *Chomelia protracta* (Bartl. ex DC.) Standl.

Pollen grains isopolar, radiosymmetric, tricolporate; suboblate; polar outline triangular convex, equatorial outline ellipsoidal. Polar axis (P): 29.8 µm (28.3–32.1 µm); equatorial axis (E): 31.5 µm (28.4–32.4 µm). Polar area small (0.16). Ectocolpus without margo and acute apex. Endoapertures lalongate, closed costae of the same width as the ectoaperture. Exine subtectate, reticulate, heterobrocate, collumelate, columellae bigger than 0.5 in diameter. Lumina of 1.52–1.94 µm, muri of 0.43–0.51 µm. Exine 2.85 µm (2.5–3.2 µm) thick. Sexine:nexine ratio 3:1. Endocracks or endofssures absent.

10. *Gonzalagunia*

Pollen grains heteropolar, radiosymmetric, tricolporate; prolate-spheroidal or subprolate; polar outline circular; equatorial outline circular. Polar area small or medium. Ectocolpus with margo and acute apex. Endoapertures convergent costae with meridional edges indistinct. Exine tectate, foveolate, collumelate, columellae less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Endocracks with irregular, trifurcate or tetrafurcate shape at both poles, 3.7–4.2 µm in width.

10.1 *Gonzalagunia chiapasensis* (Standl.) Standl. & Steyerm.

Prolate-spheroidal pollen grains. Polar axis (P): 30.6 µm (29.9–31.5µm); equatorial axis (E): 31.1µm (29.8–33.9 µm). Polar area small (0.22). Exine tectate, foveolate, foveolae diminish towards colpus edges, foveolae 0.19–0.22µm, distance among foveolae 0.35–0.54 µm. Exine 2.25 µm (1.7–2.5 µm) thick. Endocracks 4.1 µm in width.

10.2 *Gonzalagunia hirsuta* (Jacq.) K. Schum.

Subprolate pollen grains. Polar axis (P): 22.9 µm (21.3–25.0 µm); equatorial axis (E): 22.0 µm (21.6–25.4 µm). Polar area small (0.23). Exine tectate, foveolate, foveolae diminish towards mesocolpium, foveolae 0.17–0.28 µm, distance among foveolae 0.36–0.43 µm. Exine 2.1 µm (1.7–2.5 µm) thick. Endocracks 4.2 µm in width.

10.3 *Gonzalagunia osaensis* C.M. Taylor

Prolate-spheroidal pollen grains. Polar axis (P): 19.9 µm (16.4–20.4 µm); equatorial axis (E): 18.9 µm (16.2–19.9 µm). Polar area medium (0.30). Exine tectate, foveolate, foveolae 0.18–0.33µm in diameter, distance among foveolae 0.40–0.54 µm. Exine 2.14 µm (1.8–2.4 µm) thick. Endocracks 3.7 µm in width.

11. *Guettarda tikalana* Lundell

Pollen grains isopolar, radiosymmetric, tricolporate; suboblate; polar outline triangular convex, equatorial outline ellipsoidal. Polar axis (P): 29.0 µm (28.1–32.9 µm); equatorial axis (E): 31.5 µm (27.2–33.1 µm). Polar area small (0.15). Ectocolpus without margo and acute apex. Endoapertures lalongate, closed costae of the same width as the ectoaperture. Exine subtectate, reticulate, heterobrocate, collumelate, columellae bigger than 0.5 µm in diameter. Lumina of 1.43–1.92 µm, muri of 0.40–0.43 µm. Exine 2.9 µm (2.8–3.5 µm) thick. Sexine:nexine ratio 3:1. Endocracks or endofssures absent.

12. *Javorkaea*

Pollen grains heteropolar, radiosymmetric, tricolporate; spheroidal; polar outline circular, equatorial outline circular. Polar area small. Ectocolpus with margo, acute colpus apex; endoapertures lalongate, colpus equatorialis. Exine tectate foveolate or subtectate reticulate, columellate, columellae less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Endocracks with irregular, trifurcate or tetrafurcate shape at one polar area, 3.5–3.8 µm in width.

12.1 *Javorkaea acuminata* (Oerst. ex Standl.) Borhidi

Polar axis (P): 21.3 µm (15.4–22.0 µm); equatorial axis (E): 21.3 µm (15.6–21.4 µm). Polar area small (0.22). Exine subtectate, reticulate, homobrochate, lumina 0.17–0.18 µm, muri of 0.33–0.35 µm wide. Exine 1.95 µm (1.7–2.2 µm) thick. Endocracks 3.5–3.8 µm in width.

12.2 *Javorkaea uxpanapensis* (Lorence & Cast.-Campos) Borhidi

Polar axis (P): 17.2 µm (15.2–20.3 µm); equatorial axis (E): 17.1 µm (15.5–21.0 µm). Polar area small (0.24). Exine tectate, foveolate, foveolae 0.13–0.16 µm, distance among foveolae 0.29–0.34 µm. Exine 2.3 µm (1.9–2.4 µm) thick. Endocracks 3.6–3.8 µm in width.

13. *Renistipula*

Pollen grains heteropolar, radiosymmetric, tricolporate; spheroidal; polar outline circular, equatorial outline circular. Polar area medium. Ectocolpus with margo, acute colpus apex, endoapertures lalongate, colpus equatorialis. Exine tectate foveolate or subtectate reticulate, columellate, columellae less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Endocracks with irregular, trifurcate or tetrafurcate shape at one polar area, 2.8 µm in width.

13.1 *Renistipula costaricensis* (Standl.) Borhidi

Polar axis (P): 17.2 µm (15.2–19.9 µm); equatorial axis (E): 17.3 µm (15.4–20.8 µm). Polar area medium (0.37). Exine tectate, foveolate, foveolae of 0.22–0.25 µm, distance among foveolae 0.45–0.63 µm. Exine 1.92 µm (1.6–2.3 µm) thick. Sexine:nexine ratio 2:1. Endocracks 2.8 µm in width.

13.2 *Renistipula galeottii* (Standl.) Borhidi

Polar axis (P): 16.2 µm (14.5–17.9 µm); equatorial axis (E): 16.2 µm (14.9–17.6 µm). Polar area medium (0.34). Exine subtectate, reticulate, heterobrochate. Lumina 0.33–0.45 µm, muri 0.36–0.48 µm wide. Exine 2.2 µm (1.5–2.6 µm) thick. Sexine:nexine ratio 2:1. Endocracks 2.8–2.9 µm in width.

14. *Rogiera*

Pollen grains isopolar, radiosymmetric, tricolporate or tetracolporate; spheroidal; polar outline circular, equatorial outline circular. Polar area big. Ectocolpus with margo and rounded apex. Endoapertures lalongate, convergent costae with meridional edges indistinct, diameter of endoapertures equal to the width of the ectoapertures. Exine tectate foveolate, collumelate, columellae less than 0.5 µm in diameter. Sexine:nexine ratio 2:1. Endofissures at both poles, 1.6–1.7 µm in width.

14.1 *Rogiera amoena* Planch.

Polar axis (P): 18.7 µm (16.1–20.8 µm); equatorial axis (E): 18.8 µm (16.3–20.4 µm). Polar area big (0.52). Foveolae of 0.17–0.21 µm in diameter, distance among foveolae of 0.49–0.53 µm. Exine 2.2 µm (1.8–2.4 µm) thick. Endofissures 1.7 µm in width.

7.2 *Rogiera gratissima* Planch. & Linden

Polar axis (P): 18.2 µm (16.0–19.3 µm); equatorial axis (E): 18.3 µm (16.0–19.0 µm). Polar area big (0.52). Foveolae of 0.17–0.22 µm in diameter, distance among foveolae 0.44–0.53 µm. Exine 2.0 µm (1.8–2.3 µm) thick. Endofissures 1.6 µm in width.

PARTE I: LA TRIBU RONDELETIEAE

CAPÍTULO II: FILOGENIA DE LA TRIBU RONDELETIEAE

It is not a disaster: new insights from molecular and morphological phylogenetic analyses of Rondeletieae (Rubiaceae)

Alejandro Torres-Montúfar, Thomas Borsch, Susy Fuentes, Jorge Gutierrez & Helga Ochoterena2*

Preparado para Plant Systematics and Evolution

It is not a disaster: new insights from molecular and morphological phylogenetic analyses of Rondeletieae (Rubiaceae)

Running title: The Rondeletieae tribe revisited

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Abstract:

The circumscription of Rondeletieae has been debated; historically, 79 genera have been included, mainly by being small trees, with imbricate aestivation and capsular fruits. Molecular studies resulted in a narrower circumscription comprising a mainly Antillean clade with 9-17 genera. As traditionally circumscribed, Rondeletieae is both polyphyletic (involving several tribes, such as Condamineae, Sipaneae, etc.) and paraphyletic with respect to Guettardeae. Despite considerable efforts, uncertainties persist on the tribal circumscription (mainly to Guettardeae), and its generic limits and relationships. Parsimony and Bayesian analyses including 179 taxa using combined morphology, three chloroplast DNA regions (*pet*D, *trn*L-F and *trn*K-*mat*K) and DNA microstructural characters were performed to: (1) propose a circumscription for Rondeletieae according to the phylogenetic hypothesis, (2) test the monophylly and evaluate the phylogenetic relationships of the genera; (3) evaluate potential characters for the tribal and generic delimitations. The tribes Guettardeae and Rondeletieae are strongly supported as sister groups: quincuncial aestivation and spatulate corolla lobes are synapomorphic for both among subfamily Cinchonoideae. We did not find synapomorphies for each, but there is a unique combination of characters for Rondeletieae that includes the corolla ornamentation as well as fruit and seed morphology. After evaluating other potential genera not included in the phylogenies, our proposal is that Rondeletieae contains twelve genera supported by molecular and morphological data: *Acrosynanthus*, *Acunaeanthus*, *Blepharidium*, *Donnellyanthus*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella*, *Rondeletia*, *Rovaeanthus*, *Suberanthus*, *Tainus*.

Key words: taxonomy, morphology, phylogeny, *Rondeletia*complex, tribal delimitation

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Introduction

The tribe Rondeletieae is a group of predominantly Neotropical trees and shrubs, characterized by the contorted or imbricate corollas, stamens variably inserted at basal, medial, or distal positions on the corolla tube, anthers dehiscence is longitudinally and few- to many-seeded capsules or two-seeded samaras. It was proposed by De Candolle (1830) as a subtribe (Rondeletinea) within the large tribe Hedyotideae, however, this proposal was later rejected when these subtribes were later separated by the entire stipules (in Rondeletieae), in contrast to the multi-setose stipules (in Hedyotideae) and elevated to the rank of tribe by Hooker (1873).

The Rondeletieae circumscription has been re-drawn several times since then, and to date remains conflictive. In total, 79 genera have been included within Rondeletieae considering different classification systems. Robbrecht (1988) stressed out that the tribes Condamineeae, Rondeletieae, and Sipaneeae could only be separated by the corolla aestivation: Condamineeae by having valvate corolla aestivation, Rondeletieae imbricate or contorted aestivation and Sipaneeae contorted. These difficulties in establishing tribal delimitations made Robbrecht (1988) present in his graphic representation of the

Rubiaceae lineages the Condamineeae, Rondeletieae and Sipaneeae as a difficult to distinguish tribal complex.

The recent circumscription of Rondeletieae includes ten genera undoubtedly included in this tribe and six genera that have been tentatively included (Manns and Bremer 2010), the rest were transferred to many other lineages (Rova et al. 2002; Delprete and Cortés 2004; Mouly et al. 2009; Razafimandimbison et al. 2011; Delprete and Jardim 2012; Manns and Bremer 2010; Kainulainen et al. 2013; Tange 2013) (Table 1).

Table 1. Summary of tribal classification of the genera historically placed at tribe Rondeletieae.

^{1}Cinchonoideae, ^{2}Ixoroideae, ^{3}Rubioideae

Genera	**De Candolle (1830)**	**Hooker (1873)**	**Robbrecht (1988)**	**Robbrecht & Bridson (1993)**	**Delprete (1999a,b)**	**Rova et al. (2002)**	**Borhidi (2006, 2012)**	**Manns & Bremer (2010)**
Acrobotrys	-	-	RON^1	RON^1	RON^1	CON^2	-	RON^1?
Acrosynanthus	-	-	CIN^1	RON^1	RON^1	RON^1	-	RON^1
Acunaeanthus	-	-	RON^1	RON^1	RON^1	RON^1	RON^1	RON^1
Aleisanthia	-	-	RON^1	RON^1	-	IXO^2	-	-
Aleisanthiopsis	-	-	RON^1	RON^1	-	IXO^2	-	-
Arachnothryx	-	RON^1	RON^1	RON^1	-	GUE^1	RON^1	GUE^1
Argostemma	HED^3	HED^3	ARG^3	ARG^3	-	-	-	-
Augusta	HED^3	RON^1	RON^1	RON^1	RON^1	GAR^2	RON^1	-
Bathysa	-	RON^1	RON^1	RON^1	RON^1	CON^2?	-	-
Bellizinca	-	-	-	-	-	-	RON^1	HAM^1
Bikkia	HED^3	CON^2	CON^2	CON^2	-	CAT^1	-	CHI^1
Blandibractea	-	-	RON^1	RON^1	-	CON^2	-	-
Blepharidium	-	-	CIN^1	HIL^1	-	RON^1	CIN^1	RON^1
Bobea	GUE^1	GUE^1	GUE^1	GUE^1	-	RON^1?	-	GUE^1
Chalepophyllum	-	RON^1	RON^1	RON^1	RON^1	CON^2	-	-
Carphalea	HED^3	RON^1	HED^3	HED^3	-	-	-	-
Chimarrhis	HED^3	CON^2	CON^2	RON?	RON^1	CON^2	-	-
Condaminea	HED^3	CON^2	CON^2	CON^2	RON^1	CON^2	-	-
Csdapodya	-	-	-	-	-	-	RON^1	HAM^1
Cuatrecasasiodendron	-	-	RON^1	RON^1	RON^1	GUE^1	-	GUE^1
Dendrosipanea	-	-	RON^1	RON^1	RON^1	CON^2	-	-
Dentella	HED^3	HED^3	HED^3	HED^3	-	-	HED^3	-
Deppea	OPE	RON^1	HAM^1	HAM^1	-	-	RON^1	HAM^1
Dioicodendron	-	-	CON^2	RON^1?	RON^1	CON^2	-	-
Dolichodelphys	-	-	GAR^2	RON^1	RON^1	CON^2	-	-
Donnellyanthus	-	-	-	-	-	-	RON^1	RON^1
Edithea	-	-	HAM^1	HAM^1	-	-	RON^1	HAM^1
Eizia	-	-	RON^1	HAM^1	-	-	RON^1	HAM^1
Elaeagia	-	RON^1	RON^1	RON^1	RON^1	CON^2	RON^1	-
Glionnetia	-	-	RON^1	RON^1	-	RON^1	-	RON^1?

Gloneria	-	RON^1	RON^1	PSY^3	-	PSY^3	-	-
Greenea	-	RON^1	RON^1	RON^1	-	IXO^2	-	-
Habroneuron	-	-	RON^1?	RON^1?	-	RON^1	RON^1	RON^1?
Holstianthus	-	-	RON^1	RON^1	RON^1	CON^2	-	RON^1?
Isidorea	HED^3	CON^2	CON^2	CON^2	-	CAT^1	-	CHI^1
Javorkaea	-	-	RON^1	RON^1	-	GUE^1	RON^1	GUE^1
Limnosipanea	-	RON^1	SIP^2	SIP^2	RON^1	-	-	-
Lindenia	-	RON^1	RON^1	RON^1	-	GAR^2	-	-
Macbridenia	-	-	RON^1	RON^1	RON^1	CON^2	-	-
Macrocnemum	HED^3	CIN^1	CIN^1	CAL^2	-	CIN^1	-	-
Maguireothamnus	-	-	RON^1	RON^1	RON^1	SIP^2	-	-
Mazaea	-	-	RON^1	RON^1	RON^1	RON^1	-	RON^1
Molopanthera	-	CIN^1	CIN^1	RON^1	RON^1	HEN^2	-	-
Neblinathamnus	-	-	RON^1	RON^1	-	CON^2	-	-
Omiltemia	-	-	HAM^1	HAM^1	-	-	RON^1	HAM^1
Ophiorhiza	HED^3	HED^3	OPH^3	OPH^3	-	-	-	-
Pallasia	-	RON^1	CIN^1	CAL^2	-	CAL^2	-	-
Parachimarrhis	-	-	CON^2	RON^1	RON^1	CON^2	-	-
Phyllomelia	-	IXO^2	*Inc. Sedis*	*Inc. Sedis*	RON^1	RON^1	-	RON^1
Picardaea	-	-	CON^2	RON^1	RON^1	CON^2	-	-
Pinarophyllum	-	-	HAM^1	HAM^1	-	-	RON^1	HAM^1
Pogonopus	-	CON^2	CON^2	RON^1	RON^1	CON^2	-	
Portlandia	HED^3	CON^2	CON^2	CON^2	-	CAT^1	-	CHI^1
Pseudomiltemia	-	-	-	-	-	-	RON^1	HAM^1
Pteridocalyx	-	-	RON^1	RON^1	RON^1	SIP^2	-	-
Rachicallis	HED^3	RON^1	HED^3	HED^3?	-	RON^1	RON^1	RON^1
Renistipula	-	-	-	-	-	-	RON^1	-
Rogiera	-	RON^1	RON^1	RON^1	-	GUE^1	RON^1	GUE^1
Roigella	-	-	RON^1	RON^1	-	RON^1	RON^1	RON^1
Rondeletia	HED^3	RON^1	RON^1	RON^1	-	RON^1	RON^1	RON^1
Rovaeanthus	-	-	-	-	-	RON^1	RON^1	RON^1
Rustia	-	CON^2	CON^2	RON^1	RON^1	CON^2	-	
Simira	COF	PSY^3	RON^1	SIM^2	RON^1	CON^2	RON^1	-
Sipanea	HED^3	RON^1	SIP^2	SIP^2	RON^1	SIP^2	-	-
Sipaneopsis	-	-	RON^1	RON^1	RON^1	SIP^2	-	-
Spallanzania	HED^3	MUS	MUS	MUS	-	-	-	-
Spathiclamys	-	-	RON^1	RON^1	-	RON^1	-	RON^1?
Spiradiclis	HED^3	HED^3	OPH^3	OPH^3	-	-	-	-
Standleya	-	-	RON^1	RON^1	-	HED^3	-	RON^1?
Steenisia	-	-	RON^1	RON^1	-	HAM^1	-	-
Stevensia	CIN^1	RON^1	RON^1	RON^1	RON^1	RON^1	RON^1	RON^1
Steyermarkia	-	-	SIP^2	SIP^2	-	SIP^2	RON^1	-
Stylosiphonia	-	-	RON?	-	-	-	RON^1	-
Suberanthus	-	-	CIN^1	RON^1	-	RON^1	RON^1	RON^1
Tresanthera	-	CON^2	CON^2	RON^1	RON^1	CON^2	-	-
Virecta	HED^3	HED^3	SIP^2	SIP^2	-	-	-	-

Warszewiczia	-	RON[1]	RON[1]	RON[1]	RON[1]	CON[2]	-	-
Wendlandia	HED[3]	RON[1]	RON[1]	RON[1]	-	GAR[2]	-	-
Xanthophytum	HED[3]	HED[3]	HED[3]	HED[3]	-	-	-	-
ARG-Argostemaeae, CAL-Callicoophylleae, CAT-Catesbeae, CIN-Cinchoneae, COF-Coffeae, CON-Condamineeae, GAR-Gardenieae, GUE-Guettardeae, HAM-Hamelieae, HED-Hedyotideae, IXO-Ixoreae, MUS-Mussaendeae, OPE-Operculieae, OPH-Ophiorrizae, PSY-Psychotrieae, RON-Rondeletieae, SIM-Simireae, SIP-Sipaneeae.								

Despite the considerable reduction of the tribe, phylogenetic studies show Rondeletieae to be polyphyletic. Regardless of the efforts to circumscribe a natural tribe, it remains to be tested if some genera tentatively included in the tribe by different authors (Robbrecht 1988; Borhidi 2006; Manns and Bremer 2010) should be classified within Rondeletieae: *Acrobotrys, Habroneuron, Holstianthus, Renistipula, Spathichlamys, Standleya* and *Stylosiphonia*. All these genera are monotypic and many of them are only known from the type collections.

In the classification by Robbrecht (1988), Rondeletieae consists of small trees or shrubs with entire stipules, imbricate corolla lobes, heterostylic flowers, capsular or samaroid fruits and tricolporate pollen. The characters commonly used to differentiate genera within Rondeletieae (Robbrecht 1988; Delprete 1999a, 1999b; Rova et al. 2002, 2009) are: inflorescence position (axillar vs terminal), number of corolla lobes (four to six), corolla mouth ornamentation (naked or with a fleshy/hairy ring), position of the stamen insertion to the corolla (basal, on the middle or at the throat), and fruit type (capsule or samara) and dehiscence (loculicidal or septicidal capsules).

Within Rondeletieae, the circumscription of the genus *Rondeletia* has been particularly conflictive. A number of segregates have been proposed by several authors (Steyermark 1964; Borhidi et al. 1980, 2004, 2011; Borhidi and Fernández-Zequeira 1981a, 1981b; Borhidi and Jarai-Komlódi 1983), while others have argued that practically no subdivisions should be made based on morphology and recommend not accepting the segregation until more evidence is evaluated (Lorence 1991, 1999; Burger and Taylor 1993; Taylor 2001). In total, the "*Rondeletia* complex" includes nine genera directly splitted from *Rondeletia* (*Acunaeanthus*, *Arachnothryx*, *Donnellyanthus*, *Javorkaea*, *Renistipula*, *Roigella*, *Rogiera*, *Rovaeanthus*, *Suberanthus* and *Tainus*) or closely related according to molecular evidence (*Gonzalagunia*, *Mazaea*, *Phyllomellia*, *Rachicallis* and *Stevensia*). In this way, the "*Rondeletia* complex" constitutes most of the species diversity within Rondeletieae.

Molecular studies agree that the "*Rondeletia* complex" is polyphyletic (Rova et al. 2002, 2009; Robbrecht and Manen 2006) and *Arachnothryx*, *Javorkaea* and *Rogiera* should be rather classified in tribe Guettardeae (Manns and Bremer 2010). Also, the molecular studies point to the fact that there is a set of genera (*Mazaea*, *Phyllomellia*, *Rachicallis*, *Roigella* and *Stevensia*) that intermingle with *Rondeletia* and should be synonymized with it (Rova et al. 2002). Nevertheless, the lack of resolution among the genera in the *Rondeletia* assemblage leaves the possibility that these genera do not share a most recent common ancestor with *Rondeletia*. In fact, there are some distinctive morphological features that support the recognition of these genera, such as the presence/absence of brachyblasts, the leaf texture, the corolla mouth ornamentation and the position of the stamen insertion to the corolla. Furthermore, the morphological heterogeneity of *Rondeletia*, combined with its large size of (about 120 spp), calls for caution and further research, even leaving open the possibility that more genera should be segregated.

Additionally, within the tribe Rondeletieae there are still some questions about the naturalness of *Acrosynanthus*. Rova et al. (2009) found in their ITS analysis conflictive position of different *Acrosynanthus* species, in comparison to previous studies using *trn*L-F (Rova et al. 2002). Based on these results, they proposed that the genus could be polyphyletic; however, in both cases the support values of the clades were weak. The sister group of *Rondeletia* is also still in question. Molecular studies agree that neither *Acunaeanthus, Rovaeanthus* or *Suberanthus* are sister to *Rondeletia*, but question remains to which genus(genera) is(are) its sister: Rova et al. (2002) retrieved a polytomy including *Acrosynanthus*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella* and *Rondeletia*, but the analysis does not include *Donnellyanthus*. Rova et al. (2009) show *Donnellyanthus* (as *Rondeletia deamii*) to be the sister of *Rondeletia*, both in turn sister to *Mazaea*, *Phyllomelia* and *Rachicallis*, but the analysis does not include *Roigella*. The study of Manns and Bremer (2010) presented *Roigella* as sister to *Rondeletia*, both in turn sister to *Mazaea*, *Phyllomelia* and *Rachicallis*.

The main goals of our study are to reassess the limits of the Rondeletieae tribe and in particular of the *Rondeletia* complex using molecular evidence and to study the evolution of several taxonomically important characters within the tribe in order to contribute to a natural classification.

Material and methods

Taxon sampling —To define our taxon sampling we did a literature survey to discard those genera from Table 1 that from previous phylogenetic analyses have already been placed outside Rondeletieae (Bremer and Manen 2000; Rova et al. 2002; Delprete and Cortés 2004; Andersson and Antonelli 2005; Smedmark et al. 2008; Bremer and Eriksson 2009; Mouly et al. 2009; Kainulainen et al. 2010; Manns and Bremer 2010; Razafimandimbison et al. 2011; Delprete and Jardim 2012; Kainulainen et al. 2013; Tange 2013; Cortés and Motley 2015; Stranczinger et al. 2014; Ginter et al. 2015) or synonymised without controversy with genera phylogenetically placed outside Rondeletieae. We tried to include all other genera not previously discarded from Rondeletieae by phylogenetic analyses, but when it was not possible, they are incorporated in the discussion. At the end, the sampled genera include all the genera for which by consensus have been classified within a clade Rondeletieae by previous studies (Rova et al. 2002, 2009; Robbrecht and Manen 2006, Manns and Bremer 2010), but with a broader representation of species. Several genera representing other tribes of Cinchonoideae (Condamineeae, Chiococceae, Guettardeae, and Sabiceeae) and Ixoroideae (Gardenieae) were used as outgroups. Taxon names with authors, voucher specimens and GenBank accession numbers are presented in Appendix 1.

DNA extraction, amplification and sequencing — Silica gel dried leaves were used for DNA extraction when available, complemented with herbarium material. DNA was extracted using NucleoSpin Plant II kit (Macherey Nagel, Düren, Germany) following the manufacturer's protocol or a three-fraction cetyltrimethylammonium bromide (CTAB) method (Borsch et al. 2003).

Three plastid markers (*trn*K-*mat*K, *trn*L-F and *pet*D) were amplified and sequenced in this study. The amplification of each marker was performed in reaction volumes of 50 µL, containing 2 µL of extracted DNA (with a concentration of 10–20 ng/µL), 14.7 µL of H_2O, 5 µL of 10× peqLab Taq. buffer S containing $MgCl_2$, 3 µL of $MgCl_2$ (25 mM), 10 µL of betaine monohydrate (5 M), 1 µL of BSA (10 ug/µl), 2 µL of forward primer (20 pm/µl), 2 µL of reverse primer (20 pm/µl), 10 µL dNTPs (each 0.25 mM) and 0.3 µL Taq polymerase 5 units/µl (PeqLab, Erlangen Germany).

For *trn*K-*mat*K the amplification was performed in two halves using the primers trnKFbryo (Wicke and Quandt 2009) and COmatK670R (Tesfaye et al. 2007) plus NYmatK480F (Hilu et al. 2003) and psbA5R (Steele and Vilgalys 1994). PCR conditions were: 1 cycle of denaturation (90 seconds at 96°C, 60 seconds at 50°C, 120 seconds at 68°C), 35 cycles of annealing (30 seconds at 95°C, 60 seconds at 48°C, 120 seconds at 68°C), extension (20 minutes at 68°C). The *trn*L-F region was amplified using the primers trnTc and trnTf (Taberlet et al. 1991). PCR conditions were: 30 cycles of denaturation (60 seconds at 96ºC), annealing (60 seconds at 50ºC), and extension (120 seconds at 72ºC). The *pet*D intron including the *pet*B-*pet*D spacer was amplified using the primers PIpetB1411F or PIpetB1365F and PIpetD738R or PIpetD346R (Löhne and Borsch 2005). PCR conditions were: 35 cycles of denaturation (60 seconds at 97°C), annealing (60 seconds at 48°C), extension (45 seconds at 72°C) and a final extension step (7 min at 72°C).

Owing to scarcity of herbarium material for some species and technical difficulties (i.e., primer mismatches, degraded templates and possible gene loss), not all amplification products were obtained for each taxon.

All amplification products were purified by QIAquick PCR Purification Kit (QIAGEN GmbH, Hilden, Germany). Sequencing was performed by Macrogen Inc., South Korea (http://www.macrogen.com).

Sequence assembly, alignment and indel coding — The matrix comprises 179 taxa and 428 accesions, 204 of which were generated for this study; other 293 sequences were generated for a previous study (Torres-Montúfar et al. 2017, 2018), and 15 sequences generated and used by Rova et al. (2002, 2009) were downloaded from GenBank. New pherograms were edited and assembled using PhyDE v.0 995 (Müller et al. 2005). Sequences were then added to the multiple sequence alignment of Torres-Montúfar et al. (2018) following the criteria proposed by Löhne and Borsch (2005). Gaps were coded manually following the simple gap criterion of Simmons and Ochoterena (2000); Simple Sequence Repeats (SSR) and inversions were manually coded following Ochoterena (2009). Microstructural characters are presented in Appendix 2.

Regions of uncertain homology (mutational hotspots) were removed from the matrices prior to phylogenetic analyses. The final alignments and microstructural character matrices are available at TreeBase.

Phylogenetic analyses — Parsimony (P) analyses were performed using the combined matrix with nucleotides, gaps, inversions and SSRs, only including parsimony potentially informative characters. A heuristic search with 10 000 replicates of Wagner trees constructed with random taxon addition followed by TBR branch swapping was performed in TNT version 1.1 (Goloboff et al. 2003); 10 trees were saved on each replicate and a further TBR was conducted to completion saving up to 10 000 trees. These trees were submitted to further analysis using the "new technology" option, alternating ratchet parsimony (Nixon 1999a), sectorial, drift and tree fusion (Goloboff 1999) options. One hundred initial sequences were used until the consensus was stabilized 10 times using a 100% factor. All the most parsimonious trees were collected and opened in WinClada (Nixon 1999b) and summarized in a strict consensus tree. Additionally, a Jackknife analysis (JK) was executed in TNT version 1.1 (Goloboff et al. 2003), re-sampling the matrix 10 000 times with the same parameters used for the new technology searches.

For Bayesian Inference (BI) analysis, the optimal models of sequence evolution were estimated using ModelTest 3.6 (Posada 1998) using the following parameters: 203 substitution schemes, +F base frequencies, +I and +G rate variation, nCat=4 and SPR tree search. For the morphological and the microstructural characters the MK model (Lewis 2001) was implemented, which assumes that a character can change its state at any time with equal probability for all instantaneous time intervals along the branch

BI analyses of the concatenated matrix partitioned by molecular and morphological data were conducted using MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001). Four independent Markov Chain Monte Carlo (MCMC) runs were carried out, each with four parallel chains. Each chain was performed for 1 000 000 generations, saving one random tree every 1 000 generations. The burn-in was set to 1 000 (10%) when the stability of the chain was reached. Phylogenetic trees were visualized using

Figtree (Rambaut and Drummond 2010). A summary of the phylogenetic information for each dataset is disclosed in Table 2. For the support values, we considered cut off values as follows: 64% for JK (Farris et al. 1996) and 0.95 for posterior probabilities (PP) (Alfaro and Holder 2006).

Table 2. Dataset phylogenetic information

Molecular: Nucleotides				
	# Terminals	**# Characters**	**# Potentially informative**	**Evolution model**
***trn*K-*mat*K**	120	3016	546	
***trn*L-F**	155	1060	194	GTR+I+G
***pet*D**	153	1108	181	
Molecular: Microstructural characters				
***trn*K-*mat*K**	120	79	67	
***trn*L-F**	155	41	33	MK
***pet*D**	153	51	41	
Morphology				
Morphology	179	13	13	MK
Total	179	5368	1075	

Morphological data — Morphological data were predominantly obtained from original descriptions and type specimens, complemented by personal observations, from the field and specimens conserved in the following herbaria: B, F, MEXU and MO. Specialized literature (Poiteau 1804; Standley 1918; Liogier 1962, 1995; Aiello 1979; Delprete 1999a, 1999b; Lorence 2012) was used to code some characters only when they were not directly observable. Characters and character states are listed in Table 3.

Table 3. Morphological characters evaluated

Character	Character states
1. Corolla aestivation	(0) Quincuncial; (1) Valvate; (2) Contorted; (3) Induplicated
2. Number of floral parts	(0) 4; (1) 5; (2) 6
3. Corolla shape	(0) Infundibuliform; (1) Rotate
4. Corolla color	(0) White; (1) Reddish-Pinkish; (2) Yellow
5. Corolla mouth ornamentation	(0) Naked; (1) Fleshy ring; (2) Yellow hairy ring; (3) Papillate ring; (4) White hairy ring; (5) Yellow hairy and fleshy ring
6. Corolla lobes form	(0) Spatulate; (1) Triangular
7. Stamen insertion	(0) Basal; (1) Medium; (2) Throat
8. Fruit consistency	(0) Dry; (1) Fleshy
9. Fruit type	(0) Capsule; (1) Berrry; (2) Samara; (3) Mesocarpic drupe; (4) Endocarpic drupe; (5) Schizocarp
10. Fruit line dehiscence	(0) Loculicidal; (1) Septicidal; (2) Indehiscent
11. # seeds per locule	(0) one; (1) two to six; (2) >30
12. Seed type:	(0) Winged; (1) Wingless
13. Pollen exine ornamentation	(0) Echinate; (1) Smooth

Results

In all the analyses clades corresponding to tribes (Condamineeae, Chiococceae, Gardenieae, Guettardeae, Sabiceeae and Rondeletieae) have strong support values (Fig. 1). The tribal relationships are also the same independently of the different inference methods and different treatment of characters (only nucleotides, nucleotides plus DNA microstructural characters, nucleotides plus morphology, and all combined data). Fig. 1 presents a summary consensus at tribal level, indicating support values, number of synapomorphic and homoplastic DNA microstructural characters and showing the optimization and variation within tribes (including taxa not sampled here) of morphological characters traditionally used in tribal circumscriptions.

The genus *Chione* is the only one that is not unequivocally placed within a particular tribe. All tribes are supported, in addition to individual nucleotides, by DNA microstructural characters or/and morphological synapomorphies except for Guettardeae and Rondeletieae.

Some genera formerly placed in Rondeletieae (with capsular fruits) form a paraphyletic group with respect to the traditional Guettardeae (Guettardeae s.l. vs. Guettardeae s.s.): *Arachnothryx*, *Javorkaea*, *Renistipula* and *Rogiera* (herein referred to as the "*Arachnothryx* complex").

The statistical support for Guettardeae s.l. (91 JK, 1.0 PP) and Rondeletieae (97 JK, 1.0 PP) as individual tribes is similar to that of the clade that recovers them as sisters (92 JK 1.0 PP). The combination of quincuncial corolla aestivation and spatulate corolla lobes is distinctive of both Guettardeae s.l. and Rondeletieae with respect to the other Cinchonoideae tribes (results not shown in the figure). Outside these tribes *Chione* shares the quincuncial corolla, but not the corolla lobes shape; this genus is unresolved and because we do not have a comprehensive tribal representation within Cinchonoideae, we will still consider it as *incerta sedis* (Fig. 1).

The tribe Rondeletieae

Within Rondeletieae, all analyses resulted in congruent topologies. The differences between the analyses are in resolution and/or support, being the combined matrix the most resolved and supported (Fig. 2, online Appendix 3). Given that the Bayesian trees are congruent with the parsimony trees, and because the differences are mainly due to the support significance level and therefore do not affect our general conclusions, we will present the results based on the consensus of the combined parsimony trees because it is straight forward to analyze character evolution with this method.

All genera in the tribe represented with more than one species are supported as monophyletic (Fig 2): *Acrosynanthus* (99% JK, 1.0 PP), *Donnellyanthus* (95% JK, 1.0 PP), *Rachicallis* (99% JK, 1.0 PP), *Rovaeanthus* (99% JK, 1.0 PP), *Suberanthus* (92% JK, 1.0 PP) and *Tainus* (99% JK, 1.0 PP), except for *Rondeletia*, which is paraphyletic to *Stevensia* (85% JK, 0.96 PP). The genus *Stevensia*, therefore, will be treated hereafter as *Rondeletia*. In general, there is little if any structure within genera clades, but the relations among genera are overall fairly well supported.

The Fig. 3 presents a summary of the relationships among genera within Rondeletieae showing the number and type of characters supporting each clade. In general, nucleotide punctual mutations are distributed more or less evenly among the clades. DNA microstructural and morphological characters provide support and resolution at the same hierarchical level, i.e. at generic level; only few homoplastic character states are present at more inclusive clades.

Within Rondeletieae two clades are recovered: the *Blepharidium-Donnellyanthus-Rovaeanthus-Acunaeanthus-Suberanthus* clade I (67% JK, 0.92 PP) and the *Tainus- Acrosynanthus-Mazaea-Phyllomelia-Roigella-Rachicallis- Rondeletia- Roigella* - clade II (96% JK, 1.0 PP). Both clades are supported only by punctual nucleotide mutations, but clade II has more of them resulting in higher support values.

All genera in Clade I share, but not exclusively, stamens inserted at the corolla throat and capsular fruits with more than 30 winged seeds per locule, which are symplesiomorphies (Fig. 3). The Mesoamerican monotypic genus *Blepharidium* is the earlier divergent taxon within this clade, and it is sister to two subclades (65% JK, 0.89 PP). One subclade includes the Mexico-Mesoamerican genera *Donnellyanthus* and *Rovaeanthus* (97% JK, 1.0 PP); the former is monotypic, while *Rovaeanthus* has two species. Both can be distinguished between themselves by the number of floral parts (four in *Donnellyanthus*; five in *Rovaeanthus*); in addition, *Rovaeanthus* is the only genus within the tribe that has a yellow hairy ring on top of a fleshy ring at the corolla mouth. The other subclade includes the Antillean endemic genera *Acunaeanthus* and *Suberanthus* (64 JK, 0.74 PP); *Acunaeanthus* is monotypic and endemic to Cuba, while *Suberanthus* has nine species distributed in Cuba and Hispaniola. Both genera can be distinguished between themselves by the corolla mouth ornamentation (naked in *Acunaeanthus* and with a fleshy ring in *Suberanthus*) and the capsule dehiscence (loculicidal in *Acunaeanthus* and septicidal in *Suberanthus*).

All genera in Clade II are well represented in or even restricted to the Antilles (Fig. 3), and, as in the case of the genera in Clade I, they do not have morphological synapomorphies or a unique combination of morphological features in common. There is a grade at the earlier divergent point of Clade II formed by *Tainus* (99% JK, 1.0 PP), followed by *Acrosynanthus* (99% JK, 1.0 PP), and by the *Rondeletia* assemblage: *Mazaea-Phyllomelia-Rachicallis-Roigella -Rondeletia* (88% JK, 1.0 PP).

Tainus is a monotypic genus endemic to Hispaniola, characterized by the papillate corolla mouth ornamentation and two SSRs in the *trn*L-F region (TGAT in the aligned positions 396-399 and TTTTC in the aligned positions 435-439; as in Torres-Montúfar et al. 2017). The genus *Acrosynanthus* is endemic to the Antilles, with seven species easily recognizable within the tribe by the stamens inserted at the base of the corolla tube (a feature not common among Rubiaceae), a white hairy ring at the corolla mouth and an inversion in the *trn*K-*mat*K region (TTATGAAA in the aligned positions 331-338).

The *Rondeletia* assemblage includes mostly Antillean species (particularly in Cuba), but *Rachicallis* and *Rondeletia* have some representatives in Mesoamerica and even *Rondeletia* in South America. Within this clade, the monotypic Cuban genus *Roigella,* which does not have a unique feature distinguishing it among other genera in the clade, is the earlier divergent lineage. The next one is *Rondeletia,* which is the most specious and diverse genus in the entire tribe, with around 120 species. The genus *Rondeletia* does not have a unique morphological feature distinguishing it within the tribe or even within clade II, but it is supported by a SSR in the *trn*L-F region (ACTATATCAAA in aligned positions 261-271); it is sister to *Rachicallis,* which is in turn sister to *Mazaea* and *Phyllomelia*. The genus *Rachicallis* is monotypic; it is unique within the tribe by the yellow corolla, and within Clade II by the stamens inserted near the middle of the corolla tube; in addition, it has a SSR in the *pet*D region (GTAAG in the aligned positions 832-836). The genera *Mazaea* and *Phyllomelia* are endemic to Cuba; the former has two species while *Phyllomelia* is monotypic. The genus *Mazaea* could be confused with *Rondeletia* by the fleshy ring at the corolla mouth, however it does not have winged seeds and its septicidal capsules only carry a few seeds (2-6), a unique feature within the tribe. The genus *Phyllomelia* is easy to recognize by its one-seeded samaras.

Discussion

Our results are in agreement with previous studies (Rova et al. 2002; Robbrecht and Manen 2006; Manns and Bremer 2010) in that the *Arachnothryx* complex shares a most recent common ancestor with Guettardeae s.s., clade that in turn is sister to the remaining Rondeletieae. Here we identify two morphological features that support Guettardeae s.l. as sister to Rondeletieae: the quicuncial corolla aestivation and the spatulate corolla lobes. Previous authors (Robbrecht 1988) considered their corolla aestivation to be imbricate, which is a common feature within Cinchonoideae. We found that imbricate corolla buds of Rondeletieae and Guettardeae s.l. can be better described as quincuncial corolla aestivation, which is unique among Cinchonoideae. Also, we prefer to describe the corolla lobes of both as spatulate in contrast to the common triangular or linear shape in other genera of Cinchonoideae.

Since the use of molecular phylogenetics, it has become clearer that Rondeletieae is more restricted than previously thought. Despite the agreement in the general tribal composition it has become difficult to characterize Guettardeae s.l. vs Rondeletieae, even referred to as a complex of tribes by Robbrecht and Manen (2006). In our study we also did not find morphological or DNA microstructural synapomorphies for these tribes, in contrast to the two morphological synapomorphies supporting both tribes (quincuncial corolla aestivation and spatulate corolla lobes). Rova et al. (2009) already suggested sinking both tribes and accepting a larger Rondeletieae. An alternative solution could be not to include the *Arachnothryx* complex in Guettardeae, but rather identify diagnosable lineages that could be elevated to tribes. This solution is currently difficult since there is disagreement about the monophylly of Guettardeae s.s. (our results and Manns and Bremer 2010 vs. Robbrecht and Manen 2006). In any case, before any classification changes are done with respect to Guettardeae (merging it with Rondeletieae or further splitting) it necessary to conduct further studies in Guettardeae s.l., in particular with a broader taxon representation.

We believe that it is pragmatic to recognize a strict concept for Rondeletieae because both lineages (Rondeletieae and Guettardeae s.l.) are well supported and their composition has reached relative stability (see Robbrecht and Manen 2006; Rova et al. 2002; Manns and Bremer 2010). In addition, the narrower circumscription of Rondeletieae corresponds with a mainly Antillean lineage, while Guettardeae s.l. is pantropical. Furthermore, it is still possible to provide a diagnosis for Rondeletieae based on a unique combination of characters: among genera conforming the tribal complex Guettardeae s.l. and Rondeletieae, when fruits are capsular multi-seeded and bilocular, the pollen lacks endofisures or endocracks in Rondeletieae (Torres-Montúfar et al. in prep).

Because the previous diagnosis of Rondeletieae is based on pollen nexine continuity and this features are not usually reported, the following combinations of non-synapomorphic characters serve to place genera in Rondeletieae with respect to Guettardeae s.l.: if the capsular fruits bear winged seeds, the corolla mouth has a thick ring or the capsule has few seeds; if the capsular fruits bear wingless seeds the corolla mouth is ornamented or the stamens are inserted in the middle portion of the corolla tube. For instance, those taxa that were formerly placed within the *Rondeletia* complex can be excluded from Rondeletieae by the lack of some morphological features in Rondeletieae. For example, among the “*Arachnothryx* complex”, *Rogiera*, which has capsular fruits with winged seeds, does not have a fleshy ring at the corolla mouth and has pollen with endofissures (Torres-Montifar et al. in prep); *Arachnothryx* and allies do not have a fleshy ring or winged seeds and has pollen with endocracks (Torres-Montúfar et al. in prep); Guettardeae s.s shares axillar inflorescences with some Rondeletieae, but has mesocarpic drupes (Torres-Montúfar et al. 2018).

The Rondeletieae tribe—All phylogenetic studies (Rova et al. 2002; Robbrecht and Manen 2006; Rova et al. 2009; Manns and Bremer 2010) suggest that there is a set of taxa that conform a natural group which has more or less correspondence to our circumscription of Rondeletieae. In all analyses there is a clade that includes: *Blepharidium*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella*, *Rondeletia*, *Rovaeanthus* (sometimes as *Rogiera suffrutescens*) and *Suberanthus*. The genera *Acunaeanthus*, *Donnellyanthus* (Borhidi et al 2011; treated as *Rondeletia deamii*), and *Tainus* (Torres-Montúfar et al. 2017; treated as *Rondeletia pitreana*) were only included in some analyses. The genera *Ariadne* and *Stevensia* were treated as such in some studies, but they are now considered as synonyms of *Mazaea* and *Rondeletia* respectively. Both, *Acrosynanthus* and *Tainus* are sister to Guettardeae-Rondeletieae in Rova et al. (2009), but they still included them in their synthesis of Rondeletieae.

In addition, Rova et al. (2009) and Manns and Bremer (2010) suggested to include some genera that they did not sampled for their DNA molecular phylogenies. These genera are discussed below in our section of *Genera excluded from Rondeletieae.*

In summary, there is then either consensus or at least not disagreement in that there is a lineage of 12 genera (*Acrosynanthus*, *Acunaeanthus*, *Blepharidium*, *Donnellyanthus*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella*, *Rondeletia*, *Rovaeanthus*, *Suberanthus*, and *Tainus*) that we are treating as the Rondeletieae tribe.

Phylogenetic relationships within Rondeletieae tribe—Despite the general agreement in the generic Rondeletieae composition, we found alternative phylogenetic relationships within it. Our results include the largest set of genera (12 vs 9–12) and species (47 vs 17–34) within Rondeletieae. The topology presented here notoriously contrasts with the one presented by Robbrecht and Manen (2006) in which not only the branching order differs, but several genera are depicted as non-monophyletic. We believe that this could be an artifact of the phylogenetic reconstruction method, as they used a supertree approach, which has been shown to have several pitfalls (Von Haeseler 2012). This does not diminish the general contribution of their work, which aimed to provide a general classification framework for the family, but we consider it weak to assess precise relationships within Rondeletieae. Our topology also differs considerably with respect to those presented by Rova et al. (2009), but they are difficult to compare, as they got fairly different results when only ITS was analyzed vs when a subset of taxa was analyzed for ITS in combination with *rps*16 and *trn*L-F. Rova et al. (2002) presented an important contribution to clarify the previous confusions regarding the limits of Rondeletieae, but their phylogeny has very little resolution inside Rondeletieae. Our results are by large more similar to those presented in Manns & Bremer (2010), who aimed to provide a framework for the entire Cinchonoideae using *atp*B-*rbc*L, *ndh*F, *rbc*L, *rps*16, *trn*T-F, and nrITS.

In both analyses (ours and Manns & Bremer 2010) two main clades are recovered within Rondeletieae. In Clade I both analyses recover the genus *Donnellyanthus* (monotypic) as sister to *Rovaeanthus* (two species), supporting that they deserve generic recognition in contrast of respectively being synonymized (Lorence 2012) with *Arachnothryx* and *Rogiera* (Guettardeae s.l.). Although it seems extreme to recognize two genera with so few species, both are easily distinguishable by the number of floral parts (four in *Donnellyanthus* vs five in *Rovaeanthus*) and the corolla mouth ornamentation (naked in *Donnellyanthus* vs with both a fleshy and hairy ring in *Rovaeanthus*). In both studies, also in Clade I, *Acunaeanthus* (monotypic) is sister to *Suberanthus* (nine species represented here with three of them). Both genera only share a homoplastic SSR (GT) in the aligned positions 765-766 of *trn*L-F, for which in our analysis this is the weakest supported clade, but in Manns and Bremer (2010) this clade has a high support. Despite the fact that *Acunaeanthus*, being monotypic, could be sink in *Suberanthus*, we prefer to keep them as to accepted genera because *Acunaeanthus* lacks ornamentation in the corolla mouth and its fruits are loculicidal, while *Suberanthus* has a fleshy ring on the corolla mouth and the capsules are septicidal.

The monotypic genus *Blepharidium* in Manns & Bremer (2010) is the earlier divergent genus inside our Clade II, instead of inside Clade I in our results. It was not until the study by Rova et al. (2002) that this genus was placed inside Rondeletieae; before it was classified as Cinchoneae and Hillieae (Robbrecht 1988 and Robbrecht & Bridson 1993, respectively). In Rova et al. (2009) it is placed as sister to *Suberanthus*, but in the reduced combined analysis it was retrieved as part of Guettardeae s.l. The conflict in the phylogenetic placement of *Blepharidium* does not allow us to take a firm position favoring either result.

Aside from *Blepharidium*, in both analyses (ours and Manns & Bremer 2010) the genus *Tainus* is early divergent within Clade II, followed by *Acrosynanthus*, which in turn is sister to the "*Rondeletia* assemblage" (*Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella*, and *Rondeletia*). These relationships and the acceptance of both genera are discussed in detail in Torres-Montúfar et al. (2017). In particular for *Rondeletia*, some phylogenetic studies (Rova et al. 2009; Manns and Bremer 2010) retrieved it as monophyletic, while others (Rova et al. 2002; Torres-Montúfar et al. 2017, 2018) retrieved it intermingling with *Mazaea*, *Phyllomelia*, *Rachicallis,* and *Roigella*. Our results, as in Rova et al. (2009) and in Manns and Bremer (2010), corroborate that *Rondeletia* is paraphyletic with respect to *Stevensia*. The presence of a poorly developed fleshy ring and the winged seeds in *Stevensia* provide support for the taxonomic decision to reduce *Stevensia* as a synonym of *Rondeletia*. Despite this, our study provides (as well as in Manns and Bremer 2010) strong enough support for the recognition of *Mazaea*-*Phyllomelia*, *Rachicallis*, *Roigella*, and *Rondeletia* as distinct genera, support that not only includes nucleotide changes, but also morphological and for some of these genera also microstructural DNA characters.

Within the "*Rondeletia* assemblage" there is only agreement between our results and Manns & Bremer (2010) in that *Mazaea* (two species), *Rachicallis* (monotypic) and *Phyllomelia* (monotypic) share a most recent common ancestor. Nevertheless, Manns & Bremer (2010) sampled both species of *Mazaea* and retrieve it as paraphyletic with respect to *Phyllomelia*, while we could only include *M. shaferi*. Even though the paraphyly of *Mazaea* has perfect support in Manns & Bremer (2010) we prefer to maintain them as distinct genera (as they also did) because in Rova et al. (2002) these three species form a polytomy (opening the possibility of the monophyly of *Mazaea*) and because both genera are morphologically very different: *Mazaea* has a fleshy ring on the corolla mouth and capsular dehiscent fruits with two to six seeds per locule, while *Phyllomelia* has a naked corolla mouth and samaras with one-seeded locules. The genus *Rachicallis* is also morphologically very different and, in fact, it has the longest branch within the clade, including a GTAAG SSR in the aligned positions 832-836 of *pet*D. It was first classified within Hedyotideae (De Candolle 1830; now Rubioideae) probably at least in part because it is a small shrub instead of small trees, but overall it is the most distinctive genus inside Rondeletieae: the yellow corollas with the stamens inserted in the middle portion of the tube are unique; in addition, its coastline habitat is reflected in very succulent small leaves with short internodes.

In our analysis *Roigella* (monotypic) is the earliest divergent genus within the "*Rondeletia* assemblage", while in Manns & Bremer (2010) it is sister to *Rondeletia* (about 120 spp). To prefer one of these alternatives over the other would be premature. The work of Manns & Bremer (2010) is not supported by morphology but ours does not show progressively less inclusive synapomorphies. Our topology has relatively low statistical support, but it is corroborated by the homoplastic presence of four floral parts (interpreted as the plesiomorphic condition of *Rondeletia* with five or six inside the genus, while in *Roigella* these numbers would be convergent). The only significance to favor the sister relationship would be the consideration to sink *Roigella* within the already specious *Rondeletia*. Nevertheless, by doing so, *Roigella* would be the only *Rondeletia* species without a fleshy ring on the corolla mouth and with wingless seeds. Consequently, we consider this discrepancy of low relevance.

Genera excluded from Rondeletieae— Despite the fact that our study includes the most comprehensive taxon sampling for Rondeletieae, it is still necessary to test the position of a few genera never included in a phylogenetic context due to their difficult access. Other genera have been controversially included in or excluded from Rondeletieae despite phylogenetic analyses. We revised the original descriptions, the type specimens (JStor Global Plants) and further relevant literatures associated to those genera in order to apply the criteria above mentioned and suggest their inclusion or exclusion from Rondeletieae.

Although it is desirable to rediscover and include these taxa in a comprehensive phylogenetic framework, we are confident that they do not belong in our circumscription of Rondeletieae.

Manns and Bremer (2010) suggested to tentatively include in Rondeletieae six genera that they could not sample: *Acrobotrys* K. Schum. & K. Krause, *Glionnetia* Tirveng., *Habroneuron* Standl., *Holstianthus* Steyerm., *Spathichlamys* R. Parker, and *Standleya* Brade.

The Colombian monotypic genus *Acrobotrys* is only known from the type collection from 1908. Rova (1999) tentatively included it within Condamineeae. The genus *Acrobotrys* has 4-locular ovary, typical of Condamineeae (Kainulainen et al. 2010) and it does not have spatulate corolla lobes, so we agree with the exclusion of this genus from Rondeletieae.

The monotypic African genus *Glionnetia* was found with an unresolved position relative to Vanguerieae and the Aleisanthieae–Greeneeae–Ixoreae clade within Ixoroideae (Razafimandimbison et al. 2011). Furthermore, in the original description (Tirvengadum 1984) the corolla aestivation was referred to as contorted. Therefore and also based on the geographic distribution, its tentative inclusion in Rondeletieae proposed by Manns and Bremer (2010) is rejected.

The Mexican monotypic genus *Habroneuron* was described as closely related to *Plocaniophyllon* Brandegee, *Sommera* Schlechtendal, and *Sabicea* Aublet, which all have leaf lineolate venation in common (Standley 1927). Nevertheless, *Habroneuron* differs from the previous by the contorted corolla aestivation, which was used as an argument to places it within Rondeletieae (Robbrecht 1988) when the tribe had a broader circumscription. This genus is known only from two collections from the 1800 hundreds and its fruits are unknown. Darwin (1980) remarks the close morphological affinity between *Habroneuron* and *Lindenia* Benth., both classified within Rondeletieae by Hooker (1873), by the creeping habit, membranaceous and striate leaves, rounded corolla lobes and included anthers. The phylogenetic analysis by Kainulainen et al. (2013) suggested the treatment of *Lindenia* Benth. as a synonym of *Augusta* Pohl, and placed it within the Coffeae alliance (Ixoroideae). Despite the fact that the fruits of *Habroneuron* are still unknown and that it has never been included in phylogenetic studies, based on the creeping habit, the contorted corolla aestivation and the lack of spatulate corolla lobes, we support its exclusion from Rondeletieae.

The monotypic genus *Holstianthus* from the amazonian Guyana was accommodated in tribe Rondeletieae by Robbrecht (1988). However, it differs from the current Rondeletieae genera by its herbaceous habit and the indehiscent dry fruits. In the protologue, Steyermark (1986) compared it with *Sipaneopsis* also included in Rondeletieae *sensu* Robbrecht (1988). The genus *Sipaneopsis* nevertheless has a densely barbate corolla mouth with elongated yellow hairs (as in *Rogiera*, now in Guettardeae). Molecular phylogenetic analysis (Delprete and Cortés 2004) recovered *Sipaneopsis* within the

Sipaneeae tribe as part of Ixoroideae. Because *Holstianthus* is herbaceous and the corolla aestivation is undoubtedly contorted we propose to exclude it from Rondeletieae.

The monotypic Asian genus *Spathichlamys* is included within Rondeletieae by Robbrecht (1988). The morphology suggests a close relation to *Greenea*, also included within Rondeletieae by Hooker (1873), placed within Ixoreae by Rova (1999) and Greeneae by Mouly et al. (2009). The morphological affinity between both genera leaded Tange (2013) to treat them as synonyms. Following these studies, and taking into consideration the geographic distribution, we agree that *Spathichlamys* should be included within Ixoroideae.

The monotypic Brazilian genus *Standleya* was proposed to be part of Rondeletieae by Robbrecht (1988), however it is herbaceous. In the protologue, Brade (1932) suggested that it is related to *Bradea* Standl. ex Brade, traditionally placed at Hedyotideae (Robbrecht 1988). Based on morphological similarities and on unpublished DNA sequences, Delprete and Jardim (2012) suggested including both genera in Coussareeae. Based on the herbaceous habit we propose to exclude it from Rondeletieae.

In addition to the previous genera, three other genera deserve discussion: *Blandibractea*, *Renistipula*, and *Stylosiphonia*.

The monotypic Brazilian genus *Blandibractea* Wernham was originally placed in Rondeletieae (Werham 1917) and it is only known from the type collection, which lacks fruits. In the protologue it is mentioned that the corolla aestivation is imbricate, with an exterior petal, that the "corolla lobes are almost negligible", that the stamens are fused at the medium portion of the corolla tube and that the ovary is bilocular and multi-seeded. The lectotype image (designated by Delprete 1998) is not available in online resources (JStor Global Plants), but Werham highlighted the close resemblance of the species with *Warszewiczia*, mentioning that in *Blandibractea* the bracts make the inflorescence very showy instead of a petaloid clayx lobe. Later on, Delprete (1998) considered this species as a synonym of Simira glaziovii (K. Schum.) Steyerm., a proposition that has been generally accepted. Both, *Simira* and *Warszewiczia* were at some point considered part of Rondeletieae, but phylogenic analyses place them now in Condamineae (Rova et al. 2002; Kainulainen et al. 2010). Supported by the small corolla lobes, we agree that *Blandibractea* should be excluded from Rondeletieae.

The Mesoamerican genus *Renistipula* Borhidi comprises three species; it was described to encompass *Rondeletia* species with reniform stipules and hence it was included within Rondeletieae (Borhidi et al. 2004). Nevertheless, it was not included by Rova et al. (2002) or Manns and Bremer (2010). By its morphology we consider it as a synonym of *Arachnothryx* (Guettardeae), which was also proposed in the recent floristic treatment for Mesoamerica (Lorence 2012). In contrast, molecular analysis suggests its inclusion within Hamelieae (Stranczinger et al. 2014). We question this last result because *Renistipula* does not have raphides, its inflorescences are bracteated and its flowers are not yellow-reddish. When we tried to replicate their results by downloading and re-analyzing their sequences (results not shown) we corroborate the placement of *Renistipula* within Hamelieae, but we also found one species of *Deppea* (Hamelieae) inside Rondeletieae. We think that there could be a mix-up in the labeling during the sequence procedure. Our results in progress (unpublished data) suggest that *Renistipula* should indeed be considered as a synonym of *Arachnothryx* and hence, excluded from Rondeletieae.

The type species of the Mexican genus *Stylosiphonia* Brandegee is only known from the type collection made in 1913. The genus *Stylosiphonia* was placed within Rondeletieae by Robbrecht (1988), proposition that was accepted by Borhidi (2006), and that has never been disputed or, for obvious reasons, tested in phylogenetic analyses. In the original description, Brandegee (1914) mentioned that the genus has “Corollae… limbi 5 lobi, lanceolati, elongati…” and capsular fruits with “semina angulate, rugosa”. In the available images of original material (JStor Global Plants) it is not possible to corroborate the flower characteristics. In Standley (1921) it is mentioned that the corolla of the genus is contorted. Later on, Standley (1924) added a second species to the genus, *S. salvadorensis*, which is currently considered a synonym of A*rachnothryx jurgensenii* (Hemsl.) Borhidi. We agree that *S. salvadorensis* belongs in A*rachnothryx* because it has a naked corolla mouth and the seeds are wingless. In spite the fact that *Stylosiphonia glabra* needs to be re-discovered and included in a phylogenetic analysis, based on the contorted corolla aestivation, the narrow elongated lanceolate corolla lobes and the wingless seeds, we propose to exclude it from Rondeletieae.

Biogeography—Our phylogeny implies at least four colonization events between the Antilles and the continental land. Despite the fact that our sampling of *Rondeletia* is incomplete, it is still possible to say that inside the *Rondeletia* assemblage, our sampling reveals two independent migrations from the Antilles to continental land. It is only possible that by adding more species of *Rondeletia* additional migrations from continental land to the Antilles or the other way around would be revealed because the sampled Mesoamerican species (*R. thiemei*) is well nested within the genus. In contrast, our methods do not allow determining the migration directionality for the two colonization events outside the *Rondeletia* assemblage.

Sampling density of population of *Rachicallis americana*, which is widespread with populations in the Antilles and continental land are desirable to produce phylogeographic studies that might shade light upon specific patterns of migration among continental land and the Antilles.

Conclusions

The present study improves our understanding of the phylogenetic relationships and circumscription of Rondeletieae and also of the generic limits. We provided morphological characters that are phylogenetically informative at tribal and generic ranks.

Concerning to the *Rondeletia* complex, it is confirmed that *Arachnothryx*, *Javorkaea*, *Renistipula* and *Rogiera* should be excluded from Rondeletieae and that they are paraphyletic with respect to Guettardeae. Guettardeae s.l. and Rondeletieae are sister: both share quinquncial aestivation and spatulate corolla lobes.

Among genera conforming the tribal complex Guettardeae s.l.-Rondeletieae, when fruits are capsular multi-seeded and bilocular, the pollen lacks endofisures or endocracks in Rondeletieae. A character combination including features of Guettardeae s.l.-Rondeletieae and Rondeletieae allow us to confidently exclude genera that were previously tentatively included in Rondeletieae; the tribe should include 12 genera: *Acrosynanthus*, *Acunaeanthus*, *Blepharidium*, *Donnellyanthus*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella*, *Rondeletia*, *Rovaeanthus*, *Suberanthus*, and *Tainus*. With the current circumscription, the tribe comprises approximately 140 species mainly restricted to the Caribbean region.

Taxonomic synthesis

Based on the results from the present and other recent studies (Rova et al. 2002; Delprete and Cortés 2004; Mouly et al. 2009; Razafimandimbison et al. 2011; Delprete and Jardim 2012; Manns and Bremer 2010; Kainulainen et al. 2013; Tange 2013, Torres-Montúfar et al. 2017), we propose the following taxonomic synthesis for Rondeletieae.

Tribe Rondeletieae (DC.) Miq., Flora Nederl Indie 2: 130, 156. 1856. Rondeletiinae DC., Prodr. 4: 342, 401. 1830, as tribe Hedyotideae, subtribe ‘‘Rondeletieae’’. Rondeletieae DC. ex Rchb., Der Deutsche Botaniker 1: 77. 1841, TYPE: *Rondeletia* L.

Shrubs or trees; raphides absent; thorns absent. Stipules free or connate at base, mostly entire, interpetiolar, persistent to readily caducous; leaves opposite or verticillate, petiolate to sessile; brochidodromus leaf venation; domatia variably present or absent. Inflorescences terminal or axillar, cymose, paniculate or thyrsoid, bracteate. Flowers hermaphroditic, 4 to 6(7)-merous; calyx persistent or caducous; insipient calycophylls rarely present, all calyx lobes acrescent into rotate pterophylls (green to greenish white) after anthesis rare (in *Phyllomelia*); aestivation quincuncial; corolla rotate, corolla lobes spatulate, corolla mouth naked, with a fleshy ring and/or with a hairy ring; stamens mostly as many as the corolla lobes, inserted near the base (in *Acrosynanthus*), at the medial zone (in *Rachicallis*), or more often near the corolla mouth; anthers included or exserted, dorsifixed near the base or around the middle; ovary inferior or secondary half-inferior (in *Rachicallis*), bilocular, with few to many ovules per locule, rarely one (in *Phyllomelia*). Fruits woody capsules, loculicidal or septicidal, or rarely indehiscent samaras (in *Phyllomelia*); seeds angulate, winged or not.

Genera included (Figs. 4 and 5): *Acrosynanthus*, *Acunaeanthus*, *Blepharidium*, *Donnellyanthus*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella*, *Rondeletia*, *Rovaeanthus*, *Suberanthus*, *Tainus*.

Excluded genera: *Acrobotrys* (Condamineeae?); *Blandibractea* (Condamineeae); *Glionnetia* (Vanguerieeae alliance); *Habroneuron* (Coffeae alliance); *Holstianthus* (Sipaneeae?); *Spathichlamys* (Greeneae); *Standleya* (Coussareae); *Stylosiphonia* (*Incertae sedis*); *Arachnothryx*, *Javorkaea*, *Renistipula* and *Rogiera* (Guettardeae).

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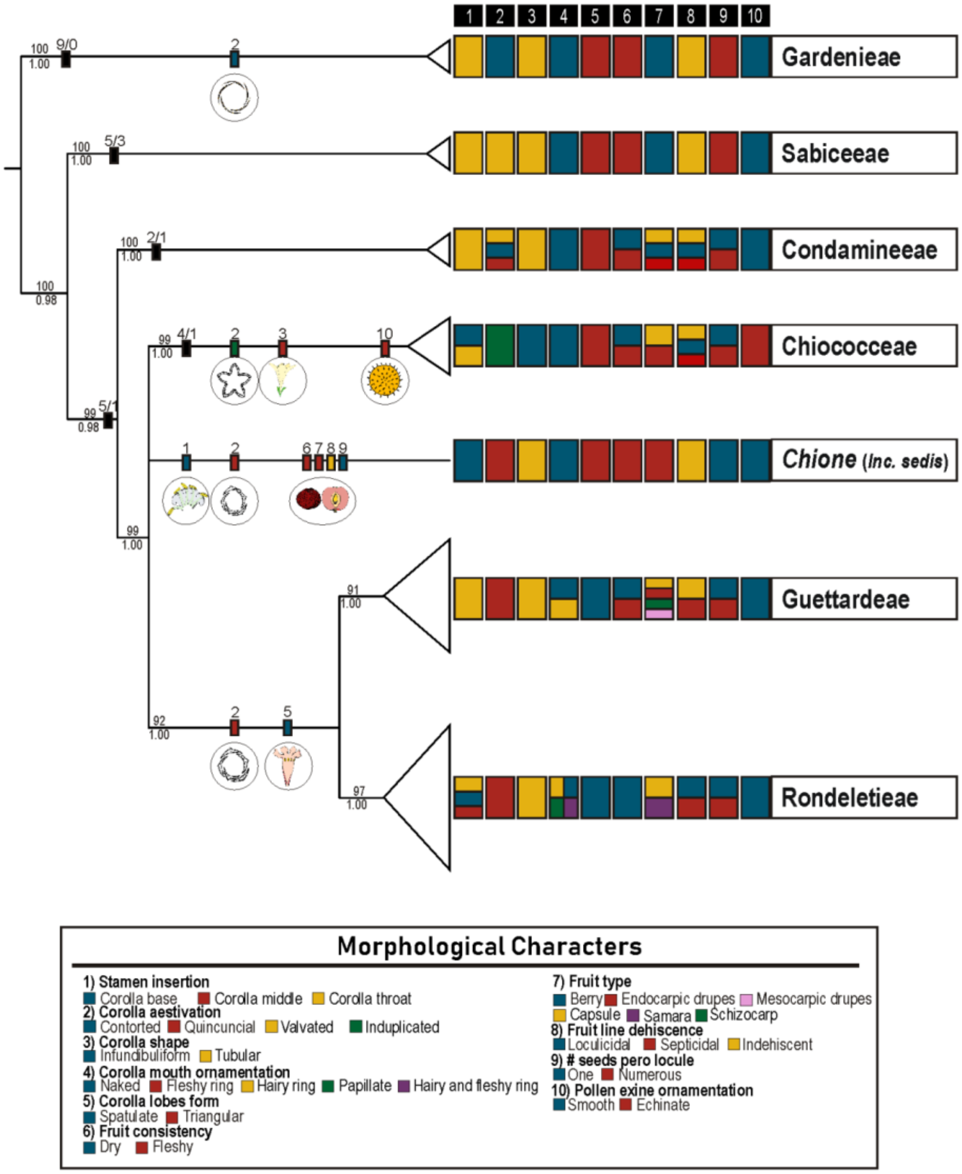


Fig. 1 Summary tree at tribal level found in all analyses, based on both the parsimony analysis and the Bayesian inference, obtain with individual nucleotides (*trn*K-*mat*K, *pet*D and *trn*L-F) and combined sequence with DNA microstructural characters and morphology. Numbers above branches correspond to Jackknife values (JK) and below to posterior probability (PP) from Bayesian analysis in the combined analyses. Numbers above black hash marks correspond to number of synapomorphic/homoplastic DNA microstructural characters. The morphological characters shown are those commonly used in tribal circumscriptions. Morphological synapomorphic character states are shown on the corresponding branches with schematic diagrams. Character variation within tribes (including that for taxa not sampled in this analysis) is shown on the left of the tribal names.

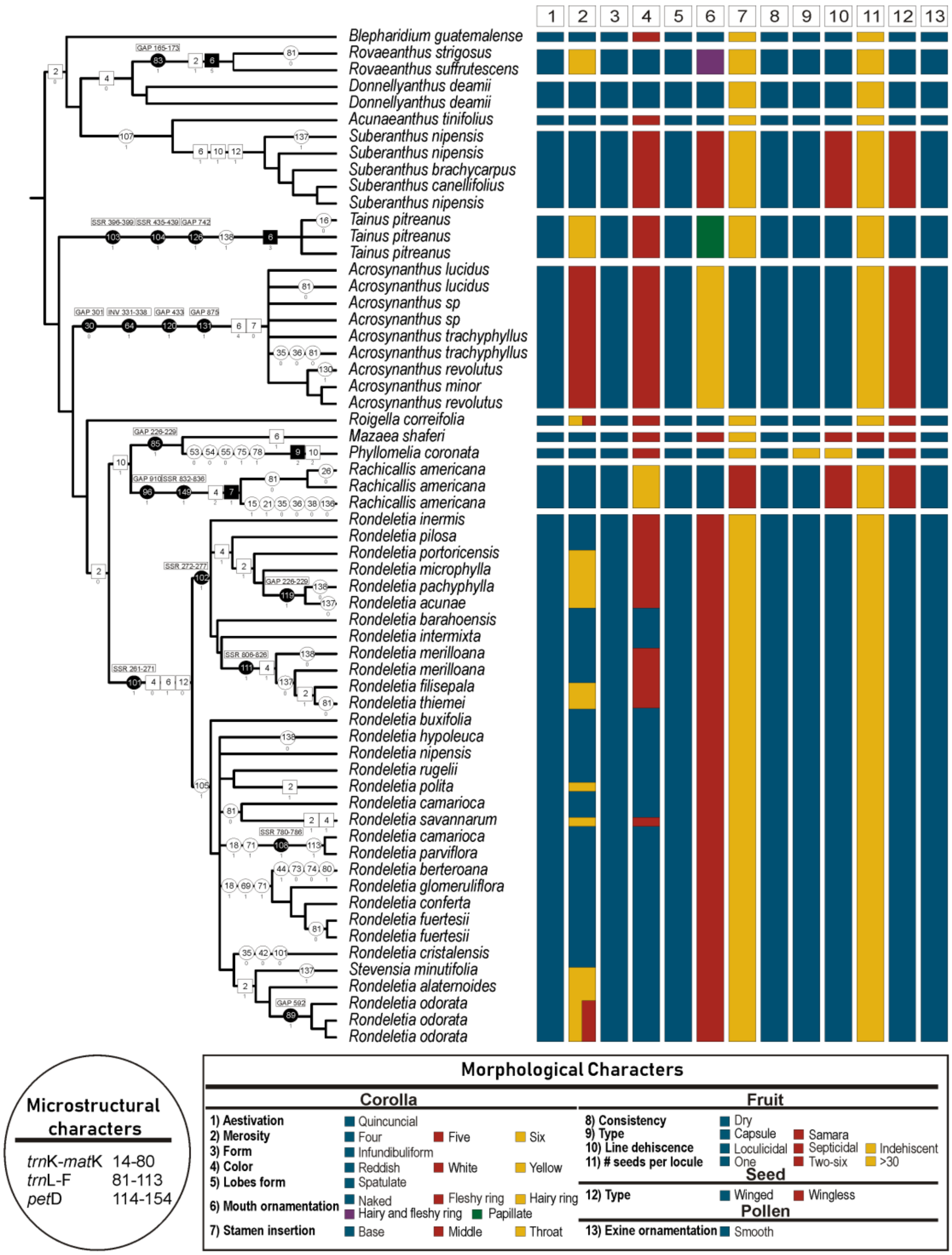


Fig. 2. Rondeletieae tree showing hashmarks for morphological (squares) and DNA microstructural characters (circles) to the left and morphological character variation to the rigth. Colored hashmarks indicate synapomorphic character states for the corresponding character type, the character number is indicated inside the hasmark and the character state is below. Above the microstructural hashmark is indicated the character and its aligned position(s) for the three plastid markers.

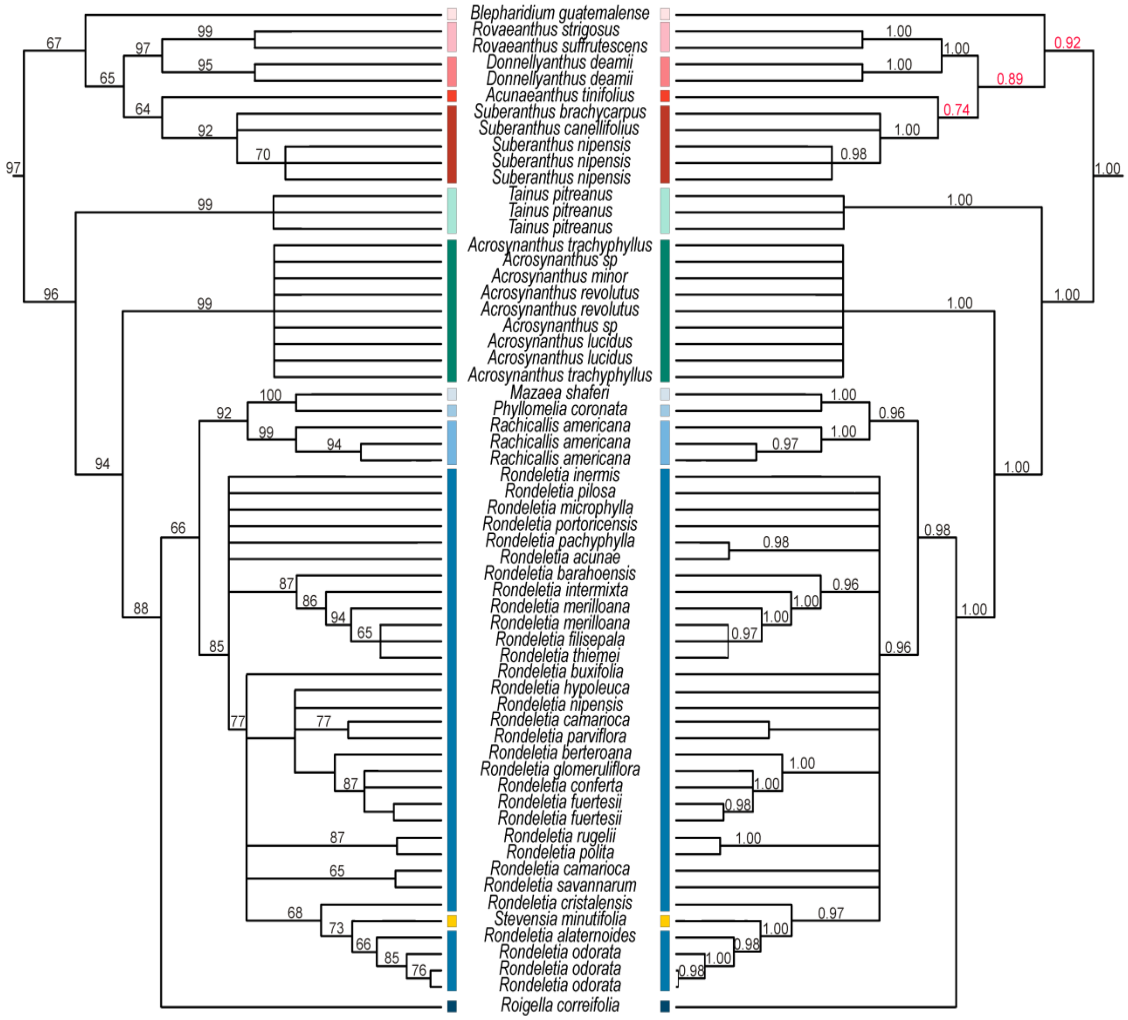


Figure 3. Comparison of the topologies obtained using combined matrix (nucleotidic plus DNA microstructural characters and morphology). To the left is showed the consensus tree (L= 2597, Ci= 0.50, Ri= 0.85) of the most parsimonious trees (L= 2440, Ci= 0.53, Ri= 0.87) obtained by Parsimony, to the right the Bayesian tree. Numbers above branches correspond to Jackknife values (JK) or to posterior probability (PP) from Bayesian analysis Numbers in red correspond weak support.

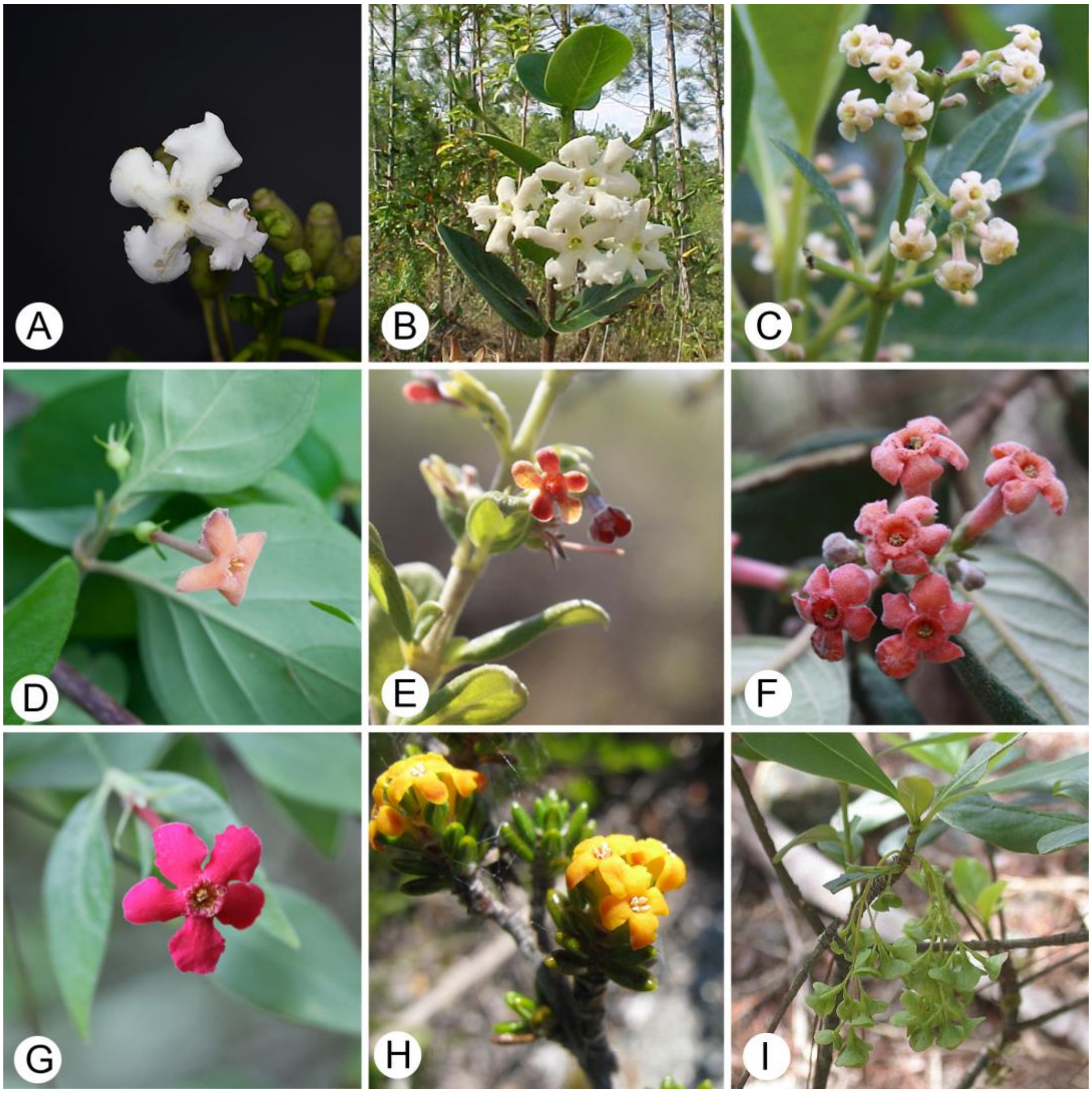


Fig. 4. Exemplar species in Rondeletieae: (A-C) Examples of genera with white flowers and lacking a fleshy corolla mouth ring. (A) *Blepharidium guatemalense* (Photo by N. Hellmuth); (B) *Roigella correifolia* (Photo by R. Rankin); (C) *Tainus pitreanus* (Photo by A. Torres-Montúfar). (D-G) Examples of genera with reddish flowers; (D) Donnellyanthus deamii. (E) *Rondeletia buxifolia* (Photo by A. Torres-Montúfar). (F) *Rondeletia merilloana* (Photo by A. Torres-Montúfar). (G) *Rovaeanthus strigosus* showing the felshy ring and the hairy ring on the corolla mouth, (Photo by I. Coronado). (H) *Rachicallis americana* with yellow flowers and succulent leaves (Photo by ; (I) *Phyllomelia coronata* samara fruits (Photo by J. Salazar).

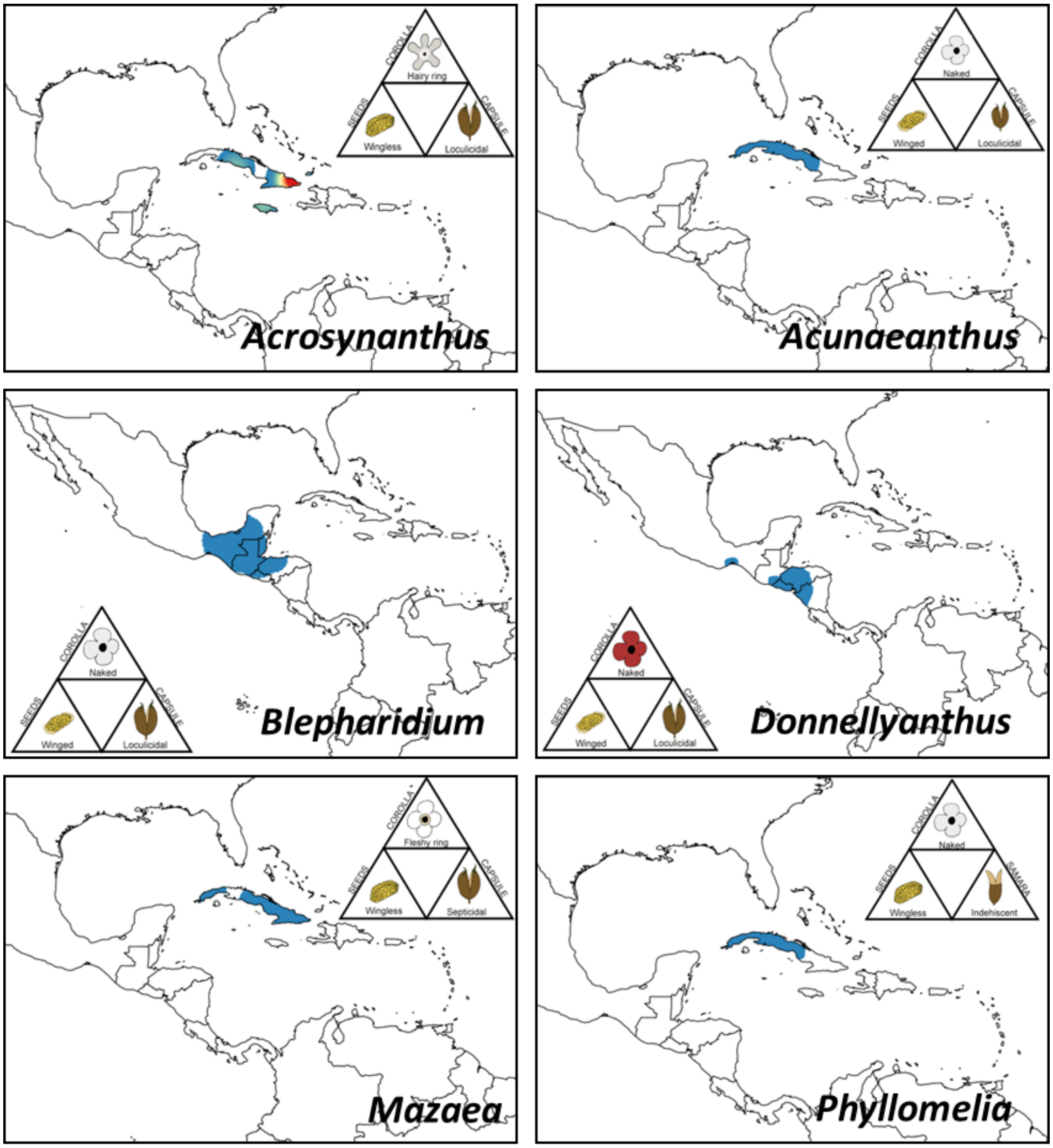


Fig. 5. Schemes summarizing the main morphological character combination to distinguish the genera within Rondeletieae and heatmaps showing their geographic distribution.

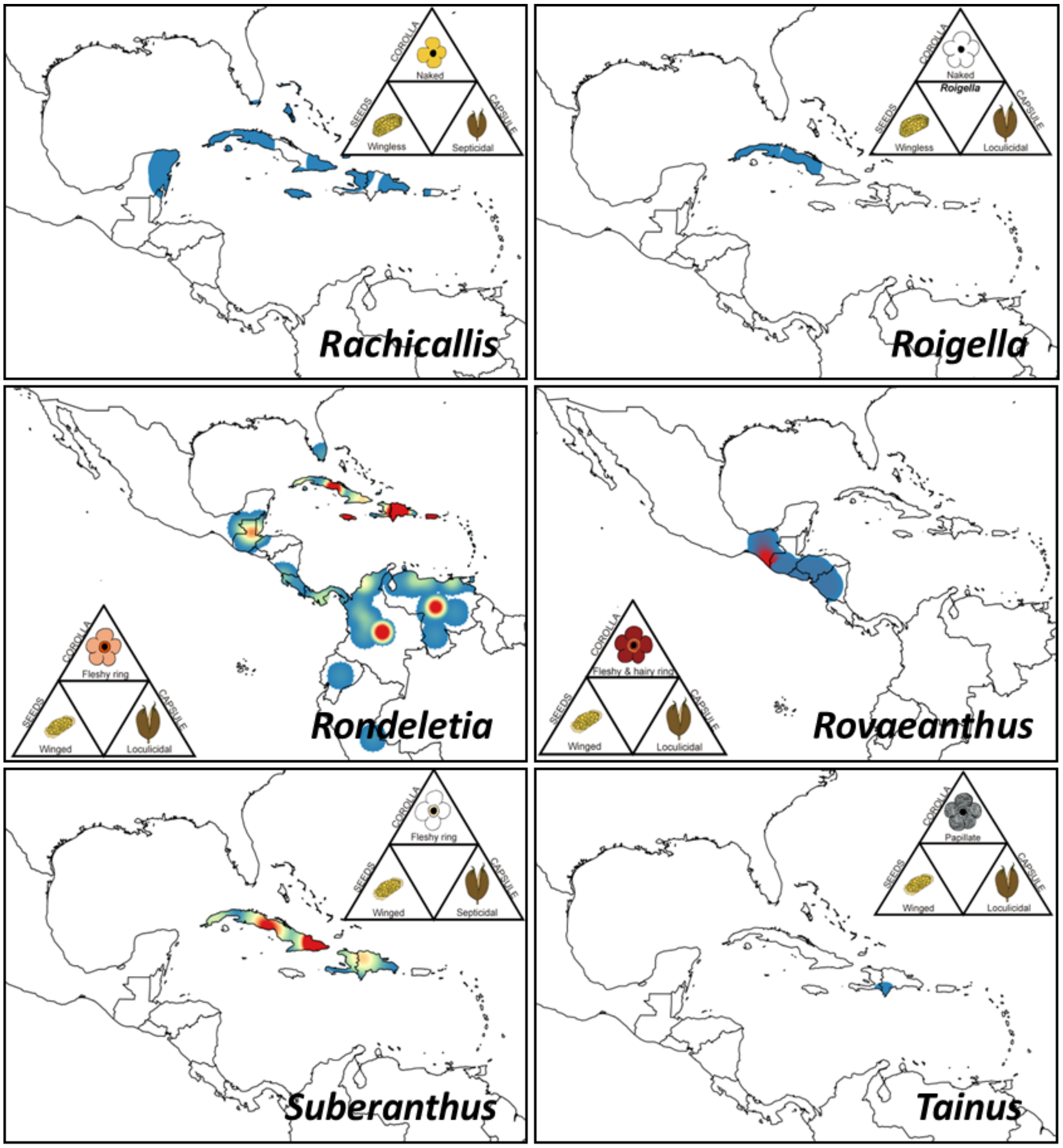


Fig. 5. Continued.

Appendix 1. Species, vouchers, geographic origin and GenBank accession numbers.

Species names of the plants included in this study, followed by the country of origin, collector(s) and collection number of the specimen (herbarium and/or silica gel dried sample), the herbarium acronym in parentheses, and the DNA project code (RUB000). GenBank accession numbers refer to sequences of genomic regions in the following order: *trn*K/*mat*K, *trn*L-F, *pet*D. For this study 204 new sequences from each of the three regions were generated, additional sequences were taken from Torres-Montúfar & al. (2017a,b) marked by an asterisk (*) and from Rova & al. (2002, 2009) marked by two asterisks (**).

Subfamily Cinchonoideae:

Tribe Chiococceae:

**Ceuthocarpus involucratus* (Wernham) Aiello, Cuba, *T. Borsch 4995* (B; HAJB; PAL), RUB233, -, KY785213, KY614097; *Chiococca alba* (L.) Hitchc., Cuba, *N. Köster 2456* (B; HAJB; PAL), RUB248, -, MF460720, MF460625; *Chiococca alba* (L.) Hitchc., Dominican Republic, *S. Fuentes 2008* (B; JBS), RUB253, -, MF460721, MF460626; *Chiococca cubensis* Urb., Cuba, *T. Borsch 4963* (B; HAJB; PAL), RUB231, MF460539, MF460722, MF460627; **Chiococca cubensis* Urb., Cuba, *S. Fuentes 535* (B; HAJB; PAL), RUB264, -, KY785214, KY614098; *Erithalis fruticosa* L., Cuba, *S. Fuentes 737* (B; HAJB; PAL), RUB209, MF460541, MF460724, MF460630; **Erithalis fruticosa* L., Dominican Republic, *S. Fuentes 221* (B; JBS), RUB183, -, KY785218, KY614101; **Erithalis vacciniifolia* (Griseb.) Wright ex Sauv., Dominican Republic, *S. Fuentes 1044* (B; JBS), RUB303, KY785272, KY785217, KY614100; *Exostema caribaeum* (Jacq.) Schult., Cuba, *T. Borsch 5295* (B; HAJB; PAL), RUB244, MF460542, MF460725, MF460631; **Exostema caribaeum* (Jacq.) Schult., Dominican Republic, *S. Fuentes 1177* (B; JBS), RUB294, -, KY785220, KY614103; **Exostema longiflorum* Roem. & Schult., Cuba, *N. Köster 2666* (B; HAJB; PAL), RUB251, -, KY785221, KY614104; **Exostema spinosum* (La Vavass) Krug & Urb., Dominican Republic, *S. Fuentes 207* (B; JBS), RUB243, KY785273, KY785219, KY614102; **Isidorea leonardii* Urb., Dominican Republic, *S. Fuentes 1210* (B; JBS), RUB302, KY785280, KY785232, KY614115; *Isidorea leptantha* Urb., Dominican Republic, *S. Fuentes 1088* (B; JBS), RUB404, -, MF460748, MF460655; **Isidorea veris* Ekman ex Aiello & Borhidi, Dominican Republic, *S. Fuentes 977* (B; JBS), RUB284, -, KY785233, KY614116; **Phialanthus resinifluus* Griseb., Cuba, *S. Fuentes 545* (B; HAJB; PAL), RUB265, -, KY785236, KY614119; **Portlandia* P. Browne, Cuba, *M. Ackerman 847* (B; HAJB; PAL), RUB226, -, KY785239, KY614122; *Schmidtottia shaferi* (Standl.) Urb., Cuba, *T. Borsch 4250* (B; HAJB; PAL), RUB225, -, -, MF460682; *Schmidtottia* Urb., Cuba, *S. Fuentes 622* (B; HAJB; PAL), RUB266, -, -, MF460681; *Scolosanthus densiflorus* Urb., Dominican Republic, *S. Fuentes 1207* (B; JBS), RUB296, -, -, MF460683; *Scolosanthus triacanthus* (Spreng.) DC., Dominican Republic, *S. Fuentes 1173* (B; JBS), RUB295, -, -, MF460684.

Tribe Guettardeae:

Antirhea abbreviata Urb., Cuba, *M. Ackerman 1011* (B; HAJB; PAL), RUB228, -, -, MF460595; **Antirhea lucida* (Sw.) Benth. & Hook. f., Cuba, *T. Borsch 5288* (B; HAJB; PAL), RUB166, KY785299, KY785196, KY614077; **Arachnothryx affinis* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 644* (MEXU), RUBmx046, KY785257, KY785197, KY614078; *Arachnothryx bourgaei* (Standl.) Borhidi, Mexico, *M. Cházaro 3636* (MEXU), RUBmx017, MF460517, MF460699, MF460602; *Arachnothryx buddleioides* (Benth.) Planch., Mexico, *A. Campos V. 1013* (MEXU, MO), RUBmx064, MF460514, MF460695, MF460597; *Arachnothryx buddleioides* (Benth.) Planch., Mexico, *H. Ochoterena B. 839* (MEXU), RUB086, MF460513, MF460694, MF460596; *Arachnothryx buddleioides* (Benth.) Planch., Mexico, *H. Ochoterena B. 875* (MEXU), RUB087, MF460519, MF460701, MF460604; **Arachnothryx buddleioides* (Benth.) Planch., Mexico, *H. Ochoterena B. 924* (MEXU), RUB130, KY785259, KY785198, KY614080; *Arachnothryx capitellata* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 817* (MEXU), RUB084, MF460523, MF460704, MF460608; *Arachnothryx* *dwyeri* (Lorence) Borhidi, Panama, *H. Herrera 1287* (MEXU), RUB139, MF460524, MF460705, MF460610; ***Arachnothryx fosbergii* Steyerm., Ecuador, *E. Rova 2082* (GB), -, AF152724, -; *Arachnothryx gracilispica* (Standl.) Borhidi, Mexico, *A. Sánchez 1897* (MO), RUBmx066, MF460525, MF460706, MF460611; **Arachnothryx heteranthera* (Brandegee) Borhidi, Mexico, *H. Ochoterena B. 823* (MEXU), RUB046, KY785261, KY785201, KY614083; *Arachnothryx heteranthera* (Brandegee) Borhidi, Mexico, *X. Munn-Estrada 1771* (MEXU), RUB059, MF460535, MF460716, MF460621; **Arachnothryx jurgensenii* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 803* (MEXU), RUB042, KY785262, -, KY614084; *Arachnothryx laniflora* (Benth.) Planch., El Salvador, *V. M. Martínez 1013* (MO), RUBmx010, MF460532, MF460713, -; **Arachnothryx leucophylla* (Kunth) Planch., Mexico, *H. Ochoterena B. 752* (MEXU), RUB043, KY785301, KY785202, KY614085; **Arachnothryx manantlanensis* (Lorence) Borhidi, Mexico, *R. Cuevas 4978* (MEXU), RUB104, KY785263, KY785203, KY614086; *Arachnothryx nebulosa* (Standl.) Borhidi, Mexico, *Linares 5936* (MEXU), RUB137, MF460571, MF460753, MF460661; *Arachnothryx nitida* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 871* (MEXU), RUB082, MF460531, MF460712, MF460617; *Arachnothryx nitida* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 872* (MEXU), RUB132, MF460521, MF460702, MF460606; *Arachnothryx pringlei* (Lorence) Borhidi, Mexico, *H. Ochoterena B. 669* (MEXU), RUB070, MF460528, MF460709, MF460614; *Arachnothryx pringlei* (Lorence) Borhidi, Mexico, *H. Ochoterena B. 854* (MEXU), RUB081, MF460529, MF460710, MF460615; **Arachnothryx pumae* J.A. Torres M. & Ochot.-Booth, Mexico, *H. Ochoterena B. 741* (MEXU), RUB069, KY785264, KY785204, KY614087; **Arachnothryx pyramidalis* (Lundell) Borhidi, Mexico, *M. Heath 414* (MEXU), RUB088, KY785302, KY785205, KY614088; *Arachnothryx rekoi* (Standl.) Borhidi, Mexico, *P. Tenorio L. 19278* (MEXU), RUB054, -, -, MF460619; *Arachnothryx secundiflora* (B.L. Rob.) Borhidi, Mexico, *H. Ochoterena B. 739* (MEXU), RUB039, MF460534, MF460715, MF460620; **Arachnothryx secundiflora* (B.L. Rob.) Borhidi, Mexico, *H. Ochoterena B. 743* (MEXU), RUB118, KY785265, KY785206, KY614089; **Arachnothryx stachyoidea* (Donn. Sm.) Borhidi, Mexico, *H. Ochoterena B. 842* (MEXU), RUB067, KY785266, KY785207, KY614090; **Arachnothryx tabascensis* Borhidi, Mexico, *H. Ochoterena B. 929* (MEXU), RUBmx069, KY785267, KY785208, KY614091; *Arachnothryx villosa* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 900* (MEXU), RUB045, MF460530, MF460711, MF460616; **Arachnothryx villosa* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 846* (MEXU), RUB124, KY785268, KY785209, KY614092; *Arachnothryx villosa* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 834* (MEXU), RUB129, MF460538, MF460718, MF460623; **Chomelia brachypoda* Donn. Sm., Mexico, *H. Ochoterena B. 746* (MEXU), RUB119, KY785270, KY785215, KY614099; *Chomelia* sp, Mexico, *H. Ochoterena B. 801* (MEXU), RUB128, MF460540, MF460723, MF460629; ***Gonzalagunia affinis* Standl. ex Steyerm., Colombia, Bremer & Thulin 1998 (GB), -, AJ847405, -; *Gonzalagunia chiapasensis* (Standl.) Standl. & Steyerm, Mexico, R. Martínez C. 885 (MO), RUBmx057, MF460543, -, MF460632; ***Gonzalagunia cornifolia* (Kunth) Standl., ND, *Stahl 1407* (GB), -, GQ852501, -; ***Gonzalagunia dependens* Ruiz & Pav., ND, *Persson et al. 462* (GB), -, GQ852502, -; ***Gonzalagunia dicocca* Cham. & Schltdl., ND, *Andersson et al. 2024* (GB), -, AF152721, -; ***Gonzalagunia kallunkiae* Dwyer, ND, *Rova & Sundbaum 2404* (GB), -, AF152723, -; **Gonzalagunia killipii* Standl., Ecuador, *M. Zak 3566* (MEXU), RUB049, KY785304, -, KY614105; *Gonzalagunia panamensis* (Cav.) K. Schum., Mexico, *H. Ochoterena B. 790* (MEXU), RUB080, MF460544, MF460726, MF460633; *Gonzalagunia panamensis* (Cav.) K. Schum., Mexico, *H. Ochoterena B. 789* (MEXU), RUB126, MF460545, MF460727, MF460634; *Gonzalagunia panamensis* (Cav.) K. Schum., Mexico, *H. Ochoterena B. 731* (MEXU), RUBmx038, MF460546, MF460728, MF460635; ***Gonzalagunia rosea* Standl., ND, *Rova 2414* (GB), -, GQ852503, -; **Gonzalagunia rudis* (Standl.) Standl., Costa Rica, *R. Forero 7419* (MEXU), RUB095, KY785305, KY785223, KY614106; **Gonzalagunia sagreana* Urb., Cuba, *N. Köster 2506* (B; HAJB; PAL), RUB418, KY785274, KY785222, -; **Gonzalagunia thyrsoidea* (Donn. Sm.) B.L. Rob., Guatemala, *M. Gonzalez 1455* (MEXU), RUB047, KY785275, KY785224, KY614107; *Guettarda clarensis* Britton, Cuba, *T.*

Borsch 4688 (B; HAJB; PAL), RUB159, MF460547, MF460729, MF460636; *Guettarda clarensis* Britton, Cuba, *T. Borsch 5098* (B; HAJB; PAL), RUB161, MF460548, MF460730, MF460637; *Guettarda echinodendron* C. Wright, Cuba, *T. Borsch 5100* (B; HAJB; PAL), RUB162, MF460550, MF460732, MF460639; *Guettarda elliptica* Sw., Mexico, *H. Ochoterena B. 794* (MEXU), RUB085, MF460551, MF460733, MF460640; **Guettarda elliptica* Sw., Mexico, *H. Ochoterena B. 894* (MEXU), RUB125, KY785306, KY785225, KY614108; *Guettarda elliptica* Sw., Dominican Republic, *S. Fuentes 216* (B; JBS), RUB180, MF460552, MF460734, MF460641; *Guettarda ferruginea* C. Wright ex Griseb., Cuba, *T. Borsch 4817* (B; HAJB; PAL), RUB148, MF460553, MF460735, MF460642; **Guettarda ferruginea* C. Wright ex Griseb., Cuba, *T. Borsch 5007* (B; HAJB; PAL), RUB152, KY785278, KY785229, KY614112; *Guettarda ferruginea* C. Wright ex Griseb., Cuba, *T. Borsch 4453* (B; HAJB; PAL), RUB155, MF460554, MF460736, MF460643; *Guettarda ferruginea* C. Wright ex Griseb., Cuba, *T. Borsch 4596* (B; HAJB; PAL), RUB157, MF460555, MF460737, MF460644; **Guettarda monocarpa* Urb., Cuba, *T. Borsch 4429* (B; HAJB; PAL), RUB153, KY785307, KY785227, KY614110; *Guettarda monocarpa* Urb., Cuba, *S. Fuentes 544* (B; HAJB; PAL), RUB201, MF460556, MF460738, MF460645; **Guettarda prenleloupii* Urb., Dominican Republic, *S. Fuentes 1205* (B; JBS), RUB292, KY785279, KY785230, KY614113; *Guettarda prenleloupii* Urb., Dominican Republic, *S. Fuentes 1186* (B; JBS), RUB299, MF460557, MF460739, MF460646; **Guettarda pungens* Urb., Dominican Republic, *S. Fuentes 238* (B; JBS), RUB184, KY785277, KY785228, KY614111; *Guettarda pungens* Urb., Dominican Republic, *S. Fuentes 908* (B; JBS), RUB291, MF460558, MF460740, MF460647; *Guettarda pungens* Urb., Dominican Republic, *S. Fuentes 1154* (B; JBS), RUB383, MF460560, MF460742, MF460649; *Guettarda scabra* (L.) Vent., Dominican Republic, *S. Fuentes 256* (B; JBS), RUB186, MF460561, MF460743, MF460650; *Guettarda scabra* (L.) Vent., Cuba, *S. Fuentes 850* (B; HAJB; PAL), RUB212, MF460562, MF460744, MF460651; *Guettarda shaferi* Standl., Cuba, *N. Köster 2852* (B; HAJB; PAL), RUB179, MF460563, MF460745, MF460652; *Guettarda shaferi* Standl., Cuba, *T. Borsch 4448* (B; HAJB; PAL), RUB238, MF460564, MF460746, MF460653; *Guettarda tortuensis* Urb. & Ekman, Dominican Republic, *S. Fuentes 218* (B; HAJB; PAL), RUB181, MF460565, MF460747, MF460654; *Javorkaea scabra* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 880* (MEXU), RUB037, MF460566, -, MF460656; **Javorkaea hondurensis* (Donn. Sm.) Borhidi & Járai-Koml., Honduras, *J. Linares 6241* (MEXU), RUBmx055, KY785281, KY785234, KY614117; **Machaonia pauciflora* Urb., Cuba, *T. Borsch 5218* (B; HAJB; PAL), RUB164, KY785282, KY785235, KY614118; *Renistipula galeotii* (Standl.) Borhidi, Mexico, A. Torres 653 (MEXU), RUBmx099, GBXX, GBXX, GBXX; **Rogiera amoena* Planch., Mexico, *H. Ochoterena B. 805* (MEXU), RUB131, KY785284, KY785240, KY614123; *Rogiera cordata* (Benth.) Planch., Mexico, *H. Ochoterena B. 777* (MEXU), RUB134, MF460573, MF460755, MF460663; *Rogiera langlassei* (Standl.) Borhidi, Mexico, *K. Velasco 431* (MEXU, SERO), RUB097, MF460574, MF460756, MF460664; *Rogiera langlassei* (Standl.) Borhidi, Mexico, *K. Velasco 2467* (MEXU; SERBO), RUBmx025, MF460572, MF460754, MF460662; **Rogiera ligustroides* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 781* (MEXU), RUB068, KY785286, KY785242, KY614125; **Rogiera ligustroides* (Hemsl.) Borhidi, Mexico, *L. Castillo H. 256* (MEXU, MO), RUB121, -, MF460757, MF460665; **Rogiera macdougalli* Lorence, Mexico, *H. Ochoterena B. 841* (MEXU), RUB073, KY785288, KY785244, KY614127; **Rogiera nicaraguensis* (Oerst.) Borhidi, Honduras, *J. Linares 3520* (MEXU), RUB064, KY785287, KY785243, KY614126; **Rogiera stenosiphon* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 749* (MEXU), RUB075, KY785289, KY785245, KY614128; **Rogiera stenosiphon* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 732* (MEXU), RUB072, KY785285, KY785241, KY614124; **Stenostomum montecristinum* (Urb. & Ekman) Borhidi, Dominican Republic, *S. Fuentes 219* (B; JBS), RUB182, -, -, MF460685.

Tribe Rondeletieae:

Acrosynanthus lucidus Britton., Cuba, *T. Borsch 5003* (B; HAJB; PAL), RUB235, -, MF460691, MF460592; *Acrosynanthus lucidus* Britton., Cuba, *T. Borsch 4447* (B; HAJB; PAL), RUB237, -, MF460692, MF460593; *Acrosynanthus minor* Urb., Cuba, *S. Fuentes 637* (B; HAJB; PAL), RUB267, -, MF460688, MF460589; **Acrosynanthus revolutus* Urb., Cuba, *T. Borsch 4156* (B; HAJB; PAL), RUB224, MF460511, MF460689, MF460590; *Acrosynanthus revolutus* Urb., Cuba, *T. Borsch 4625* (B; HAJB; PAL), RUB239, -, MF460693, MF460594; **Acrosynanthus trachyphyllus* Standl., Cuba, *T. Borsch 4444* (B; HAJB; PAL), RUB154, KY785256, KY785195, KY614076; **Acrosynanthus trachyphyllus* Standl., Cuba, *S. Fuentes 602* (B; HAJB; PAL), RUB203, MF460512, MF460690, MF460591; *Acrosynanthus* sp., RUB234 , -, -, GBXX; *Acrosynanthus* sp., RUB268 , -, -, GBXX; ***Acunaeanthus tinifolius* (Griseb.) Borhidi, Cuba, *Stahl et al. s/n* (S), -, GQ852451; ***Blepharidium guatemalense* Standl., Guatemala, *Gustafsson et al. 211* (GB), -, AF152735, -; **Donnellyanthus deamii* (Donn. Sm.) Borhidi, Honduras, *S. Duery 172* (MEXU), RUB056, KY785271, KY785216, -; ***Donnellyanthus deamii* (Donn. Sm.) Borhidi, Honduras, *Castillo 1560* (NY), -, GQ852545, -; **Mazaea shaferi* (Standl.) Delprete, Cuba, *T. Borsch 4075* (B; HAJB; PAL), RUB144, MF460567, MF460749, MF460657; **Phyllomelia coronata* Griseb., Cuba, *T. Borsch 4620* (B; HAJB; PAL), RUB158, KY785303, KY785210, KY614093; **Rachicallis americana* (Jacq.) Hitchc., Cuba, *N. Köster 2465* (B; HAJB; PAL), RUB170, KY785283, KY785238, KY614121; **Rachicallis americana* (Jacq.) Hitchc., Cuba, *T. Borsch 5625* (B; HAJB; PAL), RUB217, MF460568, MF460750, MF460658; **Rachicallis americana* (Jacq.) Hitchc., Cuba, *T. Borsch 5641* (B; HAJB; PAL), RUB218, MF460569, MF460751, MF460659; ***Roigella correifolia* (Griseb.) Borhidi & M. Fernández, Cuba, *Rova et al. 2262* (GB), -, AF152746, -; *Rondeletia acunae* Borhidi & M. Fernández, RUB195, GBXX, -, GBXX; ***Rondeletia alaternoides* A. Rich, Cuba, *Rova et al. 2228* (GB), -, AF152740, -; **Rondeletia barahonensis* Urb., Dominican Republic, *S. Fuentes 315* (B; JBS), RUB187, KY785290, KY785246, KY614129; **Rondeletia berteroana* DC., Dominican Republic, *S. Fuentes 239* (B; HAJB; PAL), RUB185, MF460575, MF460758, MF460666; ***Rondeletia buxifolia* Vahl, Montserrat islands, *Veloz et al. 1868* (MO), -, GQ852555, -; *Rondeletia camarioca* C. Wright, Cuba, *T. Borsch 5096* (B; HAJB; PAL), RUB160, MF460576, MF460759, MF460667; *Rondeletia camarioca* C. Wright, Cuba, *S. Fuentes 845* (B; HAJB; PAL), RUB211, MF460577, MF460760, MF460668; **Rondeletia conferta* Urb., Dominican Republic, *S. Fuentes 1170* (B; JBS), RUB298, KY785291, KY785247, KY614130; **Rondeletia cristalensis* Urb., Cuba, *N. Köster 2828* (B; HAJB; PAL), RUB178, MF460578, MF460761, MF460669; **Rondeletia filisepala* Borhidi, Dominican Republic, *S. Fuentes 1084* (B; JBS), RUB384, -, MF460770, MF460678; **Rondeletia fuertesii* Urb., Dominican Republic, *S. Fuentes 1184* (B; JBS), RUB293, -, MF460762, MF460670; *Rondeletia fuertesii* Urb., RUB355, GBXX, GBXX, GBXX; **Rondeletia hypoleuca* Griseb., Cuba, *T. Borsch 4204* (B; HAJB; PAL), RUB020, KY785292, KY785248, KY614131; ***Rondeletia inermis* (Spreng.) Krug & Urb., Puerto Rico, *Acevedo-Rodriguez et al. 7691* (NY), -, AF152745, -; ***Rondeletia intermixta* Britton, Cuba, *Rova et al. 2245* (GB), -, AF152742, -; **Rondeletia merilloana* Urb., Dominican Republic, *S. Fuentes 1136* (B; JBS), RUB353, KY785293, KY785249, KY614132; *Rondeletia merilloana* Urb. RUB309, GBXX, GBXX, GBXX; **Rondeletia microphylla* Griseb., Cuba, *T. Borsch 4169* (B; HAJB; PAL), RUB018, KY785308, KY785250, KY614133; ***Rondeletia nipensis* Urb., Dominican Republic, *Delprete et al. 8651* (UPS), -, GQ852547, -; *Rondeletia odorata* Jacq., Cuba, *N. Köster 2526* (B; HAJB; PAL), RUB171, MF460582, MF460766, MF460673; *Rondeletia odorata* Jacq., Cuba, *N. Köster 2546* (B; HAJB; PAL), RUB172, MF460583, MF460767, MF460674; ***Rondeletia odorata* Jacq., Cuba, *P. de Block 1407* (GB), -, -, KT218941, -; *Rondeletia pachyphylla* Krug & Urb., Cuba, *S. Fuentes 438* (B; HAJB; PAL), RUB191, MF460584, -, MF460675; *Rondeletia parviflora* Poir., RUB460, GBXX, GBXX, GBXX; ***Rondeletia pilosa* Sw., Jamaica, *P. Acevedo-Rodriguez 2836* (NY), -, AF152744, -; *Rondeletia polita* Griseb., RUB461, GBXX, GBXX, GBXX; ***Rondeletia portoricensis* Krug & Urb., Puerto Rico, *C. Taylor 11687* (MO), -, AF152743, -; **Rondeletia rugelii* C. Wright, Cuba, *T. Borsch 5601* (B; JBN; PAL), RUB215; KY785294, KY785251, KY614134; **Rondeletia savannarum* Britton, Cuba, *S. Fuentes 513* (B; HAJB; PAL), RUB198, -, MF460768, MF460676; **Rondeletia thiemei* Donn. Sm., El Salvador, *D. Rodriguez 2463* (B; LAGU), RUB308, MF460536, MF460717, -;

**Rovaeanthus strigosus* (Benth.) Borhidi, Guatemala, *M. Veliz 6539* (MEXU), RUB063, KY785295, KY785252, KY614135; ***Rovaeanthus suffrutescens* (Brandegee) Borhidi, Mexico, *B. Bremer 2712* (S), -, AF152738, -; *Stevensia minutifolia* Alain, Dominican Republic, *S. Fuentes 1193* (B; JBS), RUB300, -, MF460769, MF460677; ***Suberanthus brachycarpus* (Griseb.) Borhidi & M. Fernández, Cuba, *McDowell 4824* (DUKE), -, HM045004, -; *Suberanthus canellifolius* (Britton) Borhidi & M. Fernández, RUB146, -, -, GBXX; *Suberanthus nipensis* Borhidi & M. Fernández, RUB 193, -, -, GBXX; *Suberanthus nipensis* Borhidi & M. Fernández, RUB200, -, -, GBXX; *Suberanthus nipensis* Borhidi & M. Fernández, RUB206, -, -, GBXX; **Tainus pitreanus* (Urb. & Ekman) J. A. Torres-Montúfar, H. Ochoterena & T. Borsch, Dominican Republic, *S. Fuentes 1110* (B; JBS), RUB311, MF460587, MF460773, MF460686; **Tainus pitreanus* (Urb. & Ekman) J. A. Torres-Montúfar, H. Ochoterena & T. Borsch, Dominican Republic, *T. Clase 4228* (JBSD, MO), RUB354, MF460588, MF460774, MF460687; ***Tainus pitreanus* (Urb. & Ekman) J. A. Torres-Montúfar, H. Ochoterena & T. Borsch, Dominican Republic, *Liogier 13966* (NY), -, GQ852548, -.

Incertae sedis

Chione sp, Dominican Republic, *S. Fuentes 1135* (B), RUB310, -, -, MF460628;

Subfamily Ixoroideae:

Tribe Condamineae:

**Calycophyllum candidissimum* (Vahl) DC., Cuba, *T. Borsch 5125* (B; HAJB; PAL), RUB336, KY785298, KY614094, -; **Picardaea haitiensis* Urb., Dominican Republic, *S. Fuentes 1017* (B; JBS), RUB409, KY785297, KY785237, KY614120.

Tribe Gardenieae:

**Casasia calophylla* A. Rich., Cuba, *N. Köster 2452* (B; HAJB; PAL), RUB247, -, MF460719, MF460624; **Casasia clusiifolia* (Jacq.) Urb., Cuba, *S. Fuentes 761* (B; HAJB; PAL), RUB271, KY785269, KY785211, KY614095; **Casasia jacquinioides* (Griseb.) Standl., Cuba, *T. Borsch 4990* (B; HAJB; PAL), RUB232, -, KY785212, KY614096; **Randia aculeata* L., Cuba, *T. Borsch 5316* (B; HAJB; PAL), RUB245, KY785255, KY785194, KY614075; *Randia mitis* L. Cuba, N. Köster 2588 (B; HAJB; PAL), RUB249, MF460570, MF460752, MF460660.

Tribe Sabiceeae:

**Sabicea mexicana* Wernham, Mexico, *H. Ochoterena B. 876* (MEXU), RUB111, KY785309, KY785253, KY614136; **Sabicea villosa* Schult., Mexico, *H. Ochoterena B. 844* (MEXU), RUB078, MF460585, MF460771, MF460679; **Sabicea villosa* Schult., Mexico, *H. Ochoterena B. 858* (MEXU), RUB122, KY785296, KY785254, KY614137.

Appendix 2. Lists of microstructural characters

A. List of microstructural characters and their aligned positions found in the *pet*D region coded as absent/present.

Gaps

0. 31
1. 33-35
2. 51
3. 53-54
4. 91
5. 149
6. 366-379
7. 369-387
8. 433
9. 504-525
10. 516-547
11. 535-542
12. 655
13. 734-735
14. 742
15. 746
16. 778
17. 823
18. 839
19. 875
20. 894
21. 911
22. 917-925
23. 952-967
24. 953-963
25. 980-992
26. 1005-1009
27. 1062

Inversions

28. 122-153: CTATTCCTGTCAAATAAATAATATTGGAGAG
29. 185-210: CTATTCCTGTCAAATAAATAATATT
30. 528-534: AATAGAG

SSRs

31. 10-13: TAAAA
32. 37-44: TTGGAGAA
33. 216-221: GTTGAA
34. 317-318: AA
35. 358-362: CGTAA
36. 372-376: TATAC
37. 383-387: GAGGA
38. 476-480: TATAA
39. 481-487: AGTATAA
40. 488-496: CCAGTATAA
41. CAAAAATAGAGTTTATCTATTT 555-575

42. CTTAA 587-591
43. CAAAAATAGAGTTTATCTATTT 597-612
44. GTAAG 832-836
45. TTCTTTGGAA 876-885
46. TTAC 934-937
47. CTTAC 938-942
48. TTTATA 958-963
49. AA 974-975
50. AA 985-986

B. List of microstructural characters and their aligned positions found in the *trn*K-*mat*K region coded as absent/present unless otherwise stated.

Gaps

0. 18
1. 8
2. 41
3. 54-55
4. 55
5. 60
6. 66
7. 90
8. 94
9. 167
10. 177-178
11. 189
12. 258-259
13. 259
14. 278-286
15. 282
16. 294
17. 301
18. 317
19. 522-533
20. 538-539
21. 658
22. 919
23. 963
24. 966
25. 981
26. 985
27. 988
28. 999
29. 1009
30. 1012
31. 1015-1026
32. 1016
33. 1023
34. 1132
35. 1138-1139

36. 1267-1275
37. 1270-1275
38. 1300-1301
39. 1747
40. 1818
41. 1972
42. 2049
43. 2063
44. 2230
45. 2250
46. 2266-2267
47. 2347
48. 2359
49. 2367-2368
50. 2420-2434
51. 2500
52. 2532-2540
53. 2559
54. 2779
55. 2785-2803

Inversions

56. 331-338: TTATGAAA to TTATGAAA

SSRs

57. 80-81: GG
58. 322-328: ATTATGA
59. 352-353: GT
60. 476-485: ACTAAAAATG
61. 522-527: GTTTAT
62. 575-586: CTAGAATACTTT
63. 709-714: CAACAA
64. 1068-1073: AATTTA
65. 1258-1263: TGGAAT
66. 1336-1430: TTTTTTTCCACGAGTATTGGAATTGGAATACTCTTATTGCTACAAATAAACCCAGTTTTGATTTTTCACCAAAAAGAAGTCAAAGATTATTATTC
67. 1769-1774: ATAAAA
68. 2182-2187: TTGAAA
69. 2286-2305: AAGAACTTCTTCTACTTTTC
70. 2447-2452: GACAAA
71. 2459-2460: TT
72. 2465-2466: TT
73. 2501-2505: GGAAT
74. 2506-2513: GTGTAATT
75. 2514-2524: GTAAATGGAAT
76. 2899-2904: TTTCTA
77. 2910-2914: TTTAT

C. List of microstructural characters and their aligned positions found in the *trn*L-F region coded as absent/present.

Gaps

0. 28
1. 84-87
2. 165-173
3. 190
4. 226-229
5. 230-231
6. 310
7. 454
8. 592
9. 624-627
10. 627
11. 632-970
12. 632-980
13. 637
14. 657-664
15. 740
16. 829-838
17. 875-880
18. 903
19. 910
20. 965
21. 970

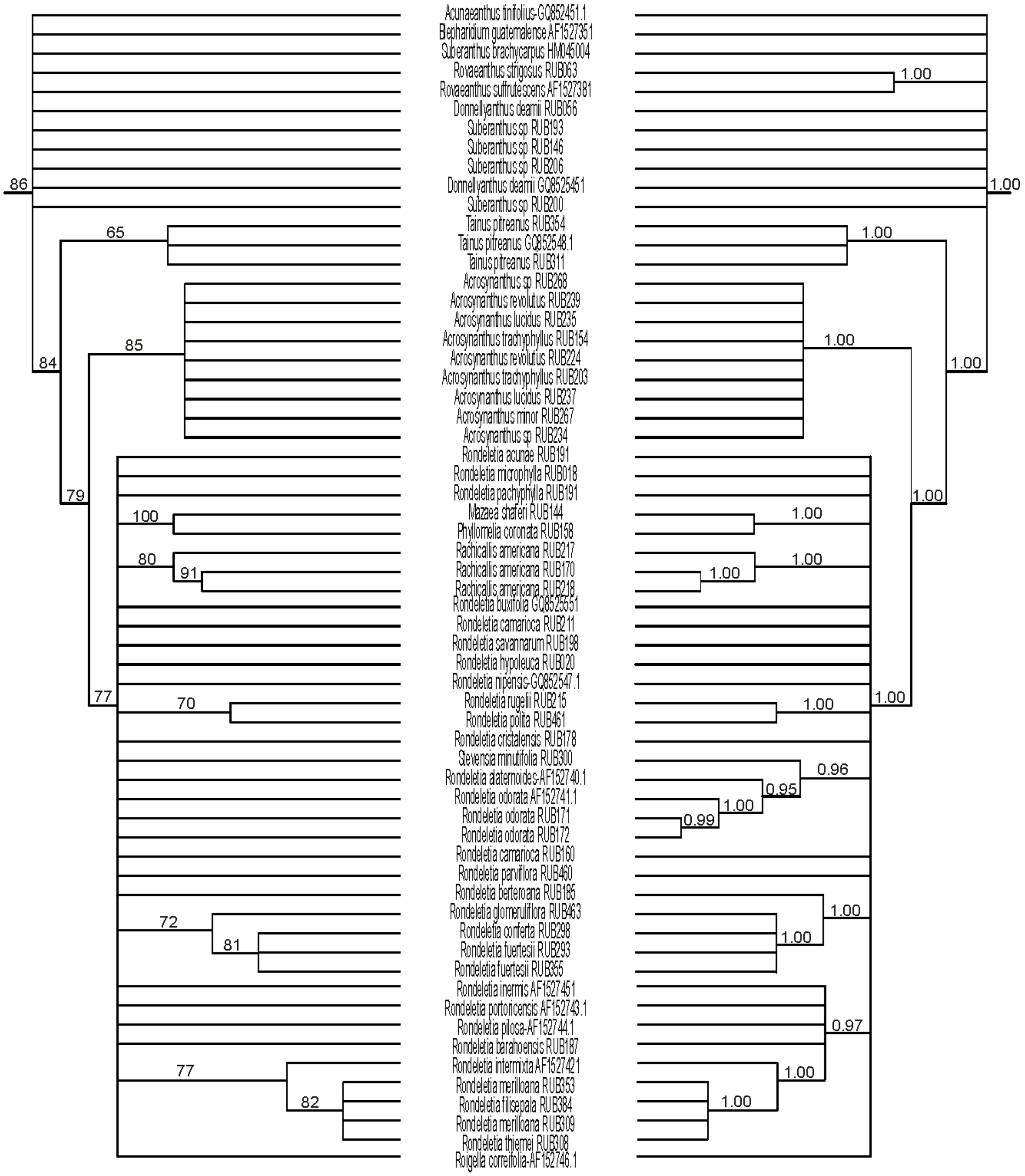
Inversions

22. 440-442: TTC to GAA

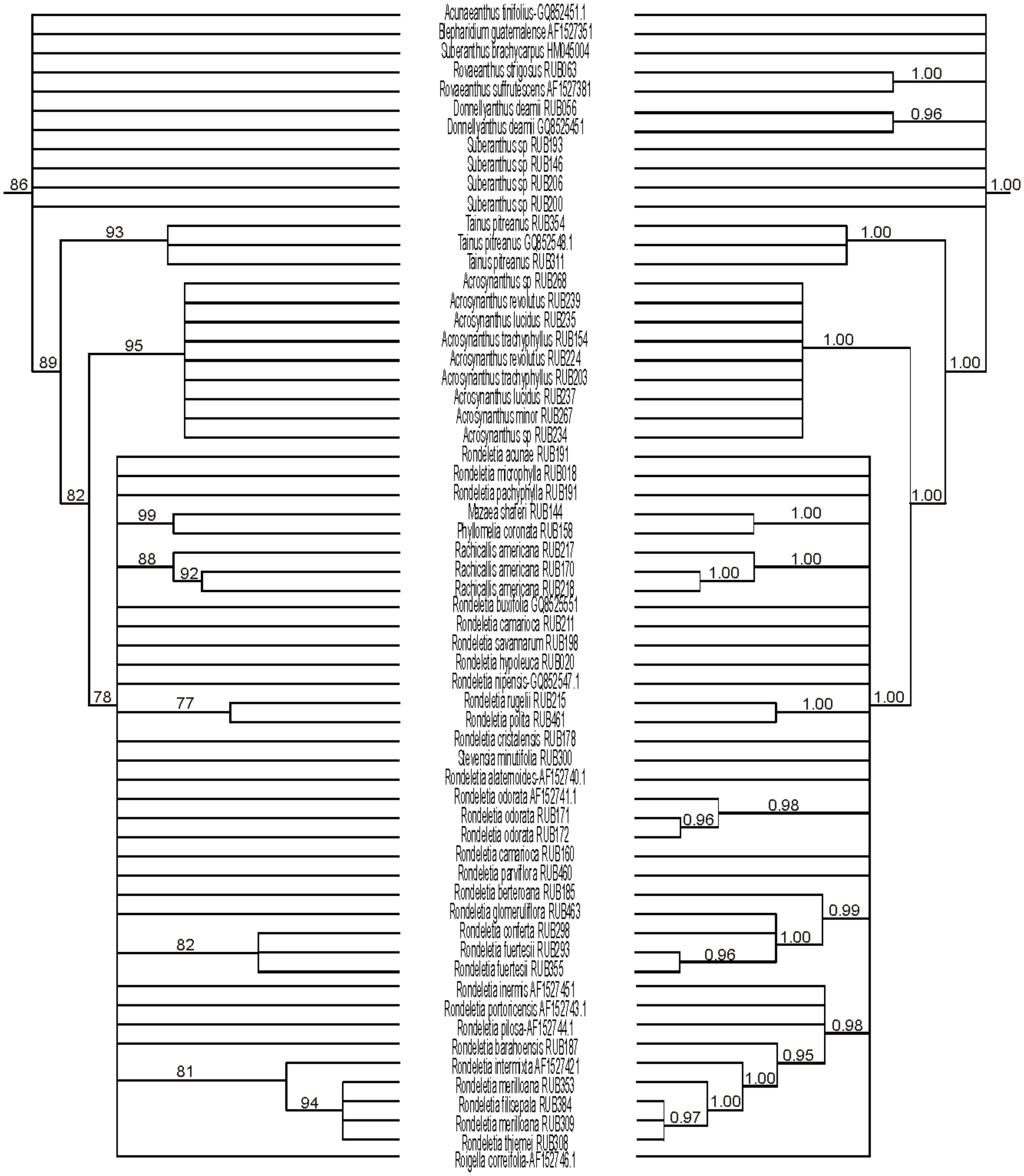
SSRs

23. 255-260: ATCAAA
24. 261-271: ACTATATCAAA
25. 272-277: ATCAAA
26. 317-322: ATTTTT
27. 396-399: TGAT
28. 435-439: TTTTC
29. 495-505: TTCTACATGTC
30. 678-682: CTCTT
31. 694-703: GAAATAGATC
32. 707-726: TCTCTTAGAAATAGATCTGG
33. 746-750: TTCTT
34. 765-766: GT
35. 780-786: TGATATA
36. 794-798: TACAA
37. 799-805: AATACAA
38. 806-826: TTATATATGATATACATACAA
39. 921-925: AAGAT
40. 987-992: TAATTG

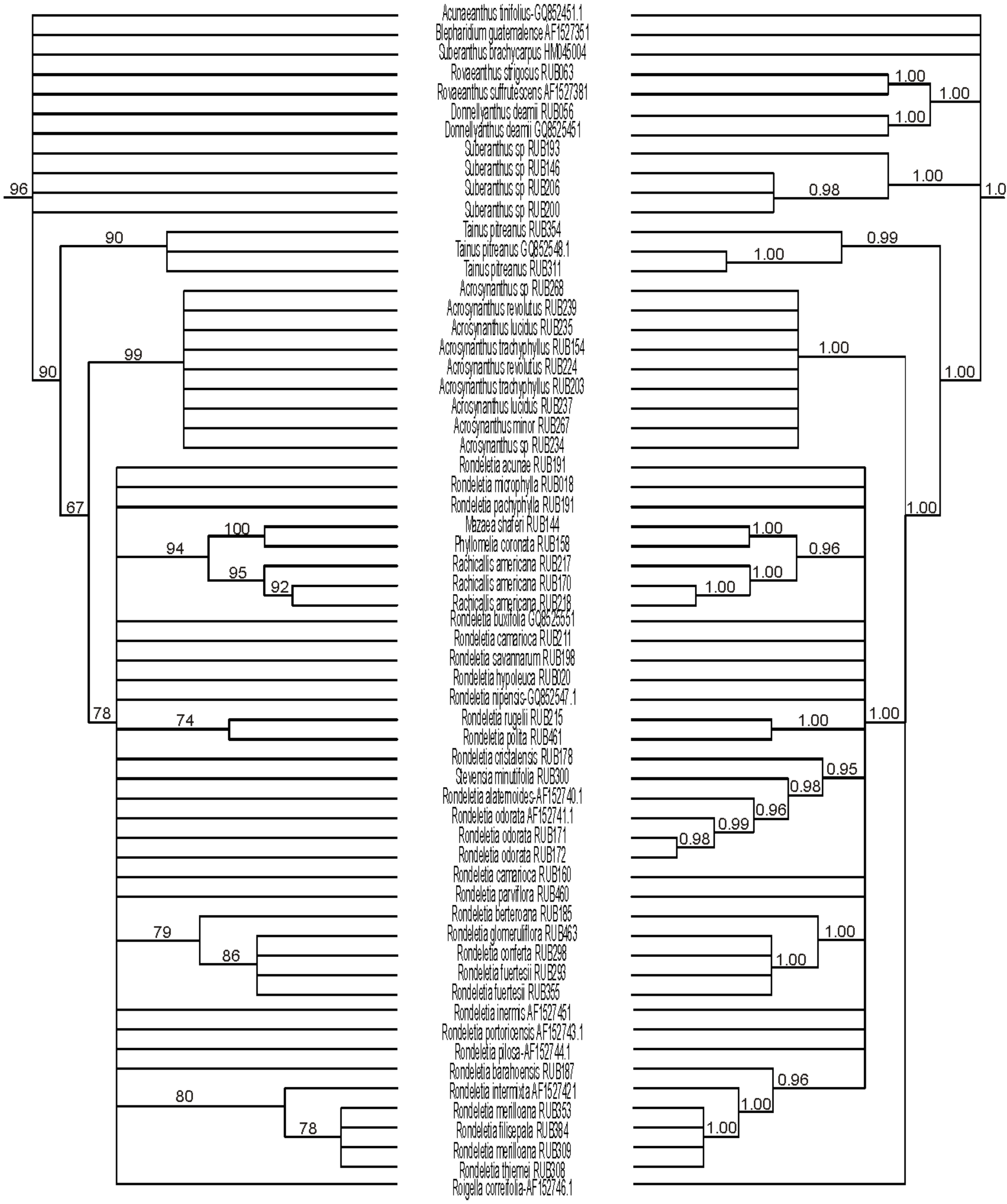
Appendix 3. Phylogenetic analyses per evidence source and inference method.



A. Comparison of the topologies obtained using nucleotidic matrix. To the left is showed the consensus tree (L= 2175, Ci= 0.52, Ri= 0.86) of the most parsimonious trees (L= 2007, Ci= 0.57, Ri= 0.88) obtained by Parsimony, to the right the Bayesian tree. Numbers above branches correspond to Jackknife values (JK) or to posterior probability (PP) from Bayesian analysis.



B. Comparison of the topologies obtained using nucleotidic matrix plus microstructural matrix. To the left is showed the consensus tree (L= 2528, Ci= 0.50, Ri= 0.85) of the most parsimonious trees (L= 2348, Ci= 0.54, Ri= 0.87) obtained by Parsimony, to the right the Bayesian tree. Numbers above branches correspond to Jackknife values (JK) or to posterior probability (PP) from Bayesian analysis.



B. Comparison of the topologies obtained using nucleotidic matrix plus morphological matrix. To the left is showed the consensus tree (L= 2341, Ci= 0.50, Ri= 0.85) of the most parsimonious trees (L= 2098, Ci= 0.55, Ri= 0.88) obtained by Parsimony, to the right the Bayesian tree. Numbers above branches correspond to Jackknife values (JK) or to posterior probability (PP) from Bayesian analysis.

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PARTE I: LA TRIBU RONDELETIEAE

CAPÍTULO III: UN NUEVO GÉNERO DE LAS ANTILLAS

The new Hispaniolan genus Tainus (Rubiaceae) constitutes an isolated lineage in the Caribbean biodiversity hotspot

Alejandro Torres-Montúfar, Thomas Borsch, Susy Fuentes, Teodoro Clase, Brigido Peguero & Helga Ochoterena

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The new Hispaniolan genus *Tainus* (*Rubiaceae*) constitutes an isolated lineage in the Caribbean biodiversity hotspot

Abstract: The Caribbean islands are a well-known biodiversity hotspot of global importance. Hispaniola (Dominican Republic and Haiti) is a highly diverse island with 42% of its species endemic. Here we describe the new monotypic genus *Tainus* (*Rubiaceae*, *Rondeletieae*), which is endemic to the Sierra de Bahoruco-La Selle. This taxon was originally published as *Rondeletia pitreana*, but its taxonomic status has been doubtful. We performed phylogenetic analyses with three chloroplast regions (*petD*, *trnK-matK* and *trnL-F*) in order to test the relationships of *R. pitreana* to other species of *Rondeletia* and allied genera. Our molecular phylogeny underscores that *R. pitreana* does not belong to *Rondeletia*, but has an isolated position within *Rondeletieae*, whereas *Acrosynanthus* is sister to an assemblage of *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella* and *Rondeletia*. The recognition of the genus *Tainus* is supported by molecular (simple sequence repeats) and morphological characters, among which the most conspicuous is the densely papillate ornamentation of the corolla mouth and lobes. Our findings reveal another case of endemism at a deeper phylogenetic level in flowering plants on Hispaniola. Furthermore, they emphasize the importance of exploring, collecting and performing phylogenetic analyses integrating samples from larger geographical areas across countries as a basis to support nature conservation.

Resumen: Las islas del Caribe son un conocido hotspot de biodiversidad mundial. Entre ellas, La Española (República Dominicana y Haití) tiene una diversidad relevante y alrededor de 42% de sus especies son endémicas. En este trabajo describimos el nuevo género *Tainus* (*Rubiaceae*, *Rondeletieae*), monotípico y endémico de la Sierra de Bahoruco-La Selle en La Española. Anteriormente, la especie que sirve para reconocer el nuevo género fue clasificada como *Rondeletia pitreana*. El estatus taxonómico de esta especie había sido puesto en duda en filogenias moleculares en las cuales se recuperaba fuera del clado de *Rondeletia*. Nuestros análisis incluyen tres marcadores de cloroplasto (*petD*, *trnK-matK* y *trnL-F*) para poner a prueba la posición filogenética de *R. pitreana* con respecto a *Rondeletia*. Nuestra filogenia molecular corrobora que *R. pitreana* no pertenece a *Rondeletia* y más bien tiene una posición aislada, en tanto que *Acrosynanthus* es hermano de un clado que incluye a *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella* y *Rondeletia*. Para ser congruentes con la filogenia, describimos el género *Tainus*, apoyado por varias sinapomorfias, incluyendo caracteres microestructurales de ADN (repeticiones simples de secuencia) y caracteres morfológicos, entre los que destaca la superficie adaxial de los lobos de la corola y la garganta densamente papilosa. La descripción de este nuevo género cambia nuestra percepción del endemismo en La Española revelando otro caso de endemismo a un nivel filogenético profundo en las plantas con flor de La Española. Esto resalta la importancia de la exploración, colecta y la realización de trabajos filogenéticos que integren muestreos de regiones geográficas más amplias para generar bases sólidas para la conservación.

Key words: Caribbean, Greater Antilles, Hispaniola, Dominican Republic, Haiti, Sierra de Bahoruco-La Selle, *Rubiaceae*, *Rondeletieae*, *Rondeletia*, *Tainus*, molecular phylogeny, taxonomy, endemism, nature conservation

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Introduction

The Caribbean islands constitute one of the global biodiversity hotspots (Myers & al. 2000) with approximately 12 300 species of vascular plants (Acevedo-Rodríguez & Strong 2012). The affinities of the Caribbean island floras are complex, as shown by the spectrum of hypotheses to explain their biogeographic origin (Santiago-Valentín & Olmstead 2004; Cano & al. 2009). Recently, Cervantes & al. (2016) provided evidence that Mexico and Mesoamerica could have played a more important role than previously thought as a source for ancestors of plants that later diversified on the Caribbean islands from the Miocene onwards.

Within the Antilles, the islands of Cuba and Hispaniola stand out by the number of species and infraspecific taxa that are endemic (51% of 5778 and 42% of 4433, respectively). From the 1210 genera reported from Cuba, 65 are considered as Caribbean endemics, whereas from the 1102 genera listed for Hispaniola, 34 are Caribbean endemics. Therefore, Cuba and Hispaniola house nearly 24% and 15%, respectively, of the endemism in the Antilles (Acevedo-Rodríguez & Strong 2012). Five of the endemic genera are restricted to Hispaniola: *Garciadelia* Jestrow & Jiménez (*Euphorbiaceae*), *Hispaniolanthus* Cornejo & Iltis (*Capparaceae*), *Hottea* Urb. (*Myrtaceae*), *Ignurbia* B. Nord. (*Asteraceae*) and *Tortuella* Urb. (*Rubiaceae*) (Nordenstam 2006; Cornejo & Iltis 2009; Borhidi 2010; Jestrow & al. 2010; Acevedo-Rodríguez & Strong 2012). However, only *Garciadelia* has so far been evaluated with phylogenetic methods.

According to Cano-Ortiz & al. (2016), Hispaniola has 19 areas of particular high diversity, which are explained by altitudinal gradients and specific soil types. Hispaniola has the highest mountains in all the Antilles (c. 2400 m) and the greatest richness in endemism is said to occur at medium altitudes (May 2001; Cano & al. 2010). The Sierra de Bahoruco-La Selle stands out by being the most diverse mountain system within Hispaniola with several different ecosystem types and c. 700 species of vascular plants, of which about two thirds are endemic (Cano-Ortiz & al. 2016).

Based on the checklist of Acevedo-Rodríguez & Strong (2012), the *Rubiaceae* are by far the most speciose family of angiosperms in the Antilles in terms of native species (c. 820) and also have the highest number of endemic species (c. 696). On the other hand, the *Asteraceae* are considered to have more native and endemic genera (145 native and 41 endemic) than *Rubiaceae* (89 and 27, respectively), whereas the total number of species in *Asteraceae* (c. 660) is considerably lower than in *Rubiaceae*. Among the Antillean islands, Cuba and Hispaniola are the most diverse for *Rubiaceae*, together housing almost 90% of the species in the Caribbean islands. With 177 species, almost all of them endemic, the tribe *Rondeletieae* is the most diverse within *Rubiaceae* (data from Acevedo-Rodríguez & Strong 2012). Nevertheless, this tribe with its nine genera (seven endemic) is not the most diverse in the Caribbean islands with respect to genera. It rather occupies the third position, after *Spermacoceae* (18 genera, four endemic) and *Chiococceae* (17, 12).

The circumscription of genera within *Rondeletieae* has varied among different authors from nine to 15 genera, whereas a diversity of c. 200 species is more commonly accepted (Fernández-Zequeira 1994; Rova & al. 2002; Borhidi & al. 2004; Robbrecht & Manen 2006; Rova & al. 2009; Manns & Bremer 2010; Borhidi & al. 2011; Tange 2013; Delprete & Jardim 2012; Razafimandimbison & al. 2011), mainly restricted to the Caribbean islands. The tribe consists of small trees or shrubs with entire stipules, imbricate corolla lobes, heterostylous flowers, tricolporate pollen and dry fruits (Robbrecht 1988). The tribe *Rondeletieae* belongs in *Cinchonoideae* according to the subfamily circumscription sensu Robbrecht & Manen (2006) and also sensu Bremer & al. (1995). Whereas molecular phylogenetic studies agree on the composition of *Rondeletieae* as a clade (Manns & Bremer 2010; Torres-Montúfar & al. 2017) and its position as sister to *Guettardeae*, a detailed understanding of phylogenetic relationships within *Rondeletieae* is still lacking.

The characters commonly used to differentiate genera within *Rondeletieae* (Robbrecht 1988; Delprete 1999a, 1999b; Rova & al. 2002, 2009) are: inflorescence position (axillary vs terminal), flower merosity (four to six), corolla mouth ornamentation (naked or with a fleshy/hairy ring), position of the insertion of the stamens on the corolla (at the base, at the middle or near the throat), and capsule dehiscence (loculicidal vs septicidal). This morphological heterogeneity has resulted in a controversial circumscription of the tribe *Rondeletieae* and particularly of the genus *Rondeletia* L. (Robbrecht 1988; Delprete 1999a, 1999b).

Rova & al. (2009), using ITS, *rps16* and *trnL-F* sequences, first noted a position of *Rondeletia pitreana* Urb. & Ekman, which was described from Haiti (Urban & Ekman 1929), outside a well-supported *Rondeletia* clade. Furthermore, they were not decisive in the inclusion of this species within *Rondeletieae*. The authors nevertheless decided to maintain the species as part of *Rondeletia* as they considered an incomplete *trnL-F* sequence for *R. pitreana* compared to other taxa as a shortcoming of their analysis. In fact, the tree published by Rova & al. (2009) depicts *R. pitreana* as an early diverging branch sister to an assemblage of genera of *Guettardeae* and *Rondeletieae* but none of the deeper nodes received any statistical support. Later, Manns & Bremer (2010) used ITS, *atpB-rbcL*, *ndhF*, *rps16* and *trnL-F* in a study of the subfamily *Cinchonoideae* and recovered *R. pitreana* as sister of a clade comprising *Acrosynanthus* Urb.–*Mazaea* Krug & Urb.–*Rachicallis* DC.–*Rondeletia*. Despite this, they also maintained the species as part of *Rondeletia* and suggested that the status of the taxon required further investigation before any change of classification would be warranted. We here took over the task to revisit the phylogenetic position of *R. pitreana* and assess its taxonomic status. For this investigation we extended our recent data set of combined intron and spacer sequence data, which has already provided a much better resolved and statistically supported phylogenetic framework for the *Cinchonoideae* (Torres Montúfar & al. 2017) compared to previous publications. We also studied morphological characters of *R. pitreana* in comparison to the other lineages of *Rondeletieae*.

Material and methods

Taxon sampling — The taxon set for *Rondeletieae* included in Torres-Montúfar & al. (2017) was extended and now includes all the genera undoubtedly classified within *Rondeletieae* by Manns & Bremer (2010) and corroborated by further studies that, although focusing on other tribes, included genera classified in *Rondeletieae* sensu Robbrecht (1988) or Delprete (1999a) (Tange 2013; Delprete & Jardim 2012; Razafimandimbison & al. 2011). Several genera representing other tribes of *Cinchonoideae* (*Chiococceae*, *Condamineeae*, *Guettardeae* and *Sabiceeae*) and *Ixoroideae* (*Gardenieae*) were used as outgroups. Taxon names with authors, vouchers and GenBank accession numbers are presented in Appendix 1.

Morphology — Information on morphological characters traditionally used to distinguish genera of *Rondeletieae* was obtained from the literature (Standley 1918; Liogier 1962, 1995; Aiello 1979; Delprete 1999a, 1999b; Lorence & Taylor 2012) and through our own examination of the voucher specimens. The phylogenetic distribution of taxonomically important floral characters is shown next to the consensus tree obtained from the plastid data (Fig. 1).

The air-dried corolla of *Rondeletia pitreana* (from herbarium material) was coated with gold and observed using a scanning electron microscope (Hitachi, model SU1510) at the Instituto de Biología, UNAM.

DNA extraction, amplification and sequencing — Silica-gel-dried leaves were used for DNA extraction when available, complemented with herbarium material. DNA was extracted using NucleoSpin Plant II kit (Macherey Nagel, Düren, Germany) following the manufacturer's protocol or a three-fraction cetyltrimethylammonium bromide (CTAB) method (Borsch & al. 2003).

Three plastid markers (*trnK-matK*, *trnL-F* and *petD*) were amplified and sequenced in this study. The amplification of each marker was performed in reaction volumes of 50 µL, containing 2 µL of extracted DNA (with a concentration of 10–20 ng/µL), 14.7 µL of H_2O, 5 µL of 10× peqLab Taq. buffer S containing $MgCl_2$, 3 µL of $MgCl_2$ (25 mM), 10 µL of betaine monohydrate (5 M), 1 µL of BSA (10 µg/µL), 2 µL of forward primer (20 pm/µL), 2 µL of reverse primer (20 pm/µL), 10 µL dNTPs (each 0.25 mM) and 0.3 µL Taq polymerase 5 units/µL (PeqLab, Erlangen Germany).

For *trnK-matK* the amplification was performed in two halves using the primers trnKFbryo (Wicke & Quandt 2009) and COmatK670R (Tesfaye & al. 2007) plus NYmatK480F (Hilu & al. 2003) and psbA5R (Steele & Vilgalys 1994). PCR conditions were: 1 cycle of denaturation (90 seconds at 96 °C, 60 seconds at 50 °C, 120 seconds at 68 °C), 35 cycles of annealing (30 seconds at 95 °C, 60 seconds at 48 °C, 120 seconds at 68 °C), extension (20 minutes at 68 °C). The *trnL-F* region was amplified using the primers trnTc and trnTf (Taberlet & al. 1991). PCR conditions were: 30 cycles of denaturation (60 seconds at 96 °C), annealing (60 seconds at 50 °C), and extension (120 seconds at 72 °C). The *petD* intron including the *petB-petD* spacer was amplified using the primers PIpetB1411F or PIpetB1365F and PIpetD738R or PIpetD346R (Löhne & Borsch 2005). PCR conditions were: 35 cycles of denaturation (60 seconds at 97 °C), annealing (60 seconds at 48 °C), extension (45 seconds at 72 °C) and a final extension step (7 min at 72 °C).

All amplification products were purified by QIAquick PCR Purification Kit (QIAGEN GmbH, Hilden, Germany). Sequencing was performed by Macrogen Inc., South Korea (http://www.macrogen.com).

Because of the availability of only older herbarium material for some species and technical difficulties to obtain PCR products, sequences were not obtained for all genomic regions for each taxon. Therefore, there are 26 terminals that only have two of the three markers (the corresponding lacking marker was coded with missing values).

Sequence assembly, alignment and indel coding — The matrix comprises 88 taxa and 217 accessions, 25 of which were generated for this study. Another 179 sequences generated for a previous study (Torres-Montúfar & al. 2017) and 13 published by Rova & al. (2002, 2009) were downloaded from GenBank. New pherograms were edited and assembled using PhyDE v.0.995 (Müller & al. 2005). Sequences were then added to the multiple sequence alignment of Torres-Montúfar & al. (2017) following the criteria proposed by Löhne & Borsch (2005). Gaps were coded manually following the simple gap criterion of Simmons & Ochoterena (2000); Simple Sequence Repeats (SSR) and inversions were manually coded following Ochoterena (2009). Regions of uncertain homology (mutational hotspots) were removed from the matrices prior to phylogenetic analyses.

Phylogenetic analyses — Parsimony (P) analyses were performed using the combined matrix with nucleotides, gaps, inversions and SSRs, only including parsimony-informative characters. A heuristic search with 10 000 replicates of Wagner trees constructed with random taxon addition followed by TBR branch swapping was performed in TNT version 1.1 (Goloboff & al. 2003); ten trees were saved on each replicate and a further TBR was conducted to completion saving up to 10 000 trees.

Table 1. Contribution of the different genomic regions to the total matrix.

	trnK-matK	*trnL-F*	*petD*	**Total**
Sequences	62	83	68	**217**
Aligned positions	2934	1046	1050	**5030**
Number of nucleotide characters (nts) without hotspots	2839	1017	1007	**4863**
Microstructural characters (mch)	47	28	40	**115**
Potentially informative characters (nts/mch)	471/39	162/23	138/34	**771/96**

These trees were submitted to further analysis using the "new technology" option, alternating ratchet parsimony (Nixon 1999a), sectorial, drift and tree fusion (Goloboff 1999) options. One hundred initial sequences were used until the consensus was stabilized ten times using a 100% factor. All the most parsimonious trees were collected and opened in WinClada (Nixon 1999b) and summarized in a strict consensus tree. Additionally, a Jackknife analysis (JK) was executed in TNT version 1.1 (Goloboff & al. 2003), re-sampling the matrix 10 000 times with the same parameters used for the new technology searches.

For Bayesian Inference (BI) and Maximum Likelihood (ML) analyses, the optimal models of sequence evolution were estimated using ModelTest 3.6 (Posada 1998) using the following parameters: 203 substitution schemes, +F base frequencies, +I and +G rate variation, nCat=4 and SPR tree search. BI analyses of the concatenated nucleotide matrix were conducted using MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001). Four independent Markov Chain Monte Carlo (MCMC) runs were carried out, each with four parallel chains. Each chain was performed for 1 000 000 generations, saving one random tree every 1000 generations. The burn-in was set to 1000 (10%) when the stability of the chain was reached. Phylogenetic trees were visualized using Figtree (Rambaut & Drummond 2010). ML topologies and Bootstrap values (BS) from 1000 replicates were inferred using the Randomized Accelerated Maximum Likelihood graphic user interface RAxMLGUI version 1.2 (Silvestro & Michalak 2011).

The P and BI consensus as well as the ML trees (Appendix 2, see Supplementary Materials online) were graphically summarized rather than presenting any of them as a preferred topology, to be conservative trusting only nodes supported by all three inference methods. This was achieved in WinClada by manually collapsing nodes that were insufficiently supported in at least one of the trees obtained by alternative methods. We considered cutoff values as follows: 64% for JK (Farris & al. 1996), 0.95 for posterior probabilities (PP; Alfaro & Holder 2006) and ≥70% for ML BS (Felsenstein & Kishino 1993; Hillis & Bull 1993).

Results

The aligned matrix with all regions consisted of 5030 characters (without mutational hotspots), of which 771 (15%) were potentially parsimony informative. The coding of microstructural mutations resulted in 115 characters (Appendix 3, see Supplementary Materials online), of which 96 (83%) were potentially parsimony informative. The general time-reversible model including parameters for invariant sites and rate variation (GTR+I+G) best fit all data sets and was used to conduct the probabilistic analyses. The alignments, microstructural matrices, the combined matrix including microstructural characters, and the matrix used for the analyses are presented as Supplementary Materials online. Detailed matrix statistics regarding each marker contribution are given in Table 1.

Fig. 1A provides an overview of the major clades that represent the tribes (*Chiococceae*, *Condamineeae*, *Gardenieae*, *Guettardeae*, *Rondeletieae* and *Sabiceeae*), which are supported by all methods. The consensus tree based on the Parsimony and Bayesian consensus as well as the ML tree presents a detailed sampling of *Rondeletieae* (Fig. 1B).

Within *Rondeletieae* there is a polytomy involving the Mesoamerican genus *Blepharidium* Standl., the Caribbean genera *Acunaeanthus* Borhidi & al. and *Suberanthus* Borhidi & M. Fernández, and to two other clades. *Rondeletia* is in a clade (9% JK, 1.00 PP, 95% BS) that also includes *Acrosynanthus*, *Mazaea*, *Phyllomelia* Griseb., *Rachicallis* and *Roigella* Borhidi & M. Fernández; this will be hereafter referred to as the *Rondeletia* assemblage. The genus *Acrosynanthus* is sister to the *Rondeletia* assemblage. The only *Rondeletia* species not sharing a common ancestor with the *Rondeletia* assemblage is *R. pitreana* (99% JK, 1.00 PP, 98% BS), which is the earliest divergent species in this clade (Fig. 1B). The two samples of this species share two *trnL-F* SSRs: TGAT (in the aligned position 389–392) and TTTTC (in the aligned position 426–430). When the incomplete *trnL-F* sequence from Rova & al. (2002) is added to our *trnL-F* matrix it groups together with our two *R. pitreana* samples (the trees are otherwise identical) and shares the mentioned SSRs (results not shown). Furthermore, *R. pitreana* lacks a conspicuous fleshy ring in the corolla mouth, which is characteristic of the genus *Rondeletia* (Fig. 2) and can be morphologically distinguished by having a papillate corolla mouth and lobes (Fig. 1B, Fig. 3).

Discussion

Phylogenetic position of Rondeletia pitreana — The phylogenetic position of *R. pitreana* is well supported as nested inside *Rondeletieae* but outside of the clade

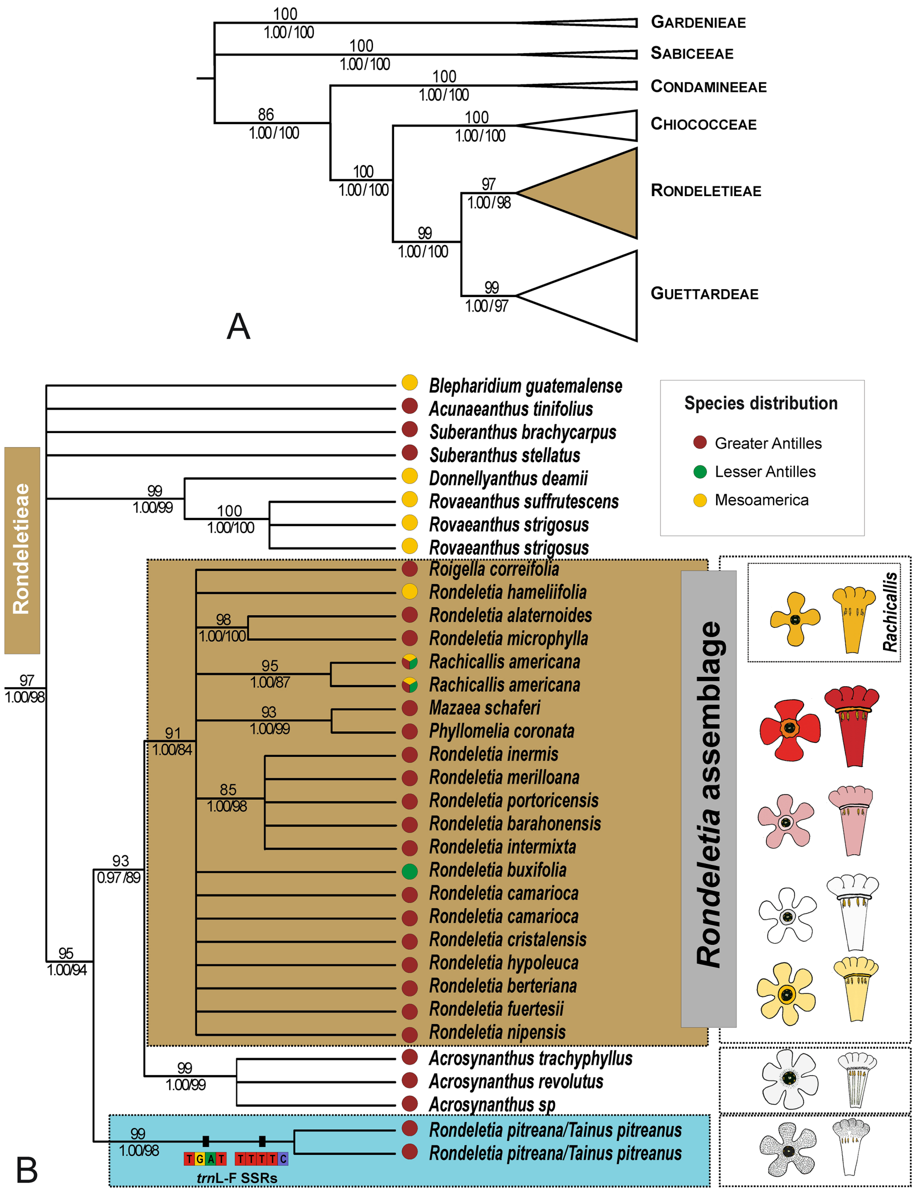

Fig. 1. Consensus of well-supported clades present in trees inferred by all three inference methods based on combined sequence data set of plastid *trnK-matK*, *petD* and *trnL-F*. – A: summary tree showing tribes; triangles are proportional to the number of taxa sampled. – B: tree depicting all samples included within *Rondeletieae*; the lineage of *Rondeletia pitreana* is highlighted by a blue box and the two apomorphic simple sequence repeats are shown below the branch. The main floral features are schematized next to each clade: ornamentation of corolla mouth, number of corolla lobes, corolla colour, and point of insertion of filament to corolla. Papillate corolla lobes (visualized as dots) are unique to *Tainus*. Numbers above branches correspond to parsimony Jackknife percentages and those below branches to Bayesian posterior probabilities (left) and Likelihood Bootstrap percentages (right).

constituted by the *Rondeletia* assemblage plus *Acrosynanthus*. Our much better-resolved and -supported trees clarify the earlier statement of Rova & al. (2009), who could not assign the species to either *Guettardeae* or *Rondeletieae*. Two factors contributed to the better understanding of the phylogenetic position of *R. pitreana*: an improved marker selection and the use of a sufficiently dense taxon sampling. The two SSRs in *trnL-F* are also present in the original but incomplete sequence generated by Rova (2002). This observation, combined with the fact that the incomplete sequence groups with our sequences in phylogenetic analyses of *trnL-F* sequences (pers. obs.), suggests that the lack of about 40 nt does not create a spurious signal and the sequence published by Rova (2002) is a correct sequence of *R. pitreana*. However, their trees were insufficiently resolved and supported because of the limited sampling of molecular characters. Whereas Manns & Bremer (2010) improved the resolution and support within *Rondeletieae* within their tree by using several DNA markers, they sampled just four other species of *Rondeletia*, thus limiting the possibility to test the monophyly of the genus. Our taxon sampling of *Rondeletia* covers the range of the genus throughout Mesoamerica and the Antilles and also its morphological diversity.

In addition, the comparative analysis of morphological features clarified the morphological differences of *Rondeletia pitreana* compared to allied taxa We found the papillate corolla to constitute a morphological apomorphy that differentiates *R. pitreana* from the rest of the *Rondeletia* assemblage (Fig. 1B, Fig. 2, Fig. 3). Furthermore, the combination of a 5-merous corolla, the presence of domatia, and stamens inserted at the corolla mouth is unique for *R. pitreana*.

The morphological and molecular characters differentiating *Rondeletia pitreana* from the rest of the *Rondeletia* species grants the recognition of a new monotypic genus that we call *Tainus*. The alternative option would be to include *R. pitreana* as well as *Acrosynanthus* within *Rondeletia* (as well as all the other currently accepted genera of the *Rondeletia* assemblage; Fig. 1). The expansion of the concept of *Rondeletia* to include all the species in the clade would result in the lack of diagnostic characters for the group and would create confusion over the well-defined monophyletic genus *Acrosynanthus*. The monophyly of *Rondeletia* (without *Tainus*) is another issue, which will require obtaining phylogenetic resolution at species level within the *Rondeletia* assemblage. As such, this will require further investigation with additional taxon sampling and considerably extended character sampling.

A new genus for Hispaniola in the Caribbean hotspot — Although *Rondeletia pitreana* was already recognized as an endemic species to Hispaniola, the description of the new genus *Tainus* adds value in our view to the endemism in Hispaniola, highlighting the importance of this island for lineage diversification. The genus *Tainus* joins the recent discoveries and description of new genera for Hispaniola of different plant lineages including now six endemic genera, but in this case phylogenetic evidence provides stronger support for the naturalness of *Tainus*.

The monotypic genus *Tainus* appears to come from one diversification event within the Antilles (Fig. 1), but it is not possible to establish further detail on its biogeographic origin in the Antilles due to bias sampling within the sister clade: in our study *Acrosynanthus* was only sampled from Cuba, but it also occurs in Jamaica; and further sampling of *Rondeletieae* is obviously needed.

The recent findings stress the need to explore, collect and carry out phylogenetic studies to increase the floristic knowledge of Hispaniola and the Antilles. Within Hispaniola, a site of particular interest is the Sierra de Bahoruco-La Selle, for which the genus *Hottea* is endemic in addition to *Tainus*, underscoring its importance as an area of high diversity in Hispaniola, as stated by Cano-Ortiz & al. (2016), and definitely highlighting the need to protect this area of Hispaniola.

Fig. 2. Conspicuous fleshy ring on corolla mouth characteristic of *Rondeletia*. – A: *Rondeletia merilloana* Urb., Dominican Republic, Sierra de Bahoruco, Apr 2013, *S. Fuentes & al. 1136*, photograph by A. Torres-Montúfar. – B: *Rondeletia odorata* Jacq., Botanical Garden, Natural History Museum of Denmark, Sep 2017, photograph by H. Ochoterena.

Taxonomic treatment

Tainus Torr.-Montúfar, H. Ochot. & Borsch, **gen. nov.** – Fig. 3.
Type: *Tainus pitreanus* (Urb. & Ekman) Torr.-Montúfar, H. Ochot. & Borsch.

Morphological diagnosis — *Tainus* is clearly distinguished

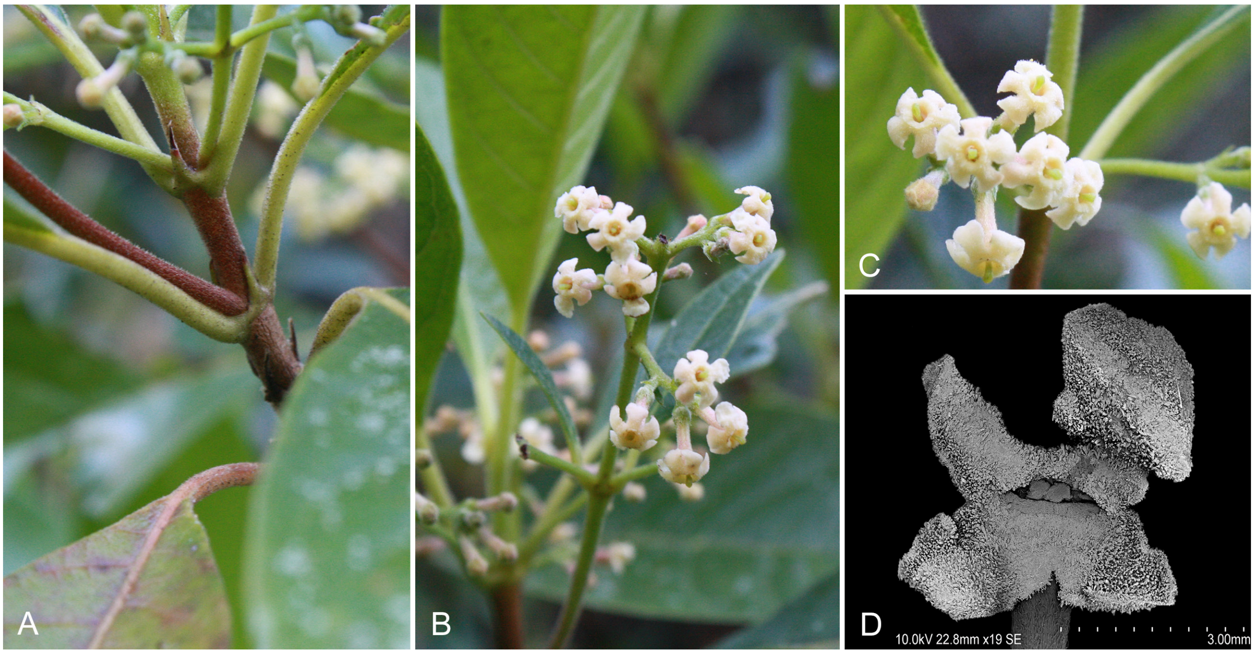

Fig. 3. *Tainus pitreanus* – A: stipules; B: inflorescence; C: longistylous flowers; D: SEM micrograph showing papillate corolla. – A–C: Dominican Republic, Sierra de Bahoruco, Apr 2013, *S. Fuentes & al. 1110*, photographs by A. Torres-Montúfar. – D: Dominican Republic, Sierra de Bahoruco, Apr 2003, *T. Clase & al. 3493*, photograph by B. García-Mendoza.

from all other genera of *Rondeletieae* by the densely papillate surface of the corolla lobes and mouth. It is distinguishable from *Rondeletia* by the lack of a conspicuous fleshy ring in the corolla mouth. *Tainus* is distinguished from *Acrosynanthus* by the stamens inserted at the distal portion of the corolla tube (vs at the basal portion of the corolla tube) and the 5-merous flower parts (vs mainly 6-merous, with only one species 5- or 6-merous).

Molecular diagnosis — *Tainus* is uniquely characterized by two *trnL-F* simple sequence repeats: a “TGAT” in positions 389–392 and a “TTTTC” in positions 426–430.

Eponymy — The name *Tainus* is dedicated to the indigenous people of the Caribbean islands. The Taino people are closely related to Mesoamerican ancient civilization, with many migrations and high cultural exchange between both regions. This resembles the biogeographic patterns in *Rondeletieae*, with several independent events of migration and diversification among the Caribbean islands and Mesoamerica.

Tainus pitreanus (Urb. & Ekman) Torr.-Montúfar, H. Ochot. & Borsch, **comb. nov.** ≡ *Rondeletia pitreana* Urb. & Ekman in Ark. Bot. 22A(10): 83. 1929. – **Lectotype (designated here):** Haiti, Massif de La Selle, group Morne des Commissaires, Anses-à-Pitres, between Banane and Tête de l’Eau, steep riverside, 26 Aug 1926, *E. L. Ekman H 6753* (S S07-14926 [online image]!; isolectotypes: A00095861 [online image]!, G00436657!, GH00095862!, K000174024 [online image]!, LL00373191!, S S07-14924! [online image], US00137618!, US00794308!).

Description — Treelets 7–10 m tall. *Stems* striate; *twigs* terete to slightly angulate, sparsely hispid with minute trichomes, glabrescent. *Stipules* erect, triangular, 2–3 × 2–3 mm, deciduous, abaxially glabrous or sparsely pubescent at base, adaxially with a row of small reddish colleters and white trichomes, margin ciliate. *Leaves* opposite, petiolate; *petiole* 3–5 mm long, slightly winged, glabrate; *leaf blade* elliptic, 4.2–9.1 × 2–3.4 cm, leathery, abaxially glabrate, adaxially lustrous and glabrate, base attenuate, apex acute; primary and secondary veins abaxially prominent, adaxially depressed, secondary veins 5–7 pairs; domatia present. *Inflorescence* axillary, pedunculate, paniculate, exceeding subtending leaf, 8.1–9.4 × c. 2.5 cm including flowers, with 4–6 pairs of secondary axes; *peduncle* 2–3 cm long, hispid to strigose; *secondary axes* 1–2 cm long, 1- or 2-flowered, strigose, each subtended by a triangular bract 2–3 mm long. *Flowers* pedicellate; each subtended by a triangular bracteole 2–3 mm long; *hypanthium* spheroid to ovoid, c. 1 × 1 mm, densely strigose; *calyx* 5-merous; *calyx lobes* erect in flower and fruit, triangular, equal, abaxially sparsely strigose toward base, margin ciliate; *corolla* 5-merous, white, salver-shaped at anthesis; *corolla tube* 6–7 mm long, externally strigose, hairs denser at tube base, sparser at apex, internally sparsely strigose on basal ½ and with a villosulous ring at base; *corolla mouth* papillate; *corolla lobes* ovate, 3–4 mm long, usually one lobe larger than others, margin slightly crisped, especially on larger lobe, abaxially strigose at base and densely papillose at margin and apex, adaxially densely papillose; *heterostyly* unknown; *anthers* adnate c. 1.5 mm below corolla mouth; *style* bilobed, c. 7 mm long, glabrate. *Capsule* loculicidal, ovoid to globose, 3–4 × c. 3 mm, woody, sparsely strigose. *Seeds* flat, winged, c. 1 × 0.5 mm, reticulate.

Phenology — The species flowers from March to July and fruits from July to August.

Distribution and ecology — The genus *Tainus* is restricted to Hispaniola, in the central southern region near the border of the Dominican Republic and Haiti (Fig. 4). The species was known only from the type collection by Ekman (1926), from La Selle in Haiti. Almost eighty years later it was collected again by botanists at the Jardín Botánico Nacional de Santo Domingo (JBN), who found another locality in the Dominican Republic, and again more recently by a joint expedition with the Botanic Garden and Botanical Museum Berlin. The species is endemic to the mainly calcareous mountain system of Sierra de Bahoruco-La Selle. It grows in riparian vegetation of tropical rain forest associated with *Fuertesia domingensis* Urb., *Guarea* sp., *Ocotea* sp. and *Piper* sp.

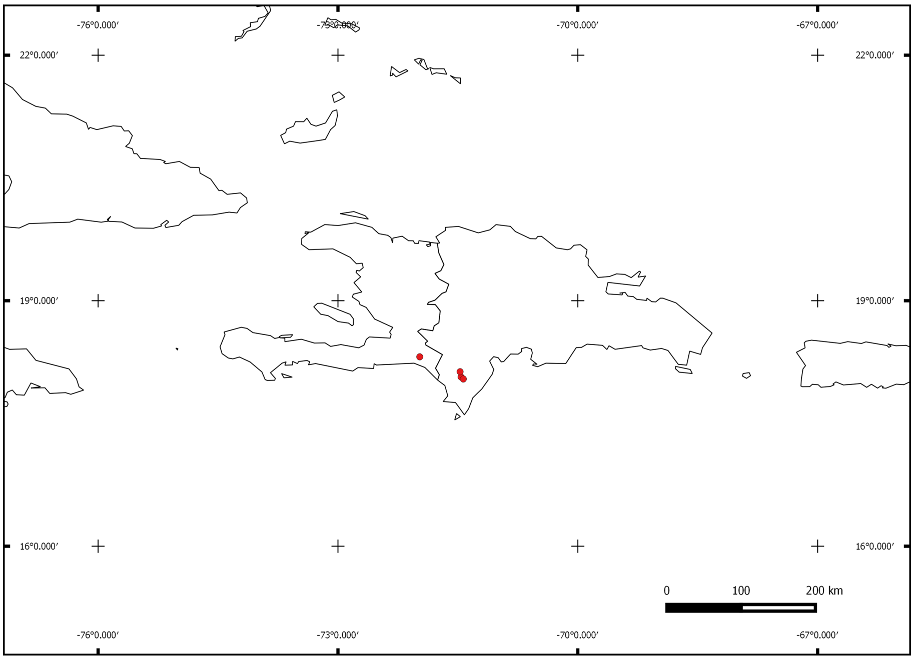

Fig. 4. Distribution map of *Tainus pitreanus*.

Conservation status — Although *Tainus pitreanus* has been collected in Haiti and the Dominican Republic, the collecting sites are nearby and share ecological conditions, so they could represent maybe one or two populations. Therefore, the species meets the criteria B1ab(iii) for the category of Critically Endangered (CR) according to the IUCN (2012). Additional exploration across this region and surrounding areas is needed to assess the density of individuals and the population status. Since there is about 50 km distance from the populations in the Dominican Republic to the type locality in Haiti, further exploration should evaluate ro what extent plants have persisted in the mountain system.

Despite the Sierra de Bahoruco National Park having been founded as a conservation area (Hoppe 1989), due to its high biodiversity it is necessary to implement efforts for its conservation. Cano & al. (2016) recommended the establishment of a Biosphere Reserve, including the Sierra de Bahoruco and La Selle (Dominican Republic and Republic of Haiti, respectively) to preserve and manage unique ecosystems in the Antilles.

Additional specimens examined — Dominican Republic: Sierra de Bahoruco, Provincia de Pedernales, Carretera Internacional, en las márgenes del Río Mulito, próximo al balneario, 18°09'N, 71°46'W, 200–300 m, fl., fr., 27 Jul 2006, *T. Clase & al. 4228* (JBSD, MO); entre Río Mulito y Cabo Duarte, 18°09'N, 71°45'W, 300 m, fl. bud, fl., 3 Apr 2003, *T. Clase & al. 3493* (JBSD); Cabo Duarte a 500 m antes del cuartel, 18°13'38.2"N, 71°47'51.2"W, 1440 m, fl., 16 Apr 2013, *S. Fuentes & al. 1110* (B, JBSD).

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Appendix 1

List of taxa used in the phylogenetic analyses with voucher information: geographic origin, collector(s) and collecting number, herbarium, project code at Botanischer Garten und Botanisches Museum Berlin (e.g. RUB000), and GenBank accession numbers per marker (*trnK-matK*, *trnL-F* and *petD*; markers for which no sequences were obtained are indicated by a dash "–"). New sequences with respect to Torres-Montúfar & al. (2017) are marked with an asterisk (*); sequences used by Rova & al. (2002, 2009) are marked with two asterisks (**).

Subfamily *Cinchonoideae*, tribe *Condamineeae*: *Calycophyllum candidissimum* (Vahl) DC., Cuba, *T. Borsch & al. 5125* (B; HAJB; PAL), RUB336, KY785298, KY614094. — **Tribe *Chiococceae*:** *Ceuthocarpus involucratus* (Wernham) Aiello, Cuba, *T. Borsch & al. 4995* (B; HAJB; PAL), RUB233, –, KY785213, KY614097; *Chiococca cubensis* Urb., Cuba, *S. Fuentes & al. 535* (B; HAJB; PAL), RUB264, –, KY785214, KY614098; *Erithalis fruticosa* L., Dominican Republic, *S. Fuentes & al. 221* (B; JBS), RUB183, –, KY785218, KY614101; *Erithalis vacciniifolia* (Griseb.) Wright ex Sauv., Dominican Republic, *S. Fuentes & al. 1044* (B;

JBS), RUB303, KY785272, KY785217, KY614100; *Exostema caribaeum* (Jacq.) Schult., Dominican Republic, *S. Fuentes & al. 1177* (B; JBS), RUB294, –, KY785220, KY614103; *Exostema longiflorum* Roem. & Schult., Cuba, *N. Köster 2666* (B; HAJB; PAL), RUB251, –, KY785221, KY614104; *Exostema spinosum* (Le Vavass) Krug & Urb., Dominican Republic, *S. Fuentes & al. 207* (B; JBS), RUB243, KY785273, KY785219, KY614102; *Isidorea leonardii* Urb., Dominican Republic, *S. Fuentes & al. 1210* (B; JBS), RUB302, KY785280, KY785232, KY614115; *Isidorea veris* Ekman ex Aiello & Borhidi, Dominican Republic, *S. Fuentes & al. 977* (B; JBS), RUB284, –, KY785233, KY614116; *Phialanthus* Griseb., Cuba, *S. Fuentes & al. 545* (B; HAJB; PAL), RUB265, –, KY785236, KY614119; *Portlandia* P. Browne, Cuba, *M. Ackerman 847* (B; HAJB; PAL), RUB226, –, KY785239, KY614122. — **Tribe *Guettardeae*:** *Antirhea lucida* (Sw.) Benth. & Hook. f., Cuba, *T. Borsch & al. 5288* (B; HAJB; PAL), RUB166, KY785299, KY785196, KY614077; *Arachnothryx affinis* (Hemsl.) Borhidi, Mexico, *H. Ochoterena & al. 644* (MEXU), RUBmx046, KY785257, KY785197, KY614078; *Arachnothryx aspera* (Standl.) Borhidi, Costa Rica, *E. Lepiz 174* (MEXU), RUB094, KY785258, –, KY614079; *Arachnothryx buddleioides* (Benth.) Planch., Mexico, *H. Ochoterena & al. 924* (MEXU), RUB130, KY785259, KY785198, KY614080; *Arachnothryx capitellata* (Hemsl.) Borhidi, Mexico, *H. Ochoterena & al. 850* (MEXU), RUB076, KY785260, KY785199, KY614081; *Arachnothryx guerrerensis* (Lorence) Borhidi, Mexico, *D. Breedlove 61973* (MEXU), RUB343, KY785300, KY785200, KY614082; *Arachnothryx heteranthera* (Brandegee) Borhidi, Mexico, *H. Ochoterena & al. 823* (MEXU), RUB046, KY785261, KY785201, KY614083; *Arachnothryx jurgensenii* (Hemsl.) Borhidi, Mexico, *H. Ochoterena & al. 803* (MEXU), RUB042, KY785262, –, KY614084; *Arachnothryx leucophylla* (Kunth) Planch., Mexico, *H. Ochoterena & al. 752* (MEXU), RUB043, KY785301, KY785202, KY614085; *Arachnothryx manantlanensis* (Lorence) Borhidi, Mexico, *R. Cuevas 4978* (MEXU), RUB104, KY785263, KY785203, KY614086; *Arachnothryx pumae* Torr.-Montúfar & H. Ochot., Mexico, *H. Ochoterena & al. 741* (MEXU), RUB069, KY785264, KY785204, KY614087; *Arachnothryx pyramidalis* (Lundell) Borhidi, Mexico, *M. Heath 414* (MEXU), RUB088, KY785302, KY785205, KY614088; *Arachnothryx secundiflora* (B. L. Rob.) Borhidi, Mexico, *H. Ochoterena & al. 743* (MEXU), RUB118, KY785265, KY785206, KY614089; *Arachnothryx stachyoidea* (Donn. Sm.) Borhidi, Mexico, *H. Ochoterena & al. 842* (MEXU), RUB067, KY785266, KY785207, KY614090; *Arachnothryx tabascensis* Borhidi, Mexico, *H. Ochoterena & al. 891* (MEXU), RUBmx069, KY785267, KY785208, KY614091; *Arachnothryx villosa* (Hemsl.) Borhidi, Mexico, *H. Ochoterena & al. 846* (MEXU), RUB124, KY785268, KY785209, KY614092; *Chomelia brachypoda* Donn. Sm., Mexico, *H. Ochoterena & al. 746* (MEXU), RUB119, KY785270, KY785215, KY614099; *Gonzalagunia killipii* Standl., Ecuador, *M. Zak 3566* (MEXU), RUB049, KY785304, –, KY614105; *Gonzalagunia panamensis* (Cav.) K. Schum., Cuba, *N. Köster & al. 2506* (B; HAJB; PAL), RUB418, KY785274, KY785222, –; *Gonzalagunia rudis* (Standl.) Standl., Costa Rica, *R. Forero 7419* (MEXU), RUB095, KY785305, KY785223, KY614106; *Gonzalagunia thyrsoidea* (Donn. Sm.) B. L. Rob., Guatemala, *M. Gonzalez 1455* (MEXU), RUB047, KY785275, KY785224, KY614107; *Guettarda camagueyensis* Britton, Cuba; *T. Borsch & al. 4028* (B; HAJB; PAL), RUB017; Cuba, –, KY785231, KY614114; *Guettarda elliptica* Sw., Mexico, *H. Ochoterena & al. 894* (MEXU), RUB125, KY785306, KY785225, KY614108; *Guettarda ferruginea* C. Wright ex Griseb., Cuba, *T. Borsch & al. 5007* (B; HAJB; PAL), RUB152, KY785278, KY785229, KY614112; *Guettarda lamprophylla* Urb., Dominican Republic, *S. Fuentes & al. 1202* (B; JBS), RUB382, KY785276, KY785226, KY614109; *Guettarda monocarpa* Urb., Cuba, *T. Borsch & al. 4429* (B; HAJB; PAL), RUB153, KY785307, KY785227, KY614110; *Guettarda prenleloupii* Urb., Dominican Republic, *S. Fuentes & al. 1205* (B; JBS), RUB292, KY785279, KY785230, KY614113; *Guettarda pungens* Urb., Dominican Republic, *S. Fuentes & al. 238* (B; JBS), RUB184, KY785277, KY785228, KY614111; *Javorkaea hondurensis* (Donn. Sm.) Borhidi & Járai-Koml., Honduras, *J. Linares 6241* (MEXU), RUBmx055, KY785281, KY785234, KY614117; *Machaonia pauciflora* Urb., Cuba, *T. Borsch & al. 5218* (B; HAJB; PAL), RUB164, KY785282, KY785235, KY614118; *Rogiera amoena* Planch., Mexico, *H. Ochoterena & al. 805* (MEXU), RUB131, KY785284, KY785240, KY614123; *Rogiera cordata* (Benth.) Planch., Mexico, *H. Ochoterena & al. 732* (MEXU), RUB072, KY785285, KY785241, KY614124; *Rogiera ligustroides* (Hemsl.) Borhidi, Mexico, *H. Ochoterena & al. 781* (MEXU), RUB068, KY785286, KY785242, KY614125; *Rogiera macdougalli* Lorence, Mexico, *H. Ochoterena & al. 841* (MEXU), RUB073, KY785288, KY785244, KY614127; *Rogiera nicaraguensis* (Oerst.) Borhidi, Honduras, *J. Linares 3520* (MEXU), RUB064, KY785287, KY785243, KY614126; *Rogiera stenosiphon* (Hemsl.) Borhidi, Mexico, *H. Ochoterena & al. 749* (MEXU), RUB075, KY785289, KY785245, KY614128. — **Tribe *Rondeletieae*:** **Acrosynanthus revolutus* Urb., Cuba, *T. Borsch & al. 4156* (B; HAJB; PAL), RUB224, MF460511, MF460689, MF460590); *Acrosynanthus trachyphyllus* Standl., Cuba, *T. Borsch & al. 4444* (B; HAJB; PAL), RUB154, KY785256, KY785195, KY614076; **Acrosynanthus trachyphyllus* Standl., Cuba, *S. Fuentes & al. 602* (B; HAJB; PAL), RUB203, (MF460512, MF460690, MF460591); ***Acunaeanthus tinifolius* (Griseb.) Borhidi, Cuba, *Stahl & al. s.n.* (S), –, GQ852451, –; ***Blepharidium guatemalense* Standl., Guatemala, *Gustafsson & al. 211* (GB), –, AF152735, –; *Donnellyanthus deamii*

(Donn. Sm.) Borhidi, Honduras, *S. Duery 172* (MEXU), RUB056, KY785271, KY785216, –; **Mazaea shaferi* (Standl.) Delprete, Cuba, *T. Borsch & al. 4075* (B; HAJB; PAL), RUB144, (MF460567, MF460749, MF460657); *Phyllomelia coronata* Griseb., Cuba, *T. Borsch & al. 4620* (B; HAJB; PAL), RUB158, KY785303, KY785210, KY614093; *Rachicallis americana* (Jacq.) Hitchc., Cuba, *N. Köster 2465* (B; HAJB; PAL), RUB170, KY785283, KY785238, KY614121; **Rachicallis americana* (Jacq.) Hitchc., Cuba, *T. Borsch & al. 5625* (B; HAJB; PAL), RUB217, (MF460568, MF460750, MF460658); ***Roigella correifolia* (Griseb.) Borhidi & M. Fernández, Cuba, *Rova & al. 2262* (GB), –, AF152746, –; ***Rondeletia alaternoides* A. Rich, Cuba, *Rova & al. 2228* (GB), –, AF152740, –; *Rondeletia barahonensis* Urb., Dominican Republic, *S. Fuentes & al. 315* (B; JBS), RUB187, KY785290, KY785246, KY614129; **Rondeletia berteroana* DC., Dominican Republic, *S. Fuentes & al. 239* (B; HAJB; PAL), RUB185, (MF460575, MF460758, MF460666); **Rondeletia buxifolia* Vahl, Montserrat islands, *Veloz & al. 1868* (MO), –, GQ852555, –; *Rondeletia camarioca* C. Wright, Cuba, *T. Borsch & al. 5601* (B; JBN; PAL), RUB215; KY785294, KY785251, KY614134; **Rondeletia camarioca* C. Wright, Cuba, *T. Borsch & al. 5096* (B; HAJB; PAL), RUB215, KY785294, KY785251, KY614134; **Rondeletia cristalensis* Urb., Cuba, *N. Köster 2828* (B; HAJB; PAL), RUB178, (MF460578, MF460761, MF460669); *Rondeletia fuertesii* Urb., Dominican Republic, *S. Fuentes & al. 1170* (B; JBS), RUB298, KY785291, KY785247, KY614130; ***Rondeletia hameliifolia* Dwyer & M. V. Hayden, Panama, *Kirkbride & Hayden 164* (NY), –, GQ852546, –; *Rondeletia hypoleuca* Griseb., Cuba, *T. Borsch & al. 4204* (B; HAJB; PAL), RUB020, KY785292, KY785248, KY614131; ***Rondeletia inermis* (Spreng.) Krug & Urb., Puerto Rico, *Acevedo-Rodríguez & al. 7691* (NY), –, AF152745, –; ***Rondeletia intermixta* Britton, Cuba, *Rova & al. 2245* (GB), –, AF152742, –; *Rondeletia merilloana* Urb., Dominican Republic, *S. Fuentes & al. 1136* (B; JBS), RUB353, KY785293, KY785249, KY614132; *Rondeletia microphylla* Griseb., Cuba, *T. Borsch & al. 4169* (B; HAJB; PAL), RUB018, KY785308, KY785250, KY614133; ***Rondeletia nipensis* Urb., Dominican Republic, *Delprete & al. 8651* (UPS), –, GQ852547, –; ***Rondeletia portoricensis* Krug & Urb., Puerto Rico, *C. Taylor 11687* (MO), –, AF152743, –; *Rovaeanthus strigosus* (Benth.) Borhidi, Guatemala, *M. Veliz 6539* (MEXU), RUB063, KY785295, KY785252, KY614135; **Rovaeanthus strigosus* (Benth.) Borhidi, Guatemala, *D. Lorence 8920* (PTGB), –, GQ852550, –; ***Rovaeanthus suffrutescens* (Brandegee) Borhidi, Mexico, *B. Bremer 2712* (S), –, AF152738, –; ***Suberanthus brachycarpus* (Griseb.) Borhidi & M. Fernández, Cuba, *McDowell 4824* (DUKE), –, HM045004, –; ***Suberanthus stellatus* (Griseb.) Borhidi & M. Fernández, Cuba, *Rova & al. 2219* (GB), –, AF152736, –; **Tainus pitreanus* (Urb. & Ekman) Torr.-Montúfar, H. Ochot. & Borsch, Dominican Republic, *S. Fuentes & al. 1110* (B; JBS), RUB311, (MF460587, MF460773, MF460686); **Tainus pitreanus* (Urb. & Ekman) Torr.-Montúfar, H. Ochot. & Borsch, Dominican Republic, *T. Clase 4228* (JBSD, MO), RUB354, (MF460588, MF460774, MF460687). — **Subfamily *Ixoroideae*, tribe *Condamineae*:** *Picardaea haitiensis* Urb., Dominican Republic, *S. Fuentes & al. 1017* (B; JBS), RUB409, KY785297, KY785237, KY614120. — **Tribe *Gardenieae*:** *Casasia clusiifolia* (Jacq.) Urb., Cuba, *S. Fuentes & al. 761* (B; HAJB; PAL), RUB271, KY785269, KY785211, KY614095; *Casasia jacquinioides* (Griseb.) Standl., Cuba, *T. Borsch & al. 4990* (B; HAJB; PAL), RUB232, –, KY785212, KY614096; *Randia aculeata* L., Cuba, *T. Borsch & al. 5316* (B; HAJB; PAL), RUB245, KY785255, KY785194, KY614075. — **Tribe *Sabiceeae*:** *Sabicea mexicana* Wernham, Mexico, *H. Ochoterena & al. 876* (MEXU), RUB111, KY785309, KY785253, KY614136; *Sabicea villosa* Schult., Mexico, *H. Ochoterena & al. 858* (MEXU), RUB122, KY785296, KY785254, KY614137.

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PARTE I: LA TRIBU RONDELETIEAE

CAPÍTULO IV: TRATAMIENTO TAXONÓMICO DE *Rovaeanthus*

Alejandro Torres-Montúfar & Helga Ochoterena

Taxonomic treatment of the Mesoamerican genus Rovaeanthus (Rondeletieae, Rubiaceae)

Introduction

Based on molecular studies the species *Rogiera strigosus* and *Rogiera suffrutescens* formed a clade within Rondeletieae while a core *Rogiera* was retrieved in Guettardeae (Rova et al., 2002; Bremer & Eriksson, 2009; Rova et al., 2009; Manns & Bremer, 2010); these results in addition to the corolla morphology supports the description of the genus *Rovaeanthus* to encompass those species (Borhidi et al., 2004). The main morphological difference between *Rogiera* and *Rovaeanthus* is the corolla mouth ornamentation, *Rogiera* has a hairy ring while *Rovaeanthus* has a unique combination of fleshy ring (occasionally not well developed) coupled with a hairy ring at the corolla mouth (Borhidi et al., 2004) (Figure 1). Despite the phylogenetic and morphological evidence, Lorence (2012) refused to accept *Rovaeanthus* as different of *Rogiera* arguing character overlapping.

Here we present a taxonomic treatment of *Rovaeanthus* as a whole in its entire range of distribution, including updated and standardized description of the species, phenological data and maps of distribution.

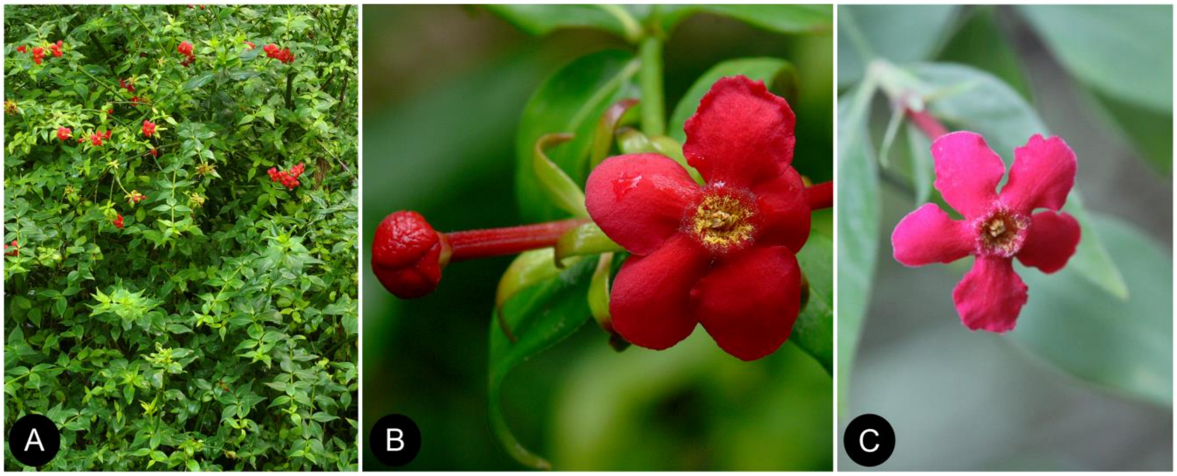

Figure 1. ***Rovaeanthus strigosus***. **A.** Habit. **B.** Bud and flower. **C.** Flower [A-B. photographs by James Gaither (flickr.com), C. Photograph by I. Coronado-González (tropicos.org)].

Materials and methods

The revision presented here is based on examination of more than 100 herbarium specimens, including type specimens of seven Herbaria (CHIP, F, IEB, LL, MEXU, MO, US). Specimens were examined during herbarium visits or received as loans, but specimen images were also examined at JStor Global Plants (http://plants.jstor.org/). The descriptions and measurements are based on herbarium specimens.

Flower buds often open prematurely in the press at a smaller size than fully developed flowers, and the succulent fruits often shrink when dried, therefore the measurements of herbarium specimens may differ from those of living plants. The descriptive terminology follows Harris & Harris (2000), distribution, phenology and habitat information comes from herbarium specimen labels. Maps were prepared using QGIS 2.8 (Quantum GIS, 2017).

Taxonomic treatment

***Rovaeanthus* Borhidi** (2004: 130) Type: *Rovaeanthus suffrutescens* (Brandegee) Borhidi ≡ *Rondeletia suffrutescens* Brandegee (1914: 70) ≡ *Rogiera suffrutescens* (Brandegee) Borhidi (1982: 67) Type:—MEXICO: Chiapas, Cerro del Boquerón, Aug 1913. *Purpus 6704*.

Shrubs, decumbent or scandent, twigs terete. **Stipules** interpetiolar, erect, persistent. **Leaves** opposite or ternate, those of a pair equal to unequal, coriaceous or chartaceous, domatia absent. **Solitary flowers, or disposed on dichasial cymes or corymbiform inflorescences,** terminal or axillar; bipartite, tripartite or 1–pedunculate. **Flowers** subsessile or pedicellate, distylous, fragant; hypanthium subglobose, turbinate to obovoid, calyx lobes 5, equal or subequal, corolla infundibuliform, red or pinkish when fresh, mouth with a ring of sparsely yellow trichomes and with a conspicuous parenchymatic fleshy ring, sometimes parenchymatic ring non conspicuous, corolla lobes 5, imbricate, crisped margins, stamens 5, partially exserted or included, dorsifixed anthers, stigmas 2, linear or ovoid, ovary 2–locular, many ovulated, axillar placentation. **Capsular fruits**, subglobose, loculicidal, woody. **Seeds** bicaudate or non caudate, angulate to polygonal.

Key to species

1. Seeds fusiform, bicaudate; leaves ternate or opposite, with 3–4 pairs of secondary veins …………………………………………..……………………...……………………..…… 1. *R. strigosus*

2. Seeds angulate to polygonal, non caudate; leaves opposite, never ternate, with 5–8 of secondary veins…………………………………………………...…………………………… 2. *R. suffrutescens*

1. *Rovaeanthus strigosus* (Benth.) Borhidi (2004: 133) ≡ *Bouvardia strigosa* Benth. (1841: 75) ≡ *Rondeletia strigosa* (Benth.) Hemsl. (1879: 27) ≡ *Rogiera strigosa* (Benth.) Borhidi (1982: 67) Type:—GUATEMALA: Quezaltenango, Zuníl, Nov 1839. *Hartweg 530* (lectotype K [online image]!, isolectotypes E [online image]!, G–DEL [online image]!, LD [online image]!, P [online image]!. Lectotype designated by Lorence (1999), Monogr. Syst. Bot. Missouri Bot. Gard. 73: 27). Figs. 2, 4.

Shrubs, erect, 1–2 m tall, twigs terete, sparsely strigose, glabrescent. **Stipules** erect, 1–2 × 2 mm, triangular, truncate when mature, strigose, persistent. **Leaves** ternate to opposite, those of a pair at a node equal, petiolate or subsessile; petioles 1–3 mm long, strigose; blade ovate, 1–5.3 × 0.7–3.1 cm, coriaceous, adaxially and abaxially strigose, mainly on costa and secondary veins margins ciliolate, revolute, base cuneate to obtuse, occasionally subcordate, apex acuminate, acumen up to 1 cm long; 3–4 pairs of secondary veins, venation prominent on abaxial surface. **Solitary flowers or inflorescences corymbiform**, terminal, 5–6 × 5–7 cm including corollas, bipartite, tripartite to 1-pedunculated, peduncle 1–3 mm long, axis strigose, bracts linear–lanceolate to subulate, 5–19 mm long. **Flowers** subtended by linear–oblong bracteoles, 2–4 mm long, pedicelate, pedicels 3–9 mm long, strigose; hypanthium subglobose turbinate to obovoid, 2–2.5 mm long, strigose; calyx lobes subequal, the larger lobe up to 9–10 mm long, the smaller ones 4–9 mm long, linear–lanceolate to linear–oblong, externally strigose, internally glabrate; corolla infundibuliform, red when fresh, the tube 15–25 × 3 mm, externally glabrate to sparsely strigose, internally hirtellous medially, lobes obovate-elliptic to elliptic, 5–10 × 3–4 mm, crisped margins, externally and internally glabrate, mouth with a ring of sparsely yellow trichomes and with a conspicuous fleshy ring; stamens in long styled flowers attached 3–4 mm below apex of tube, in short styled flowers attached 3 mm below apex of tube, anthers linear–ellipsoid, 3 mm long; style glabrous, in long styled flowers 17–21 mm long, in short styled flowers 11–13 mm long, the stigmas linear in long styled and short styled flowers, 2–3 mm long. **Fruits** subglobose-obovoid to slightly turbinate, 6–9 × 6–8 mm, slightly flattened, glabrate. **Seeds** fusiform, bicaudate, 1 mm long.

Specimens examined:—EL SALVADOR. AHUACHAPÁN: El Imposible, 14 Jun 1994, *Campos s.n.* (MO). MORAZÁN: Joateca, 1000 m, 15 Jun 2011, *Monterrosa 2349* (MO). SAN SALVADOR: Volcán San Salvador, 1650–1800 m, 4 Feb 1998, *Monro 2182* (MO); 1800 m, 22 Sep 1946, *Williams 10623* (MEXU, MO). SANTA ANA: Cerro Verde, 2030 m, 30 Jul 1977, *Croat 42183* (MO); Parque Nacional Montecristo, 1988, *Berendsohn 1056* (B, MO); 1900–2000 m, 27 Jan 1998, *Davidse 37249* (MEXU, MO). **GUATEMALA.** BAJA VERAPAZ: Rabinal, 12 Jul 1970, *Harmon 3049* (F, MO). GUATEMALA: Guatemala city, 1800 m, 22 May 1970, *Harmon 2353* (F, MO); Volcán Pacaya, 10 Aug 1975, *Torke 469* (MO). QUETZALTENANGO: Volcán Lacandón, 1500–2650 m, 10 Jul 2005, *Pérez 739* (MO); Zunil, Nov–Dec 1839, *Hartweg 530* (F, MO). SACATEPÉQUEZ: Antigua, 27 Jun 1962, *Webster 11814* (F, MO). SAN MARCOS: Toniná, 2700 m, 7 May 1987, *Martínez 20799* (LL, MEXU, MO). SANTA ROSA:

Santa Rosa, May 1892, *Heyde 3167* (MO). HONDURAS. EL PARAÍSO: Cerro Monserrat, 2000 m, 6–9 Oct 1977, *Nelson 4311* (MO); Güinope, 1400 m, 16 Aug 1946, *Williams 10319* (MO). FRANCISCO MORAZÁN: La Cumbre, 1600 m, 4 Oct 1970, *Molina 25870* (MO). **MEXICO.** CHIAPAS: Cerro Cebú, 2236 m, 16 Dec 2004, *Martínez 678* (MEXU, MO); 2200 m, 17 Jul 2005, *Martínez 1027* (MEXU, MO); Lagunas de Monte Bello National Park, 1300 m, 1 Sep 1974, *Breedlove 37065* (CHIP, MEXU, MO); Motozintla, 2100 m, 13 Oct 1980, *Breedlove 46208* (MO); Mt. Ovando, 1–16 Jul 1940, *Matuda 4152* (CHIP, LL, MEXU, MO); Pueblo Nuevo, 1450 m, 25 May 1985, *Thomas 3637* (MO); Puerto del Viento, 30 May 1965, *Breedlove 10149* (CHIP, LL, MO); San Pablo Chalchihuitán, 1600 m, 18 Nov 1987, *Pérez 91* (MO); Solistahuacán, 1830 m, 10 Aug 1975, *Davidse 9459* (MO); Yerba Buena, 25 Aug 1972, *Webster 16957* (MO). OAXACA: Guevea de Humboldt, 1800 m, 30 Aug 1986, *Torres 8883* (IEB, MEXU, MO). VERACRUZ: Soteapan, 1420 m, 8 Jan 1972, *Beaman 5433* (MEXU, MO). **NICARAGUA.** BOACO: San José de los Remates, 1100–1180 m, 11 Feb 1983, *Moreno 20228* (MO); 1100–1140 m, 4 Oct 1984, *Moreno 24896* (MO); 1160 m, 4 Dec 1984, *Moreno 25104* (MO). ESTELÍ: Condega, 400–500 m, 19–29 Jan 2008, *Blandón 225* (MO); 400–500 m, 26 Jan 2008, *Calderón 228* (MO). JINOTEGA: Los Mollejones, 1100–1300 m, 10 Apr 1981, *Moreno 8057* (MO); Wiwili, Reserva Cerro Kilambé, 950–1100 m, 26–28 Aug 2000, *Rueda 14493* (MO); Volcán Yalí, 1621 m, 04 Sep 2010, *Coronado 5417* (MO); 1500–1542 m, 9 Apr 1981, *Moreno 7954* (MO); *7977* (MO). MADRIZ: San José de Cusmapa, 1250–1300 m, 4 Jan 1982, *Moreno 14285* (MO). MATAGALPA: Cerro La Piedra del Jicote, 980–1100 m, 22 Feb 1983, *Moreno 20462* (MO).

Distribution and habitat:—*Rovaeanthus strigosus* is found from Southern Mexico to Nicaragua in tropical rain forest, cloud forest and pine-oak forest at 400 to 2650 m.

Phenology:—Collected with flowers from June to February and fruits from May to October.

2. *Rovaeanthus suffrutescens* (Brandegee) Borhidi (2004: 133) ≡ *Rondeletia suffrutescens* Brandegee (1914: 70) ≡ *Rogiera suffrutescens* (Brandegee) Borhidi (1982: 67) Type:—MEXICO: Chiapas, Cerro del Boquerón, Aug 1913. *Purpus 6704* (holotype UC [online image]!, isotypes F!, MO!, US!). Figs. 3, 4.

Shrubs, decumbent or scandent, 1–2 m tall, twigs terete, sparsely strigose, glabrescent. **Stipules** erect, 1–3 × 2–3 mm, triangular, persistent, strigose. **Leaves** opposite, those of a pair at a node subequal, occasionally one leaf one half times longer than the other, petiolate; petioles 2–5 mm long, sparsely strigose, glabrescent; blade elliptic to ovate–elliptic, 4.3–9.7 × 1.5–3.5 cm, chartaceous, adaxially and abaxially strigose, mainly on costa and secondary veins, margins ciliolate, entire, base slightly cuneate to acute, apex acuminate, acumen up to 1.5 cm long; 5–8 pairs of secondary veins, the venation prominent on abaxial surface. **Solitary flowers or disposed on dichasial cymes**, terminal or axillary, 5–8 × 4–6 cm including corollas, 1-pedunculate, peduncle 1–3 cm long, axis glabrate to sparsely strigose, soon glabrescent, bracts triangular to linear–lanceolate, 5–9 mm long. **Flowers** subtended by linear bracteoles, 1–3 mm long, pedicelate or subbsessile, pedicels 1–4 mm long, glabrate; hypanthium subglobose turbinate to ovoid, 1–1.5 mm long, glabrate to sparsely strigose, soon glabrescent; calyx lobes equal to rarely subequal, the larger lobe up to 9–11 mm long, the smaller ones 4–9 mm long, lanceolate to linear–oblong, externally strigose or glabrate, internally glabrous; corolla infundibuliform, reddish to pinkinsk when fresh, the tube 15–23 × 3–4 mm, externally glabrate, internally hirtellous medially, lobes 5, obovate–elliptic, 5–8 × 4 mm, crisped margins, externally and internally glabrate, mouth with a ring of sparsely yellow trichomes and with fleshy ring occasionally not well developed; stamens in long styled flowers attached 4 mm below apex of tube, in short styled flowers attached 3 mm below apex of tube, anthers linear–ellipsoid, 3–4 mm long; style glabrous, in long styled flowers 15–21 mm long, in short styled flowers 8–12 mm long, the stigmas linear in long styled flowers, ovoid to linear in short styled flowers, 2–3 mm long. **Fruits** subglobose, turbinate, 8–10 × 6–8 mm, glabrate. **Seeds** angulate or polygonal, non caudate, 1 mm long.

Specimens examined:—GUATEMALA. SAN MARCOS: Tajomulco, 2300 m, 31 Dec 1964, *Williams 26932* (F, MEXU, MO). **MEXICO.** CHIAPAS: Ovando Mountain, 1800 m, 14 Nov 1939, *E. Matuda s.n.* (MEXU, MO); Unión Juárez, 1700–2300 m, 3 May 1987, *Miller 2674* (MO).

Distribution and habitat:—*Rovaeanthus suffrutescens* is restricted to Chiapas, Mexico and Guatemala in cloud forest, occurring from 1700 to 2300 m.

Phenology:—Not enough collections to establish accurate phenologic status.

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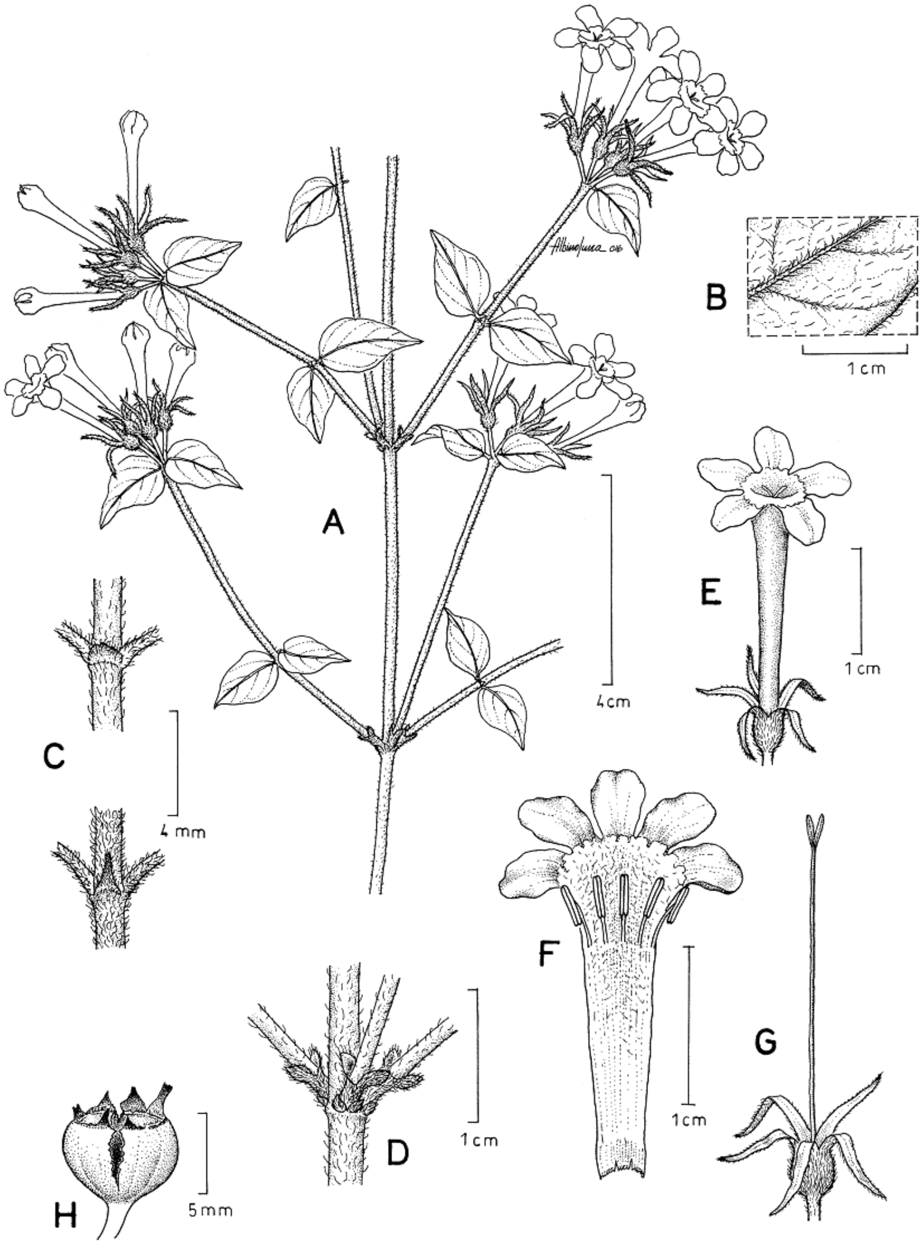

Figure 2. ***Rovaeanthus strigosus*****. A.** Fertile branch. **B.** Detail of the pubescence on the abaxial leaf surface. **C.** Stipule. **D.** Detail of a ternate branch. **E.** Longistylous flower. **F-G.** Dissected longistylous flower showing stamen insertion and internal pubescence. **G.** Calyx and gynoecium. **H.** Fruit. Illusration by Albino Luna.

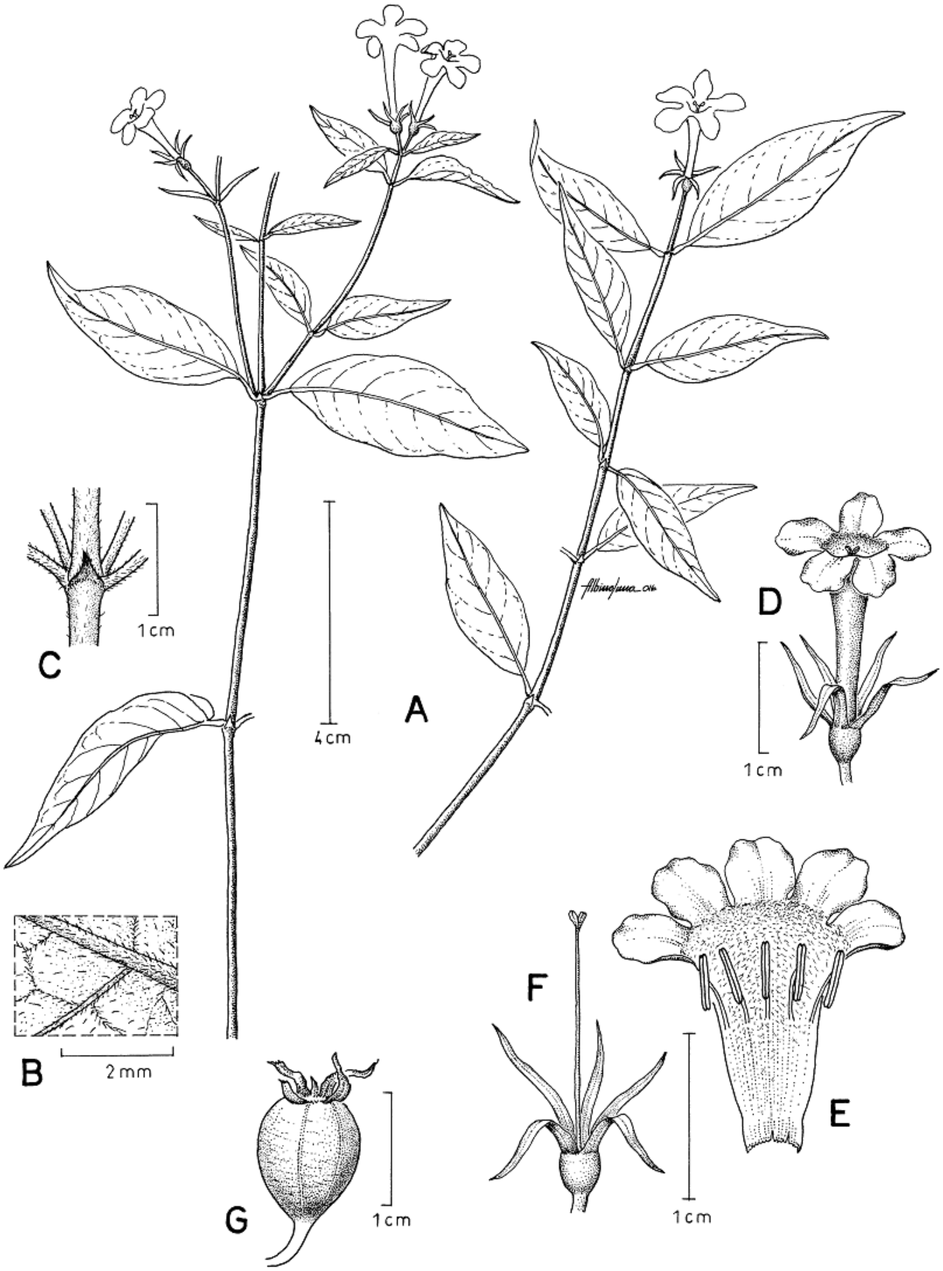

Figure 3. ***Rovaeanthus suffrutescens*****. A.** Fertile branch. **B.** Detail of the pubescence on the abaxial leaf surface. **C.** Stipule. **D.** Longistylous corolla. **E- F-.** Dissected longistylous flower showing stamen insertion and internal pubescence. **F.** Calyx and gynoecium. **G.** Fruit. Illusration by Albino Luna.

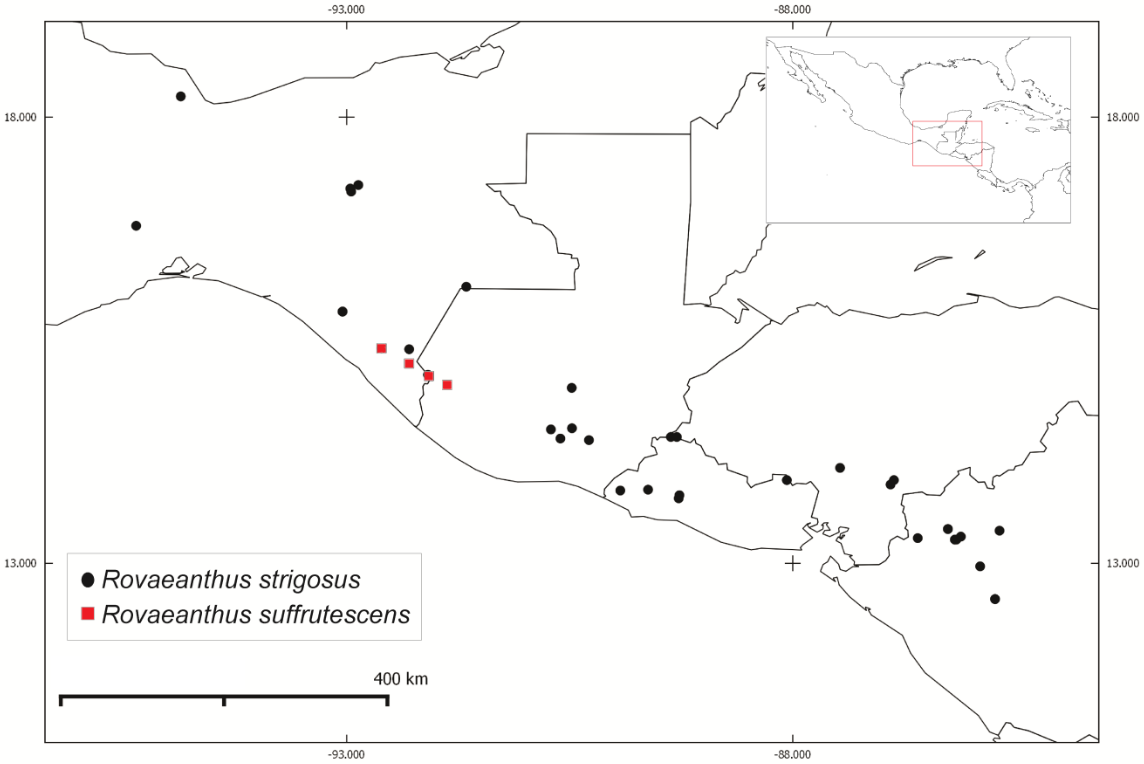

Figure 4. Geographic distribution of *Rovaeanthus* species.

PARTE II: EL GRUPO *Arachnothryx* EN LA TRIBU GUETTARDEAE

CAPÍTULO V: ESPECIES NUEVAS

Two new species of *Arachnothryx* (Rubiaceae) from Oaxaca, Mexico

Alejandro Torres-Montúfar & Helga Ochoterena

Brittonia

Two new species of *Arachnothryx* (Rubiaceae) from Oaxaca, Mexico

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Abstract. Two new species of *Arachnothryx* (Guettardeae, Rubiaceae) from the cloud forest of the Sierra Norte of Oaxaca, Mexico are described and illustrated. **Arachnothryx axillaris** together with *A. heteranthera* are the only two species in the genus with axillary inflorescences, but otherwise they are not similar. The new species is more similar to *A. capitellata*, but it differs in pubescence and inflorescence morphology. **Arachnothryx flores-olverae** can be confused with *A. buddleioides* mainly because they share discolorous leaves with densely tomentose pubescence, but they differ in stipule and inflorescence morphology. With these two new species the Sierra Norte of Oaxaca becomes more evidently the main hotspot of species diversity for the genus.

Keywords: Cloud forest, Guettardeae, Sierra Norte of Oaxaca, taxonomy.

Resumen. Se describen e ilustran dos nuevas especies de *Arachnothryx* (Guettardeae, Rubiaceae) del bosque mesófilo de montaña de la región de la Sierra Norte de Oaxaca, México. **Arachnothryx axillaris** y *Arachnothryx heteranthera* son las dos únicas especies en el género con inflorescencias axilares, pero por lo demás no son similares. Esta nueva especie puede ser confundida con *A. capitellata*, no obstante difieren en la pubescencia y la morfología de la inflorescencia. **Arachnothryx flores-olverae** se puede confundir con *Arachnothryx buddleioides* principalmente porque comparten las hojas discoloras con densa pubescencia tomentosa, pero difieren en la morfología de la estípula e inflorescencia. Con la descripción de estas dos nuevas especies se hace más evidente que la Sierra Norte de Oaxaca es el principal centro de diversidad para el género.

The neotropical genus *Arachnothryx* (Rubiaceae, Guettardeae) comprises 80 to 103 species of shrubs and trees (Lorence & Taylor, 2012; Borhidi, 2017). The genus is morphologically characterized by the interpetiolar stipules; typically terminal inflorescences; 4- (5-) merous flowers, corolla mouth glabrous, lacking a conspicuous hairy or fleshy ring, ovary 2-locular and many-ovulated; capsules, typically loculicidal; seeds angulated or rarely flattened. It was segregated from *Rondeletia* by Planchon in 1849 due to its naked corolla mouth (the mouth with a fleshy ring in *Rondeletia*) but was soon subsumed again within *Rondeletia* (Hooker, 1873; Hemsley, 1879; Standley, 1918). Subsequently, it was resurrected (Steyermark, 1967; Borhidi, 1982), reduced again to synonymy (Lorence, 1991; Burger & Taylor, 1993; Lorence, 1999), and finally accepted as a distinct genus (Borhidi, 2012; Lorence & Taylor, 2012), primarily based on molecular evidence (Rova et al., 2002, 2009).

Mexico is the center of diversity for the genus with approximately 60 species (Borhidi et al., 2004; Borhidi, 2012; Lorence & Taylor, 2012). *Arachnothryx* is one of several genera of Rubiaceae that are distributed mainly in Mexican cloud forests, other examples being *Deppea* Cham. & Schltdl., and *Rogiera* Planch. (Rzedowski, 1996; Lorence & Taylor, 2012). Within Mexico, there are three main areas that together harbor 40% of the species of the genus, mainly in cloud forests and tropical rain forests. These areas are: the Sierra of Los Tuxtlas (11 species), the Sierra Madre of Chiapas (13 species) and the Sierra Norte of Oaxaca (16 species) (Fig. 1). Although these regions have been

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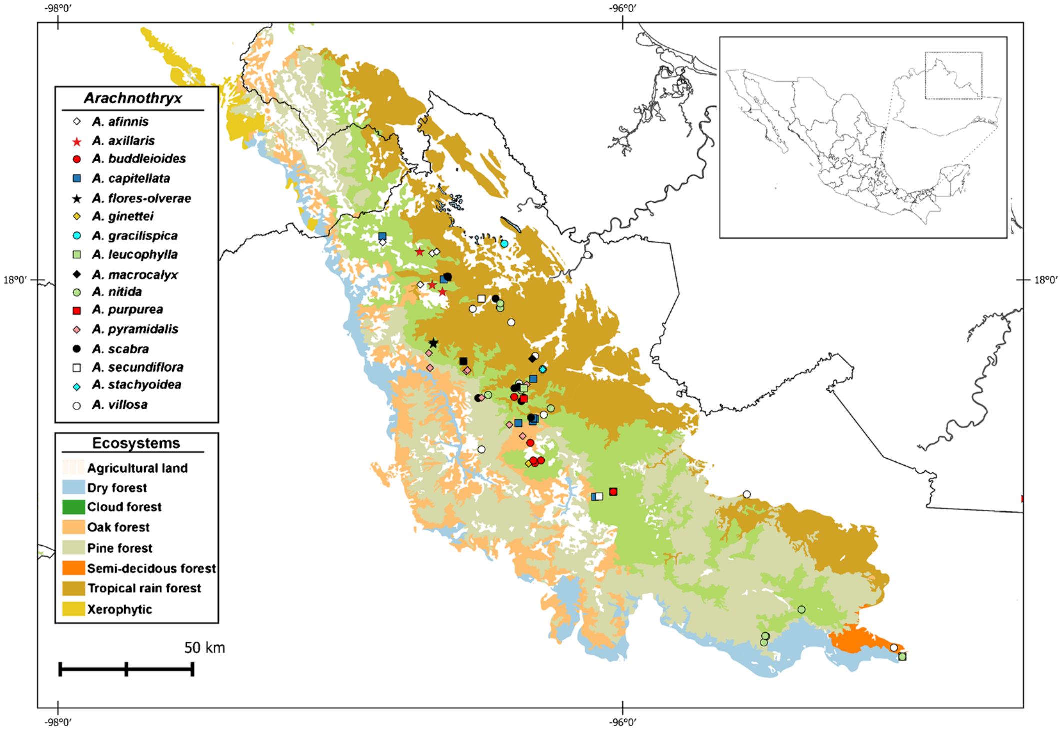

FIG. 1. Distributions of the 16 *Arachnothryx* species present in the Sierra Norte of Oaxaca, mainly concentrated in cloud and tropical rain forests. The new species are indicated with stars.

explored and are relatively well known, their biodiversity is so high that there is still need for more exploration and taxonomic work.

During the course of a systematic study of *Arachnothryx*, some specimens from the cloud forest of the Sierra Norte of Oaxaca, Mexico, were found to represent two new species, which are described herein. Their discovery highlights the high levels of plant diversity and endemism present in the Sierra Norte, which harbors a mosaic of plant formations, including temperate forest, mountain cloud forest, and tropical rain forest (Lorence & García-Mendoza, 1989; García-Mendoza, 2004). Among these formations, cloud forest occupies ca. 152,000 ha. naturally scattered along a narrow elevation belt with intense land-use changes (Arellanes, 1996; Toledo-Aceves et al., 2011; Sánchez-Ramos & Dirzo, 2014). It is undoubtedly one of the most threatened plant formations in the region.

New species

Arachnothryx axillaris A. Torres-Montúfar & H. Ochoterena, **sp. nov.** Type: México. Oaxaca: San José Tenango: zona boscosa al NE de San Martín Caballero, accesible por la vereda de San Martín a Cerro Caballero, aproximadamente 1.5 km de San Martín, 18°06′33.5″N, 96°38′ 45.7″W, 1515 m, 20 Jan 2002 [bud, fl, fr], *X. Munn-Estrada 1771* (holotype: MEXU; isotype: XAL, PTBG–n.v.) (Fig. 2).

Diagnosis: *Arachnothryx axillaris* can be recognized within the genus by the combination of strigose stems, simple, axillary racemes with 3–9 red flowers per inflorescence; it is similar to *A. capitellata* (Hemsl.) Borhidi, but differs in stem pubescence (strigose vs. hirtellous in *A. capitellata*), inflorescence position (axillary vs. terminal), and in having fewer flowers per inflorescence (3–9 vs. more than 35).

Trees 4–7 m tall; stems strigose; twigs terete. Stipules triangular, 1-aristate, erect, 1–3 × 1.5–2 mm, deciduous, margin with reddish colleters, externally strigulose, internally glabrate. Leaves opposite, those of a pair subequal, petiolate; petioles 2–4 mm long, subequal, strigillose; lamina elliptic, 2–7.3 × 1.3–3.2 cm, thickly chartaceous, adaxial surface glabrate, abaxial surface strigillose with pubescence mainly on veins, base cuneate, apex acuminate, acumen 1–2 cm long;

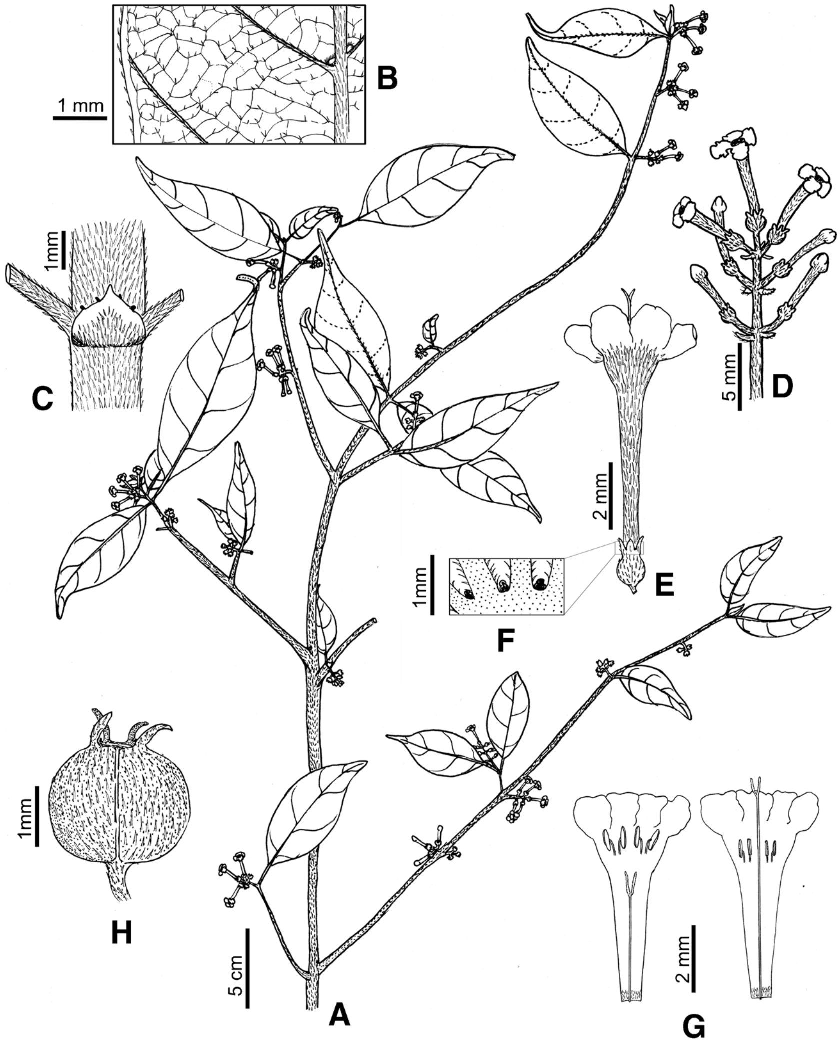

Fig. 2. *Arachnothryx axillaris*. **A.** Fertile branch. **B.** Detail of pubescence and domatia (arrow) on the abaxial leaf surface. **C.** Stipule with colleters. **D.** Inflorescence. **E.** Longistylous flower showing strigose pubescence. **F.** Calyx sinus colleters. **G.** Open brevistylous (left) and longistylous (right) corolla, showing pubescent ring at base. **H.** Mature capsule. (A–H, from *X. Munn-Estrada 1771*; G, brevistylous corolla from *G. Juárez García 1143*).

secondary veins in 6–7 pairs; domatia present abaxially in the axils of secondary veins. Inflorescences axillary, shorter than subtending leaves, determinate, lacking secondary axes, 3–9-flowered, 3 × 4 cm including the corollas, subsessile or pedunculate; peduncle 2–4 mm long, densely strigose; bracts lanceolate, 1–1.5 mm long, strigose. Flowers heterostylous; pedicellate, pedicels up to 1 mm long, strigose; hypanthium turbinate, 1.5 × 1 mm, strigose; calyx limb 0.3 mm, internally glabrous, externally sparsely strigose; calyx lobes 4, subequal, triangular, erect, 0.5–0.9 × 0.3–0.5 mm, internally glabrous, externally strigillose, each sinus with small reddish deciduous colleters; corolla red at anthesis, hypocrateriform, tube 5–8 mm long, externally strigose, internally with a villosulous ring basally, lobes 4, ovate, 2–3 × 2 mm, margin undulate or crisped, externally glabrate, internally glabrate; stamens 4, in brevistylous flowers with the tips included, in longistylous flowers with the tips exserted; style glabrous, stigma linear, bilobed, in short-styled flowers included, ca. 5 mm long, in long-styled flowers exserted, 6–7 mm long. Fruit a spheroidal capsule, loculicidal, 2–2.5 mm in diameter, strigillose, with calyx lobes persistent, reflexed. Seeds angulated, 1.0 × 0.5 mm, testa reticulate.

Geographic distribution.—Endemic to Mexico. Known only from the cloud forest of the Sierra Norte of Oaxaca (Fig. 3), from 1263 to 1515 m elevation.

Phenology.—Flowering and fruiting in January.

Etymology.—The specific epithet "*axillaris*" refers to the axillary inflorescences, atypical in *Arachnothryx*.

Conservation status.—*Arachnothryx axillaris* is known only from one region with an area smaller than 10 km^2, therefore, it meets the criteria B1ab(iii) for the category of Critically Endangered (CR) according to the IUCN (2011). Moreover, the vegetation in the area has been altered by human activities, which may also threaten the persistence of the species.

Additional specimens examined. MEXICO. Oaxaca: San Pedro Teutila: El Faro, Torre 130 de la L. T. Temascal II-Oaxaca Potencia, 17°59′23.8′N, 96°38′51″W, 1263 m, 20 Jan 2005 [fl], *G. Juárez García 1143* (MEXU); Torre 131 Bis de la Línea eléctrica Temascal II-Oaxaca Potencia, 17°59′10.4″N, 96°39′8″W, 1463 m, 14 Jan 2005 [fl], *C. A. Cruz Espinosa 2314* (MEXU).

Arachnothryx axillaris can be confused with *A. capitellata* (Hemsl.) Borhidi, *A. gracilispica* (Standl.) Borhidi and *A. secundiflora* (B. L. Rob.) Borhidi. All of these species have red flowers and occur in the same geographical area. Nevertheless, the new species differs from the other three in its deciduous stipules (vs. persistent in *A. capitellata*, *A. gracilispica* and *A. secundiflora*), domatia in the axils of the secondary leaf veins, simple racemes up to 4 cm long (vs. panicles longer than 5 cm) with 3–9 flowers (vs. more than 35-flowered) (Fig. 4).

Arachnothryx axillaris and *A. heteranthera* (Brandegee) Borhidi are the only two species in the genus with axillary inflorescences. The former species differs from the latter in having deciduous stipules (vs. persistent in *A. heteranthera*), domatia in the axils of the secondary veins of the leaves, a red corolla (vs. white), and the inflorescence up to 4 cm long (vs. more than 6 cm), 3- to 9-flowered (vs. more than 20-flowered), and lacking secondary axes.

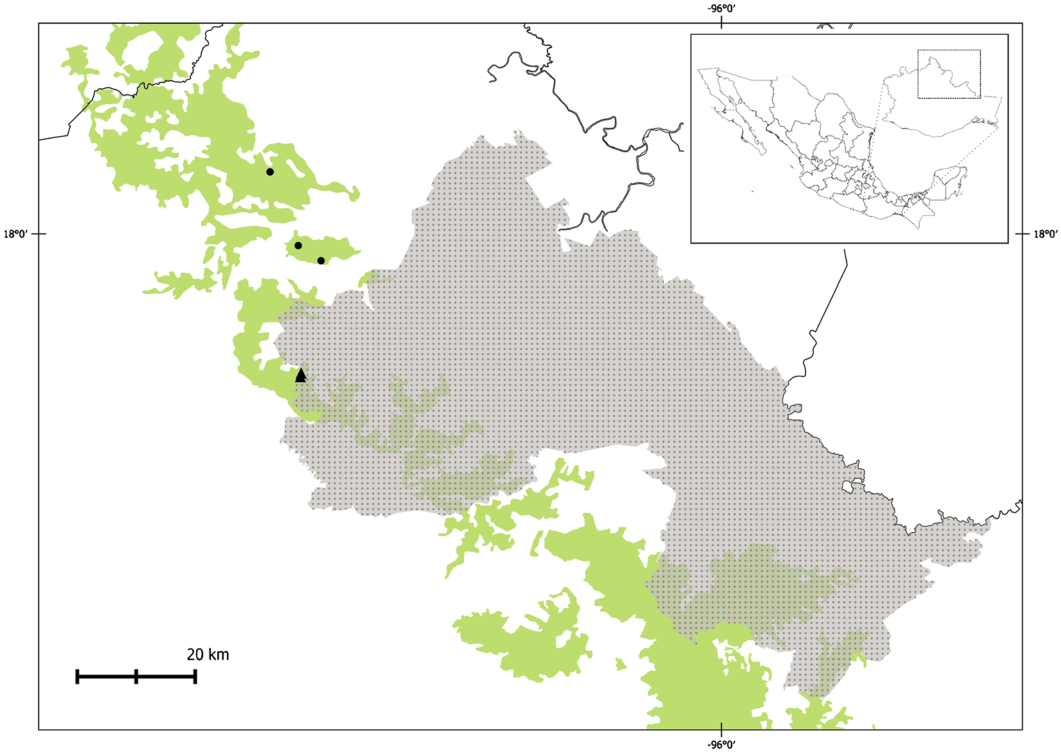

FIG. 3. Distribution of *Arachnothryx axillaris* (circles) and *A. flores-olverae* (triangles) within the cloud forest (green) and the Chinantla region (dotted gray) of the Sierra Norte of Oaxaca.

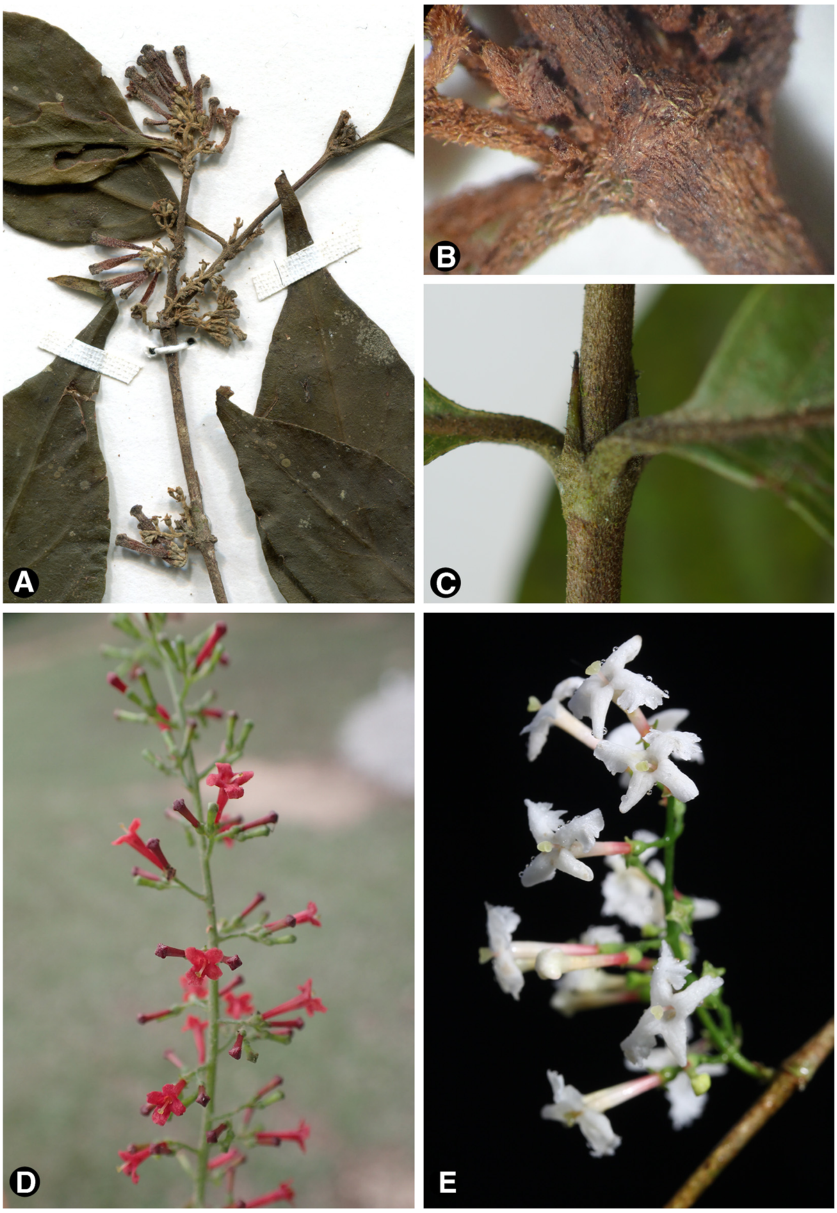

Fig. 4. Comparison of *Arachnothryx axillaris* with other morphologically similar species. **A–B.** *A. axillaris*: **A.** Fertile branch showing axillary inflorescences with red flowers; **B.** Stipule and strigose pubescence. **C–D.** *A. capitellata*: **C.** Stipule and hirsute pubescence; **D.** Terminal compound, many-flowered inflorescence with red corollas. **E.** *A. heteranthera* showing the axillary compound inflorescence with white corollas (C–D, by H. Ochoterena; E, by Canek Ledesma Corral).

Arachnothryx flores-olverae A. Torres-Montúfar & H. Ochoterena, **sp. nov.** TYPE: México. Oaxaca: Mpio. San Pedro Sochiapam, Camino entre Retumbadero y Finca Unión Francesa, 9 km NE de San Pedro Sochiapam, 17°47′53.3″N, 96°40′ 48.5″W, 1365 m, 01 Nov 2016 [bud, fl], *H. Ochoterena* et al. *1038* (holotype: MEXU; isotypes: BR, MO, NY, SERO) (Fig. 5).

Diagnosis: *Arachnothryx flores-olverae* differs from most species in the genus by the inflorescences shorter than or sometimes equal to the subtending leaves, with 4–6 pairs of secondary axes,

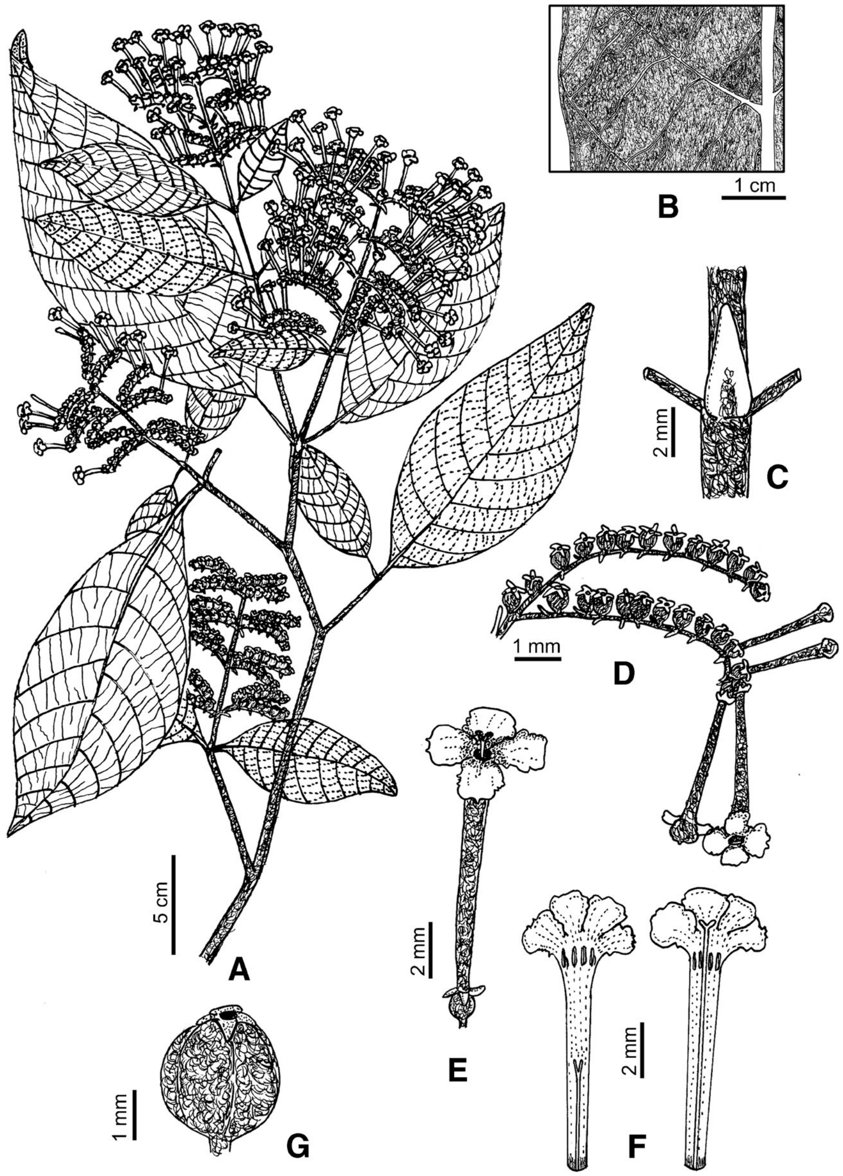

Fig. 5. *Arachnothryx flores-olverae*. **A.** Fertile branch. **B.** Detail of dense tomentose pubescence on the abaxial leaf surface. **C.** Stipule. **D.** Loose lateral branch of inflorescence. **E.** Brevistylous flower showing densely tomentose pubescence. **F.** Open brevistylous (left) and longistylous (right) corolla, showing pubescent ring at base. **H.** Mature capsule showing persistent and reflexed calyx lobes. (A–G, from *H. Ochoterena 1038;* G, longistylous corolla from *B. Velasco P. 185*).

these forming conspicuous scorpioid cymes; it differs from *A. buddleioides* (Benth.) Planch. by triangular, 4–6 mm long stipules (vs. lanceolate and longer than 6 mm in *A. buddleioides*), the inflorescences shorter than or equal to the subtending leaves (vs. longer), with 4–6 pairs of secondary axes (vs. 10–25 pairs) and loose cymes (vs. compact cymes).

Trees 4–6 m tall; stems densely tomentose, glabrescent; twigs terete. Stipules triangular, erect, 4–6 × 2–3 mm, deciduous, externally tomentulose, glabrescent, internally tomentulose. Leaves opposite, those of a pair markedly unequal, one leaf one to three times longer than the other, petiolate; petioles 3–10 mm long, unequal, tomentulose; lamina elliptic to ovate, 3.1–14.2 × 1.3–3.5 cm, chartaceous, adaxial surface tomentose, soon glabrescent, abaxial surface persistently tomentose,

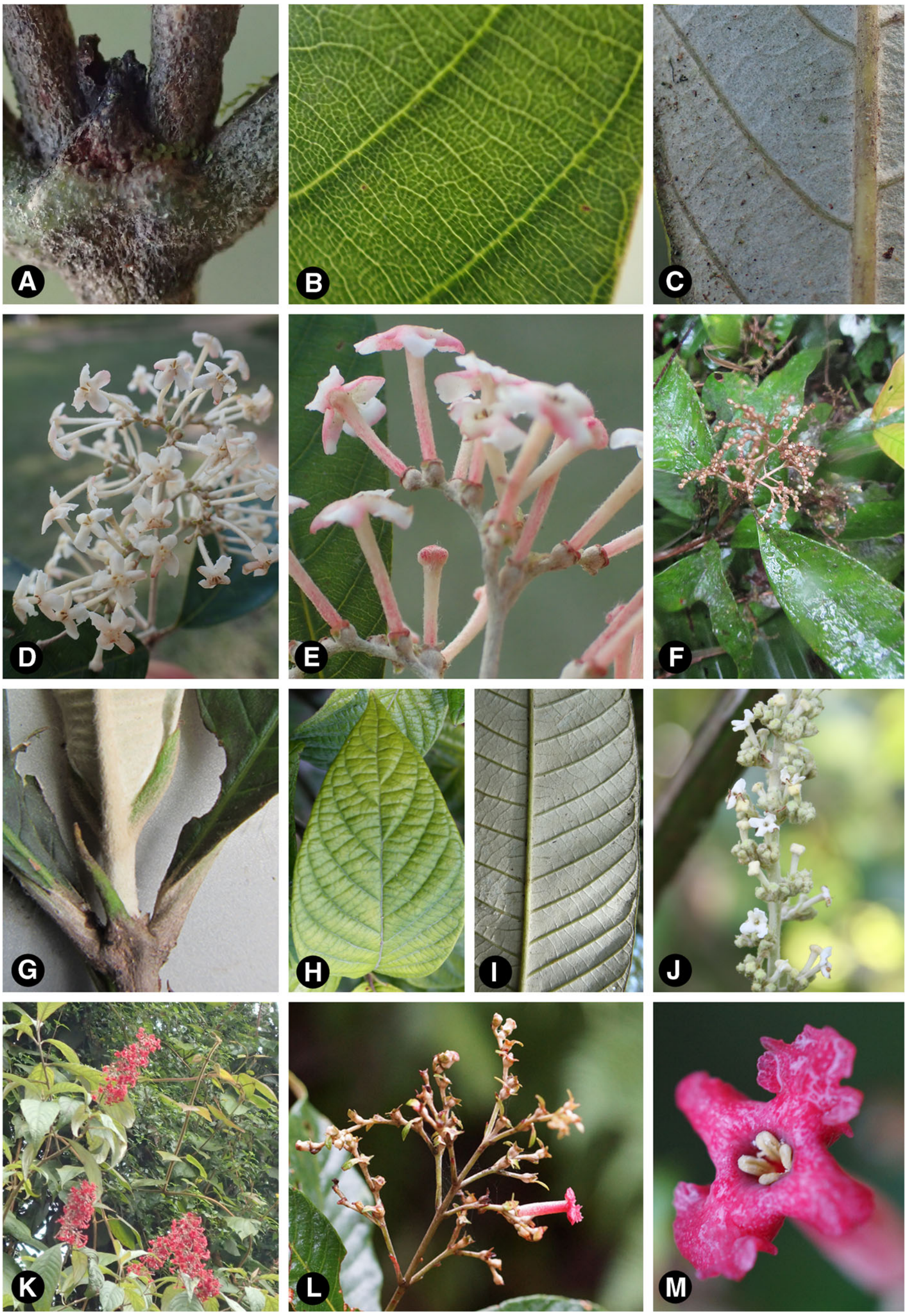

Fig. 6. Comparison of *Arachnothryx flores-olverae* with other morphologically similar species. **A–F.** *A. flores-olverae*:. **A.** Stipule. **B.** Glabrate adaxial leaf surface. **C.** Densely tomentose abaxial leaf surface. **D.** Inflorescence with few secondary axes and white flowers. **E.** Lateral loose scorpioid cymes with pinkish flowers. **F.** Fruiting branch. **G–J.** *A. buddleioides*:. **G.** Stipule and discolored leaves. **H.** Glabrate adaxial leaf surface. **I.** Densely tomentose abaxial leaf surface. **J.** White flowered inflorescence with compact secondary axes. **K.** *A. pyramidalis* showing the inflorescence with progressively decreasing secondary axes and red flowers. **L–M.** *A. nitida*: **L.** Lateral loose scorpioid cymes with pink flowers. **M.** Brevistylous pink flower.

base cuneate, apex acuminate, acumen up to 1 cm long; 13–17 pairs of secondary veins; domatia absent. Inflorescences terminal, with 4–6 secondary axes, shorter than or sometimes equal to the subtending leaves, multi-flowered, 3.3–6.2 × 3–6.5 cm including the corollas; peduncle 4–8 mm long, tomentose; each pair of secondary axes loose, scorpioid, (9-) 13- to 21-flowered, all axes of the same length, 1.5–2.5 cm long, tomentose; bracts lanceolate, 3 mm long, tomentose. Flowers heterostylous; pedicellate, pedicels up to 1.5 mm long, tomentose; hypanthium turbinate, 1–1.5 mm long, tomentose; calyx limb up to 1 mm, internally glabrate, externally tomentulose, calyx lobes 4, equal or subequal, triangular, sometimes erect, the large lobe 1–1.5 mm long, the smaller lobes up to 1 mm, externally tomentose; internally glabrous; corolla when fresh white to pinkish, hypocrateriform, tube 8–10 mm long, externally tomentulose, internally with a villosolous ring basally, 4 lobes, elliptic, 2–3 × 2 mm, margin undulate or crisped; stamens 4, in brevistylous flowers not exserted, in longistylous flowers shortly exserted; style glabrous, linear to ellipsoid stigma, bilobed, in brevistylous flowers included, 5 mm long, in longistylous flowers exserted, 7–8 mm long. Fruit a spheroidal capsule, loculicidal, 3–4 mm in diameter, tomentulose, calyx lobes persistent, reflexed. Seeds angulated, 1.0 × 1.0 mm, testa reticulate.

Geographic distribution.—Endemic to Mexico. Known from the cloud forest of the Chinantla region in the Sierra Norte of Oaxaca (Fig. 3), at 1154 to 1365 m of elevation.

Phenology.—Flowering on November to March and fruiting on December to January.

Etymology.—The specific epithet *flores-olverae* is dedicated to the botany professor, Hilda Flores-Olvera, of the Instituto de Biología of the Universidad Nacional Autónoma de México, who has intensively worked to improve the knowledge of the Mexican flora and who is a passionate trainer of new generations of botanists (including both authors).

Conservation status.—The new species *A. flores-olverae* is known only from one region with an area smaller than 10 km^2, therefore, it meets the criteria B1ab(iii) for the category of Critically Endangered (CR) according to the IUCN (2011). Even more, the vegetation in the area has been altered by human activities, conditions that could threaten the persistence of the species.

Additional specimens examined. MEXICO. Oaxaca: San Pedro Sochiapam: Finca Unión Francesa, 17°46′21″N, 96°38′29.1″W, 1154 m, 10 Feb 2016 [fr], *H. Ochoterena* et al. *942* (BR, MEXU, MO, SERO); 17 Jun 2016 [fr], *B. Velasco P.* et al. *185* (MEXU, SERO); Vereda a San Juan Teponaxtla, en el SO de la Finca Unión Francesa, ca. 22 km al SO de San Pedro Sochiapam, o bien ca. 17 km al NE de San Juan Teponaxtla, 17°46′21″N, 96°38′29.1″W, 1097 m, 01 Nov 2016 [fl, fr], *B. Velasco P.* et al. *186* (BR, MEXU).

Arachnothryx flores-olverae can be confused with *A. buddleioides*, with which it shares discolorous leaves and a white to pinkish, similarly sized corolla, but it differs by the characters listed in the diagnosis. It is also similar to *A. pyramidalis* (Lundell) Borhidi in corolla color, the inflorescence with loose secondary axes, and because the two species both grow in the same area. Nevertheless, the new species differs by having terete twigs (vs. quadrangular in *A. pyramidalis*), the inflorescences shorter than the subtending leaves (vs. longer) and with 4–6 pairs of secondary axes of about equal length (vs. 12–16 pairs decreasing in length towards the apex), and a 5–8 mm long corolla tube (vs. 10–12 mm long). On the other hand, it can be confused with *A. nitida* (Hemsl.) Borhidi by the inflorescences shorter than the subtending leaves with few loose secondary axes and the pinkish corolla, but it differs by the hypocrateriform corolla (vs. salverform in *A. nitida*), the inflorescence secondary axes usually (9-) 13- to 21-flowered (vs. 7- to 9-flowered in *A. nitida*) and the spheroidal fruit, 3–4 mm long (vs. ovoid, up to 8.8 mm long) (Fig. 6).

Acknowledgments

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PARTE II: EL GRUPO *Arachnothryx* EN LA TRIBU GUETTARDEAE

CAPÍTULO VI: FILOGENIA DEL GRUPO *Arachnothryx*

Untangling the *Arachntohryx* generic complex (Rubiaceae): insights from phylogenetics

Alejandro Torres-Montúfar, Susy Fuentes, Thomas Borsch & Helga Ochoterena

Preparado para Taxon

Untangling the *Arachnothryx* generic complex (Rubiaceae): new insights from phylogenetics

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Running title: Molecular Phylogeny of the Arachnothryx complex (Rubiaceae)

Phylogeny and taxonomy of the Arachnothryx complex (Rubiaceae)

Abstract

The taxonomy of the neotropical genus *Arachnothryx* is closely linked to *Rondeletia* and to the *Rondeletia* complex. Molecular studies are in strong overall agreement in the polyphyly of the "Rondeletia complex": some genera are closely related to *Rondeletia* in Rondeletieae, while others closely related to *Arachnothryx* are placed within Guettardeae (*Cuatrecasasiodendron*, *Gonzalagunia*, *Javorkaea*, *Renistipula* and *Rogiera*). Past studies assessing relationships had a limited sample size and generally weak support. Uncertainties persist in the generic circumscription and placement of some genera particularly related to *Arachnothryx*. Using morphological characters we identify a generic assemblage treated here as the *Arachnothryx* complex. A molecular phylogeny of was constructed with the following main objectives: (1) to test the monophylly of *Arachnothryx*, (2) to evaluate the test the position of *Gonzalagunia* within Guettardeae; (3) to corroborate the synonymy of *Cuatrecasasiodendron* and *Javorkaea* within *Arachnothryx* as proposed in previous phylogenetic results; (4) to corroborate the monophyly of *Donnellyanthus* and *Rovaeanthus* currently considered as synonyms of *Arachnothryx* and *Rogiera* by morphology, and, (5) to test if *Renistipula* belongs to Guettardeae as the morphological evidence suggest. Phylogenetic analyses were performed with combined ITS, *trn*L-F, *trn*K-*mat*K and *pet*D markers of 182 taxa. Our results showed a highly supported clade formed by *Arachnothryx* clade sister to the *Guettarda* group. The genus *Rogiera* is corroborated as monophyletic, and the genera *Donnellyanthus* and *Rovaeanthus* are also corroborated as monophyletic and even placed at tribe Rondeletieae. The genus *Arachnothryx* is confirmed to be

paraphyletic regarding to *Javorkaea*, *Gonzalagunia* and *Renistipula* with strong support. Given that these genera were found within the *Arachnothryx* clade are here synonymized as *Gonzalagunia* following the priority principle. Then 121 new combinations are proposed. Within the *Arachnothryx* clade we found that it is composed of four groups with morphological correspondence (*Buddleioides* group, *Capitellata* group, *Leucophylla* group and *Javorkaea-Renistipula*).

Introduction

The taxonomy of the neotropical genus *Arachnothryx* Planch. is closely linked to *Rondeletia* L. (tribe Rondeletieae). The genus *Arachnothryx* was segregated from *Rondeletia* by Planchon (1849) based on its corolla with a naked corolla mouth in contrast with the presence of a fleshy ring of *Rondeletia*. However, it was soon treated as a synonyms of *Rondeletia* by several authors (Hooker, 1873; Hemsley, 1879; Standley, 1918), resurrected (Steyermark, 1967; Borhidi, 1982), proposed again as synonyms (Lorence, 1991; Burger & Taylor, 1993; Lorence, 1999; Taylor, 2001) and finally accepted in recent Rubiaceae treatments (Borhidi, 2012; Lorence 2012).

The taxonomic controversy of *Rondeletia* is also seen in the segregation of many other genera from it: *Acunaeanthus* Borhidi, Járai-Koml. & Moncada, *Donnellyanthus* (Donn.Sm.) Borhidi, *Javorkaea* Borhidi & Járai-Koml., *Renistipula* Borhidi, *Suberanthus* Borhidi & Z.M. Fernández, *Renistipula* Borhidi, *Rogiera* Planch., *Roigella* Borhidi & Z.M. Fernández, *Rovaeanthus* Borhidi (Steyermark, 1964; Borhidi *& al*., 1980, 2004, 2011; Borhidi & Fernández-Zequeira, 1981a; 1981b; Borhidi & Járai-Komlodi, 1983). These genera were named the *Rondeletia* complex and traditionally placed in tribe Rondeletieae by the imbricate corolla aestivation and many-seed capsular fruits (Robbrecht, 1988; Delprete, 1999a; Borhidi, 2006).

The molecular studies strongly agree that the *Rondeletia* complex is a polyphyletic group (Rova *& al*. 2002, Robbrecht & Manen 2006, Rova *& al*. 2009, Manns & Bremer 2010). The molecular phylogenies indicate that the genera *Arachnothryx*, *Javorkaea* and *Rogiera* (*Arachnothryx* complex) are more closely related to the tribe Guettardeae than to Rondeletieae. Nevertheless, the inclusion of these genera in Guettardeae is polemical (Taylor & Gereau 2010) since Guettardeae is well characterized by the axillary inflorescences, the bi- to multi-locular ovaries with the ovules solitary in each locule and drupaceous fruits (Bremekamp 1966, Taylor & Gereau 2010). Now, the Guettardeae circumscription had to include plants with terminal inflorescences, multiple ovules per locule and capsular fruits (Achille *& al*. 2006, Taylor & Gereau 2010).

In the Flora Mesoamericana, *Renistipula* is included as synonym of *Arachnothryx* (Lorence 2012), however molecular studies treated it as a member of Hamelieae (Stranczinger *& al*. 2014) although it lacks the diagnostic characters of this tribe (raphides, ebracteolate inflorescences, yellow or yellowish flowers and granulate to tuberculate outer testa walls) (Manns & Bremer, 2010; Martínez-Cabrera *& al*. 2007). Additionally, Lorence (2012) considered the monotypic genus *Donnellyanthus* as *Arachnothryx* due to the 4-merous calyx and corolla mouth lacking a fleshy ring, however, the authors recognized that the loculicide capsule and the winged seeds are typical of *Rondeletia*, suggesting that more studies are needed to make a taxonomic decision.

In addition, the molecular evidence sustained the close relation between *Arachnothryx* and *Gonzalagunia* Ruiz & Pav. (Rova *& al*. 2002, 2009). The genus *Gonzalagunia* is morphologically quite similar to *Arachnothryx*, distinguishable only by the dry fruits in the latter and the fleshy fruits in the former. However, it is a doubtful character since Ståhl (1999) reports fruit dimorphism in *Gonzalagunia*, where both spongy and dry fruits are mixed in the same infrutescence and its dry fruits often resemble unripe capsules of *Arachnothryx*.

Although several studies include representatives of the *Rondeletia* complex and are in overall agreement on its polyphylly (Rova *& al*., 2002, 2009; Robbrecht & Manen, 2006; Manns & Bremer, 2010), uncertainty persists particularly about the naturalness of *Arachnothryx*, then our study aimed to reassess the limits of the *Arachnothryx* complex and in particular of *Arachnothryx* using molecular evidence and to propose a phylogenetic hypothesis for the intergeneric relationships.

Material and methods

Taxon sampling.—The taxon set for Rondeletieae included in Torres-Montúfar *& al*. (2017, 2018) was extended to include most of the species of *Arachnothryx*, *Gonzalagunia*, *Javorkaea*, *Renistipula* and *Rogiera* as well as other genera from Guettardeae and Rondeletieae. Several genera representing other tribes of Cinchonoideae (Condamineeae, Chiococceae and Sabiceeae) and Ixoroideae (Gardenieae) were used as outgroups. Taxon names with authors, vouchers and GenBank accession numbers are presented in Appendix 1.

DNA extraction, amplification and sequencing.—Silica gel dried leaves were used for DNA extraction when available, complemented with herbarium material. DNA was extracted using NucleoSpin Plant II kit (Macherey Nagel, Düren, Germany) following the manufacturer's protocol or a three-fraction cetyltrimethylammonium bromide (CTAB) method (Borsch *& al*. 2003).

Three plastid markers (trnK-matK, trnL-F and petD) and nuclear ITS were amplified and sequenced in this study. The amplification of each marker was performed in reaction volumes of 50 µL, containing 2 µL of extracted DNA (with a concentration of 10–20 ng/µL), 14.7 µL of H2O, 5 µL of 10× peqLab Taq. buffer S containing MgCl2, 3 µL of MgCl2 (25 mM), 10 µL of betaine monohydrate (5 M), 1 µL of BSA (10 ug/µl), 2 µL of forward primer (20 pm/µl), 2 µL of reverse primer (20 pm/µl), 10 µL dNTPs (each 0.25 mM) and 0.3 µL Taq polymerase 5 units/µl (PeqLab, Erlangen Germany).

For trnK-matK the amplification was performed in two halves using the primers trnKFbryo (Wicke & Quandt 2009) and COmatK670R (Tesfaye & al 2007) plus NYmatK480F (Hilu & al. 2003) and psbA5R (Steele & Vilgalys 1994). PCR conditions were: 1 cycle of denaturation (90 seconds at 96°C, 60 seconds at 50°C, 120 seconds at 68°C), 35 cycles of annealing (30 seconds at 95°C, 60 seconds at 48°C, 120 seconds at 68°C), extension (20 minutes at 68°C). The trnL-F region was amplified using the primers trnTc and trnTf (Taberlet & al. 1991). PCR conditions were: 30 cycles of denaturation (60 seconds at 96ºC), annealing (60 seconds at 50ºC), and extension (120 seconds at 72ºC). The petD intron including the petB-petD spacer was amplified using the primers PIpetB1411F or PIpetB1365F and PIpetD738R or PIpetD346R (Löhne & Borsch 2005). PCR conditions were: 35 cycles of denaturation (60 seconds at 97°C), annealing (60 seconds at 48°C), extension (45 seconds at 72°C) and a final extension step (7 min at 72°C).

The ITS region (ITS1 1 5.8S 1 ITS2) was amplified and sequenced using primers ITS 4 and ITS 5 (White & al. 1990). PCR conditions were: 30 cycles of denaturation (60 seconds at 96ºC), annealing (60 seconds at 50ºC), and extension (120 seconds at 72ºC). The petD intron including the petB-petD spacer was amplified using the primers PIpetB1411F or PIpetB1365F and PIpetD738R or PIpetD346R (Löhne & Borsch 2005). PCR conditions were: 35 cycles of denaturation (60 seconds at 97°C), annealing (60 seconds at 48°C), extension (45 seconds at 72°C) and a final extension step (7 min at 72°C).

Owing to scarcity of herbarium material for some species, and technical difficulties, i.e., primer mismatches, degraded templates and possible gene loss, not all amplification products were obtained for each taxon. All amplification products were purified by QIAquick PCR Purification Kit (QIAGEN GmbH, Hilden, Germany). Sequencing was performed by Macrogen Inc., South Korea (http://www.macrogen.com).

Sequence assembly, alignment and indel coding.— The matrix comprises 182 taxa and 452 sequences, 383 generated for previous studies (Torres-Montúfar *& al*. 2017, 2018), complemented with 37 sequences downloaded from GenBank generated and used by Rova *& al*. (2002, 2009). New pherograms were edited and assembled using PhyDE v.0 995 (Müller & al. 2005). Sequences were then added to the multiple sequence alignment of Torres-Montufar & al. (2017) following the criteria proposed by Löhne & Borsch (2005). Gaps were coded manually following the simple gap criterion of Simmons & Ochoterena (2000); Simple Sequence Repeats (SSR) and inversions were manually coded following Ochoterena (2009). Regions of uncertain homology (mutational hotspots) were removed from the matrices prior to phylogenetic analyses.

Phylogenetic analyses.—Parsimony (P) analyses were performed using the combined matrix with nucleotides, gaps, inversions and SSRs, only including parsimony informative characters. A heuristic search with 10 000 replicates of Wagner trees constructed with random taxon addition followed by TBR branch swapping was performed in TNT version 1.1 (Goloboff & al. 2003); 10 trees were saved on each replicate and a further TBR was conducted to completion saving up to 10 000 trees. These trees were submitted to further analysis using the "new technology" option, alternating ratchet parsimony (Nixon 1999a), sectorial, drift and tree fusion (Goloboff 1999) options. One hundred initial sequences were used until the consensus was stabilized 10 times using a 100% factor. All the most parsimonious trees were collected and opened in WinClada (Nixon 1999b) and summarized in a strict consensus tree. Additionally, a Jackknife analysis (JK) was executed in TNT version 1.1 (Goloboff & al. 2003), re-sampling the matrix 10 000 times with the same parameters used for the new technology searches.

For Bayesian Inference (BI) the optimal models of sequence evolution were estimated using ModelTest 3.6 (Posada 2008) using the following parameters: 203 substitution schemes, +F base frequencies, +I and +G rate variation, nCat=4 and SPR tree search. BI analyses of the concatenated nucleotide matrix were conducted using MrBayes v.3.1.2 (Huelsenbeck & Ronquist 2001). Four independent Markov Chain Monte Carlo (MCMC) runs were carried out, each with four parallel chains. Each chain was performed for 1 000 000 generations, saving one random tree every 1 000 generations. The burn-in was set to 1 000 (10%) when the stability of the chain was reached. Phylogenetic trees were visualized using Figtree (Rambaut & Drummond 2010). The P and BI consensus were graphically summarized rather than presenting any of them as a preferred topology to be conservative trusting only nodes supported by all three inference methods. This was achieved in WinClada by manually collapsing nodes that were insufficiently supported in at least one of the trees obtained by the alternative methods. We considered cutoff values as follows: 64% for JK (Farris & al. 1996) and for posterior probabilities 0.95 PP (Alfaro & Holder 2006).

Results

Phylogenetic analysis.—The aligned matrix with all regions consisted of 5883 characters (without hotspots), of which 1014 (17%) were potentially parsimony informative. The coding of microstructural mutations resulted in 194 characters of which 154 (79%) were potentially informative for parsimony. The alignments and microstructural matrices are available from TreeBase (Pending). Detailed matrix statistics regarding each marker contribution are given in Table 1.

Table 1. Matrix marker contribution

	*trn*K-*mat*K	*trn*L-F	*pet*D	ITS	**Total**
Sequences	121	158	153	20	**452**
Aligned positions (hotspots excluded)	2972	1076	1109	726	**5883**
Microstructural characters (mch)	72	45	55	22	**194**
Potentially informative chars. (nts/mch)	534/55	202/37	172/42	106/20	**1014/154**
Evolution model	GTR+I+G			HKY+I+G	

There were no significant conflicts between well-supported clades from the BI and parsimony analyses of individual and combined matrices. We only presented the parsimony strict consensus tree with Jackknife support values (JK) above branches and Posterior Probabilities below branches in Figure 1.

In all the analyses clades corresponding to tribes (Condamineeae, Chiococceae, Gardenieae, Guettardeae, Sabiceeae and Rondeletieae) have strong support values (Fig. 1). The genus *Chione* is the only one that is not unequivocally placed within a particular tribe, in our study is retrieved as sister to the Rondeletieae-Guettardeae clade, but we do not have a comprehensive tribal representation within Cinchonoideae then we will still consider it as incerta sedis.

The *Rondeletia* complex was corroborated as polyphyletic. *Arachnothryx*, *Javorkaea*, *Renistipula* and *Rogiera* are placed in Guettardeae (99 JK, 1.0 PP), while *Donnellyanthus, Rondeletia*, *Rovaeanthus, Tainus* and *Suberanthus* in Rondeletieae (100 JK, 1.0 PP). Rondeletieae and Guettardeae are well supported as sister tribes.

The tribe Guettardeae is divided into three well-supported clades: (1) the *Arachnothryx* assemblage (*Arachnothryx, Gonzalagunia* and *Javorkaea*) (100 JK, 1.0 PP), (2) the *Guettarda* clade (100 JK, 1.0 PP), (3) *Machaonia-Rogiera* clade (99 JK, 1.0 PP).

In particular, for the genera of the *Arachnothryx* complex, *Rogiera* is well defined by the corolla mouth with a yellow hairy ring in addition to the winged seeds. The *Arachnothryx* assemblage is characterized by the naked corolla mouth and the wingless seeds (except for Renistipula, which has briefly winged seeds). Within the *Arachnothryx* assemblage is well nested a clade formed by several species of *Gonzalagunia* which is characterized by the fleshy fruits (Figure 1).

The clade *Arachnothryx* assemblage is formed by four principal groups with morphological correspondence: (I) the *Leucophylla* group (99 JK, 1.0 PP), (II) the *Javorkaea-Renistipula* group (99 JK, 1.0 PP), (III) the *Capitellata* group (100 JK, 1.0 PP), and the (IV) the *Buddleioides* group (100 JK, 1.0 PP) including *Gonzalagunia* (Fig. 2).

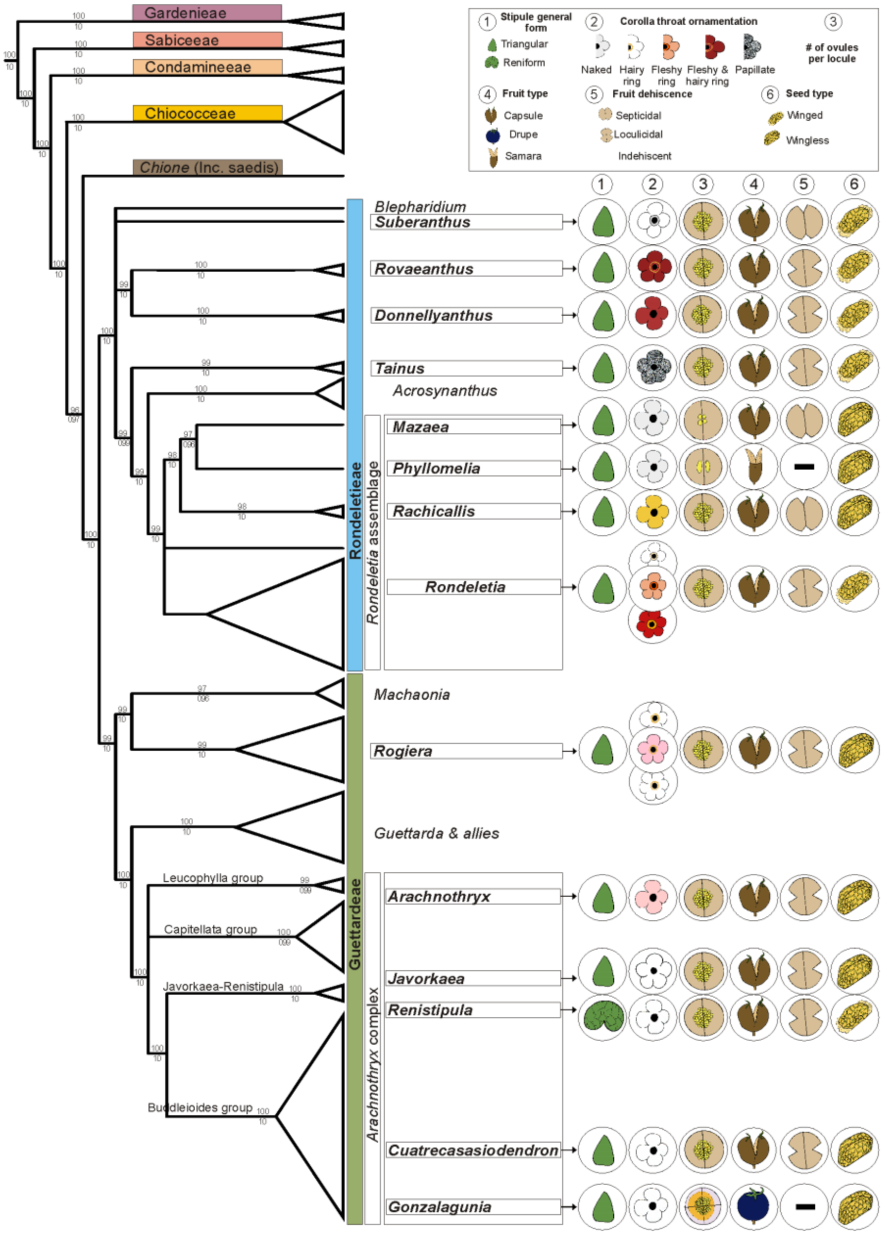

Figure 1. Consensus tree (L=2555) of the most parsimonious trees, showing the main morphological differences among the genera of the traditional *Rondeletia* complex. Numbers above branches correspond to Jackknife values (JK), number below branches correspond to posterior probability (PP) from Bayesian analysis. The genus *Cuatrecasasiodendron* is included in the phylogenetic position obtained from Rova et al. (2002).

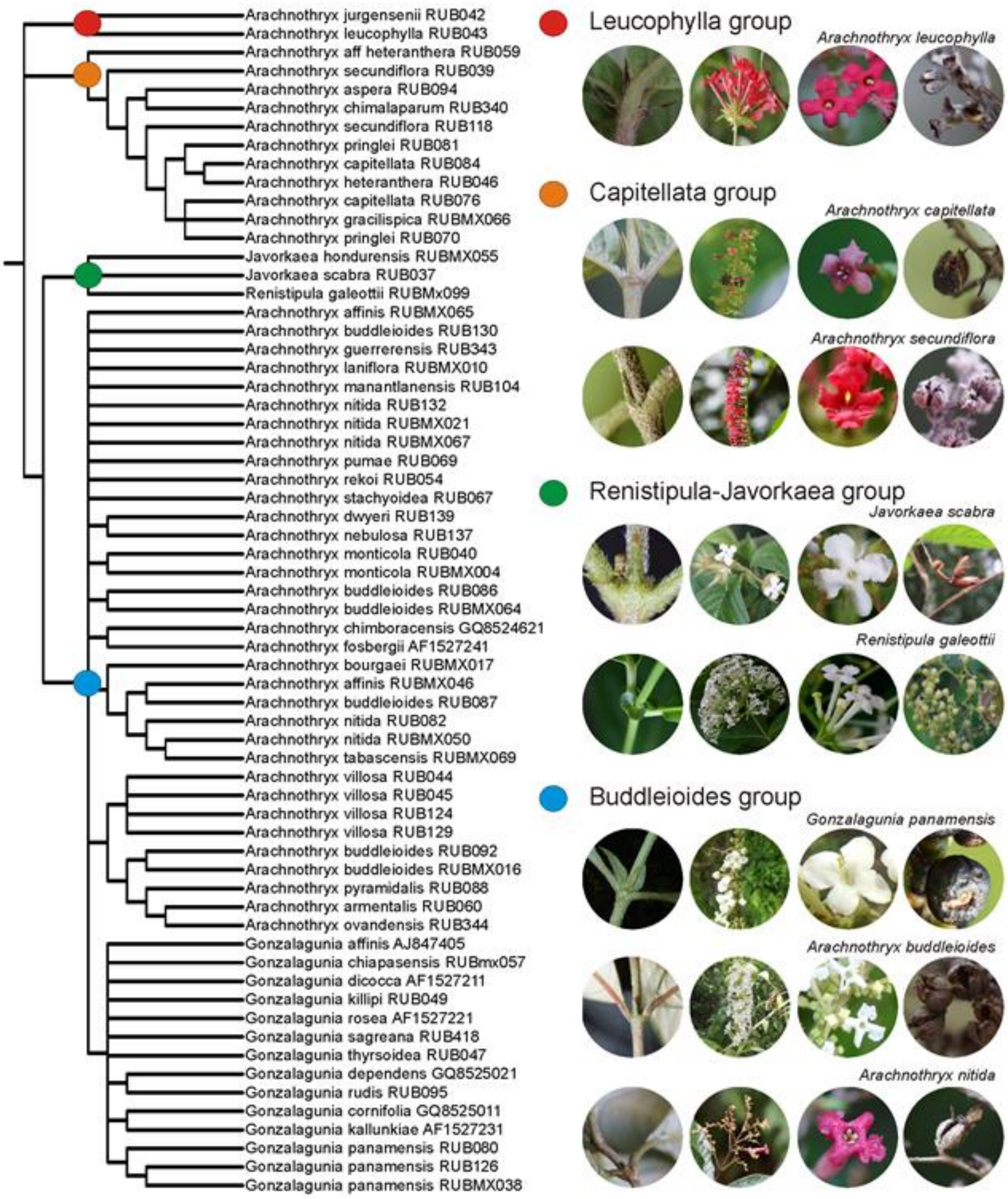

Figure 2. Subtree showing the *Arachnothryx* assemblage and its members.

Discussion

Tribe Guettardeae.**—** Our results are in agreement with previous studies (Rova & al., 2002; Robbrecht & Manen, 2006; Manns & Bremer, 2010), in that the *Arachnothryx* complex, traditionally placed in Rondeletieae, shares a most recent common ancestor with Guettardeae.

The phylogenetic affinity between Guettardeae and Rondeletieae has been suggested at the first molecular analyses of the family (Bremer *& al*., 1995) in whose studies *rbc*L sequence data resulted in a clade comprising *Rogiera*, *Rachicallis*, *Guettarda* and *Antirhea*. Since then, the major studies of the family recovered both tribes as sister groups (Robbrecht & Manen, 2006; Bremer & Eriksson, 2009; Manns & Bremer, 2010).

With the use of molecular phylogenetics, the Guettardeae limits became broader than previously thought. Despite the agreement in the general tribal composition it has become difficult to either differentiate Guettardeae from Rondeletieae, even referred to as a complex of tribes by Robbrecht & Manen (2006). Two morphological features supports the Guettardeae-Rondeletieae clade: the quicuncial corolla aestivation and the spatulate corolla lobes. Previous authors (Robbrecht, 1988) considered their corolla aestivation to be imbricate, which is a common feature within Cinchonoideae. We found that imbricate corolla buds of Rondeletieae and Guettardeae can be better described as quincuncial corolla aestivation, which is almost unique among Cinchonoideae. Also, we prefer to describe the corolla lobes of both as spatulate in contrast to the common triangular or linear shape in other genera of Cinchonoideae.

Rova & al. (2009) already suggested merge both tribes and accepting a large tribe Rondeletieae. An alternative solution could be not to include the *Arachnothryx* complex in Guettardeae, but rather identify diagnosable lineages that could be elevated to tribes. This solution is currently difficult since there is disagreement about the monophylly of Guettardeae *sensu stricto* (Manns & Bremer 2010 vs. Robbrecht & Manen 2006). In any case, before any classification changes are done with respect to Guettardeae (merging it with Rondeletieae or further splitting) it necessary to conduct further studies particularly within the Guettarda and allies clade, with a broader taxon representation.

The inclusion within Guettardeae of the *Arachnothryx* complex is controversial (Taylor & Gereau, 2010) because the tribe Guettardeae was morphologically rather isolated by the axillary inflorescences, uniovulate ovaries and usually drupaceous fruits (Robbrecht, 1988), this inclusion expanded the morphological circumscription for the tribe and plants with terminal inflorescences, multiple ovules per locule and capsular fruits (typical for Rondeletieae) should be included in Guettardeae (Achille *& al*., 2006; Taylor & Gereau, 2010).

Even more, within the Guettardeae clade, the *Arachnothryx* complex results polyphyletic: the *Arachnothryx* clade is retrieved as sister of *Guettarda* & allies as in the phylogenetic studies (Rova & al., 2002; Manns & Bremer, 2010) both groups are in turn sister to the *Rogiera* clade.

***Rogiera*.—**The genus *Rogiera* is consistently corroborated in previous studies as monophyletic as (Rova & al., 2009; Manns & Bremer, 2010). In the study of Rova & al. (2002) *Rogiera* is retrieved as polyphyletic, with a species closely related to tribe Rondeletieae. The species *Rogiera suffrutescens* and *Rogiera strigosa* are easily recognized within *Rogiera* by the ternate leaves and the corolla mouth with a yellow hairy ring in addition to a fleshy ring. These differences and the phylogenetic position found by Rova & al. (2002) lead Borhidi & al. (2004) to propose the genus *Rovaeanthus* to encompass both species. Nevertheless, in the recent taxonomic treatment of Rubiaceae the genus *Rovaeanthus* is not recognized and treated as a *Rogiera* synonym (Lorence, 2012), despite the molecular and morphological evidence that supports its recognition as separate entities (Rova & al., 2002; Manns & Bremer, 2010).

In our study, the sister group of *Rogiera* is *Machaonia* Bonpl., which is characterized by the usually ternate or fasciculate leaves, four to pentamerous flowers and schizocarpic fruits (Lorence 2012; Borhidi, 2012). In the previous phylogenetic studies the position of *Rogiera* is conflictive regarding to our results. In Manns & Bremer (2010) *Rogiera* was retrieved as the earlier divergent group within Guettardeae, and the genus *Machaonia* as the sister to the *Guettarda* & allies plus the *Arachnothryx* clade. While in Rova & al. (2002) both genera are in an unsolved position in addition to the *Guettarda* and allies plus the *Arachnothryx* clade.

***Arachnothryx*.—**Our study presents the most comprehensive phylogenetic hypothesis of *Arachnothryx* to date. The genus *Arachnothryx* is distinguished by the naked corolla mouth and the wingless seeds, in addition to the quincuncial corolla aestivation, spatulate corolla lobes and capsular fruits. The generic limits of *Arachnothryx* have been re-drawn recently, and genera were proposed as syonymys: *Donnellyanthus*, *Javorkaea* and *Renistipula*.

The genus *Donnellyanthus* was separated from *Rondeletia* based on the absence of a faucial fleshy ring at the corolla mouth and by the glabrous ovary disc (Borhidi & al., 2011). At the latest revision of Rubiaceae this taxon was treated as *Arachnothryx deamii* due to the 4-merous calyx and corolla without a fleshy ring at the corolla mouth (Lorence, 2012). However, the author pointed that the loculicide capsule and the winged seeds are typical of *Rondeletia*, suggesting that more studies were needed to make a taxonomic decision. Previous phylogenetic studies show that this taxon should be placed at Rondeletieae instead of Guettardeae (Manns & Bremer, 2010), our results undoubtedly corroborates this. The genera *Javorkaea* and *Renistipula* are discussed below.

Within *Arachnothryx* we recognize four major groups with some morphological correspondence (1) *Buddleioides* group, (2) *Javorkaea-Renistipula* group, (3) *Capitellata* group and (4) *Leucophylla* group.

The *Buddleioides* group (1) is mainly characterized by the densely arachnoid tomentose pubescence present at the abaxial surface of the leaves or at the corolla tube. This group is widely distribuited, particularly *Arachnothryx buddleioides* which is recognized as a species complex that undoubtedly needs further studies to test species limits.

Within the *Buddleioides* group is nested *Gonzalagunia*, previous authors also found this relationship (Rova & al., 2002; Manns & Bremer, 2010). It also has many taxa with the dense tomentose pubescence in abaxial leaf surface. The genus *Gonzalagunia* is quite similar to *Arachnothryx*, distinguishable only by the dry fruit in the latter and the fleshy fruit in the former (Lorence, 2012). However, it is a doubtful character since Ståhl (1999) reports fruit dimorphism in *Gonzalagunia*, where both fleshy and dry fruits are mixed in the same infrutescence and its dry fruits often resemble unripe capsules of *Arachnothryx*. Capsular fruits are unequivocally reconstructed for the common ancestor of Guettardeae and Rondeletieae (Torres-Montúfar & al., 2017); the evolution of fleshy fruits within Guettardeae independentely occurred two times (*Gonzalagunia* and *Guettarda* and allies), however, the drupes of *Gonzalgunia* are defined as endocarpic drupes while the *Guettarda* and allies correspond to mesocarpic drupes (Torres-Montúfar & al., 2018).

In our study as in previous phylogenetic studies both genera had been shown in the same clade without resolution (Rova & al., 2002; Robbrecht & Manen, 2006; Rova *& al.*, 2009, Manns & Bremer, 2010). The aims of these studies were not to test the generic limits of these genera, so the sampling design do not allowed the authors to take the accurate taxonomic decision of synonymize these genera. With a bigger sampling and new evidence we propose to synonymize *Arachnothryx* (described in 1849 by Jules Planchon) under *Gonzalagunia* (described in 1794 by Hipólito Ruiz and José Pavón), following the priority principle. The 121 new combinations are presented in the taxonomic treatment.

The clade formed by *Javorkaea-Renistipula* (2) was retrieved as sister to the *Buddleioides* group. The genus *Javorkaea* was described by Borhidi & Járai-Komlodi (1983) to encompass *Rondeletia hondurensis*, a species endemic to Honduras. According to the protologue, *Javorkaea* differs from *Arachnothryx* in having a broad connate stipular ring with 1-3-lobed stipules, 5-merous calyx and a large corolla. However, these characters are widespread within many others species of *Arachnothryx*. Then, by the dubious morphological diagnostic characters and molecular evidence, *Javorkaea* was synonymized with *Arachnothryx* (Rova & al. 2002, Borhidi & al., 2004; Lorence 2012).

The inclusion of *Javorkaea* within *Arachnothryx* clade was also retrieved in Rova & al. (2002) and Manns & Bremer (2010). For the former, the sample is only identified as *Javorkaea* and the resolution is not good enough to compare it with our results. Manns & Bremer (2010) retrieved *Javorkaea hondurensis* sister to a clade formed by *Cuatrecasasiodendron* and *Arachnothryx chimboracensis*, the former not included in our analysis and the latter is placed within our Buddleioides group, however their sampling is not good enough to reliable establish a position.

The genus *Cuatrecasasiodendron* was positioned in the Rondeletieae because of its foliaceous calyx lobes, capsular fruits, horizontal seeds, and ovary with many ovules in each locule (Steyermark, 1964). However, in the phylogenies produced by Rova & al. (2009) *Cuatrecasasiodendron* was found within *Arachnothryx* clade, the morphological affinities lead them to synonymyze both genera, decision that we adopt although we did not include in *Cuatrecasasiodendron*.

Our study recovered *Javorkaea* sister to the one species sampled of *Renistipula*. The latter was segregated from *Arachnothryx* by Borhidi *& al*. (2004) based on the foliaceous and reniform stipules. As *Javorkaea*, the genus *Renistipula* morphologically resembles *Arachnothryx;* so much so that both were treated as a synonyms in Flora Mesoamericana (Lorence 2012).

The genus *Renistipula* is not included in any confident phylogenetic study. The three species of *Renistipula* were described as *Rondeletia (*Standley, 1918; Standley & Steyermark, 1940). Subsequently transferred to *Arachnothryx* (Planchon, 1849) based on tetramerous corolla without "faucial ring" and capsules of septicidal dehiscence (Borhidi, 1982), and later encompassed in the genus *Renistipula* by Borhidi & al. (2004) based on their stipitate orbicular or reniform stipules. However, Lorence (2005) questioned the separation of the new genus and suggested further molecular analyses to reveal phylogenetic relationships among *Arachnotryx* and *Renistipula*. Recently, Stranczinger *& al.* (2014) included *Renistipula* within the tribe Hamelieae using ITS and *trn*L-F data. Nevertheless, this conclusion was weak due to *Renistipula* lacks of the diagnostic characters of Hamelieae as the raphides (Manns & Bremer, 2010; Martínez-Cabrera *& al*. 2007). Our results places *Renistipula* at Guettardeae and also supports the current synonymy with *Arachnothryx* proposed in taxonomic treatments.

The *Capitellata* group (3) is well characterized by the leaf adaxial surface strigose or glabrate, terminal or axillar (*Arachnothryx heteranthera*) inflorescences, corolla tube glabrous, white or red colored. Species with these characteristics are distribuited at the center of Mexico, Atlantic slopes and Mesoamerica. The Leucophylla group (4) is formed by plants characterized by the apparentely corymbose inflorescences formed by the axis reduction and the large red flowers (bigger than 2 cm). Species with these characteristics are distribuited at Pacific slopes and Mesoamerica.

Conclusions

The genera formerly included in the *Rondeletia* complex placed at Guettardeae conforms the *Arachnothryx* complex, well distinguished by the combination of characters from the Rondeletieae. Within the *Arachnothryx* complex two main lineages are retrieved: *Rogiera* and the *Arachnothryx-Gonzalagunia-Javorkaea-Renistipula*.

The genus *Rogiera* is confirmed as monophyletic and morphologically well defined and supported, also, the position in Rondeletieae of *Rovaeanthus* previously considered as *Rogiera* in a taxonomic treatment, is corroborated. Furthermore, the genus *Donnellyanthus* is corroborated as a Rondeletieae member instead of being synonymyzed with *Arachnothryx*.

Within the *Arachnothryx* clade four clades were retrieved with morphological correspondence as the pubescence of the abaxial leaf surface, inflorescence architecture and the corolla size and color. Also, we found that the genera *Gonzalagunia-Javorkaea-Renistipula* are intermingled within *Arachnothryx* clade, then in order to reflect our phylogenetic results 121 new combinations from *Arachnothryx* and *Renistipula* to *Gonzalagunia* are proposed.

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Taxonomy— As a consequence of the present analysis we propose the following taxonomic changes which may lead to a more natural treatment of the *Rondeletia* complex based on monophyletic groups: (i) the synonymy of *Arachnothryx, Javorkaea* and *Renistipula* with *Gonzalagunia,* and (ii) the recognition of *Donnellyanthus* and *Rovaeanthus* as accepted genera within Rondeletieae.

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= *Buena* Cav., Anales Hist. Nat. 2:278. 1800 –TYPE: *Buena panamensis* Cav.

= *Arachnothryx* Planch., **syn. nov.**, Fl. Serres Jard. Eur. 5:442. 1849 –TYPE: *Arachnothryx leucophylla* (Kunth) Planch. [≡*Rondeletia leucophylla* Kunth].

= *Duggena* Vahl ex Standl., Contr. U.S. Natl. Herb. 18:125. 1926 –TYPE: *Duggena richardii* Vahl.

= *Cuatrecasasiodendron* Standl. & Steyerm., **syn. nov.**, Acta Biol. Venez. 4:29. 1964 –TYPE: *Cuatrecasasiodendron colombianum* Standl. & Steyerm.

= *Javorkaea* Borhidi & Járai-Koml., **syn. nov.**, Acta Bot. Hung. 29:16. 1984 –TYPE: *Javorkaea hondurensis* (Donn. Sm.) Borhidi & Járai-Koml. [≡*Rondeletia hondurensis* Donn. Sm.].

= *Renistipula* Borhidi, **syn. nov.**, Acta Bot. Hung. 46:122. 2004 –TYPE: *Renistipula galeottii* (Standl.) Borhidi [≡*Rondeletia galeottii* Standl.].

New combinations for *Gonzalagunia* (Guettardeae)

Gonzalagunia angustispica (Borhidi, E. Martínez & Ramos) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx angustispica* Borhidi, E. Martínez & Ramos, Acta Bot. Hung. 57:17. 2015 – TYPE: MEXICO, Veracruz, Tezonapa, 22 Oct 2010, J.C. L. Corral 965, (HT: MEXU!; isotypes: BP [not seen]).

Gonzalagunia armentalis (L.O. Williams) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia myriantha* var. *armentalis* L.O. Williams, Phytologia 26:127. 1973 ≡ *Arachnothryx myriantha* var. *armentalis* (L.O. Williams) Borhidi, Acta Bot. Hung. 35:310. 1989 ≡ *Arachnothryx armentalis* (L.O. Williams) Lorence, Novon 15:450. 2005 – TYPE: GUATEMALA, Quiché, 22 Nov 1934, A.F. Skutch 1776, (HT: F!).

= *Rondeletia ovandensis* Lundell, Wrightia 5: 326. 1976 ≡ *Arachnothryx ovandensis* (Lundell) Borhidi, Acta Bot. Hung. 35:310. 1989 – TYPE: MEXICO, Chiapas, Mt. Ovando, 24 Oct 1941, E. Matuda 6067, (HT: LL [image!]; isotypes: F!, LL[not seen], MEXU!).

Gonzalagunia aspera (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia aspera* Standl., N. Amer. Fl. 32:54. 1918 ≡ *Arachnothryx aspera* (Standl.) Borhidi, Acta Bot. Hung. 28:68. 1982 – TYPE: COSTA RICA, San José, Pont du Rodeo, below Pacaca, Jan 1891, H. Pittier 3243, (HT: US [image!]).

Gonzalagunia atravesadensis (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia atravesadensis* Lorence, Novon 1:137. 1991 ≡ *Arachnothryx atravesadensis* (Lorence) Borhidi, Acta Bot. Hung. 38:139. 1995 – TYPE: MEXICO, Oaxaca, Cerro Atravesada to Cerro Azul, 6 Dec 1956, T. MacDougall s.n., (HT: MEXU!).

Gonzalagunia bertieroides (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia bertieroides* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4:267. 1929 ≡ *Arachnothryx bertieroides* (Standl.) Borhidi, Acta Bot. Hung. 28:70. 1982 – TYPE: PANAMA, Bocas del Toro, Chiriquí Trail, 3 Dec 1928, G.P. Cooper 598, (HT: F!; isotypes: NY [image!], WIS [image!]).

= *Rondeletia cooperi* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4:267. 1929 ≡ *Arachnothryx cooperi* (Standl.) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: PANAMA, Bocas del Toro, Buena Vista Camp, Jan-Mar 1928, G.P. Cooper 600, (HT: F!; isotypes: G [image!], NY [image!], WIS [image!]).

= *Rondeletia kirkbridei* Dwyer, Ann. Missouri Bot. Gard. 67:469. 1980 ≡ *Arachnothryx kirkbridei* (Dwyer) Borhidi, Acta Bot. Hung. 28:70. 1982 – TYPE: PANAMA, Veraguas, NW of Santa Fe, 16 May 1975, S.A. Mori 6112, (HT: MO!; isotypes: PTBG [image!]).

= *Rondeletia salicifolia* Dwyer & M.V. Hayden, Phytologia 15:58. 1967 ≡ *Arachnothryx salicifolia* (Dwyer & M.V. Hayden) Borhidi, Acta Bot. Hung. 28:70. 1982 –TYPE: PANAMA, Cerro Jefe, 27 Jan 1966, E.L. Tyson et al. 3319, (HT: MO!).

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= *Rondeletia platysepala* Standl., Ann. Missouri Bot. Gard. 27:343. 1940 ≡ *Arachnothryx platysepala* (Standl.) Borhidi, Acta Bot. Hung. 28:70. 1982 – TYPE: PANAMA, Coclé, vicinity of El Valle, 14 May 1939, P.H. Allen 1791, (HT: F!; isotypes: GH [image!], US [image!], NY [image!]).

= *Rondeletia urophylla* Standl. & L.O. Williams, Phytologia 26:129. 1973 ≡ *Arachnothryx urophylla* (Standl. & L.O. Williams) Borhidi, Acta Bot. Hung. 35:311. 1989 – TYPE: COSTA RICA, Puntarenas, 03 Aug 1951, P.H. Allen 6291, (HT: F!; isotypes: EAP [image!]).

Gonzalagunia bourgaei (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia bourgaei* Standl., N. Amer. Fl. 32:56. 1918 ≡ *Arachnothryx bourgaei* (Standl.) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: MEXICO, Veracruz, Orizaba, 8 Jul 1866, E. Bourgeau 2618, (HT: US [image!]; isotypes: P [image!]).

Gonzalagunia buddleioides (Benth.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia buddleioides* Benth., Pl. Hartw. 69. 1840 ≡ *Arachnothryx buddleioides* (Benth.) Planch., Fl. Serres Jard.

Eur. 5:442. 1849 –TYPE: MEXICO, Oaxaca, No date, K.T. Hartweg 502, (HT: K [image!]; isotypes: G [image!], K [image!], NY [image!]).

= *Arachnothryx breviflora* Borhidi, Acta Bot. Hung. 46:106. 2004 –TYPE: MEXICO, Chiapas, Pantepec, 22 Sept 1981, D.E. Breedlove 52978, (HT: MEXU!).

= *Rondeletia longipetiolata* (Lundell) Borhidi, Wrightia 5:325. 1976 ≡ *Arachnothryx longipetiolata* (Lundell) Borhidi, Acta Bot. Hung. 35:310. 1989 –TYPE: MEXICO, Chiapas, Escuintla, 14 Nov 1945, E. Matuda 6146, (HT: LL!; isotypes: LL!, MEXU!, S [image!]).

= *Gonzalea nivea* Bartl. ex DC., Podr. 4:436. 1830 ≡ *Gonzalagunia nivea* (Bartl. ex DC.) Kuntze, Revis. Gen. Pl. 1:284. 1891 ≡ *Duggena nivea* (Bartl. ex DC.) Standl., Contr. U.S. Natl. Herb. 18:125. 1916 – TYPE: MEXICO, unknown locality, Mar 1833, T. Haenke s.n., (HT: PR? [not seen]).

= *Gonzalagunia tonduzii* K. Krause, Bot. Jahrb. Syst. 54:42. 1916 – TYPE: COSTA RICA, Cerro de Roble, Apr 1898, A. Tonduz 11813, (HT: B [presumably destroyed]; isotypes: F!).

= *Rondeletia rothschuhii* Loes., Bot. Jahrb. Syst. 60: 369. 1926. – TYPE: NICARAGUA, Matagalpa, no date, E. Rothschuh 597, (HT: B [presumably destroyed]; isotypes: F [fragment]!).

Gonzalagunia buddleioides var. ***aspera*** (J.H. Kirkbr.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia buddleioides* var. *aspera* J.H. Kirkbr., Ann. Missouri Bot. Gard. 55:379. 1969 ≡ *Arachnothryx buddleioides* var. *aspera* (J.H. Kirkbr.) Borhidi, Acta Bot. Hung. 33:301. 1987 – TYPE: PANAMA, Bocas del Toro, 18 Apr 1968, J.H. Kirkbride Jr. 780, (HT:MO!; isotypes: NY [image!], US [image!]).

Gonzalagunia calycophylla (Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx calycophylla* Steyerm., Mem. New York Bot. Gard. 17:257. 1967 – TYPE: VENEZUELA, Río Táchira, 12 Jul 1944, J.A. Steyermark 57136, (HT: VEN [not seen]; isotypes: F!).

Gonzalagunia calycosa (Donn. Sm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia calycosa* Donn. Sm., Bot. Gaz. 56:59. 1913 ≡ *Arachnothryx calycosa* (Donn. Sm.) Borhidi, Acta Bot. Hung. 28:70. 1982 –TYPE: COSTA RICA, San José, Oct 1898, A. Tonduz 11633, (HT: US [image!]).

Gonzalagunia capitellata (Hemsl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia capitellata* Hemsl., Diagn. Pl. Nov. Mexic. 2:28. 1879 ≡ *Arachnothryx capitellata* (Hemsl.) Borhidi, Acta Bot. Hung. 28:69. 1982 –TYPE: MEXICO, Oaxaca, Monte Pelado, no date, Lectotype designated by Lorence, Monogr. Syst. Bot. Missouri Bot. Gard. 73: 10. 1999: C. Jürgensen 355, (LT: K [image!]; ILT: F!, K [image!]).

= *Rondeletia liebmanii* Standl., J. Wash. Acad. Sci. 17:336. 1927 ≡ *Arachnothryx liebmanii* (Standl.) Borhidi, Acta Bot. Hung. 33:302. 1987 –TYPE: MEXICO, Oaxaca, 1841–1843, F. Liebmann 11834, (HT: US [image!]; isotypes: C [not seen], P [not seen]).

= *Arachnothryx linguiloba* Borhidi & Diego-Pérez, Acta Bot. Hung. 51:11. 2009 –TYPE: MEXICO, Guerrero, Atoyac, 14 Dec 1985, J.C. Soto 11756, (HT: MEXU!).

Gonzalagunia caucana (Standl. ex Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia caucana* Standl. ex Steyerm., Acta Biol. Venez. 4:408. 1964 ≡ *Arachnothryx caucana* (Standl. ex Steyerm.) Steyerm., Mem. New York Bot. Gard. 17:260. 1967 –TYPE: COLOMBIA, Cauca, no date, C. Dryander 2094, (HT: F!; isotypes: US [image!]).

Gonzalagunia chaconii (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia chaconii* Lorence, Fieldiana 33:296. 1993 ≡ *Arachnothryx chaconii* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 ≡ *Javorkaea chaconii* (Lorence) Borhidi, Acta Bot. Hung. 43:42. 2001 –TYPE: COSTA RICA, Heredia, 21 Jan 1983, I.A. Chacón 177, (HT: CR [not seen]; isotypes: INB [image!], MO!).

Gonzalagunia chiapensis (Brandegee) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Otocalyx chiapensis* Brandegee, Univ. Calif. Publ. Bot. 6:69. 1914 ≡ *Rondeletia brandegeeana* Lorence, Novon 1:138. 1991 ≡ *Arachnothryx chiapensis* (Brandegee) Borhidi, Acta Bot. Hung. 43:42. 2001 –TYPE: MEXICO, Chiapas, Cerro Boquerón, Aug 1913, C.A. Purpus 7041, (HT: UC [image!]; isotypes: GH [image!], MO!].

= *Rondeletia zolleriana* Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:292. 1940 ≡ *Arachnothryx zolleriana* (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 33:303. 1987 – TYPE: GUATEMALA, San Marcos, 14 Mar 1940, J.A. Steyermark 37738, (HT: F!).

= *Rondeletia cordovana* Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:26. 1943 ≡ *Arachnothryx cordovana* (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 33:301. 1987 – TYPE: GUATEMALA, Zacapa, 13 Oct 1939, J.A. Steyermark 29906, (HT: F!; isotypes: US [image!]).

Gonzalagunia chimalaparum (Hemsl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx chimalaparum* Lorence ex Borhidi, Rubiáceas de México 45. 2006 –TYPE: MEXICO, Oaxaca, Santa María Chimalapa, 28 Apr 1987, Lectotype designated by Lorence, Novon 21:139. 2011, T.L. Wendt 5676, (LT: MEXU!; ILT: PTBG [image!]).

Gonzalagunia chimboracensis (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia chimboracensis* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7:203. 1931 ≡ *Arachnothryx chimboracensis* (Standl.) Steyerm., Mem. New York Bot. Gard. 17:258. 1967 –TYPE: ECUADOR, Chimborazo, July 1860, R. Spruce 6187, (HT: K [image!]; isotypes: F!).

Gonzalagunia chinajensis (Standl. & Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia chinajensis* Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:254. 1947 ≡ *Arachnothryx chinajensis* (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 33:301. 1987 –TYPE:

GUATEMALA, Alta Verapaz, Cerro Chinajá, 1–2 Apr 1942, J.A. Steyermark 45637, (HT: F; isotypes: LL [image!], MO!, US [image!]).

= *Rondeletia belizensis* var. *longiloba* Lundell, Wrightia 5:323–324. 1876 ≡ *Arachnothryx belizensis* var. *longiloba* (Lundell) Borhidi, Acta Bot. Hung. 35:310. 1989 –TYPE: GUATEMALA, Alta Verapaz, 20 Jul 1975, C.L. Lundell 19545, (HT: LL [image!]; isotypes: F!, S [image!]).

Gonzalagunia chiriquiana (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia chiriquiana* Lorence, Novon 4:129. 1994 ≡ *Arachnothryx chiriquiana* (Lorence) Borhidi, Acta Bot. Hung. 40:15. 1996 –TYPE: PANAMA, Chiriquí, 2 Aug 1984, H.W. Churchill 5924, (HT: MO!; isotypes: PMA [image!]).

Gonzalagunia colombiana (Rusby) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia colombiana* Rusby, Descr. S. Amer. Pl. 129. 1920 ≡ *Arachnothryx colombiana* (Rusby) Steyerm., Mem. New York Bot. Gard. 17:258. 1967 – TYPE: COLOMBIA, Sierra de Onaca, no date, H.H. Smith 1813, (HT: NY [image!]; isotypes: BR [image!], F!, GH [image!], S [image!], US [image!]).

Gonzalagunia costanensis (Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx costanensis* Steyerm., Mem. New York Bot. Gard. 17:259. 1967 – TYPE: VENEZUELA, Anzoategui, 07 Mar 1945, J.A. Steyermark 61424, (HT: VEN [not seen]; isotypes: F!).

Gonzalagunia cupreiflora (K. Schum. & K. Krause) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia cupreiflora* K. Schum. & K. Krause, Bot. Jahrb. Syst. 40:314. 1908 ≡ *Arachnothryx cupreiflora* (K. Schum. & K. Krause) Steyerm., Mem. New York Bot. Gard. 17:258. 1967 – TYPE: COLOMBIA, Antioquia, no date, Lectotype designated here: F.C. Lehmann 7289 (LT: F!; ILT: K [image!], NY [image!]).

Gonzalagunia darienensis (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia darienensis* Standl., N. Amer. Fl. 32:53. 1918 ≡ *Arachnothryx darienensis* (Standl.) Borhidi, Acta Bot. Hung. 28:68. 1982 – TYPE: PANAMA, Darién, Feb 1912, H. Pittier 5684, (HT: US [image!]; isotypes: F!, US [image!]).

Gonzalagunia dwyeri (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Chomelia leucophylla* Dwyer, Ann. Missouri Bot. Gard. 67:98. 1980 ≡ *Rondeletia dwyeri* Lorence, Novon 1: 139–141. 1991 ≡ *Arachnothryx dwyeri* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 –TYPE: PANAMA, Darién, 11 Feb 1972, A.H. Gentry 4262, (HT: MO!; isotypes: MO!).

Gonzalagunia educta (Standl. ex Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia educta* Standl. ex Steyerm., Acta Biol. Venez. 4:108. 1964 ≡ *Arachnothryx educta* (Standl. ex Steyerm.) Steyerm., Mem. New York Bot. Gard. 17:260. 1967 – TYPE: COLOMBIA, El Valle, no date, J. Cuatrecasas 18749, (HT: US [image!]; isotypes: F!, P [image!], BC [image!]).

Gonzalagunia euryphylla (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia euryphylla* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7:29. 1930 ≡ *Arachnothryx euryphylla* (Standl.) Steyerm., Mem. New York Bot. Gard. 17:258. 1967 – TYPE: COLOMBIA, Caldas, no date, F.W. Pennell 10627, (HT: US [image!]; isotypes: F!).

Gonzalagunia evansii (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia evansii* Lorence, Novon 7:52–54. 1997 ≡ *Arachnothryx evansii* (Lorence) Borhidi, Acta Bot. Hung. 40:15. 1996 – TYPE: HONDURAS, Celaque, 28 Jan 1992, P.R. House 1163, (HT: PTBG [image!]; isotypes: EAP [image!], MO!).

Gonzalagunia flocculosa (Borhidi) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx flocculosa* Borhidi, Acta Bot. Hung. 45:1–3. 2003 – TYPE: MEXICO, Chiapas, Unión Juárez, 18 Dec 1987, E. Martínez-Salas 22159, (HT: MEXU!).

Gonzalagunia fosbergii (Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx fosbergii* Steyerm., Mem. New York Bot. Gard. 17:255. 1967 – TYPE: ECUADOR, Loja, 10 Feb 1945, F.R. Fosberg 22964, (HT: NY, [not seen]; isotypes: S [image!]).

Gonzalagunia galeottii (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia galeottii* Standl., N. Amer. Fl. 32:59–60. 1918 ≡ *Arachnothryx galeottii* (Standl.) Borhidi, Acta Bot. Hung. 28:70. 1982 ≡ *Renistipula galeottii* (Standl.) Borhidi, Acta Bot. Hung. 46:123. 2004 – TYPE: MEXICO, no date, H. Galeotti s.n., (HT:US [image!]; isotypes: F [not seen], P [not seen]).

Gonzalagunia garciae (Standl. ex Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx garciae* Standl. ex Steyerm., Mem. New York Bot. Gard. 17:256. 1967 – TYPE: COLOMBIA, Cundinamarca, 26 Jan 1944, H. García-Barriga 11037, (HT: US [not seen]; isotypes: COL [image!], F!).

Gonzalagunia ginetteae (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia ginetteae* Lorence, Novon 1:141–143 ≡ *Arachnothryx ginetteae* (Lorence) Borhidi, Acta Bot. Hung.38:140. 1993 – TYPE: MEXICO, Oaxaca, Tuxtepec, 06 Dec 1980, D.H. Lorence & R. Cedillo T. 2973, (HT: MEXU!; isotypes: MO!).

Gonzalagunia glabrata (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia glabrata* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7:30. 1930 ≡ *Arachnothryx glabrata* (Standl.) Steyerm., Mem. New York Bot. Gard. 17:261. 1967 – TYPE: COLOMBIA, Santander, no date, E. P. Killip 15504, (HT: US [image!]; isotypes: F!, GH [image!], NY [image!]).

Gonzalagunia gonzaleoides (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia gonzaleoides* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8:169. 1930 ≡ *Arachnothryx* *gonzaleoides* (Standl.) Borhidi, Acta Bot. Hung. 33:302. 1987 – TYPE: MEXICO, Chiapas, Solistahuacán, 1840, J.J. Linden 149, (HT: LE [not seen]; isotypes: F!, G [image!], K [image!]).

Gonzalagunia gracilis (Hemsl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia gracilis* Hemsl., Diagn. Pl. Nov. Mexic. 3:53. 1880 ≡ *Arachnothryx gracilis* (Hemsl.) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: GUATEMALA, Alta Verapaz, Mar 1879, H. von Türckheim 404, (HT: K [image!]; isotypes: BR [image!]).

= *Rondeletia silvicola* L.O. Williams, Phytologia 26: 128–129. 1973 ≡ *Arachnothryx silvicola* (L.O. Williams) Borhidi, Acta Bot. Hung. 35:311. 1989 – TYPE: HONDURAS, Atlántida, 6 Dec 1927–20 Mar 1928, P.C. Standley 56885, (HT: F!).

Gonzalagunia gracilispica (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia gracilispica* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8:342. 1931 ≡ *Arachnothryx gracilispica* (Standl.) Borhidi, Acta Bot. Hung. 33:302. 1987 – TYPE: MEXICO, Oaxaca, San Pedro Nolasco, 1843–1844, C. Jürgensen 935 (HT: K [image!]).

= *Rondeletia minor* Lundell, Wrightia 5: 326. 1976 ≡ *Arachnothryx minor* (Lundell) Borhidi, Acta Bot. Hung. 35:310. 1989 – TYPE: MEXICO, Veracruz, Teziutlan, 6 Jan 1964, D.S. Correll 28736, (HT: LL [image!]; isotypes: MEXU!).

= *Arachnothryx sooiana* Borhidi, Acta Bot. Hung. 45:4–6. 2003 – TYPE: MEXICO, Veracruz, Azatlán, 5 Dec 1975, F. Ventura 12227, (HT: MEXU!).

Gonzalagunia guerrerensis (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia guerrerensis* Lorence, Novon 1:143–144. 1991 ≡ *Arachnothryx guerrerensis* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 – TYPE: MEXICO, Guerrero, Atoyac de Álvarez, 22 Nov 1983, E. Martínez 5596, (HT: MEXU!; isotypes: BM [image!], CAS [not seen], ENCB [image!], PTBG [image!]).

Gonzalagunia guettardioides (Standl. ex Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx guettardioides* Standl. ex Steyerm., Mem. New York Bot. Gard. 17:260. 1967 – TYPE: COLOMBIA, Antioquia, 25 May 1945, O. Haught 4712, (HT: F [not seen]; isotypes: COL [image!]).

Gonzalagunia hameliifolia (Dwyer & M.V. Hayden) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia hameliifolia* Dwyer & M.V. Hayden, Ann. Missouri Bot. Gard. 54:144 – 145. 1967 ≡ *Arachnothryx hameliifolia* (Dwyer & M.V. Hayden) Borhidi, Acta Bot. Hung. 28:70. 1982 – TYPE: PANAMA, Veraguas, Aug 1961, J.D. Dwyer 1350, (HT: MO!; isotypes: NY [image!]).

Gonzalagunia hennigiana (Borhidi) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** et **nom. nov.** ≡ *Arachnothryx pauciflora* Borhidi, Acta Bot. Hung. 47:28–29. 2005 – TYPE: MEXICO, Chiapas, Jaltenango, 17 jun 1990, M. Heath 1007, (HT: MEXU!).

The epithet "pauciflora" is not available in *Gonzalagunia* (*G. pauciflora* B. Ståhl); hence, a new epithet is coined, this honors to Willi Hennig (1913–1976), considered the founder of phylogenetic systematics.

Gonzalagunia heteranthera (Brandegee) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia heteranthera* Brandegee, Univ. Calif. Publ. Bot. 4:387. 1913 ≡ *Arachnothryx heteranthera* (Brandegee) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: MEXICO, Veracruz, Baños del Carrizal, Aug 1912, C.A. Purpus 6184, (HT: UC [image!]; isotypes: GH [image!], MO [image!], NY [image!], US [image!]).

= *Rondeletia falciformis* Lundell, Wrightia 5: 324–325. 1976 ≡ *Arachnothryx falciformis* (Lundell) Borhidi, Acta Bot. Hung. 35:310. 2003 – TYPE: MEXICO, Hidalgo, Chapulhuacan, 13 Jul 1943, C.L. Lundell 12234, (HT: LL [image!]; isotypes: F!, S [image!]).

Gonzalagunia hondurensis (Donn. Sm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia hondurensis* Donn. Sm., Bot. Gaz. 27:335. 1899 ≡ Javorkaea hondurensis (Donn. Sm.) Borhidi & Járai-Koml., Acta Bot. Hung. 29:16. 1983 ≡ *Arachnothryx hondurensis* (Donn. Sm.) Lorence, Novon 15: 450–451. 2005 Acta Bot. Hung. – TYPE: HONDURAS, Santa Bárbara, Dec 1888, C. Thieme 5267, (HT: MO!; isotypes: BM [image!], F!, GH [image!], K [image!], M [image!], US [image!]).

Gonzalagunia humboldtii (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** et **nom. nov.** ≡ *Rondeletia discolor* Kunth, Nov. Gen. Sp. 3:396. 1818 ≡ *Arachnothryx discolor* (Kunth) Planch., Fl. Serres Jard. Eur. 5:442. 1849 – TYPE: COLOMBIA, Mariquita, no date, A. von Humboldt & A. Bondpland s.n., (HT: P [image!]; isotypes: P [image!]).

The epithet *discolor* is not available in *Gonzalagunia* (*G. discolor* Standl.); hence, a new epithet is coined, this honors Alexander von Humboldt (1769–1859), important naturalist and explorer.

Gonzalagunia inconstans (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia inconstans* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7:31. 1930 ≡ *Arachnothryx reflexa* var. *inconstans* (Standl.) Steyerm., Mem. New York Bot. Gard. 17:252. 1967 ≡ *Arachnothryx inconstans* (Standl.) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: COLOMBIA, Quetame, no date, M. Lehmann 8751, (HT: F!).

Gonzalagunia izabalensis (Standl. & Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia izabalensis* Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:286. 1940 ≡

Arachnothryx izabalensis (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 33:302. 1987 ≡ *Renistipula izabalensis* (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 46:123. 2004 – TYPE: GUATEMALA, Izabal, 3 May 1939, P.C. Standley 72891, (HT: F!).

Gonzalagunia jurgensenii (Hemsl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia jurgensenii* Hemsl., Diagn. Pl. Nov. Mexic. 2:29. 1879 ≡ *Arachnothryx jurgensenii* (Hemsl.) Borhidi, Acta Bot. Hung. 28:70. 1982 – TYPE: MEXICO, Oaxaca, San Pedro Nolasco, no date, C. Jürgensen 248, (HT: K [image!]; isotypes: F!, G [image!]).

= *Stylosiphonia salvadorensis* Standl., J. Wash. Acad. Sci. 14:246. 1924 – TYPE: EL SALVADOR, Volcán de San Vicente, 7 Mar 1922, P.C. Standley 21559, (HT: US [image!]; isotypes: GH [image!], NY [image!]).

= *Deppea macrocarpa* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4:268. 1929 – TYPE: MEXICO, Nayarit, Cerro de San Juan, 19 Sept 1926, Y. Mexia 727, (HT: F!; isotypes: CAS [image!], E [image!], MICH [image!], MO!, NY [image!], US [image!]).

= *Deppea stenosepala* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8:161. 1930 – TYPE: MEXICO, Oaxaca, Tlaxiaco, 1844, H. Galeotti 2685, (HT: LE [not seen]; isotypes: F!).

= *Javorkaea pulcherrima* Borhidi, Acta Bot. Hung. 45:8–11. 2003 – TYPE: MEXICO, Chiapas, Jaltenango, 23 Apr 1990, M. Heath 881, (HT: MEXU!; isotypes: PTBG [image!]).

= *Arachnothryx jaliscensis* Borhidi & E. Martínez, Acta Bot. Hung. 55:223. 2013 – TYPE: MEXICO, Jalisco, San Cristóbal de la Barranca, 30 Ago 1998, P. Carrillo-Reyes 443, (HT: MEXU!).

Gonzalagunia laniflora (Benth.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia laniflora* Benth., Pl. Hartw. 85. 1841 ≡ *Arachnothryx laniflora* (Benth.) Planch., Fl. Serres Jard. Eur. 5:442. 1849 – TYPE: GUATEMALA, Las Nubes, Mar 1841, T. Hartweg 584, (HT: K [image!]; isotypes: BR [image!], E [image!], F!, G [image!], NY [image!], US [image!]).

= *Rondeletia albida* Lundell, Wrightia 5: 323. 1976 ≡ *Arachnothryx albida* (Lundell) Borhidi, Acta Bot. Hung. 35:309. 1989 – TYPE: MEXICO, Chiapas, Motozintla, Apr 1975, E. Matuda 5509, (HT: LL [image!]; isotypes: F!, LL [image!], MEXU!, S [image!]).

Gonzalagunia latiloba (Borhidi) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx latiloba* Borhidi, Acta Bot. Hung. 46:56–57. 1982 – TYPE: MEXICO, Guerrero, Atoyac de Álvarez, 26 Jan 1965, J. Rzedowski 89 (HT: ENCB [not seen]; isotypes: MICH [not seen]).

Gonzalagunia leucophylla (Kunth) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia leucophylla* Kunth, Nov. Gen. Sp. 3:395. 1818 ≡ *Arachnothryx leucophylla* (Kunth) Planch., Fl. Serres Jard. Eur. 5:442. 1849 – TYPE: MEXICO, Guerrero, April, F.W.H.A. von Humboldt s.n., (HT: P [image!]).

= *Rondeletia elongata* Bartl. ex DC., Prodr. 4:409. 1830 ≡ *Arachnothryx elongata* (Bartl. ex DC.) Planch., Fl. Serres Jard. Eur. 5:442. 1849 – TYPE: MEXICO, Guerrero, no date, T. Haenke s.n., (HT: PR [not seen]; isotypes: GOET [image!], HAL [image!]).

= *Bouvardia discolor* Hook. & Arn., Bot. Beechey Voy. 428. 1841 ≡ *Rondeletia dubia* Hemsl., Diagn. Pl. Nov. Mexic. 2:28: 1879 – TYPE: MEXICO, Oaxaca, G. Andrieux 334, (HT: K [not seen]; isotypes: P [image!]).

= *Rondeletia leucophylla* var. *calycosa* Greenm., Proc. Amer. Acad. Arts 39:92. 1904 – TYPE: MEXICO, OAXACA, Dec 1900, Lectotype designated here: C. Conzatti 970, (LT: MEXU!; ILT: BR [image!], GH [not seen]).

= *Rondeletia leptodictya* B.L. Rob., Proc. Amer. Acad. Arts 45:402. 1910 ≡ *Arachnothryx leptodictya* (B.L. Rob.) Borhidi, Acta Bot. Hung. 28:68. 1982 – TYPE: MEXICO, Michoacan/Guerrero, 24 Nov 1898, E. Langlassé 666, (HT: GH [not seen]; isotypes: F!, G [image!], K [image!], P [image!]).

= *Rondeletia yucatanensis* Lundell, Wrightia 5: 329. 1976 ≡ *Arachnothryx yucatanensis* (Lundell) Borhidi, Acta Bot. Hung. 35:311. 1989 – TYPE: MEXICO, Yucatan, Chichen Itzá, 28 Apr 1953, J.T. Baldwin Jr. 14230, (HT: LL [image!]).

Gonzalagunia lindenii (Hemsl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia villosa* Hemsl., Diagn. Pl. Nov. Mexic. 2:27. 1879 ≡ *Arachnothryx villosa* (Hemsl.) Borhidi, Acta Bot. Hung. 28:69. 1982 –TYPE: MEXICO, Oaxaca, San Pedro Nolasco, no date, Lectotype designated by Lorence, Monogr. Syst. Bot. Missouri Bot. Gard. 73: 16. 1999: C. Jürgensen 806, (LT: K [image!]; ILT: K [image!], P [image!]).

= *Arachnothryx sessilis* Borhidi & G. Ortiz, Acta Bot. Hung. 48:40. 2006 –TYPE: MEXICO, Tabasco, Huimanguillo, 13 Aug 1997, G. Ortiz 5155, (HT: MEXU!).

The epithet “villosa” is not available in *Gonzalagunia* (*G. villosa* D.R. Simpson ex C.M. Taylor); hence, a new epithet is coined, this honors to Jean Jules Linden (1817–1898), botanist and horticulturist.

Gonzalagunia linguiformis (Hemsl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia linguiformis* Hemsl., Diagn. Pl. Nov. Mexic. 2: 29–30. 1879 ≡ *Arachnothryx linguiformis* (Hemsl.) Borhidi, Acta Bot. Hung. 28:70. 1982 – TYPE: GUATEMALA, 1857, G. U. Skinner s.n., (HT: K [image!]).

= *Rondeletia aetheocalymna* Donn. Sm., Bot. Gaz. 42:298. 1906 ≡ *Arachnothryx aetheocalymna* (Donn. Sm.) Borhidi, Acta Bot. Hung. 28:70. 1982 –TYPE: GUATEMALA, Alta Verapaz, 14 Jan 1905, W.R. Maxon 3275, (HT: US [image!]).

Gonzalagunia lojensis (Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx lojensis* Steyerm., Mem. New York Bot. Gard. 17:255. 1967 – TYPE: ECUADOR, Loja, 19 Feb 1945, F.R. Fosberg 23141, (HT: NY [not seen]; isotypes: US [image!]).

Gonzalagunia macrocalyx (Standl. & Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia macrocalyx* Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23:254. 1947 ≡ *Arachnothryx macrocalyx* (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 33:302. 1987 ≡ *Javorkaea macrocalyx* (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 43:50. 2001 – TYPE: GUATEMALA, Izabal, 25 Dec 1941, J.A. Steyermark 41864, (HT: F!; isotypes: A [image!], F!, US [image!]).

Gonzalagunia manantlanensis (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia manantlanensis* Lorence, Novon 1:145–147. 1991 ≡ *Arachnothryx manantlanensis* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 – TYPE: MEXICO, Jalisco, Autlan, 7 Dec 1985, A. Vázquez 3750, (HT: WIS [image!]; isotypes: IBUG [image!]).

Gonzalagunia megalantha (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia megalantha* Lorence, Novon 4:132. 1994 ≡ *Arachnothryx megalantha* (Lorence) Lorence, Novon 15:451. 2005 ≡ *Javorkaea megalantha* (Lorence) Borhidi, Acta Bot. Hung. 40:16. 1997 – TYPE: HONDURAS, Cuyamel, 23 Aug 1924, M.A. Carleton 653 (HT: US [image!]; isotypes: US [not seen]).

Gonzalagunia mexicana (Turcz) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Siphonandra mexicana* Turcz., Bull. Soc. Imp. Naturalistes Moscou 21:582. 1848 ≡ *Rondeletia mexicana* (Turcz.) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:388. 1940 ≡ *Arachnothryx mexicana* (Turcz.) Borhidi, Acta Bot. Hung. 43:51. 2001 ≡ *Rondeletia oaxacana* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11:255–256. 1936 ≡ *Arachnothryx oaxacana* (Standl.) Borhidi, Acta Bot. Hung. 33:302. 1987 – TYPE: MEXICO, Oaxaca, no date, Lectotype designated by Borhidi et al., Acta Bot. Hung. 46:112. 2004: H. Galeotti 2664, (LT: G [not seen]; ILT: F!, P [not seen]).

= *Rondeletia polycephala* Standl., J. Wash. Acad. Sci. 17:337. 1927 ≡ *Arachnothryx polycephala* (Standl.) Borhidi, Acta Bot. Hung. 35:310. 1989 – TYPE: MEXICO, Oaxaca, no date, F. Liebmann 11826, (HT: C [image!]; isotypes: US [image!]).

Gonzalagunia michoacana (Borhidi) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx michoacana* Borhidi, Acta Bot. Hung. 46:57–59. 2004 – TYPE: MEXICO, Michoacán, Aguililla, 7 Aug 1972, M.F. Denton 2016, (HT: ENCB [not seen]; siotypes WTU [not seen]).

Gonzalagunia monteverdensis (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia monteverdensis* Lorence, Novon 1:147–148. 1991 ≡ *Arachnothryx monteverdensis*

(Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 – TYPE: COSTA RICA, Puntarenas, 24 Aug 1985, W.A. Haber 2340 (HT: MO!; isotypes: CR [not seen]).

Gonzalagunia monticola (Borhidi) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx monticola* Borhidi, Acta Bot. Hung. 46:59–60. 2004 – TYPE: MEXICO, Guerrero, Atoyac de Álvarez, Mar 1983, M.E. Millan 175, (HT: ENCB [not seen]; isotypes: FCME [not seen]).

Gonzalagunia myriantha (Standl. & Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia myriantha* Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:288. 1940 ≡ *Arachnothryx myriantha* (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 33:302. 1987 – TYPE: GUATEMALA, Suchitepequez, 31 Oct 1934, A.F. Skutch 1569, (HT: F!; isotypes: A [image!], F!, NY [image!], US [image!]).

Gonzalagunia nebulosa (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia nebulosa* Standl., Trop. Woods 37:32. 1934 ≡ *Arachnothryx nebulosa* (Standl.) Borhidi, Acta Bot. Hung. 33:302. 1987 – TYPE: HONDURAS, Tegucigalpa, 2 Apr 1932, J.B. Edwards P10, (HT: F!; isotypes: A [image!], G [image!]).

Gonzalagunia nelsonii (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx nelsonii* Lorence, Novon 15:448–450. 2005 – TYPE: HONDURAS, Copán, 30 Apr 1996, T. Hawkins 993, (HT: MO!; isotypes: EAP [image!], MEXU!, PTBG [image!]).

Gonzalagunia nitida (Hemsl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia nitida* Hemsl., Diagn. Pl. Nov. Mexic. 2:29. 1879 ≡ *Arachnothryx nitida* (Hemsl.) Borhidi, Acta Bot. Hung. 28:69.1982 – TYPE: MEXICO, Chiapas, no date, Lectotype designated by Lorence, Monogr. Syst. Bot. Missouri Bot. Gard. 73:155. 1999: J.J. Linden 1660, (LT: K [image!]; ILT: F!, G-DEL [not seen], P [image!]).

Gonzalagunia ochoterenae (Lundell) J. A. Torres-Montúfar, **comb. nov.** et **nom. nov.** ≡ *Rondeletia tacanensis* Lundell, Bull. Torrey Bot. Club 66:603. 1939 ≡ Acta Bot. Hung. – TYPE: MEXICO, Chiapas, Tacaná, 30 Mar 1939, E. Matuda 2928, (HT: MICH [image!]; isotypes: A [image!], B [image!], CAS [image!], F!, GH [image!], K [image!], LL [image!], NY [image!], US [image!]).

The epithet “tacanensis” is not available in *Gonzalagunia* (*G. tacanensis* Lundell); hence, a new epithet is coined, this honors to Helga Ochoterena, specialist in Rubiaceae and phylogenetics.

Gonzalagunia ovata (Rusby) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia ovata* Rusby, Descr. S. Amer. Pl. 129. 1920 ≡ *Arachnothryx ovata* (Rusby) Steyerm., Mem. New York Bot. Gard. 17:259. 1967 – TYPE: COLOMBIA, no date, H.H. Smith 1813, (hootype: NY [not seen]; isotypes: BM [image!], E [image!], K [image!], MPU [image!], U [image!]).

Gonzalagunia pansamalana (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia pansamalana* Standl., N. Amer. Fl. 32:58 – 59. 1918 ≡ *Arachnothryx pansamalana* (Standl.) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: GUATEMALA, Alta Verapaz, Apr 1886, H. von Türckheim 897, (HT: US [image!]; isotypes: GH [image!]).

Gonzalagunia pavonii J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** et **nom. nov.** ≡ *Rondeletia brenesii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18:1370–1371. 1938 ≡ *Arachnothryx brenesii* (Standl.) Borhidi, Acta Bot. Hung. 33:301. 1987 – TYPE: COSTA RICA, San Ramón, 20 Mar 1929, A.M. Brenes 6757, (HT: F!; isotypes: NY [image!]).

The epithet *brenesii* is not available in *Gonzalagunia* (*G. brenesii* Standl.); hence, a new epithet is coined, this honors José Antonio Pavón (1754–1844), a Spanish botanist who described the genus *Gonzalagunia* with Hipólito Ruiz.

Gonzalagunia perezii (Standl. & Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia perezii* Standl. ex Steyerm., Acta Bot. Venez. 4:109. 1964 ≡ *Arachnothryx perezii* (Standl. ex Steyerm.) Steyerm., Mem. New York Bot. Gard. 17:258. 1967 – TYPE: COLOMBIA, Cauca, no date, E. Pérez-Arbelaez 6078, (HT: US [image!]; isotypes: COL! [image!], F!, P [image!]).

Gonzalagunia peruviana (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia peruviana* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 8:342. 1931 ≡ *Arachnothryx peruviana* (Standl.) Steyerm., Mem. New York Bot. Gard. 17:251. 1967 – TYPE: PERU, Río Santiago, 7 Oct 1924, G. Tessann 4223, (HT: F!; isotypes: F!, NY [image!]).

Gonzalagunia pittieri (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** et **nom. nov.** ≡ *Rondeletia secunda* Standl., Contr. U.S. Natl. Herb. 18:141. 1916 ≡ *Arachnothryx secunda* (Standl.) Borhidi, Acta Bot. Hung. 28:70. 1982 – TYPE: PANAMA, San Blas, Aug 1911, H. Pittier 4279 (HT: US [image!]; isotypes: NY [image!]).

= *Rondeletia darcyi* Dwyer, Ann. Missouri Bot. Gard. 67:467. 1980 ≡ *Arachnothryx darcyi* (Dwyer) Borhidi, Acta Bot. Hung. 28:70. 1982 – TYPE: PANAMA, Colón, 12 Apr 1970, W.G. D'Arcy 4079, (HT: MO!; isotypes: MO!)

The epithet *secunda* is not available in *Gonzalagunia* (*G. secunda* (M. Martens & Galeotti) Kuntze); hence, a new epithet is coined, this honors Henri Pittier (1857–1950), geographer, painter, engineer and botanist.

Gonzalagunia povedae (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia povedae* Lorence, Fieldiana 33:299. 1993 ≡ *Arachnothryx povedae* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 – TYPE: COSTA RICA, San José, no date, L.J. Poveda 441, (HT: CR [not seen]; isotypes: MO!).

Gonzalagunia pringlei (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia pringlei* Lorence, Novon 7:54. 1997 ≡ *Arachnothryx pringlei* (Lorence) Borhidi, Acta Bot. Hung. 40:16. 1999 – TYPE: MEXICO, Veracruz, Orizaba, 9 Feb 1895, C.G. Pringle 6135, (HT: GH [image!]; isotypes: K [image!], MEXU!, MO!).

Gonzalagunia pumae (J. A. Torres-Montúfar & H. Ochoterena) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx pumae* J. A. Torres-Montúfar & H. Ochoterena, Revista Mex. Biodivers. 84:1082–1086. 2013 – TYPE: VERACRUZ, San Andrés Tuxtla, 29 Dec 1984, G. Ibarra 2216, (HT: MO!; isotypes: MEXU!).

Gonzalagunia purpurea (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia purpurea* Lorence, Novon 1:148–152. 1991 ≡ *Arachnothryx purpurea* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 – TYPE: MEXICO, Oaxaca, Ixtlán, 14 Apr 1982, D.H. Lorence 4009, (HT: MEXU!; isotypes: BM [image!], F!, MO!, PTBG [image!]).

Gonzalagunia pyramidalis (Lundell) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia pyramidalis* Lundell, Wrightia 5:327–328. 1976 ≡ *Arachnothryx pyramidalis* (Lundell) Borhidi, Acta Bot. Hung. 35:310. 1989 – TYPE: MEXICO, Chiapas, Siltepec, 24 Jan 1945, E. Matuda 5292, (HT: LL [image!]; isotypes: F!, LL [image!], MEXU!).

Gonzalagunia reflexa (Benth.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia reflexa* Benth., Pl. Hartw. 192. 1839 ≡ *Arachnothryx reflexa* (Benth.) Planch., Fl. Serres Jard. Eur. 5:442. 1849 – TYPE: COLOMBIA, no date, T. Hartweg 1052, (HT: K [image!]; isotypes: BR [image!], F!, LD [image!]).

= *Rondeletia trichotoma* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7:204. 1931 – TYPE: ECUADOR, Tungurahua, no date, R. Spruce 5116, (HT: GH [image!]; isotypes: F!, G [image!] K [image!], LD [image!], NY [image!]).

= *Rondeletia rosea* (Linden) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7:34. 1930 ≡ *Arachnothryx rosea* Linden, Hort. Linden 2:3. 1859 – TYPE: Plants cultivated at Brussels, brought from Colombia, L. Schlim s.n., (HT: K [image!]).

Gonzalagunia rekoi (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia rekoi* Standl., Proc. Biol. Soc. Washington 8:126. 1918 ≡ *Arachnothryx rekoi* (Standl.) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: MEXICO, Oaxaca, Las Pilas, 10 Oct 1917, B.P. Reko 3490, (HT: US [image!]; isotypes: MEXU!).

Gonzalagunia ricoi (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia ricoi* Lorence, Novon 1:152–154. 1991 ≡ *Arachnothryx ricoi* (Lorence) Borhidi, Acta Bot. Hung. 38:140.

1995 – TYPE: MEXICO, Oaxaca, Putla, 9 Dec 1982, L. Rico 566, (HT: MEXU!; isotypes: BM [image!], F!, MO!, PTBG [image!]).

= Arachnothryx brachythyrsa Borhidi, Acta Bot. Hung. 48:39–40. 2006 – TYPE: MEXICO, Oaxaca, San Jerónimo Coatlán, 7 Aug 1990, A. Campos 3255, (HT: MEXU!).

Gonzalagunia rubens (L.O. Williams) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia rubens* L.O. Williams, Phytologia 26: 128. 1973 ≡ *Arachnothryx rubens* (L.O. Williams) Borhidi, Acta Bot. Hung. 35:311. 1989 – TYPE: GUATEMALA, Quiché, 19 Nov 1934, A.F. Skutch 1725, (HT: F!; isotypes: EAP [image!]).

Gonzalagunia rufescens (B.L. Rob.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia rufescens* B.L. Rob., Proc. Amer. Acad. Arts 45:402–403. 1910 ≡ *Arachnothryx rufescens* (B.L. Rob.) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: GUATEMALA, Alta Verapaz, Mar 1881, H. von Türckheim 582, (HT: GH [image!]; isotypes: F!, MO!, K [image!]).

= *Rondeletia rufescens* var. *ovata* B.L. Rob., Proc. Amer. Acad. Arts 45:403. 1910 – TYPE: GUATEMALA, Alta Verapaz, Mar 1903, H. von Türckheim 8401, (HT: GH [image!]; isotypes: F!, US [image!]).

Gonzalagunia rugulosa (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia rugulosa* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 7:34. 1930 ≡ *Arachnothryx rugulosa* (Standl.) Steyerm., Mem. New York Bot. Gard. 17:258. 1967 – TYPE: COLOMBIA, no date, J.J. Linden 692, (HT: GH [image!]; isotypes: F!, K [image!]).

Gonzalagunia rzedowskii (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia rzedowskii* Lorence, Novon 1: 154–155. 1991 ≡ *Arachnothryx rzedowskii* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 – TYPE: MEXICO, Guerrero, Atoyac, 6 Jan 1985, Laboratorio de Biogeografía 867, (HT: MEXU!; isotypes: MEXU!).

Gonzalagunia sanchezii (Borhidi & E. Martínez) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx sanchezii* Borhidi & E. Martínez, Acta Bot. Hung. 52:77–80. 2010 – TYPE: MEXICO, Oaxaca, Tehuantepec, 7 Jun 2009, A. Sánchez M. 2602, (HT: MEXU!; isotypes: FCME [not seen], SERO [not seen], MO [not seen]).

Gonzalagunia scabra (Hemsl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia scabra* Hemsl., Diagn. Pl. Nov. Mexic. 2:29. 1879 ≡ *Javorkaea scabra* (Hemsl.) Borhidi, Acta Bot. Hung. 43:38. 2001 ≡ *Arachnothryx scabra* (Hemsl.) Borhidi, Acta Bot. Hung. 46:115. 2004 – TYPE: MEXICO, Oaxaca, San Pedro Nolasco, C. Jürgensen 926, (HT: K [image!]; isotypes: G [image!]).

= *Rondeletia mexiae* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:55–56. 1940 ≡ *Arachnothryx mexiae* (Standl.) Borhidi, Acta Bot. Hung. 33:302. 1987 – TYPE: MEXICO, Oaxaca, Choapan, 1 Apr 1938, Y. Mexia 9261, (HT: F!; isotypes: GH [image!], MO!, US [image!]).

= *Sommera acuminata* Oerst. ex Standl., J. Wash. Acad. Sci. 17:340. 1927 ≡ *Rondeletia acuminata* (Oerst. ex Standl.) Lorence & Cast.-Campos, Biótica 13:147–148. 1988 ≡ *Arachnothryx acuminata* (Oerst. ex Standl.) Borhidi, Acta Bot. Hung. 35:310. 1989 ≡ *Javorkaea acuminata* (Oerst. ex Standl.) Borhidi, Acta Bot. Hung. 40:18–19. 1997– TYPE: MEXICO, Oaxaca, Amatlán, 1841–1843, F. Liebmann 11712, (HT: C [image!]; isotypes: US [image!]).

Gonzalagunia scoti (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia scoti* Lorence, Novon 1:155–156. 1991 ≡ *Arachnothryx scoti* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 – TYPE: MEXICO, Oaxaca, 12 Mar 1953, T.B. MacDougall s.n., (HT: MEXU!; isotypes: MO!, PTBG [not seen]).

Gonzalagunia secundiflora (B.L. Rob.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia secundiflora* B.L. Rob., Proc. Amer. Acad. Arts 45:403. 1910 ≡ *Arachnothryx secundiflora* (B.L. Rob.) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: GUATEMALA, 21 Jul 1860, S. Hayes s.n., (HT: GH [image!]; isotypes: K [image!]).

= *Rondeletia vulcanicola* Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:291. 1940 ≡ *Arachnothryx vulcanicola* (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 33:303. 1987 – TYPE: GUATEMALA, Quetzaltenango, 31 Dec 1931, J.A. Steyermark 33220, (HT: F!).

Gonzalagunia sinaloae (Borhidi) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx sinaloae* Borhidi, Acta Bot. Hung. 46:115–117. 2004 – TYPE: MEXICO, Sinaloa, Cosalá, 21 Sept 1989, R. Vega 3488, (HT: MEXU!)

Gonzalagunia skutchii (Standl. & Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia skutchii* Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22:289. 1940 ≡ *Arachnothryx skutchii* (Standl. & Steyerm.) Borhidi, Acta Bot. Hung. 33:302. 1987 – TYPE: GUATEMALA, Suchitepequez, 10 Jan 1935, A.F. Skutch 2110, (HT:F!; isotypes: A [image!], NY [image!], US [image!]).

Gonzalagunia sousae (Borhidi) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx sousae* Borhidi, Acta Bot. Hung. 117–118. 2004 – TYPE: MEXICO, Chiapas, Unión Juárez, 7 Feb 1987, E. Martínez 19755 (HT: MEXU!).

Gonzalagunia stachyoidea (Donn. Sm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia stachyoidea* Donn. Sm., Bot. Gaz. 42:298–299. 1906 ≡ *Arachnothryx stachyoidea* (Donn.

Sm.) Borhidi, Acta Bot. Hung. 28:69. 1982 – TYPE: GUATEMALA, Alta Verapaz, 25 Apr 1905, R. Hay s.n., (HT: US [image!]).

Gonzalagunia subglabra (Borhidi & N.C. Jiménez) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx subglabra* Borhidi & N.C. Jiménez, Acta Bot. Hung. 48:41. 2006 – TYPE: MEXICO, Tabasco, Tenosique, 22 Jun 2002, N.C. Jiménez 665, (HT: MEXU [not seen]).

Gonzalagunia tabascensis (Borhidi) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx tabascensis* Borhidi, Acta Bot. Hung. 46:119–120. 2004 – TYPE: MEXICO, Tabasco, Huimanguillo, G. Ortiz 5160, (HT: MEXU!).

Gonzalagunia tayloriae (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia tayloriae* Lorence, Fieldiana 33:300. 1993 ≡ *Arachnothryx tayloriae* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 – TYPE: COSTA RICA, Cantón de Limón, 19 Apr 1989, G. Herrera 2656, (HT: CR [not seen]; isotypes: F!, MO!, PTBG [image!]).

Gonzalagunia tenorioi (Lorence) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia tenorioi* Lorence, Novon 1:156–157. 1991 ≡ *Arachnothryx tenorioi* (Lorence) Borhidi, Acta Bot. Hung. 38:140. 1995 – TYPE: MEXICO, Oaxaca, Juxtlahuaca, P. Tenorio 184, (HT: MEXU!; isotypes: MEXU!, MO!).

Gonzalagunia tenuisepala (Borhidi) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx tenuisepala* Borhidi, Acta Bot. Hung. 45:6–8. 2003 –TYPE: MEXICO, Veracruz, Soteapan, 7 Jan 1972, J.H. Beaman 5426, (HT: MEXU [not seen]; isotypes: MO!).

Gonzalagunia thiemei (Donn. Sm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ Rondeletia thiemei Donn. Sm., Bot. Gaz. 42:299. 1906 ≡ *Arachnothryx thiemei* (Donn. Sm.) Borhidi ≡ Acta Bot. Hung. 28:69. 1982 – TYPE: HONDURAS, Santa Bárbara, Jan 1888, C. Thieme 5276, (HT: US [not seen]; isotypes: MO!).

= *Rondeletia phyllocephala* Standl. & L.O. Williams, Ceiba 3:63. 1952 ≡ *Arachnothryx phyllocephala* (Standl. & L.O. Williams) Borhidi, Acta Bot. Hung. 33:302. 1987 – TYPE: HONDURAS, Cortés, 6 Dec 1950, A. Molina 3608, (HT: EAP [image!]; isotypes: F!).

Gonzalagunia torresii (Standl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia torresii* Standl., J. Wash. Acad. Sci. 18:163. 1928 ≡ *Arachnothryx torresii* (Standl.) Borhidi, Acta Bot. Hung. 33:303. 1987 ≡ *Javorkaea torresii* (Standl.) Borhidi, Acta Bot. Hung. 43:59. 2001 – TYPE: COSTA RICA, Alajuela, 13 Feb 1926, P.C. Standley 47839 (HT: US [image!]).

Gonzalagunia tuxtlensis (Lorence & Cast.-Campos) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia tuxtlensis* Lorence & Cast.-Campos, Biótica 13:148–150. 1988 ≡ *Arachnothryx tuxtlensis* (Lorence & Cast.-Campos) Borhidi, Acta Bot. Hung. 35:311. 1989 – TYPE: MEXICO, Veracruz, Mecayapan, 8 May 1985, J.I. Calzada 11183, (HT: XAL!; isotypes: F!, MEXU!, MO!, PTBG [image!]).

Gonzalagunia uxpanapensis (Lorence & Cast.-Campos) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia uxpanapensis* Lorence & Cast.-Campos, Biótica 13:150–154. 1988 ≡ *Arachnothryx uxpanapensis* (Lorence & Cast.-Campos) Borhidi, Acta Bot. Hung. 35:311. 1989 – TYPE: MEXICO, Veracruz, Uxpanapa, 24 Mar 1982, D.H. Lorence 3909, (HT: MEXU!; isotypes: BM [image!], ENCB [not seen], CHAPA [not seen], MO!, NY [image!], PTBG [image!], XAL!).

Gonzalagunia vallensis (Standl. & Steyerm. ex Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Cuatrecasasiodendron colombianum* Standl. & Steyerm. ex Steyerm., Acta Biol. Venez. 4:30. 1964 – TYPE: COLOMBIA, El Valle, no date, J. Cuatrecasas 13694, (HT: F!; isotypes: F!).

= *Cuatrecasasiodendron spectabile* Steyerm., Acta Biol. Venez. 4:33. 1964 ≡ *Arachnothryx spectabilis* (Steyerm.) Rova, Delprete & B. Bremer, Ann. Missouri Bot. Gard. 96:192. 2009 – TYPE: COLOMBIA, El Valle, no date, J. Cuatrecasas 17165, (HT: US [image!]; isotypes: BC [image!], F!, P [image!]).

The epithet "colombiana" is not available in *Gonzalagunia* (*G. colombiana* (Rusby) J. A. Torres-Montúfar & H. Ochoterena); hence, a new epithet is coined, this honors to El Valle (Colombia), where the type of this taxon was collected.

Gonzalagunia venezuelensis (Steyerm.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Arachnothryx venezuelensis* Steyerm., Mem. New York Bot. Gard. 17:256. 1967 – TYPE: VENEZUELA, Aragua, 26 Oct 1940, C.E. Chardon 179, (HT: VEN [not seen]).

Gonzalagunia wendtii (Lorence & Cast.-Campos) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** ≡ *Rondeletia wendtii* Lorence & Cast.-Campos, Biótica 13: 150–154. 1988 ≡ Arachnothryx wendtii (Lorence & Cast.-Campos) Borhidi, Acta Bot. Hung. 35:311. 1989 – TYPE: MEXICO, Oaxaca, Santa María Chimalapa, 21 Oct 1983, T.L. Wendt 4244, (HT: MEXU!; isotypes: CHAPA [not seen], PTBG [image!]).

Gonzalagunia zongolicana (Hemsl.) J. A. Torres-Montúfar & H. Ochoterena, **comb. nov.** et **nom. nov.** ≡ *Rondeletia affinis* Hemsl., Diagn. Pl. Nov. Mexic. 2:28. 1879 ≡ *Arachnothryx affinis* (Hemsl.) Borhidi, Acta Bot. Hung. 38:139. 1995 – TYPE: MEXICO, Veracruz, Zongolica, Jun 1866, Lectotype designated by Lorence, Monogr. Syst. Bot. Missouri Bot. Gard. 73:148. 1999: A.L.J.F. Sumichrast 1017, (LT: K [image!]; ILT: K [image!], P [image!]).

The epithet "affinis" is not available in *Gonzalagunia* (*G. affinis* Standl. ex Steyerm.); hence, a new epithet is coined, this honors to the Zongolica region, undoubtedly a hotspot of biodiversity in Mexico.

Appendix 1. Species, vouchers, geographic origin and GenBank accession numbers.

Complete names of the plants obtained from silica gel and herbarium specimens, followed by the country, collector and collection number, the herbarium abbreviation in parentheses, the project code (RUB000). The accession numbers of the regions are listed: the trnk/matK, trnL-F, petD accessions are provided. Sequences from Torres-Montúfar *et al*. (2017, 2018) are marked with an asterisk (*). Sequences from Rova *et al*. (2002, 2009) are marked with two asterisks (**).

Subfamily Cinchonoideae:

Tribe Chiococceae:

Ceuthocarpus involucratus* (Wernham) Aiello, Cuba, *T. Borsch 4995* (B; HAJB; PAL), RUB233, -, KY785213, KY614097, -; *Chiococca alba* (L.) Hitchc., Cuba, *N. Köster 2456* (B; HAJB; PAL), RUB248, -, MF460720, MF460625, -; *Chiococca alba* (L.) Hitchc., Dominican Republic, *S. Fuentes 2008* (B; JBS), RUB253, -, MF460721, MF460626, -; *Chiococca cubensis* Urb., Cuba, *T. Borsch 4963* (B; HAJB; PAL), RUB231, MF460539, MF460722, MF460627, -;Chiococca cubensis* Urb., Cuba, *S. Fuentes 535* (B; HAJB; PAL), RUB264, -, KY785214, KY614098, -; *Erithalis fruticosa* L., Cuba, *S. Fuentes 737* (B; HAJB; PAL), RUB209, MF460541, MF460724, MF460630, -; **Erithalis fruticosa* L., Dominican Republic, *S. Fuentes 221* (B; JBS), RUB183, -, KY785218, KY614101, -; **Erithalis vacciniifolia* (Griseb.) Wright ex Sauv., Dominican Republic, *S. Fuentes 1044* (B; JBS), RUB303, KY785272, KY785217, KY614100, -; *Exostema caribaeum* (Jacq.) Schult., Cuba, *T. Borsch 5295* (B; HAJB; PAL), RUB244, MF460542, MF460725, MF460631, -;**Exostema caribaeum* (Jacq.) Schult., Dominican Republic, *S. Fuentes 1177* (B; JBS), RUB294, -, KY785220, KY614103, -; **Exostema longiflorum* Roem. & Schult., Cuba, *N. Köster 2666* (B; HAJB; PAL), RUB251, -, KY785221, KY614104, -; **Exostema spinosum* (La Vavass) Krug & Urb., Dominican Republic, *S. Fuentes 207* (B; JBS), RUB243, KY785273, KY785219, KY614102, -; **Isidorea leonardii* Urb., Dominican Republic, *S. Fuentes 1210* (B; JBS), RUB302, KY785280, KY785232, KY614115, -; *Isidorea leptantha* Urb., Dominican Republic, *S. Fuentes 1088* (B; JBS), RUB404, -, MF460748, MF460655, -;**Isidorea veris* Ekman ex Aiello & Borhidi, Dominican Republic, *S. Fuentes 977* (B; JBS), RUB284, -, KY785233, KY614116, -; **Phialanthus* Griseb., Cuba, *S. Fuentes 545* (B; HAJB; PAL), RUB265, -, KY785236, KY614119, -; **Portlandia* P. Browne, Cuba, *M. Ackerman 847* (B; HAJB; PAL), RUB226, -, KY785239, KY614122, -; *Schmidtottia shaferi* (Standl.) Urb., Cuba, *T. Borsch 4250* (B; HAJB; PAL), RUB225, -, -, MF460682, -; *Schmidtottia* Urb., Cuba, *S. Fuentes 622* (B; HAJB; PAL), RUB266, -, -, MF460681, -; *Scolosanthus densiflorus* Urb., Dominican Republic, *S. Fuentes 1207* (B; JBS), RUB296, -, -, MF460683, -; *Scolosanthus triacanthus* (Spreng.) DC., Dominican Republic, *S. Fuentes 1173* (B; JBS), RUB295, -, -, MF460684, -.

Tribe Guettardeae:

***Allenanthus erythrocarpus* Standl., Panama, *Espinosa 520* (GB), -, GQ852452, -, -; ***Allenanthus hondurensis* Standl., Honduras, *M. Nee 27992* (NY), -, AF152734, -, -; *Antirhea abbreviata* Urb., Cuba, *M. Ackerman 1011* (B; HAJB; PAL), RUB228, -, -, MF460595, -; **Antirhea lucida* (Sw.) Benth. & Hook. f., Cuba, *T. Borsch 5288* (B; HAJB; PAL), RUB166, KY785299, KY785196, KY614077, -; *Arachnothryx affinis* (Hemsl.) Borhidi, Mexico, *L. Castillo 535* (MEXU), RUBmx065, MF460515, MF460696, MF460598, -; **Arachnothryx affinis* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 644* (MEXU), RUBmx046, KY785257, KY785197, KY614078, -; *Arachnothryx armentalis* (L.O. Williams) Lorence, Mexico, *A. Reyes 6755* (MEXU), RUB060, -, -, MF460599, -; **Arachnothryx aspera* (Standl.) Borhidi, Costa Rica, *E. Lepiz 174* (MEXU), RUB094, KY785258, -, KY614079, -; *Arachnothryx bourgaei* (Standl.) Borhidi, Mexico, *M. Cházaro 3636* (MEXU), RUBmx017, MF460517, MF460699, MF460602, -; *Arachnothryx buddleioides* (Benth.) Planch., Mexico, *A. Campos V. 1013* (MEXU, MO), RUBmx064, MF460514, MF460695, MF460597, -; *Arachnothryx buddleioides* (Benth.) Planch., Mexico, *H. Ochoterena B. 839* (MEXU), RUB086, MF460513, MF460694, MF460596, -; *Arachnothryx buddleioides* (Benth.) Planch., Mexico, *H. Ochoterena B. 875*

(MEXU), RUB087, MF460519, MF460701, MF460604, -; **Arachnothryx buddleioides* (Benth.) Planch., Mexico, *H. Ochoterena B. 924* (MEXU), RUB130, KY785259, KY785198, KY614080, -; *Arachnothryx buddleioides* (Benth.) Planch., Mexico, *P.J. Stafford et al. 348* (MEXU, MO), RUBmx016, MF460522, MF460703, MF460607, -; *Arachnothryx buddleioides* (Benth.) Planch., Mexico, *A. Torres M. 769* (MEXU), RUB092, MF460520, -, MF460605, -; **Arachnothryx capitellata* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 850* (MEXU), RUB076, KY785260, KY785199, KY614081, -; *Arachnothryx capitellata* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 817* (MEXU), RUB084, MF460523, MF460704, MF460608, -; *Arachnothryx chimalaparum* Lorence ex Borhidi, Mexico, *P. Tenorio L. 19319* (MEXU), RUB340, -, -, MF460609, -; ***Arachnothryx chimboracensis* (Standl.) Steyerm., Ecuador, *P. Delprete & Verduga 6398* (NY), -, GQ852462, -, AY730292; *Arachnothryx dwyeri* (Lorence) Borhidi, Panama, *H. Herrera 1287* (MEXU), RUB139, MF460524, MF460705, MF460610, -; ***Arachnothryx fosbergii* Steyerm., Ecuador, *E. Rova 2082* (GB), -, AF152724, -, AY730298; *Arachnothryx gracilispica* (Standl.) Borhidi, Mexico, *A. Sánchez 1897* (MO), RUBmx066, MF460525, MF460706, MF460611, -; **Arachnothryx guerrerensis* (Lorence) Borhidi, Mexico, *D. Breedlove 61973* (MEXU), RUB343, KY785300, KY785200, KY614082, -; **Arachnothryx heteranthera* (Brandegee) Borhidi, Mexico, *H. Ochoterena B. 823* (MEXU), RUB046, KY785261, KY785201, KY614083, -; *Arachnothryx heteranthera* (Brandegee) Borhidi, Mexico, *X. Munn-Estrada 1771* (MEXU), RUB059, MF460535, MF460716, MF460621, -; **Arachnothryx jurgensenii* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 803* (MEXU), RUB042, KY785262, -, KY614084, -; *Arachnothryx laniflora* (Benth.) Planch., El Salvador, *V. M. Martínez 1013* (MO), RUBmx010, MF460532, MF460713, -, -; **Arachnothryx leucophylla* (Kunth) Planch., Mexico, *H. Ochoterena B. 752* (MEXU), RUB043, KY785301, KY785202, KY614085, -; **Arachnothryx manantlanensis* (Lorence) Borhidi, Mexico, *R. Cuevas 4978* (MEXU), RUB104, KY785263, KY785203, KY614086, -; *Arachnothryx monticola* Borhidi, Mexico, *A. Campos V. 2741* (MEXU), RUB040, MF460516, MF460698, MF460601, -; *Arachnothryx monticola* Borhidi, Mexico, *L. C. Rodriguez 420* (FCME), RUBmx004, MF460526, MF460707, MF460612, -; *Arachnothryx nebulosa* (Standl.) Borhidi, Nicaragua, *L. Pagagua 146* (MO), RUB117, XXX, XXX, XXX, -; *Arachnothryx nitida* (Hemsl.) Borhidi, Mexico, *R. García 855* (MEXU; SERBO), RUBmx067, MF460518, MF460700, MF460603, -; *Arachnothryx nitida* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 871* (MEXU), RUB082, MF460531, MF460712, MF460617, -; *Arachnothryx nitida* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 872* (MEXU), RUB132, MF460521, MF460702, MF460606, XXXXX; *Arachnothryx nitida* (Hemsl.) Borhidi, Mexico, *K. Velasco 1479* (MEXU; SERBO), RUBmx021, MF460527, MF460708, MF460613, -; *Arachnothryx nitida* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 866* (MEXU), RUBmx050, MF460533, MF460714, MF460618, -; *Arachnothryx ovandensis* (L.O. Williams) Lorence, Mexico, *A. Reyes G. 6633* (MEXU), RUB344, -, MF460697, MF460600, -; *Arachnothryx pringlei* (Lorence) Borhidi, Mexico, *H. Ochoterena B. 669* (MEXU), RUB070, MF460528, MF460709, MF460614, -; *Arachnothryx pringlei* (Lorence) Borhidi, Mexico, *H. Ochoterena B. 854* (MEXU), RUB081, MF460529, MF460710, MF460615, -; **Arachnothryx pumae* J.A. Torres M. & Ochot.-Booth, Mexico, *H. Ochoterena B. 741* (MEXU), RUB069, KY785264, KY785204, KY614087, XXXX; **Arachnothryx pyramidalis* (Lundell) Borhidi, Mexico, *M. Heath 414* (MEXU), RUB088, KY785302, KY785205, KY614088, -; *Arachnothryx rekoi* (Standl.) Borhidi, Mexico, *P. Tenorio L. 19278* (MEXU), RUB054, -, -, MF460619, -; *Arachnothryx secundiflora* (B.L. Rob.) Borhidi, Mexico, *H. Ochoterena B. 739* (MEXU), RUB039, MF460534, MF460715, MF460620, -; **Arachnothryx secundiflora* (B.L. Rob.) Borhidi, Mexico, *H. Ochoterena B. 743* (MEXU), RUB118, KY785265, KY785206, KY614089, -; **Arachnothryx stachyoidea* (Donn. Sm.) Borhidi, Mexico, *H. Ochoterena B. 842* (MEXU), RUB067, KY785266, KY785207, KY614090, -; **Arachnothryx tabascensis* Borhidi, Mexico, *H. Ochoterena B. 929* (MEXU), RUBmx069, KY785267, KY785208, KY614091, -; *Arachnothryx villosa* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 695* (MEXU), RUB044, MF460537, -, MF460622, XXXX; *Arachnothryx villosa* (Hemsl.) Borhidi, Mexico, *H.*

Ochoterena B. 900 (MEXU), RUB045, MF460530, MF460711, MF460616, -; **Arachnothryx villosa* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 846* (MEXU), RUB124, KY785268, KY785209, KY614092, -; *Arachnothryx villosa* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 834* (MEXU), RUB129, MF460538, MF460718, MF460623, -; *Chomelia angustifolia* Benth., Brasil, *Jansen-Jacobs et al. 4361* (GB), -, GQ852478**, -, -; **Chomelia brachypoda* Donn. Sm., Mexico, *H. Ochoterena B. 746* (MEXU), RUB119, KY785270, KY785215, KY614099, -; ***Chomelia spinosa* Jacq., Colombia, *Siegler 12793* (MO), -, GQ852454, -, -; ***Chomelia tenuiflora* Benth., *Andersson et al. 2030* (GB), -, AF152729, -, -; *Chomelia* sp, Mexico, *H. Ochoterena B. 801* (MEXU), RUB128, MF460540, MF460723, MF460629, -; ***Gonzalagunia affinis* Standl. ex Steyerm., Colombia, Bremer & Thulin 1998 (GB), -, AJ847405, -, AY730295; *Gonzalagunia chiapasensis* (Standl.) Standl. & Steyerm, Mexico, R. Martínez C. 885 (MO), RUBmx057, MF460543, -, MF460632, -; ***Gonzalagunia cornifolia* (Kunth) Standl., ND, *Stahl 1407* (GB), -, GQ852501, -, GQ852128; ***Gonzalagunia dependens* Ruiz & Pav., ND, *Persson et al. 462* (GB), -, GQ852502, -, GQ852129; ***Gonzalagunia dicocca* Cham. & Schltdl., ND, *Andersson et al. 2024* (GB), -, AF152721, -; ***Gonzalagunia kallunkiae* Dwyer, ND, *Rova & Sundbaum 2404* (GB), -, AF152723, -; **Gonzalagunia killipii* Standl., Ecuador, *M. Zak 3566* (MEXU), RUB049, KY785304, -, KY614105, -; *Gonzalagunia panamensis* (Cav.) K. Schum., Mexico, *H. Ochoterena B. 790* (MEXU), RUB080, MF460544, MF460726, MF460633, XXXXX; *Gonzalagunia panamensis* (Cav.) K. Schum., Mexico, *H. Ochoterena B. 789* (MEXU), RUB126, MF460545, MF460727, MF460634, -; *Gonzalagunia panamensis* (Cav.) K. Schum., Mexico, *H. Ochoterena B. 731* (MEXU), RUBmx038, MF460546, MF460728, MF460635, -; ***Gonzalagunia rosea* Standl., ND, *Rova 2414* (GB), -, GQ852503, -, DQ063671; **Gonzalagunia rudis* (Standl.) Standl., Costa Rica, *R. Forero 7419* (MEXU), RUB095, KY785305, KY785223, KY614106, -; **Gonzalagunia sagreana* Urb., Cuba, *N. Köster 2506* (B; HAJB; PAL), RUB418, KY785274, KY785222, -, -; **Gonzalagunia thyrsoidea* (Donn. Sm.) B.L. Rob., Guatemala, *M. Gonzalez 1455* (MEXU), RUB047, KY785275, KY785224, KY614107, XXXXX; *Guettarda clarensis* Britton, Cuba, *T. Borsch 4688* (B; HAJB; PAL), RUB159, MF460547, MF460729, MF460636, -; *Guettarda clarensis* Britton, Cuba, *T. Borsch 5098* (B; HAJB; PAL), RUB161, MF460548, MF460730, MF460637, -; *Guettarda dictyophylla* Urb., Dominican Republic, *S. Fuentes 345* (B; JBS), RUB188, MF460549, MF460731, MF460638, -; *Guettarda echinodendron* C. Wright, Cuba, *T. Borsch 5100* (B; HAJB; PAL), RUB162, MF460550, MF460732, MF460639, -; *Guettarda elliptica* Sw., Mexico, *H. Ochoterena B. 794* (MEXU), RUB085, MF460551, MF460733, MF460640, -; **Guettarda elliptica* Sw., Mexico, *H. Ochoterena B. 894* (MEXU), RUB125, KY785306, KY785225, KY614108, -; *Guettarda elliptica* Sw., Dominican Republic, *S. Fuentes 216* (B; JBS), RUB180, MF460552, MF460734, MF460641, -; *Guettarda ferruginea* C. Wright ex Griseb., Cuba, *T. Borsch 4817* (B; HAJB; PAL), RUB148, MF460553, MF460735, MF460642, -; **Guettarda ferruginea* C. Wright ex Griseb., Cuba, *T. Borsch 5007* (B; HAJB; PAL), RUB152, KY785278, KY785229, KY614112, -; *Guettarda ferruginea* C. Wright ex Griseb., Cuba, *T. Borsch 4453* (B; HAJB; PAL), RUB155, MF460554, MF460736, MF460643, -; *Guettarda ferruginea* C. Wright ex Griseb., Cuba, *T. Borsch 4596* (B; HAJB; PAL), RUB157, MF460555, MF460737, MF460644, -; **Guettarda monocarpa* Urb., Cuba, *T. Borsch 4429* (B; HAJB; PAL), RUB153, KY785307, KY785227, KY614110, -; *Guettarda monocarpa* Urb., Cuba, *S. Fuentes 544* (B; HAJB; PAL), RUB201, MF460556, MF460738, MF460645, -; **Guettarda prenleloupii* Urb., Dominican Republic, *S. Fuentes 1205* (B; JBS), RUB292, KY785279, KY785230, KY614113, -; *Guettarda prenleloupii* Urb., Dominican Republic, *S. Fuentes 1186* (B; JBS), RUB299, MF460557, MF460739, MF460646, -; **Guettarda pungens* Urb., Dominican Republic, *S. Fuentes 238* (B; JBS), RUB184, KY785277, KY785228, KY614111, -; *Guettarda pungens* Urb., Dominican Republic, *S. Fuentes 908* (B; JBS), RUB291, MF460558, MF460740, MF460647, -; *Guettarda pungens* Urb., Dominican Republic, *S. Fuentes 1154* (B; JBS), RUB383, MF460560, MF460742, MF460649, -; *Guettarda scabra* (L.) Vent., Dominican Republic, *S. Fuentes 256* (B; JBS), RUB186, MF460561, MF460743, MF460650, -; *Guettarda scabra* (L.) Vent., Cuba, *S.*

Fuentes 850 (B; HAJB; PAL), RUB212, MF460562, MF460744, MF460651, -; *Guettarda shaferi* Standl., Cuba, *N. Köster 2852* (B; HAJB; PAL), RUB179, MF460563, MF460745, MF460652, -; *Guettarda shaferi* Standl., Cuba, *T. Borsch 4448* (B; HAJB; PAL), RUB238, MF460564, MF460746, MF460653, -; *Guettarda tortuensis* Urb. & Ekman, Dominican Republic, *S. Fuentes 218* (B; HAJB; PAL), RUB181, MF460565, MF460747, MF460654, -; *Javorkaea scabra* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 880* (MEXU), RUB037, MF460566, -, MF460656, -; **Javorkaea hondurensis* (Donn. Sm.) Borhidi & Járai-Koml., Honduras, *J. Linares 6241* (MEXU), RUBmx055, KY785281, KY785234, KY614117, -; ***Machaonia acuminata* Bonpl., Mexico, *S. Bullock 1432* (MO), -, GQ852523, -, -; **Machaonia pauciflora* Urb., Cuba, *T. Borsch 5218* (B; HAJB; PAL), RUB164, KY785282, KY785235, KY614118, -; ***Machaonia williamsii* Standl., ND, *Persson & Grandez 700* (GB), -, GQ852524, -, -; *Renistipula galeottii* (Standl.) Borhidi, Mexico, *A. Torres 653* (MEXU), RUBmx099, MF460571, MF460753, MF460661, -; **Rogiera amoena* Planch., Mexico, *H. Ochoterena B. 805* (MEXU), RUB131, KY785284, KY785240, KY614123, -; *Rogiera cordata* (Benth.) Planch., Mexico, *H. Ochoterena B. 777* (MEXU), RUB134, MF460573, MF460755, MF460663, -; *Rogiera langlassei* (Standl.) Borhidi, Mexico, *K. Velasco 431* (MEXU, SERO), RUB097, MF460574, MF460756, MF460664, -; *Rogiera langlassei* (Standl.) Borhidi, Mexico, *K. Velasco 2467* (MEXU; SERBO), RUBmx025, MF460572, MF460754, MF460662, -; **Rogiera ligustroides* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 781* (MEXU), RUB068, KY785286, KY785242, KY614125, -; *Rogiera ligustroides* (Hemsl.) Borhidi, Mexico, *L. Castillo H. 256* (MEXU, MO), RUB121, -, MF460757, MF460665, -; **Rogiera macdougalli* Lorence, Mexico, *H. Ochoterena B. 841* (MEXU), RUB073, KY785288, KY785244, KY614127, -; **Rogiera nicaraguensis* (Oerst.) Borhidi, Honduras, *J. Linares 3520* (MEXU), RUB064, KY785287, KY785243, KY614126, -; **Rogiera stenosiphon* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 749* (MEXU), RUB075, KY785289, KY785245, KY614128, -; **Rogiera stenosiphon* (Hemsl.) Borhidi, Mexico, *H. Ochoterena B. 732* (MEXU), RUB072, KY785285, KY785241, KY614124, -; *Stenostomum montecristinum* (Urb. & Ekman) Borhidi, Dominican Republic, *S. Fuentes 219* (B; JBS), RUB182, -, -, MF460685.

Tribe Rondeletieae:

Acrosynanthus lucidus Britton., Cuba, *T. Borsch 5003* (B; HAJB; PAL), RUB235, -, MF460691, MF460592, -; *Acrosynanthus lucidus* Britton., Cuba, *T. Borsch 4447* (B; HAJB; PAL), RUB237, -, MF460692, MF460593, -; *Acrosynanthus minor* Urb., Cuba, *S. Fuentes 637* (B; HAJB; PAL), RUB267, -, MF460688, MF460589, -; **Acrosynanthus revolutus* Urb., Cuba, *T. Borsch 4156* (B; HAJB; PAL), RUB224, MF460511, MF460689, MF460590, -; *Acrosynanthus revolutus* Urb., Cuba, *T. Borsch 4625* (B; HAJB; PAL), RUB239, -, MF460693, MF460594, -; **Acrosynanthus trachyphyllus* Standl., Cuba, *T. Borsch 4444* (B; HAJB; PAL), RUB154, KY785256, KY785195, KY614076, -; *Acrosynanthus trachyphyllus* Standl., Cuba, *S. Fuentes 602* (B; HAJB; PAL), RUB203, MF460512, MF460690, MF460591, -; ***Blepharidium guatemalense* Standl., Guatemala, *Gustafsson et al. 211* (GB), -, AF152735, -, AY730287; **Donnellyanthus deamii* (Donn. Sm.) Borhidi, Honduras, *S. Duery 172* (MEXU), RUB056, KY785271, KY785216, -, -; ***Donnellyanthus deamii* (Donn. Sm.) Borhidi, Honduras, *Castillo 1560* (NY), -, GQ852545, -, AY730305; **Mazaea shaferi* (Standl.) Delprete, Cuba, *T. Borsch 4075* (B; HAJB; PAL), RUB144, MF460567, MF460749, MF460657, -; **Phyllomelia coronata* Griseb., Cuba, *T. Borsch 4620* (B; HAJB; PAL), RUB158, KY785303, KY785210, KY614093, -; **Rachicallis americana* (Jacq.) Hitchc., Cuba, *N. Köster 2465* (B; HAJB; PAL), RUB170, KY785283, KY785238, KY614121, -; **Rachicallis americana* (Jacq.) Hitchc., Cuba, *T. Borsch 5625* (B; HAJB; PAL), RUB217, MF460568, MF460750, MF460658, -; *Rachicallis americana* (Jacq.) Hitchc., Cuba, *T. Borsch 5641* (B; HAJB; PAL), RUB218, MF460569, MF460751, MF460659, -; **Rondeletia baraconensis* Urb., Dominican Republic, *S. Fuentes 315* (B; JBS), RUB187, KY785290, KY785246, KY614129, -; **Rondeletia berteroana* DC., Dominican Republic, *S. Fuentes 239* (B; HAJB; PAL), RUB185, MF460575, MF460758, MF460666, -; ***Rondeletia buxifolia* Vahl, Montserrat islands, *Veloz et al. 1868* (MO), -, GQ852555, -, -; **Rondeletia camarioca* C. Wright, Cuba, *T. Borsch 5096* (B; HAJB; PAL), RUB160, MF460576, MF460759, MF460667, -; *Rondeletia camarioca* C. Wright, Cuba, *S. Fuentes 845* (B; HAJB; PAL), RUB211, MF460577, MF460760, MF460668, -; **Rondeletia rugelii* C. Wright, Cuba, *T. Borsch 5601* (B; JBN; PAL), RUB215; KY785294, KY785251, KY614134, -; *Rondeletia cristalensis* Urb., Cuba, *N. Köster 2828* (B; HAJB; PAL), RUB178, MF460578, MF460761, MF460669, -; *Rondeletia fuertesii* Urb., Dominican Republic, *S. Fuentes 1184* (B; JBS), RUB293, -, MF460762, MF460670; **Rondeletia conferta* Urb., Dominican Republic, *S. Fuentes 1170* (B; JBS), RUB298, KY785291, KY785247, KY614130, -; ***Rondeletia hameliifolia* Dwyer & M.V. Hayden, Panama, *Kirkbride & Hayden 164* (NY), -, GQ852546, -, AY730326; **Rondeletia hypoleuca* Griseb., Cuba, *T. Borsch 4204* (B; HAJB; PAL), RUB020, KY785292, KY785248, KY614131; ***Rondeletia inermis* (Spreng.) Krug & Urb., Puerto Rico, *Acevedo-Rodriguez et al. 7691* (NY), -, AF152745, -, AY730315; ***Rondeletia intermixta* Britton, Cuba, *Rova et al. 2245* (GB), -, AF152742, -, AY730311; **Rondeletia merilloana* Urb., Dominican Republic, *S. Fuentes 1136* (B; JBS), RUB353, KY785293, KY785249, KY614132, -; **Rondeletia microphylla* Griseb., Cuba, *T. Borsch 4169* (B; HAJB; PAL), RUB018, KY785308, KY785250, KY614133, -; **Rondeletia odorata* Jacq., Cuba, *N. Köster 2526* (B; HAJB; PAL), RUB171, MF460582, MF460766, MF460673, -; *Rondeletia odorata* Jacq., Cuba, *N. Köster 2546* (B; HAJB; PAL), RUB172, MF460583, MF460767, MF460674, -; ***Rondeletia odorata* Jacq., Cuba, *P. de Block 1407* (GB), -, -, KT218941, -, AY730307; *Rondeletia pachyphylla* Krug & Urb., Cuba, *S. Fuentes 438* (B; HAJB; PAL), RUB191, MF460584, -, MF460675, -; *Rondeletia thiemei* Donn. Sm., El Salvador, *D. Rodriguez 2463* (B; LAGU), RUB308, MF460536, MF460717, -; **Rovaeanthus strigosus* (Benth.) Borhidi, Guatemala, *M. Veliz 6539* (MEXU), RUB063, KY785295, KY785252, KY614135, -; ***Rovaeanthus suffrutescens* (Brandegee) Borhidi, Mexico, *B. Bremer 2712* (S), -, AF152738, -, AY730290; ***Suberanthus brachycarpus* (Griseb.) Borhidi & M. Fernández, Cuba, *McDowell 4824* (DUKE), -, HM045004, -, AY730300; **Tainus pitreanus* (Urb. & Ekman) J. A. Torres-Montúfar, H. Ochoterena & T. Borsch, Dominican Republic, *S. Fuentes 1110* (B; JBS), RUB311, MF460587, MF460773, MF460686; **Tainus pitreanus* (Urb. & Ekman) J. A. Torres-Montúfar, H. Ochoterena & T. Borsch, Dominican Republic, *T. Clase 4228* (JBSD, MO), RUB354, MF460588, MF460774, MF460687.

Incertae sedis

Chione sp, Dominican Republic, *S. Fuentes 1135* (B), RUB310, -, -, MF460628, -;

Subfamily Ixoroideae:

Tribe Condamineae:

**Calycophyllum candidissimum* (Vahl) DC., Cuba, *T. Borsch 5125* (B; HAJB; PAL), RUB336, KY785298, KY614094, -, -; **Picardaea haitiensis* Urb., Dominican Republic, *S. Fuentes 1017* (B; JBS), RUB409, KY785297, KY785237, KY614120.

Tribe Gardenieae:

Casasia calophylla A. Rich., Cuba, *N. Köster 2452* (B; HAJB; PAL), RUB247, -, MF460719, MF460624, -; **Casasia clusiifolia* (Jacq.) Urb., Cuba, *S. Fuentes 761* (B; HAJB; PAL), RUB271, KY785269, KY785211, KY614095, -; **Casasia jacquinioides* (Griseb.) Standl., Cuba, *T. Borsch 4990* (B; HAJB; PAL), RUB232, -, KY785212, KY614096, -; **Randia aculeata* L., Cuba, *T. Borsch 5316* (B; HAJB; PAL), RUB245, KY785255, KY785194, KY614075, -; *Randia mitis* L. Cuba, N. Köster 2588 (B; HAJB; PAL), RUB249, MF460570, MF460752, MF460660, -.

Tribe Sabiceeae:

**Sabicea mexicana* Wernham, Mexico, *H. Ochoterena B. 876* (MEXU), RUB111, KY785309, KY785253, KY614136; *Sabicea villosa* Schult., Mexico, *H. Ochoterena B. 844* (MEXU), RUB078, MF460585, MF460771, MF460679; **Sabicea villosa* Schult., Mexico, *H. Ochoterena B. 858* (MEXU), RUB122, KY785296, KY785254, KY614137.

PARTE II: EL GRUPO *Arachnothryx* EN LA TRIBU GUETTARDEAE

CAPÍTULO VII: TRATAMIENTO TAXONÓMICO DEL GÉNERO *Rogiera*

A taxonomic treatment of *Rogiera* Planch. (Guettardeae, Rubiaceae)

Alejandro Torres-Montúfar, Helga Ochoterena & Hilda Flores-Olvera

Preparado para Phytotaxa

A taxonomic treatment of *Rogiera* Planch. (Guettardeae, Rubiaceae)

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Abstract

Rogiera (Guettardeae) is a Neotropical genus distributed from Mexico to Central America that consists of nine species of shrubs, treelets or trees, which were previously treated under the taxonomically conflictive genus *Rondeletia*. *Rogiera* is recognized by the yellow hairy ring at the corolla mouth. Systematic studies in *Rogiera* are scarce, and taxonomic treatments disagree on the species circumscription as recent regional floristic treatments recognize 11 to 20 species. Here we present a taxonomic revision of *Rogiera* based on field work and the study of herbarium specimens. We provided identification keys, descriptions, distribution maps, phenological data and illustrations for nine species. Mexico is corroborated as diversity center for *Rogiera* with eight species. Here the lectotypification of *Rogiera amoena* is proposed.

Keywords

Lectotypification, Neotropical flora, *Rondeletia*, Taxonomy

Introduction

The neotropical genus *Rogiera* Planch. is formed by shrubs, treelets or trees with multiflowered inflorescences, quincuncial corolla lobes aestivation, yellow hairy ring at the corolla mouth and capsular fruits (Figure 1). It is found primarily in cloud forest and tropical rain forest mainly diverse at Mexico, also distributed in Central America to northern South America.

The circumscription of *Rogiera* has been controversial. It was segregated from *Rondeletia* by Planchon (1849) on the basis of the corolla characters: *Rogiera* includes plants with a yellow hairy ring on the corolla mouth while *Rondeletia* was characterized by flowers with a fleshy ring on the corolla mouth. This circumscription was not accepted by many authors and *Rogiera* was treated as synonyms of *Rondeletia* (i.e. Hooker 1873, Hemsley 1879, Standley 1918). Afterwards, Borhidi (1982) resurrected *Rogiera*, nevertheless, Lorence (1991, 1999) and Taylor (2001) refused to accept the segregation of *Rogiera* arguing that the characters used to distinguish them are not very useful due to morphological overlapping. Both genera were traditionally included in Rondeletieae (Hooker 1873, Robbrecht 1988, Robbrecht & Bridson 1993, Borhidi 2006).

The molecular phylogenies retrieved a polyphyletic *Rogiera*, one clade sharing a most recent common ancestor with Guettardeae and one sample just identified as *Rogiera* included in Rondeletieae (Rova *et al*. 2002). The molecular results, led to the description of *Rovaeanthus* by Borhidi *et al*. (2004) to encompass *Rogiera strigosa* (Benth.) Borhidi and *Rogiera suffrutescens* (Brandegee) Borhidi, subsequently, corroborated by other molecular studies (Robbrecht & Manen 2006, Manns & Bremer 2010, Torres-Montúfar *et al*. 2017a, b). Coupled with the molecular evidence *Rovaeanthus* is supported by morphological characters: solitary flowers or few flowered inflorescences and a fleshy ring coupled with a yellow hairy ring on the corolla mouth (Borhidi *et al*. 2004). Despite the evidence, *Rovaeanthus* is treated as *Rogiera* in the most recent Rubiaceae treatment arguing morphological and geographic overlapping (Lorence 2012).

Although recent regional floristic treatments accounts for *Rogiera* (Taylor 2001, Borhidi 2006, Borhidi 2012, Lorence 2012, Taylor *et al*. 2014), none of these treatments include all species of the genus as a whole on its entire geographical range of distribution, and species delimitation is controversial . The taxonomic treatments most inclusive for *Rogiera* shows disparity in the diversity for the genus; Borhidi (2006) in the Rubiaceae treatment for Mexico includes 11 species and cited 20 species for the genus, later in the updated version Borhidi (2012) treats 13 species and reiterates that the genus *Rogiera* has 20 species. In Mesoamerican Flora Lorence (2012) includes nine species in *Rogiera* (including *Rovaeanthus*) but recognizes 11 species for the genus. Recently, Borhidi (2018) published a "critical revision" for the genus *Rogiera* in which includes the 16 species that he recognized for the genus, nevertheless he only provided an identification key for the species and a taxonomic list, without explore species limits or even consulting specimens in herbaria. Due to this discrepancy in the total diversity reported, our main aim is to review the taxonomy of *Rogiera*, also to provide a reliable key for species identification and to update and standardize description of the species, including phenological data and maps of distribution.

Materials and methods

The treatment presented here is based on fieldwork and examination of more than 1200 herbarium specimens, including type specimens of 13 Herbaria (CAS, CICY, ENCB, F, FCME, GH, IEB, LL, MEXU, MO, TEX, US and XAL). The specimens were physical examined during herbarium visits or available as loans, but specimen images were also examined at JSTOR Global Plants (http://plants.jstor.org/). The descriptions and measurements are based primarily on dried herbarium specimens. Flower buds often open prematurely in the press at a smaller size than fully developed flowers, and the succulent fruits often shrink when dried, were also studied therefore the measurements of herbarium specimens may differ from those of living plants. The descriptive terminology follows Harris & Harris (2000), distribution, phenology and habitat information comes from herbarium specimen labels. All specimen localities were georeferenced as accurately as possible and these values were used for mapping using QGIS 2.8 (Quantum GIS 2018).

Taxonomic treatment

Rogiera Planch. (1849:442). TYPE: *Rogiera amoena* Planch. LT designated by Borhidi, Acta Bot. Hung. 28: 67. 1982.

Shrubs, treelets or **trees**, occasionally scandent, twigs terete or quadrangular. **Stipules** interpetiolar, erect or reflexed, persistent, rarely deciduous. **Leaves** opposite, those of a pair equal to unequal, coriaceous or chartaceous, domatia occasionally present. **Inflorescences** multi-flowered (>30)**,** paniculate or corymbiform, terminal or axillar; 1-pedunculate or tripartite at base. **Flowers** sessile or pedicellate, distylous, fragant; hypanthium subglobose, calyx lobes 4–7, lobes usually unequal, corolla infundibuliform, white, pink, red, or purplish, with a yellow hairy ring at the mouth, corolla lobes 4–6(–7), imbricate, entire margins or crisped, stamens 4–5, partially exserted or included, dorsifixed anthers, stigmas 2, linear, ovoid or reniform, ovary 2-locular, many ovulated, axillar placentation. **Capsular fruits**, globose to subglobose, loculicidal, woody. **Seeds** briefly winged or wingless.

Normalmente se incluiría un párrafo con una síntesis taxonómica con datos de número de especies reconocidas, distribución geográfica, endemismo, áreas de diversidad, hábitat, etc.

Key to species

1. Twigs conspicuously quadrangular, strongly angulate………………......9. *R. stenosiphon*

1. Twigs terete…………………………………………………………..………..2

2. Mature stipules evidently or slightly reflexed……………..…………….………………..3

3. Twigs densely and persistently villous; leaves abaxially villous, base acute, obtuse to slightly rounded, stipules slightly reflexed when mature...…………………….……1. *R. amoena*

3. Twigs strigose, glabrescent; leaves abaxially sparsely hirtellous at costa and veins, base slightly cordate to rounded, stipules conspicuously reflexed when mature.....…3. *R. cordata*

2. Mature stipules erect, never reflexed……………………………………………....………..4

4. Stipules up to 3 mm long; corolla glabrous………………………………...……………5

5. Flower tube 5-7 mm long; plants endemic to Veracruz…………………6. *R. ligustroides*

5. Flower tube 9-15 mm long; plants distributed from Oaxaca to Honduras ……………… ……………………………..………………………………………….…4. *R. edwardsii*

4. Stipules longer than 4 mm; corolla persistently hirtellous (rarely glabrescent in *R. gratissima*) ……………………………..…………………………………………………....6

6. Leaves elliptic-lanceolate to ovate-lanceolate, notoriously two or three times longer than broader…………………………………………………………………2. *R. breedlovei*

6. Leaves ovate, elliptic, ovate-elliptic or obovate, notoriously less than one time longer than broader……………………………………………………………………….....7

7. Adaxial leaf surface glabrate; domatia present, twigs glabrate, occasionally strigose but soon glabrescent…………..………………………………………...……5. *R. gratissima*

7. Adaxial leaf surface strigose or hirtellous; domatia absent, twigs villous or strigose…....8

8. Shrubs up to 2 m tall; pinkish corolla when fresh; twigs strigose; plants endemic to Mexico (Oaxaca)……………………..………………………………7. *R. macdougalli*

8. Shrubs or treelets 2–4 m tall; white corolla when fresh; twigs villous; plants endemic to Honduras and Nicaragua………………………...……………………8. *R. nicaraguensis*

1. *Rogiera amoena* Planch. (1849: 442) ≡*Rondeletia amoena* (Planch.) Hemsl. (1879: 26) Type:—Illustration based on plants cultivated in Belgium (Van Houtte establishment): Ilustration: Planchon, Fl. Serres Jard. Eur. 5: t. 442. 1849 (Lectotype designated here). (Figures 3, 4).

=*Rogiera elegans* Planch. (1849: 442). Type:—not designated, based on plants cultivated in Belgium (Van Houtte establishment), without illustration.

=*Rondeletia langlassei* Standl. (1918: 53) ≡ *Rogiera langlassei* (Standl.) Borhidi (1982: 67). Type:—MEXICO: Michoacán or Guerrero: Sierra Madre, 1750 m, 26 Jan 1899, *E. Langlassé 797* (holotype US!, isotypes B (destroyed), F (fragment)!, G-DEL [online image]!, K [online image]!, MEXU!, P[online image]!).

=*Rondeletia latifolia* Oerst. (1853: 43) ≡ *Rogiera latifolia* (Oerst.) Decne. (1853:121). Type:—NICARAGUA: Monte Pantasmo, Segovia. Jan 1848. *A.S. Oersted 11678* (holotype C [online image]!, isotypes K [online image]!, US!).

=*Rogiera menechma* Planch. (1849:442). Type:—not designated, based on plants cultivated in Belgium (Van Houtte establishment), without illustration.

=*Rondeletia pittieri* (1908: 316) ≡ *Rogiera pittieri* (K. Schum. & K. Krause) Borhidi (1982: 67). Type:—COSTA RICA: Bords du Río Porós et Río Legundo, 2000 m, 10 Jan 1890. *H. Pittier & T. Durand 1729* (holotype B (destroyed; photo F!, MO!), isotypes BR [online image]!, CR-n.v., US!).

=*Rogiera roezlii* Planch. (1849: 442) ≡ *Rondeletia roezlii* (Planch.) Hemsl. (1881:23). Type:—not designated, based on plants cultivated in Belgium (Van Houtte establishment), without illustration.

=*Rondeletia versicolor* Sm. ex Hook. (1851: 4579) ≡ *Rogiera versicolor* (Sm. ex Hook) Lindl. et Paxton, (1853:69–70). Type:—PANAMA: Boquete, Veraguas, based on plants cultivated at Kew (holotype K [online image]!).

=*Rondeletia rugosa* Benth. (1853: 43). Type:—COSTA RICA: Cartago, 5600 ft, no date. *Oersted s.n.* (holotype C [online image]!, isotypes US!).

=*Rondeletia schumanniana* K. Krause (1908: 315–316). Type:—PANAMA: Veraguas, Mar 1906. *Warszewicz 1168* (holotype B (destroyed; photo, F!), isotype F!).

Shrubs or **treelets,** 4–10 m tall, twigs terete, densely and persistently villous. **Stipules** erect, slightly reflexed when mature, 4–18 × 4–8 mm, triangular ovate to ovate, persistent, strigose. **Leaves** opposite, those of a pair at a node equal to slightly unequal, petiolate; petioles 3–18 mm long, hirtellous; lamina ovate-elliptic to elliptic, 5–23 × 3–15 cm, coriaceous, adaxially sparsely strigose primarily at costa and veins, abaxially villous, margins glabrate, slightly revolute, base acute, obtuse to slightly rounded, apex acute to acuminate, acumen up to 1 cm long; 5–8 pairs of secondary veins, adaxial surface sometimes bullate, venation prominent on abaxial surface, domatia absent. **Inflorescences** terminal, corymbiform, 5–19 × 5–13 cm including corollas, 1-pedunculate or tripartite at base, peduncle 1–6 cm long, axis villose, bracts ovate to elliptic, 5–13 mm long. **Flowers** subtended by triangulate to linear bracteoles, 2–4 mm long, pedicelate, pedicels 1–3 mm long, hirtellous; hypanthium subglobose, elliptic, 1–2 mm long, strigose to hirtellous; calyx lobes usually 5–6 (–7), slightly unequal, 1–3 mm long, oblong to lanceolate, strigose; corolla infundibuliform, pink or white when fresh, the tube 8–15 × 2–3 mm, externally strigose, internally sparsely puberulent to hirtellous, lobes 5(6), triangular ovate to subcircular, 2–3 × 2–3 mm, occasionally slightly crisped, externally strigulouse, internally sparsely puberulent; stamens 5, in long styled flowers attached 3 mm below apex of tube, stamens in short styled flowers attached 1 mm below apex of tube, anthers linear, 1.5–2 mm long; style glabrous, in long styled flowers 8–12 mm long, in short styled flowers 6–8 mm long, the stigmas linear, 1–2 mm long. **Fruits** globose, oblate, 3–5 × 3–6 mm, strigose. **Seeds** briefly winged, elliptic to subcircular, up to 1 mm long.

Distribution and habitat:—*Rogiera amoena* is distributed from Mexico to Colombia. Occurring from 550 to 2 250 m in tropical rain forest, deciduous forest and cloud forest.

Phenology:—Collected with flowers and fruits all along the year in the whole distribution range.

Taxonomic notes:—*Rogiera amoena* is characterized by the stipules 4–18 mm long, often reflexed when mature, the twigs and the leaf abaxial surface densely and persistently villous. It is similar to *R. cordata* by the corolla size and color, the stipule size and geographical distribution. Differs by the twigs densely and persistently villous (*vs*. twigs strigose and soon glabrescent in *R. cordata*), and the leaf base acute, obtuse to slightly rounded (vs. leaf base slightly cordate to rounded in *R. cordata*).

This species is the most widespread and also shows the most morphological variation of any *Rogiera*. Primarily based on corolla size and color, leaf form and size, many species were described, however, the diagnostic character states separating these taxa overlap. It is the most widespread species within the genus and is quite variable in which certainly derived in the many species described that are currently considered as synonyms.

Many species currently considered as synonyms of *R. amoena* were described on the same publication by Planchon (1849) based on cultivated plants in the Van Houtte establishment in Belgium. These species lacks for an illustration and there is not assignable type material, then Lorence (1999) proposed these species as synonyms probably based on the descriptions and based on the presumably type material for each species that undoubtedly fits into the *R. amoena* variation.

Specimens examined:—COLOMBIA. ANTIOQUIA: Río Tonuzco, 02 Nov 1988, *Zarucchi 7042* (MEXU). NARIÑO. Río Pielapi, 23 Jul 1988, *Gentry 63686* (MEXU). VALLE. Madroñal, 30 Jun 1988, *Devia 2213* (MEXU). **COSTA RICA.** ALAJUELA: Grecia, 1000 m, 16 Jan 1987, *Herrera et al. 397* (MEXU, MO); 1800–1850 m, 28 Mar 2006, *Vargas 1210* (MO); 1680–1680 m, 20 Apr 2010, *Vargas 4173* (MO); Monteverde, 1000 m, 08 Nov 1989, *Bello 1493* (F, MO); Zarcero, *Smith 177* (MEXU), *406* (MO). CARTAGO: La Unión, 12 May 1973, *Poveda-Álvarez 807* (MO). GUANACASTE: La Cruz, 700 m, 12 Jul 1996, *González 1100* (MO); Liberia, 980–1080 m, 17 Aug 07, *Grayum 12799* (MO). HEREDIA: Barva, 2000 m, 12 Nov 1993, *Jiménez M. 1403* (MO); Parque Nacional Braulio Castillo, 2500 m, 19 Apr 1990, *Rivera 208* (F). PUNTARENAS: Buenos Aires, 1940 m, 09 Sep 1996, *Alfaro 693* (F, MO); 1400 m, 19 Sep 1989, *Herrera 3496* (MO); 2000–2100 m, 28 Feb 2008, *Zamora 4185* (MO); 2000–2100 m, 28 Feb 2008, *Solano 5231* (MO); 1500 m, 10 Mar 1993, *Herrera 5847* (MO); Cordillera de Talamanca, 2150 m, 25 Aug 1983, *Davidse et al. 24040* (MEXU, MO); 25 Aug 1983, *Davidse et al. 24060* (MO); 1800–2000 m, 11 Mar 1984, *Davidse et al. 25522* (MEXU, MO); Coto Brus, 1850 m, 19 Jan 1997, *Navarro 618* (MO); 1500–2000 m, 01 Nov 1996, *Quesada et al. 1744* (MO); Los Angeles del Narui, 1100 m, 21 Dec 1936, *Solís 501* (MO); Monteverde, 29 Sep 1987, *Döbbeler 669* (MEXU); 1400–1500 m, 17 Jan 1977, *Dryer 1143* (MO); 20 Oct 1985, *Haber 3126* (MEXU); 1200 m, 20 Oct 1985, *Haber 3128* (MO); *3142* (MO); *3148* (MO); *3528* (MO); 1400 m, 29 Nov 1985, *Haber 3597* (MO); *3615* (MO); 30 Dec 1985, *Haber 4036* (MEXU, MO); 1200 m, 30 Dec 1985, *Haber & Bello 4036* (MO); 1500 m, 14 Nov 1986, *Haber & Bello 6238* (MO); 1400 m, 04 Jul 1988, *Haber 8489* (MO); Piedra Blanca, 1900 m, 20 Jan 1935, *Solís 153* (MO); Puntarenas, 1100 m, 04 Feb 1993, *Fuentes 164* (MO); 1400 m, 02 Feb 1979, *Haber 284* (MO); 1500 m, 01 Dec 1984, *Haber 1100* (MO); 1700 m, 24 Aug 1985, *Haber 2372* (MO). SAN JOSE: Aserri, 2000–2250 m, 13 Dec 2002, *Morales 8952* (MO); 1700–2100 m, 08 Dec 2004, *Morales 11776* (MO); Desamparados, 29 Oct 1985, *Chavarría & Chacón 30* (MEXU, MO); 1700–1800 m, 23 Apr 1985, *Grayum & Schatz 5143* (MO); Dota, 2050 m, 10 Dec 2001, *Quesada et al. 824* (MO); 2400–2500 m, 06 Jun 2004, *Solano 1123* (MO); Goicoechea, 2050–2050 m, 16 Jun 10, *Rodríguez G. 13035* (MO); Perez Zeledon, 1600 m, 29 Dec 1969, *Burger & Liesner 7072* (MO); Santa Ana, 1600–2000 m, 20 May 2006, *Solano 3174* (MO); Turrubares, 1400–1600 m, 05 Jan 1996, *Hammel et al. 20074* (MO); Vázquez de Coronado, 1500–1600 m, 17 Nov 2005, *Diego 1061* (F). **EL SALVADOR.** SANTA ANA: Monte Cristo, 2051 m, 23 Jan 2002, *Carballo et al. 128* (F, MO); 31 Jul 1977, *Croat 42371* (MEXU, MO). **GUATEMALA.** ALTA VERAPAZ: Coban, 1350 m, Sep 1907, *von Türckheim 1635* (F, MO); Sep 1912, *von Türckheim 3861* (F); 1300 m, 03 Sep 1970, *Harmon & Fuentes 4283* (MO); 1400–1500 m, 25 Jan 1969, *Williams et al. 40057* (F); 1300–1400 m, 31 Jan 1969, *Williams et al. 40708* (F); 1500 m, 4 Dec 1994, *Castillo 2411*

(F); Finca Samac, 1300 m, 23 Mar 1941, *Standley 89667* (F); San Juan Chamelco, 5 Feb 1969, *Williams 40593* (F); Feb 1969, *Williams 40861* (F); San Pedro Carchá, 1200 m, 2 Feb 1969, *Williams et al. 40486* (F); Santa Cruz, 1380 m, 09 Apr 1939, *Standley 71008* (F). BAJA VERAPAZ. Niño Perdido, 28 Aug 1975, *Lundell & Contreras 19733* (MEXU, MO); Patal, 1550 m, 4 Apr 1941, *Standley 90977* (F); Purulha, 1500 m, 23 Oct 1993, *Castillo 2005* (F, MO); 1500 m, 4 Dec 1994, *Castillo 2405* (F); Unión Barrios, 1629 m, 10 Mar 1972, *Contreras 11216* (MEXU, MO); 7 Nov 1973, *Contreras 11598* (MEXU, MO). CHIQUIMULA: El Jutal, 1700–2000 m, 2 Nov 1939, *Steyermark 31075* (F). EL PROGRESO: El Jute de Cobana, 1400–2400 m, 3 Feb 1942, *Steyermark 43375* (F); Sierra de las Minas, 1700 m, 12 Nov 1958, *Hawkes 1962* (F). HUEHUETENANGO: Cerro Huitz, 1500–2600 m, 14 Jul 1942, *Steyermark 48650* (F); Nenton, 1430 m, 13 Dec 2006, *Pérez 1818* (MO); Soloma, 21 Aug 1934, *Skutch 1051* (F). QUETZALTENANGO: Finca Chicabal, 1380 m, 8 Mar 1939, *Standley 8060* (F); Río Samalá, 2300 m, 14 Dec 1962, *Williams 23000* (F). QUICHÉ: Nebaj, 2 Jul 1964, *Contreras 5167* (MO); Pulay, 2000 m, 29 Jul 1964, *Proctor 25335* (F, MO). SOLOLA. San Lucas Tolimán, 7 Aug 1999, *Morales 401* (F). **HONDURAS.** COMAYAGUA: Barranco El Socorro, 1500 m, 5 Oct 1951, *Williams 18370* (F); Cordillera de Montecillos, 1720 m, 09 Feb 1993, *Evans 1109* (MEXU, MO); Siguatepeque, 1500 m, 12 Nov 1932, *Edwards 512* (F); 11 May 1974, *Hazlett 1551* (MO); 1350 m, 7 Aug 1936, *Yuncker et al. 6371* (F, MO); 1500 m, 11 Mar 1970, *Molina 25506* (F, MO). EL PARAÍSO: Yuscarán, 2000 m, 27 Aug 1978, *Espinal 112* (MO); 6 Oct 1977–9 Oct 1977, *Romero 4323* (MEXU, MO); 1700 m, 12 Aug 1971, *Molina 26144* (F). FRANCISCO MORAZÁN: Cordillera de Misoco, 1700 m, 18 Mar 1956, *Molina 5957* (F); Guaimaca, 1600 m, 14 May 1950, *Molina 2831* (MO); Montaña La Tigra, 2000 m, 3 Aug 1962, *Molina 11063* (F); Montaña Zanquín, 1600 m, 14 May 1950, *Molina 2875* (F); Volcán de Monserrat, 20 Jun 1996, *Linares 3393* (MEXU). INTIBUCA: El Huise, 1600 m, 21 May 1964, *Molina 13853* (F); La Esperanza, 8 Sep 1979, *Cruz 74* (MEXU); 2000 m, 8 Sep 1979, *Valladares 78* (MO); 3 Apr 1956, *Molina 6221* (F); 1800 m, 23 May 1964, *Molina 14009* (F); 2000 m, 11 Jan 1969, *Molina 23330* (F); Yamaranguila, 1800 m, 24 Mar 1969, *Molina 24432* (F, MO). LA PAZ: El Cerrón, 1700 m, 20 Mar 1969, *Molina 24235* (F); Marcala, 1466 m, 14 Mar 1986, *Mejía 134* (MO); Pinares del Huis, 1500 m, 11 Apr 1956, *Molina 6504* (F). LEMPIRA: Gracias, 1900 m, 20 Sep 1991, *Chorley 355* (MO); 20 Sep 1991, *Chorley 358* (MEXU, MO). OCOTEPEQUE: Belén Gualcho, 1500–2000 m, 2 Apr 1977–15 Apr 1977, *Romero et al. 4066* (MO); El Moral, 1600 m, 27 Aug 1968, *Molina 22278* (F). OLANCHO: Campamento, 1057 m, 25 Apr 1982, *Sosa 186* (MO); Río Olancho, 550 m, 7 Feb 1987, *Croat & Hannon 64470* (MO). **MEXICO.** CHIAPAS: Angel Albino Corzo, 2100 m, 11 Nov 1945, *Hernández & Sharp 4511* (MEXU, MO); Huistán, 2080 m, 4 Nov 1980, *Fryxell & Lott 3294* (MEXU, MO, XAL); Matsab, 5 Jan 1966, *Shilom-Ton 522* (MEXU, XAL); Nueva Independencia, 4 Mar 1989, *Bachem 390*

(MEXU); Oxchuc, 2000 m, 10 Sep 1988, *Gómez & Sántiz-Gómez 365* (MEXU, MO); Pantepec, 22 Sep 1981, *Breedlove 53014* (MEXU); Pueblo Nuevo Solistahuacán, 1900–1950 m, 25 Jan 1979, *Croat 46352* (MO); Rancho Merced–Bazom, 2 Mar 1989, *González 654* (MEXU, XAL); Raya de Oxchuc, 2600 m, 12 Sep 1988, *Santíz 782* (MEXU, MO); Rayón, 23 Mar 1967, *MacDougall 19* (MEXU); Reserva El Triunfo, 18 Feb 1990, *Hampshire 418* (MEXU); 1 Nov 1989, *Heath 578* (MEXU); 18 Jan 2005, *Martínez Meléndez 685* (MEXU); 18 May 1982, *Calzada 9137* (MEXU); Siltepec, 24 Aug 1995, *Mejía 694* (MEXU); 1 Jan 1938, *Matuda 1896* (TEX, MEXU); 1 Oct 1940, *Matuda 4028* (LL, MEXU); 30 Oct 1941, *Matuda 4036* (LL, MEXU); 23 Jan 1945, *Matuda 15309* (LL, MEXU); San Juan Cancuc, 16 Aug 1991, *Brett 310* (MO); 7 Jan 1992, *Brett 627* (MO, TEX); Tenejapa, 21 Aug 1982, *Shilom-Ton 4500* (LL, MO, XAL); 5 Oct 1982, *Shilom-Ton 4749* (IEB, LL, MEXU, MO, XAL); 10 Oct 1982, *Shilom-Ton 4800* (LL, MEXU, MO, XAL); 20 Dec 1982, *Shilom-Ton 5295* (LL, MEXU, MO, XAL); 1500 m, *Shilom-Ton 5314* (LL, MEXU, MO, XAL); Yajalon, 16 Sep 1983, *Shilom-Ton 6666* (LL, MEXU, MO, XAL); Tierra Fría, 6 Nov 1984, *Méndez 7984* (LL, MEXU); Tres Cruces, 24 Feb 1945, *Matuda 5030* (MEXU, TEX); Yashanal, 17 Mar 1965, *Breedlove 9403* (MEXU, XAL). JALISCO: Las Joyas, 21 Dec 1984, *Judziewicz & Cochrane 4822* (MEXU, MO); Rincón de Manantlán, 4 Jan 1985, *Judziewicz 5065* (MEXU); San Sebastián, 1500 m, 10 Jan. 1927, *Mexia 1440* (F, MO), Sierra de Manantlán, 5 Jan 1979, *Iltis 1239* (MEXU); Talpa de Allende, 2 Jun 1970, *Boutin 3171* (MEXU). GUERRERO: Alquitrán, 27 Nov 2003, *Diego-Pérez 439* (FCME, MEXU); *Diego-Pérez 449* (FCME, MEXU); Chichihualco, 24 Nov 1983, *Martínez 5731* (MEXU, XAL); El Balsamo, 9 Dec 1985, *Soto 11489* (MEXU); Iris, 18 Feb 1991, *Lozada 1499* (MEXU); La Esperanza, 28 Nov 1996, *Teyuco 92* (MEXU); Mina, 1500 m, 30 Nov 1939, *Hinton & Hinton 14931* (MO); Petaltina, 14 Nov 1982, *Torres et al. 1932* (MEXU, MO); Petatlan, 13 Nov 1970, *Rzedowski 27058* (ENCB, MO); Petlacala, 17 Dec 1937, *Mexia 8982* (MO); Tejamanil, 25 Jan 1993, *Diego-Pérez 6709* (FCME, MEXU); Tlatlaquitepec, 3 Oct 1981, *Nuñez 363* (MEXU); Tierras Blancas, 1740 m, 23 Oct 1936, *Hinton 9764* (MEXU, MO); Tixtla, 6 Dec 1982, *Rico et al. 494* (MEXU, MO); Toro Muerto, 2150 m, 15 Nov 1939, *Hinton & Hinton 14853* (MO); Xochipala, 15 Oct 1985, *Gómez-Campos 1877* (MEXU). OAXACA: Juxtlahuaca, 22 Oct 1990, *García-Mendoza 5127* (MEXU); 12 Jul 1996, *Calzada 21519* (CICY, MEXU, MO); Pochutla, 12 Jan 1989, *Woodruff et al. 253* (MEXU, MO, TEX); 16 Mar 2004, *Velasco et al. 431* (MEXU, MO); 6 Dec 2002, *Pascual 677* (MEXU); San Pedro Ocotepec, 3 Oct 1997, *Rivera 515* (MEXU); Tehuantepec, 18 Feb 1987, *Torres 9124* (MEXU); Tepitongo, 1 Mar 1987, *Velasco 13* (MEXU); Tlaxiaco, 13 Apr 1987, *Torres 9603* (MEXU); Tlaxiaco–Putla, 1 Nov 1985, *Torres 7656* (MEXU); Totontepec, 2 Dec 1986, *Rivera 548* (MEXU); 1 Oct 1989, *Rivera & Martin 1184* (MEXU, MO); 15 Dec 1989, *Rivera & Martin 1325* (MEXU, MO); 14 Nov 2005, *Pérez 1688*

(MEXU); 20 Feb 1984, *Torres 4705* (MEXU); La Soledad, 17 Feb 1973, *Breedlove 33501* (MEXU); 30 Sep 1981, *Breedlove 53169* (MEXU). SINALOA: La Toma, 12 Nov 1997, *Tenorio-Lezama 19615* (MEXU); Los Chirimollos, 12 Feb 2000, *Vega 10590* (MEXU); Potrerillos–Petaca, 24 Oct 1986, *Vega 2149* (MEXU). TABASCO: Tenosique, 28 Feb 1979, *García 288* (MEXU). **NICARAGUA.** ESTELI: Cerro El Fraile, 1160–1200 m, 28 Sep 1980, *Stevens & Montiel 18027* (MO); Condega, 600–800 m, 2 Jan 2008–8 Jan 2008, *Padilla 100* (MO); Laguna de Miraflores, 1400 m, 23 Oct 1983, *Moreno 22390* (MO); Puertas Azules, 1300 m, 17 Apr 1999, *Rueda & Velásquez 10852* (MO); Reserva Natural Miraflor, 1300–1400 m, 12 May 1999, *Rueda et al. 10997* (MO); 1050–1200 m, 8 Jul 1999, *Rueda et al. 11569* (MO). JINOTEGA: La Fundadora, 1100–1150 m, 31 Oct 1979, *Stevens & Grijalva 15287* (MO); 1100–1150 m, 31 Oct 1979, *Stevens & Grijalva 15366* (MO); 1200–1400 m, 31 Oct 1979, *Stevens & Grijalva 15456* (MO); 1400 m, 8 Jan 1967, *Molina & Williams 20125* (F, MO); 1300–1400 m, 22 Feb 1963, *Williams 24882* (F, MO); Las Cruces, 1000 m, 4 Mar 1980, *Araquistain 1771* (MO). Peñas Blancas, 1200–1330 m, 16 Jan 1979, *Stevens 11557* (MEXU, MO); 800–1000 m, 30 Nov 2001, *Rueda et al. 16787* (MO); 1100 m, 27 Mar 2011, *Rueda et al. 18508* (MO); Reserva Cerro Kilambé, 950–1100 m, 26 Aug 2000–28 Aug 2000, *Rueda et al. 14494* (MO); 950–1100 m, 26 Aug 2000–28 Aug 2000, *Rueda et al. 14506* (MO); 900–1200 m, 24 May 2001, *Rueda et al. 16324* (MO); 900–1200 m, 24 May 2001, *Rueda et al. 16341* (MO); San Sebastián de Yalí , 1330 m, 7 Feb 2010, *Stevens & Montiel 29470* (MO); Santa Lastenia, 1450–1550 m, 31 Oct 1982, *Stevens 21906* (MO); Santa María de Ostuma, 1450 m, 18 Jan 1965, *Williams et al. 27931* (F, MO); Volcán Yali, 1100 m, 3 Sep 2010, *Coronado 5382* (MO); 1621 m, 4 Sep 2010, *Coronado et al. 5405* (MO); 1500–1542 m, 9 Apr 1981, *Moreno & Sandino 7967* (MO); 1200–1400 m, 25 Oct 1979, *Stevens & Grijalva 15120* (MO). MADRIZ: Cerro El Fraile, 1200 m, 13 Jan 1984, *Moreno 22775* (MO); Cerro Volcán de Somoto, 1300–1500 m, 15 Feb 1981, *Moreno 6890* (MO); 1200–1400 m, 3 Feb 1983, *Moreno 20042* (MO); El Sapote, 1000 m, 23 Sep 1980, *Moreno 2765* (MO); Telpaneca, 800–900 m, 29 Jan 2008–3 Feb 2008, *Cárdenas 211* (MO); 800–900 m, 14 Feb 2008, *Cárdenas 237* (MO). MATAGALPA: Cerro Apante, 1000–1400 m, 05 Nov 1981, *Sandino & Rodríguez 1533* (MO); 1000 m, 4 Nov 1981, *Téllez et al. 4781* (MEXU, MO, XAL); 900–1050 m, 9 Aug 1983, *Moreno 21952* (MO); Cerro Matapalo, 1000–1100 m, 23 Feb 1983, *Moreno & Robleto 20508* (MO); El Tuma, 1142 m, 19 Dec 2004, *Coronado et al. 818* (MO); Matagalpa, 1350 m, 3 Dec 2001, *Rueda et al. 16835* (MO); 1500 m, 15 Jan 1963, *Williams et al. 23946* (F, MO); 1470 m, 16 Feb 2008, *Stevens & Montiel 27092* (MO); Peñas Blancas, 900–1000 m, 24 Nov 1981, *Guzmán & Castro 2202* (MO); 1000–1400 m, 18 Jan 1982–20 Jan 1982, *Stevens et al. 20984* (MO); Tepeyac, 800–1000 m, 25 Feb 1982, *Sandino 2335* (MO). **PANAMA**. BOCAS DEL TORO: Cerro Fábrega, 840 m, 16 Mar 2005, *Monro & Cafferty 4668* (MO); Changuinola, 1700 m, 15 Apr 2008, *Monro et al. 5951* (MO). CHIRIQUÍ: Bajo Mono, 1700 m, 08 Feb 86, *Grayum et al. 6444* (MEXU, MO); 1650 m, 8 Feb 1986, *McPherson & Merello 8361* (MO); Bambito, 1800–2200 m, 19 Mar 1893, *Hamilton & Stockwell 3637* (MO); 8 Apr 1979, *D'Arcy et al. 13095* (MO); Boquete, 1500 m, 13 Dec 1966, *Dwyer et al. 556* (MO); 1700–1740 m, 1 Jul 1995, *Quiroz 562* (MO); 13 Jul 1938, *Davidson 951* (MO); 1350–1680 m, 14 Apr 1982, *Huft 1810* (MEXU, MO); 24 Jul 1966, *Blum & Dwyer 2553* (MO); 19 Nov 1978, *Hammel 5726* (MO); 8 Apr 1979, *Hammel et al. 6943* (MO); Sep 1965, *Dwyer 7000* (MO); 7 Aug 1967, *Dwyer & Hayden 7669* (MO); 1200–1800 m, 21 Nov 1975, *D'Arcy 9903* (MO); 17 Mar 1979, *D'Arcy et al. 12578* (MO); 17 Mar 1979, *D'Arcy et al. 12603* (MEXU, MO); 12 May 1971, *Proctor 31807* (MEXU, MO); Bugaba, 1300 m, 26 Feb 1985, *van der Werff & Herrera 7082* (MEXU, MO); 26 Feb 1985, *van der Werff 7100* (MEXU); 1300 m, 26 Feb 1985, *van der Werff & Herrera 7101* (MEXU, MO); Cabin, 1800 m, 20 Feb 1971, *Croat 13610* (MO); Casita Alta, 1500–2000 m, 28 Jun 1938–2 Jul 1938, *Woodson Jr. et al. 810* (MO); Cerro Colorado, 1000 m, 18 Mar 1974–19 Mar 1974, *Nee 10719* (MEXU, MO); Cerro Copete, 29 Jul 1947, *Allen 4866* (MO); Cerro Punta, 1800–2200 m, 13 Jul 1983, *Hamilton & Krager 3905* (MEXU, MO); Cerro Punta, 2100 m, 5 Jun 1986, *McPherson 9335* (MO); 1700 m, 19 Jan 1968, *McDaniel 10104* (MO); Chiriquí Trail, 600–1100 m, 21 Apr 1968, *Kirkbride Jr. & Duke 1026* (MO); 1100 m, 21 Apr 1968, *Kirkbride Jr. & Duke 1036* (MO); El Volcán, 4 Mar 1962, *Tyson 819* (MO); 13 Feb 1978, *Hammel 1558* (MO); Finca Collins, 12 Mar 1963, *Stern et al. 33773* (MO); Finca La Fe, 1000 m, 26 Dec 1977, *Folsom et al. 7171* (MEXU, MO); Finca Lérida, ,7 Jul 1940–11 Jul 1940, *Woodson Jr. & Schery 227* (MO); 1750–2000 m, 9 Jul 1940, *Woodson Jr. & Schery 311* (MO); Hato de Volcán, 24 Apr 1969, *Correa & Lazor 1436* (MO); 5 Apr 1979, *Hammel et al. 6780* (MO); Llano del Volcán, 1500–1600 m, 27 May 1946, *Allen & Fairchild 3469* (MO); Nueva Suiza, 1790 m, 19 Feb 1971, *Croat 13519* (MO); Río Chiriquí Viejo, 1300–1900 m, Jul–Aug 1937, *White & White 19* (MO); 1800 m, 22 Mar 1938, *White 35* (MO); 1440 m, 14 Aug 1938, *White 231* (MO); 1800–2000 m, 6 Jan–14 Jan 1939, *Allen 1350* (MO); Río Palo Alto, 1230–1400 m, 15 Apr 1982, *Huft 1840* (MEXU, MO); Río Serano, 7 Apr 1979, *D'Arcy et al. 13050* (MEXU, MO); Volcán Baru, 1900 m, 8 Jan 1983, *Stein 1261* (MEXU, MO); 2200 m, 28 Jun 1984, *Schmalzel & Spivak 1985* (MO); 1500 m, 21 Apr 1975, *Mori & Kallunki 5700* (MO); 2500–3400 m, 23 Apr 1975, *Mori & Kallunki 5740* (MO); 13 Mar 1979, *Hammel & D'Arcy 6371* (MO); 2115 m, 20 Mar 1977, *D'Arcy 11044* (MO); 2000 m, 13 Mar 1979, *D'Arcy & Hammel 12387* (MO); 20 Mar 1979, *D'Arcy et al. 12727* (MO); Volcán de Chiriquí, 1200 m, 18 Mar 1935, *Allen 994* (MO).

2. *Rogiera breedlovei* (Lorence) Borhidi (1996:16). ≡ *Rondeletia breedlovei* Lorence (1994: 129). Type:—MEXICO: Chiapas, Tenejapa, 27 Nov 1964. *Breedlove 7682* (holotype F!, isotypes CAS [online image]!, MEXU!) (Figures 5,6)

Scandent shrubs, 3–6 m tall, twigs terete, hirtellous. **Stipules** erect, 4–7 × 3–4 mm, deltoid to linear subulate, persistent, strigose. **Leaves** opposite, those of a pair at a node equal, petiolate; petioles 3–5 mm long, sparsely hirtellous; lamina elliptic–lanceolate to ovate–lanceolate, 4–11 × 2–5.3 cm, chartaceous, adaxially sparsely hirsutulous primarily at costa and veins, abaxially hirtellous, margins ciliolate, slightly revolute, base rounded to cordate, apex acuminate, acumen up to 1 cm long; 6–8 pairs of secondary veins, venation prominent on abaxial and adaxial surface, domatia present. **Inflorescences** terminal to axillar, corymbiform, 4–8 × 4–7 cm including corollas, 1–pedunculated or tripartite at base, peduncle 2–4 cm long, axis hirtellous, bracts lanceolate, 2–9 mm long. **Flowers** subtended by triangulate to linear bracteoles, 2–4 mm long, pedicelate, pedicels 1–3 mm long, hirtellous; hypanthium subglobose, elliptic, 1–2 mm long, hirtellous; calyx lobes 4–5(6), unequal, the larger lobe 2–3 mm long, the smaller ones 1–2 mm long, linear to linear–lanceolate, hirtellous; corolla infundibuliform, pink when fresh, the tube 13–16 × 2–3 mm, externally hirtellous, internally sparsely hirtellous, lobes 5(6), obovate to subcircular, 2–3 × 3 mm, occasionally crisped, externally sparsely strigulouse, internally glabrate; stamens 5, in short styled flowers attached 3 mm below apex of tube, long styled flowers unknown, anthers linear, 1.5–2 mm long; style glabrous, in short styled flowers 6–7 mm long, the stigmas linear, 2 mm long. **Fruits** subglobose, 3–4 × 3–4 mm, slightly obovate, hirtellous. **Seeds** briefly winged, elliptic to subcircular, up to 1 mm long.

Distribution and habitat:—*Rogiera breedlovei* is restricted to Chiapas, Mexico, occurring in cloud forest from 880 to 1000 m.

Phenology:—Collected with flowers and fruits from October to November.

Taxonomic notes:—*Rogiera breedlovei* is characterized by the erect stipules 4–7 mm long, the corolla tube hirtellous and the leaves two or three times longer than broader, elliptic–lanceolate to ovate–lanceolate. It is similar to *R. gratissima* by the twig pubescence, the corolla size and color, the presence of domatia and the geographical distribution. Differs by the hirsutulous leaf adaxial surface (*vs*. glabrate in *R. gratissima*) and by the persistently hirtellous corolla tube (*vs*. corolla tube sparsely strigose and soon glabrescent in *R. gratissima*).

Specimens examined:—MEXICO. CHIAPAS: Cruz Pilar, Mahben Chauk, 28 Oct 1966, *Shilom-Ton 1448* (MEXU, XAL); Cruz Pilar, 1000 m, 28 Nov 1995, *Mejía 990* (MEXU).

3. *Rogiera cordata* (Benth.) Planch. (1849:442) ≡ *Rondeletia cordata* Benth. (1839:85). Type:—GUATEMALA. Guatemala, Jan 1841. *Hartweg 585* (holotype K [online image]!, isotypes F (fragment)!, G–DEL [online image]!, MO!, NY [online image]!)

=*Rondeletia aprica* Lundell (1942: 54). ≡ *Rogiera aprica* (Lundell) Borhidi (1987: 301). Type:—MEXICO: Chiapas: Saxchanal, Sierra Madre, 1–5 Jul 1941. *Matuda 4314* (holotype MICH [online image]!, isotypes A [online image]!, F!, MEXU!, MO!, NY [online image]!, TEX–LL!, US!).

=*Rondeletia brachistantha* Standl. et Steyerm. (1943: 25). ≡ *Rogiera brachistantha* (Standl. et Steyerm.) Borhidi (1987:301). Type:—GUATEMALA: San Marcos, 20 Feb 1940, *Steyermark 36286* (holotype F!, isotype US!).

=*Rogiera cordata* (Benth.) Planch. var. *longisepala* Borhidi (2005: 30). Type:—MEXICO: Chiapas, Ocosingo, 70 km SW of Palenque on road to Ocosingo along the Jol Ukúm, 4 Dec 1980. *Breedlove 48313* (holotype MEXU!).

=*Rondeletia intermedia* Hemsl. (1879: 26). ≡ *Rogiera intermedia* (Hemsl.) Borhidi(1982: 67). Type:—MEXICO: Chiapas, a fleurs rouges, forets de pins de Chiapas. *Linden 1661* (lectotype K [online image]!, isolectotypes F (fragment)!, P-n.v. Lectotype designated by Lorence (1999), Monogr. Syst. Bot. Mo. Bot. Gard. 73: 147–152).

Shrubs or **treelets**, 3–10 m tall, twigs terete, strigose, glabrescent. **Stipules** conspicuously reflexed when mature, 6–14 × 4–6 mm, triangular to triangular ovate, persistent, strigillose. **Leaves** opposite, those of a pair at a node equal to slightly unequal, occasionally one leaf one half times longer than the other, shortly petiolate; petioles 1–6 mm long, glabrate; lamina ovate to elliptic, 3.5–22.5 × 2–10 cm, coriaceous, adaxially sparsely strigillose, glabrescent, abaxially sparsely hirtellous at costa and veins, margins ciliolate, slightly revolute, base slightly cordate to rounded, apex acuminate to acute, acumen up to 1 cm long; 5–9 pairs of secondary veins, adaxial surface sometimes bullate, venation prominent on abaxial surface, domatia absent. **Inflorescences** terminal or axillary, corymbiform, 5–13 × 2–12 cm including corollas, 1–pedunculate or tripartite at base, peduncle 1–6 cm long, axis strigose, bracts ovate to linear–lanceolate, 6–18 mm long. **Flowers** subtended by triangulate to linear bracteoles, 1–4 mm long, pedicelate or subbsessile, pedicels 1–3 mm long, strigose; hypanthium subglobose, obovate, 1–2 mm long, strigose; calyx lobes usually (4–)5–6 (–7), unequal, the larger lobe 2–3 mm long, the smaller ones 1–2 mm long, triangular, sparsely strigose; corolla infundibuliform, pink when fresh, the tube 5–12 × 3 mm, externally strigose, glabrescent, internally hirtellous basally, lobes 4–5, triangular ovate to subcircular, 2–4 × 3–4 mm, occasionally slightly crisped, externally strigose or glabrate, internally glabrate; stamens 4–5, in long styled flowers attached 2 mm below apex of tube, in short styled flowers attached 1 mm below apex of tube, anthers linear–ellipsoid, 1–3 mm long; style glabrous, in long styled flowers 7–12 mm long, in short styled flowers 4–5 mm long, the stigmas linear in long styled flowers, ovoid in short styled flowers, 1–2 mm long. **Fruits** globose obovate to elliptic, 2–3 × 4 mm, strigose. **Seeds** winged, discoid, 1 mm long.

Distribution and habitat:—*Rogiera cordata* occurs from the south of Mexico in Chiapas and Oaxaca to Guatemala, Honduras and El Salvador, in cloud forest and tropical rain forest from 380 to 2850 m.

Phenology:—Collected with flowers from August to April and fruits from December to July.

Taxonomic notes:—*Rogiera cordata* is characterized by stipules reflexed at maturity, 6–14 mm length, the twigs strigose and glabrescent, the leaf base cordate to rounded. It is similar to *R. amoena* (see discussion below that taxon). As *R. amoena*, this species is widely distributed and somewhat variable in corolla and calyx size, variation thah lead to the description of species here considered as synonyms.

Specimens examined:—EL SALVADOR. AHUACHAPÁN: Apaneca, 11 Dec 2010, *Rodríguez & Rivera 2196* (MO); El Naranjillo, 7 Mar 1993, *Villacorta & Reyna 124* (MO); San Benito, 1200 m, 16 Jan 1994, *Chinchilla & Lucas 14* (MEXU); 7 Dec 1989, *Sermeño 16* (MEXU, MO); 21 Nov 1991, *Sandoval 36* (MEXU, MO); San Francisco Menéndez, 380 m, 7 Mar 2000, *Linares 331* (MO); 7 Dec 1995, *Castillo & Magandi 818* (F, MO). **GUATEMALA.** CHIMALTENANGO: Chimaltenango, 1500–1700 m, 22 Dec 1940, *Standley 80936* (F); Río Pixcayó, 1650–1800 m, 3 Feb 1939, *Standley 64419* (F). GUATEMALA: Concepción Pinola, 1450 m, 13 Apr 1947, *Fosberg 27234* (MO); Fraijanes, 1600 m, 20 Dec 1938, *Standley 60393* (F); 26 Feb 1970, *Harmon 1995* (F, MO); 1840 m, 26 Apr 1970, *Harmon 2253* (MO); 2000 m, 3 Dec 1963, *Molina 13503* (F); 1800 m, 12–23 Jan 1966, *Molina 15967* (F); 1600 m, 26 Nov 1969, *Molina & Molina 24856* (F, MO); Mixco, 2000 m, 19 Jan 1947, *Williams 11762* (F); San José Pinula, 2000 m, 22 Feb 1949, *Williams 15296* (F); Volcán de Pacayá, 1800–2400 m, 30 Nov 1938, *Standley 58426* (F). HUEHUETENANGO: Antigua, 19 Apr 1991, *Castillo & Ericastilla 1246* (MO). IZABAL: Petén, 9 Nov 1973, *Contreras 11628* (MEXU). QUETZALTENANGO: Calahuaché, 1020 m, 1 Mar 1939, *Standley 67125* (F); Finca Pirineos, 17 Nov 1971, *Stone 3087* (F, MO); 1300–1500 m, 31 Dec 1939, *Steyermark 33199* (F); 1300–1400 m, 5 Jan 1940, *Steyermark 33547* (F); 1350–1380 m, 11 Mar 1939, *Standley 68264* (F); 1200–1400 m, 9 Feb 1941, *Standley 86577* (F); 87081 (F); Quetzaltenango, 1200–1300 m, 22 Jan 1987, *Croat & Hannon 63420* (F, MEXU, MO); Volcán de Zunil, 2430–2850 m, 17 Feb 1939, *Standley 65343* (F). SACATEPÉQUEZ: Alotenango, 1000–1260 m, 9

Feb 1939, *Standley 64965* (F); Antigua, 2000 m, 19 Jan 1947, *Williams 11782* (F); Cuesta de las Cañas, 1650 m, 3 Feb 1949, *Molina 15428* (F); 1950 m, 6 Dec 1938, *Standley 58897* (F); Dueñas, 1590–1800 m, 21 Jan 1939, *Standley 63158* (F); Finca el Hato, 1950–2040 m, 28 Dec 1938, *Standley 61136* (F); San Juan Sacatepequez, 1800 m, 8 Dec 1938, *Standley 59223* (F); San Lucas, 2000 m, 5 Nov 1965, *Molina 15353* (F); Santa Lucia Milpas Altas, 1900 m, 10 Dec 1992, *Castillo & Luarca 1671* (F, MO); Volcán de Acatenango, 6 Oct 1999, *Véliz 100* (MEXU); 17 Jan 2003, *Véliz 12739* (MEXU); Volcán de Agua, 2000 m, 7 Nov 1965, *Molina R. 15397* (F); 1800–2100 m, 10 Dec 1938, *Standley 59461* (F); Volcán de Fuego, 1800 m, 16 Dec 1938, *Standley 60264* (F). SAN MARCOS: San Marcos, 1600–2200 m, 16 Dec 1963, *Williams 26191* (F); Volcán Tajumulco, 2300–2800 m, 26 Feb 1940, *Steyermark 36625* (F). SANTA ROSA: Volcán Jumaytepeque, Dec 1892, *Heyde & Lux 4344* (F; MO). SANTA ROSA: Volcán Tecuamburro, 20 Dec 1939, *Steyermark 33158* (F); *Steyermark 33166* (F). SOLOLÁ: Cerro Iquitu, 1700 m, 7 Aug 1999, *Morales 386* (F); Volcán Atitlán, 11 Jun 1942, *Steyermark 47362* (F); Volcán Santa Clara, 1900–2100 m, 6 Jun 1942, *Steyermark 47131* (F). SUCHITEPÉQUEZ: Acatenango, 1 Feb 2005, *Kellerman 4734* (MEXU); Patulul, 1000–1400 m, 30 Jul 2004, *Rodas & Jiménez 52* (MEXU, MO). **HONDURAS.** FRANCISCO MORAZÁN: Distrito Central, 1600 m, 16 Aug 1987, *Lagos–Witte et al. 15* (MO). **MEXICO.** CHIAPAS: Angel Albino Corzo, 1380 m, 14 Dec 1980, *Breedlove 48672* (LL, MEXU, MO); 10 Jan 1982, *Breedlove 56915* (LL, MEXU, MO); 1380 m, 10 Jan 1982, *Breedlove & Almeda 56947* (LL, MEXU, MO); 1370 m, 11 Jan 1982, *Breedlove & Almeda 57022* (LL, MEXU, MO); Cerro del Boquerón, 4 May 1945, *Matuda 5367* (LL, MEXU); Aug 1913, *Purpus 7025* (MEXU, MO); Cerro La Peña, 19 Oct 2002, *Alvarado 608* (MEXU); Cerro Tres Picos, 22 Jan 2004, *Alvarado 1088* (MEXU); 28 Feb 2002, *Reyes 4130* (MEXU); 21 Mar 2004, *Reyes 6434* (MEXU); Cintalapa, 1150 m, 30 Jan 1990, *Stafford et al. 100* (MEXU, MO); 1150 m, 30 Jan 1990, *Stafford et al. 110* (MEXU, MO); Ejido Nueva Independencia, 20 Mar 2004, *Reyes 6385* (MEXU); 20 Mar 2004, *Reyes 6416* (MEXU); Ejido Talquian, 8 Nov 1977, *Calzada 3702* (MEXU); Ejido Tres Picos, 10 Apr 2002, *Reyes 4433* (MEXU); Finca Custepec, 13 Jul 1990, *Reyes 1877* (MEXU); 10 Jan 1982, *Breedlove 56915* (MEXU); 19 Nov 1983, *Breedlove 60364* (MEXU); Jitotol, 13 Nov 1984, *Téllez 7881* (MEXU); 1700 m, 27 Sep 1971, *Breedlove 19883* (MEXU, MO); 1600 m, 8 Nov 1981, *Breedlove & Davidse 55099* (MEXU, MO); La Concordia, 1590 m, 5 Nov 2004, *Martínez 597* (MEXU); La Milpoleta, 2 Feb 1995, *Martínez–Ico 153* (MEXU); 27 Jan 1995, *Ramírez 641* (MEXU); Larráinzar, 2700 m, 3 Aug 1972, *Breedlove 26790* (MEXU); 17 Oct 1972, *Breedlove 29228* (MO); Los Angeles, 24 Aug 1995, *Mejía 6942* (MEXU); Montaña Ovando, 1 Dec 1937, *Matuda 2086* (LL, MEXU); 4 Nov 1940, *Matuda 6125* (LL, MEXU); 14 Nov 1945, *Matuda 16226* (LL, MEXU); Montaña Pasitar, 29 Dec 1936, *Matuda 396* (LL, MEXU); 28 Dec 1936, *Matuda 521* (LL, MEXU); Motozintla, 1750 m, 8 Feb

1990, *Stafford et al. 325* (MEXU, MO); 1900–2010 m, 5 May 1987, *Miller et al. 2710* (MEXU, MO); 2100 m, 27 Jun 1972, *Breedlove 25791* (MEXU, MO); 2100 m, 21 Nov 1976, *Breedlove 41694* (MEXU); Ocosingo, 5 Apr 1985, *Cabrera 8077* (MEXU, MO); 2200 m, 5 Apr 1986, *Martínez-Salas & García-Mendoza 17509* (LL, MEXU, MO); 31 Aug 1981, *Breedlove 52515* (LL, MEXU); Ocozocoautla de Espinosa, 1250–1350 m, 16 Oct 1972, *Breedlove 29107* (LL, MEXU, MO); Oxchuc, 2300 m, 25 Sep 1988, *Gómez & Sántiz 394* (MEXU, MO); Palenque, 780 m, 10 Oct 1986, *Hammel et al. 15629* (MEXU); Paraje Navemchauk, 1 Nov 1976, *Breedlove 41176* (LL, MEXU); Pichucalco, 14 Oct 1986, *Martínez-Salas 19171* (MEXU, XAL); Pueblo Nuevo, 1700 m, 11 Feb 1983, *Martínez-Salas et al. 3242* (MEXU, MO); Rancho Concepción–Cerro Brujo, 4 Jan 1949, *Miranda 5155* (MEXU); Rancho Peñaflor, 16 Mar 1989, *Bachem 564* (MEXU); Reserva del Triunfo, 1 Nov 1989, *Heath 352* (MEXU); 21 Jun 1990, *Heath 1190* (MEXU); 13 May 1982, *Calzada 8888* (MEXU); Río Hondo, 2 Oct 2005, *Zamudio 13239* (MEXU); 27 Oct 1971, *Breedlove 21390* (LL, MEXU); San Andrés Larráizar, 8 Oct 1987, *González 145* (CHIP, IEB, MEXU); San Cristóbal de las Casas, 1720 m, 26 Jan 1979, *Croat 46467* (MEXU, MO); *46474* (MEXU, MO); San Fernando, 432 m, 21 Feb 2008, *Espinosa 654* (MEXU); San Juan Chamula, 21 Sep 1987, *Santíz 169* (CHIP, MEXU); San Juan Chamula, 12 Oct 1988, *Santíz 1098* (MEXU); Santa Martha, 11 Nov 1988, *Bachem 178* (CHAP, CHIP, MEXU); Siltepec, 8 Aug 1937, *Matuda 224* (LL, MEXU); 9 Aug 1937, *Matuda 1590* (LL, MEXU, MO); 2100 m, 9 May 1987, *Miller & Myers 2773* (MEXU); 18 Jan 1973, *Breedlove 31930* (F, LL, MEXU); Talquian, 7 Oct 1985, *Ventura 2525* (MEXU); 14 Nov 1987, *Ventura 4896* (MEXU); 28 Dec 1972, *Breedlove 30964* (MEXU); 14 Dec 1976, *Breedlove 42670* (MEXU, MO, TEX); Unión Juárez, 1920 m, 10 Feb 1969, *Hernández 505* (MEXU, MO); 1800 m, 20 Oct 1985, *Martínez-Salas et al. 14164* (MEXU, MO); 2200 m, 16 Jan 1973, *Breedlove & Smith 31655* (MEXU, MO, TEX); 2200 m, 23 Nov 1980, *Breedlove & Almeda 47740* (MEXU, MO); Villa Corzo, 1500 m, 9 Feb 1972, *Breedlove 24002* (MEXU, MO); Villaflores, 1990 m, 31 Oct 2009, *Gomez 2399* (MEXU); 1500 m, 10 Dec 1972, *Breedlove & Thorne 30046* (MEXU, MO); Volcan Tacaná, 13 Mar 1978, *García 586* (MEXU); 19 Jun 1985, *Martínez-Salas 13263* (MEXU); 4 Feb 1987, *Martínez-Salas 19403* (MEXU); 8 Feb 1987, *Martínez-Salas 19788* (MEXU); Yalbante, 8 Aug 1995, *Mejía 6432* (MEXU). OAXACA: Cerro Guayabitos, 25 Sep 1986, *Maya 3948* (MEXU); Juchitán, 16 Mar 1983, *Torres 2490* (MEXU); San Miguel Chimalapa, 1250 m, 23 Dec 1984, *Wendt et al. 4705* (MEXU, MO); San Miguel Suchixtepec, 22 Nov 1983, *Breedlove 60424* (MEXU); Tehuantepec, 6 Dec 1991, *Campos 4189* (MEXU); 15 Mar 1986, *Tenorio-Lezama 11155* (MEXU); 5 Dec 1991, *Campos 4145* (MEXU); 11 Dec 1991, *Campos 4243* (MEXU).

4. *Rogiera edwardsii* (Standl.) Borhidi (2001: 44). ≡ *Rondeletia edwardsii* Standl. (1934: 31). ≡ *Arachnothryx edwardsii* (Standl.) Borhidi (1987:301). Type:—HONDURAS: Comayagua: Pito Solo, Lake Yojoa, 29 Aug 1932. *Edwards 476* (holotype F!, isotypes A [online image]!, K [online image]!, UC [online image]!, US!).

=*Rogiera oaxacensis* Borhidi & K. Velasco Gutiérrez (2012: 51–58). Type:—MEXICO: Oaxaca, Tuxtepec, camino antiguo a Valle Nacional, cerca de los límites con Monte Bello, a 5.06 km en línea recta al SE de Santa Fe y La Mar, 7 Jul 2009. *Velasco-Gutiérrez et al. 3878* (holotype MEXU!, isotypes MO!).

=*Rondeletia subscandens* Lundell (1976: 328–329). ≡ *Rogiera subscandens* (Lundell) Borhidi (1989: 311). Type:—GUATEMALA: Petén, La Cumbre in zapotal, on top of hill about 500 m. west of km. 142/143, Cadenas Road, 10 Sep 1976. *Lundell & Contreras 19830* (holotype TEX–LL [online image]!, isotypes DKE [online image]!, F!, K [online image]!, MEXU!, S [online image]!).

Shrubs or **treelets,** occasionally scandent, 4–10 m tall, twigs terete, glabrate. **Stipules** erect, 1–3 × 2–3 mm, triangular to triangular ovate, persistent, sparsely strigose. **Leaves** opposite, those of a pair at a node equal, petiolate; petioles 4–8 mm long, glabrate; lamina ovate to elliptic, 3.5–14 × 2–6 cm, chartaceous, adaxially and abaxially glabrate, margins glabrate, entire, base slightly cuneate to obtuse, apex acuminate, acumen up to 1.5 cm long, 5–8 pairs of secondary veins, venation prominent on abaxial surface, domatia absent. **Inflorescences** terminal or axillary, corymbiform, 5–13 × 4–12 cm including corollas, 1–pedunculate or tripartite at base, peduncle 1–5 cm long, axis glabrate to sparsely puberulent, soon glabrescent, bracts triangular to lanceolate, 5–12 mm long. **Flowers** subtended by triangulate to linear bracteoles, 1–4 mm long, pedicelate or subbsessile, pedicels 2–6 mm long, glabrate; hypanthium subglobose, ovoid, slightly flattened, 1–2 mm long, glabrate; calyx lobes 5, subequal, the larger lobe up to 1 mm long, the smaller ones lesser than 1 mm long, triangular, glabrate; corolla infundibuliform, reddish to pink when fresh, tube 9–15 × 3–4 mm, externally glabrate to sparsely strigose, glabrescent, internally hirtellous medially, lobes 5, triangular to ovoid, 2–4 × 3–4 mm, entire margins, externally and internally glabrate; stamens 5, in long styled flowers attached 1 mm below apex of tube, in short styled flowers attached 3 mm below apex of tube, anthers linear–ellipsoid, 2–3 mm long; style glabrous, in long styled flowers 7–12 mm long, in short styled flowers 5–6 mm long, the stigmas linear in long styled flowers, ovoid to linear in short styled flowers, 1–2 mm long. **Fruits** subglobose, flattened, 2–3 × 2–4 mm, glabrate. **Seeds** winged, subcircular, 1 mm long.

Distribution and habitat:—*Rogiera edwardsii* is restricted to tropical rain forest in southern Mexico, Guatemala and Honduras, occurring from 600 to 800 m.

Phenology:—Collected with flowers from April to June and fruits from August to November.

Taxonomic notes:—*Rogiera edwardsii* is characterized by the erect stipules 1–3 mm long, and the glabrate twigs and leaves. All these characters are share with *R. ligustroides* but differs by the corolla tube 9–15 mm long (*vs.* 5–7 mm long in *R. ligustroides*) and the domatia absent (*vs.* present in *R. ligustroides*).

Specimens examined:— GUATEMALA. PETEN: Petén, 10 Sep 1975, *Lundell s.n.* (MO). **HONDURAS.** CORTÉS: Santa Cruz, 600 m, 26 Nov 1933, *Edwards 713* (F). COMAYAGUA: Villa de Taulabé, 12 Jun 1976, *Nelson 3568* (MEXU). **MEXICO.** CHIAPAS: Chancala, 13 Apr 1986, *Martínez-Salas 18035* (MEXU); 17 Jun 1986, *Martínez-Salas 18762* (MEXU). OAXACA: Tehuantepec, 28 Aug 1991, *Campos 3861* (MEXU); 27 Oct 1991, *Campos 4079* (MEXU); 27 Oct 1991, *Campos 4101* (MEXU); 24 Aug 1984, *Torres 5905* (MEXU, XAL); 24 Aug 1984, *Torres 5919* (MEXU, MO, XAL); 18 Feb 1987, *Torres 9136* (MEXU, XAL); 11 May 1991, *Torres 13996* (MEXU, XAL). PUEBLA: Patlanalan, 27 Jun 1982, *Cházaro 2436* (MEXU).

5. *Rogiera gratissima* Planch. & Linden (1864: 133). ≡ *Rondeletia gratissima* (Planch. et Linden) Hemsl. (1879:25). Type:—Illustration based on plants cultivated at Linden establishment (Lectotype designated by Lorence (2012). Fl. Mesoamericana 4(2): 257).

=*Rogiera elegantissima* Regel (1865: 253). Type:—Illustration, Regel, 1865: f. 490, based on plants cultivated at Linden establishment.

=*Rondeletia ehrenbergii* K. Schum. ex Standl. (1918: 50–51). ≡ *Rogiera ehrenbergii* (K. Schum. ex Standl.) Borhidi (1982: 67). Type:—GUATEMALA: Totomocapan, no date. *Ehrenberg 1033* (holotype US!).

=*Rondeletia seleriana* Loes. (1923: 105). ≡ *Rogiera seleriana* (Loes.) Borhidi (1989: 311). Type:—GUATEMALA: Huehuetenango: Nentón, near Chaculá, no date. *Seler & Seler 3015* (holotype B (destroyed; photo F!, MO!, US!), isotype F (fragment)!).

=*Rogiera tabascensis* Borhidi (2012: 51–58). Type:—MEXICO: Tabasco, Parque Nacional de Agua Blanca, Macuspana, km 64 carretera Villahermosa–Escárcega, 16 Jan 1988. *López-Pintado et al. 16* (holotype MEXU!).

Shrubs or **treelets,** 4–5 m tall, twigs terete, glabrate to sparsely strigose but soon glabrescent. **Stipules** erect, 4–10 × 2–3 mm, triangular, persistent, sparsely strigose, glabrescent. **Leaves** opposite, those of a pair at a node equal, petiolate; petioles 3–11 mm long, glabrate to sparsely strigose; lamina ovate to elliptic, 3.5–12.1 × 1.5–8 cm, coriaceous, adaxially glabrate, abaxially strigose on costa, margins glabrate, revolute, base cuneate, rounded to obtuse, apex acuminate to mucronate, acumen up to 1 cm long; 5–8 pairs of secondary veins, venation prominent on abaxial surface, domatia present. **Inflorescences** terminal, corymbiform, 5–10 × 4–11 cm including corollas, tripartite at base, peduncles 1.5–5 cm long, axis strigose, bracts triangular to lanceolate, 5–19 mm long. **Flowers** subtended by subulate to linear bracteoles, 1–4 mm long, subbsessile to pedicelate, pedicels up to 2 mm long, glabrate; hypanthium subglobose, elliptic, slightly flattened, 1–1.5 mm long, strigose, calyx lobes 5, unequal, the larger lobe up to 1.5 mm long, the smaller ones up to 1 mm long, triangular to triangular ovate, glabrate; corolla infundibuliform, reddish to pink when fresh, tube 10–15 × 3 mm, sparsely strigose, rarely glabrescent, internally hirtellous medially, lobes 5, ovate, 2–3 × 2–3 mm, entire margins, externally and internally glabrate; stamens 5, in long styled flowers attached 1–2 mm below apex of tube, in short styled flowers attached 2–3 mm below apex of tube, anthers linear, 1–2 mm long; style glabrous, in long styled flowers 15–18 mm long, in short styled flowers 7–8 mm long, the stigmas triangular ovate in long styled flowers, linear in short styled flowers, 1–2 mm long. **Fruits** subglobose spheroidal, slightly flattened, 2–3 × 2–4 mm, sparsely strigose. **Seeds** winged, subcircular, 1 mm long.

Distribution and habitat:—*Rogiera gratissima* is endemic to Mexico, and San Marcos, Guatemala. Occurring in the cloud forest from 1230 to 1520 m.

Phenology:—Collected with flowers from February to May and fruits from June to November.

Taxonomic notes:—*Rogiera gratissima* is characterized by the erect stipules 4–10 mm long, the adaxial leaf surface glabrate, the domatia present and the twigs glabrate or occasionally strigose but soon glabrescent. It is similar to *R. breedlovei* (see discussion below this taxa).

Specimens examined:— MEXICO. CHIAPAS: Comitán River, 23 Oct 1971, *Breedlove 21201* (MEXU); Ejido San Antonio Buenavista, 2 May 1985, *Espejo 1641* (MEXU); 8 Aug 1985, *Espejo 1949* (MEXU); La Independencia, 1230 m, 5 Dec 1983, *Cabrera 6099* (MEXU, MO); La Trinitaria, 1500–1520 m, 23 Oct 1971, *Breedlove & Thorne 21201* (MEXU, MO); 1370 m, 9 Feb 1982, *Breedlove 58390* (MEXU, MO); 1300 m, 13 May 1973, *Breedlove 35091* (MEXU, MO); 1400 m, 5 Jul 1967, *Shilom-Ton 2632* (F, LL, MO); 27 May 1993, *Ochoa-Gaona 4209* (MEXU); 19 Apr 1995, *Mejía 254* (MEXU); Lagunas de Montebello, 22 Nov 1982, *Cabrera 3703* (MEXU); 1 Mar 1982, *Cabrera 1855*

(MEXU); 6 Jul 1988, *Cházaro 5541* (MEXU); 31 Dec 1980, *Breedlove 49024* (MEXU); 24 May 1988, *Palacios-Espinosa 451* (MEXU); 7 Oct 1978, *Schwabe 23* (MEXU); 7 Aug 1978, *Schwabe 24* (MEXU); Montebello–Tziscao, 5 Apr 1950, *Miranda 6195* (MEXU); Tziscao, 1 Oct 1983, *Cabrera 5842* (MEXU); 23 Jun 1982, *Cabrera 2961* (MEXU).

6. *Rogiera ligustroides* (Hemsl.) Borhidi (1982: 67). ≡ *Rondeletia ligustroides* Hemsl. (1879: 26–27). Type:—MEXICO: Veracruz, Orizaba, no date, *Botteri 971* (lectotype K [online image!], isolectoypes BR-*n.v.*, P [online image]!. Lectotype designated by Lorence (1999), Monogr. Syst. Bot. Mo. Bot. Gard. 73: 147–154).

Shrubs or **treelets**, occasionally scandent, 2–5 m tall, twigs terete, glabrate. **Stipules** erect, 1–2 × 2 mm, triangular, persistent, sparsely strigose. **Leaves** opposite, those of a pair at a node equal, petiolate; petioles 3–10 mm long, glabrate; lamina ovate to ovate–lanceolate, 3–8.6 × 1.3–4 cm, chartaceous, adaxially and abaxially glabrate, margins glabrate, revolute, base rounded, apex acuminate to acute, acumen up to 1 cm long, 5–7 pairs of secondary veins, the venation prominent on abaxial surface, domatia present. **Inflorescences** terminal and axillar, corymbiform, 8–17 × 5–15 cm including corollas, 1–pedunculated or sessile inflorescences and tripartite at base, peduncle 1–3 cm long, axis glabrate, bracts linear to lanceolate, 5–10 mm long. **Flowers** subtended by subulate to lanceolate bracteoles, 2–4 mm long, subbsessile to pedicelate, pedicels up to 2 mm long, glabrate; hypanthium subglobose, ovoid, 1–2 mm long, glabrate to sparsely strigose; calyx lobes 5, equal, lobes 1–2 mm long, triangular, glabrate; corolla infundibuliform, white when fresh, the tube 5–7 × 2–3 mm, externally glabrate, internally hirtellous medially, lobes 5, rounded, 2–3 × 2–3 mm, entire margins, externally and internally glabrate; stamens 5, in long styled flowers attached 2–3 mm below apex of tube, in short styled flowers attached 1 mm below apex of tube, anthers linear, 1–2 mm long; style glabrous, in long styled flowers 6–8 mm long, in short styled flowers 4–6 mm long, the stigmas rounded in long styled flowers, linear in short styled flowers, 0.5–1.5 mm long. **Fruits** subglobose, sligthly flattened, 2–3 × 2–4 mm, glabrate. **Seeds** wingless, angulate, 1 mm long.

Distribution and habitat:—*Rogiera ligustroides* is endemic to Veracruz, Mexico, occurring in cloud forest from 800 to 1800 m.

Phenology:—Collected with flowers from April to July and fruits from August to March.

Taxonomic notes:—*Rogiera ligustroides* is characterized by the erect stipules 1–2 mm long, the presence of domatia present, and the glabrate twigs, leaves and corolla tube. It is similar to *R. edwardsii* (See discussion below this taxon).

Specimens examined:—MEXICO. VERACRUZ: Atoyac, 14 May 1937, *Matuda 1521* (F, MEXU, MO, XAL); Atzacan, 1500 m, 28 Apr 1968, *Rosas 1289* (F, MEXU, XAL); Cerro de Huacapan, 7 May 1967, *Rosas 350* (MEXU, MO, XAL); Coscomatepec, 1600 m, 23 Feb 1971, *Ventura 3151* (MEXU, MO, TEX, XAL); Fortín de las Flores, 800 m, 21 Dec 1970, *Lot 1207* (F, MEXU, XAL); Huatusco, 1650 m, 12 Jul 1979, *Avendaño 380* (F, MEXU); 1580 m, 1 Aug 1979, *Avendaño 401* (F, MEXU, XAL); 11 Sep 1975, *Calzada 2001* (F, XAL); Ixhuacán de los Reyes, 6 Jul 2012, *Salazar 45* (MEXU); 3 May 1980, *Lorenzo 263* (MEXU, XAL); 24 Apr 1981, *Lorenzo 424* (MEXU, XAL); 8 Mar 1982, *Laboratorio de Biogeografía 514* (MEXU, XAL); 1280 m, 30 Oct 1981, *Nee 22508* (F); Magdalena, 1490 m, 27 Mar 1976, *Vázquez T.348* (F); Nogales, 2 May 1937, *Matuda 1124* (F, MEXU, LL, MO, XAL); Nogales, 2 May 1937, *Matuda 1126* (F, LL, MEXU, XAL); Orizaba, 1 Apr 1891, *Urbina 45* (MEXU); *47* (MEXU); no date, *Botteri 570* (F, XAL); 5 May, *Purpus 1252* (F, MO, XAL); 2 Nov 1945, *Miranda 3834* (MEXU); 1300–1600 m, 29 Aug 1985, *Lorence 4834* (MEXU, MO, XAL); 1 Nov 1948, *Miranda 4871* (MEXU, XAL); 1260–1400 m, 27 Jun 1977, *Croat 39496* (MEXU, MO, XAL); Tenango, 11 Jul 1983, *Torres 3260* (MEXU, XAL); Tequila, 1800 m, 8 Feb 1984, *Taylor 299* (F); 1500 m, 31 Jul 1983, *Lorence & Ramamoorthy 4297* (MEXU, MO, XAL); Texhuacán, 1350 m, 8 Feb 1984, *Nee & Taylor 29465* (F, MEXU, MO, XAL); Tierra Colorada, 1 Apr 1967, *González 1591* (MEXU); Zongolica, 1270 m, 26 Sep 1967, *Rosas 667* (F, XAL); 7 Apr 2000, *Rincón 1327* (MEXU); 1600 m, 12 Dec 1968, *Rosas 1484* (MEXU, MO, XAL); 1600 m, 11 Mar 1982, *Lorence & Ramamoorthy 3895* (MEXU, MO, XAL); 17 Mar 1966, *Smith 4449* (MEXU, XAL).

7. *Rogiera macdougallii* (Lorence) Borhidi (1994: 140) ≡ *Rondeletia macdougallii* Lorence (1991: 144). Type:—MEXICO: Oaxaca, Cerro Azul (top), N of Niltepec, 7000 ft, 7 Mar 1956. *MacDougall s.n.* (holotype MEXU!).

Shrubs, 1–2 m tall, twigs terete, striate, strigose. **Stipules** erect, 5–9 × 2–4 mm, triangular, persistent, strigose. **Leaves** opposite, those of a pair at a node equal, petiolate; petioles 4–9 mm long, strigose; lamina ovate to ovate–elliptic, 4.7–11.2 × 2.9–6.8 cm, coriaceous, adaxially strigose, glabrescent, abaxially strigose at costa and secondary veins, margins ciliate, revolute, base rounded to cuneate, apex acuminate to acute, acumen up to 1 cm long, 5–9 pairs of secondary veins, adaxially bullate, venation prominent on abaxial surface, domatia absent. **Inflorescences** terminal, corymbiform, 5.8–7.6 × 6.3–7.2 cm including corollas, tripartite at base, peduncle 2–3 cm long, axis strigose, bracts linear to lanceolate, 2–7 mm long. **Flowers** subtended by lanceolate bracteoles, 2–4 mm long, subbsessile to pedicelate, pedicels up to 2 mm long, strigose; hypanthium subglobose, ovoid, 1–2 mm long, strigose; calyx lobes (4–)5, subequal, the larger lobe 3–4 mm long, the smaller up to 3 mm long, triangular to triangular–obovate, adaxially and abaxially strigose; corolla infundibuliform, pinkish when fresh, the tube 8–13 × 2–3 mm, externally strigose, internally hirtellous medially, lobes (4–)5, ovate to rounded, 2–4 × 2–4 mm, entire or crisped margins, externally and internally glabrate; stamens (4–)5, in long styled flowers attached 2 mm below apex of tube, in short styled flowers attached 2 mm below apex of tube, anthers linear, 1–2 mm long; style glabrous, in long styled flowers 9–13 mm long, in short styled flowers 4–6 mm long, the stigmas elliptic in long styled flowers, linear in short styled flowers, 1–1.5 mm long. **Fruits** subglobose, sligthly flattened, 2–3 × 2–4 mm, glabrate. **Seeds** wingless, angulate, 1 mm long.

Distribution and habitat:—*Rogiera macdougalli* is endemic to Oaxaca, Mexico, in the cloud forest of the Pacific slopes.

Phenology:— Collected with flowers and fruits from February to March.

Taxonomic notes:—*Rogiera macdougallii* is characterized by the erect stipules of 5–9 mm long, the strigose adaxial leaf surface, the strigose twigs and corolla tube. It is similar to *R. nicaraguensis* by the stipule size and the strigose corolla tube; differs by the pink corolla color (*vs.* white in *A. nicaraguensis*), the strigose twigs (vs. villous in *A. nicaraguensis*), and the geographical range in México (*vs*. Honduras and Nicaragua of *A. nicaraguensis*).

Specimens examined:—MEXICO. OAXACA: San Sebastián Coatlán, 20 Feb 1988, *Campos 1237* (MEXU).

8. *Rogiera nicaraguensis* (Oerst.) Borhidi (2001: 51). ≡ *Rondeletia nicaraguensis* Oerst (1852:43). ≡ *Arachnothryx nicaraguensis* (Oerst.) Borhidi (1989: 310). Type:—NICARAGUA: Matagalpa, Segovia, in monte Pantasmo, Jan 1848. *Oersted 11825* (holotype C [online image]!, isotypes US!, MO!).

=*Rondeletia standleyana* Ant. Molina (1952: 262). ≡ *Arachnothryx standleyana* (Ant. Molina) Borhidi (1987: 302). ≡ *Rogiera standleyana* (Ant. Molina) Lorence (2005: 451). TYPE:—HONDURAS: Francisco Morazán, in pine forest above Zambrano, 20 Jul 1948. *Williams & Molina 14417* (holotype US!, isotypes BM [online image]!, F!, GH [online image]!, P [online image]!, US!, MO!).

S**hrubs** or **treelets**, 2–4 m tall, twigs terete, villous. **Stipules** erect, 4–6 × 2–4 mm, triangular to subulate, rarely bifid, strigose, persistent. **Leaves** opposite, those of a pair at a node equal, petiolate; petioles 3–13 mm long, hirtellous; lamina ovate–elliptic to obovate, 1.8–6.6 × 1–5.2 cm, chartaceous, adaxially hirtellous on the costa, abaxially hirtellous, margins glabrate, entire, base acute to cuneate, apex acute, obtuse or rounded, 5–7 pairs of secondary veins, venation prominent on abaxial surface, domatia absent. **Inflorescences** terminal, corymbiform, 4.7–8.6 × 4.5–6.8 cm including corollas, usually tripartite at base, peduncules 1–6 cm long, axis hirtellous, bracts triangular to linear–lanceolate, 4–18 mm long. **Flowers** subtended by subulate bracteoles, 1–4 mm long, subbsessile to pedicelate, pedicels up to 1 mm long, hirtellous; hypanthium subglobose, ellipsoidal, 2 mm long, hirtellous; calyx lobes 5, unequal, the larger lobe up to 3 mm long, the smaller ones less than 2 mm long, triangular to triangular ovate, sparsely hirtellous, glabrescent; corolla infundibuliform, white when fresh, the tube 10–18 × 3 mm, externally strigose, internally sparsely hirtellous medially, lobes 5, elliptic to rounded, 2–3 × 2–3 mm, entire or crisped margins, externally sparsely strigose at base, internally glabrate; stamens 5, in long styled flowers attached 2 mm below apex of tube, in short styled flowers attached 2 mm below apex of tube, anthers linear, 2 mm long; style glabrous, in long styled flowers 14–19 mm long, in short styled flowers 5–9 mm long, the stigmas reniform in long styled flowers, linear in short styled flowers, 1–2 mm long. **Fruits** subglobose, obovate, 3–4 × 3–4 mm, strigose. **Seeds** briefly winged, subcircular, 1 mm long.

Distribution and habitat:—*Rogiera nicaraguensis* is endemic to Nicaragua and Honduras, occurring from 300 to 1800 m in cloud forest and tropical rain forest.

Phenology:—Collected with flowers and fruit from June to November.

Taxonomic notes:—*Rogiera nicaraguensis* is characterized by the erect stipules 4–6 mm long, the hirtellous adaxial leaf surface, the villous twigs, strigose corolla tube and the white corolla tube. It is similar to *R. macdougalli* (See discussion below this taxa).

Specimens examined:—HONDURAS. CHOLUTECA: San Marcos de Colón, 1125 m, 17 Jun 1994, *Davidse et al. 35053* (MEXU, MO). FRANCISCO MORAZÁN: Río Las Canoas, 4 Sep 1996, *Linares 3487* (MEXU); 24 Sep 1996, *Linares 3520* (MEXU); Tatumbla, 21 Aug 2002, *Linares 6298* (MEXU); Tegucigalpa, 1000 m, 20 Aug 1978, *Castro 82* (MO); 30 Oct 1996, *Maas et al. 8468* (F, MO). **NICARAGUA.** ESTELÍ: La Gavilana, 940–1000 m, 2 Aug 1983, *Moreno 21879* (MO); La Laguna, 1280–1300 m, 29 Jun 1983, *Moreno 21610* (MO); Quetzalcayán, 900–1100 m, 15 Oct 1982, *Moreno 17802* (MO); Reserva Natural de Miraflores, 958 m, 19 Jun 2003, *Coronado & Velázquez 176* (MO); *177* (MO); San José, 5 Nov 1981, *Téllez 4798* (MEXU); San José la Laguna, 1300 m, 24 Jun 1982, *Moreno 16747* (MO); Santa Cruz Buenavista, 1000 m, 29 Jun 1983, *Moreno 21602* (MEXU, MO). JINOTEGA: La Montañita, 1100–1400 m, 29 Jun 1947, *Standley 10389* (F). LEÓN: Cerro El Nancital, 300–400 m, 22 Jun 1983, *Moreno 21574* (F, MO). MADRIZ: Somoto, 1200 m, 6 Aug 2011, *Coronado et al. 6320* (MO); 1200 m, 6 Aug 2011, *Rueda et al. 18680* (F). MANAGUA: Puertas Viejas, 400–500 m, 8 Jul 1983, *Araquistain 3604* (MO); Esquipulas, 560 m, 21 Jul 2012, *Rueda & Coronado 18837* (MO). MATAGALPA: Rincón del Diablo, 800 m, 29 Sep 1983, *Araquistain 3697* (MO); Sébaco, 600 m, 20 Jul 2012, *Rueda & Coronado 18797* (MO).

9. *Rogiera stenosiphon* (Hemsl.) Borhidi (1982: 67). ≡ *Rondeletia stenosiphon* Hemsl. (1879: 26). Type:—MEXICO: Tabasco, no date. *Johnson s.n.* (holotype K [online image]!).

=*Rondeletia lundelliana* Standl. (1940: 31). ≡ *Arachnothryx lundelliana* (Standl.) Borhidi (1987: 302). Type:—BELIZE: El Cayo district: Vaca, on hillside, 21 Apr 1938. *Gentle 2504* (holotype F!, isotypes A [online image]!, K [online image]!, LL!, MICH [online image]!, NY [online image]!, US!).

Trees or **shrubs**, 4–18 m tall, twigs quadrangular, strongly angulate, striate, sparsely strigose, glabrescent. **Stipules** erect, 7–10 × 2–4 mm, triangular to subulate, strigose, persistent, rarely deciduous. **Leaves** opposite, those of a pair at a node equal, petiolate; petioles 4–18 mm long, strigose; lamina ovate to ovate–elliptic, 4.2–15.3 × 2.3–7.8 cm, coriaceous, margins glabrate, adaxially strigose on the costa, abaxially strigose, mainly at costa and secondary veins, base acute to cuneate, apex acute to acuminate, acumen up to 1 cm long; 5–8 pairs of secondary veins, venation prominent on abaxial surface, domatia absent. **Inflorescences** terminal, corymbiform, 4.7–17.6 × 6.3–18.9 cm including corollas, tripartite at base or bipartite, peduncles 2–8 cm long, axis strigose, bracts linear to lanceolate, 8–25 mm long. **Flowers** subtended by lanceolate bracteoles, 1–3 mm long, subbsessile to pedicelate, pedicels up to 1 mm long, strigose, hypanthium subglobose, ovoid, 1–1.5 mm long, strigose, calyx lobes 5, equal, up to 1.5 mm long, triangular to deltoid, glabrate to sparsely strigose; corolla infundibuliform, white when fresh, the tube 10–13 × 3–4 mm, externally minutely strigose, internally sparsely hirtellous medially, lobes 5, ovate to rounded, 2–4 × 2–4 mm, entire or crisped margins, externally and internally glabrate; stamens 5, in long styled flowers attached 2–3mm below apex of tube, in short styled flowers attached 2 mm below apex of tube, anthers linear, 1–2 mm long; style glabrous, in long styled flowers 12–14 mm long, in short styled flowers 6–7 mm long, the stigmas elliptic in long styled flowers, linear in short styled flowers, 1–2 mm long. **Fruits** subglobose, ovoid, 2–3 × 2–4 mm, strigose. **Seeds** winged, subcircular, 1 mm long.

Distribution and habitat:—*Rogiera stenosiphon* occurs from the south of Mexico to Guatemala, Honduras and Belize. It grows in tropical rain forest, deciduous forest and cloud forest at 180 to 1350 m.

Phenology:—Collected with flowers and fruit from February to June.

Taxonomic notes:—*Rogiera stenosiphon* is characterized by the quadrangular twigs, erect stipules 7–10 mm long, the white corolla and the glabrate corolla tube. It is similar to *R. gratissima* by the glabrate twigs (or occasionally strigose but soon glabrescent) and the corolla size; differs by the white corolla color (*vs*. reddish, pink to purplish in *R. gratissima*), the strigose adaxially leaf surface (*vs*. glabrate in *R. gratissima*) and the domatia absent (*vs*. present in *R. gratissima*).

Specimens examined:—BELIZE. CAYO: Chiquibul Forest Reserve, 410 m, 15 Jul 2006, *Bayly 168* (MO); Río de la Flor, 3 Jun 1973, *Dwyer 10852* (MO); Vaca, 1050 m, 21 Apr 1938, *Gentle 2504* (MO); 19 May 1989, *Arvigo & Shropshire 253* (MO). TOLEDO: Union Camp, 700–750 m, 22 Feb 1997, *Holst 5950* (MEXU, MO); 720 m, 18 Mar 2009, *Brewer 4615* (MO); 750 m, 12 May 1979, *Whitefoord 1690* (MO). **GUATEMALA.** ALTA VERAPAZ: Coban, 1350 m, 1908, *von Türckheim 1616* (MO); San Pedro Carchá, 1200–1350 m, 20 Mar 1970, *Harmon & Fuentes 2174* (MO); 1200 m, 2 Feb 1969, *Williams et al. 40480* (MO). BAJA VERAPAZ, Purulha, 23 Feb 1990, *Castillo 990* (MO). HUEHUETENANGO: Nenton, 1050–1200 m, 9 Dec 2006, *Sánchez 1698* (MO); Petzal, 21 Feb 2003, *Véliz 13044* (MEXU); Río Azul, 17 Mar 2002, *Delgado 3* (MEXU). PETEN: Poptun, 5 May 1967, *Contreras 6850* (F, MEXU, MO); Río Machaquila, 19 Mar 1970, *Contreras 9788* (MEXU, MO). **HONDURAS.** YORO: Quebrada El Oro, 300 m, 18 May 1991, *Davidse et al. 34538* (MEXU, MO). **MEXICO.** CHIAPAS: Abasolo, 13 Jan 1982, *Breedlove 57138* (LL, MEXU); Barranca de la Toma, 15 Mar 1949, *Miranda 5293* (MEXU); Cascada Río Mezbiljas, 15 Jun 1984, *Méndez 7680* (MEXU); Cascadas de Agua Azul, 6 Apr 1985, *Cabrera 8137* (MEXU, XAL); Cerro Ak' Bana, 10 May 1984, *Méndez 6002* (LL, MEXU); Crucero Corozal, 21 Apr 1985, *Martínez-Salas 12266* (LL, MEXU, XAL); 18 Apr 1985, *Martínez-Salas 12085* (LL, MEXU); 20 May 1987, *Martínez-Salas 21165* (MEXU, XAL); 25 Apr 1986, *Martínez-Salas 17880* (LL, MEXU, XAL); Dos Lagos, 29 Dec 1981, *Breedlove 56589* (LL, MEXU); El Bosque, 1030 m, 16 Feb 1979, *Croat 47704* (MEXU, MO); 1360 m, 17 Mar 2007, *López 2* (MEXU); Ixtapa, 1280 m, 15 Apr 2007, *Meda de León 21* (MO); La Trinitaria, 8 Apr 1983, *Téllez & Villaseñor 6631* (MEXU, MO, TEX); Las Margaritas, 1300 m, 20 Feb 1973, *Breedlove 33715* (LL, MEXU, MO); Ocosingo, 1140–1145 m, 4 Mar 1982, *Cabrera et al. 1915* (MEXU, MO, XAL); 180 m, 16 Jan 1986, *Martínez-Salas 16303* (LL, MEXU, MO, XAL); 25 Apr 1986, *Martínez-Salas 17933* (MEXU, MO, TEX, XAL); 180 m, 21 Apr 1986, *Martínez-Salas 18510* (LL, MEXU, MO, XAL); 1050 m, 17 Jun 1986, *Martínez-Salas & Soto 18743* (LL, MEXU, MO, XAL); 1400 m, 7 Jul 1977, *Croat 40419* (MEXU, MO); Ocozocoautla de Espinosa, 915 m, 24 Feb 1983, *Neill 5450* (MEXU, MO); 800 m, 26 Jan 1972, *Breedlove 23841* (LL, MEXU, MO); 1000 m 1 Feb 1972, *Breedlove 23898* (MEXU); Osumacinta, 1000 m, 23 Feb 1973, *Breedlove 33800* (LL, MEXU, MO); Oxchuc, 10 Apr 1983, *Shilom-Ton 5824*

(LL, MEXU, MO, XAL); 30 Jan 1985, *Méndez 8044* (MEXU, MO, TEX); Palenque, 300 m, 24 May 1973, *Breedlove 35332* (MEXU, MO); 26 Feb 1981, *Breedlove 49853* (LL, MO); Sabanilla, 1 Mar 1984, *Shilom-Ton 7315* (LL, MEXU, MO, TEX, XAL); San Cristóbal de las Casas, 15 Nov 1986, *Shilom-Ton & Martínez-Salas 9583* (LL, MEXU, MO); Tenejapa, 11 Mar 1984, *Shilom-Ton 5392* (LL, MEXU, MO, XAL); 900 m, 5 Mar 1983, *Méndez 5608* (F, LL, MEXU, MO, XAL); 1000 m, 5 Jun 1972, *Breedlove 25515* (LL, MEXU, MO); Tila, 1000 m, 20 Mar 1983, *Shilom-Ton 5699* (MEXU, MO, TEX, XAL); 20 Mar 1984, *Shilom-Ton 7441* (MEXU, MO, TEX, XAL); Tumbalá, 350 m, 16 Mar 1983, *Fernández 1507* (MEXU, MO); 400 m, 16 Mar 1983, *Ventura 20016* (MEXU, MO); Yajalón, 1000 m, 10 Mar 1983, *Shilom-Ton 5641* (LL, MEXU, MO, XAL); 10 Feb 1983, *Shilom-Ton 5477* (MEXU, MO, XAL); 1 Apr 1984, *Shilom-Ton 7486* (LL, MEXU, MO, XAL). OAXACA: Cerro Verde, 20 Oct 1993, *de Santiago 234* (MEXU). TABASCO: Chimalapa 1º secc., 6 Nov 1994, *Guadarrama 4099* (MEXU); Tenosique, 27 Feb 1982, *Magaña 833* (MEXU).

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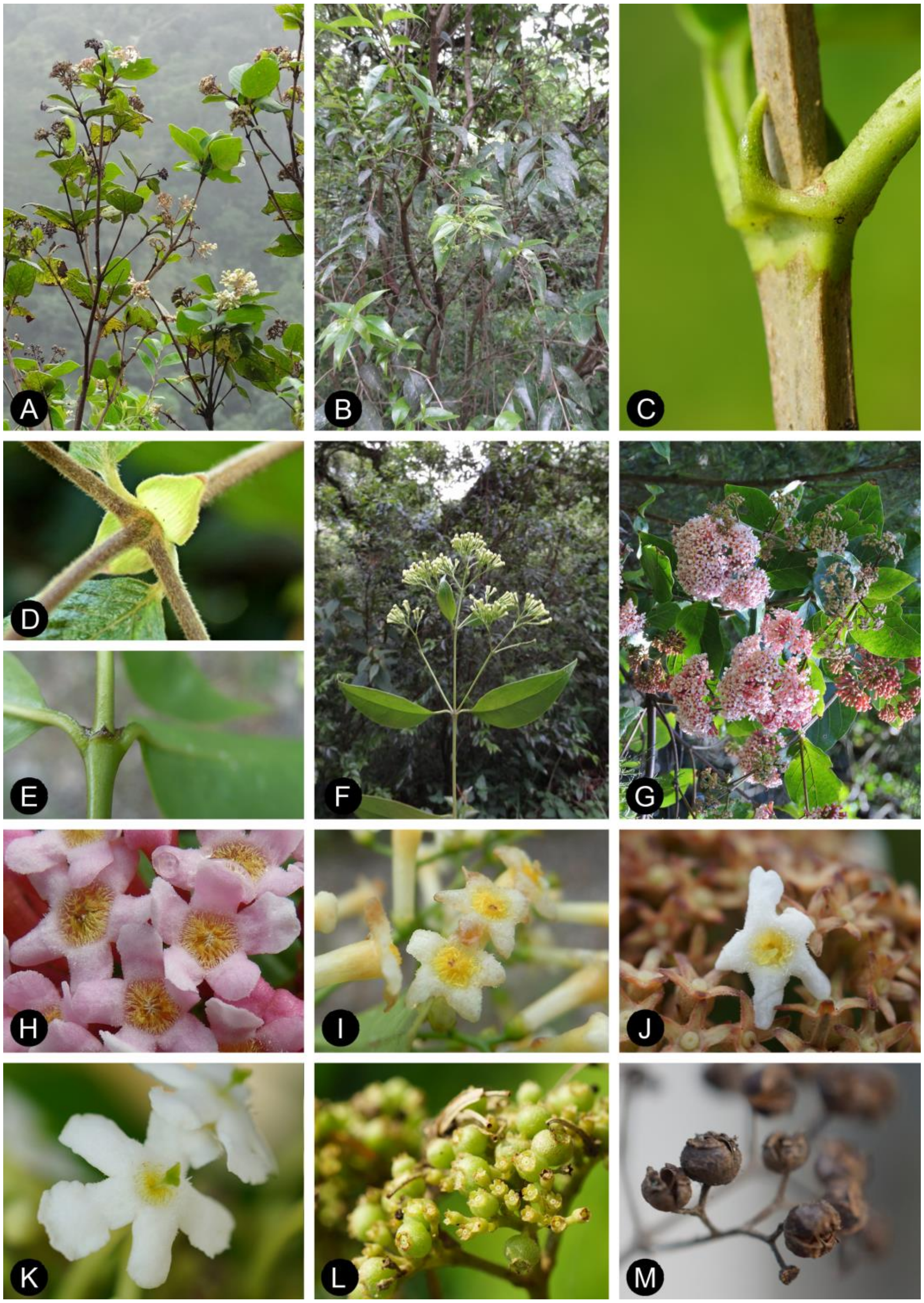

Figure 1. *Rogiera* species. **A-B. Habit. A.** *R. macdougalii*, erect shrub. **B.** *R. ligustroides*, scandent tree. **C-E. Stipules. C.** *R. stenosiphon*. **D.** *R. cordata*. **E.** *R. ligustroides*. **F-G. Inflorescence. F.** *R. ligustroides*. **G.** *R. amoena*. **H-K. Flower**. **H.** *R. amoena*. **I.** *R. ligustroides*. **J.** *R. macdougallii*. **K.** *R. stenosiphon*. **L-M. Fruits. L.** *R. amoena*, inmature fruits. **M.** *R. ligustroides*, mature fruits. Photographs by the authors.

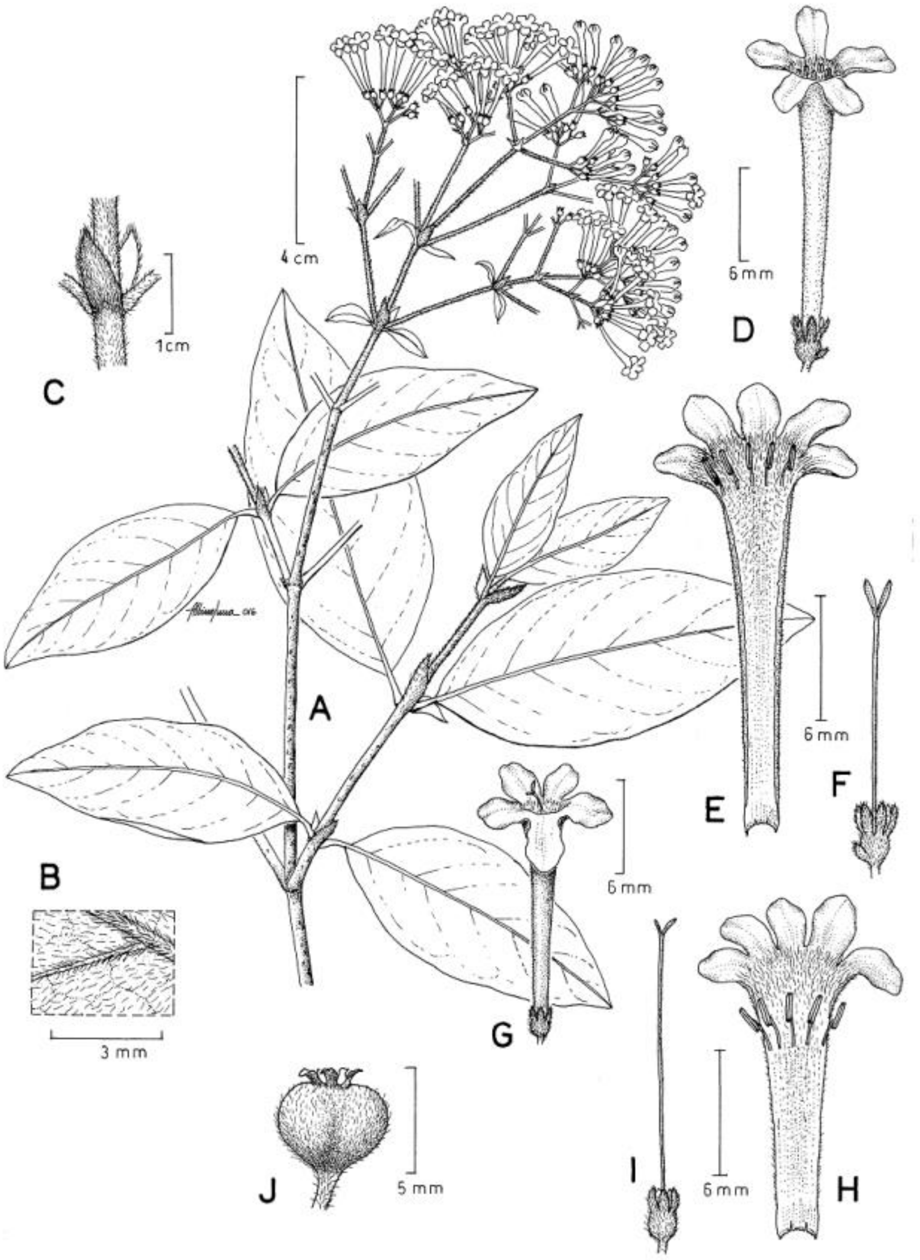

Figure 2. ***Rogiera amoena*****. A.** Fertile branch. **B.** Detail of the pubescence on the abaxial leaf surface. **C.** Stipule. **D.** Brevistylous flower. **E-F.** Dissected brevistylous flower. **E.** Open corolla showing stamen insertion and internal pubescence. **F.** Calyx and gynoecium. **G.** Longistylous flower. **H-I.** Dissected longistylous flower. **H.** Open corolla showing stamen insertion and internal pubescence. **I.** Calyx and gynoecium. **J.** Fruit.

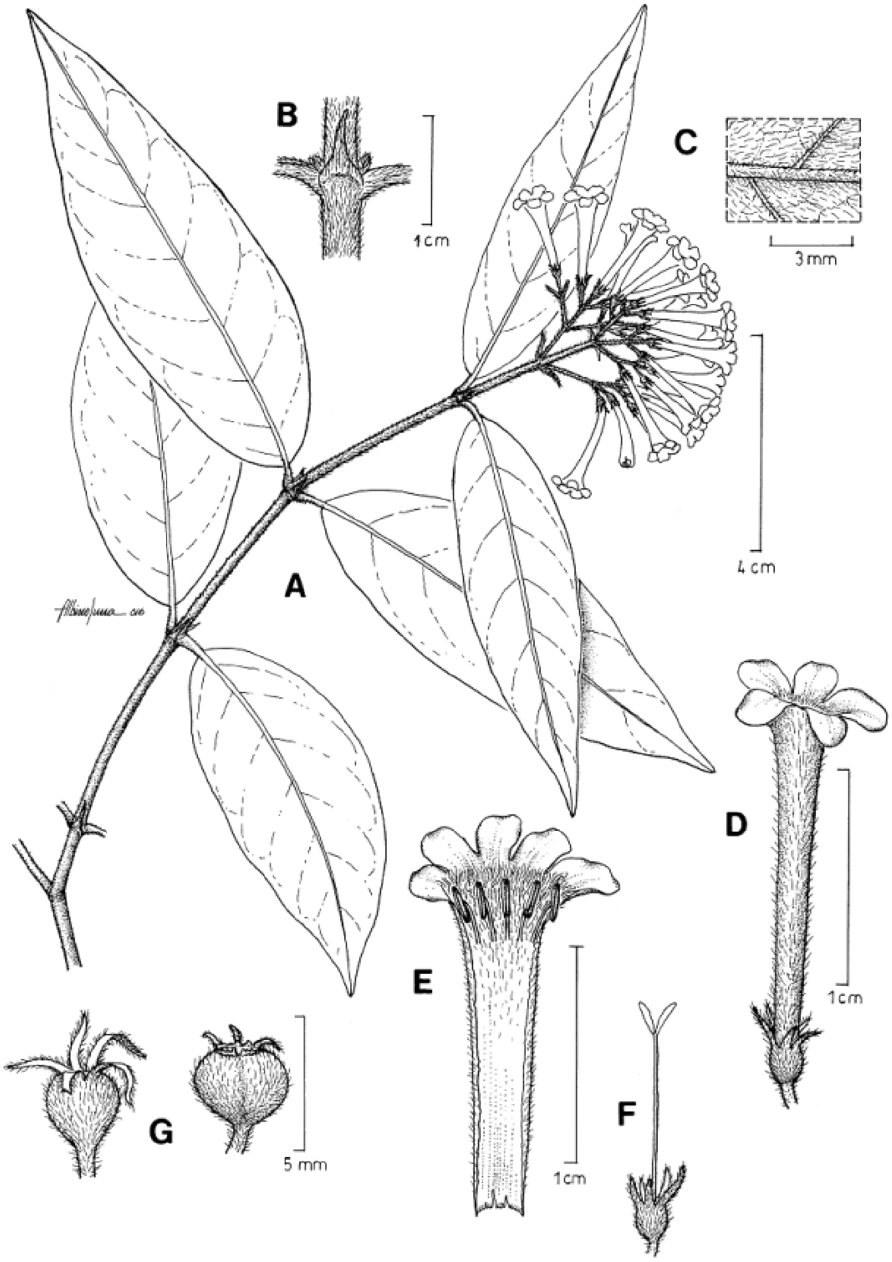

Figure 4. ***Rogiera breedlovei*****. A.** Fertile branch. **B.** Stipule. **C.** Detail of the pubescence on the abaxial leaf surface. **D.** Brevistylous flower. **E-F.** Dissected brevistylous flower. **E.** Open corolla tube showing stamen insertion and internal pubescence. **F.** Calyx and gynoecium. **G.** Fruit.

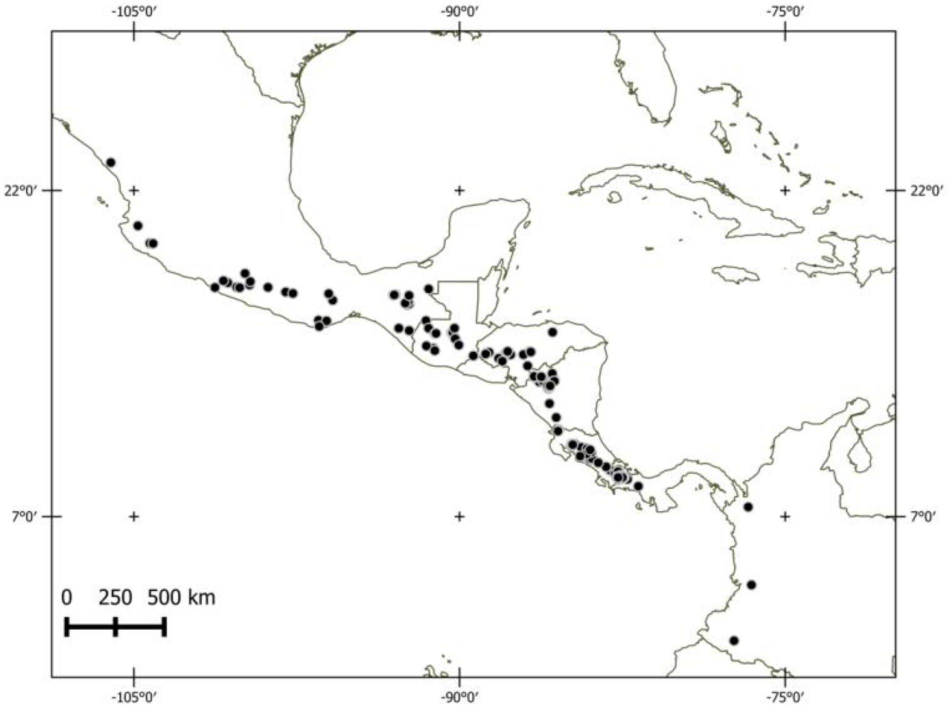

Figure 3. Geographic distribution of *Rogiera amoena*.

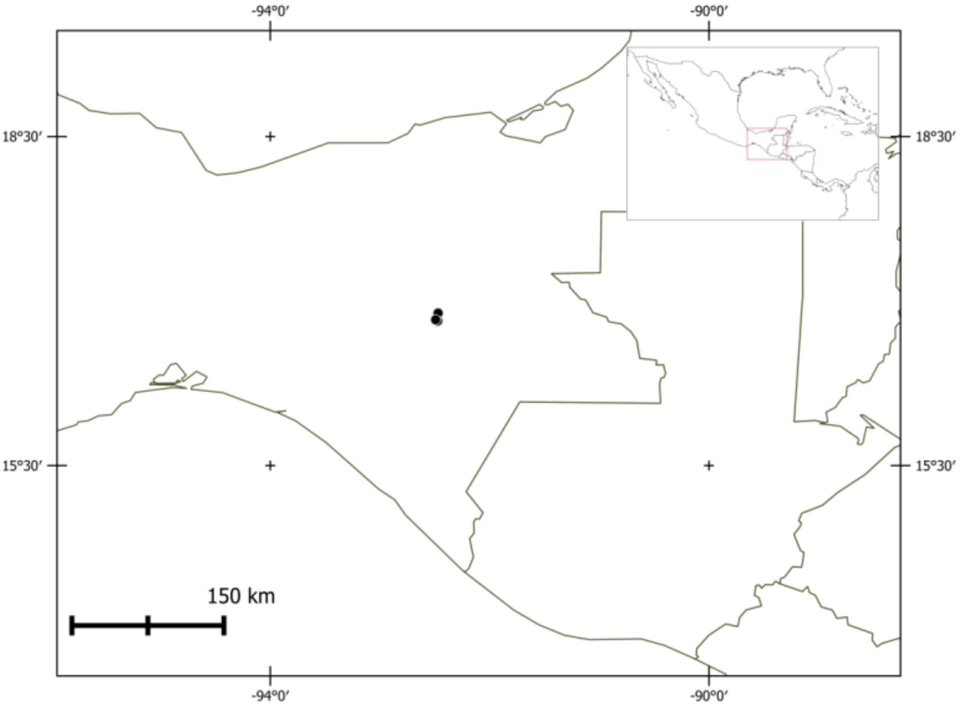

Figure 5. Geographic distribution of *Rogiera breedlovei*.

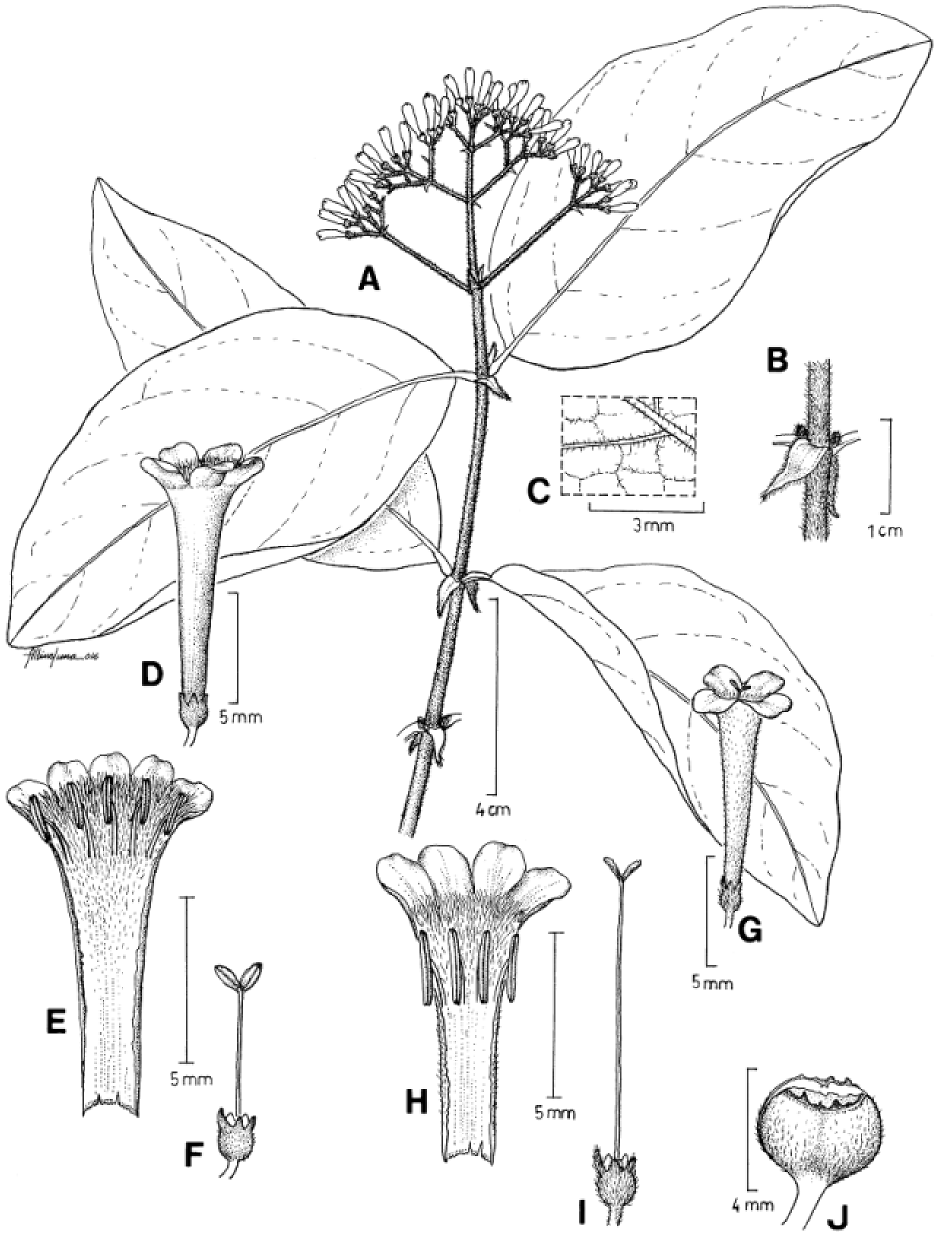

Figure 6. ***Rogiera cordata*****. A.** Fertile branch. **B.** Stipule. **C.** Detail of the pubescence on the abaxial leaf surface. **D.** Brevistylous flower. **E-F.** Dissected brevistylous flower. **E.** Open corolla tube showing stamen insertion and internal pubescence. **F.** Calyx and gynoecium. **G.** Longistylous flower. **H-I.** Dissected longistylous flower. **H.** Open corolla tube showing stamen insertion and internal pubescence. **I.** Calyx and gynoecium. **J.** Fruit.

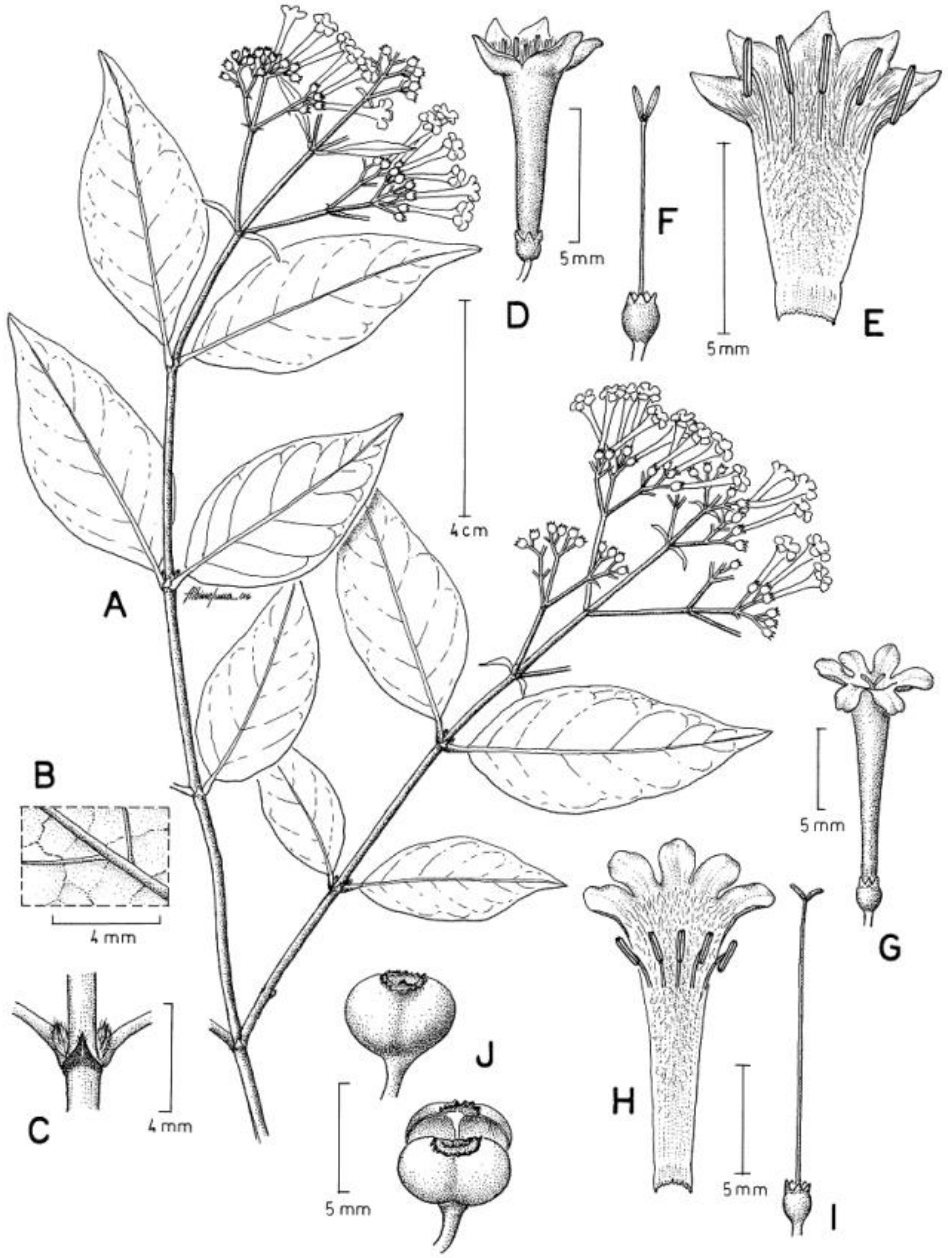

Figure 8. ***Rogiera edwardsii*****. A.** Fertile branch. **B.** Detail of the abaxial leaf surface. **C.** Stipule. **D.** Brevistylous flower. **E-F.** Dissected brevistylous flower. **E.** Open corolla tube showing stamen insertion and internal pubescence. **F.** Calyx and gynoecium. **G.** Longistylous flower. **H-I.** Dissected longistylous flower. **H.** Open corolla tube showing stamen insertion and internal pubescence. **I.** Calyx and gynoecium. **J.** Fruit.

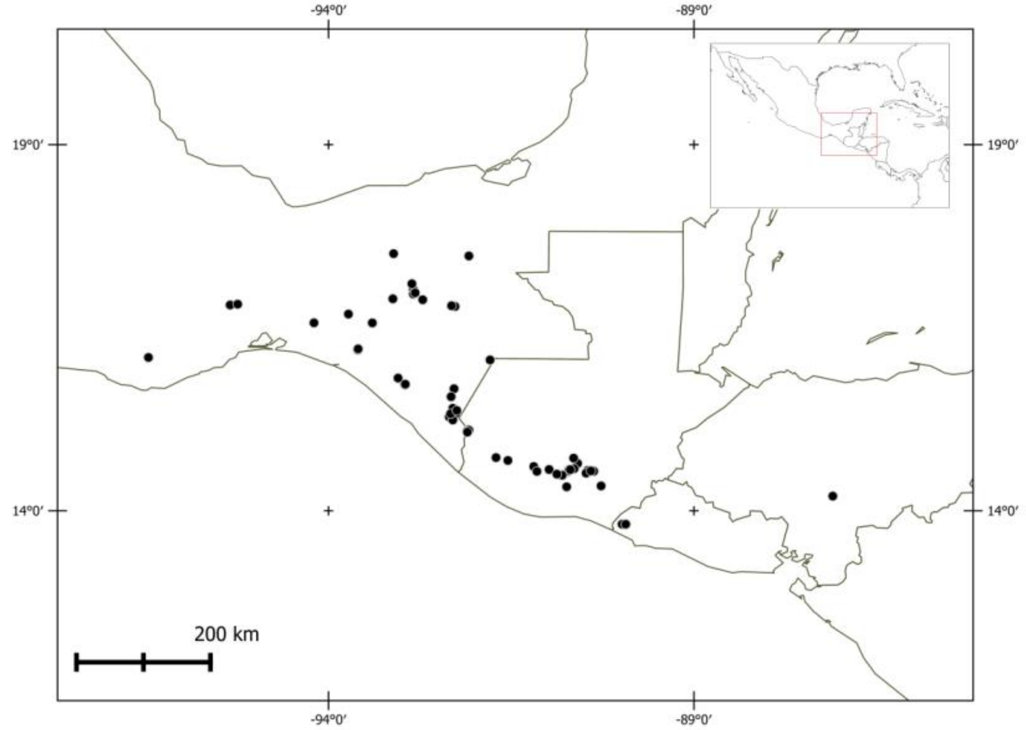

Figure 7. Geographic distribution of *Rogiera cordata*.

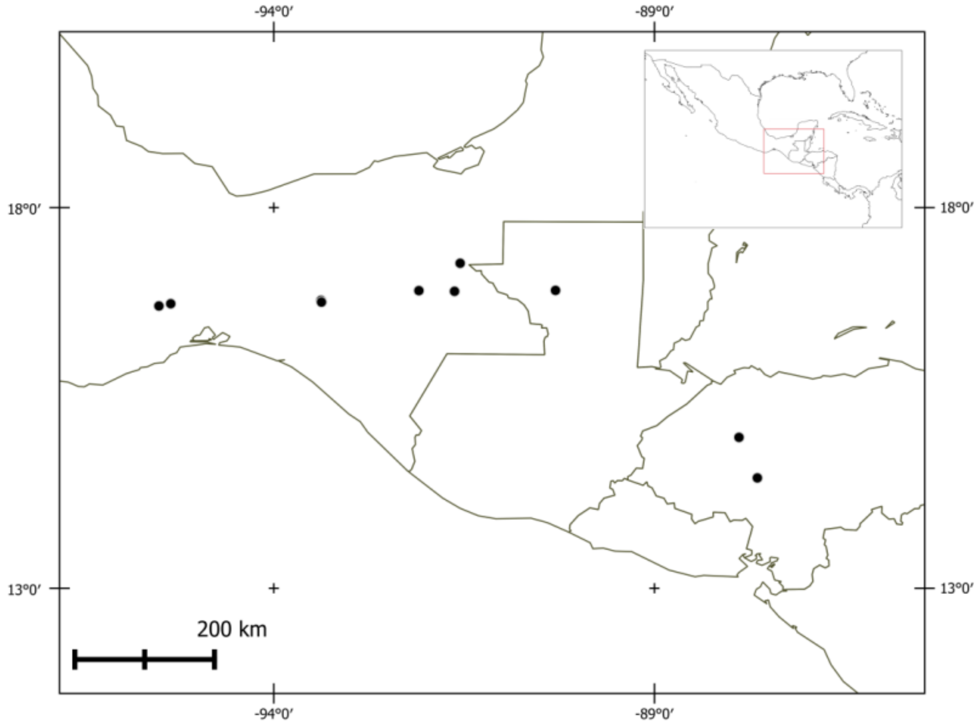

Figure 9. Geographic distribution of *Rogiera edwardsii*.

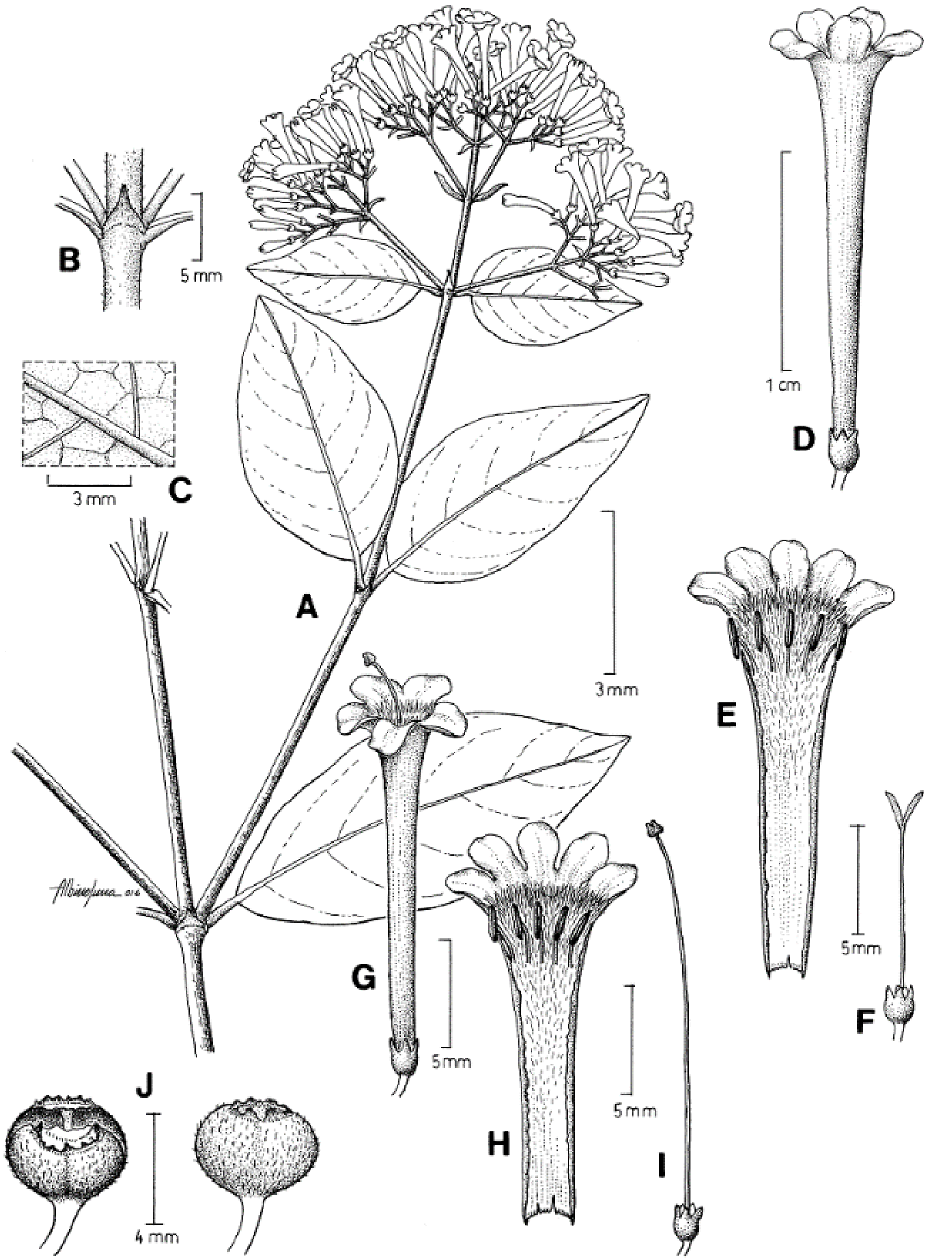

Figure 10. ***Rogiera gratissima*****. A.** Fertile branch. **B.** Stipule. **C.** Detail of the abaxial leaf surface. **D.** Brevistylous flower. **E-F.** Dissected brevistylous flower. **E.** Open corolla tube showing stamen insertion and internal pubescence. **F.** Calyx and gynoecium. **G.** Longistylous flower. **H-I.** Dissected longistylous flower. **H.** Open corolla tube showing stamen insertion and internal pubescence. **I.** Calyx and gynoecium. **J.** Fruit.

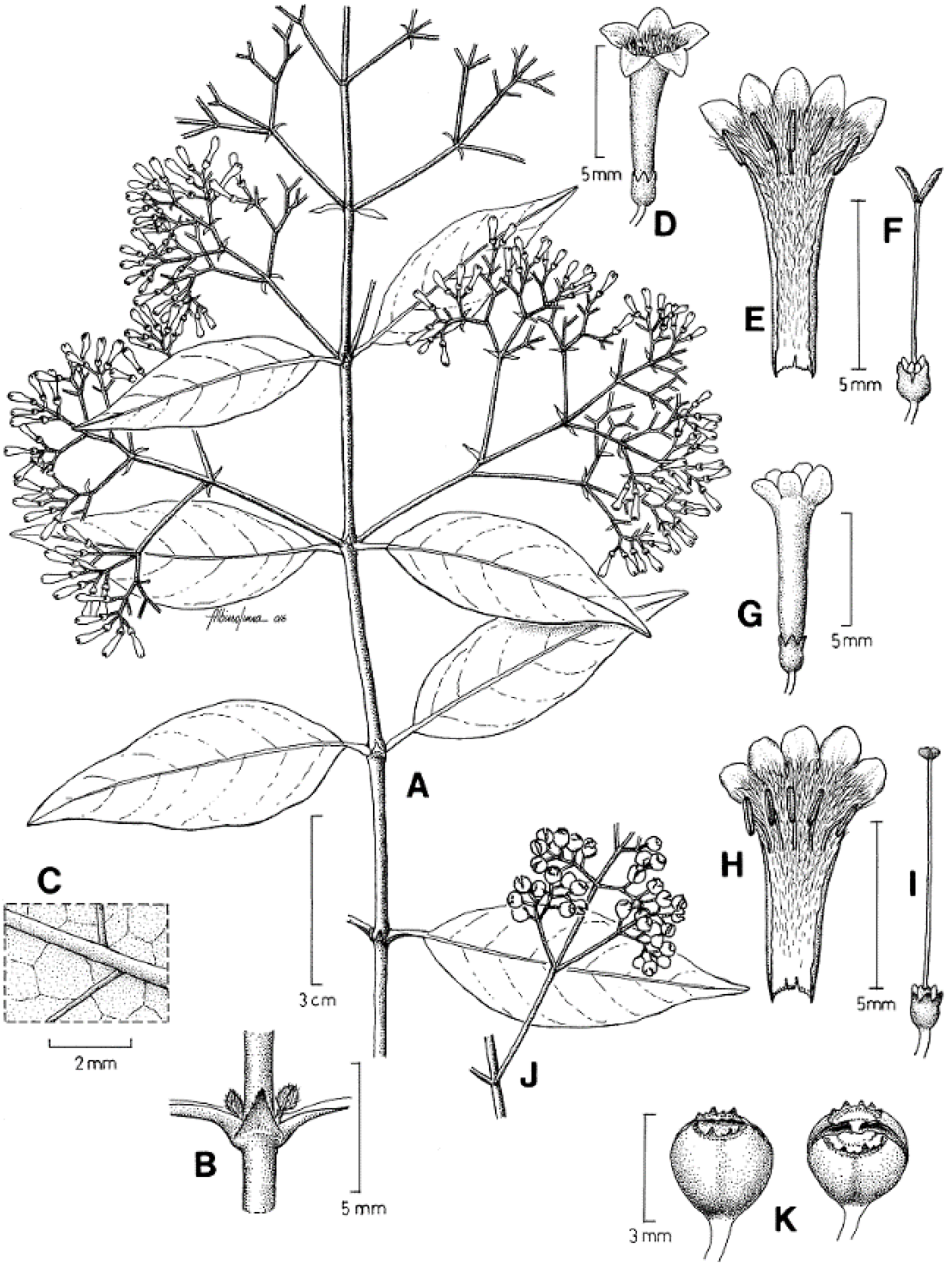

Figure 12. ***Rogiera ligustroides*****. A.** Fertile branch. **B.** Stipule. **C.** Detail of the abaxial leaf surface. **D.** Brevistylous flower. **E-F.** Dissected brevistylous flower. **E.** Open corolla tube showing stamen insertion and internal pubescence. **F.** Calyx and gynoecium. **G.** Longistylous flower. **H-I.** Dissected longistylous flower. **H.** Open corolla tube showing stamen insertion and internal pubescence. **I.** Calyx and gynoecium. **J.** Fruited branch. **K.** Fruit.

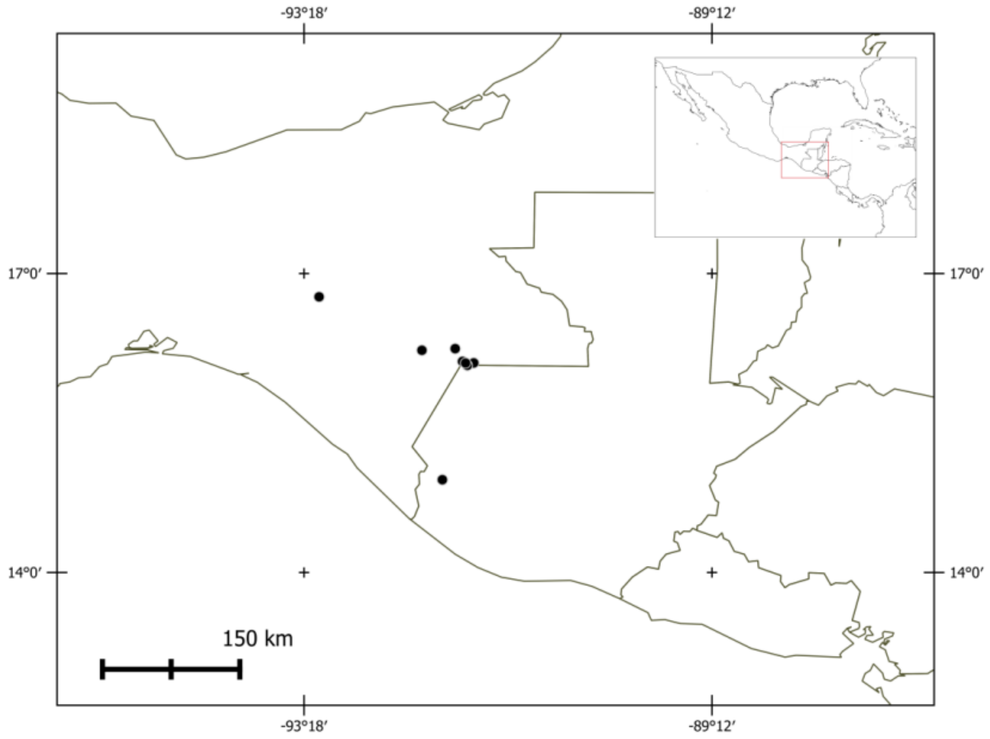

Figure 11. Geographic distribution of *Rogiera gratissima*.

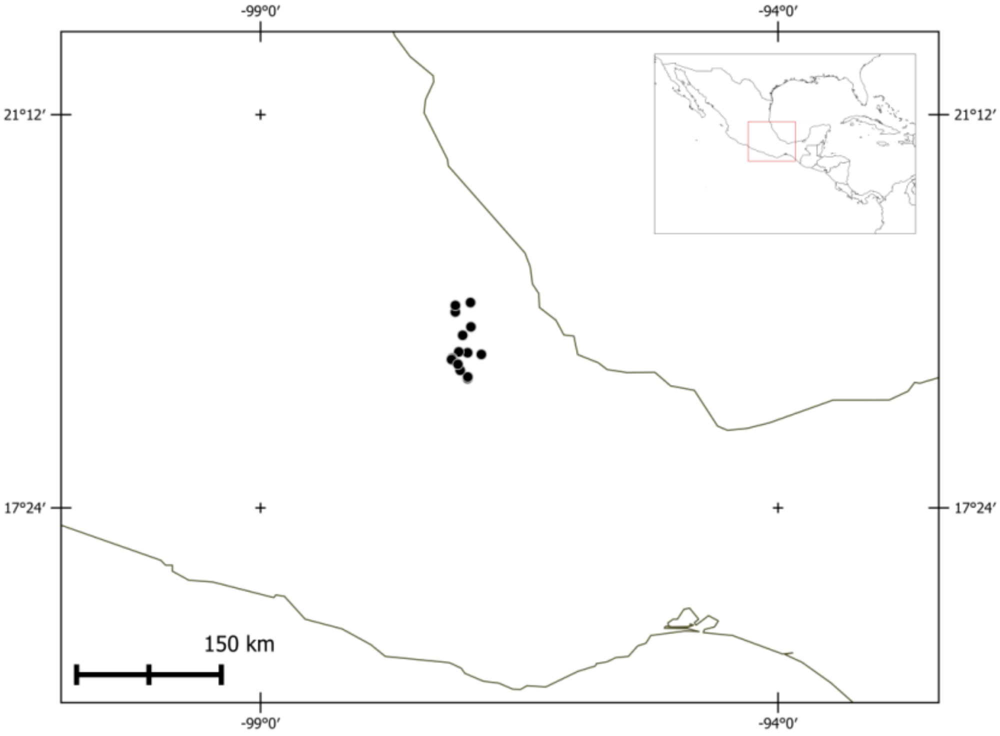

Figure 13. Geographic distribution of *Rogiera ligustroides*.

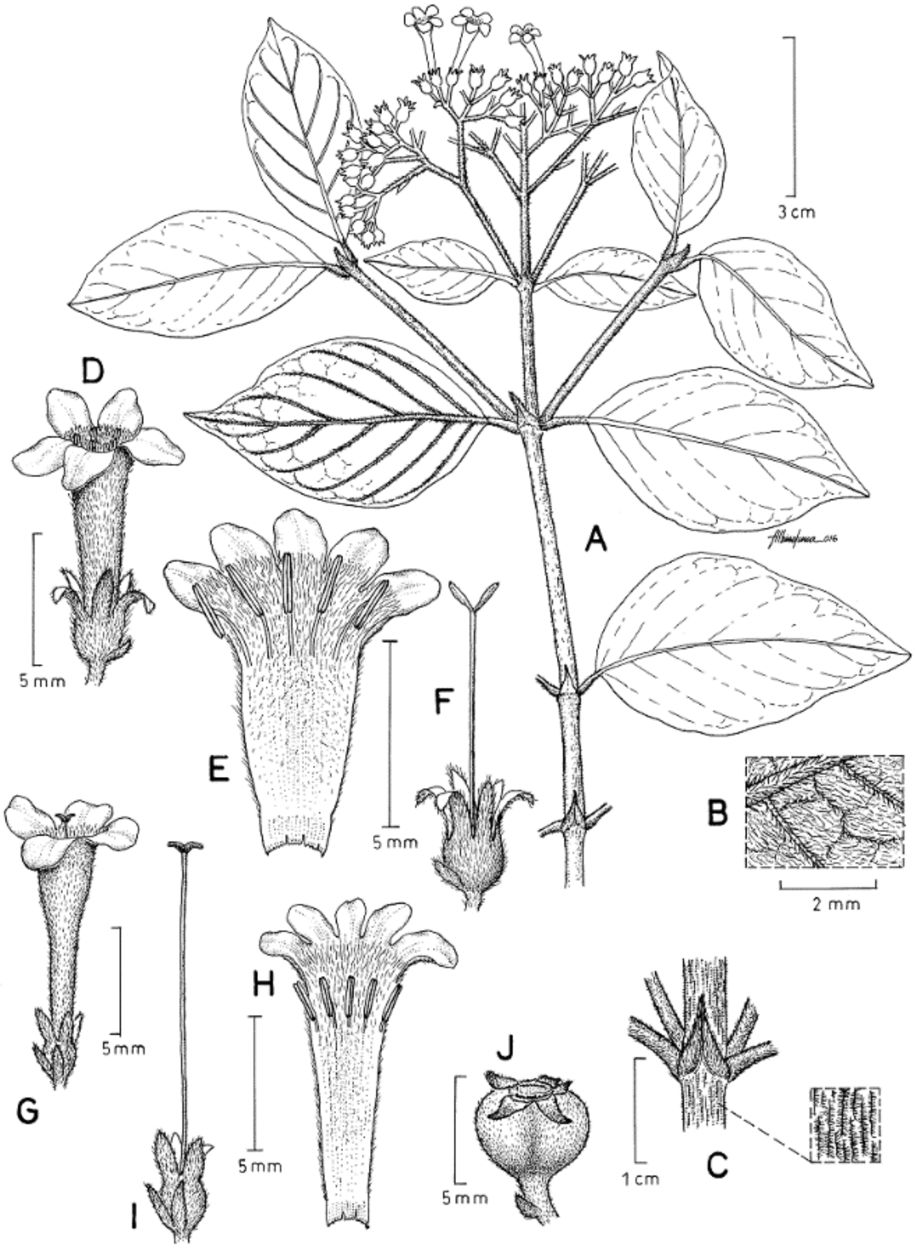

Figure 14. ***Rogiera macdougallii*****. A.** Fertile branch. **B.** Detail of the pubescence on the abaxial leaf surface. **C.** Stipule. **D.** Brevistylous flower. **E-F.** Dissected brevistylous flower. **E.** Open corolla tube showing stamen insertion and internal pubescence. **F.** Calyx and gynoecium. **G.** Longistylous flower. **H-I.** Dissected longistylous flower. **H.** Open corolla tube showing stamen insertion and internal pubescence. **I.** Calyx and gynoecium. **J.** Fruit.

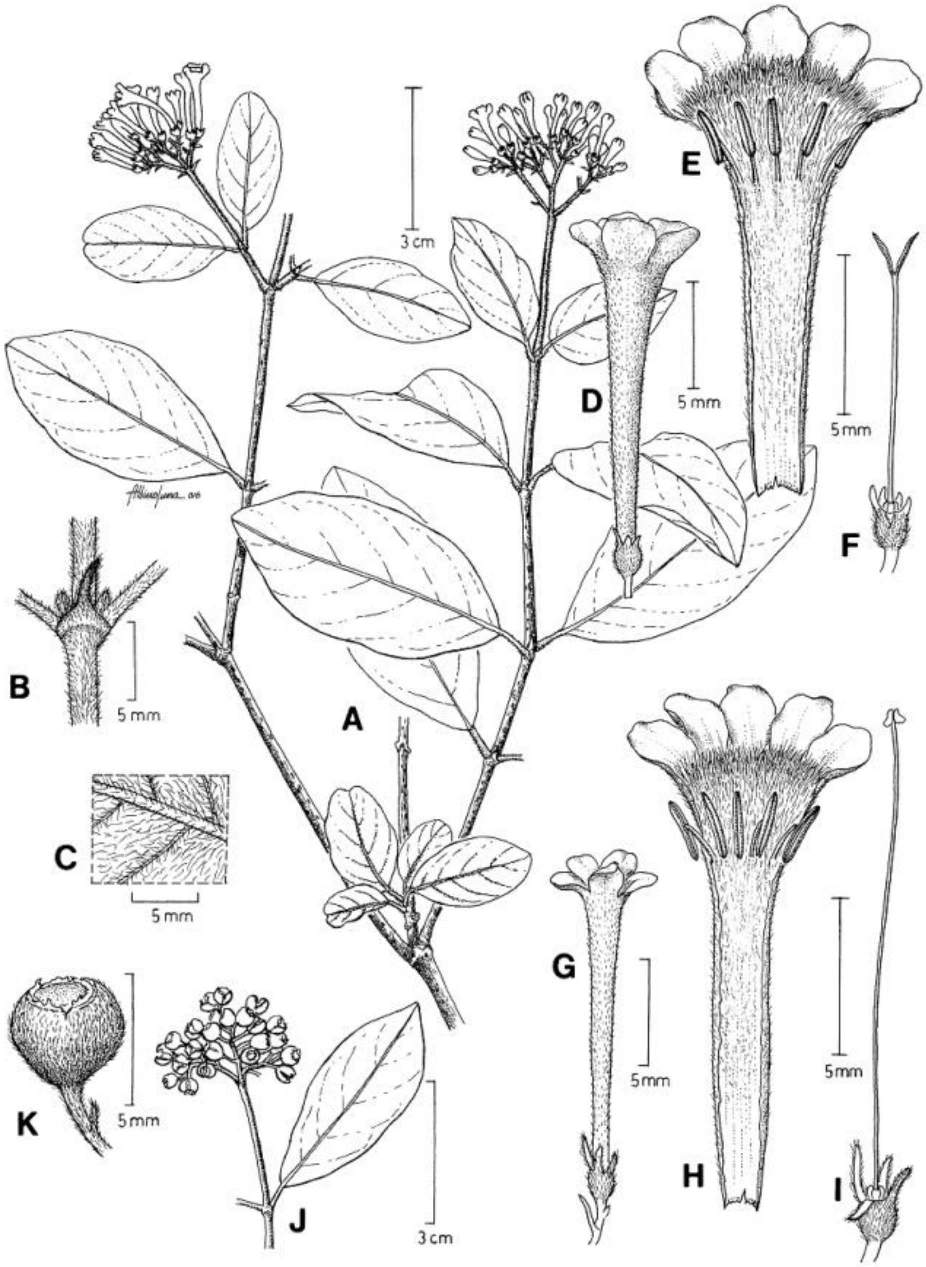

Figure 16. ***Rogiera nicaraguensis*****. A.** Fertile branch. **B.** Stipule. **C.** Detail of the pubescence on the abaxial leaf surface. **D.** Brevistylous flower. **E-F.** Open brevistylous corolla. **G.** Longistylous corolla. **H-I.** Open longistylous corolla. **J.** Fruited branch. **K.** Fruit.

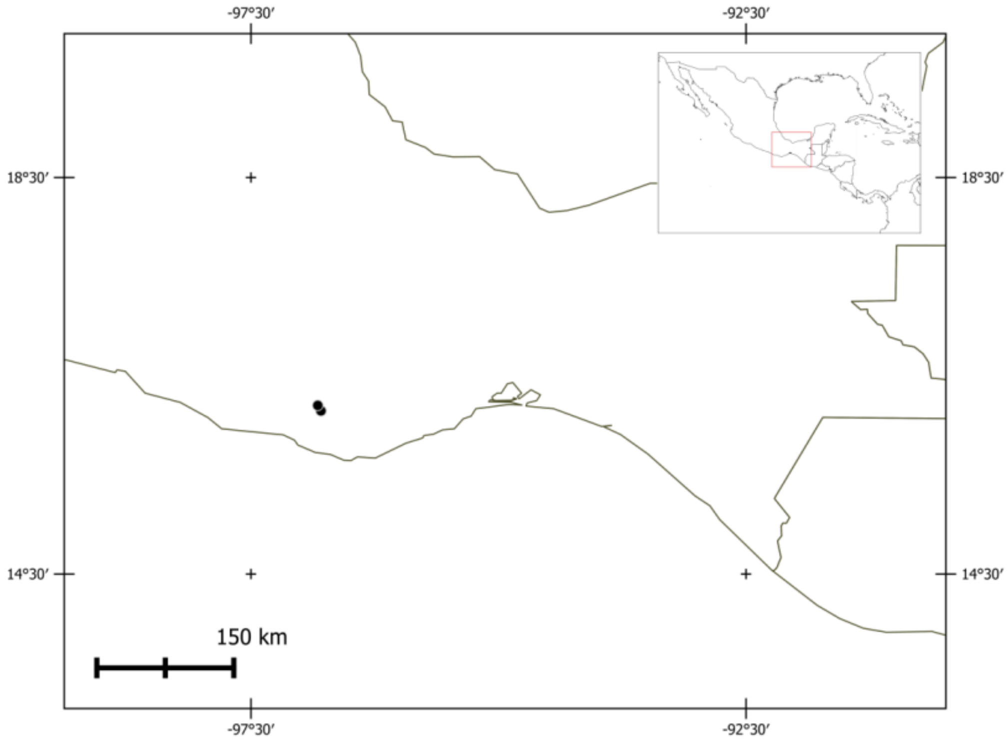

Figure 15. Geographic distribution of *Rogiera macdougallii*.

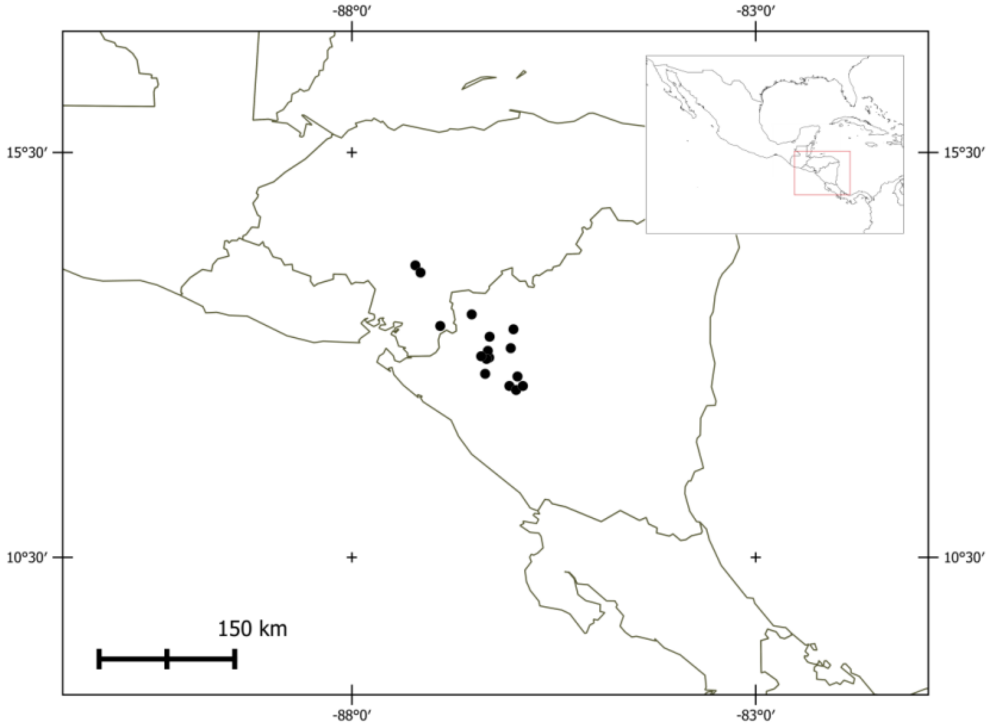

Figure 17. Geographic distribution of *Rogiera nicaraguensis*.

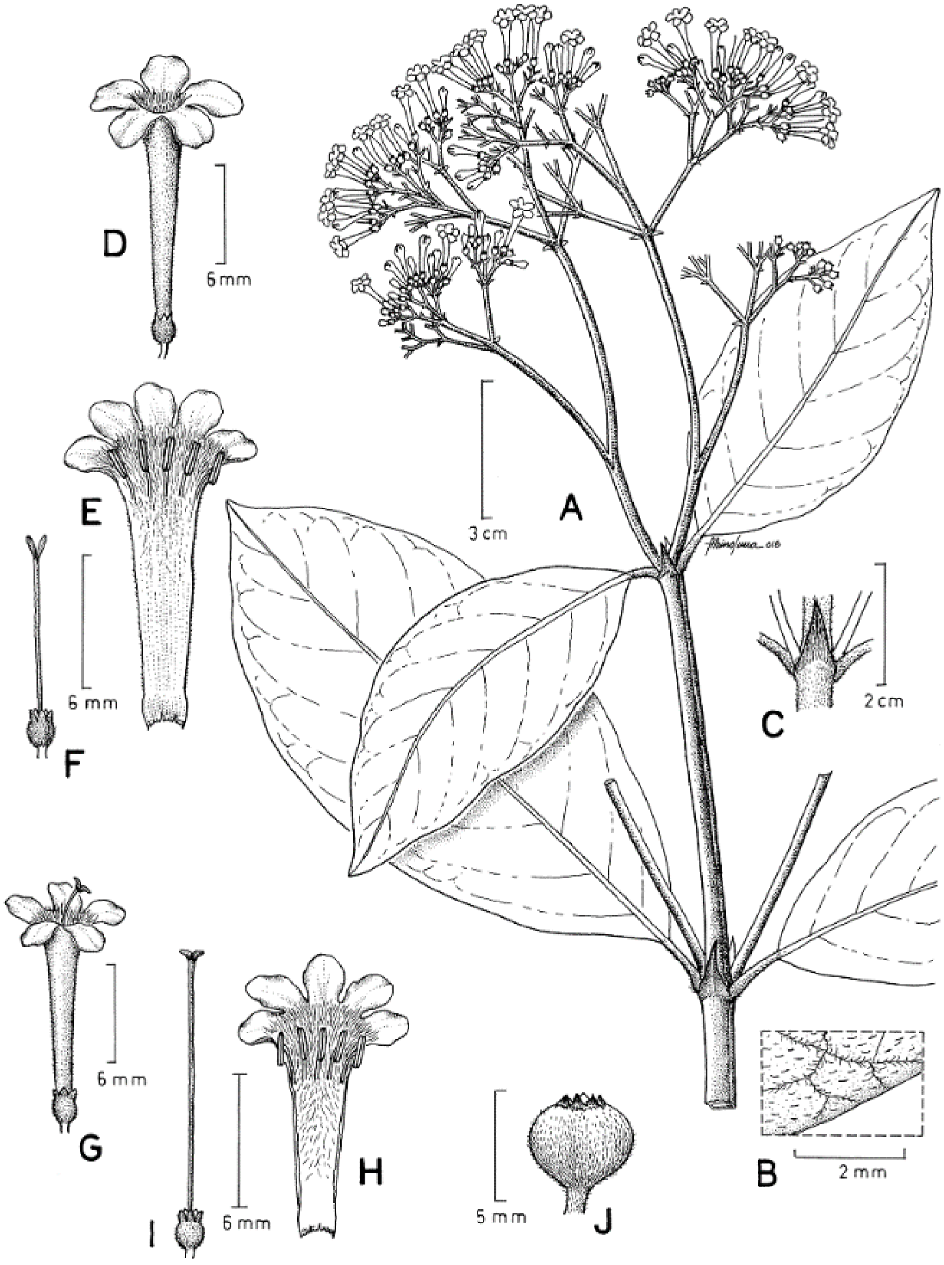

Figure 18. ***Rogiera stenosiphon*****. A.** Fertile branch. **B.** Detail of the pubescence on the abaxial leaf surface. **C.** Stipule. **D.** Brevistylous flower. **E-F.** Dissected brevistylous corolla. **E.** Open corolla tube showing stamen insertion and internal pubescence. **F.** Calyx and gynoecium. **G.** Longistylous flower. **H-I.** Dissected longistylous flower. **H.** Open corolla tube showing stamen insertion and internal pubescence. **I.** Calyx and gynoecium. **J.** Fruit.

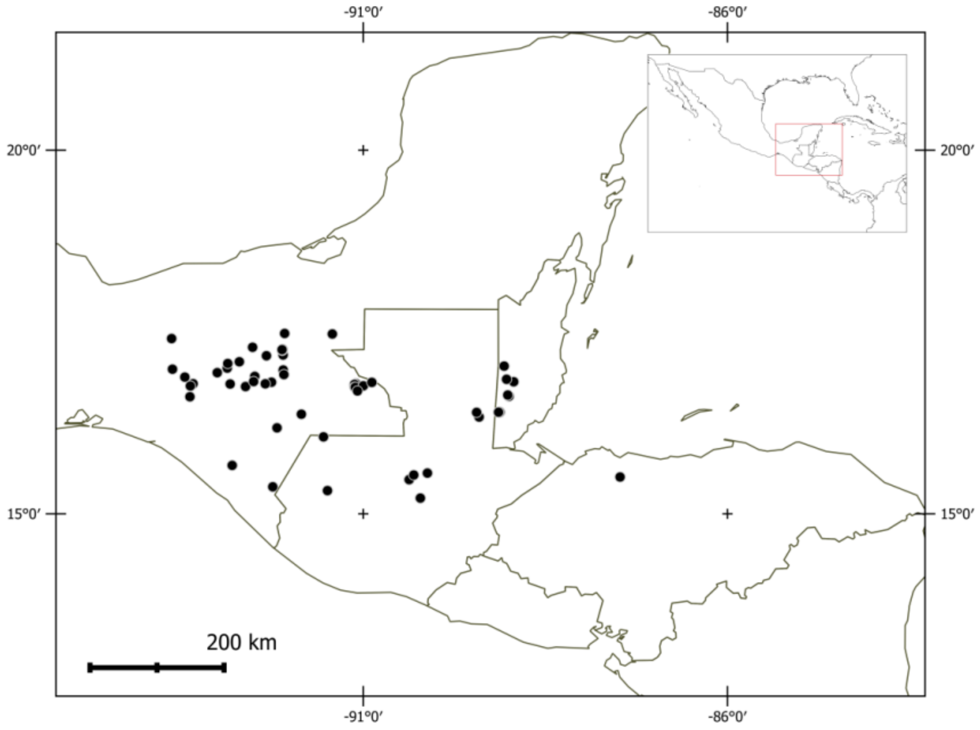

Figure 19. Geographic distribution of *Rogiera stenosiphon*.

PARTE III: COROLARIO

CAPÍTULO VIII: PROPUESTA TEÓRICA PARA ABORDAR CARACTERES COMPLEJOS

When homoplasy is not homoplasy: dissecting trait evolution by contrasting composite and reductive coding

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When Homoplasy Is Not Homoplasy: Dissecting Trait Evolution by Contrasting Composite and Reductive Coding

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Abstract.—The conceptualization and coding of characters is a difficult issue in phylogenetic systematics, no matter which inference method is used when reconstructing phylogenetic trees or if the characters are just mapped onto a specific tree. Complex characters are groups of features that can be divided into simpler hierarchical characters (reductive coding), although the implied hierarchical relational information may change depending on the type of coding (composite vs. reductive). Up to now, there is no common agreement to either code characters as complex or simple. Phylogeneticists have discussed which coding method is best but have not incorporated the heuristic process of reciprocal illumination to evaluate the coding. Composite coding allows to test whether 1) several characters were linked resulting in a structure described as a complex character or trait or 2) independently evolving characters resulted in the configuration incorrectly interpreted as a complex character. We propose that complex characters or character states should be decomposed iteratively into simpler characters when the original homology hypothesis is not corroborated by a phylogenetic analysis, and the character or character state is retrieved as homoplastic. We tested this approach using the case of fruit types within subfamily Cinchonoideae (Rubiaceae). The iterative reductive coding of characters associated with drupes allowed us to unthread fruit evolution within Cinchonoideae. Our results show that drupes and berries are not homologous. As a consequence, a more precise ontology for the Cinchonoideae drupes is required. [Character evolution; complex characters; drupes; fruit evolution; homoplasy; Rubiaceae; simple characters.]

Homology is perceived as the presence of the same (character state or character) trait in different taxa due to inheritance during phylogenesis (Hall 2007), that is, similarity due to common ancestry in the sense of Hennig (1966). Evidently, there are two steps of homology recognition: 1) the original proposition of homology *per se* (homology hypothesis based on certain criteria, such as Remane 1952 or Patterson 1988), which is stated by character coding and 2) the test (corroboration or rejection) of that hypothesis by phylogenetic inference. These were named by De Pinna (1991) as primary homology and secondary homology, respectively. Nixon and Carpenter (2012) argued that the terminology suggested by De Pinna is unfortunate, and we agree that a character shared by two or more taxa is either due to homology or not (the character is either homologous or not). Hence, we favor to use the terms *homology hypothesis* (as stated in the original character matrix) and *corroborated homology hypothesis* (as depicted after a phylogenetic analysis) for the respective cases following Fitzhugh (2016). When a homology hypothesis is corroborated by a phylogenetic test, the result is a corroborated homology hypothesis, which depends on the used set of characters and the used phylogenetic method. Consequently, it is also a homology hypothesis. For simplicity, we will hereafter use the terminology suggested by Nixon and Carpenter (2012) referring to *homology hypotheses* as stated in the matrix and merely *homology* as retrieved from the tree.

The original proposition of homology hypotheses needs a comparative approach to identify variation that can be coded in a matrix as character states. The postulation of homology hypotheses is the basis of any phylogenetic or evolutionary interpretation at the organismic or character level. Despite its importance, the assessment of homology hypotheses will be subjective and depends on the ability of the researcher to dismantle the organism or its structures into meaningful evolutionary units (Pleijel 1995; Wilkinson 1995; Strong and Lipscomb 1999).

In the case that a homology hypothesis is refuted (i.e., similarity is not due to common ancestry), the similarity is interpreted as homoplasy (Hennig 1966). Homoplasy could have two feasible explanations: 1) the similarity is a product of directional natural selection resulting in fully convergent morphologies or processes (Wake et al. 2011), so it is a “true” homoplasy or 2) the similarity is due to an incorrect homology assessment (Wake 1991; Wake et al. 2011; Nixon and Carpenter 2012), including several possibilities, such as character coding, reconstruction methods, optimization methods, and so on. In this article, we will focus on cases of homoplasy related to incorrect homology hypothesis at the level of initial character and character state conceptualization, particularly due to complex characters.

Coding Criteria and Character Complexity

The process of character coding to reflect homology hypotheses should be of major concern in phylogenetics (Pleijel 1995; Brazeau 2011). In the process of postulating homology hypotheses, the finding of similarity due to common ancestry is *the* task, regardless of the simplicity or complexity of the characters. For some data, the smallest entities that could be used to define characters are evident, for example, DNA sequences not altered by microstructural mutations, where the characters and their states simply reflect the four possible nucleotides in a certain position of a DNA molecule (Scotland et al. 2003). Nevertheless, even in these cases, one could argue that the actual evolutionary units are the proteins or amino acids, not the nucleotides (Simmons and Freudenstein 2002). Evolution does not always act at the minimal possible units, but sometimes the evolutionary units are composed of a complex set of features toward which natural selection acts. The putative homology then needs to be accordingly postulated in terms of traits responding to potential selective forces (Houle 2001; Richter and Wirkner 2014). In these cases, character coding requires to consider the postulation of complex characters (i.e., characters that can be translated into multiple simpler characters and therefore any character requiring two or more conditional qualifiers to specify it, Strong and Lipscomb 1999).

Wilkinson (1995) pointed out two ways of coding complex characters: 1) composite coding that treats the complex characters as such and 2) reductive coding in which the complex character is partitioned and analyzed as separate units. The literature presents a debate over the use of simple characters (by reductive coding) or complex characters (by composite coding) and their respective pros and cons (Strong and Lipscomb 1999; Seitz et al. 2000; Kirchoff et al. 2004, 2007; Brazeau 2011). Nevertheless, many authors apply either complex or simple coding approaches to test morphological homology hypotheses in plants and animals (Santini and Tyler 2003; Swenson and Anderberg 2005; Lehtonen 2006; Livshultz et al. 2007; Meudt and Simpson 2007; Rossie 2008; Prevosti 2010) without providing arguments for selecting either one of the methods. However, such an argumentation is needed, because complex characters contain information about the relationship between the parts, and when these types of characters are decomposed into simpler characters, the relational information of its parts can be lost.

The putative interdependency of characters is the major point in the discussion against reductive coding (Wilkinson 1995; Strong and Lipscomb 1999; Seitz et al. 2000; Fitzhugh 2006; Sereno 2007; Brazeau 2011). Wilkinson (1995) suggested that reductive coding of characters contributing to the same trait, which are not biologically independent, will lead to overweighting during phylogenetic reconstruction and thus erroneous trees. In some cases, characters that depend upon the presence of another character are only *partially* dependent. We argue that, although the presence of one character may determine the presence of the other, it is not always possible to predict which state will appear for the other character. In these cases, each simple character acts as a unit and could evolve independently from the other simple characters (Strong and Lipscomb 1999; Simmons and Freudenstein 2002). For example, the color of a flower is dependent on the presence of flowers, but once the flower is present, any color can potentially evolve. Even if the character is mapped onto the tree and not used to reconstruct the phylogeny (we suggest to distinguish both as character optimization vs. character mapping), the explicit postulation of the homology hypothesis of having or lacking flowers, independently of the color, would be lost if the character is coded as complex. Hence, no matter if a character is mapped onto or used to reconstruct a tree, the coding of complex versus simple characters affects the interpretation of the evolution of those characters.

Most authors have so far focused on the question of whether composite or reductive coding should be used. For example, Kirchoff et al. (2004) found an advantage for the use of complex characters even though highly artificial complex characters are used. They argue that this coding prevents discrepancies in the perception of the information's configuration by humans, who after all are the ones who code the characters. This perception escapes the goals of our articler, which focuses on the identification of homology.

Fitzhugh (2006) concludes that composite coding is the appropriate alternative in instances of biological nonindependence, while Simmons and Freudenstein (2002) justify reductive coding, because complex character coding assumes *a priori* dependency among characters, thus denying the opportunity of testing it. Our point of view is that whether the trait evolved as a simple or a complex unit is hardly known *a priori* and only contrasting both coding methods through the process of character coding and re-evaluation (reciprocal illumination *sensu* Hennig 1966) can shed light upon the actual units of evolution.

Reciprocal Illumination for Character Coding and Homoplasy Analysis

Hennig (1966) introduced the concept of reciprocal illumination in phylogenetic analysis, which implies "checking, correcting, and rechecking." It appears that the reciprocal illumination process is widely ignored, although it provides a unique source of character coding re-evaluation. It is "the process by which the science recognizes perceptual error" (Mickevich and Lipscomb 1991), allowing to address the need for rechecking and correcting previous statements. We consider that character conceptualization is of paramount importance to everyone who wants to evaluate characters in comparative biology with or without a phylogenetic context.

Härlin (1999) remarks that when having a phylogenetic context, the rationality of character conceptualization becomes tree dependent rather than observer dependent. That is why we propose the use of reciprocal illumination in an iterative way by which the character conceptualization can be re-evaluated and restated.

In this sense, homoplasy points to homology hypotheses that need to be re-evaluated. When homoplasy is retrieved, deeper comparative studies of the character should be conducted to exclude the possibility of coding errors. These errors can be at the level of character or character state coding, for example, when one character state is coded instead of two. For example, if red fruits are shown to be homoplasious, phytochemical studies could be performed to determine whether the red color was derived from anthocyanins or from carotenoids. In this example, the simple character state "red" would be recoded as two complex character states: "red by anthocyanins" versus "red by carotenoids." Another possibility for errors is when different characters are initially coded as character states of a single character. For example, the presence of echolocation system is homoplastic for bats and toothed whales, however, if the reductive coding is applied the echolocation system could be decomposed in several characters that consider their composition of the inner ear, number of ganglion cells per millimeter at basilar membrane, and auditory cortex thickness.

In order to evaluate homoplasy through the process of reciprocal illumination, we propose that confrontation between composite and reductive coding can be of major relevance. Homology hypotheses should be postulated according to an evolutionary hypothesis of what the researcher considers to be the functional evolutionary units. Traits (complex or simple characters), properly defined and delineated, are the actual subjects of adaptation (Wagner 2001). If the characters are corroborated through the phylogenetic test (synapomorphy is retrieved), this would be a corroboration that the evolutionary units were correctly depicted in the character coding. When a complex character results in homoplasy it should be partitioned into "simple characters," each of which describes a particular component of the character (Wilkinson 1995; Strong and Lipscomb 1999; Seitz et al. 2000; Fitzhugh 2006; Rossie 2008; Brazeau 2011). The character recoding results in a new homology hypothesis that will replace the original homology hypothesis (*contra* adding both sets of characters, as suggested by Simmons and Freudenstein 2002) conforming a "secondary matrix" that needs to be tested against the other observations through a phylogenetic method. This process could be iteratively repeated if homoplasy is again retrieved. The iterative process could stop when the last "complex character" is decomposed or when further reduction is not attainable and homoplasy needs to be accepted as in the case of nucleotide characters in a DNA molecule. A diagram summarizing the logical basis of our approach to use composite *and* reductive coding is shown in Figure 1.

Unthreading the Homoplastic Drupes within Subfamily Cinchonoideae (Rubiaceae)

We use the drupes in subfamily Cinchonoideae to provide an example of our approach. The most widely accepted features to define a drupe are the presence of three layers: 1) a skin-like, thin exocarp, (2) a thick fleshy mesocarp, and (3) a sclerenchymatic endocarp of varying thickness, the latter usually forming a "stone" or pyrene that encloses the seed (Puff 2001). It is obvious that the definition of a drupe fits to a complex character and also to a trait, as it is commonly believed that drupes represent structural units associated with animal dispersal (Jordano 1995). Because the definition of a drupe can be translated into multiple simpler characters, drupes represent a good example of a complex character believed to evolve as a complex unit, which can be tested having a phylogenetic framework.

Drupes within Cinchonoideae were treated as a single state of the character "fruit type" (Bremer and Eriksson 1992; Bremer et al. 1995). This coding implies the hypothesis that drupes are homologous. Although it has been postulated that drupes are functional units, one can also question its homologous nature, because the concept corresponds to a typological definition including several characters (Clifford and Dettmann 2001). In biology, typological definitions are often used to summarize and communicate certain features that are considered to be essential in the integration of a character (by definition a complex character). Consequently, it is often the case that typological characters are used in descriptions or even phylogenetic analyses. For logical reasons, typological characters are prompt to be homoplasious. The decomposition of drupes considering the three different layers would reflect the possible different genetic backgrounds of each of the fruit layers. Bremer and Eriksson (1992) as well as Bremer et al. (1995) mapped fruit evolution onto a Rubiaceae molecular phylogenetic tree, suggesting that dry fruits have three shifts to drupes in not closely related lineages within subfamily Cinchonoideae, thus the drupe is considered homoplastic within that subfamily. This could then be a case of "homoplasy" due to ontological issues providing a hypothesis to be tested.

Methods

To test the hypothesis that drupe homoplasy is due to incorrect ontology resulting from coding of a "drupe" as a single complex character and to identify which are the traits related to drupe evolution within Cinchonoideae, we first produced a robust phylogeny. The phylogeny was constructed using three plastid markers (*trn*K-*mat*K, *trn*L-F, and *pet*D), covering a

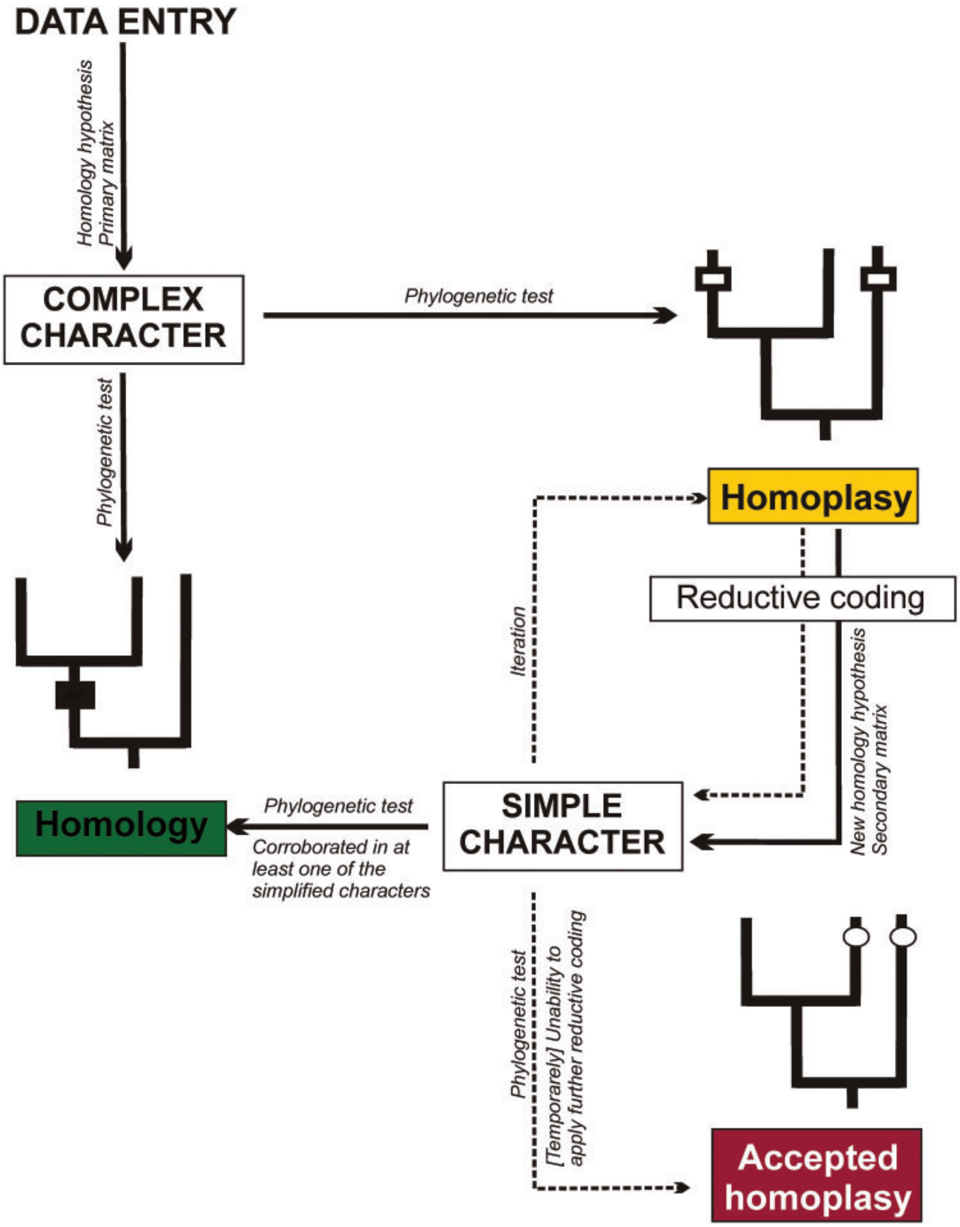

FIGURE 1. Scheme of iterative evaluation of homoplastic complex characters (states). If a homology hypothesis is corroborated by a phylogenetic test, then there is no need for further evaluation (dark gray box with black font; green box in the online version of the paper); when it corresponds to a complex feature all the characters that compose it are accepted as a trait (the evolutionary unit). However, if homoplasy is obtained (light gray box with black font; yellow box in the online version), the character state should be partitioned into simpler characters. Using reductive coding, a new matrix is created and its characters need to be tested again. The new homology hypothesis can be corroborated or, if the character state is homoplastic, once again a new reductive coding could be applied and tested iteratively until the homology hypothesis is corroborated or the homoplasy is (temporarily) accepted (dark gray box with white font; red box in the online version). The box filled in dark gray and with black font (green in the online version) suggests that the test has been successfully completed; box in light gray with black font (yellow in the online version) suggests that the test could be refined by recoding; and box in dark gray with white font (red in the online version) suggests that the test is stopped because there are no more possibilities for recoding.

wide representation of taxa with different fruit types from five tribes of Cinchonoideae. Taxon names, authors, vouchers, and GenBank accession numbers are presented in Supplementary Appendix S1 available on Dryad at http://dx.doi.org/10.5061/dryad.472s0. The extended details of the isolation, amplification, sequencing, alignment, microstructural character coding, and phylogenetic reconstruction methods are presented in Supplementary Appendix S2 available on Dryad. DNA alignments are presented as supplementary data (http://purl.org/phylo/treebase/phylows/study/TB2:S21001).

Morphological matrices were iteratively and manually created in WinClada (Nixon 1999) and analyzed for the same taxon sampling mapping them onto the DNA phylogeny. Matrix 1 used the typological fruit types (complex character states) including “drupe” (composite coding). When the character “fruit type” was mapped onto the DNA phylogeny, only the character state “drupes” was retrieved as homoplastic. Matrix 2 subdivides the homoplastic character state “drupe” into the features that typologically define it (reductive coding). Drupes were divided into origin of the fleshy layer and the pyrene or stone. These newly coded characters were again mapped onto the DNA phylogeny and a new matrix was constructed recoding the characters (states) that were retrieved as homoplasic. Matrix 3 restates the homoplasic character state “pyrene” considering more details of the pyrene morphology: pyrene number, locule number per pyrene, and seed number per locule; the homoplastic character state “fleshy undifferentiated mesocarp” cannot be further subdivided or restated, so this state is accepted as homoplasic. Table 1 summarizes the decomposition of the complex characters (states) as explained above. All complete matrices are presented in Supplementary Appendix S3 available on Dryad. Parsimony and Bayesian retrieved similar trees for which the evolutionary interpretation of character evolution does not change (Supplementary Appendix S4 available on Dryad shows the parsimony tree with Jackknife values (A) and the Bayesian tree with posterior probabilities (B) and its comparison after collapsing poorly supported branches (C)). For each matrix, the morphological characters were mapped onto the molecular parsimony consensus tree using WinClada (Nixon 1999), considering unambiguous optimizations.

RESULTS

Complex Character Coding (Matrix 1)

The mapping of “drupes” onto our phylogenetic tree obtained from Matrix 1 corroborated the existence of three previously suggested independent origins for

TABLE 1. Different iterative matrices in the coding for “drupes”

Matrix 1—Composite coding for fruit types

Character: character states

1. Fruit type: 0 = Berry, 1 = Drupe, 2 = Capsule, 3 = Samara, 4 = Schizocarp

Example of matrix coding

Char.	1
Antirhea	1
Arachnothryx	2
Chiococca	1
Gonzalagunia	1
Guettarda	1
Machaonia	4
Phyllomelia	3
Randia	0
Sabicea	0

Matrix 2—Reductive coding for “drupes” (as they were not corroborated as homologous)

1. Fruit type: 0 = Berry, 1 = Capsule, 2 = Samara, 3 = Schizocarp, ? = Drupe
2. Fleshy layer origin: 0 = undifferentiated mesocarp, 1 = outer mesocarp; inapplicable (–) for states 2, 3, and 4 of Character 1
3. Pyrene origin: 0 = endocarpic, 1 = inner mesocarp; inapplicable (–) for states 0, 2, 3, and 4 of Character 1

Chars.	1	2	3
Antirhea	?	1	1
Arachnothryx	1	–	–
Chiococca	?	0	0
Gonzalagunia	?	0	0
Guettarda	?	1	1
Machaonia	3	–	–
Phyllomelia	2	–	–
Randia	0	0	–
Sabicea	0	0	–

Matrix 3—Reductive coding for pyrens (as they were not corroborated as homologous)

1. Fruit type: 0 = Berry, 1 = Capsule, 2 = Samara, 3 = Schizocarp, ? = Drupe
2. Fleshy layer origin: 0 = undifferentiated mesocarp, 1 = outer mesocarp; inapplicable (–) for states 2, 3, and 4 of Character 1
3. Pyrene origin: 0 = endocarpic, 1 = inner mesocarp; inapplicable (–) for states 0, 2, 3, and 4 of Character 1
4. Pyrene number: 0 = 1, 1 = 2, 2 = 4; inapplicable (–) for states 0, 2, 3, and 4 of Character 1
5. Loculi number per pyrene: 0 = one pyrene, 1 = numerous pyrenes; inapplicable (–) for states 0, 2, 3, and 4 of Character 1
6. Number of seeds per locule: 0 = one seed, 1 = numerous seeds

Chars.	1	2	3	4	5	6
Antirhea	?	1	1	0	1	0
Arachnothryx	1	–	–	–	–	1
Chiococca	?	0	0	1	0	0
Gonzalagunia	?	0	0	2	0	1
Guettarda	?	1	1	0	1	0
Machaonia	3	–	–	–	–	0
Phyllomelia	2	–	–	–	–	0
Randia	0	–	–	–	–	1
Sabicea	0	–	–	–	–	1

this fruit type (Bremer and Eriksson 1992; Bremer et al. 1995) now based on a more representative molecular character sampling, generally leading to better supported nodes.

First Reductive Coding (Matrix 2)

Drupes were decomposed considering the origin of the fleshy and stony tissues (mesocarp and endocarp). In some fruits, there are two differentiable layers of stony consistency: the inner one is of identical texture as the endocarp in those fruits only have a single stony layer and the outer stony layer is more porous than the typical stony endocarps. Therefore, we interpret the outer stony layer as a modification of the inner mesocarp. Hence, the fleshy tissue can correspond to an undifferentiated mesocarp or just to the outer mesocarp; the stony tissue can correspond to the inner mesocarp or to the endocarp. A pyrene then can be formed by the inner mesocarp stony layer or by the endocarp stony layer (Matrix 2). Two homology hypotheses from Matrix 2 were retrieved as homology, but others (see Character 3 below) had to be further restated in a new Matrix. Character 1 (Fruit type): keeping this character allows understanding general fruit type evolution, including transformations among other character states. After identifying that only drupes are homoplastic, fruit type was coded with a question mark (?) for the taxa with drupes, in order to avoid character correlation. Winclada treats question marks (?) as any possible state, allowing the identification of character state correlations, relationships of character states, and homoplasy when the characters are optimized/mapped onto the tree. Therefore, keeping the character "fruit type" allows the investigation of which of the other fruit types are associated with the new characters, how many times the original state drupes evolved (which is associated with the question mark), and which characters may be correlated to the origin of drupes, in this example, preventing weighting the pyrene origin as all taxa with question mark in Character 1 will be coded either with state 0 or 1 in Character 3, while the rest of the taxa will be coded as inapplicable (−) for this same character. Character 2 (Fleshy layer origin): The fleshy undifferentiated mesocarp (character state 0) is retrieved as homoplastic, but it cannot be further subdivided, so, homoplasy is accepted. The fleshy outer mesocarp is corroborated as a synapomorphy of the clade *Guettarda* and allies. Character 3 (Pyrene origin): the endocarpic pyrenes (character state 0) is retrieved as homoplastic, so the pyrene is further reassessed into pyrene number, loculi number per pyrene, and number of seeds per locule in Matrix 3. The pyrene of inner mesocarp origin is corroborated as a synapomorphy of the clade *Guettarda* and allies.

Second Reductive Coding (Matrix 3)

Characters 1, 2, and 3 remain unchanged from Matrix 2, but the character state "drupe" is further reduced and therefore remains associated with a question mark in Character 1. Character 4 (Pyrene number): each of the states is corroborated as a synapomorphy: *Chiococca* and allies have two pyrenes; *Gonzalagunia* four and *Guettarda* and allies one. Character 5 (Loculi number per pyrene): one locule is homoplastic for *Chiococca* and allies and *Gonzalagunia*, while numerous loculi are synapomorphic to *Guettarda* and allies and correlated to the pyrene of inner mesocarpic origin. Character 6 (number of seeds per locule): one-seeded locules are homoplastic for *Chiococca* and allies and *Machaonia* (with schizocarps) plus *Guettarda* and allies and it is also present in the taxa with samaras (*Phyllomelia*). Numerous seeds per locule are plesiomorphic within Cinchonoideae.

Fruit Evolution within Cinchonoideae

With the understanding of the "drupe" evolution within Cinchonoideae the original interpretation of fruit evolution is untangled. Berries are plesiomorphic within Cinchonoideae. A regression to berries would have to be considered within Chiococceae for *Catesbaea*, but we had no samples of this genus. In the future, a similar analysis decomposing berry characters could be applied. Capsules evolved from berries, which in turn modified independently into samaras, schizocarps, and three times into drupes. Each lineage with drupes presents a unique combination of characters states among which at least one character state is a synapomorphy: 1) Chiococceae drupes have fleshy undifferentiated mesocarp, two pyrenes (synapomorphic) of endocarpic origin, one locule per pyrene, and one seed per locule; 2) *Guettarda* and allies drupes have fleshy outer mesocarp, one pyrene of inner mesocarpic origin, multilocular pyrenes, and one seed per locule (the only plesiomorphic condition); 3) *Gonzalagunia* drupes have fleshy undifferentiated mesocarp, four pyrenes (synapomorphy) of endocarpic origin, one locule per pyrene, and many seeds per locule (synapomorphy). Figure 2 summarizes the concluding interpretation of fruit trait evolution within Cinchonoideae.

Fruit Ontology within Cinchonoideae

Strictly speaking, a drupe is "a fleshy indehiscent fruit with a stony endocarp" (Harris and Harris 2001). Exceptions occur in some taxa that have drupes with more than one pyrene ("stone"), such as in the genus *Prunus* (Pérez-Zabala 2015). Our results show that structurally there are two types of pyrenes in Cinchonoideae "drupes": mesocarpic and endocarpic, the former always one per fruit, but multilocular. The fruits of *Guettarda* and allies have one pyrene of mesocarp origin, multilocular due to many seeds each covered by stony endocarp. Therefore, these fruits do not correspond to classic drupes. For clarity and simplicity, we propose to name of "mesocarpic-drupes" for those in *Guettarda* and allies. Likewise, the "drupes"

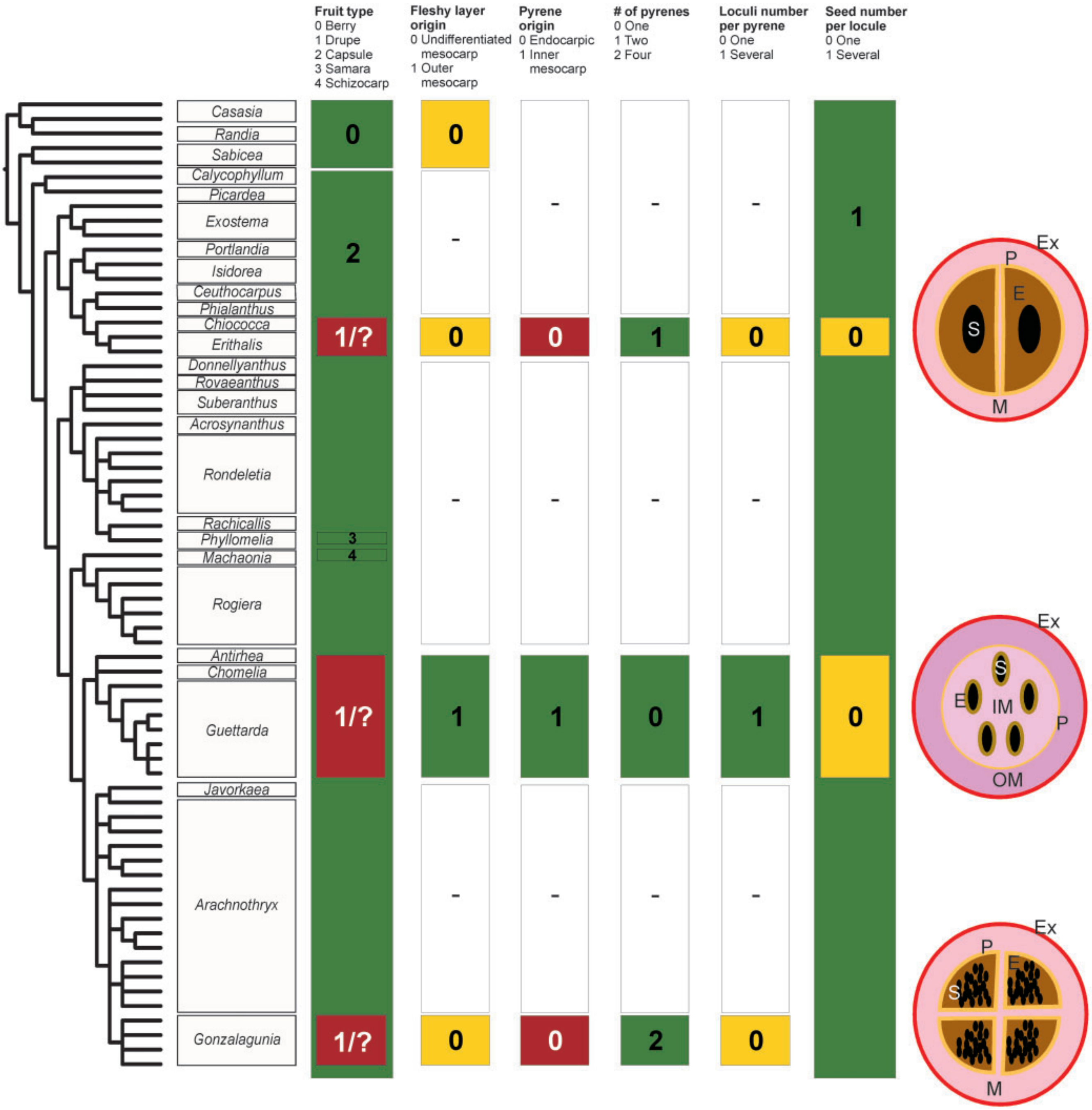

FIGURE 2. Summary of the interpretation of "drupe" evolution within Cinchonoideae. According to Figure 1, for each character state, patterns of the boxes indicate homology (dark gray with black font; green in the online version), homology hypothesis subject to further subdivision (light gray with black font; yellow in the online version), and temporarily accepted homoplasy (dark gray with white font; red in the online version). In this example, composite coding results in three independent origins of drupes. The reductive coding shows varying degrees of homoplasy, however, each lineage with drupes has synapomorphies for the simpler characters. The unique combinations of characters that conform the different types of drupes is schematized at the far right, where E = endocarp; Ex = exocarp; IM = inner mesocarp; M = undifferentiated mesocarp; OM = outer mesocarp; P = pyrene; S = seed.

of *Gonzalagunia*, although with endocarpic pyrenes, have many seeds per pyrene, which also does not fit the classic definition of a drupe. For clarity and simplicity, we propose to name "pluriseminated-drupes"for those in *Gonzalagunia*.

CONCLUSIONS

Coding complex characters allows the recognition of evolution acting on a complex character as a trait. If homoplasy is retrieved for particular character states, reductive coding can be applied, in order to recognize whether the homoplasy is due to erroneous character conceptualization or whether one has to accept independent origins of structures that cannot be further recoded, considered for simplicity at least temporarily (while new methods allow to further test it) as "true" homoplasy. Dissecting character evolution by contrasting composite and reductive coding is a useful tool to understand character evolution. The use of reciprocal illumination is here essential.

Our method does not prevail a better coding of characters as composite or as simple, the coding entirely depends on the perception of the researcher and in fact, we argue that the potential use of both coding methods could be in some instances the most appropriate. The coding of the character as complex or simple must obey only on the homology hypothesis and has to be evaluated under the light of the results. If a complex character corresponds indeed to a trait (selective unit), it is expected that all the simpler features that compose it evolve syntonically. But traits do not need to correspond to complex features. When the initial homology hypotheses are corroborated, no matter if the character was treated as complex, the coding should be accepted as the best current estimate for the conceptualization of that character. In contrast, when the results suggest homoplasy, we argue that the complex character should be iteratively decomposed by reductive coding into characters that can be further analyzed until homology is corroborated or the character state cannot be further decomposed and homoplasy has to be (at least temporarily) accepted. The temporary acceptance of homoplasy could be later tested by deeper studies using other techniques, such as anatomy, chemistry, ontogeny, or evo-devo.

In the case of Cinchonoideae, tested by reductive coding, the original idea that drupes are homoplastic is refuted: drupes are different among lineages. A unique combination of simpler characters helped unthreading "drupe" evolution within this subfamily. Our new understanding of this character can now be translated into a more accurate ontology.

Supplementary Material

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.472s0.

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CONCLUSIONES GENERALES

- La sistemática es una disciplina de la biología que se encarga de descubrir, nombrar, describir, clasificar y entender la diversidad biológica. El presente trabajo cubrió todos estos objetivos relacionados con en el complejo *Rondeletia*.
- Este estudio se basó fuertemente en trabajo de campo, que permitió el descubrimiento de un género y dos especies de *Arachnothryx* nuevos para la ciencia.
- Una de las labores en sistemática es proporcionar herramientas de identificación y síntesis taxonómicas. Aquí se presentan las de los géneros *Rovaeanthus* y *Rogiera* que, aunque morfológicamente similares, se ubican en las filogenias en tribus diferentes: Rondeletieae y Guettardeae, respectivamente. Se seleccionaron estos géneros debido a los diferentes criterios de circunscripción en los recientes tratamientos taxonómicos. En *Rovaeanthus* se reconocen dos especies, mientras que en *Rogiera* nueve.
- La morfología del polen provee información que sustenta la separación del complejo *Rondeletia* en dos tribus. Los géneros del complejo ubicados en Guettardeae poseen endofisuras o endocracks como discontinuidades de la nexina del polen, mientras que los de la tribu Rondeletieae carecen de discontinuidades en la nexina.
- Las polifilia del complejo *Rondeletia* se corroboró con respecto a los estudios previos, pues el complejo se divide en dos linajes de géneros cercanamente relacionados. Uno de ellos se ubica en la tribu Rondeletieae (*Acunaeanthus*, *Donnellyanthus*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella*, *Rondeletia*, *Rovaeanthus*, *Stevensia*, *Suberanthus* y *Tainus*) y el otro en la tribu Guettardeae (*Arachnothryx*, *Gonzalagunia*, *Javorkaea*, *Renistipula* y *Rogiera*).
- A partir de los análisis filogenéticos que incluyeron a los géneros considerados como parte del complejo *Rondeletia* y tomando en cuenta la morfología, nosotros reconocemos once: *Acunaeanthus*, *Donnellyanthus*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Rondeletia*, *Rovaeanthus*, *Suberanthus* y *Tainus* en Rondeletieae y *Gonzalagunia* y *Rogiera* en Guettardeae. Los géneros que corroborados o propuestos en sinonimia en este trabajo son *Arachnothryx*, *Cuatrecasasiodendron*, *Javorkaea* y *Renistipula* de *Gonzalagunia* en Guettardeae. En la tribu rondeletieae se corrobora la sinonimia de *Stevensia* con *Rondeletia*.
- En la tribu Rondeletieae, se descubrió y describió el género nuevo *Tainus* con el basónimo *Rondeletia pitreana*. Este género tiene sustento por su posición filogenética, además de sinapomorfias a nivel microestructural de secuencias de ADN (repeticiones simples) y morfológicas (garganta de la corola

densamente papilada), que lo distinguen inequívocamente de *Rondeletia* y de otros géneros cercanamente relacionados.

- Los géneros *Donnellyanthus* y *Rovaeanthus* deben ser aceptados, pues se apoyan en evidencia morfológica y molecular, aunque en el tratamiento más reciente (Flora Mesoamericana) sean considerados como sinónimos de *Arachnothryx* y *Rogiera*, respectivamente. Incluso se deben clasificar en una tribu diferente (Rondeletieae) a la de los géneros con los que se han sinonimizado (Guettardeae).
- El clado *Rondeletia* se recuperó como parafilético con respecto a *Phyllomelia*, *Mazaea* y *Rachicallis* haciendo uso de secuencias de ADN y con un muestreo limitado. No obstante, un muestreo más amplio de especies y el uso simultáneo de morfología y secuencias de ADN permitió reconocer a *Rondeletia* como un género monofilético. A pesar de que los análisis que aquí se presentan son los que incluyen el mayor número de especies de la tribu Rondeletieae, aún hay espacio para realizar análisis con más especies de *Rondeletia*, el cual es un género morfológicamente heterogénero.
- Dentro de la tribu Guettardeae, el género *Arachnothryx* resultó parafilético con respecto a *Javorkaea*, *Gonzalagunia* y *Renistipula*; esto también se sustenta con evidencia morfológica. Entre estos géneros, el nombre que bajo el principio de prioridad debe ser aceptado es *Gonzalagunia*, por tanto, en aras de una clasificación natural se hicieron 102 nuevas combinaciones de especies que fueron transferidas a *Gonzalagunia*.
- El género *Rogiera* se corrobora como monofilético y está más cercanamente relacionado con *Machaonia* que con el clado *Gonzalagunia-Arachnothryx* (hermano de Guettarda y aliados).
- Este estudio permitió proponer una nueva circunscripción para la tribu Rondeletieae consistente con la evidencia filogenética. Proponemos que la tribu debe incluir a los géneros *Acrosynanthus*, *Acunaeanthus*, *Blepharidium*, *Donnellyanthus*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Roigella*, *Rondeletia*, *Rovaeanthus*, *Suberanthus*, *Tainus*, caracterizados por la estivación quincuncial de los lóbulos de la corola y los frutos típicamente capsulares.
- El estudio sobre evolución del fruto dentro de la subfamilia Cinchonoideae abrió la posibilidad de un planteamiento teórico en el que se propone un método iterativo para evaluar la homoplasia en caracteres complejos. El método consiste en emplear codificación reductiva para aquellos caracteres complejos que no se hayan recuperado como homólogos. Se sugiere descomponer los caracteres en caracteres más “simples” de manera iterativa hasta corroborar homología o bien hasta que el carácter ya no pueda ser dividido y la homoplasia tenga que ser (al menos temporalmente) aceptada. Bajo este método se evaluaron los aparentes tres orígenes independientes de las drupas en la subfamilia

Cinchonoideae y se concluye que en realidad las drupas son diferentes con base en el origen anatómico de las capas que las conforman.

- El conocimiento previo en el complejo *Rondeletia* era parcial, ya sea por la carencia de un contexto filogenético robusto o bien por la falta de sustento morfológico en las decisiones taxonómicas. La presente tesis retoma estos antecedentes e indudablemente aporta al entendimiento de la problemática en el complejo *Rondeletia* al incrementar el muestreo de terminales o bien explorar nuevas fuentes de evidencia. Con el uso del marco filogenético aunado al soporte morfológico son traducidos en un esquema de clasificación natural lo cual contribuye al avance en el conocimiento no solo del grupo sino de la diversidad de Rubiaceae en el Neotrópico.
- El presente proyecto abordó diferentes líneas de investigación en la sistemática de un grupo, no obstante permitió cumplir con muchos de los objetivos inicialmente planteados, aún quedan numerosas tareas por realizarse en un futuro cercano. Desde el punto de vista morfológico, las diferencias en la ornamentación de la garganta de la corola, presentes entre géneros cercanamente relacionados, invitan a realizar estudios anatómicos. Un incremento en el muestreo de especies del género *Rondeletia* es necesario para poder responder preguntas biogeográficas y entender las relaciones entre los taxones de las Antillas y los del continente. De igual manera, es importante revisar al género *Gonzalagunia* (principalmente representado en Sudamérica en el sentido antiguo) en su nueva circunscripción. Queda pendiente establecer las relaciones filogenéticas de los géneros y la circunscripción de la tribu Guettardeae, cuya concepción se modificó fuertemente con la inclusión de géneros antes clasificados en la tribu Rondeletieae.