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João Afonso Martins do Carmo

ESTUDOS TAXONÔMICOS E FILOGENÉTICOS EM *PSYLLOCARPUS* MART. & ZUCC. (RUBIACEAE: SPERMACOCEAE), UM GÊNERO ENDÊMICO DO BRASIL

TAXONOMIC AND PHYLOGENETIC STUDIES IN *PSYLLOCARPUS* MART. & ZUCC. (RUBIACEAE: SPERMACOCEAE), AN ENDEMIC GENUS FROM BRAZIL

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Tese apresentada ao Instituto de Biologia da Universidade Estadual de Campinas como parte dos requisitos exigidos para a obtenção do título de Doutor em Biologia Vegetal

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Orientador: André Olmos Simões

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- ORCID do autor: https://orcid.org/0000-0002-7660-9918
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Prof. Dr. André Olmos Simões

Profa. Dra. Maria do Carmo Estanislau do Amaral

Dr. Gustavo Hiroaki Shimizu

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Resumo

Spermacoceae é um táxon predominantemente herbáceo em Rubiaceae, sendo considerada uma das tribos mais complexas taxonomicamente. Sua circunscrição foi alterada pela inclusão de táxons realacionados devido a filogenias moleculares. O clado Spermacoce, na tribo Spermacoceae, ocorre principalmente no Novo Mundo. A taxonomia complexa de seus gêneros está relacionada, principalmente, a *Borreria* e *Spermacoce*, que aparecem entremeados a vários gêneros menores e morfologicamente bem definidos, os quais foram recuperados em investigações filogenéticas. Entretanto a amostragem destes táxons foi esparsa, portanto sua monofilia ainda não foi testada. Um desses casos é *Psyllocarpus*, um gênero endêmico do Brasil, cuja circunscrição foi ampliada para incluir duas seções, priorizando as cápsulas comprimidas paralelamente ao septo para a sua delimitação. *Psyllocarpus* seção *Psyllocarpus* é baseada no conceito original do gênero e inclui cinco espécies no Cerrado e campo rupestre, enquanto *P.* seção *Amazonica* inclui três espécies nas campinas amazônicas. Posteriormente, o enigmático *P. densifolius* foi descrito, embora não tenha sido classificado em nenhuma seção. Os objetivos deste trabalho são testar a monofilia de *Psyllocarpus* e como este se relaciona com outros gêneros no clado Spermacoce, bem como a posição filogenética de *P. densifolius*, e formalizar estes resultados através de um tratamento taxonômico do gênero. Uma filogenia da tribo Spermacoceae foi construída com base em regiões do DNA ribossômico nuclear (espaçadores transcritos externos e internos, nrETS e nrITS, respectivamente) e plastidial (íntron *rps16* e espaçador intergênico *trnL-trnF*), e estimada por Inferência Bayesiana e Máxima Verossimilhança. No total, 162 espécies representadas por 481 sequências foram analisadas. Nossos resultados indicam que *Psyllocarpus*, como atualmente circunscrito, não é monofilético. *Psyllocarpus densifolius* não pertence ao gênero nem ao clado Spermacoce, apresentando uma posição incerta em Spermacoceae. *Psyllocarpus campinorum*, a única espécie amostrada de *P.* seção *Amazonica*, apresenta uma posição incerta no clado Spermacoce mas não relacionada ao gênero. Portanto *Psyllocarpus* é aqui circunscrito com base em seu conceito original, excluindo-se *P.* seção *Amazonica* e *P. densifolius*, tornando o gênero um táxon monofilético facilmente diagnosticável. Além disso, uma sinopse taxonômica de *Psyllocarpus* é fornecida para a formalização destes resultados, com uma descrição atualizada do gênero, uma chave de identificação e lista de nomes e tipos nomenclaturais de suas espécies. A conservação de *Psyllocarpus* contra *Tapanhuacanga*, seu nome prioritário, é proposta. Duas novas espécies são descritas, *P. bahiensis* e *P. scatignae*, do campo rupestre dos estados da Bahia e Minas Gerais, respectivamente. *Psyllocarpus laricoides* var. γ *longicornu*, anteriormente sob a sinonímia de *P. laricoides*, é tratado aqui como um novo sinônimo de *P. goiasensis*. *Psyllocarpus schwackei*, cujo tipo em B foi destruído durante a Segunda Guerra Mundial, é lectotipificado.

Abstract

Spermacoceae is the largest predominantly herbaceous taxon in the Rubiaceae and regarded as one of the most taxonomically complex tribe. Its circumscription has been amended to include several allies as a result of molecular phylogenies. The Spermacoce clade in the tribe Spermacoceae occurs mostly in the New World. The complex taxonomy regarding its genera is mostly due to *Borreria* and *Spermacoce*, which have been shown to appear intermingled with several smaller and morphologically well-defined genera, which have been recovered in phylogenetic investigations. Nonetheless, sampling of these taxa was sparse, hence their monophyly is yet to be tested. One of these genera is the Brazilian endemic *Psyllocarpus*, whose circumscription has been broadened to include two sections by prioritizing the capsules compressed parallel to the septum for its delimitation. *Psyllocarpus* sect. *Psyllocarpus* is based on the original concept of the genus and includes five species from the "Cerrado" and "campo rupestre", whereas *P.* sect. *Amazonica* includes three species from the Amazonian "campinas". Later, the rather enigmatic *P. densifolius* was described but not classified in any section. In this work we sampled across the Spermacoceae to test the monophyly of *Psyllocarpus* and how it relates to the other genera in the Spermacoce clade, as well as the phylogenetic position of *P. densifolius*, and provide a taxonomic treatment to formalize our results. A phylogenetic inference of the Spermacoceae tribe was based on nuclear ribosomal (external and internal transcribed spacers, nrETS and nrITS, respectively) and plastid (*rps16* intron and *trnL-trnF* intergenic spacer) DNA regions, and estimated with Bayesian Inference and Maximum Likelihood analysis. In total 162 species represented by 481 sequences were analyzed. Our results indicate that *Psyllocarpus* as currently circumscribed is not monophyletic. *Psyllocarpus densifolius* does not belong in the genus nor in the Spermacoce clade, but rather presents an uncertain position in the Spermacoceae. *Psyllocarpus campinorum*, the only sampled species from *P.* sect. *Amazonica*, presents an uncertain position in the Spermacoce clade but not related to the genus. *Psyllocarpus* is here circumscribed based on its original concept by the exclusion of *P.* sect. *Amazonica* and *P. densifolius*, rendering the genus to a monophyletic easily diagnosable taxon. Furthermore, we provide a synopsis of *Psyllocarpus* as a means to formalize our results, with an updated description of the genus, as well as an identification key and list of names and nomenclatural types of its species. We propose the conservation of *Psyllocarpus* against its priority name, *Tapanhuacanga*. We describe two new species, *P. bahiensis* and *P. scatignae*, from the "campo rupestre" of Bahia and Minas Gerais states, respectively. *Psyllocarpus laricoides* var. γ *longicornu*, formerly under the synonymy of *P. laricoides*, is treated here as a new synonym of *P. goiasensis*. *Psyllocarpus schwackei*, whose type in B was destroyed during the Second World War, is lectotypified.

Sumário

Introdução Geral

Rubiaceae é uma família cosmopolita, cuja diversidade e biomassa se concentram nos trópicos e subtrópicos (Davis et al., 2009), compreendendo ca. de 650 gêneros e quase 14.000 espécies (Govaerts et al., 2020). Entretanto quase um terço de seus gêneros e metade de suas espécies ocorrem nos Neotrópicos, em diversos tipos de habitats, especialmente na bacia amazônica, florestas nebulares dos Andes, Cerrado (incluindo os campos rupestres), caatinga, restingas e Mata Atlântica (Delprete & Jardim, 2012).

Spermacoceae Bercht. & J.Presl (subfamília Rubioideae Verd.) é uma de suas tribos mais complexas do ponto de vista taxonômico (Groeninckx et al., 2009; Delprete & Jardim, 2012; Salas et al., 2015). Sua circunscrição passou por várias mudanças desde que dados moleculares passaram a ser utilizados como a principal fonte de evidências para estudos filogenéticos. Bremer (1996) e Bremer & Manen (2000) propuseram uma circunscrição mais ampla para a tribo, já que Spermacoceae como delimitada tradicionalmente (e.g. Robbrecht, 1988), ou Spermacoceae s.s., foi recuperada em um clado composto por Hedyotideae DC., Manettieae Bremek., Knoxieae Hook.f. e Triainolepideae Bremek., portanto sua circunscrição deveria ser ampliada incluindo todas essas tribos. Andersson & Rova (1999) restringiram este conceito por reconhecerem Knoxieae (incluindo Triainolepideae e parte de Hedyotideae) como uma tribo a parte, irmã de Spermacoceae. Esta proposta, em geral denominada como Spermacoceae s.l., foi corroborada com pequenas modificações e seguida em estudos subsequentes (Dessein, 2003; Kårehed et al., 2008; Groeninckx et al., 2009; Salas et al., 2015; Janssens et al., 2016). Spermacoceae s.l. como atualmente circunscrita compreende ca. de 77 gêneros e 1250 espécies. Embora estípulas fimbriadas e flores geralmente tetrâmeras sejam compartilhadas por quase todas as espécies na tribo, não existem sinapomorfias morfológicas claras que possibilitem a sua distinção de Knoxieae (Groeninckx et al., 2009).

Spermacoceae s.s., ou clado Spermacoce (Kårehed et al., 2008; Salas et al., 2015), compreende atualmente 22 gêneros e ca. 500 espécies, ocorrendo principalmente nos Neotrópicos, com algumas espécies no continente africano, Austrália, Índia, Sri Lanka e Tailândia (Dessein, 2003). Seus representantes são geralmente plantas herbáceas, dotadas de ráfides, estípulas fimbriadas, lóculos do ovário contendo apenas um óvulo cada e grãos de pólen pluriaperturados (Salas et al., 2015). Dados moleculares refutam algumas circunscrições genéricas baseadas em morfologia (Kårehed et al., 2008; Salas et al., 2015), como o notável exemplo de *Spermacoce* L. e *Borreria* G.Mey. Entretanto, pelo menos nas Américas, alguns gêneros definidos morfologicamente tem sido sustentados, de maneira geral, por caracteres moleculares, apesar da sua baixa amostragem em estudos filogenéticos (Kårehed et al., 2008; Groeninckx et al., 2009; Salas et al., 2015). Um destes casos é *Psyllocarpus* Mart. & Zucc., um gênero endêmico do Brasil.

Psyllocarpus foi estabelecido por Martius & Zuccarini (1824) com base em quatro espécies. Estes autores diagnosticaram o gênero baseados no cálice bilobado, corola infundibuliforme com quatro lobos e tricomas na fauce, quatro estames inclusos, estiletes pequenos com estigmas capitados e cápsulas com duas valvas portando uma semente peltada e compressa cada. Martius (1824) proveu uma descrição mais detalhada do gênero, o qual apresenta folhas lineares a subuladas, cápsulas comprimidas e um septo membranoso paralelo às valvas. Este autor o comparou a *Borreria*, distinguindo-os pelo septo inteiro, valvas separadas e sementes peltadas em *Psyllocarpus*. Este conceito foi seguido por Schumann (1888, 1898) para sua revisão do gênero e descrição de duas novas espécies, respectivamente.

Kirkbride (1979) classificou *Psyllocarpus* em duas seções, baseado em morfologia e distribuição geográfica, expandindo o conceito original do gênero, mas priorizando as cápsulas comprimidas para a sua circunscrição. *Psyllocarpus* seção *Psyllocarpus*, que segue o conceito de Martius & Zuccarini (1824), compreende cinco espécies, endêmicas do Cerrado e campo rupestre da Cadeia do Espinhaço, nos estados de Minas Gerais e Bahia (*P. asparagoides* Mart. & Zucc., *P. laricoides* Mart. & Zucc. e *P. schwackei* K.Schum.) e do sistema de chapadas do Planalto Central, no estado de Goiás e Distrito Federal (*P. goiasensis* J.H.Kirkbr. e *P. phyllocephalus* K.Schum.), sendo caracterizada pelas folhas cilíndricas, flores homostílicas, grãos de pólen prolato-esferoidais, exina não perfurada e espinulosa ao longo de cada colpo e estigma curtamente bilobado a capitado. *Psyllocarpus* seção *Amazonica* compreende três espécies [*P. campinorum* (Krause) J.H.Kirkbr., *P. cururuensis* J.H.Kirkbr. e *P. psyllocarpoides* (Sucre) J.H.Kirkbr.] endêmicas das campinas amazônicas, nos estados de Rondônia, Amazonas e Pará, sendo caracterizada pelas folhas planas, flores heterostílicas, grãos de pólen oblato-esferoidais, exina perfurada e finamente espinulosa e estigmas profundamente bilobados. Novas espécies foram descritas para o gênero, como *Psyllocarpus intermedius* E.L.Cabral & Bacigalupo (Cabral & Bacigalupo, 1997), endêmica da Chapada Diamantina, Bahia, e *P. densifolius* Zappi & Calió (Zappi et al., 2014), endêmica da Serra do Cipó, Minas Gerais, embora não tenham sido classificadas em nenhuma das seções propostas por Kirkbride (1979).

Em estudos filogenéticos sobre a tribo Spermacoceae utilizando-se marcadores nucleares (ETS e ITS) e plastidiais (*atpB-rbcL*, *petD*, *rps16* e *trnL-F*), a única espécie de *Psyllocarpus* analisada (*P. laricoides*) formou um clado de máxima probabilidade posterior (PP) com *Hexasepalum teres* (Walter) J.H.Kirkbr. [= *Diodella teres* (Walter) Small] (Kårehed et al., 2008). Em análises posteriores, utilizando-se somente os mesmos marcadores nucleares, *P. asparagoides* e

P. phyllocephalus formaram um clado de máxima PP e altos valores de boostrap (BS; 98 e 100, para as análises de máxima parcimônia e máxima verossimilhança, respectivamente), irmão de um clado formado por espécies de *Spermacoce* e *Borreria* (Salas et al., 2015). Dessa forma, o grupo-irmão de *Psyllocarpus* permanece incógnito.

Com o objetivo de contribuir para o melhor entendimento dos limites dos gêneros e suas relações no clado Spermacoce, este trabalho tem como principal objeto de estudo o gênero *Psyllocarpus*. Dessa forma, esta tese é composta por dois capítulos. No capítulo 1, é apresentado um estudo filogenético sobre *Psyllocarpus*, no qual o gênero é delimitado com base em caracteres moleculares de DNA ribossômico do núcleo (ETS e ITS) e do cloroplasto (*rps16* e *trnL-F*) e sua relação com os outros gêneros no clado Spermacoce é investigada. Além disso, uma sinopse de *Psyllocarpus* é fornecida neste capítulo, com uma descrição atualizada do gênero e uma chave de identificação para suas espécies, bem como uma lista de nomes e tipos nomenclaturais. O capítulo 2 corresponde às novidades taxonômicas e nomenclaturais publicadas até o momento para o gênero, sendo composto por quatro artigos: o primeiro (I) corresponde a uma proposta de conservação do nome *Psyllocarpus* contra seu nome prioritário, *Tapanhuacanga*; no segundo (II), duas novas espécies são descritas para o gênero, *Psyllocarpus bahiensis* e *P. scatignae*, do campo rupestre dos estados da Bahia e Minas Gerais, respectivamente; no terceiro (III), *Psyllocarpus laricoides* var. γ *longicornu*, anteriormente sob a sinonímia de *P. laricoides*, é tratado como um novo sinônimo de *P. goiasensis*; e no quarto (IV), *Psyllocarpus schwackei*, cujo tipo em B foi destruído durante a Segunda Guerra Mundial, é lectotipificado. Este projeto foi desenvolvido no contexto da Flora do Brasil 2020 (Flora do Brasil, 2020), sendo que os seus resultados publicados alimentarão esta base de dados e contribuirão para as monografias dos gêneros aqui investigados.

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Capítulo 1:

There and back again: a phylogenetic assessment of the Brazilian endemic *Psyllocarpus* (*Rubiaceae*: *Spermacoceae*), with a recircumscription of the genus based on its original concept

(Manuscrito formatado para submissão ao periódico *Taxon*)

There and back again: a phylogenetic assessment of the Brazilian endemic *Psyllocarpus* (*Rubiaceae*: *Spermacoceae*), with a recircumscription of the genus based on its original concept

João A.M. Carmo,[1,4] Sandra V. Sobrado,[2] Javier E. Florentín,[2] Roberto M. Salas[2] & André O. Simões[3]

1 *Programa de Pós-Graduação em Biologia Vegetal, Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas – UNICAMP, CEP 13083-970, Campinas, SP, Brazil*
2 *Instituto de Botánica del Nordeste, UNNE – CONICET, Sargento Juan Bautista Cabral 2131, cc. 209, C.P. 3400. Facultad de Ciencias Exactas y Naturales y Agrimensuras, FaCENA – UNNE, Av. Libertad 5460, C.P. 3400. Corrientes, Argentina*
3 *Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas – UNICAMP, CEP 13083-970, Campinas, SP, Brazil*
4 *Author for Correspondence: João A.M. Carmo jmartinsdocarmo@gmail.com*

Abstract In contrast to the rest of the family, the Spermacoceae, with 77 genera and ca. 1250 species, is the largest predominantly herbaceous taxon in the Rubiaceae and regarded as one of its most taxonomically complex tribe. The group has been amended to include several allies due to molecular phylogenetic investigations. The Spermacoce clade in the tribe Spermacoceae, with 22 genera and ca. 500 species, occurs mostly in the New World. The complex taxonomy regarding its genera is mostly due to the unclear limits of *Borreria* and *Spermacoce*, which have been shown to appear intermingled with several smaller genera. Overall these smaller genera are morphologically well-defined, however just a few of their species have been investigated in previous phylogenies, hence their monophyly is yet to be tested. One of such genus is *Psyllocarpus*, which had its circumscription broadened to include two sections, by prioritizing the capsules compressed parallel to the septum for its delimitation. *Psyllocarpus* sect. *Psyllocarpus* is based on the original concept of the genus and includes five species distributed in the "Cerrado" and "campo rupestre", whereas *P*. sect. *Amazonica* includes three species occurring in the Amazonian "campinas". Later, *P. densifolius* was described but not classified in any section. Here, we sampled across the Spermacoceae to test the monophyly of the genus, how it relates to the other genera in the Spermacoce clade, and the phylogenetic position of *P. densifolius.* We used the nuclear ribosomal (external and internal transcribed spacers, ETS and ITS, respectively) and plastid (*rps16* intron and *trnL-trnF* intergenic spacer) DNA regions. A total 162 species and represented by 481 sequences were analyzed. Our results revealed that *Psyllocarpus* as currently circumscribed is not monophyletic. *Psyllocarpus densifolius* is not associated with the genus nor the Spermacoce clade, but rather presents an uncertain position in the Spermacoceae. *Psyllocarpus campinorum* (≡ *Borreria campinorum*), the only sampled species from *P*. sect. *Amazonica*, presents an uncertain position in the Spermacoce clade but clearly does not belong in the genus. Therefore, *Psyllocarpus* is here circumscribed based on its original concept by the exclusion of *P*. sect. *Amazonica* and *P. densifolius*, rendering the genus a monophyletic easily diagnosable taxon. Additionally, we provide a synopsis of *Psyllocarpus* to formalize our results, with an updated description of the genus, as well as an identification key and list of names and nomenclatural types of its species.

Keywords Brazil; campo rupestre; molecular phylogeny; Neotropics; Rubioideae; taxonomy

Rubiaceae (the coffee family) is regarded as the fourth family in number of species in the Angiosperms, after Orchidaceae, Asteraceae, and Leguminosae (Mabberley, 2008). It comprises more than 13,000 species worldwide (Govaerts & al., 2020) and ca. 650 genera, classified in 65 tribes and two subfamilies (Robbrecht & Manen, 2006; Rydin & al., 2017). The family is predominantly composed of shrubs and trees, and despite its cosmopolitan distribution, species diversity and biomass are concentrated in the tropics and subtropics (Davis & al., 2009). Almost one third of its genera and half of the species occur in the neotropical region, growing on a wide variety of habitats, but being especially diverse in the Amazon Basin, Andean cloud forests, "Cerrado" (Brazilian savannah, including the "campo rupestre"), "Caatinga" (seasonally dry forest occurring within the semi-arid climate region of northeast Brazil), "restingas" (vegetation complex occurring in the seaside lowlands of Brazil), and the Atlantic forest (Delprete & Jardim, 2012).

In contrast to the rest of the family, the Spermacoceae Bercht. & J.Presl (subfamily Rubioideae Verd.) is the largest predominantly herbaceous taxon in the Rubiaceae and regarded as one of its most taxonomically complex and controversial tribe (Groeninckx & al., 2009; Delprete & Jardim, 2012; Salas & al., 2015). Presenting a pantropical distribution, with a few genera extending into temperate regions (Kårehed & al., 2008), its circumscription has undergone several changes since systematists begun to utilize molecular data as the main source of evidence for phylogenetic inference. Bremer (1996) and Bremer & Manen (2000) proposed a broader circumscription for the tribe, since the traditionally delimited Spermacoceae (e.g., Robbrecht, 1988), or the Spermacoceae s.str., was recovered monophyletic deeply nested in a clade composed of the Hedyotideae DC., Manettieae Bremek., Knoxieae Hook.f., and Triainolepideae Bremek., therefore an amended tribe should include all of them. On the other hand, Andersson & Rova (1999) narrowed this concept by recognizing Knoxieae (including Triainolepideae and the *Pentas* group of Hedyotideae) as a separate tribe. This proposal, often referred to as the Spermacoceae s.l., just Spermacoceae hereafter, was corroborated with minor modifications in subsequent phylogenetic studies (e.g., Dessein, 2003; Robbrecht & Manen, 2006; Kårehed & al., 2008; Bremer & Eriksson, 2009; Groeninckx & al., 2009). Although fimbriate stipules and tetramerous flowers are shared by most species in the Spermacoceae, there are no clear morphological synapomorphies that support the clade and distinguish it from its sister tribe, the amended Knoxieae (Kårehed & Bremer, 2007; Groeninckx & al., 2009).

The works of Kårehed & al. (2008) and Groeninckx & al. (2009) are milestones in the Spermacoceae systematics, as they were the first to objectively assess the entire tribe, shedding light on non-monophyletic genera and identifying major clades in the Spermacoceae (i.e., Agathisanthemum-Hedyotis s.str. clade, Arcytophyllum-Houstonia clade, Kadua, Kohautia, Oldenlandia s.str., Pachystigma, Pentanopsis clade, and Spermacoce clade), thus providing a framework for subsequent investigation. The Spermacoceae would include 61 genera and ca. 1235 species (Groeninckx & al., 2009). Since then, some taxa have been added to this conspectus, due to the discovery of novelties (Groeninckx & al., 2010a, 2010b; Salas & al., 2015) and the resurrection (Guo & al., 2013) or proposal (Groeninckx & al., 2010c; Neupane & al., 2015) of names to accommodate newly resolved clades, which were segregated from paraphyletic genera, increasing these numbers to 77 genera and an estimate of 1250 species.

The Spermacoceae s.str., or the Spermacoce clade, as it will be referred to in this paper (Kårehed & al., 2008), occurs mostly in the New World, with some species in Africa, Australia, India, Sri Lanka, and Thailand, which has been used to base a South American origin for the clade (Dessein, 2003). It is composed of often herbaceous plants characterized by the fimbriate stipules and uniovulate ovary locules combined with the presence of raphides, and pluriaperturate pollen grains (Dessein, 2003; Kårehed & al., 2008; Salas & al., 2015). Currently, there are 22 recognized genera and ca. 500 species in the Spermacoce clade (Table 1). Recent taxonomic changes include the exclusion of *Gomphocalyx* Baker and *Phylohydrax* Puff (Thulin & Bremer, 2004; Dessein & al., 2005), the synonymization of the monotypic *Diacrodron* Sprague under *Borreria* G.Mey. (Miguel & al., 2018), and the description of *Carajasia* R.M.Salas, E.L.Cabral & Dessein (Salas & al., 2015). Of these, *Borreria* (ca. 100 spp.; Miguel & Cabral, 2013), *Galianthe* Griseb. (55 spp.; Cabral & Bacigalupo, 1997b; Cabral, 2009; Florentín & al., 2017, 2019), and *Spermacoce* L. (ca. 170 spp.) are the richest ones, while *Anthospermopsis* (K.Schum.) J.H.Kirkbr., *Carajasia*, *Emmeorhiza* Endl., *Nodocarpaea* A.Gray, *Schwendenera* K.Schum., and *Tortuella* Urb. are monotypic (Table 1).

The complex taxonomy regarding the genera in the Spermacoce clade is mostly related to the unclear limits of *Borreria* and *Spermacoce*, which ends up affecting the taxonomy of the whole clade, and has led to divergent opinions among specialists. Most specialists working on paleotropical and Australian species consider the former as a synonym of the latter (e.g., Verdcourt, 1975; Dessein & al., 2002, 2003; Harwood & Dessein, 2005). On the other hand, different concepts have been adopted by researchers of American taxa. Delprete & Jardim (2012; and others cited therein) share the same opinion with those in the Old World, recognizing only *Spermacoce* in its broader sense, which resulted in the proposal of a great number of new combinations (e.g., Delprete, 2007), impressively reaching up to 80 new ones published just in the *World checklist of seed plants* (Govaerts, 1996), mostly for neotropical species. This added confusion for the identification of species in the Americas and brought noise to other morphologically well-defined genera in the clade, such as *Staelia* Cham. & Schltdl., as new combinations also have been proposed for some of the names that have been already treated under their synonymy (for examples see Salas

& al., 2011). In contrast, our research group and others, mostly located in Argentina and Brazil, recognize the close relationship of these taxa but maintain *Borreria* as an established genus (e.g., Bacigalupo & Cabral, 1996; Miguel & Cabral, 2013; Salas & al., 2015; Miguel & al., 2018).

Whether *Borreria* should be treated as a synonym of *Spermacoce* or a distinct genus remains an open question, as available phylogenetic studies are still inconclusive (Kårehed & al., 2008; Groeninckx & al., 2009; Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018). In fact, both genera as currently circumscribed are not monophyletic, but neither is a broader concept of *Spermacoce* including *Borreria* and allies. Molecular studies have shown that these taxa often appear intermingled with several smaller and morphologically well-defined genera, such as *Mitracarpus* Zucc. ex Schult. & Schult.f., *Psyllocarpus* Mart. & Zucc., *Richardia* L., and *Staelia*, which are preliminarily well supported in phylogenies. Therefore we here recognize both genera instead of massively merging *Borreria* under *Spermacoce*, distinguishing them based on the unilateral glomerules (vs bilateral in *Borreria*), urceolate to campanulate corolla (vs infundibuliform) with pilose lobes (vs glabrous or pubescent), included stamens and styles (vs exserted), with capitate-bilobate stigmas (vs capitate-bilobate or bifid), dry indehiscent fruits or septicidally dehiscencent in only one mericarp (vs septicidal dehiscence in both mericarps), seeds with a flat ventral side (vs longitudinally grooved), and pollen grains zonocolporate (vs pantoporate or zonocolporate), with a long ectocolpi (vs short to medium) and joined endoapertures forming an endocingulum with a well-defined boundary observable under light microscopy (vs barely discernible), ectocolpi surrounded by a margin of granules (vs without margin of granules), and exine psilate at the apocolpium and spinulate at the mesocolpium (vs uniformly spinulate) in the latter (Bacigalupo & Cabral, 1996; Dessein & al., 2002a, 2002b; Cabral & al., 2010; Miguel & Cabral, 2013; Florentín & al., 2016).

Generic delimitation and relationships in the Spermacoce clade are far from being resolved. In order to tackle these questions, increasing sampling, as well as the number of characters, is vital, as representatives from some genera have never been sampled in phylogenetic studies (e.g., *Anthospermopsis*, *Denscantia* E.L.Cabral & Bacigalupo, *Micrasepalum* Urb., *Nodocarpaea*, *Planaltina* R.M.Salas & E.L.Cabral, *Tessiera* DC., *Tobagoa* Urb., *Tortuella*), and others, especially the richest ones (e.g., *Borreria*, *Galianthe*, *Mitracarpus*, *Richardia*, and *Spermacoce*), had just a few species assessed (Kårehed & al., 2008; Groeninckx & al., 2009; Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018). Similarly, even those smaller and morphologically well-defined genera had just a few species investigated, hence their monophyly is yet to be tested. This is the case of the Brazilian endemic *Psyllocarpus*, which is the main focus of this study. This is a relatively small genus (12 spp. as currently circumscribed) and has been poorly represented in phylogenetic studies (three spp.).

Kårehed & al. (2008) used nuclear ribosomal (ETS and ITS) and plastid (*atpB-rbcL*, *petD*, *rps16*, and *trnL-F*) DNA regions for their phylogenetic analysis of the Spermacoceae tribe, for which they sampled only *P. laricoides*, which formed a clade of maximum posterior probability (PP) with *Hexasepalum teres* (Walter) J.H.Kirkbr. [= *Diodella teres* (Walter) Small]. In subsequent phylogenetic studies, focusing on the Spermacoce clade and using only the same nuclear ribosomal DNA regions, two species were sampled, *P. asparagoides* and *P. phyllocephalus*, which formed a clade with high to maximum support values [PP = 1, maximum parsimony bootstrap (BS) = 98, and maximum likelihood BS = 100, Salas & al. 2015; PP = 0.99 in Florentín & al., 2017; maximum likelihood BS = 100, Miguel & al., 2018]. These studies also showed that *Psyllocarpus* is probably closely related to *Spermacoce*, with which it formed a clade with high to low support values (PP = 0.97, parsimony BS < 50, and maximum likelihood BS = 41; PP = 0.97; maximum likelihood BS = 67, respectively). Nevertheless, its sister group remains unknown at this point.

Taxonomic history of *Psyllocarpus*

Martius & Zuccarini (1824) described four *Psyllocarpus* species (*P. asparagoides* Mart. & Zucc., *P. ericoides* Mart. & Zucc., *P. laricoides* Mart. & Zucc., and *P. thymbroides* Mart. & Zucc.), diagnosing the genus based on its calyx with two distinct lobes, infundibuliform corolla with four lobes and trichomes on the throat, four included stamens, short style with capitate stigma, and bivalvate capsules with two locules bearing one peltate compressed seed each. Martius (1824) provided a more detailed description of the genus, which presents linear to subulate leaves, compressed capsules, and a membranous septum parallel to the valves. He further compared it to *Borreria*, distinguishing them by the complete septum, separate valves, and peltate seeds in *Psyllocarpus*. Schumann (1888, 1898) followed this concept for his taxonomic revision of the genus, maintaining three species in *Psyllocarpus* but transferring *P. thymbroides* to *Staelia* [≡ *Staelia thymbroides* (Mart. & Zucc.) K.Schum.], and the description of two new species (*P. phyllocephalus* K.Schum. and *P. schwackei* K.Schum.), respectively.

Kirkbride (1979) classified *Psyllocarpus* in two sections based on morphology and geographic distribution, expanding on its original concept by using only the capsules compressed parallel to the septum to circumscribe the genus. *Psyllocarpus* sect. *Psyllocarpus*, which follows the concept by Martius (1824), is characterized by the terete leaves, homostylous flowers, prolate-spheroidal pollen grains, psilate tectum with spinules along each side of the colpi exine, and weakly bilobate to rarely capitate stigma. This section occurs in the "Cerrado" and "campo rupestre" from the Espinhaço range and the Planalto Central of Brazil, in the states of Bahia, Goiás, and Minas Gerais, and the Distrito Federal, comprising five species [*P. asparagoides*, *P. goiasensis* J.H.Kirkbr., *P. laricoides* (= *P. ericoides*, although we recognize it as distinct species in the present study), *P. phyllocephalus*, and *P. schwackei*]. *Psyllocarpus* sect. *Amazonica* J.H.Kirkbr. is characterized by the planar leaves, heterostylous flowers, oblate-spheroidal pollen grains, perforated tectum, finely and evenly spinulose exine, and deeply bifid stigma. It is restricted to the white-sand Amazonian campinas in the states of Amazonas, Pará, and Rondônia, comprising three species [*P. campinorum* (K.Krause) J.H.Kirkbr. (≡ *Borreria campinorum* K.Krause), *P. cururuensis* J.H.Kirkbr., and *P. psyllocarpoides* (Sucre) J.H.Kirkbr. (≡ *Staelia psyllocarpoides* Sucre)].

More recently some taxonomic novelties have been published in the genus. Two species from the Espinhaço range were described in *Psyllocarpus*, named *P. intermedius* E.L.Cabral & Bacigalupo (Cabral & Bacigalupo, 1997a) and *P. densifolius* Zappi & Calió (Zappi & al., 2014). These species were not classified in any of the sections proposed by Kirkbride (1979), as they present morphological characteristics divergent from those of *P.* sect. *Psyllocarpus*, despite occurring in the same geographical region. The former has been recently reexamined for morphological and micromorphological characters, which led us to the conclusion that this species is actually a synonym of *Borreria catolensis* E.L.Cabral & L.M.Miguel (Miguel & al., in prep.). It is a subshrub characterized by the linear to subcylindrical leaves, terminal glomerules, 4-lobed calyx, white corolla with exserted stamens and style, bifid stigma, and subglobose fruits bearing ellipsoid seeds (Cabral & Bacigalupo, 1997a). The latter is characterized by its scarcely branched stems arising from a well-developed subterranean system, triangular acuminate sptipules, lanceolate to linear leaves, terminal 1–2-flowered inflorescences subtended by hyaline bracts, 4-lobed calyx, and exserted style (Zappi & al., 2014). Such morphological discrepancies in regards to the other species in *Psyllocarpus* have raised doubts about its placement in the genus, which will be addressed in this study.

Additionally, we described and classified *P. bahiensis* J.A.M.Carmo, Sobrado & R.M.Salas and *P. scatignae* J.A.M.Carmo, Sobrado & R.M.Salas, both also from the Espinhaço range, in *P.* sect. *Psyllocarpus* (Carmo & al., 2018b). Besides, we narrowed *P. laricoides* circumscription by treating one of its synonyms under *P. goiasensis* (Carmo & al., 2018a), and designated a lectotype for the name *P. schwackei* (Carmo & al., 2017). More recently, Moraes (2019) has undertaken 12 new combinations of *Psyllocarpus* under the obscure *Tapanhuacanga*, the priority name for the genus. Nevertheless, we proposed to conserve the former (Carmo & al., 2019) to serve stability and avoid disadvantageous changes purely based on nomenclatural reasons.

We conducted a broad phylogenetic analysis including most of the taxonomic diversity in the Spermacoceae, as a means to contribute to the discussion and further unravel the relationships of the taxa in the Spermacoce clade. Our main goals with this work are to: (1) test the monophyly of *Psyllocarpus* as currently circumscribed and delimit the genus from a phylogenetic perspective; (2) infer interspecific relationships in *Psyllocarpus*; (3) identify its sister group and assess the relationship between *Psyllocarpus* and the other genera in the Spermacoce clade; and (4) test the position of the rather enigmatic *Psyllocarpus densifolius*. Emphasis was given to the Spermacoce clade, as our sampling is larger than any previous study focusing on this group (Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018). We also provide a synopsis of *Psyllocarpus* to formalize our results, with an updated description of the genus, as well as an identification key and list of names and nomenclatural types of its species.

Material and Methods

Sampling strategy and molecular markers. — Newly generated sequences of *Psyllocarpus* species, as well as of other genera, were obtained from fresh samples of material collected in the field and dried in silica gel, or herbaria specimens (Appendix 1). We have analyzed *Psyllocarpus* collections deposited at the ALCB, B, BR, BHCB, CEN, CEPEC, CTES, DIAM, F, FURB, ESA, ESAL, HEPH, HRB, HRCB, HUEFS, IAC, IBGE, ICN, K, M, MBM, MO, NY, OUPR, P, PACA, R, RB, SP, SPF, UB, UEC, UFG, UFU, UPCB, US, and W herbaria, as well as the literature (Kirkbride, 1979; Zappi & al., 2014; Carmo & al., 2018a, b) in order to obtain data on the occurrence of the species to guide field expeditions, as we prioritized obtaining fresh samples for our study. The analysis of herbaria material, including the nomenclatural types, and the literature were also used to identify the collected specimens and produce the taxonomic treatment hereafter. We carried out five field expeditions, from May 2014 to January 2016, covering the distribution of all *Psyllocarpus* species in eastern Brazil (*P.* sect. *Psyllocarpus* and *P. densifolius*), as we collected fresh samples for all of them.

Our main goal was to sample as many *Psyllocarpus* species as possible, as well as from all the genera traditionally and currently associated with the Spermacoce clade (Table 1). After preliminary tests (not presented in this paper) we concluded that *P. densifolius* was actually not associated with the Spermacoce clade, so we broadened our sampling to test its phylogenetic position. Therefore we sampled across all of the Spermacoceae, including all of the clades identified in previous studies (Kårehed & al., 2008; Groeninckx & al., 2009; Janssens & al., 2016) and as much genera as possible, as a means to encompass most of the morphological, geographical, and taxonomic variation in the tribe but emphasizing the Spermacoce clade (we used all sequences available in GenBank for as much species in the clade as possible). We also sampled Knoxieae, sister tribe of the Spermacoceae, and used *Danais fragrans* (Lam.) Pers., tribe Danaideae B.Bremer & Manen, as outgroup (Rydin & al., 2009; Wikström & al., 2015).

We used nuclear ribosomal (both external and internal transcribed spacers, ETS and ITS, respectively) and plastid (*rps16* intron and *trnL-trnF* intergenic spacer) DNA regions for our phylogentic analysis. GenBank accession numbers of sequences of the studied taxa are summarized in Appendix 1. Discrepancies in sampling between different molecular regions are due to the availability of sequences in GenBank, and our ability to successfully produce (or not) new sequences for species that were not analyzed before.

Molecular laboratory procedures. — Total genomic DNA was extracted from fresh samples collected in the field and dried in silica gel or obtained from herbaria material (Appendix 1) utilizing a Nucleospin® Plant II (Macherey-Nagel) kit, following manufacturer instructions. Primers and temperature programs used for the amplification of the molecular markers of interest, i.e. the nuclear ribosomal ETS and ITS and the plastid *rps16* and *trnL-F*, follow the protocols outlined by Kårehed & al. (2008) and Groeninckx & al. (2009). Sequencing was performed on an ABI 3500xL Genetic Analyzer® (Applied Biosystems) at the "Centro de Biologia Molecular e Engenharia Genética" (CBMEG) at the University of Campinas (Unicamp), São Paulo, Brazil. Despite several efforts, we were unable to amplify and/or sequence DNA from herbarium material of additional *P.* sect. *Amazonica*, as we could not collect fresh samples of its species in the field, resulting in only one species from this section, *P. campinorum*, being analyzed.

Phylogenetic analyses. — Contiguous sequences were assembled using Geneious R8.1.5® (Biomatters, New Zealand). Automatic alignments were carried out with MAFFT (Katoh & al., 2002) under an E-INS-i algorithm, a 100PAM/k = 2 scoring matrix, a gap open penalty of 1.3, and an offset value of 0.123, as implemented in Geneious. The best-fit nucleotide substitution model for each nuclear and plastid regions was determined using jModelTest 2.1.4 (Darriba & al., 2012) under the Akaike information criterion (AIC). The GTR + I + G was selected for both nuclear regions, whereas the GTR + I was the best-fit substitution model for the *rps16* and the GTR + G for the *trnL-F*. All regions were first analyzed separately. The nuclear ITS and ETS were then combined into a single alignment (nrDNA), as were the plastid *rps16* and the *trnL-F* (plDNA). These datasets were analyzed separately, and had their topologies visually inspected for incongruences. Since they yielded some "hard" incongruences (i.e., alternative topologies with support values accounting for PP ≥ 0.95 and/or maximum likelihood BS ≥ 90) they were not combined for a final analysis (Pirie, 2015).

Bayesian inference (BI) analyses based on Markov Chain Monte Carlo methods (Yang & Rannala, 1997) were conducted with MrBayes v3.2 (Ronquist & al., 2012). For each Bayesian analysis, two simultaneous runs of four chains (three heated and one cold) were performed, starting from random trees and running for 50 million generations. Trees and parameters were sampled every 1000 generations. At the end of the run, chain convergence and estimated sample size (ESS) parameters were assessed with Tracer v.1.6.0 (Rambaut & al., 2014), and the first 25% of the resulting trees were discarded as burn-in. In the resulting summary 50% majority-rule consensus tree, posterior probability values (PP) ≥ 0.95 were considered to be strongly supported (Suzuki & al., 2002; Alfaro & al., 2003). Maximum Likelihood (ML) analyses were carried out using RAxML v8 (Stamatakis, 2014) under the GTRGAMMA model. Non-parametric ML bootstrapping analysis was calculated with 1000 bootstrap replicates. All analyses were run on the CIPRES Science Gateway (Miller & al., 2010).

Results

We here investigated a total of 162 species represented by 481 sequences from the nuclear ribosomal ETS and ITS and the plastid *rps16* and *trnL-F* DNA regions. Of these, 71 sequences (ca. 15%) from 24 species are newly generated. GenBank accession numbers of sequences of the studied taxa are summarized in Appendix 1. Sequence characteristics for each dataset are summarized in Table 2. Although the trees obtained from the nrDNA and plDNA both recovered major clades in the tribe, visual inspection showed some "hard" incongruences (i.e., alternative topologies with support values of PP ≥ 0.95 and/or BS ≥ 90) between them. Since we produced a more resolved and denser sampled phylogeny, at least for the Spermacoce clade, from the nrDNA dataset, discussion will be focused on this result, addressing its differences to the plDNA tree when necessary. Figures 1–2 show the Bayesian majority-rule consensus trees from the nrDNA and plDNA, respectively, and Figure 3 is a detailed view of the Spermacoce clade and closely related genera from the nrDNA tree. Only PP ≥ 0.95 and BS ≥ 90 are shown.

Phylogeny of the Spermacoceae — The tribe Knoxieae was recovered as monophyletic with maximum support in all analysis (nrDNA: PP = 1, BS = 100; plDNA: PP = 1, BS = 100). The Spermacoceae also formed a clade but with different relationships among its subclades in relation to the tress of different datasets. The nrDNA recovered a monophyletic Spermacoceae with maximum to moderate support values (PP = 1, BS = 80) but does not clarify how it relates to *Oldenlandia* *filicaulis* and *Psyllocarpus densifolius*, nor Knoxieae (Fig. 1). On the other hand, the plDNA recovered a clade composed of the Spermacoceae and both species (Fig. 2) with maximum support values (PP = 1, BS = 100), sister to Knoxieae (PP = 1).

As for the remaining Spermacoceae, we recovered almost all major clades observed in previous studies, i.e., the Arcytophyllum-Houstonia clade (nrDNA: PP = 1, BS = 95; plDNA: PP = 0.57, BS = 56), Kadua (nrDNA: PP = 1, BS = 100; plDNA: PP = 1, BS = 99), the Kohautia (nrDNA: PP = 1, BS = 100; plDNA: PP = 1, BS = 100), the Oldenlandia s.str. (nrDNA: PP = 1, BS = 100; plDNA: PP = 0.91, BS = 71), the Cordylostigma (nrDNA: PP = 1, BS = 100; plDNA: PP = 1, BS = 100), the Pentanopsis clade [nrDNA: PP = 1, BS = 98; plDNA: PP = 1, BS = 50, with the exclusion of *Phylohydrax carnosa* (Hochst.) Puff], and the Spermacoce clade (nrDNA: PP = 1, BS = 100; plDNA: PP = 0.88, BS = 14), which presented differences between datasets (more on that below). The plDNA also recovered the Madagascan endemic clades Amphistemon-Thamnoldenlandia (PP = 1, BS = 100) and Astiella-Phialiphora (PP = 1, BS = 100), which are related to each other (PP = 0.99, BS = 92) and have no nrDNA sequences available. The Agathisanthemum-Hedyotis s.str. clade appeared only in the nrDNA analysis with low support (PP = 0.76, BS = 56), although its subclades were recovered with high to maximum support, e.g., Agathisanthemum (nrDNA: PP = 1, BS = 100; plDNA: PP = 1, BS = 99) and Hedyotis s.str. (nrDNA: PP = 1, BS = 100; plDNA: PP = 1, BS = 100). Nevertheless, relationships between these clades, as well as some taxa intermingled with them, are not fully resolved.

Phylogeny of the Spermacoce clade. — The Spermacoce clade was recovered as monophyletic with maximum support by the nrDNA (PP = 1, BS = 100; Fig. 1) but not by the plDNA (PP = 0.88, BS = 14), which presented some differences (Fig. 2). *Manettia lygistum* (L.) Sw. is nested in the Spermacoce clade, while *Spermacoce prostrata* Aubl. is not, and forms a clade, at least in the BI, with *Phylohydrax carnosa* (PP = 1), a species that composes the Pentanopsis clade in the nrDNA tree. The Spermacoce clade sister group remains unclear, since its relationship with the clade composed of *Oldenlandia salzmanii* and *O. tenuis* (nrDNA: PP = 1, BS = 100) is poorly supported (nrDNA: PP = 0.61, BS = 51), and they were recovered in a polytomy (nrDNA: PP = 1, BS = 100; plDNA: PP = 1) with *Arcytophyllum serpyllaceum* (Schltdl.) Terrell, *Bouvardia ternifolia* Schltdl., *Manettia* Adans. (nrDNA: PP = 1, BS = 100; plDNA: PP = 1, BS = 100), and *Nesohedyotis arborea* (Roxb.) Bremek.

We recovered several well-supported clades (Fig. 3) which in general match the taxa they represent, e.g., *Borreria* (nrDNA: PP = 0.99, BS = 92), *Borreria* subsect. *Latifoliae* (K.Schum.) Bacigalupo & E.L.Cabral (nrDNA: PP = 1, BS = 87), *Crusea* Cham. & Schltdl. (nrDNA: PP = 1, BS = 97), *Diodia* (nrDNA: PP = 1, BS = 100), the Galianthe clade (nrDNA: PP = 1, BS = 87) and within it *Galianthe* (nrDNA: PP = 1, BS = 98; plDNA: PP = 1, BS = 76), the Hexasepalum-Ernodea clade (nrDNA: PP = 1, BS = 100) and within it *Ernodea* Sw. (nrDNA: PP = 1, BS = 100), *Hexasepalum* s.str. (nrDNA: PP = 1, BS = 100), *Mitracarpus* (nrDNA: PP = 1, BS = 99), the Psyllocarpus-Staelia clade (nrDNA: PP = 0.98, BS = 90; plDNA: PP = 0.9, BS = 79) and within it *Psyllocarpus* (nrDNA: PP = 0.99, BS = 95; plDNA: PP = 1, BS = 98) and *Staelia* (nrDNA: PP = 1, BS = 96; plDNA: PP = 0.84, BS = 79), *Richardia* (nrDNA: PP = 1, BS = 93), Old World *Spermacoce* (nrDNA: PP = 0.99, BS = 87), and *Spermacoce* s.str. (nrDNA: PP = 1, BS = 89). Relationshps between these clades remain largely unresolved, since throughout the backbone there is no support (Fig. 3). *Psyllocarpus campinorum* was recovered at an early divergent position in the Spermacoce clade, on a polytomy with *Crusea* and a clade including the remaining species. Except for *P. campinorum* and *P. densifolius*, all other species of *Psyllocarpus* clustered on a well supported clade (Fig. 3). As for the plDNA dataset, it yielded a widely unresolved Spermacoce clade, with species of *Mitracarpus*, *Richardia*, and *Spermacoce* intermingled with species of other genera.

As for the interspecific relationships in *Psyllocarpus*, *P. bahiensis* was recovered as sister to the clade formed by the remaining species of the genus (PP = 1, BS = 97) in the nrDNA analysis (Fig. 3), but not in the plDNA, in which it formed a clade with *P. asparagoides* (PP = 1, BS = 89). *Psyllocarpus laricoides*, which was sampled at its type locality, the Pico do Itambé, and at the Serra do Cipó, formed a clade with *P. schwackei* with maximum support in the BI of the nrDNA (PP = 1) but not in ML. Aside from these, interspecific relationships in the genus are generally unresolved.

Discussion

Our study is the first to objectively address the delimitation of a genus of the Spermacoce clade in the tribe Spermacoceae, as previous works aimed at clarifying the position of monotypic genera or some particular species (Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018). Our analysis retrieved the same major clades in the Spermacoceae that were previously reported in other studies (Kårehed & al., 2008; Groeninckx & al., 2009; Janssens & al., 2016), with some differences depending on the dataset (Figs. 1–2). Although our sampling is somewhat limited in terms of representing the entire tribe and the diversity within the genera it encompasses (especially those from the Old World) and relationships between clades are not fully resolved, we aimed not at presenting a detailed phylogenetic hypothesis for the whole tribe but rather to focus on the Spermacoce clade, more specifically the genus *Psyllocarpus*. Since our goals were to assess the monophyly of *Psyllocarpus* and infer interspecific relationships in the genus, to identify its sister group and assess the relationship between *Psyllocarpus* and other genera in the Spermacoce clade, as well as to test the position of the enigmatic *Psyllocarpus densifolius*, our analysis yielded adequate sampling, at least for the most part, given our objectives.

Phylogenetic position of *Psyllocarpus densifolius*. — *Psyllocarpus densifolius* is endemic to the summits of the Serra do Cipó, a component of the Espinhaço range located in Minas Gerais, southeastern Brazil (Zappi & al., 2014). This species is characterized by its scarcely branched stems arising from a well-developed subterranean system, triangular acuminate sptipules, lanceolate to linear leaves, terminal 1–2-flowered inflorescences subtended by hyaline bracts, 4-lobed calyx, and light-blue to lilac corollas. By the occasion of its description, only a few flowering and/or immature fruiting materials were available to the authors. As we have observed and collected specimens of *P. densifolius* in the field at its type locality, we were able to confirm that this is a heterostylous species (Fig. 4), a rare condition in the Spermacoce clade (reported only in most taxa from the Galianthe clade and in *P.* sect. *Amazonica*), which was not mentioned in its protologue. Such morphological discrepancies in regards to the other species in the genus in its strict sense (with the exclusion of *P.* sect. *Amazonica*; more on that below), most notably its habit, stipules, bracts, and flowers, have raised doubts about its placement in *Psyllocarpus*, or even in any other genus in the Spermacoce clade.

We here demonstrated that *P. densifolius* does not belong in *Psyllocarpus* nor any other genera in the Spermacoce clade, but most likely is a component of the Spermacoceae (Figs. 1–2). Our phylogenetic analysis provided somewhat different results regarding the position of this species depending on the dataset. The plDNA recovered a clade composed of *P. densifolius*, *Oldenlandia filicaulis*, and the remaining Spermacoceae with maximum support (PP = 1, BS = 100; Fig. 2). On the other hand, the nrDNA recovered the Spermacoceae with maximum to moderate support (PP = 1, BS = 80) but does not clarify how it relates to Knoxieae nor both species, since statistical support for these relationships is low (Fig. 1). Since we were not able to produce an ETS sequence for *P. densifolius*, we argue that the low support for a relationship with the Spermacoceae in the nrDNA analysis could be caused by a sampling artifact, as the ITS tree provided moderate support in the BI (PP = 83) and a similar topology in the ML (BS = 73).

The question could be raised if whether or not *P. densifolius* belongs in Knoxieae, since nrDNA did not provide statistical support to ascertain its relationship to the Spermacoceae. It seems unlikely, since the plDNA analysis recovered a clade composed of *P. densifolius*, *O. filicaulis*, and the remaining Spermacoceae with maximum support (PP = 1, BS = 100; Fig. 2). Furthermore, Knoxieae is a paleotropical tribe, with its distribution centered in Madagascar and continental Africa, presenting morphological characteristics divergent from those in *P. densifolius*, as the former is composed of herbs, subshrubs, shrubs or small trees, with fimbriate or rarely triangular stipules, often 5-merous or derived from the 5-merous state flowers, and calyx mostly unequal with 1 or more enlarged and often foliaceous lobes (Kårehed & Bremer, 2007; Groeninckx & al., 2009). Another possible scenario would be the recognition of *P. densifolius* in a monotypic tribe since it could represent an isolated lineage, which remains an open question, pending further studies using more molecular regions from both nuclear and plastid genomes, to try get better resolution for the internal clades in the Spermacoceae and allies.

The phylogenetic position of *O. filicaulis*, a species distributed from south Venezuela to north and northeast Brazil, is also unclear. It forms a clade (PP = 0.64) with *P. densifolius* with low support in the BI of the nrDNA (Fig. 1), but this was not recovered in any other analysis. They both have 1–2-flowered inflorescences bearing heterostylous flowers with light-blue to lilac infundibuliform corollas. Besides, such characteristics as the heterostylous flowers and filiform stigma lobes could also indicate a relationship with the Pentanopsis clade, an Afro-Madagascan clade composed of *Pentanopsis* Rendle, *Amphiasma* Bremek., *Conostomium* (Stapf) Cufod., *Gomphocalyx*, *Manostachya* Bremek., *Phylohydrax*, and three species of *Oldenlandia* L. (Kårehed & al., 2008). Such a clade, although generally well supported (nrDNA: PP = 1, BS = 98; plDNA: PP = 1, BS = 50, with the exclusion of *Phylohydrax carnosa*), is not easily morphologically characterized. The only unifying feature for this group would be the basal placentation (Thulin & Bremer, 2004), which has been questioned by Groeninckx & al. (2009) as not truly basal, but rather an axile with the placenta or ovule attached near the base of the septum. Moreover these authors argue that this kind of placentation is also found outside the Pentanopsis clade. Nevertheless, further molecular and morphological investigations are needed to test how *P. densifolius* and *O. filicaulis* relate to the Spermacoceae and each other.

New insights into the phylogeny of the Spermacoce clade. — Our phylogenetic analysis presented crucial differences between the datasets. The Spermacoce clade was recovered with maximum support by the nrDNA (PP = 1, BS = 100; Fig. 1), whereas for the plDNA it presented moderate to low support values (PP = 0.88, BS = 14) and topological differences in regards to the former, i.e. the position of *Manettia lygistum*, which appears nested within the clade, and *Spermacoce prostrata*, which does not (Fig. 2). We argue that such discrepancies with respect to the nrDNA could be caused by a sampling artifact, since both species were sampled only for *trnL-F*, a rather difficult region from the plDNA to align.

Other studies also presented conflicting results regarding support and topology of the clade with respect to the molecular regions of different genomes used as well. Kårehed & al. (2008), using both nuclear ribosomal (ETS and ITS) and plastid (*atpB-rbcL*, *petD*, *rps16*, and *trnL-F*) DNA regions, recovered a Spermacoce clade with maximum support (PP = 1) in their BI, whereas Groeninckx & al. (2009), using only plastid regions (*atpB-rbcL*, *rps16*, and *trnL-F*), recovered a clade lacking in support both for the BI and maximum parsimony analysis, with *Nesohedyotis arborea* nested within it in the former. These studies, also in agreement with ours, showed the uncertain relationship of the Spermacoce clade with respect to *Arcytophyllum serpyllaceum*, *Bouvardia*, *Manettia*, *Nesohedyotis arborea*, *O. tenuis*, and *O. salzmannii* (Figs. 1–2). Furthermore, in a study focusing on the Spermacoce clade for testing the phylogenetic position of *Carajasia*, Salas & al. (2015) obtained high to low support for the clade in their analysis, which were based only on nuclear ribosomal DNA (ETS and ITS; parsimony BS = 78, maximum likelihood BS = 82, and PP = 0.95). Although one could argue the "clade" in "Spermacoce clade" remains somewhat elusive, this is a rather morphologically cohesive group, which can be distinguished from the rest of the tribe in having ovaries with a single ovule per locule attached near the middle of the septum and often pluriaperturate pollen grains, in contrast to few to many ovules per locule and often tricolporate pollen grains.

Although our study contemplated the most of the morphological, geographical, and taxonomic variation in the Spermacoceae, emphasis was given to the Spermacoce clade. Our nrDNA sampling, which included accessions representing 91 spp., is larger than those in previous studies focusing on the clade, as Salas & al. (2015), Florentín & al. (2016), and Miguel & al. (2019), who based their phylogenetic analyses on the same molecular regions, investigated 42, 44, and 49 spp., respectively. All of these studies (including the present one) had 14 genera represented. In our nrDNA analysis, we recovered several well supported clades which in general match the concept of such genera and agree with the results presented by these authors. However, relationships between these clades, as in the aforementioned studies, remain mostly unresolved or weakly supported (Fig. 3).

Crusea is a Central American genus composed of 14 spp. characterized by the dehiscence of its fruit, which is a schizocarp that separates into two caducous mericarps leaving a basal carpophore on the pedicel. We here sampled three of its species, as the genus was recovered monophyletic with maximum to high support values (PP = 1, BS = 97) in agreement with previous studies (Kårehed & al., 2008; Groeninckx & al., 2009; Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018). The South American monotypic genus *Emmeorhiza*, which is characterized by its climbing habit and thyrsoid inflorescence, has been hypothesized to form a clade with *Crusea*

(Kårehed & al., 2008), which was not corroborated by our results.

We here follow the narrowed concept of *Diodia* L. as proposed by Bacigalupo & Cabral (1999). According to these authors *Diodia* s.str. occurs from southeast USA to Argentina, including five species that can be characterized by their palustrine habit, pauciflorous axillary inflorescences, filiform corolla tube, bifid style with two long filiform stigmatic lobes, and indehiscent fruits, as in the type species *D. virginiana* L. Species that have been ascribed to this genus despite not matching such diagnostic morphological features have been transferred to *Borreria* (Bacigalupo & Cabral, 1996), *Galianthe* (Cabral & Bacigalupo, 1997b; Florentín & al., 2017), and *Hexasepalum* Bartl. ex DC. (= *Diodella* Small; Kirkbride & Delprete, 2015). *Diodia* s.str. (*D. saponariifolia* K.Schum. and *D. virginiana*) was recovered as monophyletic with maximum support in our analysis (PP = 1, BS = 100), corroborating other studies (Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018) and the concept of Bacigalupo & Cabral (1999). The African *Diodia aulacosperma* K.Schum., which was found associated with the Old World *Spermacoce* (PP = 0.99; more on this clade below), has been treated under *Spermacoce* by Dessein (2003), but the new combination has never been formally published.

The Galianthe clade was recovered with maximum support in the BI but not in the ML (PP = 1, BS = 87). The association of *Schwendenera* with this clade have remained rather elusive (Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018). We here corroborate this relationship. The clade is also composed of *Carajasia* and *Galianthe*. Relationships between these genera are not resolved though. Most species in this clade have pollen grains with a double reticulum, which is usually associated with heterostylous flowers (except for *Carajasia*, in which flowers are homostylous). Both *Carajasia* and *Schwendenera* are monotypic genera endemic to Brazil, the former from the Carajás mountain range in the state of Pará, growing only on ferric soil or "Canga", and the latter from Paraná and São Paulo, inhabiting seasonally semideciduous forest but reaching the "Cerrado" (Dessein, 2003; Salas & al., 2015), whereas *Galianthe* is distributed from Mexico to Subtropical America, comprising ca. 55 spp. (Cabral & Bacigalupo, 1997b; Cabral, 2009; Florentín & al., 2019).

Carajasia has been recently described by Salas & al. (2015) and can be characterized, in the context of the Galianthe clade, by the dehiscence of its fruit, which is a schizocarp that separates into two caducous mericarps, leaving a basal carpophore on the pedicel, as the ventral face of each mericarp is covered by a hyaline wall that belongs to the intercarpellar septum, similar to that of *Crusea*. In *Schwendenera* the fruits are formed by three or four carpels, splitting into indehiscent mericarps. On the other hand, *Galianthe*, which was found monophyletic in our analysis with maximum to low support (nrDNA: PP = 1, BS = 98; plDNA: PP = 1, BS = 76), is mainly characterized by its lax thyrsoid or cymoid inflorescences (Cabral & Bacigalupo, 1997b; Cabral, 2009; Florentín & al., 2017). *Galianthe* has been treated under *Borreria* or *Spermacoce* until Cabral (1991) reinstated its generic status. Cabral & Bacigalupo (1997) classified it in two subgenera, *Galianthe* subg. *Galianthe* and *G.* subg. *Ebelia* (Rchb.) E.L.Cabral & Bacigalupo, based on habit, fruit, seed, and chromosome characters. Such subgenera are corroborated in our study, as well as in others (Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018). *Galianthe* subg. *Galianthe*, here represented by *G. eupatorioides* (Cham. & Schltdl.) E.L.Cabral, *G. grandifolia* E.L.Cabral, and *G. peruviana* (Pers.) E.L.Cabral, was recovered with maximum support (PP = 1, BS = 100), as *G.* subg. *Ebelia*, represented by *G. brasiliensis* (Spreng.) E.L.Cabral & Bacigalupo, *G. palustris* (Cham. & Schltdl.) Cabaña Fader & E.L.Cabral, *G. spicata* (Miq.) Cabaña Fader & Dessein, and *G. vaginata* E.L.Cabral & Bacigalupo (here investigated for the first time), with maximum to high support (PP = 1, BS = 90).

Hexasepalum, the priority name for *Diodella*, which was proposed to accommodate species from the *Diodia* s.l. with thick walled schizocarpic fruits, is mainly American distributed but also occurs in continental Africa, comprising 15 spp. (Fader & al., 2016, 2019). Its species fall in two distinct clades in the basal polytomy of the Spermacoce clade, the Hexasepalum-Ernodea clade (PP = 1, BS = 100) and the one representing the *Hexasepalum* s.str. (PP = 1, BS = 100), agreeing with previous phylogenetic investigations (Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018).

Two informal groups were recognized by Dessein (2003) in *Hexasepalum*, which match our results. The "*Diodella teres* group" corresponds to *Hexasepalum* s.str., and is characterized by the ventral face of mericarps showing two depressions (on each side of the midline), a curved embryo, and pollen grains with two types of supratectal elements (spines 1–8 µm and small granules less than 1 µm). This group includes the type species of *Diodella*, *Diodella rigida* (Cham. & Schltdl.) Small [= *Hexasepalum apiculatum* (Willd. ex Roem.) J.H. Kirkbr. & Delprete], and is here represented by five species, two of which are investigated for the first time (*Hexasepalum* sp. nov. [rio preto] and *Hexasepalum zappiae* E.L.Cabral & Cabaña Fader). The second group, called the "*Diodella sarmentosa* group," here represented by two species, as *H. mello-barretoi* (Standl.) J.H.Kirkbr. & Delprete is investigated for the first time, is distinguished by the mericarps with a flat ventral face (without depressions), usually ruminate seeds (dorsal face), a straight embryo, and pollen grains with only microspines (less than 1 µm). This group forms a grade in relation to *Ernodea* Sw. (PP = 1, BS = 100), which was recovered with maximum support. This is an unusual genus in the Spermacoceae because of its drupaceous fruits comprising nine species, distributed from southern US in Florida to northern South America, mainly in islands. This relationship was justified by Dessein (2003) based on seed morphology, but it remains rather elusive.

Richardia was recovered monophyletic with maximum to high support (PP = 1, BS = 93). There has never been much debate in regards to the monophyly of this genus (Dessein, 2003; Salas & al., 2015), which is well characterized by its 3–4-carpellate ovaries, deeply divided stigmas, fruits splitting into indehiscent mericarps, and deciduous calyx, and is distributed from southern US to temperate South America, with the exception of the Amazon basin, and introduced in some areas of the Old World, such as south and east Africa, Asia and Australia, comprising 16 spp. Lewis & Oliver (1974) classified *Richardia* into two sections based on flower merosity and morphology of the mericarps, *R.* sect. *Richardia* (PP = 1, BS = 100), here represented by *R. brasiliensis* Gomez, *R. grandiflora* (Cham. & Schltdl.) Steud., and *R. scabra* L., and *R.* sect. *Asterophyton* (K.Schum.) W.H.Lewis & R.L.Oliv. (PP = 1, BS = 100), represented by *R. humistrata* (Cham. & Schltdl.) Steud. and *R. stellaris* Steud., which are here corroborated by molecular data with maximum support for the first time. *Mitracarpus* is another morphologically well-defined genus that can be easily diagnosed by the circumscissile dehiscence of its fruits and the "X" or "Y" shaped ventral groove on the seeds, being distributed from Mexico to tropical America and comprising ca. 50 spp. (Dessein, 2003). We recovered this genus with maximum to high support in our analysis (PP = 1, BS = 99).

Spermacoce as here tentatively circumscribed is a rather heterogeneous taxon with a pantropical distribution, composed of some 165–170 spp. The *Spermacoce* species fall in two distinct clades in the polytomy of the Spermacoce clade, both with maximum to high support in the BI but moderate in the ML analysis, one corresponding to the *Spermacoce* s.str. [PP = 1, BS = 89; *S. reflexa* (J.H.Kirkbr.) Govaerts is here investigated for the first time], which accommodates the type species of the genus, *S. tenuior*, and the other recovers an Old World clade of *Spermacoce* species (PP = 0.99, BS = 87).

We here provide a general diagnose for the *Spermacoce* s.str., i.e. the unilateral glomerules, urceolate to campanulate corolla with pilose lobes, included stamens and styles with capitate-bilobate stigmas, dry indehiscent fruits or septicidal dehiscence in only one mericarp, seeds with a flat ventral side, and pollen grains zonocolporate with a long ectocolpi, joined endoapertures forming an endocingulum, ectocolpi surrounded by a margin of granules, and exine psilate at the apocolpium and spinulate at the mesocolpium (Cabral & al., 2010; Miguel & Cabral, 2013; Florentín & al., 2016). It should be noted that such a diagnosis works better for the ca. 35 American species of this group, since the two Australian *Spermacoce* (*S. breviflora* Benth. and *S. erosa* Harwood) sampled in this study, which formed a clade with maximum support (PP = 1, BS = 100) nested within the *Spermacoce* s.str., diverge from these features and present some morphological specializations, e.g. the corolla appendages (Vaes & al., 2006), which are absent in the American species.

The Old World *Spermacoce* is a rather morphologically heterogeneous group, presenting bilateral or unilateral glomerules, filiform to infundibuliform corollas with glabrous or pubescent lobes, exserted or included stamens and style, several types of fruit dehiscence, seeds longitudinally grooved on the ventral side, and pollen grains pantoporate or zonocolporate, joined endoapertures usually forming an endocingulum, with the exine variably ornamented (Dessein, 2003), with no obvious diagnosable features. Previous studies that have sampled only one species from the Old World (*Spermacoce dibrachiata* Oliv.) have found it related to *Borreria* s.str. (Salas & al., 2015; Florentín & al., 2017), whereas others have shown that the Old World *Spermacoce* form a distinct clade when more species are included, not necessarily related to *Borreria* (Dessein, 2003; Miguel & al., 2018). We here corroborate the latter, and tentatively recognize the ca. 80 spp. African and Asian taxa under *Spermacoce*.

We here tentatively adopt a circumscription for *Borreria*, which is in agreement with the morphological features in *B. suaveolens* G.Mey., its type species, yet to be sampled in a phylogenetic investigation. *Borreria* should then include species with bilateral glomerules, infundibuliform corollas with glabrous or pubescent lobes, exserted stamens and style, with capitate-bilobate or bifid stigmas, fruits with septicidal dehiscence in both mericarps, seeds longitudinally grooved on the ventral side, and pollen grains pantoporate or zonocolporate, with a barely discernible endocingulum, with the exine uniformly spinulate (Bacigalupo & Cabral, 1996; Dessein & al., 2002a, 2002b; Cabral & al., 2010; Miguel & Cabral, 2013). It is a genus almost entirely restricted to the Neotropics, composed of ca. 100 spp.

Borreria species fall in two well-supported clades, here representing *Borreria* subsect. *Latifoliae* (PP = 1, BS = 87), a well defined taxon characterized by the bifid stigmas comprising ca. 15 spp., and the remaining species of the genus, representing *Borreria* s.str. [PP = 0.99, BS = 92; of which *B. crispata* (K.Schum.) E.L.Cabral & Bacigalupo and *B. rosmariniifolia* E.L.Cabral & Bacigalupo are here investigated for the first time], with capitate-bilobate stigmas. The relationship between these clades is unclear in our analysis as in previous studies (Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018). *Spermacoce pusilla* Wall. appears nested within *Borreria* s.str. It occurs in eastern Africa to southeastern Asia and shares morphological diagnostic features with *Borreria* s.str., i.e. bilateral glomerules, infundibuliform corollas with glabrous or pubescent lobes, exserted stamens and style, capitate-bilobate stigmas, and dehiscent mericarps, hence we recommend the use of the name *B. pusilla* (Wall.) DC. for this taxon.

Both the Old World and Australian *Spermacoce* are quite diverse (ca. 80 and 50 spp., respectively) and represent morphologically heterogeneous assemblages. Despite resolving in generally well-supported clades, our sampling of these groups is limited (10 spp. and 2 spp., respectively). We here tentatively recognize these groups under *Spermacoce*, as they are traditionally recognized in those regions of the world (Dessein, 2003). Nevertheless, many independent colonization by long distance dispersal events from the Americas into such regions might have occurred (e.g. *Spermacoce pusilla*, *S. breviflora*, and *S. erosa*), as such events have already been reported for other genera in the tribe (Janssens & al., 2016). Therefore the degree to which the species from these assemblages are related to each other and to the remaining *Spermacoce* or *Borreria*, or even any other genus in the Spermacoce clade, is yet to be tested. Some of them might as well correspond to independent lineages that could be recognized as their own genera, pending further investigation with a wider sampling of these assemblages and more molecular regions.

It should be noted that the circumscriptions adopted here for both *Borreria* and *Spermacoce* are attempts on their delimitation based on preliminary phylogenetic results and morphology, primarily based on their type species, which are neotropical taxa. The monophyly of *Borreria* (as well as *Spermacoce*'s) is yet to be tested, with a wider sampling, including the type species *B. suaveolens*, and more data. At this point of our understanding of the Spermacoce clade, there is no phylogenetic evidence to corroborate a synonymization of *Borreria* under *Spermacoce*, as the relationship between clades are unclear. Furthermore, as currently circumscribed they're easily distinguishable from each other, at least in the Americas, and the name *Borreria* has been traditionally used in the literature and herbaria to identify this group of species in the Neotropics, hence our position to maintain both genera. Also, the degree to which such a synonymization might occur will depend on the phylogenetic position of *B.* subsect. *Latifoliae*, which might as well correspond to an independent lineage.

Staelia (nrDNA: PP = 1, BS = 96) and the remaining species of *Psyllocarpus*, which compose the *P.* sect. *Psyllocarpus* of Kirkbride (1979), here referred to as *Psyllocarpus* s.str. (nrDNA: PP = 0.99, BS = 95; plDNA: PP = 1, BS = 98), were recovered with maximum to high support, and both form a generally well-supported clade in all analyses, except for the ML of the plDNA, here referred to as the Psyllocarpus-Staelia clade (nrDNA: PP = 0.98, BS = 90; plDNA: PP = 0.9, BS = 79). The monophyly of such genera is in agreement with previous studies (Salas & al., 2015; Florentín & al., 2017; Miguel & al., 2018), but their relationship is here evidenced for the first time. These genera share the calyx with two lobes, the septifragal characteristic of fruit dehiscence leaving an intercarpellar septum, and pollen with long colpi and joined endoapertures forming an endocingulum.

Staelia is distributed in South America comprising 16 spp.(Salas, pers. com.). Modifications have been made to the circumscription of the genus, based on morphological studies of the sections proposed by Schumann (1888). *Anthospermopsis* and *Tessiera* were elevated to the generic rank (Kirkbride, 1997; Salas & Cabral, 2010b; respectively), whereas the two Brazilian species of the latter were segregated into a new genus, *Planaltina* (Salas & Cabral, 2010a). Unfortunately none of these genera were sampled in this study. Nevertheless, we sampled eight *Staelia* species, four of which are here investigated for the first time [*Staelia culcita* R.M.Salas & E.L.Cabral (only plDNA), *Staelia domingosii* R.M.Salas & E.L.Cabral, *Staelia hatschbachii* J.H.Kirkbr., and *Staelia thymbroides*]. This genus can be readily characterized by its fruit, which separates into three parts: two apical caducous and one basal that persists on the pedicel. The dehiscence begins longitudinally from the apex to the middle of the capsule along the carpels (septifragal), subsequently the line of dehiscence leaves the septum and goes all the way across the fruit wall of each valve from one side of the septum to the other. The persistent portion is formed by the intercarpellar septum, the base of the fruit and the pedicel (Salas & Cabral, 2011).

Reviving Martius and Zuccarini: an old new circumscription of *Psyllocarpus*. — Martius & Zuccarini (1824) described *Psyllocarpus* based on its calyx with two distinct lobes, infundibuliform corolla with four lobes and trichomes on the throat, four included stamens, short style with capitate stigma, and bivalvate capsules with two locules bearing one peltate compressed seed each. Martius (1824) provided a more detailed description of the genus, adding the linear to subulate leaves, blue corolla, compressed capsules bearing peltate seeds, and a membranous septum parallel to the valves. Their circumscription of the genus matches the results found here in this phylogenetic study, with a few amendments as discussed below. *Psyllocarpus*, as originally conceived, was recovered with maximum to high support in all analysis (nrDNA: PP = 0.99, BS = 95; plDNA: PP = 1, BS = 98), including the species described later by Schumann (1898) and Carmo & al. (2018b).

Schumann (1888) transferred one of Martius & Zuccarini (1824) species, *P. thymbroides*, to *Staelia*, creating *S. thymbroides*, which is corroborated by our study. Since *P. thymbroides* was established prior to *Staelia* (Chamisso & Schlechtendal, 1828), our hypothesis is that its blue corolla, as well as its subshrubby habit, whorled leaves with axillary brachyblasts forming fascicles, and leaf blades elliptic-lanceolate to linear-lanceolate might have been decisive for Martius & Zucarrini (1824) to treat this species under *Psyllocarpus*. They possibly overlooked characters that would later distinguish these genera, such as the exserted stamens and style and the type of fruit dehiscence in *Staelia*, a genus composed of species generally presenting white corollas.

Kirkbride (1979) expanded on the original concept of *Psyllocarpus*, gathering a rather heterogeneous group of species in the genus. By prioritizing the capsules compressed parallel to the septum to circumscribe it, its sections, i.e., *P.* sect. *Psyllocarpus* and *P.* sect. *Amazonica*, presented quite discrepant morphological traits. In a phylogenetic context, the morphology and type of dehiscence of the capsules can be of importance to support some of the well-supported genera in the Spermacoce clade (e.g. *Diodia*, *Mitracarpus*, and *Staelia*), but they can also be labile in others (e.g. *Galianthe* and *Psyllocarpus*, as discussed below), therefore caution should be regarded to this character.

Psyllocarpus campinorum is here investigated for the first time in a phylogenetic context, being one of the components of the basal polytomy of the Spermacoce clade, and distantly related to the remaining *Psyllocarpus*. Despite several efforts, we were unable to amplify and/or sequence DNA from herbarium material of additional *P.* sect. *Amazonica*, as we could not collect samples of its species in the field, pending further studies to test the monophyly of this taxon. Nevertheless, such a section, is characterized by Kirkbride (1979) by the planar leaves, heterostylous flowers, oblate-spheroidal pollen grains, perforated tectum, finely and evenly spinulose exine, and deeply bifid stigma, being restricted to the white-sand Amazonian campinas. Despite the uncertain position of *P. campinorum*, such morphological traits as the heterostylous flowers with bifid stigmas hint on a possible relation of these species to the Galianthe clade. In fact as we were able to produce only an ETS sequence for *P. campinorum*, it might have influenced on the uncertainty of its relationship to the remaining Spermacoce clade.

Recent novelties have added and broadened the circumscription of *Psyllocarpus*, as *P. bahiensis* presents a type of fruit dehiscence that is unique in the genus. In this species, the capsule is composed of two deciduous valves forming a ventral rim of carpel tissue, which keeps each seed trapped inside them after dehiscence, leaving a broadly elliptic to broadly obovate persistent septum attached to the pedicel (Carmo & al., 2018b). On the other hand, the remaining species of *Psyllocarpus* present septifragal capsules with persistent valves, from which the seeds are shed after dehiscence. Such a manner of fruit dehiscence of *P. bahiensis* has been reported for only two species in the Spermacoce clade, i.e. *Anthospermopsis catechosperma* (K.Schum.) J.H.Kirkbr., which is also endemic to Bahia, and *Spermacoce omissa* J.R.Clarkson, from Australia (Harwood & Dessein, 2005), both associated with sandy soils as well. Unfortunately, these species have never been sampled in a phylogenetic study.

In summary, *Psyllocarpus* as currently circumscribed is polyphyletic. Therefore, we here exclude from it the species from *P.* sect. *Amazonica*, as well as *P. densifolius*, in favour of a narrow circumscription of the genus, which is based on its original concept conceived by Martius & Zuccarini (1824) and Martius (1824), rendering *Psyllocarpus* to a monophyletic easily diagnosable taxon. The phylogenetic position and identity of the excluded species remain unclear, pending further investigation. Furthermore, we here provide a synopsis of *Psyllocarpus*, with an updated description of the genus and an identification key and list of names and nomenclatural types of its eight species (Fig. 5).

Concluding remarks. — Our study is the first to address the circumscription of a genus of the Spermacoce clade in the tribe Spermacoce from a phylogenetic perspective. *Psyllocarpus* is here delimited in congruence to its original concept conceived by Martius & Zuccarini (1824) and Martius (1824) almost 200 ya. Although the trees obtained from the nuclear and plastid DNA sequences both recovered major clades in the Spermacoceae, the different genomes yielded some "hard" incongruences regarding the topology of the resulting trees, pending further investigation using novel approaches to solve such conundrums, e.g. the utilization of coalescent based methods for species tree reconstructions (Pirie, 2015), which are yet to be tested in this tribe. Several genera are well supported in the Spermacoce clade, although the relationships between them remain generally unclear. The Spermacoce clade could represent a recent lineage that diversified through multiple radiations into different regions in the tropics, reaching a wide variety of habitats. For this lineage huge quantities of data, i.e. NGS, might be necessary to elucidate relationships between the taxa therein. Besides, some genera have never been sampled, as others are also yet to have their monophyly tested.

Taxonomic treatment

Psyllocarpus Mart. & Zucc. in Flora 7(1, Beil.), Suppl. 4: 130. 1824, nom. cons. prop. ≡ *Psyllocarpus* Mart. & Zucc. sect. *Psyllocarpus* in Smithson. Contr. Bot. 41: 15. 1979 – Lectotype (designated by Kirkbride, 1979): *P. laricoides* Mart. & Zucc.
= *Tapanhuacanga* Vand. in Fl. Lusit. Bras. Spec.: 9. 1788 – Type: *T. brasiliensis* Steud. (Nomencl. Bot., ed. 2, 2: 663. 1841).

Description. – Subshrubs, rarely perennial herbs, sympodial or monopodial, woody roots, stems simple to densely branched, erect, branches tetragonal to terete or compressed, glabrous to puberulous. Stipular sheath (1)3–8-fimbriate; fimbriae narrowly triangular to linear or subulate, with terminal colleters. Leaves opposite, rarely ternate, sessile; blade terete to linear, glabrous to strigose, apex narrowly acute to obtuse, sometimes with axillary brachyblasts forming fascicules. Flowering branches determinated or indeterminated, unbranched, dichasial or monchasially branched, erect or pendulous (*P. phyllocephalus*). Inflorescences in 1-flowered cymes or terminal glomerules, rarely pauciflorous cymes (*P. bahiensis*). Flowers homostylous, sessile to pedicelate; hypanthium turbinate, glabrous, hirsute (*P. bahiensis*) or the upper third puberulous (*P. goiasensis*); calyx 2(4 in *P. bahiensis*)-lobate, lobes narrowly triangular to triangular, glabrous to glabrate or sparsely ciliate, sometimes joined at base forming a tube, (0)1–8 fimbriae between the lobes, fimbriae narrowly triangular, with terminal colleters; corolla white, lilac, or blue, rarely light pink, infundibuliform or hipocrateriform, tube externally glabrous to pubescent, internally sericeous to sparsely sericeous on the upper half or third and glabrous below, lobes ovate to elliptic, narrowly to broadly acute, externally glabrous to pubescent, internally glabrous or papillate, sometimes apiculate at the apex; stamens included, fixed on the lower half of the corolla tube, filaments glabrous, anthers dorsifixed, or rarely versatile, oblong to narrowly oblong, glabrous, pollen grains prolate-spheroidal to prolate or subprolate, 4–7-zonocolporate, 15–24 µm diam in polar and 15–45 µm diam in ecuatorial view, exine perforate, finely and evenly spinulose, or with spinules concentrated along each side of the colpi; style glabrous, stigma bilobate, rarely capitate (*P. schwackei*), lobes minutely papillate, scabrous or glabrous. Capsule pedicellate, calyx persistent, elliptic to circular or obovate to broadly obovate in outline, glabrous, puberulous on the upper third or hirsute, compressed parallel to the septum, septifragally dehiscent from the apex downwards along the edge of the septum, valves persistent from which the seeds are shed or valves deciduous keeping their respective seeds trapped inside after dehiscence (*P. bahiensis*), septum entire and persistent; seeds narrowly oblong, obovate or elliptic to broadly elliptic in outline, compressed, weakly and irregularly winged, testa colliculate to verruculose, adaxial surface concave and abaxial convex, strophiole narrowly to broadly elliptic or linear to narrowly oblong, and the ends obtuse to truncate (*P. asparagoides*) or the base sagittate and the lobes spreading, broadly acute.

Distribution – Endemic from Brazil, occurring in the region of the Espinhaço range, a chain of mountains extending from Bahia to Minas Gerais, and the "chapadas" of the "Planalto Central do Brasil", in Goiás and the Distrito Federal.

Habitat and ecology – Subshrubs or rarely perennial herbs growing on sandy soils usually associated with the "campo rupestre", which is a montane, grassy-shrubby, fire-prone vegetation mosaic with rocky outcrops of quartzite, sandstone, or ironstone, along with sandy, stony, and waterlogged grasslands, at ca. 700–1500 m.

Key to species of *Psyllocarpus* (adapted from Carmo & al., 2018b)

1. Inflorescences in pauciflorous cymes; hypanthium hirsute to sparsely hirsute; capsules hirsute, valves deciduous keeping their respective seeds trapped inside after dehiscence........ **2. *P. bahiensis***

1. Inflorescences in 1-flowered cymes or glomerules; hypanthium glabrous or the upper third puberolous; capsules glabrous or the upper third sparsely puberulous, valves persistent from which the seeds are shed after dehiscence…………………………………………………………………………2

2. Flowering branches indeterminate, axillary inflorescences in 1-flowered cymes...........................3

2. Flowering branches determinate, terminal inflorescences in glomerules, rarely also with axillary inflorescences in 1-flowered cymes ………………………………………………………………………5

3. Most leaf axils without brachyblasts or pairs of smaller leaves; flowering branches with 2–4 flowers opened at the same time... **8. *P. schwackei***

3. Leaf axils with brachyblasts or short branchlets; flowering branches with 4 or more flowers opened at the same time...4

4. Sympodial subshrub; hypanthium glabrous; calyx tube 0.1–0.5 mm long; corolla lobes rounded in preanthetic buds; capsules glabrous; seeds elliptic to broadly elliptic in outline..... **5. *P. laricoides***

4. Monopodial subshrub; hypanthium with the upper 1/3 puberulous; calyx tube absent; corolla lobes capitate angulate in preanthetic buds; capsules with the upper 1/3 sparsely puberulous; seeds narrowly oblong in outline……....…………………………………………………...... **4. *P. goiasensis***

5. Flowering branches dichasial or monochasially branched, rarely unbranched; calyx lobes 4.3–4.8 mm long; corolla lobes capitate angulate in preanthetic bud....................................... **7. *P. scatignae***

5. Flowering branches unbranched; calyx lobes 1.2–3.6 mm long; corolla lobes rounded or clavate in preanthetic bud...………6

6. Mature corolla 4.1–7 mm long, lilac or blue... **3. *P. ericoides***

6. Mature corolla 1–2.6 mm long, white...7

7. Flowering branches erect; calyx lobes 1.2–2 mm long; corolla tube 1.1–1.5 mm long; seeds broadly elliptic in outline.. **1. *P. asparagoides***

7. Flowering branches pendulous; calyx lobes 2.2–3.6 mm long; corolla tube 2.2–2.6 mm long; seeds obovate in outline……….. **6. *P. phyllocephalus***

Synoptic list of species of *Psyllocarpus*

1. *Psyllocarpus asparagoides* Mart. & Zucc. in Flora 7(1, Beil.), Suppl. 4: 131. 1824 ≡ *Tapanhuacanga asparagoides* (Mart. & Zucc.) P.L.R.Moraes in Feddes Repert. 130(1): 51. 2019, **syn. nov.** – Lectotype (designated by Kirkbride, 1979): Brazil. Minas Gerais, habitat in campis altis termini Minarum Novarum prope Piedade, 1818, *Martius s.n.* (M barcode M-0189224 [annotated as lectotype by Joseph H. Kirkbride, Jr.]!; presumed isolectotypes: M barcode M-0189225 [annotated as isotype by Joseph H. Kirkbride, Jr.]! & L barcode L 0058039!).

2. ***Psyllocarpus bahiensis*** J.A.M.Carmo, Sobrado & R.M.Salas in Syst. Bot. 43(2): 582. 2018 ≡ *Tapanhuacanga bahiensis* (J.A.M.Carmo, Sobrado & R.M.Salas) P.L.R.Moraes in Feddes Repert. 130(1): 51. 2019, **syn. nov.** – Holotype: Brazil. Bahia, Macaúbas, Estrada para Tinguis, 13°05'03"S, 42°46'37"W, 904 m, 18 Apr 2015, *Carmo & Scatigna 376* (UEC!; isotypes: CTES!, MO!, RB!, & SPF!).

3. ***Psyllocarpus ericoides*** Mart. & Zucc. in Flora 7(1, Beil.), Suppl. 4: 131. 1824 – Lectotype (designated by Kirkbride, 1979): Brazil. Minas Gerais, habitat in campis ad Bandeirinha, prope Tijuco, 22 May 1818, *Martius Obs. 1295* (M barcode M-0189212 [annotated as holotype by Joseph H. Kirkbride, Jr., 1976]!; presumed isolectotypes: M barcode M-0189213 [annotated as presumed isotype by Joseph H. Kirkbride, Jr., 1976]! & M barcode M-0189214 [annotated as presumed isotype by Joseph H. Kirkbride, Jr., 1976]!).

Note – During Martius expedition to Brazil, he took notes on more than 3,000 species of plants, which were compiled in his "Adversaria Botanica". A handwritten copy of such notes was made by A. Progel, entitled "Observationes botanicae, Plantae in itinere Brasiliensi annis 1817–1820 a Car. Frid. Phil. Martio descriptae, vol. 1–6". A xerographic copy of this work housed at the Taxonomy Lab, Plant Biology Department, Institute of Biology, University of Campinas, was consulted for the elaboration of this synopsis. Notably many of the specimens collected by Martius have labels referencing those comments (Moraes & Falcade, 2015), providing an additional source of information on the species, hence "*Obs. 1295*" does not refer to a collection number but rather to Martius field observations on this particular specimen.

4. ***Psyllocarpus goiasensis*** J.H.Kirkbr. in Smithson. Contr. Bot. 41: 17. 1979 ≡ *Tapanhuacanga goiasensis* (J.H.Kirkbr.) P.L.R.Moraes in Feddes Repert. 130(1): 51. 2019, **syn. nov.** – Holotype: Brazil. Goiás, Chapada dos Veadeiros, Cerrado on outcrops with adjacent wet campo (brejo), c. 10 km N of Alto Paraíso do Goiás, ca. 1100 m, 24 Mar 1971, *Irwin & al. 33082* (UB!; isotypes: MO barcode MO2575309!, NY barcode NY00133029!, US barcode US00130113 [negative and photo!], WAG barcode WAG0003052 [photo!], WIS barcode WIS0004269 [photo!], & WIS barcode WIS0004270 [photo!]).
= *Psyllocarpus laricoides* var. *γ longicornu* K.Schum. in Mart., F1. bras. 6(6): 33, 1888 – Lectotype [first-step designated by Kirkbride (1979); second-step designated by Carmo & al. (2018a)]: Brazil. Goiás, Ouro Fino, 1819, *Pohl 1317* (W [“29a W – W46” handwritten on herbarium sheet, annotated as lectotype by Joseph H. Kirkbride, Jr.]!; presumed isolectotypes: BR barcode

BR0000005325986!, K barcode K000470420!, M barcode M-0189211!, & W ["29a W – W45" handwritten on herbarium sheet, annotated as isotype by Joseph H. Kirkbride, Jr.]!).

5. ***Psyllocarpus laricoides*** Mart. & Zucc. in Flora 7(1, Beil.), Suppl. 4: 131. 1824 ≡ *Tapanhuacanga laricoides* (Mart. & Zucc.) P.L.R.Moraes in Feddes Repert. 130(1): 49. 2019, **syn. nov.** – Lectotype (designated by Kirkbride, 1979): Brazil. Minas Gerais, in sumo Brasiliae monte Itambé, 1818, *Martius s.n.* (M barcode M-0189221 left-hand specimen [annotated as holotype by Joseph H. Kirkbride, Jr, 1976]!; presumed isolectotypes: M barcode M-0189221 center specimen!, M barcode M0189217!, & M barcode M0189220!).
= *Psyllocarpus laricoides* var. *β densifolius* Mart. in Nov. Gen. Sp. Pl. 1(3): 46. 1824 – Presumed holotype: Brazil. Minas Gerais, in sumo Brasiliae monte Itambé, 1818, *Martius s.n.* (M barcode M-0189221 right-hand specimen [annotated as holotype by Joseph H. Kirkbride, Jr, 1976]!).

6. ***Psyllocarpus phyllocephalus*** K.Schum. in Bot. Jahrb. Syst. 25(3, Beibl. 60): 17. 1898 ≡ *Tapanhuacanga phyllocephala* (K.Schum.) P.L.R.Moraes in Feddes Repert. 130(1): 51. 2019, **syn. nov.** – Lectotype [first-step designated by Kirkbride (1979); second-step designated here]: Brazil. Goiás, entre Paranaua et le Rio Torto, 12 Feb 1895, *Glaziou 21504* (P barcode P02285151 [annotated as lectotype by Joseph H. Kirkbride, Jr, 1977]!; presumed isolectotypes: BR barcode BR000000532833!, K barcode K000470419!, P barcode P02285152!, & S S05-1675 [photo!]).

Note – Kirkbride (1979) designated the specimen *Glaziou 21504* in P as lectotype of the name *Psyllocarpus phyllocephalus*. However there is a duplicate of such specimen deposited at the same herbarium. Therefore we here designate P barcode P02285151 as (second-step) lectotype to further narrow it to a single specimen (Art. 9.17; Turland & al., 2018), as this is a more complete material presenting more branches, leaves, and reproductive structures.

7. ***Psyllocarpus scatignae*** J.A.M.Carmo, Sobrado & R.M.Salas in Syst. Bot. 43(2): 587. 2018 ≡ *Tapanhuacanga scatignae* (J.A.M.Carmo, Sobrado & R.M.Salas) P.L.R.Moraes in Feddes Repert. 130(1): 52. 2019, **syn. nov.** – Holotype: Brazil. Minas Gerais, Botumirim, Areal próximo a talhão de eucalipto, 16°54'00"S, 42°53'15"W, 23 Jan 2016, *Carmo & Scatigna 446* (UEC!; isotypes: CTES!, MO!, RB!, SPF!).

8. ***Psyllocarpus schwackei*** K.Schum. in Bot. Jahrb. Syst. 25(3, Beibl. 60): 18. 1898 ≡ *Tapanhuacanga schwackei* (K.Schum.) P.L.R.Moraes in Feddes Repert. 130(1): 52. 2019, **syn. nov.** – Lectotype (designated by Carmo & al., 2017): Brazil. Minas Gerais, Serra do Cipó, Mar 1892, *Schwacke 8089* (holotype: B†, F neg. 896!; lectotype: OUPR barcode OUPR10386 [ex Herb. Magalhães Gomes 3474]!; isolectotype: BHCB barcode BHCB020828!).

Incertae sedis

Psyllocarpus* sect. *Amazonica J.H.Kirkbr. in Smithson. Contr. Bot. 41: 13. 1979 – Type: *P. cururuensis* J.H.Kirkbr.

Borreria campinorum K.Krause in Verh. Bot. Vereins Prov. Brandenburg 50(2): 118. 1908 ≡ *Psyllocarpus campinorum* (K.Krause) J.H.Kirkbr. in Smithson. Contr. Bot. 41: 13. 1979 ≡ *Tapanhuacanga campinorum* (K.Krause) P.L.R.Moraes in Feddes Repert. 130(1): 51. 2019, **syn. nov.** – Lectotype (designated by Kirkbride, 1979): Brazil. Amazonas, Campina an den Cachoeiras des Marmelos, Mar 1902, *Ule 6102* (holotype: B†, F neg. 872!; lectotype: HBG barcode HBG-521835!; isolectotypes: CTES [fragment!], F [fragment!], K barcode K000470421!).

Psyllocarpus cururuensis J.H.Kirkbr. in Smithson. Contr. Bot. 41: 14. 1979 ≡ *Tapanhuacanga cururuensis* (J.H.Kirkbr.) P.L.R.Moraes in Feddes Repert. 130(1): 51. 2019, **syn. nov.** – Holotype: Brazil. Pará, Region of village of Paratí, ca. 8°S, 57°5' W, 11 Feb 1974, *Anderson & al. 10779* (IAN; isotypes: CTES No. 226498 [fragment!], MBM barcode MBM004070!, MO barcode 2990259!, NY barcode 00133028!, R barcode 000140960!).

Psyllocarpus densifolius Zappi & Calió in Bol. Bot. Univ. São Paulo 32(1): 131. 2014 ≡ *Tapanhuacanga densifolia* (Zappi & Calió) P.L.R.Moraes in Feddes Repert. 130(1): 51. 2019, **syn. nov.** – Holotype: Brazil. Minas Gerais, Santana do Pirapama, Serra do Cipó, acesso pela Faz. Inhame, Trilha da Senhorinha, 18º57'36"S, 43º45'30"W, 9 Mar 2009, *Zappi & al. 1919* (K; isotypes: MO, NY, RB barcode 00598589!, SPF).

Staelia psyllocarpoides Sucre in Rodriguésia 26(38): 255. 1971 ≡ *Psyllocarpus psyllocarpoides* (Sucre) J.H.Kirkbr. in Smithson. Contr. Bot. 41: 15. 1979 ≡ *Tapanhuacanga psyllocarpoides* (Sucre) P.L.R.Moraes in Feddes Repert. 130(1): 52. 2019, **syn. nov.** – Holotype: Brazil. Amazonas, Rio Urubú, 17 Sep 1949, *Fróes 25262* (IAN; isotype: IAC!).

Dubious name

Tapanhuacanga brasiliensis Steud. in Nomencl. Bot., ed. 2, 2: 663. 1841 – Lectotype (designated by Moraes, 2019): [icon] t. I, fig. 5 in Vandelli (1788).

Note – Although congeneric with *Psyllocarpus*, Carmo & al. (2019) argued that the absence of an actual specimen associated with this name, and the lack of critical diagnostic features for the identification of species in the genus, which are beyond what is observable on its drawings, prevent an unequivocal application of this name. Therefore the identity of *Tapanhuacanga brasiliensis* remains unclear.

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Table 1. List of genera currently associated with the Spermacoce clade, their native distribution, total number of species, species sampled in this study and its proportion (%) relative to total.

Genus	Native distribution	Number of spp.	Number of sampled spp.	Proportion of sampled spp. (%)
Anthospermopsis (K.Schum.) J.H.Kirkbr.	NE. Brazil	1	0	0
Borreria G.Mey. (including *B.* subsect. *Latifoliae*)	Neotropical, with a few species in the Old World	ca. 100	19	ca. 19
Carajasia R.M.Salas, E.L.Cabral & Dessein	N. Brazil	1	1	100
Crusea Schltdl. & Cham.	Arizona to New Mexico and C. America	14	3	ca. 21
Denscantia E.L.Cabral & Bacigalupo	E. Brazil	5	0	0
Diodia L.	C. & E. U.S.A. to Trop. America	5	2	40
Emmeorhiza Endl.	Trinidad to S. Trop. America	1	1	100
Ernodea Sw.	Florida to Caribbean, SE. Mexico to Colombia	9	2	ca. 22
Galianthe Griseb.	Mexico to Subtrop. America	55	7	ca. 13
Hexasepalum Bartl. ex DC.	U.S.A. to Trop. America	15	7	ca. 47
Micrasepalum Urb.	Caribbean	2	0	0
Mitracarpus Schult. & Schult.f.	Mexico to Trop. America	ca. 50	6	ca. 12
Nodocarpaea A.Gray	Cuba	1	0	0
Psyllocarpus Mart. & Zucc.	Brazil (Bahia, Goiás, and Minas Gerais, and Distrito Federal)	12	10	ca. 83
Planaltina R.M.Salas & E.L.Cabral	Brazil (Goiás)	4	0	0
Richardia L.	Trop. & Subtrop. America	16	5	ca. 31
Schwendenera K.Schum.	SE. & S. Brazil	1	1	100
Spermacoce L.	Pantropical	ca. 170	20	ca. 12
Staelia Cham. & Schltdl.	Brazil to N. Argentina	16	8	50
Tessiera DC.	Mexico	2	0	0
Tobagoa Urb.	Panama to Tobago and Venezuela	2	0	0
Tortuella Urb.	Haiti	1	0	0

Table 2. Properties of data partitions used in this study, with number of terminals, taxa, bases and aligned bases, variable and phylogenetic informative sites (PIS), retention index (RI), and missing data.

	Terminals	Taxa	Bases	Aligned Bases	Variable	PIS	RI	Missing Data (%)
ETS	124	124	487 [457,526]	575	408 (71 %)	324 (56.3 %)	0.58	15.6
ITS	149	148	797 [650,972]	1068	540 (50.6 %)	410 (38.4 %)	0.63	5.5
rps16	113	112	1002 [841,1110]	1279	531 (41.5 %)	282 (22 %)	0.79	26.9
trnL-F	95	94	823 [436,1114]	1485	317 (21.3 %)	212 (14.3 %)	0.84	30.3
nrDNA	153	152	1264 [1081,1563]	1643	948 (57.7 %)	734 (44.7 %)	0.6	13.6
plDNA	121	120	1533 [972,2582]	2764	848 (30.7 %)	494 (17.9 %)	0.78	22.6

Figure legends:

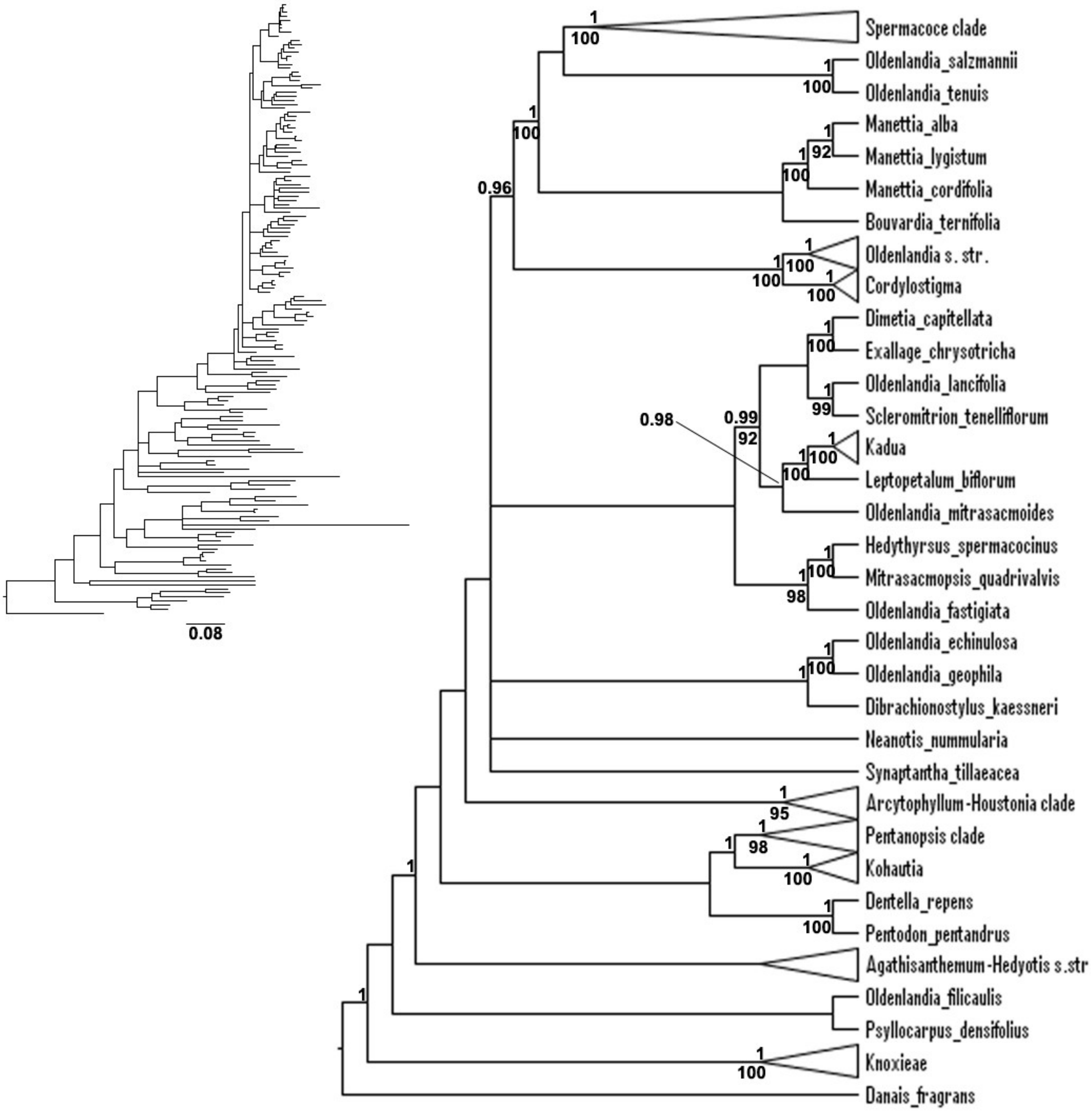
Fig. 1. Fifty-percent Bayesian majority-rule consensus tree of the Spermacoceae based on the nrDNA dataset. Posterior probabilities (PP) are indicated above branches and maximum likelihood bootstrap (BS) below. Only PP ≥ 0.95 and BS ≥ 90 are shown.

Fig. 2. Fifty-percent Bayesian majority-rule consensus tree of the Spermacoceae based on the plDNA dataset. Posterior probabilities are indicated above branches and maximum likelihood bootstrap below. Only PP ≥ 0.95 and BS ≥ 90 are shown.

Fig. 3. Detail of the Spermacoce clade and related genera in the fifty-percent Bayesian majority-rule consensus tree of the Spermacoceae based on the nrDNA dataset. Posterior probabilities are indicated above branches and maximum likelihood bootstrap below. Only PP ≥ 0.95 and BS ≥ 90 are shown.

Fig. 4. *Psyllocarpus densifolius* Zappi & Calió. **A–B**, Habit; **C**, Individual showing its subterranean system; **D**, Preanthetic bud; **E**, Short-styled flower; **F**, Long-styled flower. (photos by João A.M. Carmo).

Fig. 5. Species of *Psyllocarpus*, as circumscribed in the present study. **A**, *P. asparagoides* Mart. & Zucc.; **B**, *P. bahiensis* J.A.M.Carmo, Sobrado & R.M.Salas; **C**, *P. ericoides* Mart. & Zucc.; **D**, *P. goiasensis* J.H.Kirkbr.; **E**, *P. laricoides* Mart. & Zucc. (from the Serra do Cipó); **F**, *P. laricoides* Mart. & Zucc. (from the Pico do Itambé); **G**, *P. phyllocephalus* K.Schum.; **H**, *P. scatignae* J.A.M.Carmo, Sobrado & R.M.Salas; **I**, *P. schwackei* K.Schum. (photo by Christian Silva). (photos A–H by João A.M. Carmo).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1
100
Spermacoce clade
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100
Oldenlandia_salzmannii
Oldenlandia_tenuis
1
100
1
92
Manettia_alba
1
100
Manettia_lygistum
Manettia_cordifolia
0.96
Bouvardia_ternifolia
1
1
100
Oldenlandia s. str.
100
1
100
Cordylostigma
1
100
Dimetia_capitellata
Exallage_chrysotricha
1
99
Oldenlandia_lancifolia
Scleromitrion_tenelliflorum
0.98
0.99
92
1
1
100
Kadua
100
Leptopetalum_biflorum
Oldenlandia_mitrasacmoides
1
1
100
Hedythyrsus_spermacocinus
98
Mitrasacmopsis_quadrivalvis
Oldenlandia_fastigiata
1
1
100
Oldenlandia_echinulosa
Oldenlandia_geophila
Dibrachionostylus_kaessneri
Neanotis_nummularia
Synaptantha_tillaeacea
1
95
Arcytophyllum-Houstonia clade
1
1
98
Pentanopsis clade
1
100
Kohautia
1
100
Dentella_repens
Pentodon_pentandrus
1
Agathisanthemum-Hedyotis s.str
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Oldenlandia_filicaulis
Psyllocarpus_densifolius
1
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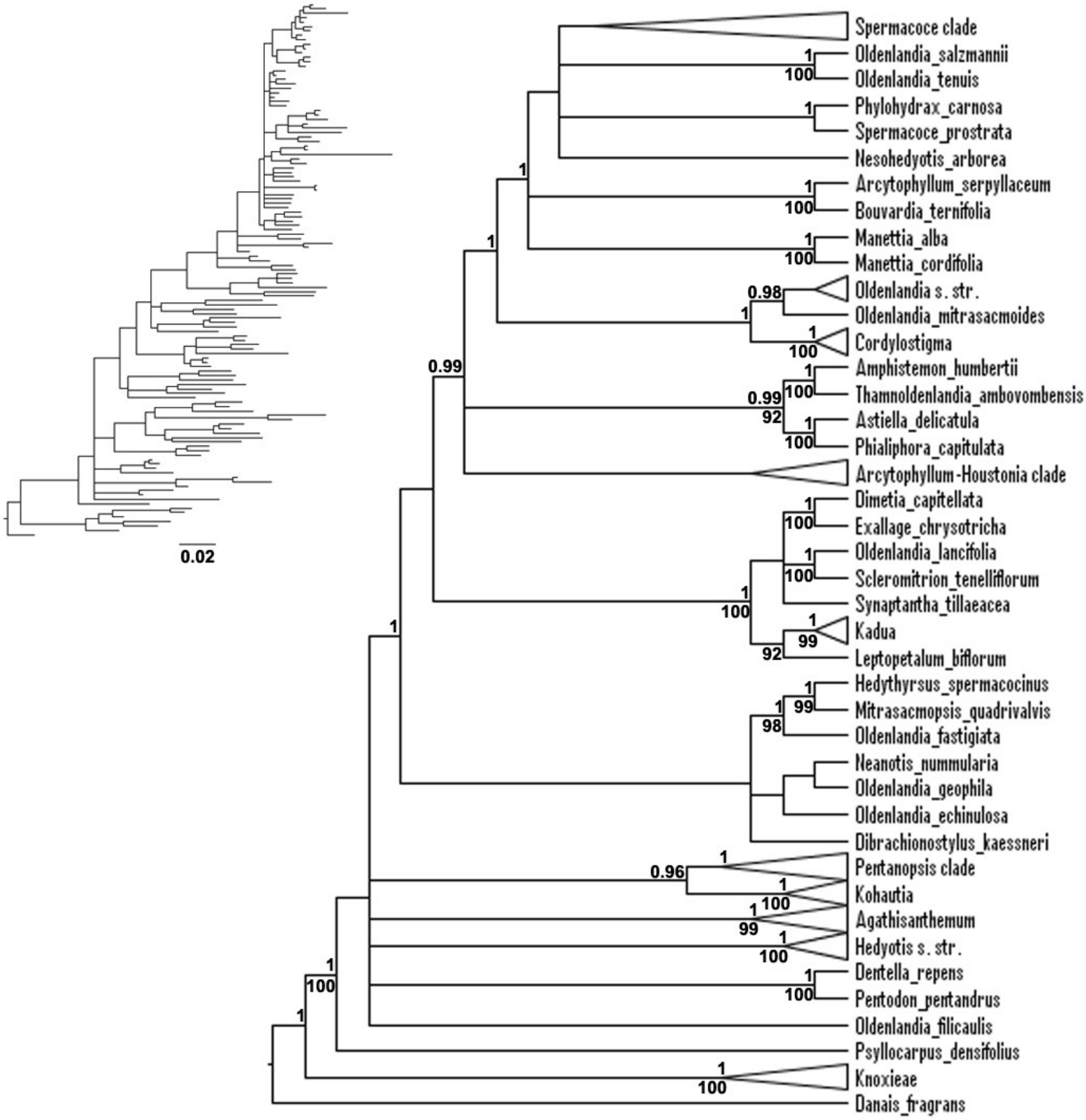
Knoxieae
Danais_fragrans

nrDNA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Oldenlandia_tenuis
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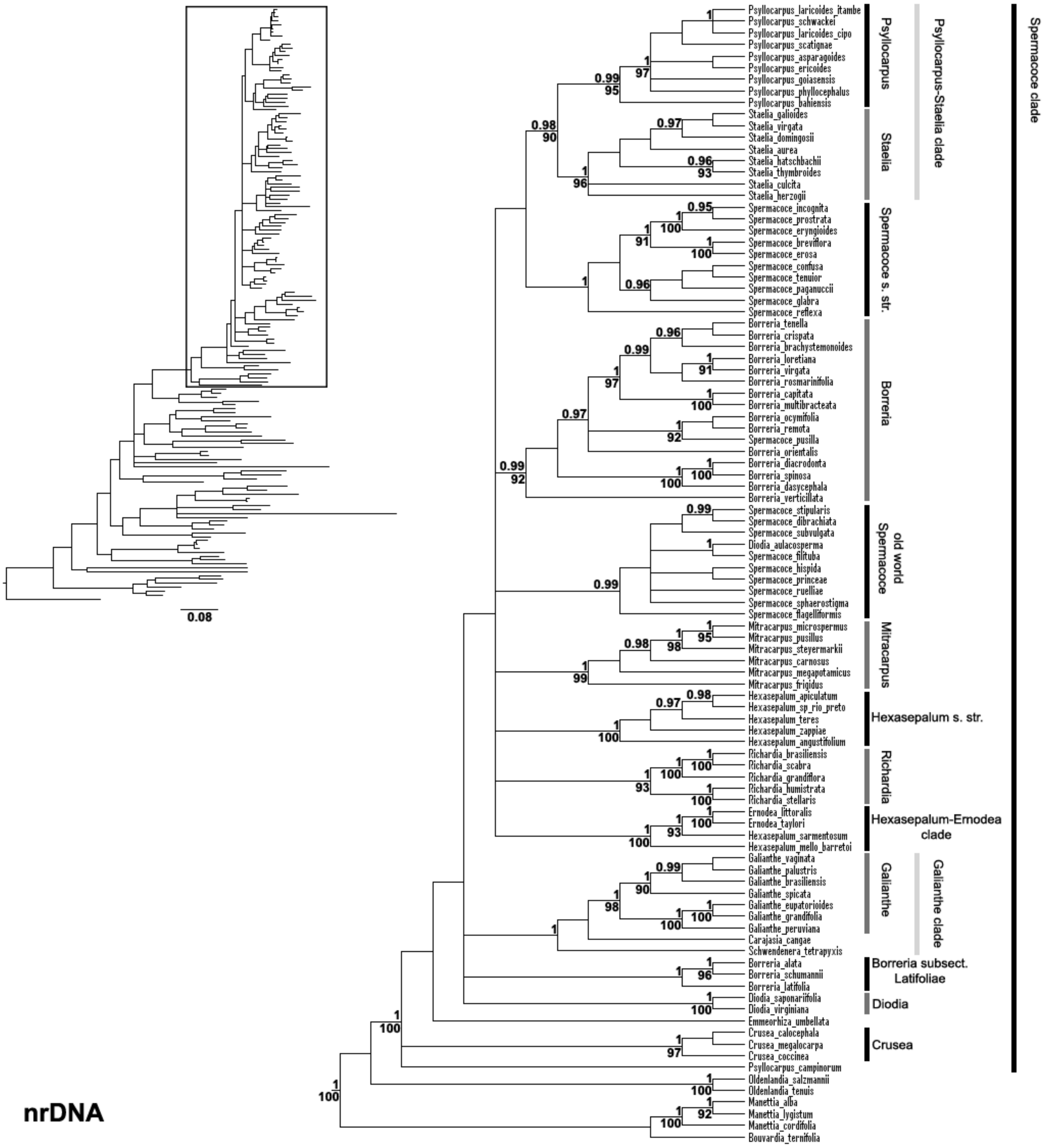
Spermacoce_prostrata
Nesohedyotis_arborea
1
1
100
Arcytophyllum_serpyllaceum
Bouvardia_ternifolia
1
1
100
Manettia_alba
Manettia_cordifolia
0.98
1
Oldenlandia s. str.
Oldenlandia_mitrasacmoides
1
100
Cordylostigma
0.99
1
100
Amphistemon_humbertii
Thamnoldenlandia_ambovombensis
0.99
92
1
100
Astiella_delicatula
Phialiphora_capitulata
Arcytophyllum-Houstonia clade
1
100
Dimetia_capitellata
Exallage_chrysotricha
1
100
Oldenlandia_lancifolia
Scleromitrion_tenelliflorum
1
100
Synaptantha_tillaeacea
1
99
Kadua
92
Leptopetalum_biflorum
1
1
99
98
Hedythyrsus_spermacocinus
Mitrasacmopsis_quadrivalvis
Oldenlandia_fastigiata
Neanotis_nummularia
Oldenlandia_geophila
Oldenlandia_echinulosa
Dibrachionostylus_kaessneri
0.96
1
Pentanopsis clade
1
100
Kohautia
1
99
Agathisanthemum
1
100
Hedyotis s. str.
1
100
1
100
Dentella_repens
Pentodon_pentandrus
Oldenlandia_filicaulis
Psyllocarpus_densifolius
1
100
Knoxieae
Danais_fragrans

plDNA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Psyllocarpus_laricoides_cipo
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Psyllocarpus_asparagoides
Psyllocarpus_ericoides
Psyllocarpus_goiasensis
Psyllocarpus_phyllocephalus
Psyllocarpus_bahiensis
Staelia_galioides
Staelia_virgata
Staelia_domingosii
Staelia_aurea
Staelia_hatschbachii
Staelia_thymbroides
Staelia_culcita
Staelia_herzogii
Spermacoce_incognita
Spermacoce_prostrata
Spermacoce_eryngioides
Spermacoce_breviflora
Spermacoce_erosa
Spermacoce_confusa
Spermacoce_tenuior
Spermacoce_paganuccii
Spermacoce_glabra
Spermacoce_reflexa
Borreria_tenella
Borreria_crispata
Borreria_brachystemonoides
Borreria_loretiana
Borreria_virgata
Borreria_rosmarinifolia
Borreria_capitata
Borreria_multibracteata
Borreria_ocymifolia
Borreria_remota
Spermacoce_pusilla
Borreria_orientalis
Borreria_diacrodonta
Borreria_spinosa
Borreria_dasycephala
Borreria_verticillata
Spermacoce_stipularis
Spermacoce_dibrachiata
Spermacoce_subvulgata
Diodia_aulacosperma
Spermacoce_filituba
Spermacoce_hispida
Spermacoce_princeae
Spermacoce_ruelliae
Spermacoce_sphaerostigma
Spermacoce_flagelliformis
Mitracarpus_microspermus
Mitracarpus_pusillus
Mitracarpus_steyermarkii
Mitracarpus_carnosus
Mitracarpus_megapotamicus
Mitracarpus_frigidus
Hexasepalum_apiculatum
Hexasepalum_sp_rio_preto
Hexasepalum_teres
Hexasepalum_zappiae
Hexasepalum_angustifolium
Richardia_brasiliensis
Richardia_scabra
Richardia_grandiflora
Richardia_humistrata
Richardia_stellaris
Ernodea_littoralis
Ernodea_taylori
Hexasepalum_sarmentosum
Hexasepalum_mello_barretoi
Galianthe_vaginata
Galianthe_palustris
Galianthe_brasiliensis
Galianthe_spicata
Galianthe_eupatorioides
Galianthe_grandifolia
Galianthe_peruviana
Carajasia_cangae
Schwendenera_tetrapyxis
Borreria_alata
Borreria_schumannii
Borreria_latifolia
Diodia_saponariifolia
Diodia_virginiana
Emmeorhiza_umbellata
Crusea_calocephala
Crusea_megalocarpa
Crusea_coccinea
Psyllocarpus_campinorum
Oldenlandia_salzmannii
Oldenlandia_tenuis
Manettia_alba
Manettia_lygistum
Manettia_cordifolia
Bouvardia_ternifolia
Psyllocarpus
Staelia
Spermacoce s. str.
Borreria
old world Spermacoce
Mitracarpus
Hexasepalum s. str.
Richardia
Hexasepalum-Ernodea clade
Galianthe
Borreria subsect. Latifoliae
Diodia
Crusea
Psyllocarpus-Staelia clade
Galianthe clade
Spermacoce clade
1
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97
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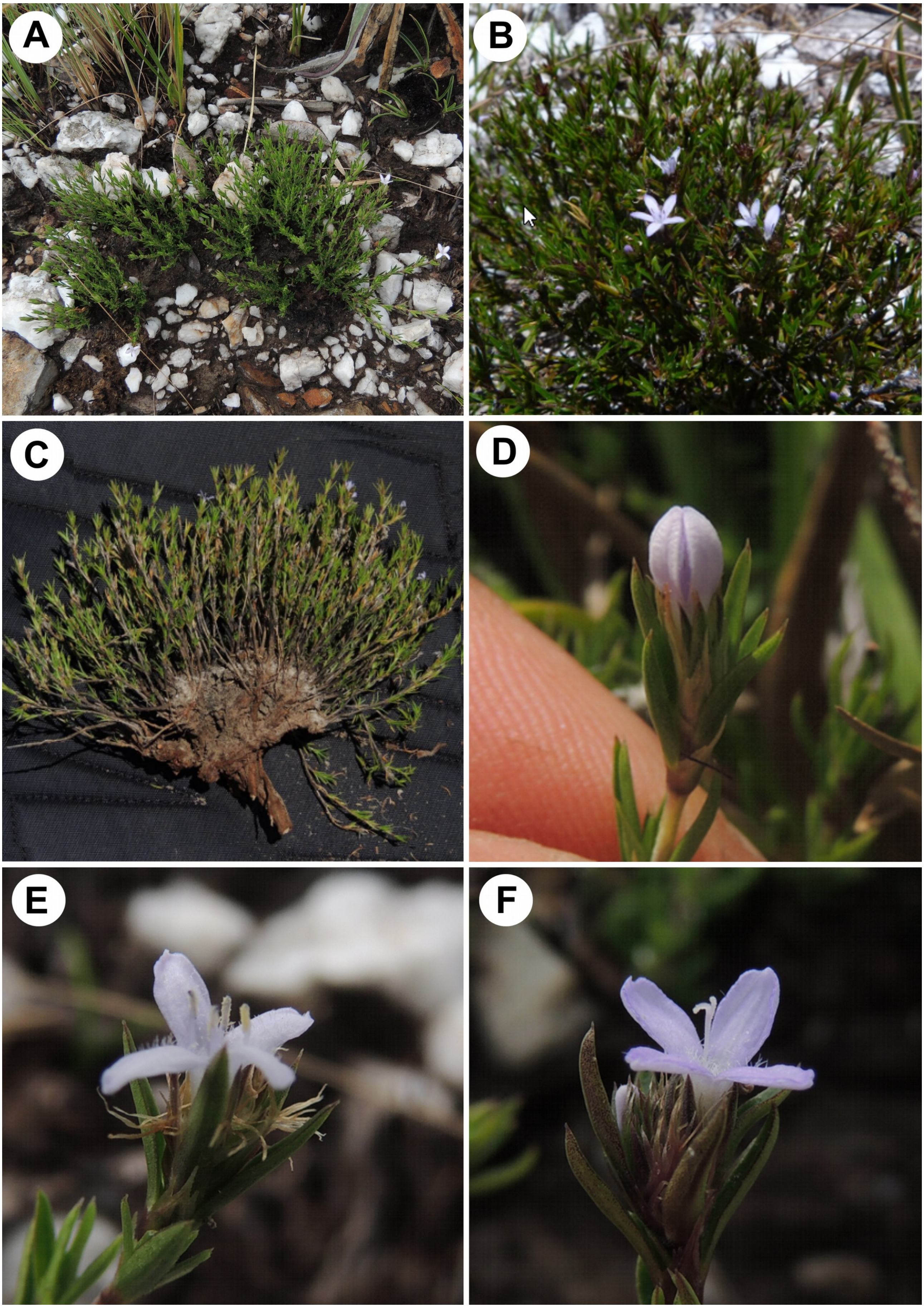
A
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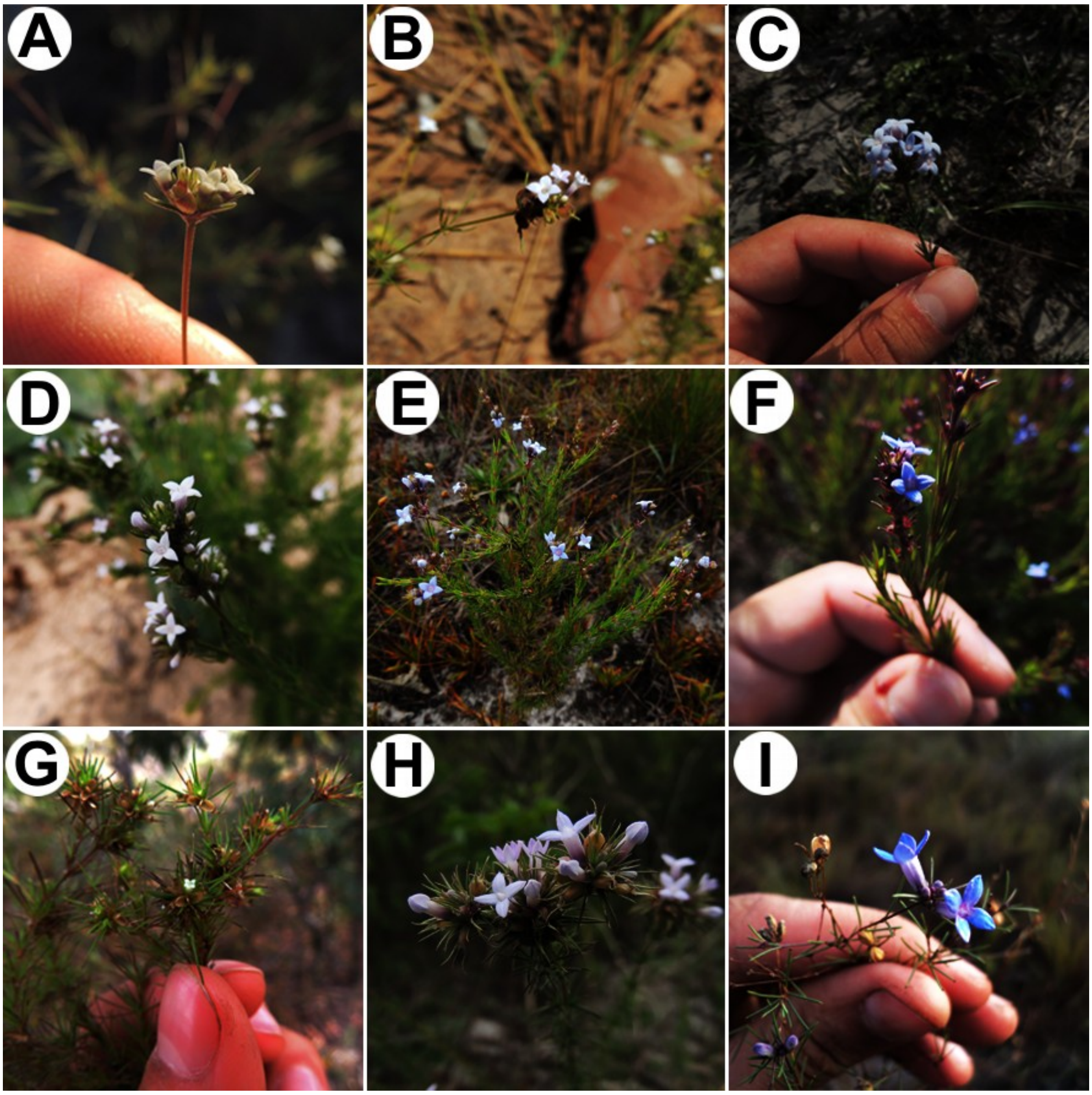
F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I

Appendix 1. GenBank accession numbers for the samples used in present study. Taxon name, accession number for ETS, ITS, *rps16*, and *trnL-F* (“–” missing data; “*” new sequences).

Name	ETS	ITS	*rps16*	*trnL-F*
Agathisanthemum bojeri	–	AM939424	EU543018	EU543077
Agathisanthemum globosum	–	AM939425	EU543019	EU543078
Amphiasma benguellense	AM932918	AM939426	AF002753	EU543079
Amphistemon humbertii	–	–	GU475977	GU475981
Arcytophyllum serpyllaceum	–	–	AF333364	–
Arcytophyllum thymifolium	AM932921	AM939431	AF333366	EU543082
Astiella delicatula	–	–	GU475979	GU475983
Batopedina pulvinellata	–	AM266989	EU543021	EU543083
Borreria alata	KF737036	KF736995	–	–
Borreria brachystemonoides	MF166810	MF166821	–	–
Borreria capitata	KF737032	MF166822	EU543069	EU543158
Borreria crispata	–	*	–	*
Borreria dasycephala	MF166807	MF166818	–	–
Borreria diacrodonta	MF166805	MF166816	–	–
Borreria latifolia	–	KF736994	–	–
Borreria loretiana	MF166809	MF166820	–	–
Borreria multibracteata	–	KF736990	–	–
Borreria ocymifolia	AM932951	AM939463	–	EU543108
Borreria orientalis	MF166812	MF166823	–	–
Borreria remota	AM933013	AM939542	–	EU543164
Borreria rosmarinifolia	–	*	–	–
Borreria schumannii	KF737038	KF736997	–	–
Borreria spinosa	MF166806	MF166817	–	–
Borreria tenella	KF737030	KF736988	–	–
Borreria verticillata	KF737039	KF736998	–	–
Borreria virgata	KF737031	KF736989	–	–
Bouvardia ternifolia	AM932922	AM939432	EU543022	EU543084
Carajasia cangae	KF737057	KF737015	–	–
Carphalea madagascariensis	KT792985	AM266995	EU543023	–
Conostomium quadrangulare	AM932926	AM939436	EU543024	EU543086
Cordylostigma microcala	AM932962	AM939480	EU543039	EU543121
Cordylostigma virgatum	AM932965	AM939483	HE798557	EU543124
Crusea calocephala	KF737051	KF737009	–	EU543088
Crusea coccinea	KF737052	KF737010	–	–
Crusea megalocarpa	AM932929	AM939439	EU543025	EU543089
Danais fragrans	–	JQ729807	JQ729693	–
Dentella repens	AM932930	AM939440	AF333370	EU543091
Dibrachionostylus kaessneri	AM932931	AM939441	AF002761	–
Dimetia capitellata	KR005765	AM939452	HE649796	JX111327
Diodia aulacosperma	AM932934	AM939444	EU543026	EU543092
Diodia saponariifolia	KF737049	KF737007	–	–
Diodia virginiana	KF737050	KF737008	AY764288	–
Edrastima goreensis	AM932985	AM939511	EU543055	EU543141
Emmeorhiza umbellata	KF737042	KF737000	AY764289	EU543094
Ernodea littoralis	KF737043	KF737001	AF002763	EU543095
Ernodea taylori	KF737044	KF737002	–	–
Exallage chrysotricha	KR005774	KP994259	KR005804	JX111377
Galianthe brasiliensis	KF737053	KF737011	AY764290	EU543096
Galianthe eupatorioides	KF737054	KF737012	EU543028	EU543097
Galianthe grandifolia	KF737055	KF737013	–	–

Appendix 1. continued.

Galianthe palustris	MF166828	MF166825	–	–
Galianthe peruviana	KF737056	KF737014	–	–
Galianthe spicata	AM933008	AM939535	EU543027	EU543093
Galianthe vaginata	*	*	*	*
Gomphocalyx herniarioides	–	–	AY764291	EU567466
Hedyotis lessertiana	AM932944	AM939466	EU543029	EU543100
Hedyotis macrostegia	–	AM942768	AF002767	EU543102
Hedyotis swertioides	HE681506	AM939460	EU543031	EU543105
Hedythyrsus spermacocinus	AM932950	AM939461	EU543032	EU543107
Hexasepalum angustifolium	KF737046	KF737004	–	–
Hexasepalum apiculatum	KF737045	KF737003	–	–
Hexasepalum mello-barretoi	*	*	*	–
Hexasepalum sarmentosum	KF737047	KF737005	AF002762	–
Hexasepalum sp. nov. (Rio Preto)	–	*	–	–
Hexasepalum teres	KF737048	KF737006	–	–
Hexasepalum zappiae	*	–	–	*
Houstonia caerulea	–	AM939464	AF333379	EU543109
Kadua littoralis	AM932954	AM939472	EU543034	EU543115
Kadua parvula	AM932955	AM939473	AF333375	EU543116
Kohautia caespitosa	AM932957	AM939474	EU543036	EU543118
Kohautia coccinea	AM932959	AM939476	EU543037	EU543119
Kohautia subverticillata	AM932964	AM939482	EU543041	EU543123
Lathraeocarpa acicularis	–	–	EU642521	EU642532
Lelya osteocarpa	–	AM939485	–	EU543125
Leptopetalum biflorum	AM932973	AM939494	EU567459	EU543132
Manettia alba	AM932966	AM939486	AF002768	–
Manettia cordifolia	KM215333	KM215368	KM215473	–
Manettia lygistum	AM932967	AM939487	–	EU543126
Manostachya ternifolia	AM932968	FJ695446	AM117328	EU543127
Mitracarpus carnosus	KF737040	KF736999	–	–
Mitracarpus frigidus	KM215319	AM939488	AF002770	EU543128
Mitracarpus megapotamicus	KF737041	KM215361	*	*
Mitracarpus microspermus	AM932969	AM939489	EU543044	–
Mitracarpus pusillus	KM215306	KM215345	KM215477	–
Mitracarpus steyermarkii	KM215311	KM215349	KM215479	–
Mitrasacmopsis quadrivalvis	AM932970	AM939490	EU543045	EU543129
Neanotis nummularia	HE681523	HE657728	HE649864	–
Nesohedyotis arborea	–	–	AF003607	–
Oldenlandia affinis	AM932971	AM939492	EU543046	EU543130
Oldenlandia capensis	AM932974	AM939496	EU543048	EU543133
Oldenlandia corymbosa	AM932979	AM939502	EU543050	EU543135
Oldenlandia echinulosa	AM932981	AM939504	EU543051	EU543136
Oldenlandia fastigiata	AM932983	AM939506	EU543052	EU543138
Oldenlandia filicaulis	KM215332	KM215377	KM215472	–
Oldenlandia geophila	–	AM939508	EU543054	EU543140
Oldenlandia herbacea	AM932989	AM939552	EU543057	EU543143
Oldenlandia lancifolia	AM932990	AM939512	EU543058	EU543144
Oldenlandia microtheca	AM932991	AM939513	EU543059	EU543145
Oldenlandia mitrasacmoides	AM932992	AM939515	AF333372	EU543146
Oldenlandia rosulata	–	AM939519	EU543043	EU567467

Appendix 1. continued.

Oldenlandia salzmannii	AM932996	AM939520	AY764294	EU543148
Oldenlandia tenuis	–	AM939523	AY764293	–
Oldenlandia wiedemannii	AM933001	AM939525	EU543063	EU543151
Paraknoxia parviflora	–	AM267020	EU543064	EU543152
Pentanisia prunelloides	KT792995	AM267033	AM266860	–
Pentanopsis fragrans	AM933002	AM939526	EU543065	EU543153
Pentas pubiflora	KT792996	AM267056	AM266885	–
Pentodon pentandrus	AM933003	AM939528	EU543066	–
Phialiphora capitulata	–	–	KT252878	KT252881
Phylohydrax carnosa	–	AM939529	EU543067	EU642534
Phylohydrax madagascariensis	–	AM939530	AY764292	EU543155
Psyllocarpus asparagoides	*	*	*	*
Psyllocarpus bahiensis	–	*	*	*
Psyllocarpus campinorum	*	–	–	–
Psyllocarpus densifolius	–	*	*	*
Psyllocarpus ericoides	*	*	*	*
Psyllocarpus goiasensis	*	*	*	*
Psyllocarpus laricoides (Cipó)	–	*	*	*
Psyllocarpus laricoides (Itambé)	*	*	*	*
Psyllocarpus phyllocephalus	*	*	*	*
Psyllocarpus scatignae	*	*	*	*
Psyllocarpus schwackei	*	*	*	*
Richardia brasiliensis	AM933007	AM939533	KM215474	–
Richardia grandiflora	KF737066	KF737027	KM215475	–
Richardia humistrata	KF737067	KF737028	–	–
Richardia scabra	AM933006	AM939532	AF003614	EU543156
Richardia stellaris	–	AM939534	EU543068	EU543157
Schwendenera tetrapyxis	KF737059	KF737017	–	–
Scleromitrion tenelliflorum	AM932949	AM939451	EU543062	EU543106
Spermacoce breviflora	KF737062	KF737019	–	–
Spermacoce confusa	KF737063	KF737020	AF003619	–
Spermacoce dibrachiata	–	KF737021	–	–
Spermacoce erosa	AM933009	AM939537	EU543070	EU543159
Spermacoce eryngioides	KF737033	KF736992	–	–
Spermacoce filifolia	–	–	KT252879	KT252882
Spermacoce filituba	AM933011	AM939539	EU543071	EU543160
Spermacoce flagelliformis	AM933010	AM939538	EU543072	EU543161
Spermacoce glabra	KF737064	KF737022	–	–
Spermacoce hispida	AM933017	AM939540	EU543073	EU543162
Spermacoce incognita	KF737034	KF736993	–	–
Spermacoce marginata	–	–	KT252880	KT252883
Spermacoce paganuccii	KM215324	–	–	–
Spermacoce princeae	HM042507	HM042452	HM042566	–
Spermacoce prostrata	KF737037	KF736996	–	EU543163
Spermacoce pusilla	–	MH768318	–	–
Spermacoce reflexa	*	*	*	*
Spermacoce ruelliae	AM933014	AM939543	EU543074	EU543165
Spermacoce sphaerostigma	MF166801	MF166813	–	–
Spermacoce stipularis	MF166802	MF166814	–	–
Spermacoce subvulgata	MF166803	MF166815	–	–

Appendix 1. continued.

Spermacoce tenuior	KF737065	KF737023	–	–
Staelia aurea	KM215338	KM215373	KM215478	–
Staelia culcita	*	–	*	*
Staelia domingosii	–	*	*	*
Staelia galioides	KM215340	KM215375	KM215481	–
Staelia hatschbachii	*	*	*	*
Staelia herzogii	–	KF737024	–	–
Staelia thymbroides	*	*	*	*
Staelia virgata	–	KF737026	–	–
Stenaria nigricans	–	AM939546	AF333373	EU543166
Synaptantha tillaeacea	–	AM939547	EU543075	EU543167
Thamnoldenlandia ambovombensis	–	–	GU475980	GU475984
Triainolepis tomentella	KT793002	AM267069	AM266900	–

Capítulo 2:
Novidades taxonômicas e nomenclaturais em *Psyllocarpus*

I: Carmo, J. A. M., Salas, R. M., Sobrado, S. V., & Simões, A. O. 2019. (2707) Proposal to conserve the name *Psyllocarpus* against *Tapanhuacanga* (Rubiaceae: Spermacoceae). Taxon, 68: 869–871. https://doi.org/10.1002/tax.12109

II: Carmo, J. A. M., Sobrado, S. V., Salas, R. M., & Simões, A. O. 2018. Two New Threatened Species of *Psyllocarpus* (Rubiaceae; Spermacoceae) from Eastern Brazil. Syst. Bot., 43: 579–590. https://doi.org/10.1600/036364418x697300

III: Carmo, J. A. M., Sobrado, S. V., Salas, R. M., & Simões, A. O. 2018. Revisiting *Psyllocarpus goiasensis* (Rubiaceae: Spermacoceae): a new synonym, notes on type specimens, and conservation status assessment of this endemic species from the campo rupestre of Goiás state, central Brazil. Kew Bull., 73: 1–6. https://doi.org/10.1007/s12225-018-9779-9

IV: Carmo, J. A. M., Scalon, V. R., Calió, M. F., & Simões, A. O. 2017. Lectotypification of *Psyllocarpus schwackei* (Spermacoceae, Rubiaceae). Phytotaxa, 329: 185–186. https://doi.org/10.11646/phytotaxa.329.2.10

Introdução

Este capítulo corresponde a novidades taxonômicas em *Psyllocarpus*. Em I, a conservação do nome *Psyllocarpus* contra o nome prioritário *Tapanhuacanga* é proposta, para que se mantenha a estabilidade nomenclatural do táxon e mudanças desvantajosas sejam evitadas. Em II, duas novas espécies no gênero, *P. bahiensis* e *P. scatignae*, do campo rupestre dos estados da Bahia e Minas Gerais, respectivamente, são descritas. Em III, *Psyllocarpus laricoides* var. γ *longicornu*, anteriormente sob a sinonímia de *P. laricoides*, é tratado como um novo sinônimo de *P. goiasensis*. Em IV, o nome *Psyllocarpus schwackei*, cujo tipo em B foi destruído durante a Segunda Guerra Mundial, é lectotipificado.

I

Carmo, J. A. M., Salas, R. M., Sobrado, S. V., & Simões, A. O. 2019. (2707) Proposal to conserve the name *Psyllocarpus* against *Tapanhuacanga* (Rubiaceae: Spermacoceae). Taxon, 68: 869–871. https://doi.org/10.1002/tax.12109

(2707) Proposal to conserve the name *Psyllocarpus* against *Tapanhuacanga* (*Rubiaceae*: *Spermacoceae*)

João A.M. Carmo,[1] Roberto M. Salas,[2] Sandra V. Sobrado[2] & André O. Simões[3]

1 *Programa de Pós-Graduação em Biologia Vegetal, Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas – UNICAMP, CEP 13083-970, Campinas, SP, Brazil*

2 *Instituto de Botánica del Nordeste, UNNE – CONICET, Sargento Juan Bautista Cabral 2131, c.c. 209, C.P. 3400, Facultad de Ciencias Exactas y Naturales y Agrimensuras, FaCENA – UNNE, Av. Libertad 5460, C.P. 3400, Corrientes, Argentina*

3 *Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas – UNICAMP, CEP 13083-970, Campinas, SP, Brazil*

Address for correspondence: *João A.M. Carmo, jmartinsdocarmo@gmail.com*

DOI

(2707) ***Psyllocarpus*** Mart. & Zucc. in Flora 7(1, Beil.): 130. Mai–Jun 1824 [*Rub.*], nom. cons. prop.
Typus: *P. laricoides* Mart. & Zucc.
(=) *Tapanhuacanga* Vand., Fl. Lusit. Bras. Spec.: 9. 1788, nom. rej. prop.
Typus (vide Smithsonian ING Staff in Index Nom. Gen.: No. 32953. 1971): *T. brasiliensis* Steud. (Nomencl. Bot., ed. 2, 2: 663. Aug 1841).

Joaquim Vellozo de Miranda sent from Brazil to Portugal original materials, which were copied as watercolor drawings and gathered as a bound folio, accounting for 133 plates containing sketches of the species he studied. These drawings were used by Domenico Vandelli as the basis for his descriptions of new Brazilian taxa. In conjunction with one of the engravings published in the *Florae Lusitanicae et Brasiliensis specimen*, showing mirror images of original drawings by Vellozo de Miranda, Vandelli (Fl. Lusit. Bras. Spec.: 9, t. 1, fig. 5. 1788; figure reprinted by Moraes in Feddes Repert. 130: 21, fig. 1A. 2019) proposed *Tapanhuacanga*, but named no species nor gave any indication that there was more than one in the genus. This name has been scarcely cited in the literature (Poiret in Lamarck, Encycl. Suppl. 5: 283. 1817; Jussieu in Mém. Mus. Hist. Nat. 6: 372.

1820; Steudel, l.c.; Pfeiffer, Nomencl. Bot. 2: 1351. 1874; Post, Lex. Gen. Phan.: 549. 1903; Stellfeld, Tribuna Farm.: 45. 1967; Farr & Zijlstra, Index Nom. Gen. 1996+ [http://botany.si.edu/ing/, accessed: 20 Apr 2019]; Govaerts, World Checkl. Sel. Pl. Fam. 2019 [https://wcsp.science.kew.org/home.do, accessed: 31 Jan 2019]), usually with doubts on its identity by authors. The only binomial in which it was used was proposed without a description or diagnosis, but since *Tapanhuacanga brasiliensis* Steud. (l.c.) was unique in the genus and established in reference to Vandelli (l.c.), it was then validly published (Art. 38.12 of the *ICN*, Turland & al. in Regnum Veg. 159. 2018). This binomial has been cited only by Farr & Zijlstra (l.c.) and Govaerts (l.c.), with doubts, more than a century and a half later.

Moraes (l.c.: 49), based on the analysis of an original drawing by Vellozo de Miranda (Brazil, Minas Gerais, [icon] [Tab. I] in an autographed letter sent by Vandelli to Joseph Banks [Library of the Natural History Museum, London: location, Botany MSS VAN; barcode 364295]) and its copy ([icon] by Manoel Piolti from original material [drawing and/or specimen] by Vellozo de Miranda [MUHNAC–UL, Biblioteca de Botânica, No. 145]), revisited Vandelli (l.c.) and concluded that *T. brasiliensis*, for which he designated the engraving in the same work as lectotype (Vandelli, l.c., [icon] t. 1, fig. 5), is *Psyllocarpus laricoides* Mart. & Zucc. (l.c.), but no objective argumentation was provided to support that conclusion. Therefore, since *Tapanhuacanga* has priority over *Psyllocarpus*, he made 12 new combinations and designated *T. laricoides* (Mart. & Zucc.) P.L.R. Moraes (l.c.), based on *P. laricoides*, as genus type. This designation would have made the two genera homotypic, since *P. laricoides* had already been selected as type of *Psyllocarpus* by Kirkbride (in Smithsonian Contr. Bot. 41: 15. 1979, under *P.* sect. *Psyllocarpus*). However, typification of *Tapanhuacanga* on *T. brasiliensis* was already established by Smithsonian ING Staff (on Index Nom. Gen. Card No. 32953, published Mar 1971).

Whether or not, as Moraes (l.c.) has stated, the fig. 5 of Vandelli, the type of *Tapanhuacanga brasiliensis*, is conspecific with *Psyllocarpus laricoides*, remains an open question. Nevertheless, *Tapanhuacanga* and *Psyllocarpus* are heterotypic synonyms. The copy by Manoel Piolti (reprinted in Moraes, l.c.: 50, fig. 10A) of the original drawing by Vellozo de Miranda depicts a subshrub with acicular leaves and flowers with lilac to blue corollas, arranged in 1-flowered cymes, allowing for the identification of the genus to which it belongs. As the engraving in Vandelli (l.c.) is a mirror image of part of Vellozo's drawing, it corresponds to some *Psyllocarpus* species, although only flower, fruit and seeds are depicted. However, we here question the synonymy between *T. brasiliensis* and *P. laricoides*.

Psyllocarpus laricoides had its circumscription amended over time. It is an endemic species from Minas Gerais and Bahia, based on original material collected by Martius, for which a lectotype was designated by Kirkbride (l.c.: 16): Brazil, Minas Gerais, in sumo Brasiliae monte Itambé, *Martius s.n.* (lectotype: M barcode M-0189221 left-hand specimen [annotated as holotype by Joseph H. Kirkbride, Jr., 1976]!; presumed isolectotypes: M barcodes M-0189221 center specimen!, M-0189217! & M0189220!). The species as currently circumscribed includes *P. ericoides* Mart. & Zucc. (l.c.) and *P. laricoides* var. β *densifolia* Mart. (Nov. Gen. Sp. Pl. 1: 45. 1824) as synonyms. It also formerly included *P. laricoides* var. *longicornu* K. Schum. (in Martius, F1. Bras. 6(6): 33. 1888) in its synonymy (Kirkbride, l.c.: 16), however Carmo & al. (in Kew Bull. 73(52): 1–6. 2018) noted that the type specimens of this variety resembled *P. goiasensis* J.H. Kirkbr. (l.c.: 17) in their morphology and that this original material was collected in Goiás, not Minas Gerais as stated by Kirkbride (l.c.), so they transferred *P. laricoides* var. *longicornu* to the synonymy of *P. goiasensis*.

The result is that *Psyllocarpus laricoides* can be characterized by its sympodial branching pattern, glabrous hypanthium, presence of a calyx tube, and triangular to linear calyx lobes 1–2 mm long. We could not observe these characters in any of the *T. brasiliensis* drawings, which depict a plant that seems to present a monopodial branching pattern. The absence of an actual specimen associated with *T. brasiliensis* and the lack of such critical details, which are beyond what is observable on these drawings, or even the presence of characteristics possibly divergent from those in relevant type specimens prevent an unequivocal assignment of *P. laricoides* to *T. brasiliensis*, even considering the former taxon in its broader sense. Even the recently described *P. bahiensis* J.A.M. Carmo & al. (in Syst. Bot. 43: 582. 2018), which presents a unique set of characters in the genus, also has been identified as *P. laricoides*, which is most likely to represent a species complex (Carmo & al., in prep.). Additionally, the origin of the material on which *T. brasiliensis* drawings were based is uncertain, although it was probably collected in the macro-region of the Serra do Espinhaço, for which several areas of endemism have been identified. According to Moraes (l.c.) it could have been collected in several localities around Ouro Preto, in a region known as the “Iron Quadrangle”, or Conceição do Mato Dentro, in the eastern slopes of Serra do Cipó, whereas Martius made his collections of *P. laricoides* specimens in the region of the Diamantina Plateau, around Santo Antônio do Itambé and Diamantina, all of which fall in different major areas of endemism in the Serra do Espinhaço (Echternacht & al. in Flora 206: 782. 2011). For these reasons we argue that the identity of *T. brasiliensis* (1841) is still unclear. Although congeneric with *P. laricoides*, it is not referable to any *Psyllocarpus* species whose name was published later than 1841, so *T. brasiliensis* does not threaten any of these names and proposing its rejection under Art. 56 is unnecessary.

Since its publication, *Psyllocarpus* has been consistently used in works, such as floras (e.g., Schumann in Martius, l.c. 1888: 30; Zappi & Stannard in Stannard, Fl. Pico das Almas: 572. 1995; Campos & al. in Bol. Bot. Univ. São Paulo 24: 61. 2006; Delprete in Rizzo, Fl. Est. Goiás Tocantins 40: 979. 2010; Delprete in Cavalcante & Dias, Fl. Distrito Federal 10: 203. 2012; Zappi & al. in Bol. Bot. Univ. São Paulo 32: 130. 2014; Borges & al. in Rodriguésia 68: 614. 2017), illustrated guides (e.g., Souza & Lorenzi, Bot. Sist., ed. 3: 570. 2012; Zappi & al., Pl. Setor Noroeste da Serra do Cipó, Minas Gerais: 167. 2014; Souza & al., Guia das Plantas do Cerrado: 462. 2018), palynological and micromorphological studies (e.g., Dessein & al. in Grana 41: 70. 2002, in Bot. Rev. (Lancaster) 71: 409. 2005; Silveira Júnior & al. in Acta Bot. Brasil. 26: 444. 2012; Salas & Cabral in Bol. Soc. Argent. Bot. 49: 52. 2014; Judkevich & al. in Int. J. Pl. Sci. 178: 382. 2017), phylogenetic/evolutionary studies (e.g., Dessein & al. in Taxon 54: 107. 2005; Kårehed & al. in Molec. Phylogen. Evol. 49: 845. 2008; Groeninckx & al. in Ann. Missouri Bot. Gard. 96: 113. 2009; Guo & al. in Molec. Phylogen. Evol. 67: 111. 2013; Neupane & al. in Taxon 64: 322. 2015, in Amer. J. Bot. 104: 420. 2017), printed checklists (e.g., Giulietti & al. in Bol. Bot. Univ. São Paulo 9: 93. 1987; Andersson, Prov. Checkl. Neotrop. Rubiaceae [Scripta Bot. Belg. 1]: 172. 1992; Zappi & al. in Bol. Bot. Univ. São Paulo 21: 387. 2003; Mourão & Stehmann in Rodriguésia 58: 780. 2007; Borges & al. in Rodriguésia 62: 147. 2011; Teixeira & Lemos Filho in Bol. Bot. Univ. São Paulo 31: 225. 2013), red list of threatened species (e.g., Zappi & al. in Martinelli & al., Livro Vermelho Fl. Brasil, Pl. Raras do Cerrado: 237. 2014), and metal accumulation studies (e.g., Jansen & al. in Ann. Bot. (Oxford) 85: 97. 2000; Schettini & al. in Flora 238: 176. 2018), or in online databases (e.g., Flora do Brasil 2020 [http://floradobrasil.jbrj.gov.br/]; Global Biodiversity Information Facility [http://gbif.org]; JSTOR Global Plants [https://plants.jstor.org/]; speciesLink [http://www.splink.org.br]; Tropicos [https://www.tropicos.org/]; World Checklist of Selected Plant Families [http://wcsp.science.kew.org]).

The application of the principle of priority is clearly disruptive in this case, as the long-established and widely used legitimate name *Psyllocarpus* would have to be abandoned in favor of *Tapanhuacanga*, a name that has been rarely cited and generally treated with uncertainty. Furthermore, the combinations of all *Psyllocarpus* names undertaken by Moraes (l.c.) were based purely on nomenclatural reasons, disregarding detailed and critical examination of herbaria material and ongoing research on the *Spermacoceae* tribe, as we've shown evidence at the VII International Rubiaceae and Gentianales Conference, held in Copenhagen, Denmark, in 2017 (Carmo & al. in VII International Rubiaceae and Gentianales Conference, Copenhagen, Denmark. 2017) that the genus as currently circumscribed is not monophyletic (Carmo & al., in prep.), therefore some of these new combinations will be relegated to synonymy.

In summary, to serve stability and avoid disadvantageous changes purely based on nomenclatural reasons (Art. 14.1 of the *ICN*) we here propose the conservation of *Psyllocarpus* against *Tapanhuacanga*.

Author information

JAMC, https://orcid.org/0000-0002-7660-9918; RMS, https://orcid.org/0000-0001-7799-9017; SVS, https://orcid.org/0000-0001-8463-0429; AOS, https://orcid.org/0000-0001-6555-8759

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II

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Two New Threatened Species of *Psyllocarpus* (Rubiaceae; Spermacoceae) from Eastern Brazil

João A. M. do Carmo,[1,4] Sandra V. Sobrado,[2] Roberto M. Salas,[2] and André O. Simões[3]

[1]Programa de Pós-Graduação em Biologia Vegetal, Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas – UNICAMP, CEP 13083-970, Campinas, São Paulo, Brazil.

[2]Instituto de Botánica del Nordeste, UNNE – CONICET, Sargento Juan Bautista Cabral 2131, cc. 209, C.P. 3400. Facultad de Ciencias Exactas y Naturales y Agrimensuras, FaCENA – UNNE, Av. Libertad 5460, C.P. 3400. Corrientes, Argentina.

[3]Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas – UNICAMP, CEP 13083-970, Campinas, São Paulo, Brazil.

[4]Author for Correspondence (jmartinsdocarmo@gmail.com)

Abstract—Two new species of *Psyllocarpus* sect. *Psyllocarpus* are here described and illustrated. ***Psyllocarpus bahiensis*** and ***Psyllocarpus scatignae***, from the campo rupestre s. l. of Bahia and Minas Gerais states, respectively. We provide comments on their distribution, habitat, conservation status, and taxonomy. In addition, we analysed floral, fruit, and seed micromorphology, as well as pollen grains of the new species. We also provide an updated identification key to the species of *P.* sect. *Psyllocarpus*.

Keywords—campo rupestre, conservation, sect. *Psyllocarpus*, *Spermacoce* clade, Spermacoceae, taxonomy.

The *Spermacoce* clade in the Spermacoceae (Rubiaceae) comprises 23 genera that were recognized as the tribe as traditionally delimited, excluding *Gomphocalyx* Baker and *Phylohydrax* Puff (Kårehed et al. 2008). Salas et al. (2015) showed that *Carajasia* R. M. Salas, E. L. Cabral & Dessein also belongs in the *Spermacoce* clade. Representatives of this clade are characterized by the presence of raphides and uniovulate ovary locules often (but not always) in combination with a herbaceous habit, fimbriate stipules, and 3–4 colporate pollen grains, with long and narrow ectocolpi, endoapertures laterally joined forming an endocingulum, psilate tectum, and spinules mainly located around ectoapertures (Pire 1996; Dessein 2003; Kårehed et al. 2008; Salas and Cabral 2014; Salas et al. 2015).

Within the *Spermacoce* clade, molecular data refute some traditional generic circumscriptions, e.g. *Borreria* G. Mey. and *Spermacoce* L., leading to divergent opinions among specialists (Delprete and Jardim 2012). Nevertheless, at least for the Americas, there are some morphologically well-defined genera which are preliminarily supported in phylogenetic studies, despite their low sampling (Kårehed et al. 2008; Groeninckx et al. 2009; Salas et al. 2015). One example of such genus is the Brazilian endemic *Psyllocarpus* Mart. & Zucc., which was found monophyletic with maximum to high support in an analysis which sampled two of its species for two nuclear regions, related to a clade composed of American and one Australian *Spermacoce* species (Salas et al. 2015).

Psyllocarpus was established by Martius and Zuccarini (1824a), who proposed four species. They diagnosed the genus based on its calyx with two distinct lobes, infundibuliform corolla with four lobes and trichomes on the throat, four included stamens, short style with capitate stigma, and bivalvate capsules with two locules bearing one peltate compressed seed each. Martius and Zuccarini (1824b) provided a more detailed description of the genus, which presents linear to subulate leaves, compressed capsules, and a membranous septum parallel to the valves. They further compared it to *Borreria*, distinguishing them by the complete septum, separate valves, and peltate seeds in *Psyllocarpus*. This concept was followed by Schumann (1888, 1898) for his taxonomic revision of the genus and description of two new species, respectively.

Kirkbride (1979) classified *Psyllocarpus* in two sections based on morphology and geographic distribution, expanding the original concept of the genus. *Psyllocarpus* sect. *Psyllocarpus*, which follows the concept of Martius and Zuccarini (1824a, b), is characterized by terete leaves, homostylous flowers, prolate-spheroidal pollen grains, psilate tectum with spinules along each side of the colpi exine, and weakly bilobate to rarely capitate stigma. This section occurs in the Cerrado and campo rupestre from the Espinhaço range and the Planalto Central of Brazil, in the states of Bahia, Goiás, and Minas Gerais, and the Distrito Federal, comprising five species (*P. asparagoides*

Mart. & Zucc., *P. goiasensis* J. H. Kirkbr., *P. laricoides* Mart. & Zucc., *P. phyllocephalus* K. Schum. and *P. schwackei* K. Schum.). *Psyllocarpus* sect. *Amazonica* J. H. Kirkbr. also presents capsules compressed parallel to the septum, but is characterized by planar leaves, heterostylous flowers, oblate-spheroidal pollen grains, perforated tectum, finely and evenly spinulose exine, and deeply bifid stigma. This section is restricted to white-sand Amazonian campinas in the states of Amazonas, Pará, and Rondônia, comprising three species [*P. campinorum* (Krause) J. H. Kirkbr., *P. cururuensis* J. H. Kirkbr. and *P. psyllocarpoides* (Sucre) J. H. Kirkbr.]. Later, two species from the Espinhaço range were described in *Psyllocarpus* [*P. intermedius* E. L. Cabral & Bacigalupo (Cabral & Bacigalupo 1997a), and *P. densifolius* Zappi & Calió (Zappi et al. 2014)], although they were not classified in any section.

Psyllocarpus is now under re-revision by the authors. The analysis of herbarium vouchers and field expeditions carried out in Minas Gerais and Bahia have revealed specimens that could not be ascribed to any described species in the genus. We propose here two new species of *Psyllocarpus* sect. *Psyllocarpus*, and provide their descriptions, illustrations, and photographs, as well as comments on their distribution, habitat, conservation status, and taxonomy. In addition, we analysed their floral, fruit, and seed micromorphology, as well as their pollen grains, which are also described and illustrated.

MATERIALS AND METHODS

This study is based on field collections and analysis of specimens deposited at the CEPEC, CTES, ESA, MBM, MO, RB, SPF, and UEC herbaria, whose acronyms are listed according to Thiers (2017). We followed Anonymous (1962), Clopton (2004), and Simpson (2010) for general morphological terminology, and Weberling et al. (1997) and Ruá (1999) for inflorescence. The distribution map was created using ArcGIS® software, intellectual property of Esri, used herein under license. Conservation status was assessed by range size (B criterion), following IUCN (2016) recommendations. The extent of occurrence (EOO) and area of occupancy (AOO) were estimated using GeoCAT (Bachman et al. 2011).

Pollen grains were acetolyzed according to Erdtman (1966) and mounted in glycerine jelly for analysis using a light microscope (LM). Conventional parameters (P, polar axis; E, equatorial axis), in at least 20 grains were measured under LM and the exine details were analysed using scanning electron microscopy (SEM). The terminology used to describe the pollen followed Punt et al. (2007). Fresh buds, mature flowers, fruits, and seeds fixed in alcohol 70% were also analysed using SEM. We utilized the terminology proposed by Stearn (1986) for seed descriptions. For the images, the dehydrated material and acetolyzed pollen grains were sputter-coated with gold and then photographed with a Jeol 5800 LV SEM (SGCyT - UNNE, Corrientes, Argentina).

TAXONOMIC TREATMENT

Psyllocarpus bahiensis Carmo, Sobrado & R. M. Salas, sp. nov. TYPE: BRAZIL, Bahia: Macaúbas, Estrada para Tinguis, 13°05’03” S 42°46’37” W, 904 m, 18 Apr 2015, *J. A. M. Carmo & A. V. Scatigna 376* (holotype: UEC!; isotypes: CTES!, MO!, RB!, SPF!).

Psyllocarpus bahiensis is similar to *P. laricoides*, but differs by the monopodial branching pattern (vs. sympodial in *P. laricoides*), determinate flowering branches (vs. indeterminate), inflorescences in terminal and axillary pauciflorous cymes (vs. axillary 1-flowered cymes), hirsute to sparsely hirsute hypanthium and capsules (vs. glabrous), calyx tube absent (vs. present), corolla lobes clavate in preanthetic bud (vs. rounded), capsules 3-ribbed on dorsal surface (vs. smooth) with deciduous valves forming a ventral rim of carpel tissue, keeping the seed inside after dehiscence (vs. persistent valves, from which the seeds are shed after dehiscence), and ventral surface of the seeds covered by diffuse strophiole (vs. delimited strophiole).

Subshrubs, 0.15–1 m tall, monopodial. Stems sparsely branched, erect, internodes 0.5–3.5 cm long, terete to slightly compressed or tetragonal, puberulent to glabrous, bark peeling from older internodes. Stipular sheaths 0.5–1 mm long, puberulent, 3–7-fimbriate on each side of the stem, fimbriae 0.3–1.5 mm long, narrowly triangular to subulate, strigulose to glabrous. Leaves opposite, 4.7–20 × 0.1–0.4 mm, sessile, linear to terete, apex acute to obtuse, strigose to glabrate, axillary brachyblasts forming fascicles. Flowering branches determinate, (1.5)3–19 cm long, internodes 1.5–3.7 cm long, tetragonal to subtetragonal, narrowly winged, glabrous, inflorescences axillary and terminal cymes, 3–9 pairs per flowering branch, (2)4–5-flowered, external bracts 2, 4.3–5.5 × 0.3–0.4 mm, narrowly triangular to linear, apex acute to obtuse, strigulose to glabrate, peduncle 0.6–1.2 mm long, internal bracts per cyme 2, 2.2–3.5 mm long, narrowly triangular, glabrous, 5–10 colleter tipped fimbriae at the base of each flower, 0.3–0.6 mm long, linear, glabrous. Flowers sessile, homostylous; hypanthium 0.5–3 × 0.8–2 mm, turbinate, hirsute to sparsely hirsute; calyx 2(4)-lobate, if four lobes then 2 longer and 2 shorter opposite to each other, 1–4 fimbriae along the calyx rim between the lobes, 0.1–0.3 mm long, colleter tipped, lobes (0.9)1.2–2 × 0.2–0.3 mm, triangular to narrowly triangular, glabrous or with sparse trichomes along the medium line; corolla infundibuliform, lower 2/3 purple, upper third white, 3.8–5(6) mm long, tube 1.5–3 mm long, 0.7–1.5 mm diam, purple, throat white, external surface papillate and scabrous, internal surface glabrous at the first third, pubescent to sparsely pubescent on the tube above the base, with a ring of moniliform trichomes on the throat, (3)4-lobate, lobes 1.1–2.3 × 1.3–1.8 mm, ovate, apex mucronulate, lilac, external surface papillate and sparsely scabrous, internal surface papillate, clavate in the preanthetic bud, ca. 1.6 mm diam, apex rounded; stamens included, filaments 0.1–0.5 mm long, anthers 0.4–0.8 mm long, orbicules present covering uniformly the inner wall of dehiscent anthers, pollen 4–5-zonocolporate, subquadrangular to circular outline in polar view, small-sized (P = 15.4–7.7; E = 12.8–14.9), prolate-spheroidal to subprolate (P/E = 1.1–1.3), long and narrow ectocolpi (9–11.6 µm long), endocingulum 2.4–3.3 µm wide, tectum psilate spinulate, tipped spinules 0.2–0.4 µm long, uniformly distributed over the entire surface, exine 0.8–1.4 µm thick; style included, 0.15–0.3 mm long, stigma 0.1–0.14 mm long, bilobate, lobes inconspicuous; nectariferous disk entire, 0.4–0.5 mm diam, with striate cells. Capsule 2.3–4.8 × 2.7–3.8 mm, broadly elliptic to broadly obovate in outline, strongly compressed parallel to the septum, 3 acrodromous ribs on the dorsal surface, hirsute to sparsely hirsute, calyx lobes persistent, dehiscent from the apex downwards, dehiscence line on the septum forming an broadly elliptic to broadly obovate section, uncovering a ventral rim of carpel tissue on the edge of the deciduous valves, 0.5–0.7 mm wide, keeping the seed inside after dehiscence, septum persistent, 3.5–4 × 2–2.6 mm, broadly elliptic to broadly obovate, attenuate at the base, white to slightly translucent. Seeds 2, 2–4.5 × 2–3.2 mm, broadly elliptic to broadly obovate in outline, strongly compressed, ventral surface covered by diffuse strophiole, 2–2.1 × 1.4–1.5 mm, dorsal surface slightly convex, testa subtuberculate, with digital-like cells pressed (66–140 × 19–21 µm), with small smooth, orbicular to elliptic apical projections (27.2–64.6 × 25.6–36 µm) radially arranged. Figures 1, 3A–J, 4A–H, 5A–C, 6A–C.

Paratypes—**Brazil**, BAHIA: Macaúbas, estrada para Canatiba, subida para a Serra Poção, próximo ao alto, 20 Apr 1996, *G. Hatschbach et al. 65130* (CEPEC, CTES, ESA, MBM, MO); Macaúbas, estrada para Tinguis, 13°04’57” S, 42°46’26” W, 904 m, 18 Apr 2015, *J. A. M. Carmo & A. V. Scatigna 368* (UEC); idem, 13°05’04” S, 42°46’41” W, 900 m, 18 Apr 2015, *J. A. M. Carmo & A. V. Scatigna 375* (UEC); idem, 13°06’43” S, 42°41’43” W, 693 m, 18 Apr 2015, *J. A. M. Carmo & A. V. Scatigna 378* (CTES, UEC).

Distribution and Habitat—*Psyllocarpus bahiensis* is endemic to the municipality of Macaúbas, Bahia (Fig. 7). The species grows on patches of sandy soil usually associated with rocky outcrops amidst the seasonally dry forest (Caatinga), at elevations from 700 to 900 m. The habitat and area where this species occurs are included in the concept of campo rupestre s. l. by Silveira et al. (2016), which is a montane, grassy-shrubby, fire-prone vegetation mosaic with rocky outcrops of quartzite, sandstone or ironstone, along with sandy, stony, and waterlogged grasslands. It is an azonal ecosystem embedded mainly within the Cerrado and Caatinga, characterized by its nutrient-poor soils supporting grassland and scrub (Mucina in press.).

Conservation—*Psyllocarpus bahiensis* does not occur within the limits of any protected area in Bahia. It was collected in two locations in Macaúbas. The first botanical collections made in this municipality date to 1924, as the more recent ones were made in 2016, accounting for ca. 1400 botanical records in 92 years (*species*Link network 2017). Except for the first collection of *P. bahiensis* (*G. Hatschbach et al. 65130*), made in 1996, this species has been collected again only by us, in 2015.

Psyllocarpus bahiensis presents EOO and AOO equal to 1.647 Km^2 and 12 Km^2 respectively (.kml file available at https://figshare.com/articles/_/4754428). According to the IUCN (2016), if EOO is less than AOO, it should be changed to make them equal and ensure consistency with the definition of AOO as an area within EOO. The IUCN (2016) also states that for species with linear elongated distributions, the EOO (minimum convex polygon) may lead to an overestimate of extinction risk. This seems to be the case for *P. bahiensis*, since we could identify patches of sandy soil along the top of the mountain range when driving on its unpaved roads trying to find new populations during fieldwork, and by analysing satellite images on Google Earth$^{©}$.

Therefore, for the purposes of this evaluation, we consider *P. bahiensis* to be endangered (EN B2abiii) based on its AOO (less than 500 Km^2), number of locations less than five, and continuing decline inferred on quality of habitat, due to human interference on the native vegetation cover. The impacts on the Caatinga, in which patches of campo rupestre s. l. are intermingled, are associated with agriculture, livestock, and logging for the production of firewood and charcoal (Martinelli and Moraes 2013), whereas in the campo rupestre s. l. with opencast mining, annual anthropogenic burnings to support the cattle industry, wood extraction, invasive species, harvesting ornamental plants (orchids, bromeliads, everlastings), road construction, and uncontrolled urbanization, especially linked to tourism expansion and eucalypt plantations (Silveira et al. 2016). *Psyllocarpus bahiensis* occurs is in the interior of Bahia, relatively far from big urban centers. Nevertheless, the advance of human occupation in this region is noticeable due to the opening of roads, yet unpaved, and the settlement of properties by the removal of significant portions of the native vegetation cover, as we observed during fieldwork and on Google Earth$^{©}$ (for reference please see the .kml file available at https://figshare.com/articles/_/4754428).

Phenology—Both flowering and fruiting and only fruiting specimens were collected in April.

Etymology—The specific epithet refers to the state of Bahia, Brazil, where *P. bahiensis* is endemic.

Taxonomy—*Psyllocarpus bahiensis* belongs in *P.* section *Psyllocarpus* due to the linear to terete leaves, homostylous flowers with included stamens and style (Fig. 1E, 3A, 6B–C), prolate-spheroidal to subprolate pollen grains with long and narrow ectocolpi, endocingulum and endoaperture, psilate spinulate exine (Fig. 5A–C), bilobate stigma with inconspicuous lobes (Fig. 3E), and capsules compressed parallel to a persistent septum (Figs. 1H, 4A). This species presents character states reported for the first time in the genus, such as the inflorescences in pauciflorous cymes (Figs. 1B, 6B), and hirsute to sparsely hirsute hypanthium and capsules (Figs. 1E–F, H–I, 3A, D), which present deciduous valves forming a ventral rim of carpel tissue, keeping the seed inside after dehiscence (Fig. 4A–D). This manner of dehiscence has been reported for only two species in the Spermacoceae, *Staelia catechosperma* K. Schum. [≡ *Anthospermopsis catechosperma* (K. Schum.) J. H. Kirkbr.], which is also endemic to Bahia (Cabral and Salas 2015), and *Spermacoce omissa* J. R. Clarkson, in Australia (Harwood and Dessein 2005), both associated with sandy soils. Further phylogenetic investigation is needed to assess how these taxa relate to each other in the *Spermacoce* clade and how the dehiscence of capsules has evolved.

The first collection of *P. bahiensis* (*G. Hatschbach et al. 65130*) has been identified as *P. laricoides*. They are both subshrubs with opposite leaves and axillary brachyblasts forming fascicles but can be easily differentiated, not only by the unique set of character states mentioned above for the new species but also by the monopodial branching pattern, determinate flowering branches bearing terminal and axillary cymes (Figs. 1B, 6B), calyx tube absent (Fig. 3D), capsules with 3 acrodromous ribs on the dorsal surface (Fig. 4B), and ventral surface of the seeds covered by diffuse strophiole (Fig. 4C, G) in *P. bahiensis*. Also, the pollen of this species present tipped spines uniformly distributed over the entire surface of the grains (Fig. 5B), unlike *P. laricoides*, which presents spinules only along the ectocolpi edges (Kirkbride 1979).

Psyllocarpus scatignae Carmo, Sobrado & R. M. Salas, sp. nov. TYPE: BRAZIL, Minas Gerais: Botumirim, Areal próximo a talhão de eucalipto, 16°54’00” S, 42°53’15” W, 23 Jan 2016, *J. A. M. Carmo & A. V. Scatigna 446* (holotype: UEC!; isotypes: CTES!, MO!, RB!, SPF!).

Psyllocarpus scatignae is similar to *P. goiasensis*, but differs by the sympodial branching pattern (vs. monopodial in *P. goiasensis*), determinate flowering branches (vs. indeterminate), unbranched, dichasially or monochasially branched (vs. unbranched), terminal glomerules (vs. axillary 1-flowered inflorescences), calyx tube present (vs. absent), calyx lobes 4.3–4.8 mm long (vs. 2.4–3 mm long), capsules glabrous (vs. capsules with the upper 1/3 sparsely puberulous), and seeds broadly obovate in outline (vs. narrowly oblong).

Subshrubs, 0.5–1 m tall, sympodial. Stems sparsely branched, erect, internodes 0.1–1.1 cm long, terete to slightly compressed or tetragonal, puberulent to glabrous, bark peeling from older internodes. Stipular sheaths 0.5–1.6 mm long, glabrous to sparsely puberulent, 4–6(8)-fimbriate on each side of the stem, fimbriae 0.2–1.6 mm long, narrowly triangular to subulate, strigulose to glabrous. Leaves opposite, (2.6)3.2–7.6 × 0.1–0.4 mm, sessile, linear to terete, apex acute to obtuse, strigose to glabrate, axillary brachyblasts forming fascicles. Flowering branches determinate, 0.5–1.4 cm long, unbranched or dichasial or monochasially branched, branches 1.8–3.7 cm long, internodes 2.7–4.9 mm long, terete to slightly compressed or tetragonal, puberulent to glabrous, inflorescences in terminal glomerules, (5)7–28-flowered, bracts 2, (2)4–6.9 × 0.2–0.9 mm, linear to terete, apex acute, glabrous, with 3–5 pairs of axillary brachyblasts forming fascicles, peduncle 2–4.4 mm long. Flowers sessile, homostylous; hypanthium 1.3–2.5 × 0.8–1.3 mm, turbinate, glabrous; calyx tube 0.3–0.8 mm long, 2-lobate, 5–10 fimbriae along the calyx rim between the lobes, 0.8–1 mm long, colleter tipped, lobes 3–4.8 × 0.4–0.7 mm, narrowly triangular, glabrous; corolla infundibuliform, lower half to 2/3 purple or pink, the upper half to third white to light blue or light pink, 6.5–7.5 mm long, tube 4.2–5.1 mm long, 2–2.8 mm diam, purple or pink, throat white to light blue or light pink, external surface papillate, internal surface glabrous at the first third, pubescent to sparsely pubescent on the tube from the base of the filaments to the throat, with a dense ring of moniliform trichomes on the throat, 4(5)-lobate, lobes 2.5–3.2 × 1.3–2.2 mm, ovate to obovate, apex mucronulate, blue, light blue, lilac or light pink, external and internal surfaces papillate, roundly ribbed on the medium line, papillae conspicuous on the rib, capitate angulate in the preanthetic bud, ca. 1.8–2 mm diam, apex acute; stamens included, filaments 0.2–0.5 mm long, anthers 0.9–1 mm long, orbicules present covering uniformly the inner wall of dehiscent anthers, pollen 4–5(6)-zonocolporate, nearly circular outline in polar view, small-sized [P = 16.4 (17.5) 19.1; E = 13.9 (15.3) 17.3], prolate-spheroidal to prolate (P/E = 1–1.8), long and narrow ectocolpi (8.3–12.8 μm long), endocingulum 2.7–4.1 μm wide, tectum psilate spinulate, spinules 0.14–0.4 μm long, uniformly distributed around the mesocolpium and sparsely over the apocolpium surface, exine 0.7–1.4 μm thick; style included, 0.4–0.5 mm long, stigma 0.1–0.3 mm long, bilobate, lobes inconspicuous; nectariferous disk entire, 0.7–1 mm diam, with striate cells and a slight transversal slit in the middle part. Capsule 4.2–4.6 × 3–3.3 mm, broadly obovate in outline, compressed parallel to the septum, smooth, glabrous, calyx lobes persistent, dehiscent from the apex downwards, valves persistent from which the seeds are shed after dehiscence, septum 4–4.5 × 2.7–3 mm. Seeds 2, 4–4.3 × 2–2.6 mm, broadly obovate in outline, strongly compressed, ventral surface partially covered by defined narrowly oblong strophiole, 1.4 × 0.5 mm, dorsal surface slightly convex, testa subtuberculate, with digital-like cells pressed (93.5–149.7 × 19.8–33.5 μm), with small striate, elliptic apical projections (47–67.4 × 27.9–28.4 µm) radially arranged. Figures 2, 3K–S, 4I–P, 5D–F, 6D–H.

Paratypes—**Brazil**, MINAS GERAIS: Botumirim, Areal próximo a talhão de eucalipto, 16°54’ S, 42°53’15” W, 23 Jan 2016, *J. A. M. Carmo & A. V. Scatigna 443* (CTES, UEC); idem, *J. A. M. Carmo & A. V. Scatigna 444* (UEC); idem, 16°54’ S, 42°53’15” W, 23 Jan 2016, *J. A. M. Carmo & A. V. Scatigna 445* (UEC); idem, 16°54’ S, 42°53’15” W, 23 Jan 2016, *J. A. M. Carmo & A. V. Scatigna 448* (CTES, UEC); Cristália, Estrada Cristália-Botumirim, 25 km de Cristália, 1 Jan 2004, *C. S. Sato et al. 20* (SPF).

Distribution and Habitat—*Psyllocarpus scatignae* is endemic to Botumirim and Cristália, Minas Gerais (Fig. 7), occurring in patches of white sand soil (“areais”; Fig. 6D) along one of the roads which connects both municipalities, surrounded by Cerrado and seasonally dry forest (Caatinga), at ca. 800 m elevation. The habitat and area where this species occurs are also included in the concept of campo rupestre s. l. (Silveira et al. 2016).

Conservation—*Psyllocarpus scatignae* does not occur within the limits of any protected area in Minas Gerais. The first botanical collections made in Botumirim date to 1960, as the more recent ones were made in 2017, accounting for ca. 1600 botanical records for the municipality in 57 years (*species*Link network 2017). Except for the first collection (*C. S. Sato et al. 20*), made in 2004, this species has been collected only by us, in 2016.

Psyllocarpus scatignae presents AOO equal to 4 Km^2 (kml. file available at https://figshare.com/articles/_/4754431). Therefore, for the purposes of this evaluation, we consider *P. scatignae* as critically endangered (CR B2abiii), based on its AOO (less than 10 Km^2), number of locations equal to one and continuing decline inferred on quality of habitat, due to major current disturbances in the campo rupestre region (Silveira et al. 2016). It was collected in the same site as the carnivorous and also critically endangered species *Philcoxia rhizomatosa* Scatigna & V. C. Souza (Scatigna et al. 2015). This area is surrounded by a eucalypt farm and is constantly under disturbance because of the extraction of sand for local housing constructions, as observed by Scatigna et al. (2015) and us, during fieldwork trying to find new populations.

Phenology—Both flowering and fruiting and only fruiting specimens were collected in January.

Etymology—The specific epithet honours the young and talented Brazilian botanist André Vito Scatigna MSc, who works on the systematics of the Plantaginaceae and related taxa. André’s fieldwork support and knowledge on habitats where *Psyllocarpus* species occur were vital for the collection of both taxa described in the present paper.

Taxonomy—*Psyllocarpus scatignae* belongs in *P.* section *Psyllocarpus* due to the linear to terete leaves, homostylous flowers with included stamens and style (Fig. 2E), prolate-spheroidal to prolate pollen grains, with long and narrow ectocolpi, endocingulum and endoaperture, psilate and spinulate exine (Fig. 5D–F), bilobate stigma with inconspicuous lobes (Fig. 3N), and capsules compressed parallel to a persistent septum (Fig. 2H, 4I). This species is unique in the genus because of its flowering branches determinate, dichasial or monochasially branched, sometimes unbranched, with terminal inflorescences in glomerules (Fig. 1A–B, 6F–H). This type of branching is rare in the *Spermacoce* clade, being reported only in some *Galianthe* [*G. cymosa* (Cham.) E. L. Cabral & Bacigalupo, *G. dichasia* (Sucre & C. G. Costa) E. L. Cabral, Cabral and Bacigalupo 1997b)] and *Spermacoce* [*S. eryngioides* Cham. & Schltdl., *S. incognita* (E. L. Cabral) Delprete, and *S. tocantinsiana* (E. L. Cabral & Bacigalupo) Delprete, Florentín et al. 2016] species.

Psyllocarpus scatignae is similar to *P. goiasensis* because they're both subshrubs with opposite leaves and axillary brachyblasts forming fascicles, corolla lobes with internal surface roundly ribbed on the medium line, mucronulate at the apex and capitate angulate in preanthetic bud, and compressed capsules, but they can be easily differentiated by the sympodial branching pattern, determinate flowering branches dichasial or monochasially branched, terminal inflorescences in glomerules (Fig. 1A–B, 6F–H), calyx tube present (Fig. 2F), glabrous capsules (Fig. 4I–J), and seeds broadly obovate in outline (Fig. 2M–N, 4N–O) in *P. scatignae*. Besides, the pollen grains of this species present spinules uniformly distributed around the mesocolpium and sparsely over the apocolpium surface (Fig. 5D–E), unlike *P. goiasensis*, which presents supratectal elements only on the edges of the colpi (Kirkbride 1979).

KEY TO THE SPECIES OF *PSYLLOCARPUS* SECT. *PSYLLOCARPUS*

1. Inflorescences in pauciflorous cymes; hypanthium hirsute to sparsely hirsute; capsules hirsute, valves deciduous keeping the seed inside after dehiscence…………………………………………………………………..*P. bahiensis*

1. Inflorescences in 1-flowered cymes or glomerules; hypanthium glabrous or the upper 1/2 puberolous; capsules glabrous or the upper 1/3 sparsely puberulous, valves persistent from which the seeds are shed after dehiscence……………………….……...2

    2. Flowering branches indeterminate, axillary inflorescences in 1-flowered cymes….3

        3. Most leaf axils without brachyblasts or pairs of smaller leaves; flowering branches with 2–4 flowers opened at the same time...*P. schwackei*

        3. Leaf axils with brachyblasts or short branchlets; flowering branches with 4 or more flowers opened at the same time...4

            4. Sympodial subshrub; hypanthium glabrous; calyx tube 0.1–0.5 mm long; corolla lobes

rounded in preanthetic buds; capsules glabrous; seeds elliptic to broadly elliptic in outline ....*P. laricoides*

4. Monopodial subshrub; hypanthium with the upper 1/3 puberulous; calyx tube absent; corolla lobes capitate angulate in preanthetic buds; capsules with the upper 1/3 sparsely puberulous; seeds narrowly oblong in outline………………………………………………….......... *P. goiasensis*

2. Flowering branches determinate, terminal inflorescences in glomerules, rarely also with axillary inflorescences in 1-flowered cymes ……………………………..........5

5. Flowering branches dichasial or monochasially branched, or unbranched; calyx lobes 4.3–4.8 mm long; corolla lobes capitate angulate in preanthetic bud, mature corolla 6.5–7.5 mm long…………………………………….......................................*P. scatignae*

5. Flowering branches unbranched; calyx lobes 1.2–3.6 mm long; corolla lobes rounded or clavate in preanthetic bud, mature corolla 1–2.6 mm long......................………6

6. Flowering branches erect; calyx lobes 1.2–2 mm long; corolla tube 1.1–1.5 mm long; seeds broadly elliptic in outline...*P. asparagoides*

6. Flowering branches pendulous; calyx lobes 2.2–3.6 mm long; corolla tube 2.2–2.6 mm long; seeds obovate in outline…………..................................*P. phyllocephalus*

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FIG. 1. *Psyllocarpus bahiensis*. A. Habit. B. Inflorescence at the apex of a flowering branch. C. Stipular sheath. D. Preanthetic flower bud. E. Flower. F. Hypanthium, calyx, style, and stigma. G. Opened corolla. H–L. Capsule: H. Dehiscent capsule, lateral view. I. Dehiscent capsule, dorsal view. J. Valve, ventral view. K. Septum. L. Valve, cross section. M–N. Seed: M. Dorsal view. N. Ventral view. [A, M–N. *G. Hastchbach et al. 65130* (CTES); B–L. *J. A. M. Carmo & A. V. Scatigna 376* (CTES)]. Illustration: L. Simón.

FIG. 2. *Psyllocarpus scatignae*. A. Branch portion. B. Inflorescence at the apex of a flowering branch. C. Stipular sheath. D. Preanthetic flower bud. E. Flower. F. Hypanthium and calyx. G. Opened corolla. H–L. Capsule: H. Dehiscent capsule, lateral view. I. Dehiscent capsule, dorsal view. J. Dehiscent valve, ventral view. K. Septum. L. Valve, cross-section. M–N. Seed: M. Dorsal view. N. Ventral view. [A–N. *J. A. M. Carmo & A. V. Scatigna 446* (CTES)]. Illustration: L. Simón.

FIG. 3. Flower morphology. A–J. *Psyllocarpus bahiensis*: A. Flower bud. B–C. Papillate and scabrous external surface of the corolla. D. Hypanthium, calyx, style, and stigma. E. Detail of style and stigma. F. Opened corolla. G. Papillate internal surface of the corolla lobes. H. Inner wall of a dehiscent anther, showing the prescence of orbicules. I. Nectariferous disk, top view. J. Detail of the striate nectariferous disk cells. K–S. *P. scatignae*: K. Flower bud. L. Papillate external surface of the corolla. M. Hypanthium, calyx, style, and stigma. N. Detail of style and stigma. O. Opened

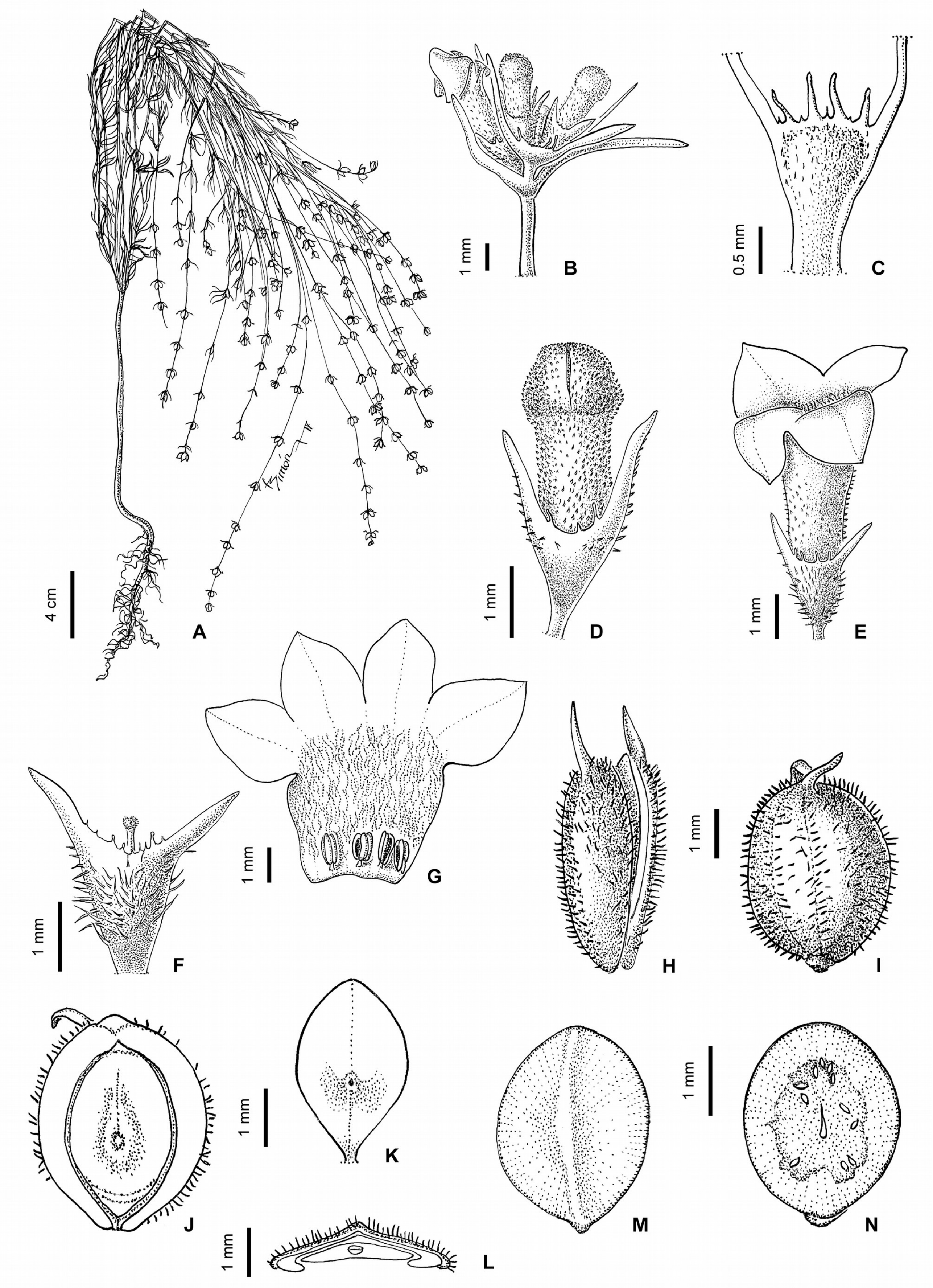
corolla. P. Papillate internal surface of the corolla lobes. Q. Inner wall of a dehiscent anther, showing the presence of orbicules. R. Nectariferous disk, top view. S. Detail of the striate nectariferous disk cells. Scale bar: 500 µm (A, F, K, M, O); 200 µm (D); 100 µm (E, I, N, R); 50 µm (B–C, G, L, P); 20 µm (J, S); 5 µm (H, Q).

FIG. 4. Fruit and seed morphology. A–H. *Psyllocarpus bahiensis*: A–E. Capsule: A. Dehiscent capsule, lateral view. B–D. Valve: B. Dorsal view. C. Ventral view. D. Cross section, showing the seed keept inside the valve after dehiscence. E. Septum. F–H. Seed: F. Dorsal view. G. Ventral view, with diffuse strophiole. H. Detail of the testa. I–P. *P. scatignae*: I–M. Capsule: I. Dehiscent capsule, lateral view. J–L. Valve: J. Dorsal view. K. Ventral view. L. Cross section, showing the seed, which is shed after dehiscence. M. Septum. N–P. Seed: N. Dorsal view. O. Ventral view. P. Detail of the testa. Abreviations: s, seed; se, septum; v, valve.

FIG. 5. Pollen morphology. A–C. *Psyllocarpus bahiensis*: A. Polar view (LM). B. Ventral view. C. Detail of the inner side of pollen fragment showing the endocingulum. D–F. *P. scatignae*: D. Polar view. E. Ventral view. F. Detail of the inner side of pollen fragment showing the endocingulum. Photographs: LM (A); SEM (B–F). Abbreviations: en, endocingulum.

FIG. 6. A–C. *Psyllocarpus bahiensis*: A. Habit. B. Inflorescences at the apex of a flowering branch. C. Detail of flowers and fruits. D–H. *P. scatignae*: D. Habitat, white sand patch in Botumirim, Minas Gerais. E. Habit. F–G. Flowering branch dichasially branched. H. Flowering branch unbranched, inflorescence in glomerule. Photographs: J. A. M. Carmo (A–C, E–H); M. A. Sartori (D).

FIG. 7. Distribution map of *Psyllocarpus bahiensis* and *P. scatignae* in Bahia and Minas Gerais states, Brazil. Symbols: star = *P. bahiensis*; circle = *P. scatignae*.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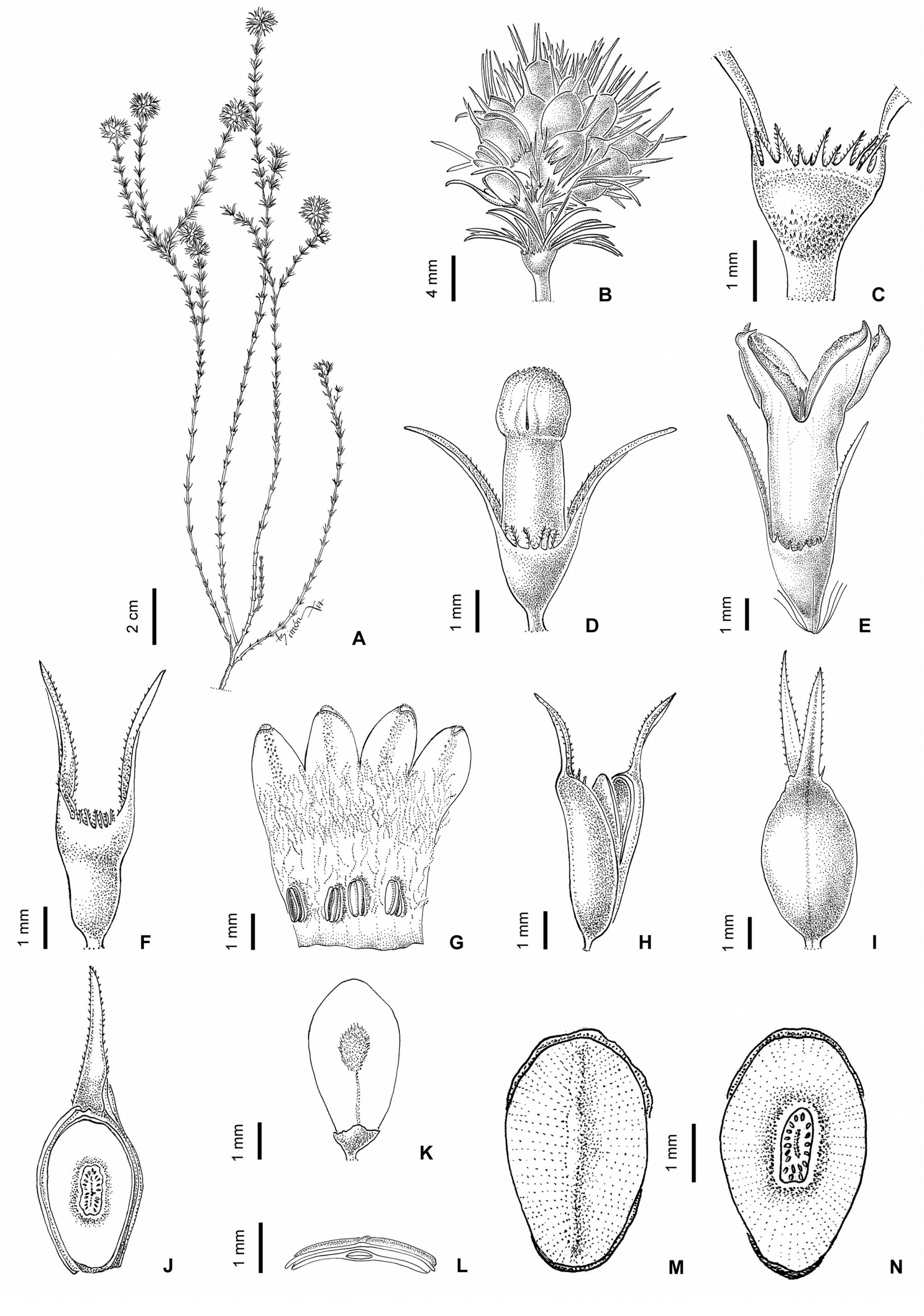
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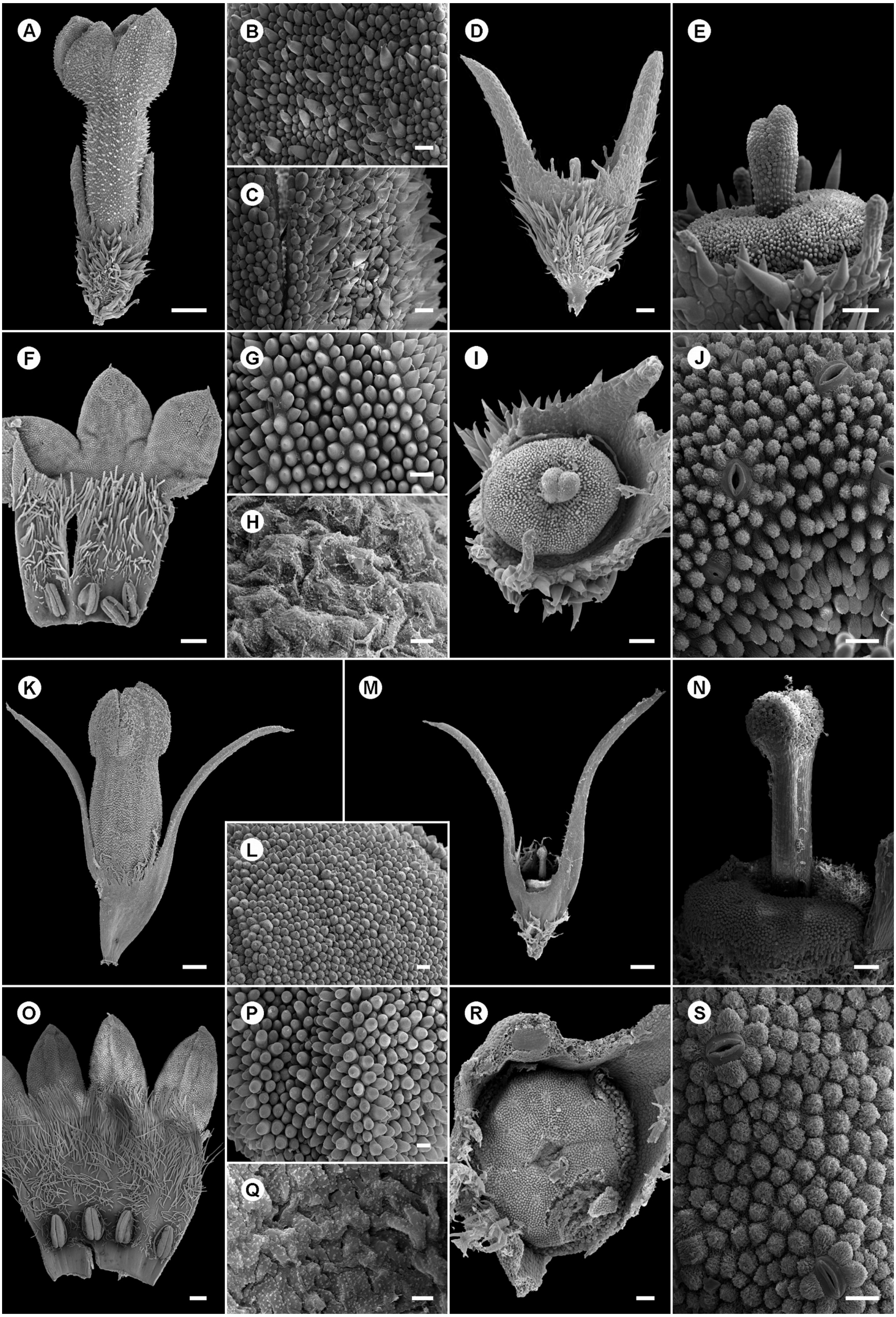
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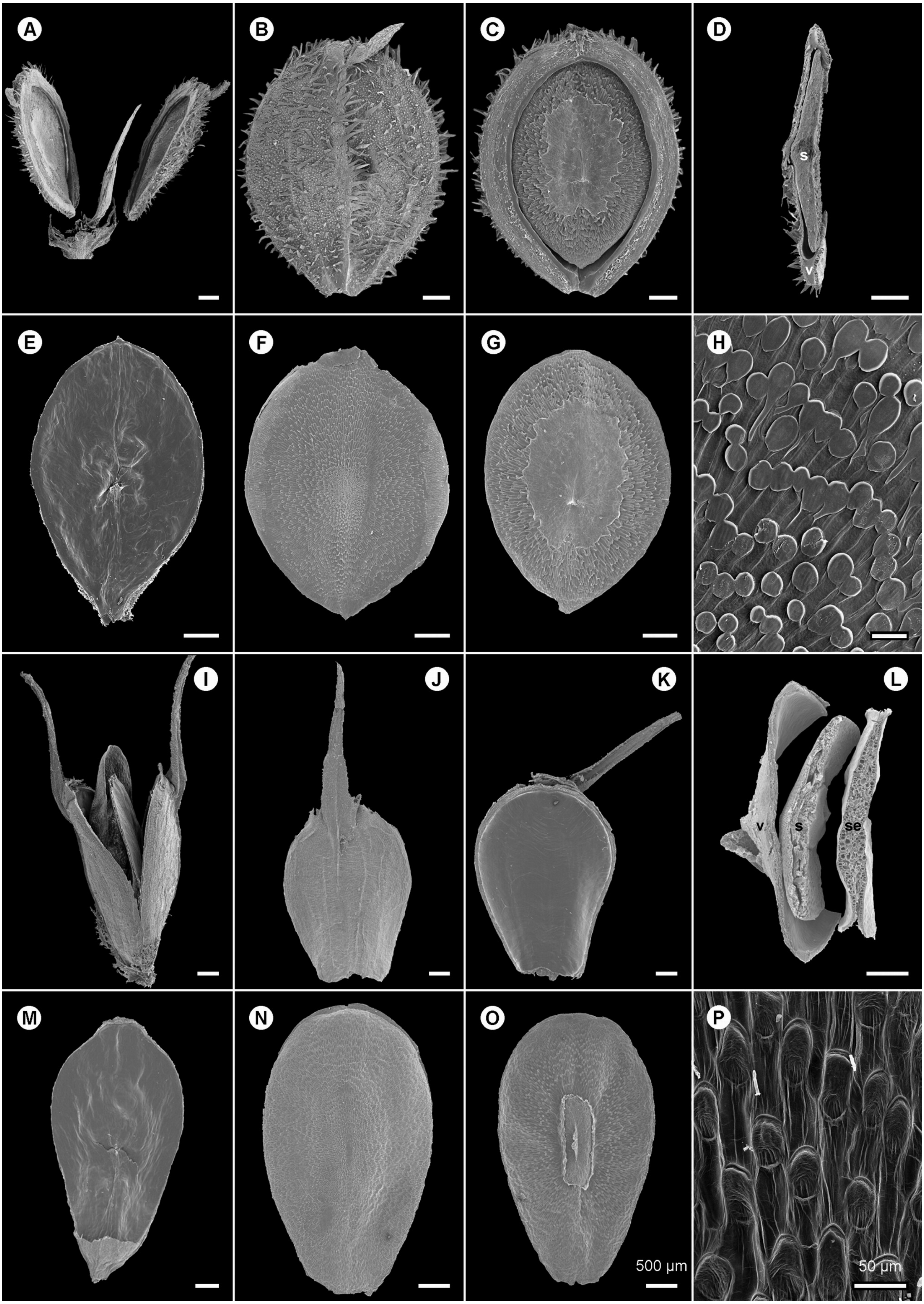
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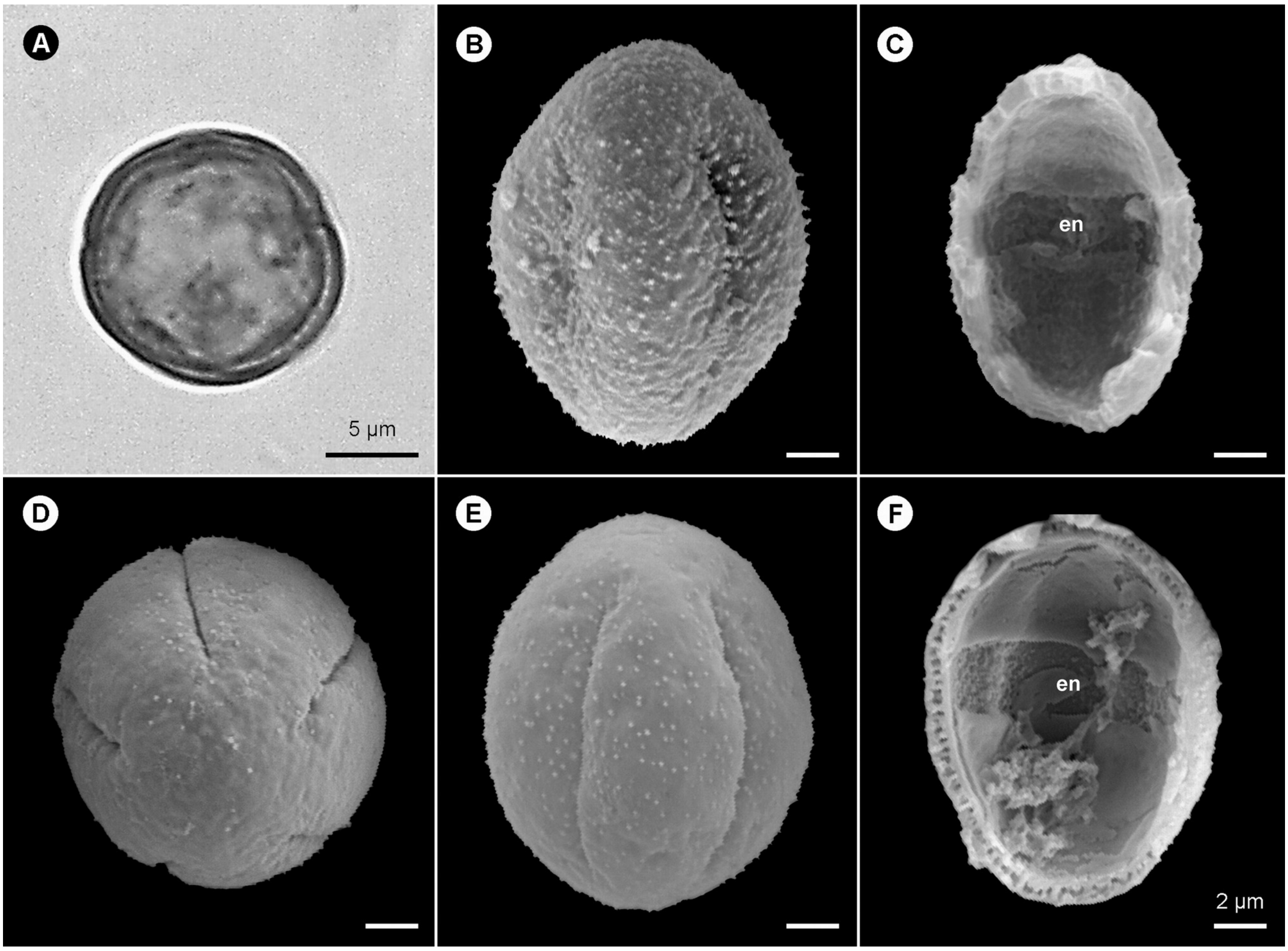
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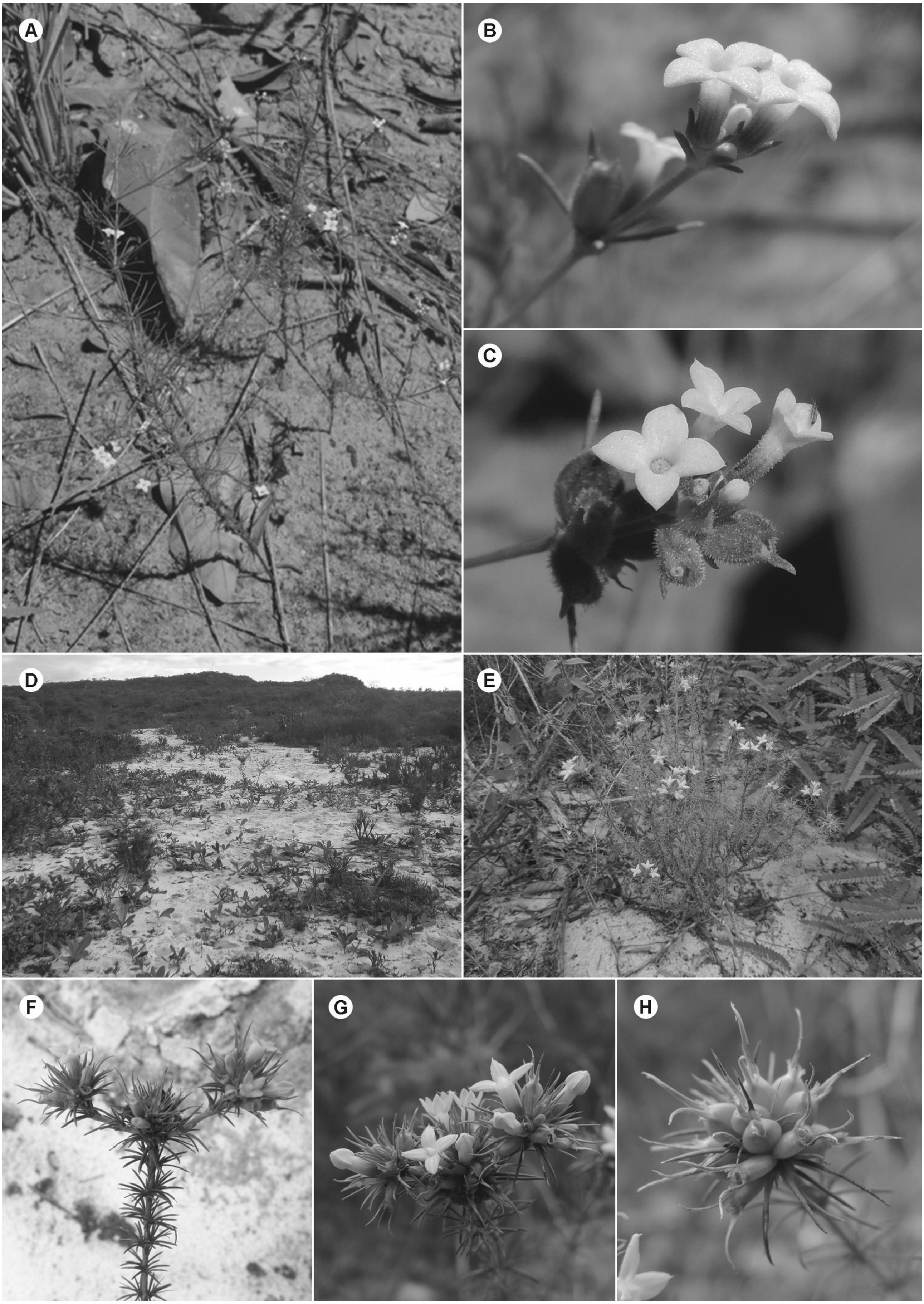
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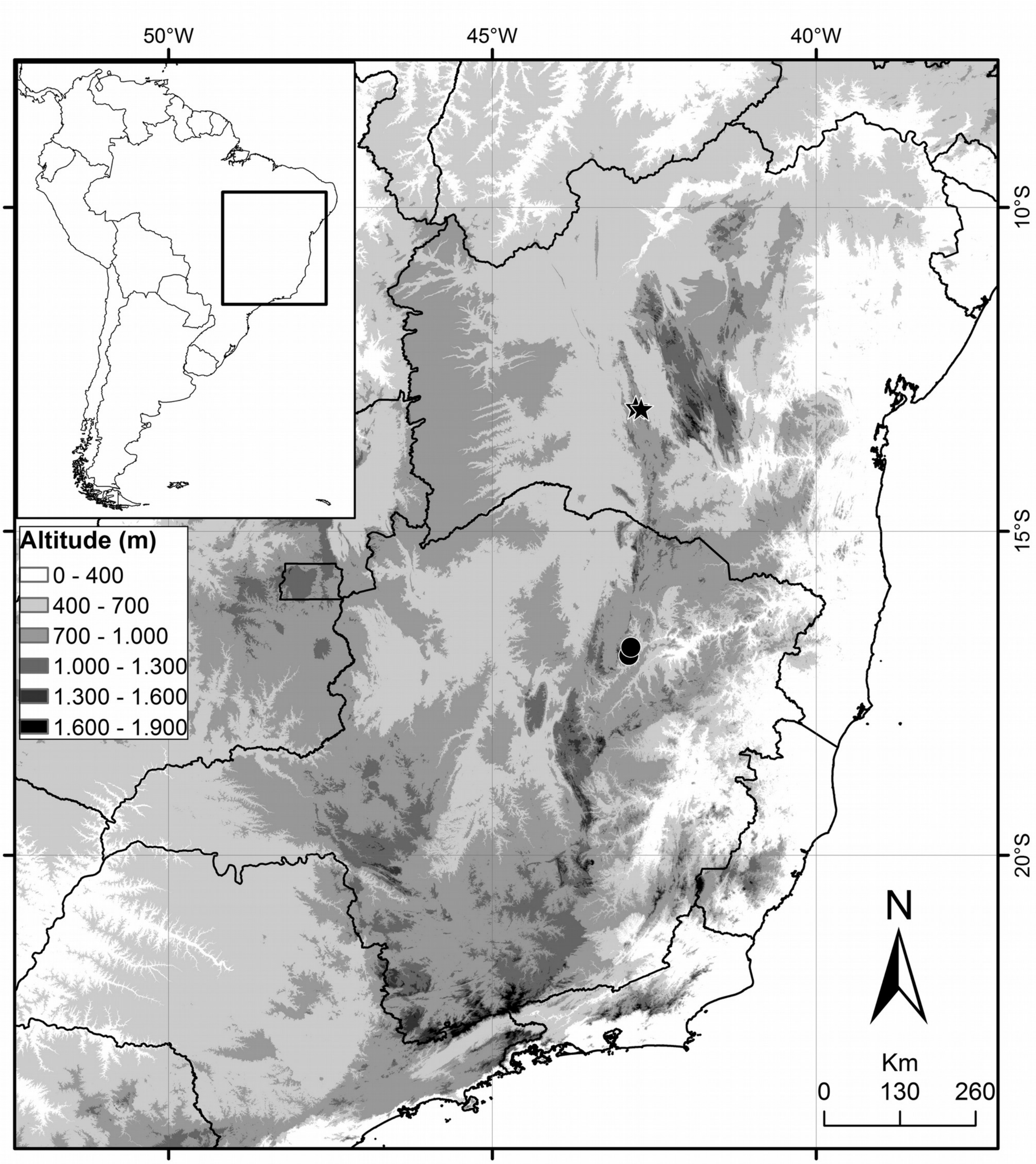
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1.300 - 1.600
1.600 - 1.900
N
Km
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130
260

III

Carmo, J. A. M., Sobrado, S. V., Salas, R. M., & Simões, A. O. 2018. Revisiting *Psyllocarpus goiasensis* (Rubiaceae: Spermacoceae): a new synonym, notes on type specimens, and conservation status assessment of this endemic species from the campo rupestre of Goiás state, central Brazil. Kew Bull., 73: 1–6. https://doi.org/10.1007/s12225-018-9779-9

Revisiting *Psyllocarpus goiasensis* (Rubiaceae: Spermacoceae): a new synonym, notes on type specimens, and conservation status assessment of this endemic species from the campo rupestre of Goiás state, central Brazil

João Afonso Martins do Carmo[1], Sandra Virginia Sobrado[2], Roberto Manuel Salas[2] & André Olmos Simões[3]

Summary. *Psyllocarpus goiasensis* J. H. Kirkbr. is an endemic species from the campo rupestre of Goiás. *Psyllocarpus laricoides* Mart. & Zucc. var. γ *longicornu* K. Schum., formerly under the synonymy of *P. laricoides*, is treated here as a new synonym of *P. goiasensis*. A second-step lectotype is designated for this variety. The first illustration and photographs of *P. goiasensis*, as well as a distribution map and comments on its ecology are presented. This species is assessed Endangered (EN) under range size (B) criterion of the IUCN.

Key Words. Chapada dos Veadeiros, Pohl, *Spermacoce* clade, taxonomy.

Introduction

Psyllocarpus Mart. & Zucc. is distinguished from other genera of the *Spermacoce* clade in the tribe Spermacoceae by its compressed capsule parallel to the septum (Martius & Zuccarini 1824; Kirkbride 1979; Kårehed *et al.* 2008; Salas *et al.* 2015). It is endemic to Brazil and as currently circumscribed comprises 10 species, occurring in the Cerrado, campo rupestre, and white-sand Amazonian campina (Kirkbride 1979; Cabral & Bacigalupo 1997; Zappi *et al.* 2014; BGF 2015). Despite being considered a morphologically well-defined genus, *Psyllocarpus* has never been the subject of a comprehensive phylogenetic study to test its monophylly and how it relates to other genera in the *Spermacoce* clade, as well as the relationships between its species. However, according to an analysis based on two species and two nuclear DNA regions, *P. asparagoides* Mart. ex Mart. & Zucc. and *P. phyllocephalus* K. Schum. and ITS and ETS, respectively, Salas *et al.* (2015) recovered the genus as sister group of a clade composed of some *Spermacoce* L. species.

Psyllocarpus goiasensis J. H. Kirkbr. is endemic to the state of Goiás, occurring in the Chapada dos Veadeiros and Serra Geral do Paranã, growing on soils composed of quartz sands (Kirkbride 1979; Delprete 2010). Kirkbride (1979) compared it with the supposedly closely related *Psyllocarpus laricoides* Mart. & Zucc., since both taxa have leaf axils with brachyblasts and flowering branches indeterminate with axillary inflorescences in 1-flowered cymes. The author distinguished *P. goiasensis* from *P. laricoides* by its hypanthium and capsule puberulous above the middle (vs. glabrous) and the absence of a calyx tube (vs. calyx tube present).

Psyllocarpus laricoides var. γ *longicornu* K. Schum. was described based on the collection "Prope Ouro fino: *Pohl* n. 1317 (d. 851)". Schumann (1888) segregated this variety from the typical *P. laricoides* based on the following morphological traits: "internodiis abbreviatis, foliis longioribus, inflorescentia elongata, sepalis majoribus tubo corollae vix brevioribus, capsulae aequilongis". Some of these features, such as the elongate flowering branches and the calyx lobes relatively longer, are diagnostic for the identification of *P. goiasensis*. Kirkbride (1979) transferred *P. laricoides* var. γ *longicornu* to the synonymy of *P. laricoides*, an endemic species from high elevation areas of the Espinhaço Range in the states of Minas Gerais and Bahia, without further explanation. He also designated a lectotype for this variety, in W, with two isolectotypes, in W and K, and annotated it was collected by Pohl in 1820, in "Ouro fino", Minas Gerais.

In the present study, we propose that *P. laricoides* var. γ *longicornu* should be treated as a synonym of *P. goiasensis*, based on morphology and geographical distribution here clarified by consulting Pohl's travel book (Pohl 1976). Since there are two type specimens for this variety deposited in W, and no specification is provided by Kirkbride (1979) on which one is the lectotype, a second-step lectotype designation is here proposed, according to the Art. 9.17 of the ICN (McNeill *et al.* 2012). We provide the first illustration and photographs of *P. goiasensis*, along with a distribution map, comments on its ecology, and conservation status assessment.

Materials and Methods

We analyzed collections deposited at the CTES, F, HUEFS, MBM, MO, NY, RB, SPF, UB, UEC, and US herbaria; digital images of type specimens deposited at K, MO, NY, US, W, WAG, and WIS available at JSTOR, the New York Botanical Garden's Virtual Herbarium, Smithsonian National Museum of Natural History, Tropicos, and the Virtual Herbaria (Naturhistorisches Museum Wien) websites; and photographs of type specimens, not yet digitized, deposited at W. Acronyms are presented according to Thiers (continuously updated). Links for digital images available online are provided in the Appendix section. A population in the Serra do Tombador, Goiás, Brazil, was sampled and photographed in the field. Conservation status was assessed by range size (B) criterion, following IUCN (2014) recommendations. We used coordinates from municipalities, when their names were given on the labels, as proxies for the specimens which were not georeferenced. Extent of occurrence (EOO) and area of occupancy (AOO) were estimated using GeoCAT (Bachman *et al.* 2011).

Psyllocarpus goiasensis *J. H. Kirkbr.* (1979: 41; 17, fig. 5). Type: Brazil, Goiás, Chapada dos

Veadeiros, Cerrado on outcrops with adjacent wet campo (brejo), ca. 10 km N of Alto Paraíso do Goiás, ca. 1100 m, 24 March 1971, *H. S. Irwin et al.* 33082 (holotype UB!; isotypes MO2575309!, NY00133029!, US00130113 [negative and digital image]!, WAG0003052 [digital image]!, WIS0004269 [digital image]!, WIS0004270 [digital image]!) (Figs. 1 & 2).

Psyllocarpus laricoides var. γ *longicornu* K. Schum. (1888: 6(6); 33), **synon. nov.** Type: Brazil, Goiás, Ouro Fino, 1819 [annotated as "Minas Gerais, Ouro fino, 1820" by Kirkbride (1979)], *J. B. E. Pohl* 1317 (lectotype W ["*29a W – W46*" handwritten on herbarium sheet, annotated as lectotype by Joseph H. Kirkbride, Jr.]!, first-step selected by Kirkbride (1979: 16); isolectotypes BR0000005325986 [digital image]!, K000470420 [digital image]!, M0189211 [digital image]!, W ["*29a W – W45*" handwritten on herbarium sheet, annotated as isotype by Joseph H. Kirkbride, Jr.]!; lectotype W ["*29a W – W46*" handwritten on herbarium sheet, annotated as lectotype by Joseph H. Kirkbride, Jr.,]!, second-step selected here).

DISTRIBUTION. *Psyllocarpus goiasensis* is endemic to the state of Goiás, in central Brazil (Map 1). From north to south, this species occurs in the Serra do Tombador, Chapada dos Veadeiros, and Serra Geral do Paranã, in the municipalities of Alto Paraíso de Goiás, Cavalcante, Formosa, and São João d'Aliança. However, most of the analyzed specimens were collected in the region of the Chapada dos Veadeiros.

SPECIMENS EXAMINED. BRAZIL. Goiás: ca. 30 km N of Formosa, 2 May 1966, *H. S. Irwin et al.* 15531 (paratypes F!, NY!, UB!, W [digital image]!), Chapada dos Veadeiros, 18 July 1964, *G. T. Prance & N. T. Silva* 58197 (paratypes NY!, UB!, US!), 15 Feb. 1966, *H. S. Irwin et al.* 12870 (paratypes F!, NY!, UB!, W [digital image]!), 6 March 1973, *W. R. Anderson* 6437 (paratypes NY!, RB!, UB!, US!), 16 March 1973, *W. R. Anderson* 7161 (paratypes MBM!, MO!, NY!, UB!), Estrada Alto Paraíso a Campo Belo, km. 8, 28 Nov. 1976, *G. J. Shepherd et al.* 3714 (UEC!), Hilly campo ca. 16 km S of Alto Paraíso (formerly Veadeiros), 20 March 1969, *H. S. Irwin et al.* 24745 (paratypes F!, NY!, RB!, UB!), Region of the Chapada dos Veadeiros, 14°30'S, 47°30'W, 24 May 1956, *E. Y. Dawson* 14619 (paratype F!), Rod. GO-118, 10-20 km S de São João da Aliança, 11 Feb. 1990, *G. Hatschbach & V. Nicolack* 53810 (MBM!, US!), Serra do Tombador, 13°32'20"S, 47°31'46"W, 14 April 2015, *J. A. M. Carmo & A. V. Scatigna* 352 (CTES, UEC!), Alto Paraíso de Goiás, Chapada dos Veadeiros, 20 Feb. 1975, *G. Hatschbach et al.* 36340 (paratypes CTES!, MBM!, MO!, NY!, US!, W [digital image]!), Fazenda São Bento, próximo a Cachoeira Almecégas II, 14°10'44"S, 47°34'59"W, 16 April 2009, *G. Martinelli et al.* 16535 (MO!, RB!), Parque Nacional da Chapada dos Veadeiros, 17 Oct. 2006, *J. P. Souza et al.* 8677

(SPF!), Cavalcante, Parque Nacional da Chapada dos Veadeiros, 1320 m, 13°56’38”S, 47°41’46”W, 15 April 2009, *G. Martinelli et al.* 16512 (RB!), Serra do Tombador, 1128 m, 13°32’22”S, 47°31’47”W, 19 April 2013, *J. Cordeiro et al.* 4966 (HUEFS!, MBM!), Formosa, Rio Tiquiri, 25 May 1967, *E. P. Heringer* 11451 (RB!).

HABITAT. *Psyllocarpus goiasensis* occurs in montane areas at elevations from 1000 to 1400 m, in campo rupestre vegetation (sensu Silveira *et al.* 2016), growing on sandy soils.

CONSERVATION STATUS. This is the first conservation status assessment for *P. goiasensis*. Its EOO and AOO account for 2,475.228 km^2 and 20 km^2, respectively (.kml file available at https://figshare.com/articles/Extent_of_Occurrence_and_Area_of_Occupancy_of_Psylocarpus_goiasensis/4216356), and it was recorded in three locations: Serra do Tombador; Chapada dos Veadeiros, including records within the limits of the Parque Nacional da Chapada dos Veadeiros; and Serra Geral do Paranã. Therefore, *P. goiasensis* should be considered as an Endangered (EN) species under the B1ab(iii) + 2ab(iii) criteria, based on its EOO < 5000 km^2 and AOO < 500 km^2, number of locations ≤ 5, and continuing decline in area, extent and quality of habitat, due to major current disturbances in the campo rupestre, which are opencast mining, annual anthropogenic fires to support the cattle industry, wood extraction, invasive species, ornamental plant indiscriminate collection, road construction and uncontrolled urbanization, especially linked to tourism expansion and eucalypt plantations (Silveira *et al.* 2016).

PHENOLOGY. Specimens were collected with flowers and fruits from October to April, and only fruits until July.

NOTES. The type specimens of *P. laricoides* var. γ *longicornu* present morphological traits coincident to *P. goiasensis*, such as the monopodial branching pattern (Fig. 1A; vs. sympodial in *P. laricoides*), no calyx tube (Fig. 1E; vs. calyx tube), and calyx lobes triangular to subulate (Fig. 1E, I; vs. narrowly triangular to linear) and longer (2.3 – 3 mm long) than those of *P. laricoides* (1 – 1.4 mm long, from syntype M0189221!). Capsules of *P. laricoides* var. γ *longicornu* seem glabrescent, as is the case for some **specimens of *P. goiasensis*, but we were not able to analyze the indumentum on the apex of the hypanthium and fruit in detail.**

According to Pohl’s travel book (Pohl 1976) he travelled in Goiás from 1818 to 1820. The locality Ouro Fino was a small village in the so-called captaincy of Goiás, which he passed by with his entourage on his way from Paracatu do Príncipe, Minas Gerais, to Vila Boa, Goiás, in 1819. Therefore, the distribution of *P. laricoides* var. γ *longicornu* in Goiás also corroborates its synonymy with *P. goiasensis*, since *P. laricoides* is an endemic species from the Espinhaço Range (Map 1) in Minas Gerais and Bahia (Kirkbride 1979). Furthermore, other species have been described based on Pohl’s collections at the same locality. Bentham (1839) described *Crotalaria* *divergens* Benth. (1839: 429) and *C. vespertilio* Benth. (1839: 429), for which he annotated the localities "Ouro fino" and Santa Cruz for the former and only "Ouro fino" for the latter, both in "Goyaz" [Goiás]. The information "Ad Ouro fino & S. Cruz in C. Goyaz" is written on the labels of two type specimens of *C. vespertilio* from the collection *Pohl* 1634 (isotypes NY00006697 [digital image]!, W0031489[digital image]!). There is a municipality in southern Minas Gerais also called Ouro Fino, but the village that originated it received its current name only in 1868 (IBGE 2016), after Pohl left Brazil.

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APPENDIX

Digital images of MO, NY, WAG, and WIS isotypes of *Psyllocarpus goiasensis* J.H.Kirkbr. available at http://www.tropicos.org/Image/51125, http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=303767, http://plants.jstor.org/stable/10.5555/al.ap.specimen.wag0003052?searchUri=plantName%3D%2522Psyllocarpus%2Bgoiasensis%2522%26syn%3D1, http://plants.jstor.org/stable/10.5555/al.ap.specimen.wisv0004269wis?searchUri=plantName%3D%2522Psyllocarpus%2Bgoiasensis%2522%26syn%3D1, and http://plants.jstor.org/stable/10.5555/al.ap.specimen.wisv0004270wis?searchUri=plantName%3D%2522Psyllocarpus%2Bgoiasensis%2522%26syn%3D1, respectively.

Digital images of BR, K, and M isolectotypes of *Psyllocarpus laricoides* var. γ *longicornu* available at http://plants.jstor.org/stable/10.5555/al.ap.specimen.br0000005325986?searchUri=plantName%3D%2522Psyllocarpus%2Blaricoides%2Bvar.%2Blongicornu%2522%26syn%3D1, http://plants.jstor.org/stable/10.5555/al.ap.specimen.k000470420?searchUri=plantName%3D%2522Psyllocarpus%2Blaricoides%2Bvar.%2Blongicornu%2522%26syn%3D1, and http://plants.jstor.org/stable/10.5555/al.ap.specimen.m0189211?searchUri=plantName%3D%2522Psyllocarpus%2Blaricoides%2Bvar.%2Blongicornu%2522%26syn%3D1, respectively.

Digital images of W paratypes of *Psyllocarpus goiasensis* J.H.Kirkbr. available at http://herbarium.univie.ac.at/database/detail.php?ID=1056921, http://herbarium.univie.ac.at/database/detail.php?ID=1056920, and http://herbarium.univie.ac.at/database/detail.php?ID=219632.

Digital image of M syntype of *Psyllocarpus laricoides* available at http://plants.jstor.org/stable/10.5555/al.ap.specimen.m0189221?searchUri=si%3D1%26plantName%3D%2522Psyllocarpus%2Blaricoides%2522%26syn%3D1.

Digital images of NY and W isotypes of *Crotalaria vespertilio* available at http://plants.jstor.org/stable/10.5555/al.ap.specimen.ny00006697?searchUri=filter%3Dname%26so%3Dps_group_by_genus_species%2Basc%26Query%3Dcrotalaria%2Bvespertilio and http://plants.jstor.org/stable/10.5555/al.ap.specimen.w0031489?searchUri=filter%3Dname%26so%3Dps_group_by_genus_species%2Basc%26Query%3Dcrotalaria%2Bvespertilio, respectively.

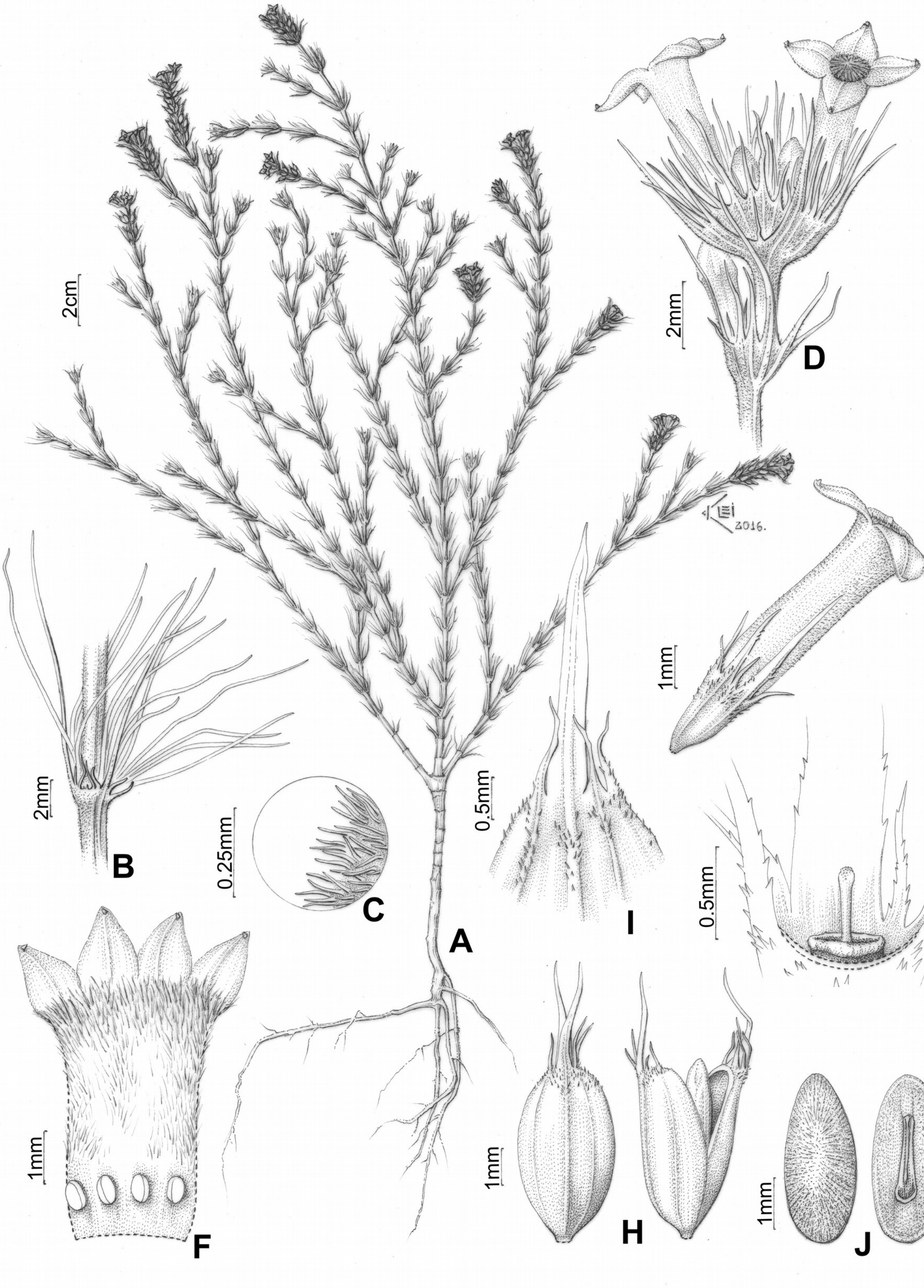
LEGENDS:

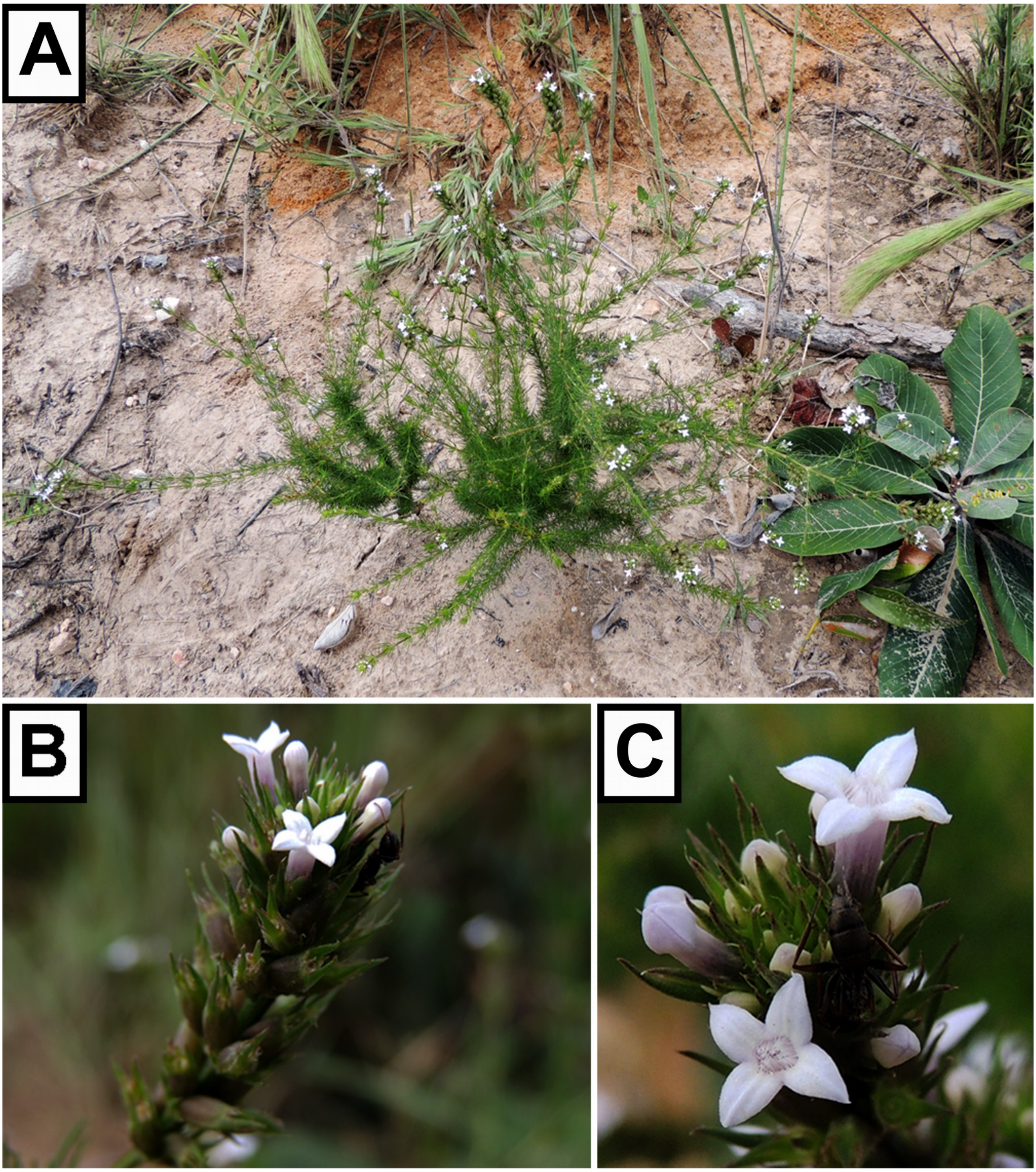
FIGURE 1. *Psyllocarpus goiasensis*. **A.** Habit. **B.** Stipule. **C.** Indumentum on the stipule. **D.** Apex

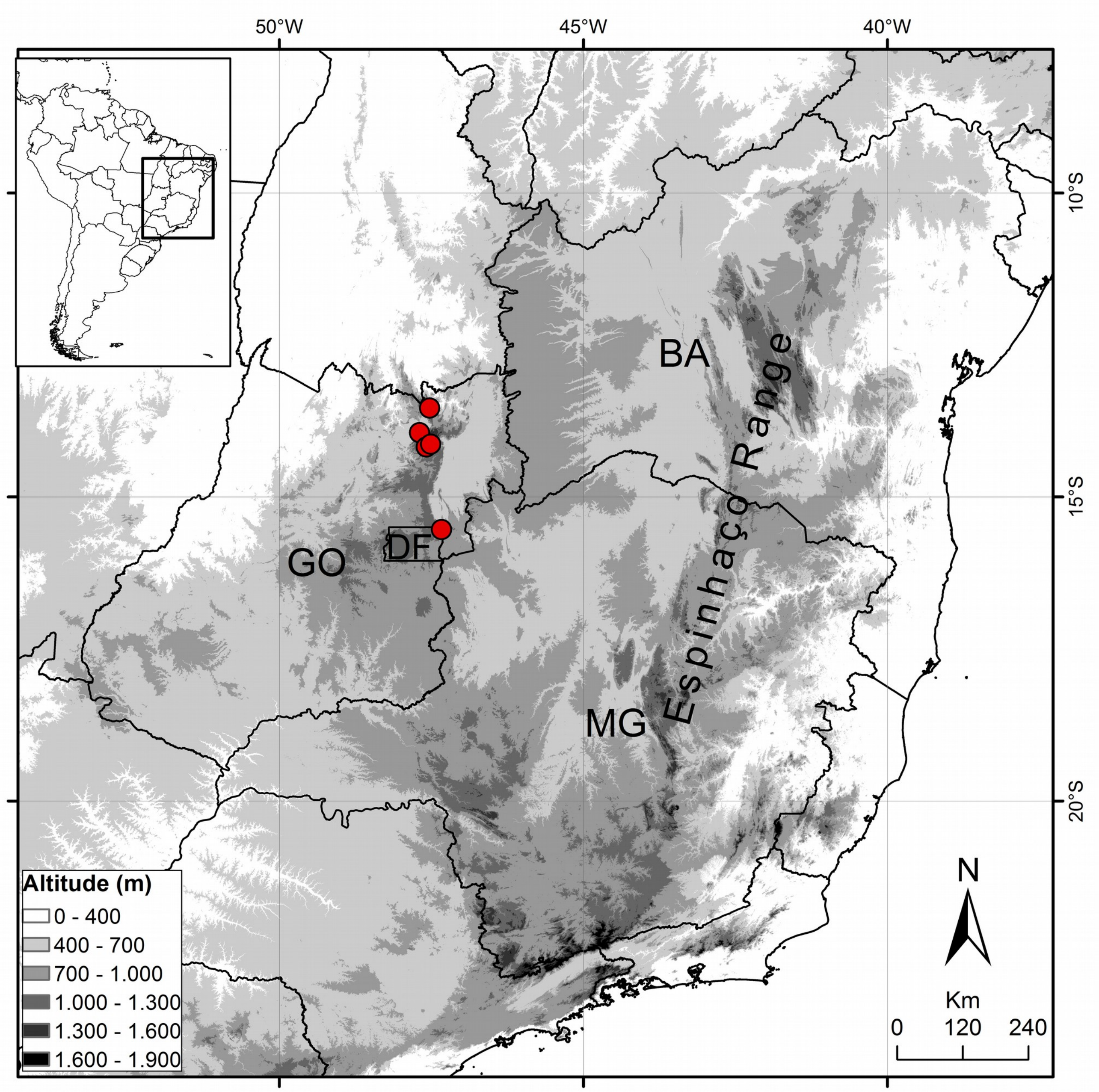
of flowering branch. **E.** Flower. **F.** Opened corolla. **G.** Nectariferous disc, style, and stigma. **H.** Capsules, dorsal and lateral view. **I.** Apex of the capsule, on dorsal view. **J.** Seeds, dorsal and ventral view. [based on *Carmo & Scatigna 352* (CTES, UEC)]. Illustration by Klei Sousa.

FIGURE 2. *Psyllocarpus goiasensis*. **A.** Individuals. **B.** Flowering branch. **C.** Flowers. (photographs by João Carmo at the Serra do Tombador, Goiás, Brazil, 4/14/2015).

MAP 1. Distribution map of *Psyllocarpus goiasensis* in the state of Goiás, Brazil, and its relative position to the Espinhaço Range, in the states of Minas Gerais and Bahia, where *Psyllocarpus laricoides* occurs. BA: Bahia; DF: Distrito Federal; GO: Goiás; MG: Minas Gerais.


2cm
A
2mm
B
0.25mm
C
2mm
D
1mm
E
1mm
F
0.5mm
G
1mm
H
0.5mm
I
1mm
J
2016.


A
B
C


50°W
45°W
40°W
10°S
15°S
20°S
BA
GO
DF
MG
Espinhaço Range
Altitude (m)
0 - 400
400 - 700
700 - 1.000
1.000 - 1.300
1.300 - 1.600
1.600 - 1.900
N
Km
0
120
240

IV

Carmo, J. A. M., Scalon, V. R., Calió, M. F., & Simões, A. O. 2017. Lectotypification of *Psyllocarpus schwackei* (Spermacoceae, Rubiaceae). Phytotaxa, 329: 185–186. https://doi.org/10.11646/phytotaxa.329.2.10

Lectotypification of *Psyllocarpus schwackei* (Spermacoceae, Rubiaceae)

JOÃO A.M. CARMO[1]*, VIVIANE R. SCALON[2], MARIA F. CALIÓ[3] & ANDRÉ O. SIMÕES[3]

[1]*Programa de Pós-Graduação em Biologia Vegetal, Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Monteiro Lobato 255, 13083-970, Campinas, São Paulo, Brazil.*
[2]*Instituto de Ciências Exatas e Biológicas, Universidade Federal de Ouro Preto, Morro do Cruzeiro s/n, 35400-000, Ouro Preto, Minas Gerais, Brazil.*
[3]*Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, Monteiro Lobato 255, 13083-862, Campinas, São Paulo, Brazil.*
**Author for correspondence: jmartinsdocarmo@gmail.com*

Psyllocarpus schwackei was described by Schumann (1898: 18), for which he cited a single collection, "in Brasiliae civitate Minas Geraes, locis arenosis in Serra do Cipo: Schwacke n, 8089, floret Aprili". Later, in a taxonomic revision of the genus, Kirkbride (1979) stated that the material studied by Schumann at the Botanical Museum in Berlin had been destroyed in the Second World War (Hiepko 1987), and that he was unable to locate any duplicates of this collection. He consulted a photograph of the specimen available in the Field Museum of Natural History type photograph series, negative number 896. Therefore, based upon the original description of the species, the photograph he analysed and his experience at the type locality, the Serra do Cipó, Minas Gerais state, he selected a neotype, the collection "Serra do Cipó, elev. ca. 1125 m, *Anderson et al. 36254* (neotype US; isoneotypes NY, UB)".

During a taxonomic study of *Psyllocarpus*, we discovered specimens from the original collection Schwacke 8089, deposited in the OUPR and BHCB herbaria, state of Minas Gerais, Brazil, rendering the neotypification made by Kirkbride (1979) superfluous. Therefore, the purpose of this paper is to lectotypify the name *Psyllocarpus schwackei*.

Psyllocarpus schwackei Schumann (1898: 18). **Type:—**BRAZIL. Minas Gerais: Serra do Cipó, March 1892, *C.A.W. Schwacke 8089* (lectotype, designated here: OUPR [OUPR10386; ex Herb. Magalhães Gomes 3474]!; isolectotype, BHCB [BHCB020828]!).

We have consulted the Berlin Negatives of Field Museum of Natural History, a collection of images originated in 1929, when J. Francis Macbride travelled to Europe to photograph herbarium specimens of nomenclatural types (Grimé & Plowman 1986), which are available on line (The Field Museum 2012). The negative number 896 (http://emuweb.fieldmuseum.org/botany/berDisplay.php?irn=229340&QueryPage=%2Fbotany%2Fsearch_berlin.php) corresponds to the original gathering of *Psyllocarpus schwackei*, and despite the information "Collector(s): C.A.W. Schwacke" and "Collector Number: 8089" on the webpage, the actual specimen used to produce the negative did not present a label, making it impossible to check the information cited by Schumann on the protologue. Nevertheless, we here treat this image as the negative of the original specimen once present in B.

The BHCB specimen carries only a typewritten label with some erroneous annotations. Its locality is "Diamantina" and date "1904", but collected by "Schwacke nº 8089". The OUPR specimen presents the annotations "ad Serra do Cipó (M. Geraes), ex Schwacke 8089, Mart. 1892, Off. Senna" handwritten on its label, thus matching the type locality, collector, and number mentioned on the protologue of the name. Therefore, we here select the specimen OUPR barcode OUPR10386 as the lectotype of *Psyllocarpus schwackei*. This specimen has a more complete material in comparison to the one deposited in BHCB (isolectotype), presenting more branches, leaves and mature flowers, whereas the BHCB specimen presents a single branch with a few leaves, flower buds and immature fruits.

According to Stafleu & Cowan (1985) Schwacke worked as travelling scientist for the Rio de Janeiro National Museum from 1874 to 1891, and as professor of botany and director at the School of Pharmacy in Ouro Preto, Minas Gerais, from 1891 to 1904, where some of his collections were deposited in the EM herbarium, which was later incorporated in OUPR in 1986 (Thiers 2017). Most of his collections are deposited in R and RB though (Stafleu & Cowan 1985). He has also sent duplicates to the extinct BHMG, which was incorporated by the BHCB (Thiers 2017), as well as to BR, C, G, GOET, IAC, NY, P, SP, U, US, and W (Stafleu & Cowan 1985). We have consulted these herbaria, in person (IAC, NY, R, RB, SP, and US) or online (BR, C, G, GOET, P, U, and W) at Global Plants on JSTOR (JSTOR 2017) and Virtual Herbaria (Herbarium WU 2017), but have not found any other collection of *Psyllocarpus* made by Schwacke.

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Conclusão

O gênero *Psyllocarpus* deve ser circunscrito de acordo com o seu conceito original (Martius & Zuccarini 1824a, b). Tanto *P.* seção *Amazonica* quanto *P. densifolius* não pertencem ao gênero, embora as suas posições filogenéticas e identidades ainda sejam incertas. Mais estudos abordando estes taxons são necessários para responder a estas questões, a partir da utilização de mais caracteres (NGS) e abordagens que solucionem as diferenças topológicas de árvores provenientes de diferentes genomas, como por exemplo métodos de coalescência para a reconstrução de árvores de espécies, bem como para elucidar as relações interespecíficas em *Psyllocarpus*. Embora este gênero seja composto por relativamente poucas espécies e tenha sido revisado um tanto quanto recentemente (Kirkbride 1979), é provável que sua real diversidade ainda seja subamostrada, já que novidades foram encontradas durante a elaboração deste estudo.

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Anexo 1. Autorização Ética

Ministério do Meio Ambiente
CONSELHO DE GESTÃO DO PATRIMÔNIO GENÉTICO
SISTEMA NACIONAL DE GESTÃO DO PATRIMÔNIO GENÉTICO E DO CONHECIMENTO TRADICIONAL ASSOCIADO

Comprovante de Cadastro de Acesso

Cadastro nº A067FE8

A atividade de acesso ao Patrimônio Genético, nos termos abaixo resumida, foi cadastrada no SisGen, em atendimento ao previsto na Lei nº 13.123/2015 e seus regulamentos.

Número do cadastro: **A067FE8**
Usuário: **João Afonso Martins do Carmo**
CPF/CNPJ: **092.611.036-50**
Objeto do Acesso: **Patrimônio Genético**
Finalidade do Acesso: **Pesquisa**

Espécie

Psyllocarpus laricoides

Título da Atividade: **ESTUDOS TAXONÔMICOS E FILOGENÉTICOS EM PSYLLOCARPUS MART. & ZUCC. (RUBIACEAE: SPERMACOCEAE), UM GÊNERO ENDÊMICO DO BRASIL**

Equipe

João Afonso Martins do Carmo	**UNICAMP**

Data do Cadastro: **06/03/2020 15:51:18**
Situação do Cadastro: **Concluído**

Conselho de Gestão do Patrimônio Genético
Situação cadastral conforme consulta ao SisGen em **17:17** de **06/03/2020**.

SISTEMA NACIONAL DE GESTÃO DO PATRIMÔNIO GENÉTICO E DO CONHECIMENTO TRADICIONAL ASSOCIADO - SISGEN

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Campinas, 26 de maio de 2020

Assinatura :

João Afonso Martins do Carmo

Nome do(a) autor(a): **João Afonso Martins do Carmo**
RG n.° MG-15.631.309

Assinatura :

Nome do(a) orientador(a): **André Olmos Simões**
RG n.° 263639824