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FILOGENIA, BIOGEOGRAFIA E TAXONOMIA DE *PRADOSIA* (SAPOTACEAE, CHRYSOPHYLLOIDEAE)

MÁRIO HENRIQUE TERRA-ARAUJO

Manaus – Amazonas
Abril / 2013

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FILOGENIA, BIOGEOGRAFIA E TAXONOMIA DE *PRADOSIA* (SAPOTACEAE, CHRYSOPHYLLOIDEAE)

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Tese apresentada ao Instituto Nacional de Pesquisas da Amazônia como parte dos requisitos para obtenção do título de Doutor em Ciências Biológicas, área de concentração em Botânica.

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Sinopse: *Pradosia* (Sapotaceae, Chrysophylloideae) comprises 23 species mostly confined to rainforests in tropical South America. Molecular data indicate that the genus is monophyletic and includes three main clades, which are also supported by morphological characters, geography and habitat preferences. The genus originated in Early Oligocene in the Amazon region and reached the Brazilian Atlantic coast ~ 24.9 Ma, followed by an expansion from the Amazon region to the northeast of South America in the Oligocene, with three independent recolonization events of the Brazilian Atlantic coast region during the Miocene-Pliocene. The association between habitat and species indicates that shift in habitat preference may have played an important role in the speciation process of *Pradosia*.

Palavras-chave: 1. Sapotaceae. 2. *Pradosia.* 3. Neotropics. 4. Molecular dating. 5. Biogeography. 6. Amazon.

“Um homem precisa viajar. Por sua conta, não por meio de histórias, imagens, livros ou TV. Precisa viajar por si, com seus olhos e pés, para entender o que é seu. Para um dia plantar as suas próprias árvores e dar-lhes valor. Conhecer o frio para desfrutar o calor. E o oposto. Sentir a distância e o desabrigo para estar bem sob o próprio teto. Um homem precisa viajar para lugares que não conhece para quebrar essa arrogância que nos faz ver o mundo como o imaginamos, e não simplesmente como é ou pode ser. Que nos faz professores e doutores do que não vimos, quando deveríamos ser alunos, e simplesmente ir ver”

Amyr Klink
(Mar sem fim)

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RESUMO

O gênero *Pradosia* (Sapotaceae, Chrysophylloideae) compreende 23 espécies com hábito variando de arbustos geófilos, arvoretas à árvores de dossel com altura superior a 35 m. O gênero é restrito à América do Sul, com apenas uma única espécie se estendendo até o Panamá e Costa Rica. As espécies podem ser encontradas em uma variedade de habitats, incluindo florestas úmidas e decíduas na Amazônia, costa Atlântica Brasileira e Andes. Estudos prévios, combinando dados moleculares e morfologia de poucas espécies de *Pradosia* indicaram que o gênero é monofilético, excluindo a espécie Africana *P. spinosa*. O presente trabalho apresenta os resultados de um estudo mais aprofundado de *Pradosia*, com uma maior amostragem das espécies e que teve como objetivos: (1) obter uma hipótese filogenética para *Pradosia*, com utilização de dados moleculares; (2) estimar o tempo de divergência dos clados e discutir a biogeografia histórica do grupo; (3) reconstruir a evolução de caracteres morfológicos selecionados, considerados úteis para o reconhecimento das espécies dentro do gênero; (4) investigar a evolução da preferência do habitat para as espécies do gênero; (5) atualizar a taxonomia do grupo com base nos resultados das análises moleculares, morfológicas, e de estudos de campo. Os resultados deste trabalho são apresentados em três capítulos. No primeiro capítulo é apresentada a filogenia molecular de *Pradosia,* reconstruída com utilização de dois marcadores moleculares, ITS e ETS. Esta filogenia é então utilizada como base para explorar a evolução de caracteres morfológicos e da preferência de habitat, bem como discutir o padrão biogeográfico do gênero. No segundo capítulo, são apresentadas as novas espécies para *Pradosia*. Por fim, no terceiro capítulo é apresentada uma sinopse taxonômica do gênero, com uma atualização da distribuição geográfica das espécies e uma chave de identificação, seguida por uma curta descrição morfológica de todas as espécies do grupo, além de informações obtidas em campo.

ABSTRACT

The genus *Pradosia* (Sapotaceae, Chrysophylloideae) comprises 23 species that vary in habit from geoxylic shrubs to medium-sized and tall canopy trees up to 35 m. The genus is confined to South America, one of which also extends into Panama and Costa Rica. The species are distributed across a wide variety of habitats, including savannas and evergreen to deciduous forests in the Amazon region, the Brazilian Atlantic coast, and the Andes. Previous studies including a few species of *Pradosia* have indicated that the genus is monophyletic, provided that the African species *P. spinosa*, is excluded. This work presents the results of a new phylogenetic study of *Pradosia*, with a broader species sampling and aimed to: (1) produce a phylogenetic hypothesis for the genus *Pradosia* using molecular data; (2) estimate species divergence times and biogeographical history; (3) reconstruct the evolution of some morphological traits that have been considered useful in distinguishing species within the genus; (4) investigate the evolution of habitat preference; (5) provide a taxonomic update to the species. These objectives correspond to the three chapters of the present thesis. The first chapter includes a molecular phylogeny of *Pradosia* based on the molecular markers ITS and ETS. The resulting phylogenetic hypothesis was used to infer the generic biogeographical history of the genus, explore the evolution of morphological characters, and habitat preferences. The second chapter presents the novelties in *Pradosia*, with description of new species. Lastly, the third chapter presents a synopsis of the species, a review of the species geographical distributions, and a new key followed by a short morphological description, as well as notes regarding species circumscriptions and information obtained in field.

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INTRODUÇÃO GERAL

Sapotaceae, um dos membros de Ericales (Stevens, 2001), compreende aproximadamente 1.250 espécies distribuídas por 58 gêneros (Swenson & Anderberg, 2005; Swenson et al., 2008). As espécies da família são principalmente árvores ou arbustos, com látex geralmente de coloração branca, encontrado no caule, ramos, folhas e frutos. As folhas são geralmente alternas, raramente opostas, com ou sem estípulas. Os estames são sempre opostos aos lobos da corola, e alguns gêneros também apresentam estaminódios localizados entre os lóbulos da corola. Outra característica da família é a presença de tricômas malpighiáceos sobre as diferentes estruturas da planta (Pennington, 1990; Anderberg & Swenson, 2003; Swenson & Anderberg, 2005; Swenson et al., 2008).

As espécies de Sapotaceae são encontradas predominantemente em florestas úmidas de regiões de baixas altitudes da América, África, Ásia e Ilhas do Pacífico (Pennington, 1991). Nos Neotrópicos, Sapotaceae é um dos grupos de maior diversidade e abundância, com ca. de 400 espécies descritas. Na Amazônia Central, a quantidade de espécies da família se iguala ou mesmo supera os índices de diversidade de outras famílias muito bem representadas na região, como Fabaceae e Lecythidaceae (Pennington, 1991; Milliken, 1998; ter Steege et al., 2000). No entanto, a diversidade de espécies aliadas à alta homoplasia em caracteres morfológicos tem resultado em diferentes opiniões sobre as delimitações genéricas e classificações infrafamiliares (Lam, 1939; Baehni, 1938, 1965; Aubréville, 1964; Pennington, 1990, 1991; Anderberg & Swenson, 2003; Swenson et al., 2008).

As espécies neotropicais de Sapotaceae foram revisadas por Pennington (1990). Nesse trabalho, o autor propôs a divisão da família nas tribos Chrysophylleae, Sideroxyleae, Mimusopeae, Isonandreae e Omphalocarpeae. Entretanto, essa classificação infrafamiliar se mostrou incongruente com os resultados de estudos cladísticos efetuados com base em caracteres moleculares (Anderberg & Swenson, 2003; Swenson & Anderberg, 2005; Swenson et al., 2008), que mostraram evidências da ocorrência de três grandes linhagens para o grupo. Com base nesses resultados, foi proposta uma nova classificação taxonômica com a subdivisão de Sapotaceae em três subfamílias: (1) Sarcospermatoideae, compeendendo apenas *Sarcosperma*, considerada pelos autores como membro de Sapotaceae devido ao forte suporte estatístico obtido com as análises para sua relação como irmão do resto da família, e ao fato desse grupo já vir sendo considerado como Sapotaceae por Pennington (1990); (2) Sapotoideae, compreendendo as tribos Isonandreae, Mimusopeae e Sideroxyleae; (3) Chrysophylloideae, compreendendo todos os membros das tribos Omphalocarpeae e Chrysophylleae mais o gênero *Diploon*.

Dentre as três subfamílias propostas por Swenson & Anderberg (2005), Chrysophylloideae é a melhor representada nos Neotrópicos. De acordo com esses autores, esse clado apresenta forte suporte, mas as relações internas de seus táxons continuam mal resolvidas. Além disso, muitos dos gêneros definidos por Pennington (1990) vêm sendo apontados como para- ou polifiléticos (Swenson et al., 2008; Faria et al., in prep.). O gênero *Pradosia,* em contrapartida, é monofilético quando excluída a espécie africana *Pradosia spinosa* (Ewango & Breteler, 2001), erroneamente descrita como uma das espécies do gênero. Uma única sinapomorfia sustenta a monofilia de *Pradosia*: o fruto do tipo drupáceo, ao contrário da baga, que é encontrada nos demais espécies de Chrysophylloideae (Pennington 1990, Swenson et al., 2008, Terra-Araujo et al., 2012a, 2013). Entretanto, pouquíssimas espécies de *Pradosia* foram amostradas em todos esses trabalhos, sendo necessário um estudo mais aprofundados, e com um maior número de táxons e caracteres para obtenção de resultados mais consistentes.

Pradosia inclui 26 espécies principalmente distribuídas na América do Sul, e pertence a uma linhagem que muito provavelmente colonizou os Neotrópicos durante o Paleoceno, ~ 59 MA (Pennington, 1990, 1991; Anderberg and Swenson, 2003; Swenson and Anderberg, 2005; Swenson et al., 2008; Bartish et al., 2011). As espécies de *Pradosia* podem ser encontradas em uma variedade de ambientes, incluindo florestas úmidas ou decíduas na Amazônia, costa Atlântica Brasileira e Andes (Pennington 1991; Alves-Araújo & Alves 2012; Terra-Araujo et al., 2012b, 2013), crescendo sobre solos oligotróficos e arenosos (campina, campinaranas e restingas), solos argilosos ou ainda, em florestas periodicamente inundadas ou sujeitas a inundação (Pennington, 1990). A região Amazônica seguida pela costa Atlântica Brasileira compreendem os dois maiores centros de diversidade para Sapotaceae e para *Pradosia* (Pennington, 2006; Terra-Araujo et al., 2012a, 2013), com 17 espécies ocorrendo nessas regiões.

Morfologicamente, *Pradosia* é facilmente distinguida dos demais gêneros da subfamília por um conjunto de caracteres que inclui: corola rotada, com tubo menor que o comprimento dos lóbulos da corola e ausência de estaminódios (caráter diagnóstico para o gênero); estames exsertos, com filletes bem desenvolvidos e geniculados no ápice e fruto drupáceo com endocarpo parcialmente transparente e cartilaginoso (Pennington, 1990; Terra-Araujo et al., 2012a, 2013).

A mais recente revisão taxonômica de *Pradosia* foi realizada por Pennington (1990). Entretanto, ao longo dos últimos 20 anos, aproximadamente metade das espécies do gênero se manteve pobremente amostrada, conhecida apenas pela coleção tipo, sem frutos e/ ou informações sobre seu local de coleta. Além disso, a ausência de coletas recentes repercutiu na inclusão de três espécies na IUCN Red List (2013) como espécies extintas e outras oito como espécies em risco de extinção ou vulneráveis.

Organização da tese

Esta tese está organizada em três capítulos. O primeiro apresenta uma hipótese filogenética para *Pradosia*, seguida pela reconstrução de sua história evolutiva, com estimativa dos eventos de divergência dentro do gênero, e reconstrução da evolução de alguns caracteres morfológicos e de hábitat. O segundo apresenta as novas espécies de *Pradosia,* descobertas e descritas durante o desenvolvimento do presente trabalho. No terceiro capítulo é apresentada uma sinopse para o gênero, novos sinônimos, revisão da distribuição geográfica das espécies, uma nova chave de identificação seguida por uma curta descrição morfológica, observações de campo e listagem de material examinado em coleções botânicas.

CAPÍTULO 1

Terra-Araujo, M. H., Vicentini, A., Faria A. D., Nylinder, S. and Swenson, U. Phylogeny and historical biogeography of Neotropical *Pradosia* (Sapotaceae, Chrysophylloideae). Manuscrito formatado para *Molecular Phylogenetics and Evolution.*

Phylogeny and historical biogeography of Neotropical *Pradosia* (Sapotaceae, Chrysophylloideae)

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ABSTRACT

The subfamily Chrysophylloideae (Sapotaceae) represents a major component of Neotropical rainforests, both in terms of species richness and abundance. Recent phylogenetic studies of the subfamily have redefined genera and their relationships, but species-level studies reconstructing the evolutionary history of such high diversity are still lacking. The Neotropical genus *Pradosia* is believed to be monophyletic and it includes 26 species. Here we reconstruct the phylogenetic relationships of *Pradosia* using two nuclear markers (ITS, ETS), and use the resulting phylogenetic hypothesis to infer the generic biogeography, explore the evolution of morphological characters, and habitat preferences. Both parsimony and Bayesian inference were used to estimate phylogenetic relationships among 21 of the 26 known species. The two nuclear markers were largely congruent and produced a phylogeny where most relationships were strongly supported. We found that *Pradosia* is monophyletic in its current circumscription and three clades are readily distinguished with morphological characters. In addition, geography and habitat preference appear to be very important for groups and even species recognition. Our dated phylogeny suggests that *Pradosia* originated in Early Oligocene in the Amazon region and reached the Brazilian Atlantic coast ~ 24.9 Ma, followed by an expansion of the genus from the Amazon region to the northeast of South America in the Oligocene, with three independent recolonization events of the Brazilian Atlantic coast region during the Miocene-Pliocene. The association between habitat and species of *Pradosia* indicate multiple transitions from an ancestor growing in white-sand forest to forest on clayish soils, and six reversals, one from rainforest to dry mountain forest and a single colonization of savannas in Central Brazil associated with the evolution of a geoxylic habit. This indicates that shift in the ancestral ecology are more common than previously suggested and has played an important role in the speciation process of *Pradosia*.

key words: Neotropics, Sapotaceae, molecular dating, Tertiary, Amazon, Atlantic forest.

1. Introduction

Neotropical rainforests have a higher plant species diversity than any other place on Earth (Richardson et al., 2001; Antonelli and Sanmartín, 2011; Baraloto et al., 2012; Fouquet et al., 2012b). The Amazon region may contain approximately 15.000 species of trees (Baraloto et al., 2012), and more than 250 species of trees may be found in just one hectare in Central Amazon (Oliveira and Nelson, 2001). However, the evolutionary history of such high diversity in flowering plants remains poorly understood, particularly because there are still few species-level phylogenetic studies for the Amazonian flora (Pennington et al., 2006; Hopkins, 2007; Fiaschi and Pirani, 2009; Hoorn et al., 2010).

The plant family Sapotaceae is widely distributed in the tropics (Bartish et al., 2005; Swenson et al., 2008a,b) and is an important component of rainforests of South America (ter Steege et al., 2000). In a single hectare of lowland forest in Central Amazon, near Manaus, one may find around 44 trees (DBH > 10 cm) of 23 different species of Sapotaceae, being one of the most abundant and species-rich families in these forests (Milliken, 1998; Oliveira and Daly, 1999; Oliveira and Nelson, 2001). However, classification of Sapotaceae has been notoriously difficult and different systems have been proposed (Lam, 1939; Baehni, 1938, 1965; Aubréville, 1964; Pennington, 1990, 1991), leading to unnatural and inconvenient classifications, mainly due to high degree of morphological homoplasy (Swenson and Anderberg, 2005; Swenson et al., 2008a,b). On top of that, generic and specific circumscriptions are prone to large uncertainties (Terra-Araujo et al., 2012b; Gomes et al., 2013). Furthermore, previous conservation assessments have suggested that many species of Neotropical Sapotaceae are extinct, threatened to extinction, or endangered (IUCN Red List, 2013).

The Sapotaceae of the Neotropics were revised by Pennington (1990), but over the last century, the number of described species for the Neotropics has increased significantly (Pennington, 2006; Alves-Araújo and Alves, 2011, 2012; Morales, 2012; Terra-Araujo 2012a, 2013). Most of these additions belong to the subfamily Chrysophylloideae (Swenson and Anderberg, 2005), but the relationships among the groups in this subfamily are still poorly understood, and some of the genera defined by Pennington (1990) are polyphyletic in their current circumscription (Swenson et al., 2008a). Recent efforts have increased the number of taxa and molecular markers, which have confirmed that the larger genera *Pouteria* and *Chrysophyllum* are indeed unnatural assemblages (Faria et al., in prep.). The genus *Pradosia* (Fig. 1), on the other hand, is supported as monophyletic by these studies, excluding the recently described species *Pradosia spinosa* from Africa (Ewango and Breteler, 2001). A single synapomorphy supports the monophyly of *Pradosia*: a drupaceous fruit with a thin cartilaginous endocarp (Fig. 1L–M; Terra-Araujo et al., 2013), unlike the berry that is found in the rest of Chrysophylloideae (Swenson and Anderberg, 2005; Swenson et al., 2008a). However, these studies only included a few species of *Pradosia*. Given the fact that previous generic limits across the subfamily usually do correspond to natural groups, the monophyly of *Pradosia* requires a rigorous test with a broader taxon sampling.

Pradosia comprises 26 species that vary in habit from geoxylic shrubs to medium-sized and large trees (Fig. 1A). The genus is confined to South America, one of which also extends into Panama and Costa Rica (Pennington, 1991). Species are distributed across a wide variety of habitats, including savannas and evergreen to deciduous forests in the Amazon region, the Brazilian Atlantic coast, and the Andes. The Amazon and Atlantic coast are the two major centres of diversity for Sapotaceae and especially for *Pradosia* (Pennington, 1990; Alves-Araújo and Alves, 2011; Terra-Araujo et al., 2013), where 80% of the species occur. The biogeographical connections between these regions are still poorly understood and, to date, only a handful studies have estimated the divergence time between taxa from these regions, finding that organisms in the two areas have been isolated from each other for tens of million years (Vicentini, 2007; Fiaschi and Pirani, 2009; Pellegrino et al., 2011; Fouquet et al., 2012a,b). Furthermore, *Pradosia* includes species inhabiting nutrient-poor white-sand forests, others that are restricted to forests on clay, and yet others that occur in periodically flooded forests. This is an interesting abiotic distribution since studies have proposed that habitat diversity in the Amazon contributes to plant species diversification (Levin, 2004; Fine et al., 2005), however, this has never been explored in Sapotaceae.

The goal of the present study was to produce a phylogenetic hypothesis for *Pradosia* using molecular data (ITS and ETS), and to use this phylogenetic framework to reconstruct the evolutionary history of the genus. We first assessed support and congruence among these datasets. We then estimated, based on a concatenated dataset, a phylogeny, divergence times, and the biogeography of the genus. The resulting phylogenetic tree was used as the basis for reconstructing the evolution of some morphological traits that have been considered useful in distinguishing species within the genus. In addition, we investigated the evolution of habitat preference to the species.

2. Material and methods

2.1. Taxon sampling

This study was based on a taxon sample of 18 of the 23 species of *Pradosia* recognized by Pennington (1990), plus three recently described species (Alves-Araújo and Alves, 2012; Terra-Araujo, 2012a, 2013). Ten of the 21 species were represented by two or more accessions (i.e. *P. atroviolacea*, *P. cochlearia, P. decipiens*, *P. granulosa*, *P. kuhlmannii*, *P. lactescens*, *P. ptychandra*, *P. restingae*, *P. schomburgkiana* and *P. verrucosa*). We opted for sampling accessions from distant geographic locations for widespread taxa. Material of four species was unavailable, including *P. argentea* and *P. glaziovii,* two narrow endemics know only from the type collections with doubtful collection sites dating back 100 and 180 years, respectively, and *P. beardii* and *P. huberi* for which DNA samples were not obtained. We chose an outgroup based on previous phylogenetic findings that the putative closest relatives of *Pradosia* is *Chromolucuma*, *Micropholis* or *Pouteria* (Swenson et al., 2008a) and all taxa, voucher information, and accession numbers are found in Appendix 1.

2.2. DNA sequencing and alignment

DNA was extracted from ca. 20 mg of silica dried leaf material for 41 accessions, and from seven herbarium specimens. Extractions were obtained using the Qiagen DNeasy tissue leasy kit using the standard protocol, with an additional elution for old herbarium material. Vouchers were deposited in herbaria of the Instituto Nacional de Pesquisas da Amazônia (INPA), the New York Botanical Garden (NY) and the Swedish Museum of Natural History (S). We also used 23 previously published sequences (Swenson et al., 2008a).

We produced molecular sequence data for two different nuclear regions: the internal transcribed spacer (ITS) and the external transcribed spacer (ETS). We selected these markers because they have proven to be useful for phylogenetic inference in Sapotaceae (Bartish et al., 2005; Swenson et al., 2008a,b, 2013). The ITS consisted of 18SF and 26RN rDNA. Primers 18SF and 26SR, developed by Rydin et al. (2004), were used for amplification and sequencing of this marker (for further details of amplification, see Bartish et al., 2005). The ETS fragments were amplified using the primers 18S-ETS (Baldwin and Markos, 1998), Ast-1 and Ast-8 (Markos and Baldwin, 2001), and Sap-1 (Swenson et al., 2008b), a primer that partially overlaps Ast-1. Marker amplification was conducted by standard polymerase chain reaction (PCR) and the amplifications were carried out in a 25 μl reaction mixture using GE beads Ready-To-Go prepared beads (GE Healthcare Bio-Sciences AB, Uppsala, Sweden). The PCR products were afterward purified with the ExoSap clean-up kit (Fermentas, St. Leon-Rot, Germany), and sequencing relied on Big Dye Terminator kits (Applied Biosystems, Foster City, CA, USA) and primers 18SF, 26SR, 18S, Ast-1, Ast-8, and Sap-1 for sequencing reactions. The reaction was analyzed on an ABI 3730 Capillary Electrophoresis Genetic Analyzer with ABI BigDye Terminator v3.1 Cycle Sequencing chemistry (Applied Biosystems Inc., Foster City, CA). The sequences were assembled using the Staden software packages Pregap4 and Gap4 (Staden et al., 1998).

Alignments were performed in MEGA vs. 5.05, using MUSCLE (Edgar, 2004) and minor manual adjustments were made to the alignment using MESQUITE vs. 2.75

(Maddison and Maddison, 2011). One region of ITS of 45 base pairs was rich in gaps, ambiguously aligned, and subsequently excluded from all analyses.

Each gene partition was tested for the best-fit substitution model using jModelTest 0.1.1 (Posada, 2008) under the Akaike Information Criterion (AIC; Akaike, 1974). Estimated parameters values and log-likelihood scores for the different models were calculated based on three schemes of model substitution and ML tree. The best fit model for ITS was TN93, whereas the HKY model was the best fit for ETS. Unambiguous gaps were coded as additional binary characters following the method of Simmons and Ochoterena (2000), treated as a separate partition, and analyzed under a simple substitution model.

2.3. Node calibration

To estimate the divergence times within *Pradosia* we used the same fossils used by Bartish et al. (2011) to infer divergence times in Chrysophylloideae. *Psilatricolporites maculosus* is a microfossil that appears in a sequence of sediments from the Palaeocene/ Eocene transition (~ 55 Ma) in the Maracaibo Basin of Western Venezuela (the oldest reported dated representative of Chrysophylloideae from the New World), and from the Early Eocene in Colombia (Rull, 2000; Jaramillo and Dilcher, 2001). The second fossil is a leaf from the Cerrejón Formation in Colombia (Wing et al., 2009), dated to the Late Palaeocene (~ 58 Ma) and is suggested to belong to Sapotaceae. Since generic limits in Neotropical Sapotaceae are still largely unclear (Swenson et al., 2008a), but all taxa in the area, together with some African species, constitute a monophyletic group (Bartish et al., 2011), we believe the safest calibration point is at the root with an “offset” of 53.8 Ma, reflecting the range estimates (59 +/- 5.2 Ma) estimated of Bartish et al. (2011). No other internal calibration is presently possible.

2.4. Operational areas

In order to obtain full distributions of each taxon, herbaria material was used in Brazil (ALCB, CEPEC, CVRD, HRB, INPA, IPA, MBML, MG, PEUFR, RB, SP, UEFS), USA (CA, PH, NY, US), and Europe (S). A geo-reference database was assembled from label information of 251 specimens, which then was used to generate distribution maps by using the MAPS packages in R program (R Core Team, 2012). This enabled the identification of six main areas of distribution: (1) Amazon basin, (2) Brazilian Atlantic coast, (3) Central Brazil–Eastern Paraguay, (4) Ecuador–Peru, (5) Chocó region, and (6) North South America–Panama–Costa Rica. These areas are well delimited geographically as well as ecologically and do not share more than one species (i.e. *P. atroviolacea*; found both in the Amazon region and in Panama and Costa Rica). Species in the Amazon basin and in the Brazilian Atlantic coast (from Pernambuco in the north to the Paraná State in the south) occur almost exclusively in wet lowland forests, but a northeast–southwest drier climatic barrier, the Cerrado-Caatinga biome, separates these areas. Two endemic species (i.e. *P. montana* and *P. cuatrecasasii*) are found in Ecuador–Peru and in Pacific coast of Colombia (Chocó region) respectively: (1) *P. montana* occurs in tropical deciduous forests in the Pacific coast of Western Ecuador and Northwestern Peru, an important zone of endemism (Linares-Palomino et al., 2010); (2) *P. cuatrecasasii* is only known from wet lowland forests, at low altitudes on the Chocó, a region that is isolated from the Amazon by the Western Cordillera of Colombia (Burnham and Graham, 1999; Frasier et al., 2008). Lastly, in the northern range of the distribution, the area of South America–Panama–Costa Rica, species of *Pradosia* occur in wet montane or deciduous forests. This area is separated from the Amazon by a dry climatic zone similar to the Cerrado (Llanos) and by the Eastern cordillera of the Andes in Colombia and reaching an altitude of 2000 m above the sea level, and from the Ecuador–Peruvian area by the North Andes.

2.5. Phylogenetic analyses

Parsimony Jackknife (JK) analyses were conducted in PAUP 4.0 (Swofford, 2003) using CIPRES Science Gateway cluster (Miller et al., 2010) and Bayesian inference (BI) (Rannala and Yang, 1996; Yang and Rannala, 1997) in BEAST 1.7.5 (Drummond and Rambaut, 2007). The parsimony settings were: heuristic search with 1000 replicates of random stepwise addition, holding 20 trees at each replicate, tree bisection reconnection branch swapping (TBR), and equal weighting of all characters. Support values were obtained with Jackknife analysis (Farris et al., 1996) as implemented in PAUP by using the same settings as above, but with 100 replicates. BEAST analyses relied on the lognormal relaxed clock model on substitution rates for each locus together with four rate categories, gamma distribution, and a Yule prior (Yule, 1925). The Monte Carlo Markov chains (MCMC) were set to run for 20 million generations, logging tree parameters every 5000 generations. Chain mixing and convergence were checked in Tracer v.1.5 (Rambaut and Drummond, 2007) to confirm that the estimated sample sizes (ESS) values for all parameters were larger than 200. A maximum clade credibility tree was calculated in TreeAnnotator (also part of the BEAST package). The summary tree with 95% highest posterior density (HPD) intervals of divergence time estimates were prepared in FigTree v.1.3.1. (Rambaut, 2009).

Phylogenetic analyses were conducted for each molecular marker as well as for ITS and ETS concatenated in a single data matrix. In order to discover incongruence between sets of characters (partitions), an ILD tests, as implemented in PAUP, and topological comparisons using the SH (Shimodaira and Hasegawa, 1999), and AU tests (Shimodaira, 2002) as implemented in CONSEL (Shimodaira and Hasegawa, 2001) were performed. For each dataset we compared for significant differences in likelihood scores between the dataset majority rule (MR) consensus tree and the MR consensus trees produced by the other datasets. To test the congruence between markers, analyses were conducted only with accessions shared by both markers. Some additional topological comparisons were conducted to test specific hypotheses (e.g. species monophyly), by comparing trees produced by unconstrained with constrained phylogenetic analyses.

2.6. Divergence time, area, habitat and morphological character reconstruction

To generate time-calibrated maximum clade credibility (MCC) trees, produce a biogeographical hypothesis, reconstruct the ancestral states of the habitat and morphology, aligned matrices were concatenated in BEAUti 1.7.5 (part of the BEAST package), as an output xml-file to be executed in BEAST. The analyses used the same parameters as defined above to BI, but using the BEAGLE library (Ayres et al., 2012) and symmetric matrix for transition rates. For ancestral areas, we built a matrix of species by area, containing presences and absences of species in the six operational areas defined above. To reconstruct the ancestral states for habitat and morphology a presence/ absent matrix of five morphological characters and habitat was assembled using our own field observations combined with published data (Pennington, 1990, 1991, 2006). The five morphological characters are: bark properties, midvein characteristics, distribution of fascicles, size of flower, and the color of the flowers (Table 1). Five habitat classes reflect the range of different ecological and vegetation adaptations. In several species of *Pradosia* the inner bark has a sweet taste, and some species are indeed locally known as *casca-doce* ("sweet-bark"), a feature characterized in character one. Character (2) scores the midvein whether it is flat/ raised or sunken. When sunken, it may be below the level of the adjacent lamina. Character (3) distinguish whether fascicles of flowers appear along the branches (ramiflorous) on old wood below the leaves without any adjacent leaf scar; along the trunk (cauliflorous); axillary; or at the apices of the branches. Character (4) is the corolla length, arbitrary set to 4 mm to distinguish between small and large flowered species. Finally, character (5) classifies the color of the corolla.

3. Results

3.1. Phylogeneric analyses

The ITS data set included 862 bp, of which 529 were constant, 145 parsimony informative, and 24 coded indels. The ETS data set included 386 bp, of which 174 were constant, 114 parsimony informative, and five coded indels. *Pradosia* was supported as monophyletic by the individual phylogenetic analyses of both the ETS and the ITS datasets. Within *Pradosia*, analyses of the separate molecular markers recovered similar trees, but they were incongruent in the placement of *P. cochlearia* MHT855, *P. restingae* JJ5588 and *P. verrucosa* MHT780 (Appendix 2). In the ETS tree the accession *P. cochlearia* was placed in a poorly supported grade with all other congeners, except *P.*

longipedicelata. *P. verrucosa* as sister to *P. lactescens,* and *P. restingae* nested in a clade with other four species with weak support. In contrast, in the ITS tree *P. cochlearia* was recovered with strong support as sister to *P. schomburgkiana,* while the placements of the other two species were inverted. When these three accessions were excluded from the analyses, the topological differences between the markers was not significant in likelihood scores according to both the SH and the AU tests ($P = 0.21$). The precise position of *P. cochlearia* MHT855, *P. restingae* JJ5588 and *P. verrucosa* MHT780 within *Pradosia* was uncertain, with different positions being found depending on the nuclear marker. However, the placement of these assessions in the ITS tree was more in agreement with morphology (see discussion). We have, therefore, focused on the ITS tree, which seems the best indication of species relationships, and opted to build our molecular matrix and perform our analyses on a combined ITS-ETS and indels, excluding the accessions *P. cochlearia* MHT855, *P. restingae* JJ5588 and *P. verrucosa* MHT780 from the ETS dataset for a total-evidence phylogenetic hypothesis.

Analyses of the combined ITS+ETS+indels dataset using JK and BI recovered similar tree topologies (Fig. 2). *Pradosia* was strongly supported (1/ 99) as monophyletic and *P. longipedicellata* appeared as sister to all other species of *Pradosia.* The genus was further subdivided into three main lineages, which were strongly supported and correlated with morphological, geographical and ecological characters. The first clade, here named "Montane", includes species that have a narrow distribution in the northeastern of Colombia, north of Venezuela and in Ecuador (e.g. *Pradosia caracasana*, *P. colombiana* and *P. montana* respectively). The second clade, here named "Sweet-bark", included almost exclusively species from the Amazon region, except for *P. kuhlmannii* that occurs along the Brazilian Atlantic coast. Within the Sweet-bark clade, the relationships between species were unresolved, and the widespread (throughout the Amazon region) and morphological variable species *Pradosia schomburgkiana* appeared as paraphyletic. However, the combined dataset did not reject a constrained monophyletic *P. schomburgkiana* (both SH and AU tests with $P = 0.62$). The third clade, here named "Red-flowers", included species from the Amazon region (eight species), the Brazilian

Atlantic coast (four species), the savannas of Central Brazil (*P. brevipes*), and the Chocó region on the Pacific Coast in Colombia (*P. cuatrecasasii*). Eight of the ten species with more than one accession appeared as monophyletic in this tree, except for *Pradosia atroviolacea* and *P. schomburgkiana*.

3.2. Divergence time estimation

The stem node of *Pradosia* was dated to the Late Eocene/ Early Oligocene (31.4 +/- 9 Ma), and *Pradosia longipedicellata*, an endemic and morphologically unique species from the Brazilian Atlantic coast in Ilhéus, Southern Bahia, appeared as sister to rest of the genus (Fig. 3). The divergence between *P. longipedicellata* and the ancestral of the rest of the genus was estimated to the Medium/ Late Oligocene. Subsequent speciation events within the Sweet-bark and Red-flowers clades were estimated to have occurred in the Miocene/ Pliocene. All speciation events were older than ~ 2.0 Ma and the speciation was quite constant throughout the history of the genus.

3.3. Biogeographical reconstruction

The Bayesian Inference indicated that the most recent common ancestor of *Pradosia* was distributed in the Amazon region, and may have reached the Brazilian Atlantic coast for the first time ~ 31.4 Ma ago, representing the divergence of *P. longipedicellata* from the common ancestor of the remaining species of *Pradosia* (Fig 3). This event is followed by an expansion of the genus from the Amazon region to the Northern and Northwestern South America, in Colombia and Venezuela, during the Late Eocene/ Oligocene ~ 24.9 +/- 7 Ma ago, as species endemic to this region form a clade. This lineage colonized afterwards the dry forests of the Pacific coast of Ecuador (~ 9.8 Ma ago). The reconstruction further indicated three additional dispersal events from the Amazon to the Atlantic coast of Brazil, two of which, may have occurred during the same period around 6 Ma ago. The last event was predated by a dispersal event to Central Brazil, ca. 2.1 Ma. A second dispersal event from the Amazon to the northwest of South

America also occurred after 3.5 Ma, represented by divergence of *P. cuatrecasasii,* which is the only species occurring in the Chocó region in Colombia.

3.4. Evolution of habitat preference

Reconstruction of habitat preference indicated that the ancestral habitat of *Pradosia* was evergreen forests on white-sand nutrient-poor soils, with one evolution to deciduous forests (the Montana clade, i.e., *P. colombiana* and *P. montana*), another to savannas (*P. brevipes*), and at least six independent shifts to evergreen forests on clayish soils (Fig. 4F). Within the Sweet-bark clade the majority of the species occurs in white-sand forests, except for *P. kuhlmannii,* which occurs in forests on clayish soils along the Atlantic coast. Otherwise, the Red-flowers clade includes species occurring on both types of soils throughout the Amazon region, Brazilian Atlantic coast and in Central Brazil.

3.5. Morphological evolution and apomorphies

Bayesian analyses indicated that sweet bark (character 1) is a derived condition within the genus and appeared to have evolved at least four times independently (Fig. 4A). Another character defining clades refers to the position of the midvein in a cross-section of the leaf blade: a flat/ raised midvein is the ancestral condition, with two shifts to sunken midvein (Fig. 4B). In *Pradosia*, there is also variation in flower placement, which may be ramiflorous, axillary, cauliflorous or terminal (Fig. 1D–F). Flowers born at the apices of the branches are present only in *P. longipedicellata*, which is sister to rest of the genus (Fig. 4C). This node was reconstructed as having fascicles along the branches below the leaves (ramiflorous), which is shared by most species of *Pradosia*. The two other conditions, flowers fascicles born along the trunk (cauliflorous), and flowers born at the leaf axils, both evolved at least twice from ramiflorous ancestors. Lastly, flowers with large corollas (> 4 mm) were reconstructed as the ancestral condition within the genus, with at least two independent events of flower reduction (corollas < 4 mm; Fig. 4D). Flower color is also conserved within *Pradosia* (Fig. 1G–I): white flowers is only present in *P. longipedicellata*, following a transition to green flowers and a single origin of reddish flowers, and at least three reversals to green flowers (Fig. 4E).

4. Discussion

4.1. Phylogenetic analyses

Our results corroborate previous studies (Swenson et al., 2008a; Bartish et al., 2011; Faria et al., in prep.) indicating that *Pradosia* forms a well-supported clade, which is sister to some species of non-monophyletic *Pouteria* (Fig. 2). A single morphological character, the drupaceous fruit, also supports the monophyly of *Pradosia* (Swenson et al., 2008a; Terra-Araujo et al., 2012a, 2013) (Fig. 1L–M).

Ten of the 21 species of *Pradosia* included in our analyses by two or more accessions. The purpose of this was to investigate if species with wide geographic distributions were monophyletic, or to clarify the species status of some closely related species and infra specific taxa. We discuss these with reference to the phylogenetic tree in Figure 2. In the Sweet-bark clade, two accessions of *P. cochlearia, P. decipiens, P. kuhlmannii,* and four of *P. schomburgkiana* were included. The first three species, represented by multiple accessions (e.g. *P. cochlearia*, *P. decipiens* and *P. kuhlmannii*) appeared as monophyletic. Because multiple accessions were from distant geographical locations, we considered these as unproblematic species. In contrast, *P. schomburgkiana* appeared as paraphyletic, but the monophyly of this species was not rejected by the combined ITS-ETS dataset. *Pradosia schomburgkiana* is widely distributed in the Amazon region, and includes two recognized subspecies that are sympatric in the Serra do Aracá region, Amazonas State, Brazil. In the past century, Ducke (1942, 1953) described several species morphologically similar to *P. schomburgkiana* from Central and Eastern Amazon. Pennington (1990), later synonymized these species, but the morphological variation within *P. schomburgkiana* induced the author to split this species into two subspecies (*P. schombugkiana* subsp. *sericea* and *P. schomburgkiana* subsp. *schomburgkiana*), which are currently recognized by the presence/ absence of a dense indumentum on the lower leaf surface respectivaly. The two subspecies were here included (*P. schombugkiana* subsp. *schomburgkiana*: FMC1577, FMC541 and DR05/1829; *P. schombugkiana* subsp. *sericea*: and FMC184), but there was no phylogenetic signal or correlation with geography or morphology. This species complex requires closer examination and a wider sampling to understand how many species it contains and their limits.

Within the Red-flowers clade, *Pradosia atroviolacea* is paraphyletic because of *P. grisebachii* – the former is a widespread species distributed from Western Amazon to Costa Rica and Panama, and is morphologically very similar to the later (which is known to be distributed in Trinidad-Tobago and Venezuela), being the only two known species having petiolar scales and flower fascicles emerging from the branches. *Pradosia atroviolacea* has been distinguished from *P. grisebachii* by its glabrous leaves, many-flowered fascicles and longer pedicels (Pennington, 1990). However, these morphological distinctions were not supported by the additional specimens we examined and the morphological variation overlap. Therefore, it seems clear that there is no support for the recognition of *P. atroviolaceae* and *P. grisebachii* as different species.

4.2. Biogeography and habitat evolution

In Chrysophylloideae, the age and ancestral area of the earliest diversification was during the Cretaceous, in Africa, around 73 to 83 Ma (Bartish et al., 2011). The ancestor of the subfamily colonized South America through a dispersal event during the Early Paleocene (~ 59 Ma), and was already very species-rich and widespread during the Eocene (Burnham and Johnson, 2004; Wing et al., 2009; Jamarillo et al., 2010).

Age estimates indicate that the ancestor of *Pradosia* started to diversify in the Early Oligocene (~ 31.4 Ma) in the Amazon region, where 11 of the 26 species occur today. The genus is mostly confined to lowland rainforests (Pennington, 1990). However, an initial split (~ 22.0 Ma) of this lineage led to colonization of high-altitudes, and dry areas in Northern South America (Fig. 4F). This was followed by the diversification of at least two species, one restricted to deciduous forests in Ecuador and Peru (*P. montana*) and another distributed through the deciduous forests of northwestern Colombia and

Venezuela (*P. colombiana*). A third species (*P. caracasana*), also recolonized lowland montane rainforests from sea level to 1900 m altitude. Colonizations of high-altitudes in the Middle/ Late Miocene are strikingly coincident with the uplift of the Eastern Cordillera in the Northern Andes during the Miocene Climatic Optimum (MCO: ~ 15 Ma; see Antonelli et al., 2010; Hoorn et al., 2010). Therefore, these results are consistent with the hypothesis that the ancestor of the Montane clade may have in fact colonized high-altitudes when the climate was warmer.

Subsequent diversification events led to the occupation of white-sand nutrient-poor forests (see Sweet-bark clade). These island-like habitats (i.e., campina, campinarana and restinga forests) surrounded by tall rainforests are found scattered across the Guiana and Brazilian Shields, as well as throughout the Amazon region (Prance, 1996; Frasier et al., 2008). The soils of these forests differ markedly from those of their surroundings because of much less nutrients, lower pH and low hydric retention (Prance and Schubart, 1978; Anderson, 1981; Frasier et al., 2008). However, in spite of such extreme conditions six independent lineages of *Pradosia* colonized white-sand forests throughout the Amazon and Atlantic forests.

Evidence of a single colonization of white-sandy soils can be seen in the Sweet-bark clade, in which three species (*P. cochlearia, P. decipiens* and *P. schomburgkiana*) are sympatric near Manaus, Central Amazon. Many other transitions from white-sand to clayish forests (Fig. 4F; see clade Red-flowers) were observed across the evolution of *Pradosia*, and each transition seems to have implicated in speciation. Other studies on habitat specialization in the Protieae (Burseraceae) throughout the Peruvian Amazon (Fine et al., 2005) have yielded similar results. Their phylogenetic analyses indicated that association with soil types evolved independently multiple times, and therefore, played an important role in diversification (Fine et al., 2005; Fine et al., 2013).

Pradosia reached the Atlantic coast of Brazil by at least four independent events. The earliest (*Pradosia longipedicellata*) event was around the Middle Eocene/ Oligocene (~ 24.9) and three subsequents during the Late Miocene (*P. kuhlmannii*, *P. restingae* and *P. lactescens*), and Early Pliocene (*P. verrucosa*). Today, a northeast–southwest drier climatic barrier, in which the Cerrado+Caatinga biomes occur, separate the evergreen forests of the Atlantic coast from that of the Amazon. However, there are biological links between these areas, with disjunct distributions in several groups of plants and animals (Vicentini, 2007; Fiaschi and Pirani, 2009; Pellegrino et al., 2011; Fouquet et al., 2012a,b), which have been attributed to historical connections through the Cenozoic (Costa, 2003; Pellegrino et al., 2011; Fouquet et al., 2012a).This first arrival of *Pradosia* in the Atlantic coast coincides with the divergence times of two major clades of frogs distributed in Amazon and the Atlantic Forest (Fouquet et al., 2012a). Nevertheless, the two subsequents recolonization of the Atlantic coast occurred in Late Miocene and Pliocene match the arrival of some lineages of frogs, lizards, mammals (Costa, 2003; Pellegrino et al., 2011; Fouquet et al., 2012b), and also coincide with the pattern of recolonization by edaphic white-sand specialist genus *Pagamea,* Rubiaceae (Vicentini, 2007).

Some biogeographical routes connecting the Amazon and the Atlantic coast have been proposed (see Por, 1992): (1) through the Paraná river basin; (2) through the coast of Northeastern Brazil; and, (3), through gallery forests crossing the drier areas of Central Brazil. *P. kuhlmannii* (Northeastern Brazilian coast) is related with species from Northwestern and Central Amazon; *Pradosia lactescens* and *P. restingae* to species from North South America and Central-West Amazon; and *P. verrucosa* is more closely related to species from Central Brazil and Eastern Amazon. Given these relationships and distributions, *P. kuhlmannii* and *P. verrucosa,* appear to represent a migration route through Central Brazil. The ancestral of the clade *P. lactescens+P. restingae* may have migrated south through the Paraná basin. The divergence times visualized for *P. kuhlmannii* and *P. lactescens+P. restingae* during the Late Miocene (~ 6 Ma) matches a period when the climatic barrier between Amazon and the Atlantic coast may have been smaller (Hoorn et al., 2010), and such conditions may have allowed dispersal events between these two large blocks of rainforests. A single transition ~ 3.2 Ma ago from Amazon through the Central Brazil towards the Atlantic forest (clade *P. granulosa+P. brevipes+P. verrucosa*) resulted in the colonization of the Cerrado and afterwards the

Atlantic forest. It seems likely that the ancestor of this clade originally occurred in Northeastern Amazon and subsequently colonized the Cerrado (*P. brevipes*) and finally reached the Atlantic forest ~ 2.1 Ma ago (*P. verrucosa*). Nonetheless, the split between the Amazon and the Atlantic forest matches a period of brake-up of the connection through the Central Brazil-Atlantic coast. During the Early Pliocene the climate became progressively cooler favoring the replacement of forests by savannas in Central Brazil (Rosseti and Toledo, 2007). The adaptation to dry conditions of Central Brazil further involved a drastic change in the morphology of *P. brevipes*, which has a specialized subterranean habit (geoxylic).

There is a single colonization (*Pradosia cuatrecasasii*) of the Chocó region. This area in Colombia became isolated from Amazon in the early Miocene by the uplift of the Western Cordillera of Colombia, which led to the development of a distinctive flora, with a high number of endemic species (Burnham and Graham, 1999; Frasier et al., 2008). *P. cuatrecasasii* is a poorly known species that is associated with riverine systems and appears to be sister to *P. atroviolacea+P. grisebachi.* Their ancestor may have crossed the Andes into the Chocó region during the Middle Miocene some 6 Ma ago. Similar pattern and age estimate also coincide with *Pagamea* (Vicentini, 2007; see *Pagamea dudleyi*) and *Potalia*, Gentianaceae (Frasier et al., 2008; see *Potalia chocoensis*).

4.3. Morphological apomorphies

Bark traits are frequently used for recognizing tree species in the field in the neotropics (Pennington, 1990). However, for Sapotaceae there are few exclusive patterns. For example, a smooth bark of yellowish-gray color, sometimes with darker spots and sweet taste is only found within *Pradosia*, not found in any other genus of the Neotropical Sapotaceae (Fig. 1A–B). Ducke highlighted the sweet taste of the inner bark in *Pradosia*, and attributed it to the presence of glycyrrhizin (Ducke, 1942). Other studies also found flavonoids in the sweet bark these species (e.g., *Pradosia huberi*; not included in this study), which may be related to protection against injury (Medeiros et al., 2010). The ancestral reconstruction revealed that the sweet taste first appears in the Sweet-bark clade (followed by one reversion in *Pradosia decipiens*), and it evolved afterwards at least three different times in the Red-flowers clade (Fig. 4A). For Sapotaceae in general, the leaf venation patterns have provided many useful characters for the recognition of genera and species (Pennington, 1990, 1991). Venation patterns have been defined in relation to the primary (midvein), secondary, tertiary, and quaternary veins (ibid.). For Chrysophylloideae, patterns of secondary veins are homoplasious (Swenson et al., 2008a). This is not the case of the type of midvein in *Pradosia*. The mapping of this character onto the phylogeny indicated that a flat/ raised midvein on the adaxial surface is the ancestral state for the genus, and that this condition have soon changed to a sunken midvein in the Montane clade, but it was maintained in the Sweet-bark clade. The type of the leaf midvein thus permits distinguish the major clades within *Pradosia*.

The position of flower fascicles may be under strong selective pressure, as it may be related to pollinators (Warren et al., 1997). A simple fasciculate inflorescence is remarkably constant throughout the family (Pennington, 1990), but the position of the fascicle on the tree may vary. In *Pradosia*, fascicles attached along the branches and below the insertion of leaves (ramiflorous) predominate, followed by flowers clustered along the trunk (cauliflorous) (Fig. 4C). Ramiflory is a plesiomorphic trait in *Pradosia*, present in 80% of the species included in our study. On the other hand, cauliflory evolved at least three times. Flowers attached along the trunk is relatively unusual within the Neotropical Chrysophylloideae, having been documented in a few species of *Chrysophyllum* (two species), *Ecclinusa* (one species) and *Micropholis* (one species) (see Pennington, 1990). Some other published studies for Melastomataceae, Moraceae and Proteaceae (Michelangeli et al., 2004; Mast et al., 2008; Zerega et al., 2010) have documented similar patterns to those shown here, indicating multiple origins of cauliflory. Furthermore, results of these studies suggests that cauliflory is a synapomorphy for clades within these families, however this is not the case for Neotropical genera of Sapotaceae.

Floral characters are very important to distinguish closely related genera and species in Sapotaceae, but the problem is that when they are mapped onto the tree most of them are homoplasious (Swenson et al., 2008a,b). Flowers in Sapotaceae have a corolla that is partly sympetalous, comprising a tube and free corolla lobes (Pennington, 1990). Furthermore, the fused part may vary in length influencing the corolla shape. In *Pradosia*, a particular set of morphological features is distinctive from other genera in Chrysophylloidea (Swenson et al., 2008a). For example, in this genus, the flowers are frequently 5-merous, with rotate corolla, short tube, and lack of staminodes. The length of the corolla was highlighted by Pennington (1990) as useful for groups recognition and here it appears to be partiality consistent with his observations. Our analysis shows that a large corolla > 4 mm is plesiomorphic in *Pradosia*, followed by a reduction in flower size in the Montane and Sweet-bark clades, and with maintenance of the plesiomorphic condition in *P. decipiens* and in the Red-flowers clade (Fig. 4D). The color of the corolla is another useful feature that seems to define clades. Whitish flowers are only present in a single species, being greenish flowers are the ancestral condition for the other species (Fig. 4E). This change in flower color may be directly associated with changes in pollinators (Jones and Reithel, 2001; Rausher, 2008). Whitish flowers are frequently associated with nocturnal visitors, while greenish and reddish are associated with bees and vertebrates (Momose et al., 1998). In *Pradosia* the change to greenish flowers evolved twice, with a single change within the Montane and in the Red-flowers clades, followed by three reversions in the latter. Reddish flowers are restrict to Red-flowers clade and are present in 70 % of the species sampled. Therefore, the length of corolla and color appears to be an important character for group and even species recognition.

5. Conclusions

Our results confirm that *Pradosia* is monophyletic in its current circumscription and three clades are strongly supported and correlated with morphological, geographical and ecological characters. The analyses suggests that two species are non-monophyletic, although one of these (i.e. *P. atroviolacea* because of *P. grisebachii*) are morphologically similar, allopatric, form a strongly supported clade and, seems to belong to a single species. The resolution of the second species complexes (i.e. *P. schomburgkiana*), however, requires a closer examination and a broader sampling to understand how many species they contains and their limits. The biogeographic history of *Pradosia* implies that the ancestor of the genus seems to have originated in the Early Oligocene in the Amazon region, reaching the Atlantic coast ~ 24.9 Ma, followed by an expansion to the Northern South America and three independent recolonizations of the Brazilian Atlantic coast region during Miocene-Pliocene. This pattern in *Pradosia* is concordant with several studies of plants and animals whose limits are more or less coincident with those from *Pradosia.* Finally, when examining the association between habitat and species in *Pradosia,* we found multiple transitions from a white-sand forest ancestor to forests on clayish soils, dry montane forests and a single colonization of Cerrado in Central Brazil. This finding indicates that habitat transitions played an important role in the diversification of *Pradosia.*

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Table 1
Characters states used in the ancestral reconstruction of habitat and selected morphological traits of *Pradosia* (Sapotaceae, Chrysophylloideae).

Characters States

1. Bark properties: (0) sweet taste, (1) non-sweet taste
2. Leaf midvein on the adaxial surface: (0) flat/ raised, (1) sunken
3. Fascicles being: (0) ramiflorous, (1) axillary, (2) cauliflorous, (3) terminal
4. Length of corolla: (0) < 4 mm, (1) > 4 mm
5. Color of corolla: (0) whitish, (1) reddish, (2) greenish
6. Habitat: (0) deciduous forest, (1) tropical savanna, (2) tropical rainforest on sandy soil, (3) tropical rainforest on clayish soils, (4) tropical flooded forest.

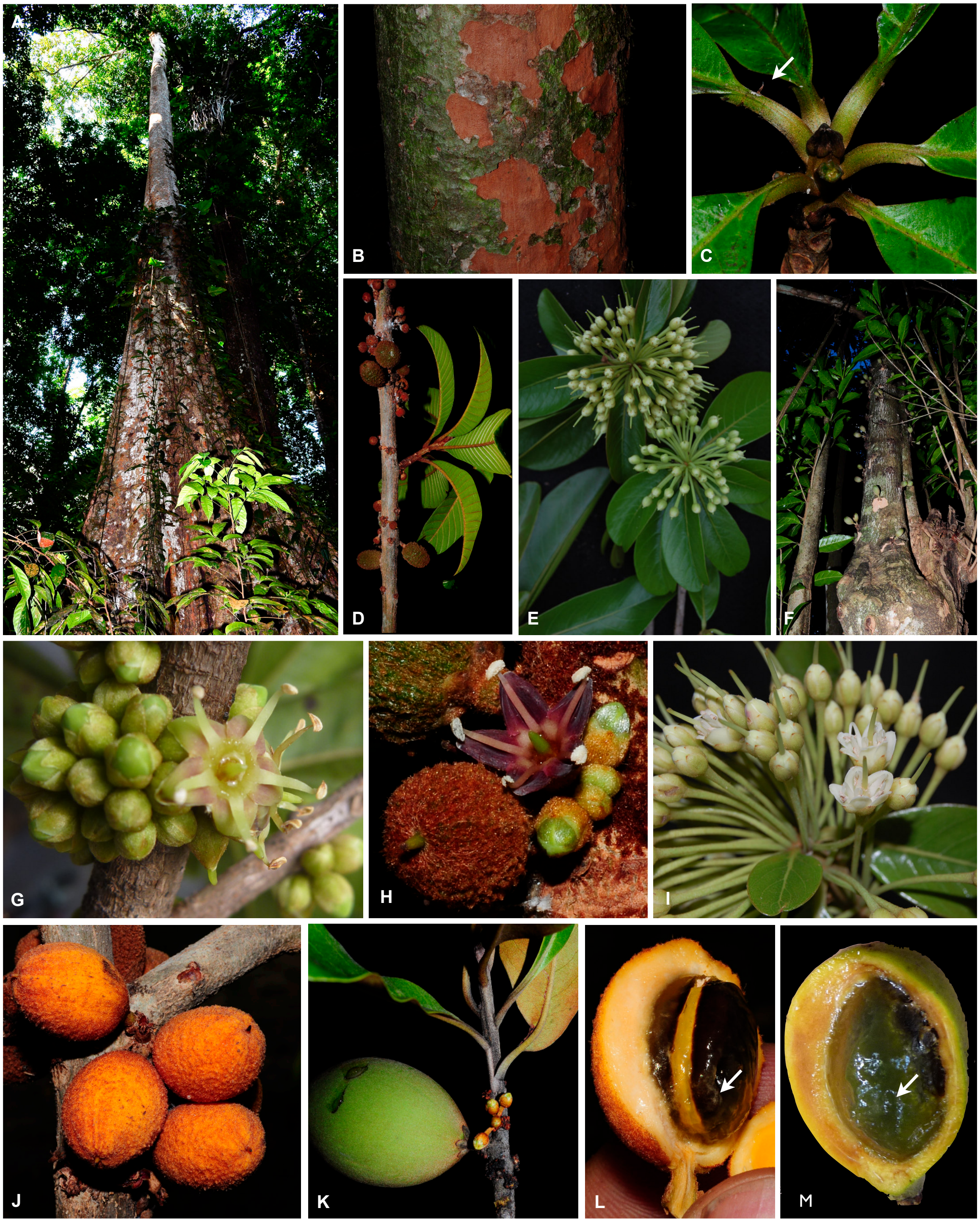


Fig. 1. Field images of *Pradosia* (Sapotaceae, Chrysophylloideae). (A) *P. cochlearia*, a canopy tree growing in rainforests of the Amazon region; (B) bark of *P. verticillata*, showing the smooth bark of greenish and brownish color, scaling in thin asymmetric plates leaving deep orange marks, a typical bark pattern of the genus; (C) Scales on the petiole of *P. lahoziana*; (D–F) fascicles of different species: (D) borne along the branches

below the leaves like in *P. granulosa*; (E) at the branch's apices, found in *P. longipedicellata*; (F) or along the trunk like in *P. lactescens*. (G–I) Rotate, open flowers, showing the variation in color; (G) *P. restingae*; (H) *P. granulosa*; (I) *P. longipedicellata*; (J) fruit of *P. granulosa* and (K) *P. cochlearia*; (L–M) transection of fruits showing the half-transparent cartilaginous endocarp in (L) *P. granulosa* and (M) *P. surinamensis.* Photos: Anderson Alves-Araújo (G), Ricardo I. Barbosa (M), Jomar Jardim (E, I), and Mário H. Terra-Araujo (A–D, F, H, J–L).

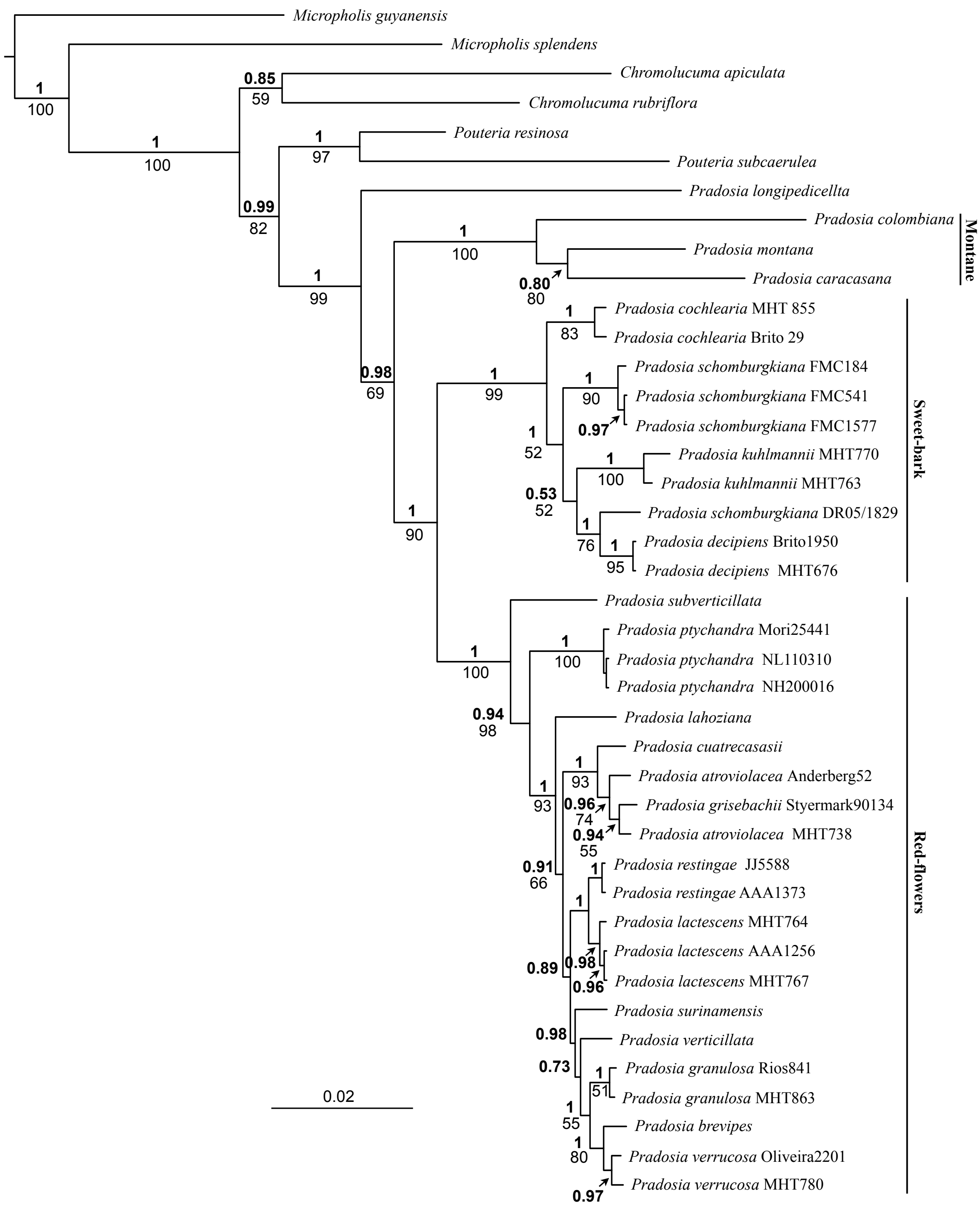


Fig. 2. Bayesian majority-rule consensus phylogram of *Pradosia* (Sapotaceae, Chrysophylloideae), with likelihood estimated branch lengths based on two concatenated nuclear markers (ITS and ETS). Numbers above (in bold) the branches indicate Posterior Probabilities (PP) and below Parsimony Jackknifing (JK) values. Branches with values below PP 0.70 and JK 50 are not indicated. The scale bar indicates the number of mutations per site.

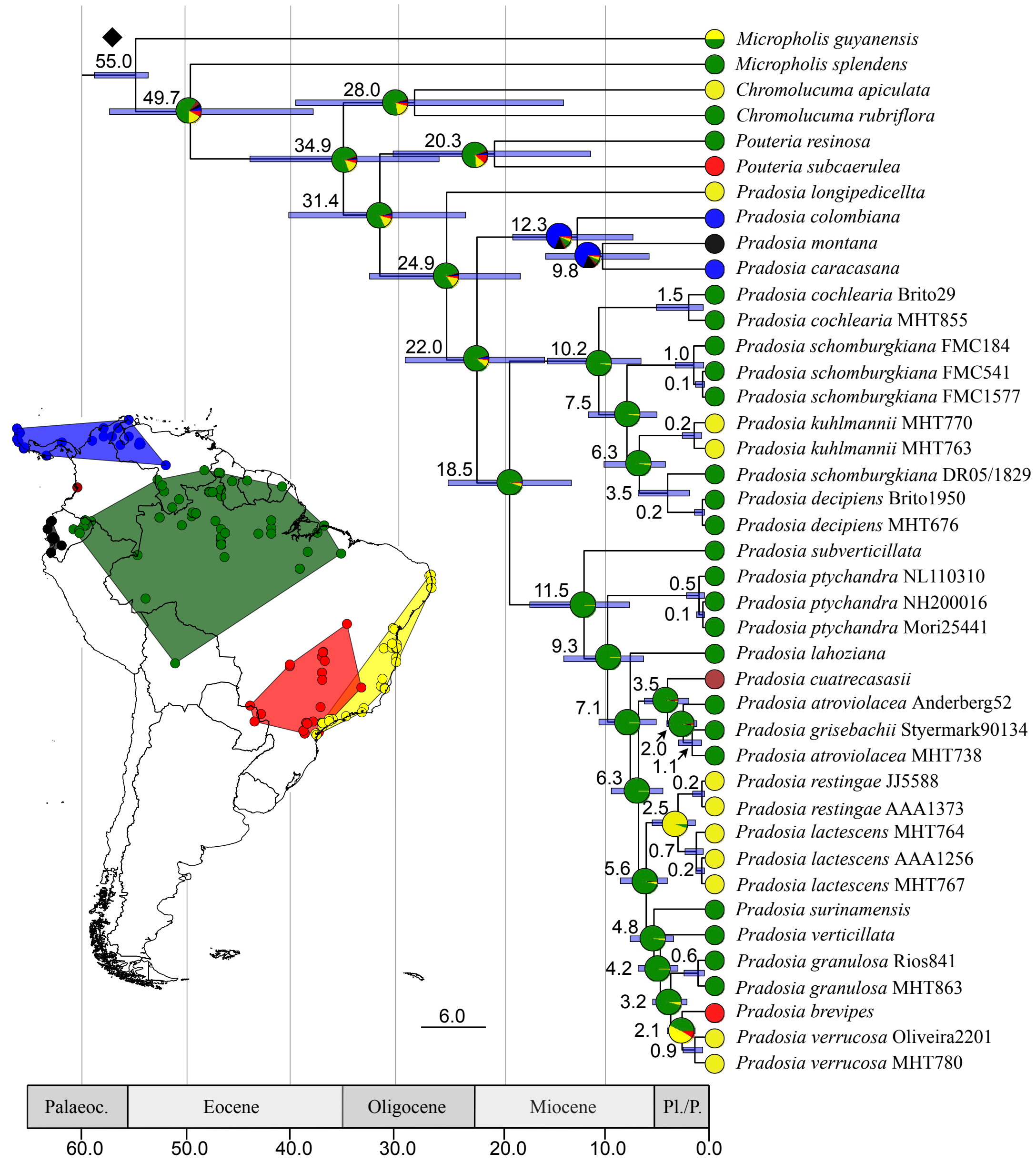


Fig. 3. Chronogram for *Pradosia* (Sapotaceae, Chrysophylloideae) obtained from a BEAST analysis using 58 Ma South America leaf fossil for calibration. Filled diamond indicate the callibration point. The node bars indicate 95% confidence intervals for age estimates. Numbers above branches indicate the mean ages. Pie charts at nodes represent relative frequencies of ancestral-area reconstructions obtained with BEAST, using BEAGLE library. The current species distributions are shown preceding the species names by six color coding that correspond with the map. The geological time scale is in million years, adapted from Walker and Geissman (2009). Abbreviations: Pl./ P. = Pliocene/ Pleistocene.

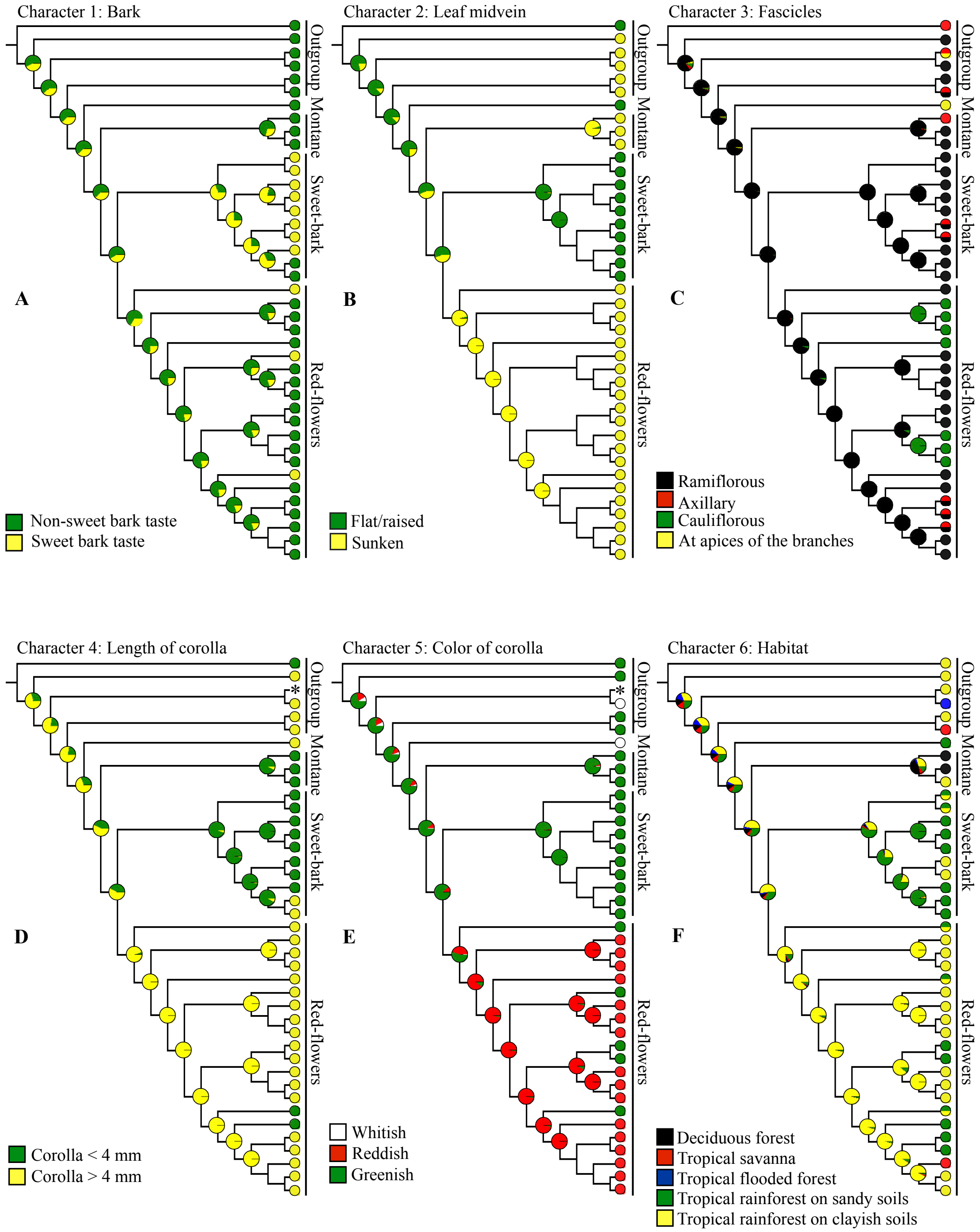


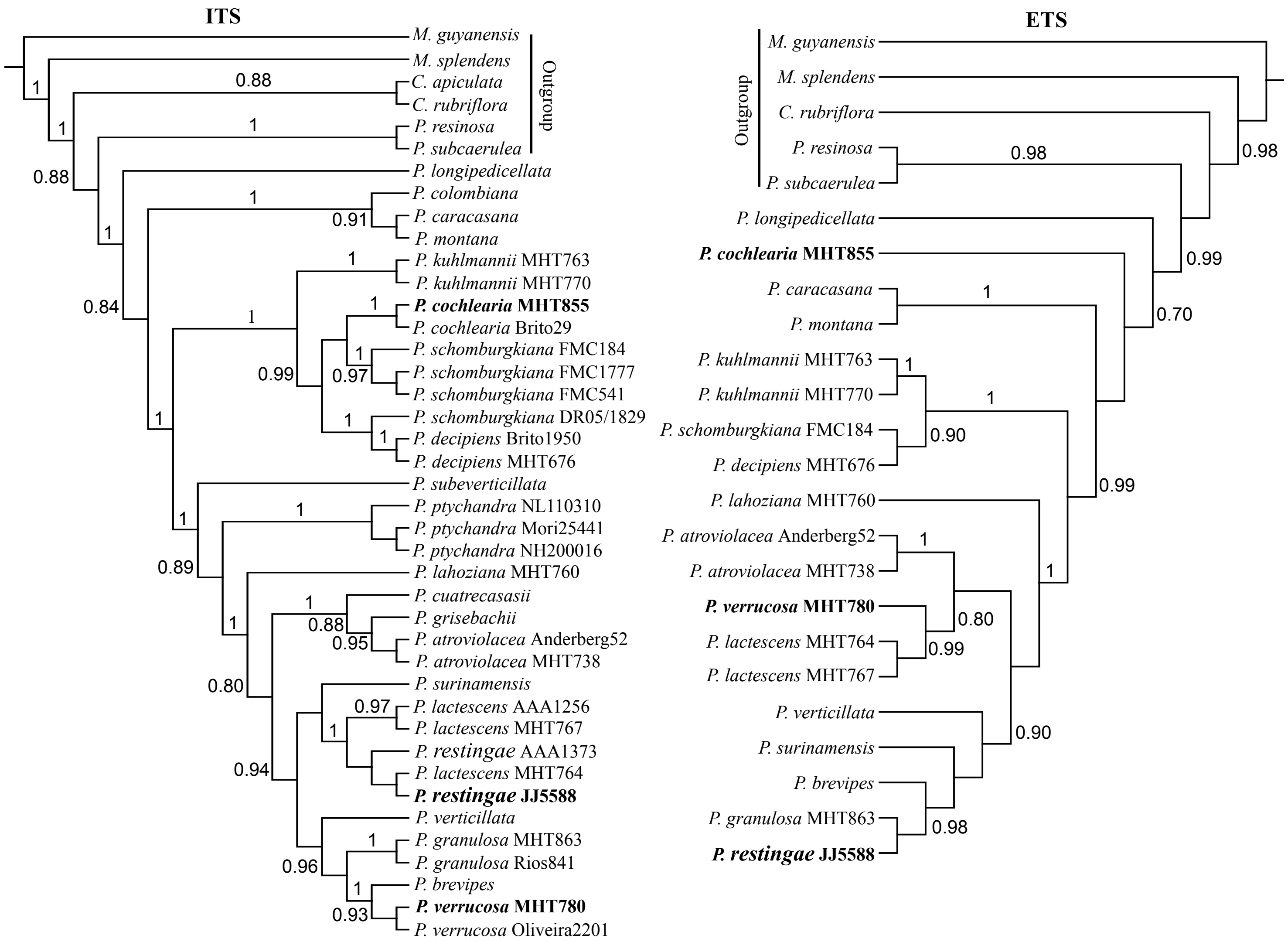
Fig. 4. Ancestral reconstruction of habitat and five morphological traits (bark, midvein, flower disposition, length of corolla, color) of *Pradosia* (Sapotaceae, Chrsophylloideae). Pie charts at nodes indicate the relative frequencies of ancestral character optimizations across the entire tree, obtained with BEAST, using the BEAGLE library. *Species that could not be scored.

Appendix 1. Taxa, voucher information, and GenBank accessions used in this phylogenetic study for *Pradosia* (Sapotaceae, Chrysophylloideae). Sequences in bold were downloaded from GenBank. *DNA extraction from herbarium specimens.

Taxon	**Voucher**	**Nuclear Markers**	
		ITS	**ETS**
Chromolucuma rubriflora Ducke	Brazil: Terra-Araujo 833 (INPA, S)	unpubl.	unpubl.
Chromolucuma apiculata Alves-Araújo & M. Alves	Brazil: Voeks 88 (CEPEC)	unpubl.	—
Micropholis guyanensis (A.DC.) Pierre	Brazil: Hopkins 1475 (INPA)	unpubl.	—
Micropholis splendens Gilly ex Aubrév.	Brazil: Assunção 13 (INPA)	unpubl.	unpubl.
Pouteria resinosa T.D. Penn.	Brazil: Faria 2007/33 (UEL)	unpubl.	unpubl.
Pouteria subcaerulea Pierre ex Dubard in Lecomte	Brazil: Faria 2008/3 (UEL)	unpubl.	unpubl.
Pradosia atroviolacea Ducke	Brazil: Terra-Araujo 738 (INPA, S)	unpubl.	unpubl.
Pradosia atroviolacea	French Guiana: Anderberg 52 (S)	unpubl.	unpubl.
Pradosia brevipes (Pierre) T.D. Penn.	Paraguay/Brazil: Lindeman 6743 (U)	**AY552158**	unpubl.
Pradosia caracasana (Pittier) T.D. Penn.*	Venezuela: Stergios 17109 (NY)	unpubl.	unpubl.
Pradosia cochlearia (Miq.) Baill.	Brazil: Brito 29 (INPA)	unpubl.	—
Pradosia cochlearia	Brazil: Terra-Araujo 855 (INPA, S)	unpubl.	unpubl.
Pradosia colombiana (Standl.) T.D. Penn. ex T.J. Ayers & Boufford*	Colombia: Haught 4303 (S)	unpubl.	—
Pradosia cuatrecasasii (Aubrév.) T.D. Penn.*	Colombia: Cuatrecasas 1398 (K)	unpubl.	—
Pradosia decipiens Ducke	Brazil: Brito 1950 (INPA)	unpubl.	—
Pradosia decipiens	Brazil: Terra-Araujo 676 (INPA, S)	unpubl.	unpubl.
Pradosia granulosa Pires & T.D. Penn.	Brazil: Terra-Araujo 863 (INPA, S)	unpubl.	unpubl.
*Pradosia granulosa**	Brazil: Rios 841 (INPA)	unpubl.	—
Pradosia grisebachii (Pierre) T.D. Penn.*	Colombia: Styermark 90134 (NY)	unpubl.	—

Appendix 1
continued

Pradosia kuhlmannii Toledo	Brazil: Terra-Araujo 763 (INPA, S)	unpubl.	unpubl.
Pradosia kuhlmannii	Brazil: Terra-Araujo 770 (INPA, S)	unpubl.	unpubl.
Pradosia lactescens (Vell.) Radlk.	Brazil: Terra-Araujo 764 (INPA, S)	unpubl.	unpubl.
Pradosia lactescens	Brazil: Terra-Araujo 767 (INPA, S)	unpubl.	unpubl.
Pradosia lactescens	Brazil: Alves-Araujo 1256 (UFP)	unpubl.	unpubl.
Pradosia lahoziana Terra-Araujo	Brazil: Terra-Araujo 760 (INPA, S)	unpubl.	unpubl.
Pradosia longipedicellata Alves-Araújo & M. Alves	Brazil: Terra-Araujo 769 (INPA, S)	unpubl.	unpubl.
Pradosia montana T.D. Penn*	Ecuador: Palacios & Rubio 9968 (NY)	unpubl.	unpubl.
Pradosia ptychandra (Eyma) T.D. Penn.	French Guiana: Mori 25441 (S)	unpubl.	—
Pradosia ptychandra	French Guiana: NH200016 (CAY)	**FJ037897**	—
Pradosia ptychandra	French Guiana: NL110310 (CAY)	**FJ037899**	n.s.
Pradosia restingae Terra-Araujo	Brazil: Jardim 5588 (INPA)	unpubl.	unpubl.
Pradosia restingae	Brazil: Alves-Araujo 1373 (INPA, RB, S, UFP, UFRN)	unpubl.	—
Pradosia schomburgkiana (A.DC.) Cronquist	Brazil: Costa 184 (INPA, S)	unpubl.	unpubl.
Pradosia schomburgkiana	Brazil: Costa 541 (INPA, S)	unpubl.	—
Pradosia schomburgkiana	Brazil: Costa 1577 (INPA, S)	unpubl.	—
Pradosia schomburgkiana	Brazil: DR05 1829 (INPA)	unpubl.	—
Pradosia subverticillata Ducke	Brazil: Terra-Araujo 579 (INPA, S)	unpubl.	—
Pradosia surinamensis (Eyma) T.D. Penn.	Guyana: Harris 1076 (U)	**AY552157**	unpubl.
Pradosia verrucosa Ducke	Brazil:Terra-Araujo 780 (INPA, S)	unpubl.	unpubl.
*Pradosia verrucosa**	Brazil: Oliveira 2201 (INPA)	unpubl.	—
Pradosia verticillata Ducke	Brazil: Terra-Araujo 857 (INPA, S)	unpubl.	unpubl.



Appendix 2. Topological congruence between the phylogenetic trees inferred from Bayesian analysis for the ITS (left) and ETS (right) datasets for the genus *Pradosia* and outgroups (Sapotaceae). Accessions with different positions recovered in the two datasets are shown in bold. Numbers at the branches indicate posterior probabilities > 0.70.

CAPÍTULO 2

Novelties on *Pradosia* (Sapotaceae, Chrysophylloideae)

Parte 1

Terra-Araujo, M. H., Faria, A. D. and Vicentini, A. 2012. A new species of *Pradosia* (Sapotaceae) from Central Amazonia. 2012. *Brittonia* 64 (2), 2012, pp. 139–142.

A new species of *Pradosia* (Sapotaceae) from Central Amazonia

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Abstract. **Pradosia lahoziana** is here described as new. It is known from four collections from wet lowland and non-flooded terra firme forests near Manaus in Central Amazonia. Illustrations are provided together with a comparison of the morphological differences with similar species.

Key Words: Amazonia, terra firme forest, Sapotaceae, *Pradosia*, taxonomy.

Pradosia consists of 23 species and belongs to the Sapotaceae subfamily Chrysophylloideae (Swenson & Anderberg, 2005; Swenson et al., 2008). The genus is distributed throughout Central and South America and has the highest number of narrowly endemic species (seven) of any genus of Sapotaceae in the New World, reaching its greatest richness in Colombia, Ecuador, northern Peru, Guyana, and northern Brazil (Pennington, 1990). In Central Amazonia near Manaus, five species have been recorded (Pennington, 1990). Species of *Pradosia* are shrubs or trees that grow mainly in lowland and non-flooded forests on sandy soils (i.e., campina and campinara forest). Variable characters within the genus include flower placement, size of the flower, the place of insertion of the stamens on the corolla tube as well as size and surface of the fruits, which range from smooth to rough and glabrous to pubescent. A single morphological character, the drupaceous fruit, appears to be a synapomorphy of *Pradosia* (Swenson & Anderberg, 2005), and is not known from other genera of Sapotaceae.

Here we describe a new species of *Pradosia* based on collections from the Manaus region.

Pradosia lahoziana Terra-Araujo, **sp. nov.** Type: Brazil. Amazonas: Manaus, Estrada do Aleixo, grounds of Companhia das Plantações, forest on terra firme [03°05'S, 59°55'W, 50–94 m], 30 Aug 1973 (fl), *G. T. Prance 18763* (holotype: INPA; isotypes: MG, MO, NY). (Fig. 1)

Species nova stipellis in medio petioli affixis proxime ad *Pradosia grisebachii* (Pierre) T. D. Penn. et *P. atroviolacea* Ducke accedit, tamen ab ea differt floribus longis in fasciculis in trunco o dispositis.

Trees up to 12 m tall, shoots puberulent, lenticels present. Leaves clustered at the shoot apex, subverticillate, obovate or elliptic, chartaceous, 9–20 × 3–7 cm, apex symmetric, acuminate, base symmetric, cuneate, adaxial surface glabrous, abaxial surface puberulous (visible with a hand-lens); venation eucamptodromous, midrib impressed above, secondary veins 13–18 pairs, intersecondaries absent, tertiaries numerous, oblique or horizontal, marginal vein present and the margin, slightly revolute; petiole 1.6–2.6 cm long, canaliculate, puberulous, stipels present, lanceolate, attached on the middle of the petiole, ca.1–2 mm long, paired. Flowers in fascicles on the trunk (cauliflorous), pedicel 7–9 mm long, puberulous; sepals 3.9–5 mm long, ovate, with a rounded apex, appressed puberulous outside with glabrous margin, glabrous inside; corolla 6.4–

Brittonia, 64(2), 2012, pp. 139–142 ISSUED: 1 June 2012

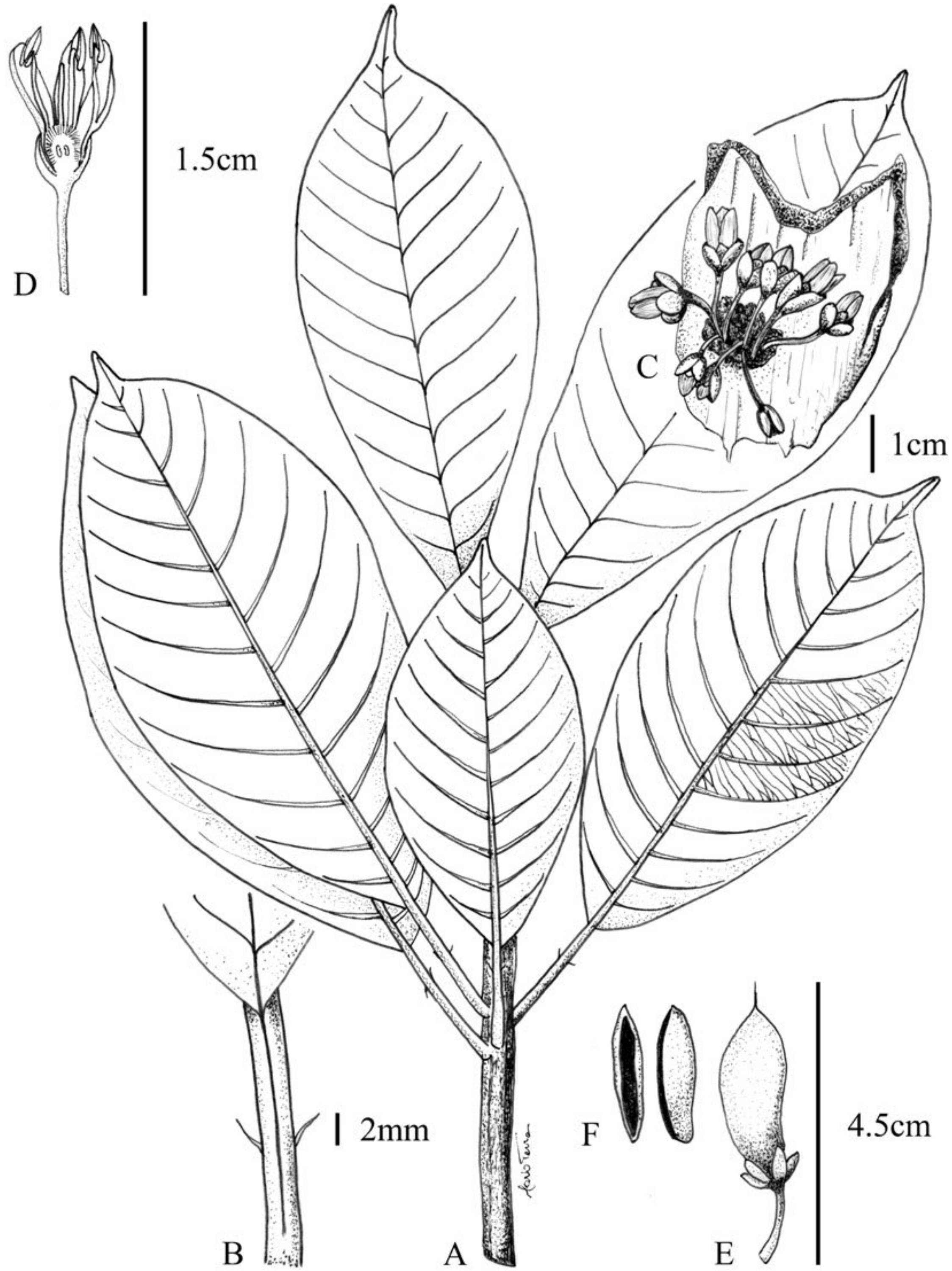

Fig. 1. *Pradosia lahoziana*. **A.** Habit. **B.** Stipels on petiole. **C.** Inflorescences on the trunk. **D.** Flower with front petal removed. **E.** Fruit. **F.** Seed. (A–D from *Prance 18763*, INPA; F from *Lemos s.n.*, INPA.)

9.5 mm long, rotate, tube 2–2.8 mm long, sparsely hairy outside, glabrous inside; stamens 5.6–6.4 mm long, glabrous, fixed at the top of the corolla tube, exserted;

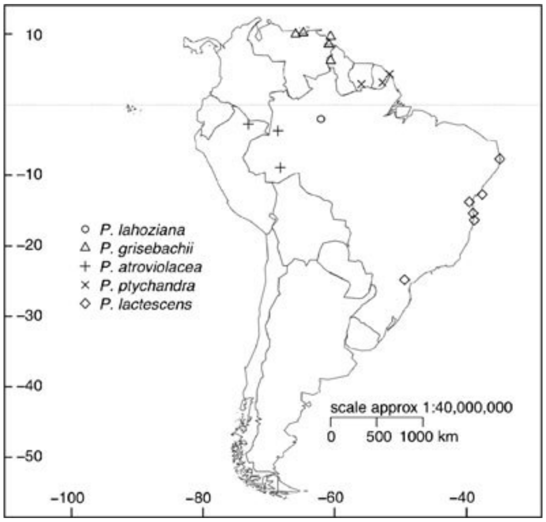

Fig. 2. Known distribution of *Pradosia lahoziana* and similar species.

filaments 3.5–7 mm long, geniculate below the apex; anthers ca. 3 mm long, sagittate; ovary 5-locular, conical and puberulent; styles glabrous, 3.6–3.9 mm long, stigmas simple. Fruit a drupe, ca. 5 × 1.2 cm, smooth, oblong, asymmetric, the apex acuminate, the base rounded, puberulent; seed solitary, approximately 3 cm long, laterally compressed, testa smooth, shiny, the scar adaxial, full-length, 2 mm wide.

Distribution and conservation.—This new species does not overlap geographically with morphologically similar species (Fig. 2). It is known only from tall terra firme forests north of Manaus, in the permanent plots of the Dinâmica Biológica de Fragmentos Florestais Project (DBFFP), Dimona Reserve and from the Estação Experimental de Sivicultura Tropical-ZF2, both from the Instituto Nacional de Pesquisas da Amazônia, in Manaus, Central Amazônia. Many individuals of *Pradosia lahoziana* have been collected at the Dimona Reserve. In the last census in 2007, however, all five individuals of this species that were tagged in permanent plots at this site were dead. The absence of information on the population size does not allow the assessment of the conservation status of this species. The occurrence only within the DBFFP reserves and the small number of individuals suggest that this species is locally rare.

Etymology.—The specific epithet honors José Eduardo Lahoz da Silva Ribeiro, for his outstanding work on the flora of Central Amazonia.

Additional specimens examined. BRAZIL. Amazonas: Manaus, Distrito Agropecuário da Suframa, Fazenda Dimona, Dinâmica Biológica de Fragmentos Florestais Project, 02°19'S 60°05'W, 50–125 m, 29 Oct 1989 (st), *P. Kukle 75* (INPA, K); Fazenda Dimona, Dinâmica Biológica de Fragmentos Florestais Project, 02°19'S, 60°05'W, 50–125 m, 22 Oct 1982 (st), *J. R. M. Nascimento s.n.* (INPA); Estação Experimental de Silvicultura Tropical-ZF2 (fr), 2°35'S, 60°06'W, *M. C. Lemos s.n.* (INPA).

This new species has a unique combination of characters in the genus: the presence of stipels attached at midway on the petiole and cauliflory. Similarly positioned stipels are also found in *Pradosia atroviolacea* Ducke and *P. grisebachii* (Pierre) T. D. Penn., which are not cauliflorous. In contrast, cauliflory occurs in *P. ptychandra* (Eyma) T. D. Penn. and *P. lactescens* (Vell.) Radlk., but these species do not present stipels attached to the petiole. *Pradosia lahoziana* can also be distinguished from these species by larger flowers (Table I).

TABLE I
COMPARISON OF *PRADOSIA LAHOZIANA* AND SIMILAR SPECIES.

	P. lahoziana	*P. atroviolacea*	*P. grisebachii*	*P. ptychandra*	*P. lactescens*
Stipels	Present	Present	Present	Absent	Absent
Inflorescences	Cauliflorous	On twigs and larger branches	On twigs and larger branches	On trunk and larger branches	On trunk and larger branches
Pedicel length	7–9 mm	2–3 mm	0–1 mm	9–12 mm	4–6 mm
Corolla length	6.4–9.5 mm	4–5 mm	4 mm	5 mm	6.5 mm
Filaments length	3.5–7 mm	2.5 mm	2 mm	4–5 mm	4.5 mm
Habitat	Wet lowland non-flooded forests, 45–125 m	Wet lowland periodically flooded or non-flooded forests ca. 100 m	Wet lowland non-flooded forest up to 700 m	Semi-evergreen seasonal forest 200–600 m	Wet lowland forest 0–300 m

Acknowledgments

We thank Wayt Thomas, Douglas Daly, Barbara Thiers, and Shannon Asencio for supporting the first author during work at the New York Botanical Garden. Ulf Swenson kindly provided helpful comments on the manuscript. This research funded by the U.S. National Science Foundation (DEB-0749751).

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———, **J. E. Richardson & I. V. Bartish.** 2008. Multigene phylogeny of the pantropical subfamily Chrysophylloideae (Sapotaceae): Evidence of generic polyphyly and extensive morphological homoplasy. Cladistics 24: 1006–1031.

Parte 2

Terra-Araujo, M. H., Faria, A. D., Alves-Araújo, A. and Alves, M. A new species of *Pradosia* from the Atlantic forest, Brazil. *Nordic Journal of Botany* (no prelo).

A new species of *Pradosia* from the Atlantic forest, Brazil

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Proposed running head: *Pradosia restingae*

Pradosia restingae Terra-Araujo, a new species of Sapotaceae (Chrysophylloideae) from the Brazilian Atlantic forest is here described and illustrated. It is only known from the southern coast of the State Rio Grande do Norte and is likely restricted to the coastal sand dune ecosystem, locally known as restinga forest, from which the epithet is derived. The species is naturally common, but due the low number of known subpopulations we assign *P. restingae* a preliminary conservation status of *Endangered*.

The genus *Pradosia,* Sapotaceae (Chrysophylloideae) is monophyletic (excluding *P. spinosa* from Africa) and belongs to a lineage that is believed to have colonized South America in the Palaeocene some 59 Ma (Anderberg and Swenson 2003; Swenson and Anderberg 2005; Swenson et al. 2008; Bartish et al. 2011). It comprises 24 species confined to South America, except for one that also occurs in Panama and Costa Rica. Most species occur in lowland and non-flooded forests on sandy soils, locally known as campina, campinara or restinga forests. In Brazil, there are around 14 species, nine restricted to Amazonia, and five to the Atlantic Forest. Conservation assessments indicate that three species are believed to be extinct, and ten are endangered (IUCN Red List 2010). However, many regions have not been properly inventoried, which was demonstrated by collections made during our recent fieldwork that extend the geographic distribution of several species. For this reason, we predict that some of the presumed extinct or endangered species are not extinct or are more abundant than previously reported.

Species of *Pradosia* are shrubs or trees, occasionally with a pair of scales along the petiole. The flowers are bisexual, frequently 5-merous and rotate with a short corolla tube, exserted stamens, and lack staminodes (Fig. 1A). Fruits of Sapotaceae are usually berries, but in *Pradosia* they are characterized as drupes with a thin cartilaginous endocarp (Pennington 1990, 1991), also used as a synapomorphy for the genus (Swenson and Anderberg 2005). However, a drupe is usually a one-seeded, indehiscent, and fleshy fruit where the endocarp is hard or stony, the mesocarp fleshy, and the exocarp skin-like (Swartz 1971; Harris and Harris 1997). This definition is inappropriate for *Pradosia* because the endocarp is rather jelly-like, partly transparent, and never becomes hard or stony (Fig. 1B–C). Therefore, we suggest that the fruit of *Pradosia* is termed *drupaceous*, which distinguish it from a genuine drupe.

The Atlantic Forest along the eastern coast of Brazil comprises, after Amazonia the second highest centre of diversity for Sapotaceae in Brazil (Pennington 1990, 2006). Five species of *Pradosia* have been recorded in the Atlantic coast region, and new species of *Pouteria* have recently been described from this region (Alves-Araújo and Alves 2011). On the Brazilian horn, in the state of Rio Grande do Norte, one species of *Pradosia* grows in restinga forest has been identified as *Pradosia lactescens* (Vell.) Radlk., a species that normally occurs in lowland non-flooded forests on clay, not on sandy soils. After a careful morphological study, it became clear that the plants from restinga forests differ from *P. lactescens* and represent a new species, which is here described and illustrated as *P. restingae.* Preliminary cladistic analyses using DNA sequences from the nucleus suggest that the closest relative to *P. restingae* is *P. lactescens* (Terra-Araujo, M.H. unpubl. data). Other congeners that grow in the Atlantic Forests are *P. longipedicellata* Alves-Araújo, *P. kuhlmanni* Toledo, and *P. verrucosa* Ducke

Pradosia restingae **Terra-Araujo sp. nov (Fig. 1, 2)**

Similar to Pradosia lactescens (Vell.) Radlk., but differs by usually being ramiflorous with subsessile (not pedicellate) flowers and a green (not red) corolla.

Type: Brazil. Rio Grande do Norte: Pipa, Estrada para o Santuário Ecológico, 06°13’43.7” S, 35°03’31.7” W, alt. 55 m a.s.l., 26 Sep 2011 (fl, fr), A. Alves-Araújo, M. Alves, A. R. Lourenço and A. Araujo 1373 (holotype: UFP, isotypes: INPA, RB, S, UFRN).

Small tree about 2–6 m tall, sometimes up to 9 m, young shoots puberulous with lenticels. Leaves subverticillate, chartaceous, 7.5–12.5 x 2.6–4.2 cm, obovate or elliptic, glabrous, apex acuminate, base cuneate; leaf venation eucamptodromous, midvein sunken on the upper surface; secondaries of 8–14 pairs, impressed above, parallel, slightly arcuate near leaf margin; intersecondaries absent; tertiaries numerous, oblique and horizontal, marginal vein present; quaternaries areolate; petiole 6–8 mm long, channelled, tomentulose. Flowers clustered in fascicles, subsessile, born along the branches below the leaves, usually not on the trunk; pedicel 0.8–1.6 mm long, tomentulose. Sepals yellow or greenish, 2.7–3.8 mm long, ovate, appressed tomentulose outside, glabrous inside, the inner ones with a ciliate margin. Corolla green, often light wine-red inside, 4.8–5.5 mm long, with a 1.6–2.2 mm long tube and five ovate lobes, slightly pubescent outside, the inner ones with a glabrous margin, glabrous inside. Stamens inserted in the corolla tube orifice; filaments 3.3–4.4 mm long, geniculate below the apex in the bud and opened flowers, glabrous; anthers, 1.6–1.9 mm long, sagittate, glabrous. Ovary 5(–6)-locular, conical, sericeous; style glabrous, 1.8–2.0 mm long. Fruit drupaceous, 25–37 mm long, yellow, smooth, ovoid to spherical, with an acuminate apex; base round and tomentose behind the sepals. Seed usually 2, 16–23 mm long, laterally compressed; testa smooth, shinning; seed scar adaxial, 100% of seed length, 25% of seed circumference, partly displaced to the lateral side; cotyledons plano-convex, radicle exserted below the cotyledons, endosperm absent.

Distribution and conservation

Pradosia restingae is only known from restinga areas from the southern coast of the state of Rio Grande do Norte in Brazil (Fig. 3A). There are two known populations of *P. restingae,* both occurring in protected areas: Parque das Dunas in Natal and Santuário Ecológico de Pipa, in the municipality of Tibau do Sul. These areas are separated by 80 km and add up to 12.5 km^2. Other unprotected populations are present in Natal, Parnamirim and Tibau do Sul, where the latter two are under serious threat due to deforestation and expansion of the city boundaries. Based on the IUCN (2010) guidelines for Red List categories, and because the estimated area of occupancy (AOO) is 160 km^2, we propose a preliminary status of *P. restingae* as *Endangered* (EN: B1ab(iv)).

Recognition

The only species *Pradosia restingae* could be confused with is *P. lactescens*. Sterile specimens of the two have similar, glabrous leaves with the same shapes and leaf venations, but *P. restingae* has cuneate leaf bases, not decurrent as in *P. lactescens*. However, flowering specimens of *P. restingae* are readily distinguished by being ramiflorous, with subsessile and green flowers, and are confined to restinga forests, whereas *P. lactescens* is cauliflorous, has pedicellate (4–6 mm long) and red flowers, and are never found growing on sandy soils. On other hand, *P. longipedicellata* grows in restinga forest, but is distinguished from *P. restingae* by its flat petiole and midvein, long pedicels (15–25 mm long), white flowers, and its distribution is limited to the area around Ilhéus, southern coast of Bahia State. The fact that *Pradosia restingae* usually has two seeds in each fruit is partly at odds with the general pattern of a single-seeded (monospermic) fruit in the genus (Pennington 2006; Swenson and Anderberg 2005), but it is still possible that some fruits of poorly known species such as *P. longipedicellata* and *P. granulosa* have more than one seed. The distributions of all *Pradosia* species occurring in the Atlantic Forest are shown in Fig. 3.

Etymology

The specific epithet refers to the distribution of *Pradosia restingae,* which is restricted to the coastal sand dune ecosystem know as restinga forest.

Additional specimens examined

Brazil. Rio Grande do Norte: Natal, Mata das Dunas, 29 Dec 1952 (fl), S. Tavares, 52-146 (IPA); Natal, between Parque das Dunas and Universidade Federal do Rio Grande do Norte (UFRN), 05° 49’30” S, 35° 11’ 00” W, 21 Oct 1997 (fl), L. A. Cestaro, 97-0144 (IPA); Tibau do Sul, Santuário Ecológico de Pipa, Mata de Vassourinha, 05 Oct 1999 (fl), K. Y. Arns, 314 (IPA); Dunas, close to Barreira D’água, 19 Dec 1964 (fl), S. Tavares, 1213 (HST); Close to Barreira D’água, 19 Dec 1964 (fl), S. Tavares, 1211 (HST); Pipa, restinga forest, 06° 14’03.3”S, 35° 03’26.0”W, 55 m a.s.l., 29 Sep 2011 (fl), A. Alves-Araújo, A. et al. 1374 (INPA, MO, NY, S); Parnamirim, Centro de Lançamento da Barreira do Inferno, 20 Nov 2008 (fl), R. A. Costa 64 (UFRN); Parnamirim, Centro de Lançamento da Barreira do Inferno, 18 Nov. 2008 (fr), A. M. G. Costa (UFRN); Natal, UFRN, 28 Jun 2006 (fl), T. Lima et al. (UFRN); Parnamirim, Campo Exp. e de Prod. do Jiqui, EMPARN, 05°55’45” S, 35°11’15” W, 16 Feb 1999 (st), L. A. Cestaro 99-0057

(UFRN); Natal, Campus da UFRN, área de entorno do Centro de Biociências, 13 Dec 2009 (fl, fr), J. G. Jardim, 5588 (INPA, UFRN); Natal, between Campus da UFRN and Parque das Dunas, 05°49'30'' S, 35°11'00'' W, 21 Oct 1997 (fl), L. A. Cestaro, 97-0144 (UFRN); Parque das Dunas, 14 Oct. 1980 (fl), A. Trindade (UFRN).

Key to the species of *Pradosia* from the Atlantic Forest

1. Bark with sweet taste; leaf venation brochidodromous, tertiaries horizontal. Plants growing on clayish soils, from Rio do Janeiro to Southern Bahia State .... *P. kuhlmannii*
1. Bark non-sweet; leaf venation eucamptodromous, tertiaries oblique 2
2. Leaves covered by whitish to golden trichomes; fruit pubescent 3
2. Leaves glabrous or with residual trichomes at the midvein; fruit glabrous 4
3. Petiole and midvein flattened; fascicles clustered at the apices of the branches; pedicels 15–25 mm long; flowers white; fruit with a smooth surface. Species occurring in forested and open vegetation on white-sandy soils; endemic to the coastal region of Southern Bahia .... *P. longipedicellata*
3. Petiole and midvein impressed; fascicles along the branches below the leaves; pedicels short, ca. 1 mm long; flowers red; fruit with a muricate surface. Species occurring in vegetation on clay, from Rio do Janeiro to Southern Pernambuco State .... *P. verrucosa*
4. Flowers born along the trunk (cauliflorous); pedicel > 4 mm long; flowers red. Species growing in vegetations on clay, from Rio do Janeiro to Pernambuco State .... *P. lactescens*
4. Flowers born along the branches (ramiflorous); pedicel < 1.6 mm long; flowers greens. Plants found in forested and open vegetation on white-sandy soils, from Rio Grande do Norte State .... *P. restingae*

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Figure 1. Field images of *Pradosia restingae*. (A) open, rotate flower, born in fascicles along branches below the leaves, (B) fruit, (C) transection of a fruit showing the half-transparent cartilaginous endocarp, (D) lateral view of seed displaying the partly displaced seed scar. Photos by Anderson Alves-Araújo.

Figure. 2. *Pradosia restingae.* (A) habit, (B) open flower, frontal view, (C) corolla, from below, evidencing the short tube and reflex corolla lobes, (D) sepals showing the outer surface, (E) ovary and style, (F) transection of ovary, (G) two fruits of different shapes, (H) transection of a fruit showing the mesocarp and distal portion of the seed, (I) longitudinal section of the fruit, showing the presence of two seeds, (J) and (K) seeds, the latter showing a partly displaced seed scar. Drawn by Regina Carvalho from holotype.

Figure 3. Known distribution of *Pradosia* from the Atlantic Forest and the new species is indicated in bold. (A) *Pradosia longipedicellata*, *P. restingae* and *P. verrucosa*, (B) *Pradosia kuhlmannii* and P. *lactescens.*

Fig. 1

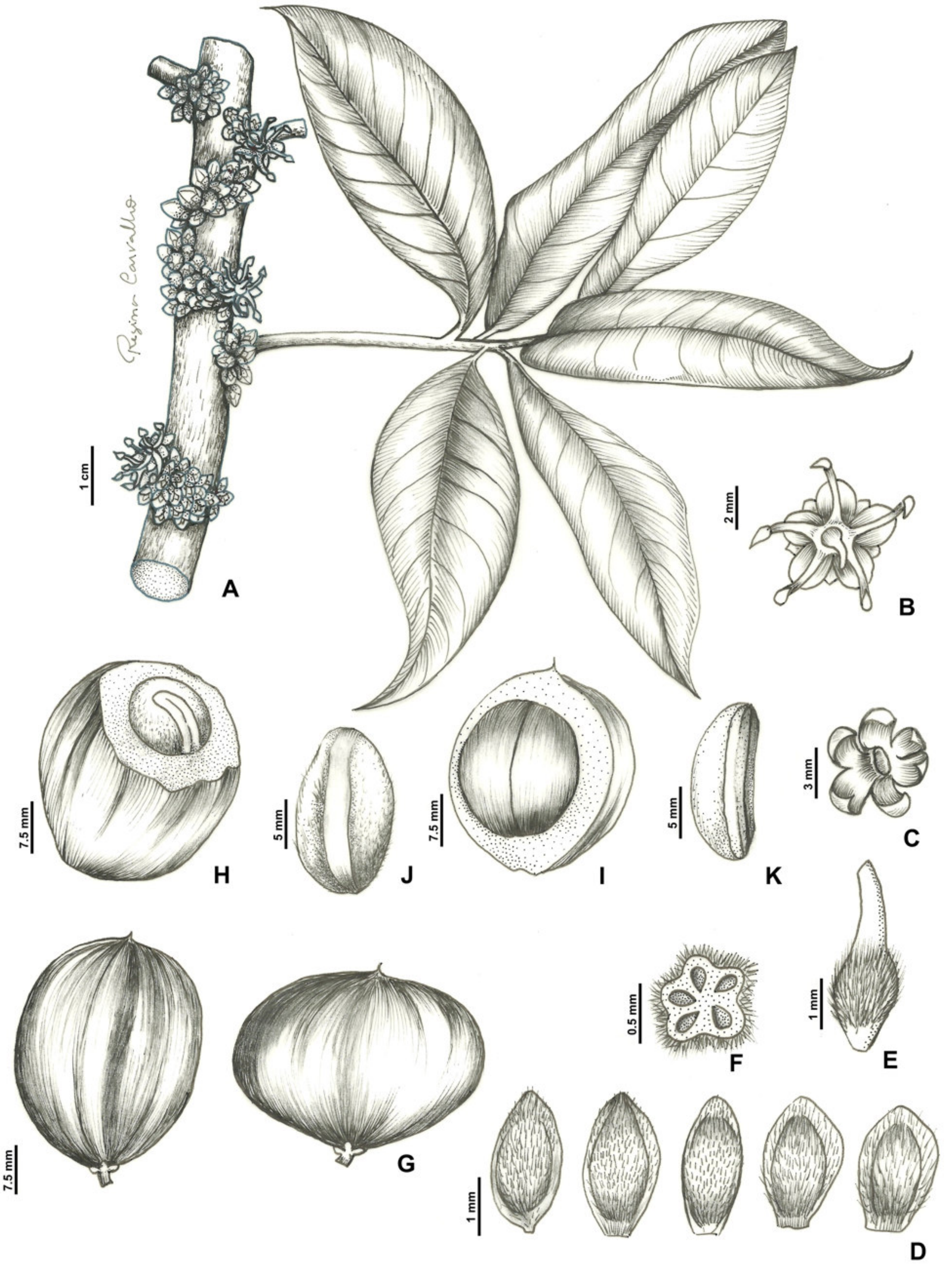
Regina Carvalho
1 cm
A
2 mm
B
7.5 mm
H
5 mm
J
7.5 mm
I
5 mm
K
3 mm
C
0.5 mm
F
1 mm
E
7.5 mm
G
1 mm
D

Fig. 2

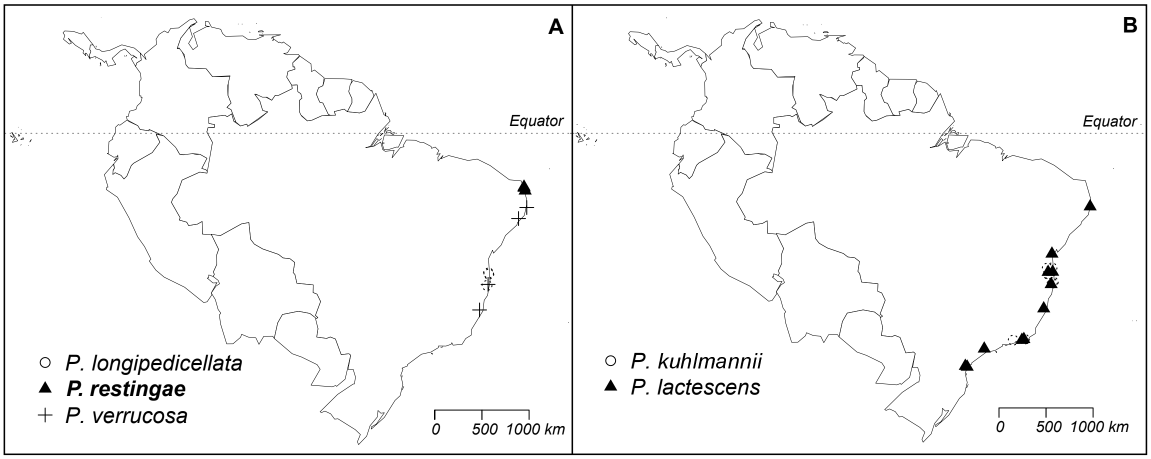
A
Equator
○ P. longipedicellata
▲ **P. restingae**
+ P. verrucosa
0 500 1000 km
B
Equator
○ P. kuhlmannii
▲ P. lactescens
0 500 1000 km

Fig. 3

CAPÍTULO 3

Terra-Araujo, M. H., Faria A. D. and Vicentini, A.
A taxonomic update of Neotropical *Pradosia*
(Sapotaceae, Chrysophylloideae). Manuscrito
formatado para *Systematic Botany*.

A taxonomic update of Neotropical *Pradosia* (Sapotaceae, Chrysophylloideae)

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Proposed running head: Novelties on *Pradosia*

Abstract – *Pradosia* (Sapotaceae, Chrysophylloideae) comprises 26 species mostly confined to rainforests in tropical South America. Molecular data indicate that the genus is monophyletic and includes three main clades, which are also supported by morphological characters, geography and habitat preferences. *Pradosia* is defined by its rotate corolla with a short tube, lack of staminodes and drupaceous fruit. Most species have narrow distributions, and because of their restricted distributions and poor sampling, 10 of the 26 known species have been considered extinct or threatened. In light of recent fieldwork and of collections of flowering material from multiple locations, we present an update to the taxonomy of the genus, including detailed morphological description, synopses of the species, geographical distribution, and key.

***key words* –** Extinct species, Neotropics, *Pradosia*, Sapotaceae, Systematics.

INTRODUCTION

Pradosia (Sapotaceae, Chrysophylloideae), is a genus of trees and shrubs that are mainly distributed throughout South America across a wide variety of habitats, including savannas, evergreen and deciduous forests in the Amazon, the Brazilian Atlantic coast, and the Andes (Pennington 1991; Alves-Araújo and Alves 2012; Terra-Araujo et al. 2012a, 2013). The Amazon region and the Brazilian Atlantic coast are major centres of diversity for the genus, with around 16 species occurring in theses areas (Pennington 2006; Terra-Araujo et al. 2012a, 2013). Many of these species are still known only by the type specimen (see Pennington 1990, 1991), or were described based on poor quality collections, lacking fruits/ flowers. This resulted in many species assessed to be either extinct or endangered (IUCN Red List 2013). However, recent fieldwork conducted in these areas demonstrated that some of these presumed extinct or endangered species are more abundant than previously reported (Terra-Araujo et al. in prep.).

The latest taxonomic revision of *Pradosia* was provided by Pennington (1990), but over the past twenty years it became outdated with newly described species, and accumulation of new material that extended the geographical distribution of many species (Alves-Araújo and Alves 2012; Terra-Araujo 2012a, 2013). Recent phylogenetic analyses have demonstrated that *Pradosia* is monophyletic, provided that the African species *Pradosia spinosa* Ewango & Breteler (Ewango and Breteler 2001) is excluded from the genus circumscription (Anderberg and Swenson 2003; Swenson and Anderberg 2005; Swenson et al. 2008). The monophyly of *Pradosia* was initially inferred based on three species only, and a single morphological character, the drupaceous fruit appears to be a synapomorphy for the genus (Swenson et al. 2008, Terra-Araujo et al. 2012a, 2013). A more detailed study, now including 18 of the 23 species in the Pennington's revision, and three recently described species (Alves-Araújo and Alves 2012; Terra-Araujo 2012a, 2013) was recently undertaken (Terra-Araujo et al. in prep.). Results indicate that *Pradosia* is monophyletic, and seems to have originated in the Early Oligocene in the

Amazon region, reaching the Brazilian Atlantic coast ~ 24.9 Ma (Terra-Araujo et al. in prep.).

This taxonomic update of *Pradosia* incorporates novel molecular phylogenetic data, field observations and the examination of herbarium collections, many of which were not available to Pennington, and the literature. The taxonomic changes here proposed include two new synonyms, a review of the species geographical distribution, and new key fellowed by a short morphological description for each recognized species, as well as notes regarding species circumscription and field tips.

MATERIAL AND METHODS

The taxonomic update on *Pradosia*, the identification key and species geographical distributions were based on our own fieldwork conducted throughout the neotropics, bibliographic review, and examination of specimens deposited in Brazil (ALCB, CEPEC, CVRD, HRB, INPA, IPA, MBML, MG, PEUFR, RB, SP, UEFS), USA (CA, PH, NY, US), and in Europe (S, P). A complete list of the examined specimens is provided in Appendix 1.

Morphological data were obtained from herbarium specimens and from fresh material collected from 2008 onwards. The habit, bark pattern, flowers, fruits and seeds traits were also studied in the field. The terminology used follows Harris and Harris (2001).

A database with species georeferences was created from label data from 260 specimens to generate distribution maps. The total distribution of the species surveyed was obtained by plotting all georeferenced specimens on maps using the MAPS packages in R program (R Core Team 2012).

The phylogeny presented here is simplified version from Terra-Araujo et al. (in prep.), and this phylogeny includes accessions for 21 of the 24 species of *Pradosia.*

Here, we adopted the general lineage-based concept (GLC) (de Queiroz 1998) in delimiting species. Under the GLC, a species is a separately evolving metapopulational lineage, where reproductive isolation, reciprocal monophyly or ecological divergence are reach independently at different times along the evolutionary history (de Queiroz 2007). Thus, a lineage do not have to be necessarily monophyletic, morphologically distinct or reproductively isolated to be a species. In practice, any propriety that provide evidence of lineage separation is relevant to inferring the boundaries and number of species. For this taxonomic treatment we considered ecology, species geographical distribution, phylogenetic relationships and morphology in delimiting the species. Two species here recognized (i.e. *P. beardii and huberi*) could not be sampled for molecular data.

RESULTS

Taxonomic history – *Pradosia* was described by Liais (1872) based on a single species published in Martius's Flora Brasiliensis. The name was in honour to "Visconde de Prados", a person with political prominence and who lived in Rio de Janeiro and Minas Gerais, Brazil in the 19th century. Diagnostic features of *Pradosia* as circumscribed at the time included opposite leaves, absence of staminodes, fruits with a soft pericarp and lack of endosperm. These characters were not attributed by Liais as belonging to *Chrysophyllum* L., neither to *Lucuma* Molina, but suggested that it may be distinct enough to warrant a new genus.

Fifty years later, Ducke (1922) noticed in Northeastern Amazonia that some trees with opposite or subopposite leaves and folded stamens (at least in bud), formed a distinct group within Sapotaceae, and named these *Glycoxylon* Ducke. In addition to the leaf arrangement, these species also shared the presence of a sweet, afterward astringent taste of the inner bark (Ducke 1922). *Glycoxylon* refers to the inner bark with a sweet taste, which is called "casca doce" or "pau doce" in Northern Brazil. Three species were first described by Ducke, and additional species were subsequently discovered nearby Manaus in Central Amazon. However, unlike the first three species, the latter presented alternate or subverticillate leaves and lacked a sweet taste. At this time, opposite leaves, folded stamens as well as the sweet taste of the bark were no longer unique to *Glycoxylon*. Ducke himself recognised the close relationship between his new species and the two species from the southeastern Brazil (*Pradosia kuhlmannii* and *P. lactescens*). Up to that time, these two species were confounded by most authors. In part, such confusion came from a swap of samples in the "Flora Brasiliensis". The diagnosis was based on two different samples: leaves from *P. lactescens* and the bark description from *P. kuhlmannii*. Kuhmann (1930) was the first to highlight this historical confusion, but only Toledo (1946) defined the position of both species and provided new descriptions.

Later Eyma (1936), after detailed review, proposed the suppression of *Glycoxylon* and placed *Pradosia* within *Pouteria* Aubl. Cronquist (1946a, 1946b) on the other hand, in his revision of several American groups of Sapotaceae maintained *Pradosia* and proposed new species and combinations to the genus. Ducke (1942) afterwards provided a synopsis to the genus, and later an identification key, illustrations and new species (see Ducke 1953). However, in spite of his endeavors, *Pradosia* and *Glycoxylon* were still considered as distinct groups by Aubréville (1964). This author recognized the forms according to leaf arrangement: opposite in *Pradosia* and alternate in *Glycoxylon*. One year later Baehni (1965) placed *Pradosia* within *Chrysophyllum*. Over the years, some authors accepted *Pradosia* at the generic level, but some species remained within *Chrysophyllum, Pouteria, Pometia* Vell. (an illegitimate homonyn of *Pometia*, Sapindaceae; renamed *Neopometia* by Aubréville) or even *Lucuma*.

Finally, Pennington (1990) in his treatment of Neotropical Sapotaceae recognized *Pradosia* as a genus with a total of 23 species. The genus was distinguished from other neotropical genera by its rotate corolla with a short tube, lack of staminodes, filets narrowed below the anthers insertion, and by its drupe fruit. *Pradosia* was further amalgamated with *Chrysophyllum, Ecclinusa* Mart., *Diploon* Cronquist, *Micropholis* (Griseb.) Pierre and *Pouteria* within the tribe Chrysophylleae.

Habit **–** As in other Neotropical Sapotaceae, *Pradosia* comprises woody taxa ranging in habit from tall canopy trees up to 35 m tall (e.g. *P. decipiens, P. cochlearia, P. glaziovii* and *P. kuhlmannii*), to treelets around 10–15 m (most of the species), or shrubs (*P. schomburgkiana*) (Fig. 2A–B). Only *P. brevipes* has specialized habit with most of the plant below ground (geoxylic subshrub), with only a few branches emerging above ground.

***Leaves* –** The species have alternate (Fig. 2F), subverticillate (Fig. 2D) and less frequently opposite leaves (Fig. 2E; *P. huberi* and *P. schomburgkiana*). The margin is entire and the leaf surface range from glabrous to densely covered by a dense golden-ferruginous indumentum as in *Pradosia beardii* (Monach.) T. D. Penn. The midvein may be deeply sunken or less frequently flat or raised. The leaf venation of the majority of species is eucamptodromous, however, brochidodromous venation with intersecondaries extending towards the midvein occur in *Pradosia kuhlmannii* Toledo, *P. schomburgkiana* (A.DC.) Cronquist. The secondaries veins are frequently arcuate, sometimes straight, and the tertiaries, when visible, are oblique (Fig. 2T), horizontal (Fig. 2R) or reticulate (Fig. 2S). The petiole may be flat or canaliculate, and paired scales attached at the midway of the petiole are found in *P. grisebachii* (Peirre) T. D. Penn. and *P. lahoziana* Terra-Araujo (Fig. 2G).

***Flowers* –** In *Pradosia,* flowers are clustered in fascicles, usually positioned below the apical clusters of leaves (ramiflorous; majority of the species), sometimes on the trunk (Fig. 2M, cauliflorous; *P. lactescens, P. lahoziana* and *P. ptychandra*), and less frequently at the apices of the branches (terminal; *P. longipedicellata*). Flowers are bisexual and frequently with five sepals and petals; the corolla is rotate, presents a short tube and their color is variable, ranging from greenish to reddish or sometimes white (*P. longipedicellata*) (Fig. 3A–F). The stamens are exserted and occur in equal number to the corolla lobes. They are further usually attached on the corolla-tube orifice, or below it. The filaments are long and geniculate below the apex in bud and in open flowers. Staminodes are lacking, a trait considered a diagnostic of the genus (Lias 1872; Ducke 1953; Pennington 1990; Swenson et al. 2008). The anthers are glabrous and the ovary is 5 (–6)-locular and puberulous; style is glabrous and the stigma simple.

***Fruits* –** In *Pradosia* fruits have been characterized as a drupe and with a thin cartilaginous endocarp (Pennington 1990, 1991; Swenson et al. 2008). However, it is better characterised as drupaceous, because the endocarp is rather jelly-like, partly transparent, and never hardened (Terra-Araujo et al. 2012a; 2013) (Fig. 3K–N). The fruits usually have an ovate or oblong form with a smooth surface (Fig. 3G–I). Only *Pradosia granulosa* Pires & T. D. Penn., *P. glaziovii* (Pierre) T. D. Penn. and *P. verrucosa* Ducke have fruits with small spicules covering the surface and giving a muricate aspect (Fig. 3J). The mesocarp is soft and most of the species are edible, having a sweet taste. Fruits are further considered as monospermic. However, they may include more than one seed, as observed in *P. cochlearia*, *P. granulosa*, *P. longipedicellata* and *P. restingae*. The seed is laterally compressed with a smooth, shinning testa, and with a seed scar as long as the seed itself; the cotyledons are plano-convex, the radicle is exserted below the cotyledons, and the endosperm is thin sheath or absent.

Distributions and habitat – *Pradosia* occurs throughout South America, although *Pradosia atroviolacea* extend to Costa Rica and Panama (Fig. 4A–D). The centre of diversity of the genus is the Amazon region, where 10 species are found, followed by the Brazilian Atlantic coast, with six species. Most of the species grows at low elevations nutrient-poor white-sand or clayish soils. However, one species has been recorded in permanent flooded-forests, or swampy land in Northeast Amazon (*P. huberi*). Only *P. brevipes* occurs in savannas ranging from 300–1000 m altitude in Central Brazil. Three species, *P. colombiana*, *P. montana and P. mutisii* are found in dry montane forest up to 400 m altitude in North and Northwest South America.

***Phylogenetic Relationships* –** A phylogenetic study of *Pradosia* was recently undertaken (Terra-Araujo et al. in prep.). The results of this study support *Pradosia* as monophyletic and indicate *P. longipedicellata* as sister to all other species of the *Pradosia* (Fig. 1). According with this study, these remaining species are grouped in three clades, which were strongly supported and are morphologically, geographically and ecological coherent. The Montane clade includes species that have a narrow distribution in the northeast of Colombia, north of Venezuela and in Ecuador. This clade includes tree species having the inner bark without a sweet taste, leaves with sunken midvein, flower fascicles born on branches below the insertion of leaves (axillary in *P. colombiana*), and greenish flowers. The Sweet-bark clade, with four species, includes almost exclusively species from the Amazon region. Within this clade the relationships between species are still unresolved, and the widespread (throughout the Amazon region) and morphological variable species *Pradosia schomburgkiana* appeared as paraphyletic. Most species have a sweet bark taste, leaves with flat/ raised midvein, flower fascicles below the leaves, and greenish flowers with small corollas. The Red-flowers clade includes species from the Amazon region (eight species), the Brazilian Atlantic coast (four species), the savanna areas of Central Brazil, and the Chocó region on the Pacific coast in Colombia. Within this clade the majority of species have non-sweet bark, leaves with sunken midvein, reddish flowers and larger corolla. The latter further includes plants with flowers borne on the trunk, scales attached at the middle of the petiole, and fruits with muricate surface, features not found in any other clade within *Pradosia*.

TAXONOMIC TREATMENT

Pradosia Liais, Clim. Geol. Geogr. Bot. Bresil: 612–616. 1872 – TYPE: BRAZIL, *Pradosia glycyphloea* (Casar.) Liais.

Tall canopy tree, treelets or geoxlylic shrub. Leaves usually alternate, subverticillate, less frequently opposite; venation bronquidodromous or eucamptodromous, midvein usually sunken, less frequently flat or raised; intersecondaries sometimes present, but rarely well-developed; tertiaries oblique, horizontal or reticulate; petiole flat or canaliculate, puberulous or glabrous, sometimes with small scales 0.5–1.5 mm long, attached at the middle way of the petiole. Flowers bisexual, clustered in fascicles, usually below the leaves (ramiflorous), sometimes on the trunk (cauliflorous) and less frequently at the apices of the branches (terminal). Calyx in a single whorl, sepals 5(–6), usually ovate, with a rounded apex; Corolla 5(–6), rotate, always with a tube shorter than lobes, reddish, greenish or less frequently whitish; Staminodes absent. Disk absent. Stamens, glabrous, exserted; filaments long, geniculate below the apex in bud and opened flowers; anthers glabrous; Ovary 5(–6)-locular, puberulous; style glabrous. Fruit drupaceous, smooth or covered by small spicules; endocarp cartilagenous; Seed usually one, laterally compressed, testa smooth, shinning, the scar adaxial, full-length; embryo with plano-convex cotyledons, exserted radicle; endosperma thin or absent.

KEY TO THE SPECIES OF *PRADOSIA*

1. Geoxylic subshrub. Species growing in savannas from Central Brazil to Paraguay .... 2. *P. brevipes*
1. Tree, treelets or shrubs found in evergreen and deciduous forests in the Amazon, the Brazilian Atlantic coast, and the Andes, but not in savannas from Central Brazil to Paraguay 2
    2. Leaves with a flat or raised midvein 3
        3. Leaves opposite 4
            4. Eucamptodromous leaf venation, secondaries veins slightly divergent, intersecondaries absent. Species growing in swampy lands or flooded forest along the coast (estuary areas) in the Northeastern Amazon .... 11. *P. huberi*
            4. Brochidodromous leaf venation, secondaries veins parallel, long intersecondaries. Species growing in rainforest on nutrient-poor white-sand soils throughout Amazon .... 20. *P. schomburgkiana*
        3. Leaves spirally arranged 5
            5. Leaf venation eucamptodromous 6
                6. Lower leaf surface covered by whitish to golden trichomes; fascicles clustered at the apices of the branches; pedicels 15–25 mm long; flowers whitish; fruit with a smooth surface. Species growing in forested and open vegetation on white-sandy soils (restinga forest) in of Southern Bahia .... 15. *P. longipedicellata*
                6. Lower leaf surface glabrous or with sparse brownish indumentum; fascicles ramiflorous; pedicel 0.5–7 mm long; flowers greenish. Plants found in rainforest on sandy or clayish soils in the Amazon 7
                    7. Inner bark without a sweet taste; leaves coriaceaous, glabrous; pedicel 5–7 mm long; corolla ca. 5 mm long ....7. *P. decipiens*

7. Inner bark with sweet taste; leaves chartaceous, glabrous or brown-pubescent; pedicels 0.5–4 mm long; corolla 1.7–3 mm long .... 4. *P. cochlearia*

5. Leaf venation brochidodromous. Species growing on clayish soils in the Brazilian Atlantic coast .... 12. *P. kuhlmannii*

2. Leaves with a sunken midvein 7

7. Petiole with scales 8

8. Flowers born along the trunk. Species known from Central Amazon .... 14. *P. lahoziana*

8. Flowers born on branches, below the leaves. Species known from Western Amazonia to Panama and Costa Rica .... 10. *P. grisebachii*

7. Petiole lacking scales 9

9. Lower leaf surface glabrous or with residual trichomes at the midvein 10

10. Intersecondary veins long and extending towards the margin. Species growing in dry montane forests of the Colombia, Ecuador and Peru .... 17. *P. mutisii*

10. Intersecondary veins short or absent. Species not found in dry montane forests 11

11. Fascicles cauliflorous; flowers reddish 12

12. Species known from the Amazon .... 18. *P. ptychandra*

12. Species known from the Brazilian Atlantic coast .... 13. *P. lactescens*

11. Fascicles ramiflorous; flowers greenish 13

13. Leaves clustered, subverticillate; pedicel 4–7 mm long .... 21. *P. subverticillata*

13. Leaves poorly clustered, spirally arranged or subverticillate; pedicel 0.5–2 mm long 15

15. Corolla 4.5–5.5 mm long. Species growing in forested and open vegetation on white-sandy soils in Northeastern Brazilian Atlantic coast ....19. *P. restingae*

15. Corolla 2.0–3.5 mm long. Species growing in wet or montane forested from

Amazon and North South America 16

16. Fruits surface smooth, finely appressed puberulous. Species growing in forest on sandy or clayish soils in Northeastern Amazon .... 22. *P. surinamensis*

16. Fruits surface densely lenticellate, glabrous. Species known from wet forests of North Colombia and Northwest Venezuela ...... 3. *P. caracasana*

9. Lower leaf surface pubescent 17

17. Covered by golden-brownish indumentum 18

18. Flowers with greenish corolla; fruits with a smooth surface, glabrous or puberulous .. 20

20. Corolla 1–3 mm long 19

19. Fruits glabrous. Species known from forests on clayish soils of Central and Eastern Amazon .... 23. *P. verticillata*

19. Fruits densely pubescent. Species known from low elevations on swampy land to forest up to 1800 m altitude of Northeastern South America .... 1. *P. beardii*

20. Corolla ca. 7.5 mm long; fruit glabrescent. Species known from wet lowland forest of the Pacific drainage in Colombia (Chocó) .... 6. *P. cuatrecasasii*

18. Flowers with reddish corolla; fruits with a muricate surface, pubescent 21

21. Pedicels ca. 1 mm long. Species occurring in vegetation on clayish

soils throughout the Brazilian Atlantic coast .... 8. *P. glaziovii*

21. Pedicels 1.5–3 mm long. Species known from rainforests on sandy soils in Northeastern Amazon .... 9. *P. granulosa*

17. Covered by sparse whitish or pale indumentum 22

22. Pedicel 2–3 mm long; fruits densely pubescent. Species known from deciduous forests in the Pacific coast of Ecuador and Peru .... 16. *P. montana*

22. Pedicel 0.5–1.2 cm long; fruits puberulous. Species growing in deciduous forests in Colombia and Venezuela ...5. *P. colombiana*

1. PRADOSIA BEARDII (Monach.) T. D. Penn., Fl. Neotrop. 52: 665–666. 1990. – TYPE: TRINIDAD. Long Stretch Reserve, nr. Turune junction, Aug 1949 (fl), *Ayliffe s.n.* (holotype: NY!; isotype: U).

Shrub 1.5–3 m tall, sometimes tree up to 20 m; buttresses short; bark smooth, reddish, scaling in thin irregular plates and leaving deep marks; inner bark sweet-tasting. Leaves opposite or verticillate, coriaceous, upper surface glabrous or glabrescent, lower surface densely covered by reddish-brown short trichomes; venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, straight or slightly arcuate, impressed above; tertiaries oblique to horizontal, obscure. Petiole channeled, pubescent. Fascicles placed below the leaves. Pedicel short, ca. 1 mm long. Corolla 2–3 mm long, greenish. Fruit brownish, smooth, pubescent.

Distribution and habitat – This species is found throughout Guiana Shield (Fig. 4D). It occurs in scrublands or tall forests, usually on sandy soils associated with periodic flooding, although it is also found in humid forest up to 1000 m altitude in Venezuela.

Note – *Pradosia beardii* is easily distinguished from other *Pradosia* species by its dense golden-brown pubescence covering the lower leaf surface and short pedicel.

2. PRADOSIA BREVIPES (Pierre) T. D. Penn., Fl. Neotrop. 52: 641–642. 1990. TYPE: BRAZIL. Paraná: São Bento, nr. Castro, Jan 1880 (fl), *Schwacke 2894* (holotype: GOET; isotype: P).

Geoxylic shrub 30–100 cm tall. Leaves clustered, spirally arranged, coriaceous, upper surface glabrous or with some residual indumentum, lower surface usually pubescent; venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, straight or slightly arcuate, impressed above; tertiaries reticulate. Petiole channeled, pubescent. Fascicles, clustered, placed below the leaves. Pedicel 0.5–3 cm long. Corolla 5.5–6.5 mm long, reddish. Fruit yellowish, with smooth surface, pubescent.

***Distribution and habitat* –** Widespread from Central Brazil, south into Paraná State and Eastern Paraguay in scrublands (Cerrado), usually on sandy soils, from 300–1000 m a. s. l (Fig. 4D).

***Note* –** *Pradosia brevipes* is placed with high support together with *P. glaziovii* and *P. granulosa*. These species are morphologically similar, sharing similar leaf shape and flower color. However, *P. brevipes* differ drastically from those by its geoxylic habit (vs. tree or treelet in *P. glaziovii* and *P. granulosa* respectively), and by its fruits with a smooth surface – *P. glaziovii* and *P. granulosa* are the only species with muricate fruits. These species differ in ecological preferences and geographical distribution – *P. granulosa* occurs in Amazonian forests on sandy soils; *P. glaziovii* occurs along the Brazilian Atlantic coast in wet forests on clayish soils; and *P. brevipes* occurs in the savannas of Central Brazil and Paraguay.

3. PRADOSIA CARACASANA (Pittier) T. D. Penn., Fl. Neotrop. 52: 668. 1990. – TYPE. VENEZUELA. Distrito Federal: Nr. Caracas, Cotiza Jul 1918 (fl), *Pittier 7955* (holotype: US!; isotypes: F, GH, MO, VEN).

Tree up to 10 m, but can reach 25 m tall; buttresses short; bark smooth, reddish-brown colored, shallowly fissured, sloughing off in thin plates and leaving deep whitish marks; inner bark non-sweet tasting. Leaves verticillate or spirally arranged, chartaceous, glabrous; venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, straight or slightly arcuate, slightly impressed above; tertiaries oblique. Petiole channeled, glabrous or with residual indumentum. Fascicles clustered, placed below the leaves. Pedicel 1.5–2 mm long. Corolla ca. 3.5 mm long, greenish. Fruit greenish-brown colored, with smooth surface, densely lenticellate, glabrous.

Distribution and habitat – *Pradosia caracasana* is found through the Northern South America in wet to montane forests, from 80–500 m a. s. l. (Fig. 4A).

Note – This species forms a strongly supported clade with *P. colombia* and *P. montana* (Fig. 1; see Montane clade). However, *Pradosia caracasana* is very distinct morphologically in its glabrous leaves and is allopatric to *P. montana,* its putative sister-species. It is more similar to *P. colombiana,* and sometimes these are confused with each other, and their ranges overlap in Zulia, Venezuela (Pennington 1990). However, *P. caracasana* differs from *P. colombiana* by its glabrous leaves (vs. pubescent), ramiflorous fascicles (vs. axillary), flowers with shorter pedicel (vs. 0.5–1.2 cm long), fruits densely lenticellate (vs. smooth). *P. caracasana* also occurs in wet to montane forests, while *P. colombiana* occurs in deciduous forests.

4. PRADOSIA COCHLEARIA (Lecomte) T. D. Penn., Fl. Neotrop. 52: 655–656. 1990. – TYPE. FRENCH GUIANA. Charvein, 13 Nov 1913 (fl), *R. Benoist 224* (holotype: P [photo]!).

Tree up to 35 m tall; buttresses up to 2 m tall; bark grayish-colored, smooth, scaling and leaving deep oranges marks; inner bark sweet-tasting. Leaves spirally arranged, chartaceous, glabrous or with brownish short trichomes covering the lower leaf surface; venation eucamptodromous; midvein raised on the upper surface; secondary veins parallel, straight or slightly arcuate, not impressed above, sometimes with short intersecondaries; tertiaries oblique to horizontal. Petiole not or slightly channeled, glabrous or with residual indumentum. Fascicles clustered, placed below the leaves.

Pedicel 0.5-3 mm long. Corolla 1.7–3 mm long, greenish. Fruits yellow-greenish colored, smooth, glabrescent.

***Distribution and Habitat* –** Widespread extending from Eastern to Central Amazon in Brazil and French Guiana (Fig. 4B). It usually grows in tall forests, non-flooded systems on sandy soils, although some plants have been collected in tall forests on clayish soils near Manaus, Central Amazon. Additional specimens have been reported for Caquetá (Colombia), and for Loreto in Peru, in upland forest on white sandy soils. However, we have not been able to examine voucher material from these areas.

***Note* –** Molecular data indicate that this species forms a well supported clade with *P. decipiens, P. schomburgkiana* and *P. kuhlmannii* (Fig. 1; see Sweet-bark clade). Relationships within this clade are poorly supported, but the monophyly of *P. cohlearia* is strongly supported, and it is sympatric with both *P. decipiens* and *P. schomburgkiana* at the Reserva Florestal Adolpho Ducke, near Manaus. It differs from *P. decipiens* by its inner bark with sweet taste, chartaceous leaves, secondary veins not impressed on the upper surface, and smaller flowers. It differs from *P. schombugkiana* by its alternate leaves, eucamptodromous venation, and by the intersecondaries absent or much shorter (*P. schomburgkiana* has opposite leaves, brochidodromous venation and long intersecondaries extending towards the margin). The other species in this clade, *P. kuhlmannii,* mainly differs by the brochidodromous venation and by the habitat preference. Specimens of *P. cochlearia* are found in lowland non-flooded forest on sandy soils throughout Amazon region, while *P. kuhlmannii* grows in rainforest on clayish soils along the Brazilian Atlantic coast.

5. PRADOSIA COLOMBIANA (Standl.) T. D. Penn. ex T. J. Ayers & Boufford, Brittonia 40 (4): 428. 1988. – TYPE. COLOMBIA. Region of Santa Marta, Aug 1898-1901 (fl), *H. H. Smith 456* (holotype: F!; isotypes: BM, BR, COL, K, MO, NY, U, US).

Tree up to 8 m, but can reach 25 m tall; buttresses short; bark red-brown colored, smooth, with irregular grayish spots along the trunk; inner bark non-sweet tasting. Leaves spaced, spirally arranged, chartaceous, upper surface glabrous, papillose, lower surface with pale indumentum; venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, slightly arcuate, not impressed above; tertiaries horizontal. Petiole slightly channeled, glabrescent. Fascicles axillary. Pedicel 0.5–1.2 cm long. Corolla ca. 3 mm long, greenish. Fruit gray-greenish colored, smooth, puberulous.

Distribution and habitat – *Pradosia colombiana* occurs from the northwestern of Colombia, along the Atlantic coast, into northeastern of Venezuela, in deciduous forests from sea level to 400 m altitude (Fig. 4A).

Note – This species is easy to recognize because is the only known species from deciduous forest with fruits densely lenticellate. *P. colombiana* is sister to *P. caracasana* +*P. montana*; see notes under *P. caracasana,*which is the most similar species, morphologically and geographically.

6. PRADOSIA CUATRECASASII (Aubrév.) T. D. Penn., Fl. Neotrop. 52: 663–664. 1990. – TYPE. COLOMBIA. Valle, Rio Naya, Puerto Merizalde, Feb 1943 (fl), *J. Cuatrecasas 13988* (holotype: P [photo]!; isotypes: F, K [photo]!, US!).

Tree, buttressed; bark grayish, scaling; inner bark sweet-tasting. Leaves coriaceous, upper surface glabrous or with some residual indumentum, lower surface covered by densely brown appressed indumentum; venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, straight or slightly arcuate, impressed above; tertiaries oblique, slightly, impressed above. Petiole channeled, pubescent. Fascicles attached to small protuberance along the branches. Pedicel ca. 0.5-1 mm long. Corolla ca. 7.5 mm long, greenish. Fruit 3.5–5 cm long, smooth, glabrescent.

Distribution and Habitat – This species is only known from wet lowland forests, at low altitudes on the Pacific coast of Colombia (Chocó) (Fig. 4C).

Note **–** *Pradosia cuatrecasasii* is only known from a few samples from collection by J. Cuatrecasas. However, this species is easy to recognize by its large, strongly coriaceous leaves, with sunken midvein, conspicuous secondary veins, and pubescent lower surface. There is no other species of *Pradosia* from the northeast of Colombia with which it may be confounded. Molecular data support that *P. cuatrecasasii* is most closely related to *P. grisebachii*, but it differ from latter by its pubescent leaves and lack of scales on the petiole.

7. PRADOSIA DECIPIENS Ducke, Trop. Woods 71: 17. 1942. – TYPE. BRAZIL. Amazonas: Nr. Manaus, Rio Tarumã, Dec 1932 (fl), *A. Ducke 385* (holotype: RB!; isotypes: K, MAD).

Tree up to 20 m tall; buttresses up to 0.5 m tall; bark grayish, smooth, scaling in asymmetric thin plates leaving orange marks; inner bark non-sweet tasting. Leaves clustered, spirally arranged, coriaceous, glabrous; venation eucamptodromous; midvein raised on the upper surface; secondary veins parallel, slightly arcuate, impressed above; tertiaries oblique, obscure. Petiole channeled in the upper half, glabrous. Fascicles many-flowered, placed below the leaves. Pedicel 5–7 mm long. Corolla ca. 5 mm long, greenish. Fruit yellowish, with smooth surface, glabrous.

Distribution and habitat **–** Two disjunct populations of *Pradosia decipiens* are known: near Manaus in Central Amazon, where it has been collected in white-sandy forest at the Reserva Florestal Adolpho Ducke; and in Solano, Caquetá, southwest of Colombia (Fig 4B). This species grows in lowland non-flooded forests or occasionally flooded forests on nutrient-poor white-sand soils (campina and campinarana).

Note **–** *Pradosia decipiens* is monophyletic and most closely related to *P. kuhlmannii and P. schomburgkiana,* although the relationships within the Sweet-bark clade lack support. See under *P. cochlearia* for further discussion.

8. PRADOSIA GLAZIOVII (Pierre) T. D. Penn. Fl. Neotrop. 52: 643. 1990. – TYPE. BRAZIL. Rio de Janeiro, (fl), *A. Glaziovii 8229* (lectotype: [photo] P!; isolectotype: BR, [photo] K!).

Pradosia verrucosa Ducke, Bol. Tecn. Inst. Agron.N. 28: 27. 1953. – TYPE. BRAZIL. Pernambuco: Recife, Estradada Aldeia, Apr 1952 (fl, fr), *A. Ducke & A. Lima 80* (holotype: IAN!; isotype: US!). syn. nov.

Tree up to 30 m tall; short buttresses; bark gray-brown colored, smooth; inner bark non-sweet tasting. Leaves clustered at the apex of the branches, spirally arranged, coriaceous, upper surface glabrous or midvein pubescent, lower surface with sparse puberulous indumentum; venation eucamptodromous; midvein sunken on upper surface; secondary veins parallel, slightly arcuate, slightly impressed above; tertiaries oblique. Petiole channeled in upper half, pubescent. Fascicles attached below the leaves. Pedicel short, ca. 1 mm long. Corolla 5–6.5 mm long, reddish. Fruit yellowish, with muricate surface, pubescent.

Distribution and Habitat – *Pradosia glaziovii* is widespread throughout the Brazilian Atlantic coast, occurring from north in Pernambuco to south in Espírito Santo State in wet lowland tall forests on clayish soils (Fig. 4D).

Note – This species is monophyletic and strongly supported as sister to *P. brevipes* (Fig. 1; see clade "b" in Red-flowers clade). To date, *Pradosia glaziovii* was an extinct species according to the IUCN Red List (2013), only known from two samples collected by A. F. M. Glaziou, in the late 19th century, in the Rio de Janeiro area; the locality remains doubtful. Pennington in his monograph suggested that *P. glaziovii* was closely related to *P. brevipes*, which has been confirmed by molecular data. The latter species is, however, a geoxylic shrub from savanna areas in Central Brazil. Sterile specimens of these species have similar leaves with short petioles and with crisped indumentum on the lower surface, but *P. glaziovii* is a tall canopy tree confined to wet forests. However, Pennington dismissed the similarities between *P. glaziovii* and *P. verrucosa* – both names refer to the only two species of *Pradosia* with muricate fruits, which are also restricted to the Atlantic coast region, occurring on wet forests on clayish soils. After comparing our specimens of *P. verrucosa* with the two existing collections of *P. glaziovii,* we did not find any morphological support for two species. These names refers to plants with similar morphology and ecological preference. Because *P. glaziovii* is the older name it has preference over *P. verrucosa*. *P. glaziovii* is mainly characterized by being a tall canopy tree with coriaceous leaves and with appressed indumentum on the lower surface, short pedicel, reddish flowers, muricate fruits surface, and by its occurrence in wet forest on clayish soils.

9. PRADOSIA GRANULOSA Pires & T. D. Penn., Fl. Neotrop. 52: 645–646. 1990. – TYPE. BRAZIL. Pará, Serra dos Carajás, AMZA camp 4-Alfa, 25 Km NW of R. Itacaiumas, Jun 1982 (fl), *C. R. Sperling et al. 5923* (holotype: K; isotype: MG!).

Treelet up to 4–6 m tall; bark grey-brownish, smooth, lenticellate; inner bark non-sweet tasting. Leaves subverticillate, coriaceous, upper surface glabrous, lower surface with sparse indumentum or glabrous; venation eucamptodromous; midvein sunken on upper surface; secondary veins parallel, straight or slightly arcuate, slightly impressed above; tertiaries oblique. Petiole channeled in the upper half, glabrous. Fascicles below the leaves or axillary. Pedicel 1.5–3.0 mm long. Corolla 4.5–5.5 mm long, reddish. Fruits yellow-orange, with muricate surface, brown-tomentose.

Distribution and habitat – *Pradosia granulosa* is known from Northeastern Amazon, occurring in the states of Goiás, Maranhão and Pará in Brazil (Fig. 4D). It grows in open lowland forests on white-sandy soils (campina, campinarana and restinga), from sea level to 250 m altitude.

Note – This species can be easily distinguished from all other Amazonian species by its fruits with muricate surface. *P. granulosa* is monophyletic and sister of *P. brevipes* +*P. glaziovii* (Fig. 1; see clade “b” in Red-flowers clade), being distinguished from the two other species by morphology, genetics and ecological preferences; see under *P. glaziovii* and *P. brevipes* for further discussion.

10. PRADOSIA GRISEBACHII (Pierre) T. D. Penn., Fl. Neotrop. 52: 655. 1990. – TYPE. TRINIDAD. Without precise locality (fl), *Crueger 157* (holotype: GOET; isotype: K, NY!, P).

Pradosia atroviolacea Ducke,Trop.Woods 90: 25. 1947. Type. Colombia. Amazonas: Leticia, Nov. 1945 (fl), *A. Ducke 1800* (holotype: RB!; isotypes: A, COL, F, IAN!, K, MG!, NY!, R, US!). syn. nov.

Tree up to 15 m tall; buttressed; bark grayish, smooth, sloughing off in thin plates and leaving dark marks; inner bark not sweet-tasting. Leaves clustered, spirally arranged or verticillate, coriaceous, upper surface glabrous, lower surface glabrous or with short appressed indumentum; venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, straight or slightly arcuate, slightly impressed above; tertiaries oblique. Petiole channeled in the upper half, glabrous; scales present, paired, ca. 1 mm long, fixed at the midway of the petiole. Fascicles placed on twigs and larger branches. Pedicel 1–3 mm long. Corolla 4–5 mm long, reddish. Fruit yellowish, smooth, sparsely puberulous.

Distribution and habitat **–** Widespread species from Southwestern Amazon, Acre, Brazil to Northwestern Amazon in Colombia, reaching the north of Venezuela and Costa Rica (Fig. 4C). *Pradosia grisebachii* grows in lowland non-flooded forests on clayish soils from 100–700 m a. s. l.

Note **–** Accessions of *Pradosia grisebachii* form a strongly support clade, which is sister to *P. cuatrecasasii* (Fig. 1; see clade “a” in Red-flowers clade). We consider *Pradosia grisebachii* and *P. atroviolacea* to be synonyms because these are the only two known species with scales on the petiole, and with flower fascicles emerging on the branches. *P. grisebachii* has been distinguished from *P. atroviolacea* by the presence of trichomes on the lower leaf surface, longer petioles and greater number of flowers in their fascicles (Pennington 1990). They are also allopatric, *P. grisebachii* is known for Trinidad and Venezuela, and *P. atroviolacea* is distributed from Western Amazonia to Costa Rica and Panama. We have seen the types and many new samples, covering the entire geographical distribution of both species, and we were not able to find any clear morphological discontinuities between the two species. The morphological characters that Pennington (1990) used to distinguish these species did not indicate distinct morphological groups. Therefore, on the basis of these findings, we consider that *P. atroviolacea* is a synonymy of *P. grisebachii*.

11. PRADOSIA HUBERI Ducke (Ducke), Trop. Woods 71:16. 1942. – TYPE. BRAZIL. Pará, R. Macujubim, Breves Jan 1920 (fl, fr), *A. Ducke RB3782* (lectotype: RB!; isolectotypes: G, IAN!, K, MG!, US).

Tree up to 30 m tall; large buttresses to 2 m tall; bark smooth, grayish-colored; inner bark sweet-tasting. Leaves poorly clustered, nearly always oppositely arranged, chartaceous, glabrous; venation eucamptodromous; midvein flat and slightly raised on upper surface; secondary veins divergent and slightly raised above; tertiaries oblique. Petiole short, flattened. Fascicles clustered, placed below the leaves. Pedicel 1–4 mm long. Corolla 4.5–5.5 mm long, greenish; Fruits with smooth surface, glabrous.

Distribution and habitat – *Pradosia huberi* occurs in Northeastern Amazon, in the states of Amapá and Pará in Brazil and nearby Cayenne in French Guiana (Fig. 4B). In spite of the low number of recent collections this has been cited (Ducke 1953) as a characteristic species of swampy lands or flooded forests along the coast (estuarine areas) and associated with riverine systems (igarapé or furo).

Note – Although *Pradosia huberi* was not included in the phylogenetic analyses, its morphology suggest that this species may belong to the Sweet-bark clade. *P. huberi* is similar to *P. cochlearia* by sharing the inner bark with sweet taste, leaves with midvein flat and slightly raised on the upper surface, and green flowers, but it differ from this species in its divergent secondary veins (vs. parallel, straight or slightly arcuate), and much longer corolla (vs. 1.7–3 mm long) (see Pennington 1990). Furthermore, *P. huberi* occurs in swampy lands or flooded forests, while *P. cochlearia* occurs in non-flooded forests on sandy soils.

12. PRADOSIA KUHLMANNII Toledo*,* Arq. Bot. Estado São Paulo 2: 29. 1946. – TYPE. BRAZIL. Rio de Janeiro: nr. Botanic Garden, May 1926 (fl, fr), *Constantino & Occhioni RB22231* (lectotype: RB!; isolectotypes: K, NY!, P, US!).

Tree up 15 m tall; buttresses well developed; bark smooth, grayish-colored, scaling in thin asymmetric plates leaving deep orange marks; inner bark sweet-tasting. Leaves poorly clustered, spirally arranged, chartaceous, glabrous; venation brochidodromous; midvein flat on the upper surface; secondary parallel, straight or slightly arcuate, not impressed above; intersecondaries present, short; tertiaries horizontal. Petiole unchanneled, glabrous. Fascicles placed at the leaf axils or below the leaves. Pedicel 0.5–1 mm long. Corolla 3–4 mm long, greenish. Fruit greenish, smooth, glabrous.

Distribution and habitat – *Pradosia kuhlmannii* is widespread along the Brazilian Atlantic coast, occurring from Pernambuco to Rio de Janeiro State, in wet lowland tall forests on clayish soils (Fig. 4B).

Note – Molecular data indicate that *Pradosia kuhlmannii* is monophyletic and belongs to the Sweet-bark clade. Sterile specimens of *Pradosia kuhlmannii* are easy to recognize because of its sweet bark tasting, unchanneled petioles, brochidodromous venation, leaves with flat midvein and horizontal tertiary veins. Other members of the Sweet-bark clade may have the inner bark with sweet taste, brochidodromous venation, flat midvein on the upper surface, but they are confined to the Amazon, and occur in rainforests on sandy soils. On the other hand, *P. kuhlmannii* have been historically confused with *Pradosia lactescens* (see Kuhlmann 1930, Toledo 1946), because both species are distributed throughout the Brazilian Atlantic coast, in wet rainforests on clayish soils. However, *P. kuhlmannii* differ in its inner bark with sweet (vs. astringent), leaves with brochidodromous venation (vs. eucamptodromous), unchanneled petiole (vs. channeled), midvein flat on the upper surface (vs. sunken), ramiflorous fascicles (vs. cauliflorous), smaller corolla (vs. ca. 6 mm long) and greenish flowers (vs. reddish). Furthermore, *P. kuhlmannii* is not closely related to *P. lactescens*.

13. PRADOSIA LACTESCENS (Vell.) Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 18: 407. 1888. – TYPE. BRAZIL (lectotype: Vellozo, Fl. flum. tab. 87. 1835).

Tree up to 15 m tall; buttresses poorly developed; bark reddish-brow colored, scaling in thin plates and leaving whitish marks; inner bark no sweet-tasting. Leaves clustered, spirally arranged, chartaceous, glabrous; venation eucamptodromous; midvein sunken on the upper surface; secondary veins convergent, arcuate, slightly sunken above; tertiaries oblique. Petiole channeled, glabrous or with residual appressed indumentum. Fascicles clustered, attached along the trunk. Pedicel 4–6 mm long. Corolla ca. 6 mm long, reddish. Fruit yellow-orange colored, smooth, glabrous.

Distribution and habitat – *Pradosia lactescens* is a very common and widespread species, occurring along the Brazilian Atlantic coast, from Pernambuco to Paraná State, in wet lowland tall forests on clayish soils from sea level to 980 m altitude (Fig. 4C).

Note – *Pradosia lactescens* is most similar morphologically to *Pradosia ptychandra*, among the other species of the Red-flowers clade. These two species have similar leaf shapes, both are cauliflorous and have flowers with similar size and color. However, they are not closely related and are allopatric – *P. lactescens* is restrict to the Brazilian Atlantic coast, while *P. ptychandra* occurs in the Northeastern Amazon, perhaps also in Central Amazon (see Pennington 2006). On the other hand, *P. lactescens* form a strongly support clade, which is sister to *P. restingae* (Fig. 1; see clade “a” in Red-flowers clade) – both these species are restricted to the Brazilian Atlantic coast region, and they are also morphologically similar, sharing glabrous leaves with similar shapes and venation patterns. However, *P. lactescens* grows in forests on clayish soils, while *P. restingae* is only known from white-sand forests from the southern coast of the state of Rio Grande do Norte in Brazil (Terra-Araujo et al. 2013). *P. lactescens* can be distinguished from *P. restingae* by its decurrent leaf base (vs. cuneate in *P. restingae*), cauliflory (vs. ramiflory), with pedicellate and reddish flowers (vs. subsessile and greenish flowers), and is never found growing on sandy soils.

14. PRADOSIA LAHOZIANA Terra-Araujo*,* Brittonia, 64 (2): 139–142. 2012. – TYPE. BRAZIL. Brazil. Amazonas: Manaus, Estrada do Aleixo, grounds of Companhia das Plantações, forest on terra firme [03° 05' S, 59° 55' W, 50–94 m], 30 Aug 1973 (fl), *G. T. Prance 18763* (holotype: INPA!; isotypes: MG!, MO!, NY!).

Trees up to 15 m tall; unbuttressed; bark rough, lenticellate, grayish-brown colored; inner bark no sweet-tasting. Leaves clustered at the shoot apex, subverticillate arranged, chartaceous, upper surface glabrous, lower surface puberulous (visible with a hand-lens); venation eucamptodromous; midvein impressed on the upper surface; secondary veins parallel, arcuate and slightly raised above; tertiaries horizontal or oblique. Petiole channeled, pubescent; stipels present, attached on the middle of the petiole, ca.1–2 mm long, paired. Flowers clustered in fascicles on the trunk. Pedicel 7–9 mm long. Corolla 6.4–9.5 mm long, reddish. Fruit smooth, puberulous.

Distribution and habitat – *Pradosia lahoziana* grows in rainforest on sandy (e.g. campina and campinarana forests) or clayish soils from 50–125 m altitude in Central Amazon (Fig. 4C).

Note – This species has a unique combination of characters in the genus: the presence of scales attached at midway on the petiole and cauliflory. Similarly positioned scales are also found in *Pradosia grisebachii*, which is not cauliflorous. In contrast, cauliflory occurs in *P. ptychandra* and *P. lactescens*, but these species do not present scales attached to the petiole.

15. PRADOSIA LONGIPEDICELLATA Alves-Araújo & M. Alves, Brittonia, 64 (1): 23–29. 2012. – TYPE. BRAZIL. Bahia: Una, Reserva Biológica do Mico-Leão- Dourado, BA-001 Km 46, 15° 09' S, 39° 05' W, 9 Mar 1993 (fl, fr), *J. G. Jardim, et al. 92* (holotype: CEPEC!; isotype: NY).

Tree up to10 m, but can reach 20 m tall; unbuttressed or occasionally with buttresses to 0.5 m tall; bark grayish-colored, rough, lenticellate, shallowly fissured, scaling; inner bark no sweet-tasting. Leaves clustered, spirally arranged, chartaceous, both leaf surfaces covered by whitish to golden trichomes; venation eucamptodromous; midvein flatted; secondary vein parallel, slightly arcuate, flat or slightly raised; tertiaries oblique. Petiole unchanneled, with whitish to golden trichomes. Fascicles clusters at the apices of short branches (terminal). Pedicel 2–3 cm long. Corolla 7–8 mm long, whitish. Fruit yellowish, smooth, brown-pubescent.

Distribution and habitat – *Pradosia longipedicellata* is endemic to the coastal region of Southern Bahia, Brazil, and is found in forested vegetation on white-sand soils (restinga), from sea-level to around 60 m altitude (Fig. 4A).

Note – This species is supported as sister to all other species of the *Pradosia.* Morphologically, *Pradosia longipedicellata* can be easily recognized by its leaves covered by whitish to golden trichomes, terminal fascicles and long flowers with whitish corolla. There are no other species of *Pradosia* with these characters.

16. PRADOSIA MONTANA T. D. Penn., Fl. Neotrop. 52: 661–663. 1990. – TYPE. ECUADOR. El Oro: Ca. 60 km SE of Arenillas on road to Loja, Nov 1982 (fl), *Pennington & Tenorio 10719* (holotype: K; isotypes, NY!, QCA).

Tree up to 8 m, but can reach 25 m tall; unbuttressed or with slight buttress to 0.5 m tall; bark light gray colored, lenticellate, rough, fissured, sloughing off in small plates; inner bark no sweet-tasting. Leaves clustered, spirally arranged, coriaceous, upper surface sparse pubescent on midvein and secondary veins, lower surface surfaces pubescent;

venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, slightly arcuate, slightly impressed above; tertiaries oblique to horizontal. Petiole channeled, pubescent. Fascicles placed below the leaves. Pedicel 2–3 mm long. Corolla ca. 3 mm long, greenish. Fruit ferruginous, smooth, densely pubescent.

***Distribution and habitat* –** This species is restricted to Western Ecuador and Northwestern Peru, being considered as a common component of tropical deciduous forests from sea level to 720 m altitude (Fig. 4A).

***Note* –** *Pradosia montana* is readily distinguished from all other species of *Pradosia* by the soft pubescence on the lower leaf surface. There are two other species associated with deciduous forests, *P. colombiana* and *P. mutisii*, but they have glabrous or glabrescent leaves, never softly pubescent like in *P. montana.*

17. PRADOSIA MUTISII Cronquist, Bull. Torrey Bot. Club 73: 470. 1946. – TYPE. COLOMBIA. (fl), *Mutis 4004* (holotype: US!).

Tree up to 8 m, but can reach 30 m tall; buttress up to 0.5 m tall; bark dark brown colored. Leaves clustered, spirally arranged, chartaceous, upper surface glabrous, lower surface glabrous or with sparse short whitish trichomes; venation eucamptodromous, midvein sunken on the upper surface, secondary veins parallel, slightly arcuate, slightly, not impressed above; intersecondaries present, long; tertiaries reticulate. Petiole channeled, glabrous. Fascicles placed below the leaves. Pedicel ca. 1 mm long. Corolla 2.5–3 mm long, greenish. Fruit brownish, with smooth surface, glabrous.

***Distribution and habitat* –** *Pradosia mutissii* occurs from Northwestern Colombia to Northweast Peru. It is a rare species found in tropical deciduous forest from 180–1200 m a. s. l. (Fig. 4A).

***Note* –** This species can be mistaken with *P. montana*, and their ranges overlap in Peru. However, *P. mutisii* can be easily distinguished from *P. montana* by its glabrous leaves (vs. pubescent), presence of long intersecondaries veins (vs. absent of intersecondaries) and glabrous fruits (vs. pubescent).

18. PRADOSIA PTYCHANDRA (Eyma) T.D. Penn., Fl. Neotrop. 52: 648–650. 1990. – TYPE. SURINAM. Upper Lucie R., Apr 1926 (fl), *BW 6943* (holotype: U; isotype: K).

Tree up to 13 m, but can reach 25 m tall; unbuttressed or with poorly developed buttress to ca. 30 cm tall; bark smooth, grayish-brown colored, scaling in thin plates and leaving pock-like depressions; inner bark no sweet-tasting. Leaves clustered, alternate, elliptic, glabrous; venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, slightly arcuate, slightly sunken above; tertiaries oblique. Petiole channeled, glabrous or with appressed indumentum. Flowers attached along the trunk. Pedicel ca. 1 cm long. Corolla ca. 5 mm long, reddish. Fruit yellow or orange colored, smooth, glabrous.

Distribution and habitat **–** This species is known from two disjunct areas: in Central Amazon, surrounds of Manaus, in DBFFP permanent plots (see Pennington 2006); and in French Guiana, Guyana and Surinam. *Pradosia ptychandra* grows in non-flooded forests on clayish soils, from 75–770 m a. s. l. (Fig. 4C).

Note **–** *Pradosia ptychandra* is morphologically more similar to *P. lasctescens* (from the Brazilian Atlantic coast) and their differences are highlighted under the latter. On the other hand, it may be confounded with *P. lahoziana*, a closely related species, which also have fascicles attached along the trunk (cauliflorous) and reddish flowers. *P. ptychandra* lack scales on the petiole (vs. present in *P. lahoziana*).

19. PRADOSIA RESTINGAE Terra-Araujo, Nord. J. Bot. (in press.). 2013. TYPE. Rio Grande do Norte: Pipa, Estrada para o Santuário Ecológico, 06° 13’ 43.7” S, 35° 03’ 31.7” W, alt. 55 m a.s.l., 26 Sep 2011 (fl, fr), *A. Alves-Araújo et al. 1373* (holotype: UFP!, isotypes: INPA!, RB!, S!, UFRN!).

Small tree about 2–6 m, sometimes up to 9 m tall. Leaves subverticillate arranged, chartaceous, glabrous; venation eucamptodromous; midvein sunken on the upper surface;

secondary veins parallel, slightly arcuate, slightly sunken above; tertiaries oblique or horizontal. Petiole channeled, tomentulose. Flowers clustered in fascicles, subsessile, born along the branches below the leaves, usually not on the trunk. Pedicel short, 0.8–1.6 mm long. Corolla 4.8–5.5 mm long, greenish. Fruit yellowish, smooth, tomentose behind the sepals.

Distribution and habitat – *Pradosia restingae* is only known from the Southern coast of the state of Rio Grande do Norte in Brazil, where it is found in both forested (restinga alta) and open (dunas) vegetation on white-sand soils, from sea-level to 55 m altitude (Fig 4C).

Note – This species can be confounded with is *P. lactescens*; see under *P. lactescens* for discussion.

20. PRADOSIA SCHOMBURGKIANA (A. DC.) Cronquist, Bull. Torrey Bot. Club 73: 311. 1946; Pennington, T. D., Fl. Neotrop. 52: 657–660. 1990. – TYPE. GUYANA, (fl), *Schomburgk 505* (holotype, G-DC; isotypes, BM, BR, F, K, NY, OXF, [photo] P!, US, W).

Shrub or small tree up to 4 m, but can reach 20 m tall; unbuttressed or occasionally with large buttresses to ca. 1 m tall; bark grayish-colored, smooth, scaling and leaving orange or reddish deep marks; inner bark sweet-tasting. Leaves opposite arranged, coriaceous**,** glabrous on the upper surface, glabrous on the lower surface or densely covered by brown indumentum; midvein flatted; venation brochidodromous; secondary veins parallel, straight or slightly arcuate, flat or slightly raised on upper leaf surface; intersecondaries long, extending towards the margin; tertiaries reticulate. Petiole unchanneled, glabrous or with appressed indumentum. Fascicles placed below the leaves. Pedicel 1–10 mm long. Corolla 2–4 mm long, greenish. Fruit greenish, smooth, glabrous or brown-puberulent.

Distribution and habitat – *Pradosia schomburgkiana* is widely distributed in the Amazon region, being found in nutrient-poor white-sandy forests (campina, campinarana and restinga forests) from sea level in Pará State up to 1200 m altitude in Guiana Shield (Fig. 4B).

Note *–* *Pradosia schomburgkiana* is sympatric to *P. cochlearia*, *P. decipiens*, *P. lahoziana, P. subverticillata* and *P. verticillata* near Manaus, in Central Amazon. However, it is easily distinguished from these species by its inner bark with sweet taste, opposite leaves, brochidodromous leaf venation, long intersecondaries veins extending towards the margin, and small flowers, a combination of characters not found in any other species from Amazon region.

This species appeared as paraphylletic within the Sweet-bark clade. However, the monophyly of the included accessions was not rejected (Terra-Araujo et al. in prep.). Pennington recognized two subspecies (subsp. *schomburgkiana* and subsp. *sericea*), which we found to be sympatric at the Serra do Aracá region. These can be distinguished by the presence/ absence of a dense indumentum on the lower leaf surface, and were included in the phylogeny, but there was no phylogenetic signal between morphological variation and habitat, nor correlation with geography. Furthermore, both subspecies are found in campina and campinarana forests. The use of infraspecific rank (e.g. subspecies) in Neotropical Sapotaceae is not exclusive to *Pradosia*, as well as it is not far to be criticised (Terra-Araujo et al. 2012b). Indeed, the criteria adopted by Pennington (1990) for subspecies recognition are based on variation of few leaf characters. However, variation is continuous and can be recognized only when the extreme morphologies are considered. For *P. schomburgkiana*, however, the complex requires closer examination and a broader sampling to understand how many species it contains, and their limits.

21. PRADOSIA SUBVERTICILLATA Ducke, Trop. Woods 71: 13. 1942. – TYPE. BRAZIL. Amazonas: Nr. Manaus, Rio Tarumã, Jun 1941 (fl), *A. Ducke 812* (lectotype: RB!; isolectotypes: F, IAN!, K, MG!, MO, NY, R, US).

Tree up to 4 m, but can reach 20 m tall; bark grayish-colored, smooth, scaling and leaving irregular oranges deep marks; inner bark sweet-tasting; Leaves clustered, spirally or subverticillate arranged, chartaceous, both surfaces glabrous; venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, slightly arcuate, slightly impressed above; tertiaries oblique. Petiole channeled, glabrous. Fascicles placed below the leaves. Pedicel 4–7 mm long. Corolla 5.5–6.5 mm long, greenish. Fruit, smooth, glabrous.

Distribution and habitat – *Pradosia subverticillata* occurs from lower Rio Negro basin, near of Manaus to upper Rio Negro river around Barcelos and Issana river in the Upper Rio Negro region (Fig. 4C). Its distribution further seems to extends to Southern Colombia, in La Uribe, Meta (*M. Gaitán 155*, COAH). However, we have not been able to examine voucher material from this area. In Brazil, along the Rio Negro it grows in non-flooded forest on white-sandy nutrient-poor soils (campina and campinarana).

Note – *Pradosia subverticillata* is strongly supported as sister to all other species of the Red-flowers clade. Within this clade, in particular when compared to other species of the Amazon region, it is morphologically most similar to *P. surinamensis.* These two species share the inner bark with sweet taste, leaves glabrous, with sunken midvein above, greenish flowers and both occur in forests on sandy soils. However, *P. subverticillata* differ from *P. surinamensis* by the secondaries veins deeply impressed above and larger flowers. On the other hand, *P. subverticillata* is also morphologically and ecologically similar to *P. cochlearia*, and *P. schomburgkiana* (Sweet-bark clade), having sweet bark tasting, flowers placed below the leaves, greenish flowers and occurring in forests on sandy soils near Manaus. However, it differ from these species by the clustered leaves, usually subverticillate, with sunken midvein on the upper surface, and larger flowers.

22. PRADOSIA SURINAMENSIS (Eyma) T. D. Penn., Fl. Neotrop. 52: 652. 1990. – TYPE. SURINAM. Surinam R., nr. Goddo, 23 Jan 1926 (fl), *Stahel 39* (holotype: U; isotype: K, MO, RB!).

Tree up to 15 m, but can reach 30 m tall; buttressed 0.30–1 m tall; bark grayish-colored, smooth, scaling and leaving orange marks; inner bark sweet-tasting. Leaves poorly clustered, spirally arranged, upper surface glabrous, lower surface glabrous or glabrescent; venation eucamptodromous; midvein sunken on the upper surface; secondary veins parallel, slightly arcuate, slightly impressed above; tertiaries oblique to reticulate. Petiole channeled, glabrous. Fascicles placed below the leaves. Pedicel short, 0.5–2 mm long. Corolla short, 2–3 mm long, greenish; Fruit yellowish, smooth, glabrous or puberulent.

Distribution and habitat – This species is known from Northeastern Amazonia, in Roraima and Pará State, Brazil and Guyana where it is found in lowland non-flooded forest from 60–600 m a. s. .l. (Fig. 4D). In Brazil, it have been collected usually on sandy soils (campinarana).

Note – *Pradosia surinamensis* is sister to *P. verticillata*, although this relation is weakly supported. Within this clade *P. surinamenis* is more similar to *P. subverticillata*; see under *P. subverticillata* for further discussion. On the other hand, this species is also similar morphologically to the distantly related *P. cochlearia* (Sweet-bark clade); both have the inner bark with sweet taste, spirally arranged leaves, small and greenish flowers, and occur in white-sand forests. However, the leaves of *P. surinamensis* have channeled petiole (vs. unchanneled or slightly channeled) and sunken midvein, raised in *P. cochlearia*.

23. PRADOSIA VERTICILLATA Ducke. Trop. Woods 71: 12. 1942. – TYPE.BRAZIL. Amazonas, Manaus, Villa Municipal, Oct 1941 (fl, fr), *A. Ducke 811* (holotype, RB!; isotypes, F, IAN!, K, MG, MO, NY, R, US).

Tree up to 15 m, but can reach 30 m tall; buttresses up to. 0.5 m tall; bark grayish-colored, smooth, scaling and leaving oranges deep mark; inner bark no sweet-tasting. Leaves clustered, verticillate arranged, coriaceous, upper surface glabrous or with some residual indumentum, lower surface brown-pubescent; venation eucamptodromous;

midvein sunken on the upper surface; secondary veins parallel, slightly arcuate, impressed above; tertiaries oblique. Petiole channeled, pubescent. Fascicles placed below the leaves. Pedicel ca. 1.0–1.7 mm long. Corolla 4.0–4.6 mm long, reddish. Fruit smooth, glabrous.

Distribution and habitat – *Pradosia verticillata* is known from two disjunct areas, one in the lower Rio Negro basin, near of Manaus; and in La Fumée Mountain, French Guiana (Fig. 4D). It grows in lowland non-flooded forest on clayish soils, from 59–400 m a .s l.

Note – A very distinct species from all other Amazonian species of *Pradosi*a because the leaves are clustered at the apex of the branches, verticillate arranged, and have impressed secondary veins, and a dark brown indumentum on the lower leaf surface.

Doubtful and Excluded Names –

Pradosia spinosa Ewango & Breteler, Adansonia 23, 147–150. 2001. TYPE. – CONGO-KINSHASA. Epulu, Jun (fl) *Ewango 631* (holotype: WAG; isotype: BR, P).

This is the only non-Neotropical species misplaced in this genus (Swenson et al., 2008a; see clade F). *Pradosia spinosa* was described from Africa and is mainly characterized by its conspicuous woody spines. However, the partly fused calyx as well as variation in the presence/ absence of stipules, staminodes, and a 5-merous flowers indicated that *P. spinosa* in fact, does not belong to *Pradosia*, but may be associated with Synsepalum-Englerophytum complex (Swenson and Anderberg, 2005). The fruits of *P. spinosa* are still unknown, so it is unclear whether it has drupaceous fruits.

Pradosia argentea (Kunth) T. D. Penn., Nov. gen. sp. 3: 238, tab. 244. 1819. TYPE. – PERU. Cajamarca: Nr. Jaen de Bracamoro (fl), *Humboldt & Bonpland s.n.* (holotype: P [photo]!).

Pradosia argenta is only known from the type collection dating back about 180 years and lacking fruits. No record of this species has been made since then, and *P. argentea* received the conservation status of regionally extinct in Peru (IUCN Red List 2013). Pennington (1990) in his monograph placed this species within *Pradosia* because of its pentamerous rotate flowers with long exserted stamens and lack of staminodes. It was further considered as morphologically similar to *Pradosia schomburgkiana* due their brochidodromous venation with long intersecondaries, but readily distinct from latter in its spirally arranged leaves with fine silvery indumentum. However, we only examined photos of *P. argentea* and could not confirm that this species belongs to *Pradosia*.

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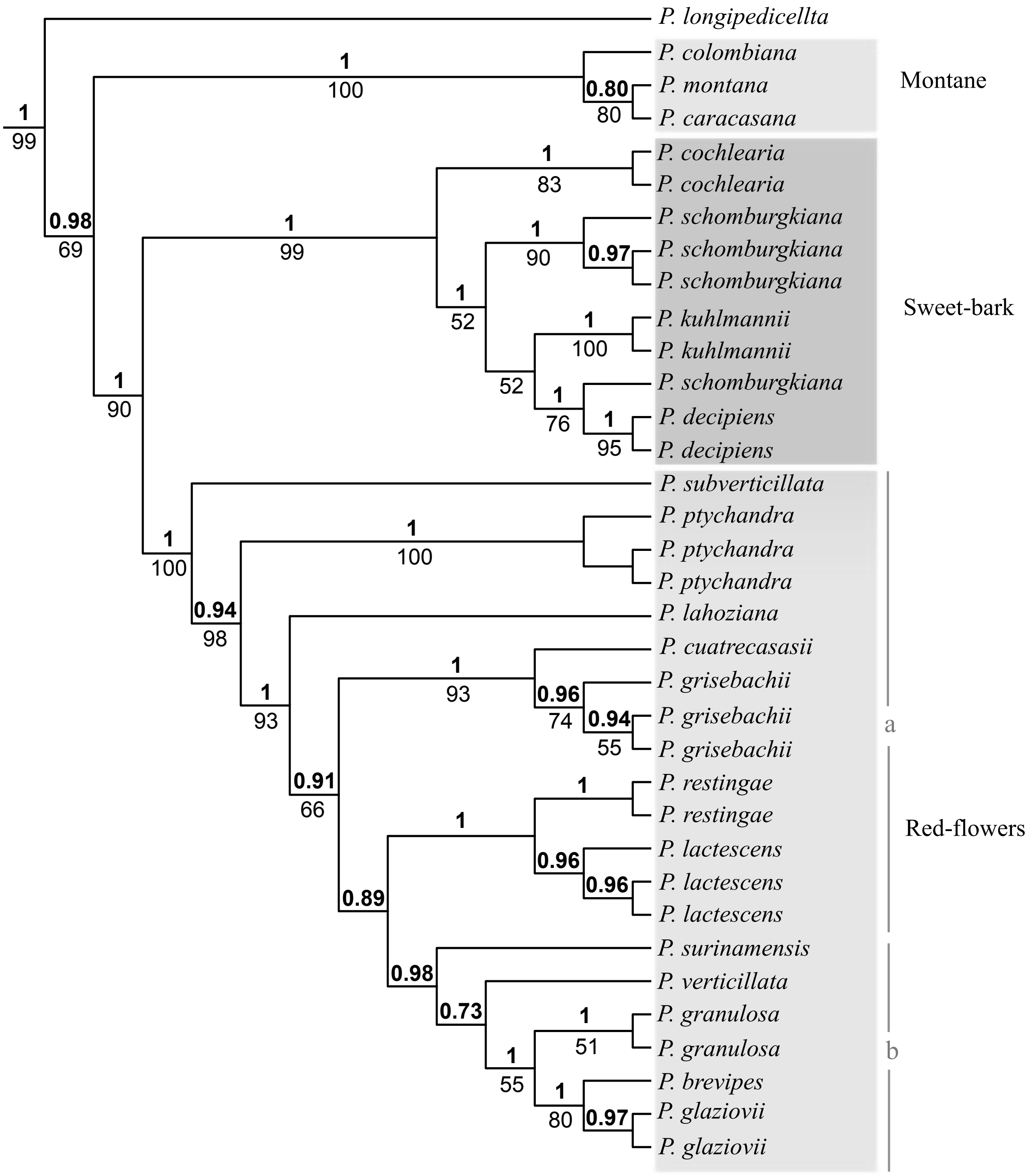

Figure 1. Phylogenetic tree of *Pradosia* (Sapotaceae, Chrysophylloideae) obtained from a bayesian analysis based on two nuclear markers (ITS and ETS). Numbers above (in bold) the branches indicate Posterior Probabilities (PP) and below, the Parsimony Jackknifing (JK) values. Branches with values below 0.75 for PP and 50 for PF are not indicated.

Figure 2. Habitat, bark variation and leaf venation in *Pradosia* (Sapotaceae, Chrysophylloideae): Habit (A–B); A. *P. granulosa*, an understored tree growing in rainforests of the Amazon region. B. *P. kuhlmannii,* a tall canopy tree from Brazilian Atlantic coast. C. buttresses to 1.5 m high in *P. cochlearia.* Leaf arrangement (D–F); D.

verticillate in *P. verticillata*. E. opposite in *P. schomburgkiana*. F. alternate in *P. granulosa*. G. Scales on the petiole of *P. lahoziana*. Patterns and colors of the bark and the outer and inner bark for ten species (H–Q). Lower leaf surface showing the midvein, secondaries or higher leaf venation and indumentum (R–V); R. *P. schomburgkiana*. S. *P. longipedicellata.* T. *P. granulosa*; U. *P. cochlearia*; V. *P. beardii.* The scale bar correspond to 1 cm long. Photos: M. H. Terra-Araujo (A–D, F–V), A. Vicentini (E).

Figure 3. Flowers and fruits of *Pradosia* (Sapotaceae, Chrysophylloideae): Flowers (A–F); A. *P. longipedicellata.* B. *P. schomburgkiana.* C. *P. montana.* D. *P. restingae.* E. *P. lactescens.* F. *P. granulosa.* Fruit (G–J); G. *P. restingae.* H. *P. lactescens.* I. *P. surinamensis.* J. *P. granulosa.* Transection of fruits showing the half-transparent cartilaginous endocarp (K–N); K. *P. cochlearia*. L. *P. granulosa*. M. *P. restingae.* N. *P.*

surinamensis. Photos: A. Alves-Araújo (D, G, M), R. I. Barbosa (I, N), J. Jardim (A), M. H. Terra-Araujo (E, F, H, J, K, L), A. Vicentini (B).

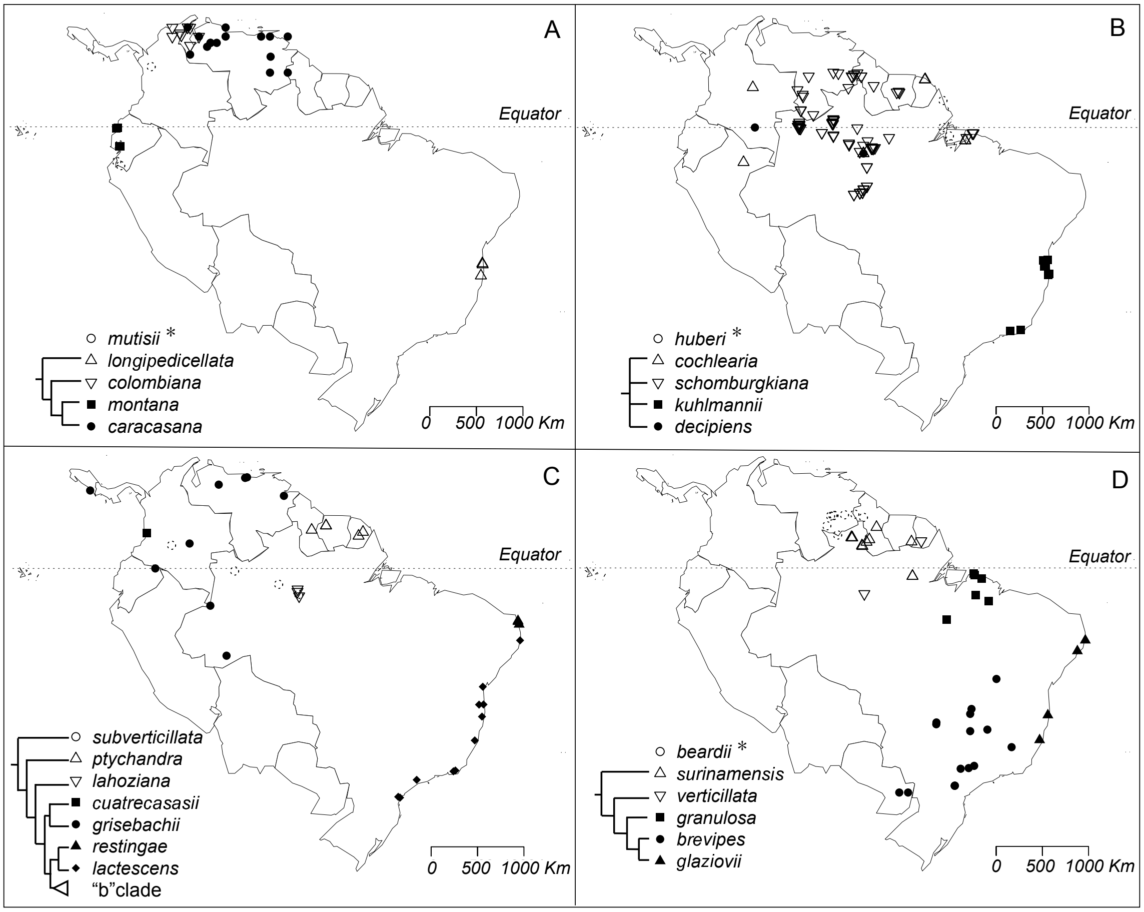

Figure 4. Known geographic distribution to the species of *Pradosia* (Sapotaceae, Chrysophylloideae). A. the ancestral species and Montane clade. B. Sweet-bark clade. C. clade "a" from Red-flowers clade. D. clade "b" from Red-flowers clade.
*Species not included in the phylogeny of the genus.

Appendix 1. Representative Specimens Examined.

1. ***Pradosia beardii*** **–** VENEZUELA. Bolivar: summit of southerly portion of Cerro Uroi, alt. 1000 m, 14 Sep 1962 (fl), *B. Maguire et al. 53842* (NY); Ptari-tepuí, southeast-facing slopes, alt. 1585–1600 m, 10–11 Nov 1944 (fl), *J. A. Steyermark 60040* (NY); En el drenaje del Río Cuyuní, al sur de El Dorado, alt. 1300–1380 m, 22–28 Dec 1970 (bud), *J. A. Steyermark 104253* (NY); Río Paragua, Cerro Guaiquinima, alt. 1600–1700 m, 04 Jan 1952 (fr), *B. Maguire 32959* (NY). Heres: Meseta del Guaiquinima, sector suroriental de la cumbre, 05° 51' N, 63° 25' W, alt. 1350 m, 26 Set 1985 (fl), *O. Huber & G. Medina C. 10903* (NY); Sierra Pakaraima, Cabeceras del Río Paragua (Aguapira), a lo largo de la fronteira Venezolana-Brasileira, fronteira n. 15, 03° 40' N, 63° 00' W, alt. 1400 m, 4–5 May 1973 (fr), *J. A. Steyermark 107288* (NY).

GUYANA. Cuyuni-Mazaruni, Holitipu, trail between camp and airstrip an surroundin area, 05° 59' N, 61° 03' W, alt. 1100 m, 07 Feb 1996 (fl), *D. Clarke 1067* (NY); Cuyuni-Mazaruni, Ayanganna Plateau, 05° 38' N, 61° 04'W, alt. 1100 m, 27 Feb 1987 (fr), *J. J. Pipoly & G. Samuels* 10758 (NY).

2. ***Pradosia brevipes*** **–** BRAZIL. São Paulo: Brotas, Campo Alegre, 24 Aug 1940 (fl), *J. F. de Toledo & A. Gehrt s.n.* (NY); Itirapina, 23 Oct 1996 (fl), *C. E. Carneiro s.n.* (HUEFS). Goiás: Luziania, Margem do Rio Vermelho, 02 Oct 1980 (fl), *E. P. Heringer 17873* (NY); Ribeirão Sobradinho, ca. 5 km S of Sobradinho, D.F., alt. 950 m, 29 Jan 1966 (fr), *H. S. Irwin et al. 12111* (NY); Serra do Caiapó, ca. 60 km S of Caiaponja on road to Jataí, 17° 12' S, 51° 47' W, alt. 800–1000 m, 27 Oct 1964 (fl), *H. S. Irwin & T. R. Soderstrom 7428* (MG); Serra do Facão, ca. 25 km NE of Catalão, alt. 900 m , 24 Jan 1970 (fr), *H. S. Irwin et al. 25258* (NY). Minas Gerais: Rio Paranaíba, Faz. olhos D'Água, ca. 12 Km da cidade, 15 Feb 1986 (fr), *M. A. Silva & E. One 143* (INPA). Paraná: Jaguariaíva, Parque Estadual do Cerrado, 15 Oct 1994 (fl), *A. Uhlmann & D. J. S. Carrião 75* (NY)

PARAGUAY. Amambay: Aquidaban, Cerro Cora, 10 Dec 1978 (fl) *L. Bernardi 19117* (NY); Caaguazú, unos 5 km al N de Yhú, en una zona inundable en mayor o menor grado, alt. 320 m, 12 Dec 1982 (fl), *F. Casas & Schinini 7451* (NY). Canindeyú: Nanduro kai nuncupato, Ype-jhu, 01 Nov. 1978 (fl), *M. Bernardi 18313* (NY).

3. ***Pradosia caracasana*** **–** VENEZUELA. Barinas: Cruz Paredes, Lomas entre las represas Masparro-Boconó, de 2–3 km arriba de la Plataforma "Barrancas A", alt. 330 m, 30 Jun 1997 (fr), *B. Stergios et al. 17109* (NY). Bolívar: Cerro Cotorro (El Vigía), forest slopes along south side of Rio Paragua, between La Pargua and San Pedro de las Bocas, alt. 500 m, 5 Aug 1960 (fl), *J. A. Steyermark 86853* (IAN); Piar, 07° 46' N, 62°56' W, alt. 125 m (fr), *W. Diaz & A. Valera 2147* (NY). Portuguesa: Guanare, entre Agua Sucia y las Panelas, 24 Jun 1981 (fr), *F. Ortega & G. Aymard 1268* (NY); Faldas pedregosas arriba del puente sobre el Río Maria, NE de Boca de Monte, 28–32 km al NNE de Guanare, 09° 18-19' N, 69° 42-43' W, alt. 400–500 m, 02 Nov 1982 (bud), *J. A. Steyermark et al. 127041* (NY). Mara, vicinity of experimental open pit coal mine, 1 km west of Coporzulia Campmento Carichuano, 11° 00' 30" N, 72° 17' 00" W, alt. 80 m, 02 Jun 1980 (fl), *J. A. Steyermark et al.123173* (CA). Zulia: Bolívar, áreas al este de Cabimas, entre Tolosa y El Zamuro, 01 Dec 1981 (fr), *G. S. Bunting 10522* (NY); Colón, alrededores de Casigua El Cubo, sector Los Manueles, entre Casigua y el Pozo CM-43, trayecto de 17 km al norte de Casigua, 30 Apr 1979 (fl), *G. S. Bunting et al. 7435* (NY); Perija, ca. 20 km N of Machiques, on hacienda La Cuiva, alt. 200 m, 20 Oct 1966 (fr), *J. de Bruijn 1254* (NY); Sierra de Perija, Estación Biológica de la Universidad de Zulia, al Suroeste de Machiques, alt. 300–700 m, 25 Aug 1967 (fr), *J. A. Steyermark & J. E. Fernández 99737* (IAN).

4. ***Pradosia cochlearia*** **–** BRAZIL. Amazonas: Manaus Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, 02° 56' S, 59° 58' W, 01 Oct 1997 (fl), *M. R. Mesquita 20* (INPA); 20 Fev. 1998 (fr), *P. A. C. L. Assunção 797* (INPA); 02° 55' 44" S, 59° 55' 09" W, 14 Jan 2002 (fr), *C. V. Castilho 543* (INPA). Pará: Ananindeua, Mata da Pirelli, 08 Jan

1958 (st), *N. T. Silva 502* (IAN); Belém, Bosque Municipal, 24 Aug. 1944 (fl), *A. Ducke 1612* (IAN); Bosque Municipal, 01 Dec 1944 (fr), *A. Ducke 1663* (IAN);

FRENCH GUIANE. Piste de Saint-Elie, Interfluve Sinnamary/ Counamama, 05° 20' N, 53° 00' W, 05 May 1995 (fr), *D. Sabatier & M. F. Prévost* 4344 (NY); Station de la Piste de Saint-Elie (ECEREX), PK 15,5, Parcelle Biodiversité 7B, 05° 20' N, 53° 18' W, 14 Nov 1997 (st), *M. F. Prévost & D. Sabatier 3377* (NY).

5. ***Pradosia colombiana*** **–** COLOMBIA. Atlantico: Cota del Caribe, carretera a Puerto Colombia, cerca de Barranquilla, alt. 70 m, 07 Jan 1941 (fr) *A. Dugand 2738* (NY); Magdalena: South of Fonseca, alt. 400 m, 12 Aug 1944 (fl), *O. Haught 4303* (RB).

VENEZUELA. Zulia: Maracaibo, alrededores de Maracaibo, prox. 10 km al noroeste de "La Curva" de Av. La Limpia, frente de la Planta de tratamiento de INOS, 3 km al oeste de la Univ. Rafael Urdaneta, 125 m (fl), *G. S. Bunting 5481* (NY); Jesús Enrique Lossada, La Concepción, Vía Cuatro Bocas, 21 Nov 1968 (fl), *L. Aristeguieta et al. 6826* (NY); Mara, cuenca de los ríos Socuy-Guasare alrededores del Campamento Carichuano de Carbozulia, vía Caño Colorado, entre campamento y km 5 al norte del caño Vaqueta, alt. 100 m, 3 Aug 1981 (fl), *G. S. Bunting 10120* (NY); Mara, vía entre Carrasquero y Playa Bonita, en el trayecto entre la carretera Carrasquero-Maracaibo y km 12 hacia Playa Bonita, alt. 0–50 m, 11 Jul 1981 (fl), *G. S. Bunting 10059* (NY); Urdaneta, carretra Maracaibo-Machiques entre km 5–56 de la vía, alt. 100 m, 20 Jul 1981 (fl), *G. S. Bunting 10087* (NY); A unos 20 km de la Villa del Rosario 21 Nov 1968 (fr), *L. Aristeguieta et al. 6819* (NY).

6. ***Pradosia cuatrecasasii*** **–** COLOMBIA. Del Valle del Cauca: Costa del Pacífico, Río Naya, Puerto Merizalde, 5–20 m, 20 Feb 1943 (fl), *J. Cuatrecasas 13988* (P); Río Calima (region del Chocó), La Trojita, 5–50 m, 28 Feb 1944 (fr), *J. Cuatrecasas 16560* (US);

7. ***Pradosia decipiens*** – BRAZIL. Amazonas: Manaus, Reserva Florestal Adolpho Ducke, Manaus-Itacoatiara, km 26. Igarapé do Acará, 02° 53' S, 59° 58' W, 28 Oct. 1994 (fl), *M.*

J. G. Hopkins 1499 (INPA ,MG, NY); 22 Mar 1995 (fr), *J. E. L. S. Ribeiro & P. A. C. L. Assunção 1579* (IAN, INPA); 09 Sep. 1997 (bud), *J. M. Brito et al. 31* (IAN, INPA); 09 Apr 1998 (fr), *P. A. C. L. Assunção et al. 833* (INPA, MG, RB); 19 Nov 1997 (fl), *J.E.L.S Ribeiro et al.1950* (INPA); 02 Dec 1997 (fl), *M. A. D. Souza, et al. 474* (INPA); Trilha L-O2, Km 6.5, 09 Jan 2002 (fr), *C. V. Castilho 503* (INPA).

COLOMBIA. Caquetá: Solano, margen der. Río Mesay, 2 km de la bocana del Río Yavilla, 17 Nov 1995 (fl), *D. Cárdenas et al. 6786* (COAH).

8. ***Pradosia glaziovii*** – BRAZIL. Alagoas: Ibatequara, Coimbra, 01 Jun 2005 (fr), *M. Oliveira & Aguiar Neto 2201* (INPA). Bahia: Santa Cruz de Cabrália, Área da Estação Ecológica do Pau-Brasil, 16° 23' S, 39° 08' W, 13 Jul 1985 (fr), *F. S. Santos 487* (CEPEC). Espírito Santo: Linhares, Reserva Natural Vale, RFL-120, Linha 2, Parcela 3, 13 Jun 2003 (fl), *D. A. Foli 4553* (CVRD); Linhares, fazenda Cobra Verde, 1.5 km antes da sede, 01 Dec 2006 (fl), *A. A. da Luz 363* (CVRD); Reserva Natural Vale, 12 Jul 2011 (fr), *M. H. Terra-Araujo 780* (INPA, S, CVRD). Pernambuco: Recife, 18 Dec 1951 (fr), *A. Ducke 80* (IAN, US); Recife, Mata Usina de Mussurepe, 30 Apr 1952 (fl), *A. Ducke & A. Lima 96* (MG); Recife, 30 May 1971 (fr), *E. P. Heringer et al. 1007* (IPA, RB)

9. ***Pradosia granulosa* –** BRAZIL. Goiás: Northen Goiás, Estrada para Tocantinópolis, 10 Aug 1964 (fl), *G. T. Prance & N. T. Silva 58636* (MG). Pará: Bragança, Comunidade Benjamin Constant, 01°11'S, 46°40'W, alt. 30 m, 25 Mar 2002 (fr), *M. Rios & I. M. de Brito 841* (INPA, IAN); Marabá, Serra dos Carajás, estrada do estéril sul, as proximidades da barragem, 06 Feb 1985 (fr), *O. C. Nascimento & R. P. Bahia 1181* (MG); Maracanã, Campo de Martius Pinheiro, 19 Mar 1965 (fr), *N.T. Silva 59715* (IAN); Maracanã, Fortalezinha, 19 Nov 2011 (fr), *M. H. Terra-Araujo et al. 863* (INPA, S); Monte Alegre, região da Colônia da Mulata, 28 Sep 1953 (fl), *N.T. Silva* 30429 (IAN); Paragominas, Itinga do Pará, Faz. Caboré, 14 Dec. 1979 (fr) *U. N. Maciel et al. 533* (MG); Serra dos Carajás, AMZA, camp 4-Alfa, ca. 25 km by road NW of Rio Itacaiúnas, 05° 46'S, 50° 36' W, alt. 225 m, 06 Jun 1982 (fl), *C. R. Sperling et al. 5923* (MG); Rio

Itacaiunas, afl. do R. Tocantins, Serra Buritirana (B4), região com minério de manganês, 05° 31’ S 50° 13’ W, Sep 1970 (fl), *J. M. Pires & R. P. Belem* (IAN). Maranhão: Santa Luzia, Mineirinho, margem direita do rio Pindaré, 03° 40’S, 45° 50’ W, alt. 0-100 m, 25 May 1979 (fl), *J. Jangoux & R. P. Bahia 862* (MG).

10. ***Pradosia grisebachii*** – BRAZIL. Acre: near mouth of Rio Macauhan, 09° 20' S, 69° 00' W, 11 Aug 1933 (fr), *B. A. Krukoff 5410* (NY, US); Bujari, Rodovia BR-364 Km 52, 09° 43' 0.01" S, 68° 07' 0.11" W, 29 Mar 2011 (st), *M. H. Terra-Araujo, et al. 738* (INPA, S). Amazonas: Basin of Rio Javary, Mun. Esperança, Genipapo, 02 Jun 1941(st), *R. L. Fróes 85* (NY). Rondônia: Rio Jarú, BR-29, 21 Sep 1962 (fr), *A. P. Duarte 6564* (MG, RB).

COLOMBIA. Caquetá: Solano, Estación Biológica Puerto Abeja, sector SE PNN Serranía de Chiribiquete, 01 Jun 2002 (st), *J. G. Ramírez 199* (COAH). Guaviare: San José del Guaviare, Inpección de la fuga, en llanura aluvial del Río Guaviare, 02° 46’ 31.1” N, 72° 17’33.6” W, 30 Oct 1995 (st), *R. López et al. 496* (COAH).

COSTA RICA: Puntarenas: Osa Peninsula, Along road to Bahia Drake, N of Corcovado National Park, 08° 40' 47" N, 83° 31' 39" W, 21 Mar 2006 (st), *A. A. Anderberg 52* (S, MO); Parque Nacional Manuel Antonio, 09° 23’N 84° 09’W, 30 Jun 1990 (fr), *P. Harmon 114* (CAS).

ECUADOR. Napo: Cuyabeno, Laguna Grande, Pica Saladero de Dantas, 00° 00’ 00” N, 76° 12’ 45”W, 30 Jul 1984 (fr), *J. Jaramillo 6877* (NY). Sucumbíos: Reserva Faunística Cuyabeno, Laguna Grande and surroundings, including Río Cuyabeno from Pto. Bolívar to above Laguna Cañangueno, 00° 00' S, 76°10' W, alt. 265 m, 11 Mar 1990 (fr), *H. Balslev et al. 97516* (QCNE).

VENEZUELA. Miranda: Páez, drainage of the Río Guapo, Cerro Riberón, between Río Guapo and Río Chiquito, 44.5 km directly (in a straight line) Southeast of Caucagua, 10° 05' N, 66° 01' W, 01 Jun 1977 (fr), *G. Davidse and A. C. González 13611* (MO); Parque Nacional de Guatopo, alt. 600–700 m 27 Nov 1961 (fr), *J. A. Steyermark 90134* (IAN, NY); Cerros Del Bachiller, near East end, 10° 09' N, 65° 48' W, 20–26 Mar

1978 (fr), *J. A. Steyermark 116861* (MO); Delta Amacuro, Bosque Pluvial, Este de Río Grande, este-noreste de El Palmar, cerca de los límites del Estado Bolívar, 08° 05' 00" N, 61° 38' 00" W, Aug–Sep 1964 (st), *L. M. Berti 360* (NY, MO).

11. ***Pradosia huberi*** **–** BRAZIL. Pará: Breves, perto da cidade, 14 Sep 1923 (fl), A. Ducke (RB); Rio Macajubim, margem, (st), *A. Ducke 3782* (IAN); Portel, Rio Cariatuba, Região de Anapú, 18, May 1956 (fr), *R. L. Fróes 33001* (IAN); Anajás, Rio Jipuru, Ilha de Marajó, São Sebastião, 23 Oct 1987 (fr), *B. V. Rabelo et al. 3599* (CA).

FRENCH GUIANE. Cayenne: 1979 (st), *Jacquemin 2410* (NY).

12. ***Pradosia kuhlmannii*** – BRAZIL. Rio de Janeiro: Nova Iguaçu, Reserva Biológica do Tinguá, trilha próxima da represa do Barrelão, 06 Dec 1995 (st), *P. R. Farág et al. 184* (RB). Rio de Janeiro, Jardim Botânico do Rio de Janeiro, coleção de plantas medicinais, canteiro 31K, n. 6429, 22° 08' 0.4" S, 43° 13' 37.6" W, 22 Jun 2011 (st), *M. H. Terra-Araujo 762* (INPA, S); canteiro 10A, n. 2471, 22° 57' 59.5" S, 43° 13' 28.8" W, 22 Jun 2011 (st), *M. H. Terra-Araujo 763* (INPA, S); Magé, Paraíso, Reserva do Centro de Primatologia do Rio de Janeiro, 24 Oct 1984 (st), *H. C. de Lima 2311* (RB). Bahia: Ilhéus, Faz. Retiro, estrada Ilheus-Urucúca, km 14, 14° 42' 24" S, 39° 09' 16" W, 22 Oct 2008 (fl), *J. L. Paixão et al. 1499* (CEPEC, RB); Santa Cruz de Cabrália, Estação Ecológica do Pau-Brasil, 16° 23' S, 39° 08' W, 20 Oct 1987 (st), *F. S. Santos 656* (CEPEC); Almadina, Rod. Almadina-Ibitupã, entrada ca. 7 Km Serra do Sete-paus, ca. 12 km da Estrada, Faz. Cruzeiro do Sul, 14° 44' 6" S, 39° 40' 46"W, 20 Apr 2005 (st), *J. L. Paixão et al. 388* (CEPEC); Camacan, RPPN Serra Bonita, 15° 23'45 S, 39° 33'58" W, 15 May 2010 (st), *D. Rocha 1082* (CEPEC); Reserva Florestal de Porto Seguro, 03 Oct 1988 (fl), *G. L. Farias 165* (CVRD). Espírito Santo: Linhares, Povoação, 19 Mar 2008 (fr), *D. A. Foli* 5968 (CVRD). Pernambuco: Rio Formoso, Cupe, Praia do Muro Alto, 06 Feb 1970 (fl), *Andrade-Lima 70-5714* (IPA).

13. ***Pradosia lactescens*** – BRAZIL. Alagoas: Ibateguara, Coimbra, Grota da Burra, 25 Jan 2003 (fr), *M. Oliveira & A. A. Grilo 1227* (INPA). Bahia: Almadina, Serra do Corcovado, 9.8 km SW de Coarací, na estrada para Almadina, N até Faz. São José, 14° 42' 21" S, 39° 36' 12" W, 650-750 m, 21 Jun 2005 (fr), *P. Fiaschi et al. 2903* (RB); Itagibá, Mata do Laterítico, 14° 10' 36" S, 39° 44'W, 08 Jan 2009 (bud), *M. L. Guedes et al. 16510* (ALCB); Ituberá/ Grapiúna, Fragmento da Pancada Grande, próximo ao rio, 14 Jul 2007 (fr), *R. Valadão & M. L. Guedes 769* (ALCB); Recôncavo Sul, Amargosa, 13° 01' S, 39° 36' W, 29 Jan 2006 (fr), *M. A. de A. Costa et al. 162* (HRB); 20 km N along road from Una to Ilhéus, 39° 02' W, 15° 11' S, 23 Jan 1977 (st), *R. M. Harley 18203* (HRB); Santa Terezinha, Serra da Jibóia, 12° 52' 10" S, 39° 28' 18" W, 18 Sep 2004 (fr), *M. L. C. Neves et al. 127* (HUEFS); Santa Cruz de Cabrália, Antiga rodovia que liga à Estação Ecológica do Pau-Brasil à Santa Cruz, 5–7 km NW da Estação, ca. 12 km NW Porto Seguro, 16° 23'S, 39° 08'W, alt. 80-100 m, 05 Jul 1979 (fr), *S. A. Mori et al. s.n.* (RB); Una, Reserva Biológica do Mico-Leão, entrada no km 46 rod. BA-001 Ilhéus-Una, 15° 09' S, 39° 05' W, 09 Mar 1993 (fr), S. C. Sant'Ana et al. 789 (RB). Espírito Santo: Colatina, estrada Beira Rio Colatina, 01 Sep 2004 (fl), *A. A. da Luz 241* (CVRD); Linhares, Reserva da Companhia vale do Rio Doce, Estrada Cinco Folhas, 19° 08' 58.9" S, 40° 04' 7.6" W, alt. 61 m, 09 Mar 2006 (st), *G. O. Romão et al. 1293* (RB); Santa Leopoldina, Chaves, Cachoeira Recanto da Mata, 20° 00' 72" S, 40° 32' 45" W, al t. 534 m, 26 Jan 2007 (fr), *A. P. Fontana et al. 2732* (RB); Santa Teresa, Reserva Biológica Santa Lúcia, alt. 600 m, 25 Set 1986 (fr), *G. Martinelli et al. 11614* (RB). Paraná: Antonina, Caixa d'água, 19 Jan. 1966 (fr), *G. Hatschbach et al. 13521* (INPA). Pernambuco: Igarassu, Usina São José, Mata do Cabu, 11 Dec. 2008 (fl), *L.V. Cumha 281* (HST); Moreno, Reserva Ecológica de Carnijó, Trilha da Comadre Florzinha, 18 Sep 2003 (fr), *M. B. Costa e Silva et al.166* (IPA). Rio de Janeiro: Búzios, mata de São José Gonçalves, vizinha à Faz. Rancho 10, 25 Feb 1997 (st), *P. R. Farág 585* (RB); Nova Iguaçú, Reserva Biológica do Tinguá, Catanudo, picada para Serra do Beco, ind. F0041, 16 Nov 1995 (fr), *H. C. Lima et al. 5235* (RB); Petrópolis, Araras, alt. 850–980 m, 04 Fev 1974 (fl), *G. Martinelli 217* (RB); Silva Jardim, Distrito de Imbaú, Faz. Santa Fé, 22° 35'

36” S, 42° 28’ 36”W, 15 May 2004 (st), *A. G. Cristo et al. 376* (RB); Reserva Biológica Poço das Antas, trilha do morro do calcário, 22° 30–33’ S, 42° 15–19’ W, 21 Jan 1994 (st) *D. S. Farias et al. 92* (RB); São Pedro da Aldeia, Morro de Sapiatiba, alt. 200–400 m, 09 Sep 1987 (fr), *G. Martinelli et al. 12194* (RB); São José do Vale do Rio Preto, Sítio Serra do Capim, 22° 09’ 16” S, 42° 52’ 30” W, alt. 943 m, 31 Jan 2001 (fr), *F. B. Pereira 29/ 63* (RB); Saquarema, Reserva Ecológica Estadual Jacarepiá, 22° 07’ S, 42° 03’W, 20 Aug 1980 (fr), *C. Farney et al. 3220* (RB); Valença, Distrito de Barão de Juparanã, Faz. Santa Mônica, Sub parcela C9, Indivíduo 7, 22° 21’ S, 43° 43’ ’W, 01 Sep 2000 (st), *M .L. C. V. Spolidoro et al. 288* (RB).

14. ***Pradosia lahoziana*** **–** BRAZIL. Amazonas: Manaus, Distrito Agropecuário da Suframa, Fazenda Dimona, Dinâmica Biológica de Fragmentos Florestais Project, 02° 19' S 60° 05' W, alt. 50–125 m, 29 Oct 1989 (st), *P. Kukle 75* (INPA); Fazenda Dimona, Dinâmica Biológica de Fragmentos Florestais Project, 02° 19' S, 60° 05' W, alt. 50–125 m, 22 Oct 1982 (st), *J. R. M. Nascimento s.n.* (INPA); Estação Experimental de Silvicultura Tropical-ZF2 (fr), 02° 35’ S, 60° 06’ W (st), *M. C. Lemos s.n.* (INPA); Instituto Federal de Educação, Ciência e Tecnologia do Amazonas (IFAM), Campus Manaus-Zona Leste, Fragmento florestal próximo à zootecnia 3, 03° 4' 49.29" S, 59° 55' 36" W, alt. 59 m , 02 Jun 2011 (st), *M. H. Terra-Araujo & J. G. Carvalho-Sobrinho 760* (INPA).

15. ***Pradosia longipedicellata*** – BRAZIL. Bahia: Ihéus, Faz. Guanabara, ramal de entrada no km 10 da Rod. Pontal-Olivença, lado direito, à 0-3 km da entrada, 16 Oct 1980 (fr), *L. A. Matos et al. 1166* (CEPEC); Maraú, estrada à direita para uma propriedade particular, ca. 3.0 km da entrada da cidade de Maraú, 14° 09’ 32”S, 39° 00’ 71” W, 19 Aug 2008 (fr), *L. P. de Quiroz et al. 13816* (HUEFS); Maraú, ca. 8 km na estrada Maraú-Ubaitaba, 14° 09’ 54”S, 39° 00’ 58” W, 05 Sep 1999 (fr), *A. M. de Carvalho et al. 6730* (RB, NY); Una, Reserva Biológica do Mico-Leão, entrada no km 46 rod. BA-001 Ilhéus-Una, 15° 09’ S, 39° 05’ W, 09 Mar 1993 (fl, fr), *J. G. Jardim et al. 92*

(RB); estrada que leva a sede da reserva, 09 Nov 1993 (fr), *A. M. A. Amorim et al 1424* (NY); Rod. BA-001 Una/ Ilhéus, estrada para o povoado de Pedras de Una, 500–700 m da rodovia, 15° 16’ 12” S, 39° 03’ 06” W, 23 Dec 2008 (fl), *J. G. Jardim & A. Jardim 5443* (CEPEC). Una, Estação Experimental Lemos Maia, CEPLAC, ao lado da sede da Estação, 24 Oct 1980 (fr), *A. Rylands 48/ 1980* (MG); Itacaré, Marambaia, ca. 6 a 8 km na estrada de Itacaré-Serra Grande, 15 Jul 1995 (fr), *A. M. de Carvalho et al. 6067* (NY); Mun. Uruçuca, 7.3 km N of Serra Grande on road to Itacaré, Faz. Lagoa do Conjunto Faz. Santa Cruz, 14° 25’ S, 39° 01’ W, 1-12 Jul 1991 (st), *W. W. Thomas et al. 8256* (NY).

16. ***Pradosia montana* –** ECUADOR. El Oro: Arenillas, 25 Jun 1943 (st), *E. L. Little Jr. 6715* (NY). Guayas: Guayaquil Cantón, Cerro Azul, Via a la Costa, km 12, 02° 10’ S, 79° 58’ W, alt. 500 m, 12 Mar 1992 (fr), *W. Palacios & D. Rubio 9968* (NY). Guayas: Guyaquil, 02° 11’ S, 79° 53’ W, May 1994 (st), *C. Bonifaz 2410* (GUAY); Bosque Protector Cerro Blanco, 02° 10’ S, 79° 50’ W, alt. 100 m, 06 May 1992 (fr), *G. Tipaz et al. 894* (QCNE); Bosque Protector Paraíso, 02° 12’ S, 79° 57’ W, alt. 150 m, 19 Apr 1997 (st), *X. Cornejo & C. Bonifaz 5592* (GUAY); Cerro San Eduardo, 02° 11’ S, 79° 58’ W, alt. 140 m, 27 Oct 1996 (st), *C. Bonifaz & X. Cornejo 3526* (GUAY); Cerro del Cementerio, 02° 11’ S, 79° 53’ W, alt. 80 m, 19 Apr 1994 (fr), *X. Cornejo 2394* (GUAY). Manabí: Jama Cantón, km 5 vía Pedernales, 00° 10’ S, 80° 14’ W, alt. 50 m, 24 Oct 1997 (fl), *X. Cornejo & C. Bonifaz 5835* (GUAY); Cerro del Matal, 3 km NW of Jama, 1 km inland from seashore, 00° 11’ S, 80° 18’W, 100 m, 17 Dec 1998 (fl), *D. Neill et al. 11601* (NY).

PERU. Tumbes: Zarumilla Province, Matapalo, parcela “V” de evaluación permanente, 3° 50’29”S 80° 15’33”W, 720 m, 9 Nov 1992 (fl), *Camilo Díaz et al.* 5899 (CA); Matapalo, zona “El Caucho-Campo Verde”, parcela “V” de evaluación permanente, 03° 50’29”S 80° 15’33”W, alt. 500 m, 16 Feb 1993 (fl, fr), *Camilo Díaz et al.* 6543 (CA).

17. ***Pradosia mutisii*** – COLOMBIA. Antioquia: Vereda San Andrés, vía Dabeiba-Fuemia, 13-88 Km, 06° 40' N, 76° 23'W, alt. 960–1200 m, 23 Nov 1987 (fr), *R. Callejas et al. 5857* (NY); Dabaiba-Chigorodo, alt. 180–400 m, 30 Jul 1987 (bud, fr), *R. Callejas et al. 4748* (NY).

ECUADOR. Loja: Cantón Maracá, Achima en la Quebrada Papayal, 04° 18'S, 79° 49' W, alt. 900 m, 02 Jan 1989 (bt, fl), *W. Palacios, 3343* (NY). El Oro: Piedras, alt. 500 m, 18 Jun 1943 (st), *E. L. Little Jr. 6629* (NY). Guayas: Guayaquil, Cantón, Bosque Protector Cerro Blanco, 02° 09' S, 80° 01' W, 12 Aug 1996 (st), *T. David Neill et al. 10675* (GUAY).

PERU. Tumbes: Zarumilla Province, Matapalo, parcela "V" de evaluación permanente, n.741, 03° 50' 29" S, 80° 15' 33" W, alt. 720 m, 02 Nov 1992 (st), *Camilo Díaz et al.* 5535 (MO); n. 742, alt. 720 m, 02 Nov 1992 (st), *Camilo Díaz et al.* 5536 (MO); n. 362, alt. 720 m, 10 Nov 1992 (bud), *Camilo Díaz et al. 5982* (MO); n. 362, 03° 50' 29" S, 80° 15' 30" W, alt. 500 m, 17 Feb 1993 (fr), *Camilo Díaz et al.* 6604 (MO); n. 365, 03° 50' 29" S, 80° 15'33"W, alt. 500 m, 17 Feb 1993 (fr), *Camilo Díaz et al.* 6608 (MO).

18. ***Pradosia ptychandra*** – BRAZIL. Amazonas, Manaus, PDBFF, Reserva 3209 (st), *Ferreira et al. 3209.1291*. (*PDBFF collection).*

FRENCH GUIANA. Compté River, Belizon, 80 km SSW of Cayenne, 24 Jan 1977 (fl), *S. A. Mori & Y. Veyret 8982* (MG); Saül, Monts La Fumée, 03° 37' N, 53° 12' W, alt. 200-400 m, 21 Sep 1982 (st), *B. Boom & S. A. Mori 1773* (NY); alt. 770 m, 27 Oct 1982 (st), *B. Boom & S. A. Mori 2427* (NY); La Fumée Mountain Trail, Antenne Nord., 03° 37'N, 53° 12' W, alt. 350–400 m, 27 Jul 1987 (st), *S. A. Mori et al. 18585* (NY); Station des Nouragues, Bassin de l'Approuague, 04° 03'N, 52° 42' W, 25 Mar 1992 (fl), *O. Poncy 885* (NY);

GUYANA. Potaro-Siparuni, Iwokrama Rainforest Reserve, Essequibo River, Ladysmith transect, 04° 17'N, 58° 30' W, alt. 75–100 m, 04 Oct 1995 (fr), *D. Clark 331* (NY).

SURINAME. Sipaliwini, Vicinity of Blanche Marie Waterfall on the Nickerie River, 04° 45’30” N, 56° 52’ 50”W, alt. 50 m, 30 Mar 1997 (fr), *R. Evans et al. 2692* (NY);

19. ***Pradosia restingae***– BRAZIL. Rio Grande do Norte: Natal, Mata das Dunas, 29 Dec 1952 (fl), *S. Tavares 52-146* (IPA); Natal, between Parque das Dunas and Universidade Federal do Rio Grande do Norte (UFRN), 05° 49’30” S, 35° 11’ 00” W, 21 Oct 1997 (fl), *L. A. Cestaro 97-0144* (IPA); Tibau do Sul, Santuário Ecológico de Pipa, Mata de Vassourinha, 05 Oct 1999 (fl), *K. Y. Arns 314* (IPA); Dunas, close to Barreira D’água, 19 Dec. 1964 (fl), *S. Tavares 1213* (HST); Close to Barreira D’água, 19 Dec 1964 (fl), *S. Tavares 1211* (HST); Pipa, restinga forest, 06° 14’03.3”S, 35° 03’26.0”W, alt. 55 m, 29 Sep 2011 (fl), *A. Alves-Araújo, A. et al. 1374* (INPA, MO, NY, S); Parnamirim, Centro de Lançamento da Barreira do Inferno, 20 Nov 2008 (fl), *R. A. Costa 64* (UFRN); Parnamirim, Centro de Lançamento da Barreira do Inferno, 18 Nov 2008 (fr), *A. M. G. Costa s.n.* (UFRN); Natal, UFRN, 28 Jun 2006 (fl), *T. Lima et al. s.n.* (UFRN); Parnamirim, Campo Exp. Prod. do Jiqui, EMPARN, 05° 55’ 45” S, 35° 11’ 15” W, 16 Feb 1999 (st), *L. A. Cestaro 99-0057* (UFRN); Natal, Campus da UFRN, área de entorno do Centro de Biociências, 13 Dec 2009 (fl, fr), *J. G. Jardim 5588* (INPA, UFRN); Natal, between Campus da UFRN and Parque das Dunas, 05°49’30” S, 35°11’00” W, 21 Oct 1997 (fl), *L. A. Cestaro, 97-0144* (UFRN); Parque das Dunas, 14 Oct 1980 (fl), *A. Trindade s.n.* (UFRN).

20. ***Pradosia schomburgkiana*** – BRAZIL. Amazonas: Manaus, Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, Igarapé do Acará, planta n. 3713-05, 02° 53’ S, 59° 58’ W, 27 Mar 1996 (fl), *J. M. Brito et al. 21* (RB); Igarapé da Bolívia, 09 Feb. 1995 (fr), *A. Vicentini et al. 862* (RB); Estação Biológica do INPA, Reserva da Campina, Km 45, N of Manaus, 26 Dec 1982 (fl), *T. Plowman et al. 12666* (RB); Borba, Rio Madeira, 3 miles E of the town, 04° 23’ S, 59° 35’ W, 22 Jun 1983 (st), *C. Todzia et al. 2227* (RB), São Gabriel da Cachoeira, estrada para Cucuí, km 30–35, beira da estrada, 01 Dec 1987

(bud), *H. C. Lima et al. 3366* (RB); Plateau of northen massif of Serra do Aracá, 00° 51-57' N, 63° 21-22' W, alt. 1200 m , 16 Feb 1984 (fr), *G. T. Prance et al. 29122* (INPA); 00° 51' N, 63° 22' W, alt.1150-1250 m , 15 Feb 1984 (fl), *I. L. Amaral 1586* (INPA). Pará: Marapanim, 00° 37' S, 47° 41'W, alt. 2-20 m , 3-4 Apr 1980 (fr), *G. Davidse et al. s.n.* (HRB); Maracanã, Ilha de Maiandeua, 15 Feb. 2002 (fl), *L. C. B. Lobato 2912* (MG); Oriximiná, Margem esquerda do Rio Mapuera, próximo às três ilhas, 01° 08' S, 57° 05' W, 25 Nov 1987 (bud), *C. A. Cid Ferreira 9679* (RB); Marapanim, E of fishing village of Camara which is ca. 11 km NW of Marudá, 00° 37' S, 47° 41' W, 2-20 m, 3-4 Apr 1980 (fr), *G. Davidse et al. 17792* (IAN); Tucuruí, 16 Km E of Represa Tucuruí, along the road (PA-263), 03° 45' S, 49° 39 W, alt. 70 m , 18 Mar 1980 (fr), *T. Plowman et al. 9724* (HRB).

GUYANA. Serrania Yutaje, Rio Manapiare, alt. 1300 m, 09 Feb 1953 (fl), *B. Maguire & C. K. Maguire 35095* (IAN); Potaro-Siparuni, Iwokrama Rainforest Reserve, Burro-Burro r., W along 5 Km long transect, km 1.4, 04° 38' N, 58° 49' W, alt. 75 m, 17 Nov 1995 (fr), *D. Clark & B. Hoffman 536* (NY); Region Cuyuni-Mazaruni, Waleliwatipu (Aymatoi), N of Paruima, in vic. of camp. 05° 53'N, 61° 01' W, alt. 1090 m, 05 Feb 1996 (fl), *D. Clark 997* (NY).

SURINAM. Tafelberg, Table Mountains, 11 Aug 1944 (fl), *B. Maguire 24305* (NY).

VENEZUELA. Atabapo, cabeça de Caño Cotúa (Yapacana), 03° 40' N, 66° 50' W, 25 May 1978 (fr), *O. Huber 1772* (INPA). Amazonas: San Carlos de Río Negro, ca. 20 km S of confluence of Rio Negro and Brazo Casiquiare, 01° 56' N, 67° 03' W, alt. 119 m, 04 Oct 1979 (fl), *H. L. Clark & P. Maquirino 7303* (NY); Carretera San Carlos de Río Negro-Solano, a unos 2–4 km de San Carlos, 01° 54'N, 67° 02' W, alt. 120 m, 25 Mar 2000 (fl), *P. E. Berry & G. Aymard 7137* (NY); Rio Negro, Slopes of Cerro Aracamuni, Quebrada camp. 01° 24' N, 65° 38' W, alt. 600 m, 20 Oct 1987 (fl), *R. Liesner & F. Delascio 22218* (NY); Atures, 8 km NW of settlement of Ytaje, plateau 3 km W of Río Coro-Coro, W of Serranía de Yutaje, 05° 41' N, 66° 09' W, alt. 1000–1050 m, 03 Mar 1987 (fr), *R. Liesner & B. Holst 21555* (NY). Bolivar: Alto Rio Cuyuni, Cerro Pitón, Cordillera Epicara, 04 Sep 1962 (fl), *B. Maguire et al. 53581* (IAN); Dist. Roscio, al S de Cantarana, aprox. 20 km al NE de Ikabarú, aprox. 95 km al W de Santa Elena de Uairén, 04° 25' N, 61° 40' W, alt. 850 m, 14 Aug 1984 (fr), *O. Huber & Clara Alarcon 9652* (NY).

21. ***Pradosia subverticillata*** – BRAZIL. Amazonas: Barcelos, 01° 46' S, 62° 14' W, 27 Sep 2010 (st), *J. F. L. Santos 471* (INPA); São Gabriel da Cachoeira, Rio Marié, 30 Jan 1942 (st), *R. Fróes 568* (NY); Rio Içana, Comunidade Boa Vista, 00° 16' 59.55" S, 67° 12' 25.92" W, 24 Jun 2009 (st), *M. H. Terra-Araujo et al. 579* (INPA, S).

22. ***Pradosia surinamensis*** – BRAZIL. Pará: Sete Varas airstrip on Rio Curua, 0° 95' S, 54° 92'W, 10 Aug 1981 (fr), *J. J. Strudwick et al. 4461* (INPA); Rio Maicuru, igarapé do Mutum, 3.30 hrs por canoa a motor de poupa acima da pista de pouso do Lageiro, 00° 55' S, 54° 30'W, 28-29 Sep 1981 (st), *J. Jangoux & B. G. S. Ribeiro 1563* (INPA). Roraima: SEMA Ecological Station Ilha de Maracá, 03° 22' S, 61° 25' W, 19 Mar 1987 (fr), *J. A. Ratter et al. 5774* (INPA); 03° 24' S, 61° 26'W, 10 Jun 1986 (fr), *M. J. G. Hopkins et al. 645* (INPA); Posto Mucajaí, Rio Mucajaí, 26 Mar 1971 (fr), *G. T. Prance et al. 11228* (INPA); Perto da Boca do Rio Ajarani, com Rio Branco 28 Apr 1974 (fr), *J. M. Pires et al. 14381* (IAN); Banks of Rio Apiaú, 30 km from mouth, 29 Jan 1967 (st), *G.T. Prance et al. 4165* (INPA); 10 km SE of Serra da Lua, 2° 25–29' N, 60° 11–14'W, 17 Jan 1969 (st), *G.T. Prance et al. 9332* (INPA)

GUYANA. Potaro-Siparuni, Essequibo R., 0-5 km N of Tiger Creek, 04° 32 N, 58° 35 ' W, alt. 60 m, 03 Oct 1996 (fr), *D. Clark 2758* (NY); Western extremity of Kanuku Mountains, in drainage of Takutu River, alt. 250 m, 4-22 Mar 1938 (fr), *A. C. Smith 3112* (IAN); Kanuko Mountains, Rupununi R., Crabwood Creek, 03° 10' N, 59° 24' W, 100 m, 03 Jul 1995 (fr), *M. J. Jansen-Jacobs et al. 4315* (NY).

23. ***Pradosia verticillata*** **–** BRAZIL. Amazonas: Manaus, Estação de Silvicultura Tropical, ZF2, (fr), *M. C. Lemos 228* (INPA); Reserva Florestal Ducke, Manaus-

Itacoatiara, km 26, Marco 512, tree n. 724, 02°56’S, 59°58’W, 9 Nov 2011 (st) *M. H. Terra-Araujo 857* (S).

FRENCH GUIANE. Saül, La Fumée Mountain, 03° N, 53° W, alt. 200–400 m, 14 May 1986 (st), *T. D. Pennington & S. A. Mori et al. 12128* (NY); 15 May 1986 (st), *T. D. Pennington & S. A. Mori et al. 12134* (NY).

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APÊNDICE

ARTIGOS PUBLICADOS

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1. Terra-Araujo, M. H., Faria A. D., Ribeiro, J. E. L. S. and Swenson, U. Flower biology and subspecies concepts in *Micropholis guyanensis* (Sapotaceae): evidence of ephemeral fowers in the family. *Australian Systematic Botany*, 25, 2012, pp. 295–303.

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