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INSTITUTO DE BIOLOGIA

CÁSSIO AUGUSTO PATROCÍNIO TOLEDO

A TAXONOMIC REVISION OF NEOTROPICAL *CONNARUS* L.
(CONNARACEAE)

REVISÃO TAXONÔMICA DAS ESPÉCIES NEOTROPICAIS
DE *CONNARUS* L. (CONNARACEAE)

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CONNARUS L. (CONNARACEAE)**

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Co-Orientador: DRA. EVELYNE JILL LUCAS

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Resumo

Connarus é o maior gênero dentro de Connaraceae e inclui aproximadamente 80 espécies no mundo, sendo a maioria delas distribuídas na região neotropical, em especial na Amazônia e Mata Atlântica. Dentre os representantes da família, *Connarus* se distingue morfológicamente pelo perianto com pontos glandulosos, gineceu unicarpelar, frutos em folículos relativamente mais largos que nos demais gêneros e sementes sem endosperma. O estudo filogenético mais abrangente em Connaraceae, baseado exclusivamente em morfologia, indica que *Connarus* é grupo irmão do clado formado por quatro gêneros nativos da África, embora novos dados genômicos sugiram algumas modificações. A presente revisão taxonômica permitiu identificar características morfológicas anteriormente não utilizadas, resultando em uma redefinição no conceito das espécies e publicação de novos táxons. Além disso, novas tipificações se mostraram necessárias. Por meio de uma análise extensa de materiais de herbário (mais de 3 mil espécimes), bem como expedições de campo, este trabalho de revisão reconhece 57 espécies de *Connarus* para a região neotropical, além de duas variedades e duas subespécies. A partir disso, descrições morfológicas completas para estes táxons são aqui apresentadas, acompanhadas de ilustrações e pranchas fotográficas, chaves de identificação e discussões detalhadas sobre distribuição geográfica, taxonomia e nomenclatura.

Palavras-chave: Morfologia; Nomenclatura; Oxalidales; Região Neotropical; Sistemática; Taxonomia.

Abstract

Connarus is the largest genus in Connaraceae and comprises approximately 80 species worldwide, mostly distributed in the Neotropical region, especially in the Amazonia and Atlantic Forest. Among the members of this plant family, *Connarus* is morphologically distinguished by the perianth with glandular dots, unilocular gynoeceum, follicular fruits relatively broader than in the other genera and seeds without endosperm. The most inclusive phylogenetic study on Connaraceae, based exclusively on morphology, indicates *Connarus* as sister to a clade formed by some African genera, although recent genomic data have suggested that modifications are needed. The present taxonomic revision allowed identification of morphological characters previously overlooked, leading to redefinition of species concept and the publication of new taxa. Moreover, new typifications have shown to be necessary. Though intense analyses of herbarium material (more than 3 thousand specimens), as well as field expeditions, this taxonomic work recognizes 57 species of Neotropical *Connarus*, along with two varieties and two subspecies. Therefore, complete morphological descriptions of these taxa are here presented, accompanied by illustrations and photographic plates, identification keys and detailed discussions on geographic distribution, taxonomy and nomenclature.

Key-words: Morphology; Neotropics; Nomenclature; Oxalidales; Systematics; Taxonomy.

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Introdução

Connaraceae possui 12 gêneros – ou 13 com a inclusão de *Bernardinia* Planch., gênero monoespecífico e restrito ao Brasil, reconhecido nos últimos trabalhos para os táxons neotropicais (Schellenberg 1938; Forero 1983; Toledo & Souza 2020), embora também tratado dentro de *Rourea* Aubl. (Lemmens 1989b; Lemmens et al. 2004) – e cerca de 200 espécies no mundo, morfologicamente reconhecidas pelas folhas alternas, compostas e sem estípulas, estames alternados em tamanho, carpelos 1 ou 5 livres e frutos em folículos (Lemmens 1989b; Lemmens et al. 2004). A família possui distribuição pantropical, com espécies ocorrendo principalmente na África Central, América do Sul e Ásia (Lemmens 1989b), com algumas poucas se estendendo além dos trópicos (Forero 1983; Lemmens et al. 2004). A África Central tem sido considerada como possível centro de diversificação da família, muito provavelmente porque a maioria dos gêneros – representando todas as quatro tribos – ocorre neste território (Lemmens et al. 2004), embora a maior parte da riqueza esteja distribuída na região neotropical, que abriga aproximadamente 100 espécies (Forero 1983).

Economicamente, Connaraceae se destaca por apresentar algumas espécies de interesse medicinal (Paim et al. 2020). Uma das propriedades mais referidas é a ação de compostos secundários antimicrobianos e antioxidantes, tal como mostram os trabalhos de Kalegari et al. (2011, 2014) e Reanmongkok et al. (2000) para *Rourea induta* Planch. e *Connarus semidecandrus* Jack, respectivamente. Além disso, *Connarus perrottetii* (DC.) Planch. é usada de forma similar ao barbatimão (*Stryphnodendron* spp. – Fabaceae) e possui propriedades anti-inflamatórias (Paracampo 2011), enquanto extratos de *Connarus favosus* Planch. têm sido utilizados por sua ação anti-hemorrágica (Silva et al. 2016).

A literatura referente aos aspectos de polinização em Connaraceae ainda é muito escassa. Devido ao tamanho reduzido das flores, à coloração no geral branca ou creme e ao perfume exalado, entende-se que as Connaraceae sejam polinizadas por pequenos insetos, em especial abelhas (Forero 1983). Os estudos mais recentes em biologia reprodutiva, baseados em *Connarus suberosus* Planch. (Paz 2019) e *Rourea induta* Planch. (Lenza et al. 2008), têm indicado que a entomofilia é predominante, com a grande maioria das visitas sendo feita por pequenas abelhas. Já os estudos relacionados aos processos de dispersão em Connaraceae são ainda mais limitados. Contudo, como os frutos são geralmente folículos chamativos (vermelhos ou alaranjados), contendo sementes negras de arilo vistoso, a hipótese mais aceita é de que as sementes sejam dispersas por aves (Forero 1983; Lemmens et al. 2004).

Linnaeus (1753) descreveu *Connarus*, posteriormente considerado como parte da família Terebinthaceae por Jussieu (1789), juntamente com *Cnetis* Juss., *Rourea* Aubl. e outros gêneros que vêm sendo reconhecidos como parte de Rutaceae ou Sapindaceae. De Candolle (1825) seguiu o trabalho de Jussieu (1789), mas considerou os gêneros de Connaraceae como uma tribo separada dentro de Terebinthaceae.

Antes disso, no entanto, Connaraceae havia sido descrita por Brown (1818), que propôs a separação de parte dos representantes de Terebinthaceae, baseando-se principalmente na posição e número de óvulos inseridos nos carpelos, além de dar grande importância ao número de carpelos para separar os gêneros. O autor incluiu *Cnetis*, *Connarus* e *Rourea* em Connaraceae e sinonimizou *Omphalobium* em *Connarus*, transferindo as espécies de Connaraceae com apenas um carpelo para este gênero.

Planchon (1850) também seguiu a proposta de Brown (1818) e tratou Connaraceae como família distinta, estabelecendo uma classificação que incluía a divisão desta em duas tribos (Connareae e Cnestideae Planch.), baseando-se principalmente na abertura das sépalas durante a prefloração e na presença ou ausência de endosperma. O autor ainda incluiu novos gêneros dentro da família, sendo a tribo Connareae formada por *Agelaea* Sol., *Bernardinia*, *Byrsocarpus* Schumach., *Connarus*, *Rourea*, e *Roureopsis* Planch. e Cnestideae formada por *Cnestidium* Planch., *Cnetis* e *Manotes* Sol.

Contudo, Gilg (1897), a fim de incluir o gênero recém-descrito *Jollydora* Pierre (nativo da África), sugeriu uma nova classificação para Connaraceae, dividindo a família em duas subfamílias: Jollydoroideae Gilg (com apenas *Jollydora*) e Connaroideae Gilg (demais gêneros). Schellenberg (1938) reconheceu as duas subfamílias propostas por Gilg (1897) e adotou a mesma circunscrição, mas subdividiu Connaroideae em cinco tribos (Agelaeae G. Schellenb., Byrsocarpeae G. Schellenb., Castanoleae G. Schellenb., Cnestideae e Connareae), com base principalmente na abertura das sépalas, número de carpelos, abertura e indumento dos frutos e presença ou ausência de endosperma nas sementes, além de propor novos gêneros (24 no total) e reconhecer 385 espécies dentro de Connaraceae.

A fim de propor uma classificação que refletisse o grau de parentesco entre os gêneros, Lemmens (1989c) propôs uma nova subdivisão da família, utilizando caracteres morfológicos para construção de um cladograma, tais como número de folíolos, número de carpelos, número de estames férteis e presença ou ausência de endosperma. Assim, a classificação mais recente para a família engloba quatro tribos: Cnestideae (incluindo cinco

gêneros), Connareae (incluindo cinco gêneros), Jollydoreae (Gilg.) Lemmens (com apenas *Jollydora*) e Manoteae Lemmens (com apenas *Manotes*).

Os estudos filogenéticos vêm demonstrando, com grande suporte, que a família é monofilética e pertence à ordem Oxalidales, juntamente com Brunelliaceae, Cephalotaceae, Cunoniaceae, Elaeocarpaceae, Huaceae e Oxalidaceae (APG IV 2016). Dentro da ordem, Connaraceae forma um grupo irmão com Oxalidaceae, sendo este posicionamento seguido por APG IV (2016) e por estudos comparativos de anatomia e histologia floral (Matthews & Endress 2002).

No que se refere ao gênero *Connarus*, historicamente o número de espécies reconhecidas variou muito ao longo dos anos. Os táxons até então tratados como *Omphalobium* foram transferidos para *Connarus* por Planchon (1850), que reconheceu 33 espécies para o gênero, enquanto Schellenberg (1938) reconheceu 121. Tais discrepâncias se devem, provavelmente, às diferenças nos conceitos de espécie adotados pelos autores, o que tem sido observado para Connaraceae de uma maneira geral (Breteler 1989; Lemmens et al. 2004).

Schellenberg (1938) propôs uma subdivisão para o gênero que incluía três subgêneros, separados com base na abertura e formato dos frutos: *Connarus* subg. *Connarus* – folículos semelhantes a legumes e ligeiramente assimétricos; *Connarus* subg. *Connarellus* – frutos exclusivamente em folículos; e *Connarus* subg. *Neoconnarus* – folículos semelhantes a legumes assimétricos. Contudo, Forero (1983) e Lemmens (1989a) argumentam que tais classificações infragenéricas são duvidosas e devem ser abandonadas até que estudos mais embasados sejam apresentados. Forero (1983) também sugeriu que somente *C.* subg. *Neoconnarus* sect. *Pseudotricholobus*, que inclui as espécies com tricomas dendroides nos ramos e inflorescências, parece representar um grupo natural e bem definido.

Embora a classificação infragenérica de *Connarus* seja um assunto em aberto e seu posicionamento filogenético dentro de Connaraceae ainda careça de análises baseadas em abordagens moleculares, o cladograma apresentado por Lemmens (1989c), ainda que baseado unicamente em dados morfológicos, fornece um importante panorama acerca das suas relações de parentesco dentro da família, principalmente porque neste estudo todos os gêneros de Connaraceae foram amostrados. De acordo com o autor, *Connarus* é um grupo irmão do clado formado pelos gêneros *Burttia* Baker f. & Exell, *Ellipanthus* Hook.f., *Hemandradenia* Stapf e *Vismianthus* Mildbr., que são táxons predominantemente africanos. Uma recente abordagem genômica acerca da Árvore da Vida das plantas e fungos (PAFTOL), ainda que preliminar,

identificou que *Jollydora* Pierre ex Gilg, um pequeno gênero restrito à África, faz parte do mesmo clado que inclui *Connarus* e alguns dos gêneros africanos citados acima (<https://treeoflife.kew.org/tree-of-life>). Contudo, uma amostragem mais abrangente ainda se faz necessária, uma vez que nem todos os gêneros de Connaraceae foram sequenciados, em especial *Hemandradenia* e *Burtia*, apontados como próximos filogeneticamente de *Connarus*, segundo Lemmens (1989c).

De acordo com a circunscrição de Lemmens et al. (2004), *Connarus* é o maior gênero de Connaraceae, consistindo de aproximadamente 75 espécies, morfologicamente caracterizadas pelo perianto com pontos glandulosos, gineceu unicarpelar e sementes sem endosperma (Forero 1983; Lemmens et al. 2004). Apesar da distribuição pantropical de *Connarus*, a maioria das espécies ocorre na região neotropical, que abriga 57 espécies do gênero.

O último tratamento taxonômico extenso lidando com as espécies neotropicais de *Connarus* foi proposto por Forero (1983), cujo trabalho ampliou os conhecimentos sobre o gênero na região, em especial na delimitação das espécies – até então reconhecidas com base majoritariamente em Baker (1871) e Schellenberg (1938), na indicação de tipos nomenclaturais e na publicação de novos táxons. Contudo, mais de 30 anos após a publicação da *Flora Neotropica* de Connaraceae (Forero 1983), ficou claro que os limites morfológicos das espécies de *Connarus* ainda careciam de um melhor entendimento e caracteres anteriormente desprezados deveriam ser utilizados, o que foi evidenciado, em um primeiro momento, a partir de um estudo taxonômico abrangendo *Connarus* na Amazônia brasileira (Toledo et al. 2020a). Além disso, novas espécies ainda têm sido descobertas (ver Toledo & Souza 2018; Toledo et al. 2019; Toledo et al. 2021). Por fim, ressalta-se a necessidade por atualizações nomenclaturais e de tipificação que, além de acompanhar as novas versões do código de nomenclatura Botânica, permitiram identificar lectotipificações equivocadas com implicações práticas (ver discussão sobre *Connarus ruber* (Poepp.) Planch. em Toledo et al. 2020b).

Somando-se a estes fatores, a incorporação de novas coleções de Connaraceae neotropicais em herbários nacionais e estrangeiros também contribuiu para o processo de delimitação dos táxons, principalmente considerando que diversas das espécies tratadas por Forero (1983) eram, até então, conhecidas por um único ou apenas poucos materiais.

Diante do exposto, o presente trabalho de revisão nomenclatural e taxonômica apresenta descrições morfológicas completas das 57 espécies neotropicais de *Connarus* aqui

reconhecidas, bem como ilustrações e pranchas fotográficas, chaves de identificação e mapas de ocorrência, além de discussões detalhadas sobre o reconhecimento dos táxons e questões nomenclaturais e de distribuição.

Objetivos

Geral:

- Ampliar o conhecimento taxonômico das espécies neotropicais de *Connarus*.

Específicos:

- Realizar o levantamento dos nomes publicados em *Connarus* para a região neotropical;
- Esclarecer os limites morfológicos entre as espécies neotropicais do gênero;
- Realizar a revisão nomenclatural e taxonômica das espécies neotropicais de *Connarus*;
- Apresentar descrições morfológicas completas das espécies reconhecidas;
- Discutir aspectos relacionados à distribuição e habitat das espécies estudadas.

Material e métodos

1) Levantamento bibliográfico e de espécies

O levantamento bibliográfico para o gênero está sendo baseado, principalmente, em Planchon (1850), Baker (1871), Schellenberg (1925, 1938), Forero (1983) e Breteler (1989b), além das obras originais onde os nomes foram publicados.

2) Análise dos materiais

Para a elaboração das chaves de identificação, descrição das espécies e discussões sobre ecologia e distribuição, foram utilizadas as informações disponíveis nas bibliografias citadas acima, nas etiquetas dos materiais depositados nos principais herbários do Brasil e exterior e em expedições de campo.

As atividades de laboratório foram realizadas nas dependências do Laboratório de Botânica Sistemática da Escola Superior de Agricultura “Luiz de Queiroz” (ESALQ-USP, Piracicaba), bem como no herbário de Kew (Londres, Reino Unido) durante o período de novembro/2018 a abril/2019. A análise morfológica foi feita a partir de materiais herborizados e as estruturas com tamanho reduzido (partes florais e tricomas) foram observadas com auxílio

de um estereomicroscópio. Para este último procedimento, as flores presentes nos materiais herborizados foram reidratadas com água fervida, possibilitando o manuseio das estruturas.

Os herbários que tiveram, até o momento, suas coleções analisadas (pessoalmente, por imagem nos herbários virtuais ou por meio de empréstimos) são aqueles com coleções representativas para o gênero *Connarus* na região neotropical, e estão discriminados na seção “Material and Methods” da versão para publicação do trabalho (ver “Resultados” logo abaixo). Informações adicionais pertinentes à realização e metodologia do projeto também são discutidas nesta seção subsequente.

3) Expedições de coleta

Para a coleta e registro fotográfico de algumas das espécies tratadas neste estudo, foram realizadas expedições de campo em diferentes domínios fitogeográficos do Brasil e em diferentes épocas do ano. Tais viagens foram organizadas com base nas localidades referidas em coletas disponíveis nos herbários virtuais do CRIA (<http://www.splink.org.br>) e REFLORA (<http://reflora.jbrj.gov.br/reflora/>). Estas atividades foram importantes para ampliar a quantidade de espécimes disponíveis, bem como observar as plantas em seu ambiente natural, adquirir informações que só podem ser visualizadas em campo e obter amostras de folhas a serem armazenadas em sílica gel para posterior extração e sequenciamento de DNA.

A lista completa das localidades amostradas é apresentada na versão para publicação (ver “Material and Methods”).

Resultados

Os resultados referentes a este projeto de doutorado são apresentados a seguir, sob forma de artigo científico, preparado para submissão na revista “Plant Systematics and Evolution”:

A taxonomic revision of Neotropical *Connarus* L. (Connaraceae)

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Abstract

The pantropical genus *Connarus* L. is the largest within Connaraceae and comprises ca. 80 species, most of which occur in the Neotropics. The genus is potentially economically important as several taxa produce metabolites of medicinal interest. Morphologically, *Connarus* differs from other members of the family mainly by the punctate perianth, the single carpel and follicular and relatively broader fruits than in the other genera. In the decades after the publication of the *Flora Neotropica* monograph of Connaraceae, new botanical collections have become available, especially in American herbaria, allowing identification of overlooked characters and, hence, redefinition of species circumscription. In addition, a significant number of typifications were outdated and taxonomic novelties have been recently proposed, all elements that justify a revisional work. After intensive examination of herbarium specimens and field expeditions, the present study recognizes 57 species, two varieties and two subspecies of *Connarus* in the Neotropics, ranging from south Mexico to south Brazil. Although most of these taxa occur in dense wet forests, especially in the Amazonia and Atlantic Forest, some are dispersed in savannahs from Brazil, Colombia and Venezuela, in Brazilian coastal vegetations or in montane formations; wide distributions are commonly seen in wet forests from Central America to north South America, while restricted occurrence or endemism are mainly observed in the Atlantic Forest, Peru and Venezuela. Complete morphological descriptions for the species of Neotropical *Connarus* are here provided, as well as illustrative images, identification keys, and detailed discussions on their taxonomy, nomenclature, distribution and habitat.

Introduction

Connarus L. is the largest genus in Connaraceae, comprising ca. 80 species (Lemmens et al. 2004), mainly from low land tropical wet forests or savannahs of South America, Central Africa, Madagascar and Southeast Asia (Leenhouts 1958; Forero 1983; Lemmens 1989b). Although the genus is pantropical, its species richness lies on the Neotropics, where approximately three-quarters of the total taxa occur (57 species are here recognized). In the Neotropical region, most species are distributed in the Amazon, followed by the Atlantic Forest, where nearly all taxa are restricted to each of these domains. Some species are dispersed in Central America, occasionally reaching adjacent islands of the Caribbean; only a few taxa surpass the Tropic of Cancer in south Mexico (Forero 1983).

Economically, several species of the genus have been used in traditional medicine and their pharmacological potential has been scientifically demonstrated (Paim et al. 2020). Some of the metabolites of medicinal interest include substances to treat bleedings, reported for *Connarus angustifolius* (Paracampo 2011), venom-induced haemorrhage from snakebites, reported for *C. favosus* Planch. (Silva et al. 2016), viral infestation, for *C. cochinchinensis* Pierre (Rizwana et al. 2010), among others (Coe et al. 2010; Farias et al. 2013; Castilho et al. 2014). The wood of some Neotropical species is appreciated for local folkcraft and construction (Baillon 1869; Forero 1983; Lorenzi 2008; Lorenzi 2009).

Species of *Connarus* are normally lianas, shrubs, scandent shrubs or treelets (less frequently trees), morphologically characterized by alternate, compound and imparipinnate leaves without stipules, pentamerous and actinomorphic flowers, androecium with two whorls of 10 stamens alternating in length, and follicular, attractive fruits with black seeds bearing colorful arils, differing from other Connaraceae especially by the punctate perianth and the single carpel (Forero 1983; Lemmens 1989a; Lemmens et al. 2004). Among the Neotropical genera of the family, the punctate perianth, the single carpel and the broader fruits are exclusively found in *Connarus* (Forero 1983; Toledo et al. 2020b).

The flowers in *Connarus*, as well as in other Connaraceae, have been treated as heterostylic and different reproductive systems can be recognized, such as heterodistyly, heterotristyly and homostyly (Burck 1887; Hemsley 1956; Baker 1962; Lemmens 1989c; Paz 2019). Some authors have pointed to a complex of polymorphisms and reproductive mechanisms in Connaraceae, while others have argued tendency towards dioecy (Hemsley 1956; Leenhouts 1958), with Lemmens (1989c) making particular reference to the Neotropical

species of *Connarus*. This latter case has been supported by a recent experimental study showing that, although the flowers of *C. suberosus* Planch. are morphologically perfect, they are functionally unisexual because anthers/ovules are sterile depending on the floral morph (i.e. relative variation in the length of stamens and ovaries among different individuals) (Paz 2019).

Lemmens (1989e), exclusively based on morphological data, recognized 12 genera in Connaraceae and found *Connarus* to be sister to a clade formed by the African genera *Vismianthus* Mildbr., *Ellipanthus* Hook.f., *Hemandradenia* Stapf and *Burtia* Baker f. & Exell. These, along with *Connarus*, have flowers with a single carpel (vs. 5 in other Connaraceae members), but *Connarus* differs from the formers mainly by the imparipinnate leaves, hairy petals and dehiscent fruits (Lemmens et al. 2004). Recently, a preliminary genomic study to the Plant and Fungal Tree of Life (<https://treeoflife.kew.org/tree-of-life>) found *Jollydora* Pierre ex Gilg, a small genus endemic to Africa, included in the same clade containing *Connarus*. This suggests that additional effort should be undertaken since *Hemandradenia* and *Burtia* were not sampled.

Connarus was described by Linnaeus (1753) based on *C. monocarpus* L. Ever since this publication, the number of species included in the genus varied greatly depending on author's concept and several generic names were published and then synonymized (Forero 1983). The first attempt to describe a significant number of new taxa in *Connarus* was made by De Candolle (1825a), but the author treated most of the species of the genus known at the time in *Omphalobium* Gaertn., considering it distinct from *Connarus* by the 1-carpellate flowers (vs. normally 5-carpellate). The same confusing concept was adopted by Poeppig (1845). Later, Planchon (1850) considered *Omphalobium* a synonym of *Connarus* and recognized 33 species in his work, 21 of which were newly described. Schellenberg (1938) followed Planchon's (1850) synonymization of *Omphalobium* and described most of the species in the genus, increasing to 121 the number of recognized species. Leenhouts (1958) found the number of recognized taxa by Schellenberg (1938) excessive and considered his concepts too narrow. Forero (1983) dealt only with the Neotropical species and followed some of Schellenberg's (1938) concepts, although considered *Connarus* to include 80–100 species worldwide. Lemmens (1989a) also found that too many taxa of the genus were being recognized and, in the same work (Lemmens 1989b), suggested that 77 species should be recognized. Following recent descriptions of new Neotropical *Connarus* and with the outcomes of the present revision, about at least 82 species of the genus should be considered.

In his extensive treatment, Schellenberg (1938) also proposed an infra-generic classification for *Connarus*, dividing the genus into three subgenera (*Connarus* subg. *Connarus* – referred to as *Euconnarus* –, *C. subg. Connarelus* and *C. subg. Neoconnarus*) and ten sections, mainly based on shape and dehiscence of the fruits. Leenhouts (1958), Forero (1983) and Lemmens (1989a) argued that this classification does not reflect species relationship and should not be taken up. Forero (1983), however, suggested that only *C. subg. Neoconnarus* sect. *Pseudotricholobus*, which includes species with dendroid trichomes, seems to be a well-defined group.

The last extensive systematic study on Neotropical *Connarus* was undertaken by Forero (1983). His contribution to the knowledge of the genus was enormous: new synonyms were proposed, eliminating several names of ambiguous identity. New species were described, some of which were widely distributed in herbarium collections, remaining undescribed for a long time. A more comprehensive identification key was presented and enhanced descriptions of species known only by few collections were also provided.

Nearly 40 years after Forero's (1983) work, a taxonomic treatment of *Connarus* from the Brazilian Amazon (Toledo et al. 2020a) revealed that still more species of the genus remained undescribed, overlooked morphological characters should be re-considered and typifications were needed. In addition, new collections of Neotropical *Connarus* have been made available in herbaria, which allowed re-evaluation of species concepts. It became clear that revisionary work was necessary, which is here provided. Therefore, the present study presents complete morphological descriptions of 57 species, identification keys, lists of synonyms, line-drawings, fully illustrated photographic plates, distribution maps and discussions on nomenclature, taxonomy, occurrence, habitat and phenology.

Methods

This study was primarily based on examination of specimens deposited in the following herbaria: A, ALCB, ASE, BHCB, BM, BR, C, CAY, CEN, CEPEC, COL, CR, CVRD, EAC, EAP, ECON, ESA, F, FI, FMB, FURB, G, GH, GOET, GUAY, HAL, HB, HBRA, HRCB, HSTM, HUA, HUVA, IAC, IAN, IBGE, IFAM, INB, INPA, JPB, K, LL, LOJA, LPB, M, MA, MAC, MBM, MBML, MEXU, MFS, MG, MIRR, MO, MSC, NY, OXS, P, PH, R, RB, RBR, RON, S, SAMES, SLUI, SP, SPF, U, UB, UC, UEC, UFACPZ, UFG,

UFMT, UFRN, UNIP, US, USM, VEN, VIC, VIES, W, WAG, XALU and YU (acronyms according to Thiers 2020). Some of the specimens destroyed at B during World War II were seen thanks to the negatives available in F. Therefore, practically all information provided in the descriptions is based on herbarium specimens. To describe habit and arrangement of petals, field observations were taken into account, complementing the morphological descriptions. Field expeditions were undertaken in Brazil, covering the following states and localities: Acre (Mâncio Lima, Rio Branco and Tarauacá), Bahia (Ilhéus and Porto Seguro), Espírito Santo (Conceição da Barra, Linhares and Marilândia), Pará (Itaituba and Santarém), Rio de Janeiro (Petrópolis, Rio de Janeiro and Saquarema), Roraima (Boa Vista) and São Paulo (Bertioga, Itirapina and Piedade). Specific literature for the genus (Planchon 1850; Baker 1871; Schellenberg 1925, 1938; Forero 1983) was accessed, essential to prepare a preliminary species list, consult previous proposed typifications and compare disagreements among authors.

General morphological terms follow Font Quer (1953), while venation patterns are based on Ellis et al. (2009) and inflorescence architecture mainly on Endress (2010), with a few adaptations from Weberling (1992). Relevant information on how morphological terminology was applied in the descriptions is discussed in the section “Morphology of the Neotropical species” (see below).

Geographic distribution maps were prepared using ArcGIS 10.5 (ESRI 2016), with precise/approximate coordinates based on the localities indicated on herbarium sheet labels. Distribution points on the maps were plotted over a shape file on Latin American ecoregions, proposed by Olson et al. (2001). Morphologically similar species were included in the same map when possible.

Synonyms and typifications

Homotypic synonyms are cited in the same paragraph as the accepted name for the taxon concerned, following the publication date of the species. When there are more than one homotypic synonym, they are cited in chronological order of publication (starting with the earlier). Heterotypic synonyms are cited in separate paragraphs, also according to chronological order of publication.

The designation “*pro syn.*” is frequently used when a name is merely cited as a synonym of an accepted species name, mostly observed in Schellenberg’s (1938) treatment of

Connaraceae from *Pflanzenreich* and in Baker's (1871) *Flora Brasiliensis* of Connaraceae, probably reflecting the use of a name which was written on herbarium specimens.

Most lectotypes proposed in the present study are second step lectotypifications. These are applied when Schellenberg (1938) or Forero (1983) selected a lectotype from available syntypes, but did not indicate in which herbarium the specimen was deposited or when they indicated a specimen and herbarium, but more than one specimen is deposited in the same designated herbarium. In the last case, such specimens are considered duplicates because they are in disagreement with article 8.3 of the *Code* (Turland et al. 2018). When a unicate has been mounted on more than one sheet, then all barcodes/accession numbers are cited. Comments on such issues are provided for the species concerned. Inadvertent lectotypifications are here considered when previous authors referred to a syntype as “type” or “holotype”, following Art. 7.11, Ex. 13 of the *Code* (Turland et al. 2018).

Results

During the development of the present taxonomic study, more than 3,000 herbarium specimens were analyzed, allowing the recognition of 57 Neotropical species of *Connarus* and two varieties and two subspecies. In the subsequent sections, morphological characters displayed by these taxa are discussed, followed by detailed descriptions.

All specific names described in the Neotropics were evaluated, accounting for 102 names (among accepted taxa, their basionyms and synonyms). From this total, 36 are here listed as heterotypic synonyms, nine of which are *nomida nuda* and three are illegitimate names. For specific and infraspecific names, 15 new synonyms (*syn. nov.*) are firstly considered here. Seven new species have been described since 2018 as part of the present study.

Morphology of the Neotropical species

Habit and branchlets: Most Neotropical species of *Connarus* are scandent shrubs or at least start development as shrubs with climbing branches that, in the undergrowth, climb on other trees towards the canopies so they are also treated as lianas (or woody vines). Following the most recent terminology for climbing habit (Sperotto et al. 2020), the Neotropical lianescent species have prehensile branches. When exposed in open fields, shrubby plants may

develop into small trees. In some cases, individuals of this genus are truly trees, either from savannahs, such as *C. suberosus*, or dense wet forest, such as the emergent Amazonian tree *C. angustifolius*.

Branchlets are fully covered by abundant lenticels which vary from inconspicuous to conspicuous; only a few species are not lenticellate. The majority of species have slightly striate branchlets, with few exceptions, including *C. suberosus*, a representative species of the Brazilian Cerrado, easily recognized by its suberized branchlets, and others with slightly fissured twigs.

Trichomes and indumentum: Several trichome types are found in different structures of the studied species. Tector trichomes can be simple unicellular, simple multicellular or ramified (dendroid); these are dispersed in vegetative and reproductive structures, such as branchlets, petioles, leaflet blades, inflorescence rachises, sepals, petals and fruits, and have proven to be of taxonomic importance. Glandular trichomes, on the other hand, are considered highly specialized, mainly found in reproductive parts, such as petals, stamens, and internal surface of fruits, although Denardi (2008) found them to be dispersed over petioles, rachises and leaflets when these structures are in early stages of development in *C. suberosus*. This study also found that such glandular trichomes function as secretory cells and accumulate pectin, starch and lipid, probably as a food resource (Denardi 2008). These trichomes consist of a multicellular stalk supporting a globose head, also multicellular and broader than the stalk. Denardi (2008) also suggested that glandular trichomes in such species are deciduous due to programmed cell death, reducing their use as a diagnostic feature.

Tector trichomes form the different indumentum types observed in the Neotropical species, defined here as follows: 1) pubescent, characterized by short or medium size trichomes, erect or almost so, not appressed; 2) sericeous, short or medium size trichomes, always appressed; 3) tomentose, densely covered by short or medium size trichomes, usually curved, matted; 4) lanate, densely covered by very long trichomes, erect, usually matted; and 5) hirsute, erect and long-sized trichomes, similar to lanate, though not as long, and not forming a dense and continued indumentum. The term “hairy” is used to name any indumentum other than glabrous or subglabrous, to simplify the comparison between pubescent/tomentose/sericeous/hirsute and glabrous/subglabrous. Some structures may become glabrescent with age, resulting in indumentum existing on young or early mature surfaces, followed by trichome loss over time.

Leaves and leaflets: Among Neotropical species of *Connarus*, leaflets vary in number from three to 25, and the basal pairs are slightly or significantly smaller than the apicals, so separate measurements are provided to the proximal and distal leaflets. When leaves are 3–7-foliolate, basal pairs refer to the first pair of leaflets; when the leaves are 9–25-foliolate, then basal pairs refer to the first and second pairs of leaflets; apical blades refer to all leaflets other than the basal ones. Some exclusively 3-foliolate species are occasionally found with unifoliolate or even bifoliolate leaves. However, this seems to be an unusual development of young branchlets, confirmed by the fact that, in those cases, vestiges of other leaflets can be seen in such leaves. These species are therefore treated as 3-foliolate. In the identification keys, leaflet number is frequently used as diagnostic so that, in several cases, exclusively 3-foliolate species are compared to those with three or more leaflets, but in the last scenario, herbarium specimens of the taxon concerned have the large majority of leaves with a variable number of leaflets, preventing these overlapping states from interfering with the key.

Most species with only simple trichomes have 3–7 leaflets, while those with dendroid trichomes are mostly multifoliolate. Leaflets vary considerably in texture, size and shape, while margins vary from flat to revolute. Blade bases are always subpeltate, varying from symmetric to asymmetric and with variable shape. Apices are almost exclusively acuminate, with the acumen varying in length. A separate measurement for the acumen is here provided, starting from the point where the apex becomes concave to the apex tip.

Leaflet venation is pinnate, with primary venation uninervate and secondary venation usually brochidodromous (although secondary veins may become slender around anastomosing areas). Secondary veins are here considered linear when they form a straight line from the midvein to the leaflet margin, ending where secondary veins diverge and merge into each other (Fig. 1A, D), or arcuate, when they form a concave ascending line, even after dichotomizing marginally (Fig. 1B, E). Secondary veins also vary in number and prominence. Tertiary venation is described with respect to its prominence and architecture, in which case intercostal veins can be opposite (Fig. 1E), alternate (Fig. 1C) or mixed percurrent (Fig. 1B) or reticulate (Fig. 1A), while the epidermal veins can be opposite percurrent (Figs. 1B, C, E) or reticulate (Figs. 1A, D).

Inflorescences: Both main axes and lateral branches are determinate, i. e. ending in a flower or bud (Fig. 2). Different taxonomic treatments for the genus have been ambiguous in defining whether inflorescences are determinate or not and which is the basic architecture. Most

studies treated the inflorescence of *Connarus* as a panicle, traditionally recognized as a ramified structure, but different authors diverge in defining whether it is determinate or not. Forero (1983), for example, described most *Connarus* inflorescences as panicles, or occasionally racemes, suggesting that the inflorescences are indeterminate. Lemmens (1989a) also used panicles to define inflorescences in *Connarus*, but his illustrations (Lemmens 1989d) show that he considered them determinate. An ongoing ontogenetic study on Connaraceae (Toledo et al., unpublished data) has found that inflorescences in *Connarus* are determinate.

The basic inflorescence unit in Neotropical *Connarus* is a thyrsoïd, composed of a primary determinate axis with several lateral branches formed by cymes (dichasia or monochasia) (Fig. 2A, 3C), as presented by Endress (2010). Such inflorescence architecture can be repeated laterally along the main axis of a larger inflorescence so that lateral branches are composed of thyrsoïds (the same basic unit described above), as well as the apex of the main axis. This pattern is here treated as a double thyrsoïd (Fig. 2E), in which case each first order ramification is a sub-thyrsoïd (Weberling 1992). Occasionally, primary axes in double thyrsoïds are extremely reduced in length (the internodes) so that several thyrsoïds appear to emerge from the same proximal point, displaying a fasciculate inflorescence formed of multiple thyrsoïds (Fig. 2F). Both double thyrsoïds and fasciculate thyrsoïds are occasionally seen in the same species, suggesting variance in which the rachis in a double thyrsoïd reduces to a fasciculate inflorescence composed of thyrsoïds, and/or that this fasciculate inflorescence can expand, giving rise to a double thyrsoïd (Fig. 2E–F). In a few species, inflorescences are mostly double thyrsoïds, but another ramification order may appear in the sub-thyrsoïds, leading to a pleiothyrsoïd (Weberling 1992).

Stachyoid spikes can also occur (sessile flowers and a determinate axis with no ramifications), as can botryoid racemes (a determinate inflorescence with pedicellate flowers and no lateral branches). These arrangements are found in *C. erianthus* (Fig. 2B) and *C. fasciculatus* (Fig. 2C), respectively.

Most inflorescences are axillary. Lemmens (1989d) recorded no terminal inflorescences in Connaraceae, but these are frequently disposed in the apex of a vegetative shoot where their axillary origin can be confirmed by the fact that, in some cases, leafy bracts subtend each inflorescence unit (Fig. 2D). This pattern is also observed in Neotropical species of *Connarus*, referred here as ‘pseudo-terminal’. Ramiflorous inflorescences are found in *C.*

ramiflorus and sometimes in *C. erianthus*, while cauliflory is observed in *C. fasciculatus* and *C. foreroi*.

Flowers: These structures are normally short pedicellate (up to 2(–5) mm long), with only a few species with sessile flowers. Flowers are subtended by solitary and usually triangulate bracts, also present in lateral branches.

Flowers are relatively small, aromatic, actinomorphic and pentamerous, with imbricate aestivation of sepals. Heterostyly has been widely described for *Connarus* and Connaraceae as a whole (Burck 1887; Hemsley 1956; Baker 1962; Lemmens 1989c; Paz 2019), implying, generally speaking, that pistils and stamens alternate in length depending on the individual: some with longistylous flowers (pistils longer than the stamens – Fig. 3F), others with brevistylous flowers (stamens longer than the pistils – Fig. 3E) or even medistylous flowers (short series of stamens shorter than pistils and long series of stamens longer than pistils). These are the basic types traditionally applied to members of this family, but studies have shown that heterostyly is highly diversified in Connaraceae so several reproductive systems can be recognized (heterodistyly, heterotristyly, homostyly, dioecy) depending on the species or specific group (Lemmens 1989c; Paz 2019).

Lemmens (1989c) extensively measured stamens and carpels of all 12 genera and 21 species of Connaraceae, mainly from Africa, while Paz (2019) analyzed ten genera and 86 species, mostly Neotropical. The former study subdivided heterostyly in Connaraceae based on eight different types, from which the two studied *Connarus* species (both African) were considered heterodistylous, one with ten fertile stamens and the other with five fertile plus five rudimentary stamens. Lemmens (1989c), however, highlighted potential difficulties in identifying fertile stamens and noted that Neotropical species present a different pattern in which carpels can be shorter than the two series of stamens (not seen in the African taxa), including a tendency towards dioecy. The latter study (Paz 2019) went further, identifying six different reproductive systems in 20 species of New World *Connarus*, including, for example, homostyly, distyly, dioecy and androdioecy. Paz (2019) also confirmed dioecy in *C. suberosus* by experimentally showing that “longistylous” flowers have sterile stamens and “brevistylous” flowers have sterile ovules. This was previously hypothesized by Denardi (2008), after noticing that microgametophyte development is interrupted in “longistylous” flowers and that glandular trichomes are dispersed only on filaments of “brevistylous” flowers, suggesting they may play a role for attracting pollinators, which may discriminate among different floral morphs.

Some of these reproductive patterns are easily observed in herbarium specimens of Neotropical *Connarus* as longistylous flowers have rudimentary stamens (very short with poorly developed anthers), while brevistylous flowers have rudimentary pistils (shorter ovaries with rudimentary or not developed styles and stigmas). Such findings might also help explain why individuals in the field can have fully matured fruits in the absence of developed seeds (Fig. 4G).

Taking all these factors into account, it seems coherent to suggest that different species of *Connarus* have different reproductive systems, in which heterostyly is highly diversified and a tendency towards dioecy can be hypothesized, as recorded for other flowering plant families (Ornduff 1966; Lloyd 1979; Naiki & Kato 1999; Watanabe et al. 2013). Therefore, considering the complexity of floral and reproductive mechanisms in *Connarus*, difficulties in establishing which floral organs are fertile/sterile and a lack of sufficient specimens for several Neotropical species, androecium and gynoecium measurements are here reported regardless of floral morph, i.e. size variations include any floral morph so no distinction of reproductive systems is presented in the subsequent descriptions.

Regarding floral structures, there are usually five sepals that are slightly basally connate to ca. 0.2 mm. Therefore, this length is not repeated in the descriptions and sepal measurements refer to the “lobes”, i.e. only the free portion of these structures. Some species with dendroid trichomes have four to five sepals and, in these cases, some sepals are connate to each other half their length or entirely, as specified in the descriptions. Sepals are short (ca. 2 mm long), normally ovate or triangulate, with external surfaces covered by sparse to dense indumentum, while the internal surfaces vary from glabrous to hairy. Normally, both surfaces are fully covered by glandular dots.

There are five petals per flower, cream or white-coloured, usually covered by glandular dots as well, which are brownish in nature (Fig. 3G), becoming black or colorless in herbarium specimens. Petals are narrow, slightly to significantly longer than the sepals, with broader apices (usually rounded) and narrower bases. Petals are normally erect (straight, oriented upwards, occasionally giving an impression of a false tube – Fig. 3G) or reflexed (curved downwards – Figs. 3A, E); some species appear to have an urceolate corolla (Fig. 8F). These variable arrangements have not previously been recorded in *Connarus*, although Forero (1983) described and illustrated petals in few species, as relatively united in their median portion, suggesting a possible diagnostic feature. This is indeed the case of some species, but

as petals are not truly fused, “adhered” seems to be the best term to refer to the erect petals forming a false tube. It is still unclear if such differences in arrangement are related to heterostyly, so this information was largely based on flowering specimens in which stamens are longer than pistils (brevistylous flowers). Corolla indumentum may be absent or sparse to hairy, with tector and/or glandular trichomes, usually denser on external surfaces.

The androecium is composed of ten stamens always connate at the base, with one series of five shorter epipetalous filaments alternating with another series of five longer episepalous filaments. In the descriptions, stamen lengths were measured from the base of the united portion to the anther apex, but the length of the fused tissue is provided separately. Glandular trichomes are usually dispersed on filaments. Anthers are obcordate, rimose.

Unlike other Neotropical genera of Connaraceae, the gynoecium in *Connarus* is 1-carpellate (vs. 5-carpellate). The ovary is short (ca. 1 mm long), suborbicular and externally densely hairy. When observed using a stereomicroscope, ovaries are clearly sessile, although Denardi (2008) used gynophore to define a particular tissue between the receptacle and the ovary. Styles are usually hairy in the base, becoming glabrescent towards the apex; the insertion point between the ovary and style is slightly laterally dislocated, becoming more evident during fruit development. The stigmatic surface is usually bilobate due to the carpel leaf, which is not entirely folded apically in the early stages of floral development (Fig. 3H). An exception is found in *C. erianthus*, whose stigmas are discoid with more than two inconspicuous lobes. Ovary placentation is marginal, with two ovules disposed side by side, only one developing into a seed.

Fruits: Fruits in *Connarus* are follicles, i.e. opening on a single side, but Schellenberg (1938) considered some species to have legume-like fruits with both sides opening during maturation, a characteristic the author used to define a subgenus in *Connarus*. Fruits in several herbarium specimens appear opened via two sutures, perhaps due to pressing technics as, when the fruits of the same species are observed in nature, they open just one side. This fact may have influenced Schellenberg’s (1938) infrageneric classification, which does not seem to reflect natural species relationships. In the Neotropics, *C. erianthus* and *C. fasciculatus* were found with legume-like fruits in nature, but evolutionary trends related to this character have not yet been addressed.

Immature follicles are greenish, then they become yellowish and subsequently orangish, finishing their maturity (when opening) reddish or red-orangish. These fruits vary in

shape from obovate to semi orbicular and laterally compressed (Fig. 4A). The dehiscent side is rounded (although not perfectly symmetric as apical portions are broader than basal), while the indehiscent side varies from linear to sigmoid, rarely concave. Although ovaries are sessile, a stipe occasionally develops in the fruits of some species, with length of taxonomic importance (see sessile fruit in Fig. 4D and long stipitate fruit in Fig. 4E). Styles usually develop a relatively prominent apiculus on fruit apices, which are occasionally spinescent or inconspicuous.

As ovaries are always externally hairy, the outer surfaces of fruits are hairy in early stages of development. In some species, the indumentum becomes rapidly glabrescent so that mature fruits are externally sparsely hairy, occasionally only or at least more densely on the stipe, base, sutures and/or apex. In other species, fruits are externally hairy even in late stages of development, becoming glabrescent only at maturity. Internally, fruits can be glabrous, pubescent, tomentose, hirsute, lanate or with sparse indumentum, and glandular trichomes may be present or absent.

Persistent calyces are quite common among Connaraceae members, so sepals can be ascending, patent or reflexed in Neotropical *Connarus*, but never accrescent (characteristic of *Rourea*). In the ascending case, *Connarus* sepals can be erect (straight, completely oriented upwards – Fig. 4B) or curved (base of sepal laterally oriented with tips arranged upwards – Fig. 4C). Patent sepals are erect and laterally oriented, while in the reflexed ones, apices are arranged downwards (Fig. 4F). In some species of *Connarus*, calyces are completely deciduous or at least partially persistent. Under such arrangement, a few sparse sepals or their remains are still attached to the base of the fruit/stipe in the same specimen, at least at some point during maturation (Fig. 4E).

Seeds: These are always black, ellipsoid and covered by a colorful aril embracing approximately one-third of the seed around the hilum. Lemmens (1989a) used the term sarcotesta to define the fleshy tissue in the seeds of *Connarus*, but Denardi (2008) showed that this structure is actually an aril. Mature seeds do not have endosperm.

Taxonomic treatment

Connarus L., Sp. Pl. 2: 675. 1753. Type species: *Connarus monocarpus* L.

Tali Adans., Fam. Pl. 2: 319. 1763.

Tapomana Adans., Fam. Pl. 2: 343. 1763, *nom. illeg.*

Omphalobium Gaertn., Fruct. Sem. Pl. 1: 217, t. 46. 1788.

Canicidia Vell., Fl. Flum.: 184. 1835.

Mathrancia Steud., Nomencl. Bot. ed 2: 404. 1840, *pro syn.*

Erythrostigma Hassk., Flora 25(2, Beibl.): 45. 1842.

Anisostemon Turcz., Bull. Soc. Imp. Naturalistes Moscou 20(1): 152. 1847.

Tricholobus Blume, Mus. Bot. 1: 236. 1850.

Lianas, shrubs, scandent shrubs or treelets, less frequently trees; branchlets glabrous to densely hairy, indumentum with simple and/or dendroid trichomes, usually lenticellate. *Leaves* alternate, compound, 3–17(–25)-foliolate, exstipulate; petioles and rachises cylindrical, pulvini and pulvinuli rugous; leaflets subpeltate, the basal ones slightly to significantly smaller than the apical ones, bases symmetric to asymmetric, apices usually acuminate, abaxial surfaces glabrous, subglabrous, sericeous, tomentose or lanate, frequently glabrescent with age, adaxial surfaces usually glabrous or subglabrous, when densely hairy, then glabrescent with age, dull to shining, margins entire, flat to revolute; venation pinnate, midveins uninervate, secondary veins brochidodromous, linear to arcuate, tertiary veins percurrent or reticulate. *Inflorescences* in thyrsoids or double thyrsoids, rarely stachyoid spikes or botryoid racemes, usually fasciculate, axillary or pseudo-terminal, rarely cauliflorous or ramiflorous, indumentum with simple and/or dendroid trichomes; bracts triangulate, subtending lateral branches and flowers. *Flowers* bisexual, frequently functionally unisexual due to rudimentary/sterile organs, short pedicellate, rarely sessile; sepals (4–)5, slightly basally connate by ca. 0.2 mm, rarely 2 or 4 connate entirely or half their length, both surfaces covered by abundant glandular dots; petals 5, free, white or cream, both surfaces covered by sparse to abundant glandular dots, rarely absent; stamens 10, basally connate, one series of 5 shorter epipetalous filaments alternating with another series of five longer episepalous filaments, glabrous or with glandular trichomes, anthers obcordate, rimose; carpel 1, sessile, externally densely hairy, stigma usually bilobate, ovules 2, placentation marginal, only one developing into a seed. *Fruits* follicular, reddish or red-orangish when mature, obovate (or variations of it), compressed laterally, sessile to stipitate, outer surfaces sparsely sericeous to glabrescent or

occasionally tomentose or lanate to glabrescent, inner surfaces glabrous to densely hairy, glandular trichomes present or absent, calyces persistent, partially persistent or deciduous, sepals ascending, patent or reflexed; seed 1, black, ellipsoid, usually without endosperm, outer surface with a colorful aril, covering ca. 1/3 of the seed around the hilum.

Diversity and distribution: *Connarus* is the largest genus in Connaraceae, comprising at least 82 species worldwide, pantropical (mainly Neotropics, central and south Africa, south Asia and north Australia). In the Neotropics, the limits of *Connarus* range from south Mexico (Guerrero) to south Brazil (Santa Catarina), comprising 57 species, most of which occur in wet forests of South America.

Key to the Neotropical species of *Connarus*

- 1a. Branchlets and inflorescences with dendroid trichomes 2
- 1b. Branchlets and inflorescences with only simple trichomes 19
- 2a. Branchlets suberized *C. suberosus*
- 2b. Branchlets slightly striate or slightly fissured, never suberized 3
- 3a. Leaflet bases asymmetric 4
- 3b. Leaflet bases symmetric, rarely slightly asymmetric 6
- 4a. Inflorescences in stachyoid spikes, rachises lanate *C. erianthus*
- 4b. Inflorescences in botryoid racemes or thyrsoids, rachises tomentose 5
- 5a. Secondary veins adaxially impressed or slightly so; inflorescences in botryoid racemes, cauliflorous or ramiflorous *C. fasciculatus*
- 5b. Secondary veins adaxially flat, rarely slightly impressed; inflorescences in botryoid racemes, axillary, rarely ramiflorous *C. pedicellatus*
- 6a. Leaflets abaxially tomentose 7
- 6b. Leaflets abaxially glabrous, subglabrous, tomentose or lanate to glabrescent or tomentose only on midvein, never tomentose when mature 9
- 7a. Trees; calyx with at least 2 sepals connate half their length or entirely *C. angustifolius*

- 7b. Lianas or scandent shrubs; calyx with all sepals slightly basally connate 8
- 8a. Leaflets adaxially dull, margins flat, rarely slightly revolute; secondary veins forming angles of 50–75° with midvein, epidermal tertiary veins percurrent; fruits internally pubescent, sparsely pubescent and/or with sparse to abundant glandular trichomes, rarely glabrous; Amazon Forest *C. perrottetii*
- 8b. Leaflets adaxially shining, margins revolute; secondary veins forming angles of ca. 80° with midvein, epidermal tertiary veins reticulate; fruits internally tomentose; Atlantic Rain Forest *C. tomentosus*
- 9a. Fruits 2.9–3.4 cm long *C. grandifolius*
- 9b. Fruits up to 2.2 cm long 10
- 10a. Calyces with at least 2 sepals connate half their length or entirely 11
- 10b. Calyces with all sepals slightly basally connate 15
- 11a. Midveins adaxially prominent; fruits externally lanate to glabrescent *C. wurdackii*
- 11b. Midveins adaxially impressed or slightly so; fruits externally tomentose to glabrescent 12
- 12a. Leaves 3–5-foliolate; tertiary veins adaxially slightly prominent *C. oblongus*
- 12b. Leaves 5–11-foliolate; tertiary veins adaxially flat 13
- 13a. Lianas; fruit stipes 1–3 mm long; Amazon Forest (north South America) *C. patrisii*
- 13b. Trees, treelets or shrubs; fruit stipes 2–6 mm long; Atlantic Forest, Caatinga and Cerrado (central, northeast or southeast Brazil) 14
- 14a. Length/width ratio of leaflets 3–4:1; petals 3–4 mm long, both surfaces with glandular trichomes; Atlantic Forest and Caatinga *C. deterrentus*
- 14b. Length/width ratio of leaflets 1.5–2.5:1, rarely 3:1; petals 4–4.5 mm long, both surfaces without glandular trichomes; Cerrado *C. suberosus*
- 15a. Secondary veins 8–12 pairs, forming angles of 60–80° with midvein; fruits 1–1.6 cm long *C. incomptus*
- 15b. Secondary veins 6–8(–9) pairs, forming angles of 40–65° with midvein; fruits 1.7–2.2 cm long 16
- 16a. Leaflets 3–5 foliolate; petioles 1.2–2.8 cm long; rachises 1.5–3.3 cm long *C. oblongus*

- 16b. Leaflets 5–11 foliolate; petioles 3.2–10.5 cm long; rachises 3.5–12.2 cm long 17
- 17a. Inflorescences in thyrsoids; north Venezuela *C. steyermarkii*
- 17b. Inflorescences in double thyrsoids; north Colombia and north Brazil 18
- 18a. Leaves 9–11 foliolate; apical leaflets narrowly ovate or narrowly elliptic, length/width ratio 3–3.5:1; north Colombia *C. guggenheimii*
- 18b. Leaves 5–9 foliolate; apical leaflets ovate, length/width ratio 2.5–2.75:1; north Brazil (Amazonas) *C. manausensis*
- 19a. Leaflets abaxially sericeous or tomentose throughout the blade 20
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Connarus acutissimus G. Schellenb., in Engler, Pflanzenr. IV. 127(Heft 103): 226. 1938.
Connarus ruber (Poepp.) Planch. var. *acutissimus* (G. Schellenb.) Forero, Fl. Neotrop. Monogr. 36: 115. 1983.—TYPE: Brazil. Amazonas: Rio Negro, May 1910, fl., *Ule* 8855 (holotype: B†; lectotype designated by Forero 1983: MG barcode MG013877!; isoelectotype: IAN!).

Connarus laevis G. Schellenb., Pflanzenr. (Engler) IV. 127(Heft 103): 226. 1938.—TYPE: Brazil. Minas Gerais: Caraça, entrada para o Rio, Feb 1881, fl., *A. F. M. Glaziov* 13676 (holotype: B†; lectotype **designated here**: P barcode P01819591!; isoelectotypes: C [photo!], F [n. v.], MO [n. v.]).

Lianas; branchlets slightly striate, glabrous or subglabrous, rarely sparsely sericeous, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3-foliolate; petioles 3.2–8.5 cm long, glabrous or subglabrous; rachises 0.8–1.8 cm long, glabrous or subglabrous; pulvinuli 4–6 mm long, glabrous or subglabrous; leaflets chartaceous to subcoriaceous, slightly discoloured or concolorous, flat, basal pairs 7.3–13.3 × 2.6–5 cm, symmetric, narrowly ovate, elliptic or narrowly elliptic, bases symmetric, rounded or obtuse, the apical ones 9.5–13.8 × 3.4–7 cm, symmetric, narrowly ovate, elliptic or narrowly elliptic, bases symmetric, rounded or obtuse, apices acuminate to long acuminate, acumen 6–13 mm

long, abaxial surfaces glabrous or subglabrous, occasionally irregularly sparsely sericeous on midvein or nearby, indumentum griseous, adaxial surfaces glabrous or subglabrous, rarely irregularly sparsely sericeous, dull, margins slightly revolute, rarely flat; midveins abaxially prominent, adaxially slightly impressed, secondary veins (9–)10–11 pairs, abaxially flat, rarely slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of 60–80° with midvein, linear, rarely slightly arcuate, tertiary veins flat on both surfaces, intercostals mixed percurrent or reticulate, epidermals reticulate. *Inflorescences* in thyrsoids, axillary, 2–5 per axil, trichomes simple unicellular, peduncles 0.2–0.9 cm long, sericeous or sparsely so, rachises 5–9 cm long, sericeous or sparsely so, lateral cymes 0.2–0.5 cm long, sericeous or sparsely so, indumentum of these structures ferruginous or brown; bracts 0.7–1 mm long, sericeous. *Flowers* with pedicels 0.3–0.5(–1) mm long; buds ca. 2×1.2 mm, ovate; sepals 5, slightly basally connate, $2\text{--}2.8 \times 0.5\text{--}1$ mm, ovate or narrowly so, occasionally narrowly triangulate, apices acute, outer surfaces sericeous or sparsely so, usually more densely at margin and apex, indumentum ferruginous or brown, inner surfaces subglabrous or sparsely sericeous, usually tomentose at apex; petals $3.5\text{--}5 \times 1\text{--}1.5$ mm, erect, narrowly obovate or narrowly elliptic, apices rounded or obtuse, glandular dots more than 10, loosely distributed, black or colorless, conspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous, rarely with sparse glandular trichomes; stamens basally connate by 0.5–1 mm, shorter series (1.2–)2.5–3.5 mm long, longer series (1.5–)3.3–4 mm long, filaments with glandular trichomes sparse to abundant; ovaries 0.8–2 mm long, densely pubescent, styles 1–2.5 mm long, stigmas bilobate, lobes ca. 0.5 mm long. *Fruits* $1.7\text{--}2 \times 1.2\text{--}1.4$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes (2–)3–4 mm long, styles partially persistent, apiculate, 1–2 mm long, outer surfaces irregularly sparsely sericeous, more densely at stipe and base, rarely subglabrous, indumentum ferruginous, black dots sparse to abundant, inner surfaces subglabrous or sparsely pubescent, glandular trichomes absent, calyx persistent, sepals ascending, rarely patent; seeds $0.9\text{--}1.1 \times 0.5\text{--}1$ cm, arils whitish.

Specimens examined: **Brazil.** Amazonas: In vicinibus Barra, Prov. Rio Negro, *s. d.*, fl., *R. Spruce* 1335* (P barcode P05615113); Lago do Janauari, margem direita do Rio Negro, 5 May 1961, fr., *W. Rodrigues & D. Coêlho* 2493 (INPA, NY); Lower Rio Negro, 20 km below mouth of Rio Cuieras, 24 Sep 1971, fr., *G. T. Prance et al.* 14786 (COL, INPA, K, MG, NY); Manaus. Capoeira baixa do Tarumã, 10 Feb 1958, fr., *W. Rodrigues & D. Coêlho* 1330 (INPA, NY); Comunidade Nossa Senhora de Fátima, Rio Taruma-mirim, 03°02'S, 60°17'W, 16 May 1992, fl., *L. V. Ferreira* 248 (INPA, K); Igarapé da Cachoeira, 28 Mar 1937, fl., *A. Ducke* 437

(IAN, K, NY, US); Ponta Negra, 22 Jun 1961, fr., *W. Rodrigues & D. Coêlho* 2875 (INPA, K). Rio Tiririca, afluyente do Rio Preto, 1 Jun 1964, fr., *W. Rodrigues & D. Coêlho* 5866 (F, INPA). Tefé, Nogueira, 25 Feb 1973, fr., *L. Krieger & Marilene* 12570 (INPA, SPF). *S. loc.*, *s. d.*, *A. F. Regnell* III395 (P barcode P05613564).

Distribution, habitat and phenology: *Connarus acutissimus* is exclusive to the Brazilian state of Amazonas, represented by few collections with no precise locations. It is apparently distributed along Rio Negro, with most of the records from the municipality of Manaus (Fig. 5). Individuals of this species are lianas, growing along river margins and in flooded areas, at low elevations. Specimens have been collected with flowers from February to May and with fruits in February, May, June and September.

The location of the type collection of *C. laevis* (*Glaziou* 13676) is likely to be inaccurate as the species is restricted to Amazonas state and there is no evidence of such disjunct distribution among the Brazilian species of the genus. In addition, it is well known that several Glaziou's collections have had their location intentionally changed (see, for example, Wurdack 1970).

Notes: *Connarus acutissimus* is morphologically recognized by the exclusively 3-foliolate leaves, leaflet margins usually slightly revolute, secondary veins with (9–)10–11 pairs, and inflorescences in thyrsoids. It can be mistaken for other lianescent species exclusively 3-foliolate, such as *C. lambertii* and *C. negrensis*, also for *C. araucanus*, although the latter being represented by shrubs or treelets. These four species share similar characteristics of inflorescence architecture, indumentum and punctuation of petals, and size, shape and indumentum of fruits. In addition, some of them are morphologically very variable, so that overlapping might occur. Therefore, differentiation of these species may be problematic, and this relies on very few and discrete characters; they can be separated by a careful analysis of leaflet shape and margin, number and orientation of secondary veins, and length of fruit stipe (Table 1).

Specimens of *Spruce* 1335 are deposited in K and P, but they seem to be a mixture of different species. Among all duplicates, only the one deposited in P (barcode P05615113) belongs to *C. acutissimus*; the others, both from K and P, represent *C. negrensis*. Specimen *Regnell* III395 from P (barcode P05613564) might not belong to this collector as this number correspond to the type of *C. regnellii*; in addition, *C. acutissimus* is exclusive to the Brazilian

Amazon, where Regnell never collected (Stafleu & Cowan 1983). Therefore, it seems that Regnell's name was erroneously included in the sheet label from collection P05613564.

Connarus acutissimus was once treated at varietal rank under *C. ruber* by Forero (1983). However, the former has linear secondary veins, inflorescences in thyrsoids, and fruits with sepals ascending and stipe (2–)3–4 mm long, while the latter has arcuate secondary veins, inflorescences in double thyrsoids, and fruits with reflexed sepals and the stipe 1–2(–3) mm long. These characteristics are sufficient to recognize *C. acutissimus* as a distinct species, following Schellenberg (1938) and Toledo et al. (2020a).

Connarus angustifolius (Radlk.) G. Schellenb., Candollea 2: 117. 1925. *Connarus perrottetii* var. *angustifolius* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20: 194. 1890.—TYPE: Brazil. Pará. [In sylvis aliariginibus prope Jacuary], 23 Aug 1819, fl., C. F. P. von Martius 2626 (lectotype first step designated by Schellenberg 1938: M; lectotype second step **designated here**: M barcode M-0243861 [photo!]; isoelectotypes: M [photo!]).

Trees, 2–30 m tall; branchlets slightly striate, tomentose or sparsely so, trichomes dendroid and simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 5–13-foliate (occasionally 3 in young branchlets); petioles 4–10 cm long, tomentose to glabrescent; rachises 4–18 cm long, tomentose to glabrescent; pulvinuli 4–8 mm long, tomentose to glabrescent; leaflets chartaceous to coriaceous, discolorous, flat, basal pairs $3.5\text{--}17 \times 2\text{--}6.5$ cm, symmetric, narrowly ovate, ovate, narrowly elliptic or elliptic, bases symmetric, rounded or obtuse, the apical ones $7\text{--}25 \times 2.4\text{--}7$ cm, symmetric, narrowly ovate, narrowly elliptic, lanceolate, oblong or narrowly obovate, bases symmetric, rounded or obtuse, apices short acuminate to acuminate, acumen 2–10 mm long, usually retuse, abaxial surfaces tomentose, indumentum griseous or brown, adaxial surfaces glabrous, shining or dull, margins slightly revolute, less frequently flat; midveins abaxially prominent, adaxially impressed, secondary veins 10–14 pairs, abaxially slightly prominent or almost flat, adaxially flat, concolorous in relation to the blade, rarely discolorous, forming angles of $45\text{--}65^\circ$ with midvein, arcuate or slightly so, tertiary veins flat on both surfaces, occasionally slightly prominent abaxially, intercostals mixed percurrent, epidermals opposite percurrent. *Inflorescences* in double thyrsoids, occasionally pleiothyrsoids,

axillary, 1–2 per axil, trichomes dendroid and simple unicellular, peduncles 0.3–4 cm long, tomentose, rachises 8–24.5 cm long, tomentose, lateral sub-thyrsoids 2.5–10.5 cm long, tomentose, indumentum of these structures ferruginous or brown; bracts 0.7–0.8 mm long, tomentose. *Flowers* with pedicels 0.8–2 mm long; buds ca. 2×2 mm, orbicular; sepals 5, 1–2 pairs with 2 sepals each connate entirely, $2\text{--}2.8 \times 1.5$ mm, ovate, apices obtuse, 1–3 sepals connate to the others at base or half their length, $1\text{--}2 \times 1$ mm, narrowly ovate or elliptic, apices acute, outer surfaces tomentose, indumentum brown, inner surfaces glabrous; petals $4 \times 0.8\text{--}1.5$ mm, reflexed, oblong, narrowly obovate or narrowly elliptic, apices rounded or obtuse, glandular dots 5 or more than 10, occasionally absent, loosely distributed, black, conspicuous or inconspicuous, both surfaces glabrous or subglabrous, outer surfaces occasionally sparsely pubescent, glandular trichomes absent, margins with only sparse to abundant glandular trichomes, rarely glabrous; stamens basally connate by 0.5–2 mm, shorter series 1.5–4 mm long, longer series 2.5–5 mm long, filaments with abundant glandular trichomes; ovaries ca. 1 mm long, tomentose, styles 1.2–3 mm long, stigmas bilobate, lobes ca. 0.2 mm long. *Fruits* $1.5\text{--}2.3 \times 1.2\text{--}1.7$ cm, semi-orbicular or obovate, indehiscent side sigmoid or almost linear, pericarps up to 2 mm thick, stipes 2–5 mm long, styles partially persistent, inconspicuous or apiculate, 0.2–2 mm long, outer surfaces tomentose to glabrescent, indumentum griseous, brown or ferruginous, black dots absent or abundant, inner surfaces with only sparse to abundant glandular trichomes, calyx deciduous or partially persistent, sepals reflexed; seeds $1.1\text{--}1.5 \times 0.7\text{--}0.9$ cm, arils yellowish.

Selected specimens examined: **Brazil.** Amapá: 10 km de Macapá, margem da Rodovia Macapá-Santana, 5 May 1982, fr., *N. A. Rosa & M. R. Santos 4308* (INPA, NY); Camaipi, EMBRAPA reserve and vicinity, 18 Sep 1983, fl., *S. Mori et al. s. n.* (NY); Macapá, APA de Curiaú, 3 Aug 1993, fl., *S. Bridgewater et al. 93* (INPA); Macapá, Parque Estadual da Fazendinha, 12km S of Macapá, 3 Aug 1983, fl., fr., *B. V. Rabelo 2289* (NY); Mazagão, BR 156, complete road toward Monte Dourado, 75–80 km WSW of Macapá, 5–10 km SE of Rio Preto, approx. $0^{\circ}08'S$, $51^{\circ}48'W$, 20 Dec 1984, fr., *D. C. Daly & R. Souza 3941* (NY); Porto Platon, 29 Oct 1957, fr., *E. Pereira 3370* (COL, NY, RB). Amazonas: Estrada Manaus-Itacoatiara, km 26, Reserva Florestal Ducke, estrada da Petrobrás, 29 Jul 1971, fl., *B. W. P. Albuquerque & L. F. Coêlho 1220* (INPA); Manaus, Reserva Ambiental Adolfo Ducke, estrada do Acará marco 1.10 km, 9 Dec 2015, fr., *M. C. Rodrigues et al. 429* (ESA). Maranhão: São Luis, Praia do Aracagi, 14 Aug 1989, fl., *M. C. L. C. Marques 243* (HRCB). Mato Grosso: Alto Araguaia, Serra da Saudade, camp 120 km beyond Alto Araguaia, Brasília-Acre Highway, 26

Aug 1963, fr., *B. Maguire et al. s. n.* (NY, RB); Cuiabá, mata ciliar no alto da Chapada dos Guimarães, perto da Cachoeira Véu da Noiva, Rio Coxipozinho, 15°30'S, 55°45'W, 21 Oct 1985, fr., *J. Pirani 1316* (INPA, SPF); Estação Ecológica de Iquê-Juruena, 8 Dec 1981, fr., *G. Guarim Neto & L. A. Neto 544* (INPA, UFMT); Gaúcha do Norte, propriedade de Alfredo Zingles, 13°10'S, 53°27', 5 Oct 2000, fr., *N. M. Ivanauskas 4404* (UEC, UFMT); Nobres, BR-163, Rod. Cuiabá-Sinop, Estr. da Fazenda Santa Maria do Amazonas a 65 km S de Sinop, 12°25'S, 55°45'W, 19 Sep 1985, fr., *C. A. C. Ferreira et al. 6154* (INPA); Nova Suiá, 14 Aug 1997, fr., *L. C. Bernacci 2446* (ESA, IAC); Pontes e Lacerda, quinto braço da Mineradora Santa Elina, 12 Sep 1997, fr., *A. G. Nave et al. 2105* (ESA, UFMT, UNIP); São Félix do Araguaia, área da Fazenda Jamaica, 28 km S do cruzamento das estradas BR-158 e MT-242 (Posto da Mata), 11°12'S, 51°52'W, 16 Oct 1985, fr., *C. A. C. Ferreira et al. 6476* (INPA); Tapurah, Estrada entre a Fazenda Contagro e o assentamento do INCRA (antiga fazenda Agrolasa), 12°22'S, 56°43'W, 300 m alt., 7 Jun 1997, fl., *V. C. Souza et al. 17311* (ESA, UFMT). Pará: Almeirim, 21 Jun 1984, fl., *N. T. Silva 5477* (INPA); Barcarena, Ilha da Trambioca, 19 Nov 2001, fr., *M. N. Bastos et al. 2370* (RB); Belém, IPEAN, 27 May 1964, fl., *N. T. Silva 57889* (NY, UB); Bragança, 13 Oct 1923, fl., *A. Ducke s. n.* (NY, RB); Curuçá, Abade, 14 Dec 1973, fl., *M. G. Silva 4056* (NY); Ilha de Marajó, 11 Apr 1927, fr., *A. Ducke s. n.* (NY, RB); Igarapé-Açu, estrada velha do cafezal, 00°58'38"S, 47°37'77"W, 27 Oct 2009, fr., *J. C. L. de Oliveira et al. 491* (IAN, RB); Jacundá, 3 km towards Jatobal, area to be flooded by Tucuruí dam, Rio Tocantins, 21 Oct 1977, fl., *A. S. Silva et al. 139* (NY); Juruti, estrada da PA Translago, 02°11'59"S, 56°53'85"W, 17 Jun 2007, fl., *M. B. Ramos et al. 263* (INPA); Marabá, Carajás, Serra Norte, Estrada H-7, 30 km do acampamento, 4 Aug 1982, fl., *U. N. Maciel et al. 747* (INPA, MG, NY); Maracanã, a 300 m do centro, 5 Jul 1977, fl., *E. Oliveira 6667* (NY, UB); Marapánin-Castanhal, km 12, 47°47'W, 0°44'S, 4 Jan 1976, fr., *P. Bamps 5110* (P); Martins Pinheiro, Campina do Mangaba, 28 Feb 1975, fr., *L. Coradin 123* (RB); Faro, 19 Aug 1907, fl., *A. Ducke 8394* (RB); Óbidos, Campos de Ariramba no lugar Tabuleta, 18km do Rio Jaramacaru, 01°10'S, 55°35'W, 6 Dec 1987, fl., *C. A. C. Ferreira 9798* (MG, RB); Porto Trombetas-Viveiro, estrada da mina, Km 7, área de campina, 20 Jun 1986, fl., *E. Soares 133* (INPA); Santa Isabel do Pará, Prope Santa Isabel (ad viam ferream inter Belém do Pará et Bragança), 22 Sep 1908, fl., *Herb. Amaz. Mus. Pará 9677* (P); Santarém, Km 35 da estrada do Palhão, arredores do acampamento do Igarapé Curupira, 20 Sep 1969, fl., *M. Silva & R. Souza 2653* (NY); Serra do Cachimbo, BR 163, Cuiabá-Santarém Highway, 8 Nov 1977, fr., *G. T. Prance 25069* (NY, RB); Serra dos Carajás, 7 km west of camp ECB on the ferrovia, ca. 52 km west of BR-150, 05°35'S, 49°15'W, 26 Mar 1982, fl., *C. R. Sperling et al. 6358* (NY); Serra

dos Carajás, Serra do Norte, ca 20 km N of AMZA Exploracion Camp, ca. 6°S, 50°15'W, 18 Oct 1977, fr., *C. C. Berg et al. BG621* (INPA, MG, NY, P); Sete Varas airstrip on Rio Curua, 00°95'S, 54°92'W, 7 Aug 1981, fl., *J. J. Strudwick et al. 4275* (INPA, MG, MO, NY, US); Tucuruí, Rio Tocantins, ca. 3 km NE of Repartimento (ca 140km on the road Marabá-Altamira), 26 Oct 1977, fr., *C. C. Berg et al. BG715* (NY, RB, UEC). Rondônia: Chapada dos Parecis a 29 km de Vilhena, 12°45'S, 60°10'W, 28 Oct 1979, fr., *M. G. Vieira et al. 740* (INPA, NY, RB); Colorado do Oeste, BR-364, Porto Velho-Cuiabá, estrada para Colorado do Oeste, km 18, Serra da Biquinha, 12°13'S, 60°61'W, 8 Jun 1984, fl., *C. A. C. Ferreira et al. 4375* (INPA, MG, MO, NY); Porto Velho, linha de transmissão Jirau/Sto Antonio, ponto 17, 13 Aug 2012, fl., *G. Pereira-Silva 16288* (RB); Road Vilhena to Colorado, 10 km from Vilhena (2 km from BR-264), 25 Oct 1979, fr., *J. L. Zarucchi et al. 2797* (INPA, NY, RB); Vilhena, estrada de Vilhena para Juína (MT) (BR-174), estrada vicinal à dir., pouco mais de 10 km de Vilhena, 8 Jun 2006, fl., *P. Fiaschi & I. J. Geremias 3010* (SPF).

Distribution, habitat and phenology: *Connarus angustifolius* is characteristic of the Brazilian Amazon, where it is widely distributed, occurring mainly in the states of Amazonas, Pará and Rondônia, also reaching transitional areas between the Amazon and the Cerrado in Mato Grosso (Fig. 6). It is the only representative of Neotropical *Connarus* with arborescent individuals reaching 30 m tall, thus being emergent trees in some areas. This species grows primarily in upland ombrophilous forests, but it is also found in semideciduous forests, arborescent cerrado or on top of dunes, in clay or sandy soils, at approximately 50–600 m elevation. Specimens have been collected with flowers, especially from April to October, and with fruits from August to April.

Notes: *Connarus angustifolius* is easily recognized by being tall trees with branchlets and inflorescences with dendroid trichomes, leaflets abaxially tomentose, inflorescences in double thyrsoids, calyx with at least 2 sepals connate up to the apex, and fruits with calyx deciduous or sepals reflexed. It resembles *C. deterrentus* due to their arborescence habit, narrow leaflets and at least 2 sepals connate up to the apex, but differs because the leaflets are abaxially tomentose and with 10–14 pairs of secondary veins in *C. angustifolius*, while they are glabrescent and with 6–9 pairs in *C. deterrentus*. In addition, the former occurs in the Brazilian Amazon, while the latter occurs in the Atlantic, Cerrado or Caatinga domains.

Connarus angustifolius was treated either at species level (Schellenberg 1938) or as a variety of *C. perrottetii* (Forero 1983; Toledo et al. 2020a). After conducting this revision,

it became clear that these taxa should be considered distinct species, even though they have similarities, such as leaflets and fruits tomentose. Therefore, *C. angustifolius* differs from the type variety of *C. perrottetii* by being trees (vs. lianas or scandent shrubs), with at least 2 sepals entirely connate (vs. all sepals only slightly basally connate), margin petals with glandular trichomes (vs. eglandular) and fruits with stipes 2–5 mm long (vs. fruits sessile or stipes 1–2(–4) mm long), apices usually apiculate (vs. apices usually rounded) and calyx deciduous or with sepals reflexed (vs. calyx persistent with sepals ascending or patent).

A second step lectotypification concerning the type of *C. angustifolius* was here adopted because there are at least four specimens of *Martius 2626* deposited in M and Schellenberg (1938), who firstly indicated the herbarium, did not make clear which sheet he referred to. These specimens are considered duplicates and each sheet bears a different barcode. The specimen with barcode M-0243861 was chosen as lectotype because it is the most complete material and includes original annotations and drawings.

Connarus araucanus Cuatrec., Brittonia 11(3): 164. 1959. *Connarus venezuelanus* Baill. var. *orinocensis* Forero, Brittonia 32(1): 41. 1980. *Connarus venezuelanus* Baill. subsp. *araucanus* (Cuatrec.) Cuatrec., Phytologia 49(1): 75. 1981, *syn. nov.*—TYPE: Colombia. Arauca: Corregimiento de Cravo Norte, región de Caño Rico, 20 Jan 1955, fl., J. Gómez J. 16 (holotype: US barcode US 00130987!). Fig. 7

Shrubs or treelets, rarely trees, 2–8(–12) m tall; branchlets striate, glabrous, subglabrous or sparsely sericeous, trichomes simple unicellular, lenticels conspicuous. *Leaves* 3-foliolate; petioles 3–7.5(–10) cm long, glabrous, subglabrous or sparsely sericeous; rachises 1.3–2.7(–3.9) cm long, glabrous, subglabrous or sparsely sericeous; pulvinuli 3–6 mm long, glabrous, subglabrous or sparsely sericeous; leaflets chartaceous to subcoriaceous, rarely coriaceous, slightly discolorous or concolorous, flat or conduplicate, basal pairs 6.2–13 × 2–4.6 cm, symmetric, narrowly ovate, narrowly elliptic or oblong, bases symmetric, rounded or obtuse, rarely subcordate, the apical ones 7.2–15 × 2.5–5.2 cm, symmetric, narrowly ovate, narrowly elliptic or oblong, bases symmetric, rounded or obtuse, rarely subcordate, apices short acuminate to acuminate, acumen 2–8 mm long, abaxial surfaces glabrous, subglabrous or sparsely sericeous to glabrescent, usually more densely on midvein or nearby, indumentum

brown or griseous, adaxial surfaces glabrous or subglabrous, shining, rarely dull, margins flat, rarely slightly revolute; midveins abaxially prominent, adaxially impressed or slightly so, secondary veins 9–14 pairs, abaxially flat, rarely slightly prominent, adaxially flat, rarely slightly prominent, discolorous in relation to the blade, rarely concolorous, forming angles of 55–75° with midvein, arcuate or slightly so, tertiary veins flat on both surfaces, occasionally abaxially slightly prominent, intercostals opposite percurrent, epidermals mixed percurrent. *Inflorescences* in thyrsoids, axillary or pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncles 0.2–1 cm long, sericeous or sparsely so, rachises 7–24 cm long, sericeous or sparsely so, lateral cymes 0.2–0.8(–2) cm long, sericeous or sparsely so, indumentum of these structures ferruginous; bracts 0.5–1 mm long, sericeous. *Flowers* with pedicels 0.5–2 mm long; buds ca. 2 × 2 mm, orbicular; sepals 5, slightly basally connate, (2.2–)2.5–3.5 × (0.5–)0.8–1.5 mm, ovate or narrowly so, occasionally narrowly triangulate, apices acute or obtuse, outer surfaces sericeous or tomentose, indumentum ferruginous or brown, inner surfaces glabrous, subglabrous or sparsely sericeous, pubescent or sericeous only at apex; petals 3.2–5 × 1.3–2 mm, erect, narrowly obovate, apices rounded or obtuse, glandular dots more than 10, loosely distributed, black, conspicuous or inconspicuous, both surfaces glabrous or subglabrous, rarely sparsely pubescent, glandular trichomes absent or sparse, margins glabrous or with sparse to abundant glandular trichomes; stamens basally connate by (0.3–)0.8–1(–1.5) mm, shorter series 1.5–3.5 mm long, longer series (2.2–)2.5–5 mm long, filaments with sparse to abundant glandular trichomes, rarely glabrous; ovaries 0.7–1 mm long, densely pubescent, styles 1.5–2.5 mm long, stigmas bilobate, lobes 0.5–0.8 mm long. *Fruits* (1.5–)1.7–2.2 × (1–)1.2–1.6 cm, obovate, indehiscent side sigmoid or slightly so, pericarps up to 2 mm thick, stipes 3–7 mm long, styles partially persistent, apiculate, (0.5–)1–2 mm long, outer surfaces subglabrous or irregularly sparsely sericeous, more densely at stipe, base and sutures, indumentum ferruginous or brown, black dots sparse to abundant, inner surfaces sparsely tomentose or sparsely pubescent, rarely subglabrous, glandular trichomes absent, calyx deciduous to persistent, sepals reflexed, patent or ascending erect; seeds 1.1–1.4 × 0.6–0.8 cm, arils yellowish, rarely whitish.

Selected specimens examined: **Bolivia.** Beni: Ballivián, Espiritu en la zona de influencia del rio Yacuma, 200 m., 24 Aug 1985, fr., *S. G. Beck* 5709 (COL, K). La Paz: Larecacha, Copacabana (about 10 km. south of Mapiri), alt. 850–950 m, 8 Oct–15 Nov 1939, fl., *B. A. Krukoff* 11172 (G). **Colombia.** Boyacá: 2 Km NE de Mani, cano de las Panelas, 19 Feb 1971, fl., *C. Sastre* 740 (P); 34 km SW de Hato Yarumito, 45 km de Mani, cano Guira, 23 Feb

1971, fl., *C. Sastre* 841 (P). Casanare: Orocué, Río Meta, 25 Jul 1897, fr., *F. C. Lehmann* 8797 (K). Meta: Carretera Puerto Gaitán-San Pedro de Arimena, sitio “Nieblina”, 4°35’N, 71°38’W, alt. 220 m, 9 Dec 1993, fr., *R. Sastre & G. González* 1115 (P). **Venezuela.** Amazonas: Átures, Puerto Ayacucho, end of road from airport to Río Orinoco, 4 Apr 1984, fl., *T. Plowman* 13471 (F); Puerto Ayacucho, 100 m, May 1931, fr., *E. G. Holt & E. R. Blake* 794 (F, US); Region of San Fernando de Atabapo, occasional in sabanita on right bank of Cano Cupueni 0.5 km above mouth, 120-130 m, 16 Feb 1964, fl., *B. Maguire et al.* 37686 (K, NY); Sabana Jivao, Caño Jivao on right bank of Río Orinoco opposite Minicio, 125 m, 1 Aug 1959, fr., *J. J. Wurdack & L. S. Adderley* 42728 (K, NY); Seasonally inundated forest mostly on sandy river bank along Río Orinoco behind Puerto Ayacucho airport, alt. 100 m, ca. 5°40’N, 67°40’W, 100 m, 5 Apr 1984, fr., *A. H. Gentry & B. Stein* 46361 (K, MO); *S. loc.*, 100 m, 20 May 1940, fr., *L. Williams* 13033 (K). Anzoátegui: Río Mapire, afluente norte del Río Orinoco Medio, 7°30’-8°30’N, 64°30’-65°00’W, 10 Aug 1986, fr., *J. Rosales & J. L. Valles* 12 (NY); Río Mapire, distrito Monagas, a 10 minutos de la población de Mapire, 7°30’N, 64°30’W, 20 Jan 1995, fr., *S. Flores et al.* 77 (NY). Apure: Near La Guama, S. of San Fernando de Apure, on road to San Juan de Payara, 18 May 1964, fr., *F. R. Fosberg* 45316 (NY); Pedro Camejo, banks of Río Orinoco on Isla Poyatón opposite the Serranía de Baraguán on the Apure side of Estrecho de Baraguán of the Río Orinoco, 7°02’N, 67°05’W, 27 Apr 1977, fr., *G. Davidse & A. González* 12224A (P); Pedro Camejo, Parque Nacional “Santos Luzardo”, bosque de galería a lo largo del caño “El Porvenir” a 500 m de la base E de Las Galerías del Cinaruco, 6°39’N, 67°16’W, Mar 1992, fl., *G. Aynard & R. Schargel* 10284 (NY); Pedro Camejo, southern bank of Río Cinaruco, 3 km directly S of Pesquero (in a straight line), 6°36’N, 67°14’W, 28 Apr 1977, fr., *G. Davidse & A. González* 12246A (P); San Fernando, ca. 4.5 airline miles ESSE of San Carlos del Meta along the banks of the Río Meta, 6°19’N, 67°50’W, 9–11 Feb 1978, fl., *G. Davidse & A. González* 13814 (P); Barinas: El Morrocroy, Sta Lucía, 100-150 m, 6 Apr 1954, fl., *Bernardi* 1198 (K); Reserva Florestal Caparo. Unidade Uno, 15 Mar 1971, fr., *H. J. Saa* 1316 (NY); Zonas inundadas em invierno, unidad I, al este del Campamento Cachicamo, este de El Cantón, 100 m, 11 Apr 1968, fr., *J. A. Steyermark et al.* 102121 (NY). Bolívar: 1 km east of Río Orinoco between mouth of Río Horeda and Cerro Gavilan (Cerro Carichana), 100 m, 16 Jul 1955, fl., *J. J. Wurdack & J. V. Monachino* 39914 (NY, P); Cadeño, margen derecha del Río Cuchivero, em los alrededores del embarcadero, 25 Mar 1988, fr., *C. E. de Rojas et al.* 3912 (F, MO, NY); Canton de Upatá, Puerto de Tallus, 1864, fl., *R. Grosourdy* 13 (P); Cerro Altamira, 10 km east of Ciudad Piar, 425-650 m, 19 Oct 1953, fr., *B. Maguire et al.* 35884 (K, NY, P); Guyana, canton de Upata, Puerto de tullus, 1864, fl., *R. Grosourdy* 13 (P); La Urbana, Orinoco River,

80 m, 08 Mar 1949, fl., *B. Maguire & B. Maguire Jr* 29009 (NY); Río Parguaza, locally frequent at savana margins near Pilon, 5 km. Northeast of river mouth, 100 m, 5 Jan 1956, fl., *J. J. Wurdack & J. V. Monachino* 41121 (K, NY); Sucre, Hato el Torno, 7°56'N, 64°28'W, Apr 1987, fl., *A. Fernandez* 4249 (NY). Guárico: Estación Biológica de los Llanos, 24 Feb 1980, fl., *N. Ramírez* 250 (NY); Estación Biológica de los Llanos de la Sociedad Venezolana de Ciencias Natulares, ubicada aproximadamente a 12 km S. E. de Calabozo, 08°56'N, 67°25'W, 22 Jul 1987, fr., *N. Ramírez* 2304 (K); Montaña (parque) de Carapa, Parmana, 28 Apr 1955, fr., *F. Tamayo* 4054 (P); Río Orituco, aprox. 8 km de la Estación Biológica de los Llanos, 24 Feb 1980, fl., *N. Ramírez* 257 (K); Monagas. A 5 km al oeste de la compuerta del cano Monamo, 08°53'N, 62°03'W, 11 Aug 1989, fr., *F. Zuloaga et al.* 4385 (K, VEN); Carretera a unos 10 km de Tucupita, 13 Jun 1979, fr., *G. Ferrari* 1923 (F, NY). *S. loc.* Hato los Cocos, 14 Mar 1985, fl., fr., *J. M. Lorde* 85/31 (K); *s. d.*, fl., *W. Gehringer* 129 (G). *S. loc.*, *s. d.*, fl., *R. Grosourdy s. n.* (F-frag.).

Distribution, habitat and phenology: *Connarus araucanus* mainly occurs in northeast Colombia and in Venezuela, especially along Orinoco River, but also reaching the northwest portion of the country (Fig. 5). Two specimens were found in north Bolivia, departments of Beni and La Paz, which represents an unusual disjunction among Neotropical *Connarus*. However, although separated by hundreds of kilometers, the populations from north South America and north Bolivia occupy similar environments as they are distributed in seasonally flooded savannahs of the Orinoco and the Llanos de Moxos, respectively. A more comprehensive floristic comparison between these two similar ecosystems has not yet been carried out, but they show similarities in floristic composition (Huber et al. 2006; Plotkin 2011), aside from the hypothesis that connections may have existed in the past (Silva & Bates 2002). Nevertheless, additional efforts should be undertaken in order to understand this disjunct distribution of *C. araucanus* and evaluate how these populations diverge morphologically.

Individuals of *C. araucanus* are shrubs or usually small trees occurring in savannahs influenced by river courses, especially in seasonally flooded areas of the Venezuelan Llanos, growing on sandy soils, at elevations ranging from ca. 100–650 m. Specimens have been collected with flowers from January to April and with fruits irregularly from January to October.

Notes: *Connarus araucanus* is recognized by the exclusively 3-foliolate leaves, leaflets narrowly ovate, narrowly elliptic or oblong, 9–14 pairs of secondary veins,

inflorescences in thyrsoids, and fruits usually sparsely pubescent or sparsely tomentose internally. It is morphologically similar to *C. acutissimus* and *C. lambertii*, but differs mainly in leaflet shape, number of secondary veins, inflorescence rachis length, and fruit stipe (Table 1).

Forero (1980a, 1983) treated *C. araucanus* as a variety of *C. venezuelanus*, while Cuatrecasas (1981) included it at subspecies level under the same species, even though Cuatrecasas (1959) had previously published this taxon at species level. It seems that Forero (1980a, 1983) took his decision after noticing that both *C. araucanus* and *C. venezuelanus* have leaflets abaxially sparsely sericeous, similar inflorescence architectures and sepals internally sparsely sericeous in the upper half. Following Forero's varietal name, Cuatrecasas (1981) agreed to the recognition of two infraspecific taxa, but considered that they should be treated at subspecies level, given the consistent morphological differences and their distributions. However, after analyzing additional collections, it was found that leaflet indumentum in both species seems to be deciduous, so that trichomes are denser in young leaflets, becoming glabrous when mature, which is the case of several other Neotropical *Connarus*. Additionally, most *Connarus* have inflorescences in thyrsoids, and several have sepals internally sparsely sericeous. Therefore, this review considers *C. araucanus* and *C. venezuelanus* as two separate species: the former has leaflets chartaceous to subcoriaceous, rarely coriaceous, which are narrowly ovate, narrowly elliptic or oblong, acumen not spinescent 2–8 mm long, 9–14 pairs of secondary veins, and fruits usually sparsely pubescent or sparsely tomentose internally, while the latter has leaflets coriaceous, which are elliptic, ovate or obovate, acumen spinescent usually 6–13 mm long, 7–10 pairs of secondary veins, and fruits glabrous or subglabrous internally. Also, the recognition of two infraspecific taxa does not make much sense as both species are sympatric.

Connarus aureus C. Toledo, Phytotaxa 415(1): 66. 2019.—TYPE: Brazil. Espírito Santo: Marilândia, Alto Liberdade, propriedade de Deuclecio Lorenzini, 19°21'12"S, 40°31'02"W, 18 Oct 2018, bd., fr., C. A. P. Toledo & N. C. Bígio 397 (holotype: ESA 141713!; isotypes: K!, RB!). Fig. 8

Scandent shrubs, ca. 4 m tall; branchlets slightly striate, sparsely sericeous, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3–7-foliolate, occasionally 1-foliolate when subtending inflorescences; petioles 2.7–3.8 cm long, subglabrous or sparsely sericeous; rachises 1.7–5 cm long, subglabrous or sparsely sericeous; pulvinuli ca. 3 mm long, subglabrous; leaflets chartaceous, discolorous, flat, basal pairs $2.6\text{--}4 \times 1.4\text{--}2.2$ cm, symmetric, elliptic, obovate or ovate, bases symmetric, rounded or obtuse, the apical ones $4.5\text{--}9.5 \times 2.2\text{--}4$ cm, symmetric, elliptic, obovate or ovate, bases symmetric, rounded or obtuse, apices short acuminate, acumen 2–4 mm long, abaxial surfaces sericeous, indumentum aureous, adaxial surfaces glabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed, secondary veins 7–9 pairs, abaxially flat or slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of $70\text{--}80^\circ$ with midvein, linear, tertiary veins abaxially flat or slightly prominent, adaxially flat, intercostals and epidermals reticulate. *Inflorescences* in thyrsoids or double thyrsoids, axillary or pseudo-terminal, 1–2 per axil, trichomes simple unicellular, peduncles 0.3–0.6 cm long or inflorescences subsessile, sericeous or densely pubescent, rachises 10.5–16 cm long, sericeous or densely pubescent, lateral cymes ca. 0.5 mm long, sericeous or densely pubescent, lateral sub-thyrsoids 2.2–4.8 cm long, sericeous or densely pubescent, indumentum of these structures aureous; bracts ca. 2 mm long, sericeous. *Flowers* with pedicels 1–2 mm long; buds ca. 2×2 mm, orbicular; sepals 5, slightly basally connate, $3 \times 1.3\text{--}1.5$ mm, narrowly ovate, apices acute, outer surfaces sericeous, indumentum aureous, inner surfaces glabrous or subglabrous; petals ca. 4×1.5 mm, slightly reflexed (urceolate-like), narrowly obovate or oblanceolate, apices obtuse, glandular dots more than 10, loosely distributed, black or brown, conspicuous or inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous; stamens basally connate by ca. 0.5 mm, shorter series ca. 1.2 mm long, longer series ca. 1.8 mm long, filaments glabrous; ovaries ca. 1.2 mm long, densely pubescent, styles ca. 1.5 mm long, stigmas bilobate, lobes ca. 0.3 mm long. *Fruits* $1.7\text{--}2.3 \times 1.3\text{--}1.7$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 1–3 mm long, styles partially persistent, apiculate, ca. 0.2 mm long, outer surfaces densely velutinous or tomentose to glabrescent, indumentum ferruginous, black dots absent, inner surfaces subglabrous or sparsely pubescent, glandular trichomes absent, calyx persistent, sepals ascending erect; seeds $1.1\text{--}1.3 \times 0.7\text{--}0.8$ cm, arils yellowish.

Specimens examined: **Brazil.** Espírito Santo: Marilândia, Alto Liberdade, Prop. Delclecio. $19^\circ 21' 7''\text{S}$, $40^\circ 30' 51''\text{W}$, alt. 150–350 m, 13 Sep 2007, fr., R. R. Vervloet et al. 3516

(MBML, UB); 19°21'13"S, 40°31'01"W, alt.: 300–400 m, 19 Apr 2006, fr., *L. F. S. Magnago et al.* 952 (MBML, RB, UB).

Distribution, habitat and phenology: *Connarus aureus* is represented by scandent shrubs, apparently restricted to central Espírito Santo, southeast Brazil (Fig. 9). Only one population of this species has been identified and the three specimens cited here might be the same individual, collected in a degraded slope surrounded by eucalyptus or coffee plantations, at ca. 320 m elevation. Specimens have been collected with fruits in September, October and April.

Notes: Although only known by few collections, *C. aureus* is easily distinguished by the 3–7-foliolate leaves, leaflets discolorous, abaxially sericeous, and fruits externally densely velutinous or tomentose, with calyx persistent and sepals ascending. Among the species with only simple trichomes, *C. aureus* can be confused with *C. favosus* due to the number of leaflets and indumentum on the abaxial surfaces, but the former differs by the leaflets chartaceous with flat margins (vs. leaflets coriaceous with revolute margins) and fruits internally subglabrous, with stipes 1–3 mm long (vs. fruits internally sparsely hirsute or sparsely pubescent, sessile or with stipes 0.5–1 mm long). In addition, *C. aureus* is restricted to the Atlantic Forest in southeast Brazil, while *C. favosus* is restricted to the Amazon in north Brazil.

Connarus beyrichii Planch., *Linnaea* 23: 430. 1850.—TYPE: Brazil. *S. loc.*, *s. d.*, fr., *F. Sellow s. n.* (holotype: K barcode K000633789!; isotype: US [photo!]). Fig. 10

Omphalobium beyrichii Vogel ex Baker, in Martius, *Fl. Bras.* 14(2): 189. 1871, *pro syn.*

Copaifera beyrichii Hayne ex Baker, in Martius, *Fl. Bras.* 14(2): 189. 1871, *pro syn.*

Connarus salicifolius G. Schellenb., *Candollea* 2: 115. 1925.—TYPE: Brazil. Rio de Janeiro: *S. loc.*, *s. d.*, fl., *F. Sellow s. n.* (lectotype designated by Schellenberg 1938: B†). Brazil. Minas Gerais: Quartel do Biribiry, pres de Diamantina, 1907, fl., *A. F. M. Glaziou 19017* (lectotype designated by Toledo et al. in prep.: P barcode P05615134!; isoelectotypes: K!, R [photo!]).

Treelets or trees, 2–4 m tall; branchlets slightly striate, sparsely sericeous to glabrescent, trichomes simples unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3–7-foliolate; petioles 2.5–6.5 cm long, sparsely sericeous to glabrescent; rachises 0.9–4.5 cm long, sparsely sericeous to glabrescent; pulvinuli 4–6 mm long, glabrous; leaflets coriaceous, concolorous or slightly discolorous, conduplicate, basal pairs $4.5\text{--}11.5 \times 1.7\text{--}2.8$ cm, symmetric, narrowly obovate or narrowly elliptic, bases symmetric, acute or obtuse, rarely rounded, the apical ones $5.7\text{--}13.5 \times 2.2\text{--}3.8$ cm, symmetric, narrowly obovate or narrowly elliptic, bases symmetric, acute or obtuse, rarely rounded, apices short acuminate to acuminate, acumen 3–6(–9) mm long, abaxial surfaces sericeous to glabrescent, adaxial surfaces glabrous, dull or shining, margins revolute or slightly so; midveins abaxially prominent, adaxially impressed, secondary veins 9–13 pairs, abaxially flat or slightly prominent, adaxially flat, rarely slightly prominent, concolorous in relation to the blade, forming angles of $50\text{--}65^\circ$ with midvein, linear, tertiary veins flat or rarely slightly prominent on both surfaces, intercostals and epidermals reticulate. *Inflorescences* in thyrsoids, axillary, 1–4 per axil, trichomes simple unicellular, peduncles 0.3–0.7 cm long or inflorescences subsessile, sericeous or sparsely so, rachises 4–11 cm long, sericeous or densely pubescent, lateral cymes 0.5–2 cm long, sericeous or densely pubescent, indumentum of these structures ferruginous; bracts 0.5–1 mm long, sericeous or tomentose. *Flowers* with pedicels 0.5–2 mm long; buds ca. 2×1.7 mm, elliptic; sepals 5, slightly basally connate, $2.5\text{--}3.3 \times 1\text{--}1.8$ mm, narrowly ovate, ovate or narrowly triangulate, apices acute or obtuse, outer surfaces sericeous, indumentum ferruginous, inner surfaces glabrous or subglabrous, more densely at apex; petals $4\text{--}5 \times 1.3\text{--}2$ mm, reflexed, narrowly obovate or oblanceolate, apices rounded, obtuse or acute, glandular dots more than 10, loosely distributed, black or brown, conspicuous or inconspicuous, outer surfaces subglabrous to sparsely pubescent, glandular trichomes sparse to abundant, inner surfaces glabrous or with sparse glandular trichomes, margins glabrous or with sparse to abundant glandular trichomes; stamens basally connate by ca. 0.5 mm, shorter series 1.5–2 mm long, longer series 2–3.3 mm long, filaments glabrous or with sparse glandular trichomes; ovaries 1.2–1.5 mm long, densely pubescent, styles 1.5–1.8 mm long, stigmas bilobate, lobes ca. 0.3 mm long. *Fruits* $2.1\text{--}2.7 \times 1.4\text{--}1.7$ cm, obovate or semi orbicular, indehiscent side slightly sigmoid or almost linear, pericarps 2–3 mm thick, stipes 1–4 mm long, styles partially persistent, apiculate or spinescent, 1–3 mm long, outer surfaces subglabrous to sparsely sericeous, more densely so at base and apex, indumentum ferruginous, black dots abundant, inner surfaces subglabrous to sparsely pubescent, glandular trichomes absent or sparse, calyx persistent, sepals ascending erect or curved; seeds $1.3\text{--}1.8 \times 0.9\text{--}1$, arils yellowish.

Specimens examined: **Brazil.** Minas Gerais: Ad Saramenha, *s. d.*, fr., *C. T. M. Gomes 11993* (RB). Rio de Janeiro: Petrópolis. Araras, trilha para a Pedra da Cuca, lado esquerdo da trilha, área com afloramento rochoso, 22°25'10.3"S, 43°17'12.9"W, alt. 1260 m, 06 Oct 2020, fl., *C. A. P. Toledo et al. 466* (ESA); Araras, trilha para a Pedra da Cuca, próximo ao mirante, área com afloramento rochoso, na encosta, 22°25'15.7"S, 43°17'27.6"W, alt. 1260 m, 06 Oct 2020, fr., *C. A. P. Toledo et al. 467* (ESA); Araras, Vale das Videiras, trilha na cumieira entre o mirante e o Morro do Cuca, Área de Proteção Ambiental Petrópolis, 22°25'6"S a 22°25' 6"S, 43°16'35"W a 43°16'35"W, alt. 1524 m, 26 Jun 2011, fr., *C. N. Fraga et al. 3303* (RB); Pedra da Cuca-Araras, APA Petrópolis, 22°25'10"S, 43°16'58"W, 11 Oct 2017, fl., fr., *M. S. Wängler et al. 2192* (RB); Vale das Videiras, Pedra da Índia, zona de amortecimento da Rebio Araras, 22°25'54"S, 43°16'17"W, alt. 1432 m, 01 Aug 2016, fr., *M. S. Wängler et al. 1793* (RB). State unknown: *S. loc. S. d.*, fl., *F. Custodio 135* (P); *s. d.*, fl., *Schuch s. n.* (W); *s. d.*, fr., *F. Sellow 1108* (IAN, NY); *s. d.*, fr., *F. Sellow 1192* (BM); *s. d.*, fl., *F. Sellow s. n.* (NY barcode NY 00010911).

Distribution, habitat and phenology: *Connarus beyrichii* had been known from very few and old collections with no precise location. Thanks to modern botanical collections in the municipality of Petrópolis, central Rio de Janeiro, living populations of this species have recently been identified. Two collections are known from Minas Gerais state, probably from around Ouro Preto and Diamantina (type collection of *C. salicifolius*). The type collection of *C. beyrichii* is hypothesized to come from adjacent areas between Petrópolis and montane formation of Minas Gerais (Toledo et al., in prep.). This species is, therefore, considered to be rare and endemic to montane outcrops between Petrópolis and southeastern Minas Gerais (Fig. 11). Individuals are relatively small trees growing on top of hills associated with rocky soils. Specimens have been collected with flowers in October and with fruits from June to October.

Notes: *Connarus beyrichii* is morphologically recognized by the 3–7-foliolate leaves, leaflets narrowly obovate or narrowly elliptic, secondary veins linear and tertiary veins reticulate. It resembles *C. cuneifolius* (also known from Rio de Janeiro) due to the narrowly obovate leaflets but differs by the number of secondary veins (9–13 vs. 6–7), tertiary veins adaxially flat or rarely slightly prominent (vs. prominent) and inflorescence rachises sericeous or densely pubescent (vs. hirsute). *Connarus beyrichii* can also be confused with *C. rostratus* (also from southeast Brazil) but differs mainly by the narrower leaflets with revolute or narrowly revolute margins (vs. flat margins), reticulate tertiary veins (vs. percurrent) and petals 4.5–5 long (vs. petals 3–4 mm long).

Planchon (1850) described *C. beyrichii* based only on the collection *Sellow s. n.* from “herb. Hook. ex herb. reg. Berol.”, suggesting that he consulted a duplicate today deposited in K with a label from B. This specimen (barcode K000633789) is considered the holotype because no other belonging to the same collection has been identified.

In accordance with Forero (1983), *C. salicifolius* is here considered a synonym of *C. beyrichii* as the type of the former is identical to *C. beyrichii*: the leaves are 3–5-foliolate, leaflets are narrowly obovate or narrowly elliptic, secondary veins are composed of 9–11 pairs, tertiary veins are reticulate and the petals are 4.5–5 mm long. This combination of characteristics fits in the concept of *C. beyrichii*. Schellenberg (1925) described *C. salicifolius* citing two syntypes (*Sellow s. n.* and *Glaziou 19017*). The former was later selected as lectotype by Schellenberg (1938), but was deposited in B, and is now considered destroyed. Accordingly, the syntype *Glaziou 19017* is here designated as lectotype of *C. salicifolius*.

Connarus blanchetii Planch., Linnaea 23: 431. 1850. *Connarus blanchetii* Planch. var. *blanchetii*.—TYPE: Brazil. Bahia: Ilhéus [Ilheos], *s. d.*, fl., *J. S. Blanchet 2344* (lectotype first step designated by Schellenberg 1938: P!; lectotype second step **designated here**: P barcode P 01819583!; isoelectotypes: BM!, F [photo!], G!, K!, M [n. v.], NY [photo!], P!).
Fig. 12

Omphalobium ovatifolium Mart. ex Baker, in Martius, Fl. Bras. 14(2): 187. 1871, *pro syn.*

Connarus ovatifolius G. Schellenb., in Engler, Pflanzenreich IV. 127(Heft 103): 243. 1938.—TYPE: Brazil. Bahia: Ilhéus, *s. d.*, fl., fr., *B. Luschnath, Martii Herbar. Florae Bras. 1266* (lectotype **designated here**: M barcode M-0244190!; isoelectotypes: BR [photo!], G!, HAL [photo!], K!, M!, NY [photo!], W [photo!]), *syn. nov.*

Lianas or scandent shrubs, 2–5 m tall; branchlets slightly striate, glabrous or subglabrous, trichomes simples unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3-foliolate; petioles (1.4–)3–7(–9) cm long, glabrous or subglabrous, rarely sparsely sericeous; rachises 0.7–1.8(–4.2) cm long, glabrous or subglabrous, rarely sparsely sericeous; pulvinuli 3–8 mm long, glabrous or subglabrous; leaflets coriaceous, less frequently chartaceous, concolorous, less frequently slightly discoloured, conduplicate, basal pairs 5.5–12 × 3–5.8 cm,

symmetric, elliptic to broadly so, or ovate, bases symmetric, rounded or subcordate, the apical ones $6.5\text{--}19.5 \times 4\text{--}9.2$ cm, symmetric, elliptic or broadly so, or ovate, bases symmetric, rounded or subcordate, apices acuminate, acumen $1\text{--}4(-7)$ mm long, both surfaces glabrous, adaxial surfaces shining or slightly so, less frequently dull, margins flat or slightly revolute; midveins abaxially prominent, adaxially impressed or slightly so, secondary veins 8–11 pairs, abaxially prominent or slightly so, adaxially flat or slightly prominent, concolorous in relation to the blade, forming angles of $45\text{--}65^\circ$ with midvein, linear, arcuate or slightly so, tertiary veins prominent or slightly so on both surfaces, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids or double thyrsoids, axillary, rarely pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncle 0.2–1.5 cm long or inflorescences sessile, sericeous or sparsely so, rachises $6\text{--}16.5(-24)$ cm long, sericeous or sparsely so, lateral cymes 0.3–0.8 cm long, sericeous or densely pubescent, lateral sub-thyrsoids 0.9–8 cm long, sericeous or densely pubescent, indumentum of these structures brown or aureous; bracts 0.5–1 mm long, sericeous. *Flowers* subsessile or pedicels 0.3–1 mm long; buds $1.8\text{--}2 \times 1.5$ mm, ovate or elliptic; sepals 5, slightly basally connate, $2\text{--}3 \times 1\text{--}1.2$ mm, ovate, narrowly ovate or triangulate, apices acute or obtuse, outer surfaces sericeous, indumentum brown or ferruginous, inner surfaces sparsely sericeous, occasionally more densely at apex; petals $2.5\text{--}4 \times 1\text{--}1.3(-1.5)$ mm, erect, oblong, narrowly obovate or narrowly elliptic, rarely narrowly ovate, apices rounded, obtuse or acute, glandular dots more than 10, loosely distributed, black, conspicuous, outer surfaces glabrous or with sparse to abundant glandular trichomes, inner surfaces with only abundant glandular trichomes, margins with glandular trichomes sparse to abundant; stamens basally connate by 0.5–1 mm, shorter series (1–)1.5–3 mm long, longer series (1.6–)2–4 mm long, filaments glabrous or with sparse glandular trichomes; ovaries 0.8–1 mm long, densely pubescent, styles 1–1.3 mm long, stigmas bilobate, lobes 0.2–0.3 mm long. *Fruits* $1.5\text{--}2.1 \times 1.1\text{--}1.5$ cm, obovate or orbicular, indehiscent side sigmoid or slightly so, pericarps up to 2 mm thick, stipes (1–)2–3 mm long, styles partially persistent, inconspicuous, ca. 0.3 mm long, rarely apiculate ca. 1 mm long, outer surfaces sparsely sericeous, indumentum brown, black dots abundant, less frequently sparse, inner surfaces pubescent or sparsely so, glandular trichomes sparse to abundant, calyx deciduous or partially persistent, sepals reflexed or patent; seeds $1.1\text{--}1.2 \times 0.6\text{--}0.8$ cm, arils orangish.

Selected specimens examined: **Brazil.** Alagoas: Marechal Deodoro. Campo Grande, $09^\circ45'38''\text{S}$, $35^\circ50'45''\text{W}$, 10 Aug 1999, fr., R. P. Lyra-Lemos et al. 4239 (MAC); Dunas do Cavalo Russo, 12 Feb 2009, fl., Chagas-Mota 1974 (MAC); Rodovia AL 101, 500 m do Posto

Rodoviário, 9°45'41"S, 35°50'45"W, 18 Jun 2000, fr., *A. M. Amorim et al.* 3487 (CEPEC, NY). Bahia: Belmonte. Ca. 26 km S.W. of Belmonte along road to Itapebi, and 4 km alongside road towards the see, 16°03'S, 39°02'W, 25 Mar 1974, fl., *R. M. Harley* 17399 (CEPEC, K, NY, P, US); Lat – 16,123559, Long -39,17731, 23 Oct 2018, fl., *D. A. Folli* 6771 (CVRD, ESA). Ilhéus. Estrada de acesso a Vila Brasil, Olivença/Vila Brasil, acesso a esquerda pelo areal chegando a área de depósito de lixo, 6 May 2001, fl., *F. Juchum et al.* 121 (CEPEC, NY); Estrada Olivença para Vila Brasil, 5 km SW de Olivença, 8 Feb 1982, fr., *G. P. Lewis et al.* 1169 (CEPEC, K, RB); Km 19 da estrada Ilhéus/Uma, Cana Brava, 11 Feb 1983, fr., *A. M. de Carvalho & T. Plowman* 1607 (CEPEC, F); Road from Olivença to Uma, 2 km S of Olivença, 19 Abr 1981, fr., *S. A. Mori et al.* 13659 (K, NY). Itabuna. 65 km N. E. of Itabuna, at the mouth of the Rio Contas on the N. bank opposite Itacaré, 14°15'S, 39°01'W, 1 Abr 1974, fl., *R. M. Harley* 17607 (CEPEC, K, NY, RB); 65 km N.E. of Itabuna, at the mouth of the Rio de Contas on the N. bank opposite to Itacaré, 1 Abr 1974, fl., fr., *R. M. Harley* 17627 (ALCB, CEPEC, NY, RB); Estrada entre Ilhéus e Olivença, 14°58'S, 39°00'W, 4 Dec 2006, fr., *E. J. Lucas et al.* 1015 (ESA, K, RB). Porto Seguro, Caraíva, próximo à entrada do condomínio Outeiros das Brisas, 16°42'55.2"S, 39°07'44"W, 23 Oct 2018, fr., *C. A. P. Toledo & N. C. Bígio* 402 (ESA); Salvador. Dunas da Armação, 23 Aug 1959, fl., fr., *A. L. Costa s. n.* (NY); Região Metropolitana de Salvador, 12°58'S, 30°30'W, Jun 2013, fl., fr., *D. Oliveira & M. L. Guedes s. n.* (ALCB 109780). *S. loc.*, s. d., fl., *J. S. Blanchet* 3184 (P). Sergipe: Mata dos Coqueiros, Restinga (área localizada após o rio Parnamirim), 5 Dec 1997, fr., *C. Amaral & E. Santos* 39 (ASE); Pirambu, Ass. Sambaíba, 13 Feb 2012, fr., *L. A. S. Santos et al.* 714 (ASE).

Distribution, habitat and phenology: *Connarus blanchetii* is exclusively found in northeastern Brazil, occurring in the coastal zone ranging from the municipality of Maceió (Alagoas) to south Bahia (Fig. 13). This species is represented by lianas or scandent shrubs, frequently collected in areas of “restinga” or “muçununga” with sandy soils, usually at sea level. Specimens have been collected with flowers from October to May and with fruits almost throughout the year.

Notes: *Connarus blanchetii* is recognized by the 3-foliolate leaves, tertiary veins usually prominent on both surfaces, petals 2.5–4 mm long with glandular trichomes on both surfaces and in the margin, and broad fruits with stipe (1–)2–3 mm long and calyx deciduous or partially persistent with sepals reflexed or patent.

Forero (1983) recognized two varieties of *C. blanchetii*: the type variety and *C. blanchetii* var. *laurifolius*. The latter, however, was published at species level and this position is here sustained. *Connarus blanchetii* differs from *C. laurifolius* by the ovate, elliptic or broadly elliptic leaflets, tertiary veins prominent adaxially with the epidermals percurrent, and fruits internally pubescent or sparsely so, with calyx deciduous or partially persistent with sepals reflexed or patent, while in *C. laurifolius* the leaflets are narrowly elliptic or narrowly obovate, tertiary veins are flat adaxially with the epidermals reticulate, and fruits are internally glabrous or with only glandular trichomes, and calyx persistent with sepals always ascending.

In the protologue, Planchon (1850) indicated the collection *Blanchet 2234* as type, but this number is likely to have been transcribed wrongly so the correct collection is *Blanchet 2344*. This confusion in collectors' number is frequent in Planchon's (1850) whole work. While describing this species, the author did not indicate the herbarium in which the type was deposited, so Schellenberg (1938) inadvertently designated a lectotype from P. However, there are three specimens of *Blanchet 2344* in P and they do not bear the same original label. These are considered duplicates (Turland et al. 2018, Art. 8.3) and, therefore, a second step lectotypification is here proposed.

This revision also recognizes *C. ovatifolius* as a synonym of *C. blanchetii* because the characteristic pointed out by Schellenberg (1938) and Forero (1983), such as the size and indumentum of the petals, overlap in the analyzed specimens and thus cannot be used as diagnostics. A lectotype for *C. ovatifolius* is here selected because there are duplicates of the type specimen in M and neither Schellenberg (1938) nor Forero (1983) indicated a specific sheet.

Connarus brachybotryosus Donn. Sm., Bot. Gaz. 57(5): 417. 1914.—TYPE: Guatemala. Alta Verapaz: Cubilquitz, Feb 1913, fl., *H. Türkheim 4027* (lectotype first step designated by Schellenberg 1938: US; lectotype second step **designated here**: US barcode US 00130991 [photo!]; isolectotypes: BM [photo!], ECON [photo!], K!, L [photo!], NY [photo!], U [photo!], US [photo!]).

Trees, ca. 9 m tall; branchlets slightly striate, subglabrous to sparsely pubescent, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3-foliolate;

petioles 3–9 cm long, sericeous to glabrescent; rachises 1.6–4, sericeous to glabrescent; pulvinuli 5–6 mm long, tomentose; leaflets chartaceous, slightly discoloured, flat, basal pairs $7.5\text{--}16 \times 4\text{--}8$ cm, symmetric, elliptic or ovate, bases symmetric, rounded, the apical ones $9.5\text{--}17 \times 4.8\text{--}9$ cm, symmetric, elliptic or ovate, bases symmetric, rounded, apices acuminate, acumens 3–10 mm long, abaxial surfaces subglabrous to sparsely pubescent, sparsely sericeous only on midvein, indumentum ferruginous, adaxial surfaces sparsely pubescent, sparsely sericeous on midvein, dull, margins flat; midveins abaxially prominent, adaxially flat, secondary veins 6–8 pairs, abaxially prominent, adaxially flat, concolorous in relation to the blade, forming angles of $55\text{--}65^\circ$ with midvein, arcuate, tertiary veins slightly prominent on both surfaces, intercostals and epidermals opposite percurrent. *Inflorescences* in thyrsoids, axillary, 1–3 per axil, trichomes simple unicellular, peduncles 0.6–1.2 cm long, sericeous, rachises 2.8–8.8 cm long, sericeous, lateral cymes ca. 0.5 cm long, sericeous, indumentum of these structures ferruginous; bracts ca. 0.7 mm long, sericeous. *Flowers* with pedicels 0.8–1.5 mm long; buds ca. 2×1.5 mm, ovate; sepals 5, slightly basally connate, $3 \times 1\text{--}1.5$ mm, ovate or narrowly triangulate, apices acute or obtuse, outer surfaces sericeous, indumentum ferruginous, inner surfaces sparsely sericeous; petals $3\text{--}3.2 \times 1.3\text{--}1.5$ mm, erect, narrowly obovate or oblong, apices rounded, glandular dots ca. 5 or more than 10, loosely distributed, black or colorless, inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous; stamens basally connate by 0.5–0.8 mm, shorter series ca. 0.8 mm long, longer series ca. 1.2 mm long, filaments glabrous; ovaries ca. 1 mm long, densely pubescent, styles ca. 1.5 mm long, stigmas bilobate, lobes ca. 0.5 mm long. *Fruits* not seen.

Specimens examined: **Guatemala.** Alta Verapaz: Woods between Finca Cubilgüitz and Hacienda Yaxcabanal, 7 Mar 1942, fl., *J. A. Steyermark 44811* (F).

Distribution, habitat and phenology: This species is only known to occur in Alta Verapaz, Guatemala, and is represented by only two collections (Fig. 14). It is a tree up to 9 m tall, but there is no further information on its habitat. Specimens have been collected with flowers from February to March.

Notes: *Connarus brachybotryosus* is morphologically recognized by its leaflets with 6–8 pairs of arcuate secondary veins, intercostal and epidermal tertiary veins opposite percurrent and short inflorescence rachis (3.5–8.8 cm long). This species can be confused with *C. costaricensis* due to the number of secondary veins, but differs by the midvein, which is adaxially flat in *C. brachybotryosus* and prominent or slightly so in *C. costaricensis*. *Connarus*

brachybotryosus is also similar to *C. lambertii* as both have 3-foliolate leaves with few secondary veins but differ by the abaxially prominent secondary veins (vs. flat, rarely slightly prominent) and sepals and petals nearly of the same length (vs. petals significantly longer than the sepals).

Smith (1914) published *C. brachybotryosus* without indicating in which herbarium the type was deposited, so Schellenberg (1938) inadvertently selected the lectotype from US. However, two specimens of *Türckheim 4027* are deposited in this herbarium and they can be considered as duplicates since each sheet bears its own and different collection label (Turland et al. 2018, Art. 8.3), so a second step lectotypification is here proposed.

Connarus bracteosovillosus Forero, Ann. Missouri Bot. Gard. 68(1): 218. 1981.—TYPE: Peru. Huánuco: Pachitea, Dtto. Honoria, Bosque Nacional de Iparia, región de “bosque seco tropical” a lo largo del Río Pachitea cerca del Miel de Abeja (1 km. arriba del pueblo de Tournavista a unos 20 km. arriba de la confluencia con el Río Ucayali), altura sobre el mar 300-400 m, 5 Jun 1967, fl., *J. Schunke Vigo 2040* (holotype: F 1690963!).

Shrubs, ca. 1 m tall; branchlets slightly striate, glabrous or subglabrous, trichomes simple unicellular, lenticels conspicuous. *Leaves* 7–9-foliolate; petioles 6.5–8.5 cm long, glabrous or subglabrous; rachises 7.5–11.5 cm long, glabrous or subglabrous; pulvinuli 5–6 mm long, glabrous or subglabrous; leaflets chartaceous, slightly discoloured, flat, basal pairs ca. 4.6 × 2.6 cm, symmetric, ovate, bases symmetric, rounded, the apical ones 7–11.7 × 3.2–4.5 cm, symmetric, narrowly elliptic, bases symmetric, obtuse or rounded, apices acuminate, acumen 7–9 mm long, abaxial surfaces glabrous or subglabrous, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially slightly impressed, secondary veins 9–11(–13) pairs, abaxially slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of 60–70° with midvein, slightly arcuate or linear, tertiary veins flat on both surfaces, intercostals alternate percurrent, epidermals opposite percurrent. *Inflorescences* in double thyrsoids, axillary, 1 per axil, trichomes simple unicellular, peduncles ca. 0.5 cm long, densely pubescent, rachises 13.5–19.5 cm long, densely pubescent or sparsely so, lateral sub-thyrsoids 4–12 cm long, sparsely pubescent, indumentum of these structures brown; bracts 2–3.5 mm long, densely pubescent. *Flowers* with pedicels 0.6–1 mm long; buds

ca. 3×1.5 mm, elliptic; sepals 5, slightly basally connate, $3 \times 1\text{--}1.3$ mm, ovate or narrowly triangulate, apices obtuse or acute, rarely rounded, outer surfaces sparsely sericeous or pubescent, indumentum brown, inner surfaces subglabrous, sparsely sericeous only at apex; petals $3.5\text{--}4.5 \times 1.3$, erect, narrowly obovate, apices rounded or obtuse, glandular dots absent or 1–4, usually distributed in the upper half, black, conspicuous or rarely inconspicuous, both surfaces with only sparse glandular trichomes, margins with glandular trichomes abundant; stamens basally connate by ca. 1 mm, shorter series ca. 2.5 mm long, longer series 3–3.5 mm long, filaments with sparse to abundant glandular trichomes; ovaries ca. 1 mm long, densely pubescent, styles and stigmas not seen. *Fruits* not seen.

Distribution, habitat and phenology: *Connarus bracteosovillosus* is only known from the type location, district of Honoria, Peru, along Pachitea River (Fig. 15). This species is apparently represented by small shrubs, and the type was found in a tropical dry forest, at 300–400 m elevation. This material was collected flowering in June.

Notes: Among species with only simple trichomes, *Connarus bracteosovillosus* is recognized by 7–9-foliolate leaves, secondary veins with more than 8 pairs and occasionally epunctate petals, so it can be confused with *C. elsaе*, but differs by the pubescent inflorescence rachis (vs. sericeous) and 2–3 mm long bracts (vs. 0.5–1.5 mm long).

Connarus cordatus L. A. Vidal, Carbonó & Forero, Revista Brasil. Bot. 7(1): 65. 1984.—

TYPE: Venezuela. Amazonas: Casiquiare, sabanas ubicadas a pocos Km al sur del bajo río Guasacavi, 03°06'N, 67°33'W, alt. 120 m., 11 Feb 1981, fl., fr., *O. Huber & E. Medina 5975* (holotype: COL barcode COL000001580 [photo!]; isotype: VEN [photo!]).

Shrubs, scandent shrubs or treelets, 0.75–4 m tall; branchlets slightly striate, glabrous or subglabrous, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3-foliolate; petioles 3.2–5.2 cm long, glabrous, subglabrous or irregularly sparsely sericeous; rachises 0.9–2 cm long, glabrous, subglabrous or irregularly sparsely sericeous; pulvinuli 4–6 mm long, glabrous or subglabrous; leaflets coriaceous, discolorous or slightly so, conduplicate, basal pairs $7\text{--}12.5 \times 3.3\text{--}8$ cm, symmetric, cordate or ovate, bases symmetric, cordate or subcordate, the apical ones $8\text{--}15.2 \times 3.8\text{--}11.2$ cm, cordate or ovate, bases symmetric, cordate or subcordate, apices short acuminate to acuminate, acumen 3–8 mm long, abaxial surfaces

glabrous or subglabrous, adaxial surfaces glabrous, shining, margins slightly revolute; midveins abaxially prominent, adaxially impressed, secondary veins 6–9 pairs, slightly prominent on both surfaces, adaxially concolorous in relation to the blade, forming angles of 45–55° with midvein, arcuate or slightly so, tertiary veins abaxially prominent, adaxially slightly prominent, intercostals mixed percurrent, epidermals opposite percurrent. *Inflorescences* in double thyrsoids, rarely thyrsoids, axillary, 1–2 per axil, trichomes simple unicellular, peduncles 0.2–0.5 cm long, sericeous or sparsely so, rachises 6–12 cm long, sericeous or sparsely so, lateral cymes ca. 0.4 cm long, sericeous or sparsely so, lateral sub-thyrsoids 2.5–12 cm long, sericeous or sparsely so, indumentum these structures ferruginous; bracts ca. 1 mm long, sericeous. *Flowers* with pedicels ca. 1 mm long; buds ca. 1.5 × 1.5 mm, orbicular; sepals 5, slightly basally connate, ca. 2 × 1 mm, ovate or narrowly ovate, apices acute, outer surfaces sparsely sericeous, indumentum ferruginous, inner surfaces glabrous; petals ca. 3 × 1 mm, narrowly elliptic, apices acute, glandular dots more than 10, loosely distributed, black, inconspicuous, outer surfaces glabrous or subglabrous, inner surfaces glabrous, glandular trichomes absent, margins glabrous; stamens (Forero et al. 1984) basally connate by ca. 0.4 mm, shorter series 1–1.2 mm long, longer series 1.5–1.8 mm long, filaments with sparse glandular trichomes; ovaries length not seen, densely pubescent, styles and stigmas not seen. *Fruits* 1.3–1.8 × 0.9–1.2 cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 2–4 mm long, styles partially persistent, inconspicuous, ca. 0.2 mm long, outer surfaces glabrous, black dots absent or sparse, inner surfaces glabrous or subglabrous, glandular trichomes absent, calyx persistent or partially persistent, sepals ascending erect, rarely patent or reflexed; seeds (Forero et al. 1984) 0.7–1.3 × 0.4–0.7 cm, arils yellowish.

Specimens examined: **Colombia.** Guainía: Maimachi, Serranía del Naquén, Cerro Minas, alrededores del Helipuerto-15 y camino hasta la cima del Cerro, 02°12'N, 68°13'W, alt. 900 m, 7 Apr 1993, fr., *C. Barbosa & S. Madriñán* 8352 (COL, MO). Santander: Bucaramanga, Agua blanca 320 mts., 11 Dec 1977, fr., *R. R. Llanos & F. Sierra* 0.59 (COL). Vichada: Puerto Carreño, corregimiento departamental de Casuarino, por la vía que conduce del caserio a Puerto Carreño, 05°41'25.2"N, 67°39'10.8"W, 135 m, 21 Mar 2005, fl., fr., *R. López C. & R. Garces* 10161 (COL). **Venezuela.** Amazonas: Atapabo. Caño Caname (afluente derecho (oriental) del medio río Atapabo), aprox. 20 km al E de la boca, 3°40'N, 67°22'W, alt. aprox. 100 m, 29 Apr–4 May 1979, fr., *O. Huber et al.* 3670 (COL); Cucurital de Caname, southern bank of the middle part of Caño Caname, 3°40'N, 67°22'W, 30 Apr–1 May 1979, fl., *Davidse et al.* 16899 (COL, K, MO); Sabana abierta a unos 10 Km. al S. del medio Caño Caname, 3°33'N, 67°12'W, alt.

100 m, 10 Mar 1980, fr., *O. Huber 5154* (COL, VEN); Sabana sobre arena blanca a unos 2 km al W de San Antonio del Orinoco, 3°27'N, 66°47'W, alt. 120 m, 20 Jun 1980, fr., *O. Huber & S. S. Tillett 5433* (COL, VEN). Atunes. Extensas sabanas a unos 10 km. al SW. del río Guayapo medio, 4°14'N, 67°30'W, alt. 110 m, 9 Mar 1980, fr., *O. Huber 5110* (COL, VEN); Sabana ubicada em unos 6-8 Km. al SE del río Guayapo, 4°10'N, 67°25'W, alt. 110 m, 29 Jul 1979, fr., *O. Huber 3918* (COL, VEN); Sabana ubicada a unos 6-8 km. al SE del medio río Guayapo, 4°10'N, 67°25'W, alt. 110 m, 29 Jun 1979, fr., *O. Huber 3913* (COL, VEN). Casiquiare, sabana y caatinga abierta a unos 2-3 km. al SE. del bajo río Guasacavi, 3°08'N, 67°30'W, alt. 90 m, 10 Mar 1980, fr., *O. Huber 5117* (COL, VEN); Sabana El Venado, on left bank of Caño Pimichín above Pimichín, 140 m, 23 Nov 1953, fl., *B. Maguire & J. J. Wurdack 36355* (NY); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, Bana (low Amazon caatinga), 10.8 km NE of San Carlos on Solano road, 1°56'N, 67°03'W, alt. 119 m, 20 Apr 1978, fr., *H. L. Clark 6633* (COL); Sn. Carlos de Río Negro, carretera Sn. Carlos-Solano, 28 Jul 1982, fr., *B. Stergios et al. 4270* (COL). Zulía: Colón, alrededores de Casigua El Cubo, sector Las Cruces, em el Cerro El Mirador, a lo largo de la antigua vía entre El Carmelo y Estación Concordia, al sur del Pozo T-221, traysecto de aproximadamente 4 km, alt. ca. 350-450 m, 1 Aug 1979, fl., *G. S. Bunting 7779* (COL).

Distribution, habitat and phenology: *Connarus cordatus* occurs in east Colombia and west Venezuela, comprising most provinces that fall along the border between these countries (Fig. 13). Individuals of this species are shrubs, scandent shrubs or small trees up to 4 m tall, normally growing in shrubby Amazonian savannas (especially in the province of Amazonas, Venezuela) with white sandy soils, at approximately 100–450 m elevation. Specimens have been collected with flowers in February, April, August and November, and with fruits mainly from February to July.

Notes: *Connarus cordatus* is characterized by exclusively 3-foliolate leaves and coriaceous, discoloured leaflets, with cordate or subcordate bases and shining adaxial surfaces. It is vegetatively very similar to *C. coriaceus* due to the characteristics noted above, but differs by the inflorescences with ferruginous indumentum (vs. aureous), internally glabrous sepals (vs. pubescent or sericeous), petals ca. 3 mm long (vs. 3.5–5.5 mm long), and fruits 1.3–1.8 long (vs. (1.7–)2–3.2 cm long), internally glabrous or subglabrous (vs. pubescent or densely so), and with stipes 2–4 mm long (vs. stipes (3–)6–13 mm long). In addition, *C. cordatus* is a shrub or small tree from Amazonian savannas, while *C. coriaceus* is a liana mainly from flooded areas of the same domain.

Connarus coriaceus G. Schellenb., Candollea 2: 108. 1925.—TYPE: Guyana. Roraima, Mar 1842, fl., *Rob. Schomburgk 996* (lectotype first step designated by Forero 1983: W; lectotype second step **designated here**: W 0077899!; isoelectotypes: F-frag. [photo!], BM!, G!, K!, M, P!, W!).

Connarus neglectus G. Schellenb., Candollea 2: 109. 1925.—TYPE: Guyana. *S. loc.*, Jan 1843, fl., *Rich. Schomburgk 1116* (lectotype designated by Schellenberg 1938: B†; lectotype **designated here**: US barcode 00130748 [photo!]).

Connarus martii G. Schellenb., Candollea 2: 116. 1925.—TYPE: Brazil. *S. loc.*, Igapó ad Solimões, *s. d.*, fl., *C. F. P. von Martius s. n.* (lectotype designated by Schellenberg 1938: M; lectotype second step **designated here**: M barcode M-0243562!; isoelectotypes: M), *syn. nov.*

Connarus opacus G. Schellenb., in Engler, Pflanzenr. IV. 127(Heft 103): 244. 1938.—TYPE: Guyana. *S. loc.*, *s. d.*, fl., *Rich. Schomburgk 456* (holotype: B†). Guyana. U. Takutu-U, Essequibo Region, Rewa River, between camp & confluence of Rewa with Rupununi R., 3°48'35"N, 58°46'20"W, 25 Sep 1997, fl., *H. D. Clarke et al. 6714* (neotype **designated here**: K barcode K000066179!).

Connarus rigidus Forero, Brittonia 32(1): 38. 1980.—TYPE: Venezuela. Amazonas: Between Rio Negro and Comunidad, 100 m alt., 12 Apr 1953, fl., *B. Maguire & J. J. Wurdack 35546* (holotype: COL barcode COL000001593 [photo!]; isotypes: MO [photo!], NY!, VEN [photo!]).

Lianas; branchlets slightly striate, glabrous or subglabrous, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3-foliate; petioles (2–)3–7.5(–12) cm long, glabrous; rachises 1–3 cm long, glabrous; pulvinuli 3–7 mm long, glabrous or subglabrous; leaflets coriaceous or subcoriaceous, less frequently chartaceous, concolorous or slightly discolorous, flat, basal pairs 5.5–13(–29) × 2.8–6.5(–10.5) cm, symmetric, ovate or elliptic, bases symmetric, subcordate, cordate, rounded or obtuse, the apical ones 6.8–6(–32) × 3.8–8.2(–11) cm, ovate or elliptic, bases symmetric, subcordate, cordate, rounded or obtuse, apices acuminate to long acuminate, acumen 4–17 mm long, abaxial surfaces glabrous or subglabrous,

indumentum brown, both surfaces glabrous or subglabrous, adaxial surfaces shining, less frequently dull, margins flat or slightly revolute; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 6–12 pairs, abaxially flat or slightly prominent, adaxially flat or slightly prominent, concolorous or slightly discolorous in relation to the blade, forming angles of 50–65° with midvein, arcuate or slightly so, tertiary veins abaxially flat or slightly prominent, adaxially flat or slightly prominent, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids or double thyrsoids, axillary or pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncles 0.2–3 cm long, subglabrous or sparsely sericeous, rachises 8.5–26 cm long, sparsely sericeous, lateral cymes 0.2–1.2 cm long, sericeous or sparsely so, lateral sub-thyrsoids 1–7.2 cm long, sericeous or sparsely so, indumentum of these structures aureous; bracts 0.5–0.8 mm long, sericeous. *Flowers* with pedicels 0.8–2 mm long; buds 2–2.5 × 1.5–1.6 mm, elliptic; sepals 5, slightly basally connate, 2–3 × 0.8–1.3 mm, ovate or narrowly ovate, apices acute, outer surfaces sericeous or sparsely so, indumentum aureous, inner surfaces pubescent, sericeous or sparsely so, occasionally subglabrous in the lower half; petals 3–5.5 × 1–1.5 mm, erect, narrowly obovate, narrowly elliptic or oblong, apices rounded, acute or obtuse, glandular dots more than 10, loosely distributed, black or colorless, conspicuous or inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent or sparse, margins glabrous or with sparse glandular trichomes; stamens basally connate by 0.5–1 mm, shorter series 1.5–2.8 mm long, longer series 2–4 mm long, filaments with sparse glandular trichomes; ovaries 0.7–1.5 mm long, densely pubescent, styles 0.3–1.5 mm long, stigmas bilobate, lobes 0.2–0.3 mm long. *Fruits* 1.9–3.2 × 1.3–2 cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes (4–)6–13 mm long, styles partially persistent, inconspicuous, rarely apiculate, 0.2–0.5(–1) mm long, outer surfaces glabrous, black dots absent or abundant, inner surfaces densely pubescent, glandular trichomes absent or sparse, calyx deciduous or partially persistent, sepals reflexed; seeds 1.3–1.9 × 0.6–0.9 cm, arils whitish or yellowish.

Selected specimens examined: **Bolivia.** *S. loc.*, 26 Oct 1954, fr., Mandon s. n. (P).

Brazil. Amapá: Cachoeira Utussansain, 2°8'S, 52°55'W, 4 Sep 1960, fr., H. S. Irwin et al. 47995 (NY). Amazonas: Barcelos, beira do Rio Jauari passando do igarapé Pretinho, 00°42'S, 63°22'W, 28 Jun 1985, fr., J. A. Silva 169 (MG, NY); Borba, acima da Terra Preta, campina do Rio Surubim, afluenta do Rio Abacaxis, 7 Jul 1983, fr., C. A. C. Ferreira 4055 (INPA); Humaitá, estrada Humaitá-Jacarecanga, km 45, rio Maici-Mirim, 7°45'S, 62°32'W, 19 Jun 1982, fr., L. O. A. Teixeira et al. 1229 (INPA, RB); Ilha Gavião, near mouth of Rio Branco, 5

Jul 1967, fr., *R. E. Schultes* 24525 (INPA); Manicoré, BR 230, 110 km ao L de Humaitá, Rio Marcelos entre a Rod. E a Cachoeira do Paricá (R.I. dos Tenharim), 07°50'S, 61°15'W, 15 Apr 1985, fr., *C. A. C. Ferreira* 5567 (HRCB, INPA, NY, UB); Maués, basin of Rio Maués, along Rio Parauari above mouth of Rio Amazã, 04°40'S, 57°55'W, 13 Jul 1983, fr., *J. L. Zarucchi et al.* 3030 (INPA, NY); Rio Negro, Praia Grande, 12 Jun 1989, fr., *S. Mori et al. s. n.* (NY); Santa Isabel do Rio Negro, Igarapé do Daará, 14 Oct 1978, fr., *M. Madison et al.* PFE247 (INPA); São Gabriel da Cachoeira, Rio Içana, above mouth of Rio Cubate, 2 Nov 1987, fr., *D. C. Daly & D. W. Stevenson* 5556 (NY); Serra Aracá, southern massif, W facing talus slope, 00°48'N, 63°18'W, 1 Mar 1984, fr., *J. J. Pipoly et al.* 6757 (INPA, NY, W). Pará: Almeirim, distrito de Monte Dourado, Comunidade de Freguesia, coletas ao longo do Rio Arraiólos, 01°14'S, 52°24'W, 3 Jun 2010, fr., *E. S. Leal & R. C. Forzza* 222 (RB); Belém, Água Preta, 29 Oct 1914, fl., *A. Ducke s. n.* (MG 15518); Região de Jutaby de Almeirim, Pirapetinga, 13 Nov 1923, fl., *A. Ducke s. n.* (IAN, RB); Furos de Breves, Rio Anapu, Bahia Pracajai, 25 Mar 1985, fr., *K. Kubitzki* 85-54 (MG, NY); Melgaço, Caxiuanã, 18 May 2002, fr., *D. D. Amaral et al.* 307 (MFS, MG); Santarém, Rio Curuá Una, acima da cachoeira do Palhão, 6 Dec 1966, fr., *P. Cavalcante & M. Silva* 1645 (MG); Melgaço, Estação Científica Ferreira Penna, margem esquerda do rio Caxiuanã, 15 Dec 1999, fr., *A. S. L. da Silva et al.* 3795 (MG, RB); Moju, Campo Experimental da Embrapa Amazônia Oriental, Km-30 da rodovia PA-150, ramal do Km-34, 19 Oct 2000, fl., *M. R. Mesquita et al.* 375 (IAN); Rio Xingú, em frente Souzel, mun. Porto de Moz, 18 Nov 1955, fl., *R. L. Fróes* 32356 (IAN); Rio Preto, localidade Vitória, município de Melgaço, Comarca de Breves, 3 Oct 1989, fl., *C. Rosário & M. das Graças* 1267 (MG); Rio Tapajós, Itaituba, margem do rio, 10 Nov 1978, fr., *M. G. Silva & C. Rosário* 3637 (NY); Rios Pacaja and Muirapiranga, 02°33'S, 50°50'W, 22 Sep 1965, fr., *G. T. Prance et al.* 1443 (NY); São Domingos do Capim, 01°40'33"S, 47°45'57"W, 10 Jan 2003, fr., *F. C. A. Lucas* 1168 (MFS); Tapajós, Itaituba, 21 Aug 1902, fl., *A. Ducke s. n.* (RB barcode 00260781). Rondônia: Porto Velho, Represa Samuel, 09°05'S, 63°13'W, 14 Jun 1986, fr., *W. Thomas et al.* 5090 (INPA). Roraima: Caracará, Parque Nacional do Viruá, km 17, próximo à entrada do Parque, lado esquerdo, 1 Sep 2002, fr., *C. A. C. Ferreira et al.* 12404 (INPA); Dormida, foothills of Serra da Lua, 2°25'–29'N, 60°11'–14'W, 15 Jan 1969, fr., *G. T. Prance et al.* 9291 (INPA, NY, R); Rio Branco, margem do rio Anauá, 6 Mar 1978, fl., *N. T. Silva* 4548 (MG, NY, RB); Rio Uraricoera, Cachoeira Tocuxema, 9 Mar 1979, fr., *J. M. Pires et al.* 16902 (MG); Vicinity of Uaicá airstrip, Rio Uraricoeira, 03°33'N, 63°11'W, 26 Feb 1971, fl., *G. T. Prance et al.* 10716 (NY). **Guyana.** 4 km from Santa Mission, 06°30'N, 58°23'W, 25 Nov 1992, fr., *A. R. A. Görts et al.* 398 (K, U); Demerara-Mahaica, along Linden Highway, 6 km S of Kuru-Kuru Creek,

6°23'5"N, 58°14'36"W, 3 Jan 1992, fr., *B. Hoffman et al.* 703 (K); Essequibo Isl-W, Demerera, Arawak Amerindian land, Timberhead Resort, 3 km up Pokerero River from Santa Mission, near compound, 6°34'39"N, 58°21'15"W, 29 Jan 1992, fr., *B. Hoffman et al.* 902 (K); Mabura Hill, Ekuk compartment, 05°10'N, 58°45'W, alt. 75 m, 12 Oct 1989, fr., *M. J. Jansen-Jacobs* 1983 (K); U. Takutu-U, Essequibo, S Pakaraima Mts, Tipuru R., 1-2 km upstream from Tipuru Village, 4°13'N, 59°33'W, alt. 330–360 m, 1 Mar 1992, fr., *B. Hoffman et al.* 116 (K). **Suriname.** Bank of upper Wayombo R. near Fosibergi, 18 Apr 1956, fr., *J. C. Lindeman* 7610 (COL). Sipaliwini: summit of Tafelberg, along trail from airplane crash site to Arrowhead, basin, ca. 100 m. NE of Augustus Creek, 03°54'42"N, 56°10'59"W, 650 m, 2 Jul 2001, fr., *R. Evans* 3268 (COL, MO). **Venezuela.** Amazonas: A los lados de las márgenes inundadas del río Pacimoni, arriba de la desembocadura del río Pacimoni con el río Casiquiare, 1°50'N, 66°30'W, alt. 100 m, 8 Apr 1970, fl., *J. A. Steyermark & G. Bunting* 102467 (NY); Alto Pasimoni, 25 Jul 1982, fr., *B. Stergios & G. Aymard* 4126 (COL); Atapabo y Casiquiare, a lo largo del río Atacavi, del Caño Caname y del río Atapabo, entre los 3°05' y 3°50'N y entre los 66°50' y 67°30'W, alt. Aprox. 100 m, 10–24 Nov 1990, fr., *P. Piñate & E. Mondolfi* 1011 (COL).

Distribution, habitat and phenology: *Connarus coriaceus* is widely distributed across the Guiana Shield, especially in north Brazil and Guyana, with few specimens known from Bolivia, Suriname and Venezuela (Fig. 13). It is a lianescent species growing in ombrophilous forests usually associated with flooded soils, such as ciliary and “igapó” forests, at 30–400 m elevation. Specimens have been collected with flowers from August to November and from February to April, and with fruits almost throughout the year.

Notes: *Connarus coriaceus* is a widely distributed species and therefore morphologically variable, this probably being the reason why several names were published and now recognized in the synonymy of *C. coriaceus*. Despite these inconsistencies among different authors, this species can be characterized by the combination of the following characteristics: leaves exclusively 3-foliolate, leaflets usually coriaceous with tertiary veins percurrent, inflorescences with aureous indumentum, sepals internally completely sericeous, and large fruits with stipe normally 6–13 mm long. It can be confused with *C. cordatus* due to similar leaflet characteristics, but differs in inflorescence and sepal indumentum, petal length, and fruit size, internal indumentum and stipe length (see “Notes” section of *C. cordatus*).

Connarus costaricensis G. Schellenb., in Engler, Pflanzenr. IV. 127(Heft 103): 224. 1938.—

TYPE: Costa Rica. Limón: Finca Montecristo, on the Río Reventazón below Cairo, 25 m, 18–19 Feb 1926, fr., *P. C. Standley & J. Valerio 48624* (holotype: US barcode US 00130996!).

Connarus vulcanicus J.F. Morales, Rodriguésia 58(1): 45. 2007.—TYPE: Costa Rica. Alajuela:

Guatuso, Parque Nacional Volcán Tenorio, cuenca del Río Frío, Alto Masís, 8 Apr 2000, fl., *J. Chaves & Muñoz 373* (holotype: INB [photo!]), *syn. nov.*

Lianas or scandent shrubs, ca. 2.5 m tall; branchlets slightly striate, glabrous, subglabrous or sparsely tomentose, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3-foliate; petioles (2.7–)3.5–12 cm long, subglabrous; rachises 0.8–2.7 cm long, subglabrous; pulvinuli 3–5(–7) mm long, subglabrous, rarely irregularly tomentose; leaflets chartaceous to subcoriaceous, concolorous or slightly discoloured, flat, basal blades 4.8–12 × 2.5–4.7 cm, symmetric, obovate or elliptic, bases symmetric, acute or obtuse, the apical ones 7.8–15.5 × 3–6.8 cm, symmetric, obovate or elliptic, bases symmetric, acute or obtuse, apices short to long acuminate, acumen 2–10 mm long, abaxial surfaces glabrous or subglabrous, occasionally irregularly sparsely sericeous on midvein, indumentum brown, adaxial surfaces glabrous, dull, margins flat or slightly revolute; midveins abaxially prominent, adaxially prominent or slightly so (at least up to the lower half), secondary veins 5–6(–7) pairs, abaxially prominent or slightly so, adaxially flat or prominent, concolorous in relation to the blade, forming angles of 35–45° with midvein, strongly arcuate, basal ones usually ascending, tertiary veins abaxially flat or slightly prominent, adaxially flat, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids, axillary, 1–2 per axil, trichomes simple unicellular, peduncles 0.4–2.5 cm long or inflorescences sessile, sparsely sericeous, rachises 3–5.5 cm long, sericeous or sparsely so, lateral cymes 0.5–1.2 cm long, sericeous, indumentum of these structures brown; bracts not seen. *Flowers* not seen, pedicels 1–2 mm long; buds ca. 2 × 1.7 mm, elliptic; sepals (few persistent on fruits) slightly basally connate, outer surfaces sparsely sericeous, indumentum brown, inner surfaces subglabrous, pubescent only at apex; petals (Morales 2007) 2.5–2.8 mm long. *Fruits* (2–)2.3–3 × (1.4–)1.6–2 cm, obovate, rarely semi-orbicular, indehiscent side linear or sigmoid, pericarps ca. 2 mm thick, stipes 5–10 mm long, style partially persistent, inconspicuous, ca. 0.2 mm long, outer surfaces subglabrous or irregularly sparsely sericeous at stipe, base or apex, indumentum

ferruginous, black dots absent or abundant, inner surfaces subglabrous, sparsely pubescent or densely tomentose, glandular trichomes absent, calyx deciduous, rarely partially persistent, sepals ascending erect; seeds $(1.4\text{--})1.7\text{--}2.2 \times 0.8\text{--}1.1(-1.3)$ cm, arils yellowish or yellow-orangish.

Specimens examined: **Costa Rica.** Heredia: Between Quebrada Tigre and east fork of Río Sardinel, ca. 9 km SW of Las Horquetas, route crossing several branches of Río Sardomal, 2 Feb 1985, fr., *M. Grayum et al.* 5023 (BM, MO, NY). Guanacaste: Liberia. Cordillera de Guanacaste, Estación Cacao, Cerro Cacao, $10^{\circ}55'43''\text{N}$, $85^{\circ}28'10''\text{W}$, 1100 m, 8 Feb 1995, fr., *F. Quesada* 245 (BM); Cordillera de Guanacaste, Estación Cacao, Sendero Maritza, $10^{\circ}55'43''\text{N}$, $85^{\circ}28'10''\text{W}$, 1100 m, 9 Feb 1995, fr., *L. Angulo* 48 (COL, INB, MO); Cordillera de Guanacaste, Estación Cacao, Sendero Pedregal, $10^{\circ}55'43''\text{N}$, $85^{\circ}28'10''\text{W}$, 1100 m, 18 Feb 1995, fr., *B. Gamboa* 64 (COL, INB, MO); Parque Nacional Guanacaste, Estación Cacao, $10^{\circ}55'45''\text{N}$, $85^{\circ}28'15''\text{W}$, 1100 m, 22 Jun 1990, fr., *C. Chávez* 377 (CR, INB, MO, NY).

Distribution, habitat and phenology: *Connarus costaricensis* is restricted to Costa Rica and it is represented by only few collections, occurring from Limon up to the Guanacaste mountain range (Fig. 14), in ombrophilous forests, probably associated with water courses, at 20–1000 m elevation. This species is represented by lianas or scandent shrubs; the information in the sheet label of collection *Gamboa 64* states that the individual was a tree, but it is likely that it was a liana collected in the canopy. Specimens have been collected with flowers in April and with fruits in February and June.

Notes: *Connarus costaricensis* is mainly recognized by the midveins prominent adaxially, arcuate secondary veins in 5–6(–7) pairs, with the basal pairs ascending, and fruits measuring $(2\text{--})2.3\text{--}3 \times (1.4\text{--})1.6\text{--}2$ cm, with stipe 5–10 mm long. This species can be confused with *C. brachybotryosus* and *C. lambertii*, but differs from the former by the midveins adaxially prominent (vs. midveins adaxially flat), and from the latter by the stipe 5–10 mm long (vs. 2–3 mm long).

Morales (2007) published *C. vulcanicus* apart from *C. costaricensis* based on the indumentum of fruits' internal surfaces (puberulent vs. tomentose, respectively). However, there seems to be a gradient of continuous variation related to this character as the fruits in the specimens cited here vary from subglabrous to densely tomentose. Therefore, recognizing two separate species based solely on one character does not seem appropriate, also because the

characteristic leaflet venation arrangement and salience (see comments above) are clearly seen in both the type and additional specimens previously included in *C. vulcanicus*, so this name is here treated as a synonym of *C. costaricensis*.

Connarus cuneifolius Baker, in Martius, Fl. Bras. 14(2): 194. 1871.—TYPE: Brazil. Rio de Janeiro: Paraíba do Sul? [Engshade. Paraíba], *s. d.*, fl., *F. Sellow B.1824 c.1280* (lectotype **designated here**: US barcode US 00130998 [photo!]; isolectotypes: M!, NY [photo!]).

Habit not seen; branchlets slightly striate, glabrous or subglabrous, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3–5-foliolate; petioles 3–4.8 cm long, irregularly sericeous to glabrescent; rachises 1.7–4.7 cm long, irregularly sericeous to glabrescent; pulvinuli 4–6 mm long, subglabrous; leaflets chartaceous, slightly discoloured, flat, basal pairs $4.2\text{--}5.5 \times 2\text{--}2.4$ cm, symmetric, narrowly obovate or narrowly elliptic, bases symmetric, acute or obtuse, the apical ones $5.5\text{--}9.5 \times 2.5\text{--}3.8$ cm, symmetric, narrowly obovate, bases symmetric, acute or obtuse, apices short acuminate, acumen ca. 1 mm long, abaxial surfaces glabrous, occasionally irregularly sparsely sericeous on midvein, indumentum ferruginous, adaxial surfaces glabrous, shining, margins flat or slightly revolute; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 6–7 pairs, slightly prominent on both surfaces, adaxially concolorous in relation to the blade, forming angle of $45\text{--}55^\circ$ with midvein, linear, tertiary veins prominent on both surfaces, intercostals and epidermals reticulate. *Inflorescences* apparently in double thyrsoids, axillary, 1 per axil, trichomes simple unicellular, peduncles 0.5–1 cm long, sparsely hirsute, rachises 13.5–15.5 cm long, sparsely to densely hirsute, lateral sub-thyrsoids 2–7 cm long, densely hirsute, indumentum of these structures ferruginous; bracts ca. 1.8 mm long, straight, hirsute. *Flowers* with pedicels ca. 0.5 mm long; buds ca. 2×2 mm, orbicular; sepals 5, slightly basally connate, ca. 3×1 mm, narrowly triangulate or elliptic, apices acute, outer surfaces hirsute, indumentum ferruginous, inner surfaces glabrous or subglabrous; petals $4\text{--}5 \times 1.2$ mm, erect, narrowly elliptic, apices acute, glandular dots more than 10, loosely distributed, black, conspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous; stamens basally connate by ca. 0.5 mm long, shorter series ca. 2 mm long, longer series ca. 3 mm long, filaments glabrous; ovaries ca. 1 mm long, tomentose, styles and stigmas not seen. *Fruits* not seen.

Distribution, habitat and phenology: *Connarus cuneifolius* is only known from the type specimen, which was collected by F. Sellow during his expedition to Brazil, but with no precise location. In the protologue, Baker (1871) cited only the specimen *Sellow* collected in “Rio de Janeiro ad Engenho do Paraiba”. This is likely to stand for the municipality of Paraíba do Sul (Fig. 11), west Rio de Janeiro, which can be confirmed by the fact that Sellow visited adjacent areas around 1818, according to the description of collector’s itinerary provided in the first volume of *Flora Brasiliensis* (Urban 1906: 105).

Notes: Despite no further available collections, *Connarus cuneifolius* is morphologically recognized by the leaves 3–5-foliolate, apical leaflets narrowly obovate, tertiary veins reticulate and adaxially prominent, and inflorescence rachis with indumentum hirsute. It resembles *C. beyrichii* due to leaflet shape but differs by having fewer secondary veins (6–7 pairs vs. 9–13), tertiary veins adaxially prominent (vs. flat tertiary veins, rarely slightly prominent), and inflorescence rachises hirsute (vs. sericeous). Additionally, it seems that the inflorescences in *C. cuneifolius* are double thyrsoids, while in *C. beyrichii* they are thyrsoids.

Forero (1983) indicated the specimen *Sellow 1824* from M as lectotype of *C. cuneifolius*, but the present work considers that the lectotype should be replaced for the specimen *Sellow B.1824 c.1280* from US, as it bears an original label of herbarium Berolinense (where Sellow worked for a time) with indication of the locality “Engade. Paraiba”, which matches accurately with the original description. The specimen from M, on the other hand, does not have an original label from B, nor an annotation that matches the description. No mention of the collector number is made in the protologue, but on the sheet label from the US duplicate, two numbers are included: “B.1824”, followed by “c.1280”. According to Urban (1893), who provided detailed information on Sellow’s expedition to Brazil and numbering, the specimens collected in Minas Gerais, Rio de Janeiro and São Paulo between 1818–21 were double numbered, just like the type of *C. cuneifolius*, suggesting the lectotype proposed here is an original material of *Flora Brasiliensis*.

Connarus detersus Planch., Linnaea 23: 435. 1850.—TYPE: Brazil. State unknown: *s. loc.*, *s. d.*, fl., *J. E. Pohl 1941* (holotype: K barcode K000633763!; probable isotypes: F-frag. [photo!], W [photo!]).

Shrubs, treelets or trees, 3–7(–22) m tall; branchlets slightly striate or slightly fissured, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels inconspicuous. *Leaves* 5–11-foliolate, occasionally 3 in young branchlets; petioles 2.2–7 cm long, tomentose to glabrescent; rachises 4–11.5 cm long, tomentose to glabrescent; pulvinuli 4–6 mm long, tomentose to glabrescent; leaflets coriaceous, less frequently chartaceous, concolorous, flat or conduplicate, basal pairs $4.5\text{--}10 \times 1.8\text{--}3.2$ cm, symmetric, narrowly ovate, narrowly elliptic or lanceolate, rarely ovate or elliptic, bases symmetric, acute or obtuse, rarely rounded, the apical ones $5.2\text{--}14.5 \times 1.8\text{--}3.7$ cm, symmetric, narrowly ovate, narrowly elliptic or lanceolate, bases symmetric, acute or obtuse, rarely rounded, apices short acuminate to acuminate, acumen 2–14 mm long, occasionally retuse, abaxial surfaces tomentose to glabrescent, mature leaflets abaxially tomentose only on midvein, indumentum ferruginous, adaxial surfaces glabrous or subglabrous, slightly shining, rarely dull, margins slightly revolute or flat; midveins abaxially prominent, adaxially impressed or slightly so, secondary veins 6–9 pairs, abaxially slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of $45\text{--}60^\circ$ with midvein, arcuate or slightly so, tertiary veins abaxially flat or slightly prominent, adaxially flat, intercostals and epidermals mixed percurrent or reticulate. *Inflorescences* in thyrsoids or double thyrsoids, axillary, 1–4 per axil, trichomes dendroid and simple unicellular, peduncles 0.5–3 cm long or inflorescences sessile, tomentose, rachises 6–15 cm long, tomentose, lateral cymes 0.5–2.5 cm long, tomentose, lateral sub-thyrsoids 2–10.5 cm long, tomentose, indumentum of these structures ferruginous or brown; bracts 1.5–2 mm long, tomentose. *Flowers* with pedicels 0.3–1.2 mm long; buds $2.3\text{--}2.5 \times 2.2\text{--}2.3$ mm, orbicular; sepals 5, 1 pair with 2 sepals connate entirely, $2.5\text{--}3 \times 1.8\text{--}2.1$ mm, ovate, apices acute, 3 sepals connate to the others basally or half their length, $2.5\text{--}3 \times 1.2\text{--}1.8$ mm, narrowly ovate, apices acute, outer surfaces tomentose, indumentum brown, inner surfaces glabrous, pubescent only at apex; petals $3\text{--}3.5 \times 1.2\text{--}1.5$ mm, reflexed, narrowly elliptic, apices rounded or obtuse, glandular dots more than 10, loosely distributed, black, conspicuous, outer surfaces subglabrous to sparsely pubescent, glandular trichomes sparse to abundant, inner surfaces with only sparse to abundant glandular trichomes, margins glabrous or ciliate, glandular trichomes absent or sparse; stamens basally connate by ca. 0.8 mm, shorter series 2–3 mm long, longer

series 2.5–4.5 mm long, filaments with sparse glandular trichomes; ovaries ca. 1.2 mm long, tomentose, styles and stigmas not seen. *Fruits* 1.8–2.1 × 1.3–1.4 cm, obovate, indehiscent side sigmoid or slightly so, pericarps up to 2 mm thick, stipes 2–6 mm long, styles partially persistent, inconspicuous or apiculate, 0.2–1 mm long, outer surfaces tomentose to glabrescent, indumentum ferruginous, black dots absent or abundant, inner surfaces with only sparse to abundant glandular trichomes, calyx deciduous, persistent or partially persistent, sepals reflexed or patent; seeds ca. 1.4–1.6 × 0.8–0.9 cm, arils whitish or yellowish.

Selected specimens examined: **Brazil.** Bahia: 20 km S. of Andaraí on road to Macugé, 12°56'S, 41°20'W, alt. 1000 m, 16 Feb 1977, fr., *R. M. Harley 18774* (CEPEC, K, SPF); Ca. 6 km N. of Barra da Estiva not far from Rio Preto, aprox. 13°35'S, 41°18'W, alt. 1100 m, 29 Jan 1974, fr., *R. M. Harley et al. 15653* (K); Chapada Diamantina, Mucêgê, Fazenda Caraíbas, 13°08'98"S, 41°24'85"W, 12 Dec 2004, fr., *M. T. S. Stradmann & P. Castilho 1053* (MBM); Ibicoara, Chapada Diamantina, Pediplano Central, 13°14'S, 41°29'W, alt. 1040 m, 21 Nov 2000, fr., *M. Araújo-Nóbrega 232* (SPF); Jacobina. Estrada a 8 Km na Rod. Jacobina/Capim Grosso, distrito de Itaitú, situado a 20 Km da Rodovia, 27 Oct 1995, fr., *J. G. Jardim et al. 712* (CEPEC); Serra do Tombador, ca. 25 km na estrada Jacobina/Morro do Chapéu, alt. 750 m, 20 Feb 1993, fr., *A. M. V. de Carvalho et al. 4135* (ALCB, CEPEC, K, US). Seabra, alt. 950 m, 13 Sep 1956, fl., *E. Pereira 2171* (RB). Ceará: Barbalha, Flora no Araripe, proximidades da Casa de Guarda da Santa Rita, ICMBio, lat.: 7.230192, long.: 39.211597, alt. 929 m, 10 Aug 2014, fl., *V. M. Mascena 209B* (EAC); Crato. Flona do Araripe, 15 Sep 1999, fr., *L. W. Lima-Verde 1694* (EAC); Serra dos Prazeres, Chapada do Araripe, 11 Mar 1993, fr., *E. Silveira & A. Fernandes s. n.* (EAC). Serra do Araripe, 17 Aug 1948, fr., *A. P. Duarte 1391* (NY); Nova Olinda, estrada de Nova Olinda, 19 Sep 1996, fl., *F. A. S. Clemente s. n.* (EAC). Espírito Santo: Linhares. Reserva Florestal da CVRD, Est. X-2, Km 12,950 lado direito, 10 Oct 1979, fl., *I. A. S. 084/79* (CVRD, RB); Reserva Florestal de Linhares, estrada Gávea, em frente a matriz nº 1 da Farinha Seca, próxima a um Paraj, 27 Aug 1979, fl., *D. A. Folli 92* (CVRD). Minas Gerais: Pedra Azul, ligação Rod. BR-116 a Divisópolis, 13 Sep 1984, fl., *G. Hatschbach 48168* (MBM, SPF); Quatituba, estrada Quatituba a Com Sta Angélica, 11 Dec 2005, fr., *A. A. da Luz 307* (CVRD, ESA); Santa Maria do Itabira, estrada Santa Maria do Itabira à Hematita, 8 Feb 2003, fr., *A. A. da Luz 106* (CVRD, ESA). Rio de Janeiro: Botafogo, *s. d.*, *A. F. M. Glaziou 8363* (P); Estrada do Redentor, 10 Jul 1971, fr., *J. G. Kuhlmann 1921* (RB); Mata do Corcovado, 26 Jul 1950, fl., *F. Gonçalves 2758* (IAN, RB); *S. loc.*, Jul 1892, fl., *A. F. M. Glaziou 19018* (K).

Distribution, habitat and phenology: *Connarus deterrentus* is exclusive to Brazil, ranging from central Rio de Janeiro (southern limit) to Chapada Diamantina, central Bahia; several individuals have also been found in south Ceará (norther limit) (Fig. 6). This species is represented by shrubs or small trees, with few individuals reported as large trees ca. 22 m tall, occurring in areas of Cerrado or in the transition with the Caatinga, but also in tableland (Tabuleiro) or evergreen dense forests, rarely in ciliary forests, at low (Linhares, ES) or high (Chapada Diamantina, BA; Serra do Araripe, CE) elevations. Specimens have been collected with flowers from July to October and with fruits from July to February.

Notes: *Connarus deterrentus* is morphologically recognized by its shrubby or arboreal habit, narrow leaflets and calyx with at least two sepals entirely connate. Due to these characteristics, it can be confused with *C. angustifolius*, but differs by leaflet indumentum and number of secondary veins (see “Notes” under *C. angustifolius*), aside of the fact that *C. deterrentus* is an extra Amazonian species.

While originally describing *C. deterrentus*, Planchon (1850) mistakenly cited “1341” as collector number for *Pohl 1941*. This is actually a common error in Planchon’s (1850) whole work, so the correct collector numbers are here applied for his new taxa.

It is here considered that the type collection of *C. deterrentus* (as indicated above) includes two possible isotypes, one from W and a fragment from F. These specimens do not have Pohl’s collection number on their labels, but they seem duplicated of the holotype from K, as noted by Forero (1983).

Connarus ecuadorensis G. Schellenb., in Engler, Pflanzenr. IV. 127(Heft 103): 238. 1938.—
TYPE: Ecuador. Guayas: Balao, Feb 1892, fl., *H. F. A. Eggers 14398* (lectotype **designated here**: M barcode M-0244175!; isolectotype: M!).

Connarus nervatus Cuatrec., Fieldiana, Bot. 27(2): 100. 1951.—TYPE: Colombia. Valle: Costa del Pacífico, río Cajambre, Quebrada de Guapecito, 0–5 met. alt., 16 May 1944, fr., *J. Cuatrecasas 17713* (lectotype **designated here**: F 1365613!; isotype: F!), *syn. nov.*

Scandent shrubs or trees, 3–6(–15) m tall, rarely lianas; branchlets slightly striate, sparsely sericeous to glabrescent, trichomes simples unicellular, lenticels conspicuous or

inconspicuous. *Leaves* 3–7-foliolate; petioles 4.7–12 cm long, sparsely sericeous to glabrescent; rachises 3.5–9(–11) cm long, sparsely sericeous to glabrescent; pulvinuli 6–8 mm long, sericeous to glabrescent; leaflets chartaceous to subcoriaceous, slightly discoloured, rarely concolorous, flat, basal blades 6.8–16 × 3.6–6.5 cm, symmetric, elliptic, ovate or obovate, bases symmetric, obtuse or rounded, rarely acute, the apical ones 10.5–22 × 4.8–8.5 cm, symmetric, elliptic, ovate or obovate, bases symmetric, obtuse or rounded, rarely acute, apices acuminate, acumen 4–10(–15) mm long, abaxial surfaces sparsely sericeous to glabrescent, usually more densely on the veins, indumentum brown or griseous, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially strongly prominent, adaxially flat or slightly impressed, secondary veins 9–14 pairs, abaxially strongly prominent, adaxially flat or slightly impressed, concolorous or discoloured in relation to the blade, forming angles of 50–60° with midvein, arcuate, tertiary veins abaxially prominent, adaxially flat or slightly prominent, intercostals and epidermals opposite percurrent. *Inflorescences* in double thyrsoids, axillary, 1 per axil, trichomes simple unicellular, peduncles 1.8–2.5 cm long, sericeous or sparsely so, rachises 11–27 cm long, sericeous, lateral sub-thyrsoids 5.5–16 cm long, sericeous, indumentum of these structures ferruginous; bracts 0.5–0.8 mm long, sericeous. *Flowers* with pedicels 0.5–1 mm long; buds ca. 2 × 2 mm, orbicular; sepals 5, slightly basally connate, 2.5–3.1 × 1–1.1(–1.3) mm, elliptic, triangulate or narrowly triangulate, apices acute or obtuse, outer surfaces sericeous or sparsely so, indumentum ferruginous or brown, inner surfaces glabrous or subglabrous, pubescent only at apex; petals 3.5–4 × (0.8–)1–1.5 mm, erect, oblong, narrowly elliptic or narrowly obovate, apices rounded, obtuse or acute, glandular dots more than 10, loosely distributed, or 1–5 distributed in the upper half, black, conspicuous or inconspicuous, outer surfaces sericeous or sparsely so, glandular trichomes absent or sparse, inner surfaces with only sparse to abundant glandular trichomes concentrated in the upper half, margins with abundant glandular trichomes; stamens basally connate by 0.7–1 mm long, shorter series 1.2–2.2 mm long, longer series 2–3.5 mm long, filaments with glandular trichomes sparse to abundant, shorter filaments occasionally glabrous; ovaries 0.8–1 mm long, densely pubescent, styles ca. 2 mm long, stigmas bilobate, lobes ca. 0.2 mm long. *Fruits* 2–2.9 × 1.5–1.8(–2) cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 4–9 mm long, styles partially persistent, apiculate, 1–3 mm long, outer surfaces subglabrous or sparsely sericeous on stipe and apex, indumentum brown or ferruginous, black dots abundant, inner surfaces subglabrous or sparsely pubescent, rarely sparsely tomentose, glandular trichomes absent, calyx persistent, sepals ascending erect, patent or reflexed; seeds 1.6–1.8 × 0.9–1 cm, arils yellowish.

Specimens examined: **Colombia.** Chocó: Area of Baudó, on left bank of Río Baudó, about 1.5 km above estuary, slightly above estuary of Estero del Medio, 11 Feb–29 Mar 1967, fr., *H. P. Fuchs & L. Zanella 21891* (F, G, K, P); Hoya del Río San Juan, Quebrada la Sierpe, afluyente del Río San Ruan, al frente de Palestina, ca. 5 m. alt., 4°10'N, 77°10'W, 25 Mar 1979, fr. *E. Forero et al. 3950* (COL); *E. Forero et al. 4000* (COL); Río San Juan, margen derecha, Quebrada del Taparal, 5–20 met. alt., 5–10 m, 30 May 1946, fl., *J. Cuatrecasas 21450* (F). Nariño: Tumaco, alrededores del Estero de Las Cargas, afluyente del Brazo del Mira, 28 Feb 1956, fr., *R. R. Castañeda 5560* (COL). Valle: Bajo Calima, 25 Apr 1961, fl., *I. Cabera 524* (COL); Costa del Pacífico, Río Naya, brazo Ají, orilla derecha em Calle Larga, 1–4 m alt., 28 Feb 1943, fr., *J. Cuatrecasas 14287* (F). **Ecuador.** El Oro: Hcda. Daucay antes de Limón-Playa, -03,29, -79,45, 450 m, 21 Nov 1994, fl., fr., *X. Cornejo & C. Bonifaz 3635* (GUAY, K); Km 2, dirt road El Tigre-Balsas, 03°47'804"S, 80°00'417"W, 800 m, 28 Feb 1997, fl., *B. B. Klitgaard et al. 434* (K, LOJA). Esmeraldas: Cantón, Quinindé, Reserva Ecológica Mache-Chindul, 35 km W of Quinindé, The Bilsa Biological Station, Cordillera Mache-Chindul, Sendero Blanco, 0°21'N, 79°44'W, 14 May 2008, fr., *J. L. Clark 10135* (US); Quininde Cantón Bilsa Biological Station, Mache mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, 00°21'N, 79°44'W, 400–600 m. 2 Apr 1995, fr., *J. L. Clark & Y. Troya 572* (MO, US); 23 Jan 1995, fl., *J. L. Clark 408* (MO, US). Napo: Río Cuyabeno, riverside vegetation from Lagunas de Cuyabeno to about 6 km upstream from Puerto Bolívar, 0°1'S, 76°10'W, alt. 300 m. 26 Aug 1981, fl., *J. Brandbyge et al. 36168* (G); *J. Brandbyge et al. 36172* (G). Orellana: Coca, concession Palm Oriente, 7 Sep 1983, fr., *Lescure 2030* (P). Pastaza: Curaray, Valle de la Muerte, 1°25'S, 76°52'W, 240 m, 22 Mar 1980, fr., *L. B. Holm-Nielsen et al. 22464* (P). Pichincha: 20 km W. of Santo Domingo de Los Colorados, 1000 m, 22 Oct 1961, fr., *P. C. D. Cazalet & T. D. Pennington 5116* (K, NY, US). *S. loc.* Coast plain, Jul 1932, fr., *A. Rimbach 95* (F).

Distribution, habitat and phenology: *Connarus ecuadorensis* is distributed in the coastal zone from Chocó (Colombia) to El Oro (Ecuador), with few collections acquired in the center of the latter country (Fig. 16). This species is usually represented by scandent shrubs or trees up to 6 m tall, occurring in ombrophilous forests along river margins close to Pacific Ocean, or in montane formations, at sea level to up to 800 m elevation. Specimens have been collected with flowers from January to May and in August and November, and with fruits from February to June and from September to November.

Notes: *Connarus ecuadorensis* resembles *C. ruber* due to the leaflets with secondary veins abaxially strongly prominent and large inflorescences in double thyrsoids.

However, the former has 3–7-foliolate leaves, longer sepals (2.5–3.1 mm long), longer petals (3.5–4 mm long) and fruits with stipes 4–9 mm long, while the later has 3-foliolate leaves, smaller sepals (1.5–1.8 mm long), smaller petals (2.5–3.3 mm long) and fruits with stipe 1–3 mm long. It is also similar to *C. lentiginosus*, but differs by the pulvinuli 6–8 mm long (vs. 4–5 mm long), fruits 2–2.9 cm long (vs. 1.8–2.2 cm long) internally eglandular (vs. fruits internally with glandular trichomes), and fruit stipes 4–9 mm long (vs. (1–)3–5 mm long). Additionally, *C. lentiginosus* occurs in south Mexico and Central America, while *C. ecuadorensis* is distributed close to the Pacific Coast in Colombia and Ecuador.

Connarus nervatus is here recognized as a synonym of *C. ecuadorensis*. The specimens of *C. ecuadorensis* included in our analyses were mostly named as *C. nervatus* in herbarium collections and even Forero (1983) recognized these two names as distinct species. This position was taken by Forero (1983) probably because the type specimen of *C. ecuadorensis* has leaflets abaxially sparsely sericeous, while in other materials this indumentum is abaxially irregular. However, the leaflets in the type specimen of *C. ecuadorensis* are very immature and, after analyzing more materials, it was noticed that the indumentum on the abaxial surface becomes glabrescent in this species. Therefore, there is no reason to recognize *C. ecuadorensis* and *C. nervatus* as separate taxa.

The type collection of *C. ecuadorensis* is deposited only in M (Eggers 14398), but is composed of two herbarium sheets. As they do not bear the same original label, they are interpreted as duplicates (Turland et al. 2018, Art. 8.3), so a lectotype is here designated. The specimen with the barcode M-0244175 was chosen because its label matches the original description.

A similar case was observed concerning the type of *C. nervatus*, composed of two specimens of *Cuatrecasas 17713* deposited in F. They do not bear the same original label and both are kept apart in different folders, so the specimen F 1365613 was selected as lectotype because it is the only one fertile.

Connarus elsaе Forero, Ann. Missouri Bot. Gard. 68(1): 220. 1981.—TYPE: Peru. San Martín: San Martín, road from Puente Colombia to Shapaja, along Río Mayo, alt. 280 m, 30 Apr 1976, fr., *T. Plowman 6017* (holotype: F 1818282!; isotypes: US [photo!], USM [photo!]).

Shrubs or trees, 3–8 m tall; branchlets striate, glabrous, glabrous or subglabrous, rarely sparsely sericeous, trichomes simple unicellular, lenticels inconspicuous, rarely conspicuous. *Leaves* 3–7-foliolate; petioles 3.5–7.5 cm long, glabrous or subglabrous, rarely sparsely sericeous; rachises (1.5–)3–10.5 cm long, glabrous or subglabrous, rarely sparsely sericeous; pulvinuli 3–4 mm long, glabrous or subglabrous; leaflets chartaceous, concolorous, flat, basal pairs $4.5\text{--}9.5 \times 1.8\text{--}3.8$ cm, symmetric, elliptic, bases symmetric, rounded or obtuse, the apical ones $7\text{--}15 \times 2.6\text{--}4.5$ cm, symmetric, narrowly elliptic or narrowly obovate, bases symmetric, acute, obtuse or rounded, apices acuminate, acumen 3–10 mm long, abaxial surfaces glabrous, occasionally subglabrous only on midvein, indumentum brown, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially slightly impressed, secondary veins 8–12 pairs, abaxially flat, rarely slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of $45\text{--}60^\circ$ with midvein, arcuate or slightly so, tertiary veins flat on both surfaces, intercostals mixed percurrent, epidermals opposite percurrent or reticulate. *Inflorescences* in thyrsoids or double thyrsoids, axillary, 1–3 per axil, trichomes simple unicellular, peduncles 0.4–1.5 cm long or inflorescences subsessile, sericeous or sparsely so, rachises 5.5–13.3 cm long, sericeous, lateral cymes 0.3–1.3 cm long, sericeous, lateral sub-thyrsoids 3.3–9 cm long, sericeous, indumentum of these structures brown or ferruginous; bracts 0.5–1.5 mm long, sericeous. *Flowers* with pedicels 0.5–1 mm long; buds ca. 2×1.2 mm, elliptic; sepals 5, slightly basally connate, $2.2\text{--}2.5 \times 1\text{--}1.5$ mm, ovate or narrowly so, occasionally narrowly triangulate, apices acute or obtuse, outer surfaces sericeous or sparsely so, indumentum ferruginous or brown, inner surfaces glabrous or subglabrous; petals $3\text{--}4.2 \times 1\text{--}1.5$ mm, erect, narrowly obovate or narrowly elliptic, apices rounded, acute or obtuse, glandular dots absent, rarely 1 distributed at apex, black, inconspicuous, outer surfaces sparsely pubescent, glandular trichomes sparse, inner surfaces sparsely pubescent only in the upper half, glandular trichomes abundant, margins with abundant glandular trichomes; stamens basally connate by 0.5–0.8 mm, shorter series 2–3 mm long, longer series 3–3.5 mm long, filaments with sparse glandular trichomes, occasionally glabrous in the shorter filaments; ovaries ca. 1 mm long, densely pubescent, styles and stigmas not seen. *Fruits* $2.2\text{--}2.5 \times 1.5\text{--}1.6$ cm, semi-orbicular, indehiscent side slightly sigmoid, pericarps up to 2 mm thick, stipes 4–6 mm long, styles partially persistent, apiculate, ca. 1 mm long, outer surfaces irregularly sparsely sericeous, more densely at stipe, indumentum brown, black dots abundant, inner surfaces tomentose, glandular trichomes not seen, calyx persistent, sepals patent; seeds not seen.

Specimens examined: **Peru.** San Martín: Alto Río Huallaga, alt. 360–900 m, Dec 1929, fl. *L. Williams* 5733 (G); *L. Williams* s. n. (BM). Juan Jui, alto Río Huallaga, altitude about 400 m, Oct 1934, fl., *G. Klug* 3855 (BM, F, GH, K, MO, NY, US); Tarapoto, Apr 1856, fl., *R. Spruce* s. n. (K).

Distribution, habitat and phenology: *Connarus elsae* is only known by few collections, and it seems to be restricted to the province of San Martín, Peru (Fig. 15). It is represented by shrubs or trees up to 8 m tall, occurring in the margins along Mayo and Huallaga rivers, at 280–900 m elevation. Specimens have been collected with flowers in April, October and December, and with fruits in April.

Notes: Among species with exclusively simple trichomes, *C. elsae* is morphologically recognized by the 3–7-foliolate leaves, flat or slightly prominent abaxial secondary veins, and epunctate petals or rarely with 1 inconspicuous black dot. Due to the number of leaflets and epunctate petals, this species can be confused with *C. bracteosovillosus* but differs by the inflorescence rachis sericeous (vs. pubescent) and bracts 0.5–1.5 mm long (vs. 2–3 mm long).

Connarus erianthus Benth. ex Baker, in Martius, Fl. Bras. 14(2): 191. 1871. *Connarus erianthus* Benth. ex Baker var. *erianthus*, syn. nov.—TYPE: Brazil. Pará: Santarém [In vicinibus Sanratém], Apr–Aug 1850, fl., fr., *R. Spruce* 794 (lectotype first step designated by Schellenberg 1938; lectotype second step designated by Forero 1983: M barcode M-0244182!; isolectotypes: NY [photo!]; probable isolectotypes: BM!, FI [photo!], GH [photo!], K [photo!], P [photo!]). Fig. 17

Shrubs, treelets or trees, 1–7(–20) m tall; branchlets slightly striate, densely velutinous or lanate to glabrescent, trichomes dendroid, simple unicellular and simple multicellular, lenticels absent or inconspicuous. *Leaves* 9–15-foliolate; petioles 2.8–7.2 cm long, lanate to glabrescent; rachises 10–28 cm long, lanate to glabrescent; pulvinuli 3–6 mm long, lanate to glabrescent; leaflets usually coriaceous, less frequently chartaceous, concolorous or slightly discolorous, flat, basal pairs 3–12.6 × 1.7–4.8 cm, symmetric or slightly asymmetric, narrowly ovate, ovate, oblong, narrowly elliptic or elliptic, rarely narrowly obovate, bases asymmetric or slightly so, rounded, obtuse or acute, the apical ones 6–19.2 × 2–5.7 cm,

symmetric or slightly asymmetric, oblong, narrowly elliptic or narrowly ovate, rarely narrowly obovate, the distal usually elliptic, bases asymmetric or slightly so, rounded, obtuse or acute, apices acuminate to long acuminate, acumen 3–13(–22) mm long, both surfaces lanate to glabrescent, mature leaflets glabrous or subglabrous, adaxial surfaces slightly shining or dull, margins revolute or slightly so; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 6–9 pairs, abaxially prominent or slightly so, adaxially flat or slightly prominent, concolorous in relation to the blade, forming angles of 50–65° with midvein, arcuate or slightly so, tertiary veins abaxially prominent or slightly so, adaxially slightly prominent, rarely flat, intercostals mixed percurrent, epidermals opposite percurrent. *Inflorescences* in stachyoid spikes, axillary or ramiflorous, 1–5 per axil, trichomes dendroid, simple unicellular and simple multicellular, inflorescences sessile or subsessile, lanate, rachises 3–11 cm long, lanate, indumentum of these structures ferruginous; bracts 0.8–2 mm long, hirsute. *Flowers* sessile; buds 2–3 × 2 mm, orbicular or elliptic; sepals 4–5, 2 pairs with 2 sepals or all 4 or 5 connate half their length, 2–3.5 × 2.5–2.5 mm, ovate, apices obtuse or rounded, 1 sepal occasionally connate to the others at base, 3 × 1–1.2 mm, narrowly ovate, apices acute, outer surfaces hirsute or tomentose, indumentum ferruginous, inner surfaces glabrous, occasionally pubescent at apex; petals 3–4 × 1.2–1.8 mm, reflexed, narrowly obovate or oblong, apices rounded, glandular dots absent or 1–5, distributed at apex, black, inconspicuous, both surfaces glabrous, margins glabrous; stamens basally connate by 0.2–0.7 mm long, shorter series ca. 1.5 mm long, longer series 2–2.5 mm long, filaments glabrous; ovaries 1.2–2.5 mm long, densely pubescent, styles ca. 1 mm long, stigmas discoid, surfaces cordate with 2 lobes ca. 0.2 mm long. *Fruits* 1.8–2.6 × 1–1.6 cm, obovate or narrowly obovate, indehiscent side sigmoid, slightly sigmoid or almost linear, pericarps up to 2 mm thick, fruits sessile, styles partially persistent, apiculate or spinescent, 0.5–3 mm long, outer surfaces lanate to glabrescent, indumentum ferruginous, black dots absent or abundant, inner surfaces tomentose or densely so, glandular trichomes absent or sparse, calyx persistent, sepals ascending erect or patent; seeds 1.5–1.8 × 0.7–0.8 cm, arils yellowish.

Selected specimens examined: **Brazil.** Amapá: Serra do Navio, Rio Amapari. 9 Nov 1954, fr., *R. S. Cowan* 38179 (NY, RB); 10 Nov 1954, fr., *R. S. Cowan* 38218 (IAN, NY). Pará: Along E side of road to Punta Piedra, about 3.4 km from where the road departs to the NW from the Santarém–Alter do Chão road (PA-457), ca. 21.5 km E and somewhat S of Santarém, 24 Nov 2011, fr., *B. M. Torke et al.* 1289 (IAN, MG, NY, RB); Alter do Chão. 7–8 km from Alter do Chão on the Santarém road, c. 2°29'S, 54°55'W, 2 Oct 1993, fl., *J. A. Ratter & T. M.*

Sanaïotti 6919 (K); Estrada do Pindobal, savanna amazônica, beira da estrada, 2°33'13.1"S, 54°57'37.7"W, 19 Jan 2020, fr., *C. A. P. Toledo 418* (ESA). Centro de Treinamento da FAO, Santarém, 5 Oct 1962, fr., *A. P. Duarte 7068* (INPA, RB); Monte Alegre. Serra do Ererê, parte do Mirante, 01°55'S, 54°15'W, 6 Nov 1987, fr., *C. A. C. Ferreira 9499* (INPA, MG, NY, RB); Região do Igarapé da Mulata, 26 Sep 1953, fl., *R. L. Fróes 30384* (IAN); Terra de Ereré, baixo Amazonas, Rio Negro, 21 Jul 1908, st., *E. Snethlage s. n.* (MG barcode MG 09501). Perto do aeroporto de Santarém, 18 Aug 1955, fr., *G. C. Black 55-18739* (IAN); Óbidos. 5 Nov 1920, fl., *A. Ducke s. n.* (MG barcode MG011021); 10 Jan 1920, fr., *A. Ducke s. n.* (RB barcode RB 00260802). Região de campos a E. de Faro, 2 Sep 1907, fl., *A. Ducke s. n.* (MG barcode MG 008701); Rio Arapiuns, Rio Mentái, 11 Nov 1952, fl., *J. N. Pires & N. T. Silva 4358* (IAN, NY); Santarém. (Alter do Chão), vegetação de Cerrado, 1 Jan 2009, fr., *L. C. B. Lobato et al. 3560* (MG); APA Alter do Chão; em savana às margens da rodovia PA-457 (Everaldo Matins), que liga Santarém a Alter do Chão, mancha de savana próximo a comunidade de São Pedro, 2°31'43"S, 54°53'59"W, alt. 76 m, 10 Oct 2015, fl., fr., *L. L. Giacomini 2702* (HSTM); Estrada que liga Alter do Chão, 12 Dec 1978, fl., *R. Vilhena et al. 217* (MG); Open campos, Apr–Oct 1850, fl., *R. Spruce 1002* (K); Região do Tapajós, próximo de Porto Novo, estrada para Belterra, 29 Nov 1978, fr., *U. N. Maciel & M. R. Cordeiro 67* (MG, NY).

Distribution, habitat and phenology: *Connarus erianthus* is a frequently collected species, restricted to far north Brazil (north Pará and Amapá), occurring especially along the Tapajós River in Amazonian savannas (Fig. 18). It is represented by shrubs or trees usually up to 7 m tall, growing in non-flooded areas with sandy soils, at low elevations, except in Serra do Navio (Amapá), where individuals have been found up to 260 m elevation. Specimens have been collected with flowers from September to December and with fruits from August to January.

Notes: *Connarus erianthus* is easily distinguished from the species with dendroid trichomes by the branchlets lanate to glabrescent, leaflet bases asymmetric, inflorescences in stachyoid spikes with simple multicellular trichomes (rachises and bracts), calyces with at least 2 sepals connate to half their length and externally lanate to glabrescent fruits.

This species was subdivided into three varieties (*Connarus erianthus* var. *erianthus*, *C. erianthus* var. *pedicellatus* and *C. erianthus* var. *stipitatus*) by Forero (1980a, 1983), while Toledo et al. (2020) did not recognize varietal entities. After conducting this revision, it became clear that, among these three varieties, two taxa should be recognized, but at species level.

Therefore, *C. erianthus* var. *pedicellatus* and *C. erianthus* var. *stipitatus* are here treated under *C. pedicellatus* (for a complete discussion, see “Notes” section of *C. pedicellatus*). *Connarus erianthus* and *C. pedicellatus* are morphologically closely related due to their leaflet bases asymmetric, connation of sepals and fruits externally lanate to glabrescent. However, they differ by consistent characters, which suggested the recognition of two separate species: *C. erianthus* has middle and apical leaflets usually coriaceous, comparatively narrower (oblong, narrowly elliptic or narrowly obovate) and with revolute margins, inflorescences unbranched with simple multicellular trichomes (rachises and bracts), flowers and fruits sessile, while *C. pedicellatus* has middle and apical leaflets chartaceous, usually ovate or elliptic with flat margins, inflorescences in thyrsoids without simple multicellular trichomes, flowers pedicellate, and fruits with stipes 2–4 mm long. In addition, both species occur sympatrically in Pará, but *C. pedicellatus* extends far westwards, reaching the state of Acre in Brazil, suggesting that *C. erianthus* and *C. pedicellatus* co-occur only in the limits of their distribution range.

Baker (1871) published *C. erianthus* and cited only syntypes; one of them (*Spruce* 794) was indicated in synonymy, referring to a Spruce specimen identified by Bentham as *Connarus erianthus*. This means that Baker (1871) described *C. erianthus* and gave credit to Bentham, who first noticed – but did not describe – that the specimen represented a new taxon. Therefore, authorship of this name has been attributed to Bentham ex Baker. Later, Schellenberg (1938) inadvertently selected the lectotype *Spruce* 794 by referring to it as type, and Forero (1983) inadvertently designated a second step lectotype by citing the specimen *Spruce* 794 from M as holotype.

Connarus fasciculatus (DC.) Planch., *Linnaea* 23: 432. 1850. *Omphalobium fasciculatum* DC., *Prodr.* 2: 86. 1825.—TYPE: French Guiana. Cayenne, *s. d.*, fr., *Martin s. n.* (holotype: P barcode P01819588!; isotype: G-frag!).

Shrubs, treelets or trees, 2–8(–12) m tall; branchlets slightly striate, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 9–25-foliolate; petioles 5.5–19 cm long, glabrous or subglabrous; rachises 18–56 cm long, glabrous or subglabrous; pulvinuli 4–8 mm long, tomentose to glabrescent; leaflets chartaceous, concolorous or slightly discolorous, flat, basal pairs 5.5–17.3 × 2.5–6 cm, slightly

asymmetric, ovate, elliptic, narrowly elliptic, oblong or narrowly obovate, bases asymmetric or slightly so, rounded, obtuse or acute, the apical ones $12.5\text{--}33 \times 3.2\text{--}9(-11)$ cm, slightly asymmetric, oblong, narrowly elliptic, ovate, narrowly ovate, bases asymmetric or slightly so, rounded, obtuse or acute, apices long acuminate to cuspidate, acumen $(9\text{--})13\text{--}34$ mm long, both surfaces lanate to glabrescent, mature leaflets glabrous or subglabrous, abaxially more densely on midvein, indumentum brown, adaxial surfaces dull, margins flat or slightly revolute; midveins abaxially prominent, adaxially impressed, secondary veins 5–12 pairs, abaxially prominent, adaxially impressed or slightly so, concolorous in relation to the blade, forming angles of $45\text{--}65^\circ$ with midvein, arcuate, tertiary veins abaxially prominent, adaxially flat to impressed, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in botryoid racemes, ramiflorous or cauliflorous, trichomes dendroid and simple unicellular, peduncles 0.2–0.5 cm long or inflorescences subsessile, tomentose, rachises 2–7(–12.5) cm long, tomentose, indumentum of these structures ferruginous; bracts ca. 0.8 mm long, straight, tomentose. *Flowers* with pedicels 0.5–1.5 mm long; buds $2\text{--}2.2 \times 1.7\text{--}2$ mm, orbicular or elliptic; sepals 5, 1–2 pairs with 2 sepals each connate entirely, $2.8\text{--}3.2 \times 2$ mm, ovate, apices obtuse or rounded, 1–3 sepals connate to the others at base or half their length, $2.8\text{--}3 \times 1\text{--}1.2$ mm, narrowly ovate or elliptic, apices acute, outer surfaces tomentose, indumentum ferruginous, inner surfaces glabrous; petals $3.8\text{--}5 \times 1.1\text{--}1.5$ mm, reflexed, narrowly obovate or narrowly elliptic, apices acute, obtuse or rounded, glandular dots more than 10, rarely 5, loosely distributed, black, inconspicuous, both surfaces glabrous, margins glabrous; stamens basally connate by 0.5–2 mm long, shorter series 2–3.5 mm long, longer series 2.3–4.5 mm long, filaments glabrous; ovaries 1–1.5 mm long, tomentose, styles 1.5–2.8 mm long, stigmas bilobate, lobes 0.7–1 mm long. *Fruits* $1.5\text{--}2.5 \times 0.9\text{--}1.5$ cm, narrowly obovate, indehiscent side slightly sigmoid or linear, pericarps up to 2 mm thick, stipes 1–4 mm long, styles partially persistent, apiculate or spinescent, 0.3–2 mm long, outer surfaces lanate or tomentose to glabrescent, indumentum ferruginous, black dots absent or abundant, inner surfaces pubescent or sparsely so (with or without glandular trichomes) or with only sparse to abundant glandular trichomes, rarely glabrous, calyx deciduous or partially persistent, sepals reflexed, less frequently ascending erect; seeds $1.2\text{--}1.6 \times 0.6\text{--}1$ cm, arils yellowish.

Notes: Among the species with dendroid trichomes, *C. fasciculatus* is easily distinguished by being shrubs to trees with leaflet bases asymmetric and inflorescences ramiflorous or cauliflorous. It can be confused with *C. pedicellatus* due to the number of leaflets, their asymmetric bases, acumen length, connation of sepals and fruits externally

densely hairy to glabrescent, but the former differs from the latter by the relatively larger apical leaflets with secondary veins adaxially impressed or slightly so (vs. flat or rarely slightly impressed) and inflorescences cauliflorous or ramiflorous, unbranched (vs. branched inflorescences, axillary, rarely ramiflorous).

Two subspecies are here recognized under *C. fasciculatus*; these are morphologically differentiated by number and width of leaflets, number of secondary veins, and fruit indumentum. Moreover, these subspecies are geographically isolated within the Amazon of South America (see discussions below).

Key to the subspecies of *C. fasciculatus*

- 1a. Leaves 15–25-foliolate; secondary veins 8–12 pairs; fruits externally tomentose to glabrescent, internally with only sparse to abundant glandular trichomes or glabrous, rarely subglabrous with stellate trichomes *C. fasciculatus* subsp. *fasciculatus*
- 1b. Leaves 9–13-foliolate; secondary veins 5–8 pairs; fruits externally lanate to glabrescent, internally pubescent or sparsely so formed by stellate or dendroid trichomes, glandular trichomes absent or sparse, never with only glandular trichomes *C. fasciculatus* subsp. *pachyneurus*

Connarus fasciculatus (DC.) Planch. subsp. *fasciculatus*

Shrubs, treelets or trees, 2–4 m tall. *Leaves* 15–25-foliolate; leaflets 2.5–6.7 cm wide; secondary veins 8–12 pairs. *Fruits* with outer surfaces tomentose to glabrescent, inner surfaces with only sparse to abundant glandular trichomes or glabrous, rarely subglabrous with stellate trichomes.

Selected specimens examined: **Brazil.** Amapá: First cachoeira on Rio Iauê, 02°53'N, 52°22'W, 0.5 km east of confluence with Rio Oiapoque, 22 Aug 1960, fl., *H. S. Irwin & L. Y. T. Westra* 47701 (UB); Pedra Branca do Amapari, Parque Nacional Montanhas do Tumucumaque, trilha T1 no trecho 2.500–4.000 m, 1°12'14"N, 52°23'29"W, ele. 100 m, 10 Sep 2018, fl., *R. Goldenberg* 2558 (NY, RB); Rio Oiapoque, 1.5 km south of Pedra Alice, 17 Aug 1960, fl., *H. S. Irwin et al.* 47591 (COL, IAN, MG, NY). **French Guiana.** Basse crique

Courouaie (affluent basse Approuague) su deuxième camp, 11 Jan 1970, fr., *R. A. A. Oldeman B 2704* (P); Cayenne, Haute Approuague, sur la crique Parépou entre le premier et le deuxième campement, 20 Sep 1968, fl., *R. A. A. Oldeman T-175* (K); Cayenne, Monts Atachi Bacca, 3 Mar 1971, fr., *de Granville 744* (COL, NY, P, U); Mont Galbao, secteur Est., 3°36'N, 53°17'W, alt. 700 m, 17 Jan 1986, fr., *J. J. de Granville et al. 8784* (P); Monts Kotika, versant Ouest, 3°55'N, 54°12'20"W, alt. 400 m, 19 Feb 2005, fr., *J. J. de Granville et al. 16793* (K); Régina, Réserve naturelle des Nourages, Station de Recherches permanente des Nourages, site "Inselberg", petit plateau, quadrat 21G, 4°3'N, 52°42'W, alt. 150 m, 9 Dec 1999, fl., *O. Poncy & F. Crozier 1326* (P); Riv. Approuague, crique Tortue, layon LUTERMA, 27 Jan 1967 (st), *R. A. A. Oldeman 2380* (COL, IAN, NY, P, U). **Suriname.** Kabalebo: In Montibus Bakhuis inter flum. Kabalebo et Coppename Sinistrum, alt. 550 m, 3 Mar 1965, fr., *P. A. Florschütz & P. J. M. Maas 3102* (NY). Morowijne: Nassau Mountains, Marowijne River, "A" Line, 150 m west of Line 25, Plateau B, alt. 400–550 m, 8 Mar 1955, fr., *B. Maguire 40781* (K); Nassau Mountains, Marowijne River, Plateau A, Line 12 to about Line R, alt. 525 m, 28 Feb 1955, fl., *B. Maguire 40709* (NY); Nassau Mts., Plateau C, 4°50'N, 54°37'W, 2 Feb 2003, fr., *M. J. Jansen-Jacobs et al. 6505* (K); W ridge of Plateau, 4°12'04"N, 54°45'57"W, alt. 550–600 m, 8 Dec 2004, fl., fr., *M. J. Jansen-Jacobs et al. 6953* (K, U). Sipaliwini: Central Suriname Nature Reserve, on the upper slopes and summit of the first peak in Eilerts de Haan mountain range ca. 7 km ENE of Kayserberg, 20 Jun 2003, fr., *C. Herrera et al. 9986* (COL, MO). Province unknown: Tumuc Humac Mts., Talouakem, second base camp, 2°29'00"N, 59°45'W, alt. 330 m, 8 Aug 1993, fl., *P. Acevedo-Rodriguez et al. 5948* (K, US).

Distribution, habitat and phenology: *Connarus fasciculatus* var. *fasciculatus* is only found in the extreme north of South America, distributed in Amapá (Brazil), French Guiana and Suriname (Fig. 14). It is geographically isolated from *C. fasciculatus* subsp. *pachyneurus* (mainly in Acre, Amazonas and Pará, Brazil, south Colombia and northeast Peru). It is represented by shrubs or small treed up to 4 m tall, mainly from montane formations, at 150–700 m elevation. Specimens have been collected with flowers especially from August to December and with fruits from December to March.

Connarus fasciculatus (DC.) Planch. subsp. ***pachyneurus*** (Radlk.) Forero, Fl. Neotrop. Monogr. 36: 54. 1983. *Connarus pachyneurus* Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 16: 365. 1886.—TYPE: Brazil. Amazonas: [in sylvis

Yapurensibus], Jan, fr., *C. F. P. von Martius s. n.* (holotype: M barcode M-0244177!). Fig. 19

Connarus klugii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 157. 1936.—TYPE: Peru. Loreto: Mishuyacu, near Iquitos, alt. 100 meters, May–Jun 1930, fl., *G. Klug 1494* (holotype: F 627497 [photo!]; isotypes: G-frag.!, NY [photo!], US [photo!]).

Treelets or trees, 2–8(–12) m tall. *Leaves* 9–13-foliolate; leaflets (2.5–)3.5–9(–11) cm wide; secondary veins 5–8 pairs. *Fruits* with outer surfaces lanate to glabrescent, inner surfaces pubescent or sparsely so formed by stellate or dendroid trichomes, glandular trichomes absent or sparse.

Selected specimens examined: **Brazil.** Acre: Cruzeiro do Sul, Igarapé Humaitá, afluente da margem direita do Rio Juruá, Colocação Sto. Antônio, 08°19'S, 72°47'W, 30 Oct 1991, fr., *C. A. C. Ferreira et al. 10481* (NY, UFACPZ); Estrada da Alemanha, Cruzeiro do Sul, 14 Apr 1971, fr., *G. T. Prance et al. 11879* (INPA, NY); 4 Nov 1966, fr., *G. T. Prance et al. 3007* (NY). Mâncio Lima, Bacia do Alto Juruá, Rio Moa, Parque Nacional da Serra do Divisor, margem direita, Apertado da Horta, 07°31'15"S, 73°45'W, 8 May 1996, fr., *M. Silveira et al. 1306* (NY); Manoel Urbano, Lago Novo, Rio Purus, colocação Lago Novo, próximo ao roçado, 19 Nov 1996, fr., *M. Silveira et al. 1412* (INPA); Proj. RADAM, sub-base Cruzeiro do Sul, Feb 1976, fr., *Marinho 349* (IAN); Tarauacá, Rio Tarauacá, river at low water, Seringal Universo, Colocação Cumaru, 08°16'S, 71°05'W, 23 Sep 1994, fr., *D. C. Daly et al. 8344* (NY, UFACPZ). Amazonas: Autazes, Campo da Tupana, 04°15'76"S, 60°13'18"W, 3 Jul 2007, fr., *D. O. Maurenza & P. L. Viana 13* (INPA); Boca do Acre, Rio São Domingos, Floresta Nacional do Mapiá-Inauini, 08°21'67"S, 67°52'76"W, 12 Aug 2009, fr., *A. Quinet et al. 1833* (ESA, RB); Borba, bacia do Rio Amazonas, afluente do Rio Madeira, Igarapé das Onças, 3 km ao Norte da Vila de Canumã, Rio Canumã, 30 Jun 1983, fr., *C. A. C. Ferreira 3958* (NY); Carauari, Noroeste do Rio Juruá, Poço NEJ I, 28 Jun 1980, fr., *A. S. L. da Silva et al. 403* (INPA); Esperança, Javará, 27 Oct 1945, fl., *A. Ducke 1875* (NY, RB); São Paulo de Olivença, 5 Nov 1927, fr., *A. Ducke 19714* (IAN, NY, RB); Estr. Manaus-Porto Velho, trecho Castanho-Tupana, 7 Jul 1972, fr., *M. F. Silva et al. 165* (INPA); Fonte Boa, Paraná Mimeruá (tributary of Rio Juruá), Paraná Mamupina, right bank, near mouth of paraná, 02°42'S, 65°59'W, 3 Nov 1986, fr., *D. C. Daly et al. 4223* (INPA, NY); Humaitá, estrada Humaitá-Porto Velho, km 60, 3 May 1982, fr., *L. O. A. Teixeira et al. 191* (INPA, NY); Manaus, km 50 da estrada Manaus-

Itacoatiara, 28 Aug 1961, fr., *W. A. Rodrigues & J. Lima* 2395 (INPA); Maués, Rio Apoquिताua, acima do lugar São Sebastião, 03°50'S, 57°33'W, 23 Jul 1983, fr., *C. A. C. Ferreira* 4280 (INPA, NY); Rio Curuquetê, vicinity of Cachoeira Santo Antonio, 17 Jul 1971, fr., *G. T. Prance et al.* 14389 (K, NY); Rio Javari, behind Angamo Garrison, 3 Aug 1973, fr., *E. Lleras et al.* P17152 (INPA, NY); Rio Javari, behind Palmeiras Army Post, 72°49'W, 5°8'S, 31 Jul 1973, fr., *E. Lleras et al.* P16978 (K); Rio Abacaxis, Terra Preta, 04°22'S, 58°40'W, 5 Jul 1983, fr., *C. Todzia et al.* 2316 (NY); São Gabriel da Cachoeira, Morro dos Seis Lagos, Igarapé Yá-mirim, 24 Sep 2008, fr., *M. H. Terra-Araújo* 393 (INPA); Tabatinga, estrada de assentamento do INCRA, ramal paralelo à Geodésia, Jan 1989, fr., *C. A. C. Ferreira et al.* 9986 (NY). Pará: Altamira, Estação Experimental da Embrapa, rodovia Transamazônica, trecho Altamira-Itaituba, km 23, 12 Aug 1978, fr., *R. P. Bahia* 1 (MG, NY); Planalto de Santarém, estrada do Japonês, Jul 1954, fr., *R. L. Fróes* 30910 (IAN); Santarém, boca do Tapajós, terrenos da SUDAM, Oct 1969, fl., *M. Silva & R. Souza* 2660 (MG); Santarém, Fazenda Experimental da Universidade Federal do Oeste do Pará, Divisa da Fazenda, floresta densa na altura do Km 46 da PA-350 (Santarém Curuá Uma), 2°41'34"S, 54°31'51"W, Aug 2016, fr., *J. J. Lucas & Rossy s. n.* (HSTM). Rondônia: Porto Velho, Represa Samuel, forest along PR-3 road, ca. 10 km SE of dam, 08°49'S, 63°24'W, 17 Jun 1986, fr., *W. Thomas et al.* 5142 (INPA, NY); Santa Barbara, Rodovia BR 364, km 120, 9°10'S, 63°07'W, 10 km ao Norte da Sede da Mineração, 20 May 1982, fr., *L. O. A. Teixeira et al.* 740 (INPA, NY). **Colombia.** Amazonas: Tarapacá, Paisage B1, Caño Villa Flor, K0+ 1900 m, Lin 19 Par 4, 2°29'26"S, 70°20'28"W, 8 Dec 2004, fr., *J. S. Barreto et al.* 278 (COL). **Peru.** Loreto: Requena, Dtto. Sapuena, basin of Río Ucayali, Jenaro Herrera and vicinity, 3 km E of Jenaro Herrera town, then 2 km NE of Centro de Investigaciones Jenero Herrera, 4°55'S, 73°45'W, 28 Nov 1988, fr., *D. C. Daly et al.* 5775 (NY). Yarinacocha: Estacion Experimental Alexander von Humboldt, Arb. "Adolfo Salazar C", 25 May 1980, fl., *N. Begazo* 158 (COL).

Distribution, habitat and phenology: This subspecies is widely distributed in the Brazilian Amazon, especially in the states of Acre, Amazonas and Pará, with few collections known from northeast Peru and south Colombia (Fig. 14). Individuals are small trees up to 12 m tall, found in upland forests or frequently flooded areas (igapós), normally growing on clay soils, at 50–260 m elevation. Specimens have been collected with flowers from April to October and with fruits irregularly throughout the year.

Connarus favosus Planch., Linnaea 23: 434. 1850.—TYPE: Brazil. Maranhão: *S. loc.*, Jun 1841, fl., fr., *G. Gardner 6011* (holotype: K barcode K000633799!; isotypes: BM!, K!, OXF [n. v.]). Fig. 20

Connarus crassifolius Benth. ex Baker, in Martius, Fl. Bras. 14(2): 186. 1871, *pro syn.*

Lianas, shrubs or scandent shrubs, 1–5(–8) m tall; branchlets slightly striate, velutinous or tomentose, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3–5(–7)-foliolate; petioles 2–6.2 cm long, velutinous or tomentose; rachises 0.8–6 cm long, velutinous or tomentose; pulvinuli 3–5 mm long, velutinous or tomentose; leaflets coriaceous, discolorous, flat, basal pairs $4.3\text{--}11.2 \times 2\text{--}5$ cm, symmetric, elliptic or obovate, bases symmetric, rarely asymmetric, rounded, subcordate or cordate, the apical ones $5.4\text{--}13.5 \times 2.5\text{--}5.3$ cm, symmetric, elliptic or obovate, bases symmetric, rarely asymmetric, rounded, subcordate or cordate, apices short acuminate to acuminate, acumen 2–9 mm long, retuse, abaxial surfaces densely sericeous, indumentum brown or griseous, adaxial surfaces glabrous, shining, margins revolute or slightly so; midveins abaxially prominent, adaxially impressed or slightly so, secondary veins 7–10 pairs, flat on both surfaces, less frequently abaxially slightly prominent, adaxially concolorous in relation to the blade, forming angles of $50\text{--}65^\circ$ with midvein, slightly arcuate, tertiary veins flat on both surfaces, less frequently abaxially slightly prominent, intercostals and epidermals reticulate. *Inflorescences* in double thyrsoids, axillary or pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncles 0.2–3 cm long, densely pubescent, rachises 6–20 cm long, densely pubescent, lateral sub-thyrsoids 1–6 cm long, densely pubescent, indumentum of these structures brown or ferruginous; bracts 0.8–1 mm long, sericeous. *Flowers* subsessile or pedicels 0.5–1 mm long; buds $2\text{--}2.2 \times 1.2$ mm, elliptic; sepals 5, slightly basally connate, $1.8\text{--}2.5 \times 0.5\text{--}1$ mm, ovate, narrowly ovate or narrowly triangulate, apices acute, outer surfaces sericeous, indumentum brown or ferruginous, inner surfaces glabrous, pubescent only at apex; petals $3\text{--}4 \times 1\text{--}1.5$ mm, erect, narrowly obovate or oblong, apices rounded, obtuse or acute, glandular dots more than 10, loosely distributed, black or colorless, conspicuous or inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent or sparse, margins with only sparse glandular trichomes; stamens basally connate by 0.3–0.8 mm long, shorter series 1.2–2 mm long, longer series 2.2–2.5 mm long, filaments glabrous; ovaries 0.8–1.5 mm long, densely pubescent, styles 0.8–1.5 mm long, stigmas bilobate, lobes 0.15–0.25 mm long. *Fruits* $1.3\text{--}2 \times 1\text{--}1.5$ cm, obovate or semi-orbicular,

indehiscent side sigmoid or slightly so, pericarps up to 2 mm thick, stipes 0.5–1 mm long or fruits sessile, styles partially persistent, apiculate or inconspicuous, 0.1–1 mm long, outer surfaces tomentose or velutinous, occasionally glabrescent, indumentum brown or ferruginous, black dots absent or sparse, inner surfaces sparsely hirsute or sparsely pubescent, rarely subglabrous, glandular trichomes sparse to abundant, calyx persistent, sepals ascending erect or patent; seeds $1\text{--}1.6 \times 0.6\text{--}0.9$ cm, arils yellowish.

Selected specimens examined: **Brazil.** Ceará: Estrada para Guaraciaba, Reriutaba, 10 Dec, fr., *A. S. F. Castro* 913 (EAC); Pacujá, Serrinha, 16 Feb 2009, fr., *F. A. M. da Ponte Filho* 140 (HUVA). Maranhão: Caxias, 2 Jul 1907, fr., *A. Ducke* RB19720 (RB, IAN); Mineirinho, Rio Pindaré, $03^{\circ}40'S$, $45^{\circ}50'W$, 30 m alt., 25 May 1979, fl., *J. Jangoux & R. P. Bahia* 837 (RB); Lago da Pedra, 1 Jul 1978, fl., fr., *M. Ribeiro* 39 (SLUI); Maracaçumé River Region, 28 Nov 1932, fl., *R. L. Fróes* 2006 (P); São Luis, Praia do Calhau, 18 Mar 1989, fl., *M. C. L. C. Marques & J. Ferreira* 96 (HRCB). Pará: Almeirim, Serra de Tabatinga, 29 Apr 1923, fl., fr., *A. Ducke* 18386 (RB); Altamira, Ilha Belo-Horizonte, Rio Xingu, 11 Oct 1986, fr., *A. T. G. Dias* 505 (MG); Alter do Chão, Estrada do Pindobal, savana amazônica, beira da estrada, $2^{\circ}33'13.1''S$, $54^{\circ}57'37.7''W$, 19 Jan 2020, fr., *C. A. P. Toledo* 417 (ESA, RB); Aprox. 18 km east of Tucuruí and Rio Tocantins, by BR 263, $03^{\circ}30'S$, $49^{\circ}32'W$, 28 Oct 1981, fr., *D. C. Daly et al.* 940 (INPA); BR 230, Transamazon Highway, branch road north off km 20 of Transamazon Altamira-Itaituba, 31 Oct 1977, fr., *G. T. Prance et al.* P24746 (MG, NY); Campos Altos do Jutay, Almeirim, 15 Apr 1923, fl., fr., *A. Ducke* RB18385 (IAN, RB); Melgaço, Estação Científica Ferreira Penna, margem do Rio Curuá, 16 Dec 1999, fr., *A. S. L. da Silva et al.* 3818 (MG, RB); Itaituba, Vila no lado direito do Rio Tapajós, Campo dos Perdidos, área antropizada, solo arenoso, $4^{\circ}26.368'S$, $56^{\circ}13.326'W$, 23 Jan 2020, fl., *C. A. P. Toledo et al.* 420 (ESA, RB); Monte Alegre, altos da Serra do Ereré, 15 May 1953, fl., *D. A. Lima* 1593 (IAN); Monte Dourado, área da Água Azul, Almeirim, $01^{\circ}05'S$, $52^{\circ}70'W$, 26 Mar 1986, fl., *M. J. P. Pires et al.* 835 (INPA, MG); Pinhel, vegetação de savana sobre solo arenoso, $03^{\circ}08'S$, $55^{\circ}15'W$, 5 Jun 1990, fr., *T. M. Sanaiotii* 115 (INPA); Rio Capim, entre Aproaga e Igarapé Candirú, 23 Mar 1949, fl., *R. L. Fróes & J. M. Pires* 24106 (INPA); Santarém, península em frente a Alter do Chão, $54^{\circ}57'S$, $02^{\circ}29'W$, 30 May 1990, fr., *T. M. Sanaiotii* 114 (INPA); Santarém, região do Tapajós, Cajutuba, praia de rio, 2 Dec 1978, fr., *U. N. Maciel & M. R. Cordeiro* 126 (INPA, MG); São Domingos do Capim, Rio Capim, 3 Jul 1974 fr., *Cavalcante* 2955 (MG); Tapajos, Itaituba, 26 Apr 1933, fl., *R. M. da Costa* 1029 (F, IAN); Tucuruí, PA 263, km 15, sentido Tucuruí-Goianésia, 1.5 km do Ramal do Dique Dois, entrada a direita,

antes de atravessar o Dique, 03°44'34"S, 49°32'05"W, 3 Aug 2000, fr., *E. S. Leal et al.* 276 (RB, US). Piauí: Teresina, rod. BR 316, 24 km south of Teresina in direction of Demerval Lobão, ca. 5°15'S, 42°40'W, alt. 150 m., 14 Jan 1985, fr., *G. P. Lewis* 1364 (K).

Distribution, habitat and phenology: *Connarus favosus* is exclusive of north Brazil, where it is mainly distributed in the states of Maranhão and Pará, with few collections from Ceará and Piauí (Fig. 9). This is a lianescent species occurring in savanna vegetations or ciliary forests of the Amazon, or in semideciduous forests of the Caatinga, usually associated with sandy soils, at 40–150 m elevation. Specimens have been collected with flowers from November to April and with fruits irregularly almost throughout the year.

Notes: *Connarus favosus* is easily recognized by the combination of the following characteristics: leaflets coriaceous, discolorous, abaxially sericeous, adaxially shining, with margins revolute, and fruits sessile or with short stipes (0.5–1 mm long). Among the species with only simple trichomes, it can be confused with *C. megacarpus* due to leaflet indumentum, but differs by the leaves 3–5(–7)-foliolate (vs. leaves 7–9-foliolate), petals externally glabrous or subglabrous (vs. petals externally tomentose), and fruits 1.3–2 × 1–1.5 cm (vs. fruits 3.2–3.5 × 2–2.2 cm).

The specimen *Gardner 6011* (barcode K000633799) is here considered as the holotype because Planchon (1850) indicated that the type was deposited in the Hookerianum herbarium and it is the only specimen that belonged to this collection currently available in K.

Connarus foreroi C. Toledo, Willdenowia 51: 171. 2021.—TYPE: Peru. Huánuco: Pachitea, Dtto. Honoria, Bosque Nacional de Iparia, región de "bosque seco tropical" a lo largo del Río Pachitea cerca del campamento Miel de Abeja (1 km. arriba del pueblo de Tournavista a unos 20 km. arriba de la confluencia con el Río Ucayali), alt. 300–400 m., 14 Nov 1967, fr., *J. Schunke* V. 2317 (holotype: US 2859402!; isotype: F [n. v.]).

Shrubs, ca. 1.5 m tall; branchlets slightly fissured, subglabrous, trichomes simple unicellular, lenticels conspicuous. *Leaves* 5-foliolate; petioles ca. 13 cm long, glabrous; rachises ca. 9 cm long, glabrous; pulvinuli ca. 4 mm long, glabrous; leaflets chartaceous, slightly discolorous, flat, basal pairs ca. 16 × 7.5 cm, symmetric, obovate, bases symmetric, acute, the

apical ones $21.5\text{--}23.3 \times 9.5\text{--}10.2$ cm, obovate, bases symmetric, acute, apices acuminate, acumen 9–14 mm long, abaxial surfaces sparsely sericeous, indumentum brown, adaxial surfaces glabrous, dull, margins flat; midveins abaxially prominent, adaxially flat, secondary veins 11–12 pairs, abaxially prominent, adaxially flat, concolorous in relation to the blade, forming angles of $45\text{--}55^\circ$ with midvein, slightly arcuate, tertiary veins abaxially prominent, adaxially flat, intercostals mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids, cauliflorous, trichomes simple unicellular, peduncles ca. 0.5 cm long, sparsely sericeous, rachises mature not seen, sparsely sericeous, lateral cymes not seen, indumentum of these structures brown; bracts not seen. *Flowers* not seen, pedicellate; sepals 5 (persistent on fruits), slightly basally connate, outer surfaces sericeous, indumentum brown, inner surfaces subglabrous, sparsely sericeous at apex. *Fruits* $2.2\text{--}2.3 \times 1.4\text{--}1.6$ cm, obovate, indehiscent side slightly sigmoid or almost linear, pericarps up to 2 mm thick, stipes 2–5 mm long, styles partially persistent, apiculate or spinescent, ca. 1 mm long, outer surfaces subglabrous, black dots abundant, inner surfaces glabrous or subglabrous, glandular trichomes absent, calyx deciduous or partially persistent, sepals reflexed or patent; seeds 1.5×0.7 cm, arils color not seen.

Distribution, habitat and phenology: This species is only known from the type location, collected in the department of Huánuco, west Peru, close to the east side of the Andes (Fig. 16). It is a shrubby species ca. 1.5 m tall, occurring along river margins of dense wet forests, at 300–400 m elevation. The only known specimen was collected with fruits in November.

Notes: Although *C. foreroi* is represented by a single collection, it can be differentiated from other Neotropical *Connarus* with only simple trichomes by the leaves 5-foliolate, large obovate leaflets, cauliflorous inflorescences and fruits internally glabrous or subglabrous. Another Neotropical species with cauliflorous inflorescences is *C. fasciculatus*, but the latter possesses dendroid trichomes, not seen in *C. foreroi*. It can also be confused with other species of large obovate leaflets, such as *C. jaramilloi*, *C. popenoei* or *C. silvanensis*, but differs from the latter by the leaves 5-foliolate (vs. 9–11-foliolate) and from the latter two by the same characteristic (vs. leaves 3-foliolate), aside of the cauliflorous inflorescences (vs. axillary or pseudo-terminal, occasionally ramiflorous in *C. silvanensis*).

Connarus grandifolius Planch., Linnaea 23: 432. 1850.—TYPE: Dominica. *S. loc.*, *s. d.*, fl., *J. Imray 294* (lectotype first step designated by Forero 1983: K; lectotype second step **designated here**: K barcode K000633758!; islectotype: K!).

Lianas; branchlets slightly striate, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels conspicuous. *Leaves* 3–5-foliolate; petioles 3–8(–12) cm long, tomentose to glabrescent; rachises 1.5–6(–9.5) cm long, tomentose to glabrescent; pulvinuli 6–10 mm long, tomentose to glabrescent; leaflets chartaceous to coriaceous, discolorous, flat, basal pairs $10.7\text{--}19.8 \times 4.5\text{--}9.3$ cm, symmetric, elliptic or obovate, bases symmetric, rounded, obtuse or subcordate, the apical ones $13.7\text{--}24 \times 6.5\text{--}11.2$ cm, symmetric, elliptic or obovate, bases symmetric, rounded, obtuse or subcordate, apices short acuminate, acumen 1–4 mm long, rarely rounded, abaxial surfaces glabrous or tomentose to glabrescent on the midvein, indumentum ferruginous, adaxial surfaces glabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed, secondary veins 9–12 pairs, abaxially prominent, adaxially impressed or slightly so, concolorous in relation to the blade, rarely slightly discolorous, forming angles of $45\text{--}55^\circ$ with midvein, arcuate or slightly so, rarely linear, tertiary veins abaxially flat to prominent, adaxially flat, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in double thyrsoids, axillary, 1(–3) per axil, trichomes dendroid and simple unicellular, peduncles 0.3–1 cm long or inflorescences subsessile, tomentose, rachises 7–21(–32) cm long, tomentose, lateral sub-thyrsoids 2.5–5(–10.5) cm long, tomentose, indumentum of these structures ferruginous; bracts 0.5–1 mm long, tomentose. *Flowers* sessile or subsessile; buds $2\text{--}3 \times 2\text{--}3$ mm, orbicular; sepals 5, slightly basally connate or occasionally 2 adhered through trichomes, $2.5\text{--}3 \times 1\text{--}1.5$ mm, triangulate or elliptic, apices acute, outer surfaces densely tomentose, indumentum ferruginous, inner surfaces glabrous or subglabrous, occasionally pubescent at apex; petals $2.5\text{--}4 \times 1\text{--}1.5$ mm, erect, oblong, narrowly obovate or narrowly elliptic, apices rounded, acute or obtuse, glandular dots more than 10, loosely distributed, black or colorless, conspicuous or inconspicuous, both surfaces tomentose or sparsely so, glandular trichomes abundant, margins with sparse to abundant glandular trichomes; stamens basally connate by 0.2–0.3 mm long, shorter series (1.5–)2–2.5 mm long, longer series (2.5–)3–3.5 mm long, filaments with sparse to abundant glandular trichomes; ovaries ca. 1 mm long, densely pubescent, styles and stigmas not seen. *Fruits* $2.9\text{--}3.4 \times 1.9\text{--}2.3$ cm, obovate, indehiscent side linear to sigmoid, pericarps up to 2 mm thick, stipes 4–8 mm long, styles partially persistent, slightly apiculate, 0.5–1 mm long, outer surfaces tomentose to

glabrescent, indumentum ferruginous, black dots abundant, inner surfaces pubescent or sparsely so, glandular trichomes sparse, calyx deciduous, rarely partially persistent, sepals reflexed; seeds $2.1\text{--}2.6 \times 1.1\text{--}1.2$ cm, arils yellowish.

Specimens examined: **Dominica.** Ad Prince Rupert, Apr 1882, fl., *B. Eggers* 717 (G); Castle Bruce windward. 6 Feb 1889, fr., *G. A. Ramage s. n.* (BM); Jul 1982, fl., fr., *B. Eggers* 1063 (K). La Chaudiere, moist forests in valley of Hampstead River, ca. 2 miles from mouth, 10–14 May 1940, fr., *W. H. Hodge & B. T. Hodge* 3553 (GH); Loubiere Valley, GR 77 88, 13 Apr 1990, fr., *C. Pendry* 330 (BM, K); Palmiste Ridge, St. Andrew, pathside along the crest of the ridge, Mar–Apr 1996, st., *C. Whitefoord* 7344 (BM); *S. loc.*, 16 Jun 1888, fr., *G. A. Ramage s. n.* (BM, K); *S. loc.*, 1839, fl., *Imray* 282 (K). **Guadeloupe.** Bons des Banis Iannes, May 1894, fl., *A. Duss* 3454 (NY); Camp Jacobs, 1892, fr., *A. Duss* 2441 (NY); *S. loc.*, 13 Apr 1935, fl., *H. Stehlé* 57 (NY); *S. loc.*, *s. d.*, fl., *Duchassing s. n.* (K); Martinique. *S. loc.*, 1887, fl., *A. Duss* 833 (GH, NY).

Distribution habitat and phenology: *Connarus grandifolius* is only known from Dominica, Guadeloupe and Martinique islands, in the Caribbean, Central America (Fig. 14). This lianescent species is found in ombrophilous forests, approximately at sea level. Specimens have been collected with flowers from April to July and with fruits from February to July.

Notes: Among the species with dendroid trichomes, *C. grandifolius* is easily recognized by the 3–5-foliolate leaves, large leaflets ($10.7\text{--}24 \times 4.5\text{--}11.2$ cm), petals externally tomentose and large fruits ($2.9\text{--}3.3 \times 1.9\text{--}2.2$ cm).

Planchon (1850) described *C. grandifolius* based on *Imray* 282 and 294 (probably miswritten for 254), so Forero (1983) selected the specimen *Imray* 294 from K as lectotype. There are two sheets belonging to this collection in K and, although Forero (1983) cited lectotype and isolectotype from K, he did not indicate any barcode or accession number, so a second step lectotypification is here proposed. Despite the fact that the two preparations from K are kept in the same folder, they can be interpreted as duplicates as they do not bear the same original label (Turland et al. 2018, Art. 8.3).

Connarus guggenheimii Forero, *Caldasia* 13(61): 1980.—TYPE: Colombia. Santander: Secondary forest (?) near Carare, 45 km S. S. W. of Barrancabermeja, 74°5'W, 6°40'N, alt. 100–200 m., 9 Mar 1967, fr., *J. de Brujin* 1615 (holotype: COL barcode COL000001582 [photo!]; isotypes: K!, MO [photo!], U [n. v.], US [photo!], VEN [photo!], WAG [n. v.]).

Lianas; branchlets slightly striate, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels inconspicuous. *Leaves* 9–11-foliolate; petioles 3.2–3.5 cm long, tomentose to glabrescent; rachises 5.8–12.2 cm long, tomentose to glabrescent; pulvinuli ca. 4 mm long, tomentose to glabrescent; leaflets subcoriaceous, slightly discoloured, conduplicate or flat, basal pairs $4\text{--}4.5 \times 1.7\text{--}2$ cm, symmetric, ovate or narrowly ovate, bases symmetric, subcordate or rounded, the apical ones $6.4\text{--}9.2 \times 2\text{--}2.7$ cm, symmetric, narrowly ovate or narrowly elliptic, bases symmetric, rounded or subcordate, apices acuminate to long acuminate, acumen 6–9 mm long, abaxial surfaces glabrous or irregularly tomentose to glabrescent on midvein, indumentum ferruginous, shining or dull, margins flat; midveins abaxially prominent, adaxially slightly impressed, secondary veins 8–9 pairs, abaxially slightly prominent, adaxially slightly prominent or flat, concolorous in relation to the blade, forming angles of 50–60° with midvein, arcuate or slightly so, tertiary veins abaxially slightly prominent, adaxially slightly prominent or flat, intercostals mixed percurrent, epidermals opposite percurrent or reticulate. *Inflorescences* in double thyrsoids, axillary or pseudo-terminal, 1 per axil, trichomes dendroid and simple unicellular, peduncles 0.4–1.2 cm long, tomentose, rachises 10–13.5 cm long, tomentose, lateral sub-thyrsoids 2.3–8 cm long, tomentose, indumentum of these structures ferruginous; bracts ca. 0.5 mm long, tomentose. *Flowers* not seen, short pedicellate; sepals (persistent on fruits) slightly basally connate, outer surfaces tomentose, indumentum ferruginous, inner surfaces glabrous, pubescent only at apex; petals (few persistent on fruits) with glandular dots abundant, black, inconspicuous. *Fruits* 1.7–1.9 $\times$ 1–1.1 cm, obovate or semi orbicular, indehiscent side linear or slightly sigmoid, pericarps up to 2 mm thick, stipes 2–4 mm long, styles partially persistent, apiculate, 0.5–1 mm long, outer surfaces tomentose to glabrescent, indumentum ferruginous, black dots abundant, inner surfaces with only abundant glandular trichomes, calyx persistent or partially persistent, sepals reflexed or patent erect; seeds not seen.

Specimens examined: **Colombia.** Santander: Puerto Wilches, entre la Gómez y el kilómetro 80 del ferrocarril del Atlántico, alt. 100-200 m, 21 Apr 1960, fr., *R. Romero-Castañeda* 8382 (COL).

Distribution, habitat and phenology: *Connarus guggenheimii* is a liana exclusive to Colombia, where it is found in the department of Santander (Fig. 21), at approximately 100–200 m elevation. Specimens have been collected with fruits from March to April.

Notes: Among the species with dendroid trichomes, *C. guggenheimii* can be confused with *C. incomptus*, *C. manausensis* and *C. patrisii* by the lianescent habit and number of leaflets. However, *C. guggenheimii* mainly differs from these species by the leaflet shape, inflorescence architecture, union of sepals and fruit size (Table 2).

Connarus incomptus Planch., *Linnaea* 23: 433. 1850. *Connarus incomptus* Planch. var. *incomptus*.—TYPE: Guyana. *S. loc.*, 1840, fl., *Rob. Schomburgk* 827 (holotype: K barcode K000633772!; isotypes: BM!, G!, K!, P!, U [n. v.], W [n. v.]). Fig. 22

Connarus incomptus Planch. var. *subcordatus* Baker, in Martius, *Fl. Bras.* 14(2): 193. 1871.—TYPE: Guyana. *S. loc.*, *s. d.*, fl., *Rob. Schomburgk* 439 (686R) (lectotype designated by Forero 1983: K barcode K000633770!; isoelectotypes: BM!, F [photo!], G!, GH [photo!], W [n. v.]).

Lianas, shrubs, scandent shrubs or treelets, rarely trees, 1–3(–8) m tall; branchlets slightly striate, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels inconspicuous. *Leaves* (5–)7–9-foliolate; petioles 2.2–7.2 cm long, tomentose to glabrescent; rachises 2.2–6.5(–12.5) cm long, tomentose to glabrescent; pulvinuli 3–4 mm long, tomentose to glabrescent; leaflets chartaceous, rarely coriaceous, concolorous or slightly discolorous, conduplicate, basal pairs 4–7.5 × 1.6–3.2 cm, symmetric or slightly asymmetric, oblong, narrowly elliptic or narrowly ovate, bases symmetric or slightly asymmetric, rounded or subcordate, the apical ones 5.5–14.5 × 1.9–5.5 cm, symmetric or slightly asymmetric, oblong, narrowly elliptic or narrowly ovate, bases symmetric or slightly asymmetric, rounded or subcordate, apices short acuminate to acuminate, acumen 3–7 mm long, abaxial surfaces glabrous or subglabrous, adaxial surfaces glabrous, dull or slightly shining, margins flat;

midveins abaxially prominent, adaxially impressed or slightly so, secondary veins 8–12 pairs, both surfaces slightly prominent or flat, adaxially concolorous in relation to the blade, less frequently discolorous, forming angles of 60–80° with midvein, arcuate, rarely linear, tertiary veins slightly prominent or flat on both surfaces, intercostals mixed percurrent or reticulate, epidermals opposite percurrent or reticulate. *Inflorescences* in thyrsoids, axillary, 2–5 per axil, trichomes dendroid and simple unicellular, peduncles 0.3–1 cm long or inflorescences subsessile, tomentose, rachises 5.5–18 cm long, tomentose, lateral cymes 0.2–0.8 cm long, tomentose, indumentum of these structures ferruginous; bracts 1.3–2 mm long, tomentose. *Flowers* subsessile or pedicels 0.5–2 mm long; buds 2–2.5 × 2–2.2 mm, orbicular; sepals 5, slightly basally connate, 2.5–3 × 1–1.2 mm, triangulate or narrowly ovate, apices acute, outer surfaces densely tomentose, indumentum ferruginous, inner surfaces glabrous, occasionally pubescent at apex; petals 3–4.5 × 1–1.5 mm, reflexed, oblong or narrowly obovate, apices rounded, glandular dots more than 10, loosely distributed, black or colorless, inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous or with sparse glandular trichomes; stamens basally connate by 0.5–1 mm long, shorter series 1.2–3 mm long, longer series 1.5–5 mm long, filaments glabrous or with sparse glandular trichomes; ovaries 1–1.5 mm long, tomentose, styles ca. 1.5 mm long, stigmas bilobate, lobes 0.5–0.7 mm long. *Fruits* (1–)1.2–1.6 × 0.7–1.1 cm, obovate or semi-orbicular, indehiscent side sigmoid or linear, pericarps up to 2 mm thick, stipes 1–2.5 mm long, styles partially persistent, apiculate, 0.3–1 mm long, outer surfaces lanate to glabrescent, indumentum ferruginous, black dots absent, inner surfaces with only sparse to abundant glandular trichomes, calyx persistent, sepals ascending erect; seeds 1.1–1.2 × 0.4–0.5 cm, arils color not seen.

Specimens examined: **Brasil.** Roraima: Boa Vista. BR-321, em direção à zona rural do Bom Intento, lote pertencente à Maria Cecília O. P. da Silveira, ao lado do portão de entrada do jardim, 2°52'14"N, 60°39'38"W, 23 Aug 2011, fr., *R. de O. Perdiz* 879 (CEPEC, RB); Campus Cauamé UFRR, área grande PPBIO Amazônia, Oct 2011, fr., *Turma de graduação Biologia UERR s. n.* (MIRR, RB); *S. loc.*, Aug 1951, fl., *G. A. Black* 51-12499 (NY). Caminho de Samauma ao campo de aviação de Mucajaí, kms 14-15 da estrada Boa Vista-Caracará, 25 Aug 1951, fl., *G. A. Black & Magalhães* 12937 (IAN); Caracará, Estrada Perimetral Norte (BR 210), 09 km do entroncamento com Estrada Manaus-Caracará (BR 174), próximo a Novo Paraíso, 01°15'N, 60°27'W, 26 Aug 1987, fl., *C. A. C. Ferreira* 9213 (INPA, NY); Estrada BR-174 (Boa Vista-Venezuela), na beira do Rio Caomé, lado direito, 02°50'N, 60°40'W, 75 m alt., 5 Aug 1986, fl., *J. A. Silva et al.* 619 (INPA, NY, UB); Estrada da Serra Grande, 02°50'N,

60°40'W, 2 Aug 1986, fr., *J. A. Silva et al.* 574 (NY); Lago Redondo, 5 Jan 1992, fr., *M. L. Absy* 24 (INPA); Ramal no km 47 da estrada para Passarão, NE de Boa Vista, 03°13'N, 60°36'W, 15 Sep 1993 fr., *T. M. Sanaïotti* 265 (ESA, INPA); Rio Cantá, 10 Aug 1851, fl., *G. A. Black* 13820 (IAN); Rio Contigo, aldeia do Contão, Maloca Cauari, 3 Mar 1964, fr., *M. Silva* 102 (MG); Rio Branco, campo ao redor da cidade, 15 Aug 1951, fl., *G. A. Black* 51-12547 (RB); *S. loc.*, Aug 1909, fl., *E. H. G. Ule* 8128 (MG, US); Rio Murupu, 28 km NW of Boa Vista, road to Taiano, 8 Jan 1969 fr., *G. T. Prance* 9102 (INPA, MG, NY, P). **Guyana.** Alto Takutu-Alto Essequibo: Kapo, near Karanambo, N Rupununi savanna, 04°04'N, 59°19'W, 100–250 m, 19 Nov 1992, fr., *A. R. A. Görts et al.* 318 (NY); Maby Hill, at left bank of Rupununi River a few miles upstream from Karanambo, 3°45'N, 59°20'W, 6 Sep 1988, fl., *P. J. M. Maas et al.* 7306 (NY); Near Dadanawa Ranch, Rupununi savanna, 02°50'N, 59°30'W, 100–150 m, 16 Nov 1992, fr., *A. R. A. Görts et al.* 227 (NY); Rupununi District, Dadanawa, Rupununi River, along river, 100–150 m, 14 Jan 1991, fr., *M. J. Jansen-Jacobs et al.* 2046 (NY, P); Yupukarri, Rupununi River, 400 m, 16 Sep 1931, fl., *Forest Department* D183 (K). *S. loc.*, Yukutu, 4 Jun 1863, fl., *C. Appun* 1616 (K).

Distribution, habitat and phenology: *Connarus incomptus* is restricted to the state of Roraima (north Brazil) and AltoTakutu-Alto Essequibo region (south Guyana) (Fig. 21), occurring in the Amazonian savanna (campinarana), characterized by open fields with sandy soils. This species is represented by lianescent individuals, shrubs or small trees, growing at 75–400 m elevation. Specimens have been collected with flowers mainly from August to September and with fruits from August to March.

Notes: *Connarus incomptus* is easily recognized by the presence of dendroid trichomes, leaflets with 8–12 pairs of secondary veins which form angles of 60–80° with midvein, inflorescences in thyrsoids, and small fruits (1–1.6 × 0.7–1.1 cm). It can be confused with *C. guggenheimii*, but differs by the number of leaflets and secondary veins, inflorescences architecture and fruits size (Table 2).

Planchon (1850) described *C. incomptus* and cited a single specimen (*Schomburgk* 827), from Hooker herbarium, which now belong to K. There are three specimens of *Schomburgk* 827 in K, but only one with “Herbarium Hookerianum” stamp, so this is considered the holotype.

Connarus jaramilloi Forero, Caldasia 13(61): 5. 1980.—TYPE: Colombia. Meta: Sierra de la Macarena, Rio Guapaya, alt. 450 m, 29 Nov 1949, fr., *W. R. Philipson et al. 1644* (holotype: COL [photo!]; isotypes: BM!, US [photo!]).

Lianas or trees, height not seen; branchlets slightly striate, glabrous, lenticels conspicuous. *Leaves* 9–11-foliolate; petioles 15–23 cm long, sparsely sericeous; rachises 15–29.5 cm long, sparsely sericeous; pulvinuli ca. 6 mm long, glabrous or subglabrous; leaflets subcoriaceous, concolorous, flat, basal pairs $11.5\text{--}14.7 \times 5\text{--}5.8$ cm, symmetric, narrowly obovate, bases symmetric, rounded or obtuse, rarely subcordate, the apical ones $13\text{--}20 \times 5.2\text{--}7.5$ cm, symmetric, narrowly obovate, bases symmetric, rounded or obtuse, apices short acuminate, acumen 3–6 mm long, abaxial surfaces subglabrous or sparsely sericeous, indumentum griseous, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed, secondary veins 10–13 pairs, abaxially prominent, adaxially impressed or slightly so, concolorous in relation to the blade, forming angles of $60\text{--}75^\circ$ with midvein, arcuate, tertiary veins abaxially prominent or slightly so, adaxially flat or slightly prominent, intercostals and epidermals opposite percurrent. *Inflorescences* in double thyrsoids, axillary, 1 per axil, trichomes simple unicellular, peduncle ca. 4 cm long, sericeous, rachises length not seen, sericeous, lateral sub-thyrsoids length not seen, sericeous, indumentum of these structures brown; bracts not seen. *Flowers* not seen, pedicellate; sepals 5 (persistent on fruits), slightly basally connate, outer surfaces sericeous, indumentum brown, inner surfaces glabrous or subglabrous; petals, stamens and ovaries not seen. *Fruits* $1.8\text{--}2.1 \times 1.2\text{--}1.5$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 2–4 mm long, styles partially persistent, apiculate, ca. 1 mm long, outer surfaces glabrous or sparsely sericeous only on stipe, indumentum brown, black dots abundant, inner surfaces tomentose or sparsely so, glandular trichomes absent, calyx deciduous, partially persistent or persistent, sepals reflexed or patent; seeds ca. 1.2×0.7 cm, arils color not seen.

Specimens examined: **Colombia.** Meta: Sierra de la Macarena, Rio Guapaya, alt. 500 m, 18 Jan 1950, fr., *W. R. Philipson et al. 2118* (BM, COL, US).

Distribution, habitat and phenology: *Connarus jaramilloi* is apparently restricted to the department of Meta, Colombia, where the only two individuals reported here were collected in the Macarena mountain range, along Guapaya river (Fig. 23), at 450–500 m elevation. Specimens have been collected with fruits in November and January.

Notes: Among the species with only simple trichomes, *Connarus jaramilloi* differs by the leaves 9–11-foliolate, petioles 15–23 cm long, and fruits internally tomentose or sparsely so. Due to the number of leaflets, it can be confused with *C. punctatus*, although it is differentiated by the fruits with sepals patent or reflexed vs. sepals ascending.

Connarus lambertii (DC.) Sagot, Ann. Sci. Nat., Bot., sér. 6, 13: 295. 1882. *Omphalobium lambertii* DC., Prodr. 2: 85. 1825. *Connarus lambertii* (DC.) Britton, N. Am. Fl. 22(3): 234. 1908—TYPE: Saint Vincent. *S. loc.*, 1816, fl., fr., *A. B. Lambert s. n.* (holotype: G barcode G00476384!).

Connarus guianensis Lamb. ex DC., Prod. 2: 85. 1825, *pro syn.*

Connarus schomburgkii Planch., Linnaea 23: 431. 1850.—TYPE: Guyana. Berbice, 1837, fl., fr., *Rob. Schomburgk 333* (lectotype first step designated by Forero 1983: K; lectotype second step **designated here**: K barcode K000633802!; isoelectotypes: BM!, E [photo!], G!, K!, KW [photo!]).

Connarus pottsii S. Watson, Proc. Amer. Acad. Arts 21: 463. 1886.—TYPE: Guatemala. Shore of Lake Izabal, 30 Mar 1885, fr., *S. Watson 55* (lectotype designated by Schellenberg 1938: US [n. v.]; isoelectotypes: GH [photo!], K-frag.!, M [n. v.], NY-frag. [photo!]), *syn. nov.*

Connarus merizaldinus Cuatrec., Fieldiana, Bot. 27(2): 101. 1951.—TYPE: Colombia. Valle: Costa del Pacífico, río Naya, Puerto Merizalde, alt. 5–20 m, 20–23 Feb 1943, fl., *J. Cuatrecasas 14067* (holotype: F 1372249 [photo!]; isotypes: COL [photo!], U [photo!], US!).

Lianas, shrubs or scandent shrubs, rarely treelets, 1.5–5(–9) m tall; branchlets slightly striate, glabrous or subglabrous, rarely sparsely sericeous, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3-foliolate; petioles 2.7–8.5 cm long, glabrous or subglabrous, rarely irregularly sparsely sericeous; rachises 0.6–2.5 cm long, glabrous or subglabrous, rarely irregularly sparsely sericeous; pulvinuli 3–6 mm long, glabrous or subglabrous, rarely sparsely sericeous; leaflets chartaceous, slightly discoloured, flat, basal pairs 5.2–12(–14) × 2.3–5(–6.3) cm, symmetric, ovate or elliptic, rarely narrowly ovate or narrowly elliptic, bases symmetric, rounded, less frequently obtuse, the apical ones 7–13.5(–

15.5) $\times$ 2–6.6(–8) cm, symmetric, ovate or elliptic, rarely narrowly ovate or narrowly elliptic, bases symmetric, rounded, less frequently obtuse, apices acuminate short acuminate to acuminate, acumen 3–12 mm long, abaxial surfaces glabrous or subglabrous, rarely irregularly sparsely sericeous on the midvein or nearby, indumentum brown, adaxial surfaces glabrous, dull, margins flat, rarely slightly revolute; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 6–9 pairs, abaxially flat, rarely slightly prominent, adaxially flat, concolorous or discolorous in relation to the blade, forming angles of 50–65° with midvein, arcuate, rarely slightly arcuate, tertiary veins flat on both surfaces, intercostals mixed percurrent, epidermals opposite percurrent, the intersecondary occasionally reticulate. *Inflorescences* in thyrsoids, axillary or pseudo-terminal, 1–5 per axil, trichomes simple unicellular, peduncles 0.2–1.7 cm long or inflorescences sessile, sericeous, sparsely sericeous or pubescent, rachises 5–14 cm long, sericeous, sparsely sericeous, pubescent or densely pubescent, lateral cymes 0.3–2 cm long, sericeous or densely pubescent, indumentum ferruginous, brown or flavous; bracts 0.5–1.2 mm long, sericeous or pubescent. *Flowers* with pedicels 0.5–1.3 mm long; buds 2–2.8 $\times$ 1.1–1.5 mm, elliptic or ovate; sepals 5, slightly basally connate, 2.2–3 $\times$ 0.6–1.1 mm, ovate, narrowly ovate or narrowly triangulate, apices acute or obtuse, outer surfaces sericeous or sparsely so, indumentum ferruginous, brown or flavous, inner surfaces sparsely sericeous, usually more densely at apex and subglabrous in the lower half; petals 3.5–5 $\times$ 0.8–1.5 mm, erect, narrowly obovate, or narrowly elliptic or oblong, apices rounded, obtuse or acute, glandular dots more than 10, loosely distributed, black or colorless, conspicuous or inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent or sparse, margins glabrous or with sparse glandular trichomes; stamens basally connate by (0.3–)0.5–1.3 mm, shorter series 1.2–3 mm long, longer series 1.5–4.2 mm long, filaments glabrous or with sparse glandular trichomes; ovaries 0.7–1 mm long, densely pubescent, styles 1–1.5 mm long, stigmas bilobate, lobes ca. 0.5 mm long. *Fruits* 1.6–1.9 $\times$ 1–1.3 cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 2–3(–4) mm long, styles partially persistent, apiculate or spinescent, 0.5–3 mm long, outer surfaces irregularly sparsely sericeous, more densely at stipe and base, indumentum brown or griseous, black dots absent or sparse to abundant, inner surfaces glabrous or subglabrous, rarely sparsely pubescent, glandular trichomes absent, rarely sparse, calyces deciduous, persistent or partially persistent, sepals patent or reflexed, less frequently ascending erect; seeds 0.9–1.3 $\times$ 0.5–0.8 cm, arils color not seen.

Selected specimens examined: **Belize.** Lemonal: Bermudian Landing, School Fragment, 17°40'N, 88°35'W to 17°30'N, 88°25'W, *s. d.*, fr., *L. Marsh* 120 (F). Stann Creek: Melinda, Pine Ridge, 12 Aug 1937, fr., *P. H. Gentle* 2130 (NY); Sittee Road, 21 Feb 1953, fl., *P. H. Gentle* 7885 (NY); Mullins River road, 25 Mar 1937, fr., *P. H. Gentle* 1949 (K); Railway 11 mile, 22 Feb 1929, fl., *W. A. Schipp* 22 (K); Railway 12 mile, 11 Apr 1929, fr., *W. A. Schipp* 118 (K). Toledo: Of highway from Dangriga to Punta Gorda, road to Laguna Village, 16°10'N, 88°54'W, 13 Mar 1993, fr., *M. J. Balick et al.* 3607 (NY); San Antonio, in acahual, base of hill near San Antonio, 7 Mar 1952, fl., *P. H. Gentle* 7587 (NY). District unknown: Between Mullins River and Manatee, 16 Aug 1940, fl., *P. H. Gentle* 3380 (NY). **Colombia.** Guaviare: El Retorno, Vereda San Antonio, grania experimental "El Trueno", alt. 200 m, 7 Mar 1994, fr., *D. Cardenas et al.* 4382 (COL). Meta: Carretera Puerto López-Puerto Caitán, alrededores del puente sobre el río Yucao, 16 Mar 1986, fr., *E. Forero et al.* 10242 (COL); Puerto Gaitán, caño La Emma, afluyente del Yucao, Hacienda Maraure, alt. ca. 200 m, 7 Jan 1981, fl., *R. Jaramillo M.* 6770 (COL). Vaupés: Maviso, 24 Nov 1948, fr., *R. Romero-Castañeda* 1256 (COL). Vichada: Pto. Carreño, corregimiento de Santa Rita, loma granítica em los alrededores del Pueblo, 4°54'N, 68°20'W, alt. 150 m, 13 Dec 1993, fl., *C. González & R. Cortés* 9096 (COL). **Costa Rica.** Limón: Tortuguero, Reserva Biológica Caño Palma, Sandero Raphia, 10°35'00"N, 83°32'00"W, 10 m, 26 Apr 1995, fr., *G. Herrera* 7787 (K). **Guatemala.** Izabal: Bananera, swamps of Salomón Creek, 1/2–1 mi. south of Bananera, 6 Apr 1940, fr., *J. A. Steyermark* 38910 (F); Lago Izabal, south shore of Lake Izabal, east of Izabal, 15°15'N, 89°25'W, 2 May 1966, fr., *G. C. Jones & L. Facey* 3226 (NY). **Guyana.** E. Berbice-Corentyne, Corentyne River, Marabunta Creek, 10 m, 4°56'4"N, 57°49'27"W, 24 Mar 1995, fr., *P. Mutchnick* 992 (K); Georgetown, Mahayconi, Amary rice areas, about 35 miles S. E. of Georgetown, 15 Oct 1995, fr., *E. L. Little Jr.* 16867 (NY); U. Demerera-Berbice, Berbice River, Melissa Falls to the Gate, 120 m, 4°51'39"N, 58°14'45"W, alt. 120 m, 5 May 1995, fr., *P. Mutchnick & P. K. Harmon* 1294 (K); U. Takutu-U, Essequibo, Conservation International concession on the Essequibo River, right side of river bank going down river, 3°37'39.2"N, 58°17'31.9"W, alt. 76 m, 20 Jan 2007, fr., *K. M. Redden et al.* 5101 (K). **Honduras.** Atlantida: Jutiapa, 5 km before Jutiapa on road to La Ceiba, 15°45'N, 86°32'W, 11 Jul 1987, fr., *M. J. Balick et al.* 1721 (K, NY). Colón: 1.8 mi strip in the north bank of rio Guaimoreto between old bridge and opening of Laguna Guaimoreto 4.5 mi NE of Trujillo on old road to Castilla, 15°57'30"N, 85°54'30"W, 10 Jul 1980, fr., *J. Saunders & J. S. Buckley* 454 (NY); Capuchin site east, 1.8 mi strip in the north bank of rio Guaimoreto between old bridge and opening of Laguna Guaimoreto 4.5 mi NE of Trujillo on old road to Castilla, 15°57'30"N, 85°54'30"W, 30 Jan 1981, fl., *J. Saunders* 992

(NY). **Nicaragua.** Zelaya: Costa N de Puerto Cabezas, 14°02'N, 83°22'W, alt. 12 m, 5 Feb 1983, fl., *J. C. Sandino 3969* (COL); S de Tuapí, sucesión secundaria y bosque de pinos, 14°05'N, 83°22'W, 8 Feb 1983, fr., *J. C. Sandino 4065A* (COL). **Panama.** Colon: Remnants and much disturbed secondary tropical moist forest along Quebrada Bonita, 3 km NW of Salamanca, 13 km NE of Buenos Aires, 100-170 m, 30 Jul 1973, fl., *M. Nee 9113* (COL, MO). **Saint Vincent and Granadines.** Locality unknown, Jan 1823, fl., *M. Caley s. n.* (G); Locality unknown, 1828, fl., *J. D. Hooker 20* (G). **Suriname.** Province unknown: Matappi, Corantyn, 15 Jun 1916, fr., *B. W. 2055* (K). **Trinidad and Tobago.** Dibe Valley, 15 Apr 1920, fl., *N. L. Britton et al. 1755* (NY). Locality unknown, 10 Mar 1928, fl., *B. O. Williams 11950* (F, NY). **Venezuela.** Amazonas: Rio Pacimoni-Yatuam between Laja Catipan and Piedra Araucaua, 120 m, 14 Jul 1959, fl., *J. J. Wurdack & L. S. Adderley 43449* (NY); Savanna Santa Barbara, at junction of rios Ventuari and Orinoco, 21 Feb 1950, fr., *B. Maguire et al. 32021* (NY). Apure: Pedro Camejo, bank of the Río Meta, ca. 19 airline km WSW of Paraquito, 6°14'N, 68°05'W, alt. ca. 75 m, 12–13 Feb 1978, fr., *G. Davidse & A. González* (COL). Barinas: Barinas, Carretera rural Santa Barbara de Barinas, Los Diques del río Zulia, 19 Oct 1990, fl., *L. Valverde & I. Peña 1254* (NY). Bolívar: A lo largo de la pica maderera entre el Caño Maracapra y el Campamento La Esperanza, Reserva Florestal La Paragua, Feb 1970, fl., *C. Blanco 736* (NY); Along river side at El Foco, 29 Aug 1962, fl., *B. Maguire et al. 46994* (NY); En las margens del río Asa en la “Reserva Florestal La Paragua”, Feb 1970, fl., *C. Blanco 690* (NY). Táchira: San Antonio, Río Orinoco, 26 Apr 1942, fr., *L. Williams 15012* (G).

Distribution, habitat and phenology: *Connarus lambertii* is the most widely distributed species of the genus in the Neotropics, occurring from north Central America (Belize, Guatemala) to north South America (Colombia, Venezuela, Guyana and Suriname), also including islands from the Caribbean (Trinidad and Tobago and Saint Vincent) (Fig. 5). This species is mainly represented by lianescent individuals, although some collections refer to it as small trees. It is found in a wide variety of vegetation types, mainly along water courses of the Amazon, but also in Amazonian savannas, disturbed areas, roadsides and pine ridges, at low elevations (sea level to 450 m). Specimens have been collected with flowers especially from December to March and irregularly from July to October, and with fruits especially in the first semester, but also from July to October.

Notes: As a widely distributed species, *Connarus lambertii* is very plastic and does not show an evident diagnostic character, but it can be distinguished by the leaves exclusively 3-foliolate, leaflets relatively smaller, usually glabrous, inflorescences in thyrsoids, and fruits

normally internally glabrous or subglabrous, with short stipes (2–3(–4) mm long). It is frequently confused with other Amazonian species exclusively 3-foliolate, such as *C. acutissimus*, *C. araucanus* and *C. negrensis*, but differs mainly by the number, prominence and disposition of secondary veins and acumen length (Table 1). *Connarus lambertii* is also similar to *C. turczaninowii*, but differs by the leaves 3-foliolate (vs. leaves 3–7-foliolate), secondary veins arcuate (vs. linear) and fruit stipes 2–3(–4) mm long (vs. 3–6 mm long).

According to De Candolle (1826), the type specimen of *C. lambertii* was acquired by Lambert in the Saint Vincent Botanic Garden and was cultivated under the name “*Connarus guianensis*”, originally collected in savannas from Guyana.

Connarus laurifolius Baker, in Martius, Fl. Bras. 14(2): 186. 1871. *Connarus blanchetii* var. *laurifolius* (Baker) Forero, Fl. Neotrop. Monogr. 36: 79. 1983.—TYPE: Brazil. Pernambuco: *S. loc.*, Nov 1837, fr., *G. Gardner* 963 (lectotype designated by Forero 1983: K barcode K000633793!; isolectotype: BM!).

Connarus portosegurensis Forero, Brittonia 32(1): 36. 1980.—TYPE: Brazil. Bahia: Porto Seguro, Km 18 do ramal da BR-5, 22 Nov 1963, fr., *A. P. Duarte* 8042 (holotype: HB barcode HB000029652; isotype: RB!), *syn. nov.*

Lianas, scandent shrubs or shrubs, 2–4 m tall; branchlets slightly striate, glabrous or subglabrous, trichomes simples unicellular, lenticels conspicuous. *Leaves* 3-foliolate; petioles 2.5–13 cm long, glabrous; rachises 0.4–1.3(–2.2) cm long, glabrous; pulvinuli 3–7 mm long, glabrous or subglabrous; leaflets coriaceous, less frequently chartaceous, concolorous, rarely slightly discolorous, flat, basal pairs 6.7–22(–25) × 2.7–8(–11.5) cm, symmetric, narrowly obovate or narrowly elliptic, bases symmetric, obtuse, acute or rounded, the apical ones 7–23(–26.5) × 2.8–9(–12) cm, symmetric, narrowly obovate or narrowly elliptic, bases symmetric, obtuse, acute or rounded, apices short acuminate to acuminate, acumen 1–7 mm long, both surfaces glabrous or subglabrous, adaxial surfaces slightly shining or dull, margins slightly revolute, rarely flat; midveins abaxially prominent, adaxially flat to impressed, secondary veins 9–12 pairs, abaxially flat or slightly prominent, adaxially flat, rarely slightly prominent, concolorous in relation to the blade, forming angles of 55–70° with midvein, linear, tertiary veins abaxially flat or slightly prominent, adaxially flat, rarely slightly prominent,

intercostals and epidermals reticulate. *Inflorescences* in thyrsoids or double thyrsoids, axillary, 1–2 per axil, trichomes simple unicellular, peduncles 0.2–0.7 cm long or inflorescences sessile, subglabrous or sparsely sericeous, rachises 5.8–9 cm long, sparsely sericeous, lateral cymes ca. 0.3–1.5 cm long, sericeous or sparsely so, lateral sub-thyrsoids 3–8 cm long, sericeous or sparsely so, indumentum of these structures brown or ferruginous; bracts 0.8–1 mm long, sericeous. *Flowers* with pedicels 0.5–2 mm long; buds ca. 2.5×2 mm, elliptic; sepals 5, slightly basally connate, $2.5\text{--}3 \times 1\text{--}1.3$ mm, ovate or narrowly ovate, apices acute, outer surfaces sericeous or sparsely so, indumentum brown or ferruginous, inner surfaces glabrous; petals $4\text{--}4.5 \times 1.2\text{--}1.5$ mm, erect, narrowly obovate, apices rounded, glandular dots more than 10, loosely distributed, black, conspicuous, both surfaces subglabrous, glandular trichomes sparse to abundant, margins with sparse to abundant glandular trichomes; stamens basally connate by 0.5–1.2 mm, shorter series 1.5–2.8 mm long, longer series 2–3.8 mm long, filaments with sparse glandular trichomes; ovaries ca. 1 mm long, densely pubescent, styles ca. 1.8 mm long, stigmas bilobate, lobes ca. 0.5 mm long. *Fruits* $1.8\text{--}2.4\text{--}(2.8) \times 1.2\text{--}1.6$ cm, obovate or narrowly obovate, indehiscent side slightly sigmoid or almost linear, pericarps up to 2 mm thick, stipes 2–4(–6) mm long, styles partially persistent, inconspicuous or apiculate, ca. 0.3 mm long, outer surfaces irregularly sparsely sericeous, indumentum ferruginous, black dots abundant, inner surfaces glabrous or with sparse glandular trichomes, calyces persistent, sepals ascending erect; seeds $1.2\text{--}1.5 \times 0.7\text{--}0.9$ cm, arils yellowish.

Selected specimens examined: **Brazil.** Alagoas: Chã Preta, Serra Lisa, 16 Oct 2010, fl., fr., *Chagas-Mota & J. M. Ferreira* 9065 (MAC); Coruripe, Usina Coruripe, Fazenda Capitã, 20 Jan 2011, fr., *Chagas-Mota* 10013 (MAC); Maceió. Complexo Serra da Saudinha, Fazenda Boa Vista, 20 Oct 2007, fl., *E. C. O. Chagas & M. C. S. Mota* 79 (MAC); Serra da Saudinha, Fazenda Cela, 20 Oct 2007, fl., *Chagas-Mota* 64 (MAC); Serra da Saudinha, Fazenda Cela, 27 Dec 2007, fr., *E. C. O. Chagas & M. C. S. Mota* 173 (MAC). Mar Vermelho, Fazenda Canadá, 29 Jan 2010, fr., *Chagas-Mota* 7324 (MAC); Quebrangulo, Reserva Biológica Pedra Falhada, 5 Oct 2010, fr., *Chagas-Mota* 8884 (MAC). Bahia: Ba. Km 10 a 15 da BR 367 Porto Seguro para Eunapolis, 18 Oct 1973, fl., *A. Eupunino* 322 (CEPEC, NY, RB); Ilhéus. Estrada Olivença/Uma, a 7 km NE de Olivença, 7 Dec 1981, fr., *A. M. de Carvalho & E. Fernandes* 351 (CEPEC); Mata da Esperança, ca. de 3 Km ao W da sede, próximo à Represa para captação de água, $14^{\circ}46'S$, $39^{\circ}05'W$, 29 Sep 1994, fr., *J. G. Jardim et al.* 562 (CEPEC, NY). Jussari. Entrada 7,5 km da Rod. Jussari/Palmira, Faz. Teimoso, 1,7 km da entrada, Reserva Particular do Patrimônio Natural (RPPN), Serra do Teimoso, sede da Reserva, $15^{\circ}9'37''S$, $39^{\circ}31'74''W$,

alt. 450–600 m, 15 Sep 2001, fr., *J. G. Jardim et al. 3930* (CEPEC, NY); Fazenda Serra do Teimoso, RPPN Serra do Teimoso, 15°09'330"S, 39°31'745"W, alt. 300–330 m, 3 Oct 2000, fr., *W. W. Thomas et al. 12196* (G, NY); Rod. Jussari-Palmira, entrada ca. 7,5 km. Faz. Teimoso a 1,5 km E da entrada, Reserva do Patrimônio Natural (RPPN), Serra do Teimoso, 39°35'W e 15°10'S, alt. 400 m, 1 Jan 1999, fr., *J. G. Jardim et al. 1864* (CEPEC, G, NY); Rodovia Jussari-Palmira, estrada ca. 7.5 km de Jussari, Fazenda Teimoso, RPPN Serra do Teimoso, 19 Sep 2002, fr., *P. Fiaschi & S. C. Sant'Ana 1082* (CEPEC, NY). Prado, Reserva Florestal da Brasil de Holanda Industrias S. A., the entrance at Km 18 east of Itamaraju on road to Prado, 8 km from entrance, 17°11'S, 39°20'W, 22 Oct 1993, fr., *W. W. Thomas et al. 10157* (NY); Santa Cruz da Cabralia e Porto Seguro, entre os Kms 45-56 da Rod. Eunápolis/Porto Seguro (BR-367), 22 Oct 1978, fr., *S. A. Mori et al. 10952* (CEPEC, K, NY); Una. Reserva Biológica de Una, Picada do Marimbondo, 15°10'S, 39°04'W, 24 Nov 1996, fr., *W. W. Thomas et al. 11389* (G, NY); Reserva Biológica do Mico Leão (IBAMA), entrada no km 46 da Rod. BA-001 Ilhéus-Uma, 30 Aug 1995, fr., *A. M. de Carvalho et al. 6089* (CEPEC, G). Paraíba: Marcação, Aldeira Jacaré de São Domingos, 30 Aug 2006, fl., *G. B. Freitas et al. 99* (JPB, RB); Pernambuco: Goiana, RPPN Fazenda Tabatinga, borda do fragmento, 7°36'22"S, 34°49'14"W, 29 Nov 2011, fr., *D. Cavalcanti et al. 640* (NY); In a woods, Tapera, 5 Jul 1935, fl., *D. B. Pickel 4019* (F); *S. loc.*, 25 Jun 1887, fr., *G. A. Ramage s. n.* (BM). Rio Grande do Norte: Tibau do Sul, Parque Estadual de Pipa, trilha com acesso a oeste do Polígono do Parque, 6°15'13"S, 35°03'11"W, alt. 45–60 m, 14 Aug 2012, bd., *J. G. Jardim & L. A. Cestaro 6374* (UB, UFRN).

Distribution, habitat and phenology: *Connarus laurifolius* is exclusive of northeast Brazil, occurring in coastal zones from south Bahia, Sergipe, Alagoas to Pernambuco (Fig. 13). It is a lianescent species, mostly found in tableland forests (Tabuleiro) or inside dense wet forests, growing on clay or sandy soils, at low elevations (close to sea level) or up to 600 m (Serrado do Teimoso, Bahia). Specimens have been collected with flowers in January, July and October, and with fruits especially from August to January.

Notes: *Connarus laurifolius* is morphologically recognized by the exclusively 3-foliolate leaves, usually large, coriaceous, narrowly elliptic or narrowly obovate leaflets, linear secondary veins, reticulate tertiary veins and fruits with calyx persistent and sepals ascending. This species was treated as a variety of *C. blanchetii* by Forero (1983), but they differ in leaflet shape, disposition of tertiary veins, disposition of sepals on fruits and fruit indumentum (see "Notes" under *C. blanchetii*). This combination of characteristics is consistent with the recognition of two separate species.

Connarus portosegurensis is here treated as a synonym of *C. laurifolius*. They were previously separated by the narrowly obovate and larger leaflets in *C. portosegurensis*, which is evident when their type collections are compared. However, both characters have shown to be variable as additional specimens were analyzed. In addition, they are morphologically identical in several diagnostic features, naming 9–12 pairs of linear secondary veins, reticulate tertiary veins and obovate fruits, internally glabrous or with only sparse glandular trichomes, and with a persistent calyx composed of ascending sepals.

The specimen *Gardner 963* was used by Planchon (1850) to described a variety of *C. blanchetii*, but the author named it as “var. β ”, which is considered not validly published according to the *Code* (Turland et al. 2018, Art. 32.1). Later, Baker (1871) validly published the referred taxon under *C. laurifolius*.

Connarus lentiginosus Brandegee, Univ. Calif. Publ. Bot. 6(8): 186. 1915.—TYPE: Mexico.

Chiapas: Finca Irlanda and Huitla, Jun 1914, fl., fr., *C. A. Purpus 7379* (holotype: UC barcode UC 178083 [photo!]; isotypes: A [photo!], BM!, F [photo!], GH [photo!], LL-frag. [photo], MO [photo], NY [photo!], UC [photo!], US [photo!]).

Lianas, scandent shrubs, shrubs or treelets, 3–8 m tall; branchlets slightly striate, sparsely sericeous to glabrescent, trichomes simple unicellular, lenticels inconspicuous or conspicuous. *Leaves* 3–5-foliolate; petioles 3–9.5 cm long, sparsely sericeous to glabrescent; rachises 1.5–3.5 cm long, sparsely sericeous to glabrescent; pulvinuli 4–5 mm long, sparsely sericeous to glabrescent; leaflets chartaceous, concolorous, rarely slightly discoloured, flat, basal pairs $7.5\text{--}16.5 \times 3\text{--}6.6$ cm, symmetric, elliptic, ovate or obovate, bases symmetric, obtuse or acute, the apical ones $8.2\text{--}18 \times 4.7\text{--}6.7$ cm, symmetric, elliptic, ovate or obovate, less frequently narrowly elliptic or narrowly obovate, bases symmetric, obtuse or acute, apices acuminate, acumen 3–12 mm long, abaxial surfaces glabrous or sparsely sericeous on midvein, occasionally on secondary veins, indumentum brown, adaxial surfaces glabrous, dull, margins flat; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 8–11 pairs, abaxially prominent or slightly so, adaxially flat, concolorous in relation to the blade, forming angles of $45\text{--}65^\circ$ with midvein, arcuate or slightly so, tertiary veins abaxially slightly prominent, adaxially flat or slightly prominent, intercostals mixed percurrent, epidermals

opposite percurrent. *Inflorescences* in thyrsoids or double thyrsoids, axillary or pseudo-terminal, 1–4 per axil, trichomes simple unicellular, peduncles 0.2–1 cm long or inflorescences subsessile, sericeous or sparsely so, rachises 6.5–18(–30) cm long, sericeous or sparsely so, lateral cymes 0.3–0.6 cm long, sericeous or sparsely so, lateral sub-thyrsoids 3–9(–18) cm long, sericeous or sparsely so, indumentum of these structures brown or ferruginous; bracts 0.5–1 mm long, sericeous. *Flowers* with pedicels 0.5–1 mm long; buds ca. 2×1.5 mm, elliptic; sepals 5, slightly basally connate, $2\text{--}2.5 \times 0.9\text{--}1.2$ mm, ovate, narrowly ovate, triangulate or narrowly triangulate, apices acute or obtuse, outer surfaces sparsely sericeous in the central portion and more densely in the edges, indumentum brown, inner surfaces glabrous, subglabrous or sparsely sericeous; petals $3.5\text{--}4 \times 1\text{--}1.3$ mm, erect, narrowly obovate or narrowly elliptic, apices rounded or obtuse, glandular dots more than 10, rarely 5–10, loosely distributed, black, conspicuous, outer surfaces subglabrous or sparsely pubescent, inner surfaces subglabrous, glandular trichomes sparse to abundant on both surfaces, margins with glandular trichomes sparse to abundant; stamens basally connate by 0.5–0.8 mm long, shorter series 2–2.5 mm long, longer series 2.5–3.5 mm long, filaments glabrous or with sparse glandular trichomes; ovaries 0.8–1.2 mm long, densely pubescent, styles ca. 1.5 mm long, stigmas bilobate, lobes ca. 0.5 mm long. *Fruits* $(1.8\text{--})2\text{--}2.2 \times (1.2\text{--})1.3\text{--}1.6$ cm, obovate or semi-orbicular, indehiscent side sigmoid or slightly so, pericarps up to 2 mm thick, stipes (1–)3–5 mm long, styles partially persistent, apiculate, 0.5–2 mm long, outer surfaces sparsely sericeous to glabrescent, indumentum brown, black dots abundant, inner surfaces subglabrous, glandular trichomes sparse to abundant, calyces persistent, rarely partially persistent, sepals ascending erect, rarely patent; seeds $1.4\text{--}1.5 \times 0.7\text{--}0.8$ cm, arils yellowish.

Selected specimens examined: **Costa Rica.** Guanacaste: Parque Nacional Guanacaste Estación Pitilla, $10^{\circ}5'2''\text{N}$, $85^{\circ}25'40''\text{W}$, 700 m, 1 Apr 1991, fr., *C. Moraga* 256 (K, CR). Limón: Banana and cacao plantations on leve areas between Siquerres and the Río Pacuare, and remnant forest on steep hills south of the railroad bridge over the Río Pacuare, at 50–100 m. altitude, $10^{\circ}5'\text{N}$, $83^{\circ}29'\text{W}$, 20–22 Jul 1969, fl., *W. C. Burger & R. L. Lierner* 6957 (NY); Cantón de Talamanca, Sukut de las juntas de Río Urén y Río Sukut 1.5 Km aguas arriba sobre éste, margen derecha, $9^{\circ}24'30''\text{N}$, $82^{\circ}58'10''\text{W}$, 350 m, 6 Jul 1989, fl., *G. Herrera* 3153 (MEXU, NY, US). Puntaneras: Entre playas de Jacó y Esterillos, 6 Feb 1964, fr., *A. Jiménez M.* 1696 (NY, US); Garabito, P. N. Carara, cuenca del Tárcoles, Parque Nacional Carara, 0,6 Km después del portón en el Sendero Laguna Meandrica, $9:47:50.0000\text{ N}$, $-84:35:40.0004\text{ W}$, 70 m, 4 Apr 2000, fl., *L. Acosta et al.* 777 (NY); Parque Nacional Corcovado Sirena,

8°28'00"N, 83°35'00"W, 1-20 m, 6 Jul 1991, fr., *P. Delpetre 5184* (CR, NY); Road to Golfito Dairy pastures, 11 Nov 1952, fl., *P. H. Allen 6619(?)* (US). *S. loc.* Arenal, 12 Jul 1923, fl., *J. Valerio 144* (US). **Guatemala.** Retalhuleu: Along Río Vil, west of Retalhuleu, 300 m, 24 Feb 1941, st., *P. C. Standley 88332* (F). Suchitepéquez: Tiquisate, near Santiago farm, 100 m, 17 Jun 1942, fr., *J. A. Steyermark 47657* (F). **Mexico.** Chiapas: Acacoyagua. Escuintla, Chris, 12 Jun 1947, fr., *E. Matuda 16427* (F); Hidalgo, Chris, 15 Jun 1948, fl., *E. Matuda 17952* (F); Mt. Ovando, trail toca, 5 km above Fianca La Magnolia (formerly owned by E. Matuda), which is 3 km N of Los Cacao and 13 km N of Acacoyagua on rd to Olondrina, 1200–1500 m, 29 May 1985, fl., *W. Thomas & J. L. Villaseñor 3673* (MEXU); Acapetahua, Ejido Acapetahua cerca de Zacoalpita, 15 Apr 1979, fr., *F. González et al. 11324* (MEXU); Huixtla, Cafetal in seasonal Evergreen Forest along small streams 6–8 km northeast of Huixtla, elevation 200 m, 27 Dec 1992, fr., *D. E. Breedlove & R. F. Thorne 30924* (MEXU); Mapastepec, forest along Rui Testacapa 10 km southeast of Mapastepec, 180 m, 24 Jul 1972, fl., *D. E. Breedlove & R. F. Thorne 30694* (NY); Tapachula. Cantón Monte Negro, alt. 200 m, 1 Mar 1985, fr., *E. Ventura & E. López 1226* (MEXU); La Escondida, 50 m, 13 Aug 1984, fr., *E. Ventura & E. López 161* (P); Esperanza, Escuintla, Chris, 27 Apr 1947, fl., *E. Matuda 16537* (F). Tuxtla Chico, a 2 km al W de Cacahoatan caminho al río Suchiate, alt. 300 m., 9 Feb 1987, fr., *E. Martínez S. et al. 19873* (MEXU); *S. loc.* Jilguero, Chris, 10 May 1947, fr., *E. Matuda 16473* (BR). Guerrero: Petatlán Rabo de Iguana, al Norte de Petatlán, Nov 1973, fr., *F. G. Medrano 6601* (MEXU). **Nicaragua.** Chontales: Near Santo Domingo, along small river a short distance from town, 09 Apr 1961, fr., *G. S. Bunting & L. Licht 1169* (NY, US). Jinotega: Wiwili, Reserva de la Biosfera de Bosawas, transecto Wayawas, comunidad de Inipawas, 14°24'N, 85°08'W, 160 m, 23 Feb 2008, fr., *I. Colorado & A. Fernández 4255* (P). Zelaya: Guamil o breñas sobre áreas pantanosas a lo largo del Río Grande, 0.15 m, 26 Apr 1949, fl., *Molina 2448* (GH).

Distribution, habitat and phenology: *Connarus lentiginosus* occurs from southeast Costa Rica to south Mexico (Fig. 16). It is represented by lianas, shrubs, scandent shrubs or small trees, growing apparently in ombrophilous forests, at elevations ranging from sea level to 1500 m. Specimens have been collected with flowers from April to July and in November, and with fruits irregularly almost throughout the year.

Notes: *Connarus lentiginosus* is recognized by the leaves 3–5-foliolate, tertiary veins percurrent, large inflorescences usually in double thyrsoids, and petals with abundant glandular trichomes. Unusual characters in this species include: perianth strongly punctate and sepals externally sparsely sericeous in the central portion and more densely in the edges. It is

similar to *C. ecuadorensis* due to the numerous secondary veins abaxially prominent and large inflorescences in double thyrsoids, but differs in pulvinulus length, fruit size and indumentum, and stipe length (see Notes section of *C. ecuadorensis*).

Connarus lonchotus S. F. Blake, Contr. Gray Herb. 52: 69. 1917.—TYPE: Belize [British Honduras]. Moho River, 16 Mar 1907, fl., *M. E. Peck* 727 (holotype: GH [photo!]; isotype: K!). Figs. 24A–D

Connarus stenophyllus Standl. & L. O. Williams ex Ant. Molina, Ceiba 14(1): 2. 1968.—TYPE: Mexico. Chiapas: Los Lagos, 3 miles northwest of Rancho San Jose, which is 34 miles southeast of Comitán, alt. 5,000 feet, 15–20 Apr 1949, fl., *M. C. Carlson* 1860 (holotype: EAP barcode EAP89491 [photo!]; isotype: F!), *syn. nov.*

Lianas, shrubs or trees, 3–8 m tall; branchlets slightly striate, sericeous to glabrescent, trichomes simple unicellular, lenticels conspicuous. *Leaves* 3-foliolate; petioles 4–9.5 cm long, sericeous to glabrescent; rachises 1–1.4 cm long, sericeous to glabrescent; pulvinuli 4–7 mm long, sparsely sericeous to glabrescent; leaflets chartaceous, slightly discoloured, flat, basal pairs $5.5\text{--}10 \times 1.7\text{--}3.7$ cm, symmetric or slightly asymmetric, narrowly elliptic or narrowly ovate, rarely elliptic, bases asymmetric or slightly so, rarely symmetric, acute or obtuse, occasionally rounded in the broader side, the apical ones $7\text{--}12.5 \times 1.7\text{--}3.8(-5)$ cm, symmetric, narrowly elliptic or narrowly ovate, bases symmetric, obtuse, acute or rounded, apices acuminate or long acuminate, acumen 4–10(–15) mm long, abaxial surfaces glabrous or occasionally subglabrous on midvein, adaxial surfaces glabrous, dull, margins flat, rarely slightly revolute; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 7–12 pairs, abaxially slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of $45\text{--}65^\circ$ with midvein, linear, rarely slightly arcuate, tertiary veins abaxially slightly prominent, adaxially flat, intercostals reticulate or opposite percurrent, epidermals reticulate, opposite or alternate percurrent. *Inflorescences* in thyrsoids, axillary or pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncles 0.4–1 cm long, sericeous or sparsely so, rachises 7–15 cm long, sericeous or sparsely so, lateral cymes 0.5–0.7 cm long, sericeous, indumentum of these structures ferruginous; bracts 1–1.2 mm long, sericeous. *Flowers* mature not seen, pedicels 0.7–1 mm long; buds ca. 2×2 mm, orbicular; sepals 5,

slightly basally connate, at least 2 mm long, ovate, apices obtuse, outer surfaces sericeous, indumentum ferruginous, inner surfaces glabrous or subglabrous, pubescent only at apex; petals erect, glandular dots 5–10 or more than 10, loosely distributed, black, conspicuous, both surfaces glabrous or subglabrous, glandular trichomes sparse, margins with abundant glandular trichomes, pubescent only at apex; stamen filaments glabrous; ovaries densely pubescent, stigmas bilobate. *Fruits* 2.2–2.6 × 1.3–1.5(–1.8) cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 4–10 mm long, styles partially persistent, apiculate, 0.5–1.5 mm long, outer surfaces irregularly sparsely sericeous, more densely at stipe, base, sutures and apex, indumentum brown, black dots abundant, inner surfaces densely pubescent, glandular trichomes absent, calyces persistent, sepals ascending erect, rarely reflexed; seeds not seen; arils yellowish.

Selected specimens examined: **Mexico.** Chiapas: Trinitaria. Along the Comitan River at its sumidero, Lagos de Montebello, 42 km northeast of La Trinitaria, alt. 1300 m, 23 Oct 1971, fr., *D. E. Breedlove & R. F. Thorne 21102* (MEXU); Lago de Monte Bello, 25 miles east of La Trinitaria, alt. 1580 m, 17 Aug 1966, fr., *D. E. Breedlove 14975* (F, NY, US); Slopes with Montane Rain Forest, *Liquidambar*, *Magnolia*, *Vochysia*, east of Laguna Tziscaco, Monte Bello National Park, alt. 1380 m, 18 Jul 1980, fr., *D. E. Breedlove 48783* (MEXU, NY). Guerrero: San Luis Acatlán. 37 km adelante de San Luis Acatlán, rumbo a Iliatenco, alt. 1030 m, s. d., fr., *R. M. Fonseca 217* (MEXU); a 12.5 km al N de Horcasitas, camino San Luis Acatlán-Horcasitas-El Potrerillo-El Rincon, 7 Mar 1983, fr., *E. M. Martínez S. et al. 3476* (MEXU). Tlacoachistlahuaca. 6 kms. al N de Tlacoachistlahuaca, 27 Nov 1983, fr., *G. Campos R. 1052* (MEXU); 33 km al N de Ometepec, camino Tlacoachistlahuaca-San Isidro, alt. 490 m., 26 Nov 1983, fr., *E. Martínez S & F. Barrie 5785* (MEXU). Oaxaca: Putla Villa de Guerrero. 14 Km, al SW de Putla, hacia Pinotepa Nacional, alt. 1960 m, 5 Apr 1982, fr., *R. Torres C. & P. Tenorio L. 219* (MEXU); ca. 15 Km de la carretera Putla-Pinotepa Nal siguiendo el camino de terracería al Sesteadero, alt. 810 m, 1 Sep 1988, fr., *E. Solano C. 516* (MEXU). Jamiltepec, 7.7 km al N de Sta. Cruz Flores Magón y 20 km al N Jamiltepec, hacia San José de las Flores, 22 Oct 1982, fr., *R. Torres C et al. 1653* (MEXU); La Reforma, Alrededores de Llano Grande, alt. 660 m, 14 Jun 1985, fr., *R. López A. 670* (MEXU).

Distribution, habitat and phenology: *Connarus lonchotus* is restricted to the states of Chiapas, Guerrero and Oaxaca, southern Mexico (previously treated under *C. stenophyllus*), except for the type collection from Belize (Fig. 16). Individuals of this species are lianas, shrubs or trees, growing in montane wet, semi-deciduous or ciliary forests, at ca. 500–1950 m

elevation. Specimens have been collected with flowers from March to April and with fruits irregularly almost throughout the year.

Notes: *Connarus lonchotus* can be recognized by the 3-foliolate leaves, usually narrowly elliptic or narrowly ovate leaflets up to 3.8 cm wide, reticulate tertiary veins, inflorescences in thyrsoids and fruits internally densely pubescent, with stipe 4–10 mm long. It can be confused with *C. schultesii*, but differs in leaflet width, and fruit indumentum and stipe length (see Notes section of *C. schultesii*).

This species was considered a synonym of *C. lambertii* by Forero (1983). However, *C. lonchotus* differs by the leaflets comparatively narrower and basal leaflets with bases slightly asymmetric. These characteristics, in combination to the inflorescences in thyrsoids, make *C. lonchotus* identical to *C. stenophyllus*, so the latter is here considered a later heterotypic synonym of the former.

Connarus manausensis C. Toledo & V. C. Souza, Syst. Bot. 43(3): 754. 2018.—TYPE: Brazil. Amazonas: Manaus, 17 Jun 1932, fl., *A. Ducke s. n.* (holotype: RB barcode RB 00260845!; isotype: NY!).

Lianas; branchlets slightly striate, subglabrous, trichomes dendroid and simple unicellular, lenticels inconspicuous. *Leaves* 5–9-foliolate; petioles 3.2–5.3 cm long, subglabrous; rachises 3.5–8 cm long, subglabrous; pulvinuli 3–5 mm long, subglabrous; leaflets chartaceous, concolorous, flat, basal pairs 3.5–7 × 2–3 cm, symmetric, ovate, bases symmetric or slightly asymmetric, rounded or subcordate, the apical ones 6.8–10.5 × 2.5–4 cm, symmetric, ovate, bases symmetric or slightly asymmetric, rounded or subcordate, apices long acuminate, acumen 8–18 mm long, abaxial surfaces glabrous or sparsely pubescent on midvein, indumentum ferruginous, adaxial surfaces glabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed, secondary veins 7–8 pairs, abaxially slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of 60–65° with midvein, arcuate, tertiary veins flat on both surfaces, intercostals mixed percurrent, epidermals opposite percurrent or reticulate. *Inflorescences* in double thyrsoids, axillary, 1–2 per axil, trichomes dendroid and simple unicellular, peduncles 1–2 cm long, tomentose, rachises 11–16 cm long, tomentose, lateral sub-thyrsoids 0.8–5.5 cm long, tomentose, indumentum of these structures

ferruginous; bracts ca. 2 mm long, tomentose. *Flowers* with pedicels 1–2 mm long; buds not seen; sepals 5, slightly basally connate, $2\text{--}2.5 \times 1$ mm, narrowly ovate or narrowly triangulate, apices acute, outer surfaces tomentose, indumentum ferruginous, inner surfaces subglabrous to sparsely pubescent; petals $2.5\text{--}3.5 \times 1.2$ mm, erect, narrowly obovate or narrowly elliptic, apices acute, glandular dots absent or 1–4, loosely distributed, black, inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, glabrous; stamens basally connate by ca. 0.3 mm, shorter series ca. 1 mm long, longer series ca. 1.5 mm long, filaments glabrous; ovaries ca. 1 mm long, tomentose, styles ca. 2 mm long, stigmas bilobate, lobes ca. 0.8 mm long. *Fruits* not seen.

Specimens examined: **Brazil.** Amazonas: Manaus, Km 9 da BR-17 road, 5 Jul 1955, fl., J. C. de Almeida s. n. (INPA 1324, MG 21846).

Distribution, habitat and phenology: *Connarus manausensis* is only known by two collections, both from Manaus, Amazonas (Brazil) (Fig. 21). It is a lianescent species collected in upland forests of the Amazon, growing on sandy soils, at ca. 100 m elevation. Specimens have been collected with flowers from June to July.

Notes: *Connarus manausensis* is characterized by being a liana with dendroid trichomes, ovate leaflets, acumen 8–18 mm long and all sepals slightly basally connate. It is similar to *C. patrisii*, but mainly differs by leaflet texture and shape, and connation of sepals (Table 2).

Connarus marginatus Planch., Linnaea 23: 429. 1850.—TYPE: Brazil. Rio de Janeiro:

Corcovado, fl., G. Gardner 5426 (lectotype first step designated by Schellenberg 1938: K; lectotype **second step designated here:** K barcode K000633805!; isoelectotypes: BM!, K!, OXF [n. v.], W [photo!]).

Omphalobium brasiliense A. Richard ex Baker, in Martius, Fl. Bras. 14(2): 185. 1871, *pro syn.*

Lianas or shrubs, height not seen; branchlets slightly striate or slightly fissured, glabrous or subglabrous, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3(–5)-foliolate; petioles 1.3–4 cm long, glabrous or subglabrous, rarely sparsely pubescent; rachises 0.5–2.2 cm long, glabrous or subglabrous, rarely sparsely pubescent; pulvinuli 2–5 mm long,

subglabrous, rarely sparsely pubescent; leaflets chartaceous, slightly discoloured, flat, basal pairs $2.8\text{--}7.5 \times 1.4\text{--}3.4$ cm, symmetric, elliptic or ovate, bases symmetric, rounded, rarely obtuse, the apical ones $3.5\text{--}8 \times 1.8\text{--}3.7$ cm, symmetric, elliptic or ovate, bases symmetric, rounded, rarely obtuse, apices short to long acuminate, acumen 2–14 mm long, abaxial surfaces glabrous, subglabrous or sparsely pubescent on midvein or nearby, indumentum brown, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 6–8 pairs, abaxially slightly prominent, adaxially flat or slightly prominent, concolorous in relation to the blade, forming angles of $50\text{--}70^\circ$ with midvein, linear, tertiary veins abaxially slightly prominent, adaxially flat or slightly prominent, intercostals and epidermals reticulate. *Inflorescences* in thyrsoids, axillary, 1–3 per axil, trichomes simple unicellular, peduncles 0.9–2 cm long, subglabrous, rachises 3.8–11.5 cm long, subglabrous, lateral cymes 0.7–2.5 cm long, subglabrous to sparsely sericeous, indumentum of these structures brown or ferruginous; bracts 0.5–1 mm long, sericeous. *Flowers* with pedicels 2–5 mm long; buds ca. 1.5×1.5 mm, orbicular; sepals 5, slightly basally connate, $2\text{--}2.5 \times 1\text{--}1.2$ mm, ovate, narrowly ovate or elliptic, apices acute or obtuse, outer surfaces sericeous, indumentum brown or ferruginous, inner surfaces glabrous; petals $2.5\text{--}3.5 \times 1.1\text{--}1.3$ mm, reflexed, narrowly obovate or oblong, apices rounded, obtuse or acute, glandular dots more than 10, loosely distributed, black or colorless, conspicuous or inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous; stamens basally connate by 0.2–0.5 mm long, shorter series ca. 1 mm long, longer series 1.2–1.5 mm long, filaments glabrous or with sparse glandular trichomes; ovaries 0.8–1 mm long, densely pubescent, styles 1–1.5 mm long, stigmas bilobate, lobes ca. 0.5 mm long. *Fruits* $1.8\text{--}2.2 \times 1.3\text{--}1.4$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 2–4 mm long, styles partially persistent, apiculate or spinescent, 2–5 mm long, outer surfaces subglabrous or sparsely sericeous only at base, indumentum ferruginous, black dots absent, inner surfaces pubescent or sparsely so, glandular trichomes sparse, calyces persistent, rarely partially persistent, sepals ascending erect; seeds mature not seen.

Specimens examined: **Brazil.** Rio de Janeiro: Colinas dos environs de Copacabana, *s. d.*, fl, fr., *J. Nadeaud s. n.* (P barcode P05613559); Copacabana, Apr 1862, fl., *J. Nadeaud s. n.* (P barcode P05613560); Guanabara, Agulhinha de Copacabana, 25 Apr 1965, fr., *H. E. Strang s. n.* (US barcode US 01857582); Morro da Agulhinha de Inhangá, Copacabana, 11 Jan 1969, fr., *D. Sucre 4364* (NY, RB); Morro da Babylonía, 12 Aug 1871, fl., *A. F. M. Glaziou 4968* (K, P). *S. loc.*, *s. d.*, fl., *M. Gaudichaud 816* (NY, P); *S. loc.*, *s. d.*, fl., *P. Luetzelburg 15462*

(NY barcode NY 00393483); *S. loc.*, *s. d.*, fl., fr., *J. Miers s. n.* (NY barcode NY 01081411, P barcode P05613561). State unknown: *S. loc.*, *s. d.*, fl., *Tweedie 11039* (K); *S. loc.*, *s. d.*, fl., *Tweedie 11095* (K); *S. loc.*, *s. d.*, fl., fr., *L. Riedel s. n.* (K, P barcode P05613547); *S. loc.*, *s. d.*, fl., *J. Nadeaud s. n.* (P barcode P05613556).

Distribution, habitat and phenology: *Connarus marginatus* seems to be restricted to the state of Rio de Janeiro (Fig. 11), southeast Brazil, although it is represented by few and old collections. Individuals of this species are apparently lianas or small shrubs from dense ombrophilous forests of the Atlantic Forest, probably growing in mountain slopes. Specimens have been collected with flowers in April and with fruits from January to April.

Notes: *Connarus marginatus* is recognized by the 3–(5)-foliolate leaves, small leaflets, 6–8 pairs of linear secondary veins, reticulate tertiary veins, subglabrous inflorescence peduncle and rachis, and fruits with a prominent apex. It is morphologically very close to *C. nodosus*, which also occurs in Rio de Janeiro and has small leaflets with linear secondary veins and reticulate tertiary veins, but the former differs by the 6–8 pairs of secondary veins (vs. 9–13 pairs) and subglabrous inflorescence rachises (vs. pubescent or sericeous). In addition, it seems that inflorescence rachises in *C. marginatus* are very thin and bear a reduced number of flowers, which should be investigated when additional collections of this species become available.

Planchon (1850) described *C. marginatus* based on the syntypes *Gardner 5426* and *Tweedie s. n.* Schellenberg (1938) inadvertently selected the former as lectotype without indicating in which herbarium it was deposited, while Forero (1983) indicated that the type collection was deposited in K. As there are two specimens of this collection in K, the one that belonged to Hooker herbarium is here designated under a second step lectotypification because Planchon (1850) cited the collection *Gardner 5426* from this collection.

Connarus marleneae Forero, Brittonia 32(1): 35. 1980 (“*marlenei*”).—TYPE: Brazil. Amazonas: Lago do Janauacá, south of Rio Solimões, 28 Aug 1973, fr., *C. C. Berg et al. P19800* (holotype: INPA 43284!; isotypes: COL [photo!], MG!, NY [photo!]).

Connarus celatus Forero, Brittonia 32(1): 33. 1980.—TYPE: Brazil. Pará: Prainha, Rio Jauary, beira, 14 May 1903, fl., *A. Ducke s. n.* (holotype: MG barcode MG003566!; isotypes: IAN!, RB!), *syn. nov.*

Treelets to trees, 2–14 m tall; branchlets slightly striate, subglabrous or sparsely pubescent, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3-foliolate; petioles 2.5–9 cm long, glabrous or subglabrous; rachises 0.5–3 cm long, glabrous or subglabrous; pulvinuli 3–5 mm long, glabrous or subglabrous; leaflets chartaceous, slightly discoloured, flat, basal pairs $5.2\text{--}12.5 \times 2.3\text{--}4.7$ cm, symmetric, elliptic, narrowly elliptic, ovate or narrowly ovate, bases symmetric, rounded or subcordate, the apical ones $7.4\text{--}16 \times 2.8\text{--}6$ cm, symmetric, elliptic, narrowly elliptic, ovate or narrowly ovate, bases symmetric, rounded or subcordate, apices long acuminate to cuspidate, acumen 7–23 mm long, abaxial surfaces glabrous, subglabrous or occasionally irregularly sparsely pubescent on midvein, indumentum ferruginous, adaxial surfaces glabrous or subglabrous, dull or slightly shining, margins flat; midveins abaxially prominent, adaxially slightly impressed or slightly so, secondary veins 7–10 pairs, abaxially slightly prominent, adaxially flat, discoloured or slightly so in relation to the blade, forming angles of $50\text{--}65^\circ$ with midvein, arcuate, tertiary veins abaxially slightly prominent, adaxially flat or slightly prominent, intercostals alternate percurrent, epidermals opposite percurrent or reticulate. *Inflorescences* in thyrsoids, rarely double thyrsoids, axillary, 1–4 per axil, trichomes simple unicellular, peduncles 0.5–2 cm long or inflorescences subsessile, tomentose, rachises 5–23 cm long, tomentose, lateral cymes 0.2–0.7 cm long, tomentose, lateral sub-thyrsoids 3–4.5 cm long, tomentose, indumentum of these structures ferruginous; bracts 0.7–1.5 mm long, tomentose. *Flowers* subsessile or pedicels 1–2 mm long; buds $1.5\text{--}2 \times 1.5$ mm, elliptic or orbicular; sepals 5, slightly basally connate, $2\text{--}3 \times 1\text{--}1.5$ mm, narrowly ovate or narrowly triangulate, apices acute, outer surfaces tomentose or pubescent, indumentum ferruginous, inner surfaces glabrous or subglabrous, pubescent only at apex; petals $4\text{--}7 \times 1.2\text{--}2$ mm, reflexed, narrowly obovate, narrowly elliptic or narrowly ovate, apices acute, glandular dots absent or 1–4, distributed at apex, black, inconspicuous, both surfaces glabrous, margins glabrous; stamens basally connate by 0.3–1 mm, shorter series 2.5–4 mm long, longer series 4–5 mm long, filaments glabrous; ovaries ca. 1.5 mm long, densely pubescent, styles and stigmas not seen. *Fruits* $1.5\text{--}2.2 \times 0.9\text{--}1.5$ cm, obovate, indehiscent side sigmoid or slightly so, pericarps up to 2 mm thick, stipes (3–)4–6 mm long, styles partially persistent, apiculate or spinescent, 0.5–1 mm long, outer surfaces irregularly sparsely sericeous, more densely at stipe and base, indumentum brown, black dots abundant, inner surfaces pubescent or sparsely so, glandular trichomes sparse, calyces persistent, sepals ascending erect; seeds $0.9\text{--}1.9 \times 0.5\text{--}0.7$ cm, arils color not seen.

Specimens examined: **Brazil.** Amazonas: Enseada Grande, Ponta Negra, 9 Mar 1961, fr., *W. A. Rodrigues & J. Lima* 2202 (INPA, NY); Estrada Manaus-Porto Velho, Lago do Castanho, margem esquerda, 9 Jul 1972, fr., *M. F. da Silva* 304 (INPA, NY); Ilha do Marapatá, boca do Rio Negro, 20 Jun 1961, fl., fr., *W. Rodrigues & D. Coelho* 2827 (INPA, NY); Janauari, Rio Negro opposite Manaus, 1 Apr 1971, fl., *G. T. Prance et al.* 11242 (INPA, NY); Lago do Castanho-Mirim, igarapé Andiroba, 19 Jun 1973, fr., *B. Albuquerque et al.* 733 (INPA); Lago do Arapari, Paraná do Autraz-Mirim, 11 May 1966, fl., *F. Mello* 13 (INPA); Lago do Castanho-Mirim, igarapé do Itauba, 3 Jul 1973, fl., *B. Albuquerque et al.* 1062 (INPA, NY); Lago do Janauari, boca do Rio Negro, 2 Jun 1961, fr., *W. Rodrigues et al.* 2690 (INPA, NY); Lago do Janauacá, Italiano, 9 Jul 1969, fr., *Byron* 203 (INPA, UEC); Lago Janauacá, sul do Rio Solimões, Água Preta, 28 Aug 1973, fr., *C. C. Berg et al.* P19800 (INPA, NY); Manaus. Autaz-Mirim, Rosa Branca, 16 Jun 1973, fr., *A. Loureiro et al.* s. n. (INPA, NY); Rio Preto, local das 3 Bocas, 21 Jun 1964, fl., *W. Rodrigues & D. Coelho* 5877 (F, INPA, NY). Pará: Cacaual Grande, Águas Pretas, Jun 1952, fl., *G. A. Black* 15460 (IAN, UB); Igarapé das fazendas, Fazenda São Joaquim (Lago Grande), 02°11'S, 55°46'W, 8 May 1984, fl., *I. A. Rodrigues & M. R. Cordeiro* 1099 (IAN); Lago Grande, s. d., fr., *Projeto IARA* s. n. (IAN 164468); Monte Alegre, Floresta em Paituma, 2°00'09"S, 54°04'09"W, alt. 38 m, 3 Apr 2009, fl., *C. Suemitsu & A. S. S. Holanda* 929 (HSTM); Monte Alegre. Lago do Jacaré, 9 Jul 1908, fr., *E. Snethlage* s. n. (MG); Matas ciliares do Lago Grande, 1 May 1996, fl., *Projeto IARA* s. n. (IAN 164434). Oriximiná, rio Trombeta, margem direita ao Norte de Porto Trombetas, 23 Jul 1980, fr., *C. A. C. Ferreira* 1731 (COL, INPA); Santarém. Cacaual Grande, Igarapé Água Preta, 28 Oct 1950, fl., *G. A. Black & P. Ledoux* 10348 (INPA, P); Enseada de Alter do Chão, margem direita do Rio Tapajós, 13 Aug 1978, fl., *U. N. Maciel & M. R. Cordeiro* 305 (NY). Várzea do Gurupatuba, 23 Apr 1916, fl., *A. Ducke* s. n. (MG 16043, IAN, RB).

Distribution, habitat and phenology: *Connarus marleneae* is restricted to north Brazil, where it is found in central-east Amazonas and north Pará (Fig. 15). This species is represented by trees or treelets up to 14 m tall from the Brazilian Amazon, occurring in floodplain (várzea) or ciliary forests, at low elevations (40–150 m). Specimens have been collected with flowers from April to October and with fruits especially from June to August.

Notes: Among the 3-foliolate species with only simple trichomes, *C. marleneae* is easily distinguished by few but unusual characteristics: the individuals are trees with inflorescence rachises tomentose and petals epunctate or with 1–4 black dots distributed apically. It can be confused with *C. acutissimus*, but the latter is represented by lianescent

species with inflorescence rachises sericeous and petals with abundant evenly distributed glandular dots.

Connarus marleneae was separated from *C. celatus* based on pedicel length (Forero 1983) and inflorescence architecture (Toledo et al. 2020). However, the holotype of *C. celatus* has short pedicels or measuring up to 2 mm long, and inflorescences in both species are thyrsoids. Besides, both species are trees and share unusually characteristics among Neotropical *Connarus*, such as inflorescences rachises tomentose and petals epunctate or with 1–4 glandular dots. These factors suggest that only one species should be recognized and, although both names were published in the same work (Forero 1980), *C. marleneae* was chosen over *C. celatus* because the former has been more largely used in herbarium collections.

Forero (1980a) published *C. marleneae* spelled as “*marlenei*”, a name given in honor to Dr. Marlene da Silva, ex curator of INPA herbarium. However, this epithet should retain its feminine gender (Turland et al. 2018, Art. 60.8), so the correct spelling is here applied.

Connarus megacarpus S. F. Blake, Bull. Torrey Bot. Club 50(8): 273. 1923.—TYPE: Guyana.

Along the Demerara River, 25 Nov 1913, fr., *C. D. Mell s. n.* (holotype: US barcode US 00130745!; isotype: US!).

Scandent shrubs or trees, height not seen; branchlets slightly striate, densely tomentose, trichomes simple unicellular, lenticels absent. *Leaves* 7–9-foliolate; petioles 3.2–8 cm long, densely tomentose; rachises 4.5–13.5 cm long, densely tomentose; pulvinuli 4–5 mm long; leaflets coriaceous, discolorous, flat, basal pairs 4.2–9 × 2.2–3.9 cm, symmetric, elliptic, narrowly elliptic or ovate, bases symmetric, rounded or subcordate, the apical ones 5.5–16 × 3.4–5.4 cm, symmetric, narrowly elliptic, narrowly obovate or oblong, bases symmetric, rounded or subcordate, apices short acuminate, acumen 2–4 mm long, retuse, abaxial surfaces densely tomentose, indumentum brown or griseous, adaxial surfaces glabrous or subglabrous, slightly shining, margins revolute or slightly so; midveins abaxially prominent, adaxially impressed, secondary veins 7–9 pairs, abaxially prominent, adaxially flat, concolorous in relation to the blade, forming angles of 70–80° with midvein, linear, tertiary veins abaxially flat, rarely slightly prominent, adaxially flat, intercostals and epidermais reticulate. *Inflorescences* in thyrsoids, axillary, 1–3 per axil, trichomes simple unicellular, peduncle 0.1–

0.3 cm long or inflorescences sessile, densely tomentose, rachises 5–9 cm long, densely tomentose, lateral cymes 0.3–1.2 cm long, densely velutinous, indumentum of these structures brown; bracts ca. 1 mm long, tomentose. *Flowers* sessile; buds ca. 2×1.7 mm, elliptic; sepals 5, slightly basally connate, $2.5\text{--}3 \times 1$ mm, ovate, apices acute or obtuse, outer surfaces tomentose, indumentum brown, inner surfaces glabrous; petals $3\text{--}4 \times 1\text{--}1.2$ mm, slightly reflexed (urceolate-like), narrowly obovate, apices acute, glandular dots more than 10, loosely distributed, colorless, conspicuous, outer surfaces tomentose, inner surfaces tomentose in the upper half, glabrous in the lower half, glandular trichomes sparse only in the inner surface, margins ciliate, glandular trichomes absent; stamens basally connate by ca. 0.5 mm long, shorter series ca. 1 mm long, longer series 3–3.5 mm long, filaments with sparse glandular trichomes; ovaries ca. 0.8 mm long, densely pubescent, styles and stigmas not seen. *Fruits* $3.2\text{--}3.5 \times 2\text{--}2.2$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 7–8 mm long, styles partially persistent, apiculate, ca. 5 mm long, outer surfaces densely tomentose, indumentum brown, black dots absent, inner surfaces glabrous, calyces persistent, sepals ascending erect; seeds ca. 2×1 cm, arils color not seen.

Specimens examined: **Guyana.** Dukalikuru Creek, Berbice River, 31 Mar 1938, fl., *Fanshawe in Forest Department* 2683 (K).

Distribution, habitat and phenology: *Connarus megacarpus* is only found in Guyana, where the two individuals reported here were collected along Berbice and Demerara Rivers (Fig. 9), without precise locations. It is a scandent shrub or tree growing probably in ciliary forests. Specimens have been collected with flowers in March and with fruits in November.

Notes: *Connarus megacarpus* was described by Schellenberg (1938) and Forero (1983) as possessing dendroid trichomes, but none of these were found in the two specimens analyzed by both authors. Therefore, among the species with exclusively simple trichomes, *Connarus megacarpus* can be easily recognized by the 7–9-foliolate leaves, densely tomentose leaflets on abaxial surfaces, sessile flowers, externally tomentose petals and large fruits ($3.2\text{--}3.5 \times 2\text{--}2.2$ cm), externally densely tomentose and with stipe 7–8 mm long. This species can be confused with *C. favosus* by the leaflet shape and indumentum, retuse acumen and revolute leaflet margins, but mainly differs by the 7–9-foliolate leaves (vs. 3–7), inflorescences in thyrsoids (vs. double thyrsoids) and fruits 3.2–3.5 cm long (vs. 1.3–2 cm long) with stipe 7–8 mm long (vs. fruits sessile or stipe ca. 1 mm long).

Connarus negrensis Huber, Bol. Mus. Para 5: 374. 1909.—TYPE: Brazil. Amazonas: Barcelos, Rio Negro, 1 Jul 1905, fr., *A. Ducke MG 7208* (lectotype designated by Toledo et al. 2020b: RB barcode RB 00542191!).

Lianas or scandent shrubs; branchlets slightly striate, rarely smooth, glabrous or subglabrous, trichomes simple unicellular, lenticels inconspicuous or conspicuous. *Leaves* 3-foliolate; petioles 5.5–15(–22) cm long, glabrous or subglabrous, rarely sparsely sericeous; rachises 1.4–4(–5.7) cm long, glabrous or subglabrous, rarely sparsely sericeous; pulvinuli 4–8 mm long, glabrous or subglabrous; leaflets chartaceous to subcoriaceous, concolorous or slightly discolorous, flat, basal pairs 10.5–28 × 3.7–10.5 cm, symmetric, elliptic or ovate, rarely narrowly elliptic, bases symmetric or slightly asymmetric, rounded or obtuse, less frequently acute, the apical ones 12.5–33 × 5–13 cm, symmetric, elliptic or ovate, rarely narrowly elliptic, bases symmetric, rounded or obtuse, less frequently acute, apices long acuminate to cuspidate, acumen 15–42 mm long, abaxial surfaces glabrous or subglabrous, rarely sparsely sericeous only on midvein, indumentum brown, adaxial surfaces glabrous or subglabrous, dull, margins flat, rarely slightly revolute; midveins abaxially prominent, adaxially slightly prominent or flat, secondary veins (8–)10–12 pairs, abaxially prominent, adaxially flat or slightly impressed, concolorous in relation to the blade, forming angles of 50–65° with midvein, arcuate or slightly so, tertiary veins abaxially prominent, adaxially flat, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids, axillary or pseudo-terminal, 1–4 per axil, trichomes simple unicellular, peduncles 0.2–0.8 cm long or inflorescences subsessile, sericeous or sparsely so, rachises 8–20 cm long, sericeous or sparsely so, lateral cymes 0.5–1.6 cm long, sericeous, indumentum of these structures brown or ferruginous; bracts 0.8–1 mm long, sericeous. *Flowers* with pedicels 0.8–1 mm long; buds 2 × 1.2–1.3 mm, ovate; sepals 5, slightly basally connate, 2.3–3 × 0.8–1.2 mm, ovate, narrowly triangulate or narrowly elliptic, apices acute, outer surfaces sericeous or sparsely so, indumentum brown or ferruginous, inner surfaces subglabrous in the lower half, sericeous or sparsely so in the upper half; petals 3.5–5 × 1–1.5 mm, erect, narrowly obovate or oblong, apices rounded or obtuse, rarely acute, glandular dots more than 10, loosely distributed, colorless, rarely black, conspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent or sparse, margins glabrous or with sparse to abundant glandular trichomes; stamens basally connate by 0.3–1 mm long,

shorter series 1.2–3 mm long, longer series 2–4 mm long, filaments with sparse to abundant glandular trichomes, shorter filaments rarely glabrous; ovaries 0.8–1 mm long, densely pubescent, styles 1.3–1.5 mm long, stigmas bilobate, lobes 0.3–0.6 mm long. *Fruits* 1.7–2.4 × 1.1–1.6 cm, obovate, indehiscent side linear or slightly sigmoid, pericarps up to 2 mm thick, stipes 2–4 mm long, styles partially persistent, apiculate or spinescent, 0.5–2(–4) mm long, outer surfaces sparsely sericeous to glabrescent, indumentum brown, black dots sparse to abundant, inner surfaces glabrous, subglabrous or sparsely pubescent, glandular trichomes sparse or absent, calyces persistent, sepals ascending erect or patent, rarely reflexed; seeds 1–1.3 × 0.6–0.7 cm, arils yellowish or whitish.

Specimens examined: **Brazil.** Acre: Cruzeiro do Sul, BR 364 (C. do Sul a Tarauacá, km 40), linha n° 01, 13 Sep 1985, fr., *A. Rosas et al.* 291 (NY, RB). Amazonas: Barra, Rio Negro. Feb 1857, fl., *R. Spruce* 1335 (K, P), *s. d.*, fl., *Spruce s. n.* (RB barcode RB 00260883); Ega (Tefê), Oct 1831, fl., *E. F. Poeppig* 2759 (W); Fontebôa, 27 Nov 1927, fl., *A. Ducke* 19713 (RB); Jauaretê, Voupês, Rio Negro, 23 Oct 1945, *R. L. Fróes* 21267 (IAN, NY); Manaus. 17 Apr 1932, fl., *A. Ducke s. n.* (IAN 67510, RB 260878); Estrada do Aleixo, 26 Mar 1947, fl., *R. L. Fróes* 22048 (IAN); Parintins, 5 Apr 1946, fl., *J. P. Pires & G. A. Black* 1224 (IAN, P, US); Maués, mata baixa na beira de um igapó, 5 Oct 1929, fl., *A. Ducke s. n.* (IAN 67570, RB 25666); São Gabriel da Cachoeira, ad Rio Negro, Jan–Aug 1952, fl., *R. Spruce* 2363 (G, K, P, W); Slopes of Serra de Jacumim, between Manaus and São Gabriel, 00°25'S, 65°32'W, 2 Jul 1979, fr., *L. Alencar* 323 (NY); Tefê, 15 Sep 1947, fr., *G. A. Black* 47-1438 (IAN). Roraima: Rio Branco, margem esquerda do Paraná do Marará, ponto B-1 B-2, 4 Mar 1977, fr., *M. R. Santos* 128 (MG, NY). **Colombia.** Amazonas: Río Caquetá, cerca al chorro Córdoba, en zona de rebalse del río Caquetá, 12 Mar 1990, fr., *G. Galeano et al.* 2065 (COL, NY).

Distribution, habitat and phenology: *Connarus negrensis* is mainly distributed in the Brazilian state of Amazonas, with few collections known from Acre and Roraima (Brazil), and Colombia (Amazonas) (Fig. 5). A lianescent species, occurring in flooded areas or upland forests, at low elevations (75–200 m). Specimens have been collected with flowers from October to April and with fruits sparsely from March to September.

Notes: This species is mainly characterized by the exclusively 3-foliolate leaves, large leaflets with acumen 15–42 mm long and inflorescences in thyrsoids. Its flowers and fruits are similar to those found in *C. lambertii*, so *C. negrensis* differs by the leaflet and acumen length, number of secondary veins and type of tertiary veins (Table 1). Distribution may also

be useful for distinction as the limits of their distribution ranges are close, but not in sympatry: *C. negrensis* is found in north Brazil (Acre, Amazonas, Roraima) and south Colombia, while *C. lambertii* is distributed from north Central America, with southern limit in central Colombia and south Venezuela (Fig. 5).

Connarus negrensis was considered a synonym of *C. ruber* var. *sprucei* by Forero (1983), but this position is inconsistent as the characteristics presented in the type of *C. negrensis* match with Forero's (1983) concept of *C. ruber* var. *ruber*. Nevertheless, after a careful revision of collections and names regarding *C. ruber* (Toledo et al. 2020b), typifications were proposed and varietal taxa were disregarded, so *C. negrensis* was reestablished. Therefore, this species differs from *C. ruber* by the inflorescence architecture, sepals and petals size, and fruits stipe and indumentum (Table 3).

Forero (1983) inadvertently selected the lectotype of *C. negrensis* as Huber (1909) did not indicate in which herbarium the type was deposited. However, the specimen designated by Forero (1983) from MG is apparently missing, so the collection from RB was considered the lectotype (for a complete discussion, see Toledo et al. 2020b).

Connarus nodosus Baker, in Martius, Fl. Bras. 14(2): 190. 1871.—TYPE: Brazil. Rio de Janeiro: S. Juan et Tapebussú, Distr. Goyatacazes, 1815, fl., *M. A. P. Wied-Neuwied s. n.* (lectotype designated by Forero 1983: BR barcode BR 658891). Fig. 25

Omphalobium simonianum Casar. ex G. Schellenb., in Engler, Pflanzenr. IV. 127(Heft 103): 239. 1938, *pro syn.*

Lianas, shrubs or scandent shrubs, 1–4 m tall; branchlets slightly striate, glabrous or subglabrous, occasionally sparsely sericeous, trichomes simple unicellular, lenticels conspicuous, rarely inconspicuous. *Leaves* 3–5(–7)-foliolate; petioles 2.2–5.7 cm long, glabrous, subglabrous, sparsely sericeous or sparsely tomentose; rachises 1.3–4.8 cm long, glabrous, subglabrous, sparsely sericeous or sparsely tomentose; pulvinuli 3–5 mm long, glabrous, subglabrous or sparsely tomentose to glabrescent; leaflets chartaceous, slightly discolorous, flat, basal pairs 4.6–11 × 2.5–4 cm, symmetric, elliptic or narrowly elliptic, bases symmetric, rounded or obtuse, the apical ones 5.3–12.3 × 2.8–4 cm, symmetric, elliptic or

narrowly elliptic, bases symmetric, rounded or obtuse, apices short acuminate to long acuminate, acumen 2–11 mm long, abaxial surfaces glabrous or subglabrous, occasionally sparsely tomentose at base or midvein, indumentum ferruginous, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed, secondary veins 9–13(–16) pairs, abaxially flat or slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of 60–80° with midvein, linear, tertiary veins abaxially flat or slightly prominent, adaxially flat, intercostals and epidermals reticulate. *Inflorescences* in double thyrsoids, axillary or pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncles 0.2–2 cm long or inflorescences subsessile, pubescent or sparsely sericeous, rachises 6.5–17 cm long, densely pubescent, sericeous or sparsely so, lateral sub-thyrsoids 1–4 cm long, densely pubescent or sericeous, indumentum of these structures ferruginous; bracts ca. 1 mm long, tomentose. *Flowers* subsessile or pedicels 1–2 mm long; buds ca. 2 × 2 mm, orbicular; sepals 5, slightly basally connate, 2–2.5 × 1–1.3 mm, narrowly ovate or triangulate, apices acute, outer surfaces tomentose, indumentum ferruginous, inner surfaces glabrous or subglabrous; petals 2.5–3.5 × 1.2–1.5 mm, reflexed, narrowly obovate, narrowly elliptic or oblong, apices rounded or acute, glandular dots more than 10, loosely distributed, black or colorless, conspicuous or inconspicuous, both surfaces glabrous, subglabrous or sparsely pubescent, glandular trichomes absent, margins glabrous or sparsely ciliate, more densely at apex, glandular trichomes absent; stamens basally connate by 0.2–0.5 mm, shorter series 1.5–3 mm long, longer series 2–4 mm long, filaments glabrous or with sparse glandular trichomes; ovaries 1–1.2 mm long, densely pubescent, styles 0.5–1 mm long, stigmas bilobate, lobes 0.3–0.5 mm long. *Fruits* 1.5–2.3 × 1.1–1.5 cm, obovate or semi orbicular, indehiscent side sigmoid or almost linear, pericarps up to 2 mm thick, stipes 3–6 mm long, styles partially persistent, apiculate or spinescent, 0.5–3 mm long, outer surfaces irregularly sparsely sericeous to glabrescent, more densely at stipe and base, indumentum ferruginous, black dots abundant, inner surfaces glabrous, subglabrous or with only sparse glandular trichomes, calyces persistent, rarely partially persistent, sepals ascending erect; seeds 1–1.5 × 0.5–0.7 cm, arils whitish.

Selected specimens examined: **Brazil.** Bahia: Rod. Uma x Santa Luzia, 3 Sep 1971, fr., *R. S. Pinheiro 1572* (CEPEC). Espírito Santo: Linhares. Pontal do Ipiranga. 10 Nov 1996, fl., *R. L. Dutra 143* (VIES); Lado direito da estrada chegando em Pontal do Ipiranga, 31 May 1993, fr., *V. de Souza 496* (CVRD, NY); Reserva Goytacazes, BR-101, -19,420826, -40,067273, alt. 30 m, 10 Aug 2010, fl., *D. A. Folli 6663* (CVRD, NY, RB); Reserva Natural

Vale, aceiro Bragato, 26 Oct 2010, fr., *T. B. Flores & G. S. Siqueira* 948 (CVRD, ESA, RB, VIES); Reserva Natural Vale, aceiro catelã João Pedro, -19,18039 S, -39,975015, 8 May 2009, fr., *Maas et al.* 9850 (CVRD). Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, alt. 800 m, 4 Oct 2001, fr., *L. Kollmann & E. Bausen* 4803 (MBML, UB). Rio de Janeiro: Ad Tapebussú, 1829, fl., *M. A. P. Wied-Neuwied s. n.* (BR barcode BR 586509); Dunas da Praia do Pero, Cabo Frio, 14 Nov 1968, fl., *D. Sucre* 3623 (RB); Macaé, Cabiunas, próx. a estação ferroviária, alt. 0–40 m, 28 Jul 1987, fl., *H. C. de Lima & J. Caruzo* 3065 (RB); Maricá, Ponta do Fundão, na margem da Lagoa da Barra, 9 Dec 1994, fr., *M. C. L. Ramos & C. E. dos S. Dina* 313 (RB); Paraíba do Sul(?) [Parahyba], 1829, fl., *M. A. P. Wied-Neuwied s. n.* (BR barcode BR 584760); Paraty, Paratimirim, Ilha do Grumari, 24 Apr 1989, fl., *E. L. Jacques et al.* 127 9RB); R. da Tijuca, 21 Jul 1945, fr., *O. Machado s. n.* (RB); Restinga Recreio dos Bandeirantes, 29 Feb 1972, fr., *J. Almeida* 1296 (RB); Rio de Janeiro. APA de Grumari, Restinga de Grumari, estrada perpendicular a praia, ca. 50 m da praia, 14 Dec 2002, fl., *J. M. A. Braga & R. H. P. Andreato* 7130 (K, MBM, NY, RB, SP); Campos dos Goytacazes, Guarus, Mata do Bom Jesus (também conhecida como Mata do Caixão), 21°42'46"S, 41°15'50"W, 9 Oct 2019, fl., fr., *E. A. Fortes et al.* 146 (RB); Grumari, restinga arbustivo-arbórea, 23°02'46.7"S, 43°32'07.6"W, 8 Dec 2019, fr., *C. A. P. Toledo & M. Falcão* 410 (ESA); Restinga da Praia de Grumari, 21 May 2000, fr., *D. Fernandes & A. Oliveira* 507 (RB); Restinga de Grumari, mata de restinga a cerca de 100 metros da estrada interna do Grumari, 23°02'41"S, 43°31'58"W, 24 Oct 2007, fr., *M. C. Souza* 634 (K, RB); Restinga do Mauá, 16 Nov 1990, fr., *Schwacke* 6997 (RB). Saquarema. Parque Estadual da Costa do Sol, antiga Reserva Ecológica de Jacarepiá ("Vilatur"), 22°55'34"S, 42°27'22"W, alt. 7 m, 21 Mar 2018, fr., *C. Baez et al.* 1527 (RB); Restinga de Ipitangas, 7 Mar 1989, fr., *C. Farney et al.* 2227 (RB). Sapopemba, 19 Oct 1876, fr., *A. M. F. Glaziou* 8624 (P). *S. loc.*, *A. F. M. Glaziou* 19019 (K).

Distribution, habitat and phenology: *Connarus nodosus* is almost exclusively found in southeast Brazil, except for one collection known from south Bahia. It mainly occurs in the coastal zone with limits ranging from Linhares, ES (north) to Rio de Janeiro, RJ (south) (Fig. 11). This species is represented by shrubs or scandent shrubs up to 4 m tall, usually found in coastal vegetations (restinga), but also in tableland forests (Tabuleiro) or rarely close to river margins, always associated to sandy soils, normally at low elevations (sea level to ca. 40 m). Specimens have been collected with flowers mainly from July to December and with fruits irregularly almost throughout the year.

Notes: *Connarus nodosus* is recognized by the 3–5(–7)-foliolate leaves, relatively small leaflets, 9–13 pairs of linear secondary veins, reticulate tertiary veins and externally punctate fruits, with stipe 3–6 mm long and style partially persistent, usually strongly prominent. It can be confused to *C. marginatus* as both species occur in Rio de Janeiro and have relatively small leaflets, but *C. nodosus* differs mainly by the number of secondary veins (9–13 vs. 6–8 pairs) and inflorescence rachises indumentum (tomentose or sericeous vs. subglabrous).

In the protologue (Baker 1871), *C. nodosus* was erroneously presented in the identification key as “*C. nodulosus*”, but the correct spelling was applied in the header of its description.

Forero (1983) included *C. uleanus* Gilg ex Ruebsaamen (*nomen nudum*) in the synonymy of *C. nodosus*, but it is unclear why the author took this decision as no specimen of the referred name was indicated.

Connarus oblongus G. Schellenb., in Engler, Pflanzenr. IV. 127(Heft 103): 250. 1938.—

TYPE: Brazil. Minas Gerais(?): Environs de Rio de Janeiro et d’Ouro Preto, 1883–84, fl., fr., *A. F. M. Glaziou 14606* (holotype: B $\dagger$; lectotype designated by Forero 1983: P barcode P01819593!; isoelectotype: K!).

Habit not seen; branchlets slightly striate, sparsely puberulent, trichomes dendroid and simple unicellular, lenticels conspicuous. *Leaves* 3–5-foliolate; petioles 1.2–2.8 cm long, sparsely puberulent; rachises 1.5–3.3 cm long, sparsely puberulent; pulvinuli ca. 4 mm long, sparsely tomentose; leaflets coriaceous, concolorous, conduplicate, basal pairs 6.7–7 × 3.8–4.6 cm, symmetric, ovate, bases symmetric, rounded, the apical ones 9.3–13 × 4.1–5.8 cm, symmetric, ovate, narrowly ovate or narrowly elliptic, bases symmetric, rounded or obtuse, apices acuminate, acumen 4–8 mm long, abaxial surfaces subglabrous, sparsely tomentose only on midvein, indumentum ferruginous, adaxial surfaces glabrous, occasionally subglabrous on midvein, dull, margins flat; midveins abaxially prominent, adaxially impressed, secondary veins 6–7 pairs, both surfaces slightly prominent, concolorous in relation to the blade, forming angles of 40–60° with midvein, arcuate, basal pairs ascending, tertiary veins abaxially flat, adaxially slightly prominent, intercostals and epidermals reticulate or mixed percurrent. *Inflorescences* in thyrsoids or double thyrsoids, axillary, 1–4 per axil, trichomes dendroid and

simple unicellular, peduncles 0.1–0.2 cm long or inflorescences subsessile, densely tomentose, rachises 5–13 cm long, densely tomentose, lateral cymes 0.3–1.5 cm long, densely tomentose, lateral sub-thyrsoids 3.2–3.8 cm long, densely tomentose, indumentum of these structures ferruginous; bracts 1–2 mm long, tomentose. *Flowers* sessile; buds ca. 2×2 mm, orbicular; sepals 5, slightly basally connate or occasionally 2 connate half their length, ca. $3\text{--}3.5 \times 1.5$ mm, narrowly triangulate, apices acute, outer surfaces tomentose, indumentum ferruginous, inner surfaces glabrous or subglabrous; petals ca. 3.5×1 cm, arrangement not seen, narrowly obovate, apices acute, glandular dots more than 10, loosely distributed, black, conspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins subglabrous, glandular trichomes sparse; stamens basally connate by ca. 0.3 mm long, shorter series ca. 1 mm long, longer series ca. 1.5 mm long, filaments glabrous; ovaries ca. 1.2 mm long, tomentose, styles ca. 1.5 mm long, stigmas bilobate, lobes ca. 0.3 mm long. *Fruits* $1.9\text{--}2.2 \times 1.1\text{--}1.4$ cm, obovate or semi-orbicular, indehiscent side linear, pericarps up to 2 mm thick, stipes 5–7 mm long, styles partially persistent, inconspicuous, ca. 0.5 mm long, outer surfaces tomentose to glabrescent, indumentum ferruginous, black dots absent, inner surfaces subglabrous, glandular trichomes abundant, calyces deciduous; seeds not seen.

Distribution, habitat and phenology: *Connarus oblongus* is only known from the type location, probably collected between Minas Gerais and Rio de Janeiro states, Brazil (Fig. 18). No information on habitat and phenology is currently available.

Notes: Among the species with dendroid trichomes, *C. oblongus* is recognized by the 3–5-foliolate leaves, tertiary veins adaxially slightly prominent on leaflets, and fruit stipes 5–7 mm long. It can be confused with *C. grandifolius* due to the 3–5-foliolate leaves; however, the former differs in having 6–7 pairs of secondary veins, externally glabrous or subglabrous petals, and fruits $1.9\text{--}2.2 \times 1.1\text{--}1.4$ cm, while the latter has 9–12 pairs of secondary veins, sparsely to tomentose petals on outer surface, and fruits $2.9\text{--}3.3 \times 1.9\text{--}2.2$ cm.

Connarus panamensis Griseb., Bonplandia 6(1): 6. 1858.—TYPE: Panama. *S. loc.*, 1850, fl., fr., *E. P. Duchassaing s. n.* (lectotype designated by Schellenberg 1938: GOET barcode GOET002279 [photo!]; isotype: P!; probable isoelectotypes: GH!, GOET [photo], NY-frag. [photo!]). Fig. 26

Connarus haemorrhoeus H. Karst., Florae Columbiae 2: 73. 1863.—TYPE: Colombia. Magdalena: Tomarazón, *s. d.*, fl., *G. K. W. H. Karsten s. n.* (holotype: W0077902! and W0077904!).

Connarus cooksii Pittier ex G. Schellenb., in Engler, Pflanzenr. IV. 127(Heft 103): 223. 1938, *pro syn.*

Lianas, shrubs or scandent shrubs, rarely treelets, 3–4 m tall; branchlets slightly striate, tomentose, occasionally glabrescent, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3(–5)-foliolate; petioles 2.1–8(–12) cm long, tomentose to glabrescent; rachises 1–3(–4) cm long, tomentose to glabrescent; pulvinuli 4–7 mm long, tomentose to glabrescent; leaflets subcoriaceous to coriaceous, slightly discoloured, flat, basal pairs (5–)7.5–16.5(–21) × (2.5–)3–7(–8.8) cm, asymmetric or slightly so, elliptic, narrowly elliptic or ovate, rarely obovate, bases asymmetric or slightly so, subcordate, less frequently rounded or narrowly rounded, the apical ones (7.5–)9–16.5(–26) × (3.3–)3.7–7.5(–12) cm, symmetric, elliptic, narrowly elliptic or ovate, rarely obovate, bases symmetric, subcordate, less frequently rounded or narrowly rounded, apices acuminate to long acuminate, acumen 4–16 mm long, occasionally spinescent, abaxial surfaces sparsely tomentose to glabrescent, more densely on midvein, indumentum brown, adaxial surfaces glabrous, occasionally subglabrous on midvein, dull, margins flat; midveins abaxially prominent, adaxially flat or slightly prominent, secondary veins 8–10(–11) pairs, abaxially slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of 65–80° with midvein, arcuate, tertiary veins abaxially flat or slightly prominent, adaxially flat, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in double thyrsoids, axillary or pseudo-terminal, 1–4 per axil, trichomes simple unicellular, peduncles 0.3–4.5 cm long or inflorescences subsessile, tomentose, rachises 15.5–34 cm long, tomentose, lateral sub-thyrsoids 3.5–11 cm long, tomentose, indumentum of these structures brown or ferruginous; bracts 0.8–1.5 mm long, hirsute. *Flowers* sessile; buds 1.8–2 × 1.5–1.8 mm, orbicular; sepals 5, slightly basally connate, 1.8–2.5 × 0.8–1.2 mm, ovate or narrowly ovate, rarely triangulate, apices acute or obtuse, outer

surfaces tomentose, rarely sericeous, indumentum brown or ferruginous, inner surfaces glabrous or subglabrous, occasionally pubescent only at apex; petals $2.5\text{--}3.5 \times 0.8\text{--}1.3\text{--}(1.5)$ cm, erect, narrowly obovate or oblong, apices rounded or obtuse, glandular dots more than 10, loosely distributed, black, conspicuous, both surfaces glabrous, margins glabrous; stamens basally connate by 0.3–1 mm long, shorter series (0.8–)2 mm long, longer series (1.5–)2.5–3 mm long, filaments glabrous or with sparsely glandular trichomes, rarely abundant; ovaries 0.8–1 mm long, densely pubescent, styles 0.7–1 mm long, stigmas bilobate, lobes 0.2–0.8 mm long. *Fruits* $1.7\text{--}2.2 \times 1.1\text{--}1.7$ cm, obovate or semi-orbicular, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes (3–)4–10 mm long, styles partially persistent, inconspicuous, ca. 0.5 mm long, outer surfaces densely tomentose to glabrescent, indumentum brown or ferruginous, black dots sparse to abundant, inner surfaces tomentose or sparsely so, glandular trichomes absent, calyces persistent or partially so, sepals ascending erect or patent; seeds $1.3\text{--}1.6 \times 0.7\text{--}0.9$ cm, arils yellowish.

Selected specimens examined: **Colombia.** Chocó: Riosucio, Parque Natural Nal. Los Katyos, Cacaricas camino a Cristales, 70–120 m, 1 Dec 1976, fl., *H. León 634* (MO). Cordoba: Montelibano, corregimiento Ure, Cerromatoso, áreas aledañas a la explotación de Ferroniquel, 30–60 msnm, $7^{\circ}54'N$, $75^{\circ}33'W$, 24–25 Oct 1990, fl., *F. J. Roldám et al. 1448* (NY). **Costa Rica.** Puntarenas: Golfito, Playa Cacao, Punta Voladera, $08^{\circ}37'35''N$, $83^{\circ}11'00''W$, 100 m, 6 Jun 1994, fl., *G. Herrera & G. Rivera 7136* (K); Osa Peninsula. Aguabuena, 3 km W of Rincón, at trail leading to one-hectare permanent sample plot 700 m N of the house of Henry Monge, $8^{\circ}42'N$, $83^{\circ}30'W$, 100 m, 15 Apr 1993, fr., *K. Thomsen 339* (K); Aguabuena, 3 km W of Rincón, at trail leading to one-hectare permanent sample plot 700 m N of the house of Henry Monge, $8^{\circ}42'N$, $83^{\circ}30'W$, 100 m, 15 Apr 1993, fr., *K. Thomsen 339* (K). **Panamá.** Canal Zone: Barro Colorado Island. B. C. I. WMW 4R, 31 Dec 1931, fr., *Shattuck s. n.* (US); Colorado Point, 30 Nov 1981, fl., *R. J. Schmalzel 173* (MEXU); Large cove S. E. of Gross Point, 11 Apr 1970, fl., *T. B. Croat 9565* (MO); N. side of shoreline of Fuertes Cove, 1 Apr 1968, fl., fr., *T. B. Croat 5266* (MO); Shore of Gigante Bay, peninsula between Drayton and Bangs House, 6 Jun 1969, fr., *R. Foster 930* (F); Shoreline north of dock vine, 10 Jan 1969, fr., *T. B. Croat 7122* (F, MO, NY). Pipeline Rd., 11 Apr 1972, fr., *A. Gentry 5063* (F, MO); Rio Agua Salud, near Frijoles, 6 Mar 1923, fl., *C. V. Piper 5862* (US); *S. loc.*, Apr 1969, fr., *W. H. Lewis et al. s. n.* (P). Coclé: Between Paso del Arado and Olá, in savannas and thickets, alt. 20 to 280 meters, 7–9 Dec 1911, fl., *H. Pittier 5010* (P). Darién: Gallery Forest near Chepigana, 10 m, 14 Feb 1967, fr., *J. A. Ducke 10021(3)* (MO); Periaque Hill near Rio Sabanas & Lara, 16

Jul 1966, fl., *E. Tyson et al.* 4723 (GH); Rio Cucunati at Puente Quemado, 30 Nov 1966, fr., *J. A. Ducke* 8818 (US). Panama: Along R. Tecumen, north of Chepo road, up to 30 m, 27 Jan 1935, fl., *A. A. Hunter & P. H. Allen* 230 (P). San Jose Island: Pearl Archipelago, east road, between 8°15'–8°16'N, 79°07'–79°08'W, 5 Nov 1945, fl., fr., *J. Harlow* 32 (US); Perlas archipelago, Gulf of Panama, about 55 miles SSE of Balboa. Oct 1944, fr., *I. M. Johnston* 57 (P); 24 Jan 1946, fr., *I. M. Johnston* 1244 (GH); 24 Jan 1946, fl., *I. M. Johnston* 1244 (GH). Veraguas: Uva Island, of the Contreras Islands, 25 Aug 1970, fl., *R. Foster* 1571 (F). **Venezuela.** Zulia: 6 km west of main road and 2 km south of Río Catatumbo, ca 20 to 100 m alt., 9°6'N, 72°42'W, 27 Mar 1982, fr., *R. Liesner & A. González* 13242 (NY).

Distribution, habitat and phenology: *Connarus panamensis* occurs from northwest Venezuela and north Colombia to Guatemala, although it is more commonly distributed in Panama, and reported by only few collections in the other countries (Fig. 23). This species is mainly represented by lianas or scandent shrubs, frequently found in coastal vegetations, mangroves and ciliary forests, at low elevations (ca. 20–200 m). Specimens have been collected with flowers irregularly almost throughout the year and with fruits specially from November to April.

Notes: *Connarus panamensis* is morphologically recognized by the combination of the following characters: asymmetric or slightly asymmetric basal leaflets, large inflorescences in double thyrsoids, with tomentose peduncles and rachises, sessile flowers and externally tomentose fruits. In herbarium specimens, *C. panamensis* is confused with another Panamanian species, *C. turczaninowii*, but differs in the arcuate secondary veins (vs. linear), percurrent intercostal tertiary veins (vs. reticulate), inflorescence rachises tomentose (vs. sericeous or pubescent), sessile flowers (vs. pedicellate) and externally tomentose fruits (vs. sparsely sericeous). In addition, basal leaflets are asymmetric or slightly so in *C. panamensis*, with bases usually subcordate, while in *C. turczaninowii* they are symmetric, with bases usually obtuse or rounded.

Grisebach (1858) described *C. panamensis* and indicated only collector name, with no mention of herbarium, so Schellenberg (1938) inadvertently selected the lectotype from GOET. It must be emphasized that there are apparently only two specimens with an original label of *Duchassaing*, one in GOET and another in P, so these are considered lectotype and islectotype, respectively; other specimens previously cited from GH, GOET and NY do not have an original label and, thus, are here considered as probable islectotypes.

Connarus patrisii (DC.) Planch., Linnaea 23: 432. 1850. *Omphalobium patrisii* DC., Prodr. 2: 86. 1825.—TYPE: French Guiana. Cayenne [Cayenna], s. d., fr., *M. Patris* s. n. (lectotype first step designated by Forero 1983: G; lectotype second step **designated here**: G barcode G00476355!; isoelectotype: G!).

Omphalobium magicum Mart. ex Baker, in Martius, Fl. Bras. 14(2): 189. 1871, *pro syn.*

Connarus confertiflorus Baker, in Martius, Fl. Bras. 14(2): 193. 1871.—TYPE: French Guiana. Borda de la mana, 1854, fl., *P. A. Sagot* 238 (holotype: K barcode K000066180!).

Lianas; branchlets slightly striate, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels inconspicuous. *Leaves* (5–)7–9-foliolate; petioles 3–11.5(–13) cm long, sparsely tomentose to glabrescent; rachises 5.5–11.8(–14) cm long, sparsely tomentose to glabrescent; pulvinuli 4–7 mm long, tomentose to glabrescent; leaflets coriaceous, concolorous or slightly discolorous, flat, basal pairs 4–11.2 × 2.7–5 cm, symmetric, ovate, oblong, elliptic or narrowly elliptic, bases symmetric or slightly asymmetric, rounded or subcordate, the apical ones 6.8–13.5(–18) × 3.2–5.5(–7.3) cm, symmetric, oblong, narrowly ovate or narrowly elliptic, rarely narrowly obovate, bases symmetric or slightly asymmetric, rounded or subcordate, rarely obtuse, apices short acuminate to acuminate, acumen 2–10 mm long, abaxial surfaces glabrous or subglabrous, occasionally sparsely tomentose on midvein, indumentum ferruginous, adaxial surfaces glabrous, shining, rarely dull, margins slightly revolute, less frequently flat; midveins abaxially prominent, adaxially impressed, secondary veins 5–9(–10) pairs, abaxially prominent or slightly so, adaxially flat or slightly impressed, concolorous in relation to the blade, forming angles of 45–65° with midvein, arcuate, the basal pairs usually ascending, tertiary veins flat on both surfaces, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in double thyrsoids, occasionally pleiothyrsoids, axillary, 1–3 per axil, trichomes dendroid and simple unicellular, peduncles 1–4.5 cm long or inflorescences subsessile, tomentose, rachises 8–35 cm long, tomentose, lateral sub-thyrsoids 2–12 cm long, tomentose, indumentum of these structures ferruginous; bracts 0.8–1 mm long, tomentose. *Flowers* sessile or pedicels 0.3–1 mm long; buds ca. 2 × 2 mm, orbicular; sepals 4–5, 1–2 pairs with 2 sepals each connate entirely or half their length, 2–2.5 × 1.4–1.5 mm, ovate, apices obtuse or acute, 1–3 sepals connate to the others at base or half their

length, $2\text{--}2.5 \times 1$ mm, narrowly ovate or elliptic, apices acute, outer surfaces tomentose, indumentum ferruginous, inner surfaces glabrous; petals $2\text{--}3 \times 1\text{--}1.5$ mm, reflexed, oblong or narrowly obovate, apices rounded or obtuse, rarely acute, glandular dots 5 or more than 10, occasionally absent, loosely distributed, black, conspicuous or inconspicuous, outer surfaces tomentose to glabrescent, inner surfaces glabrous or subglabrous, glandular trichomes absent or sparse, margins sparsely ciliate, glandular trichomes absent; stamens basally connate by $0.5\text{--}1.5$ mm, shorter series $1\text{--}3$ mm long, longer series $1.5\text{--}4$ mm long, filaments with sparse glandular trichomes; ovaries ca. 1 mm long, tomentose, styles $1\text{--}1.7$ mm long, stigmas bilobate, lobes $0.7\text{--}0.8$ mm long. *Fruits* $1.4\text{--}2.1 \times 1.1\text{--}1.5$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes $1\text{--}3$ mm long, styles partially persistent, inconspicuous or apiculate, $0.2\text{--}0.5$ mm long, outer surfaces tomentose to glabrescent, indumentum ferruginous, black dots absent, inner surfaces subglabrous, glandular trichomes sparse or abundant, calyces deciduous, less frequently partially persistent, sepals reflexed; seeds $1\text{--}1.2 \times 0.7\text{--}0.8$ cm, arils color not seen.

Selected specimens examined: **Brazil.** Amapá: Serra do Navio, Rio Amapari, 70–300 m alt., 16 Nov 1964, fl., *R. S. Cowan 38347* (NY). Amazonas: Between Camp Tatu and Camp III, 200–400 m, 22 Dec 1965, fr., *N. T. Silva & U. Brazão 60716* (NY); Jataí, margem direita do Rio Solimões, localidade Copessu, logo abaixo da cidade de Jataí a 5 km da margem, $02^{\circ}43'S$, $66^{\circ}42'W$, 23 Oct 1987, fl., *C. A. C. Ferreira et al. 8264* (INPA); Rio Negro, Rio Jauaperi, Estirão Tacuera, 10 Feb 1977, fr., *M. R. Santos 79* (MG); Rio Negro, Rio Cauaburi, Rio Maturacá, 200–400 m alt., 22 Dec 1965, fr., *N. T. Silva & U. Brazão 60716* (MG, NY). Pará: Ilha de Marajó, Rio Anajás, $01^{\circ}00'S$, $50^{\circ}10'W$, 29 Oct 1987, fr., *H. T. Beck & R. Souza 234* (INPA, MG, NY); Juruti, Estrada do Barroso em sentido da Comunidade São Francisco, $02^{\circ}28'43''S$, $55^{\circ}59'57''W$, 15 Jun 2007, fr., *M. B. Ramos et al. 216* (INPA). Roraima: Posto Mucajaí, Rio Mucajaí, 19 Mar 1971, fr., *G. T. Prance et al. 11118* (INPA, NY). **Colombia.** Caqueta: Sierra de Chiribiquete, Campamento Norte, recorrido por el cauce casi seco de um arroyo al NE del campamento, $1^{\circ}7'N$, $72^{\circ}50'W$, 500–350 m., 12 Dec 1991, fl., *S. Castroviejo et al. 12040* (COL). **Ecuador.** Napo: Añangu, NW corner of the “Parque Nacional Yasuní”, $76^{\circ}22'W$, $0^{\circ}33'S$, 355–365 m, 1–15 Feb 1986, st., *J. Korning & K. Thomsen 47675* (G). **French Guiana.** Crique Plomb, bassin du Sinnamary, $53^{\circ}1'W$, $5^{\circ}1'N$, 16 Jul 1992, fl., *D. Loubry 1697* (CAY, NY, P); *S. loc.*, 1792, fl., *M. Leblond 57* (G); *S. loc.*, s. d., fl., *M. Mélinon 1845* (P); *S. loc.*, s. d., fl., *M. Mélinon s. n.* (P05615221); *S. loc.*, 1820, fr., *G. S. Perrottet s. n.* (G 00476346). **Guyana.** Malali, Demerara River, about $5^{\circ}35'N$, 30 Oct–5 Nov 1922, fl., *J. S. de la Cruz 2736*

(F); Tapakuma [Tapacooma] Creek, Jun 1893, fl., *Jenman 6609* (K); Tapakuma [Tapacooma] Creek, Jun 1893, fl., *Jenman 6606A* (K); U. Takutu-U, Essequibo, Kamoia Mts., 2 Km S of Kamoia River, 1°31'04"N, 58°48'54"W, 450 m, 12 Nov 1996, fr., *D. Clarke 3119* (P, US); *S. loc.*, *s. d.*, fr., *L. C. Richard s. n.* (P). **Peru.** Loreto: Maynas, rio Yuvinetto affluent du Putumayo, territoire des indiens Secoya, 21 Dec 1977, fl., *S. Barrier 105* (P). **Suriname.** Nickerie, area of Kabalebo Dam project, rain forest 1.5 km S of road camp, ca. 20 km SW of Avanavero dam site, 14 Nov 1976, fr., *N. M. Heyde & J. C. Lindeman 83* (NY); Tafelberg (Table Mountain), 8 Sep 1944, fl., *B. Maguire 24663* (COL, MG, NY); Wilhelmina Cebergte, lower slopes of Frederik Top, 3 km south of Juliana Top, 3°36'–3°41'N, 56°34'W, alt. 500 m, 21 Aug 1963, fl., *H. S. Irwin et al. 54932* (NY).

Distribution, habitat and phenology: *Connarus patrisii* mainly occurs in north Brazil, French Guiana, Guyana and Suriname, with only few collections from south Colombia, northwest Ecuador and north Peru (Fig. 21). It is a lianescent species growing in upland forests, with sandy or clay soils, at 160–450 m elevation. Specimens have been collected with flowers from June to August and from October to December, and with fruits mainly from November to March.

Notes: *Connarus patrisii* is recognized by possessing dendroid trichomes, coriaceous leaflets, inflorescences in large double thyrsoids, and calyx with 1–2 pairs of sepals connate entirely or half their length. It can be confused with other lianescent species with dendroid trichomes, such as *C. guggenheimii* and *C. manausensis*, but differs by the number and texture of leaflets, and connation of sepals (Table 2). In previous studies (Toledo & Souza 2018; Toledo et al. 2020a), *C. patrisii* was described as bearing a discoid stigma, which was inaccurate as stigmas in this species are bilobate.

The basionym of *C. patrisii* was originally described by De Candolle (1825a), who indicated only the specimen *Patris s. n.* and cited an illustration. Schellenberg (1938) inadvertently designated a lectotype from P, which was not found in the herbarium during the present revision. Forero (1983), on the other hand, chose a specimen from G, which was an appropriate decision considering that the specimens collected by Patris were sent as unicates to De Candolle herbarium and, although their sheet labels do not have Patris name written on them, they can be identified because the labels are solely indicated as coming from Cayenne (De Candolle 1880). Even though De Candolle (1880) had stated that Patris' collections were represented by unicates, two specimens of *C. patrisii* that fit in the condition described above were found in G. One of them (barcode G00305719) was indicated as holotype by Forero (1983)

and it is accompanied by an attached label of this author. This specimen, however, was given from DC herbarium to Moricand as gift, who in 1908 donated it to G. The other specimen (barcode G00476355) is an original DC collection. Both specimens are here considered as duplicates and it seems that the one donated by Moricand correspond to a fragment of the main collection. Therefore, a second step lectotypification is here proposed and the specimen that always belonged to DC collection was chosen to serve as so. Finally, the illustration of *Omphalobium patrisii* indicated in the protologue was published separately (De Candolle 1825b), but it is not considered an original element as De Candolle (1825a) did not clearly indicate which illustration he was referring to.

Connarus pedicellatus (Forero) C. Toledo, Willdenowia 51: 173. 2021. *Connarus erianthus* Benth. ex Baker var. *pedicellatus* Forero, Brittonia 32(1): 40. 1980.—TYPE: Brazil. Pará: Estrada entre Planalto A e Tinguelim, km 14, 10 Jul 1969, fl., N. T. Silva 2387 (holotype: IAN 134211!).

Connarus erianthus Benth. ex Baker var. *stipitatus* Forero, Brittonia 32(1): 40. 1980.—TYPE: Brazil. Pará: Santarém, km 70 da estrada do Palhão, ramal do Caetetú, 11 Sep 1969, fr., M. Silva & R. Souza 2551 (holotype: MG barcode MG037357!; isotypes: COL [photo!], NY [photo!]).

Shrubs, treelets or trees, 2–14(–18) m tall; branchlets slightly striate or fissured, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels absent or inconspicuous. *Leaves* 7–11-foliolate; petioles 2.5–9 cm long, glabrous; rachises 6.5–17.2(–28) cm long, glabrous; pulvinuli 3–7 mm long, glabrous or subglabrous; leaflets chartaceous, concolorous or slightly discolorous, flat, basal pairs 3.8–10.3 × 2–4.5 cm, symmetric to asymmetric, ovate or elliptic, less frequently narrowly ovate, bases asymmetric or slightly so, rounded or obtuse, the apical ones 5–16.4 × 2.5–5.7 cm, symmetric to asymmetric, ovate, narrowly ovate, elliptic or narrowly elliptic, the distal usually elliptic, bases asymmetric or slightly so, rounded, obtuse or acute, apices long acuminate to cuspidate, acumen 5–23 mm long, both surfaces glabrous or subglabrous, adaxial surfaces dull, margins flat; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 5–7 pairs, abaxially slightly prominent, adaxially flat, rarely slightly impressed, concolorous in relation to the blade, forming angles of 45–65° with midvein, arcuate or slightly so, tertiary veins abaxially flat or

slightly prominent, adaxially flat, rarely slightly prominent, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids, axillary, rarely ramiflorous, 1–6 per axil, trichomes dendroid and simple unicellular, peduncles 0.2–1 cm long or inflorescences subsessile, tomentose, rachises 4.5–15 cm long, tomentose, lateral cymes ca. 0.3 mm long, tomentose, indumentum of these structures brown or ferruginous; bracts 1–2 mm long, tomentose. *Flowers* subsessile or pedicels 0.5–2 mm long; buds $1.5\text{--}2 \times 1\text{--}1.8$ mm, orbicular or elliptic; sepals 4–5, 1–2 pairs with 2 sepals each connate half their length, $2\text{--}2.2 \times 2.2$ mm, ovate or orbicular, apices obtuse, 1–3 sepals connate to the others at base, $2\text{--}3 \times 1$ mm, narrowly ovate, apices acute, outer surfaces tomentose, indumentum brown or ferruginous, inner surfaces glabrous, occasionally pubescent at apex; petals $3\text{--}4 \times 1\text{--}1.5$ mm, reflexed, narrowly obovate or oblong, apices acute or obtuse, glandular dots absent or 1–5, loosely distributed, black, inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent or sparse, margins glabrous; stamens basally connate by ca. 0.5 mm long, shorter series ca. 2 mm long, longer series 3–3.5 mm long, filaments glabrous or with sparse glandular trichomes; ovaries ca. 2.5 mm long, densely pubescent, styles ca. 0.5 mm long, stigmas discoid, surfaces multilobate, lobes ca. 0.1 mm long. *Fruits* $1.7\text{--}2.2 \times 1.2\text{--}1.4$ cm, obovate, indehiscent slightly sigmoid or almost linear, pericarps up to 2 mm thick, stipes 2–4 mm long, styles partially persistent, apiculate, 0.3–1 mm long, outer surfaces lanate to glabrescent, indumentum ferruginous, black dots abundant, inner surfaces tomentose or densely so, glandular trichomes absent, calyces persistent or partially persistent, sepals reflexed, patent or ascending erect; seeds $1.2\text{--}1.4 \times 0.6\text{--}0.7$ cm, arils yellowish.

Selected specimens examined: **Brazil.** Acre: Cruzeiro do Sul, Rio Juruá & Rio Moa, Igarapé São Francisco, 9 May 1971, fl., *P. J. M. Maas et al.* PI2837 (INPA, NY); Estrada Rio Branco/Porto Acre, km 33, 11 Oct 1980, *B. Nelson* 691 (NY, UB); Mâncio Lima, Parque Nacional Serra do Divisor, Serra do Moa, Hunting trail leading from Boca da Serra to Igarapé Anil (=Ig. República), $07^{\circ}21'30''\text{S}$, $73^{\circ}27'37''\text{W}$, 9 May 1996, fl., *D. C. Daly et al.* 8975 (NY); Manoel Urbano, Lago Novo, Rio Purus, colocação Lago Novo, próximo ao roçado, 19 Nov 1996, fr., *M. Silveira et al.* 1412 (INPA); Tarauacá, $07^{\circ}55'50''\text{S}$, $71^{\circ}32'15''\text{W}$, 20 Jun 2006, fr., *M. Silveira et al.* 3863 (RB). Amapá: Coastal region, Igarapé Ariramba, $1^{\circ}13'\text{N}$ – $51^{\circ}3'\text{W}$, 3 Aug 1962, fr., *J. M. Pires & P. B. Cavalcante* 52320 (IAN, K, MG, NY); Mazagão, margem esquerda do rio Jarí, morro do Felipe VI, 18 Aug 1985, fl., *J. M. P. Pires et al.* 553 (INPA, K); Rio Araguari, along road between Porto Platon and Macapá, 18 Sep 1961, fr., *M. J. Pires et al.* 51100 (NY). Amazonas: Boca do Acre. Entrada do Igarapé São Francisco, $08^{\circ}29'22''\text{S}$,

67°38'36"W, 5 Jul 2009, fr., *M. G. Bovini et al.* 2909 (MBM, RB, VIC); Boca do Acre, Rio Santo Antônio, Floresta Nacional do Mapiá, Inauini, 8°07'549"S, 68°08'108"W, 12 Dec 2009, fr., *A. Quinet et al.* 1974 (RB). Manaus, estrada Manaus-Itacoatiara, km 60, 21 Oct 1961, fr., *W. Rodrigues & D. Coêlho* 3522 (NY); Manaus-Itacoatiara Road, km 69–70, 5 Sep 1973, fr., *G. T. Prance et al.* 17542 (INPA, K, MG, NY); Manicoré, near Santa Fé, basin of Rio Madeira, 8–11 Sep 1934, fr., *B. A. Krukoff* 6042 (K, NY). Mato Grosso: Picadão que dá acesso ao Rio Juruena à pista do garimpo do mesmo nome, 12 Jun 1977, fl., *N. A. Rosa & M. S. Santos* 2110 (RB). Pará: Almeirim. Gleba Monte Dourado da Reserva Genética, 0°52'S, 52°32'W, 10 Jul 1987, fl., *J. M. Pires* 1724 (K); Monte Dourado, gleba Monte Dourado da Reserva Genética do Jari, 0°51'S, 52°33'W, 8 Oct 1987, fr., *J. M. Pires* 1791 (INPA, NY, W). Gurupi, 50–65 km north of Gurupi, Belém-Brasília, 12 Aug 1964, fr., *G. T. Prance & N. T. Silva* 58680 (NY, P, UB); Jarí, estrada de Munguba, km 10, 10 Jul 1969, fl., *N. T. Silva* 2387 (MG, NY); Oriximiná, Rio Trombetas, a jusante de Cach, porteira, margem do Lago Abui, 01°16'S, 57°00'W, 22 Aug 1986, fr., *C. C. C. Ferreira et al.* 7987 (MG); Paragominas. Área do Projeto Sustentabilidade dos Usos da Terra na Amazônia, B: 549, T: 4, 22 Apr 2011, fl., *E. A. P. Nascimento* 147 (IAN, RB); Belém-Brasília Highway, km. 161, 28 Oct 1964, fr., *G. T. Prance & N. T. Silva* 58925 (K, NY). Rio Jarí, estrada que liga Monte Dourado a Caracurú, 6 Dec 1967, fr., *E. de Oliveira* 3759 (IAN, NY); Serra dos Carajás, AMZA camp. 3-Alfa, 05°48'S, 50°33'W, 525m, 7 Jun 1982, fl., *C. R. Sperlinng et al.* 5936 (NY). **Peru.** Loreto: Varadera de Mazan, 26 Sep 1972, fr., *B. Croat* 20754 (MO). **Suriname.** S. base of Vier-Gebroeders-Mts, alt. 325 m, 23 Oct 1968, fr., *F. H. F. Oldenburger et al.* 331 (K, NY, U, US).

Distribution, habitat and phenology: *Connarus pedicellatus* is a common species in the Brazilian Amazon, occurring in the states of Acre, Amapá, Amazonas and Pará, with one collection known from Mato Grosso (Brazil), Peru and south Suriname (Fig. 18). It is represented by shrubs or trees normally up to 14 m tall, mainly from ombrophilous forests, including upland forests or flooded areas (igarapé or igapó), at ca. 50–500 m elevation. Specimens have been collected with flowers from April to August and with fruits from June to December.

Notes: Among the species with dendroid trichomes, *C. pedicellatus* is recognized by being shrubs or trees with leaflet bases asymmetric, inflorescences in thyrsoids and fruits externally lanate to glabrescent, with stipes 2–4 mm long. It was previously treated as a variety of *C. erianthus* (Forero 1980a, 1983), but it is here considered a separate species, mainly based

on the characteristics of leaflet texture, shape and margin, inflorescence architecture and indumentum, and pedicel and fruit stipe length (see “Notes” section under *C. erianthus*).

Two of the three varieties proposed by Forero (1980a) under *C. erianthus* are here considered a separate species. *Connarus erianthus* var. *pedicellatus* and *C. erianthus* var. *stipitatus* were published in the same work (Forero 1980a), separated based on pedicel and fruit stipe length (Forero 1983). However, the former was described based only on flowering specimens, while the latter, only on fruiting specimens. When fruiting specimens are analyzed, it is possible to note that inflorescences are thyrsoids and the flowers are pedicellate with variable length, so Forero’s concept of *C. erianthus* var. *stipitatus* also includes specimens with pedicellate flowers. In addition, both varieties are identical in leaflet size and shape and, most importantly, they have inflorescences in thyrsoids. These characters, together with the fruit stipes 2–4 mm long, seem to be consistent enough to recognizing a taxon at species level.

The basionym *C. erianthus* var. *pedicellatus*, to serve *C. pedicellatus*, was chosen over *C. erianthus* var. *stipitatus* because the presence of pedicellate flowers can be seen in both flowering and fruiting specimens (the main diagnostic feature to distinguish from *C. erianthus*), so the epithet referring to the pedicellate flowers seems more appropriate to designate the species. Therefore, *C. erianthus* var. *stipitatus* is considered a synonym of *C. pedicellatus*.

Connarus perrottetii (DC.) Planch., *Linnaea* 23: 432. 1850. *Omphalobium perrottetii* DC., *Prodr.* 2: 86. 1825.—TYPE: French Guiana. *S. loc.*, 1820, fr., *G. S. Perrottet s. n.* (lectotype designated by Schellenberg 1938: P barcode P01819558!; isolectotype: G!).

Lianas or scandent shrubs, ca. 1.5 m tall; branchlets slightly striate, tomentose to glabrescent or tomentose, trichomes dendroid and simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 7–11(–13)-foliolate, occasionally 5 in young branchlets; petioles 2.7–9 cm long, tomentose to glabrescent or tomentose; rachises 3.5–17 cm long, tomentose to glabrescent or tomentose; pulvinuli 4–6 mm long, tomentose; leaflets chartaceous to coriaceous, discolorous, flat, basal pairs 4–13 × 2.2–4.3 cm, symmetric, elliptic, narrowly elliptic, obovate or narrowly obovate, rarely ovate, bases symmetric, rounded or subcordate, rarely acute or obtuse, the apical ones 5–17 × 2.2–6.3 cm, symmetric, elliptic, narrowly elliptic, obovate or narrowly obovate, bases symmetric, rounded or subcordate, rarely acute or obtuse,

apices short acuminate to long acuminate, acumen 2–13(–17) mm long, abaxial surfaces tomentose, indumentum ferruginous, light brown, flavous or rufous, adaxial surfaces glabrous, dull, rarely shining, margins flat, less frequently slightly revolute; midveins abaxially prominent, adaxially impressed, secondary veins 8–12 pairs, abaxially prominent or slightly so, adaxially flat or slightly impressed, concolorous in relation to the blade, forming angles of 50–80° with midvein, linear or slightly arcuate, tertiary veins abaxially prominent or slightly so, adaxially flat, rarely slightly prominent, intercostals opposite or mixed percurrent or reticulate, epidermals opposite percurrent, the intersecondary occasionally reticulate. *Inflorescences* in double thyrsoids, axillary or pseudo-terminal, 1–2 per axil, trichomes dendroid and simple unicellular, peduncles 0.2–3 cm long, tomentose, rachises 6–18 cm long, tomentose, lateral subthyrsoids 2–9 cm long, tomentose, indumentum of these structures ferruginous; bracts 0.8–2 mm long, tomentose. *Flowers* with pedicels 0.5–1.5 mm long, rarely subsessile; buds ca. 1.8–2 × 1.6–2 mm, orbicular; sepals 5, slightly basally connate, 2–2.5 × 0.7–1 mm, ovate, elliptic, triangulate or narrowly triangulate, apices acute, outer surfaces tomentose, indumentum ferruginous, inner surfaces glabrous or subglabrous, usually tomentose only at apex; petals 2.8–3 × 0.8–1 mm, erect, oblong or narrowly elliptic, apices acute or obtuse, glandular dots 5 or more than 10, loosely distributed, black, rarely colorless, conspicuous or inconspicuous, outer surfaces pubescent or densely so, inner surfaces glabrous or subglabrous, glandular trichomes absent, margins densely ciliate, glandular trichomes absent; stamens basally connate by 0.5–1.2 mm, shorter series 1.2–2.5 mm long, longer series 1.5–3.5 mm long, filaments with sparse to abundant glandular trichomes, rarely glabrous; ovaries ca. 1 mm long, tomentose, styles 1.3–1.8 mm long, stigmas bilobate, lobes 0.2–1 mm long. *Fruits* 1.7–2.3 × 1.2–1.7 cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 1–5 mm long or fruits sessile or subsessile, styles partially persistent or absent, inconspicuous, ca. 0.2 mm long, outer surfaces tomentose to glabrescent, indumentum ferruginous, black dots absent or abundant, inner surfaces pubescent or with only sparse to abundant glandular trichomes, rarely subglabrous, calyces persistent or partially persistent, sepals ascending erect or patent; seeds 1.2–1.6 × 0.6–0.8 cm, arils color not seen.

Notes: Among the species with dendroid trichomes, *C. perrottetii* is distinguished by being lianas or scandent shrubs with 7–11(–13)-foliolate leaves, abaxially tomentose leaflets, slightly basally connate sepals, externally pubescent petals and externally tomentose fruits.

Connarus perrottetii was treated by Forero (1983) including three varieties. One of them (*C. perrottetii* var. *angustifolius*) is here considered a distinct species, mainly due to its habit, sepal connation, petal indumentum, fruit stipe and orientation of sepals on fruits (see “Notes” under *C. angustifolius*). Therefore, *C. perrottetii* is here treated under two varieties: *C. perrottetii* var. *perrottetii* and *C. perrottetii* var. *rufus*. These are recognized under the same species because they share peculiar characteristics, such as abaxially tomentose leaflets, slightly basally connate sepals, externally pubescent petals and externally tomentose fruits with apex usually rounded. They differ mainly in color of indumentum (leaflets abaxially), orientation of secondary veins, architecture of tertiary veins and fruit stipe length.

De Candolle (1825a) described the basionym of *C. perrottetii* citing only collector name, with no mention of herbarium. Schellenberg (1938) cited the specimen *Perrottet s. n.* from P as type, and Forero (1983) considered it the holotype because no other collection was identified. In the present study, the specimen from P is considered lectotype following Schellenberg (1938) designation, and a specimen from G is treated as isoelectotype. The specimen from P was accurately chosen as it bears a label with De Candolle’s handwriting naming the specimen as “*Perrottetia*”, indicating his first intention of describing a new genus that he thought it belonged to Fabaceae, a confusion he admitted after the description of his new Connaraceae (De Candolle 1825b). This specimen clearly indicates the collector Perrottet, which is not seen in the specimen from G. However, as both specimens seem to belong to the same collection (based on morphology) and De Candolle (1880) stated that most specimens from Perrottet were sent to G, then this is here considered an isoelectotype.

Key to the varieties of *C. perrottetii*

- 1a. Leaflets abaxially with indumentum flavous or light brown; secondary veins (8–)10–12 pairs, forming angles of 50–65(–70)° with midvein, intercostal tertiary veins percurrent; fruits sessile, subsessile or stipes 1–2(–4) mm long, inner surfaces pubescent formed by stellate trichomes *C. perrottetii* var. *perrottetii*
- 1b. Leaflets abaxially with indumentum ferruginous or rufous; secondary veins 8–10 pairs, forming angles of 65–80° with midvein, intercostal tertiary veins reticulate; fruits with stipes 2–5 mm long, inner surfaces glabrous or with only glandular trichomes *C. perrottetii* var. *rufus*

Connarus perrottetii (DC.) Planch. var. *perrottetii*. Fig. 27

Connarus floribundus Planch., Linnaea 23: 435. 1850.—TYPE: Suriname. *S. loc.*, *s. d.*, fl., *W. R. Hostmann 1052* (holotype: K barcode K000633777!; isotypes: BM!, F [photo!], G!, K!, MO [photo!], P!, U [photo!], W [photo!]), *nom. illeg.*, *non. C. floribundus* Thonn. ex Schum. (1827).

Branchlets tomentose to glabrescent. *Leaves* 7–9-foliate; leaflets abaxially with indumentum flavous or light brown; secondary veins (8–)10–12 pairs, forming angles of 50–65(–70)° with midvein, intercostal tertiary veins percurrent. *Fruits* sessile, subsessile or stipes 1–2(–4) mm long, inner surfaces pubescent formed by stellate trichomes.

Selected specimens examined: **Brazil.** Amapá: At margin of river, confluence of Rio Iuae with Rio Oiapoque, 02°53'N, 52°22'W, 140 m alt., 24 Aug 1960, fr., *H. S. Irwin et al. 47791* (IAN, MG, NY, UB, W); Calçoene, Parque Nacional do Cabo Orange, Vila de Cunani, Programa de Monitoramento da Biodiversidade, acampamento cachoeira, Rio Cunani, margem do rio, 2°50'12"N, 51°12'9"W, 12 Nov 2017, fr., *H. Medeiros et al. 2866* (RB); Contagem entre Porto Platon e Serra do Navio, 10 Oct 1976, st., *Rosa 1356* (MG); Rio Araguaí, 4 Oct 1961, fr., *Pires et al. 51504* (IAN, MG, NY, P); Rio Oiapoque, margin of river, about 3km northeast of mouth of Riv. Eureupucigne, 14 Sep 1960, fr., *H. S. Irwin et al. 48250* (NY, RB); Serra do Navio, Rio Amapari, 24 Nov 1954, fr., *R. S. Cowan 38570* (IAN, NY, RB). Amazonas: Itapiranga. Rio Pitinga, margem direita, 24 Aug 1979, fr., *C. A. C. Ferreira 687* (INPA, MG); Rio Uatumã, próximo à cachoeira do Tucumari, 19 Aug 1979, fr., *C. A. C. Ferreira et al. 502* (INPA). Presidente Figueiredo. Reserva de Balbina, along Rio Pitinga, 2–4 km N of confluence with Rio Uatumã, 8 Jul 1986, fl., *W. W. Thomas 5398* (INPA); Rio Pitinga, a 2 horas acima da confluência com Rio Uatumã (a montante da UHE de Balbina), 01°02'S, 59°60'W, 21 Mar 1986, fl., *C. A. C. Ferreira et al. 6918* (INPA, NY). Rio Uatumã, lado direito do rio, 3° Acampamento, 23 Feb 1978, fr., *P. Ivo 3463* (INPA). Pará: BR 163, km 1414, beside Rio Itapacurá, 25 Nov 1977, fr., *G. T. Prance et al. P25769* (NY, RB, UEC); Faro, beira do Rio Jamundá, acima de São Jorge, 12 Nov 1950, fr., *G. A. Black 50-10741* (IAN, INPA, NY); Itaituba, Rodovia Transamazônica Itaituba-Jacareacanga, coletada na beira da estrada, 4°53'41.1"S, 56°51'38.1"W, 25 Jan 2020, fl., *C. A. P. Toledo et al. 424* (ESA, RB); Lago

Salgado, Rio Trombetas, 24 Oct 1919, fl., *A. Ducke s. n.* (IAN, RB); Oriximiná, alto Rio Erepecuru, próximo ao campo de pouco do acampamento da Cachoeira Paciência, 00°20'N, 56°00'W, 20 Nov 1987, fr., *C. A. C. Ferreira 9646* (INPA, NY, RB, UFACPZ); Oriximiná, margem direita do Rio Mapuera, próx. à Cach. São Marçal, 01°S, 57°30'W, 14 Aug 1986, fl., *C. A. C. Ferreira et al. 7755* (INPA, MG); Rio Erepecurú, Serra de Tumucumaque via Rio Cuminá, 30 Sep 1928, fr., *A. J. Sampaio 5134* (R); Rio Jamundá, abaixo da boca da Parnatinga, 15 May 1911, fl., fr., *A. Ducke 11718* (RB); Serra Norte, 19 Jul 1973, fr., *Pires & Passos 13182* (IAN). **French Guiana.** Bas-Camopi, 21 May 1965, fl., *Oldeman 1306* (CAY, K, MO, P); Camp n° 1 Ouman fou Langa Soula, Bassin du Haut-Marouini 1 Km em aval, 2°53'N, 54°0'W, 24 Aug 1987, fr., *J. J. de Granville et al. 9630* (P); Cyequé Baboune, amount de la orique Forte Affluent de la Riv. Mana, 29 Jul 1971, fr., *G. Cremers 7349* (P); Guiques Ouquai, 7–13 Sep 1981, fr., Lemoine 7817 (P). **Guyana.** Basin of Essequibo River, near mouth of Onoro Creek, about 1°35'N, 15–24 Dec 1937, fr., *A. C. Smith 2817* (F, G, MO, NY, P, U, US); Kamakusa, upper Mazaruni River, 12 Nov 1922, fr., *H. Leng 102* (NY). **Suriname.** Sipaliwini: 3 km S (190°) from Kwamalasamutu village center, access trail from confl. Peritu Eeku (Creek) and Sipaliwini R (1.0 há research plot KW4), 2°19'30"N, 56°47'20"W, 29 Mar 2005, fr., *B. Hoffman 6096* (F); Jacob Kondre, Saramacca River, river banks, below rapids, 16 Jun 1944, fl., *B. Maguire 23815* (K); N side of Kuruni Island, E of trail from airstrip to N branch of Kuruni River around island, ca. 30 airline km E of confluence on Corantijn River, 03°22'12"N, 57°20'36"W, alt. 180 m, 18 Nov 1994, fr., *R. Evans et al. 1974* (K, RB); Saramacca River, 3 km above Boschland, 3 Jun 1944, fr., *B. Maguire 24041* (K). Province unknown: Ad ripas fluv. Marowije, above base camp, 14 Feb 1949, fl., *J. Lanjouw & J. C. Linderman 2043* (K).

Distribution, habitat and phenology: *Connarus perrottetii* var. *perrottetii* is widely distributed in north Brazil (Amapá, Amazonas and Pará), French Guiana, Guyana and Suriname (Fig. 6). It is represented by lianas or scandent shrubs, occurring in dense wet forests of the Amazon, especially in upland forests, but also in ciliary forests or periodically flooded areas, with clay or sandy soils, at 45–300 m elevation. Specimens have been collected with flowers irregularly almost throughout the year and with fruits especially from July to December.

Connarus perrottetii (DC.) Planch. var. *rufus* Forero, Brittonia 32(1): 41. 1980.—TYPE: Guyana. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, alt. 850 m, 22–

23 Apr 1938, fr., *A. C. Smith* 3622 (holotype: MO 1165482 [photo!]; isotypes: A [n. v.], F [photo!], G!, IAN!, K!, MO [photo!], NY [photo!], P!, U [photo!], US [photo!]).

Branchlets tomentose. *Leaves* 7–11(–13)-foliolate; leaflets abaxially with indumentum ferruginous or rufous; secondary veins 8–10 pairs, forming angles of 65–80° with midvein, intercostal tertiary veins reticulate. *Fruits* with stipes 2–5 mm long, inner surfaces glabrous or with only glandular trichomes.

Specimens examined: **Guyana.** Cuyuni-Mazaruni region, Mazaruni River, 1.47 miles SW of base camp, 5°48'8.6"N, 59°35'27.1"W, alt. 70 m, 6 Oct 2004, fr., *K. M. Redden et al.* 3240 (K); Kamo River, Toucan Mountain, 01°33'N, 58°50'W, alt. 260–360 m, 17 Sep 1989, fr., *M. J. Jansen-Jacobs et al.* (K, P); Madray-Babu trail, Essequibo-Demerera, 5 Feb 1944, fl., *Fanshawe* F1682 (K); Pomerron-Sepenaam, Pomerron River watershed, Kurushi Creek, trib. of Arapiaco R, 2–4 km SW of lading along logging road, 10–20 m, 7°8'N, 58°43'W, 23 Sep 1992, fr., *B. Hoffman & L. Roberts* 2794 (K); Upper Essequibo Region, Rewa River, near Camp 2 at foot of Spider Mountains, 03°08'N, 058°32'W, 24 Jul 1999, fr., *M. J. Jansen-Jacobs et al.* 6128 (K); Waraputa compartment, ca. 25 km S of Mabura, 05°15'N, 58°45'W, alt. 100 m, 20 Jul 1990, fl., fr., *M. Polak* 211 (K). **Venezuela.** Bolivar: N. E. of Upata, primary forest near El Paraiso camp, 8°16'N, 62°13'W, alt. 500 m, 13 Apr 1967, fl., *Brujin* 1709 (COL, K, MO, NY, U, VEN, WAG). Delta Amacuro: East side of Rio Cuyubini, vicinity of large granitic boulders and steep slopes around summit of cerro, alt. 100–200 m, 16 Nov 1960, st., *J. A. Steyermark* 87582 (NY).

Distribution, habitat and phenology: This variety is found in west and north Guyana and east Venezuela (Fig. 6). It is represented by lianas or scandent shrubs from dense wet forests, usually in mountain formations associated with water courses, growing in sandy soils, at 50–850 m elevation. Specimens have been collected with flowers irregularly from February to July and with fruits irregularly from July to October.

Connarus popenoei Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 4(8): 307. 1929.—TYPE: Honduras. Atlántida: Lancetilla Valley, near Tela, altitude 20 to 600 meters, 6 Dec 1927–20 Mar 1928, fr., *P. C. Standley 54130* (holotype: F 583960!; isotypes: A [photo!], US [photo!]). Figs. 28A–D

Lianas; branchlets slightly striate, densely lanate to glabrescent, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3-foliolate; petioles 4–12.5 cm long, densely lanate to glabrescent; rachises 0.5–2 cm long, densely lanate to glabrescent; pulvinuli 5–7 mm long, sparsely hirsute to glabrescent; leaflets chartaceous, concolorous or slightly discolorous, flat, basal pairs $9.5\text{--}17 \times 5.5\text{--}7.7$ cm, slightly asymmetric, obovate or narrowly obovate, bases asymmetric, acute or obtuse, the apical ones $12\text{--}22 \times 7.3\text{--}9.8$ cm, symmetric, obovate, bases symmetric, acute or obtuse, rarely narrowly rounded, apices short acuminate, rarely rounded, acumen 1–3(–5) mm long, abaxial surfaces glabrous or subglabrous, sparsely sericeous only on the veins, occasionally with tuft of trichomes on midvein, indumentum brown, adaxial surfaces glabrous, occasionally subglabrous on midvein, dull, margins flat; midveins abaxially prominent, adaxially slightly prominent or flat, secondary veins 7–9 pairs, abaxially strongly prominent, adaxially impressed or slightly so, concolorous in relation to the blade, forming angles of (50–)55–70° with midvein, arcuate or slightly so, tertiary veins abaxially prominent, adaxially flat, rarely slightly prominent, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids, axillary or pseudo-terminal, 2–5 per axil, trichomes simple unicellular, peduncles 0.2–0.6 cm long or inflorescences sessile or subsessile, lanate, rachises 7–16 cm long, lanate, lateral cymes (extremely contracted dichasia) ca. 0.2 cm long, lanate, indumentum of these structures ferruginous; bracts 0.8–1 mm long, densely hirsute. *Flowers* sessile; buds not seen; sepals 5, slightly basally connate, ca. 3×1.2 mm, ovate, elliptic or narrowly triangulate, apices acute or obtuse, outer surfaces densely hirsute, indumentum ferruginous, inner surfaces glabrous or subglabrous; petals ca. 3.5×1.5 cm, arrangement not seen, narrowly obovate, apices rounded, glandular dots more than 10, loosely distributed, black, conspicuous, outer surfaces with only sparse glandular trichomes, inner surfaces with only abundant glandular trichomes, margins with abundant glandular trichomes; stamens basally connate by ca. 0.5 mm long, shorter series ca. 3 mm long, longer series ca. 3.5 mm long, filaments glabrous; ovaries ca. 0.8 mm long, densely pubescent, styles and stigmas not seen. *Fruits* (2.3–)2.6–2.9 $\times$ (1.6–)2–2.4 cm, semi-orbicular, indehiscent side linear, rarely slightly sigmoid, pericarps up to 2 mm thick, stipes 4–6 mm long, styles partially persistent,

inconspicuous, ca. 0.5 mm long, outer surfaces densely lanate to glabrescent, indumentum ferruginous, black dots sparse to abundant, inner surfaces hirsute or sparsely lanate, glandular trichomes absent, calyces persistent, sepals ascending erect, rarely patent; seeds ca. 2×1.1 cm, arils color not seen.

Specimens examined: **Honduras.** Atlántida: Base of N slope of Pico Bonito, E of new CURLA (Centro Universitario Regional del Litoral Atlántico) camp building on the Quebrada Grande, ca. 1/3 km above its confluence with the Río Bonito, ca. 10 km SW of La Ceiba, Parque Nacional Pico Bonito, 15°42'N, 86°51'W, 160 m alt., 15 May 1993, fr., *R. Evans 1677* (MO, NY); Esparta, 41.5 km E of Tela on the Tela-Ceiba Hwy then ca. 6 km N along old timber road, 15°39'N, 87°16'W, 100–200 m alt., 24 Apr 1994, fr., *A. E. Brant & R. Zúñiga 2921* (BM, MO); In forest near Lancetilla, 100 feet alt., 8 Aug 1934, fr., *T. G. Yuncker 4964* (F, NY); Lancetilla Valley, near Tela, altitude 20 to 600 meters, 6 Jul 1927–20 Mar 1928, fl., *P. C. Standley 55276* (F). Yoro: Watershed of Leon River, near town of Lempira, 200 m alt., 9 Nov 1978, fr., *D. Hazlett 2963* (BM).

Distribution, habitat and phenology: *Connarus popenoei* is only found in the departments of Atlántida and Yoro, Honduras (Fig. 23). This species is represented by lianas growing in upland wet forests at 200–600 m elevation. Specimens have been collected with flowers in April and with fruits from April to November.

Notes: *Connarus popenoei* is morphologically recognized by the densely lanate indumentum on branchlets, leaves and fruits, usually obovate leaflets with adaxially impressed secondary veins, sessile flowers and externally hirsute sepals. It is similar to *C. silvanensis* due to large leaflets with impressed secondary veins above, but differs by the externally hirsute sepals (vs. sericeous) and semi-orbicular fruits (vs. narrowly obovate), externally lanate (vs. sericeous), with stipe 4–6 mm long (vs. 1–3 mm long).

Connarus punctatus Planch., Linnaea 23: 433. 1850.—TYPE: Suriname. *S. loc.*, *s. d.*, fl., *W. R. Hostmann 1146* (holotype: K barcode K000633808!; isotypes: F [photo!], G!, K!, L [photo!], MO [photo!], P!, U [photo!], US [photo!], W [photo!]). Fig. 29

Connarus penningtonii Prance, Mem. New York Bot. Gard. 15: 129. 1966.—TYPE: Brazil. Pará: Road Braganca to Viseu, banks of Rio Piria, south of Curupati, 9 Nov 1965, fr., *G. T.*

Prance & T. D. Pennington 2051 (holotype: NY barcodes NY 00011178 and NY 00011179 [photo!]; isotypes: K!, RB!, US [photo!]).

Connarus perturbatus Forero, *Caldasia* 13(61): 7. 1980.—TYPE: Colombia. Meta: Al sur de la Macarena, margen derecho del caño losada, junto a su desembocadura al río Guayamero, peña de los Conejos, 300 m. alt., 10 Mar 1959, fr., *R. Jaramillo M. & J. Hernández C. 2135* (holotype: COL barcodes COL000001589 and COL000001590 [photo!]; isotypes: FMB [photo!], HUA [photo!], MBM [photo!], NY [photo!], SP [photo!]), *syn. nov.*

Lianas or scandent shrubs, 3–8 m tall; branchlets slightly striate, glabrous, subglabrous or sparsely sericeous, trichomes simple unicellular, lenticels conspicuous. *Leaves* (3–)5–7(–9)-foliolate; petioles 2.5–10(–11) cm long, glabrous, subglabrous or irregularly sparsely sericeous; rachises 2–10(–13) cm long, glabrous, subglabrous or irregularly sparsely sericeous; pulvinuli 3–6 mm long, glabrous or subglabrous; leaflets chartaceous to coriaceous, concolorous or slightly discolorous, flat, basal pairs 7.3–11.5 × 3.2–4.8 cm, symmetric, elliptic, narrowly elliptic, oblong, narrowly obovate or obovate bases symmetric, rounded, subcordate or obtuse, the apical ones 10.4–18 × 3.6–6 cm, symmetric, narrowly elliptic, oblong or narrowly obovate, less frequently elliptic or obovate, bases symmetric, rounded, subcordate or obtuse, apices acuminate to long acuminate, acumen 5–15 mm long, abaxial surfaces glabrous, subglabrous or irregularly sparsely sericeous on midvein, indumentum brown, adaxial surfaces glabrous, dull or slightly shining, margins flat; midveins abaxially prominent, adaxially impressed or slightly so, secondary veins (9–)10–15 pairs, abaxially prominent, adaxially prominent or slightly so, concolorous in relation to the blade, rarely slightly discolorous, forming angles of 65–80° with midvein, slightly arcuate, less frequently linear or arcuate, tertiary veins prominent or slightly so on both surfaces, intercostals opposite or mixed percurrent, epidermals opposite percurrent, the intersecondary usually reticulate. *Inflorescences* in thyrsoids or double thyrsoids, axillary or pseudo-terminal, 1–4 per axil, trichomes simple unicellular, peduncles 0.4–4 cm long or inflorescences subsessile, sericeous or sparsely so, rachises 5–27 cm long, sericeous or sparsely so, lateral cymes 0.3–0.7 cm long, sericeous, lateral sub-thyrsoids 2–8 when, sericeous, indumentum of these structures brown or ferruginous; bracts 0.5–0.8 mm long, sericeous. *Flowers* with pedicels 0.5–1.7 mm long; buds 2.5 × 1.5–1.8 mm, elliptic; sepals 5, slightly basally connate, 2–3 × 0.8–1.4 mm, elliptic, narrowly ovate or narrowly triangulate, apices acute or obtuse, outer surfaces sericeous or

sparsely so, indumentum ferruginous, inner surfaces glabrous or subglabrous, pubescent only at apex; petals $3.5\text{--}6 \times 1.2\text{--}1.5$ mm, erect, narrowly obovate or narrowly elliptic, apices rounded or obtuse, glandular dots more than 10, loosely distributed, black, conspicuous, both surfaces glabrous, subglabrous or sparsely pubescent, glandular trichomes absent or sparse to abundant, margins ciliate, glandular trichomes absent or sparse to abundant; stamens basally connate by 0.3–1.5 mm long, shorter series 1–3.5 mm long, longer series 1.5–4.5 mm long, filaments with sparse to abundant glandular trichomes, shorter filaments occasionally glabrous; ovaries 0.8–2 mm long, densely pubescent, styles 1–2 mm long, stigmas bilobate, lobes ca. 0.5 mm long. *Fruits* $1.8\text{--}2.8 \times (1.1\text{--})1.3\text{--}1.6$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 3–7 mm long, styles partially persistent, apiculate, 0.5–4 mm long, outer surfaces irregularly sparsely sericeous, more densely on stipe, base and apex, indumentum brown, black dots abundant, inner surfaces subglabrous to sparsely pubescent, glandular trichomes sparse to abundant, calyces persistent, sepals ascending erect; seeds $1.2\text{--}2 \times 0.7\text{--}0.9$ cm, arils yellowish.

Selected specimens examined: **Brazil.** Acre: Mâncio Lima, Rio Moa (Japiim), 07°35'53"S, 72°54'07"W, 1–5 Jun 2007, fr., *F. Obermuller & E. C. Oliveira* 302 (RB). Amapá: Macapá, Igarapé do Ambé, no afluyente do Rio Pedreira, 8 Jul 1951, fr., *R. L. Fróes & G. A. Black* 27327 (IAN); Município de Apuã, Rio Urucú, mata de várzea, 12 Sep 1992, fl., *U. N. Maciel & M. R. Santos* 1975 (MG); Parque Nacional Montanhas do Tumucumaque, Rio Anotaié, Cachoeira do Lampião, 03°05'33"N, 52°01'39"W, 11 Sep 2005, fr., *A. Lobão et al.* 912 (RB); Rio Oiapoque, 20 Jun 1904, fl., fr., *A. Ducke* MG4785 (IAN, MG). Amazonas: Along Dermuni River (a tributary of Aracá River), 00°18'05"S, 62°46'00"W, 11 Aug 1996, fr., *P. Acevedo-Rodriguez et al.* 8226 (INPA); Estrada Manaus-Caracará, km 58, Reserva Biológica INPA-SUFRAMA, Sep 1976, fl., *D. F. Coêlho & C. D. A. da Mota* 860 (IFAM, INPA); Ilha Tipinambarana, paraná Urariá, between rio Abacaxis and rio Paraconi, várzea, 03°50'S, 58°30'W, 9 Jul 1983, fr., *R. S. Hill* 13051 (INPA); Lábrea, Rio Purus, 30 Oct 1978, fr., *G. T. Prance & L. G. Farias* 8075 (INPA); Rio Purús, Lago Mapongapá, 30 Mar 1904 fr., *J. Huber s. n.* (MG). Maranhão: Campo da Boa Esperança, Maracassumé River Region, 19 Aug 1932, fr., *R. de L. Fróes* 1813 (NY); Carutapera, margem do Rio Gurupi, 01°18'00"S, 46°00'36"W, 27 May 2010, fl., *R. C. Forzza et al.* 5864 (ESA, K, MG, RB); Cândido Mendes, Maracassumé River Region, 17 Jul, 1932 fl., *R. de L. Fróes* 1782 (NY). Mato Grosso: Novo Mundo, Parque Estadual Cristalino, acampamento 35 km da pousada, 09°28'56"S, 55°28'34"W, 257 m alt., 11 Feb 2008, fl. fr., *D. Zappi et al.* 1187 (SPF). Pará: Bragança, Península de Ajuruteua, Salinas dos Roques/Jabuti, 00°55'38"S, 46°40'09"W, Jan 2006, fr., *N. B. Vale et al.* 22 (HBRA); Bragança

to Viseu Road, banks of Rio Piria, south of Curapati, 9 Nov 1965, fr., *G. T. Prance & T. D. Pennington 2051* (IAN, K); Jarí, estrada do Munguba, km 16, 20 May 1969, fl., *N. T. Silva 1999* (NY); Belém, I.A.N., 3 Oct 1951, fl., *J. M. Pires s. n.* (INPA 2322); Marajó, Chaves, 4 Dec 1901, fl., *A. Ducke 2535* (MG); Melgaço, Rio Camuim, 15 Jan 1993, fr., *L. C. B. Lobato 570* (MG); Monte Dourado, Jarí, margem do Rio Jarí, 12 Jul 1969, fr., *N. T. Silva 2411* (IAN, NY); Oriximiná, Rio Trombetas, margem esquerda em frente à Mineração Patricia, 7 Jul 1980, fr., *C. A. C. Ferreira et al. 1344* (RB); Pau D'arco, Marajoara, 10 Sep 1997, fr., *J. Grogan 101* (INPA); Santana do Araguaia, 100 km south of Redenção on road PA-150 to Barreiras dos Campos, Fazenda Inajaporã, 08°45'S, 50°25'W, 18 Feb 1980, fl., *T. Plowman et al. 8840* (INPA, MG); Serra dos Carajás, Riverbanks of Rio Itacaiúnas near ferry crossing to AMZA camp 3-Alfa, 05°53'S, 50°30'W, 120 m alt., 12 Jun 1982, fr., *C. R. Sperling et al. 6118* (MG); Vitória do Xingu, 03°13'46"S, 51°45'05"W, 22 Apr 2015, fl., *A. C. Gonçalves s. n.* (RB). Rondônia: Ariquemes, 21 km SE of Ariquemes on hwy BR-364, then 1 km E of "Linea 45," 10°07'S, 62°56'W, 200 m alt., 17 Mar 1987, fl., *M. Nee 34425* (INPA); Porto Velho, margem esquerda do Rio Madeira, 09°23'20"S, 64°50'49"W, 23 Jun 2010, fr., *G. Pereira-Silva et al. 15469* (CEN, INPA, UFACPZ); Rio Machado, curso inferior, Jan 1981, fr., *M. Goulding 1342* (MG). Tocantins: Tocantinópolis, 2 Aug 1949, fr., *J. M. Pires & G. A. Black 1675a* (IAN).

Colombia. Meta: Parque Nacional Natural Tinigua, Serranía Chamusa, Centro de Investigaciones Primatológicas La Macarena, trocha FI 460 m 10 der., Jan 1993, fr., *P. Steverson 430* (COL).

Ecuador. Napo: Río Cuyabeno, collections made from the canoe along the riverside, from 2 hours upstream from the outlet in Río Aguarico to Puerto Bolívar, ca. 0°10–6'S, 76°0–10'W, 17 Aug 1981, fr., *J. Brandbyge et al. 33629* (K).

French Guiana. Bord de l'Oyapock à Paola, 13 Sep 1980, fl., *M. F. Prévost & P. Grenand 1013* (P); Fleuve Oyapock, entre Carbets Pekeía et Roche Mon Père, 13 Jul 1969, fr., *Oldeman s. n.* (P); Rive droite de l'Approuague village Takoudou au Saut Athanase, 26 Jan 1967, fl., *Oldeman B-901* (P); Site de Fort Saint-Louis, place forte abandonnée vers 1945, em amont de Trois-Palétuviers Bas-Oyapock, rive gauche de fleuve, 4°2'5"N, 51°41'15"W, alt. 30 m, 10 Feb 2011, fl., *O. Poncy & F. Crozier 2584* (P).

Guyana. *S. loc., s. d.*, fl., *R. Schomburgk 804* (K).

Peru. Huánuco: Vicinity of Tingo María, 19 Sep 1962, fr., *J. S. Vigo 6163* (K). Loreto: Florída, Río Putumayo, at mouth of Río Zubineta, alt. 180 m, Oct–Dec 1931, fl., *G. Klug 2366* (K). San Matín: Mirascal Caceres, Quebrada de Tananta (margen izquierda del río Huallaga), 16 Jun 1970, fr., *J. Schunke 4054* (P).

Suriname. Concession Haenen, west of mouth of Coppename R., 23 Mar 1954, fl., *J. C. Lindeman 5673* (K).

Distribution, habitat and phenology: *Connarus punctatus* is one of the most common species of the genus in the Amazon, and it is mainly distributed in the Guiana Shield, although few collections have been made in Colombia, Ecuador and Peru (Fig. 15). Some individuals were found in transitional areas between the Amazon and the Cerrado in Tocantins, Brazil. It is represented by lianas or scandent shrubs, occurring mainly in ombrophilous forests, usually river margins or flooded areas, at 20–300 m elevation. Specimens have been collected with flowers and fruits practically throughout the year.

Notes: *Connarus punctatus* has conspicuous lenticels in its branchlets, usually 5–7-foliolate leaves, secondary vein with 9–15 pairs forming angles of 65–80° with midvein, prominent or slightly prominent tertiary veins on adaxial surface, and fruits with sepals ascending. It can be confused with *C. jaramilloi* due to the number and shape of leaflets, but mainly differs by the ascending sepals on fruits vs. patent or reflexed sepals. In addition, leaflets are a bit numerous (9–11) and larger in *C. jaramilloi*.

The specimen *Hostmann 1146* (barcode K000633808) is here considered the holotype because when Planchon (1850) originally described *C. punctatus*, the only specimen he cited belonged to Hooker Herbarium, now incorporated to K. A duplicate is also found in K, but it belonged to Bentham Herbarium, which makes it an isotype.

Forero (1980b) described *C. perturbatus* and differentiated it from *C. punctatus* based on its sessile flowers (Forero 1983). Although the type specimen has only fruits, it is possible to note that the flowers are short pedicellate. In addition, the similarities between *C. perturbatus* and *C. punctatus* in leaflet size and shape, disposition of secondary veins, fruit size and shape, and disposition of sepals on fruits, are consistent enough to consider the former as a synonym of *C. punctatus*.

Connarus ramiflorus C. Toledo & V. C. Souza, Syst. Bot. 43(3): 758. 2018.—TYPE: Brazil. Amazonas: Tefé, Road of Luc 6, Porto Urucú, Kms 2 to 3, 20 Jul 1991, fr., *A. S. Tavares et al.* 526 (holotype: INPA 198821!; isotype: ESA!).

Lianas; branchlets slightly striate, sparsely sericeous, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3-foliolate; petioles 4.5–9.5 cm long, sparsely sericeous;

rachises ca. 2.5 cm long, sparsely sericeous; pulvinuli 6–8 mm long, subglabrous; leaflets chartaceous, discolorous, flat, basal pairs $10.3\text{--}13 \times 5.4\text{--}6.8$ cm, symmetric, ovate or elliptic, bases symmetric, rounded, the apical ones $11\text{--}16 \times 6.5\text{--}8.5$ cm, symmetric, ovate or elliptic, bases symmetric, rounded, apices short acuminate, acumen 3–5 mm long, abaxial surfaces sericeous or sparsely so, indumentum ferruginous, adaxial surfaces glabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed, secondary veins 5–7 pairs, abaxially prominent, adaxially flat, slightly discolorous in relation to the blade, forming angles of $45\text{--}50^\circ$ with midvein, arcuate, tertiary veins abaxially slightly prominent, adaxially flat, intercostals and epidermals opposite percurrent. *Inflorescences* in thyrsoids, ramiflorous, 1–4 per axil, trichomes simple unicellular, peduncles 0.3–0.5 cm long, sericeous, rachises 2–6 cm long, sericeous, lateral cymes 0.3–0.7 cm long, sericeous, indumentum of these structures ferruginous; bracts ca. 0.7 mm long, sericeous. *Flowers* not seen, pedicellate; buds not seen; sepals 5 (persistent on fruits), slightly basally connate, narrowly ovate, apices acute, outer surfaces sparsely sericeous, indumentum brown or ferruginous, inner surfaces subglabrous; petals (few persistent on fruits) with glandular dots ca. 5, loosely distributed, black, inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous. *Fruits* $1.4\text{--}1.8 \times 1\text{--}1.2$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 3–5 mm long, styles partially persistent, rostrate, 2–3 mm long, outer surfaces sparsely sericeous to glabrescent, indumentum ferruginous, black dots absent, inner surfaces sparsely pubescent, glandular trichomes sparse, calyces persistent or partially persistent, sepals patent or reflexed; seeds $1\text{--}1.2 \times 0.6\text{--}0.7$ cm, arils yellowish.

Distribution, habitat and phenology: *Connarus ramiflorus* is only known from the type location, collected in the municipality of Tefé, countryside of Amazonas, Brazil (Fig. 9). It is a lianescent species, found in upland forests of the Amazon, at ca. 60 m elevation. The only known specimen was collected with fruits in July.

Notes: Among the species exclusively with simple trichomes, *C. ramiflorus* is easily distinguished by the discolorous and abaxially sericeous leaflets, ramiflorous inflorescences and fruits with rostrate apex. It is similar to other Amazonian species with abaxially hairy leaflets, *C. favosus*, but differs by the flat leaflet margins (vs. revolute), percurrent tertiary veins (vs. reticulate), ramiflorous inflorescences (vs. axillary or pseudo-terminal) and fruits stipes 3–5 mm long (vs. fruits sessile or stipes 0.5–1 mm long).

Connarus regnellii G. Schellenb., Candollea 2: 114. 1925.—TYPE: Brazil. Minas Gerais: Caldas, 3 Oct 1861, *A. F. Regnell III*395 (lectotype designated by Schellenberg 1938: S [n. v.]). Fig. 30

Tress or treelets, 3–12 m tall; branchlets slightly striate, rarely slightly fissured, glabrous or subglabrous, trichomes simple unicellular, lenticels inconspicuous. *Leaves* 3–5-foliolate; petioles 3.5–7.3 cm long, glabrous or subglabrous; rachises 0.7–5.5 cm long, glabrous or subglabrous; pulvinuli 3–5 mm long, glabrous or subglabrous; leaflets chartaceous, discolorous or slightly so, flat, basal pairs $6.2\text{--}11.3 \times 2.4\text{--}4.2$ cm, symmetric, elliptic or narrowly elliptic, bases symmetric, rounded or obtuse, the apical ones $8\text{--}14.8 \times 2.5\text{--}5.8$ cm, symmetric, elliptic or narrowly elliptic, rarely narrowly obovate, bases symmetric, obtuse or rounded, rarely acute, apices acuminate, acumen 4–11 mm long, abaxial surfaces glabrous or subglabrous, occasionally sparsely sericeous on midvein, indumentum brown or ferruginous, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed or slightly so, secondary veins 7–10(–11) pairs, abaxially slightly prominent, rarely flat, adaxially flat, discolorous in relation to the blade, rarely concolorous, forming angles of $50\text{--}65^\circ$ with midvein, arcuate or slightly so, tertiary veins abaxially slightly prominent, adaxially flat or slightly prominent, intercostals mixed or opposite percurrent, epidermals opposite percurrent, the invervenal occasionally reticulate. *Inflorescences* in thyrsoids or double thyrsoids, axillary, 1–4 per axil, trichomes simple unicellular, peduncles 0.3–1.3 cm long, sericeous or sparsely so, rachises 7–12 cm long, sericeous or sparsely so, lateral cymes 0.7–1.8 cm long, sericeous, lateral sub-thyrsoids 0.7–5 cm long, sericeous, indumentum of these structures brown or ferruginous; bracts 1–1.5 mm long, sericeous. *Flowers* with pedicels 0.5–2 mm long; buds ca. 2×1.5 mm, ovate or elliptic; sepals 5, slightly basally connate, $2.2\text{--}2.8 \times 0.8\text{--}1.3$ mm, narrowly ovate or narrowly triangular, apices acute or obtuse, outer surfaces sericeous, indumentum brown or ferruginous, inner surfaces glabrous or subglabrous; petals $4\text{--}5 \times 1\text{--}1.5$ mm, reflexed, narrowly obovate, narrowly elliptic or oblanceolate, apices rounded, obtuse or acute, glandular dots more than 10, loosely distributed, black or colorless, inconspicuous, outer surfaces sparsely pubescent, with abundant glandular trichomes, inner surfaces glabrous, subglabrous or with only sparse glandular trichomes; stamens basally connate by 0.3–0.5 mm long, shorter series 1.5–2 mm long, longer series 2–2.5 mm long, filaments with sparse glandular trichomes; ovaries 1.2–1.3 mm long, densely pubescent, styles 2–2.5 mm long, stigmas bilobate, lobes ca. 0.3 mm long. *Fruits* $1.7\text{--}2.2 \times 1.3\text{--}$

1.7 cm, obovate or semi-orbicular, indehiscent side sigmoid or linear, pericarps up to 2 mm thick, stipes 2–4 mm long, styles partially persistent, spinescent or apiculate, 1–3 mm long, outer surfaces irregularly sparsely sericeous, more densely on stipe and sutures, indumentum brown, black dots abundant, inner surfaces with only sparse to abundant glandular trichomes, calyces persistent, rarely partially persistent, sepals ascending erect or patent; seeds $1.5\text{--}1.6 \times 1\text{--}1.2$ cm, arils yellowish.

Selected specimens examined: **Brazil.** Minas Gerais: Extrema, Serra do Lopo, estrada para Joanópolis, alt. 1300 m, 19 Dec 2002, fr., *L. F. Yamamoto* 985 (UEC); Monte Santo de Minas, Fazenda Barreiro, 03 Sep 1986, fr., *H. F. Paulino Filho* 1186 (CEN, UEC); Santa Bárbara, 20°05'39"S, 43°39'97"W, 05 Jul 2013, fr., *E. Temeirão Neto & T. Mansur* 5327 (BHCB, RB). Rio de Janeiro: Petrópolis, Serra da Estrella, 250 m, 09 Aug 1979, fr., *K. Kubitzky & H. H. Poppendieck* 79-1 (NY); Serra da Estrella, a Quitadinha, 24 Oct 1875, fl., *A. F. M. Glaziou* 8329^a (P). São Paulo: Campinas, Mata do Macuco (Fragmento G1), 22.47 S, 46.56 W, alt. 739 m, 29 Sep 1999, fr., *K. Santos & R. Belinello* 498 (UEC); Mairiporã, fazenda Paineira, 27 Feb 1997, fr., *A. Cassalho s. n.* (RB, SPSF); Piedade, Área de transição entre Floresta Ombrófila e Floresta Estacional, 23°42'05.5"S, 47°30'38.5"W, alt. 800, 03 Jun 2018, fr., *C. A. P. Toledo* 377 (ESA); São Roque, Mata da Câmara, 23°31'26"S, 47°06'45", 03 Oct 1993, fl., *E. Cardoso-Leite & A. Oliveira* 244 (ESA, UEC); *S. loc.*, 31 Oct 1847, fl., *A. F. Regnell* III395 (F, P, S, US).

Distribution, habitat and phenology: *Connarus regnellii* includes relatively small trees, characteristics of seasonal semideciduous forests of southeast Brazil (Fig. 11), growing on clay soils, at 250–1300 m elevation. Specimens have been collected with flowers from September to October and with fruits from June to December.

Notes: Although never brought out in previous treatments, *C. regnellii* is morphologically very similar to *C. rostratus*, especially due to the normally 3–5-foliolate leaves, percurrent tertiary veins and fruits with prominent apices, in addition to the interesting fact that, in herbarium specimens, secondary veins are mostly discolorous in relation to the blade. The distribution of these species should also be taken into account as both are found in the Atlantic Forest, especially of southeast Brazil; however, *C. regnellii* occurs mainly in semideciduous forests of the interior of São Paulo and Minas Gerais states, while *C. rostratus* is characteristic of coastal “restingas” and ombrophilous forests, especially from Santa Catarina up to São Paulo state. (Fig. 11). Morphologically, both species are separated by very few

discrete features: in *C. regnellii*, apical pairs of leaflets are normally elliptic or narrowly so, petals are 4–5 mm long with glandular trichomes and fruits are internally covered only by glandular trichomes (rarely glabrous), while in *C. rostratus*, apical leaflets are normally narrowly obovate, petals are 3–4 mm long, glabrous, and fruits are internally pubescent, without glandular trichomes.

While originally describing *C. regnellii*, Schellenberg (1925) did not indicate the holotype, instead nine syntypes. The author (1938) subsequently designated a proper lectotype by indicating the specimen *Regnell III395* from S, collected in Caldas (Minas Gerais) in “03.10.1861”, as “type”. However, no specimen including all these requirements has been found; during the development of the present work, Herbarium S was kept under maintenance, which made it impossible to check the existence of such sheet. It is of note, in addition, that there are several specimens under *Regnell III395* in European herbaria, all of them collected in São Paulo and mostly seen by Schellenberg, although the author never indicated this locality when citing the analyzed specimens of *C. regnellii*, which may serve as a hint to hypothesize that Schellenberg (1925, 1938) considered all these specimens as belonging to the same collection, coming from Caldas (Minas Gerais), not São Paulo. Only a single collection of Regnell from Caldas has been identified. It is incorporated in P (barcode P01819561), but the specimen includes two different sheet labels (one from Caldas containing Regnell’s number “III395” and the other from São Paulo state with Regnell’s name and number “III395”, collected in October 31st 1847); nevertheless, the collection date as referred to the lectotype (Schellenberg 1938) is not included anywhere else in this specimen. Therefore, as the existence of the specimen from S, that indicated in Schellenberg (1938) is considered the lectotype, with the remarks that it has not been seen, as also adopted by Forero (1983).

Connarus renteriae Carbonó, Forero & L. A. Vidal, *Revista Brasil. Bot.* 7(1): 67. 1984.—

TYPE: Colombia. Santander: Cerro La Paz, 600 mts., 16 Oct 1977, fl., *E. Rentería et al.* 757 (holotype: HUA barcode HUA0000363 [photo!]; isotypes: COL [photo!], MO [photo!], NY!).

Scandent shrubs or treelets, 3–5 m tall; branchlets slightly striate, subglabrous or sparsely sericeous, trichomes simple unicellular, lenticels conspicuous or inconspicuous.

Leaves (3–)5-foliolate; petioles 3.7–6 cm long, subglabrous or sparsely sericeous; rachises (1.5–)2.8–5 cm long, subglabrous or sparsely sericeous; pulvinuli 3–5 mm long, glabrous or subglabrous; leaflets chartaceous, slightly discoloured, flat, basal pairs $4.5\text{--}8 \times 1.6\text{--}3.7$ cm, symmetric, narrowly ovate or narrowly elliptic, rarely ovate, bases symmetric, rounded or subcordate, the apical ones $5.8\text{--}14.5 \times 2\text{--}5.5$ cm, symmetric, narrowly ovate or narrowly elliptic, rarely ovate, bases symmetric, rounded or subcordate, apices acuminate, acumen 5–10 mm long, abaxial surfaces subglabrous or irregularly sparsely sericeous on midvein, indumentum brown, adaxial surfaces glabrous or subglabrous, dull or slightly shining, margins flat; midveins abaxially prominent, adaxially slightly impressed, secondary veins 9–10 pairs, flat on both surfaces, adaxially concolorous in relation to the blade, forming angles of $50\text{--}70^\circ$ with midvein, arcuate, tertiary veins flat on both surfaces, intercostals mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids or double thyrsoids, axillary or pseudo-terminal, 1–2 per axil, trichomes simple unicellular, peduncles 0.2–2 cm long, sparsely sericeous, rachises 7.5–19.5 cm long, sparsely sericeous, lateral cymes 0.2–1.2 cm long, sericeous or densely pubescent, lateral sub-thyrsoids 1.8–7.3 cm long, sericeous or densely pubescent, indumentum of these structures ferruginous; bracts ca. 0.8 mm long, sericeous. *Flowers* with pedicels 0.3–0.8 mm long; buds ca. 2×1.3 mm, elliptic; sepals 5, slightly basally connate, $2\text{--}2.5 \times 0.6\text{--}1$ mm, narrowly ovate or narrowly triangulate, apices acute, outer surfaces sericeous or sparsely so, indumentum ferruginous, inner surfaces sparsely sericeous, more densely at apex; petals $3\text{--}4 \times 0.8\text{--}1.2$ mm, erect, narrowly obovate, apices rounded, glandular dots more than 10, loosely distributed, colorless, inconspicuous, both surfaces glabrous, margins glabrous; stamens basally connate by ca. 0.5 mm long, shorter series 1.8–2 mm long, longer series 2.2–3 mm long, filaments glabrous or with sparse glandular trichomes; ovaries ca. 0.8 mm long, densely pubescent, styles ca. 1.2 mm long, stigmas bilobate, lobes ca. 0.2 mm long. *Fruits* $1.5\text{--}1.8 \times 1.1\text{--}1.2$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 2–3 mm long, styles partially persistent, apiculate, ca. 0.5 mm long, outer surfaces sparsely sericeous to glabrescent, indumentum ferruginous, black dots abundant, inner surfaces subglabrous to sparsely pubescent, glandular trichomes absent, calyces persistent, sepals ascending erect; seeds $1.2\text{--}1.4 \times 0.7\text{--}0.8$ cm, arils yellowish.

Specimens examined: **Colombia.** Santander: Cerro La Paz, alt. 600 m, 16 Oct 1977, fr., *E. Rentería et al.* 752 (NY). **Venezuela.** Zulia: Colón, alrededores de Casigua El Cubo, sector Las Cruces, en cerro El Mirador, a lo largo de la vía antigua entre El Carmelo y Estación Concordia, al sur de Pozo T-221, trayecto de aprox. 4 km, alt. 350–450 m, 27 Apr 1979, fr., *G.*

S. Bunting & L. Alfonzo G. 7276 (NY); Colón, alrededores de Casigua El Cubo, sector Las Cruces, en la vecindad de pozo T-52, unos 4 km al sur de El Carmelo, alt. 150 m, 13 Dec 1979, fr., *G. S. Bunting & M. Fucci 8388* (NY); Perijá, carretera Machiques-La Fría, em km 69 al sur del desvío hacia Machiques, 4 Feb 1979, fr., *G. S. Bunting & L. Alfonzo G. 6846* (NY).

Distribution, habitat and phenology: *Connarus renteriae* was described based on a single specimen, collected in the department of Santander, Colombia, but additional collections were identified, so this species is now known to occur in north Colombia (Santander) and northwest Venezuela (Zulia) (Fig. 15). Individuals are scandent shrubs or small trees up to 5 m tall, occurring in ombrophilous forests of the Amazon, at 150–600 m elevation. Specimens have been collected with flowers in October and with fruits irregularly from October to February.

Notes: Among the species with exclusively simple trichomes, *C. renteriae* can be confused with *C. punctatus* due to the leaves usually with more than 3 leaflets, but differs by the narrower leaflets, secondary veins arcuate (vs. linear or slightly arcuate), flat tertiary veins on both surfaces (vs. conspicuous on both surfaces) and fruit stipes 2–3 mm long (vs. 3–7 mm long).

Connarus reticulatus Griseb., Cat. Pl. Cub.: 84. 1866.—TYPE: Cuba. Santiago de Cuba [Orientalis]: *S. loc.*, 1861, fl., fr., *C. Wright 59* (lectotype first step designated by Schellenberg 1938: GOET; lectotype second step **designated here**: GOET barcode GOET002280 [photo!]; isoelectotypes: BM!, BR [n. v.], G!, GH [photo!], GOET [photo!], K!, MO [photo!], NY [photo!], P!, PH [photo], S [photo!], YU [photo!]).

Lianas or shrubs, 1–2 m tall; branchlets slightly striate, sericeous to glabrescent, trichomes simple unicellular, lenticels conspicuous. *Leaves* 3-foliolate; petioles 1.3–4.2 cm long, sericeous to glabrescent; rachises 0.6–1.5(–2) cm long, sericeous to glabrescent; pulvinuli 3–5 mm long, pubescent to glabrescent; leaflets coriaceous, slightly discoloured, flat or conduplicate, basal pairs 4.5–7.7 × 2–3.7 cm, symmetric, ovate or elliptic, bases symmetric, rounded or subcordate, the apical ones 5–10.2 × 2.3–4.4 cm, symmetric, ovate or elliptic, bases symmetric, rounded or subcordate, apices acuminate or long acuminate, acumen 4–11(–14) mm long, abaxial surfaces glabrous or subglabrous, adaxial surfaces glabrous, slightly shining, margins revolute or slightly so; midveins abaxially prominent, adaxially flat or slightly

impressed, secondary veins 6–7 pairs, abaxially slightly prominent, rarely flat, adaxially flat or slightly prominent, concolorous in relation to the blade, forming angles of 45–60° with midvein, linear, tertiary veins abaxially prominent, adaxially flat or slightly prominent, intercostals and epidermals reticulate. *Inflorescences* in thyrsoids, axillary or pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncles 0.2–1.1 cm long, sericeous or sparsely so, occasionally tomentose, rachises 5–17.5(–26) cm long, sericeous or tomentose, lateral cymes 0.3–1 cm long, sericeous or tomentose, indumentum of these structures rufous or ferruginous; bracts 0.7–1 mm long, sericeous. *Flowers* with pedicels 1–2 mm long; buds 2.5×1.5 –1.7 mm, ovate; sepals 5, slightly basally connate, $2-3 \times 1$ –1.2 mm, ovate, apices acute, rarely obtuse, outer surfaces sericeous, indumentum ferruginous, inner surfaces glabrous or subglabrous, occasionally pubescent only at apex; petals $3.5-4(-5) \times 1.2$ –1.5 mm, erect, narrowly obovate or narrowly elliptic, apices rounded or obtuse, glandular dots more than 10, loosely distributed, black, rarely colorless, inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous or subglabrous, pubescent only at apex, glandular trichomes absent; stamens basally connate by 0.5–0.6 mm long, shorter series 1.5–2.5 mm long, longer series 2–3.5 mm long, filaments glabrous or with sparse glandular trichomes, rarely abundant; ovaries 0.8–1.2 mm long, densely pubescent, styles 1–1.5 mm long, stigmas bilobate, lobes ca. 0.4 mm long. *Fruits* $1.8-2.4 \times 1.2$ –1.6 cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 2–5 mm long, stigmas partially persistent, apiculate, 0.5–2 mm long, outer surfaces subglabrous or irregularly sparsely tomentose, more densely at stipe, base and apex, indumentum ferruginous or rufous, black dots sparse to abundant, inner surfaces tomentose or densely pubescent, glandular trichomes sparse, calyces deciduous, rarely partially persistent, sepals patent or ascending erect; seeds ca. 1.2×0.7 cm, arils yellowish.

Specimens examined: **Cuba.** Guantánamo: Southern Baracoa region. Charrascales, Jauco arriba, 17 Jul–4 Aug 1924, fl., *F. Leon 12014* (NY); Slope of Mesa de Prada, 450 m alt., 17 Jul–4 Aug 1924, fr., *F. Leon 11961* (NY). Holguín: Along banks of Rio Levisa, Jul 1941, fl., fr., *R. A. Howard 5848* (NY, US); Carretera Hulgóin-Cueto, 30 May 1954, fl., fr., *M. L. Figueiras 1396* (US); Barren Savannas, south east of Holguín, 26–29 Nov 1909, fl., fr., *J. A. Shafer 2945* (NY); Cerro de Fraile, in thickets, 25 Aug 1916, fl., *E. L. Ekman 7557* (K, NY); Mina cromita cayoguan, Moa, *s. d.*, fl., *B. Clemente 4067* (US); Moa. Bosque do Centeno, Jun 1945, fl., *B. Clement 4334* (F); Campo de aviación, Jul 1941, fr., *B. Leoni 20135* (US); *S. loc.*, 9 Apr 1945, fr., *J. Acuña 12429* (US). Moa Bay, east of Rio Moa, 2–3 Jan 1911, fr., *J. A. Shafer 8346* (K, NY, US). Monte Picote. A foothill at the southern end of Sierra de Nipe, near

Palmarito del Cauto, 400 m alt. 29 Jan 1956, fr., *C. V. Morton* 9732 (US); *C. V. Morton* 9667 (US); Sierra de Nipe. Cayo del Rey, Río Canapú, 23 May 1940, fl., fr., *J. P. Carabia* 4073 (NY); Loma de Estrella, in carrascales, 3 Jul 1914, fl., *E. L. Ekman* 1741 (K, NY); Prop Rio Piloto, 1 Apr 1914, fl., *E. L. Ekman* 2695 (S, US). Santiago de Cuba: Bayate, in carrascales at Rio Piedra, 5 Jun 1915, fl., *E. L. Ekman* 5922 (K, US); Bayate, Monte Oscuro, limestone foothill of Sierra de Vipe, in forest, 13 Feb 1915, st., *E. L. Ekman* 4636 (NY); Foot of upper incline down Arroyo to Piedra Gorda, 150 m alt., 8–13 Jan 1910, fr., *J. A. Shafer* 3524 (NY, US).

Distribution, habitat and phenology: *Connarus reticulatus* is only found in Cuba island, where individuals are distributed in the provinces of Guantánamo, Holguín and Santiago de Cuba (Fig. 16). It is represented by lianas or shrubs up to 2 m tall, most likely growing in mountainous areas at 150–450 m elevation, although the specimen *Shafer* 2945 was collected at sea level. Specimens were collected with flowers irregularly from April to August and in November, and with fruits irregularly from January to July and in November.

Notes: *Connarus reticulatus* is recognized by its short petiole (1.3–4.2 cm long), small and coriaceous leaflets (4.5–10.2 cm long), abaxially prominent and reticulate tertiary veins, inflorescences in thyrsoids, and tomentose or densely pubescent fruits on internal surfaces, with calyx usually deciduous. Another feature that may help identifying this species is the rufous indumentum, which covers petioles and leaf rachises and peduncles and inflorescence rachises.

Grisebach (1866) did not indicate the herbarium when he originally described *C. reticulatus*, so Schellenberg (1938) inadvertently selected the lectotype from GOET. However, two specimens of *Wright* 59 are deposited in this herbarium and, as they do not bear the same original label and should be regarded as duplicates (Turland et al. 2018, Art. 8.3), a second step lectotypification is here proposed.

Connarus revolutus C. Toledo, Willdenowia 51: 177. 2021.—TYPE: Brazil. Espírito Santo: Linhares, Reserva Natural Vale, estrada Jacarandá, 28 Sep 1994, fl., *D. A. Folli* 2379 (holotype: CVRD 5016!; isotypes: ESA!, NY [photo!], UB!).

Lianas or scandent shrubs, 3–4 m tall; branchlets slightly striate, glabrous, subglabrous or irregularly sparsely sericeous, trichomes simple unicellular, lenticels absent or inconspicuous. *Leaves* 3-foliolate; petioles 3–11.7 cm long, glabrous, subglabrous or irregularly sparsely sericeous; rachises 0.5–2.3 cm long, glabrous, subglabrous or irregularly sparsely sericeous; pulvinuli 4–7 mm long, glabrous or subglabrous; leaflets coriaceous, slightly discoloured, flat, basal pairs $7.5\text{--}16(-19) \times 2.5\text{--}5.7(-8)$ cm, symmetric or slightly asymmetric, narrowly ovate or lanceolate, less frequently elliptic, bases symmetric or slightly asymmetric, rounded, subcordate or obtuse, the apical ones $9.5\text{--}17.3(-21.5) \times 2.8\text{--}7(-8.7)$ cm, symmetric, narrowly ovate or lanceolate, less frequently elliptic, bases symmetric, rounded, subcordate or obtuse, apices acuminate or acute, acumen 5–7 mm long, abaxial surfaces subglabrous or irregularly sparsely sericeous, more densely close to the veins and margins, indumentum ferruginous, adaxial surfaces glabrous or subglabrous, dull to shining, margins revolute; midveins abaxially prominent, adaxially flat or slightly impressed, rarely slightly prominent, secondary veins 8–9 pairs, abaxially prominent, adaxially flat or slightly impressed, rarely slightly prominent, concolorous in relation to the blade, forming angles of $45\text{--}60^\circ$ with midvein, arcuate, tertiary veins abaxially prominent, adaxially flat or slightly prominent, intercostals and epidermals opposite percurrent. *Inflorescences* in thyrsoids or double thyrsoids, axillary or pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncles 0.2–0.8 cm long or inflorescences subsessile, sericeous, rachises 4–12.5 cm long, sericeous, lateral cymes 0.3–1.5 cm long, sericeous, lateral sub-thyrsoids 0.3–8 cm long, sericeous, indumentum of these structures ferruginous; bracts 1–1.2 mm long, sericeous. *Flowers* with pedicels 0.5–1.3 mm long; buds ca. 2×1.5 mm, elliptic or ovate; sepals 5, slightly basally connate, $2.3\text{--}3 \times 0.8\text{--}1.2$ mm, ovate, narrowly ovate, triangulate or narrowly triangulate, apices acute, outer surfaces sericeous or densely pubescent, indumentum brown or ferruginous, inner surfaces pubescent or sparsely so, more densely close to the margins and apex; petals $3.5\text{--}4.8 \times 1\text{--}1.3$ mm, erect, narrowly obovate or oblanceolate, apices acute, glandular dots more than 10, loosely distributed, black, conspicuous, outer surfaces sparsely to densely pubescent, trichomes occasionally concentrated in the ventral portion, glandular trichomes abundant, inner surfaces with only sparse to abundant glandular trichomes, margins with only sparse glandular trichomes; stamens basally connate by ca. 0.5 mm long, shorter series ca. 1.5 mm long, longer series ca. 2.5 mm long, filaments with sparse glandular trichomes; ovaries 1–1.2 mm long, densely pubescent, styles 1.5–1.8 mm long, stigmas bilobate, lobes 0.3–0.5 mm long. *Fruits* $2\text{--}2.2 \times 1.4\text{--}1.6$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 4–8 mm long, stigmas partially persistent, apiculate, ca. 0.5 mm long, outer surfaces subglabrous, black

dots abundant, inner surfaces pubescent or sparsely so, glandular trichomes sparse to abundant, calyces persistent or partially persistent, sepals reflexed or patent; seeds ca. 1.2×0.6 cm, arils yellowish.

Specimens examined: **Brazil.** Bahia: Porto Seguro, Trancoso, estrada Porto Seguro à Trancoso, -16,566331, -39,168533, 12 Sep 2010, bd., *D. A. Folli 6726* (CVRD, ESA, UB). Espírito Santo: Conceição da Barra. Área 214 da Aracruz Celulose S. A., 5 Nov 1992, fr., *O. J. Pereira 4147* (VIES); Área 214 da Aracruz Celulose S. A., 24 Aug 1993, fl., *O. J. Pereira & J. M. L. Gomes 4769* (VIES); Área 215 da Aracruz Celulose S. A., 17 Dec 1992, fr., *O. J. Pereira 4505* (VIES); Área da Veracruz, 22 Oct 2018, st., *C. A. P. Toledo & N. C. Bígio 401* (ESA); Lajinha, próximo ao rio São Mateus, seguindo a estrada de terra atrás do campus do CEUNES, próximo ao Bairro Litorâneo, 1 Aug 2007, fl., *R. F. A. Martins 162* (VIES); Parque Estadual de Itaúnas, área atrás da Fazenda Jequitaita, 18.4239°S, 39.7392°W, 12 Oct 2009, fr., *A. O. Giaretta & M. M. Monteiro 673* (RB, SAMES, VIES); Rancho Tropical II, Comunidade de Lajinha, 05 Sep 2007, bd., *R. D. Ribeiro et al. 860* (RB). Linhares, Reserva Natural Vale, 28 Sep 2015, fl., *D. A. Folli 7410* (CVRD, ESA, RB, UB); Sooretama, trilha próxima ao herbário, 17 Oct 2018, st., *C. A. P. Toledo & N. C. Bígio 398* (ESA).

Distribution, habitat and phenology: *Connarus revolutus* is restricted to northeast Espírito Santo and south Bahia, Brazil (Fig. 13). Individuals are lianas or scandent shrubs up to 3 m tall from the Atlantic Forest, occurring close to coastal zones, in tableland (Tabuleiro) or “restinga” formations, growing on sandy soils, at low elevations. Specimens have been collected with flowers in September and with fruits in October.

Notes: *Connarus revolutus* is easily recognized by the combination of the following characteristics: 3-foliolate leaves, coriaceous leaflets, usually narrowly ovate or lanceolate with revolute margins, arcuate secondary veins, externally pubescent petals and fruit stipes 4–8 mm long. This species is similar to *C. coriaceus* due to the sepals internally hairy and long stipitate fruits, but differs by being exclusive to the Atlantic Forest, with revolute leaflet margins, ferruginous indumentum of inflorescence rachises and externally pubescent petals, while *C. coriaceus* is widely distributed in the Amazon and possesses leaflets with margins flat or slightly revolute, inflorescence rachises with indumentum aureous and petals externally glabrous or subglabrous. *Connarus revolutus* can be confused with *C. blanchetii* as well (also occurring in south Bahia), but differs by the flat leaflets (vs. conduplicate) and fruit stipes 4–8 mm long (vs. 1–3 mm long).

Connarus rostratus (Vell.) L. B. Sm., J. Wash. Acad. Sci. 45: 195. 1955. *Canicidia rostrata* Vell., Fl. Flum.: 184. 1825[1829], Fl. Flum. Icon. 4. *Connarus rostratus* (Vell.) Segadas-Vianna & Trindade, Fl. Ecol. Restingas 15: 21. 1970, *nom. illeg.*—TYPE: Vellozo, Fl. Flum. Icon. 4, t. 139. 1831 (lectotype designated by Forero 1983). Fig. 31

Connarus cymosus Planch., Linnaea 23: 430. 1850.—TYPE: Brazil. Rio de Janeiro: Serra dos Órgãos [Organ Mt.], near Magé, Mar 1837, fl., *G. Gardner* 728 (lectotype designated by Schellenberg 1938: K barcode K000633814!; isolectotypes: BM!, G!, P-frag!).

Connarus cymosus Planch. var. *angustifolius* Baker, in Martius, Fl. Bras. 14(2): 191. 1871.—TYPE: Brazil. Rio de Janeiro: Serra dos Órgãos, s. d., fl., *C. F. P. von Martius* s. n. (lectotype designated by Forero 1983: M [n. v.]).

Lianas or scandent shrubs, rarely treelets 3–5 m tall; branchlets slightly striate, rarely slightly fissured, glabrous or subglabrous, less frequently sparsely sericeous, trichomes simple unicellular, lenticels conspicuous. *Leaves* 3–7-foliolate; petioles 2.5–7.2(–8) cm long, glabrous or subglabrous, occasionally sparsely sericeous; rachises 1.5–6.3(–8) cm long, glabrous or subglabrous, occasionally sparsely sericeous; pulvinuli 4–6 mm long, glabrous or subglabrous, occasionally sparsely sericeous; leaflets chartaceous, slightly discoloured, flat, basal pairs 4.2–11.5 × 1.8–5.2 cm, symmetric, ovate, elliptic, narrowly ovate or narrowly elliptic, bases symmetric, rounded, subcordate, obtuse or narrowly rounded, the apical ones 5.5–16.8 × 2.5–5.8 cm, symmetric, narrowly ovate, rarely narrowly elliptic, bases symmetric, rounded, subcordate, obtuse or narrowly rounded, apices rounded or short acuminate, acumen 1–6 mm long, abaxial surfaces glabrous or subglabrous, occasionally sparsely sericeous on midvein or nearby, indumentum brown, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 8–11 pairs, abaxially slightly prominent, adaxially flat, discoloured in relation to the blade, rarely concolorous, forming angles of 45–65° with midvein, arcuate or slightly so, tertiary veins abaxially slightly prominent, adaxially flat or slightly prominent, intercostals mixed percurrent, epidermals opposite percurrent, the intervenal occasionally reticulate. *Inflorescences* in thyrsoids or double thyrsoids, axillary, 1–3 per axil, trichomes simple unicellular, peduncles 0.2–1.5(–3) cm long, sericeous or sparsely so, rachises 7.5–21 cm long, sericeous or sparsely

so, lateral cymes 0.7–2.5 cm long, sericeous, lateral sub-thyrsoids 0.7–5.5 cm long, sericeous, indumentum of these structures brown, ferruginous or griseous; bracts 0.5–1 mm long, sericeous. *Flowers* with pedicels 0.7–2 mm long; buds ca. 2×2 mm, orbicular; sepals 5, slightly basally connate, $2-2.5(-2.8) \times 0.8-1.3$ mm, ovate or narrowly ovate, apices acute or obtuse, outer surfaces sericeous or sparsely so, indumentum brown or ferruginous, inner surfaces glabrous or subglabrous, occasionally pubescent only at apex; petals $3-4 \times 1-1.5$ mm, reflexed, narrowly obovate, narrowly elliptic or oblanceolate, apices rounded or obtuse, glandular dots more than 10, loosely distributed, black, inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous; stamens basally connate by 0.3–0.8 mm long, shorter series 1–2.5 mm long, longer series 1.5–3.5 mm long, filaments with sparse glandular trichomes, rarely glabrous; ovaries 0.8–1.2 mm long, densely pubescent, styles 0.7–1.2 mm long, stigmas bilobate, lobes 0.3–0.5 mm long. *Fruits* $1.6-2 \times 1.2-1.5$ cm, obovate or semi-orbicular falcate, indehiscent side sigmoid or semi-annular, pericarps up to 2 mm thick, stipes 2–4 mm long, styles partially persistent, rostrate, spinescent or apiculate, (1–)2–5 mm long, outer surfaces irregularly sparsely sericeous, more densely on stipe and sutures, indumentum brown, black dots abundant, inner surfaces pubescent, glandular trichomes absent, calyces persistent or partially persistent, sepals ascending curved; seeds $1.1-1.2 \times 0.6-0.7$ cm, arils yellowish.

Selected specimens examined: **Brazil.** Paraná: Adrianópolis, Parque Estadual das Lauráceas, 29 Jul 2010, fr., *J. M. Silva & C. B. Poliquesi* 7633 (MBM, RB); Campinas Grande do Sul, Serra Virgem, 12 Nov 1968, fl., *G. Hatschbach* 20292 (K, MBM, P). Rio de Janeiro: Freixal, s. d., fl., *G. Gardner* 3442 (BM); Serra dos Órgãos [Organ Montains], Mar 1941, fl., *G. Gardner* 5687 (BM, K); *S. loc.*, s. d., fl., *J. Miers* 4174 (K). Santa Catarina: Florianópolis, Morro do Ribeirão, alt. 400 m, 19 Dec 1967, fl., *R. Klein & Besolin* 7679 (MBM); Ibirama, 24 Oct 1997, fr., *A. Krambech s. n.* (FURB 22548); Itajaí, Braço Joaquim, Luis Alves, alt. 350 m, 14 Dec 1954, fl., *R. Klein* 915 (NY); Schroeder Barragem 8° Salto, $26^{\circ}17'42''\text{S}$, $49^{\circ}03'26''\text{W}$, alt. 715 m, 26 Jun 2018, fr., *A. Kassner-Filho* 2902 (FURB); Serra do Matador, Rio do Sul, 12 Mar 1959, fr., *Reitz & Klein* 8535 (G, K); Três Barras, Guaruva, S. Francisco do Sul, 150 m, 7 Nov 1957, fl., *Reitz & Klein* 5641 (G). São Paulo: Bertioga, Parque Nacional da Restinga de Bertioga, praia de Itaguapé, trilha próxima ao encontro do rio com o mar, $23^{\circ}46'45.0''\text{S}$, $45^{\circ}58'20.0''\text{W}$, 21 Dec 2019, fr., *C. A. P. Toledo* 413 (ESA); Eldorado, Parque Estadual de Jacupiranga, Núcleo da Caverna do Diabo, trilha do rolado, $24^{\circ}38'41''\text{S}$, $48^{\circ}23'41''\text{W}$, 3 Sep 1995, fr., *R. R. Rodrigues et al.* 145 (ESA); Pariquera-Açu, Estação Experimental do IAC,

24°36'30"S, 47°53'06"W. 24 May 1995, fr., *N. M. Ivanauskas* 168 (ESA); 9 Nov 1995, fl., *N. M. Ivanauskas* 542 (ESA, UB, UEC). Santos, 1 Jan 1899, fl., *Debeaux* 38 (P); São Miguel Arcanjo, 6 Aug 1994, fr., *P. L. R. Moraes* 1030 (ESA, RB); Ubatuba, Paruba, 23°21'05.3"S, 44°56'05.2"W, 1 Jul 1993, fl., *K. D. Barreto et al.* 1698 (ESA, UEC). State unknown: *S. loc. S. d.*, fl., *L. Riedel s. n.* (P); *s. d.*, fl., fr., *W. J. Burchell* 2533 (K, P); *s. d.*, fl., *W. J. Burchell* 3658 (P).

Distribution, habitat and phenology: *Connarus rostratus* is exclusively found in south and southeast Brazil, establishing the austral distribution of the genus in the Neotropics (Fig. 11). Individuals of this species are normally scandent shrubs from the Atlantic domain, growing in the undergrowth of arboreal coastal vegetations (restinga) or ombrophilous forests, on clay or sandy soils, at elevations ranging from sea level to ca. 700 m. Specimens have been collected with flowers mainly from November to March and with fruits irregularly almost throughout the year.

Notes: This species is morphologically recognized by the 3–7-foliolate leaves, usually narrowly obovate or narrowly elliptic leaflets, short acumen and internally pubescent fruits, with apex normally rostrate or spinescent. It is similar to *C. regnellii*, differing in leaflet shape, petal length and fruit indumentum (see “Notes” section of *C. regnellii*). *Connarus rostratus* is commonly confused with *C. beyrichii* (also occurring in southeast Brazil), but differs by the slightly broader leaflets, disposition of tertiary veins and petals length (see “Notes” section of *C. beyrichii*).

The basionym of *C. rostratus* was described by Vellozo (1829) and no physical specimen has been found. Consequently, Smith (1955) proposed a neotype for the name, which was refused by Forero (1983), under the argument that illustrations are eligible as type collections according to the *Code* (Turland et al. 2018, Art. 9.1 and 9.3). The present treatment agrees with Forero’s (1983) position, but considers that the illustration in Vellozo (1831) is the lectotype of *Canicidia rostrata*, which was selected by Forero (1983) after the author referred to the illustration as “type”. This should be regarded as lectotype because no specimen has been found and the illustration, despite published after the protologue, is considered part of the original description as it was cited by Vellozo (1829).

Connarus ruber (Poepp.) Planch., Linnaea 23: 436. 1850. *Omphalobium rubrum* Poepp., Nov. Gen. Sp. Pl. 3: 76. 1845. *Connarus ruber* (Poepp.) Planch. var. *ruber*.—TYPE: Brazil. Amazonas. In sylvis ad Ega, Sep 1831, fr., *E. F. Poeppig* 2608 (lectotype designated by Toledo et al. 2020b: W 0048757!; isolectotype: P!). Fig. 32

Connarus sprucei Baker, in Martius, Fl. Bras. 14(2): 187. 1871. *Connarus ruber* var. *sprucei* (Baker) Forero, Fl. Neotrop. Monogr. 36: 116. 1983.—TYPE: Brazil. Amazonas. Falls of S. Gabriel, gapó, Apr 1852, fl., *R. Spruce* 2264 (lectotype first step designated by Forero 1983: K; lectotype second step designated by Toledo et al. 2020b: K barcode K 000633817!; isolectotypes: F!, G!, GH [n. v.], K!, NY!, P!, W!).

Lianas or scandent shrubs, less frequently treelets 3–9(–12) m tall; branchlets slightly striate, glabrous or subglabrous, less frequently sparsely sericeous, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3-foliate; petioles 3.5–13.5(–18) cm long, glabrous or subglabrous, rarely sparsely sericeous; rachises 0.5–3 cm long, glabrous or subglabrous, rarely sparsely sericeous; pulvinuli 4–6 mm long, glabrous or subglabrous; leaflets chartaceous to subcoriaceous, concolorous or slightly discolorous, flat, basal pairs 8.3–23 × 4.5–9.5 cm, symmetric or slightly asymmetric, elliptic or ovate, occasionally narrowly elliptic, bases symmetric or slightly asymmetric, rounded, subcordate or obtuse, rarely acute, the apical ones 11.5–25 × 5–11.5 cm, symmetric, elliptic or ovate, occasionally narrowly elliptic, bases symmetric, rounded, subcordate or obtuse, rarely acute, apices acuminate to cuspidate, acumen (7–)10–25 mm long, abaxial surfaces glabrous or subglabrous, occasionally sparsely sericeous on midvein, indumentum brown, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins (9–)10–14 pairs, abaxially prominent, adaxially flat, occasionally slightly impressed, concolorous or discolorous in relation to the blade, forming angles of 45–60° with midvein, arcuate, tertiary veins abaxially prominent or slightly so, adaxially flat or slightly prominent, intercostals and epidermals opposite percurrent. *Inflorescences* in double thyrsoids, axillary or pseudo-terminal, 1–4 per axil, trichomes simple unicellular, peduncles 0.2–1.5 cm long or inflorescences subsessile, sericeous or sparsely so, occasionally densely pubescent, rachises 10–35 cm long, sericeous or sparsely so, occasionally densely pubescent, lateral sub-thyrsoids 3.5–16 cm long, sericeous or densely pubescent, indumentum of these structures brown or ferruginous; bracts 0.5–1 mm long, sericeous. *Flowers* with pedicels 0.5–1 mm long; buds 1 ×

0.8–1 mm, orbicular or elliptic; sepals 5, slightly basally connate, 1.5–1.8 × 0.6–0.8 mm, elliptic, ovate or narrowly triangulate, apices acute, outer surfaces sericeous or sparsely so, indumentum brown or ferruginous, inner surfaces sparsely sericeous, pubescent only at apex; petals 2.5–3.5 × 0.7–1 mm, erect, narrowly obovate or oblong, apices rounded or obtuse, rarely acute, glandular dots more than 10, loosely distributed, black or colorless, conspicuous or inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent or sparse, margins glabrous or with only sparse glandular trichomes; stamens basally connate by 0.2–0.8 mm long, shorter series 0.7–1.5 mm long, longer series 1–3 mm long, filaments glabrous or with sparse glandular trichomes; ovaries 0.5–0.8 mm long, densely pubescent, styles ca. 0.5 mm long, stigmas bilobate, lobes 0.1–0.3 mm long. *Fruits* 1.5–1.9 × 1.1–1.5 cm, obovate or semi-orbicular, indehiscent side linear, pericarps up to 2 mm thick, stipes 1–2(–3) mm long, styles partially persistent, inconspicuous, rarely apiculate, 0.2(–1) mm long, outer surfaces sparsely sericeous to glabrescent, indumentum brown, black dots abundant or sparse, inner surfaces densely pubescent, glandular trichomes absent, calyces deciduous, rarely partially persistent, sepals reflexed; seeds 1–1.3 × 0.6–0.7 cm, arils yellowish.

Selected specimens examined: **Bolivia.** Beni: Km 1 & 2 along road to Hamburgo, at SE edge of Riberalta, 11°02'S, 66°06'W, 220 m alt., 30 May 1982, fl., *J. C. Salomon* 7865 (G, MO). Pando: Madre de Dios, Blanca Flor, de la Carretera de Sena a Riberalta, 10 km al sureste del pueblo Naranjal casi hasta el Río Beni, camino cruzando “Pampa de Blanca Flor” a 4 km ao suroeste de Blanca Flor, 11°43.84'S, 66°57.54'W, 150–200 m alt., 9 Jul 2002, fl., *J. Urrelo et al.* 130 (F, LPB). Santa Cruz: Velasco Province, Parque Nacional Noel Kempff Mercado, Campamento Las Gamas, 14°48'23''S, 60°23'12''W, 825 m alt., 30 Oct 1925, fr., *P. F. Foster et al.* 560 (G, MO). **Brazil.** Acre: Feijó, Basin of Rio Muru, village of Colombo, 08°46'S, 71°06'W, 200 m alt., 15 Apr 2002, fl., *P. Delprete et al.* 8503 (COL, NY); Mâncio Lima, Ramal do Chaparal a beira de um afluente do igarapé preto, 12 Jul 2013, fl., *D. S. Costa et al.* 181 (RB). Amazonas: Humaitá, Tenharins, km 132 pela Transamazônica em direção a Pará, a 07°31' Lat., 63°10' Lon., 6 Jun 1980, fr., *A. Janssen* 467 (M); Manicoré, BR 230, Rod. Transamazônica km 302, Rio Aripuanã entre a Rod. e a Cachoeira Matamatá, 07°35'S, 60°40'W, 24 Apr 1985, fl., *C. A. C. Ferreira* 5772 (INPA, RB); Pauíni, Floresta Nacional do Purus, igarapé Mapiá, 08°25'32.6''S, 67°31'10.5''W, 22 Jul 2008, fr., *A. Quinet* 1297 (RB); Prope Panure ad Rio Uaupés, *s. d.*, fr., *R. Spruce* 2562 (K, P); Rio Uatumã, margem direita subindo o rio, entre cachoeira Morena e Balbina, 10 Aug 1979, fr., *C. A. C. Ferreira et al.* 104 (INPA, NY). Mato Grosso: Itauba, margem do Rio Teles Pires, entre a Balsa J. F. Grimas e o

Rancho do Rogerio, 13 Jul 2008, fr., *V. Maioli et al.* 678 (RB); Nucleo Pioneiro de Humboldt, Aripuanã, forest along margin of Rio Aripuanã, 10°12'S, 59°21'W, 20 Oct 1973, fr., *C. C. Berg et al.* P19801 (INPA, NY); Santa Cruz do Xingu, Parque Estadual do Xingu, Rio Fontourinha, após a ponte, 8°43'36''S, 52°21'50''W, 257 m alt., 12 Mar 2011, fl., *W. Milliken et al.* 4272 (RB). Pará: Novo Progresso, Serra do Cachimbo, rio Braço Norte, 21 Aug 2013, fr., *F. Bonadeu & A. K. Koch* 736 (NY, RB). Rondônia: Alvorada do Oeste, quintal de sítio, 11°21'26''S, 62°17'46''W, 183 m alt., 29 Sep 2013, fr., *N. C. Bígio et al.* 1126 (RB, RON); Porto Velho, margens do Rio Cotia, 09°41'58''S, 63°00'05''W, 90 m alt., 25 Apr 2012, fr., *G. Pereira-Silva et al.* 16231 (CEN, RB). **Colombia.** Vuapés: Mitú, Río Caduyari, afluente del Río Vuapés, resguardo indígena de la Comunidad Indígena de Piracemo (Comunidad Cubes), 1°21'14.6''N, 70°23'54.9''W, 29 Sep 2001, fr., *C. R. López et al.* 7356 (COL). **French Guiana.** Comté, entre Roche Fendée et Bélizon, 21 Jul 1965, fr., *Oldeman* 1444 (P); Sinnamary, route de Ste. Elie, camp N° 2, 14 Jul 1977, fr., *C. Sastre* 5450 (P); Station de la Piste de St. Elie (Ecerex), km 15,5, 5°17'N, 53°3'O, 15 May 2002, fr., *M. F. Prévost & D. Sabatier* 4527 (NY, P). **Peru.** Amazonas: Cerros Kampankis, Serranía entre los ríos Santiago y Morona, desde río Marañon hasta frontera com Ecuador, 03°07'01.52''S, 77°46'55.14''W, 520 m alt., 3 Aug 2011, fl., *I. Huamantupa et al.* 15229 (F). Loreto: Balsapuerto, 220 m alt., *s. d.*, fl., *G. Klug* 2937 (G); Lower Rio Huallaga, 155–210 m alt., Oct–Nov 1929, fr., *L. Williams* 3806 (G); Rio Monon near Rio Nanay, 4 Sep 1972, fl., *T. B. Croat* 19973 (COL, MO); Maynas, Indiana, Río Amazonas, Quebrada de Yanayacu, Bombonaje, margen del pasto del Sr. Victor Novoa, ca. 90 m alt., 15 Nov 1988, fr., *Y. M. Rimachi* 9001 (NY, US). **Venezuela.** Amazonas: Alto Orinoco, Río Orinoco, entre Laulau y la boca del Río Cunucunuma, 03°09'02''N, 66°02'21''W, Oct 1999, fr., *A. Fernández et al.* 15880 (NY); Atures, bosque alto denso, a orillas del río Cataniapo, desde el lugar de la futura represa hasta el caserío San Pedro de Cataniapo, 5°38'N, 67°11'W, 90–110 m alt., 5 Aug 1980, fr., *F. Guanchez* 112 (COL); Cerro Sipapo (Paráque), vicinity of Base Camp, 28 Dec 1948, fr., *B. Maguire & L. Politi* 27979 (NY); Río Mavaca, river below basecamp, 02°01'N, 65°07'W, 228 m alt., 6 Feb 1989, fr., *A. Henderson et al.* 980 (NY). Bolivar: Rio Parguaza, river banks 3–5 km. below El Carmen (about 50 river km. from mouth), 110 m alt., 24 Dec 1955, fr., *J. J. Wurdack & J. V. Monachino* 40927 (NY). *S. loc.*, En la margen poblada del Orinoco llegando hasta la superficie del agua, arriba de Tamata, Alto Orinoco, 121 m. alt., 6 May 1942, fr., *L. Williams* 15195 (G).

Distribution, habitat and phenology: *Connarus ruber* is one of the most common species of the genus in the Neotropics and it is widely distributed in the Brazilian Amazon,

especially in Amazonas, also with representative collections from south Venezuela, less common in Bolivia, Colombia, French Guiana and Peru (Fig. 16). Some individuals have also been found in the transition between the Amazon and the Cerrado in Mato Grosso (Brazil), establishing the austral distribution of this species. It is represented by lianas or scandent shrubs, with few individuals reported as small trees, which is unusual and probably related to the condition of growing in open fields. *Connarus ruber* mainly occurs in flooded areas, such as ciliary or “igapó” forests, but also growing in disturbed environments, in clay or sandy soils, at 40–400 m elevation. Specimens have been collected with flowers and fruits practically throughout the year.

Notes: Although *C. ruber* is a widely distributed species, it is easily recognized by the exclusively 3-foliolate leaves, 10–14 pairs of abaxially prominent secondary veins, inflorescences in large double thyrsoids, sepals 1.5–1.8 mm long, petals 2.5–3.5 mm long, and fruits stipes usually 1–2 mm long. It is morphologically similar to *C. ecuadorensis* due to the number of secondary veins and large inflorescences, but differs by the number of leaflets, sepal and petal sizes, and stipe length (see “Notes” section under *C. ecuadorensis*). *Connarus ruber* can also be mistaken for *C. negrensis* (previously treated as a variety of *C. ruber*, but see discussion below), but differs in flowers size, fruit indumentum and stipe length, and disposition of sepals on fruits (see “Notes” section of *C. negrensis*).

Connarus ruber was divided into three varieties by Forero (1983), but the differences presented in Table 3 are consistent enough to recognize three taxa at species level, also in accordance with Schellenberg (1938).

Poeppig (1845) described *Omphalobium rubrum* (the basionym of *C. ruber*), without prompt indicating which material he used to described his new species. Then Schellenberg (1938) inadvertently selected as lectotype the specimen *Poeppig* 2759. After analyzing Poeppig’s collections, it became clear the lectotype should be replaced to *Poeppig* 2608 as this specimen has Poeppig’s handwriting fully indicating *O. rubrum* and where he described it, and the information on its herbarium sheet label matches accurately with the original description, which is not observed in the specimen *Poeppig* 2759. Another lectotype was therefore proposed to *O. rubrum* (= *C. ruber*) by Toledo et al. (2020b), who presented detailed information on this issue, with discussions of practical applications. By proposing a different lectotype, another name had to be reestablished (*C. negrensis*), and *C. sprucei* was placed in the synonymy of *C. ruber* (Toledo et al. 2020b).

Connarus schultesii Standl., in Schultes, Bot. Mus. Leaf. 9(9): 173. 1971.—TYPE: Mexico.

Oaxaca: Choapam, Montains southeast of San Juan Lalana, 17°25'N, 95°45'W, alt. 700 m, 9 May 1939, fr., *R. E. Schultes & B. P. Reko* 833 (holotype: F 1016861!; isotypes: ECON [photo!], GH [photo!], US [photo!]). Figs. 24E–H

Lianas, scandent shrubs or trees, ca. 5 m tall; branchlets slightly striate, tomentose or lanate to glabrescent, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3-foliolate; petioles 3.6–9.5 cm long, tomentose or lanate to glabrescent; rachises 0.5–2.2 cm long, tomentose or lanate to glabrescent; pulvinuli 5–9 mm long, tomentose to glabrescent; leaflets chartaceous to subcoriaceous, concolorous, flat, basal pairs $9.2\text{--}21.5 \times 2.7\text{--}7.3(-9)$ cm, asymmetric, narrowly elliptic, obovate or narrowly so, or oblong, bases asymmetric, acute or obtuse, occasionally rounded in the broader side, the apical ones $9.3\text{--}23 \times 3.2\text{--}7.6(-10)$ cm, symmetric, obovate or narrowly so, or oblong, bases symmetric, rounded or obtuse, apices short acuminate, rarely long acuminate, acumen 1–3(–12) mm long, abaxial surfaces tomentose to glabrescent, usually more densely on midvein, indumentum brown, adaxial surfaces glabrous or subglabrous, dull, margins flat, rarely slightly revolute; midveins abaxially prominent, adaxially flat, secondary veins 8–11 pairs, abaxially prominent, adaxially flat, rarely slightly impressed, concolorous in relation to the blade, forming angles of 45–55(–65)° with midvein, arcuate or slightly so, tertiary veins abaxially prominent or slightly so, adaxially flat, rarely slightly prominent, intercostals reticulate or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids, rarely double thyrsoids, axillary, 3–5 per axil, rarely ramiflorous, trichomes simple unicellular, peduncles 0.2–2 cm long, tomentose, rachises 7–16.5 cm long, tomentose, lateral cymes 0.3–1.5 cm long, tomentose, lateral sub-thyrsoids 2.3–5 cm long, tomentose, indumentum of these structures brown or ferruginous; bracts 1–1.3 mm long, tomentose. *Flowers* with pedicels 1–2 mm long; buds ca. 2.5×2 mm, ovate; sepals 5, slightly basally connate, $2\text{--}2.5 \times 1.2\text{--}1.3$ mm, ovate, apices acute, outer surfaces tomentose, indumentum ferruginous, inner surfaces tomentose or sparsely so, more densely at apex; petals $4.5\text{--}5 \times 1.5\text{--}2$ mm, reflexed, narrowly obovate or narrowly elliptic, apices rounded or acute, glandular dots absent or up to 5, loosely distributed, black, inconspicuous, both surfaces subglabrous or sparsely sericeous, glandular trichomes sparse, margins with abundant glandular trichomes; stamens basally connate by 0.3–1 mm, shorter series 1.7–3.5 mm long, longer series

2.5–4.5 mm long, filaments glabrous, occasionally with sparse glandular trichomes only on longer filaments; ovaries 1–1.2 mm long, densely pubescent, styles 0.8–1 mm long, stigmas bilobate, lobes ca. 0.3 mm long. *Fruits* 2.1–3.1 × 1.5–2.3 cm, obovate or semi-orbicular, indehiscent side sigmoid or linear, pericarps up to 2 mm thick, stipes 4–7 mm long, styles partially persistent, inconspicuous, ca. 0.5 mm long, outer surfaces tomentose or lanate to glabrescent, indumentum brown or ferruginous, black dots absent or abundant, inner surfaces sparsely tomentose to densely tomentose or hirsute, glandular trichomes sparse or absent, calyces deciduous or partially persistent, sepals ascending erect, patent or reflexed; seeds 1.6–1.8 × 0.8–1.3 cm, arils yellowish.

Selected specimens examined: **Mexico.** Veracruz: Catemaco. Cerro de Pipiapan, 18°27'N, 95°02'W, 500 m, 24 Apr 1987, fl., *R. Acosta et al.* 1566 (NY, XALU); lado S. E. de Lago Caramaco, arriba de Rio Cuetzalapan, 18-23 N, 95-01 W, 25 Oct 1971, fr., *J. H. Beaman* 5168 (F, NY, MEXU, MSC). Coatzacoalcos, a 0.8 km al E de los quemadores de PEMEX, 18°06'03"N, 94°19'53"W, 1 Apr 2003, fr., *C. H. Ramos & E. Martínez* 2207 (BM, MEXU); El Majahual, Los Tuxtlas, alt. 100 m., 8 Nov 1967, fr., *M Sousa* 3294 (MEXU); Estacion Biologica Tropical de Los Tuxtlas. 4 Jul 1970, st., *G. Martinez* 3034 (F); 180 m, 26 May 1970, fr., *G. Martinez* 3014 (F, K); UNAM camino a la Laguna Escondida, 18°35'N, 95°04'W, 29 Mar 1979, fl., *M. Dillon et al.* 1848 (F, NY, K). Ixhuatlán del Sureste, 2.34 km al SO de Ixhuatlán del Sureste 18°00'49.50"N, 94°24'31.90"W, alt. 28 m, 26 Oct 2012, fr., *J. C. Soto & P. S. Colin* 28627 (MEXU); Laguna Majahual, Los Tuxtlas, 110 m, 8 Jun 1967, fr., *M. Sousa* 3294 (US); Mecayapan, Volcán de San Martín Pajapan, al S del Ejito La Valentina, 5 Aug 1985, fl., fr., *J. I. Calzada* 11214 (MEXU); Poblado de Laguna escondida a 5 km de la estacion de Biologia Tropical "Los Tuxtlas", San Andres Textla, 18°35'N, 95°05'W, 170 m, 21 Mar 1975, fl., fr., *J. I. Calzada* 1778 (F, US); San Andres Tuxtla. Estación de Biología Tropical Los Tuxtlas, lote 67, 95°04'S, 95°09'W, 18°34' y 18°36'N, alt. 200 m, 30 Mar 1984, fl., *G. I. Manriquez* 1427 (MEXU); Lote 67, Est. Biol. Trop. Los Tuxtlas, 22 Jul 1983, fr., *G. I. Manriquez* 761 (NY); Wallace 100 y el límite de la Estación de Biol. Los Tuxtlas 30 Km al N de Catemaco camino a Monte Pio, 20 Mar 1984, fl., *R. Cedillo T. & S. Sinaca* 2679 (MEXU, US). Tebanca (camino a la Magdalena), 20 Oct 1971, fr., *J. I. Calzada* 614 (F, GH).

Distribution, habitat and phenology: *Connarus schultesii* is restricted to the states of Oaxaca (type specimen) and Veracruz in Mexico, being widely collected in the latter state, especially in the Biological Station of Los Tuxtlas, municipality of San Andrés Tuxtla (Fig. 16). It is a lianescent or arboreal species occurring in evergreen forests, occasionally associated

to ciliary forests, on clay soils, at approximately 30–700 m elevation. Specimens have been collected with flowers from March to April and in August, and with fruits irregularly almost throughout the year.

Notes: *Connarus schultesii* is morphologically characterized by the 3-foliolate leaves, asymmetric basal leaflets (as well as their bases), inflorescences usually in thyrsoids and fruits $2.1\text{--}3.1 \times 1.5\text{--}2.3$ cm, externally with a dense indumentum. This species can be confused with another Mexican species, *C. lonchotus*, which occasionally has slightly asymmetric basal leaflets, but differs by the leaflets 2.7–7.6(–10) cm wide (vs. usually 1.7–3.8 cm wide), 8–11 pairs of secondary veins (vs. 7–9 pairs), inflorescence rachis tomentose (vs. sericeous or sparsely so) and fruits 1.5–2.3 cm wide, externally tomentose or lanate to glabrescent (vs. fruits 1.4–1.5 cm wide, externally irregularly sparsely sericeous). In addition, basal leaflets are notably asymmetric in *C. schultesii*, while in *C. lonchotus* they are slightly asymmetric or even symmetric. Geographic distribution may also assist in differentiating these species: *C. schultesii* is only found in the states of Oaxaca and Veracruz, occurring in evergreen forests at lower elevations (up to 700 m), while *C. lonchotus* is only found in the state of Chiapas, distributed mainly in montane semi deciduous forests at 500–1950 m elevation.

Connarus schultesii also resembles *C. popenoei* due to the large leaflets with asymmetric base and fruits with a dense indumentum, but differs by the usually flat secondary veins on adaxial surfaces (vs. secondary veins adaxially impressed) and pedicellate flowers (vs. sessile flowers). In addition, the former only occurs in south Mexico, while the latter, only in Honduras.

Connarus silvanensis Cuatrec., Fieldiana, Bot. 27(2): 102. 1951.—TYPE: Colombia. Valle: Costa del Pacífico, Río Cajambre, Silva, 5–80 m alt., 5–15 May 1944, fr., *J. Cuatrecasas* 17454 (lectotype **designated here**: F 1366107!; isoelectotypes: F!, U [photo!], US [photo!]). Figs. 28E–G

Lianas, scandent shrubs, treelets or trees, 3–7 m tall; branchlets slightly striate, subglabrous, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3-foliolate; petioles 5–17 cm long, subglabrous, rarely sparsely sericeous; rachises 1.3–3.7(–5) cm long, subglabrous, rarely sparsely sericeous; pulvinuli 6–8 mm long, subglabrous; leaflets

chartaceous or subcoriaceous, slightly discoloured, flat, basal pairs $13\text{--}28 \times 6.2\text{--}16$ cm, symmetric, elliptic or obovate, bases symmetric, acute or obtuse, the apical ones $17.5\text{--}36.5 \times 9\text{--}19.2$ cm, symmetric, elliptic or obovate, bases symmetric, acute or obtuse, apices short acuminate, rarely long acuminate, acumen $(1\text{--})3\text{--}8(21)$ mm long, abaxial surfaces glabrous or subglabrous, irregularly sparsely sericeous only on the veins, indumentum brown, adaxial surfaces glabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed or slightly so, secondary veins 9–14 pairs, abaxially strongly prominent, adaxially impressed, discoloured or concolorous in relation to the blade, forming angles of $45\text{--}60^\circ$ with midvein, arcuate or slightly so, tertiary veins abaxially prominent or slightly so, adaxially flat, intercostals and epidermals opposite percurrent. *Inflorescences* in thyrsoids, axillary or ramiflorous, 2–4 per axil, trichomes simple unicellular, inflorescences subsessile, rachises 7–8.2 cm long, sericeous, lateral cymes ca. 0.3 cm long, sericeous, indumentum of these structures brown or aureous; bracts ca. 1 mm long, sericeous. *Flowers* mature not seen, pedicels 0.5–1 mm long; buds ca. 2×2 mm, orbicular; sepals 5, slightly basally connate, at least 2 mm long, outer surfaces sericeous, indumentum aureous, inner surfaces sparsely sericeous; petals with glandular dots more than 10, loosely distributed, black, conspicuous, outer surfaces sparsely sericeous, inner surfaces subglabrous, glandular trichomes absent, margins glabrous; stamen filaments with sparse glandular trichomes; ovaries densely pubescent. *Fruits* $2\text{--}3.2 \times 1\text{--}1.8$ cm, narrowly obovate, indehiscent side straight, pericarps up to 2 mm thick, stipes 1–2 mm long or fruits sessile, styles partially persistent, inconspicuous or apiculate, 0.2–1 mm long, outer surfaces sericeous to glabrescent, indumentum brown, black dots absent, inner surfaces pubescent, rarely subglabrous, glandular trichomes abundant or absent, calyces persistent, sepals ascending erect, rarely patent; seeds $1.1\text{--}2 \times 1$ cm, arils yellowish.

Specimens examined: **Colombia.** Chocó: Bahía de Soano, subiendo por Quebrada Seca hacia la Chorrera, 11 Jun 1950, fl., fr., *A. Fernandez 321* (US). Valle: Buenaventura, corregimiento San Cipriano, Reserva Natural de Escalerente, sendero a saragoza, sector norte casa Administración, 18 Nov 1992, bd., *W. Devia et al. 3514* (COL). **Panamá.** Colón: Río Ganche, ca. 3 km upriver from bridge on road to Portobelo, 25 m alt., 24 Mar 1975, fr., *S. Mori & J. Kallunki 5200* (MO). Darién: Casi-Cana trail on Cerro Campamiento E of Tres Bocas, head water of Río Coas, 29 Apr 1968, fr., *J. H. Kirkbridge & J. A. Ducke 1231* (NY); Cerro Campamento (south of Cerro Pirre), 20–22 Mar 1968, fl., *J. A. Ducke 15571(3)* (MO); Foothills of Cerro Coasi, headwaters of Río Coasi, 20–22 Mar 1968, fr., *J. A. Ducke 15627(3)* (MO); North Slopes of Cerro Pirre, 300–700 m alt., 6 Apr 1975, fr., *S. Mori & J. Kallunki 5437* (MO);

Summit of Cerro Pirre, 1000–1400 m alt., 29 Jul 1972, fr., *A. Gentry & A. Clewell 7104* (MO).
Panamá: Along El Llano to Carti road, 09°15'04"N, 79°00'04"W, 6 Mar 1987, fr., *G. McPherson 10617* (BM, MO, NY).

Distribution, habitat and phenology: *Connarus silvanensis* occurs from west Colombia to central Panamá (Fig. 23). Individuals of this species have been reported as lianas, scandent shrubs or trees, distributed mainly in wet upland forests at elevations ranging from 5–1400 m. Specimens have been collected with flowers in March and June and with fruits from March to July.

Notes: *Connarus silvanensis* is morphologically recognized by the large leaflets, adaxially impressed secondary veins and inflorescences in fasciculate thyrsoids, which are axillary or ramiflorous. This species is similar to *C. popenoei* due to the large and usually obovate leaflets with secondary veins adaxially impressed. However, *C. silvanensis* differs by the subglabrous branchlets, externally aureous-sericeous sepals and narrowly obovate fruits, externally sericeous, with stipe up to 2 mm long, while in *C. popenoei* branchlets are densely lanate, sepals are externally ferruginous-hirsute and fruits are semi-orbicular, externally lanate, with stipe 4–6 mm long.

Connarus steyermarkii Prance, Mem. New York Bot. Gard. 15: 129. 1966.—TYPE: Venezuela. Distrito Federal: Cerro Naiguatá, laderas pendientes del lado del mar que miran hacia el Norte, arriba del pueblo de Naiguatá, bosque húmedo denso, Lomas de Las Delicias, entre Quebrada de Basenilla y Quebrada Guayoyo, 9–12 Km. Suroeste de Hacienda Cocuizal, alt. 1500–1635 m, 15–19 Nov 1963, fl., *J. A. Steyermark 91995* (holotype: VEN barcode VEN 67751 [photo!]; isotypes: F [photo!], K!, US [photo!]).

Lianas; branchlets slightly striate or smooth, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels inconspicuous. *Leaves* 5–7-foliolate; petioles 4–10.5 cm long, tomentose to glabrescent; rachises 4.7–10.8 cm long, tomentose to glabrescent; pulvinuli 5–8 mm long, tomentose to glabrescent; leaflets chartaceous, concolorous or slightly discoloured, flat, basal pairs 6.5–12.8 × 3.2–6.5 cm, asymmetric or slightly so, ovate, elliptic, narrowly elliptic or narrowly obovate, bases asymmetric or slightly so, obtuse, rarely rounded, the apical ones 10.5–16.5 × 4–9 cm, symmetric or slightly asymmetric, ovate, elliptic, narrowly

elliptic, ovate or narrowly obovate, bases symmetric or slightly asymmetric, obtuse or acute, rarely rounded, apices acuminate or shortly so, acumen 2–8 mm long, both surfaces tomentose to glabrescent, occasionally abaxially tomentose only on midvein, indumentum brown or ferruginous, adaxial surfaces dull, margins flat; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins 6–9 pairs, abaxially prominent, adaxially flat, rarely slightly prominent, concolorous in relation to the blade, forming angles of 55–65° with midvein, arcuate, tertiary veins abaxially slightly prominent or flat, adaxially flat, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in thyrsoids, axillary or pseudo-terminal, 1–2 per axil, trichomes dendroid and simple unicellular, peduncles 0.2–3 cm long, tomentose, rachises 10.5–24 cm long, tomentose, lateral cymes 0.3–2 cm long, tomentose, indumentum of these structures ferruginous; bracts 1–2 mm long, tomentose. *Flowers* with pedicels ca. 1 mm long; buds ca. 2 × 2 mm, orbicular; sepals slightly basally connate, 3.5–4 × 1.5 mm, narrowly ovate, apices acute, outer surfaces tomentose, indumentum ferruginous, inner surfaces glabrous; petals 4–4.5 × 1.5 mm, erect, oblong, apices obtuse or acuminate, glandular dots more than 10, loosely distributed, black, conspicuous or inconspicuous, both surfaces glabrous, margins glabrous; stamens basally connate by ca. 0.3 mm, shorter series ca. 2.5 mm long, longer series ca. 3.5 mm long, filaments glabrous; ovaries mature not seen, tomentose, styles and stigmas not seen. *Fruits* 1.9–2.1 × 1.5–1.6 cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 2–5 mm long, styles partially persistent, inconspicuous, ca. 0.4 mm long, outer surfaces tomentose to glabrescent, indumentum ferruginous, black dots absent or abundant, inner surfaces tomentose, glandular trichomes abundant, calyces deciduous or partially persistent, sepals patent or reflexed; seeds 1.1–1.3 × 0.6–0.7 cm, arils color not seen.

Specimens examined: **Venezuela.** Carabobo: Selve siempre verde em las quebradas al norte de Los Tanques, arriba de la Planta Eléctrica, em las cabeceras del Río Gián, al sur de Borburata, alt. 750 m, 1 Apr 1966, fl., *J. A. Steyermark & C. Steyermark* 95426 (M, NY). Sucre: Península de Paria. Cerro Espejo, entre Manacal y Pauji, arriba de Mundo Nuevo, arriba de Río Seco de Irapa, alt. 750–850 m, 6 Aug 1966, fl., *J. A. Steyermark & M Rabe* 96033 (G, NY); fr., *J. A. Steyermark & M Rabe* 96059 (NY, P); Cerro Patao, Norte de Puerto de Hierro, Noroeste de Güiría. Alt. 875 m. 25 Jul 1962, fr., *J. A. Steyermark & G. Agostini* 91338 (K). Vecindades del Campamento selva siempre verde a lo largo de la fila, debajo de la cumbre, alt. 850 m, 18 Jul 1962, fl., *J. A. Steyermark & G. Agostini* 91028 (K). Yaracuy: San Felipe, Cordillera de la Costa, Macizo de Nirgua, al noroeste de Nirgua, Montaña El Zapatero, parte del “refugio

Nirgua”, lado sureste, camino La Alegria a El Terrón, 10°13’N, 68°37’W, alt. 900–1000 m, 31 Jul 2003, fr., *W. Meier & N. Flauger 9810* (G, VEN).

Distribution, habitat and phenology: *Connarus steyermarkii* is restricted to north Venezuela, occurring close to coastal areas in ombrophilous forests, usually associated with river margins (Fig. 21), at 750–1600 m elevation. Specimens have been collected with flowers irregularly from April to August and in November, and with fruits from July to August and in November.

Notes: Among the species with dendroid trichomes, *Connarus steyermarkii* is recognized by the asymmetric basal leaflets usually with acute or obtuse bases, inflorescences in thyrsoids and fruits internally with dense indumentum. It is similar to *C. patrisii*, but differs by the usually acute or obtuse leaflet bases (vs. rounded or subcordate), inflorescences in thyrsoids (vs. double thyrsoids) and sepals slightly connate only at base (vs. at least 2 sepals connate up to the middle or apical portions). In addition, *C. steyermarkii* is only found in north Venezuela, while *C. patrisii* extends horizontally from French Guiana to Ecuador and do not reach central areas of Venezuela (Fig. 21).

Connarus suberosus Planch., *Linnaea* 23: 433. 1850. *Connarus suberosus* Planch. var. *suberosus*.—TYPE: Brazil. Minas Gerais: *S. loc.*, *s. d.*, fl., fr., *P. Claussen s. n.* (lectotype first step designated by Schellenberg 1938; lectotype second step **designated here**: K barcode K000633782!; isoelectotypes: G!, K!, P!). Fig. 33

Connarus fulvus Planch., *Linnaea* 23: 434. 1850. *Connarus suberosus* var. *fulvus* (Planch.) Forero, *Fl. Neotrop. Monogr.* 36: 71. 1983.—TYPE: Brazil. State unknown: *S. loc.*, 1837, fl., *J. E. Pohl 721* (lectotype **designated here**: K barcode K000633788!; isoelectotype: K!).

Cnestidium lasiocarpum Baker, in Martius, *Fl. Bras.* 14(2): 195. 1871.—TYPE: Brazil. State unknown: [Rio Crixas ad Lavrinhas], *s. d.*, *J. E. Pohl 1822* (lectotype designated by Forero 1983: BR barcode BR 697 275 [photo!]; isoelectotypes: W [photo!]).

Connarus deterrentoides G. Schellenb., *Candollea* 2: 118. 1925.—TYPE: Brazil. State unknown: *S. loc.*, *s. d.*, fr., *J. E. Pohl s. n.* (lectotype designated by Schellenberg 1938: W 0062101!; isoelectotype: F-frag. [photo!]), *syn. nov.*

Shrubs, treelets or trees, (0.80–)1.5–7(–10) m tall; branchlets suberized, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels inconspicuous. *Leaves* 5–11(–13)-foliolate; petioles 3–8.2(–10.8) cm long, tomentose to glabrescent; rachises 5.5–17.5 cm long, tomentose to glabrescent; pulvinuli 4–6 mm long, tomentose to glabrescent; leaflets coriaceous, discolorous or slightly so, conduplicate, basal pairs $3.5\text{--}9.8 \times 2.5\text{--}5.5$ cm, symmetric, ovate, broadly ovate, suborbicular or cordate, bases symmetric, subcordate, cordate or rounded, the apical ones $4.7\text{--}11.5 \times 2.7\text{--}7.4$ cm, symmetric, ovate, broadly ovate, suborbicular, cordate or elliptic, rarely narrowly ovate, bases symmetric, subcordate, cordate or rounded, apices short acuminate, acumen 1–4 mm long, abaxial surfaces densely tomentose to glabrescent, mature leaflets abaxially entirely tomentose or only on midvein, indumentum ferruginous or griseous, adaxial surfaces tomentose to glabrescent, dull, margins or flat; midveins abaxially prominent, adaxially flat to impressed, secondary veins 6–7 pairs, abaxially slightly prominent, adaxially flat, less frequently slightly impressed or slightly prominent, concolorous or slightly discolorous in relation to the blade, forming angles of $45\text{--}60^\circ$ with midvein, linear or slightly arcuate, tertiary veins flat or slightly prominent on both surfaces, intercostals mixed percurrent, epidermals reticulate, rarely opposite percurrent. *Inflorescences* in thyrsoids or double thyrsoids, axillary, 1–6 per axil, rarely pseudo-terminal, trichomes dendroid and simple unicellular, peduncles 0.2–1 cm long or inflorescences sessile, densely tomentose, rachises 7–26 cm long, densely tomentose, lateral cymes 0.5–2.2 cm long, densely tomentose, lateral sub-thyrsoids 2.5–11.5 cm long, densely tomentose, indumentum of these structures ferruginous or brown; bracts 1–3 mm long, tomentose. *Flowers* sessile, subsessile or pedicels 0.3–1 mm long; buds $1.5\text{--}2 \times 1.4\text{--}2$ mm, orbicular or broadly elliptic; sepals 5, 1–2 pairs with 2 sepals each connate entirely or half their length, $2.2\text{--}3 \times 1.5\text{--}1.9$ mm, ovate or suborbicular, apices obtuse, 1–3 sepals connate to the others at base or half their length, $2.2\text{--}3.2 \times 0.9\text{--}1.2$ mm, narrowly ovate, ovate or narrowly triangulate, apices acute, outer surfaces tomentose, indumentum ferruginous or brown, inner surfaces glabrous or subglabrous, tomentose only at apex; petals $4\text{--}4.5 \times 1.1\text{--}1.3$ mm, reflexed, oblanceolate or oblong, apices rounded, obtuse or acute, glandular dots more than 10, loosely distributed, black, conspicuous or inconspicuous, outer surfaces glabrous or subglabrous, glandular trichomes absent, inner surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous or with only sparse to abundant glandular trichomes; stamens basally connate by 0.5–0.8 mm, shorter series 2–3 mm long, longer series 2.5–5 mm long, filaments glabrous or with sparse to abundant glandular trichomes; ovaries 1–1.2 mm long, tomentose, styles ca. 2.2 mm long, stigmas bilobate, lobes ca. 0.4 mm long. *Fruits* $1.8\text{--}2.3 \times 1.2\text{--}1.7$ cm, obovate or semi orbicular,

indehiscent side sigmoid or linear, pericarps up to 2 mm thick, stipes 2–7 mm long, styles partially persistent, inconspicuous or apiculate, 0.2–0.5 mm long, outer surfaces densely tomentose to glabrescent, indumentum ferruginous, black dots abundant, inner surfaces with only sparse to abundant glandular trichomes, calyces deciduous or partially persistent, sepals reflexed or patent; seeds ca. $1.1\text{--}1.2 \times 0.6\text{--}0.9$ cm, arils yellowish.

Selected specimens examined: **Bolivia.** Nuflo de Chavez: Santa Cruz, Comunidad El Carmen, 40 km S of Concepcion on road to Lomerio, $16^{\circ}30'S$, $62^{\circ}00'W$, alt. 750 m, 13 Nov 1985, fr., *T. Killeen 1452* (F, NY). Valesco: Estación Flor de Oro, margen del Río Iténez (Guaporé), frontera com Rondonia, ca. 20 km norte del Serrania de Huanchaca, ca. 85 km este del Río Paragua, $13^{\circ}33'S$, $61^{\circ}00'W$, alt. 200 m, 22 May 1991, fl., *M. Peña et al. 122* (F, NY); Santa Cruz. Parque Nacional “Prof. Noel Kempff Mercado”, campamento Los Fierros, 10 km SE y e 2 km ES del campamento, $14^{\circ}35'04''S$, $60^{\circ}50'26''W$, 30 Oct 1994, fr., *B. Mostacedo 2441* (NY); Serrania de Huanchaca, Parque Nacional “Prof. Noel Kempff Mercado”, $13^{\circ}59'S$, $60^{\circ}43'W$, alt. 800 m, 3–4 Dec 1987, fr., *W. W. Thomas et al. 5582* (NY). **Brazil.** Amazonas: Manicoré, $8^{\circ}32'04''S$, $61^{\circ}28'31''W$, 2 Oct 2007, fr., *A. L. P. Silveira 290* (RON). Bahia: Barreiras, arredores da Cachoeira do Acaba Vida, 22 Jul 2017, fl., *V. C. Souza 40980* (ESA); Drainage of the Rio Corrente, western Bahia, near Rio Piau, ca. 150 km. S. W. of Barreiras, alt. 850 m, 14 Apr 1966, fl., *H. S. Irwin et al. 14789* (NY); São Desidério. 74 km da vila Roda Velha em direção a Estiva, estrada de terra, próximo ao asfalto, $12^{\circ}29'28''S$, $45^{\circ}15'28''W$, alt. 675 m, 8 Nov 1997, fr., *M. A. da Silva et al. 3530* (IBGE, RB); Localidade Ribeirão Grande, 24 Jul 2008, fl., *A. M. Miranda & J. Ferraz 5825* (MAC). Distrito Federal: Brasília. Memorial das Idades do Brasil, 26 Aug 2009, fl., *T. Nogales & M. L. Ianhez 79* (RB); Parque Nacional de Brasília, cerrado entorno da estrada de acesso à Cascalheira do Entroncamento, $15^{\circ}44'04.5''S$, $47^{\circ}55'58.0''W$, 7 Sep 2015, fl., *C. R. Martins 1836* (RB); Reserva Ecológica IBGE, 1 Sep 1983, fl., *B. A. S. Pereira 697* (SPF). Goiás: Alexânia. Após entrada para Corumbá, 1 km, cerca de 200 metros após a ponte sobre o rio Corumbá, $16^{\circ}08'31''S$, $48^{\circ}36'55''W$, alt. 866 m, 24 Nov 2003, fr., *A. A. Santos et al. 2159* (CEN); Estrada de terra que liga a BR-060 à Corumbá de Goiás, próximo à ponte que divide Alexânia de Abadiânia, $16^{\circ}08'10''S$, $48^{\circ}37'44''W$, alt. 941 m, 04 Aug 2003, fl., *J. M. Rezende et al. 270* (CEN, ESA). Alto Paraíso de Goiás, Parque Nacional da Chapada dos Veadeiros, Vila de São Jorge, trilha entre a sede do PARNA e os saltos do Rio Preto (I e II), $14^{\circ}10'18''S$, $47^{\circ}49'38''W$, alt. 1000–1050 m, 24 Nov 2014, fr., *E. P. Fernandez et al. 134* (ESA, RB); Araguapaz, próxima a Serra Dourada, $15^{\circ}14'S$, $50^{\circ}54'W$, alt. 650 m, 23 Oct 1996, fr., *S. de S. e Silva 96* (IBGE, NY, RB, SP, UFG); Cristalina, Fazenda

Campanha (prop. Luís Rodrigues), estrada que dá acesso a Palmital/AHE Queimado, à esquerda, 16°08'59"S, 47°18'11"W, 01 Jul 2003, fl., *A. A. Santos & J. B. Pereira* 2067 (CEN, ESA); Luziânia, canteiro de obras, margem direita do Rio Corumbá a montante da barragem, Fazenda Corumbá, 16°19'31"S, 48°12'11"W, alt. 885 m, *J. M. Rezende et al.* 215 (CEN, ESA); Minacu, Serra da Mesa (área 1—proposta p/ unidade de conservação), mais ou menos 3 km da entrada norte do canteiro, 19 Nov 1991, fr., *B. M. T. Walter et al.* 721 (CEN); Pirenópolis, Serra dos Pirineus, subida para o Parque Cerrado, 15°49'29"S, 48°54'24"W, alt. 1070 m, 18 Jan 2005, fr., *J. Paula-Souza et al.* 4064 (ESA, RB). Maranhão: Alto Parnaíba, 8°54'29"S, 45°59'21"W, alt. 274 m, 11 Oct 2013, fr., *P. M. Santos et al.* 433 (MBM); Loreto, by football field, 7°6'S, 45°8'W, alt. 150 m, 29 Jan 1970, fr., *G. Eiten & L. T. Eiten* 10396 (NY); Transect area, Fazenda Madeira, approximately 17 km N of Carolina, 7°11'S, 47°25'W, 30 Jun 1993, fl., *J. A Ratter et al.* 6699 (NY). Mato Grosso: 1–10 km West of Alto Araguaia, along watershed between Amazonas and Rio Paraguaya, 21 Aug 1963, fl., *B. Maguire et al.* 56240 (NY); 80 miles out of Campo Grande on road to São Paulo, alt. 1500 feet, 24 Nov 1959, fr., *B. Maguire & C. K. Maguire* 44527 (NY, US); Alto Araguaia, arredores do Rio Ariranha, 17°31'28.8"S, 53°33'8.9"W, alt. 544 m, 10 Feb 2013, fr., *J. Paula-Souza & J. C. Oliveira* 11573 (ESA); Alto Paraguay, road Currupira–Arenápolis, 14°57'S, 56°51'W, 24 Aug 1994, fl., *B. Dubs* 1709 (ESA, UFMT); Diamantino, Fazenda Caeté (parte da Fazenda Baronesa), 15 km ESSE (em linha reta) de Diamantino, 23 May 1997, fl., *V. C. Souza et al.* 16989 (ESA, UFMT); Nova Mutum, estrada para Nova Brasilândia, ca. 50 km da BR163, 13°58'38.1"S, 55°44'00"W, 23 Oct 2004, fr., *V. C. Souza* 30058 (ESA); Rosário Oeste, ca. 75 km E de Rosário Oeste, estrada entre Riolândia (Frieira) e Marzagão, 14°43'S, 55°10'W, 7 Oct 1997, fr., *V. C. Souza et al.* 20225 (ESA, EFMT, UNIP). Mato Grosso do Sul: Coxim, Rodovia MS0217, 500 m do trevo com a Rod. BR-163, direção a Silviolândia, 18 Oct 1995, fr., *G. Hatschbach et al.* 63456 (MBM, RB, US); Fazenda Salina, Pantanal do Rio Negro, 19°30'S, 56°10'W, 11 Sep 1987, fl., *B. Dubs* 337 (MBM, NY); Piraputanga, arredores, 15 Oct 2003, fl., *G. Hatschbach et al.* 76374 (MBM). Minas Gerais: Formoso, Fazenda do Sr. Edgar, limite com o Parque Nacional Grande Sertão Veredas, 15°15'18"S, 45°59'02"W, alt. 750 m, 28 Nov 1997, fr., *M. L. M. Azevedo et al.* 1206 (IBGE, RB); Morada Nova de Minas Gerais, Estação Ecológica de Pirapitinga, Jul 2008, fl., *R. G. Giácomo et al. s. n.* (RBR 33749); Nova Ponte, 26 Jun 1996, fl., *E. Temeirão Neto* 2063 (BHCB, ESA); Patrocínio, Fazenda Daterra, Chachoeira Dourada, 15 Dec 1998, fr., *F. T. Farah & C. A. Freitas* 831 (ESA). Pará: Conceição do Araguaia, 25 Jul 1962, fr., *N. T. Silva* 648 (IAN); Pau D'arco, Marajoara, 18 Aug 1998, fl., *J. Grogan* 102 (INPA); Serra do Cachimbo, BR 163, Cuiabá-Santarém Highway, km 807.5, alt. 520 m, 9 Nov 1977, fr., *G. T.*

Prance et al. P25092 (NY); São Geraldo do Araguaia, Santa Cruz to Araguaia, Serra do Riacho Fundo, 6°14'S, 48°26'W, 11 Jul 1995, fl., *I. Aragão 152* (IAN); Terra Indígena Las Casas, Aldeira Las Casas, 18 Aug 2010, fl., fr., *M. Coelho-Ferreira et al. 595* (IAN, MG). Piauí: Entre Jerumenia e Marcos Parente, 7 Jul 1980, fl., *A. Fernandes & E. Nunes s. n.* (EAC barcode EAC0008821); Gilbués, 12 Jun 2011, fl., *S. M. C. Barbeiro s. n.* (RB barcode RB 01001199); Near Paranagoá, Aug 1839, fl., fr., *G. Gardner 2521* (BM, F, G, K, NY, P); Redenção do Gurguéia, 18 km de Redenção, estrada para Bom Jesus, 09.2047 S, 44.3243 W, 23 Oct 2008, fr., *A. S. F. Castro 2106* (EAC). São Paulo: Itirapina, coletada na beira da Rodovia Engenheiro Paulo Nilo Romano, que liga Itirapina a Analândia, próximo ao trevo, 22°13'08.3"S, 47°46'13.5"W, 7 Nov 2019, fl., *C. A. P. Toledo & A. Gibau 414* (ESA); Mogi Guaçu, Padua Sales, Fazenda Campininha, alt. 650 m, 22 Sep 1980, *E. Forero et al. 8180* (COL, RB); Pedregulho, Estreito, Usina de Estreito (Acampamento de Estreito), encosta à margem da represa, próxima à barragem, 20°09'28"S, 47°16'38"W, alt. 720 m, 23 Aug 2003, fl., *D. Sasaki & A. B. Junqueira 655* (SPF); São José do Rio Preto, Bairro Vale do Sol, 20°48'36"S, 49°22'50"W, 25 Aug 1995, fl., *N. Tarola 151* (SPF, UEC); São Manoel, Santa Lúcia, 3 Oct 2008, fl., *G. H. Aguirre et al. 696* (ESA). Tocantins: Between Cristalandia and Gurupi, Belém-Brasília Highway, alt. 300 m, 13 Aug 1963, fl., fr., *B. Maguire et al. 56146* (NY); Dianapolis, 11°36'37"S, 46°28'09"W, alt. 722 m, 25 Sep 2003, fl., *A. O. Scariot et al. 739* (CEN); Gurupi, bacia do Tocantins, sub-bacia do Rio Santo Antônio, 11°46'33"S, 48°46'22"W, alt. 260 m 10 Oct 2008, fr., *L. L. Guimarães et al. 32* (IBGE); Mateiros, Parque Estadual do Jalapão, povoado Mumbuca, 10°22'09"S, 46°34'19"W, alt. 458 m, 2 Dec 2012, fr., *M. L. Fonseca et al. 6747* (IBGE); Palmas, a oeste do reservatório Luís Eduardo Magalhães, próximo ao ribeirão Santa Luzia, 14 Aug 2002, fl., *D. Sasaki & A. G. Fuentes 55* (SPF); Porto Nacional, estrada para Natividade, ca. 6 km de Porto Nacional, 10°44'57"S, 48°23'46"W, 16 Jul 2000, fl., *V. C. Souza et al. 24001* (ESA, RB).

Distribution, habitat and phenology: *Connarus suberosus* is almost exclusively found in Brazil, except for few collections from Bolivia, mainly in the border between these countries. It is one of the most common and widely distributed Brazilian species of *Connarus*, occurring practically throughout the Cerrado domain (Fig. 6). When collected outside the boundaries of the Cerrado, this species is restricted to enclaves of savannas, particularly in Amazonas and Pará. *Connarus suberosus* is a species of tortuous shrubs or small trees, growing in different vegetation types of the Cerrado (Cerradão, campo sujo, serrado *s. s.*), normally at

altitudes ranging from 150–100 m. Specimens have been collected with flowers from April to September and with fruits especially from October to February.

Notes: As widely distributed across the Brazilian Cerrado, *C. suberosus* is the most recognizable species of the genus in Brazil. It has several morphological features regarded as adaptations to the savannas, some of which are used here as diagnostic of this species, namely: branchlets usually suberized and leaflets coriaceous, conduplicate and hairy to glabrescent on both surfaces. In addition, apical leaflets are normally as broad as long (not seen in other Neotropical species), there are at least 2 sepals connate medially or entirely, and the fruits are externally densely tomentose to glabrescent and internally covered only by glandular trichomes.

Forero (1983) separated *C. suberosus* into two varieties based on *C. suberosus* and *C. fulvus*, which were treated at species level by Planchon (1850) and Schellenberg (1938). While the former author mainly used sepal, petal and filament length and presence/absence of glandular trichomes on stamens as diagnostic, the latter two authors employed leaflet indumentum. The present treatment has adopted a broader concept and recognizes only *C. suberosus* as a biological entity. Firstly, leaflet indumentum cannot be used as diagnostic because trichomes on this structure become glabrescent with age. Regarding floral characters used by Forero (1983), these represent floral morphs related to heterostyly or possibly dioecy in *Connarus suberosus* (Denardi 2008; Paz 2019). As discussed by the former author, *C. suberosus* var. *suberosus* corresponds to individuals with long-styled flowers (shorter stamens), while *C. suberosus* var. *fulvus* corresponds to those with short-styled flowers (longer stamens). This becomes even more evident when the illustrations of the two varieties presented by Forero (1983) are compared. Finally, Denardi (2008) also discussed that glandular trichomes become deciduous with age and they might be related to heterostyly as well.

Planchon (1850) originally described *C. suberosus* and cited two syntypes, so Schellenberg (1938) indicated the collection *Claussen s. n.* as type, but, as he did not mention herbarium, a second step lectotype is here designated.

The basionym of *C. suberosus* var. *fulvus* was also published by Planchon (1850), who cited only one specimen (*Pohl 721*), but with no herbarium designation, so Forero (1983) inadvertently designated a specimen from F as lectotype. However, this specimen was not found, so the collection from K (barcode K000633788) is here considered as lectotype of *C. fulvus*. This decision is more appropriate as Planchon described most of his new Connaraceae

species based on specimens from Hooker herbarium (now incorporated to K), aside from the fact that the lectotype here designated has Planchon's handwriting.

Planchon (1850) also intended to describe a variety of *C. fulvus* based on *Gardner 2521*, but he named it as “var. β .”, thus not validly published according to the *Code* (Turland et al. 2018, Art. 32.1). Nevertheless, the specimen *Gardner 2521* fits the concept of *C. suberosus*.

Lastly, the inclusion of *C. deterrentoides* in the synonymy of *C. suberosus* should be discussed. The later name was firstly described by Schellenberg (1925) based on a single collection of J. E. Pohl, which lacks collector number, date and location. Subsequently, Schellenberg (1938) designated a proper lectotype after indicating the specimen *Pohl s. n.* (W) as “type”. It was regarded as holotype by Forero (1983) because it seemed the only existing specimen of this collection, but a fragment has been identified in F. The basis for recognizing *C. deterrentoides* as a distinct species has relied only on the type collection (Schellenberg 1925, 1938; Forero 1983), which may have led them to use very few and dubious characteristics to distinguish it: inflorescence architecture, for example, was used by both authors as diagnostic, even though the collection contains only few and dispersed fruits. Another issue is that there is no information on the type location, thus impossible for comparing it with possible sympatric species. However, it is here hypothesized that Pohl's specimen was collected in central Brazil, most likely Goiás state, during his expedition for the *Flora Brasiliensis* (an annotation “H. Bras.” is handwritten in the sheet label from W). According to Pohl's itinerary, provided by Urban (1906: 79), the botanist collected in many sites across central Goiás, such as Cristalina (Serra dos Cristais), Luziânia (“S. Luzia”) and São Bartolomeu (“S. Bortholomeo”). Several specimens of *Connarus* have been recently collected around those sites (namely, *Rezende et al. 270*, *Rezende et al. 715*, *Santos et al. 2159*, among others), which morphologically resemble the type of *C. deterrentoides*. At first sight, such collections differ from *C. suberosus* by the fissured branchlets (rather than suberized) and narrowly ovate leaflets, although flowers and fruits features are identical. Some of these individuals were found on the field, where it became clear that they may represent an extreme of variation in *C. suberosus*, especially because barks and branchlets of these plants vary from fissured to slightly or completely suberized (Fig. 33). It is also of note that the referred individuals were found close to water courses, where vegetations are typically forestry, contrasting with the typical open habitat of *C. suberosus*, hence supporting the ideal of a local variation. Taking this into account, *C. deterrentoides* is here considered a synonym of *C. suberosus*.

Connarus tomentosus C. Toledo, Phytotaxa 415(1): 69. 2019.—TYPE: Brazil. Bahia: Porto Seguro, Reserva Florestal de Porto Seguro, próximo ao aceiro, no Córrego Camorogi, 5 Jul 1990, fr., *D. A. Folli 1197* (holotype: CEN barcode CEN 00057291!; isotypes: CVRD!, NY [photo!]).

Lianas; branchlets smooth, tomentose to glabrescent, trichomes dendroid and simple unicellular, lenticels absent. *Leaves* 9–13-foliolate; petioles 1.3–2.8 cm long, tomentose to glabrescent; rachises 3.2–8.5 cm long, tomentose to glabrescent; pulvinuli 2–3 mm long, tomentose; leaflets coriaceous, slightly discoloured, flat, basal pairs $3.9\text{--}5.5 \times 1.7\text{--}2.7$ cm, symmetric, oblong, narrowly obovate or elliptic, bases symmetric, rounded or subcordate, the apical ones $5.2\text{--}7.6 \times 1.9\text{--}2.8$ cm, symmetric, oblong or narrowly obovate, the apical usually elliptic, bases symmetric, rounded or subcordate, rarely obtuse, apices rounded or short acuminate, acumen ca. 2 mm long, abaxial surfaces tomentose, indumentum ferruginous, adaxial surfaces glabrous, shining, margins slightly revolute; midveins abaxially prominent, adaxially impressed, secondary veins 9–10 pairs, abaxially flat, adaxially flat or slightly prominent, concolorous in relation to the blade, forming angles of ca. 80° with midvein, linear, tertiary veins flat on both surfaces, intercostals and epidermals reticulate. *Inflorescences* in double thyrsoids, axillary, 1–2 per axil, trichomes dendroid and simple unicellular, peduncles 0.2–0.8 cm long or inflorescences subsessile, tomentose, rachises 6.4–13 cm long, tomentose, lateral sub-thyrsoids 4–5.5 cm long, tomentose, indumentum of these structures ferruginous; bracts ca. 3 mm long, tomentose. *Flowers* not seen, pedicellate; sepals 5 (persistent on fruits), slightly basally connate, narrowly ovate, apices acute, outer surfaces tomentose, indumentum brown or ferruginous, inner surfaces glabrous; petals (few persistent on fruits) with more than 10 glandular dots, loosely distributed, black. *Fruits* $1.6\text{--}1.9 \times 1.1\text{--}1.3$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes ca. 1 mm long or fruits sessile or subsessile, styles partially persistent, apiculate, 0.2–1.5 mm long, outer surfaces tomentose, indumentum ferruginous, black dots absent, inner surfaces tomentose, glandular trichomes abundant, calyces persistent, sepals ascending erect or patent; seeds mature not seen.

Distribution, habitat and phenology: *Connarus tomentosus* is only known from the type location, municipality of Porto Seguro, south Bahia (Brazil) (Fig. 6). It is a lianescent

species from tableland forests (“Tabuleiro”) of the Atlantic Forest, growing on sandy soils, at ca. 80 m elevation. The type specimen was collected with fruits in July.

Notes: Even though *C. tomentosus* is known from a single collection, it is easily distinguished by possessing dendroid trichomes, 9–13-foliolate leaves, coriaceous and abaxially tomentose leaflets, which are normally oblong with slightly revolute margins, secondary veins forming angles of ca. 80° with midvein, and fruits internally and externally tomentose, with sepals ascending or patent. It is morphologically similar to *C. perrottetii*, but differs by the adaxially shining leaflets (vs. dull, rarely shining) with slightly revolute margins (vs. margins flat, rarely slightly revolute), secondary veins forming angles of ca. 80° with midvein (vs. angles of 50–80° with midvein), and internally tomentose fruits (vs. pubescent, sparsely pubescent, subglabrous or with only glandular trichomes). In addition, *C. tomentosus* is restricted to the Atlantic Forest, while *C. perrottetii* is more widely distributed in the Amazonia.

Connarus turczaninowii Triana, Ann. Sci. Nat., Bot., sér. 5, 16: 364. 1872. *Connarus panamensis* Turcz., Bull. Soc. Imp. Naturalistes Moscou 32(1): 277. 1859., *nom. illeg., non* Griseb. 1858.—TYPE: Panama. Chagres, Mar 1850, fl., fr., *A. Fendler 128* (lectotype first step designated by Forero 1983: K; lectotype second step **designated here**: K barcode K000633823!; isoelectotypes: BM [n. v.], F [n. v.], GH [photo!], K!, MO [photo!], NY-frag. [photo!], P!, US [n. v.], W [photo!]).

Connarus turczaninowii Hemsl., Biol. Cent.-Amer., Bot., 1(3): 224. 1879, *nom. illeg.*

Lianas or scandent shrubs, 2–3 m tall; branchlets slightly striate, sericeous to glabrescent, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3–7-foliolate; petioles 2.5–8.2 cm long, sericeous to glabrescent; rachises 2–7 cm long, sericeous to glabrescent; pulvinuli 4–6 mm long, sericeous to glabrescent; leaflets chartaceous, rarely subcoriaceous, slightly discoloured, flat, basal pairs 4–9.3 × 2.2–4.4 cm, symmetric, elliptic, obovate or ovate, rarely narrowly elliptic, bases symmetric, rounded or obtuse, rarely subcordate, the apical ones 5.7–13.5 × 3.3–6.1 cm, symmetric, elliptic, obovate or ovate, rarely narrowly elliptic, bases symmetric, rounded or obtuse, rarely acute or subcordate, apices acuminate, rarely long acuminate, acumen 2–10(–17) mm long, abaxial surfaces sparsely

sericeous to glabrescent, usually more densely on midvein, indumentum brown or aureous, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed or slightly so, secondary veins 7–9 pairs, abaxially flat or slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of 45–55(–60)° with midvein, linear, tertiary veins flat on both surfaces, intercostals and epidermals reticulate. *Inflorescences* in thyrsoids, rarely double thyrsoids, axillary or pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncles 0.1–0.5 cm long or inflorescences sessile, sericeous or densely pubescent, rachises 9–22 cm long, sericeous or densely pubescent, lateral cymes 0.2–0.5 cm long, sericeous or densely pubescent, lateral sub-thyrsoids 2.5–5.3 cm long, sericeous or densely pubescent, indumentum of these structures brown or ferruginous; bracts 1–1.3 mm long, sericeous. *Flowers* with pedicels 0.5–1 mm long; buds ca. 2×1.5 mm, elliptic; sepals 5, slightly basally connate, (2–)2.5–2.8 $\times$ 0.8–1.3 mm, elliptic, ovate or narrowly ovate, apices acute or obtuse, outer surfaces sericeous or sparsely so, indumentum brown, inner surfaces subglabrous or sparsely sericeous, usually more densely at apex; petals 3–4.5 $\times$ 1–1.3 mm, erect, oblong, narrowly oblong or narrowly elliptic, apices rounded, obtuse or acute, glandular dots 5–10 or more than 10, loosely distributed, black, inconspicuous, both surfaces glabrous or subglabrous, glandular trichomes absent, margins glabrous; stamens basally connate by 0.5–0.8 mm, shorter series 1.5–2 mm long, longer series 2–3 mm long, filaments with sparse glandular trichomes only on longer series; ovaries ca. 1 mm long, densely pubescent, styles 1.3–1.7 mm long, stigmas bilobate, lobes 0.5–0.8 mm long. *Fruits* 1.6–2.2 $\times$ 1.2–1.5 cm, obovate or semi-orbicular, indehiscent side sigmoid, rarely linear, pericarps up to 2 mm thick, stipes 3–6 mm long, styles partially persistent, apiculate, 0.5–1.5 mm long, outer surfaces sparsely sericeous to glabrescent, indumentum brown, black dots abundant, inner surfaces subglabrous or sparsely pubescent, rarely glabrous, glandular trichomes absent, calyces deciduous to persistent, sepals reflexed or patent; seeds 1.1–1.2 $\times$ 0.5–0.7 cm, arils yellowish.

Specimens examined: **Panama.** Canal Zone: Area west of Limon Bay, Gatun Locks and Gatun Lake, 4 Apr 1956, fr., *I. M. Johnston 1785* (MO); Barro Colorado Island. 8 Aug 1961, fr., *J. D. Dwyer 1464* (MO); Cump cove south of dock, 6 Jul 1970, fr., *T. B. Croat 11120* (NY); Forest along shore of Gatun Lake, east of laboratories, 24 Nov 1948, fl., *E. P. Killip 40027* (US); Lakeshore of Dump cove, 17 Apr 1968, fl., *T. B. Croat 4883* (F); Shore north of lab, 17 Feb 1971, fl., fr., *R. Foster 2159* (US); Shoreline north of dock, 10 Jan 1969, fl., *T. B. Croat 7130* (F); Shoreline of large cove S of Orchid Island, 15 Feb 1971, fl., *T. B. Croat 13485* (F). Chagres, 7 Jan 1850, fl., *A Fendler 128* (K); Coco Solo. 19 Jul 1972, fr., *A. Gentry 6064*

(MO); U. S. Army Tropic Test Center, Mine Emplacement Center, 13 Aug 1967, fr., *J. D. Dwyer & J. A. Ducke 7904* (K, US). End of Pipeline Road, 19 km NW of Gamboa, alt. 25-50 m, at bay of Gatun Lake, 1 km S of Pueblo Limone, 6 Apr 1974, fl., fr., *M. Nee & D. Smith 11076* (US); Frijoles, 3 Mar 1923, fr., *C. V. Piper 5797* (US); Frijoles, *s. d.*, fr., *S. Hayes 332* (K); Gatún, Nov 1859, fl., *Y. Hayes 166* (NY); Near Fort Randolph, 28 Dec 1923, fr., *P. C. Standley 28603* (K, US); Near Piña, 100 m, 7 Dec 1973, fl., *A. Gentry 8728* (MO). Colón: Between France Field, Canal Zone, and Catival, 9 Jan 1924, fr., *P. C. Standley 30273* (US); Colón, Frijoles, 3 Mar 1923, fr., *C. V. Piper 5832* (US). Darién: Near Helipad at Hydro Camp on Rio Morti in premontane Rain Forest, 15 Mar 1968, fr., *J. A. Ducke 15411(3)* (MO); Tumaganti, elev. ca. 300 m, 18 Sep 1967, fr., *J. A. Ducke 14140* (MEXU).

Distribution, habitat and phenology: *Connarus turczaninowii* is only found in Panama, where populations seem to be restricted to the region of the Canal Zone, center of the country (Fig. 5). Individuals of this species are lianas or scandent shrubs, mainly distributed in the coastal vegetation or around Lake Gatún, at approximately sea level. Specimens have been collected with flowers from November to April and with fruits irregularly almost throughout the year.

Notes: *Connarus turczaninowii* is mainly recognized by the leaves 3–7-foliate, 7–9 pairs of linear secondary veins, tertiary veins reticulate, and inflorescences usually in thyrsoids. It is morphologically similar to *C. lambertii*, but differs by a careful analysis of the number of leaflets, disposition of secondary veins, and fruit stipe length (Table 1). In herbarium specimens, this species is also confused with another Panamanian species, *C. panamensis*, but *C. turczaninowii* differs in disposition of secondary veins, architecture of tertiary veins, inflorescence indumentum, flower pedicels, and fruit indumentum (see Notes section of *C. panamensis*).

Forero (1983) selected the specimen *Fendler 128* from K as lectotype of *C. turczaninowii* after the name was published based on syntypes. However, there are three duplicates of this collection in K and, considering that they belonged to different collections in the past (one from Benthonianum herbarium, one from Hookerianum, and the other without stamp), then these are regarded as duplicates, so a second step lectotypification is here proposed. An additional specimen *Fendler 128* is available in K, but has a different collection date, so it is not believed to be part of the type.

Connarus venezuelanus Baill., *Adansonia* 9: 151. 1868. *Connarus venezuelanus* Baill. var. *venezuelanus*, *syn. nov.*—TYPE: Venezuela. Bolívar: Guyana, villa de Upata, 1804, fl., *R. Grosourdy* 13 (holotype: P barcode P01819571!).

Shrubs or trees, 1.5–7 m tall; branchlets slightly striate or fissured, sparsely sericeous to glabrescent, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3-foliolate; petioles 2.5–8 cm long, sparsely sericeous; rachises 0.5–2.2 cm long, sparsely sericeous; pulvinuli 3–7 mm long, glabrous, subglabrous or sparsely sericeous; leaflets coriaceous, discolorous, conduplicate or flat, basal pairs 5.2–13 × 2.4–5.7 cm, symmetric, elliptic or ovate, rarely obovate, bases symmetric, rounded or subcordate, rarely obtuse, the apical ones 6.2–14.5 × 2.8–5.7 cm, elliptic or ovate, rarely obovate, bases symmetric, rounded or subcordate, rarely acute, apices acuminate, rarely short acuminate, acumen 2–13 mm long, spinescent, abaxial surfaces sparsely sericeous to glabrescent, indumentum griseous or brown, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially impressed or slightly so, secondary veins 7–10 pairs, abaxially prominent or slightly so, adaxially flat, occasionally slightly prominent, concolorous in relation to the blade, forming angles of 55–75° with midvein, linear, rarely slightly arcuate, tertiary veins abaxially prominent or slightly so, adaxially flat or slightly prominent, intercostals and epidermals reticulate, intercostals occasionally mixed percurrent. *Inflorescences* in thyrsoids, rarely double thyrsoids, axillary or pseudo-terminal, 1–3 per axil, trichomes simple unicellular, peduncles 0.1–1.2 cm long or inflorescences subsessile, sericeous or sparsely so, rachises 8.5–18 cm long, sericeous or sparsely so, lateral cymes 0.5–1.5 cm long, sericeous, lateral sub-thyrsoids 1.8–7 cm long, sericeous, indumentum of these structures brown or ferruginous; bracts 0.8–1.2 mm long, sericeous. *Flowers* sessile or pedicels 0.3–1 mm long; buds ca. 1.8 × 1.3 mm, elliptic; sepals 5, slightly basally connate, 2.5–3 × 0.8–1 mm, narrowly elliptic, ovate or narrowly ovate, apices acute, outer surfaces sericeous, indumentum brown or ferruginous, inner surfaces sericeous or sparsely so, usually more densely at apex; petals 3.3–4.5 × 1–1.3 mm, erect, narrowly obovate, oblong, or narrowly elliptic, apices rounded or obtuse, glandular dots more than 10, loosely distributed, black or colorless, inconspicuous, both surfaces glabrous, subglabrous or sparsely sericeous, glandular trichomes absent or sparse to abundant, margins glabrous; stamens basally connate by 0.5–0.8 mm, shorter series 1.2–2.5 mm long, longer series 2.2–3.3 mm long, filaments with sparse glandular trichomes; ovaries (0.7–)1 mm long, densely pubescent, styles 1.3–1.8 mm long, stigmas bilobate, lobes 0.1–0.4 mm long. *Fruits* 1.8–2.2 × 1.3–1.6 cm,

obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 3–7 mm long, styles partially persistent, apiculate, 0.5–2 mm long, outer surfaces sparsely sericeous to glabrescent, more densely on stipe, indumentum brown, black dots absent or sparse to abundant, inner surfaces glabrous or subglabrous, glandular trichomes absent, calyces persistent or partially persistent, sepals ascending erect or patent, rarely reflexed; seeds $1.1\text{--}1.3\text{--}(1.6) \times 0.7\text{--}1$ cm, arils yellowish.

Specimens examined: **Venezuela.** Amazonas: Puerto Ayacucho, 100 m, Jun 1940, fr., *L. Williams 13465* (US). Anzoátegui: Farallones de la Mesa de Guanipa, 24 Mar 1940, fr., *H. Pittier 14333* (G, VEN). Bolívar: Bolívar and vicinity, on the Orinoco. 27 Feb 1921, fl., *L. H. Bailey & E. Z. Bailey 1375* (US); 60 m, Feb–Mar 1921, fr., *L. H. Bailey & E. Z. Bailey A3* (US). Jobo Liso, 9 Feb 1939, fl., *E. Delgado 218* (US); La Mariquita, 100 m, 10–18 Apr 1954, fl., fr., *L. Aristeguieta 2158* (NY, VEN); Near Pilon, 5 km northeast of river mouth, 100 m, 5 Jan 1956, fl., *J. J. Wurdack & J. V. Monachino 41115* (NY); On upper slopes of Cerro Toribio (east of Cerro Bolívar), 450–500, 22 Oct 1953, fr., *B. Maguire et al. 35949* (US); Piar, Bajo Caroli, sector III, $67^{\circ}04'N$, $62^{\circ}05'W$, 100 m, May 1994, fr., *A. Valeria 500* (NY). Guarico: 80 km S of Las Mercedes along Hwy. 12 to Cabruta, 170 m, 20 Nov 1973, fl., *G. Davidse 4279* (MO). Merida: El Dorado, entre vegetación arborea de Calseta de la Botella, 100 m, 14 Apr 1957, fl., *A. L. Bernardi 6738* (NY). Monagas: Ca. 2 km N. W. (60° N. of W.) of Jusepin, 185 m, 7 Mar 1967, fr., *R. A. Pursell et al. 8255* (US); Forested slopes along top of sandstone escarpment above Río Amana, at La Traviesa Mene Grande Oil Company Camp, 7 kilometers west of Santa Barbara, 240 m, 01 Apr 1945, fl., *J. A. Steyermark 61761* (NY). Sucre: Parque Nacional Mochima, vía Mochima-Cumaná, a lo largo de la carretera, 9 Nov 1992, fr., *B. Garófalo 1096* (P, VEN).

Distribution, habitat and phenology: *Connarus venezuelanus* is only found in Venezuela, where it is distributed in the states of Amazonas, Anzoátegui, Bolívar, Merida, Monagas and Sucre (Fig. 9). This species includes shrubs or trees up to 8 m tall, occurring along river margins, usually at low elevations (ca. 100–250 m). Specimens have been collected with flowers from January to April and in November, and with fruits from March to May and from October to November.

Notes: *Connarus venezuelanus* is recognized by the exclusively 3-foliolate leaves, coriaceous and abaxially sparsely sericeous leaflets, spinescent acumen, internally sericeous sepals and internally glabrous or subglabrous fruits. It can be mistaken for *C. lambertii* or *C.*

turczaninowii, but differs from the former by the coriaceous leaflets with indumentum sericeous abaxially (vs. chartaceous leaflets, glabrous abaxially) and usually linear secondary veins (vs. secondary veins arcuate), and differs from the latter by being a shrub or tree (vs. lianescent habit), with 3-foliolate leaves (vs. 3–7-foliolate leaves) and coriaceous leaflets (vs. chartaceous, rarely subcoriaceous). Another Amazonian species with coriaceous and abaxially hairy leaflets is *C. favosus*, from which *C. venezuelanus* differs, despite their disjunct distribution (Fig. 9), in the flat leaflet margins (vs. revolute) and longer fruit stipes (3–7 mm long vs. stipes up to 1 mm long).

The type collection of *C. venezuelanus* from P is composed of a folder with two specimens belonging to two different species. Although both are attributed to *Grosourdy 13*, the holotype (barcode P01819571) has a label annotated as “Guyana – Villa de Upata” and matches perfectly with the original description (Baillon 1868), while the other (barcode P01819572) correspond to *C. araucanus*, with location indicated as “Guyana – canton de Upata, Puerto de tullus”, which is not in accordance with the protologue of *C. venezuelanus*. Curiously, the fragment of *Grosourdy s. n.* from F (937700) had been treated as isotype of *C. venezuelanus* (Forero 1983), but as it has no collector number and it is composed of a single leaflet that belong to *C. araucanus*, therefore not an isotype.

Connarus williamsii Britton, N. Amer. Fl. 22(6): 560. 1913. *Connarus williamsii* Britton var. *williamsii*, *syn. nov.*—TYPE: Panama. Marraganti and Vicinity, 10–200 ft, 3–9 Apr 1908, fr., *R. S. Williams 1006* (lectotype **designated here**: NY barcode NY 00010891!; isolectotypes: NY!).

Connarus allenii Steyerm., Ann. Missouri Bot. Gard. 28(4): 430. 1941. *Connarus williamsii* Britton var. *allenii* (Steyerm.) Forero, Fl. Neotrop. Monogr. 36: 129. 1983.—TYPE: Panama. Darién: Trail between Pinogana and Yavisa, ca. 15 m, 17 Mar 1937, fr., *P. H. Allen 249* (holotype: US barcode US 00130986!; isotypes: A [photo!], F-frag. [n. v.], GH [photo!], MO [photo!], NY [n. v.]), *syn. nov.*

Lianas, scandent shrubs, shrubs or treelets, 3–6 m tall; branchlets slightly striate, glabrous or subglabrous, trichomes simple unicellular, lenticels conspicuous or inconspicuous. *Leaves* 3–5(–7)-foliolate; petioles (2.3–)5.2–13.5(–21) cm long, glabrous, subglabrous or

irregularly sparsely sericeous; rachises (1.5–)3.7–8.5 cm long, glabrous, subglabrous or irregularly sparsely sericeous; pulvinuli 2–6 mm long, glabrous, subglabrous or pubescent; leaflets chartaceous, concolorous or slightly discolorous, flat, basal pairs 8–21.8 × 2.3–5.8 cm, symmetric, narrowly elliptic or narrowly obovate, rarely obovate, bases symmetric, acute or attenuate, rarely obtuse, the apical ones 10.5–28 × 2.9–6.8 cm, narrowly elliptic or narrowly obovate, bases symmetric, acute or attenuate, apices short to long acuminate, acumen 3–17 mm long, abaxial surfaces glabrous or subglabrous, occasionally irregularly sparsely sericeous on midvein, indumentum brown, adaxial surfaces glabrous or subglabrous, dull, margins flat; midveins abaxially prominent, adaxially flat or slightly impressed, secondary veins (9–)11–16 pairs, abaxially slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of 60–80° with midvein, linear or slightly arcuate, tertiary veins abaxially slightly prominent, adaxially flat, rarely slightly prominent, intercostals and epidermals reticulate. *Inflorescences* in thyrsoids, axillary, 1–6 per axil, trichomes simple unicellular, peduncles 0.2–0.5 cm long or inflorescences subsessile, sericeous or sparsely so, rachises 4–8.5 cm long, sericeous or sparsely so, lateral cymes ca. 0.2 cm long, sericeous, indumentum of these structures brown; bracts 0.3–0.7 mm long, sericeous. *Flowers* with pedicels 1.5–2 mm long; buds ca. 3 × 2 mm, elliptic or orbicular; sepals 5, slightly basally connate, 2–2.5 × 0.8–0.9 mm, narrowly ovate or elliptic, apices acute or obtuse, outer surfaces sparsely sericeous, indumentum brown, inner surfaces glabrous or subglabrous; petals 4.5–5.2 × 1.1–1.3 mm, erect, narrowly obovate, narrowly elliptic or oblong, apices rounded, obtuse or acute, glandular dots more than 10, loosely distributed, black, conspicuous or inconspicuous, both surfaces glabrous, margins glabrous; stamens basally connate by 0.3–1 mm, shorter series 1–2.2 mm long, longer series 1.4–3.2 mm long, filaments with sparse glandular trichomes; ovaries ca 1 mm long, densely pubescent, styles ca. 1.3 mm long, stigmas not seen. *Fruits* 1.6–2.1 × 1.2–1.6 cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 2–3 mm long, styles partially persistent, apiculate, 0.5–1 mm long, outer surfaces sparsely sericeous to glabrescent, more densely on stipe and base, indumentum brown, black dots sparse to abundant, inner surfaces glabrous, subglabrous or sparsely pubescent, glandular trichomes absent, calyces persistent or partially persistent, sepals ascending erect or patent; seeds 1.1–1.4 × 0.6–0.9 cm, arils color not seen.

Specimens examined: **Colombia.** Antioquia: Necocli, ca 15 km NE of Necocli on road to Arboletes (Km 17.3 of road), 8°31'N, 76°43'W, 20 m, 24 Mar 1987, fl., *J. Zarucchi et al.* 4976 (COL). Chocó: Riosucio, Peyé, camino al Alto del Limón, 3 Jun 1976, fr., *E. Forero*

& R. Jaramillo 1805 (COL, MO). **Panama.** Canal Zone: Fort Clayton, Cerro Piriaque between 100–1000, 23 Apr 1966, fr., E. L. Tyson *et al.* 3829 (MO). Darién: Cerro Yaviza river, near the town of Yaviza, 1966, fl., J. A. Duke & N. Bristan 426 (MO); Cruce de Mono Field Station, Parque Nacional de Darién, ca. 20 km SSW of Boca de Cupe, 07°58'N, 77°40'W, 200 m, 29 Apr 1990, fr., R. C. Moran 4185 (COL); El Rio Yape, 26 Oct 1967, fl., N. Bristan 1413(2) (MO); Loma Piriaque, 14 Apr 1966, fr., J. A. Ducke 8105 (MO); Ridge NW of Yaviza ca. 2 miles, 12 Dec 1962, fl., J. A. Ducke 6540 (MO); Río Chico, from Yaviza at junction with Río Chucunaque to ca 1 hour by outboard from junction, 19 Dec 1966, fl., D. Burch *et al.* 1111 (GH, MO, US).

Distribution, habitat and phenology: *Connarus williamsii* is distributed from Canal Zone (central Panama) to northwest Colombia (Fig. 23), and it is known only from a few collections. Individuals of this species are either lianas, shrubs, scandent shrubs or small trees, occurring in wet dense forests along river margins or hills, at 10–200 m elevation. Specimens have been collected with flowers in October, December and March, and with fruits from March to April.

Notes: *Connarus williamsii* is recognized by the 3–7-folliolate leaves, usually narrowly obovate or narrowly elliptic leaflets, inflorescences in short thyrsoids and fruit stipes 2–3 mm long. It can be mistaken for *C. silvanensis* due to the short inflorescence rachises, but differs by the 3–7-folliolate leaves (vs. always 3-folliolate) and adaxially flat secondary veins (vs. impressed).

Forero (1983) separated *C. williamsii* into two different varieties mainly based on leaflet size; however, the specimens analyzed by the author represented extremes of variation in leaflet size and, after revising additional specimens, it has been found that this character presents continuous values, so *C. allenii* and *C. williamsii* var. *allenii* are here considered synonyms of *C. williamsii*.

When Britton (1913) originally described *C. williamsii*, the designated type was attributed to the collection *Williams 1006* from NY; however, three specimens of this collection are deposited in NY and they are kept in separate folders and considered duplicates, so a lectotype is here proposed.

Connarus wurdackii Prance, Brittonia 23(4): 443. 1971.—TYPE: Peru. Loreto: Alto Amazonas, rainforest on middle north slopes of Cerros Campanquiz at Pongo de Manseriche, right bank of Río Marañón, ele. 550-750 m, 22 Oct 1962, fl., J. J. Wurdack 2383 (holotype: NY barcode NY00010920!; isotype: K!).

Lianas or scandent shrubs; branchlets slightly striate, lanate to glabrescent, trichomes dendroid and simple unicellular, lenticels inconspicuous. *Leaves* 5–7-foliolate; petioles 5–8.8 cm long, lanate to glabrescent; rachises 5.5–12.7(–14.5) cm long, lanate to glabrescent; pulvinuli 5–7 mm long, lanate to glabrescent; leaflets chartaceous to subcoriaceous, slightly discoloured or concolorous, flat, basal pairs $6.5\text{--}13 \times (2.2\text{--})3\text{--}4.8$ cm, symmetric or slightly asymmetric, oblong, narrowly obovate or obovate, bases symmetric to asymmetric, acute or obtuse, the apical ones $8\text{--}22 \times (3\text{--})3.5\text{--}7$ cm, symmetric or slightly asymmetric, oblong or narrowly obovate, bases symmetric to asymmetric, acute or obtuse, apices acuminate to long acuminate, rarely short acuminate, acumen (3–)8–15 mm long, both surfaces lanate to glabrescent, mature leaflets glabrous or subglabrous, indumentum brown or brown-grayish, adaxial surfaces dull or slightly shining, margins flat or slightly revolute; midveins abaxially prominent, adaxially prominent or slightly so, secondary veins 8–10 pairs, abaxially prominent, adaxially slightly prominent or flat, concolorous in relation to the blade, forming angles of $50\text{--}70^\circ$ with midvein, linear to slightly arcuate, tertiary veins abaxially prominent, adaxially slightly prominent or flat, intercostals opposite or mixed percurrent, epidermals opposite percurrent. *Inflorescences* in double thyrsoids, axillary, 1 per axil, trichomes dendroid and simple unicellular, peduncles 3–7 cm long, lanate, rachises 11–19 cm long, lanate, lateral sub-thyrsoids 4–12.8 cm long, lanate, indumentum of these structures ferruginous; bracts 1.5–3 mm long, lanate. *Flowers* sessile; buds $2.5\text{--}3 \times 2.5\text{--}4$ mm, orbicular; sepals 5, 2 pairs with 2 sepals each connate entirely, ca. 2.5×2.5 mm, broadly ovate, apices obtuse, 1 sepal ca. 2.5×1.5 mm, ovate, apices obtuse, outer surfaces tomentose, indumentum ferruginous, inner surfaces glabrous at base, pubescent only at apex; petals ca. 4×1.5 mm, reflexed, narrowly obovate, apices rounded, glandular dots more than 10, loosely distributed, black, conspicuous, both surfaces glabrous, margins glabrous; stamens basally connate by ca. 0.6 mm, shorter series ca. 4 mm long, longer series ca. 4.5 mm long, filaments glabrous; ovaries ca. 1 mm long, densely pubescent, styles and stigmas not seen. *Fruits* $2\text{--}2.2 \times 1.5\text{--}1.6$ cm, obovate, indehiscent side sigmoid, pericarps up to 2 mm thick, stipes 3–5 mm long, styles partially persistent, apiculate, ca. 0.1–1 mm long, outer surfaces lanate to glabrescent,

indumentum ferruginous, black dots absent, inner surfaces lanate, glandular trichomes absent, calyces persistent, sepals reflexed; seeds $1.1\text{--}1.4 \times 0.6$ cm, arils color not seen.

Specimens examined: **Brazil.** Pará: Rio Tapajós, Bela Vista, 23 Aug 1923, fl., *A. Ducke s. n.* (IAN 67557, RB barcode 0260921). **Peru.** Loreto: Iquitos, carretera de Iquitos-Nauta, km 7.5, trocha del caserio de Varillal, em terreno arenoso, monte alto, 150 m alt., 20 Nov 1987, fr., *M. Rimachi* 8422 (US); Maynas. Distrito de Medio Putumayo, inventario Rápido #25, Campamento Medio Campuya, $01^{\circ}31'03.4''\text{S}$, $73^{\circ}48'58.2''\text{W}$, 135–200 m alt., 28 Oct 2012, fl., *M. Ríos et al.* 2860 (F); Dtto. Iquitos, Quebrada Aucaya and Yanaquilla, “cotohuasca”, 17 May 1973, fr., *M. Rimachi* 390 (US); Mishana, Río Nanay, halfway between Iquitos and Santa María de Nanay, $73^{\circ}30'\text{W}$, $03^{\circ}50'\text{S}$, 19 May 1979, fr., *C. Diaz et al.* 1104 (F); Rio Nanay, Caseria Mishana 30 km SW of Iquitos, Aug 1978, st., *R. B. Foster* 4795 (F); Rio Yubinetto, affluent du Rio Putumayo, 23 Apr 1978, fr., *G. Haxaire* 952 (P). Requena, Dtto. Saquena, Rio Ucayali, trail from the creek of Aucayacu above Genaro Herrera, 7 Feb 1979, fr., *M. Rimachi* 4237 (US); Via Nauta-Iquitos, trocha lateral izquierda a 3 km de Nauta, $73^{\circ}32'\text{W}$, $04^{\circ}30'\text{S}$, 27 Jun 1979, fr., *C. Diaz & N. Jaramillo* 1228 (F).

Distribution, habitat and phenology: *Connarus wurdackii* is restricted to the region of Loreto, Peru, although one collection is known from the Tapajós River, west portion of Pará state, Brazil (Fig. 18). These locations are about 1,500 km away from each other, so this represents an unusual disjunction among Neotropical *Connarus*, which might be due to the lack of botanical collections in the Amazon. *Connarus wurdackii* is a lianescent species and grows in the Amazonia, reported to upland forests with clay or sandy soils, at approximately 120–200 m elevation. Specimens have been collected with flowers from August to October and with fruits from February to June and in November.

Notes: Among the species with dendroid trichomes, *Connarus wurdackii* is easily recognized by the acute or obtuse leaflet base, adaxially prominent or slightly prominent midveins and lanate inflorescences. It is morphologically similar to *C. erianthus* due to the lanate indumentum and sessile flowers, but differs by the lianescent habit (vs. shrubs or treelets), 5–7-foliolate leaves (vs. usually more than 7 leaflets), and inflorescences in double thyrsoids (vs. stachyoid spikes).

Connarus xylocarpus L.A. Vidal, Carbonó & Forero, Revista Brasil. Bot. 71(1): 68. 1984.—

TYPE: Brazil. Bahia: Maracás, Rod. BA-250, 13–15 Km a E de Maracás, margem da estrada e mata perturbada, 18 Nov 1978, fr., *S. A. Mori et al. 11147* (holotype: CEPEC 15301!; isotype: COL [photo!]).

Lianas; branchlets slightly striate, glabrous or subglabrous, trichomes simples unicellular, lenticels conspicuous. *Leaves* 3-foliolate; petioles 3.2–4.6 cm long, glabrous; rachises 0.5–1 cm long, glabrous; pulvinuli ca. 5 mm long, glabrous or subglabrous; leaflets coriaceous, concolorous, conduplicate, basal pairs $5.3\text{--}7.2 \times 3.1\text{--}3.9$ cm, symmetric, elliptic or ovate, bases symmetric, obtuse rounded, the apical ones $6.8\text{--}8.5 \times 3.5\text{--}4.7$ cm, symmetric, elliptic or ovate, bases symmetric, rounded, apices short acuminate, acumen 1–2 mm long, both surfaces glabrous or subglabrous, adaxial surfaces shining, margins slightly revolute; midveins abaxially prominent, adaxially impressed, secondary veins ca. 7 pairs, abaxially slightly prominent, adaxially flat, concolorous in relation to the blade, forming angles of $65\text{--}70^\circ$ with midvein, linear, tertiary veins flat on both surfaces, intercostals and epidermals reticulate. *Inflorescences* in thyrsoids, axillary, trichomes simple unicellular, peduncles 0.2–0.5 cm long or inflorescences subsessile, subglabrous or sparsely sericeous, rachises 11.2–14.8 cm long, sparsely sericeous, lateral cymes not seen, indumentum of these structures brown; bracts not seen. *Flowers* not seen. *Fruits* $2.1\text{--}2.5 \times 1.3\text{--}1.4$ cm, obovate, indehiscent side slightly sigmoid, pericarps ca. 3 mm thick, stipes 4–7 mm long, styles partially persistent, inconspicuous or apiculate, ca. 0.3 mm long, outer surfaces irregularly sparsely sericeous, indumentum ferruginous, black dots abundant, inner surfaces with sparse glandular trichomes, calyces persistent or partially so, sepals ascending erect or patent; seeds ca. 1.6×0.7 cm, arils color not seen.

Distribution, habitat and phenology: *Connarus xylocarpus* is only known from the type specimen, collected in a seasonal forest with high incidence of lianas, Bahia state (Brazil) (Fig. 13). It is a lianescent species, growing at ca. 900 m elevation. The only known specimens was collected with fruits in November.

Notes: This species is morphologically close to *C. laurifolius* (also from Bahia state) due to the exclusively 3-foliolate leaves, coriaceous leaflets with slightly revolute margins, linear secondary veins, reticulate tertiary veins and fruits internally with only glandular trichomes. However, *C. xylocarpus* seems restricted to seasonal forests in higher elevations and

it has elliptic or ovate leaflets, ca. 7 pairs of secondary veins and fruits pericarp ca. 3 mm thick, while *C. laurifolius* is associated to coastal vegetations with low elevations and it has narrowly obovate or narrowly elliptic leaflets, 9–12 pairs of secondary veins and fruits pericarp up to 2 mm thick.

Excluded taxa

Connarus fecundus Baker, in Martius, Fl. Bras. 14(2): 185. 1871. = *Pseudoconnarus macrophyllus* (Poepp.) Radlk.

Connarus gilgianus Pilg., Bot. Jahrb. Syst. 30: 154. 1901. = *Rourea puberula* Baker.

Connarus glaber (Kunth) DC., Prod. 2: 85. 1825. = *Rourea glabra* Kunth.

Connarus macrophyllus Poepp., Nov. Gen. Sp. Pl. 3: 76. 1845. = *Pseudoconnarus macrophyllus* (Poepp.) Radlk.

Connarus pubescens DC., Prod. 2: 85. 1825. = *Rourea pubescens* (DC.) Radlk.

Connarus oblongifolius (Hook. & Arn.) Mart. ex Baker, in Martius, Fl. Bras. 14(2): 179. 1871, *pro syn.* = *Rourea puberula* Baker.

Connarus simplicifolius Sessé & Moc., Pl. Nov. Hisp.: 106. 1887[1889]. = *Triumfetta simplicifolia* (Sessé & Moc.) Fryxell.

Connarus subpeltatus G. Schellenb., Candollea 2: 111. 1925, *nom. illeg.* = *Connarus neurocalyx* Planch.

Connarus subpeltatus was published by Schellenberg (1925) based on the collection *Gardner 1762* from G, indicated as coming from Brazil, although with no precise location. This specimen, however, was probably mistakenly labeled in G and it actually belongs to a collection made in southeast Asia, which is supported by several evidences. Firstly, according to Gardner's original collection book, available in K, his 1762 number refers to an Apocynaceae species. Secondly, the original label attached to the specimen in G does not resemble Gardner's original labels. Finally, the number 1762 is curiously the same as that of the type collection of *Connarus neurocalyx* (*Cuming 1762*, deposited in K), described from the Philippines. When both specimens from G and K are compared, they are identical with respect

to the number, size and shape of leaflets, flower structures sizes and fruits size and indumentum. This has led to the conclusion that the specimen from G is actually a duplicate of *Cuming 1762*, which was erroneously labeled during herbarium processing. Schellenberg (1925, 1938) did not notice the resemblance between the two specimens and described *C. subpeltatus*, which is very distinct from other Neotropical *Connarus*. As Schellenberg (1925) described a species based on the same type of a previously published species, then the name *C. subpeltatus* becomes illegitimate.

Connarus tricarplus Kuntze, Revis. Gen. Pl. 3(3): 47. 1898. = Sapindaceae.

Unidentified specimens

In this final section, a list of unidentified specimens is presented to indicate those of dubious identity, most of which collected with none or very few reproductive structures (or eventually in early stages of development) or whose morphology resembles more than one species:

M. Dantas & M. R. Cordeiro 1371 (IAN): in Toledo et al. (2020a), this specimen was identified as *C. acutissimus*. However, it differs from this species by the arcuate tertiary veins and percurrent tertiary veins, which are not seen in *C. acutissimus*. In addition, the specimen was collected in Amapá (Brazil), whereas *C. acutissimus* is restricted to Amazonas (Brazil). Following the concept of this taxonomic revision, the referred collection is more closely related to *C. lambertii* due to the relatively small leaflets with arcuate secondary veins, abaxially flat. Still, it differs significantly by the coriaceous leaflets with slightly revolute margins.

B. Hammel et al. 16880 (BM): this specimen resembles *C. silvanensis* due to the 3-foliolate leaves and large obovate leaflets with secondary veins adaxially impressed, but its fruits have longer stipes (ca. 5 mm long), which differs significantly from *C. silvanensis*, characterized by sessile fruits or with stipes up to 2 mm long. It could also be seen as a borderline individual among *C. ecuadorensis*, *C. lentiginosus* and *C. silvanensis* because of

their morphological resemblance in leaflet shape and size. Aside from this, the specimen was collected in Costa Rica, thus representing the boundary of their limits of occurrence.

J. C. Mutis 1113 (US): this specimen appeared to be a new species at first sight as the leaflets are broadly obovate, not seen in any other Neotropical *Connarus*. However, it is an old collection with no precise location and, moreover, the sample is composed of loose leaflets and there is only one fruit attached to the specimen branchlet. Given the poor condition in which the specimen is preserved, it is prudent to wait until more collections are examined.

J. A. Steyermark 90483 (US): this individual was collected with fruits in early stages of development, so it was not possible to confirm its identification. It resembles *C. lambertii* as the leaves are 3-foliolate and the leaflets are relatively small, with secondary veins arcuate and the tertiary ones abaxially flat. In addition, this specimen was collected in the range of occurrence of *C. lambertii* (Bolívar, Venezuela).

L. Valverde & Ismael 1254 (NY): it is closely similar to *C. lambertii* due to the leaves 3-foliolate, relatively small leaflets, secondary veins abaxially flat and inflorescences in thyrsoids, but slightly differs by the linear secondary veins and the floral buds, which are narrowly elliptic and whose aestivation is composed of imbricate sepals that become free in the central portion but maintain attached at the apex. It was also in the range of occurrence of *C. lambertii* (Barinas, Venezuela).

R. Vásquez et al. 24024 (F, NY): this specimen is very distinctive from other Neotropical *Connarus* due to its multifoliolate leaves and large inflorescences with rachises tomentose, without dendroid trichomes. However, only flower buds are presented in this specimen, so it is included in the list of unidentified specimens until additional data are available. It was collected close to Cenepa River, district of Cenepa, Peru, where only few *Connarus* species occur.

Considerações finais

Com o reconhecimento de 57 espécies neotropicais de *Connarus*, este trabalho de revisão representa uma importante contribuição para o conhecimento taxonômico e nomenclatural do grupo, apresentando consideráveis mudanças em relação aos últimos tratamentos para o gênero na região (Schellenberg 1938; Forero 1983), em especial no que se refere à utilização de caracteres morfológicos adicionais, ao reconhecimento de novos sinônimos (16 no total) e à publicação de espécies novas para a ciências (sete).

Embora tenha havido avanço no entendimento morfológico das espécies estudadas, ainda é necessária a utilização de novas informação que visem facilitar o reconhecimento de alguns táxons, principalmente daqueles cuja distinção esbarra em discretas sobreposições, mesmo que respaldadas por aspectos relacionados à distribuição geográfica e a algumas particularidades referentes ao número de folíolos (ver discussão anterior na seção “Morphology of the Neotropical species”). Tais dificuldades também permearam os trabalhos de Schellenberg (1938) e Forero (1983).

Portanto, considera-se que, com o advento de estudos anatômicos e/ou filogenéticos, é possível alcançar uma robustez ainda maior no reconhecimento das espécies neotropicais de *Connarus*. Além disso, ressalta-se a necessidade por futuros trabalhos relacionados à biologia reprodutiva/floral, uma vez que a aparente complexidade de sistemas reprodutivos no gênero pode ter desempenhado papel crucial na diversificação do grupo. Tais estudos encontram-se em fase de elaboração e representam a continuidade desta tese.

No que se refere à distribuição geográfica das espécies estudadas, considera-se que houve expressiva ampliação do conhecimento neste quesito, resultado alcançado a partir de uma extensa análise de materiais de herbário, aliado à execução de expedições de campo, importantes para dar respaldo às informações fornecidas nos espécimes. Com isso, é possível afirmar que, na região neotropical, as espécies de *Connarus* podem apresentar desde amplas distribuições, como *C. lambertii* (norte da América Central até norte da América do Sul) e *C. ruber* (praticamente ao longo de toda a Amazônia), restritas, como é o caso de *C. ecuadorensis* (Equador e parte da costa da Colômbia), *C. reticulatus* (ilha de Cuba) e *C. turczaninowii* (Panamá), ou até endêmicas, como *C. beyrichii* (conhecida somente para afloramentos rochosos entre os estados do Rio de Janeiro e Minas Gerais), *C. incomptus* (em savanas entre o estado de Roraima e os limites com a Guiana) e *C. steyermarkii* (em florestas úmidas na costa norte da Venezuela).

Do total de espécies, 24 apresentam ampla distribuição em seu domínio fitogeográfico, 17 são restritas a uma determinada área, cinco ocorrem em mais de um domínio e 11 são restritas a uma única localidade. A maior parte das espécies (37) ocorrem em florestas úmidas sempre verdes do sul do México até a floresta Amazônica (Perú e região norte do Brasil). Na Mata Atlântica (incluindo florestas sempre verdes, estacionais e as áreas de restinga), são encontradas 13 espécies de *Connarus*. Já em áreas mais abertas de savana ou em matas secas da América do Sul, seis espécies estão presentes, com destaque para *C. suberosus*, amplamente distribuída ao longo de praticamente todo o Cerrado brasileiro e em parte da Bolívia.

Tais constatações sugerem que grande parte das espécies neotropicais do gênero apresenta, ao menos, certo grau de especificidade com o ambiente onde habitam. Essa hipótese pode ser embasada pela ausência de grandes disjunções; dentre todas as espécies analisadas, apenas *C. araucanus* conta com populações disjuntas: embora sua distribuição seja primordialmente concentrada entre as savanas da Colômbia e Venezuela, duas coletas foram identificadas para a Bolívia, mas provavelmente em ambientes similares àqueles encontrados no limite norte de ocorrência. Análises filogenéticas também seriam essenciais no sentido de permitir uma discussão mais detalhada acerca da biogeografia de *Connarus* na região neotropical.

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ANEXO I

Figuras

Tabelas

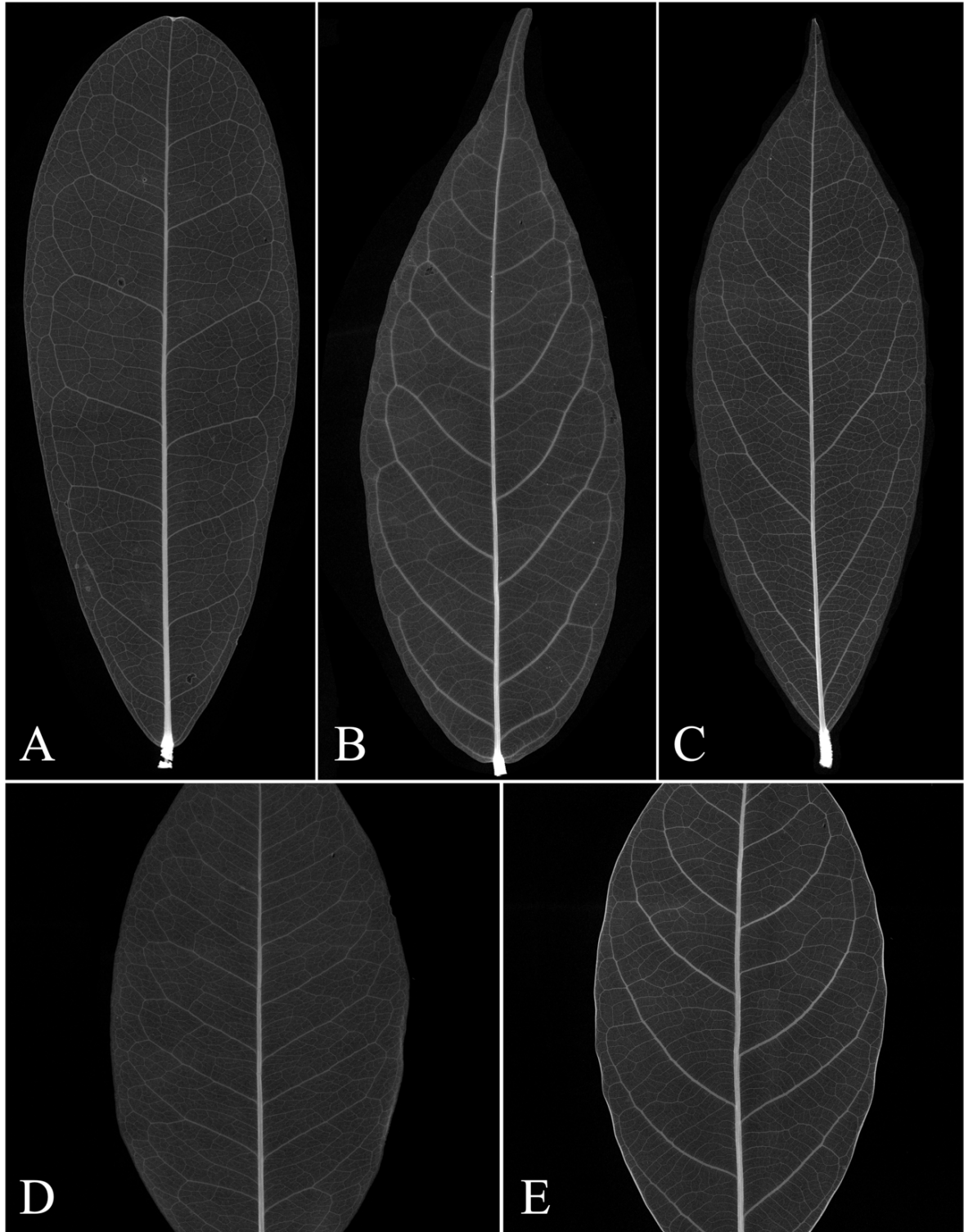


Figure 1. Venation pattern in Neotropical *Connarus*. A–*Connarus laurifolius*: linear secondary veins and intercostal and epidermal reticulate tertiary veins; B–*Connarus ruber*: arcuate secondary veins, mixed percurrent intercostal tertiary veins and opposite percurrent epidermal tertiary veins; C–*Connarus regnellii*: slightly arcuate secondary veins, alternate percurrent intercostal tertiary veins and opposite percurrent epidermal tertiary veins; D–*Connarus nodosus*: linear secondary veins and intercostal and epidermal reticulate tertiary veins; E–*Connarus revolutus*: arcuate secondary veins and opposite percurrent intercostal and epidermal tertiary veins.

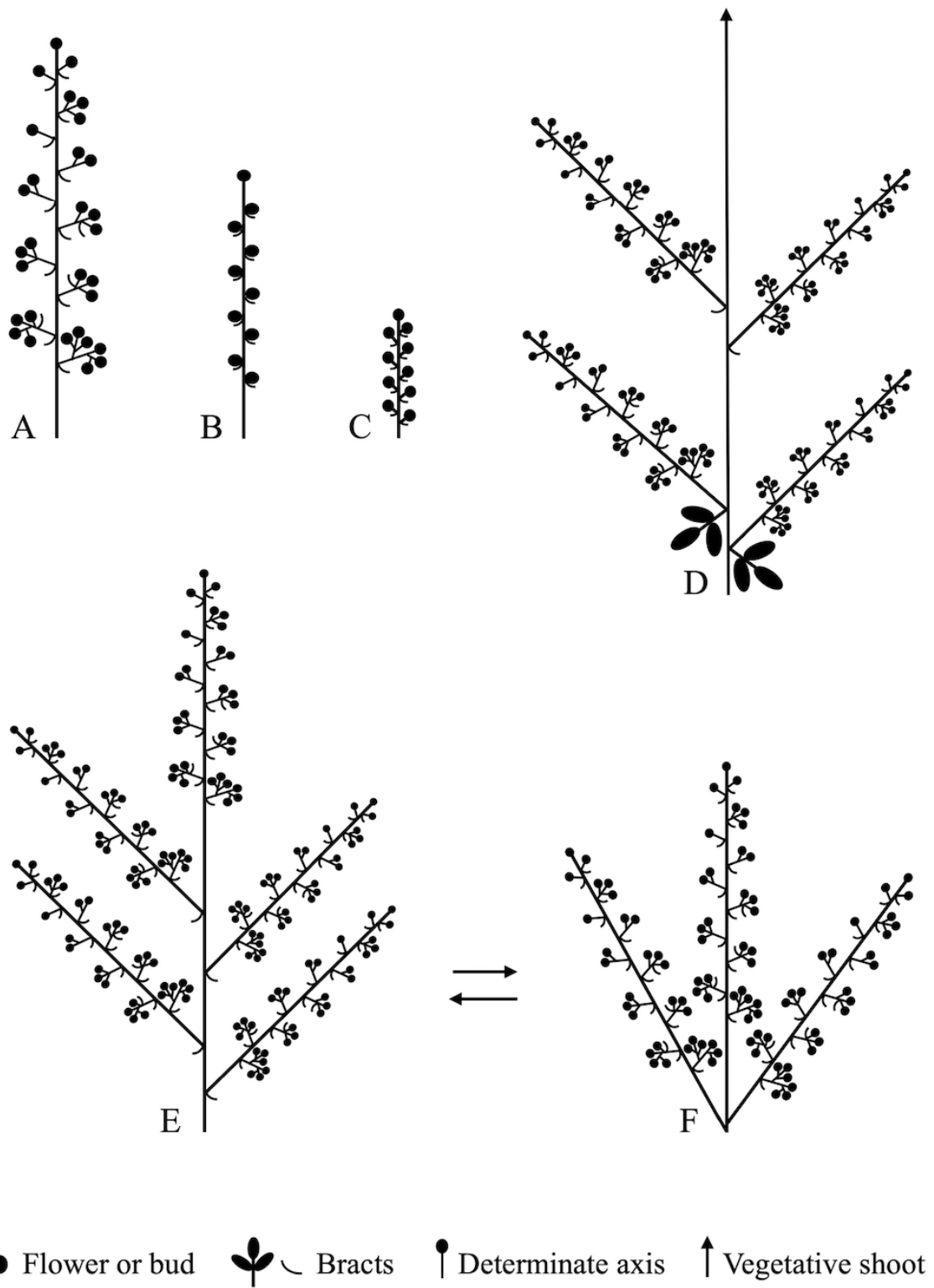


Figure 2. Inflorescence architecture in Neotropical *Connarus*. A–thyrsoid; B– stachyoid spikes; C– botryoid racemes; D–pseudo-terminal inflorescences; E–double thyrsoid; F–fasciculate thyrsoids.



Figure 3. Inflorescence architecture and flower characters in Neotropical *Connarus*. A–*Connarus fasciculatus* subsp. *fasciculatus*: cauliflorous inflorescences; B–C–*Connarus incomptus*: fasciculate thyrsoids and a single thyrsoid, respectively; D–*Connarus punctatus*: double thyrsoid; E–F–*Connarus incomptus*: brevistylous and longistylous flowers, respectively; G–*Connarus blanchetii*: detailed flowers showing the punctate perianth; H–K–*Connarus suberosus*: androecium and gynoecium (H), with red arrow indicating the carpel leaf suture, detailed stamens (I), detailed carpel (J), ovary in internal view (K), showing initial development of the marginal ovules.

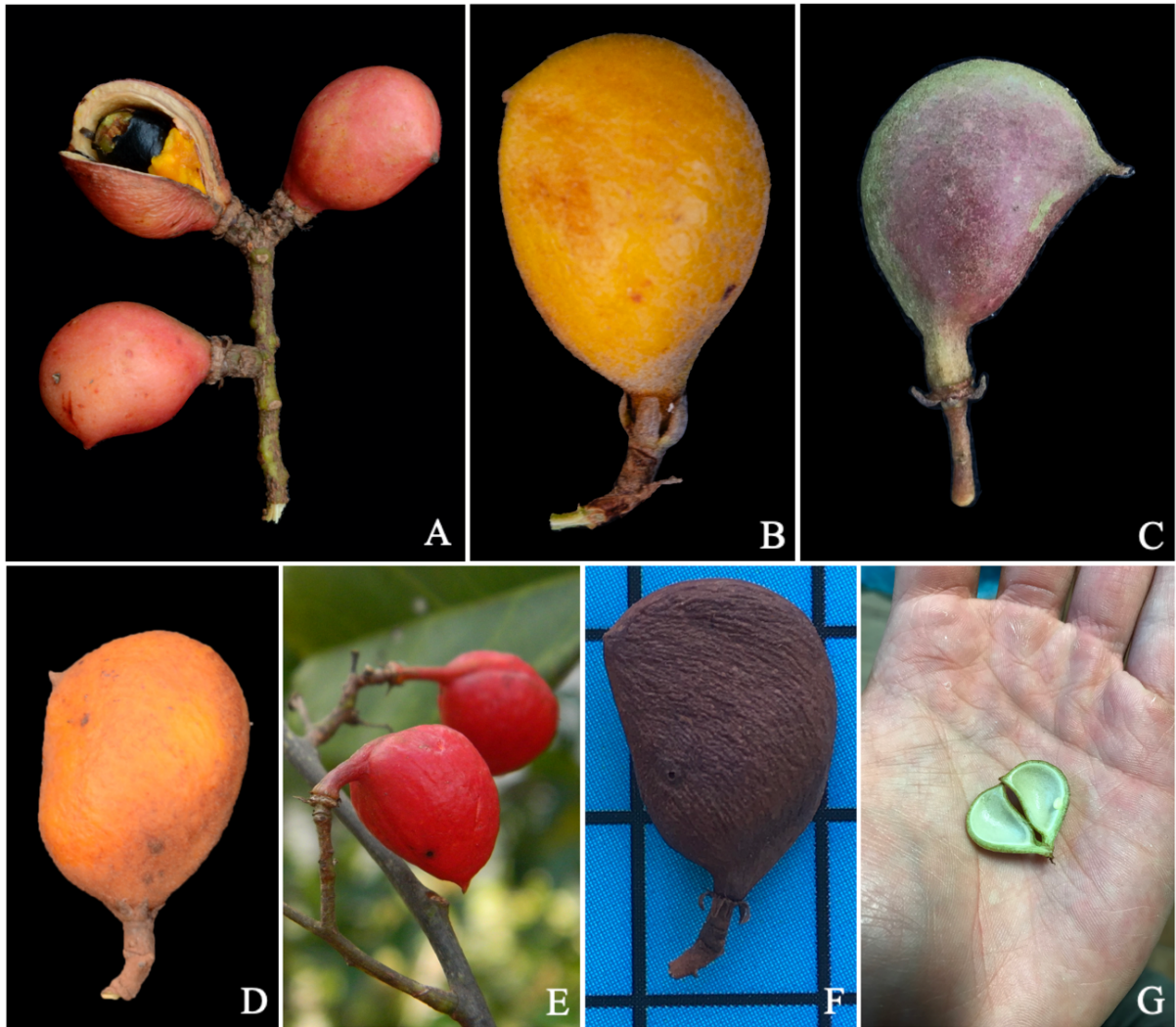


Figure 4. Fruit details in Neotropical *Connarus*. A–*Connarus beyrichii*: follicle showing the black seed with yellowish aril; B–*Connarus aureus*: persistent calyx with ascending erect sepals; C–*Connarus rostratus*: persistent calyx with ascending curved sepals; D–*Connarus favosus*: sessile fruit; E–*Connarus coriaceus*: long stipitate fruits; F–*Connarus ruber*: reflexed sepals; G–*Connarus rostratus*: fruit with non-developed seed. Photo in E by Mayara Pastore.

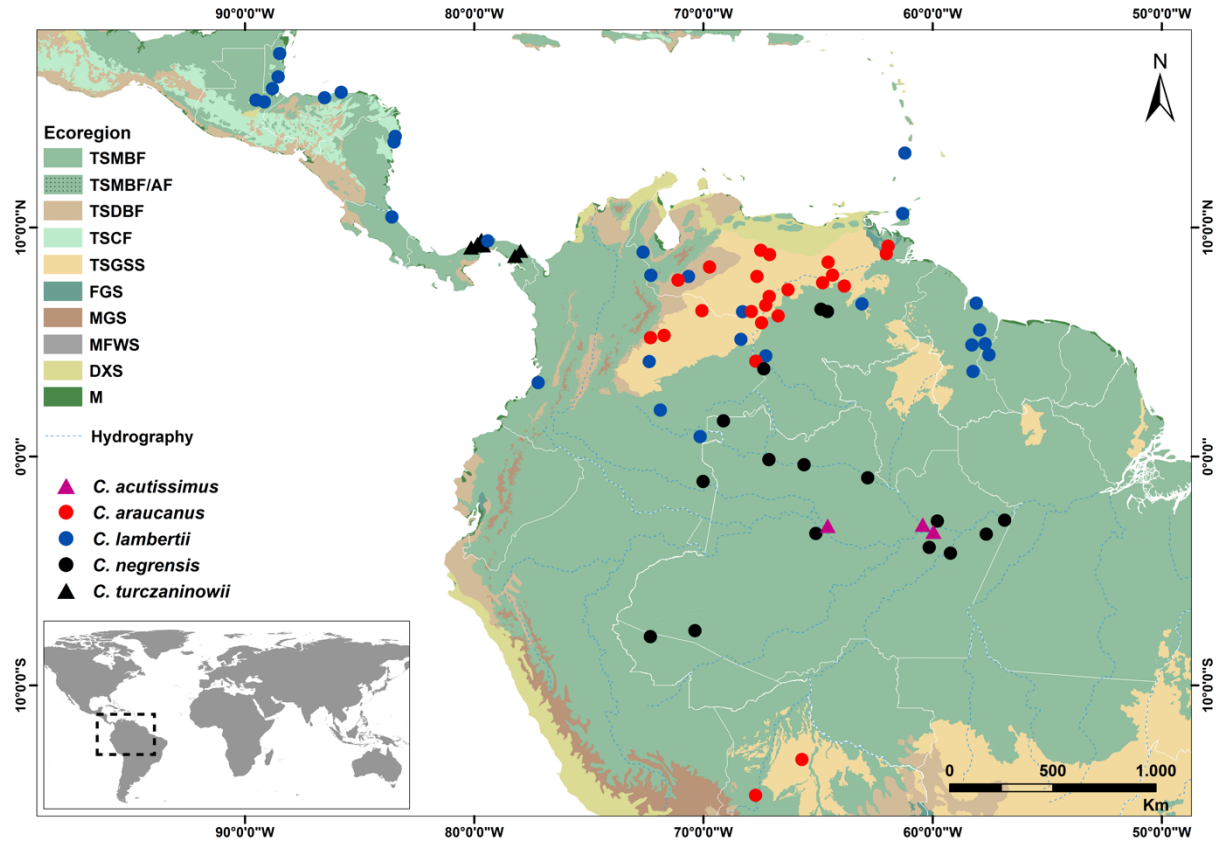


Figure 5. Geographic distribution of *Connarus acutissimus*, *C. araucanus*, *C. lambertii*, *C. negrensis* and *C. turczaninowii* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

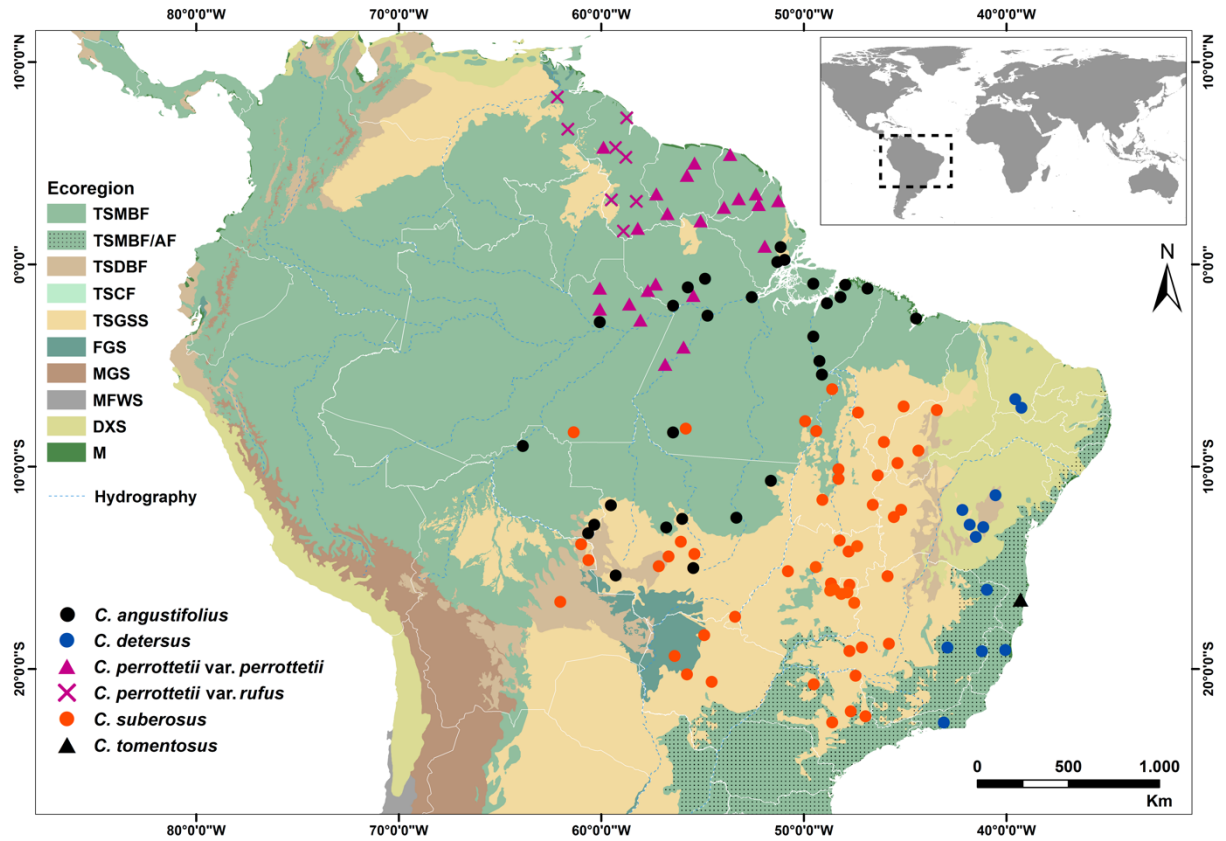


Figure 6. Geographic distribution of *Connarus angustifolius*, *C. deterrentus*, *C. lambertii*, *C. perrottetii*, *C. suberosus* and *C. tomentosus* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

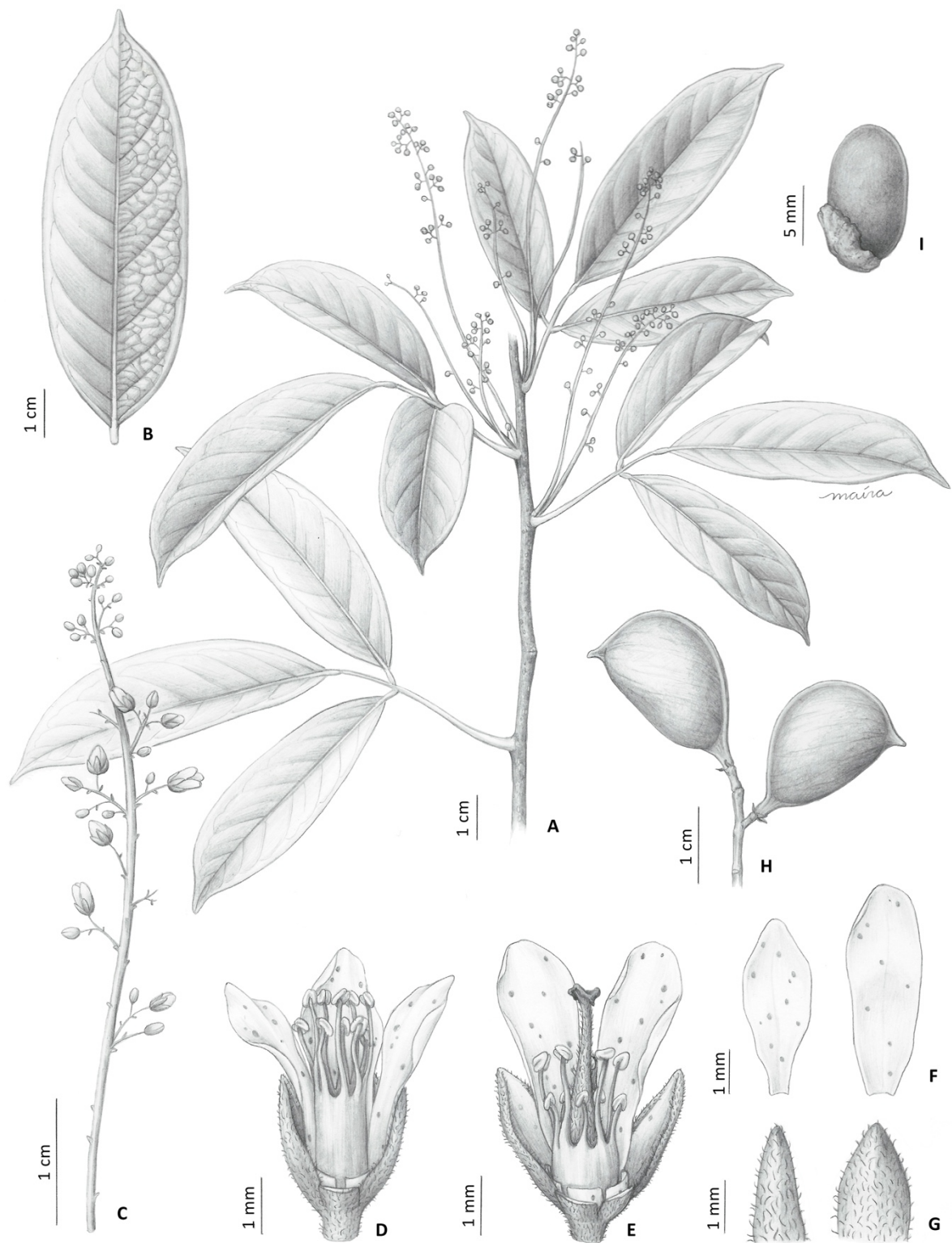


Figure 7. *Connarus araucanus*: A—flowering branchlet; B—leaflet showing venation, abaxial surface; C—thyrsoid inflorescence; D—brevistylous flower, external view; E—longistylous flower, external view; F—petals, external view; G—sepals, external view; H—fruits, external view; I—seed with aril.

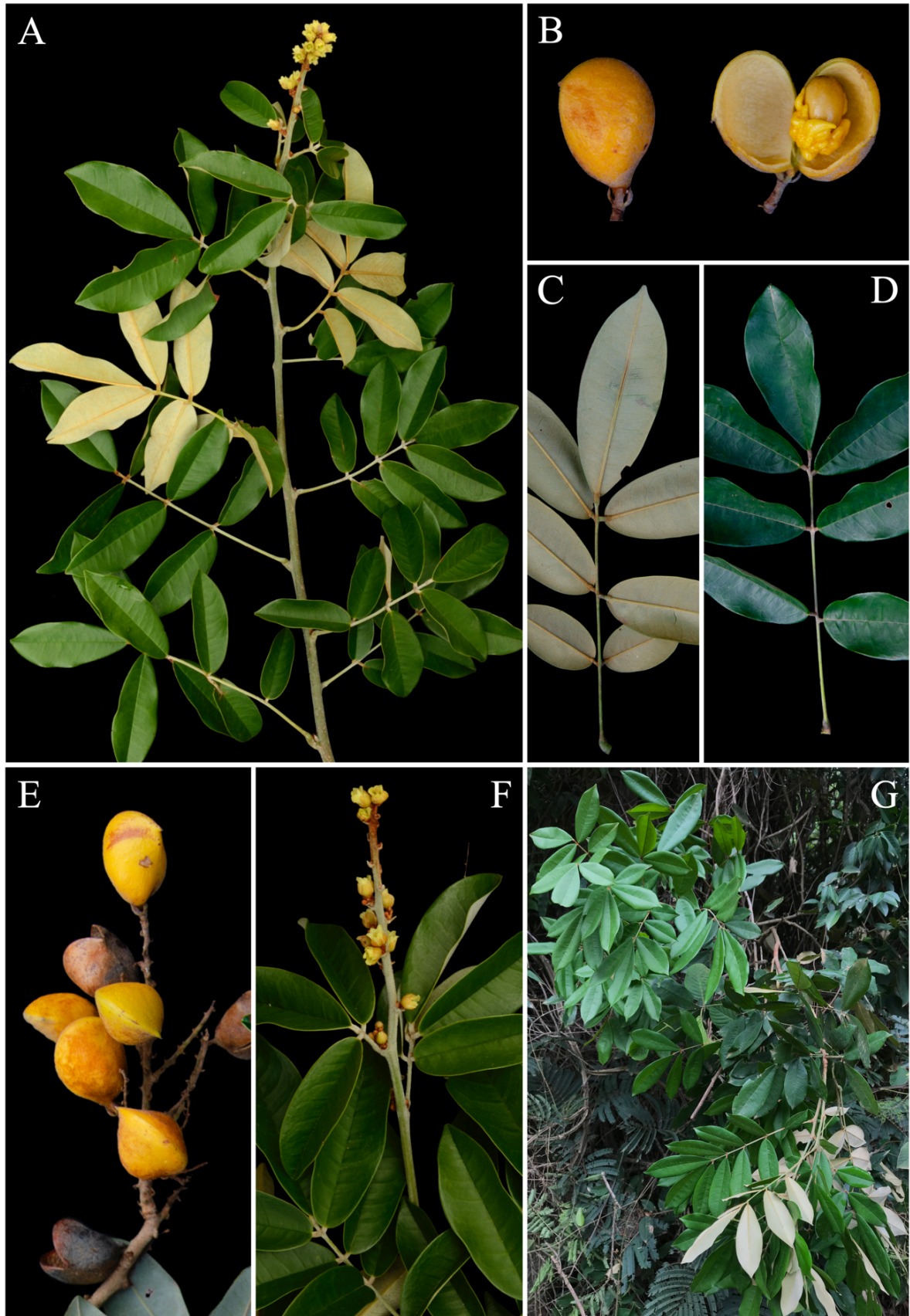


Figure 8. *Connarus aureus*: A–flowering branchlet; B–fruits, external and internal views showing immature seed; C–leaf, abaxial surface; D–leaf, adaxial surface; E–infructescence; F–detailed inflorescence; G–habit.

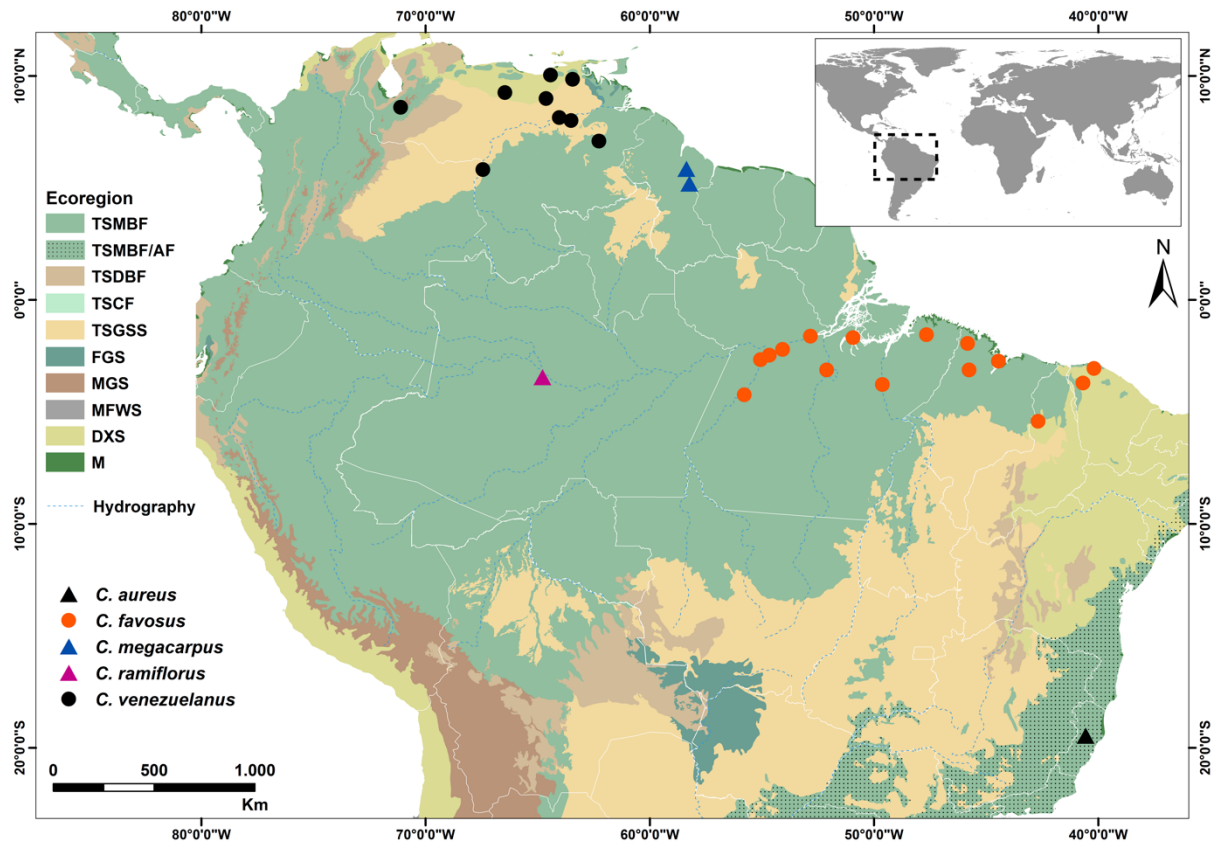


Figure 9. Geographic distribution of *Connarus aureus*, *C. favosus*, *C. megacarpus*, *C. ramiflorus* and *C. venezuelanus* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

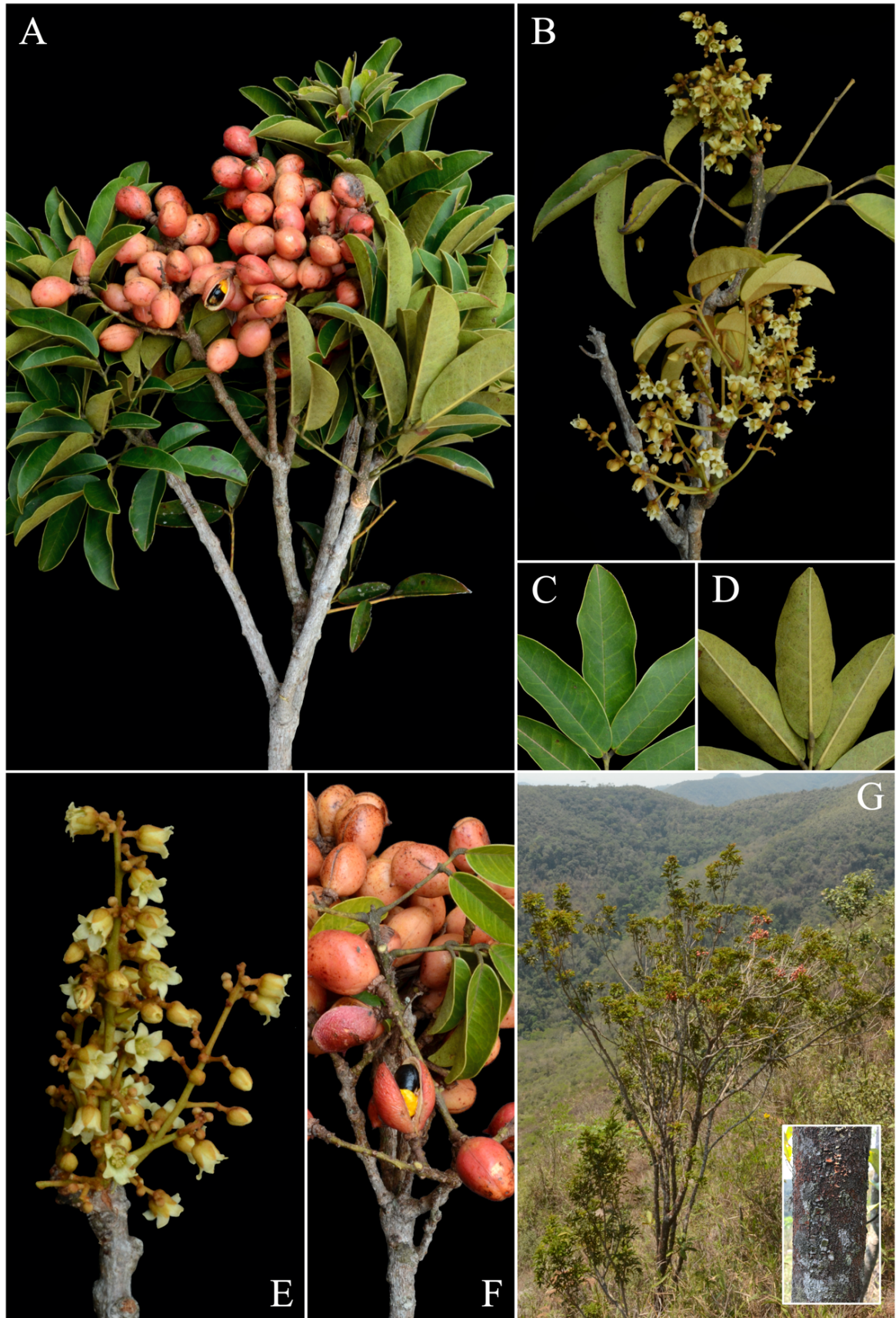


Figure 10. *Connarus beyrichii*: A—fruiting branchlet; B—flowering branchlet; C—leaf, adaxial surface; D—leaf, abaxial surface; E—detailed flowers; F—detailed fruits; G—habit with detail of the trunk.

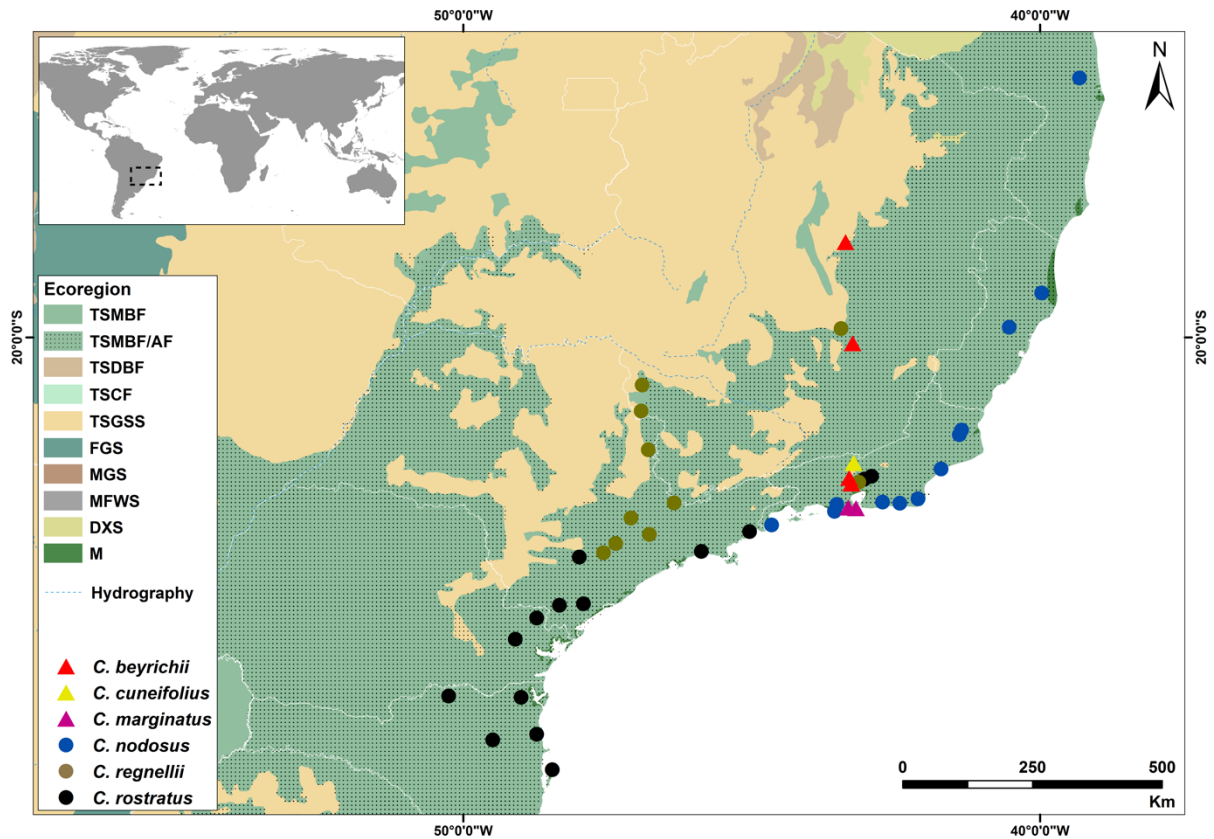


Figure 11. Geographic distribution of *Connarus beyrichii*, *C. cuneifolius*, *C. marginatus*, *C. nodosus*, *C. regnellii* and *C. rostratus* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

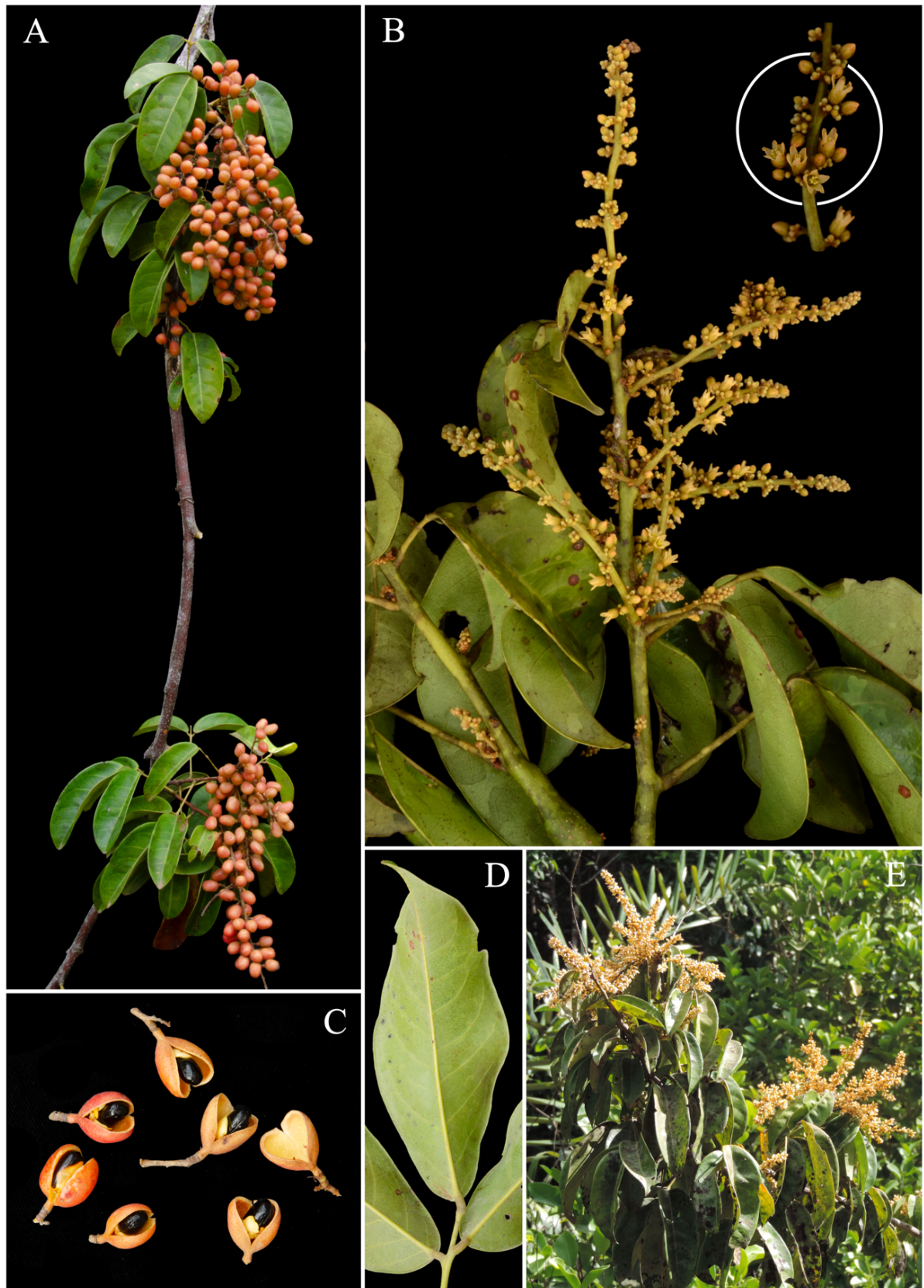


Figure 12. *Connarus blanchetii*: A—lianescent habit with fruiting branchlets; B—flowering branchlet with detailed flowers; C—detailed fruits showing seeds with aril; D—leaf, abaxial surface; E—scandent shrub.

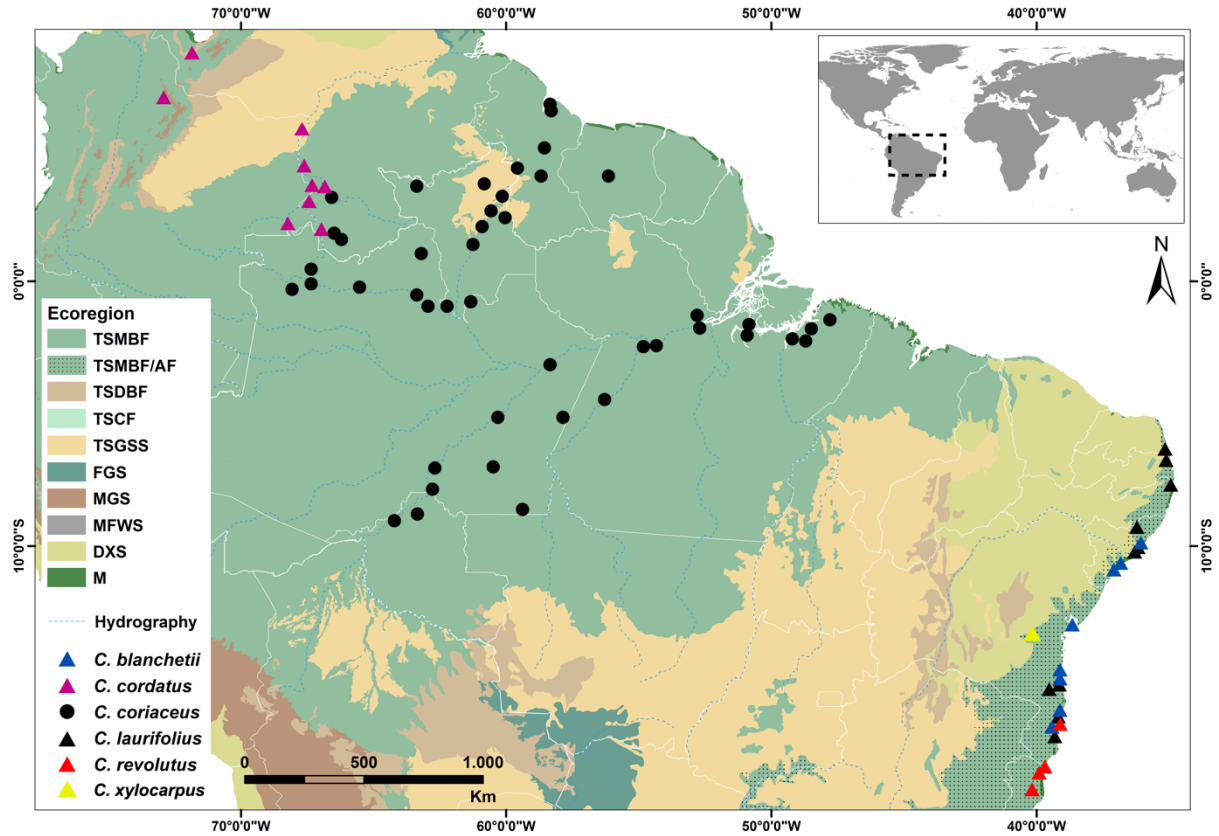


Figure 13. Geographic distribution of *Connarus blanchetii*, *C. cordatus*, *C. coriaceus*, *C. laurifolius*, *C. revolutus* and *C. xylocarpus* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

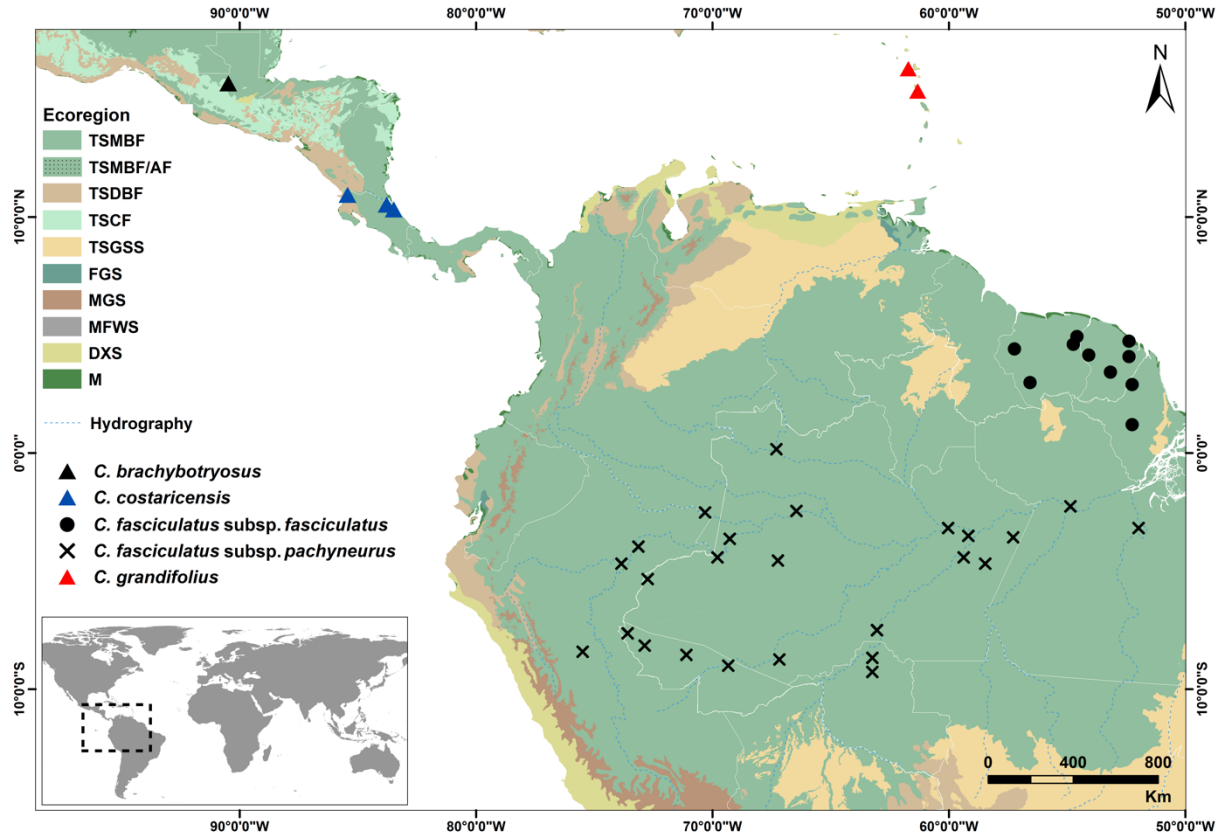


Figure 14. Geographic distribution of *Connarus brachybotryosus*, *C. costaricensis*, *C. fasciculatus* and *C. grandifolius* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

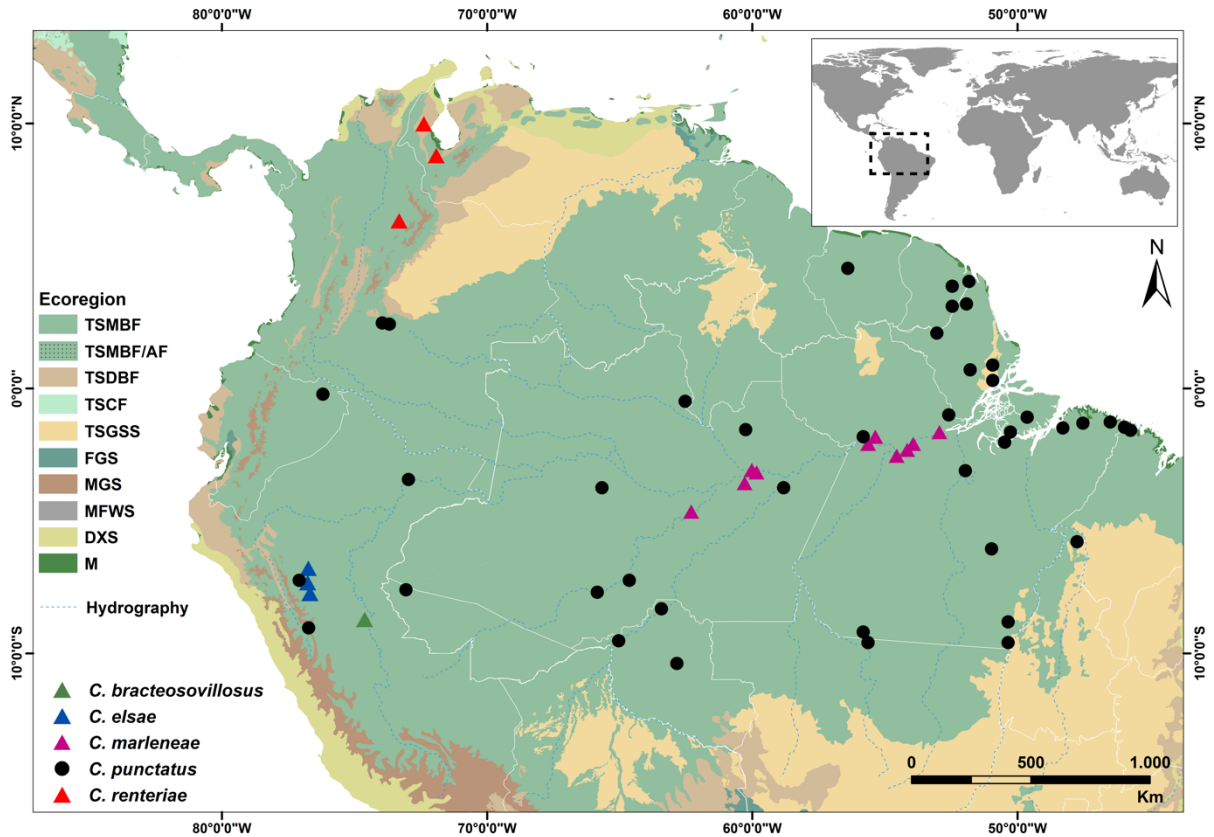


Figure 15. Geographic distribution of *Connarus bracteosovillosus*, *C. elsae*, *C. marleneae*, *C. punctatus* and *C. renteriae* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

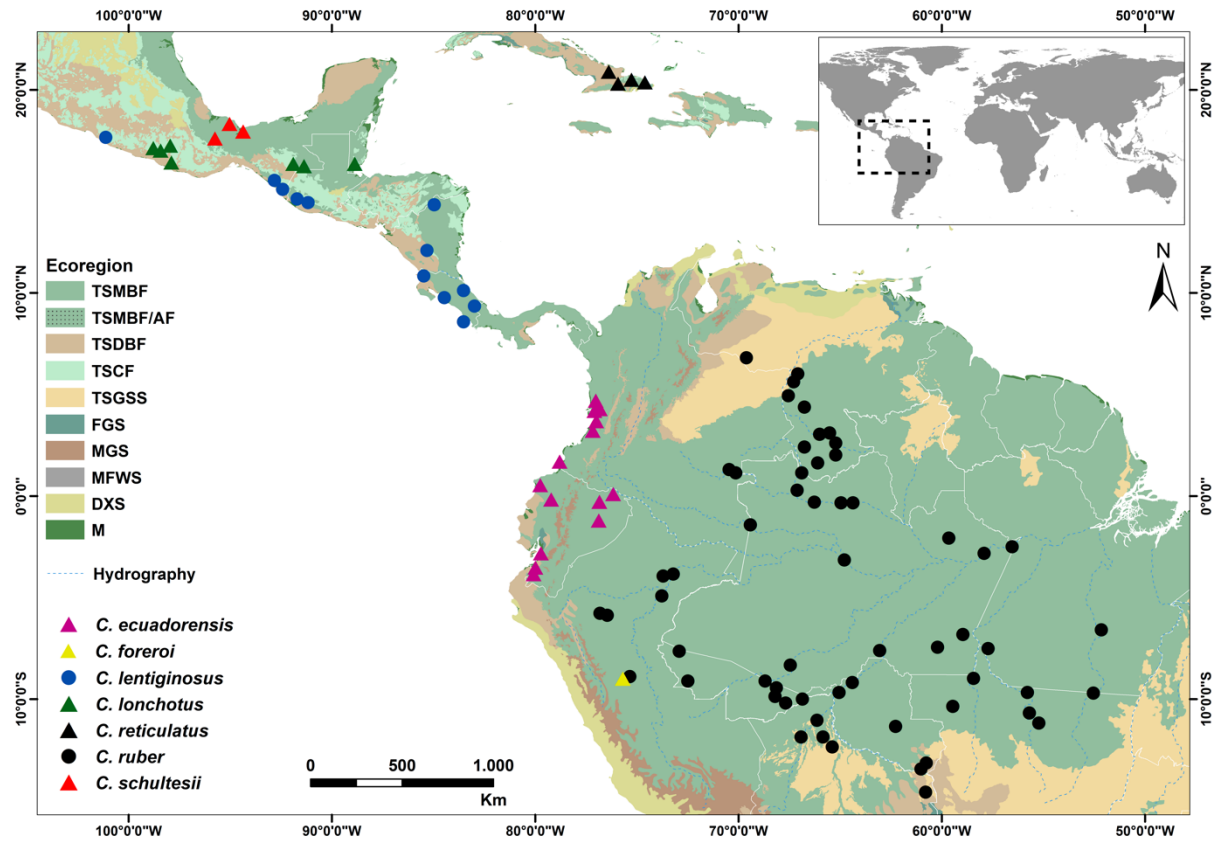


Figure 16. Geographic distribution of *Connarus ecuadorensis*, *C. foreroi*, *C. lentiginosus*, *C. lonchotus*, *C. reticulatus*, *C. ruber* and *C. schultesii* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

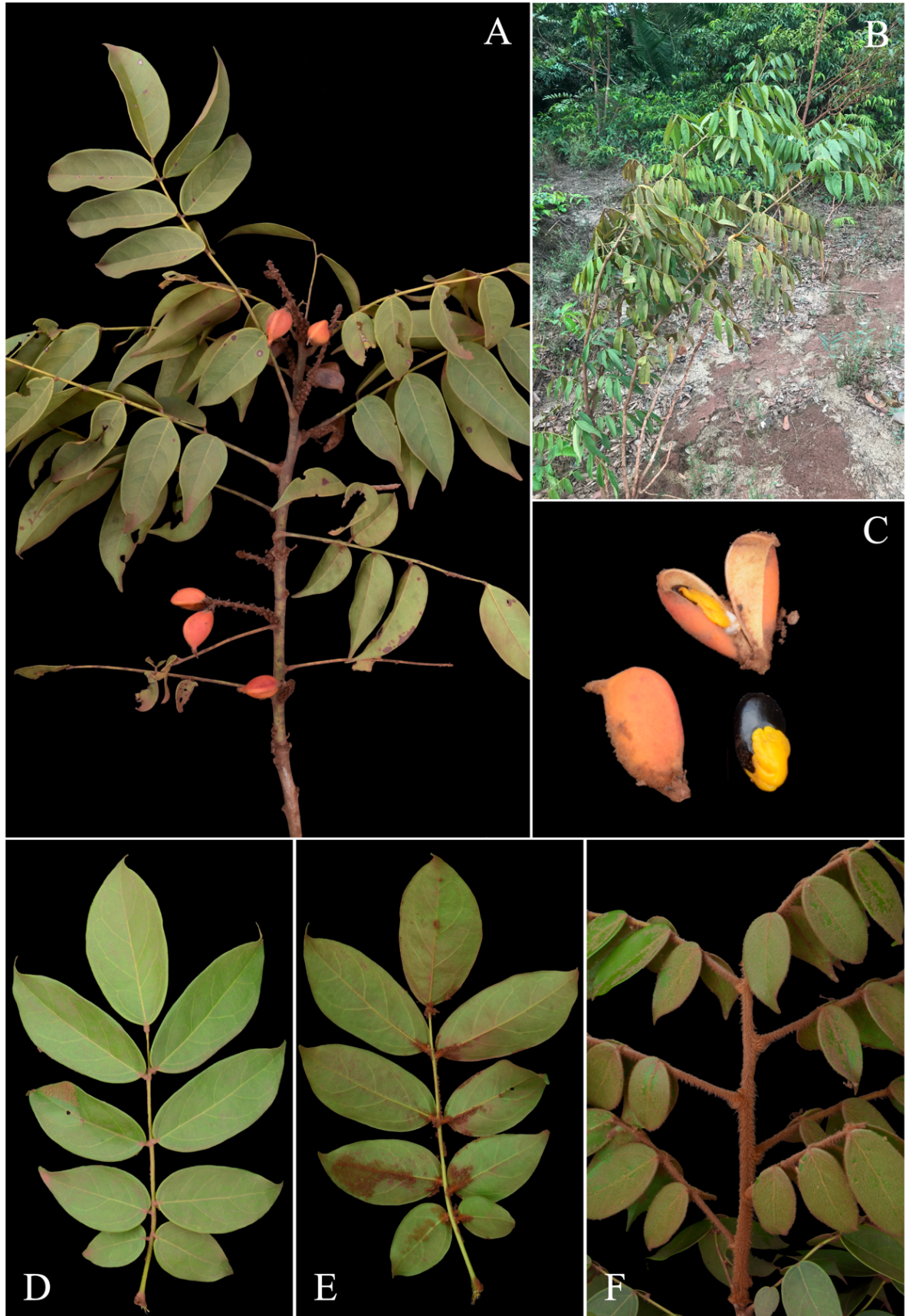


Figure 17. *Connarus erianthus*: A—fruiting branchlet; B—habit; C—detailed fruits showing seeds with aril; D—leaf, adaxial surface; E—leaf, abaxial surface; F—detailed indumentum of young branchlets.

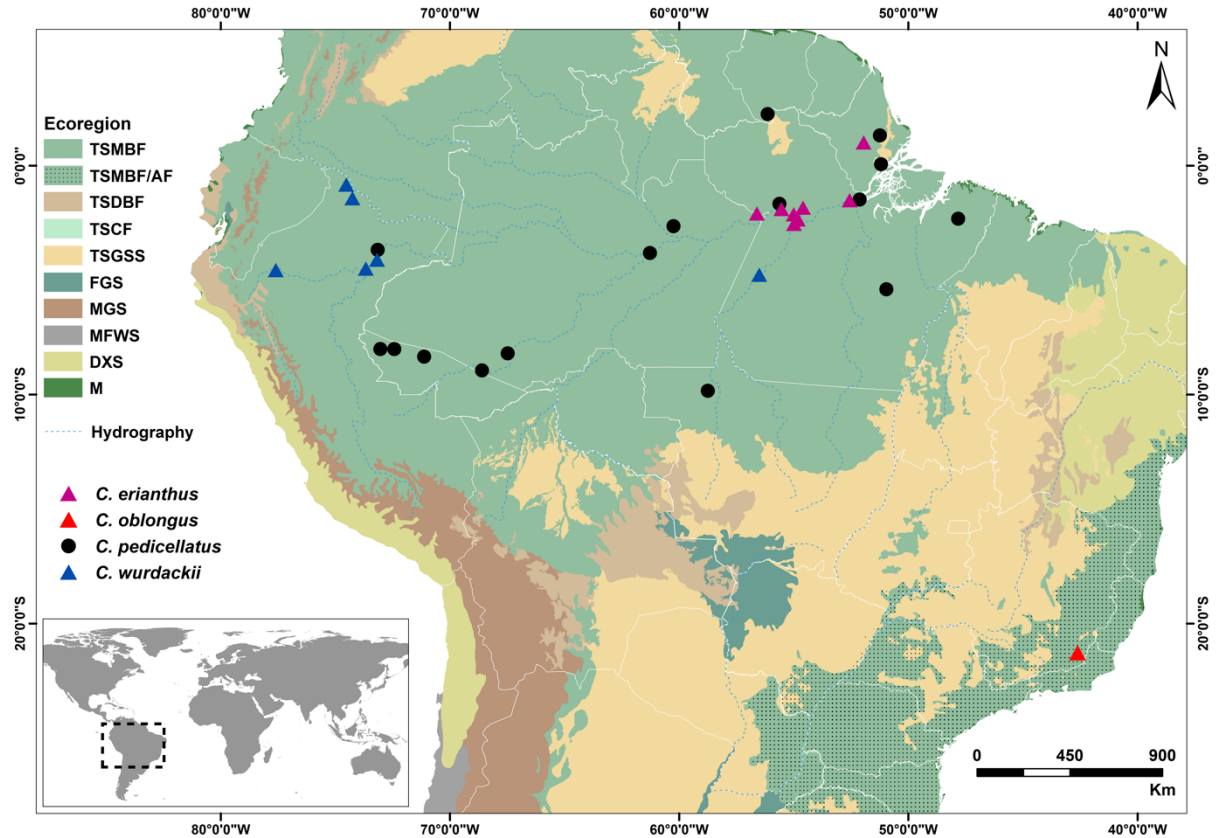


Figure 18. Geographic distribution of *Connarus erianthus*, *C. oblongus*, *C. pedicellatus* and *C. wurdackii* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

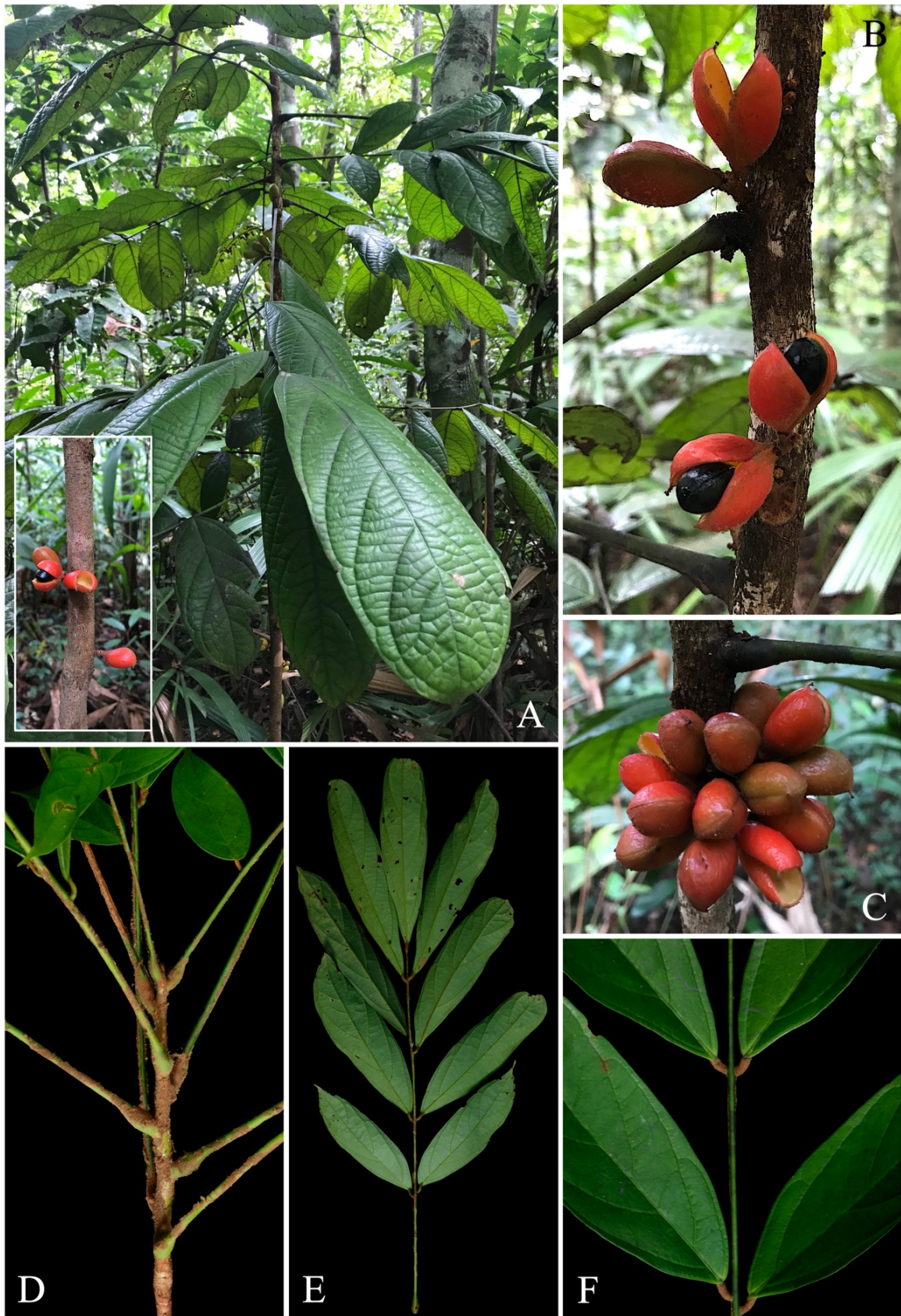


Figure 19. *Connarus fasciculatus* subsp. *pachyneurus*: A–habit showing the cauliflorous fruits; B–detailed fruits showing the seeds; C–detailed fruits; D–detailed indumentum of branchlets; E–leaf, abaxial surface; F–asymmetric leaflet bases. Photos in B and C by Iracema Moll.

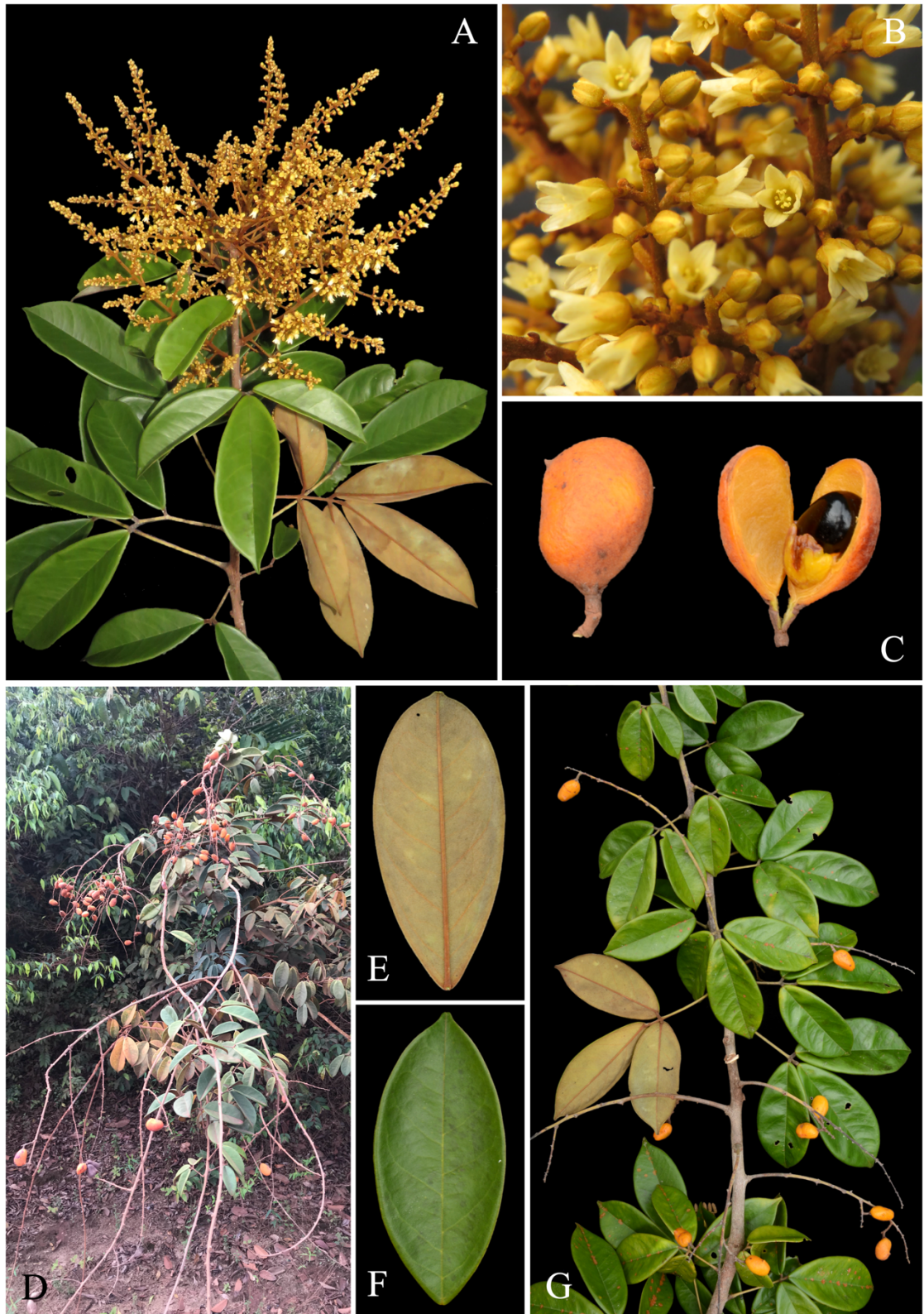


Figure 20. *Connarus favosus*: A—flowering branchlet; B—detailed flowers; C—detailed fruits showing seed with aril; D—habit; E—leaflet, abaxial surface; F—leaflet, adaxial surface; G—fruiting branchlet.

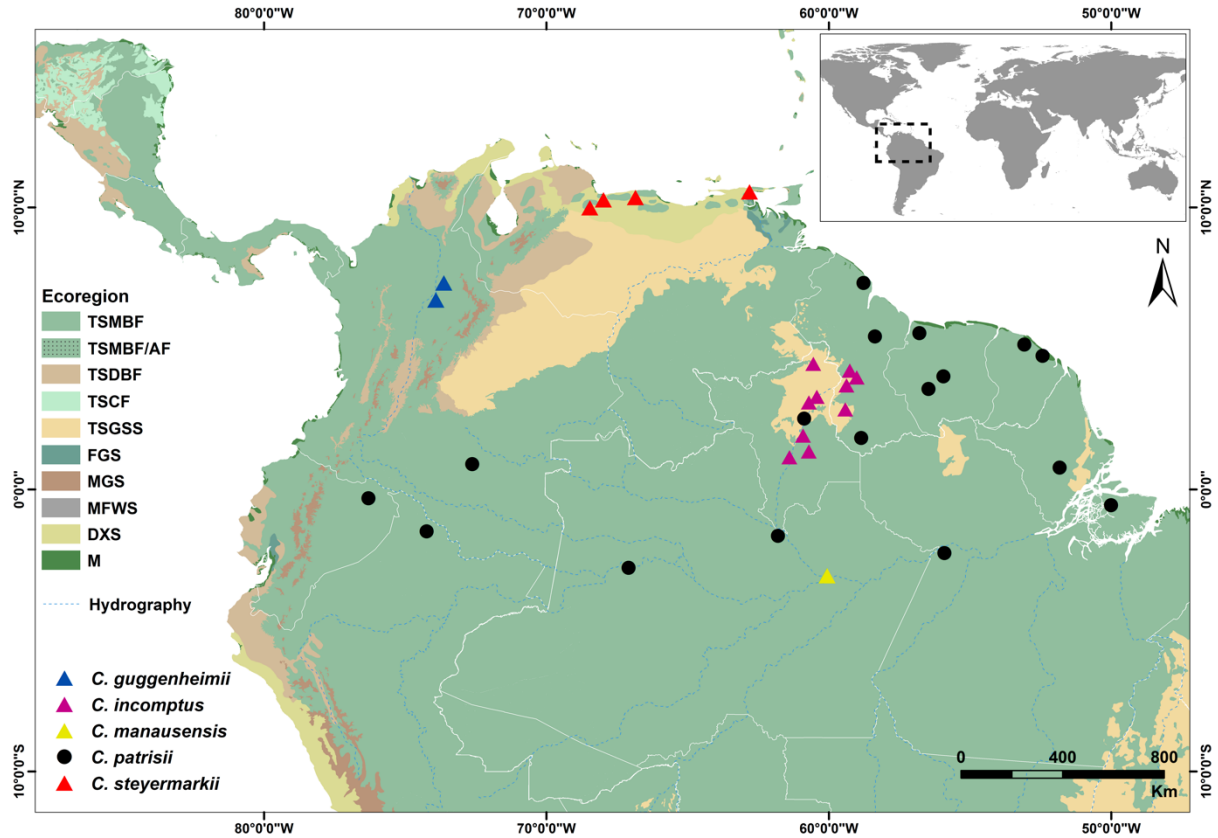


Figure 21. Geographic distribution of *Connarus guggenheimii*, *C. incomptus*, *C. manausensis*, *C. patrisii* and *C. steyermarkii* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

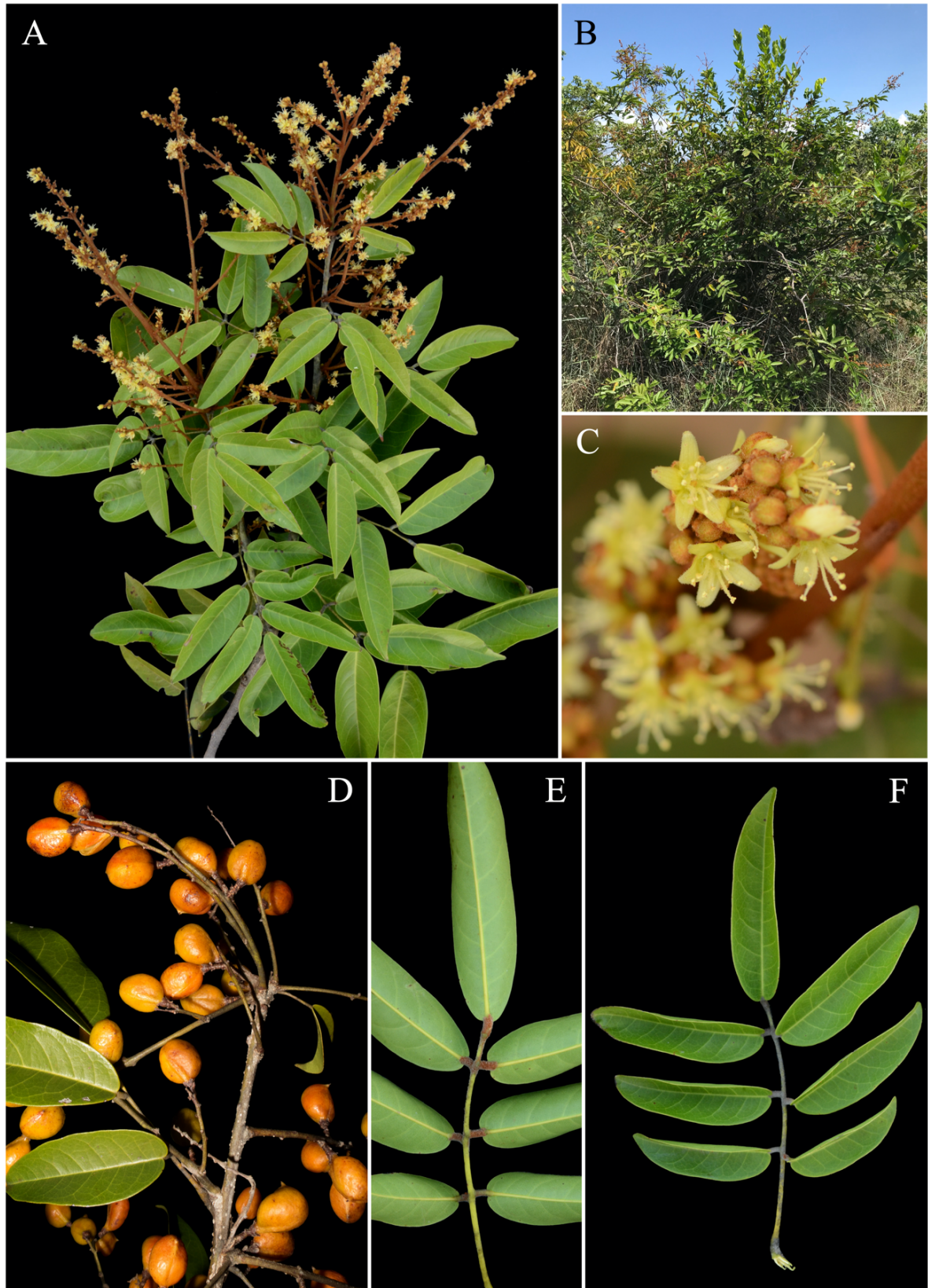


Figure 22. *Connarus incomptus*: A–flowering branchlet; B–habit; C–detailed flowers; D–fruiting branchlet; E–leaf, abaxial surface; F–leaf, adaxial surface. Photo in D by Ricardo Perdiz.

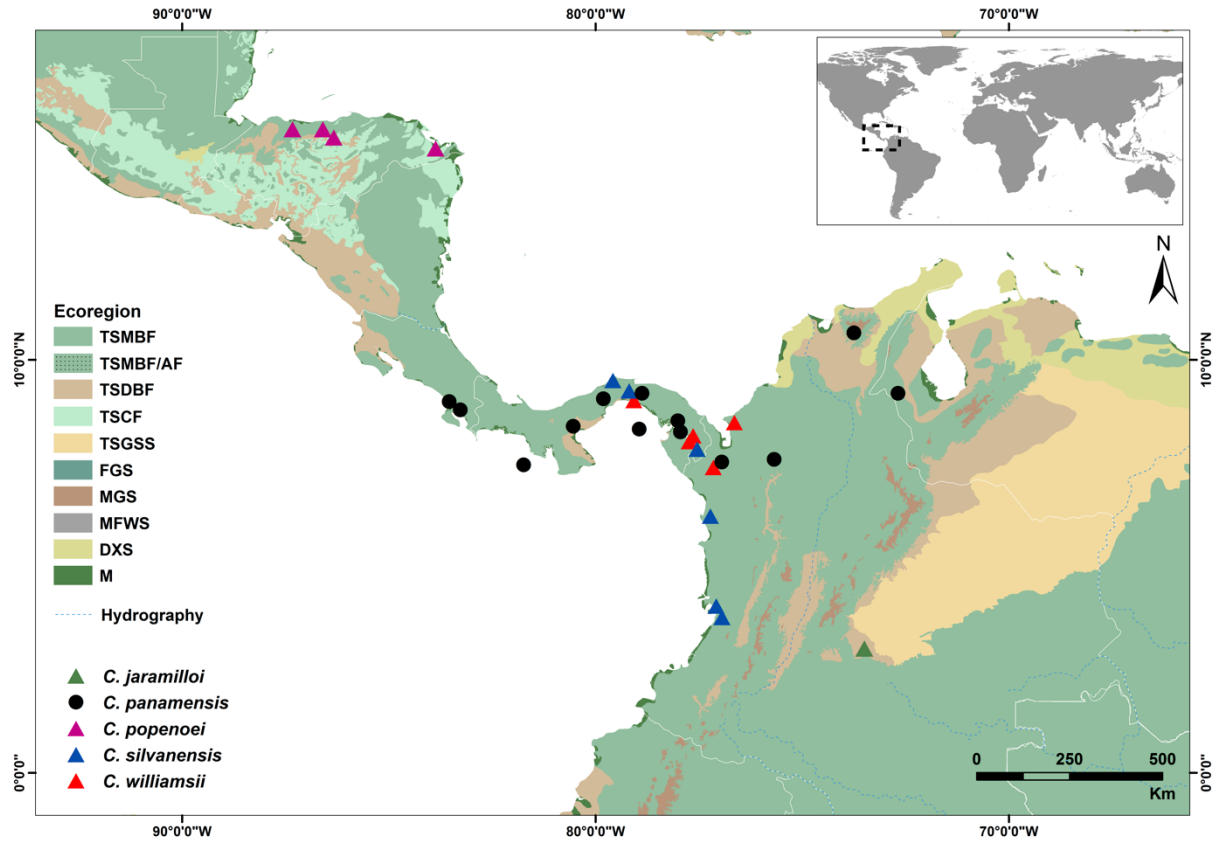


Figure 23. Geographic distribution of *Connarus jaramilloi*, *C. panamensis*, *C. popenoei*, *C. silvanensis* and *C. williamsii* in the Neotropics. (TSMBF=Tropical and Subtropical Moist Broadleaf Forests; TSMBF/AF=Tropical and Subtropical Moist Broadleaf Forests/Atlantic Forest; TSDBF=Tropical and Subtropical Dry Broadleaf Forest; TSCF= Tropical and Subtropical Coniferous Forests; TSGSS=Tropical and Subtropical Grasslands, Savannas and Shrublands; FGS=Flooded Grasslands and Savannas; MGS=Montane Grasslands and Shrublands; MFWS=Mediterranean Forests, Woodlands and Scrub; DXS=Desert and Xeric Shrublands; M=Mangroves)

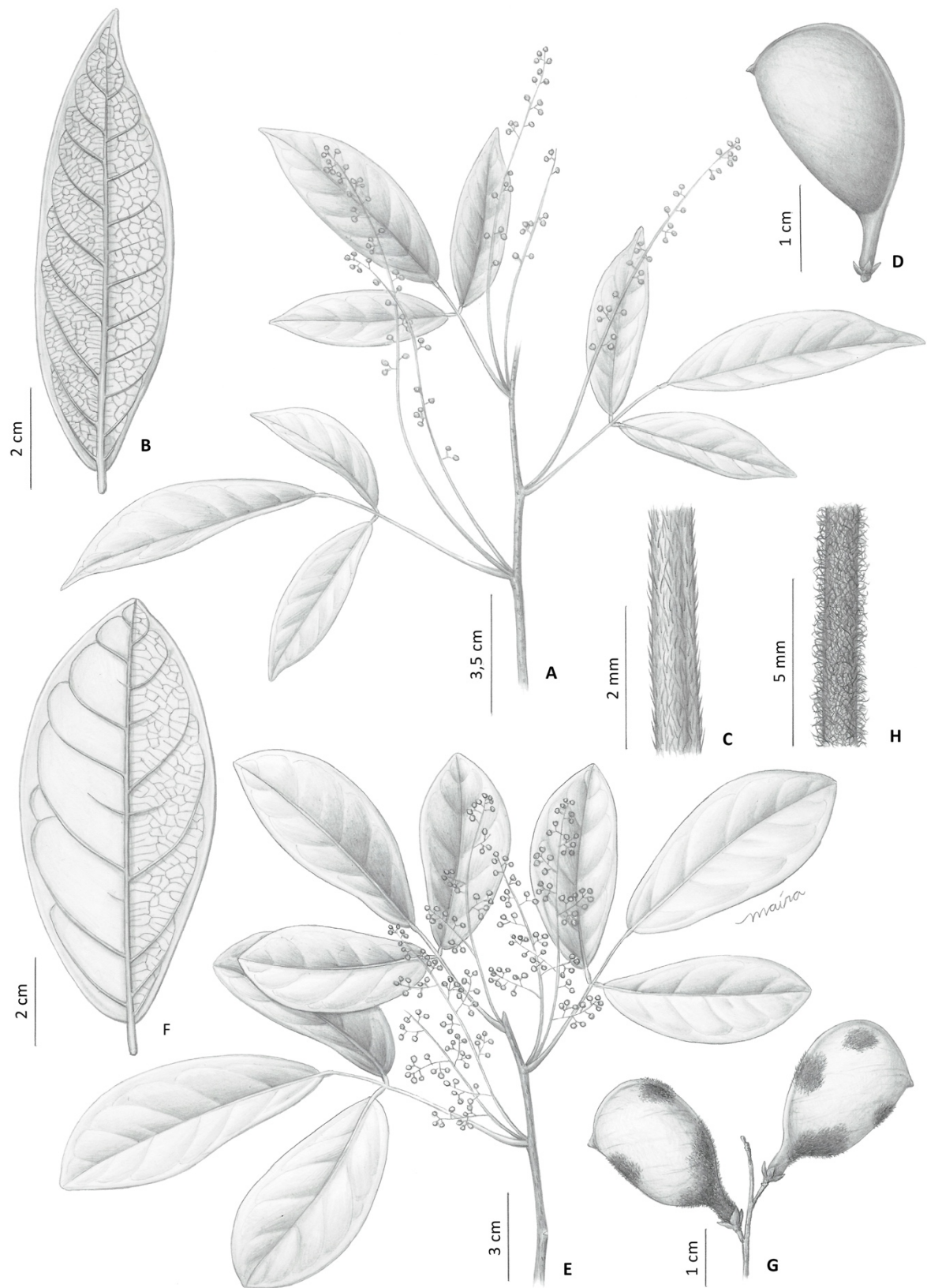


Figure 24. *Connarus lonchotus*: A—flowering branchlet; B—leaflet showing venation, abaxial surface; C—sericeous indumentum on inflorescence rachis; D—fruit, external view. *Connarus schultesii*: E—flowering branchlet; F—leaflet showing venation, abaxial surface; G—fruits, external surface; H—indumentum on inflorescence rachis.

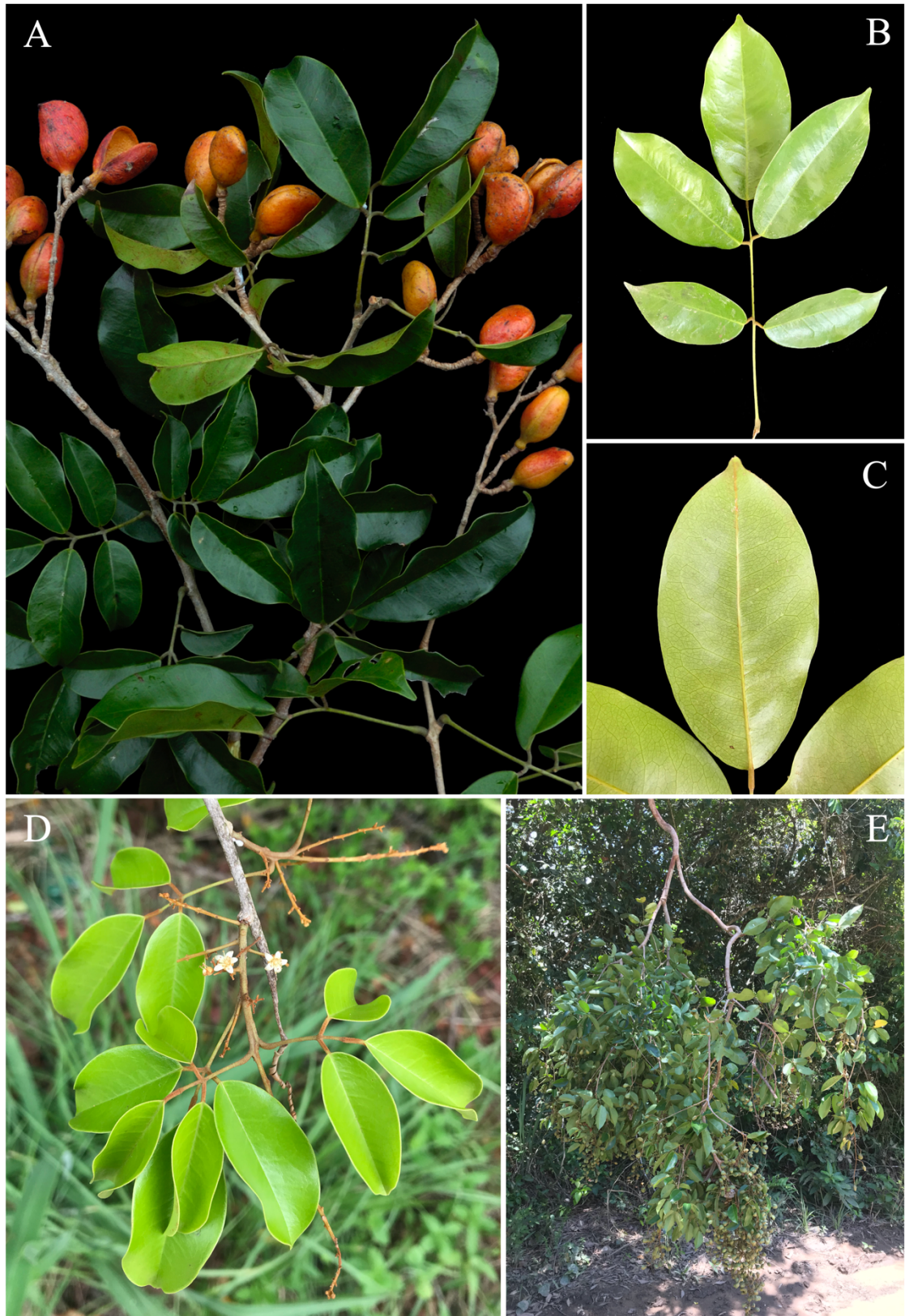


Figure 25. *Connarus nodosus*: A–fruiting branchlet; B–leaf, adaxial surface; C–leaflet, abaxial surface showing venation; D–flowering branchlet; E–habit. Photo in A by Thiago Flores.



Figure 26. *Connarus panamensis*: A—detailed flowers; B—fruiting branchlet; C—flowering branchlet; D—inflorescences. All photos by Pedro Acevedo-Rodríguez.

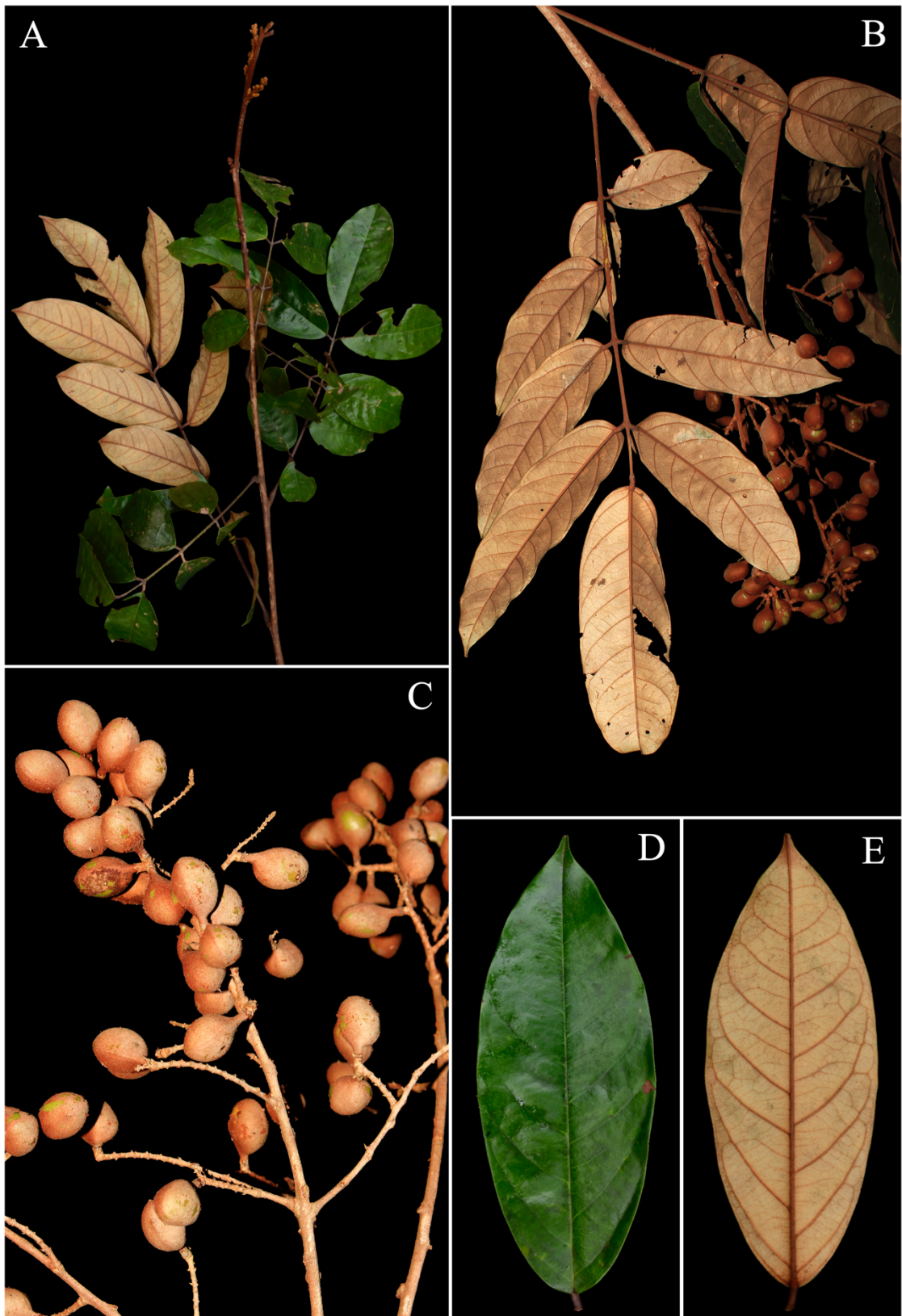


Figure 27. *Connarus perrottetii* var. *perrottetii*: A—flowering branchlet (buds); B—fruiting branchlet; C—detailed fruits; D—leaf, adaxial surface; E—leaf, abaxial surface. Photos in B and C by Herison Medeiros.

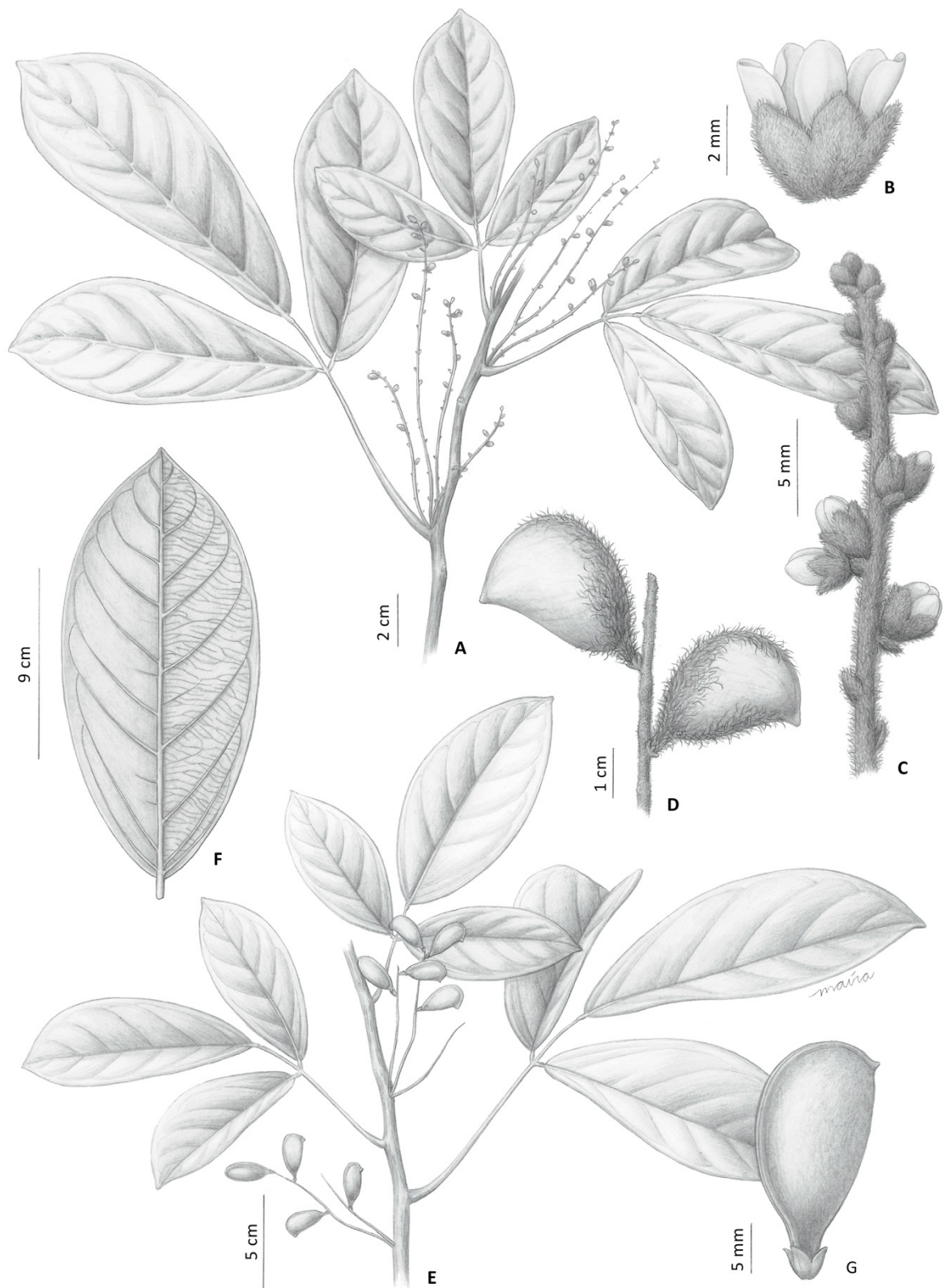


Figure 28. *Connarus popenoei*: A—flowering branchlet; B—flowers, external view; C—thyrsoid inflorescence with sessile flowers; D—fruits, external view. *Connarus silvanensis*: E—fruiting branchlet; F—leaflet showing venation, abaxial surface; G—fruit, external view.



Figure 29. *Connarus punctatus*: A-B—fruiting branchlet; C—habit; D—fruit and seed with aril, external view.



Figure 30. *Conarus regnellii*: A-B–fruiting branchlet; C–leaf, adaxial surface; D–leaf, abaxial surface; E–fruiting branchlets on arboreal individual; F–trunk; G–fruits and seeds with aril. Photo in G by Jeniffer Fernandes.

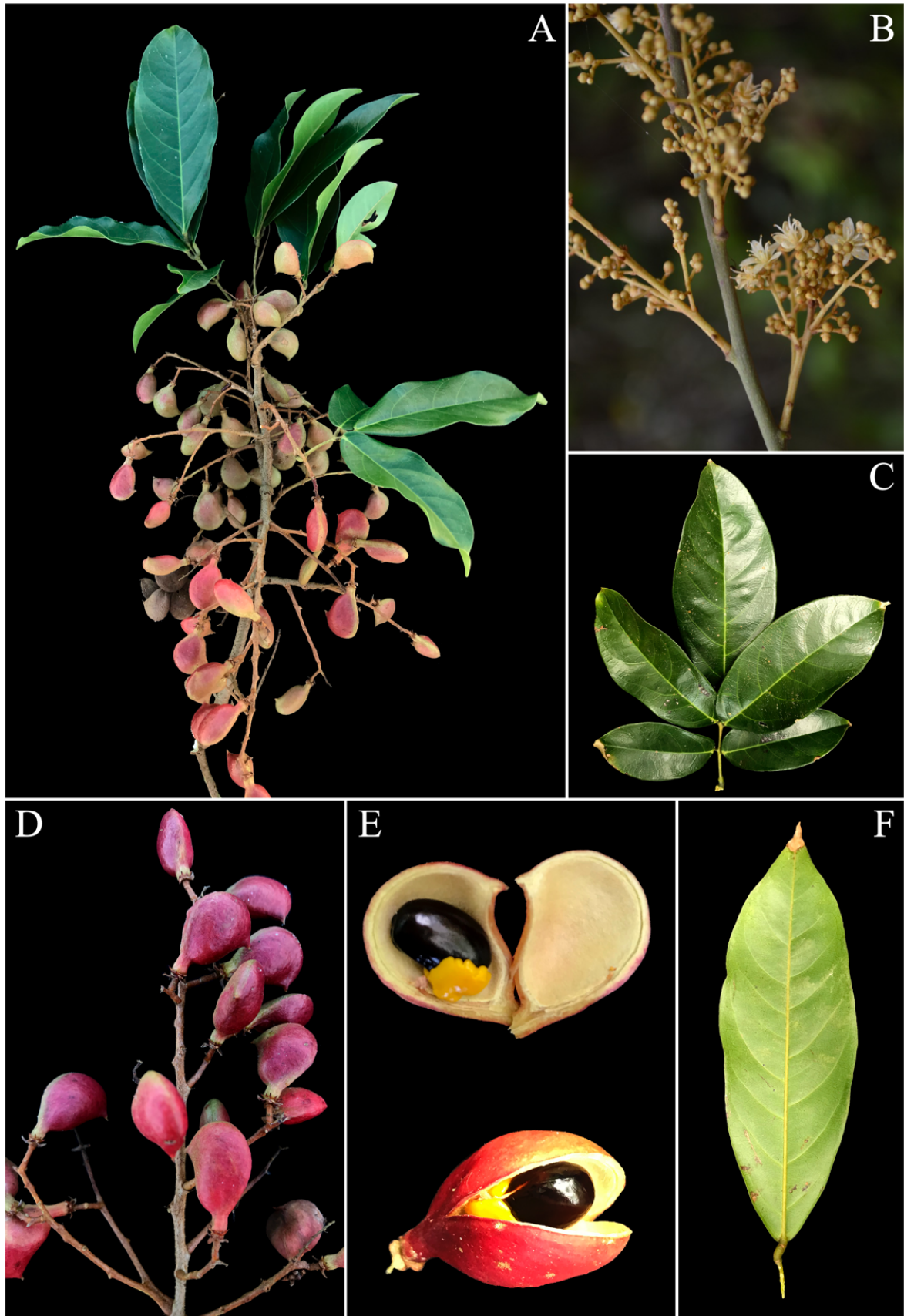


Figure 31. *Connarus rostratus*: A–fruiting branchlet; B–inflorescence; C–leaf, adaxial surface; D–fruits, external view; E–detailed fruits showing seeds, external and internal view; F–leaflet, abaxial surface.



Figure 32. *Connarus ruber*: fruiting branchlet. Photo by Herison Medeiros.



Figure 33. *Connarus suberosus*: A—flowering branchlet; B—inflorescence; C—indumentum on young branchlets; D—habit and fruiting branchlets; E—suberized trunk. Photo in D by Narcísio Bígio and in E by Bianca Schindler.

Table 1. Differentiation of *C. acutissimus*, *C. araucanus*, *C. lambertii*, *C. negrensis* and *C. turczaninowii*.

	Leaflets	2nd veins	3rd veins	Inflorescence rachis	Fruit stipe
<i>C. acutissimus</i>	3, narrowly ovate or elliptic, margin slightly revolute, acumen 6–13 mm long	(9–)10–11 pairs, abaxially usually flat, linear, rarely slightly prominent	Epidermals percurrent	5–9 cm long	(2–)3–4 mm long
<i>C. araucanus</i>	3, oblong, narrowly ovate or narrowly elliptic, margin usually flat, acumen 2–8 mm long	9–14 pairs, abaxially slightly prominent, linear or slightly arcuate	Epidermals reticulate	7–24 cm long	3–7 mm long
<i>C. lambertii</i>	3, ovate or elliptic, margin flat, acumen 3–12 mm long	6–9 pairs, abaxially flat, rarely slightly prominent, arcuate	Epidermals percurrent	5–14 cm long	2–3(–4) mm long
<i>C. negrensis</i>	3, ovate or elliptic, margin flat, rarely slightly revolute, acumen 15–42 mm long	10–12 pairs, abaxially prominent, arcuate	Epidermals percurrent	8–20 cm long	2–4 mm long
<i>C. turczaninowii</i>	3–7, ovate, elliptic or obovate, rarely narrowly elliptic, margin flat, acumen 2–12 mm long	7–9 pairs, abaxially flat, linear	Epidermals reticulate	9–22 cm long	3–6 mm long

Table 2. Differentiation of *C. guggenheimii*, *C. incomptus*, *C. manausensis* and *C. patrisii*.

	Leaflets	2nd veins	Inflorescences	Sepals	Fruits
<i>C. guggenheimii</i>	9–11, apicals narrowly ovate or narrowly elliptic	8–9 pairs, forming angles of 50–60° with midvein	Double thyrsoids	All slightly basally connate	1.7–1.9 cm long, stipe 2–4 mm long
<i>C. incomptus</i>	5–9, apicals narrowly ovate, narrowly elliptic or oblong	8–12 pairs, forming angles of 60–80° with midvein	Thyrsoids	All slightly basally connate	1–1.5 cm long, stipe 1–2 mm long
<i>C. manausensis</i>	5–9, apicals ovate	7–8 pairs, forming angles of ca. 45° with midvein	Double thyrsoids	All slightly basally connate	Not seen
<i>C. patrisii</i>	5–9, apicals oblong, narrowly ovate or narrowly elliptic	5–8 pairs, forming angles of ca. 45° with midvein	Double thyrsoids	2–4 sepals connate up to middle portion	1.5–2.2 cm long, stipe 2–4 mm long

Table 3. Differentiation of *C. acutissimus*, *C. negrensis* and *C. ruber*, previously treated by Forero (1983) as varieties under *C. ruber*.

	Veins	Inflorescences	Flowers	Fruit stipes
<i>C. acutissimus</i>	Secondary abaxially flat or slightly prominent; tertiary epidermals reticulate	Thyrsoids	Sepals 2–2.8 mm long; petals 3.5–5 mm long	Internally subglabrous or sparsely pubescent, stipes (2–)3–4 mm long
<i>C. negrensis</i>	Secondary abaxially prominent; tertiary epidermals percurrent	Thyrsoids	Sepals 2.3–3 mm long; petals 3.5–5 mm long	Internally subglabrous or sparsely pubescent stipes 1–4 mm long
<i>C. ruber</i>	Secondary abaxially prominent; tertiary epidermals percurrent	Double thyrsoids	Sepals 1.5–1.8 mm long; petals 2.5–3.5 mm long	Internally densely pubescent, stipes 1–2(–3) mm long

ANEXO II

Bioética

Direitos autorais



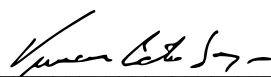
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DECLARAÇÃO

Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada “***A taxonomic revision of Neotropical Connarus L. (Connaraceae)***”, desenvolvida no Programa de Pós-Graduação em Biologia Vegetal do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

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Assinatura: 
Nome do(a) orientador(a): Dr. Vinicius Castro Souza

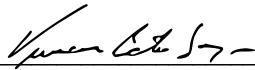
Data: 14 de outubro de 2021

Declaração

As cópias de artigos de minha autoria ou de minha co-autoria, já publicados ou submetidos para publicação em revistas científicas ou anais de congressos sujeitos a arbitragem, que constam da minha Dissertação/Tese de Mestrado/Doutorado, intitulada **A taxomic revision of Neotropical Connarus L. (Connaraceae)**, não infringem os dispositivos da Lei n.º 9.610/98, nem o direito autoral de qualquer editora.

Campinas, 14 de outubro de 2021

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