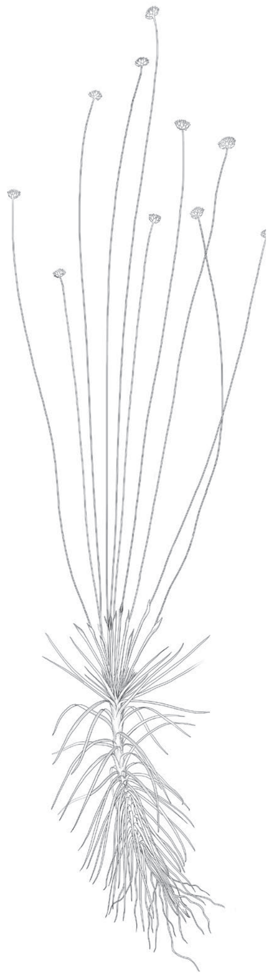
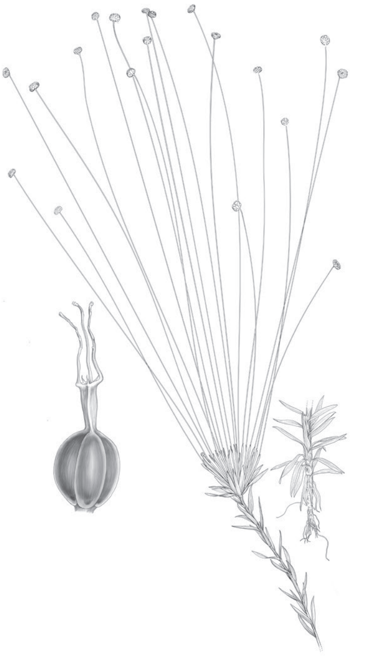
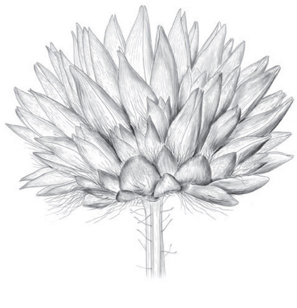
Maurício Takashi Coutinho Watanabe

Sistemática de *Syngonanthus*
(Eriocaulaceae)







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Sistemática de *Syngonanthus*

Systematics of *Syngonanthus*

Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências, na Área de Botânica.

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Aos meus pais e aos meus mestres,
com carinho

“...Olha o pião do tempo com sua ponta afiada
indo aprontando no quengo deste bando de guris
só acredita quem souber
levou um tombo e não parou de rodar
veloz
do lado errado da palma da nossa mão”

Gonzaguinha (Belo Balão)

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Índice

Resumo Geral

Esta tese consta de três capítulos nos quais são abordados questões relacionadas à sistemática de *Syngonanthus* (Eriocaulaceae). No primeiro capítulo são apresentadas novidades taxonômicas, com descrições de novas espécies do gênero, incluindo a primeira espécie de flor exclusivamente trímera e bissexual da família. No segundo capítulo, uma análise filogenética com amostragem expandida de *Syngonanthus* é apresentada, para tentar elucidar questões relacionadas ao posicionamento do gênero em Paepalanthoideae; verificação e sustentação de classificações infragenéricas anteriores; e correlação de grupos bem sustentados com padrões morfológicos. O último capítulo é composto por uma revisão taxonômica de *Syngonanthus* sect. *Carphocephalus*, um dos grupos morfologicamente mais complexos no gênero. A revisão constou de um total de 13 espécies, nos quais foram propostos novos sinônimos, lectotipificações e descrição de novos táxons.

Abstract

This thesis consists of three parts involving systematics of *Syngonanthus* (Eriocaulaceae). The chapter I consists on taxonomic novelties, with descriptions of new species, including the first species with exclusively trimerous and bisexual flowers in the family. The second chapter is the phylogenetic study of *Syngonanthus* with expanded sampling This study is an attempt to clarify issues related to the placement of *Syngonanthus* in Paepalanthoideae; to check the support and previous infrageneric classifications; and to correlate well supported groups with morphological patterns. The chapter three consists on a taxonomic revision of *Syngonanthus* sect. *Carphocephalus*, one of the most complex groups in the genus. The revision consisted of a total of 13 species. It has been proposed new synonyms, lectotypifications and description of new taxa.

Introdução Geral

Caracterização geral e breve histórico

Com cerca de 1200 espécies distribuídas em 10 gêneros, Eriocaulaceae Martinov são monocotiledôneas de distribuição pantropical. Morfologicamente são bem caracterizadas pelo hábito herbáceo, geralmente apresentando uma roseta basal, de onde emergem escapos portando as inflorescências em forma de capítulo, que contêm flores unissexuais, com raríssimos casos de flores bissexuais (Giulietti & Hensold 1990).

A primeira documentação da família foi realizada por Linneaus (1754), ao descrever *Eriocaulon* L. Em pouco menos de um século, a família passou por duas grandes revisões. A primeira realizada por Bongard (1831), na qual descreveu inicialmente cerca de 80 espécies em *Eriocaulon*. O segundo grande estudo taxonômico foi realizado por Martius (1835), que sinonimizou alguns gêneros em *Eriocaulon*, reconheceu o gênero monoespecífico *Tonina* Aubl. descrito por Aublet (1775) e descreveu os gêneros *Philodice* Mart. e *Paepalanthus* Mart. Pouco depois, Kunth (1841) descreveu *Lachnocaulon* Kunth, gênero restrito à América do Norte. Koërnicke (1854) realizou a segunda revisão para a família e ampliou o conhecimento das espécies neotropicais, especialmente brasileiras (Koërnicke, 1863). Além disso, descreveu *Mesanthemum* Koern. e classificou a família em duas tribos (Eriocaulae e Paepalanthae), acomodando os gêneros de acordo com suas afinidades morfológicas. Ruhland (1900, 1903) realizou a última grande revisão para toda a família, sugerindo mudanças taxonômicas e nomenclaturais adotadas até os dias atuais. Na ocasião, foram propostas duas subfamílias, baseando-se nas mesmas características empregadas por Koernicke (1863) para a delimitação de suas tribos e alocando os mesmos gêneros. Eriocauloideae apresentaria o número de pétalas igual ao dobro do número de estames, pétalas glandulosas e gineceu sem apêndices. Os representantes de Paepalanthoideae possuiriam número de estames igual (ou inferior) ao número de pétalas, pétalas eglandulosas e gineceu com apêndices. Os novos gêneros descritos nesta obra (*Blastocaulon* Ruhland, *Leiothrix* Ruhland e *Syngonanthus* Ruhland) estariam inclusos nesta última subfamília. Dentre as contribuições que se seguiram, deve-se citar Silveira (1908, 1928), que descreveu dezenas de espécies brasileiras; Herzog (1931) que descreveu *Rodonanthus* Herzog; Sano (2004) que elevou *Actinocephalus* (Koern.) Sano à categoria genérica e o recente restabelecimento de *Comanthera* L.B. SM (Parra & al. 2010).

Popularmente, as Eriocaulaceae são conhecidas como "sempre-vivas" pelo fato de manterem a aparência conservada mesmo após sua retirada da natureza. A comercialização e a exportação destas plantas são estimuladas principalmente pela alta durabilidade e beleza das inflorescências, utilizadas para ornamentação de ambientes (Giulietti & al. 1988) e até mesmo na confecção de acessórios (Schmidt & al. 2007).

Dessa maneira, a importância econômica da família reside praticamente no extrativismo, que é realizado, sobretudo, em municípios localizados na Cadeia do Espinhaço (BA e MG), e que surgiu como resposta alternativa ao declínio da atividade mineradora na região. Tal movimentação econômica nas cidades envolvidas gera empregos durante todo o processo de comercialização e constitui uma importante fonte de renda para as comunidades coletoras de sempre-vivas (Giulietti & al. 1988; Giulietti & al. 1996). Contudo, frequentemente, as coletas de sempre-vivas acontecem de forma precoce, antes mesmo da maturação completa dos frutos, acarretando numa diminuição crítica das populações naturais. Tal exploração caótica e desenfreada levou muitas espécies ao risco iminente de extinção (Giulietti & al. 1996), o que tem conduzido a uma série de trabalhos de conservação e conscientização com as comunidades coletoras, apoiando a adoção de formas de manejo racional (Schmidt & al. 2007).

Quanto à distribuição pantropical da família, esta se deve, principalmente, a *Eriocaulon*, gênero de ampla distribuição com ca. 400 espécies, algumas ocorrendo em áreas temperadas (Giulietti & Hensold 1990; Stützel 1998). Os demais gêneros apresentam limites mais restritos à América e/ou África, com vasta diversidade concentrada principalmente nas elevadas altitudes da Cadeia do Espinhaço (Giulietti & al. 1987; Giulietti & Hensold 1990), região conhecida pela riqueza dos campos rupestres e por sua alta taxa de endemismos de flora e fauna (Harley 1995), o que se verifica também nas espécies da família (Giulietti & al. 2000). Assim, a Cadeia do Espinhaço constitui-se como o principal centro de diversidade de Eriocaulaceae, com aprox. 60% das espécies da família restritas a essa região. Outro centro de diversidade importante está localizado nas regiões dos Tepuis venezuelanos (Giulietti & Pirani 1988).

O gênero *Syngonanthus*

Syngonanthus apresenta distribuição disjunta, possuindo grande diversidade de espécies nas Américas (especialmente concentradas na Cadeia do Espinhaço) além de dezoito taxa ocorrentes na África. É caracterizado pelas flores isostêmones, anteras bitecas e pétalas das flores pistiladas unidas na região mediana (Giulietti & Hensold 1990). Ruhland (1900) descreveu o gênero a partir de espécies antes incluídas em *Paepalanthus*. Um sistema de classificação infragenérico também foi proposto por Ruhland (1903): tendo como referência subgêneros de *Paepalanthus*, o autor propôs cinco seções. A maior delas foi *S.* sect. *Dimorphocaulon*, sinonimizada em *S.* sect. *Syngonanthus* por Parra & Giulietti (1997), por conter a espécie-tipo do gênero. Conta com aproximadamente 130 espécies e compreende toda distribuição geográfica do gênero (Giulietti & Hensold 1990). Já *S.* sect *Eulepis* e *S* sect. *Thysanocephalus* apresentam distribuição somente em países sul-americanos como Brasil, Colômbia, Guianas e Venezuela (Giulietti & Hensold 1990) e foram recentemente re-circunscritos integrando subgêneros do restabelecido *Comanthera* (Parra & al. 2010). A única espécie pertencente à *S.* sect. *Chalarocaulon*, *S. macrocaulon* Ruhland, foi sinonimizada em *S. anomalus* (Köern.) Ruhland. (*S.* sect. *Carphocephalus*) por Hensold (1999).

Syngonanthus sect. *Carphocephalus* também possui uma distribuição limitada à América do Sul. Nessa seção, encontra-se a espécie com a distribuição geográfica mais ampla do gênero: *S. caulescens* (Poir.) Ruhland, com pouco mais de uma dezena de variedades descritas somente para este táxon, refletindo a complexidade morfológica desse grupo. A seção é caracterizada por apresentar espécies com flores estaminadas de corola espessada e ápice involuto, além das brácteas involucrais não ultrapassando a altura das flores.

A Sistemática Filogenética nos estudos de Eriocaulaceae

Nas últimas décadas, o estudo das relações filogenéticas entre os organismos tem alcançado avanços significativos, com alterações expressivas na classificação dos táxons. A incorporação de dados moleculares às filogenias (Judd & al. 2002) forneceu subsídios para a realização de análises mais robustas e tornaram os trabalhos taxonômicos mais consistentes. Isso se deve, em parte, à adoção dos princípios das classificações filogenéticas em que todos os táxons devem ser monofiléticos, gerando um sistema de nomes que busca refletir a filogenia em todos os níveis (Amorim 2002).

Eriocaulaceae tem passado por dinamismos em sua classificação. Anteriormente, a família era posicionada em uma ordem exclusiva (Eriocaulales) (Takhtajan 1980; Cronquist 1988) tendo como base somente os caracteres morfológicos. Estudos mais recentes, utilizando marcadores moleculares, além dos próprios dados morfológicos, têm apontado a família como um grupo monofilético demonstrando grandes afinidades com Xyridaceae (Chase & al. 1995; Linder & Kellogg 1995). Atualmente, está inclusa na ordem Poales (APG 2009) e estudos cladísticos na família com as mais diversas abordagens foram realizados (Giulietti & al. 1995; Giulietti & al. 2000; Unwin 2004). A própria condição monofilética das subfamílias já foi testada por Unwin (2004) e Andrade & al. (2010), corroborando as hipóteses precursoras baseadas somente em dados morfológicos. Em relação aos estudos envolvendo *Syngonanthus s.l.*, Giulietti & al. (1995), em suas análises cladísticas com dados morfológicos, confirmaram seu monofiletismo (com a inclusão informal de *Philodice*) e obtiveram um bom suporte para *Leiothrix* como seu provável grupo-irmão. Giulietti & al. (2000), com dados anatômicos e morfológicos, realizaram novas análises cladísticas com a família e, novamente, confirmaram o monofiletismo e as relações mais próximas entre *Leiothrix* e *Syngonanthus s.l.*. No mesmo trabalho, ainda foi possível observar a formação de um clado entre *S.* sect. *Eulepis* e *S.* sect. *Thysanocephalus*, sustentado por caracteres anatômicos. Estes resultados também são congruentes com os obtidos por Ricci & al. (1996), em que fitoquimicamente *S.* sect. *Eulepis* e *S.* sect. *Thysanocephalus* têm mais afinidades por partilharem, como derivados da luteolina, os compostos C-glicosídeos, ao passo que *S.* sect. *Syngonanthus* e *S.* sect. *Carphocephalus* possuem compostos de 6-hidroxiluteolina. Unwin (2004) também encontrou resultados semelhantes aos anteriores, utilizando dados moleculares, porém sem grandes resoluções em relação às seções (fig.1). Entretanto, Andrade & al. (2010), também valendo-se de marcadores moleculares, observaram que *Syngonanthus* constitui um grupo polifilético (fig.2), tal como circunscrito. A análise infra-genérica apontou novamente um grupo monofilético formado por *S.* sect *Eulepis* e *S.* sect. *Thysanocephalus*, como havia sido sustentado em outros trabalhos (Giulietti & al. 2000; Parra 2000). Com base nesses resultados, foi proposto que tais seções fossem delimitadas em um novo gênero, tendo assim restabelecido o nome *Comanthera* (Parra & al. 2010). *S.* sect. *Syngonanthus*, *S.* sect. *Carphocephalus* e *Philodice* formaram um grupo monofilético com alta sustentação. Como reflexo dos dados químicos, morfológicos e moleculares, foi proposto o reconhecimento de um único gênero: *Philodice*, uma vez que *Syngonanthus* é o nome posterior. Uma proposta de conservação do nome *Syngonanthus* (Giulietti & al. 2009) foi encaminhada, levando-se em consideração que este nome é mais amplamente reconhecido na família. A proposta também envolve questões práticas, já que *Philodice* é um gênero monoespecífico e *Syngonanthus,* em sua nova circunscrição, apresentava ca. 120 espécies, o que forjaria mudanças nomenclaturais em um número muito maior de espécies. Echternarcht & al. (2014), em uma análise filogenética mais exploratória envolvendo os gêneros *Comanthera* e *Syngonathus*, também encontrou resultados bastante consistentes a respeito da condição monofilética desses gêneros. No entanto, *S.* sect. *syngonanthus* revelou-se parafilética, ao passo que *S.* sect. *Carphocephalus* mostrou-se polifilética, necessitando um maior refinamento de suporte, amostragem e resolução destes grupos para maiores decisões taxonômicas. A relação entre esses dois gêneros também não foi claramente definida. Enquanto Echternacht et al. (2014) encontraram uma relação mais estreita entre *Syngonanthus* e *Comanthera*, Giulietti et al. (2012), em seus resultados, demonstraram que *Syngonanthus* na verdade é um gênero que divergiu primeiro em Paepalanthioideae, sendo irmão de um grande clado contendo as demais espécies da subfamília. Estas hipóteses foram testadas e são apresentadas no capítulo 2 desta tese.

Novas perspectivas têm sido cada vez mais abordadas em Eriocaulaceae e têm elucidado muitas questões com respeito à distribuição, diversificação e às afinidades filogenéticas entre os táxons. Trovó & al. (2013), em estudo abrangendo toda a subfamília Paepalanthoideae com ênfase em *Paepalanthus*, corroborou várias hipóteses filogenéticas levantadas por Andrade & al. (2010) e incrementou suas análises com reconstruções biogeográficas, sugerindo que os padrões de distribuição geográfica encontrados na família podem ter sido gerados por processos de vicariância e por poucos eventos de dispersão a longa distância.

Sob esta nova perspectiva e utilizando abordagens até então não utilizadas para a família como trabalhos de polinização (Ramos & al. 2005; Oriani & al. 2009) e morfometria (Pereira & al. 2007; Trovó & al. 2008; Watanabe 2009), a família tem ganhado um maior dinamismo com muitos grupos ainda por ser explorados sob as mais diversas metodologias. Dessa maneira, os estudos apresentados nessa tese pretendem elucidar algumas questões pendentes em *Syngonanthus*, como por exemplo: sua relação com os demais gêneros em Paepalanthoideae; as relações filogenéticas entre as espécies; delimitação e identidade de grupos no gênero; e revisão das espécies da seção *Carphocephalus*, um grupo morfologicamente complexo e "obscuro".

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Chapter One

Novelties in *Syngonanthus*

Chapter One: Part one

Two new and endangered species of *Syngonanthus* (Eriocaulaceae) from Chapada dos Veadeiros, Goiás, Brazil.[1]

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[1] Artigo submetido à Phytotaxa. Aceito com pequenas revisões em 12 de abril de 2015. Autores: Mauricio T. C. Watanabe, Lívia Echternacht, Nancy Hensold & Paulo Takeo Sano.

Abstract

We describe and illustrate two new species of *Syngonanthus* from Chapada dos Veadeiros (Central highlands of Brazil), an area known for its high number of endemic and threatened species, such as those described here. These species have a restricted distribution and inhabit critical areas. *Syngonanthus incurvifolius* has not been collected since 1994 and is critically endangered; *Syngonanthus vittatus* is known only from a small somewhat disturbed area, on private property, and is endangered. Evaluation of threatened status was provided by CNCFlora, the IUCN Red List Authority in Brazil.

Key words: Brazil, Cerrado, Conservation, Everlasting plants, Monocotyledons, new species, Taxonomy.

Resumo

Duas novas espécies de *Syngonanthus* são descritas para a Chapada dos Veadeiros, na região do Brasil Central. Conhecida pela grande quantidade de endemismos, esta área abriga muitas espécies ameaçadas como as descritas aqui. Não há Registro de coleta para *Syngonanthus incurvifolius* desde 1994, que é criticamente ameaçada de extinção; *Syngonanthus vittatus* é uma espécie conhecida apenas para pequenas áreas em propriedades particulares e está ameaçada. A avaliação do estado de ameaça foi provida pelo CNCFlora, a autoridade da Lista Vermelha da IUCN no Brasil.

Palavras chave: Brasil, Cerrado, Conservação, Monocotiledôneas, espécies novas, Sempre-vivas, Taxonomia.

Introduction

Syngonanthus Ruhland (1900: 487) is characterized by pistillate flowers with petals fused in the middle and free at the base and apex, a character also attributed to *Mesanthemun* Körn. (1856:572) and *Comanthera* L.B.Sm. (1937:38) *emend.* Parra *et al.* (2010:1136), a genus recently reestablished and recircumscribed based on molecular and morphological data (Giulietti *et al.* 2000; Andrade *et al.* 2010; Echternacht *et al.* 2014; Echternacht *et al.* 2015). The features that distinguish *Syngonanthus* from *Comanthera* are petals shorter than sepals in pistillate flowers (*vs.* pistillate flowers with sepals shorter than petals), petals fused in the distal part with short lobes (*vs.* fused in a narrow region leaving long free apices), seed surface reticulate (*vs.* rough) (Giulietti *et al.* 2012, Echternacht *et al.* 2014) and predominance of flavonoids as 6–hydroxyluteoline derivatives (*vs.* C-glucosides) (Ricci *et al.* 1996). *Syngonanthus* contains approximately 110 species, distributed in Africa and the Neotropics. Species diversity is concentrated in the mountains of the Espinhaço Range, in Minas Gerais and Bahia States; in Chapada dos Veadeiros, in Goiás State; and in the Amazonian savannas (Echternacht 2012), where micro-endemic species are common, some of them restricted to a few mountaintops. However, some species are widespread, accounting in large part for the distribution of the genus from southern South America to northern Central America. In Brazil, the genus is well represented in open areas, especially on sandy streambanks, grasslands and rock outcrops.

The new species described here occur in Alto Paraíso de Goiás municipality (Goiás State, Central Brazil) on the Veadeiros Plateau ("Chapada dos Veadeiros") (FIG. 1). This region has a species-rich flora and high levels of endemism, especially in Eriocaulaceae, Cyperaceae, Poaceae and Xyridaceae (Munhoz & Felfili 2006) at elevations ranging from 800 to 1650 m. This plateau encompasses open grass savannas, *campo rupestre* vegetation and *Cerrado* woodlands located among rock outcrops and over shallow, acid soils derived from sandstone and quartzite rocks (Munhoz & Felfili 2006; Simon *et al.* 2010; Trovó & Sano 2011). This region corresponds to a small portion of the Brazilian Cerrado hotspot under constant threat. An aggravating factor is that these new species occur outside protected areas of Chapada dos Veadeiros National Park (PNCV), near to tourist areas and cattle grazing. Even now, new species are still being described and discovered in this region, including recent examples in Eriocaulaceae (Trovó & Sano 2011; Echternacht *et al.* 2015). This fact shows that Chapada dos Veadeiros is still in need of basic taxonomic studies and its biodiversity is still poorly known (Simon et al. 2010).

Syngonanthus is divided into two sections, *S.* sect. *Syngonanthus* and *S.* sect. *Carphocephalus*; the former includes most of the morphological and species diversity and the latter includes species with spongy petals, usually free filaments, and elongated vegetative stems. *Syngonanthus* sect. *Syngonanthus* appears paraphyletic, encompassing a polyphyletic *S.* sect. *Carphocephalus* (Echternacht *et al.* 2014), but further phylogenetic studies are necessary to provide stable phylogenies and a corresponding taxonomy (Watanabe *et al.* in prep.). The species described herein are included in the morphological concept of *S.* sect. *Syngonanthus* and, more precisely, are similar to the species of *Syngonanthus* previously placed within *Paepalanthus* Martius (1834:28) subg. *Andraspidopsis* Koern. Ruhland (1903) did the last worldwide revision for the family and transferred these species from *Paepalanthus* to *Syngonanthus*.

To avoid any confusion, we would like to explain that several of the "varieties" that will be mentioned here in the text are to be treated as different species. A taxonomic treatment is being done to change the status of these taxa by Echternacht *et al.* (in prep.).

Taxonomic treatment

Syngonanthus incurvifolius M.T.C.Watan. & Echternacht, *sp. nov.* Type:— BRAZIL. Goiás: Alto Paraíso de Goiás, ca. 15 km south of Veadeiros, road to São João da Aliança, cerrado on outcrops, in wet sand, adjacent campo, 1000 m alt., 19 March 1969, *H. S. Irwin*, *R. Reis dos Santos*, *R. Souza & S. F. da Fonseca 24648* (Holotype UB!, Isotypes F!, MO!, NY! RB!). Figures 2 A–G & 3.

Syngonanthus incurvifolius differs from all other New World species of *Syngonanthus* by the rosette leaves incurved from the middle to the apex. It differs from *Syngonanthus arenarius*, the most similar species, by pistillate flowers with cream sepals and adpressed trichomes on the leaves. *Syngonanthus incurvifolius* is also similar to *Syngonanthus densifolius* var. *majus* but differs by pistillate flowers with pilose petals, sepals cream with a light castaneous longitudinal band, and individuals smaller.

Perennial herbs, 7.5–18.0 cm tall. *Roots* 0.75–1.4 mm in diameter, cream-colored, spongy. *Rosettes* 1.7–3.4 cm in diameter. *Rhizome* 1.0–2.5(–5) cm × 2.5–7.5 mm, horizontal to oblique, often branched, tomentose to villous, with white, dense and interwoven trichomes ca. 1 cm long; each branch giving rise to a rosette of leaves, each rosette bearing 1–5 synflorescences. *Leaves* 0.5–2.0

cm × 0.75–1.20 mm, linear, flat to semi-terete, apex acute to round, base truncate, sinuous, recurved at base, becoming incurved from the middle to the apex, firm to rigid, striate adaxially with 3–veins prominent, or only the midvein perceptible in young leaves; densely pilose adaxially, glabrescent to pilose abaxially, with adpressed hairs, and patent, simple hairs ca. 0.5 mm long; basal sheath not enlarged. *Synflorescences* with a primary axis bearing a lax umbel of 1–18 inflorescences at the apex. *Synflorescence axes* 2–8 cm long, 0.2–1.0 mm in diameter, emerging from the center of the rosette, erect to curved, brown, sometimes with a dark-reddish tinge, glabrescent to pilose with simple filamentous trichomes ca. 0.3 mm long. *Bracts of synflorescence axis* restricted to the apex, 0.2–3.0 cm × 0.5 mm, whorled and numerous, patent, progressively elongating from the outer toward the inner series, linear to narrowly lanceolate, apex acute, erect to uncinate, pubescent on both surfaces with adpressed trichomes, and patent, capitate and simple, filamentous trichomes, capitate trichomes mostly on abaxial surface, simple trichomes concentrated at margins. *Inflorescences* composed of a closed spathe subtending a scape with a capitulum at the apex. *Spathes* 1–4 cm long, chartaceous, cylindrical, lax at apex, obliquely opened, apex acute to obtuse, erect to recurved, tip erect to uncinate, margin entire, not involute, glabrous adaxially, pubescent abaxially with capitate and simple, filamentous trichomes. *Scapes* erect, 3–12 cm long, green to straw-colored with age, 3–costate, pilose, pubescent near the apex with erect to patent, simple and capitate hairs. *Capitula* 4–8 mm in diameter, radiate. *Involucral bracts* in 5–7 series, castaneous, reddish-brown to brown, sometimes with a lighter stramineous longitudinal band in the middle and on the margins, glabrous on adaxial surface, pilose to glabrescent abaxially, ciliate, with simple filamentous hairs, rarely also capitate hairs, these concentrated at the apex, ca. 0.3 mm long; external series 1.0–1.8 × 0.5–0.8 mm, triangular to ovate, apex acute, progressively longer toward the internal series, middle series ca. 2.5–3.0 × 0.9–1.2 mm, obovate, apex acute to obtuse, internal series 2.5–3.0 × 0.3–0.7 mm, equaling the flower height, elliptic to slightly oblanceolate, apex acute to obtuse, sometimes membranous, lighter-colored than the external series; receptacle obconic, pilose. *Floral bracts absent*. *Flowers* 3–merous, 40–100 per capitulum, the staminate and pistillate generally equal in number, with contrasting colors, staminate flowers darker and concentrated at the border of the capitulum or mixed. *Staminate flowers* with pedicels 0.5–1.0 mm long, pilose in the bottom part of pedicel with simple trichomes ca. 1 mm long; sepals 1.5–2.0 mm long, coppery brown, shortly fused at base, concave, membranous, the sepals slightly different from each other, or two sepals similar to each other and a third different, falcate-asymmetrical, oblanceolate, elliptic or irregular-subspathulate, apex mucronate, cuspidate, rounded or obtuse to acute, glabrous adaxially, pubescent abaxially, especially at apex and margin, with simple filamentous hairs ca. 0.4 mm long; petals 1–2 mm long, hyaline, membranous, fused, tubulose, lobes obtuse to rounded, involute after anthesis, glabrous; stamens adnate to the petals at base, anthers ca. 0.3 mm long, cream to yellowish; anthophore ca. 0.3 mm long; pistillodes 3, ca. 0.3 mm long, clavate, papillose at apex. *Pistillate flowers* 2–3 mm long, including pedicels; pedicels 0.4–1.0 mm long, with filamentous hairs at insertion with receptacle, actinomorphic; sepals equaling the petal height, 1.2–2.0 mm long, oblong to widely ovate, concave, apex acute, base thickened, free, white with a light castaneous longitudinal band, adaxially glabrous, abaxially pubescent near the apex, ciliate, with simple filamentous hairs up to 0.5 mm long; petals about equaling the sepals, 1–2 mm long, linear to oblong, fused at the upper half, free at base and at the very top, lobe triangular, apex acute, membranous, white to hyaline when hydrated, pilose with simple filamentous hairs up to 0.5 mm; gynoecium ca. 2 mm long; ovary 0.4–0.6 mm long; style column ca. 0.2 mm long, cream-colored to castaneous; appendages ca. 0.4 mm long, the glandular apex capitate; stigmatic branches simple, ca. 1.5 mm long. *Seed* 0.4–0.6 × 0.2–0.3 mm, ellipsoid, brown-colored.

Etymology:— The specific epithet refers to the orientation of the rosette leaves, which are curved inward and upward at the distal middle, a unique feature within Brazilian *Syngonanthus*. Only *Syngonanthus wahlbergii* Ruhland (1903:247) in Africa has leaves like this.

Notes and taxonomic affinities:— Several species share a similar architecture with *Syngonanthus incurvifolius*, including: a rhizome with apical rosettes of leaves, bearing synflorescences with verticillate bracts at the apex and scapes arranged in lax umbels. The following taxa also share dark and pilose involucral bracts (FIG 3H), usually with a lighter longitudinal band abaxially: *Syngonanthus arenarius* (Gardner) Ruhland (1903:260), *S. densifolius* var. *brachyphyllus* Moldenke (1984: 372), *S. densifolius* var. *majus* Moldenke (1972:499), and *S. vittatus,* the new species described here below. *Syngonanthus densifolius* var. *majus* and *S. densifolius* var. *brachyphyllus*, actually do not belong to *S. densifolius*, which possess golden to cream, glabrous involucral bracts, and shall be elevated to species status (Echternacht *et al.* in prep.). We consider these five taxa to form a cohesive morphological group due to the characters mentioned above. All of them, except *S. arenarius*, occur in Chapada dos Veadeiros and they are possibly sympatric.

Syngonanthus incurvifolius also shares with these four taxa an unusual floral trait: sepals of staminate flowers are always clearly asymmetrical (FIG. 3D; 3F). The three sepals might differ in form and curvature or two might be similar and the third different.

Syngonanthus incurvifolius differs from the congeneric species that have synflorescences by the remarkable form of the rosette leaves, which are recurved at base and incurved at the upper half. This feature persists even after diaphanization. *Syngonanthus densifolius* var. *brachyphyllus* can be easily distinguished from *S. incurvifolius* by its broader leaves (ca. 2–5 *vs.* 0.5–2 mm), with arachnoid trichomes on the adaxial surface (*vs.* not arachnoid), which is reticulate (*vs.* striate), and leaf bases achlorophyllous and pale (*vs.* chlorophyllous and green) (FIG. 3C). *Syngonanthus densifolius* var. *majus* differs by pistillate flowers with glabrous petals (*vs.* pilose), and darker sepals, light-brown at the upper half (FIG. 3G; 3J) (*vs.* cream with a longitudinal light castaneous band); moreover, individuals are bigger than *S. incurvifolius* and the rosette leaves are erect and flexuous. *Syngonanthus arenarius* var. *arenarius* shares with *S. incurvifolius* the small size and pilose petals of pistillate flowers (FIG. 3E; 3I); it differs by the cup-shaped bracts of the synflorescence (equal size), which are fewer (*vs.* progressively elongating from the outer toward the inner series and more numerous), and pistillate flowers with sepals cream at base and dark reddish-brown on the upper half (*vs.* cream with a longitudinal light castaneous band). *Syngonanthus incurvifolius* also differs from *S. vittatus* by the synflorescence axis bearing bracts only at the apex (*vs.* tiny bracts scattered along axis), the petals of the pistillate flowers pilose (*vs.* glabrous), and the involucral bracts of the middle series obovate (*vs.* narrow-elliptic).

Syngonanthus incurvifolius has been determined as *S. densifolius* var. *pilosior* Silveira (1928:320) in some herbaria. Actually, *S. densifolius* var. *pilosior* is probably a synonym of *S. anthemiflorus* var. *similis* (Ruhland) L.R.Parra & Giul. (1997:228) (Echternacht 2012), which can be easily distinguished from *S. incurvifolius* by the involucral bracts surpassing the capitulum disc (*vs.* not surpassing), the outer series golden to straw-colored and the internal series cream (*vs.* all series castaneous to reddish-brown). Furthermore, the distributions of these taxa do not overlap, as *S. anthemiflorus* is restricted to the Espinhaço Range in Minas Gerais State.

Phenology:— The flowering season of *Syngonanthus incurvifolius* is somewhat different from congeneric sympatric species. Most species of *Syngonanthus* bloom during the dry season but the blooming period of *S. incurvifolius* recorded in herbaria is between February and May (the rainy season). Exceptions are *S. densifolius* var. *majus* and *S. densifolius* var. *brachyphyllus*, whose records also attest for a blooming in the first semester of the year. Flowers of *S. incurvifolius* are in anthesis from February to April, corresponding to the latter half of the rainy season in the region. Fruits were observed only in herbarium specimens collected in May, suggesting that seeds are dispersed during the dry season.

Habitat and distribution:— Records for this species have only been reported from the municipality of Alto Paraíso de Goiás, along a small stretch of GO–118 highway, that connects Alto Paraíso de Goiás and São João da Aliança, between 5–15 km south of Alto Paraíso de Goiás. According to herbarium labels, *S. incurvifolius* occurs on *campos rupestres* within the Cerrado biome, over quartzitic sandy soils and in wet meadows, typical habitats at the border of the highway at the described locality. Field observations (*King & Bishop 8900*, MO) reported the species to be locally abundant. However, we have done fieldwork in Chapada dos Veadeiros over a large area and we did not find the reported population neither did we see any other subpopulation. This fact indicates that the populations probably occupy narrow areas. The roadside along GO–118 northwest of Alto Paraíso de Goiás belongs to the PNCV; roads to the south and northeast are privately owned, used for cattle grazing and farming, fragmenting the original *campo rupestre* habitat. *Syngonanthus incurvifolius* is registered southward, outside the PNCV and therefore might be threatened by human activities.

Conservation status:— *Syngonanthus incurvifolius* is known from a stretch no longer than 10 km along GO–118 highway, where the natural habitat is severely fragmented. The species is not recorded from a protected area and the region is affected by fire, pasturage and farming, with great impact on natural habitats. As it has not been collected since 1994 and there was no success to find it in recent fieldwork, the species could be classified as extinct. However, the region is still poorly collected and a careful search might discover new populations. Because there is reasonable doubt that the last individual has died, a more thorough check of expected habitat of this species is needed to confirm it. CNCFlora (Brazilian National Center for Plant Conservation, cncflora.jbrj.gov.br) evaluated the species threatened status, following the criteria of the IUCN Red List (IUCN 2001, 2015). *Syngonanthus incurvifolius* has an area of occupancy of 8 km^2, which tend to contract and deteriorate in quality. According to criteria A2ac and B2ab(i,ii,iii) this species is currently considered critically endangered (Negrão 2014a).

Additional specimens examined:— BRAZIL. Goiás: Alto Paraíso de Goiás, Region of the Chapada dos Veadeiros at 14°30’ S 47°30’ W, 7 km south of Veadeiros, wet meadowland below sandstone outcrop 7, 24 May 1956, *Y. Dawson 14639* (LL); Rod. GO–12, km 5–10 ao Sul de Alto Paraíso, campo arenoso, 26 May 1975, *G. Hatschbach 36814* (C, LL, MBM); 5–12 km S of Alto Paraíso de Goiás, mostly E of road to São João da Aliança, 3300–3800 feet, 8 February 1981, *L. R. M. King & L. E. Bishop 8900* (MO, UB); 10 km S of Alto Paraíso de Goiás (GO–118) heading for Brasília, adjacent to Chapada dos Veadeiros, 14°30’S, 47°30’W, 23 February 1990, *J. Saunders, L. Breyer & G. Eiten 3020* (LL); Rod. GO–118, 10 km S de Alto Paraíso, campo rupestre, solo arenoso úmido, 1150 m, 10 February 1994, *G. Hatschbach, M. Hatschbach & J. M. Silva 60290* (F, MBM).

Syngonanthus vittatus M.T.C.Watan. & Echternacht, *sp. nov.* Type:— BRAZIL. Goiás: Alto Paraíso de Goiás, Chapada dos Veadeiros, estrada Alto Paraíso de Goiás - Teresina de Goiás, Fazenda Água Fria, em campo limpo após a piscina, próximo a vereda e mata de galeria, 14°06'21.7"S, 47°30'33.6"W. 19 July 2012 (fl), *M. Watanabe & W. Watanabe 377* (holotype SPF!, isotype F!). Figures 2H–N & 4.

The new species is similar to *Syngonanthus arenarius* var. *heterophyllus* but differs by involucral bracts narrowly lanceolate with apex markedly acute and petals glabrous in pistillate flowers. *Syngonanthus vittatus* is also similar to *Syngonanthus densifolius* var. *majus* differing by all characteristics mentioned above as well the rosette leaves recurved.

Perennial herbs, 20–40 cm tall. *Roots* 0.2–1.5 mm in diameter, white to cream-colored, spongy. *Rhizome* 0.7–3.3 cm × 2.5–3.5 mm, horizontal to oblique, often branched, tomentose to villous, with white, dense and woolly curled hairs; each branch giving rise to a rosette of leaves, each rosette bearing 1–3 synflorescences. *Rosettes* 19–41 mm in diameter. *Leaves* 9.0–22.5 × 0.3–1.0 mm, linear to narrowly lanceolate, flat to semi-terete, apex acute, base truncate, recurved, coriaceous, striate abaxially with 3–5 conspicuous veins, only the midvein visible on upper surface in young leaves; pilose on both surfaces, with arachnoid trichomes and adpressed trichomes adaxially, filamentous hairs and adpressed trichomes abaxially, mainly concentrated on midvein, ca. 0.3 mm long; basal sheath slightly enlarged, 0.5–1.0 mm wide, pale and achlorophyllous at base. *Synflorescences* with a primary axis bearing a lax umbel of 1–5 inflorescences at the apex. *Synflorescence axis* 5.0–8.5 cm long, emerging from the center of the rosette, erect to flexuous, yellow-reddish when young, dark reddish brown in maturity, pilose at base with filamentous trichomes, glabrescent, becoming tomentose near the apex with simple filamentous and capitate trichomes. *Bracts of synflorescence axis* usually restricted to the apex, rarely a few tiny scattered bracts along the axis ca. 3 mm long; apical bracts 1–30 × 0.3–1.0 mm, whorled, patent, the external series lanceolate, progressively elongating from the outer toward the inner series, the internal series linear, apex acute to rounded, erect, pubescent on both surfaces with capitate filamentous trichomes. *Inflorescences* composed of a closed spathe subtending a scape with a capitulum at the apex. *Spathes* 3.5–5.5 cm long, chartaceous, cylindrical, obliquely opened, apex acute, erect, recurved or rarely involute, tip erect to uncinate, margin minutely involute, ciliate, adaxial surface glabrous to glabrescent, abaxial surface pubescent with capitate trichomes. *Scapes* erect, 9–30 cm long, greenish to straw-colored with age, 4(–5)-costate, sparsely hairy to densely pilose with erect to patent glandular hairs and appressed, and simple trichomes, pubescent near the apex with a collar of patent, simple filamentous and capitate [gland-tipped] hairs. *Capitula* 5–12 mm in diameter, obconic, later becoming depressed-hemispherical. *Involucral bracts* in 4–6 series, all similar in color, light to dark brown, often with a reddish tinge, with a lighter longitudinal band in center and a darker pigmentation on the margins, adaxial surface glabrous, abaxial surface strigose, ciliate, with patent, simple trichomes, rarely also capitate hairs ca. 0.5 mm long; external series 1.5–2.0 × 0.5–0.8 mm, triangular to ovate, apex acute, bracts progressively elongating toward the internal series, middle series 4–5 × 1 mm, narrow elliptic, apex acute, internal series 3.0–5.5 × 0.7–1.0 mm, inner series surpassing the flowers by 0.1–0.3 mm, narrow-lanceolate, elliptic, rarely narrow-oblanceolate, apex acute; receptacle hemispheric, pilose. *Floral bracts* absent. *Flowers* 3–merous, 60–110 per capitulum, staminate and pistillate generally equal in number, with contrasting colors, staminate flowers darker and concentrated at the border of the capitulum. *Staminate flowers* 2.5–3.5 mm long, including pedicels; pedicels 0.5–1.0 mm long; sepals 2.0–2.5 mm long, coppery brown, shortly fused at base, concave, membranous, usually two sepals similar in form, elliptic to lanceolate (-oblanceolate) with acute apex, slightly curved, asymmetrical, and the third different, slightly irregular-subspathulate with round to truncate apex, but occasionally occurs a reversal of forms, or occasionally the three sepals slightly different, margins ciliate, adaxially glabrous, abaxially setose with simple filamentous hairs ca. 0.5 mm long; petals ca. 2 mm long, hyaline, membranous, fused, tubulose, lobes triangular, obtuse, involute after anthesis, glabrous; filaments free, anthers ca. 0.6 mm long, white; anthophore ca. 0.3 mm long; pistillodes 3, ca. 0.2 mm long, clavate, papillose at apex. *Pistillate flowers* 2.4–3.5 mm long, including pedicels of 0.4–1.5 mm long; sepals ca. 2 mm long, elliptic, concave, apex acute to obtuse, base thickened, free, cream to light castaneous, hyaline and membranous toward the apex, dark reddish brown-colored at apex, ciliate, hairy on the inside, with simple filamentous trichomes up to 1 mm long, glabrous outside; petals about equaling the sepals, 1.8–2.7 mm long, oblanceolate, fused at the distal third, membranous, white to hyaline, glabrous, the lobes triangular-rounded to obtuse, involute after anthesis; ovary ca. 0.6 mm long; style column 0.2–0.4 mm long, cream-colored; appendages ca. 0.5 mm long, the glandular apex capitate-curved; stigmatic branches simple, ca. 1.5 mm long. *Seed* ca. 0.40 × 0.25 mm, ellipsoid, reddish-brown colored.

Etymology:— The specific epithet refers to the well-marked longitudinal stripe evident in the center of the involucral bracts.

Notes and taxonomic affinities:— In the field, the species looks superficially similar to *Paepalanthus* (FIG. 4A), because of its pilose capitula and dark involucral bracts. However, a closer examination reveals the compound inflorescences (synflorescences), with a differentiated, usually leafless primary axis, a feature that does not occur in *Paepalanthus*. In addition, the species has petals of pistillate flowers fused in the distal part and free at the base, and staminate flowers isomerous an exclusive set of characters of *Syngonanthus* (Giulietti *et al.* 2012).

Syngonanthus vittatus belongs to the same morphological group as *S. incurvifolius,* which also includes *Syngonanthus arenarius*, *S. densifolius* var. *brachyphyllus* and *S. densifolius* var. *majus.* All these species share a similar architecture and dark and pilose involucral bracts with a contrasting pale longitudinal band. *Syngonanthus vittatus* differs from all of them by the involucral bracts narrowly lanceolate to linear, with a narrower and more conspicuous pale stripe, composing a laxer involucre (FIG. 4G); the other species have large elliptical to obovate bracts, forming a denser involucre (Fig. 4F, 4H–I).

The flowers of *Syngonanthus vittatus* are very similar to those of *S. arenarius* var. *heterophyllus* (1903:260), except that the former has petals of pistillate flowers glabrous (FIG. 4J–K; *vs.* petals pilose, FIG. 4L) and smaller flowers (up to 3.5 *vs.* 4.5 mm). In addition, *S. vittatus* has pistillate and staminate flowers strongly contrasting in colour, the staminate with brown sepals and the pistillate with cream sepals (FIG. 4M–N and 4K–J, respectively), whereas both types of flowers in *S. arenarius* var. *heterophyllus* have a similar pigmentation (FIG. 4L; 4O), cream at base and reddish-brown at apex.

Other features differentiating *Syngonanthus vittatus* from *S. incurvifolius* and *S. densifolius* var. *majus* are the rosette leaves recurved (FIG. 4B) (*vs.* incurved in the distal half or flexuous, respectively, FIG 3A–B), the synflorescence axis often bearing tiny scattered bracts along its length (*vs.* bracts restricted to the apex), and the petals of pistillate flowers glabrous (*vs.* pilose). *Syngonanthus vittatus* also differs from *Syngonanthus densifolius* var. *brachyphyllus* by the narrower leaves (0.3–1.0 mm *vs.* 2.0–5.0 mm), with simple and adpressed trichomes (*vs.* only simple) and striate adaxial surface (*vs.* reticulate).

Additionally, the evident asymmetrical sepals of staminate flowers are an important characteristic shared with *S. incurvifolius* and the other species previously cited (FIG. 4C–E).

Phenology:— Flowering of *Syngonanthus vittatus* occurs during the dry season (winter), from July to September. This period coincides with all collections reported for this species. Most *Syngonanthus* from Chapada dos Veadeiros bloom at the same time, for example, *S. decorus* Moldenke (1976:485) and *S. densifolius* var. *majus*. Seeds mature at the end of the dry season, implying a dispersal period concomitant with the rains and possible hydrochory.

Habitat and distribution:— All collections are known from the same population as the type, at the farm called "Água Fria", except by a single record from waterfall "São Bento". These localities are about 10 km apart and close to recreational and agricultural areas. The expansion and intensification of human activities in the area threatens the natural surroundings. The limited distribution of the known populations contrasts with a local abundance of individuals, and further fieldwork may reveal other populations. *Syngonanthus vittatus* occurs outside conservation units, although very close to the boundaries of the PNCV. The species occurs over hydromorphic soils, in moist grasslands or wet campo, a common physiognomy on *floodplains* between Cerrado *sensu stricto* and gallery forest (Ratter et al. 1997). These wet *campos* occur on well-drained sandy soils, which become waterlogged during summer and quite dry in winter, a variation that constrains tree growth and prevents forest formations (Ratter et al. 1997), favoring the occurrence of herbs such as *S. vittatus*.

Conservation status:— This species is classified as critically endangered, according to criteria B1ab and B2ab of IUCN (2001, 2015). The taxon is known only from two populations, both on privately owned land hosting human activities that may threaten the species with extinction. *Syngonanthus vittatus* has an area of occupancy of 12 km^2. Conservation status is endangered, as evaluated by CNCFlora according to the IUCN (2001, 2015), matching criteria B2ab(i,ii,iii) (Negrão 2014b).

Additional specimens examined:— BRAZIL. Goiás: Alto Paraíso de Goiás. Est. 11 – Chapada dos Veadeiros, mata, 06 August 1972, *Rizzo 8236* (SPF); 9 km de Alto Paraíso / São Jorge, cachoeira São Bento, campo úmido próximo a floresta de galeria, 09 September 1994, *Silva et al. 2315* (IBGE, SPF); Fazenda Água Fria 3, próximo a sede da fazenda, borda de mata de galeria, 14º09'07" S, 47º37'08"W, 06 June 1997, *Munhoz et al.* 462; Fazenda Água Fria, cerca de 10 km em direção a Teresina de Goiás, campo limpo úmido, borda de cerrado rupestre e mata de galeria, 14°04'21.7"S, 47°30'33.6"W, altitude 1488 m, 17 June 2000, *Munhoz et al. 1651* (IBGE, SPF); idem, 01 July 2000, *Munhoz et al. 1721* (IBGE, SPF); idem, 01 July 2000, *Munhoz et al. 1729* (IBGE, SPF); idem, 19 July 2000, *Munhoz et al. 1764* (IBGE, SPF); idem, 19 July 2000, *Munhoz et al. 1797* (F, IBGE, SPF); idem, 16 August 2000, *Munhoz et al. 1831* (F, IBGE, SPF)

Conclusion

Probably, the new *Syngonanthus* species described here are closely related. The similarity in several aspects including floral attributes, vegetative characters and geographical proximity of taxa suggest close relationship, except for the different flowering times. Ongoing phylogenetic studies investigate this hypothesis (Watanabe *et al.* in prep.). The pilose and castaneous to reddish-brown involucral bracts are common features, shared with a small group of plants in Minas Gerais and Goiás states. These phylogenetic studies in preparation confirm that *S. vittatus* and *S. densifolius* var. *majus* are sister species, although the relationship is not clear among similar species such as *S. incurvifolius, S. arenarius* and *S. densifolius* var. *brachyphyllus* (Watanabe *et al.* in prep.).

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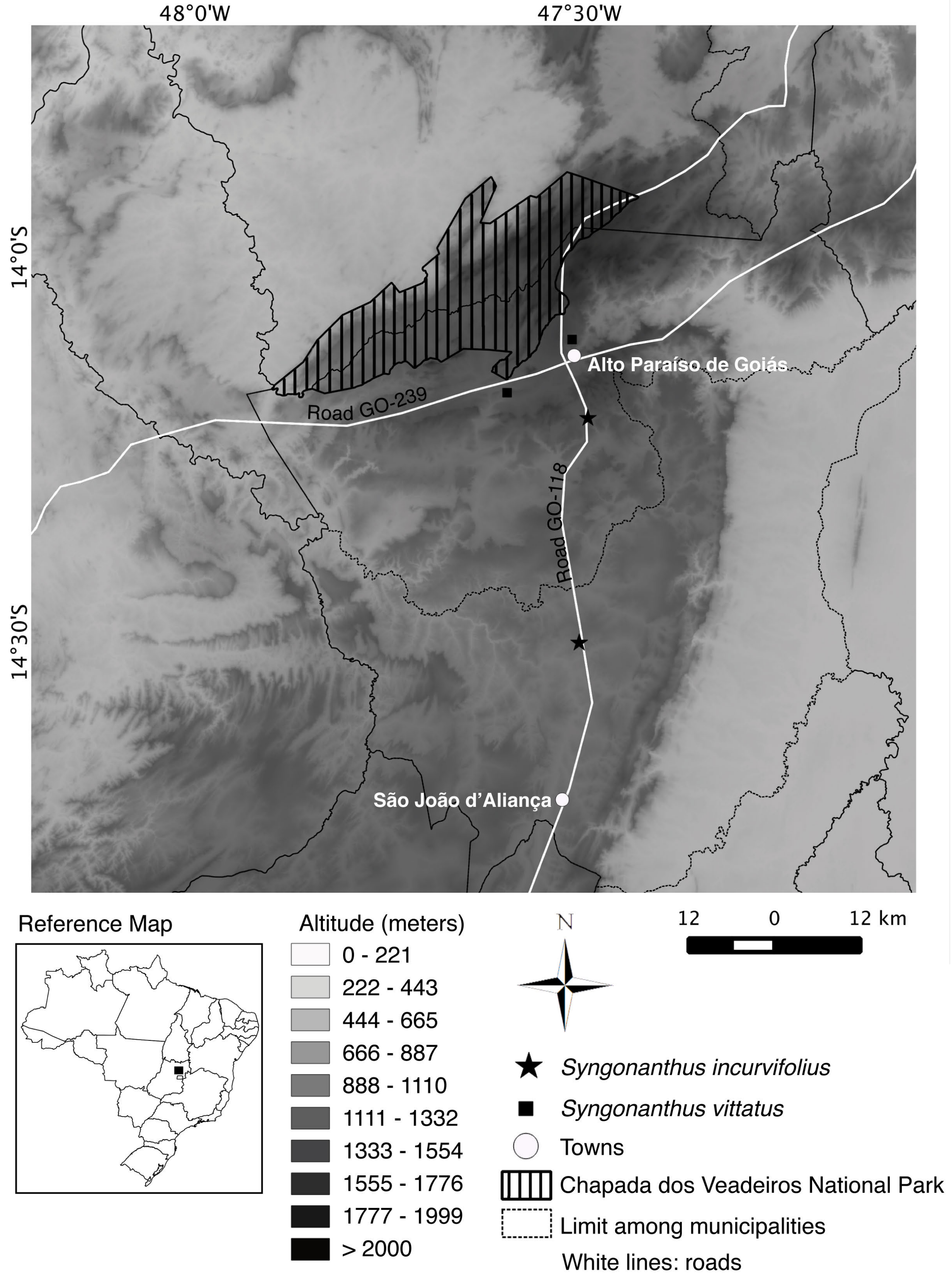
Legends

FIGURE 1. Map of Chapada dos Veadeiros region showing collection localities of *Syngonanthus incurvifolius* and *S. vittatus*.

FIGURE 2 A–G. *Syngonanthus incurvifolius* (based on *Irwin et al. 24648*). **A.** Habit; **B.** Capitulum detail; **C.** From outermost to innermost series of involucral bracts; **D.** Staminate flower; **E.** Various forms of sepals of staminate flower; **F.** Pistillate flower with one sepal removed; **G.** Gynoecium. **H–N.** *S. vittatus* (based on *Watanabe & Watanabe 377*). **H.** Habit; **I.** Capitulum detail; **J.** From outermost to innermost series of involucral bracts; **K.** Staminate flower; **L.** Various forms of sepals of staminate flower; **M.** Pistillate flower with one sepal removed; **N**. Gynoecium. Illustrated by Marcelo Kubo.

FIGURE 3. *Syngonanthus incurvifolius* and other morphologically similar *Syngonanthus* species. **A–C.** Comparison among leaves: **A.** *Syngonanthus densifolius* var. *majus* showing erect, flexuous leaves in a rosette; **B.** Incurved leaves of *S. incurvifolius*; **C.** Leaf of *S. densifolius* var. *brachyphyllus*, showing achlorophyllous base. **D–G.** Comparison among sexual traits of *S. incurvifolius* and *S. densifolius* var. *majus*: **D.** Staminate flower of *S. incurvifolius* (trichomes removed from pedicel); **E.** Pistillate flower of *S. incurvifolius* with filamentous trichomes; **F.** Staminate flower of *S. densifolius* var. *majus*; **G.** Pistillate flower of *S. densifolius* var. *majus* exhibiting trichomes only at upper portion of the sepals; **H.** Capitulum detail of *S. incurvifolius*; **I–J.** Comparative vestiture of the petals in pistillate flowers: **I.** *S. incurvifolius* showing pilose petals; **J.** Petals glabrous in *S. densifolius* var. *majus*. Scale bars: B= 3 mm. C,H= 2mm. D-G, I–J: 500 µm. (Photos by Mauricio T. C. Watanabe)

FIGURE 4. *Syngonanthus vittatus* and other morphologically similar *Syngonanthus* species. **A–E**. *S. vittatus*: **A.** Habit detail showing specimen at flowering; **B.** Rosette and roots; **C.** Elliptic sepal of staminate flower; **D.** Other forms of sepals revealing concave shapes in staminate flowers; **E.** Three different shapes of sepals in the same staminate flower revealing asymmetry among the sepals. **F–I.** Comparison among capitula in *Syngonanthus* species: **F.** *S. arenarius* var. *heterophyllus*; **G.** *S. vittatus*; **H.** *S. densifolius* var. *brachyphyllus*; **I.** *S. densifolius* var. *majus*; **J–K**. Pistillate flower of *S. vittatus*: **J.** Flower exhibiting trichomes on sepals; **K.** Flower with two sepals removed, the remaining sepal with hairs deciduous, showing the glabrous petals; **L.** Pistillate flower of *S. arenarius* var. *heterophyllus*; **M–N.** Staminate flowers of *S. vittatus*: **M.** Young flower; **N.** Mature flower; **O.** Staminate flower of *S. arenarius* var. *heterophyllus*. Scale bars: C,M= 500 µm. D–E, J–L, N–O= 1 mm. F–I= 2 mm. (Photos by Mauricio T. C. Watanabe).



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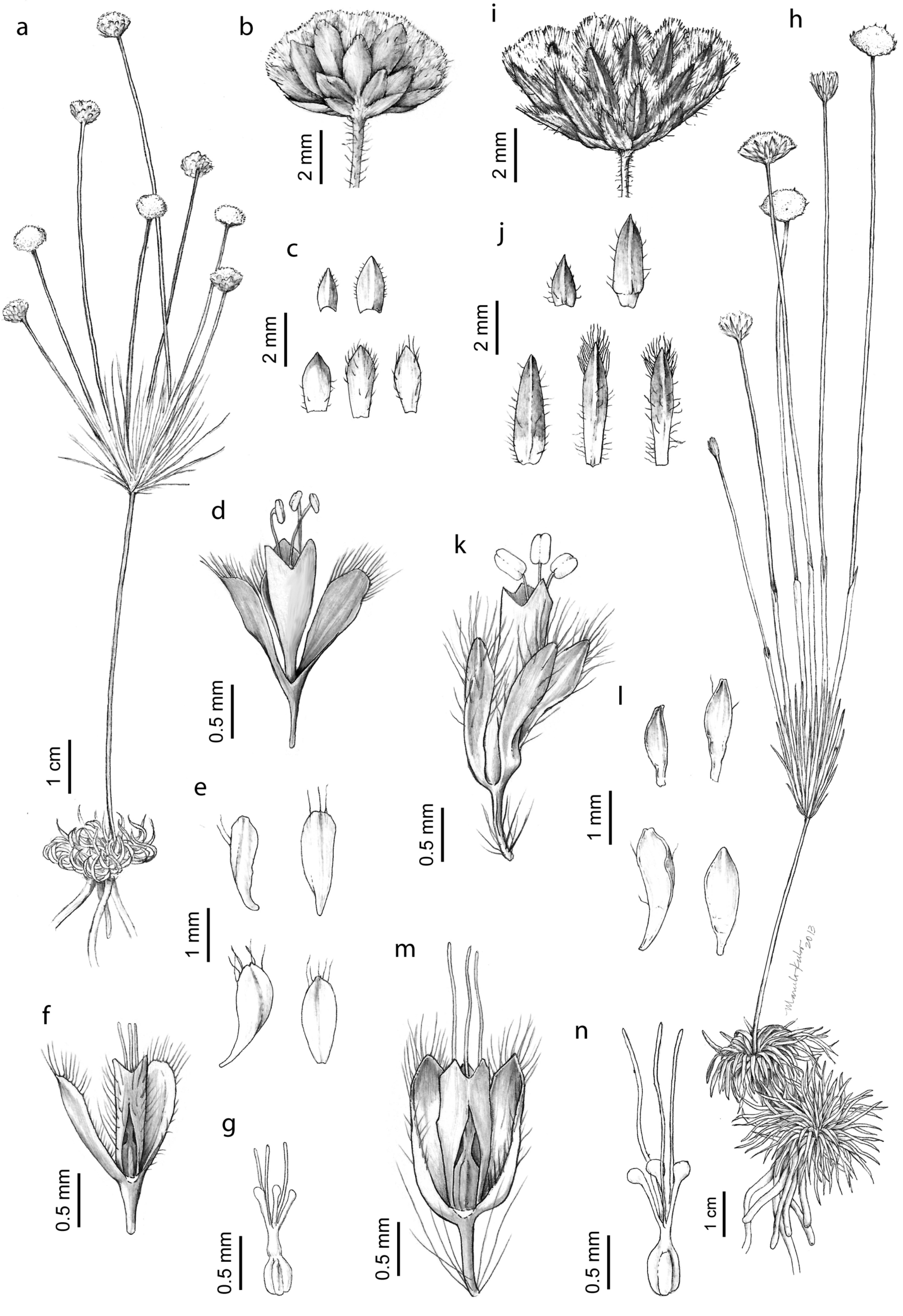
Source: altitudinal data from TOPODATA project
http://www.dsr.inpe.br/topodata/, accessed November 2013

Figure 1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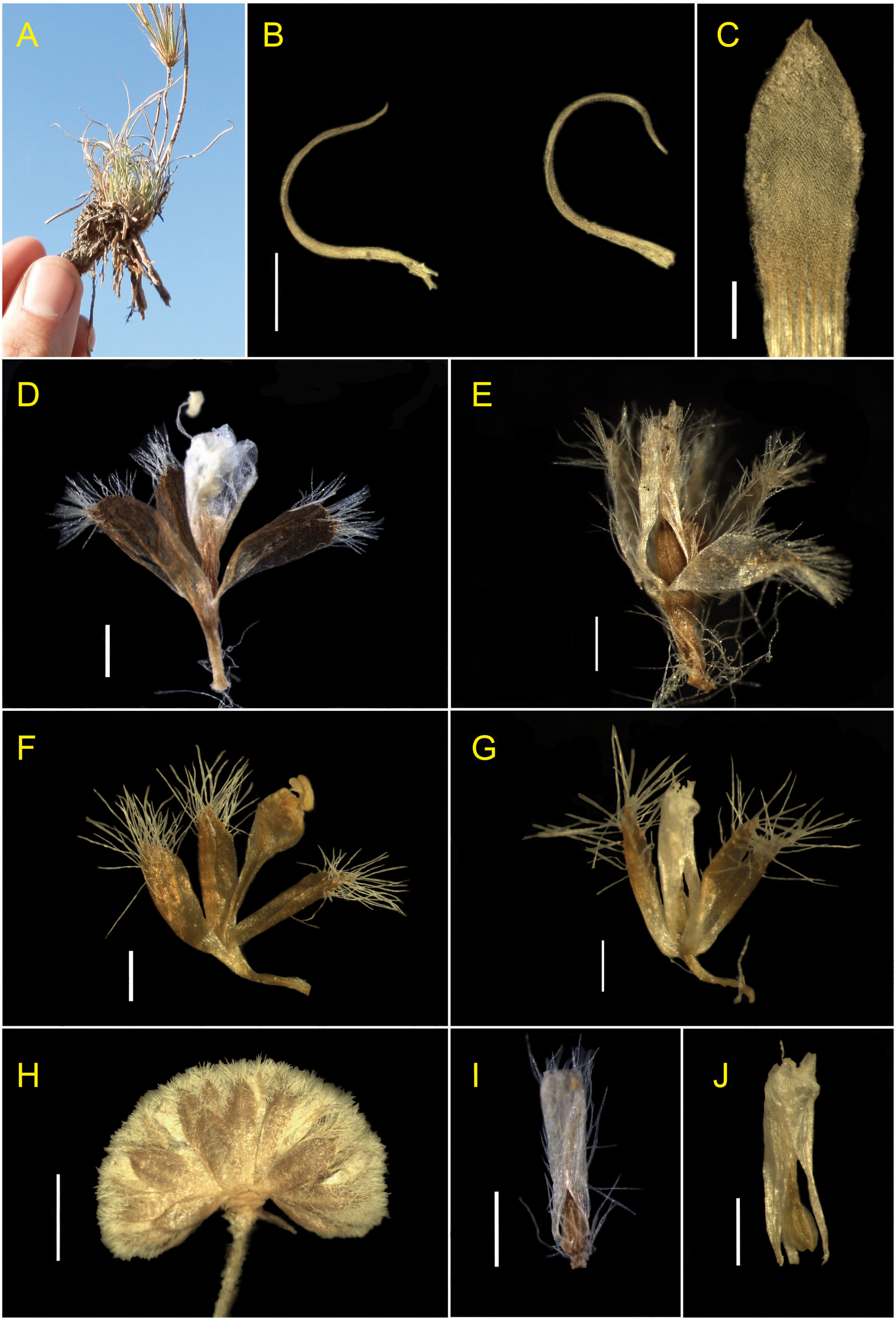

Figure 3

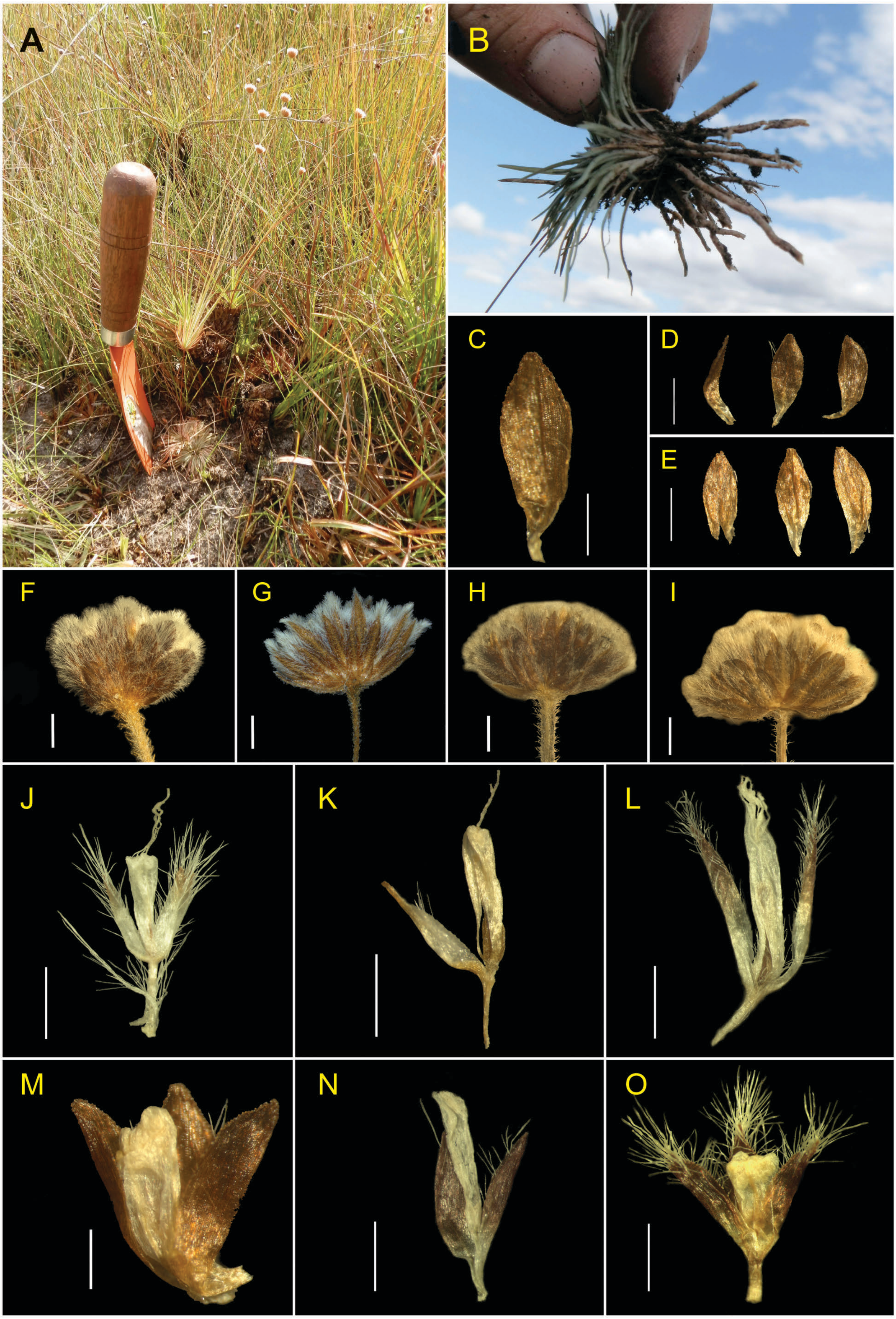

Figure 4

Chapter One: Part two

Syngonanthus androgynus, a striking new species from South America, its phylogenetic placement and implications for evolution of bisexuality in Eriocaulaceae.[2]

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[2] Artigo submetido à PLoS ONE em 26 de Março de 2015. Autores: Mauricio T. C. Watanabe, Nancy Hensold & Paulo Takeo Sano.

Abstract

In the present study, we described and illustrated a remarkable new species of *Syngonanthus* from South America (records to Bolivia, Brazil and Peru). The description was based on morphological observations and comparisons, and specific literature. This new species is quickly distinguished from all species in the genus by trimerous and bisexual flowers, an exclusively set of characteristics in *Syngonanthus*. Complementary, sequences of 33 species were downloaded from GenBank and four species had newly generated sequences for this study. Molecular phylogenetic analyses based on nuclear ribosomal ITS and the plastids *psb*A-*trn*H and *trn*L-F regions were performed to determine its systematic position. The results have shown *S. androgynus* closely related to a well-supported clade that has been considered as *Syngonanthus* sect. *Carphocephalus*. Floral traits associated with this new plant also were surveyed. Character reconstruction has appointed that the bisexual flowers appears to be originated independently more than once in the genus. However, trimerous flowers appear to be an ancestral condition of the whole genus.

Introduction

Eriocaulaceae is a pantropical family consisting of 11 genera and approximately 1200 species [1,2,3]. In Brazil, various species of Eriocaulaceae have been gathered and used as dried ornamental plants for more than a century. This trade provides main and alternative income sources for hundreds of families in the Brazilian countryside [4, 5]. Most Eriocaulaceae possess unisexual and trimerous flowers, with bisexual or dimerous flowers extremely rare [6]. The inflorescences are capitulum-like composed of flowers borne on a flattened receptacle at the peduncle apex [7], with involucral bracts at the border. A single inflorescence usually has staminate and pistillate flowers in the same capitulum [1].

Syngonanthus Ruhland has been recognized as the third largest genus in Eriocaulaceae. The genus comprises approximately 120 species that exhibit a disjunct distribution in the American and African continents [1]. Some species of *Syngonanthus* occur in rupestrian grassland, upon shallow and sandy soils, over quartzites and sandstones, like most taxa in the Eriocaulaceae [8]. However, fieldwork observations have shown that most species of *Syngonanthus* inhabit marshy or poorly drained soils. The genus is distinguished by the follow character sets: isostemonous flowers, pistillate flowers with petals fused at middle and bithecous anthers (except *S. cuyabensis* (Bong.) Giul., Hensold & L.R. Parra) [1]. Other characteristics are spongiose roots, nectariferous and stigmatic branches free at the same level and some species exhibit synflorescence axes.

During revisionary studies involving *Syngonanthus* sect. *Carphocephalus*, an unidentified material was selected from some herbaria in Brazil and United States of America for detailed observation. The material was shown to be surprising for its exclusively bisexual 3-parted flowers, which is the only known occurrence in this family. The goals of the present study are to describe this new remarkable taxon and check its placement in the genus. Furthermore, we have tested reconstruction of character for two characteristics of flowers in *Syngonanthus*.

Material and Methods

Ethics Statement

Vegetal tissue for DNA analysis was donated by major collectors or extracted from herborized materials deposited in the herbaria ANDES, INPA, F and SPF. The policies for each herbarium were followed. The samples were used only for the purpose of supporting molecular phylogenetics. We attest that the samples will not be available for screening for genes of interest in applied research or bioprospecting endeavors.

Nomenclature

The electronic version of this article in Portable Document Format (PDF) in a work with an ISSN or ISBN will represent a published work according to the International Code of Nomenclature for algae, fungi, and plants, and hence the new names contained in the electronic publication of a PLOS ONE article are effectively published under that Code from the electronic edition alone, so there is no longer any need to provide printed copies.

In addition, new names contained in this work have been submitted to IPNI, from where they will be made available to the Global Names Index. The IPNI LSIDs can be resolved and the associated information viewed through any standard web browser by appending the LSID contained in this publication to the prefix http://ipni.org/. The online version of this work is archived and available from the following digital repositories: PubMed Central, LOCKSS.

Morphological observations

The new species was described based on examination of pressed and rehydrated material under a stereomicroscope (Leica M125) and flowers were photographed for accurate observation (Leica DFC425). For morphological comparison, we additionally observed under stereomicroscope other *Syngonanthus* species with similar morphological aspect, such as *S. weddellii,* and Brazilian and Colombian species with bisexual flowers, dimerous flowers, such as S. *amazonicus*, *S. trichophyllus* and *S. acephalus*. The study also was based on information gathered in taxonomic literature, live plants in the field and other herborized materials. The material selected to be the holotype is deposited in the herbarium of University of São Paulo (SPF) and duplicates (isotypes) are deposited in Jardim Botânico do Rio de Janeiro (RB) and Instituto Brasileiro de Geografia e Estatística (IBGE). Additional specimens (paratypes) were observed in the Field Museum of Natural History (F) and Missouri Botanical Garden (MO).

Sampling

Sequences of 33 species belonging to 6 genera of Eriocaulaceae were downloaded from GenBank. Both subfamilies (Eriocauloideae and Paepalanthoideae) are represented. Additionally, sequences of four species were newly generated for this work: *Syngonanthus acephalus* Hensold, *S. trichophyllus* Moldenke, *S. weddellii* Moldenke and the new species. The ingroup consists of a total of 31 species, representing both sections still supported for inclusion in *Syngonanthus*: *Syngonanthus* sect. *Syngonanthus* and *Syngonanthus* sect. *Carphocephalus* [9, 10]. The voucher specimen information and the GenBank accession numbers of the sequences used and generated in this study are listed in Table S1.

Molecular markers

For phylogenetic reconstruction in *Syngonanthus* and investigation of the placement of the new taxon, we analyzed data from DNA sequences of the internal transcribed spacer region of the nrDNA tandem repeat (ITS) and plastid *psb*A-*trn*H and *trn*L-F regions. Genomic DNA from silica-gel dried tissue or herbarium specimens were extracted using a modified 2X cetyl trimethylammonium bromide (CTAB) protocol [11]. To generate sequences used in this study we amplified the DNA regions using polymerase chain reaction (PCR) protocols previously used for Eriocaulaceae [12, 13]. The chromatograms were assembled and edited with Geneious software (Geneious Pro v7.1.7 software Biomatters Ltd., Auckland, New Zealand).

Sequence alignment, phylogenetic analysis and character reconstruction

Alignment of the DNA sequences was initially carried out using MAFFT v.7 [14] followed by minor manual adjustments in Geneious. Echternacht et al. [13] evaluated congruence among trees resulting from analyses of individual markers and no conflict in supporting clades was identified. We analyzed combined data sets conducting maximum parsimony (MP) and Bayesian inference (BI) analyses as implemented in PAUP [15] and MrBayes 3.2.3 [16], respectively. The best-fit model of nucleotide evolution for Bayesian analyses was chosen separately for each marker using JModelTest 2 [17]. The models were selected using Akaike information criteria (AIC) for all data sets. The best models fitted were TPM1uf + I + G for *psb*A-*trn*H, TVM + I + G for *trn*L-F, and GTR + I + G for ITS. The combined analysis consisted a partitioned data with each marker decoupled. The heuristic search was composed by two independent runs of four Markov chains Monte Carlo (MCMC) running 10 million generations, sampling results every 1,000 generations. Trees were discard as burn-in (25%) of the sampled trees after checking the stability using Tracer v1.6 [18]. Posterior Probabilities (PP) and the majority rule consensus tree were determined by combination of two runs using the trees sampled after the convergence of the chains. Internal support clades were evaluated by non-parametric bootstrapping (BS) based on 10,000 bootstrap replicates. Branch support was assessed by Bayesian posterior probabilities (PP).

To reconstruct the evolution of morphological characters associated with flowers in *Syngonanthus,* and to determine primitive ancestral states, the analyses were carried out on the Bayesian consensus tree based on the combined plastid and nuclear data set. The reconstructions were performed with maximum likelihood in Mesquite 3.75 [19] using the model Mk1 (Markov k-state 1 parameter model). Two characters were examined: floral merism: (0) dimerous, (1) trimerous; and flower type: (0) unisexual, (1) bisexual.

Results and Discussion

Taxonomic treatment

Syngonanthus androgynus M.T.C.Watan. sp. nov. (Figs. 1; 2)

Type: BRAZIL, Goiás: Alto Paraíso de Goiás, Chapada dos Veadeiros, Km 11 da estrada Alto Paraíso de Goiás / São Jorge, estrada para a cachoeira São Bento, ca. 1.5 km após a cachoeira, 09 Sep 1994, M. Fonseca & T. Filgueiras 115 (HOLOTYPE: SPF; ISOTYPES: IBGE, RB).

This new species is similar to S. weddellii but differs by lax leaves on aerial stem (versus patent leaves). S. androgynus also differs from all described Syngonanthus by the exclusively trimerous and bisexual flowers.

Caulescent herbs, 12–37 cm tall, unbranched at base, lacking basal rosette. Roots white, 0.1–0.2(-0.6) mm in diameter, spongy. Aerial stem 2–13 cm long, villous with white crooked trichomes mainly concentrated next to the apex, bearing an umbel of 1-30 inflorescences at the apex. Leaves abundant, spirally arranged and equally distributed on the stem, ascending, fenestrate, lax, sometimes more congested at the apex near the synflorescence, 0.5–4.5 cm × 0.25–2.0 mm, linear to threadlike or capillary, acuminate or filiform, both surfaces pilose with capitate filamentous hairs and malpighian trichomes, later glabrescent, veins 3–6 prominent. Leaves more congested on the top, 0.3–2.0 cm long, linear or acicular, apex recurved and thick, pubescence of malpighian trichomes and capitate hairs. Spathes 1.0–5.5 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute or cuspidate, tip curved or slightly uncinate, triangular or auriculate, margin entire, ciliate, not involute, both surfaces pilose with capitate filamentous and malpighian trichomes. Scapes erect, 3–34 cm long, greenish or straw-colored to golden with age, 3-costate, pilose throughout, pubescent near the apex with capitate hairs and malpighian trichomes. Capitula 3–7 mm in diameter, radiate, hemispherical at anthesis. Involucral bracts in 2–5 series, cream-colored, all similar in color or sometimes the outer castaneous, the inner becoming cream, hyaline when wet, glabrous, those of the external series 1.05–1.55 × 0.5–0.9 mm, varying from triangular to slightly ovate, obovate or oblong, apex acute or obtuse, progressively thinner toward the apex, those of the internal series 1.0–1.8 × 0.5–0.75 mm, almost equaling the flower height, oblanceolate, apex obtuse to rounded, sometimes bifid; receptacle discoid, pilose. Floral bracts absent. Flowers bisexual, 3-merous, 20–60 per capitulum, flowers 1.45–2.55 mm long including pedicels; pedicels 0.15–0.45 mm long, with long white villous trichomes at base and insertion with receptacle; sepals 1.5–2.0 mm long, membranous, glabrous, white to cream, hyaline when hydrated, slightly white at longitudinal band at middle, shortly connate at base, margin revolute, lanceolate, rhombic or narrowly obtrullate, very slightly thickened, toward apex acute; petals 1.0–2.2 mm long, rhombic, connate at the upper margin, free at base and apex, lobe triangular, apex acute, lower half of petal fleshy, upper half membranous, pilose abaxially with simple filamentous hairs, involute after anthesis; filaments adnate to the petals, anthers 0.15–0.3 mm long, white; gynoecium 1.3–1.5 mm long; ovary 0.5–0.75 mm long; style column ca. 0.1–0.2 mm long, cream-colored; appendages ca. 0.15–0.3 mm long, the glandular apex capitate; style branches broad and membranous at base, apex narrow and papillose, 0.5–1.0 mm long. Seed 0.45–0.6 × 0.25–0.35 mm, ovoid, brown-colored, striate with very short pseudotrichomes in longitudinal lines.

Etymology. The specific epithet refers to the developed male and female structures in the same flower (bisexual flowers), a very uncommon characteristic in the family.

Habitat, distribution and phenology. *Syngonanthus androgynus* has a disjunct distribution. It has been collected in the Amazonian region of Bolivia and Peru in a region comprising the border of both countries in the floodplain of the "Río Heath". Two other populations have been detected from Brazil, over 2000 km away. These collections are from Grande Sertão Veredas National Park and near Chapada dos Veadeiros National Park (Central Brazil). This terrestrial species grows in wetlands, over shallow sandy soils and "Pampas" vegetation. However we cannot eliminate the possibility that it is facultatively aquatic, since it inhabits seasonally inundated habitats. Flowers have been recorded from May-September. Fruit abundant from September.

Conservation status. The disjunct distribution, occupying threatened regions allows categorization of this species as endangered following the criteria B (geographic range) of World Conservation Union Red List Categories and Criteria [20]. Area of occupancy < 500 km^2, number of locations ≤ 5 and extreme fluctuations in number of locations and area of occupancy accord with the requirements of criterion B2ac.

Species recognition. *Syngonanthus androgynus* shares bisexual flowers with three other Amazonian *Syngonanthus*. Unlike *S. androgynus*, all species included in this small group have two-parted flowers with inflorescences and flowers reduced. *S. acephalus* is a small clump-forming species with flowers solitary or paired, lacking involucral bracts. *Syngonanthus amazonicus* and *S. trichophyllus* have conical capitula, two spathaceously fused sepals, and stamens two and one in number, respectively, also differing from each other by the leaf width and consistency of petals of pistillate flowers (membranous in *S. trichophyllus versus* thick in *S. amazonicus*). *Syngonanthus androgynus* is very distinctive among all species of Eriocaulaceae because there is no reduction in the number of parts in its exclusively bisexual flowers (there are three sepals, petals and stamens). *Rondonanthus flabelliformis* (Moldenke) Hensold & Giul. is another Eriocaulaceae described with 3-parted bisexual flowers but this species shows also staminate flowers in the same capitulum. The pistillate flowers of *S. weddellii* Moldenke are similar to the bisexual flowers of *S. androgynus*. Both species have the same texture and form of petals: connate at the upper margin, free at base and apex very top, lower half of petal fleshy, upper half membranous. *Syngonanthus androgynus* is distinguished from *S. weddellii* by the characteristics mentioned in the *diagnosis*. *S. weddellii* was only known by type-collection but it was rediscovered recently by senior author in Tocantins state (Brazil).

This new species could be the first reported case of cleistogamy for Eriocaulaceae. The petals are hooked inward over each other at apex and apparently do not completely open, in all stages observed, and the stamens and style branch are wrapped around each other. Petals are not completely fused at very top portion but strongly uncinate without exposition of sexual parts. The collection chosen as the holotype includes well-developed individuals (from Chapada dos Veadeiros, Central Brazil), while specimens from Grande Sertão Veredas National Park (ca 200 km away) comprise smaller plants. Collections from the Río Heath usually have leaves scattered on aerial stem but congested apically near scapes, unlike those from Central Brazil that have leaves longer, more congested and more equally distributed over the length of the stem. Plants from Río Heath also exhibit petals of pistillate flowers glabrous, while those from Brazil have petals of pistillate flowers pilose in most cases, rarely glabrescent, and also the flowers slightly flattened and stamens larger than specimens from Río Heath. We do not treat these as two different taxa because of the small sample size and the inherent variability of wetland species. In addition, the floral structure and vegetative arrangement is very similar in all specimens and the pilosity in the flowers as well as the distribution of leaves on stem showed slight gradation in plants from Brazil.

Paratypes. BOLIVIA. La Paz: Abel Iturralde, Puerto Muscoso, donde llega la pampa mas cerca del río Heath, 25 Jul 1995, *N. Helme & L. Kruger 678* (F). BRAZIL. Minas Gerais: Formoso, Parque Nacional Grande Sertão Veredas, próximo a ponte da barra do Rio Preto / Santa Rita, em vereda, 15°10’35”S 45°46’09”W, 21 May 1998, *F. Oliveira et al. 1056* (F, IBGE). PERU. Madre de Dios: Tambopata, Parque Nacional “Bahuaja-Sonere”, ex Santuario Nacional “Pampa de Heath”, formación de pampa inundada permanentemente, 25 Sep 1997, *C. Diáz et al. 9201* (F, MO); Río Heath, Santuario Nacional de las Pampas del Heath, lado este de la

Pampa, 3-4 km oeste del río, camino del Refugio Juliaca, hasta el bosque de galería y campamento Aguas Claras, 15 Jun 1992, *J. Albán Castillo & R. Foster 6968* (F).

Phylogenetic analysis

Sequences for ITS (nuclear), *trn*L-F and *psb*A (both plastid loci) were combined for 37 accessions (31 ingroup and 6 outgroup). The final alignment comprised 2440 pb, of which 1000 (41%) were variable and 557 (23%) were parsimony-informative. The heuristic source found 14 most parsimonious trees with a length of 2313 steps (both consistence and retention index = 0.66). Topologies from MP and Bayesian analyses were similar in the most inclusive clades but the relationships among genera and the most exclusive clades in *Syngonanthus* are unclear in MP analysis, with some groups collapsed (see Figure S2). Collapsed branches in MP were not represented by BS values in the Figure 3.

The Figure 3 shows unclear relationships among *Syngonanthus*, *Comanthera* and *Leiothrix* with low statistical support for the *Syngonanthus* + *Leiothrix* clade (PP 0.47). Some indicated nodes received high statistical support (except clade B, moderate). The clade A (PP 1, BS 97) is a well-supported clade, which comprises robust species with thick synflorescence axes, including *S. macrolepis* as basal species. This clade also shows *S. niger* as sister to a well-supported clade with *S. longipes* and *S. densiflorus* (PP 1, BS 96).

Clade B has moderate to high statistical support (PP 0.93, BS 64) consisting of two subgroups: the "bisexual dimerous species" clade consists of *S. trichophyllus* and *S. acephalus* as sister species (PP 0.63, BS 72); another subgroup consists of *S. chrysanthus* and *S. flavidulus* (PP 1, BS 89). Clade C (PP 1, BS 100) is strongly supported and consists of a group of *Syngonanthus* from *Cadeia do Espinhaço* (mainly in Minas Gerais State, Brazil). This small group shares a conspicuous character of showy and dimorphic involucral bracts.

Clade D has been considered as *Syngonanthus* sect. *Carphocephalus* (excluding *S. anomalus*) and it is well supported (PP 1, BS 95). Here, *S. caulescens* is the first divergent species and the new species appears as sister of *S. weddellii*. The taxonomic placement of *S. androgynus* (within *Syngonanthus* sect. *Carphocephalus*) corroborated our original hypothesis. The new species shares characteristics observed in this group like fleshy petals, and well-developed aerial stem with leaves spirally distributed.

The phylogenetic analysis also reveals multiple origins for bisexual flowers in *Syngonanthus*. *Syngonanthus trichophyllus* and *S. acephalus* share the same ancestor for bisexual flowers and they are more related to plants from clade B and C. It is surprising because they are groups with distinct morphological structure, inflorescence and geographical distribution.

Clade E shows a known strong group (PP 1, BS 96) that consists of rosette plants without synflorescence axes, such as *S. minutulus*, *S. heteropeplus*, *S. costatus*, *S. davidsei*, *S. nitens*, *S. gracilis* and *S. poggeanus*.

Character reconstruction

Character reconstruction based on MP analyses resulted in trimerous flowers as ancestral character state for *Syngonanthus* ($p > 99\%$), with only one transition for dimerous flowers (Figure 4). This implies that 3-parted flowers proved to be the plesiomorphic state, explicitly, a shared state observed for almost all Eriocaulaceae. Dimerous flowers, a character state shared by *S. acephalus* and *S. trichophyllus* appears to be a synapomorphy with a unique shift in *Syngonanthus*. According to parsimony assignations, there is about 94% of probability for ancestral character of *S. acephalus* and *S. trichophyllus* to be represented by 2-merous flowers.

On the other hand, the bisexual condition of the flowers appears to have originated independently twice in the genus, at least. This scenario makes sense, since the bisexual-flowered species form two morphologically very distinctive groups: *S. androgynus* has 3-parted flowers and *S. acephalus* and *S. trichophyllus* are dimerous. The character state for type of the flowers revealed that unisexual flowers represent the ancestral character state in *Syngonanthus* ($p > 99\%$). The bisexual condition of *S. androgynus* seems to be an isolated transition. The probability is more than 99% that unisexual flowers represent the ancestral character state in the clade *S. androgynus / S. weddellii* while the ancestral character state of *S. acephalus* and *S. trichophyllus* had bisexual flowers ($p = 88\%$).

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Legends

Figure 1. Illustration of *Syngonanthus androgynus*. A. habit; B. distribution of leaves on aerial stem; C. details of spathe and scape; D. capitulum; E-F. flower variation: E. flower with shorter and pilose corolla; F. flower with longer and glabrous corolla; G. dissected flower showing petals, anthers and styles; H. petal dorsal view; I. petal ventral view; J. seed. Drawn by Natanael Nascimento from *Fonseca & Filgueiras 115* (A; C-E; G-J) and *Albán Castillo & Foster 6968* (B; F).

Figure 3. Phylogenetic tree. Cladogram of Bayesian analysis of the combined plastid and nuclear data (psbA-trnH, trnL-F and ITS) showing the position of *Syngonanthus androgynus*. Numbers above the branches represent posterior probabilities (PP more than 0.60), numbers below branches are bootstrap percentages. Branches without parsimony bootstrap proportions are collapsed in the strict consensus.

S2 Figure. Strict consensus tree of the maximum parsimony. Maximum parsimony tree resulting from analysis of the combined plastid and nuclear markers (*psb*A-*trn*H, *trn*L-F and ITS). Numbers below the branches are bootstrap values.

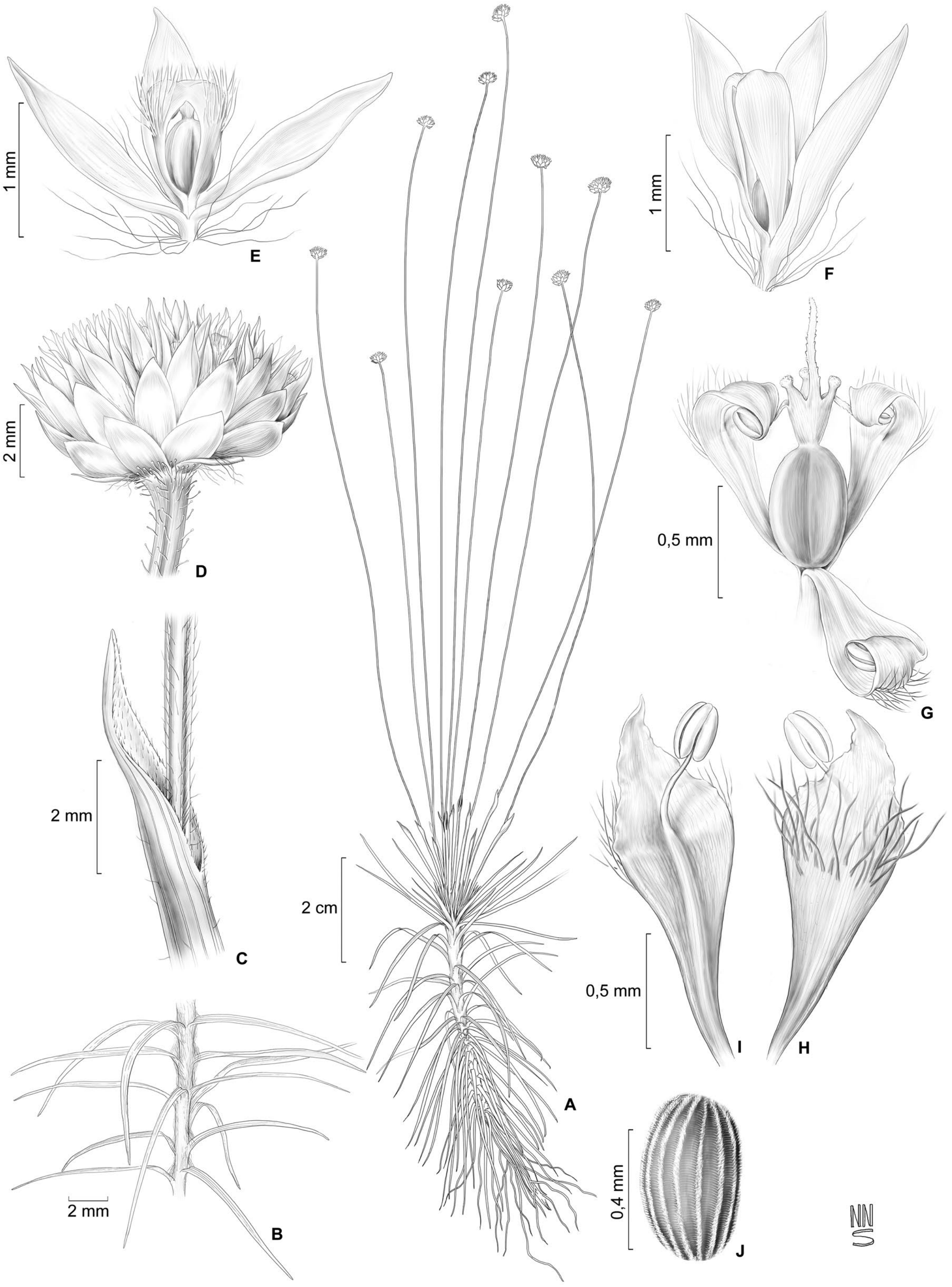
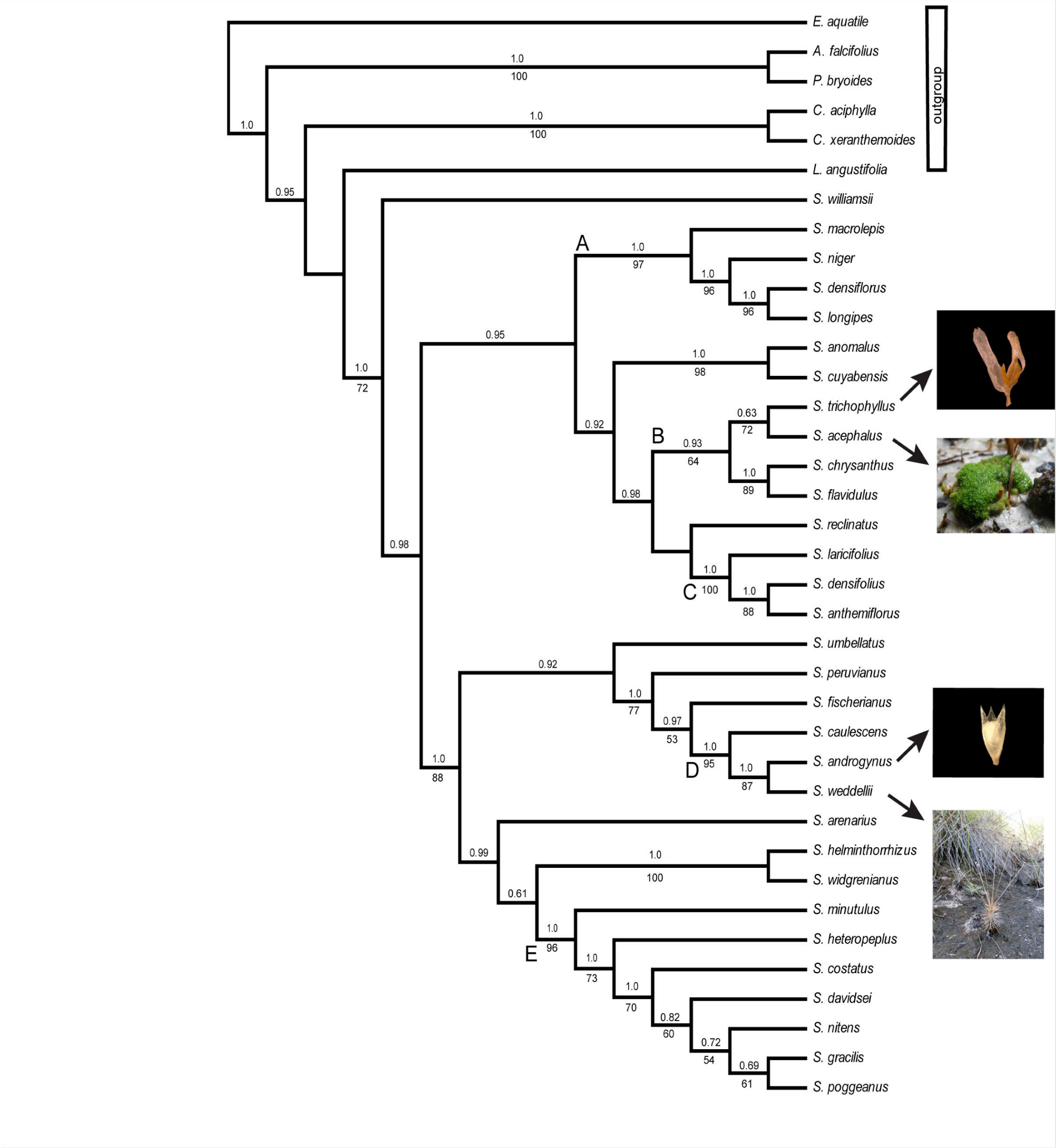


Figure 1

Figure 2. *Syngonanthus androgynus* details. A-B. Capitula. **A.** specimen from Brazil. **B.** specimen from Peru. **C.** bisexual flower with one sepal removed. **D.** dissected bisexual flower. **E.** petal with evidently adnate filament. **F.** seed. Scale bars: 0.4 mm (F), 0.5 mm (C-E), 1 mm (A,B). Photos from *Oliveira et al. 1056* (A) and *Albán Castillo & Foster 6968* (B-F).


E. aquatile
A. falcifolius
P. bryoides
C. aciphylla
C. xeranthemoides
outgroup
L. angustifolia
S. williamsii
S. macrolepis
S. niger
S. densiflorus
S. longipes
S. anomalus
S. cuyabensis
S. trichophyllus
S. acephalus
S. chrysanthus
S. flavidulus
S. reclinatus
S. laricifolius
S. densifolius
S. anthemiflorus
S. umbellatus
S. peruvianus
S. fischerianus
S. caulescens
S. androgynus
S. weddellii
S. arenarius
S. helminthorrhizus
S. widgrenianus
S. minutulus
S. heteropeplus
S. costatus
S. davidsei
S. nitens
S. gracilis
S. poggeanus
A
B
C
D
E
1.0
100
1.0
100
1.0
0.95
1.0
72
1.0
97
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64
1.0
89
0.98
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77
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87
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96
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73
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0.82
60
0.72
54
0.69
61

Figure 3

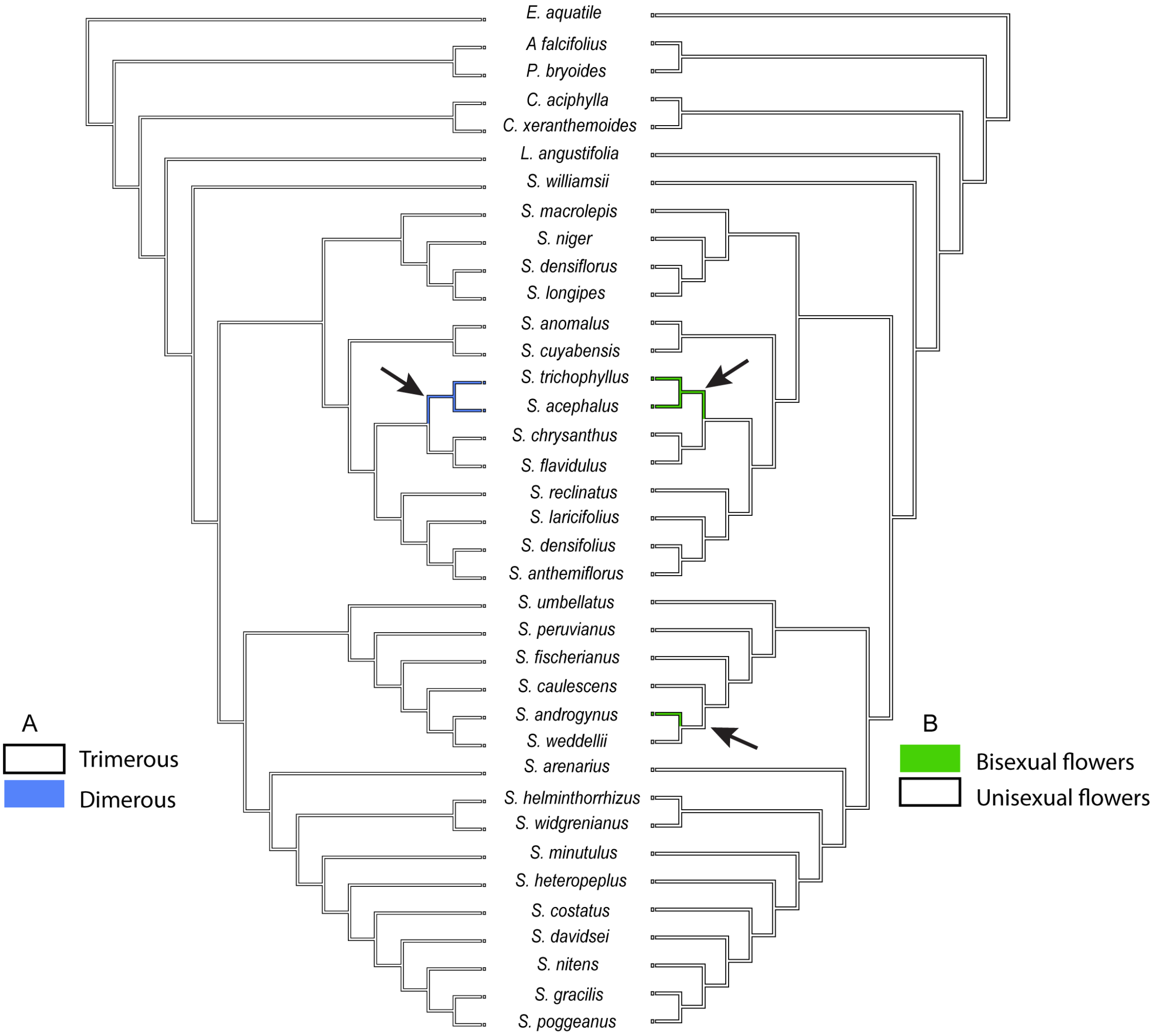
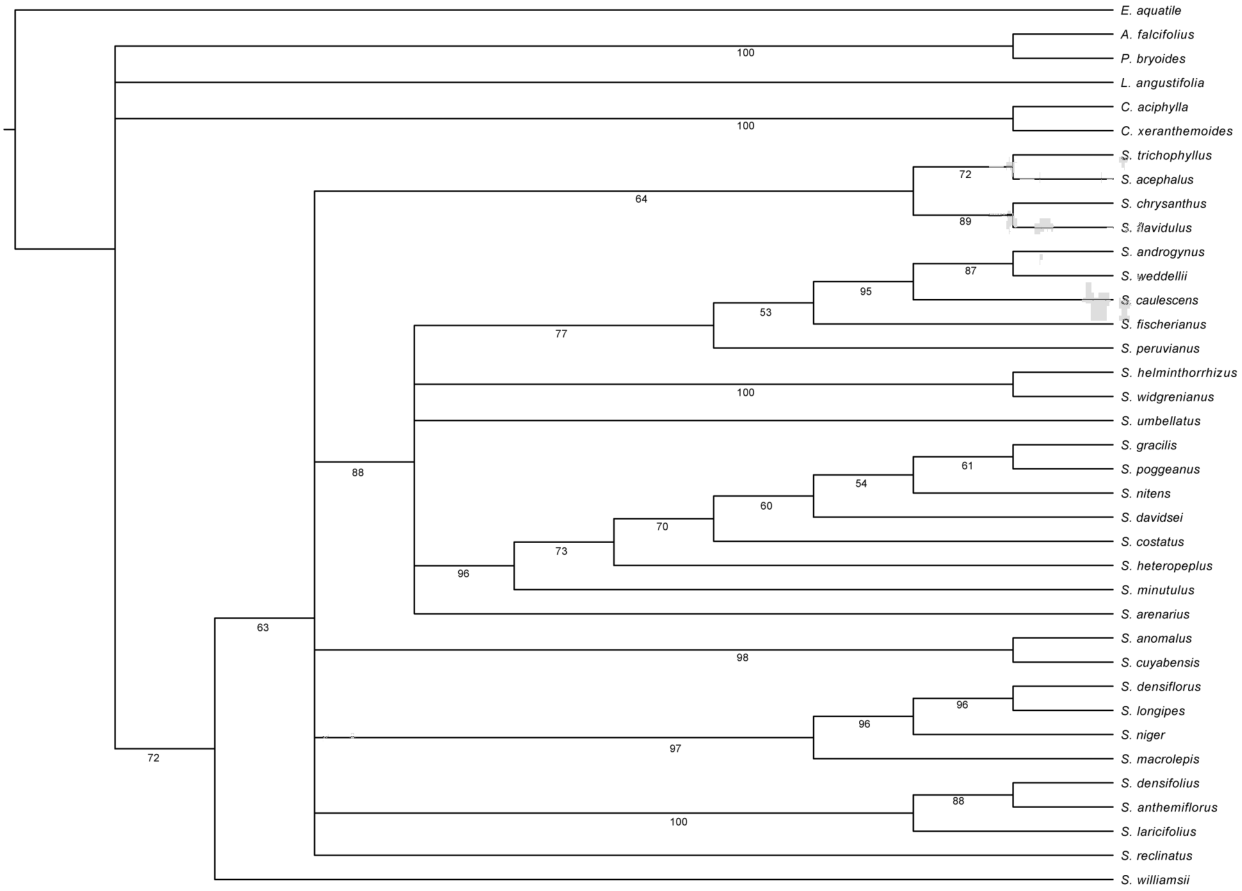


Figure 4. Character reconstruction. Ancestral character reconstruction for floral traits based on the Bayesian tree inference of the combined plastid and nuclear data (*psb*A-*trn*H, *trn*L-F and ITS). (A) Number of parts in the whorl (merism). (B) Type of flower. Branch colors indicate the ancestral reconstruction under maximum likelihood. The arrowheads indicate the nodes where change occurs to dimerous and bisexual flowers.

Table I. List of investigated species in the molecular analysis with voucher information and GenBank acession numbers for three regions (*psba*A-*trn*H, *trn*L-F and ITS). An en-dash indicates that the region was not sequenced for the taxon. An asterisk (*) indicates newly sequences generated for this study.

Taxa	**Locality**	**Voucher**	**GenBank accession**		
			psb**A-*****trn*****H**	***trn*****L-F**	**ITS**
Actinocephalus falcifolius (Koern.) Sano	Brazil, MG	*Echternacht 1635* (SPF)	KF840892	KF840832	KF840799
Comanthera aciphylla (Bong.) L.R.Parra & Giul.	Brazil, MG	*Echternacht 1692* (SPF)	KF840907	EU924491	EU924339
Comanthera xeranthemoides (Bong.) L.R.Parra & Giul.	Brazil, GO	*Echternacht 1963* (SPF)	KF840906	KF840845	KF840808
Eriocaulon aquatile Koern.	Brazil, MG	*Echternacht 1845* (SPF)	KF840891	KF840831	KF840798
Leiothrix angustifolia (Koern.) Ruhland	Brazil, BA	*Harley 54660* (HEFS)	EU924364	EU924443	EU924290
Syngonanthus acephalus Hensold	Colombia, GUA	*Lucero 190* (ANDES)	*xxxxxx	-	-
Syngonanthus androgynus M.T.C. Watan.	Brazil, MG	*Oliveira 1056* (F)	*xxxxxx	*xxxxxx	*xxxxxx
Syngonanthus anomalus (Koern.) Ruhland	Suriname	*Irwin 55267* (P)	KF840925	KF840866	-
Syngonanthus anthemiflorus (Bong.) Ruhland	Brazil, MG	*Echternacht 1649* (SPF)	KF840926	KF840867	KF840818
Syngonanthus arenarius (Gardner) Ruhland	Brazil, MG	*Andrade 493* (HUEFS)	EU924422	EU924498	EU924342
Syngonanthus caulescens (Poir.) Ruhland	Brazil, BA	*Andrade 452* (HUEFS)	EU924424	EU924500	EU924344
Syngonanthus chrysanthus (Bong.) Ruhland	Brazil, RS	*Trovó 115* (SPF)	KF840927	-	-
Syngonanthus costatus Ruhland	Brazil, MG	*Echternacht 2066* (SPF)	-	KF840871	-
Syngonanthus cuyabensis (Bong.) Giul., Hensold & L.R. Parra	Brazil, MT	*Giulietti 2483* (HUEFS)	EU924412	EU924489	EU924336
Syngonanthus davidsei Huft	Brazil, MT	*Argent 6454* (P)	-	KF840872	-
Syngonanthus densiflorus (Koern.) Ruhland	Brazil, TO	*Trovó 292* (SPF)	KF840930	KF840873	-
Syngonanthus densifolius Silveira	Brazil, MG	*Echternacht 1689* (SPF)	KF840931	KF840874	-
Syngonanthus fischerianus (Bong.) Ruhland	Brazil, SP	*Trovó 171* (SPF)	KF840934	KF840877	KF840820
Syngonanthus flavidulus (Michx.) Ruhland	United States, NC	*Masssey 3284* (P)	KF840932	KF840875	-
Syngonanthus gracilis (Bong.) Ruhland	Brazil, MG	*Echternacht 1709* (SPF)	KF840936	KF840879	KF840822
Syngonanthus helminthorrhizus (Mart. ex koern.) Ruhland	Brazil, SP	*Trovó 315* (SPF)	KF840937	KF840880	KF840823
Syngonanthus heteropeplus (Koern.) Ruhland	Brazil, AM	*Carvalho 1443* (INPA)	KF840945	KF840888	KF840828

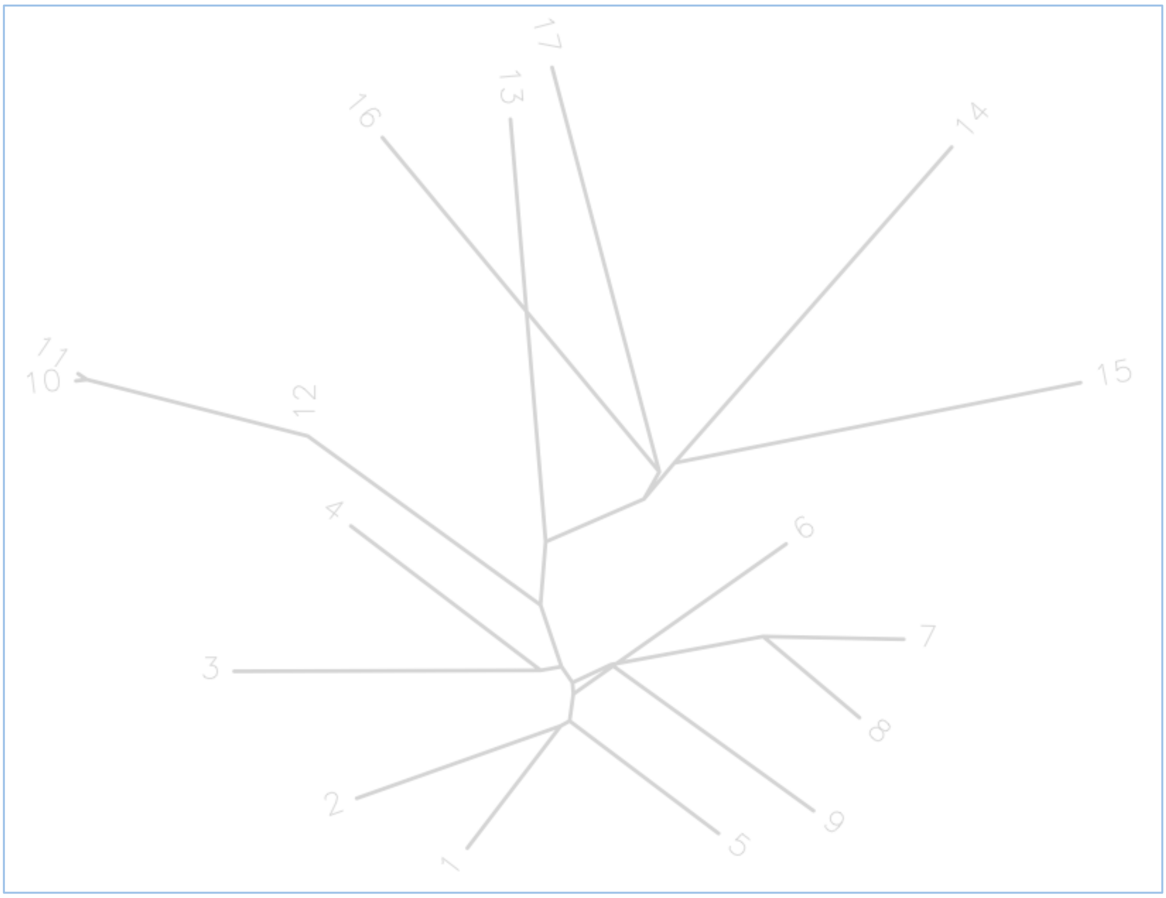
Syngonanthus laricifolius (Gardner) Ruhland	Brazil, MG	*Echternacht 1870* (SPF)	KF840938	KF840881	KF840824
Syngonanthus longipes Gleason	Brazil, AM	*Carvalho 1831* (INPA)	KF840939	KF840882	-
Syngonanthus macrolepis Silveira	Brazil, MG	*Echternacht 1902* (SPF)	KF840940	KF840883	KF840825
Syngonanthus minutulus (Steud.) Moldenke	Brazil, MG	*Echternacht 1797* (SPF)	KF840935	KF840878	KF840821
Syngonanthus niger Silveira	Brazil, MG	*Echternacht 1840* (SPF)	KF840941	KF840884	-
Syngonanthus nitens (Bong.) Ruhland	Brazil, MT	*Echternacht 1815* (SPF)	KF840942	KF840885	KF840826
Syngonanthus peruvianus Ruhland ex Ule	Peru	*Hutchison 556* (P)	KF840928	KF840870	KF840819
Syngonanthus poggeanus Ruhland	DR Congo	*Duvigneaud 1342* (BRLU)	KF840943	KF840886	-
Syngonanthus reclinatus (Koern.) Ruhland	Brazil, TO	*Echternacht 2118* (SPF)	KF840944	KF840887	KF840827
Syngonanthus trichophyllus Moldenke	Brazil, RR	*Carvalho 1580B-B* (INPA)	*xxxxx	*xxxxx	*xxxxx
Syngonanthus umbellatus (Lam.) Ruhland	Brazil, AM	*Echternacht 2097* (SPF)	KF840946	KF840889	KF840829
Syngonanthus weddellii Moldenke	Brazil, TO	*Watanabe 381 (SPF)*	*xxxxx	*xxxxx	*xxxxx
Syngonanthus widgrenianus (Koern.) Ruhland	Brazil, MG	*Echternacht 1952* (SPF)	KF840947	KF840890	KF840830
Syngonanthus williamsii (Moldenke) Hensold	Brazil, AM	*Carvalho 2208b* (INPA)	KF840948	-	-
Paepalanthus bryoides (Bong.) Kunth	Brazil, MG	*Costa 263* (HUEFS) / *Echternacht 1804* (SPF)	EU924373	KF840834	KF840801


E. aquatile
A. falcifolius
100
P. bryoides
L. angustifolia
C. aciphylla
100
C. xeranthemoides
S. trichophyllus
72
S. acephalus
64
S. chrysanthus
89
S. flavidulus
S. androgynus
87
S. weddellii
95
S. caulescens
53
S. fischerianus
77
S. peruvianus
S. helminthorrhizus
100
S. widgrenianus
S. umbellatus
S. gracilis
61
S. poggeanus
88
54
S. nitens
60
S. davidsei
70
S. costatus
73
S. heteropeplus
96
S. minutulus
S. arenarius
63
S. anomalus
98
S. cuyabensis
S. densiflorus
96
S. longipes
96
S. niger
72
97
S. macrolepis
S. densifolius
88
S. anthemiflorus
100
S. laricifolius
S. reclinatus
S. williamsii

(S2)

Chapter Two

Trends in *Syngonanthus* (Eriocaulaceae: Poales) based on molecular phylogeny: Have DNA sequences reflected morphological groups?



Abstract

Syngonanthus is the third largest genus in Eriocaulaceae and one of the most economically important genera in the family. Traditionally, the genus is classified in two sections: *Syngonanthus* sect. *Syngonanthus* and *S.* sect. *Carphocephalus*. Moreover, this classification is controversial due to the high levels of convergence and homoplasy of the morphological characters. In this present study, phylogenetic analyses of *Syngonanthus* were conducted with maximum parsimony and Bayesian analyzes using two nuclear genes (ITS and ETS) and three chloroplast regions (*psb*A-*trn*H, *trn*L-F and *rps*16). The subjects of this study explore the placement of the genus in Paepalanthoideae, infrageneric categories and morphological groups. The results of this phylogeny study corroborated the placement of *Syngonanthus* as sister group of the remaining genera in Paepalanthoideae and evidenced that the traditional infrageneric groups are non-monophyletic. Additionally, new morphological groups emerged with strong support and a new circumscription can be proposed in the future. Despite the general geographical patterns have been scarcely observed in the genus, molecular data corroborated most of morphological groups in *Syngonanthus*.

Keywords: Eriocaulaceae; Paepalanthoideae; phylogeny; morphology; taxonomy.

1. Introduction

Eriocaulaceae is a pantropical family consisting of 11 genera and 1200 species (Giulietti & Hensold 1990; Stützel 1998; Sano 2004; Parra et al. 2010; Andrade et al. 2011; Echternacht et al. 2011; Trovó et al. 2013). The family is characterized by herbaceous plants with compact involucrate capitula, orthotropous ovules and uniovulate locules. Most Eriocaulaceae have unisexual and trimerous flowers showing extremely rare bisexual or dimerous flowers (Rosa & Scatena 2007; Oriani et al. 2008). A single inflorescence shows staminate and pistillate flowers (Giulietti & Hensold 1990).

Commonly, Eriocaulaceae are known as "everlasting plants" because remain the alive appearance even after harvesting. Commercialization and exportation of these plants are primarily stimulated by the beauty and high durability of inflorescences, used for ornamental purposes (Giulietti et al. 1988) or for manufacturing accessories (Schmidt et al. 2007). However, frequently harvests of these plants are premature, before the full fruiting. This entails a critical decrease of natural populations. This chaotic scenery has left many species at imminent risk of extinction (Giulietti et al. 1996). Many conservation actions have been proposed by the scientific community, NGOs and Brazilian governmental institutions. This includes specific actions to raise awareness of the collectors and forms suitable of management. Several species of *Syngonanthus* Ruhland (Paepalanthoideae) are covered by these goals, such as *Syngonanthus nitens* (Bong.) Ruhland (common name "golden grass"), *Syngonanthus niger* Silveira, *Syngonanthus macrolepis* Silveira, among others species of the genus.

Syngonanthus has been recognized as the third largest genus in Eriocaulaceae. The genus comprises about 120 species, which exhibit a disjunction distribution in American and African continents (Giulietti & Hensold 1990). Only about a sixth of *Syngonanthus* occurs in Africa (Phillips, 1997). The most of the diversity is concentrated in Eastern Brazil mainly in Espinhaço range. This region has high elevations (above 900 m) and rich mountaintop endemisms of fauna and flora (Giulietti et al. 1987; Harley 1995; Giulietti et al. 2000). Giulietti & Pirani (1988) claim that about 60 percent of species in Eriocaulaceae occur in this area, and Venezuelan tepuis have been reported as another rich endemism area to Eriocaulaceae (Hensold 1999). Some species in the *Syngonanthus* genera occur in ruspestrian grassland, up shallow and Sandy soils, and rocks quartzites and sandstones, like in the most taxa in Eriocaulaceae (Giulietti et al. 1987). However, fieldwork observations have shown that the most species of *Syngonanthus* inhabit marshy or easily water drainage soils.

Syngonanthus is distinguished by the follow character sets: isostemonous flowers, bitec anthers (except *S. cuyabensis* and *S. infimus*) and pistillate flowers with fusioned petals at middle (Giulietti & Hensold 1990). Others characteristics are spongiate roots, nectariferous and stigmatic branches free at the same level and some species exhibit sinflorescence axis. Ruhland (1900) described the genus from taxa previously included in *Paepalanthus*. Subsequently, an infrageneric classification was also proposed by Ruhland (1903). Taking the reference point a subgenus of *Paepalanthus*, the author proposed five sections. The largest section was *Syngonanthus* sect. *Dimorphocaulon*, synonymized with *Syngonanthus* sect. *Syngonanthus* by Parra & Giulietti (1997). This section has about 130 species and includes all geographical distribution of the genus (Giulietti & Hensold 1990). Recently, *Syngonanthus* sect *Eulepis* and *Syngonanthus* sect. *Thysanocephalus* were recircumscribed and transferred to the reestablished *Comanthera* (Parra & al. 2010), that presents restricted geographical distribution in South America, including Brazil, Colombia, Guyana and Venezuela (Giulietti & Hensold 1990). *Syngonanthus* sect. *Chalarocaulon* and *S. macrocaulon* Ruhland were synonymized with *S. anomalus* (Köern.) Ruhland. (*S.* sect. *Carphocephalus*) by Hensold (1999). The current circumscription of *S.* sect. *Carphocephalus* is restricted to approximately 15 species; most of all is rare or not seen in natural fields.

The goals of the present study are to expand a phylogenetic analyzes of *Syngonanthus* with a broader taxon sampling and an increased number of molecular markers, a total of five. All studies conducted with Eriocaulaceae at this moment have used only *psb*A-*trn*H, *trn*L-F and ITS regions. Furthermore, we are investigating the circumscription of the sections currently accepted: *Syngonanthus* sect. *Syngonanthus* and *Syngonanthus* sect. *Carphocephalus*; and to check other infrageneric relationships.

2. Materials and Methods

2.1 Taxon sampling

In this study, a total of 111 accessions belonging to 77 *Syngonanthus* taxa (ingroup) were included in the analyzes (table 1), in order to cover the morphological diversity and geographical distribution of the genus. We covered the complete geographical distribution of the genus with representative taxa from Africa and North, Central and South America. Most of taxa were collected in Brazil but some of that species occur in South and/or Central America (e.g. *S. davidsei*, *S. caulescens*, *S. trichophyllus* and *S. heteropeplus*, for detailed information see table 2). The traditional subdivision of the genus also had covered with species from *Syngonanthus* sect. *Syngonanthus* and *Syngonanthus* sect. *Carphocephalus* (Ruhland 1903; Andrade et al. 2010;

Echternacht et al. 2014). Most of this diversity was sampled from Brazil, mainly in Espinhaço Range (Minas Gerais state) and Central Brazil (Goiás and Mato Grosso states). Leaves, scapes or spathe were collected from natural habitats, dried and stored in silica gel or removed from herbarium material. The outgroup was composed by recognized genera of the two subfamilies in Eriocaulaceae. The representative taxa of the Paepalanthoideae were *Actinocephalus* (1), *Comanthera* (11), *Leiothrix* (9), and *Paepalanthus* (11). In Eriocauloideae, only two species of Eriocaulon were included. The small number of samples in Eriocauloideae is justified since the monophyletism of the subfamilies has been already proved and well-supported as well as *Syngonanthus* has consistently appeared as a monophyletic group. (Andrade et al. 2010; Gilulietti et al. 2012a; Trovó et al. 2013; Echternacht et al. 2014). The most of ITS, *psb*A-*trn*H and *trn*L-F outgroup sequences were obtained from GenBank. The species, voucher specimens, herbarium, localization and the GenBank accession number of the sequences generated in this study are listed in the table 1.

2.2 DNA extraction, PCR amplification, and cycle sequencing

Genomic DNA from silica-gel dried tissue or herbarium specimens were extracted using modified 2X cetyl trimethylammonium bromide (CTAB) protocol (Doyle & Doyle 1987). For the phylogenetic reconstruction of *Syngonanthus,* data set from DNA sequences of two nuclear markers (ETS, the external transcribed spacer of 18S-26S nuclear ribosomal nuclear and; ITS, the internal transcribed spacer region of the nrDNA tandem repeat) and three plastid markers (*psb*A-*trn*H, *trn*L-F and *rps*16). PCR primers information used in this phylogeny are listed in the table 3 and 4.

To generate a data-set sequences used in this study, we amplify the DNA regions using PCR (polimerase chain reaction) protocols previously used for Eriocaulaceae (Andrade et al. 2010, Echternacht et al. 2014). Most *trn*L-F and *psb*A-*trn*H amplifications were carried in a 25µL volume with the following reagents: 2µL of total DNA, 15.1µL sterile water, 2.5µL with 10X *Taq* Qiagen buffer with $MgCl_2$, 1.25µL of DMSO, 2µL dNTPs (at concentration 8mM), 1µL of each primer and 0.15µL of *Taq* DNA polymerase (5U/µL). The 25µL- *rps*16 PCR reactions contained 14.6µL of purified water, 2.5µL with 10X Taq Qiagen buffer with $MgCl_2$, 0.75µL of BSA, 0.5µL of DMSO, 2.5µL dNTPs (8mM), 1µL of each 10µM primer and 0.15µL of *Taq* DNA polymerase (5U/µL) and 2 µL of total DNA. The ITS region was performed in a final reaction volume of 25µL, containg 1-2µL of genomic DNA with unkonwn concentration, 2.5µL with 10X *Taq* Qiagen buffer with $MgCl_2$, 1µL of BSA, 1.25µL of DMSO, 2µL dNTPs (at concentration 8mM), 1µL of each 10µM primer and 0.25µL of *Taq* DNA polymerase (5U/µL), and sterile water was added to totalize the final volume. To amplifly ETS region, a total of 25µL of reaction was performed with 2µL total DNA, 2.5µL with 10X *Taq* Qiagen buffer with $MgCl_2$, 0.75µL of BSA, 0.5µL of DMSO, 2.5µL dNTPs (8mM), 1µL of each 10µM primer and 0.2µL of *Taq* DNA polymerase (5U/µL), and 14.55µL of sterile water. The PCR profile reactions are described in the table 4.

The 10µL sequencing reactions contained 5.75µL of sterile water, 2µL of 5X Big Dye buffer, 0.25µl of Big Dye, 0.25µL of each primer and 1.5µL DNA template. The final product of the cycle sequencing and purification was sequenced for the auto-run profile of the 3730 sequencer, in the Pritzker DNA Lab, Field Museum. Sequences were assembled and edited using Geneious Pro 5.5.2 (Drummond et al. 2011)

2.3 Sequences Alignments and Phylogenetic Analyzes

Alignments of the DNA sequences were initially carried out using MAFFT v.7 (Katoh et al. 2013). Ambiguously aligned portions were removed manually using Geneious Pro 5.5.2 (Drummond et al. 2011). We analyzed combined data sets conducting maximum parsimony (MP) and Bayesian inference (BI) analyzes as implemented in PAUP (Swofford 2003) and MrBayes 3.2.3 (Ronquist et al. 2012), respectively. The best-fit model of nucleotide evolution for Bayesian analyzes was chosen separately for each marker using JModelTest 2 (Posada 2008). The models were selected using Akaike information criteria (AIC) for all datasets. The best models fitted were TVM + I + G for *trn*L-F, *psb*A-trnH and *rps*16; GTR + I + G for ITS; and TVM +G for ETS. The combined analyzes consisted a partitioned data with each marker decoupled. The heuristic search was composed by two independent runs of four Markov chains Monte Carlo (MCMC) running 10 million generations, sampling results every 1,000 generations. Trees were discard as burn-in (25%) of the sampled trees after checking the stability using Tracer v1.6 (Rambaut & Drummond 2007). Posterior Probabilities (PP) and the majority rule consensus tree were determined by combination of two runs using the trees sampled after the convergence of the chains. Internal support clades were evaluated by non-parametric bootstrapping (BS) based on 10,000 bootstrap replicates. Branch support was assessed by Bayesian posterior probabilities (PP). Clades with PP higher than 0.95 or BS higher than 75% were considered strongly supported (Cummings et al. 2003; Simmons et al. 2004). Three concatenated data matrices for phylogenetic analyzes were performed for the plastid dataset (*psba*A-*trn*H, *trn*L-F and *rps*16), nuclear dataset (ITS, ETS), excluding the outgroup, and total dataset (plastid + nuclear).

3. Results

Molecular datasets and phylogenetic analyzes

Summary statistics for each dataset are exposed in the table 5. The most informative data was provided by ETS with high support for different levels in the genus, while *psb*A-*trn*H was less informative, although it did support to infrageneric groups and major clades in *Syngonanthus*. In the combined analyzes, Bayesian analyzes yielded better-supported trees than those inferred by maximum parsimony. Statistical and visual representation of all topologies indicate that the BI tree that resulted from the analyzes of the total evidence dataset represent the best phylogenetic hypothesis of *Syngonanthus* (Figure 1). Sequences of the five gene combined result in the final alignment comprised 4180 pb, of which 2056 (49%) were variable and 1574 (38%) were parsimony-informative. Collapsed branches in MP were not represented by BS values in the Figure 1.

Individual data supported some major clades, but provided little resolution regarding relationships among genera. All genera sampled were strongly supported in all analyzes (BS=100, PP=1.00) and appears to be monophyletic, except for *Paepalanthus*, which proved to be paraphyletic with the emergence of *Actinocephalus falcifolius* within the clade. Individual topologies for BI can be checked in the support information for all markers, and for nuclear and chloroplast combined dataset.

The topology of infrageneric clades of *Syngonanthus* were similar with few controversial positions. Most of internal clades in the genus are well-supported. The first divergent clade (I) is composed by two taxa (*Syngonanthus williamsii* and *S. densiflorus* var. *longifolius*) strongly supported (BS=99, PP=1.00). Clade II, which shelter *S. cuyabensis* (x-*Philodice*), is also strongly supported (BS=100, PP=1.00). Clade III, which comprises a diverse group, with plants of bisexual flowers or dimorphic involucral bracts, is well-supported (BS=86, PP=1.00). Following inside the topology of the genus, the next big clade with strong support (BS=96, PP=1.00, clade IV) has *S. restingensis* as sister species to the remaining clade. Clades that deserve special attention are denominated as clade VI (BS=91, PP=1.0), VII (PP=0.96) and VIII (BS=66, PP=1.0), and commentaries about morphology and geographical distribution of the species included in these clades are provided in the discussion.

4. Discussion

4.1. Placement of Syngonanthus in Paepalanthoideae.

In the present study, an updated phylogeny of *Syngonanthus* was proposed based on more comprehensive samplings of both DNA sequences and species. This is the first study involving five DNA markers for Eriocaulaceae. The monophyly of *Comanthera*, *Leiothrix*, *Paepalanthus* / *Actinocephalus* group and *Syngonanthus* is strongly supported (PP 1.0, BS 100) for all analyzes. The placement of *Syngonanthus* in Paepalanthoideae does not corroborate previously phylogenetic studies in Eriocaulaceae (Andrade et al. 2010; Trovó et al. 2013; Echternacht et al. 2014), but is coherent with the findings of Giulietti et al. (2012). Here, *Syngonanthus* (clade A) is strongly positioned as sister to the remainder of Paepalanthoideae (clade B), in Bayesian analyzes. Probably, the greatly increased sampling effort of *Syngonanthus*, covering an extensive geographical and morphological diversity of the genus led to this result. In general, the relationships among other genera of Paepalanthoideae are still unclear, with weak support.

4.2. Synapomorphies of Syngonanthus

Fusion of the sepals in the pistillate flowers appears to be a character homoplastic in the floral evolution of Eriocaulaceae, with multiple events. Because the weak support, the relationships among the genera are unclear; but, at least, two times this character emerged in the family, with occurrence in *Mesanthemum* (Eriocauloideae) and *Comanthera* and *Syngonanthus* (Paepalanthoideae). In Paepalanthoideae, *Syngonanthus* and *Comanthera* share this floral trait but the fusion zone is different in each other. *Syngonanthus* has pistillate flowers with petals shorter than sepals and petals fused in the upper part, leaving a short free apex. *Comanthera* has pistillate flowers with sepals shorter than petals and petals fused in the middle leaving long free apex with apices erect (Echternacht et al. 2014). Synflorescence axes (sometimes denominated "modified aerial stem") and unequal sepals of the staminate flowers emerged early in the evolutionary history of *Syngonanthus* and can also be considered synapomorphies of the genus.

4.3. Infrageneric taxonomic implications

The historical and current infrageneric classification of *Syngonanthus* is not corroborated, according with our findings and previous phylogenetic studies (Andrade et al. 2010; Echternacht et al. 2014). Koernicke (1863) placed some species of *Syngonanthus* in subgenera of *Paepalanthus*, suggesting morphological affinities and close relationship among *Paepalanthus* subg. *Andraspidopsis*

Koern., *P.* subg. *Carphocephalus* Koern. and *P.* subg. *Psilocephalus* Koern. Neither of these groups emerged as monophyletic in our analyzes. Currently, *Syngonanthus* is composed by two sections: *S.* sect. *Syngonanthus* and *S.* sect. *Carphocephalus* (Ruhland 1903), both non-monophyletic groups. In our analysis, *Syngonanthus* sect. *Syngonanthus* is paraphyletic, despite the formal inclusion of *Philodice* in the genus (*S. cuyabensis*) (Giulietti et al. 2012b). Following the circumscription proposed by Ruhland (1903), *Syngonanthus* sect. *Carphocephalus* appears as polyphyletic group in our analysis. However, a new circumscription for this section is proposed (chapter three), excluding some species traditionally included in this group, based on morphological and molecular evidences. Other species previously included in *S.* sect. *Syngonanthus* have added to the *S.* sect. *Carphocephalus*, such as *S. fischerianus*, *S. hygrotrichus* and *S. peruvianus*.

4.4. Formal and informal groups in Syngonanthus: morphology, geographic distribution and taxonomic implications

Informal group "Gigantum" (Clade I)

Syngonanthus williamsii and *S. densiflorus* var. *longifolius* are sister species and the early divergent lineage within *Syngonanthus*. Both species are robust plants with developed synflorescence axis with foliaceous bracts over its structure, a probable synapomorphy of this small group. Another autopomorphy is the leaves of the rosette with apex bifid, an uncommon character, which was not seen in another species of the genus. These species share the presence of floral bracts, arachnoid trichomes on the leaves of the rosette, involucral bracts pilose, and synflorescence axis segmented (with ribs). This small group have a curious geographical pattern. *Syngonanthus williamsii* occurs only in Amazonian region of Brazil, Colombia and Venezuela. *Syngonanthus densiflorus* var. *longifolius* is representative in the Brazilian Cerrado in Mato Grosso and Tocantins states; in other words, these species do not have a geographical distribution overlapped, although phylogenetically closer related.

Informal group "Philodicoides" (clade II)

This is another small group, which has appeared consistently in all analysis with high support. It includes *Philodice,* the genus recently transferred to *Syngonanthu*s for nomenclatural and taxonomic issues (Giulietti et al. 2012b). For a long time, some species included in this clade were considered as belonging to *Syngonanthus* sect. *Carphocephalus* (*Paepalanthus* subg. *Carphocephalus sensu* Koernicke, 1863), such as *S. anomalus* and *S. philodicoides* (Ruhland 1903). Previous phylogenetic studies indicated *S.* sect. *Carphocephalus* polyphyletic, as currently circumscribed (Andrade et al.

2010; Echternacht et al. 2014). We excluded these species from *S.* sect. *Carphocephalus* and a new circumscription and revisionary studies of this section are detailed in the chapter 3, and below. Although, we have not sampled *S. xinguensis* and *S. philodicoides* in this phylogenetic study, for morphological inference, it is supposed that those species belong to the same group of *S. anomalus*, *S. fenestratus*, *S. cuyabensis* and *Syngonanthus sp.nov.1* (clade 2). Pistillate flowers with upper half of the petal spongy, and staminate flowers with flesh (rigid) corolla are homoplastic synapomorphies for this group. Both pistillate and staminate flowers have corolla non-involute after anthesis, and rhomboidal petals, features of easy visualization. The species in the "Philodicoides group" have a variable habit showing plants with aerial stem and/or synflorescence apex, since plants without scapes. This evidence shows that floral traits are decisive for coherence and morphological identity of this group, regardless of the pattern shown in the arrangement of inflorescences. The geographical distribution of "Philodicoides group" is widely spread, and basically covers the Amazonian region, mainly in wet grasslands, with occurrence in Bolivia, Brazil, Colombia, Ecuador, Guyana, Guyane, Peru, Suriname and Venezuela.

Informal group "Altibracteatum" (clade III)

Another clade with robust support in our analysis is composed by species of the clade III. This group has a large morphological variability, but shares the character of involucral bracts surpassing the flowers in height. The first divergent species in this clade is *S. reclinatus*, a plant with occurrence in the Central Brazil, in Cerrado phytophysiognomy. This species has pistillate flowers with upper half membranous and lower half fleshy. Additionally, it has staminate flowers with spongy corolla as observed in *S.* sect. *Carphocephalus*. Clearly, these floral traits are convergences in the genus, since they emerge two times, at least. The "*Altibracteatum* group" has also two distinctive clades in its phylogeny. The smaller includes two species with bisexual and dimerous flowers (*S. acephalus* and *S. trichophyllus*), a rare condition in Eriocaulaceae. Probably, *S. amazonicus*, a species not included in the sampling, is confined to this group, since it also shares those floral traits. Species in this clade are restricted to the Northern Amazonian region in Brazil, Colombia, Guyana, Suriname and Venezuela. The other group comprises endemic species of Espinhaço range in Minas Gerais, Brazil (except *S. laricifolius*, which also occurs in Bahia). This group shares an outstanding character of evident and 2-differentiated involucral bracts. Particularly, species in this subgroup occupy *campo rupestre* vegetation (for example *S. anthemiflorus*, *S. densifolius*, among others), resulting a complex mosaic of distribution in the major group with plants exclusive of *campo rupestre, cerrado* or Amazonian domain.

Informal group "Variabilis" (clade IV)

The majority of *Syngonanthus* species are concentrated in the huge clade (IV) with good support (BS=76, PP=0.99), observed in all analyzes, which encompasses the whole morphological variability of the genus. The first clade includes two subclades. One of them has *S. niger*, (endemic species of Serra do Cabral, Minas Gerais [MG]) and *S. macrolepis*, (also restricted to mountain ranges of Espinhaço) as sister species; the second subclade comprises *S. densiflorus* (typical species of *Syngonanthus* in the *Veredas* of Central Brazil) sister to *S. longipes*, which occurs in Amazonia. One more time the geographical pattern of species that occurs in Amazonian domain, Brazilian Cerrado and campo rupestre is observed in the same clade (also I and III).

Next, *S. restingensis* arises as sister to remaining species of the clade IV with high support (BS=96, PP=1.0). This striking species accumulates a series of autopomorphies as floral bracts, hydathodes and pseudovivipary (Hensold et al. 2012). It is endemic to *restingas* of Bahia and Rio de Janeiro.

Syngonanthus umbellatus, type species of the genus, emerges in the next clade, sister to core *Syngonanthus,* which comprises two major clades inside clade IV (clades V and VIII). This relationship is also well-supported (BS=91, PP=1.0). This species has synflorescence axis, a plesiomorphy retained and a trend in *Syngonanthus* species. This is another species belonging to Amazonian domain.

Informal group "Membrananthum" Clade V

The clade V is composed by a major group including clades VI and VII and *Syngonanthus oblonglus* (the typical variety and *S. oblongus* var. *aequinoctialis*). Most species in this clade has both membranous corolla. "Membrananthum group" is embedded by a small clade with weak support (involving *S. tenuis*, *S. umbellatus* var. *liebmannianus* and *S. bracteosus* var. *scrupulosus*), and then, the relationships between these groups are still unclear. *Syngonanthus oblongus* is a widespread species, and basically occupies fields of Cerrado in Bahia, and Amazonian domain in Brazil, Colombia and Venezuela. See commentaries about clades VI and VII below.

Informal group "Bracteosus" (clade VI)

One of the most morphologically distinct groups within *Syngonanthus* is "*Bracteosus group*". Most species of this clade have pilose involucral bracts, dark brown/castaneous-colored. All species in this group have compound inflorescences (synflorescence axis) and leaf-like bracts scattered on the axis. Usually, the synflorescence axis is not segmented (with ribs), as observed in the previous groups. Species with bracts arranged in verticils as *S. verticillatus* and *S. humboldtii* are splitted in two different subclades, according to geographical distribution. *Syngonanthus verticillatus* and *S. graomogolense*, species from Espinhaço range (Minas Gerais) are sister species, whereas *S. humboldtii* var. *humboldtii*, *S. humboldtii* var. *fuscus* and *S. bellus* are confined to subclade of species occurring in Amazonia and Brazilian Cerrado. Another subclade, sister to *S. verticillatus/S. graomogolense* clade, has species restricted to Chapada dos Veadeiros region, in Central Brazil. *Syngonanthus decorus*, *S. densifolius* var. *majus* and *S. vittatus* are morphologically similar species, often mistakenly identified in herbaria. One more time, the mosaic of patterns merging different domains in the same clade is similar to other clades in the genus, as observed in the clades I, III and IV.

Informal group "Sineaxem" (clade VII)

Clade VII is defined by the absence of synflorescence axis, except for *Syngonanthus bisumbellatus*, the early divergent species in the basal topology of the clade. It is surprising, because it would suppose that the morphological characters of *S. bisumbellatus* have more affinities with the clade VI, which has species with bracts along the synflorescence axis. This species occurs in Amazonia (Brazil, Colombia and Venezuela) and Brazilian Cerrado. The major remaining group embedded in the clade VII has exclusively species without synflorescence axis, such as *S. gracilis*, *S. latifolius*, *S. nitens* and others. This group has a high support (BS=100, PP=1.00), and consistently emerges in all analyzes. There is no geographical pattern observed in this group and species occurs in both American and African continents. Species in this clade occurs in African savannas, Atlantic forest, Cerrado, campo rupestre and Amazonian domain. This type of habit may be an innovation-key in the genus, and could explain the success of this group to explore the most different habitats and its diversification.

Informal group "Carphocephalus" (clade VIII)

This clade has a large morphological variability, and three well-supported groups are observed. The first group includes species with synflorescence axis and castaneous involucral bracts as *S. arenarius* and *S. densifolius* var. *brachyphyllus*. The first occurs in the Espinhaço range and the later in the Chapada dos Veadeiros. Other consistent group encompasses plants without synflorescence axis and basically, occurs in the restingas, except by *S. goyazensis*, a species known from Goiás and Western of Bahia, occupying wetlands in Cerrado. The major clade in this group partly corresponds to *Syngonanthus* sect. *Carphocephalus*. Excluding *S. anomalus* in the new circumscription proposed (chapter III), this group is clearly monophyletic and well supported in all analyzes. Species of *S.* sect *Carphocephalus* basically have two vegetative morphology-like very distinctive. The first species divergent in this group is *S. peruvianus*, an Andean species. Its morphology is similar to other species grouped in this clade as *S. fischerianus* and *S. hygrotrichus*. These three species has a short synflorescence axis and sometimes can show aerial stem slightly elongated. Despite these plants do not have pistillate flowers with carnose petals, the staminate flowers have petals, at least partly, carnose. *S. caulescens*, *S. appressus*, *S. weddellii*, *S. androgynus* and *Syngonanthus sp. nov*. show staminate and pistillate flowers with carnose corolla, a character observed in other groups in Syngonanthus. "Philodicoides group" (clade II) shares the same floral traits, however there are evident contrasts, which can expose different ontogeny of the flowers in these groups. "Philodicoides group" has pistillate flowers with corolla fleshy, but the texture is extremely rigid compared with *S.* sect *Carphocephalus* (the texture is spongy) and flowers are non-involute after anthesis. The pistillate flowers also reveals differences in the ontogeny of these groups. In "Philodicoides group", the petals of pistillate flowers are fleshy, mainly in the upper half, but in *S.* sect. *Carphocephalus* flowers are membranous in this same part and fleshy in the lower half.

General conclusions

Morphological patterns are observed in the most of clades in *Syngonanthus*, but traditional infrageneric classifications do not show monophyletic groups. Floral traits and reproductive characters such as absence/presence of synflorescence axis, characteristics of involucral bracts and floral texture have a great significance for evolutionary morphology of the groups. However, geographical distribution patterns of the clades are not observed and species occurring in many different domains can be included in the same group.

Synapomorphies of the genus can be related to pollination/dispersal mechanisms and floral biology studies are encouraged. The different level of fusion of the petals in pistillate flowers in *Comanthera* and *Syngonanthus* may reveal different strategies. Concave sepals are common features observed in many species of *Syngonanthus*. This shape sometimes implies the involvement of the seeds by sepals like it was seed storage. Some raised hypotheses converge to assist in aerodynamics dispersion over long distances. On the other hand, that could be a strategy for seed stock and protection of the propagule (e.g. torrential rains or predation). In any event, both are positive hypothesis. More studies are necessary to elucidate those issues.

The sepals of the staminate flowers are asymmetric. Most of all species in *Syngonanthus* have this characteristic. In addition, the whorl of sepals has a slight rotation. More studies are necessary to investigate and ascertain whether these features have relationship with ecological attraction of pollinator or evolutionary aspects.

Syngonanthus is a promising model for evolutionary research, because it has the most morphological diversity in Eriocaulaceae, along with *Paepalanthus*. Much of this richness and diversity of species is concentrated in specific areas, such as mountains of Espinhaço range and Central Brazil. Moreover, this morphological diversity is associated with molecular data, and morphological groups are corroborated by phylogenetic analyses.

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Table I. List of investigated species in the molecular analysis with voucher information and GenBank acession numbers for five regions (*psba*A-*trn*H, *trn*L-F, *rps*16, ETS and ITS). An en-dash indicates that the region was not sequenced for the taxon. Collector's name is only indicated for new sequences. An asterisk (*) indicates newly sequences generated for this study. Taxa named as "*Syngonanthus* sp." are new species that have been described and submitted for publication.

Taxa	Locality	Voucher	GenBank accession				
			*psb*A-*trn*H	*trn*L-F	*rps*16	ETS	ITS
Actinocephalus falcifolius (Koern.) Sano			KF840892	KF840832	-	-	KF840799
Comanthera aciphylla (Bong.) L.R.Parra & Giul.	Brazil, MG		KF840907	EU924491	-	-	EU924339
Comanthera curralensis (Moldenke) L.R.Parra & Giul.			KF840909	KF840849	-	-	EU924340
Comanthera elegans (Bong.) L.R.Parra & Giul.			KF840911	KF840851	-	-	KF840809
Comanthera floccosa (Moldenke) L.R.Parra & Giul.			KF840913	KF840853	-	-	KF840810
Comanthera jenmanii (Gleason) L.R.Parra & Giul.			KF840902	KF840843	-	-	KF840807
Comanthera nítida (Bong.) L.R.Parra & Giul.			EU924418	EU924495	-	-	KF840813
Comanthera nivea (Bong.) L.R.Parra & Giul.			KF840922	KF840862	-	-	KF840814
Comanthera reflexa (Gleason) L.R.Parra & Giul.	Brazil, AM	*Carvalho 2210d* (INPA)	KF840903	-	-	*xxxxx	-
Comanthera suberosa (Giul.) L.R.Parra & Giul.	Brazil, MG		KF840924	KF840864	-	-	KF840816
Comanthera vernonioides (Kunth) L.R.Parra & Giul.			KF840905	EU924499	-	-	EU924343
Comanthera xeranthemoides (Bong.) L.R.Parra & Giul.	Brazil, GO		KF840906	KF840845	-	-	KF840808
Eriocaulon aquatile Koern.	Brazil, MG		KF840891	KF840831	-	-	KF840798
Eriocaulon ligulatum (Vell.) L.B.Sm.	Brazil, BA		EU924430	EU92435	-	-	EU924278
Leiothrix angustifolia (Koern.) Ruhland	Brazil, BA		EU924364	EU924443	-	-	EU924290
Leiothrix arrecta Ruhland			EU924370	EU924449	-	-	EU924296
Leiothrix crassifolia (Bong.) Ruhland			EU924366	EU924445	-	-	EU924292
Leiothrix distichoclada Herzog			EU924368	EU924447	-	-	EU924294
Leiothrix flagellaris (Giul.) Ruhland			EU924371	EU924371	-	-	EU924297
Leiothrix flavescens (Bong.) Ruhland			EU924365	EU924444	-	-	EU924291
Leiothrix gomesii Silveira			KF840898	KF840839	-	-	KF840806

Leiothrix vivipara			EU924372	EU924451	-	-	EU924298
Paepalanthus bryoides (Bong.) Kunth.			EU924373	KF840834	-	-	KF840801
Paepalanthus calvulus (Ruhland) Hensold			KF840894	KF840835	-	-	KF840802
Paepalanthus comans Silveira			EU924404	EU924482	-	-	EU924329
Paepalanthus erectifolius Ruhland			KF840893	KF840833	-	-	KF840800
Paepalanthus flaccidus (Bong.) Kunth			KF840895	KF840836	-	-	KF840803
Paepalanthus macrocaulon Silveira			EU924392	EU924470	-	-	EU924317
Paepalanthus neglectus Koern.			EU924382	EU924460	-	-	EU924308
Paepalanthus vellozioides Koern.	Brazil, MG		KF840897	KF840838	-	-	KF840805
Paepalanthus paulinus Ruhland			KF840896	KF840837	-	-	KF840804
Paepalanthus tortilis (Bong.) Mart.			EU924302	EU924376	-	-	EU924455
Syngonanthus acephalus Hensold	Colombia, GUA	*Lucero 190* (ANDES)	*xxxxx	-	-	-	*xxxxx
Syngonanthus albopulvinatus (Moldenke) Moldenke	Brazil, MT	*Watanabe 343* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanhus angolensis H.E.Hess	Zambia	*Harder 3176* (MO)	*xxxxx	*xxxxx	-	-	-
Syngonanthus anomalus (Koern.) Ruhland	Brazil, RR / Suriname	*Amaral 2011/7* (F)	KF840925	KF840866	-	*xxxxx	*xxxxx
Syngonanthus anthemiflorus var. *anthemiflorus* (Bong.) Ruhland	Brazil, MG	*Watanabe 257* (SPF)	-	-	*xxxxx	*xxxxx	-
Syngonanthus anthemiflorus var. *similis* (Ruhland) L.R. Parra & Giul.	Brazil, MG	*Watanabe 305* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus appressus var. *appressus* (Koern.) Ruhland	Brazil, DF	*Watanabe 253* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus appressus var. *chapadensis* Moldenke	Brazil, GO	*Watanabe 243* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus arenarius var. *arenarius* (Gardner) Ruhland	Brazil, MG	*Watanabe 209* (SPF)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus arenarius var. *heterophyllus* (Koern.) Ruhland	Brazil, MG	*Watanabe 205* (SPF)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus bartlettii Moldenke	Belize, Stan Creek	*Goodwin 1751* (MO)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus bellus Moldenke	Brazil, MT	*Watanabe 341* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus bisumbellatus (Steud.) Ruhland	Brazil	*Mendonça 494* (SPF)	-	*xxxxx	*xxxxx	-	-
Syngonanthus bracteosus var. *scrupulosus* Moldenke	Brazil, RO	*Carvalho 2075* (INPA)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus cabralensis Silveira	Brazil, MG	*Watanabe 285* (SPF)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
"	Brazil, GO	*Watanabe 228* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus canaliculatus Silveira	Brazil, MG	*Watanabe 276* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	-
Syngonanthus capillaceus Silveira	Brazil, MG	*Watanabe 326* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus caulescens (Poir.) Ruhland	Brazil, MG	*Watanabe 318* (SPF)	EU924424	EU924500	*xxxxx	*xxxxx	EU924344

Syngonanthus chrysanthus (Bong.) Ruhland	Brazil, RS	*Trovó 115* (SPF)	KF840927	KF840869	-	*xxxxx	*xxxxx
Syngonanthus costatus Ruhland	Brazil, MG	*Abreu 245* (SPF)	*xxxxx	KF840871	*xxxxx	-	-
Syngonanthus crassinervius Silveira	Brazil, MG	*Watanabe 169* (SPF)	*xxxxx	*xxxxx	-	-	*xxxxx
Syngonanthus cuyabensis (Bong.) Giul., Hensold & L.R. Parra	Brazil, MT		EU924412	EU924489	-	-	EU924336
Syngonanthus davidsei Huft	Brazil, MT	*Watanabe 328* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus decorus Moldenke	Brazil, GO	*Watanabe 224* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus densiflorus var. *densiflorus* (Koern.) Ruhland	Brazil, MT	*Watanabe 334* (SPF)	*xxxxx	KF840873	*xxxxx	-	*xxxxx
Syngonanthus densiflorus var. *longifolius* Moldenke	Brazil, TO	*Watanabe 383* (SPF)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus densifolius var. *densifolius* Silveira	Brazil, MG	*Watanabe 316* (SPF)	KF840931	KF840874	*xxxxx	*xxxxx	-
Syngonanthus densifolius var. *brachyphyllus* Moldenke	Brazil, GO	*Watanabe 178* (SPF)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus densifolius var. *majus* Moldenke	Brazil, GO	*Watanabe 239* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus densus (Koern.) Ruhland	Brazil, MT	*Watanabe 345* (SPF)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus dichroanthus Hensold	Brazil, MT	*Watanabe 340* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus fenestratus Hensold	Brazil, RR	*Amaral 2011/26* (F)	*xxxxx	*xxxxx	*xxxxx	-	-
Syngonanthus fertilis var. *fuscus* Moldenke	Brazil, MT	*Watanabe 344* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus fischerianus (Bong.) Ruhland	Brazil, SP		KF840934	KF840877	-	-	KF840820
Syngonanthus flavidulus (Michx.) Ruhland	United States, FL	*Allen 28* (F)	KF840932	KF840875	-	*xxxxx	*xxxxx
Syngonanthus goyazensis (Koern.) Ruhland	Brazil, BA	*Watanabe 371* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus gracilis (Bong.) Ruhland	Brazil, MG	*Echternacht 1709* (SPF)	KF840936	KF840879	-	-	KF840822
Syngonanthus graomogolensis Silveira	Brazil, MG	*Watanabe 196* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus helminthorrhizus (Mart. ex koern.) Ruhland	Brazil, DF	*Watanabe 252* (SPF)	*xxxxx	KF840880	*xxxxx	-	KF840823
Syngonanthus heteropeplus (Koern.) Ruhland	Brazil, AM	*Watanabe 213* (SPF)	KF840945	KF840888	*xxxxx	*xxxxx	KF840828
Syngonanthus humbertii Moldenke	Madagascar	*Rakotoarivelo 332* (MO)	*xxxxx	-	*xxxxx	-	-
Syngonanthus humboldtii var. *humboldtii* (Kunth) Ruhland	Brazil, MT	*Watanabe 362* (SPF)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus hygrotrichus Ruhland	Brazil, MG	*Watanabe 313* (SPF)	*xxxxx	*xxxxx	-	*xxxxx	*xxxxx
Syngonanthus insularis Moldenke	Cuba	*Killip 45613* (NY)	*xxxxx	-	-	-	-
Syngonanthus itambeensis Silveira	Brazil, MG	*Watanabe 327* (SPF)	*xxxxx	*xxxxx	-	*xxxxx	*xxxxx
Syngonanthus lagopodioides (Griseb.) Ruhland	Cuba	*Greuter 25983* (NY)	*xxxxx	*xxxxx	-	-	-
Syngonanthus laricifolius (Gardner) Ruhland	Brazil, MG	*Watanabe 324* (SPF)	KF840938	KF840881	*xxxxx	*xxxxx	KF840824
Syngonanthus latifolius (Moldenke) Hensold	Brazil, MT	*Watanabe 384* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx

Syngonanthus longipes Gleason	Brazil, AM		KF840939	KF840882	-	-	-
Syngonanthus macrolepis Silveira	Brazil, MG		KF840940	KF840883	-	-	KF840825
Syngonanthus minutulus (Steud.) Moldenke	Brazil, MG	*Watanabe 319* (SPF)	KF840935	KF840878	*xxxxx	*xxxxx	KF840821
Syngonanthus multipes Silveira	Brazil, MG	*Watanabe 272* (SPF)	*xxxxx	*xxxxx	-	-	-
Syngonanthus niger Silveira	Brazil, MG	*Watanabe 270* (SPF)	KF840941	KF840884	-	-	*xxxxx
Syngonanthus nitens (Bong.) Ruhland	Brazil, MT	*Watanabe 329* (SPF)	KF840942	KF840885	*xxxxx	-	KF840826
Syngonanthus oblongus var. *aequinoctialis* Ruhland	Brazil, AM	*Watanabe 215* (SPF)	*xxxxx	*xxxxx	-	*xxxxx	*xxxxx
Syngonanthus oblongus var. *oblongus* Ruhland	Brazil, BA	*Watanabe 370* (SPF)	*xxxxx	*xxxxx	-	-	*xxxxx
Syngonanthus peruvianus Ruhland ex Ule	Peru		KF840928	KF840870	-	-	KF840819
Syngonanthus philcoxii Moldenke	Brazil, DF	*Watanabe 391 (SPF)*	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus poggeanus Ruhland	DR Congo		KF840943	KF840886	-	-	-
Syngonanthus reclinatus (Koern.) Ruhland	Brazil, TO		KF840944	KF840887	-	-	KF840827
Syngonanthus restingensis Hensold & A. Oliveira	Brazil, RJ	*Oliveira 269* (R)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus spongiosus Hensold	Brazil, RR	*Amaral et al. 2011/5* (F)	*xxxxx	*xxxxx	-	*xxxxx	*xxxxx
Syngonanthus tenuis var. *bulbifer* (Huber) Hensold	Brazil, AM	*Carvalho 1935* (INPA)	*xxxxx	*xxxxx	-	-	*xxxxx
Syngonanthus tenuis var. *tenuis* (H.B.K.) Ruhland	Brazil, AM	*Watanabe* 214 (SPF)	*xxxxx	*xxxxx	-	*xxxxx	*xxxxx
Syngonanthus trichophyllus Moldenke	Brazil, RR	*Carvalho 1580B-B* (INPA)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus umbellatus var. *liebmannianus* (Koern.) Ruhland	Brazil, GO	*Watanabe 380 (SPF)*	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus umbellatus var. *umbellatus* (Lam.) Ruhland	Brazil, AM	*Watanabe 211* (SPF)	KF840946	*xxxxx	*xxxxx	*xxxxx	KF840829
Syngonanthus verticillatus (Bong.) Ruhland	Brazil, MG	*Watanabe 197* (SPF)	*xxxxx	-	*xxxxx	*xxxxx	*xxxxx
Syngonanthus weddellii Moldenke	Brazil, TO	*Watanabe 381 (SPF)*	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus widgrenianus (Koern.) Ruhland	Brazil, BA		KF840947	KF840890	-	-	KF840830
Syngonanthus williamsii (Moldenke) Hensold	Brazil, AM	*Carvalho 2019* (INPA)	KF840948	*xxxxx	-	-	*xxxxx
Syngonanthus sp. 1 (*S. ruhlandii*)	Brazil, BA	*Watanabe 394* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus sp. 2 (*S. minimus*)	Brazil, MT	*Watanabe et al. 355* (SPF)	*xxxxx	*xxxxx	*xxxxx	-	*xxxxx
Syngonanthus sp. 3 (*S. laxifolius*)	Brazil, GO	*Watanabe 375* (SPF)	*xxxxx	*xxxxx	*xxxxx	*xxxxx	*xxxxx
Syngonanthus sp. 4 (*S. vittatus*)	Brazil, GO	*Watanabe 377* (SPF)	*xxxxx	-	*xxxxx	*xxxxx	*xxxxx
Syngonanthus sp. 5 (*S. androgynus*)	Brazil, MG	*Oliveira 1056* (F)	*xxxxx	*xxxxx	-	-	*xxxxx

Table 2. Geographical distribution records for taxa represented in this phylogenetic study.

South America	**Central America**	**North America**	**Africa**
Argentina: 1	Belize: 1	Mexico: 2	Angola: 2
Bolivia: 13	Costa Rica: 1	United States: 1	Burundi: 1
Brazil: 76	Cuba: 2		DR Congo: 1
Colombia: 18	Dominican Republic: 1		Madagascar: 1
Equator: 2			Malawi: 1
French Guyana: 5			Tanzania: 1
Guyana: 13			Zaire: 1
Paraguay: 4			Zambia: 2
Peru: 6			
Suriname: 9			
Uruguay: 1			
Venezuela: 22			

Table 3. PCR primers information.

Region	**Primer**	**Sequence (5'-3')**	**Reference**
*psb*A-*trn*H	psbAF	GTT ATG CAT GAA GCT AAT GCT C	Sang et al. (1997)
	trnHR	CGC GCA TGG ATT CAC AAA TC	
*trn*L-F	tabC	CGA AAT CGG TAG ACG CTA CG	Tarberlet et al. (1991)
	tabF	ATT TGA ACT GGT GAC ACG AG	
*rps*16	rpsF	GTG GTA GAA AGC AAC GTG CGA CTT	Oxelman et al. 1997
	rpsR2	TCG GGA TCG AAC ATC AAT TGC AAC	
ETS	18SE	ACT TAC ACA TGC ATG GCT TAA TCT	Linder et al (2000)
	ETS1f	GCG GCC GCA TGG TAT CGG ATA TCG ACA CG	
ITS	17SE	ACG AAT TCA TGG TCC GGT GAA GTG TCC	Desfeaux et al. (1996)
	26SE	G TAG AAT TCC CCG GTT CGC TCG CCG TTA C	

Table 4. PRC reaction profile

Region	Initial denaturation temp./time	Denaturation temp./time	Annealing temp./time	Extension temp./time	Final extension temp./time	Number of cycles
*psb*A-*trn*H	94°C / 3 min	94°C / 30 sec	53°C / 40 sec	72°C / 40 sec	72°C / 5 min	40
*trn*L-F	94°C / 3 min	94°C / 1 min	50°-52°C / 1 min	72°C / 2 min	72°C / 5 min	35
*rps*16	94°C / 3 min	94°C / 1 min	59°C / 35 sec	72°C / 90 sec	72°C / 5 min	30
ETS	94°C / 2 min	95°C / 30 sec	54°C / 1 min	72°C / 80 sec	72°C / 7 min	35
ITS	94°C / 7 min	94°C / 1 min	58°C / 1 min	72°C / 40 sec	72°C / 7 min	30

Table 5. Summary statistics of dataset used for phylogenetic inference.

	*psb*A-*trn*H	*trn*L-F	*rps*16	ETS	ITS	5-gene
Number of accessions	106	102	48	42	92	111
Aligned sequence length	737	1149	900	491	903	4180
Variable DNA sites (%)	415 (56)	955 (83)	629 (70)	460 (94)	724 (80)	–

Legend

Figure 1. Phylogenetic tree. Cladogram of Bayesian analysis of the combined plastid and nuclear data (*psb*A-*trn*H, *trn*L-F, *rps*16 ETS and ITS) showing the position of *Syngonanthus androgynus*. Numbers above the branches represent posterior probabilities (PP more than 0.75), and bootstrap percentages, respectively. Branches without parsimony bootstrap proportions are collapsed in the strict consensus.

Supplementary materials (Legends)

(S1) Bayesian tree obtained from analysis of nuclear sequences (ETS and ITS).
(S2) Bayesian tree obtained from analysis of chloroplasr sequences (*psb*A-*trn*H, *trn*L-F, and *rps*16)
(S3) Bayesian tree obtained from analysis of *psb*A-*trn*H sequences.
(S4) Bayesian tree obtained from analysis of *trn*L-F sequences.
(S5) Bayesian tree obtained from analysis of *rps*16 sequences.
(S6) Bayesian tree obtained from analysis of ITS sequences.
(S7) Bayesian tree obtained from analysis of ETS sequences.
(S8) Strict consensus tree from the parsimony analysis resulting from the combination of chloroplast (*psb*A-*trn*H, *trn*L-F, *rps*16) and nuclear (ETS and ITS) sequences.

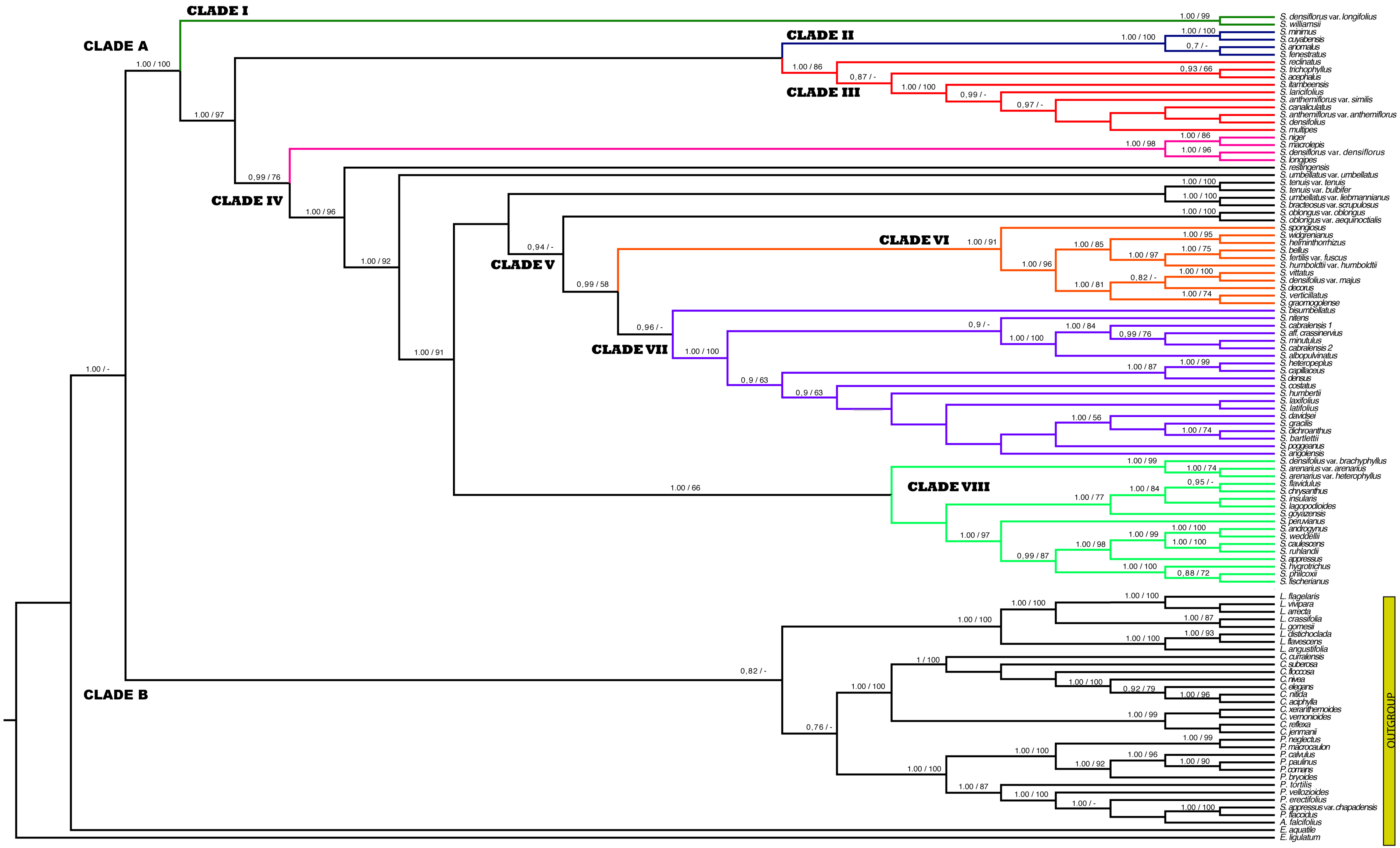
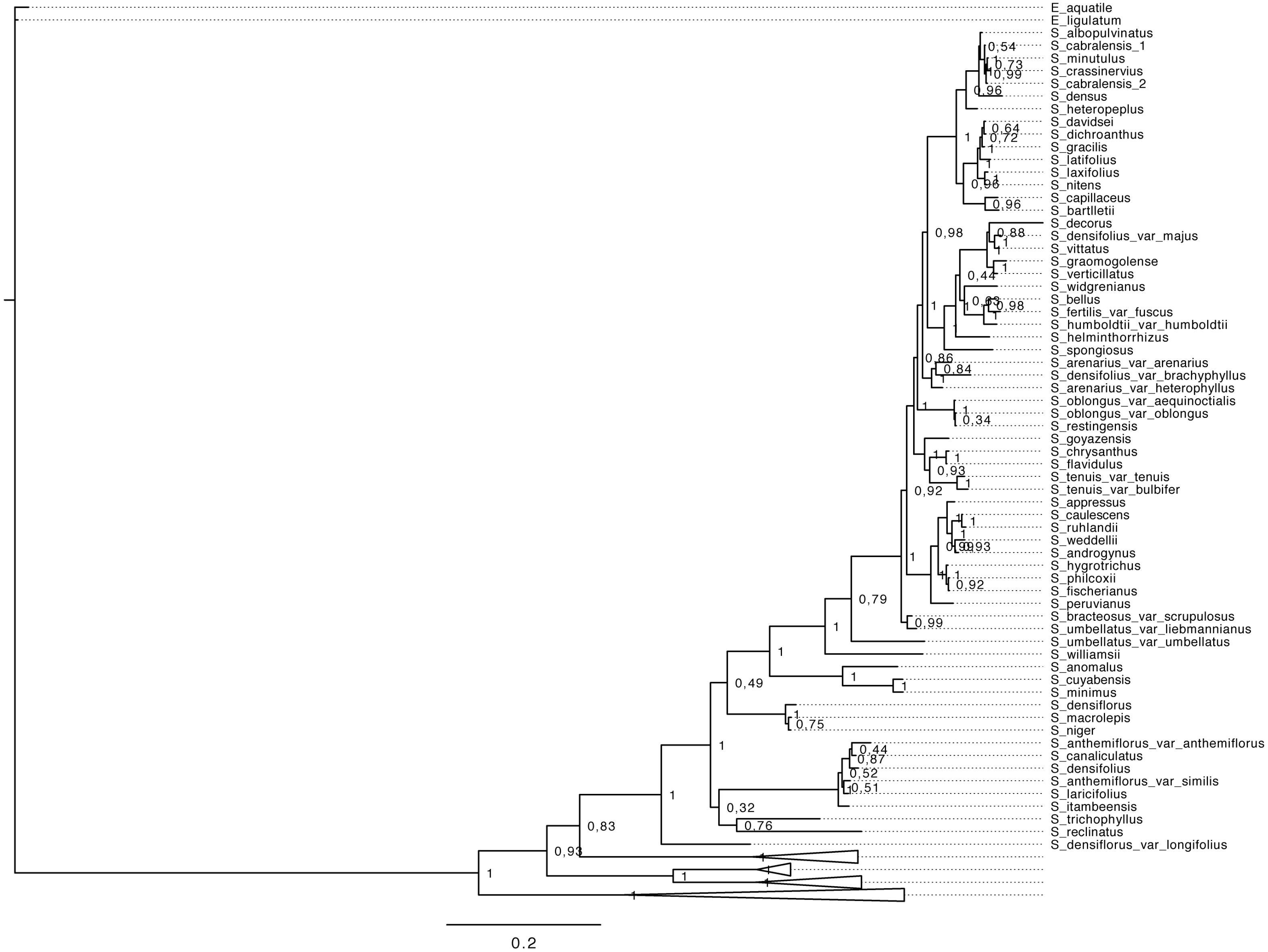
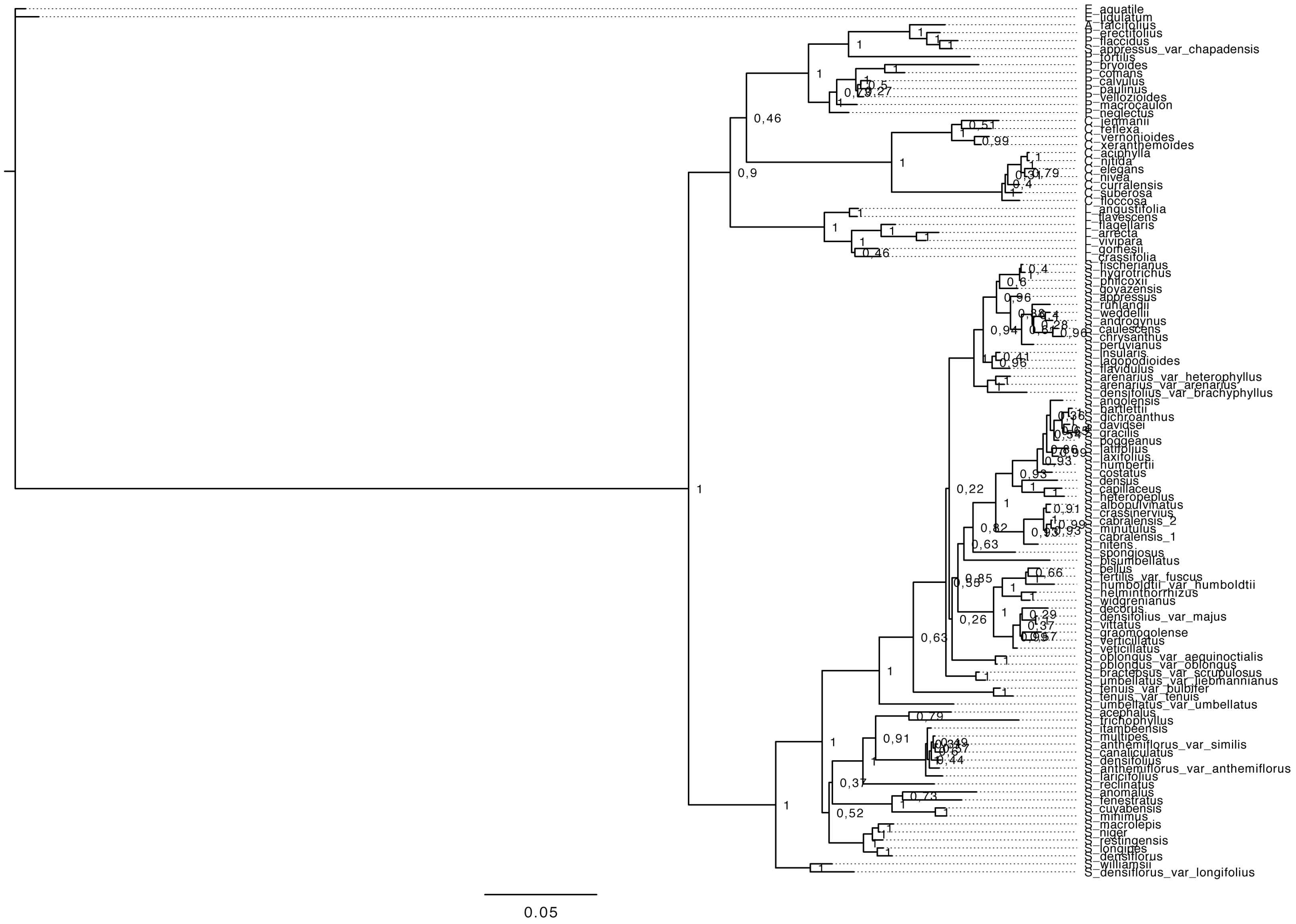

CLADE I
CLADE A
CLADE II
CLADE III
CLADE IV
CLADE V
CLADE VI
CLADE VII
CLADE VIII
CLADE B
OUTGROUP
1.00 / 99
1.00 / 100
1.00 / 100
0,7 / -
1.00 / 86
0,87 / -
0,93 / 66
1.00 / 100
0,99 / -
0,97 / -
1.00 / 97
1.00 / 86
1.00 / 98
1.00 / 96
0,99 / 76
1.00 / 96
1.00 / 100
1.00 / 100
1.00 / 100
1.00 / 92
0,94 / -
1.00 / 91
1.00 / 95
1.00 / 85
1.00 / 75
1.00 / 97
1.00 / 96
1.00 / 100
0,82 / -
1.00 / 81
1.00 / 74
0,99 / 58
0,96 / -
0,9 / -
1.00 / 84
0,99 / 76
1.00 / 100
1.00 / 100
1.00 / 91
1.00 / 99
1.00 / 87
0,9 / 63
0,9 / 63
1.00 / 56
1.00 / 74
1.00 / 99
1.00 / 74
0,95 / -
1.00 / 84
1.00 / 77
1.00 / 66
1.00 / 100
1.00 / 99
1.00 / 100
1.00 / 98
1.00 / 97
0,99 / 87
1.00 / 100
0,88 / 72
1.00 / -
1.00 / 100
1.00 / 100
1.00 / 100
1.00 / 87
1.00 / 100
1.00 / 93
0,82 / -
1 / 100
1.00 / 100
1.00 / 100
0,92 / 79
1.00 / 96
1.00 / 99
0,76 / -
1.00 / 99
1.00 / 100
1.00 / 96
1.00 / 92
1.00 / 90
1.00 / 100
1.00 / 87
1.00 / 100
1.00 / -
1.00 / 100
S. densiflorus var. longifolius
S. williamsii
S. minimus
S. cuyabensis
S. anomalus
S. fenestratus
S. reclinatus
S. trichophyllus
S. acephalus
S. itambeensis
S. laricifolius
S. anthemiflorus var. similis
S. canaliculatus
S. anthemiflorus var. anthemiflorus
S. densifolius
S. multipes
S. niger
S. macrolepis
S. densiflorus var. densiflorus
S. longipes
S. restingensis
S. umbellatus var. umbellatus
S. tenuis var. tenuis
S. tenuis var. bulbifer
S. umbellatus var. liebmannianus
S. bracteosus var. scrupulosus
S. oblongus var. oblongus
S. oblongus var. aequinoctialis
S. spongiosus
S. widgrenianus
S. helminthorrhizus
S. bellus
S. fertilis var. fuscus
S. humboldtii var. humboldtii
S. vittatus
S. densifolius var. majus
S. decorus
S. verticillatus
S. graomogolense
S. bisumbellatus
S. nitens
S. cabralensis 1
S. aff. crassinervius
S. minutulus
S. cabralensis 2
S. albopulvinatus
S. heteropeplus
S. capillaceus
S. densus
S. costatus
S. humbertii
S. laxifolius
S. latifolius
S. davidsei
S. gracilis
S. dichroanthus
S. bartlettii
S. poggeanus
S. angolensis
S. densifolius var. brachyphyllus
S. arenarius var. arenarius
S. arenarius var. heterophyllus
S. flavidulus
S. chrysanthus
S. insularis
S. lagopodioides
S. goyazensis
S. peruvianus
S. androgynus
S. weddellii
S. caulescens
S. ruhlandii
S. appressus
S. hygrotrichus
S. philcoxii
S. fischerianus
L. flagelaris
L. vivipara
L. arrecta
L. crassifolia
L. gomesii
L. distichoclada
L. flavescens
L. angustifolia
C. curralensis
C. suberosa
C. floccosa
C. nivea
C. elegans
C. nitida
C. aciphylla
C. xeranthemoides
C. vernonioides
C. reflexa
C. jenmanii
P. neglectus
P. macrocaulon
P. calvulus
P. paulinus
P. comans
P. bryoides
P. tortilis
P. vellozioides
P. erectifolius
S. appressus var. chapadensis
P. flaccidus
A. falcifolius
E. aquatile
E. ligulatum

Figure 1

Supplementary materials. All derived trees, from analyzes done, are not edited. (S1)



Supplementary materials. All derived trees, from analyzes done, are not edited. (S2)



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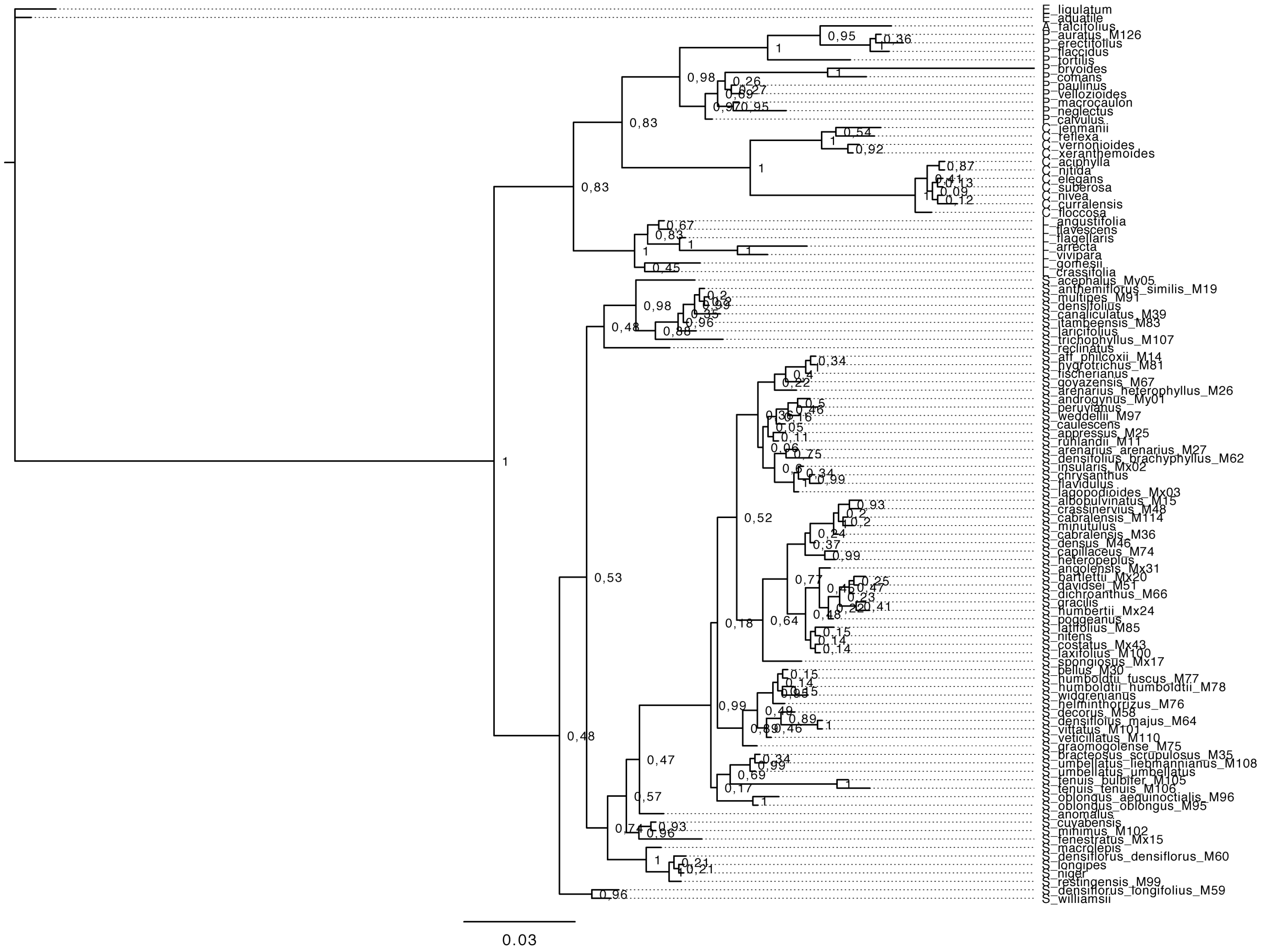

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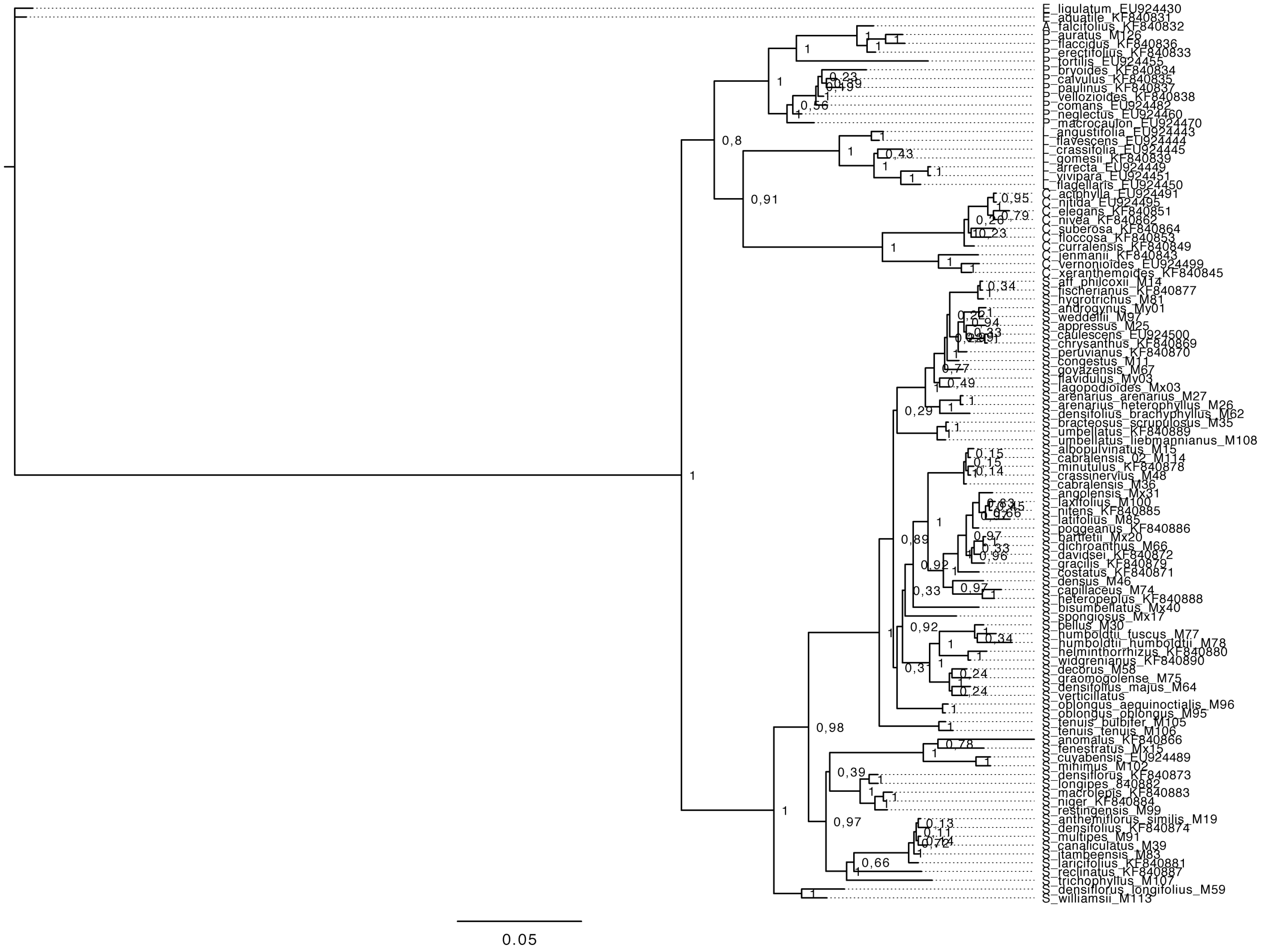
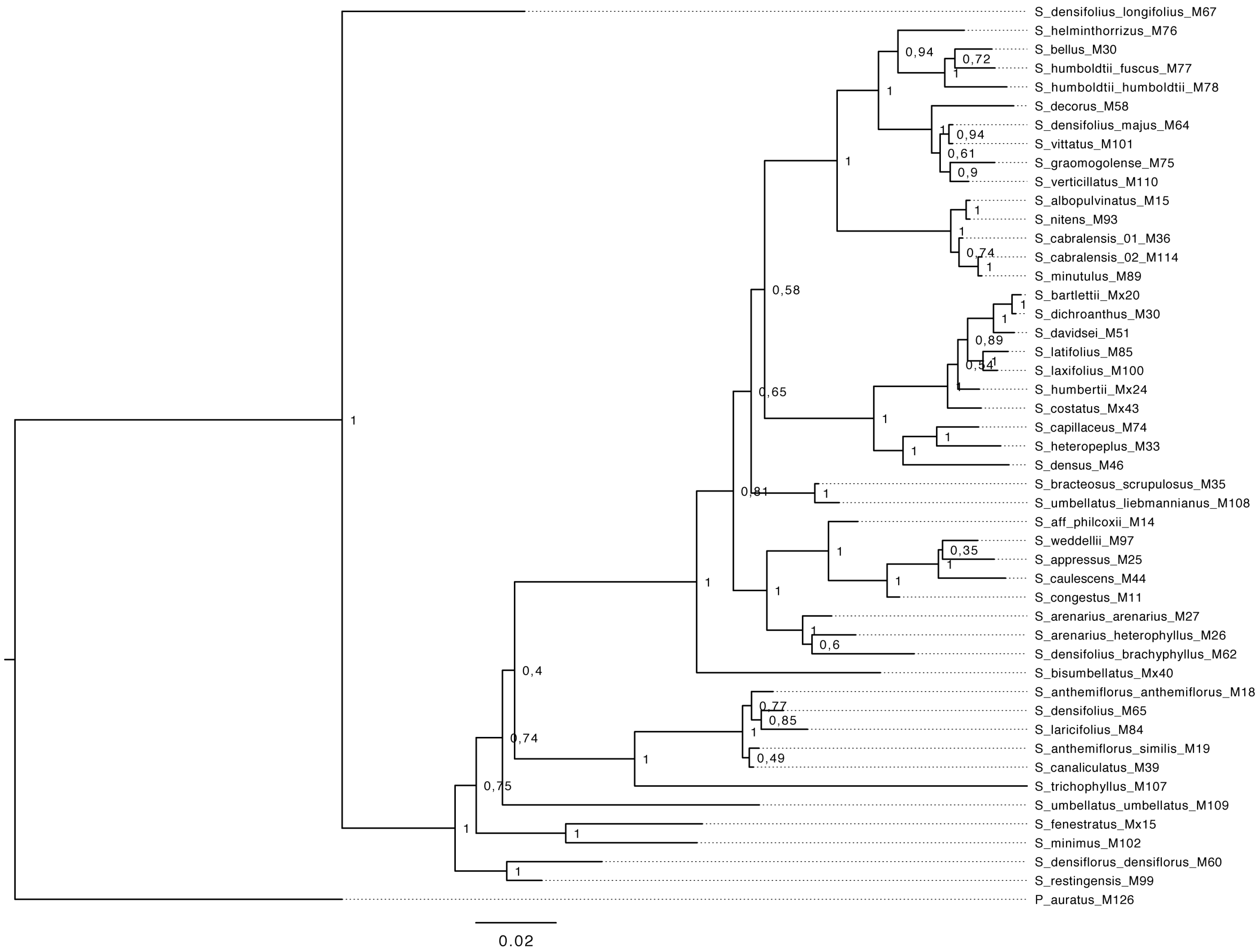
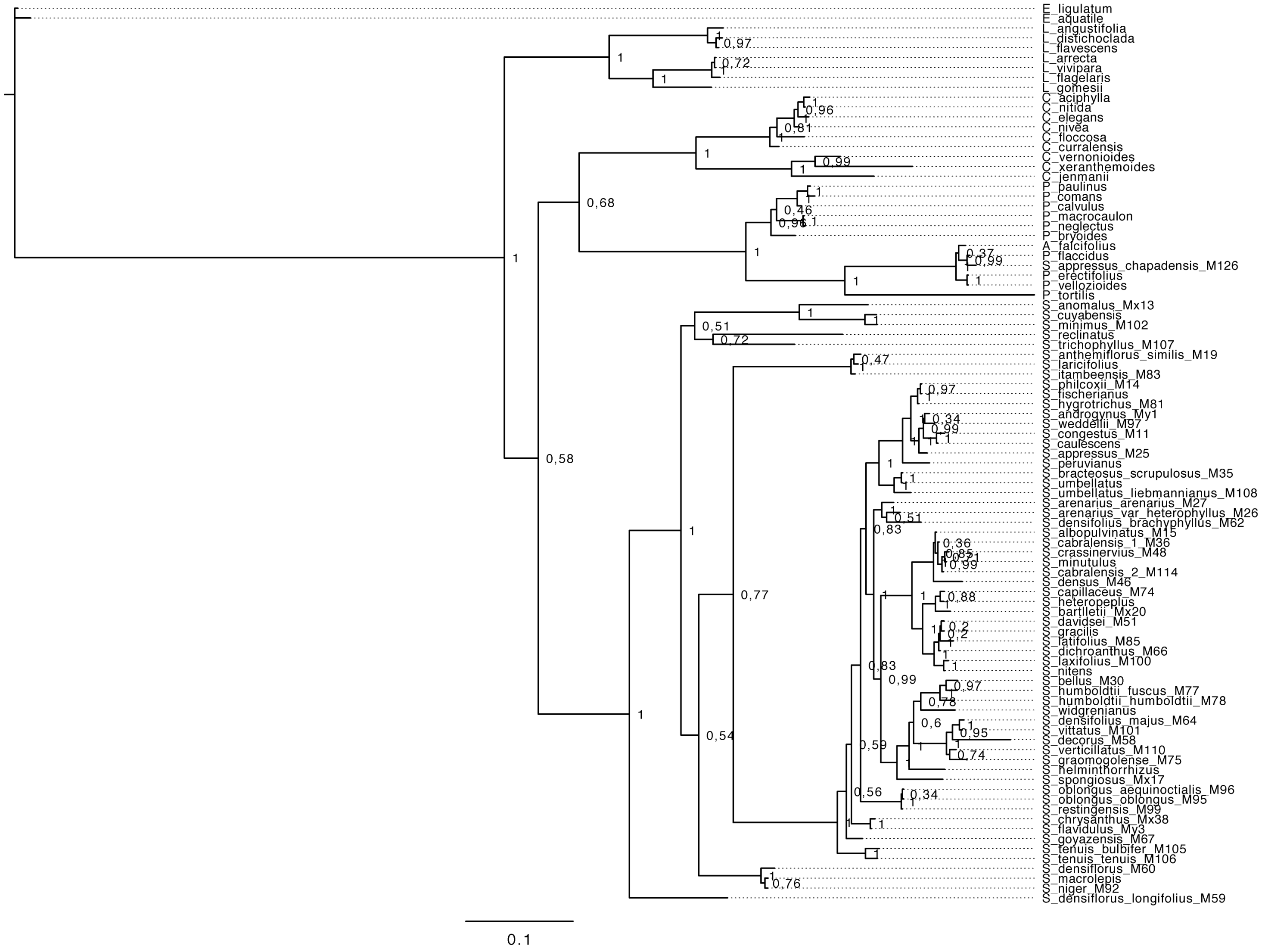


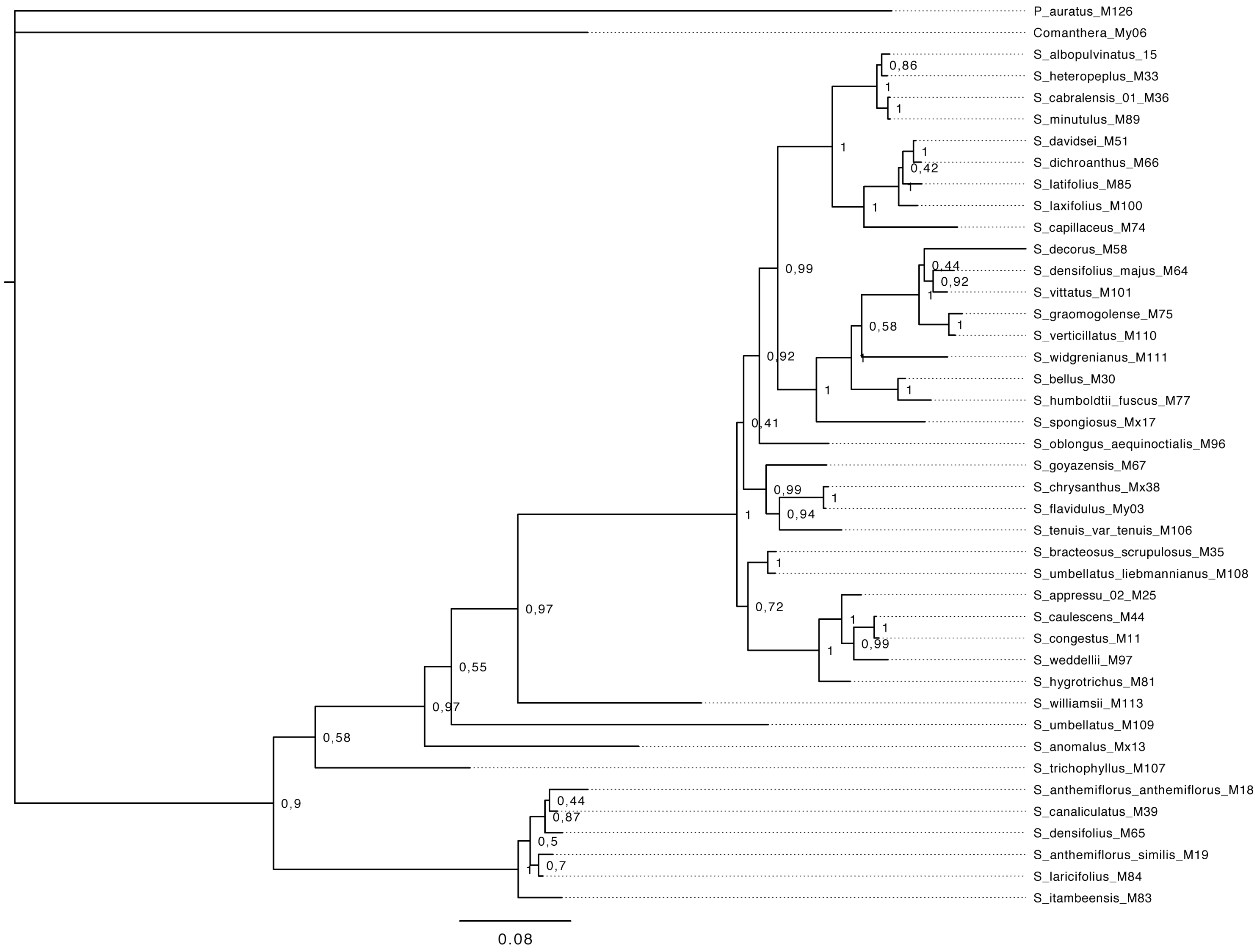
Supplementary materials. All derived trees, from analyzes done, are not edited. (S5)



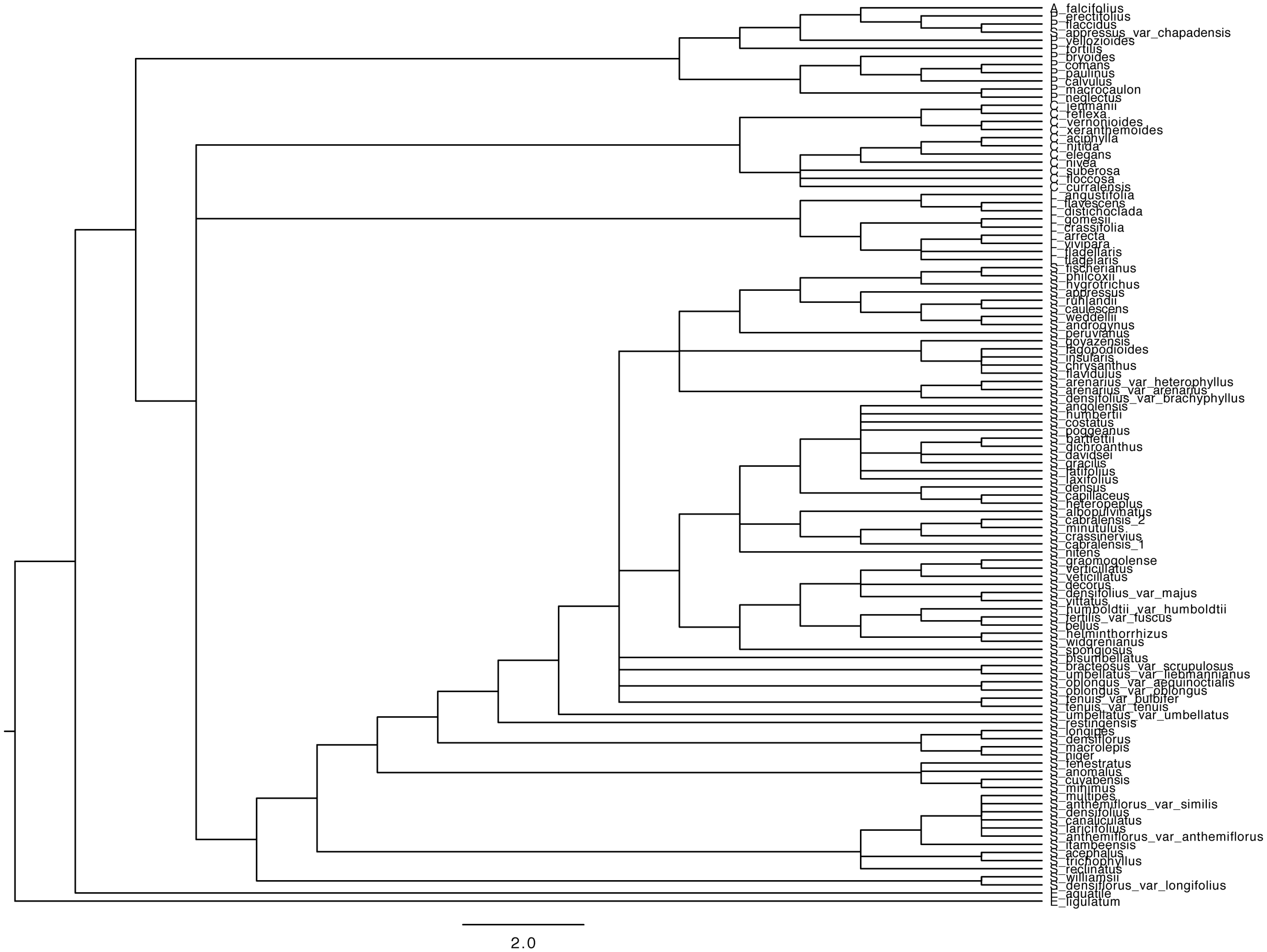
Supplementary materials. All derived trees, from analyzes done, are not edited. (S6)



Supplementary materials. All derived trees, from analyzes done, are not edited. (S7)



Supplementary materials. All derived trees, from analyzes done, are not edited. (S8)



Chapter three

Systematics of *Syngonanthus* sect. *Carphocephalus* (Eriocaulaceae)

Resumo

Apresentamos aqui a revisão taxonômica de *Syngonanthus* sect. *Carphocephalus* (Eriocaulaceae), com ênfase na morfologia do grupo. O estudo é baseado na análise de materiais de herbário e em observações de campo. Esta seção consta de 12 espécies localmente restritas ao continente americano, com espécies de ampla distribuição, como *S. caulescens*, mas também espécies raras ou conhecidas apenas pelo material-tipo, caso de *S. cachimboensis*. A seção é caracterizada por plantas de caule aéreo desenvolvido, recoberto por folhas dispostas espiraladamente, com inflorescências sempre apicais e também pelas pétalas crassas das flores estaminadas. Todas as espécies são trímeras e possuem flores unissexuais, com exceção da nova espécie aqui descrita (*S. androgynus*), que possui flores bissexuais. Os taxa possuem morfologia bastante semelhante, o que torna a taxonomia deste grupo um tanto complexa. *Syngonanthus ruhlandii* é um exemplo dessa realidade: esta espécie, restrita ao extremo oeste da Bahia, é distinguida de *S. caulescens* com base em dados moleculares e sutis caracteres fenotípicos. As espécies podem ser reconhecidas principalmente pela disposição e forma das folhas no caule aéreo, pela forma das brácteas involucrais e por caracteres florais como ausência/presença/redução dos apêndices. Os espécimes geralmente ocorrem em locais úmidos, como veredas, brejos e campos úmidos, principalmente no Brasil. Somente três espécies possuem ocorrência extra-brasileira, casos de *S. androgynus*, *S. caulescens* e *S. peruvianus*. Devido aos escassos registros nos herbários e à restrita extensão geográfica de alguns taxa, a maioria das espécies foi categorizada como criticamente ameaçada de extinção. Neste tratamento taxonômico, são apresentadas descrições para a seção e suas espécies, comentários, chave de identificação, mapas, ilustrações botânicas e fotografias. Paralelamente, algumas questões relacionadas à nomenclatura também foram verificadas, com indicação de lectótipos, novas sinonimizações e mudança de status.

Palavras chave: Taxonomia; *Syngonanthus*; Cerrado; Paepalanthoideae; Espécies raras; Savanas; Espécies novas.

Abstract

A revisionary study of *Syngonanthus* sect. *Carphocephalus* (Eriocaulaceae) with emphasis on its morphology is presented here. This study is based on thorough analyses of herborized materials and field observations. The section contains 12 species, all restricted to South, Central and North America. Some species are widely distributed, such as *S. caulescens,* but most are rare or only known from the holotype (as in the case *S. cachimboensis*). Plants are characterized by well-developed aerial stems with leaves spirally distributed, apical inflorescences, and petals of staminate flowers thickened, at least partially. Generally, the flowers are 3-merous and unisexual as in most Eriocaulaceae, except for *S. androgynus* (a new species described with bisexual flowers). The species have a similar morphology making their identification difficult. Taxa can be distinguished by arrangement and form of leaves on aerial stem, form of involucral bracts and floral traits such as appendages present/absent/reduced. Populations occur in wetlands, "veredas" and swamps, mainly in Brazil. Only three species occur in extra-Brazilian territory (*S. androgynus*, *S. caulescens* and *S. peruvianus*). Due to scarce records in herbaria and restricted geographical distribution, most species were categorized as endangered or critically endangered. This taxonomic treatment presents detailed descriptions to *S.* sect. *Carphocephalus* and species included, commentaries, identification keys, maps, line drawings and photos. Additionally, nomenclatural issues also have been checked and some lectotype selections, new synonyms and change of status are reported.

Keywords: Taxonomy; *Syngonanthus*; Cerrado; Paepalanthoideae; Rare Species; Savanas; New Species.

Systematics of *Syngonanthus* sect. *Carphocephalus* (Eriocaulaceae)

Syngonanthus Ruhland is the third largest genus in Eriocaulaceae and comprises about 120 species. It has a disjunct distribution and the diversity is concentrated in South America, mainly in the Espinhaço Range (Bahia and Minas Gerais states – Brazil) and Guiana Highlands. Other species occur in Central America and only one species, *Syngonanthus flavidulus* (Michx.) Ruhland, in North America (United States of America). Furthermore, less than twenty taxa occur in Africa. The genus is characterized by isostemonous flowers, bithecous anthers and pistillate flowers with petals fused in the middle (Giulietti & Hensold 1990), characteristics shared with *Comanthera* L.B.Sm., in Paepalanthoideae. The differences between these two genera reside in the floral traits. *Syngonanthus* has pistillate flowers with petals fused in the upper part, leaving a short free apex and *Comanthera* has petals fused in the narrow part, leaving long free apices, and sepals smaller than petals (*vs*. petals smaller than sepals) (Echternacht et al. 2014). Ruhland (1900) described *Syngonanthus* from species previously included in *Paepalanthus* Mart. Ruhland (1903) also proposed an infrageneric system for *Syngonanthus* based on subgenera previously described in *Paepalanthus* by Koernicke (1863). A total of five sections were described. *Syngonanthus* sect. *Dimorphocaulon* is the largest section, later synonymized in *Syngonanthus* sect. *Syngonanthus* by Parra & Giulietti (1997), for nomenclatural issues and because it contained the type of the genus, *Syngonanthus umbellatus* (Lam.) Ruhland. *Syngonanthus* sect. *Eulepis* and *Syngonanthus* sect. *Thysanocephalus* were recently transferred to the reestablished *Comanthera* (Parra et al. 2010). The monospecific section *Syngonanthus* sect. *Chalarocaulon* was synonymized in *Syngonanthus* sect. *Carphocephalus* by Hensold (1999). *S.* sect. *Carphocephalus* is a small group that occurs in South America. Only *S. caulescens* (Poir.) Ruhland (belonging to this section) occurs in Central America and Mexico.

Phylogenetic studies based on molecular and morphological data corroborated the monophyly of *Syngonanthus* and *Comanthera* (Andrade et al. 2010; Trovó et al. 2013; Echternacht et al. 2014). However, the phylogenetic results obtained for Echternacht et al. (2014) do not confirm *S.* sect. *Syngonanthus* and *S.* sect. *Carphocephalus* as monophyletic. Apomorphies were homoplastic and probably new circumscriptions are needed for these sections. This analysis revealed *S.* sect. *Syngonanthus* as paraphyletic and *S.* sect. *Carphocephalus* as polyphyletic. Our phylogenetic study (Watanabe 2015; chapter 2) showed *Syngonanthus* sister to remaining genera of Paepalanthoideae and *S.* sect. *Carphocephalus* as a monophyletic group considering a new circumscription proposal. Some species described by Moldenke (1951; 1973) after the classification proposed by Ruhland (1903) were included in this group. Other taxa were synonymized, described and excluded from the section or had their status changed. We consider species included in *S.* sect. *Carphocephalus* characterized by aerial stem with leaves in spiral, terminal inflorescences and staminate flowers with fleshy petals (or partly basal species) and pistillate flowers with membranous corolla, at least in the upper part, corolla involute when senescent. Most of these characters are homoplastic and plesiomorphic but are indicators to separate this section from another similar group, which emerged in our analysis, the "*Philodice* group" (chapter 2).

Taxonomic history

Poiret (1813) described the first species of *Syngonathus* sect. *Carphocephalus*. *Syngonanthus caulescens* (Poir.) Ruhland was initially described as *Eriocaulon caulescens* Poir., but the holotype was not designated. Due to large morphological variability, this taxon had many synonyms and infraspecific categories associated to it. Bongard (1831) described *E. fischerianum* Bong. [*Syngonanthus fischerianus* (Bong.) Ruhland] in the unranked taxonomic category *Acaulia*, probably a group gathering acaulescent plants. In the first major taxonomic treatment for Brazilian Flora (*Flora Brasiliensis*), Koernicke (1863) described *Paepalanthus appressus* Koern., *P. inundatus* Koern. and *P. philodicoides* Koern. in the new *P.* subg. *Carphocephalus* (etymology: capitulum stramineous) he proposed. *Paepalanthus* subg. *Carphocephalus* included species with elongated stems, terminal inflorescences and staminate flowers with urceolate and fleshy corolla. Koernicke also placed *P. caulescens* (Bong.) Koern. in this group.

Later, Ruhland (1903) described *Syngonanthus hygrotrichus* Ruhland and *S. peruvianus* Ruhland. He placed these species in the new *S.* sect. *Dimorphocaulon*. In this review, we are transferring *S. hygrotrichus*, *S. peruvianus* and *S. fischerianus* to *S.* sect. *Carphocephalus*. Ruhland also combined *Paepalanthus* subg. *Carphocephalus* in *Syngonanthus* sect. *Carphocephalus*. In his revisionary study, the circumscription of the section *Carphocephalus* was very similar to Koernicke's concept, the only modification included the addition of species with lateral/axial inflorescences. *S.* sect. *Carphocephalus sensu* Ruhland had 11 species, many of which are synonyms of *S. caulescens* and *S. anomalus* (Koern.) Ruhland. These synonyms were proposed by Hensold (1991) and Echternacht (2012). We do not consider *S. anomalus* and *S. philodicoides* as representative species of *S.* sect. *Carphocephalus*. In this treatment, Ruhland (1903) described *S. rhizonema* Ruhland.

After the new circumscription proposed by Ruhland (1903), there were no other revisionary studies on a global scale involving *S.* sect. *Carphocephalus*. Moldenke (1951; 1960; 1973; 1977) described some species, which could be considered as *S.* sect. *Carphocephalus*: *S.*

weddellii Moldenke, *S. cachimboensis, S. philcoxii* Moldenke and *S. caulescens* var. *discretifolius* Moldenke (with status changed here).

During the phylogenetic study to clarify relationships among species in *Syngonanthus*, Watanabe (chapter 2) detected that the circumscription of *S.* sect. *Carphocephalus* based on Ruhland's concept (including *S. anomalus* and *S. philodicoides*) is polyphyletic. On the other hand, *Carphocephalus sensu* Koernicke (1863) is monophyletic (excluding *S. philodicoides*). This present revisionary study of *S.* sect. *Carphocephalus* formalizes new status, new synonyms and three new species. Some of the synonyms and lectotypification involving *S.* sect. *Carphocephalus* were previously released by Echternacht et al. (*in* Echternacht 2012) in a collaborative synopsis of *Syngonanthus*. A new formal proposal for *S.* sect. *Carphocephalus* is presented here, including species described previously by Moldenke (1973; 1977). This proposal excludes *S. anomalus* (and its related synonyms) and *S. philodicoides* from *S.* sect. *Carphocephalus sensu* Ruhland. Some species with short aerial stems (frequently not evident) described in *Syngonanthus* sect. *Syngonanthus sensu* Ruhland are transferred to *S.* sect. *Carphocephalus: S. fischerianus*, *S. hygrotrichus* and *S. peruvianus*.

Morphology

Habit, stem and roots

Syngonanthus sect. *Carphocephalus* contains mostly monocarpic species. Most species do not form clones. These species occur in sandy soils, over quartzites and sandstones, like most taxa in Eriocaulaceae. However, fieldwork observations have shown that most species of *S.* sect. *Carphocephalus* inhabit marshy, poorly drained soils or seasonal inundated areas. In the field, only *S. hygrotrichus* has aquatic habit with its inflorescences emergent. Probably, *S. rhizonema* also is aquatic, but this plant is only known from the type collection and was not observed in the field.

In general, individuals are composed of a very short subterranean stem, an aerial stem, which is an extension of the subterranean stem with rosette absent, and terminal inflorescences. There are exceptions such as *S. appressus*, which eventually can show lateral ramifications and rosettes, able to produce some clones. *S. philcoxii* and *S. cachimboensis* also produces lateral branches but the inflorescence emerges directly from rosette. Horizontal subterranean branching under the soil is not usual and the species have an erect aerial stem, sometimes prostrate due to mechanical damage. *S. ruhlandii* (a new species described here) is a notable exception with its aerial stem decumbent.

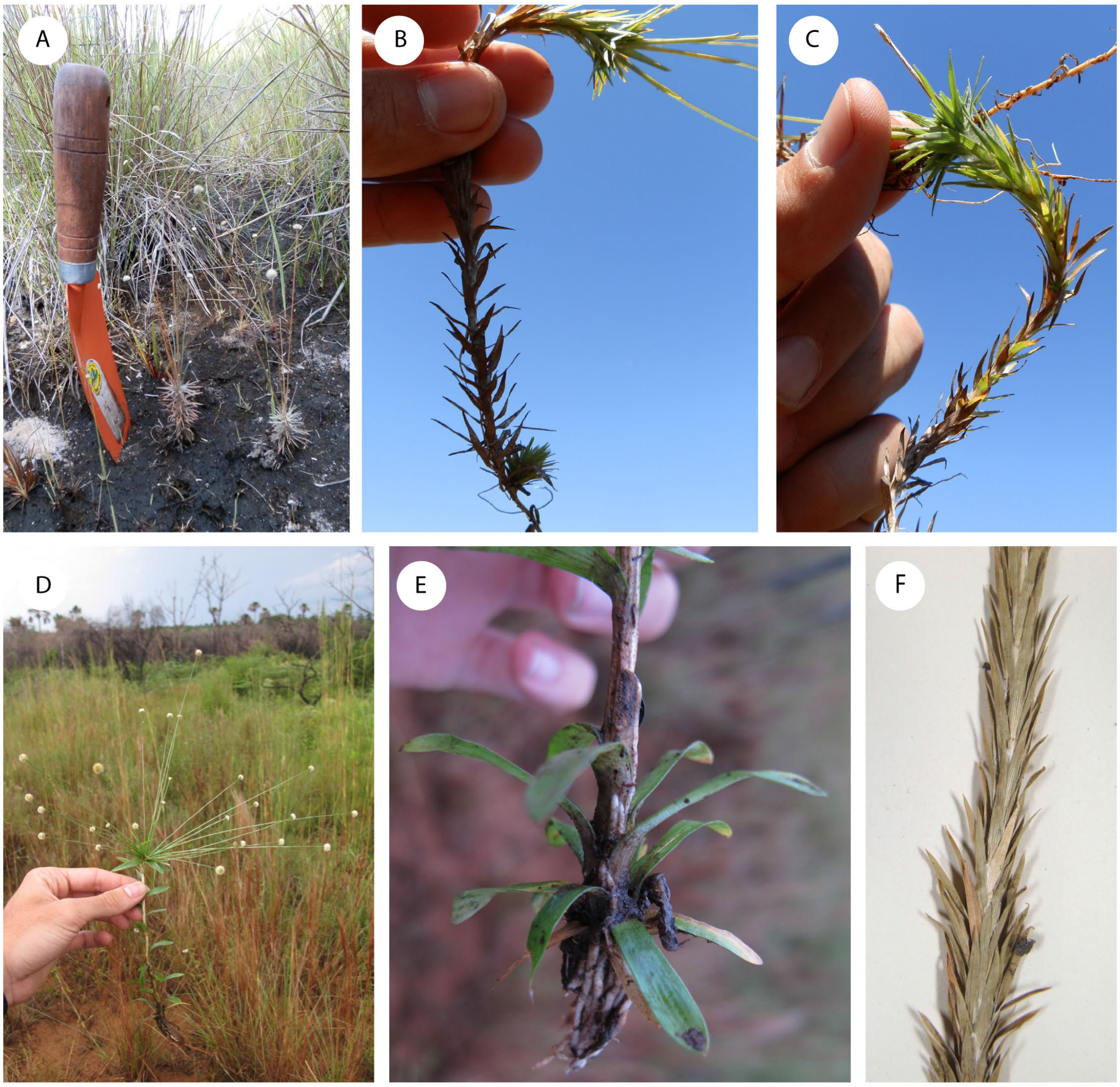


Figure 01. A. Individuals of *Syngonanthus weddellii* in the field; **B.** *Syngonanthus ruhlandii* showing anomalous growth; **C.** *S. ruhlandii* with its ascendent leaves; **D.** Individual of *Syngonanthus caulecens*; **E.** Roots and basal leaves of *S. caulescens*; **F.** Stem of *Syngonanthus appressus* with its adpressed leaves.

The aerial stem is covered by leaves throughout its length, with distinct internodes. The length of the aerial stem is somewhat variable (Fig. 1). Some species as *S. caulescens* show extreme variation in stem length with plants more than 0.5 m tall. On the other hand, plants with undeveloped stems have leaves congested in the basal part of the plant, providing a false rosette aspect. The aerial stem always is covered by white crooked and villous trichomes.

The roots are similar in *S.* sect. *Carphocephalus*: they are white/cream colored, tiny and spongy. Roots are restricted to the bottom part of the stem, to fix the individuals in the soil, but in some species, the roots can be disposed throughout the aerial stem, as observed in *S. rhizonema*, *S. cachimboensis* and some specimens of *S. appressus* and *S. caulescens* (especially when the aerial stem comes into contact with water or soil cover). Scatena & Menezes (1996) observed that almost all species in *Syngonanthus* have aerenchyma. This is a common pattern in Eriocaulaceae, particularly in species inhabiting soggy soils. The root anatomy is aimed to air storage. The uniseriate cortex is composed of isodiametric cells with only slightly thickened cell walls. There are long braciform cells but in small number. The endodermis also is uniseriate but the cells are thickened.

Leaves

Species of *S.* sect. *Carphocephalus* have evergreen annual leaves disposed spirally in distinct internodes on the aerial stem. Only some specimens of *S. appressus* occasionally show a rosette of leaves, which are threadlike and appressed to the soil. Other species included within *S.* sect. *Carphocephalus* apparently have a rosette (*S. peruvianus*, *S. philcoxii*, *S. hygrotrichus* and *S. fischerianus*). In general, the leaves are persistent and equally distributed on the stem. Most species have congested leaves as observed in *S. ruhlandii*, *S. cachimboensis, S. appressus*, *S. hygrotrichus*, *S. fischerianus* and *S. weddellii*. Other species have more widely spaced internodes as *S. discretifolius* and *S. rhizonema*. *S. caulescens*, *S. androgynu*s and *S. mollis* have variable distribution of leaves on the aerial stem. In *S. caulescens*, the leaves usually are spaced, the exception occurs when the aerial stem is undeveloped and the leaves becomes congested at the base. *S. mollis* has leaves congested in young individuals with leaves concentrated at the apex and base. When the plant becomes older, the leaves are spaced from each other. *S. androgynus* has leaves congested in specimens from Brazil but specimens from Heath river (Bolivia/Peru) have leaves congested only at the apex (probably leaves are deciduous below).

Only in some cases, shape of leaves are taxonomically informative in *S.* sect. *Carphocephalus*. More than one kind of leaf can be found on the same specimen. Most leaves are linear, threadlike and lanceolate, although filiform, oblong, capillary, elliptic and linear-triangular leaves can also be found. The only species with capillary leaves are *S. androgynus*, *S. hygrotrichus* and *S. philcoxii*. The apex of leaves is also taxonomically informative, but somewhat variable in some species. Only *S. mollis* has apex retuse, although it can show apex round and obtuse. Most apices are acute as observed in *S. appressus*, *S. ruhlandii*, *S. discretifolius*, *S. rhizonema* and *S. weddellii*. *S. androgynus* has apex acuminate and recurved. *S. cachimboensis* is the unique with apex mucronate to mucronulate.

Pilosity is the most variable character in the leaves. Frequently the leaves are pilose or glabrescent (*S. androgynus*, *S. cachimboensis, S. ruhlandii*, *S. rhizonema* and *S. weddellii*) but in *S. appressus*, *S. discretifolius* and *S. mollis* are tomentose. Several types of trichomes are found on the leaves, generally on both surfaces. The most common are adpressed trichomes (in *S. androgynus*, *S. appressus*, *S. cachimboensis, S. ruhlandii*, *S. mollis*, *S. philcoxii*, *S. rhizonema* and *S. weddelli*). A few species have capitate hairs as observed in *S. androgynus*, *S. discretifolius* and *S. weddelli*. The most common kind of trichomes in the genus is the filamentous hairs, present in *S. appressus*, *S. caulescens*, *S. ruhlandii*, *S. mollis* and *S. rhizonema* and others.

In relation to the leaves, the most informative taxonomic character is their disposition and arrangement on the aerial stem. Leaves are appressed on the aerial stem in *S. appressus* but notably recurved at the base (in *S. caulescens* they are recurved or oblique throughout stem). Leaves can be patent to ascending in *S. androgynus*; flat to ascendant in *S. cachimboensis;* oblique to adpressed in *S. ruhlandii*; patent to oblique in *S. discretifolius*, *S. mollis* and *S. weddellii*, and visibly lax in *S. rhizonema*.

In the integrative study of anatomy and taxonomy organized by Scatena et al. (2005), the authors enumerate the relevant characteristics for systematics of Eriocaulaceae. Leaves of *Syngonanthus* (both *S.* sect. *Syngonanthus* and *S.* sect. *Carphocephalus*) are anatomically characterized by epidermis with thin cell wall, loosely aggregated chlorenchyma, parenchymatous bundle sheath extensions and fewer vascular bundles.

Synflorescences and inflorescences (figure 2)

Inflorescences are basically composed of scapes, sheath and capitula. These structures are present in all species of *S.* sect. *Carphocephalus*. However, a few species in the section can also have a synflorescence axis: *S. hygrotrichus*, *S. fischerianus* and *S. peruvianus*. All these species have a small axis hidden by congested leaves of the aerial stem. This axis is glabrescent and dark brown-colored and it culminates with the inflorescence *per se*. The inflorescences in these three species are surrounded at their base by foliaceous bracts. Usually these bracts are chartaceous, linear to lanceolate, green or brown-colored, glabrous to glabrescent and spirally arranged.

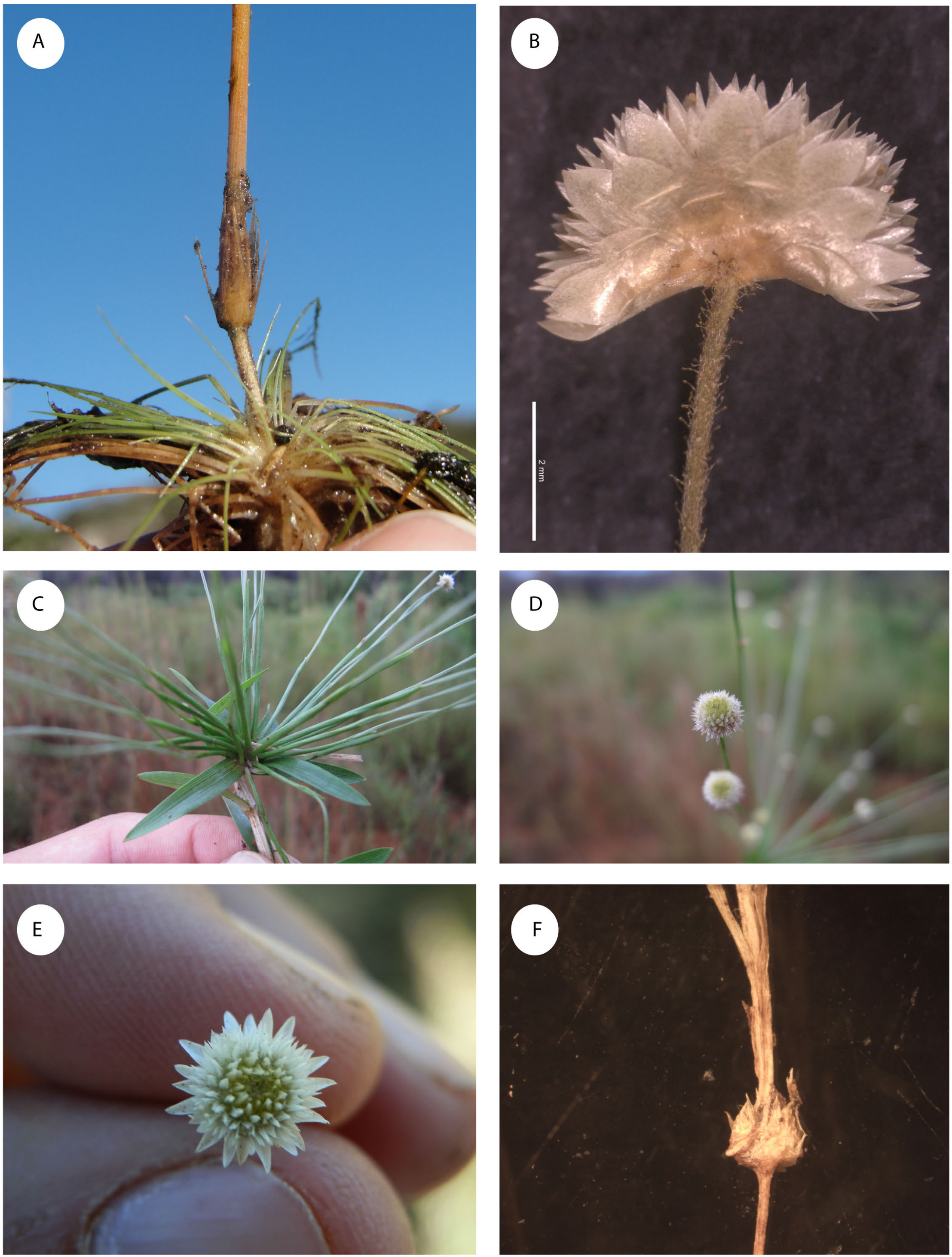


Figure 2. A. Synflorescence axis of *Syngonanthus hygrotrichus*; **B.** Capitulum detail of *S. appressus*; **C.** Detail of terminal inflorescences of *S. caulescens*; **D.** Capitulum of *S. caulescens*; **E.** Capitulum of *S. ruhlandii*; **F.** Viviparous capitulum of *S. rhizonema*.

Every scape is enclosed by a modified leave called spathe, which is cylindrical, chartaceous, greenish, erect and obliquely opened. Spathes can measure from 1 cm to 7 cm. The apices are acute or obtuse, uncinate, margin entire, not involute. Usually, the adaxial surface is glabrous or glabrescent, but they are pilose in *S. androgynus*, *S. cachimboensis* and *S. mollis*. Abaxially, the spathe may vary from glabrescent to pubescent or tomentose with capitate and simple filamentous hairs and adpressed trichomes.

Scapes are elongated axes, usually 3-costate. The number of scapes varies from 1 to 35 per stem and their length extends up to 40 cm. They are erect to flexuous and slightly twisted. The color may be green in young individuals but when older they are straw-colored to golden. The pilosity is variable. In most species they are pilose (glabrescent when older) or pubescent. Some species such as *S. appressus, S. discretifolius* and *S. weddellii* have a collar of trichomes near the apex. In this zone, there are more capitate and adpressed trichomes, rarely simple filamentous hairs.

The capitulum is composed by flowers disposed on a receptacle surrounded by involucral bracts at border. Most of capitula are discoid or obconic. The number of series of involucral bracts is from 1 to 6, relatively few for this family. For example, *S. cachimboensis* has only 1-2 series. In general, the outer series are smaller than those of the internal series, which are progressively longer with golden or cream color and they almost equal the flowers. The form of involucral bracts is one of the most informative taxonomic characters for this group. The shapes are triangular, ovate, obovate, oblong, lanceolate, oblanceolate and elliptic. The apex of the bracts can distinguish very similar species such as *S. discretifolius* and *S. caulescens*, which have bracts round and acute, respectively. Other species have retuse, mucronate, obtuse, round and acute apices. Usually, involucral bracts are glabrous. *S. weddellii* has bracts pilose abaxially with adpressed trichomes. *S. rhizonema* has bracts with simple filamentous hairs adaxially.

Flowers, fruit, and seeds (figure 3)

Flowers in *S.* sect. *Carphocephalus* are diclinous and the species are monoecious (both staminate and pistillate flowers are in the same capitulum) as in the majority of Eriocaulaceae. The exception is *S. androgynus*, a new species with bisexual flowers (see chapter 1.2). Only *S. trichophyllus*, *S. amazonicus* and *S. acephalus* shared this characteristic with *S. androgynus* in the genus. These species occur in another clade (chapter 2), which indicates that bisexual flowers emerged at least twice in the genus. All species of *S.* sect. *Carphocephalus* are trimerous. The maturation of flowers on the receptacle is centripetal and cyclic. This pattern is similar that found in other

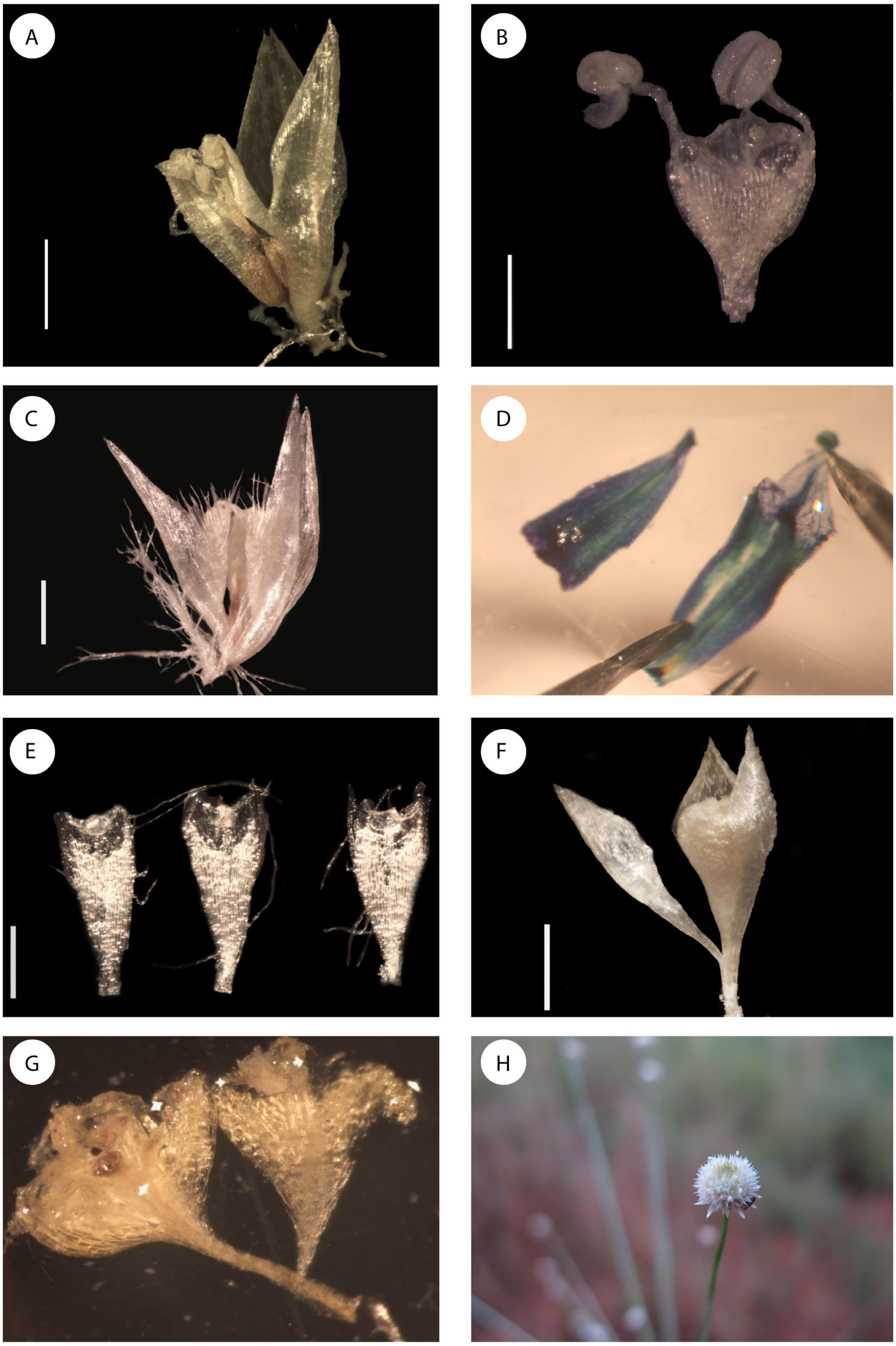


Figure 3. A. Bisexual flower of *S. androgynus*; **B.** Staminate corolla of *S. appressus*; **C.** Pistillate flower of *S. mollis*; **D.** Dissected petal of *S. androgynus*; **E.** Pistillate petals of *S. weddellii*; **F.** Staminate flower of *S. discretifolius*; **G.** Staminate flower of *S. rhizonema* dissected; **H.** Visitor on the capitulum of *S. caulescens* in the field.

groups of Eriocaulaceae as *Paepalanthus* sect. *Diphyomene* (Trovó 2010) and *Comanthera* subg. *Thysanocephalus* (Echternacht 2012). The distribution of flowers is also alternate with groups of staminate or pistillate flowers aggregated together. This condition varies in different specimens with alternation of pistillate or staminate flowers whorls; or merely isolate. Staminate flowers usually bloom first. Pistillate and staminate flowers are almost equal in number but depending on phenophase, one of them can be slightly more numerous. The exception is *S. appressus*, which has twice as many pistillate as staminate flowers. The number of flowers is from 10 to 160 per capitulum. The species with the smaller number of flowers per capitulum is *S. cachimboensis* with 10-30 flowers and the species with the largest number of flowers is *S. fischerianus* with up to 250. *S.* sect. *Carphocephalus* species do not have floral bracts. In its protologue, *S. cachimboensis* is described as species with floral bracts but we found no traces of this structure in the holotype.

Staminate flowers are variable in *S.* sect. *Carphocephalus*. The common character is the fleshy petals of the flowers. The corolla is urceolate or infundibuliform and usually is involute after anthesis. Other characteristics are similar to *Syngonanthus* species, in general. The flowers are long pedicellate with trichomes at base. Sepals are membranous (hyaline when hydrated) and fused in the short base. The sepals in the upper part are slightly thickened. In *S.* sect. *Carphocephalus*, sepals are slightly asymmetrical, cymbiform/concave with margin involute. The shapes are lanceolate, oblanceolate, rhombic, obtrullate, elliptic or obovate. The pilosity of the sepals is variable. In some species one or both surfaces is glabrous. In *S. weddellii* and *S. appressus*, sepals are pubescent adaxially and glabrous abaxially while in *S. discretifolius* and *S. mollis* they are glabrous adaxially and pilose abaxially, which could indicate this character as taxonomically important. There are three stamens (usually exsert) with dorsifixed anthers and three very small pistillodes. The stamens are adnate (e.g. *S. androgynus*, in which only the anthers and the very distal part of the filament are free) or partly free (most species).

Pistillate flowers of *S.* sect. *Carphocephalus* are subsessile or short-pedicellate with trichomes at insertion with receptacle. The sepals are connate at base with margin revolute. The shape is quite variable: lanceolate, oblanceolate, rhombic, obtrullate, oblong, obovate and cymbiform. The texture of the sepals in *S.* sect. *Carphocephalus* is chartaceous, except for *S. appressus*, which is rigid-chartaceous. They are glabrous abaxially and pilose or pubescent adaxially. Petals are fused in the upper part, with a short free apex, a floral trait shared with almost all *Syngonanthus* species. Usually the apex is involute after anthesis. The lobes are rhombic, obtrullate or oblanceolate. Usually, petals of *S.* sect. *Carphocephalus* species are fleshy in the lower half, while the upper half is membranous. A similar pattern is observed in the bisexual flowers of *S. androgynus*. In *S. appressus*, petals are thickened medially in the fusion zone, and in *S. mollis*, they are thickened throughout. Petals are glabrous adaxially and pilose, pubescent or scarcely pilose abaxially. The ovary is composed of three carpels, each one containing one locule and one ovule. The stigmatic branches are completely fused (branches simple) and fused at base with nectariferous branches (appendages). The appendages have a glandular capitate apex. In *S. discretifolius* the appendages are very short or undeveloped. Below this fusion zone there is the cream-colored to castaneous column. Stigmatic and nectariferous branches are free at the same level of the column. Usually, the nectariferous branches are shorter than stigmatic branches.

Fruit is similar to that of most Eriocaulaceae, a loculicidal capsule. After the fruiting, the remaining parts of pistillate flower and gynoecium are retained in the fruit. Usually, staminate flowers and involucral bracts are deciduous, exposing the seeds in the free basal part of the petals. Some seeds are released from the fruit but they remain retained in the concave sepals. Seeds are ovoid or obovoid, brown-colored, striate with pseudotrichomes.

Phenology and Reproductive Biology

Most species of *S.* sect. *Carphocephalu*s bloom in four to six months, usually in the dry season, but exceptions are observed in *S. caulescens*. This species has a large geographical distribution, probably this is the reason for its variable period of blooming with flowers and fruit observed all the year. On the other hand, *S. discretifolius* was collected only in May. Few collections in this period can indicate this plant as monocarpic or simply that it has an observed flowering peak only in this month. Plants with occurrence near the Equator bloom in the January to June and plants with occurrence further South this line bloom in the next to second half of the year. The reproductive cycle of *S.* sect. *Carphocephalus* appears to be linked to dry season. Flowers become mature from May to September and the dispersal of seeds occurs after this period. In *S. discretifolius* and some specimens of *S. caulescens* (that occur north of the Equator) this period is reversed with seeds dispersed in the first semester of the year, in the rainy season.

The reported pollination process in Eriocaulaceae is entomophily (insect pollination) or wind pollination (anemophily) (Ruhland 1903; Hensold 1988). For a long time, anemophily was considered as the main pollination process, but recent studies involving reproductive biology suggest insect pollination (Ramos et al. 2005; Oriani et al. 2009). Structures like appendages (nectariferous branches of the style) in pistillate flowers and pistillodes in staminate flowers strengthen this current. In some field trips, Coleoptera and Hemiptera were observed visiting capitula of *Syngonanthus* species, in general. In *S. androgynus*, it is possible that the self-pollination plays an important mechanism. The apices of the petals are not completely free at any observed stage, and the stamens and style branch are wrapped around each other. Petal apices are not completely fused but strongly involute without exposition of sexual parts. There are no focused studies in pollination of *S.* sect. *Carphocephalus* species in the literature.

Dispersal mechanisms in *S.* sect. *Carphocephalus* are also unknown. Morphological observations can lead us to deduce that autochory and hydrochory are possible mechanisms. In older capitula, involucral bracts are deciduous, exposing fruits. There was observed in the field some dispersal mechanisms as “elevator mechanisms” (Trovó & Stützel 2011), in which diaspores consisting of retained parts of the flower (petals) and fruit (locules opened) are raised to the top of the capitulum surface. Some seeds are retained in the concave and cymbiform sepals, maybe to float the seeds in the water. The fructification coincides with the rainy season, which suggests hydrochory as the real mechanism of dispersal, or it may just suggest that it’s a good time for seeds to germinate.

Hybridization appears to be a common process in Eriocaulaceae. Some specimens have intermediate characteristics between species that occur in the same area. In *Syngonanthus*, this fact suggests that hybridization is a natural process (Hensold 1991; Phillips 1997; personal observations in the field), mainly for African specimens and species of *S. nitens* and *S. gracilis* complex. In *S.* sect. *Carphocephalus* there is no evidence of hybridization among the species, which could be not detected because species in this group have an enormous morphological variation.

Geographic Distribution, Habitat and Conservation

All but one of the 13 species of *S.* sect. *Carphocephalus* are restricted to South America. The unique exception is *Syngonanthus caulescens* that occurs in North and Central America, in addition to South America. Brazil is the center of diversity of the section. At least nine species occur in that country, and seven are restricted to it. In Brazil, it occurs in almost all states. Minas Gerais and Goiás states have the major number of species with five each. Although many species occur in Brazil, the distribution of the section is curiously spread and patterns were not identified. Most of species have been collected at borders of rivers and “cerrado” biome (savannas), particularly in landscapes with soggy soils such as swamps and “veredas”, but they can occur in other domains.

Apparently, only two species are microendemic in *S.* sect. *Carphocephalus*. *Syngonanthus discretifolius* is only known from Serra dos Carajás (Pará state – Brazil). This area is characterized by soils with a rich ferriferous component with peculiar “canga” vegetation and intensive mining activity. *Syngonanthus ruhlandii* is another endemic species that occurs in the extreme west of Bahia, in the municipality of Luís Eduardo Magalhães.

Syngonanthus caulescens is the most widespread species in the genus. Its geographical distribution encompasses the section distribution. This plant occurs in many different environments and probably this is the reason of the large morphological variability of the taxon. *S. caulescens* has a large capacity of adaptation, occupying the Amazonian domain, in the North of Brazil and the countries of Northern South America. In Bahia and Rio de Janeiro, there are records in areas belonging to "mata atlântica" domain, in Itaparica and Serra dos Órgãos, respectively. It is the only species in the section occurring in this domain. In Central Brazil, *S. caulescens* occupies areas of Cerrado domain, in typical savannas; and in Bahia and Minas Gerais, in campos rupestres. In Central America, it occurs only in Costa Rica and in North America only in Mexico.

Syngonanthus androgynus is distributed in Bolivia, Brazil and Peru. It was collected in the Amazonian region of Bolivia and Peru at border of both countries in the flow of the Heath River. It was also collected in Brazil Central in the Grande Sertão Veredas National Park and Chapada dos Veadeiros region. *S. weddellii* is another species collected in the flow of rivers. There are historical records for this species in the flow of Araguaia and Tocantins rivers (Goodman 1972), in the region of Central Brazil (probably in Goiás). Recently, *S. weddellii* was also collected in Tocantins (Brazil) in Cerrado phytophysiognomy, specifically in *Campo limpo* with "buritis" and next to the margin of Rio Tocantins. *S. hygrotrichus* is narrowly distributed in the South of the Espinhaço range in Minas Gerais, specially in the Diamantina plateau and Serra do Cipó. It is an aquatic plant collected next to waterfalls, with only its inflorescences emergent.

Syngonanthus appressus is restricted to a few localities in Minas Gerais, São Paulo, Distrito Federal and Goiás. In Minas Gerais, it is widely distributed but in São Paulo there is only one collection in São Carlos. The collections for this taxon are also scattered in Goiás and Distrito Federal. *S. fischerianus* is widely distributed in the South of the Espinhaço range (Minas Gerais). The species is also known further South of Brazil in São Paulo, Paraná and Santa Catarina, occupying Cerrado areas next to border of rivers and swamps.

Except for *S. caulescens*, there are few collections for species of *S.* sect. *Carphocephalus* in the herbaria. The scarcity of specimens found in field trips and the small number of exsiccates lead to the deduction that there are few naturally occurring populations. For example, *S. rhizonema* is only known by the type collection. The locality indicated for the holotype is São Paulo but some collections of Glaziou revealed historical misconceptions of geographic distribution and date of collection. Roots throughout the aerial stem are evidence of an aquatic habit for this species. *S. philcoxii* is another rare species in the section. It was only known by the holotype from Central Brazilian plateau in Mato Grosso, in the road connecting Xavantina and Serra do Cachimbo, in the wet campo between grass tussocks. Another population has been collected in Planaltina in the Estação Ecológica de Águas Emendadas and in Brasília.

Only two species do not occur in Brazil. *S. mollis* is a new species distributed in Bolivia and Peru. *S. androgynus* and *S. mollis* are sympatric species, especially in the flow of Heath river. Some collections have mixed material of both plants and their taxonomic interpretations previously were obscure. *S. peruvianus* is the other extra-Brazilian species, restricted to Peru and Ecuador. It is known from the Andean formations and Páramos, Neotropical ecosystems, which can reach elevations above 3000 m.

Lack of populational studies about *S.* sect. *Carphocephalus* species make it difficult to rank the taxa in the risk categories based on IUCN (2014) criteria. The unknown information about population size and its dynamics, as well as detailed information about area of occupancy makes classification a difficult task. For suggestion, inferences and projection are allowed and the absence of high-quality data should not be an impediment to apply the criteria. The major problem is concentrated in the species only known by holotype, i.e. *S. rhizonema*, which additionally has dubious data in the exsiccate. For caution, we prefer not to classify this species in any category.

Geographical distribution is the unique applicable criterion (B) to evaluate if a taxon belongs to threatened category (IUCN 2014). The evaluation is based on extent of occurrence, area of occupancy, inferred decline in area of extent and number of locations. The scenario in *S.* sect. *Carphocephalus* is diversified but most species are narrowly distributed, and thus are considered endangered, here. Only *S. caulescens* is considered of least concern, since it is a widespread and abundant taxon. *S. appressus* is considered near threatened, with populations occurring in few National Parks. *S. discretifolius* is critically endangered. Only few individuals were detected in a critical area with intensive mining exploitation, with severe fragmentation of the habitat.

Phylogeny

Syngonanthus emerged as a monophyletic group since the first phylogenetic study involving Eriocaulaceae. Giulietti et al. (1995) performed a cladistic analysis with morphological data. This analysis considered *Philodice* informally included in *Syngonanthus s.l.* and show *Leiothrix* as sister group of *Syngonanthus*. Giulietti et al. (2000) in another cladistic study prioritizing anatomical and morphological data, one more time confirmed *Syngonanthu*s as monophyletic group and sister group of *Leiothrix*. This study also showed the emergence of the clade joining *S.* sect. *Eulepis* and *S.*

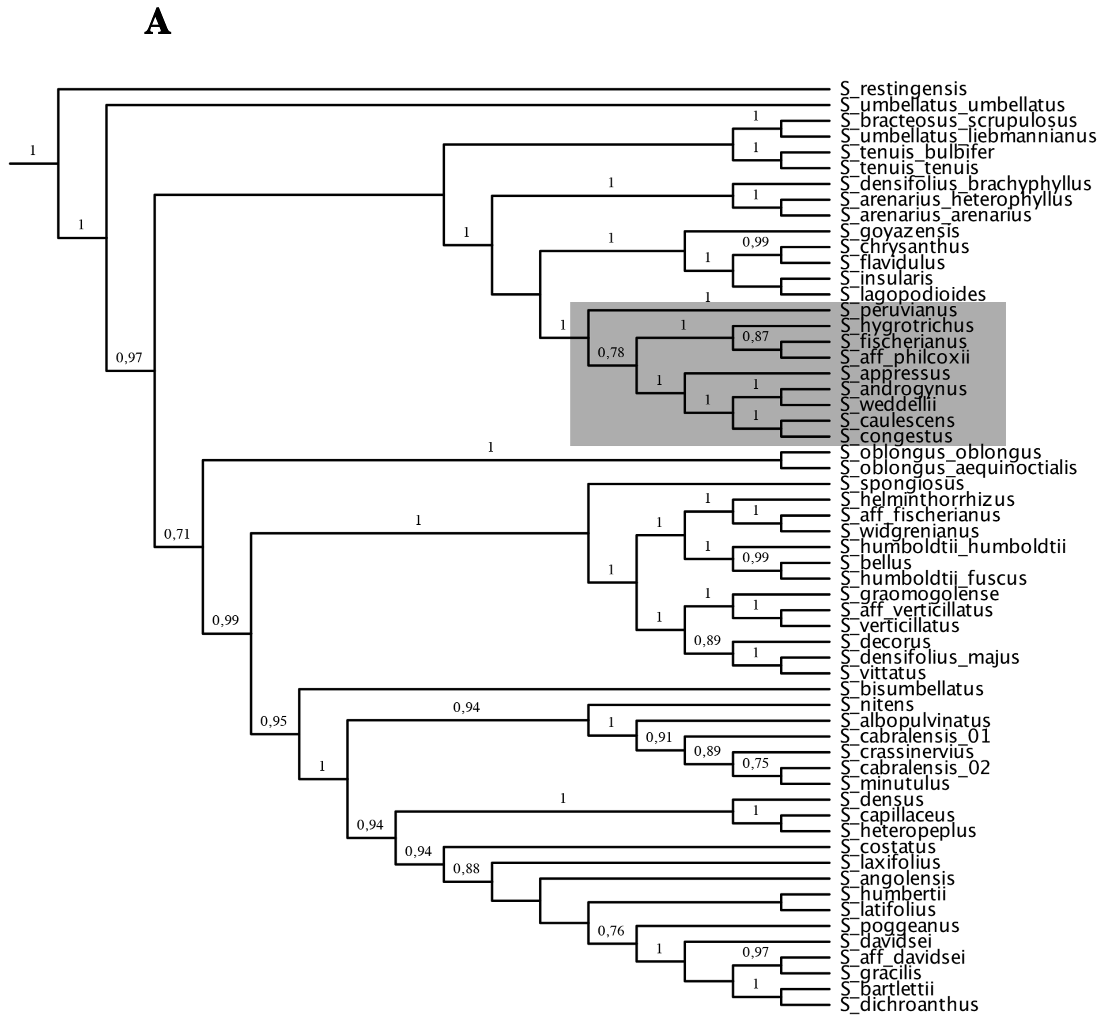
sect. *Thysanocephalus*, based on anatomical characters. This result corroborated the findings of Ricci et al. (1996), showing that these sections do not have only phytochemical affinities. Later, Andrade et al. (2010) using molecular data ascertained that *S.* sect. *Eulepis* and *S.* sect. *Thysanocephalus* appear as sister groups and *S.* sect. *Syngonanthus* and *S.* sect. *Carphocephalus* are in another clade (including *Philodice*), forming another group. However, as so circumscribed *S.* sect. *Syngonanthus* was paraphyletic and *S.* sect. *Carphocephalus* was polyphyletic. Based on these results, Parra et al. (2010) to solve the topological conflict in *Syngonanthus s.l.,* proposed the reestablishment of *Comanthera*, a genus with *S.* sect. *Eulepis* (now *Comanthera* subg. *Comanthera*) and *S.* sect. *Thysanocephalus* (*C.* subg. *Thysanocephalus*). In the face of chemical, molecular and morphological data, Giulietti et al. (2009; 2012) synonymized *Philodice* in *Syngonanthus* and required the conservation of the name *Syngonanthus*.

In the most recent phylogenies of Eriocaulaceae, the panorama was not different. Giulietti et al. (2012) recognized *Syngonanthus*, *Comanthera*, *Leiothrix* and *Rondonanthus* as monophyletic genera in Paepalanthoideae. In this study, *Syngonanthus* was positioned as sister to the remainder of Paepalanthoideae, a new scenario that had not been discerned previously. Although both *S.* sect. *Syngonanthus* and *S.* sect. *Carphocephalus* were represented, the small sampling of the species in the genus did not allow any further consideration of these groups. Echternacht et al. (2014) exploring data from an expanded sampling of *Comanthera* and *Syngonanthus*, had strong support for the monophyly for these genera. However, *S.* sect. *Syngonanthus* also appears paraphyletic and *S.* sect. *Carphocephalus* was polyphyletic.

All these studies (Andrade et al. 2010; Echternacht et al. 2014), which considered *S.* sect. *Carphocephalus* as a polyphyletic group, included *Syngonanthus anomalus* as a representative species of the section. In our analysis (chapter 2), We excluded this taxon from *S.* sect. *Carphocephalus* and substantially increased the sampling of the sections, in general. *S. anomalus* and other species considered as *S.* sect. *Carphocephalus* (e.g. *S. philodicoides* by morphological inference) are in another monophyletic group with homoplastic characters, such as elongated stems with leaves spiral and corolla fleshy in staminate flowers, the "*Philodice* group". Our definition of *S.* sect. *Carphocephalus* species was explained above. The "*Philodicoides* group" has a set of characters not found in *S.* sect. *Carphocephalus*, as for example, regular axillary inflorescences, carnose and not involute corolla of pistillate flowers, stamens free, staminate flowers with corolla partially fused and not involute. In our analysis, *S.* sect. *Carphocephalus* appears always monophyletic for all results using different molecular markers.

Syngonanthus peruvianus is the early divergent species in the clade. This species has basal leaves in the rosette, synflorescence axis very short or undeveloped, and the staminate flowers carnose only in the basal portion of the urceolate corolla. Sepals in both types of flowers have the upper portion slightly thickened. Maybe, these are the major synapomorphies for this clade.

Syngonanthus sect. *Carphocephalus* also is composed of two other clades. The smaller group includes *S. philcoxii*, *S. hygrotrichus* and *S. fischerianus*. These species are very similar morphologically and few characters are divergent. *S. hygrotrichus* and *S. fischerianus* have an evident synflorescence axis and *S. philcoxii* has axillary sterile aerial stems emerging from the rosette. The other group includes *S.* sect. *Carphocephalus sensu stricto*. The main morphological characters and floral traits are the developed aerial stem, staminate flowers with corolla fleshy and involute after anthesis, and pistillate flowers with corolla fleshy and lobes membranous.



B

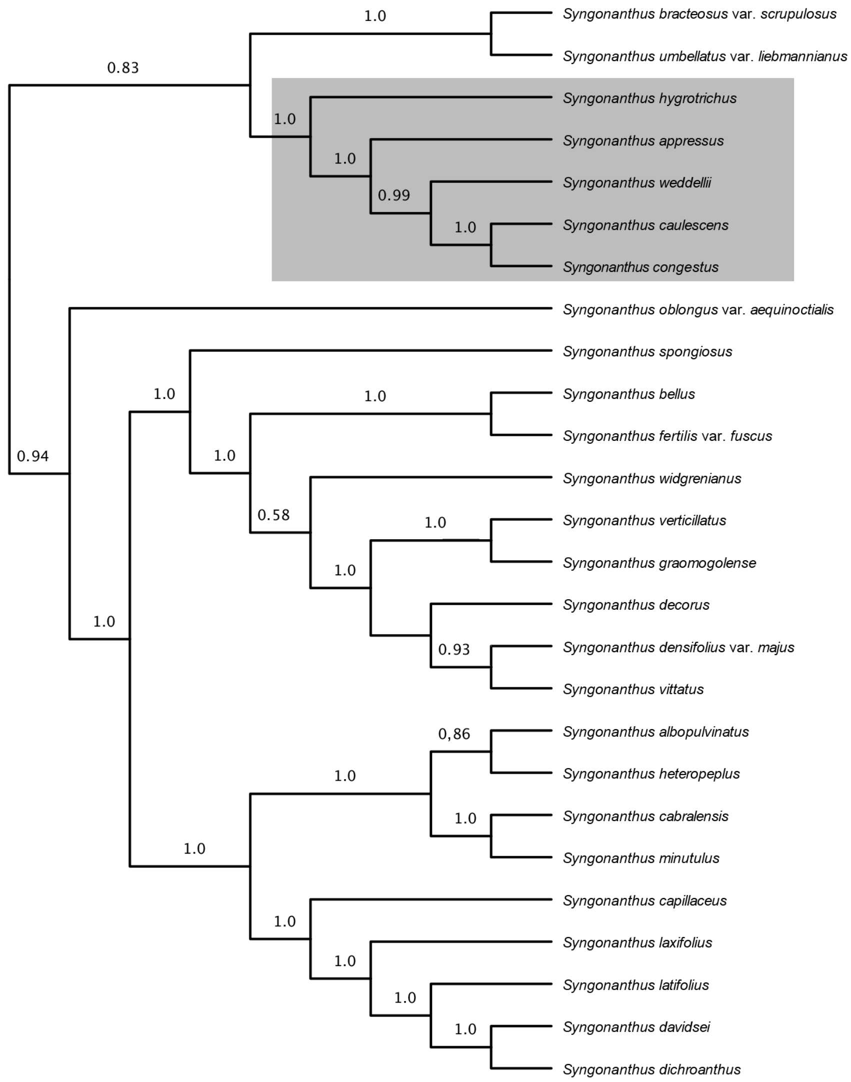


Figure 04. **A.** Cladogram of Bayesian analysis of the combined plastid and nuclear data (*psb*A-*trn*H, trnL-F, *rps*16 ETS and ITS) showing the position of *Carphocepahlus* within *Syngonanthus*. Numbers above the branches represent posterior probabilities (PP more than 0.70). *Carphocephalus* group is represented by the grey rectangle. **B.** Cladogram of Bayesian analysis of ETS showing the position of *Carphocepahlus* within *Syngonanthus*.

Materials and Methods

The monograph of *Syngonanthus* sect. *Carphocephalus* is based on a detailed study of herbarium specimens and field expeditions by Watanabe to Brazil between 2010 and 2014. The examination includes database of photographs and materials analyzed in person from the following herbaria: ALCB, BHCB, CEN, CEPEC, CESJ, ESA, ESAL, F, HEPH, HRCB, HRB,

HUEFS, IBGE, INPA, LL, MBM, MO, NY, OUPR, PAMG, R, RB, SP, SPF, UB, UEC and VIC (acronyms according to Thiers, 2014).

Descriptions of species are listed in alphabetical order, and were prepared by examining dried specimens. Particular structures such as flowers were boiled for dissection and observed under a stereomicroscope for measurements using their corresponding scale. The morphological terminology follows Radford *et al.* (1974) and Stearn (1992) and abbreviations of the author's names follow Brummitt & Powell (1992).

The species concept adopted for this revisionary study takes into account the intra- and interpopulational morphological discontinuities. The species have been identified by stable morphological character state. Although the taxonomy of this group can be complex, with large morphological variation, the morphological species concept proposed by Davis & Heywood (1963) is considered. According to this concept, species are ***assemblages of individuals with morphological features in common and separable from other such assemblages by correlated morphological discontinuity in a number of features***. However, we are aware that this concept can be limited and we also consider data from genetics and ecology relevant to robust taxonomic decisions.

We present, in this taxonomic study, general comments about taxonomic history, morphology, geographical distribution, phenology, reproductive biology, conservation, notes about similar species and identification keys. The taxonomic treatment consists of descriptions, commentaries, botanical illustrations and photos.

Taxonomic Treatment

Syngonanthus sect. ***Carphocephalus*** Ruhland in Engler, Pflanzenr. 13 (IV.30): 264. 1903. *Paepalanthus* subg. *Carphocephalus* Koern., Fl. Bras. (Martius) 3(1): 465. 1863. — Lectotype, designated here: *Syngonanthus caulescens* (Poir.) Ruhland [≡ *Eriocaulon caulescens* Poir.]

Aquatic or terrestrial herbs, monocarpic, viviparous or not, caulescent or with leaves in basal rosette, erect or decumbent, sometimes branching at base to form clumps; or axillary stem without inflorescences. **Roots** white, spongy. **Leaves** linear, linear-lanceolate, or capillaceous, apex round to truncate, acute, mucronate, or uncinate, base truncate, fenestrate, recurved, patent, ascending or adpressed; ciliate, glabrescent, pilose to glabrescent or tomentose on both surfaces, with adpressed, simple filamentous and/or small glandular trichomes, villous hairs at the insertion of the leaves. **Aerial stem** sometimes branching at the apex, sometimes not developed, with leaves congested at base, villous or woolly, with white crooked trichomes, sometimes concentrated next to the apex, bearing an umbel of 1-75 inflorescences at the apex, or purely vegetative, without inflorescences at the apex. Cauline leaves spirally arranged, equally or unequally distributed on the stem, lax or congested at the apex near synflorescence, recurved, appressed, patent, ascendant or oblique; acicular, capillaceous, linear to triangular to lanceolate to elliptic or oblong, apex acute, retuse, round, mucronate, acuminate, obtuse or uncinate; glabrescent to pilose, with adpressed trichomes, capitated and simple filamentous hairs on both surfaces. Synflorescences with a primary axis bearing inflorescences at the apex. **Synflorescence axis** emerging from the center of the rosette, erect, straw-colored, pubescent with adpressed trichomes and filamentous hairs. Bracts of synflorescence axis restricted to the apex, whorled and numerous, progressively elongating from the outer toward the inner series, ascending, paleaceous to membranous, linear-lanceolate or linear-triangular, apex acuminate, scarcely pilose to glabrescent on both surface with simple filamentous hairs and adpressed trichomes. Inflorescences composed of a closed spathe subtending a scape with a capitulum at the apex. **Spathes** chartaceous, cylindrical, erect, obliquely opened, apex acute to obtuse, retuse, acuminate, lacerate or cuspidate, tip curved or uncinate, margin entire, not involute, ciliate or glabrous, glabrescent, pilose or tomentose, with capitate and simple filamentous hairs and adpressed trichomes. **Scapes** erect to flexuous, green or straw-colored with age, 3-8-costate, glabrescent, pilose, pubescent, sometimes a collar of trichomes near the apex with capitate and simple hairs and adpressed trichomes. **Capitula** obconic or hemispherical. **Involucral bracts** in 2–6 series, those of the external series triangular, obovate ovate, elliptic, lanceolate, or oblong, apex acute, obtuse, acuminate, mucronate, rounded or apiculate, glabrous, those of the internal series progressively longer, obovate, linear, elliptic, lanceolate, oblanceolate, apex acute, acuminate, apiculate, obtuse, mucronate, round or retuse; inner bracts glabrous or ciliate, sparsely pilose with simple filamentous hairs. Floral bracts absent. **Flowers** 3-merous, unisexual or bisexual, 20–250 per capitulum. **Bisexual flowers**, when present, pedicellate, with long white villous trichomes at base and insertion with receptacle; sepals chartaceous, glabrous, white to cream, hyaline when hydrated, slightly white in longitudinal band at middle, shortly connate at base, lanceolate, rhombic or narrowly obtrullate, very slightly thickened, margin revolute, toward apex acute; petals rhombic, connate at the upper margin, free at base and apex, lobe triangular, apex acute, lower half of petal fleshy, upper half membranous, pilose abaxially with simple filamentous hairs, involute after anthesis; filaments adnate to the petals, anthers white; gynoecium 3-carpellate; style column cream-colored; appendages 3, the glandular apex capitate; style branches broad and membranous at base, apex narrow and papillose. **Staminate flowers** pedicellate with filamentous trichomes at insertion with receptacle, sometimes at the bottom part of pedicel; sepals cream, sometimes slightly golden in longitudinal band at middle, or upper part white, lower part hyaline, shortly fused at base, cymbiform, chartaceous, oblanceolate, lanceolate, rhombic or elliptic, apex rounded, acuminate or acute, margin involute; glabrous, or pilose with simple filamentous hairs or adpressed trichomes; corolla partly fleshy, at last the lobes membranous, urceolate, tubular, lobes obtuse to rounded, involute after anthesis, glabrous; the anthophore approximately the half the length of the corolla; filaments free or adnate to the petals, anthers cream to yellowish or whitish; pistillodes 3, clavate, papillose at apex. **Pistillate flowers** short pedicellate, with filamentous hairs at insertion with receptacle or bottom part of pedicel; sepals oblong, obovate, rhombic, elliptic, oblanceolate or lanceolate, cymbiform, rigid-chartaceous toward apex, acute or acuminate, margin involute, white to hyaline, pilose as in staminate flower; petals oblong, obtrullate, oblanceolate or spatulate, fused at the upper margin, free at base and apex, lobes triangular, oblong, acute or obtuse, lower half of petal fleshy, upper half membranous, or thickened medially in fusion zone and otherwise membranous, pilose abaxially with simple filamentous hairs; gynoecium 3-carpellate; style column cream-colored to castaneous; appendages 3 or lacking, the glandular apex capitate; style branches simple. **Seeds** ovoid, ellipsoid or elliptic, brown-colored, striate with very short pseudotrichomes.

Key to the species of *Syngonanthus* sect. *Carphocephalus*

1. Plants with bisexual flowers .... ***S. androgynus***

1’. Plants with unisexual flowers **2**

  2. Plants without synflorescence axis; aerial stem developed, sometimes very short; petals of pistillate flowers fleshy in the lower half **3**

    3. Aerial stem vegetative, without inflorescences; leaves capillaceous; rosette always present .... ***S. philcoxii***

    3’. Aerial stem fertile, with inflorescences at apex; leaves never capillaceous; rosettes may be produced in addition to elongate aerial stem and only the aerial stems are fertile **4**

      4. Pistillate flowers with appendages (nectariferous portions of the style) reduced or absent .... ***S. discretifolius***

      4’. Pistillate flowers with appendages evident **5**

        5. Leaves on the aerial stem completely appressed and strongly recurved at stem base; sometimes rosette present .... ***S. appressus***

5'. Leaves on the aerial stem not totally appressed and curved; rosette absent **6**

6. Capitula viviparous; roots on the aerial stem throughout the length; involucral bracts pilose; axillar inflorescences present .... ***S. rhizonema***

6'. Capitula non-viviparous; roots on the aerial stem when present, not throughout the length; involucral bracts glabrous; axillar inflorescence usually absent **7**

7. Plants decumbent/prostrate **8**

8. Capitula up to 1.5 (-3) mm in diameter; leaves narrowly oblong to obovate, elliptic or lanceolate; leaves persistent .... ***S. cachimboensis***

8'. Capitula more than 3 mm in diameter; leaves linear or narrowly lanceolate; leaves deciduous near stem base .... ***S. ruhlandii***

7'. Plants erect **9**

9. Involucral bracts with apex mucronate or retuse .... ***S. mollis***

9'. Involucral bracts with apex acute, acuminate, apiculate or obtuse **10**

10. Leaves on the aerial stem patent to slightly oblique; leaves linear-lanceolate; scapes pubescent near the apex with capitate trichomes .... ***S. weddellii***

10'. Leaves on the aerial stem oblique/patent to ascending; leaves lanceolate, elliptic, linear or oblong; scapes with adpressed and filamentous trichomes only, not pubescent near the apex .... ***S. caulescens***

2'. Plants with short synflorescence axis; aerial stem usually undeveloped; petals of pistillate flowers membranous/chartaceous **10**

10. Aquatic plants; leaves capillaceous .... ***S. hygrotrichus***

10'. Terrestrial or semi-aquatic plants; leaves lanceolate, linear **11**

11. Leaves fenestrate at base, linear-lanceolate, apex acute, mucronate or uncinate; style branches robust .... ***S. peruvianus***

11'. Leaves non-fenestrate, linear, apex round to truncate; style branches thin .... ***S. fischerianus***

Syngonanthus androgynus M.T.C.Watan. *sp. nov.* Type: Brazil, Goiás, Alto Paraíso de Goiás, Chapada dos Veadeiros, Km 11 da estrada Alto Paraíso de Goiás / São Jorge, estrada para a cachoeira São Bento, ca. 1.5 km após a cachoeira, 09 Sep 1994, Fonseca & Filgueiras 115 (Holotype: SPF; Isotype: IBGE, RB).

Caulescent herbs, 12–37 cm tall, unbranched at base, lacking basal rosette. Roots white, 0.1–0.2(-0.6) mm in diameter, spongy. Aerial stem 2–13 cm long, villous with white crooked trichomes mainly concentrated next to the apex, bearing an umbel of 1-30 inflorescences at the apex. Leaves abundant spirally arranged and equally distributed on the stem, patent to ascending, fenestrate, lax, sometimes more congested at the apex near the synflorescence, 5–45 × 0.25–2 mm, linear to threadlike or capillary, acuminate or filiform, both surface pilose with capitated filamentous hairs and adpressed trichomes, latter glabrescent, veins 3–6 prominent. Leaves more congested on the top, 0.3–2 cm long, linear or acicular, apex recurved and thick, pubescence of adpressed trichomes and capitate hairs. Spathes 1.0–5.5 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute or cuspidate, tip curved or slightly uncinate, triangular or auriculate, margin entire, ciliate, not involute, both surfaces pilose with capitate filamentous and adpressed trichomes. Scapes erect, 3–34 cm long, greenish or straw-colored to golden with age, 3-costate, pilose in all extension, pubescent near the apex with capitated hairs and adpressed trichomes. Capitula 3–7 mm in diameter, radiate, hemispherical in anthesis. Involucral bracts in 2–5 series, cream-colored, all similar in color or sometimes the outer castaneous, the inner becoming cream inward, hyaline when wet, glabrous, those of the external series 1.05–1.55 × 0.5–0.9 mm, varying form to triangular to slightly ovate, obovate or oblong, apex acute or obtuse, progressively thinner toward the apex, those of the internal series 1.0–1.8 × 0.5–0.75 mm, almost equaling the flower height, oblanceolate, apex obtuse to rounded, sometimes bifid; receptacle discoid, pilose. Floral bracts absent. Flowers bisexual, 3-merous, 20–60 per capitulum, flowers 1.45–2.55 mm long including pedicels; pedicels 0.15–0.45 mm long, with long white villous trichomes at base and insertion with receptacle; sepals 1.5–2.1 mm long, membranous, glabrous, white to cream, hyaline when hydrated, slightly white at longitudinal band at middle, shortly connate at base, margin revolute, lanceolate, rhombic or narrowly obtrullate, very slightly thickened, toward apex acute; petals 1–2.2 mm long, rhombic, connate at the upper margin, free at base and apex very top, lobe triangular, apex acute, lower half of petal fleshy, upper half membranous, pilose abaxially with simple filamentous hairs, involute after anthesis; filaments adnate to the petals, anthers 0.15–0.3 mm long, white; gynoecium 1.3–1.5 mm long; ovary 0.5–0.75 mm long; style column ca. 0.1–0.2 mm long, cream-colored; appendages ca. 0.15–0.3 mm long, the glandular apex capitate; style branches broad and membranous at base, apex narrow and papillose, 0.4–1 mm long. Seed 0.45–0.6 × 0.25–0.35 mm, ovoid, brown-colored, striate with very short pseudotrichomes in longitudinal lines.

Phenology— Flowers have been recorded from May-September. Fruit abundant from September.

Habitat and Distribution— This new species was collected in the Amazonian region of Bolivia and Peru at border of both countries in the flow of the Heath River. Also known from Grande Sertão Veredas National Park and near Chapada dos Veadeiros National Park (east-central region of Brazil). Grows on wetlands, over shallow sandy soils and "Pampas" vegetation.

Conservation status— The disjunct distribution, occupying threatened regions allowed categorize this species as endangered following the criteria B (geographic range) of IUCN 2014. Area of occupancy < 500 km^2, number of locations ≤ 5 and extreme fluctuations in number of locations and area of occupancy comply with the requirements of criteria B2ac.

Commentaries— Bisexual flowers represent an exception among species of Eriocaulaceae. *Rondonanthus flabelliformis* (Moldenke) Hensold & Giul. and only three *Syngonanthus* (*S. acephalus* Hensold, *S. amazonicus* Moldenke and *S. trichophyllus* Moldenke) share this floral trait. This is a particular situation because the other three species in the genus, which share this characteristic, have 2-merous flowers. *S. acephalus* is a small species forming clumps that contain only 1-2 flowers per capitulum without involucral bracts. *S. amazonicus* and *S. trichophyllus* have two spathaceous sepals and two and one stamens, respectively, both species also differing by the width leaves and consistency of petals of pistillate flowers (membranous in *S. trichophyllus versus* thick in *S. amazonicus*). This new species has an unique combination with bisexual flowers and 3-merous flowers.

We suggest the taxonomic placement of *S. androgynus* in *S.* sect. *Carphocephalus* because the taxon shares characteristics observed in this group like fleshy petals, well-developed aerial stem with leaves spirally distributed. Phylogenetic studies showed close relationship of this taxon with sect. *Carphocephalus* (Watanabe et al. submitted; Chapter 1.2 and 2)

This new species could be the first reported case of cleistogamy for Eriocaulaceae. The apex petals are not completely free, in all stages observed, and the stamens and style branch are wrapped each other. Petals are not completely fused but strongly involute without exposition of sexual parts (Watanabe et al. submitted).

An intriguing morphological variation was noted between specimens from Brazil and Bolivia/Peru. Specimens from Brazil have petals of pistillate flowers pilose in most cases, rarely glabrescent. The collection that has been chosen to be the holotype includes well-developed individuals (from Chapada dos Veadeiros) as opposed to specimens from Grande Sertão Veredas

National Park that comprise smaller plants. Collections from the Heath River have a similar form, usually with leaves scattered on aerial stem but congested appicaly near scapes, unlike those from Central Brazil that have leaves longer and more congested on the stem. Plants from River Heath always exhibit petals of pistillate flowers glabrous. Specimens from Brazil show flowers slightly flattened and stamens larger than specimens from Heath River.

We do not consider two different taxa because have been observed discrete variation among individuals in the same population. In addition, the floral structure and vegetative arrangement is very similar in all specimens and the pilosity in the flowers had a slight gradation in plants from Brazil as well as the distribution of leaves on stem.

See figures of *Syngonanthus androgynus* in the chapter 1.2.

Specimens examined— BOLIVIA. La Paz, Abel Iturralde, Puerto Muscoso, donde llega la pampa mas cerca del río Heath, 25 Jul 1995, *Helme & Kruger 678* (F).

BRAZIL. Minas Gerais, Formoso, Parque Nacional Grande Sertão Veredas, próximo a ponte da barra do Rio Preto / Santa Rita, em vereda, 15º10'35"S 45º46'09"W, 21 May 1998, *Oliveira et al. 1056* (F, IBGE).

PERU. Madre de Dios, Tambopata, Parque Nacional "Bahuaja-Sonere", ex Santuario Nacional "Pampa de Heath", formación de pampa inundada permanentemente, 25 Sep 1997, *C. Diáz et al. 9201* (F, MO); Río Heath, Santuario Nacional de las Pampas del Heath, lado este de la Pampa, 3-4 km oeste del río, camino del RefugioJuliaca, hasta el bosque de galería y campamento Aguas Claras, 15 Jun 1992, *Castillo & Foster 6968* (F).

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HERBÁRIO DA RESERVA ECOLÓGICA DO IBGE
Brasília - DF. Brasil
Eriocaulaceae

GO. CHAPADA DOS VEADEIROS. Alto Paraiso. Km 11 da estrada Alto Paraiso / São Jorge. Entrada para cahoeira de São.Bento, 1,5 Km após a cachoeira. Erva anual ereta, ca. 0,20 m alt.; folhas basais; capítulos esbranquiçados em fase de dispersão de sementes. Campo úmido.

115 9.IX.1994

Leg: M.L.Fonseca & T.S.Filgueiras.

Figure 05. Isotype of *Syngonanthus androgynus* deposited in RB herbarium.

Syngonanthus appressus (Koern.) Ruhland in Engler, Pflanzenr. 13 (IV. 30): 269. 1903. *Paepalanthus appressus* Koern., Fl. Bras. (Martius) 3(1): 468. 1863. *Dupatya appressa* (Koern.) Kuntze, Revis. Gen. Pl. 2: 745. 1891. Type: Brazil. Minas Gerais: G. Gardner 5255 (Lectotype designated here: HAL [0109780]; Isolectotypes: B, BM, E, F, G, K, LE, NY, OXF, P, R, S, US).

Syngonanthus inundatus (Koern.) Ruhland in Engler, Pflanzenr. 13 (IV.30): 267. 1903. *Paepalanthus inundatus* Koern., Fl. Bras. (Martius) 3(1): 468. 1863. *Dupatya inundata* (Koern.) Kuntze, Revis. Gen. Pl. 2: 746. 1891. Type: Brazil. Goiás: In aquis fluentibus Chapadão de S. Marcos, *L. Riedel 2745* (Lectotype designated here: LE [00001176]; Isolectotypes: B, G, K, L, LE [00001175; 00001177] M, NY, P, S, U, UPS). ***syn nov.***

Caulescent herbs, 12–54 cm tall, rarely branching at base to form clumps up to five stems. Roots white, 0.3–1.3 mm in diameter, spongy. Rosette sometimes present, 14–30 mm diam., leaves linear to lanceolate, 4.0–9.0 × 1.0–2.0 mm, recurved to flat, tomentose, with adpressed and filamentous trichomes. Aerial stem 2–26 cm long, villous, with white crooked trichomes, bearing an umbel of 1-8 inflorescences at the apex. Cauline leaves recurved near stem base and appressed toward stem apex, congested at the apex near synflorescence, 6.0–28.5 × 0.8–2.6 mm, linear, apex acute, pubescence strigose, with adpressed trichomes, veins 5–7 prominent. Spathes 2.0–6.5 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute to obtuse, tip uncinate, margin entire, not involute, glabrous to glabrescent adaxially, tomentose abaxially with capitate filamentous hairs and adpressed trichomes. Scapes erect, 6–37 cm long, green or straw-colored with age, 3-costate, pilose, pubescent near the apex with capitate hairs and adpressed trichomes. Capitula 4–8.5 mm in diameter, radiate. Involucral bracts in 4–6 series, those of the external series 1.35–2 × 0.75–1 mm, triangular to ovate or oblong, apex rounded or apiculate, golden to cream-colored, glabrous, those of the internal series progressively longer 2.25–2.7 × 0.6–0.9 mm, almost equaling the flower height, oblanceolate, apex acute to obtuse, cream to white-colored with a slight golden band on the center, rarely ciliate, sparsely pilose with simple filamentous hairs on abaxial surface; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 60–160 per capitulum, the staminate and pistillate generally equal in number but depending on phenophase, pistillate can be almost twice as many as staminate, pistillate flowers concentrated in inner whorls. Staminate flowers 1.6–2.5 mm including pedicels; pedicels 0.5–0.85 mm long with filamentous trichomes at insertion with receptacle; sepals 1.15–1.7 mm long, cream, slightly golden at longitudinal band at middle, shortly fused at base, cymbiform, membranous, oblanceolate to lanceolate or elliptic, apex rounded to acute, pubescent adaxially, especially distally, with simple filamentous hairs, glabrous abaxially; corolla 0.6–1.15 mm long, fused ca. 2/3 their length, fleshy, tubular, lobes obtuse to rounded, involute after anthesis, glabrous; filaments adnate to the petals, anthers 0.2–0.35 mm long, cream to yellowish; pistillodes 3, ca. 0.2 mm long, clavate, papillose at apex. Pistillate flowers 1.1–2.6 mm including pedicels; pedicels 0.3–0.6 mm long with filamentous hairs at insertion with receptacle; sepals 1.45–1.75 mm long, oblong to lanceolate, cymbiform, rigid-chartaceous toward apex, acute, white to hyaline, pubescent as in staminate flower; petals 0.8–2.0 mm long, oblong, fused at the upper margin, free at base and apex, lobes triangular, acute, thickened medially in fusion zone otherwise membranous, or lower half of petal fleshy, upper half membranous, white to hyaline when hydrated, glabrous adaxially, pilose abaxially with simple filamentous hairs; gynoecium 1.3–1.85 mm long; ovary 0.45–0.65 mm long; style column 0.2–0.35 mm long, cream-colored to castaneous; appendages 0.25–0.35 mm long, the glandular apex capitate; style branches simple, 065–0.85 mm long. Seeds 0.45 × 0.25–0.35 mm, ovoid, brown-colored, striate with very short pseudotrichomes.

Phenology— The flowering is similar to other species of *Syngonanthus* from São Paulo and Minas Gerais with mature flowers in the beginning of June with intensified fruiting concentrated in September.

Habitat and Distribution— *S. appressus* has been registered in Distrito Federal, Goiás, Minas Gerais and São Paulo (Brazil). Occurs in the "cerrado" biome, particularly in landscapes with soggy soils such as swamps and "veredas".

Conservation status—*S. appressus* was categorized as near Threatened following IUCN 2014 criteria because the best estimate of number of individuals is 2000 mature individuals, but this estimate is very uncertain, and as low as 1000 mature individuals cannot be ruled out.

Commentaries— *Syngonanthus appressus* is a typical species from *Syngonanthus* sect. *Carphocephalus* with well-developed leaves on evident aerial stem. It is very similar to *S. caulescens* differing by leaves adpressed on stem, with adpressed trichomes concentrated at apex and, involucral bracts with obtuse, rounded or apiculate apex (*S. caulescens* has involucral bracts with acute apex, distribution of trichomes more regular on the scape, and leaves not adpressed on the stem). In addition to adpressed leaves, there can be recurved leaves near base at plant also leaves from basal rosette (which are plane to curved). The leaves subtending the synflorescence (bracts) are undifferentiated form as those other cauline leaves, basically differing by the greater length.

Scapes usually bear a "collar" of capitate trichomes at base of capitulum. Generally the capitula have two types of involucral bracts: the outer are pale golden with apex rounded or apiculate and the inner are cream with apex acute to obtuse. The apex of the sepals of pistillate flowers is rigid, cymbiform and sometimes slightly involute near apex. Petals are abaxially pilose and spongy in the central part. Sepals of staminate flowers are cymbiform and internally pilose.

Koernicke (1863) described this taxon based on materials of *Riedel 2302* and *Gardner 5255* from São Paulo and Minas Gerais, respectively. The collection of *Riedel 2302* has plants with immature inflorescences in contrast the material *Gardner 5255* has mature inflorescences and represents the most abundant geographical distribution (*versu*s only three colections known in São Paulo). For this reason this material has been chosen to be the lectotype (HAL 0109780). Koernicke probably saw Gardner's specimens deposited in herbarium LE and some of this material has been transferred to herbarium HAL. The material deposited in LE has a unique specimen and the condition of the capitula suggest that there is no fruit to exam in the sheet. On the other hand, the material deposited in HAL has two mature specimens with capitula at different phenological stages.

Syngonanthus inundatus is only known from the type-collection. There is no significant morphological variation between specimens of *S. appressus* and *S. inundatus*. A similar form of capitulum, disposition of leaves on aerial stem, pilosity and floral structures support our decison to synonymize *S. inundatus*. Basically, taxonomists distinguished the two taxa on the basis of two types of leaves on aerial stem of *S. inundatus*, one type very similar to that observed in *S. appressus* (adpressed leaves), and the other type much thinner. In fact, the latter appears to be the same type that we found in the rosette of *S. appressus* and it is possible to notice that these thin leaves are consistently associated with roots. This observation leads us to consider these leaves not to just be another kind of leaf but anomalous growth on the stem. This situation mainly occurs when the stem is submerged in water or covered up by soil.

Specimens examined— **BRAZIL**. **Distrito Federal**: Brasília, Jardim Botânico, anexo, campo úmido, na margem de um lago pequeno, dentro d'água, 24 Aug 1990, *Splett 21* (HEPH), matas do zoobotânico, em solo alagado, 26 Aug 1965, *Sucre 804* (UB); Planaltina, Estação Ecológica Águas Emendadas, vereda do marco, 14 Jul 2008, *Amaral & Eugênio 2131* (HEPH); **Minas Gerais**: Couto Magalhães, fazenda das Abóboras, brejo próx. a Cerrado, 16 Jul 1984, *Giulietti et al. [CFCR 4572]* (HUEFS, SPF), Itacambira, Plantar MG 15, fazenda Tamanduá, 09 Oct 2005, *Tameirão Neto 4051* (BHCB), Santana do Riacho, Serra do Cipó, estrada da usina de força Dr. Pacífico Mascarenhas, campo limpo brejoso ao lado de mata ciliar do córrego Braúna, 19°15´54´´S 43°35´48´´W, 12 Jun 1996, Mello-Silva et al. 1094 (SPF), Uberlândia, fundo direito da vereda 1, reserva do clube caça e pesca Itororó, 2 Jul 1999, *Barbosa & Faria 2170* (F), idem, 11 Aug 1999, *Barbosa & Amaral s.n.* (F), idem, 13 Aug 1999, *Barbosa 2252* (F), Unaí, fazenda São Miguel (grupo Votorantin), em vereda, 07 Nov 1993, Aparecida da Silva et al. 1754 (IBGE, SPF); **Goiás**: Niquelândia, estrada Niquelândia – Colinas, em brejo, 17 Sep 1998, *Forzza et al. 1068* (SPF); **São Paulo**: São Carlos, 5 km NWW of center of São Carlos, in open marsh at head of east, 19 June 1961, *Eiten et al. 3029* (NY), about 4 km due N of center of São Carlos on road to Ribeirão Preto, 5 August 1961, *Campos 3* (LL, NY).

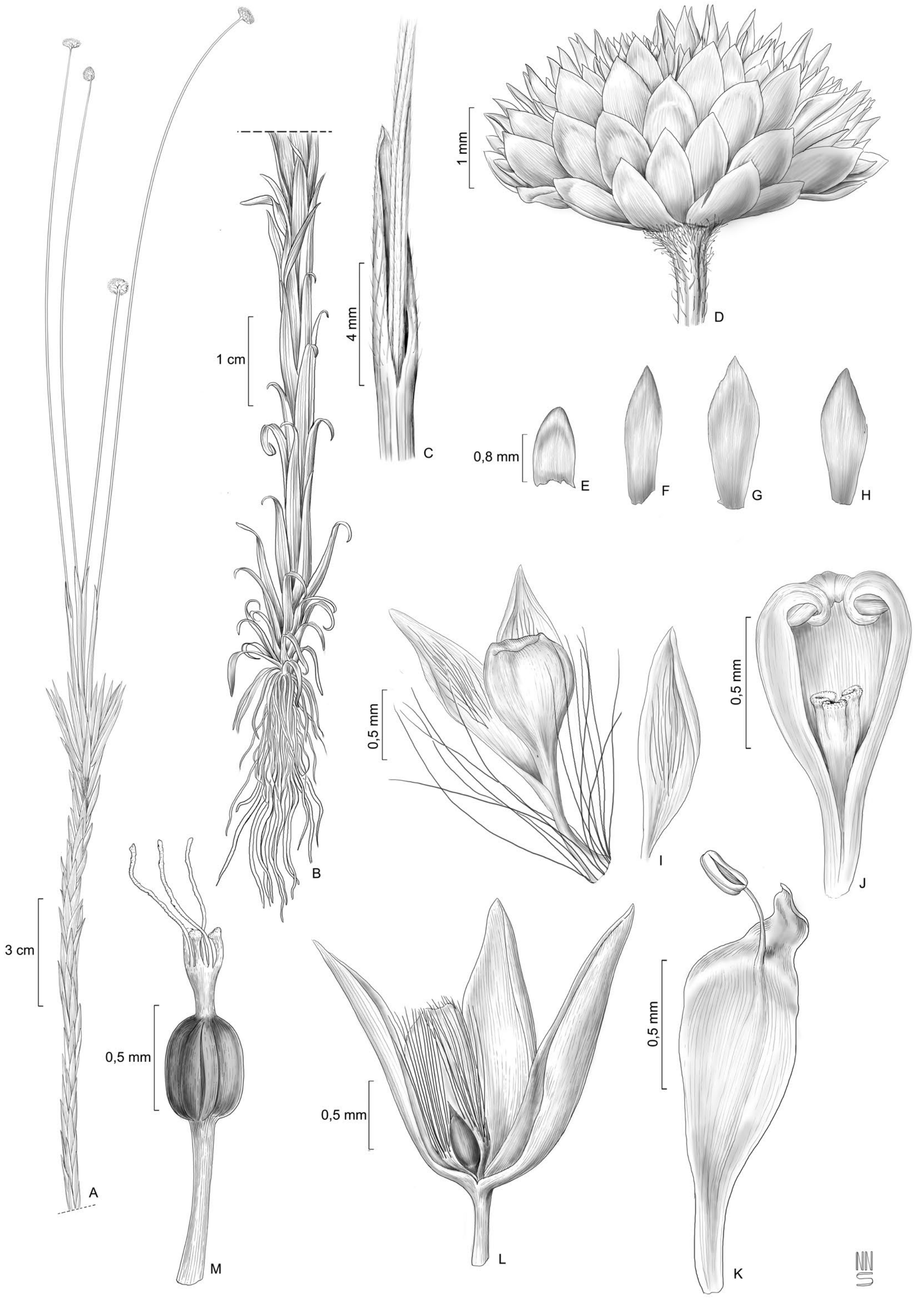

Figure 06. ***Syngonanthus appressus*****. A-B.** habit; **A.** Aerial stem and inflorescences; **B.** Roots and basal leaves in the aerial stem; **C.** Details of spath and scape; **D.** Capitulum; **E-H.** Involucral bracts; **I.** Staminate flower with one sepal removed; **J.** Dissected staminate flower showing pistillodes; **K.** part of the corolla with adnate stamen; **L.** Pistillate flower; **M.** Gynoecium.

Figure 7. Lectotype of *Syngonanthus appressus* deposited in HAL herbarium.*

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* Available at http://herbarium.univie.ac.at/database/image.php?filename=hal_0109780&method=download&format=tiff [Accessed September 24, 2014]

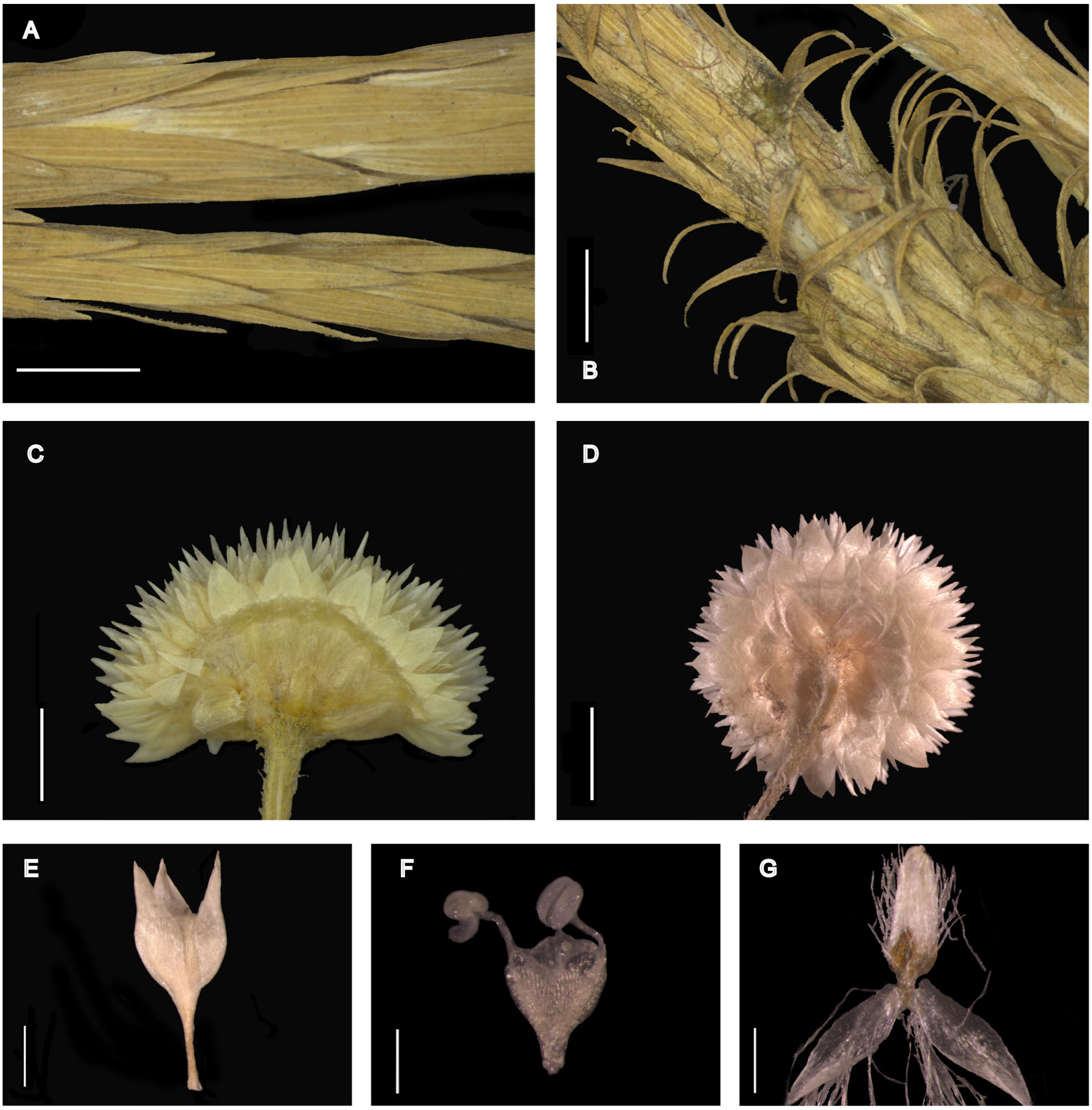


Figure 08. *Syngonanthus appressus*. **A.** adpressed leaves on aerial stem. **B.** recurved leaves in the base of aerial stem. **C-D.** capitula. **C.** lateral view. **D.** medial/ventral view showing graduation of involucral bracts. **E.** staminate flower. **F.** staminate flower with dissected corolla showing stamens. **G.** pistillate flower. Scale bars, 0.4 mm (F), 0.5 mm (E), 0.6 mm (G), 2 mm (C, D), 3 mm (B), 4 mm (A).

Syngonanthus cachimboensis Moldenke, Bol. Mus. Paraense Emilio Goeldi, N.S., Bot. 3: 2. 1960. Type: Brazil. Pará: "Serra do Cachimbo, 425 m alt., na chuva da cachoeira, sobre pedra. 12 Dec 1956, J.M. Pires et al. 6168 (Holotype: NY!; Isotype: R!).

Caulescent herbs branched from base, 4–17 cm tall; grow in clumps, prostrate, decumbent. Roots white, very branched and elongated, 0.1–0.6 mm in diameter, spongy. Rosette apparently absent. Leaves 0.5–2.3 × 0.1–0.6 cm, distributed on lateral ramifications on stem, very congested, persistent, narrowly oblong to obovate, elliptic or lanceolate, apex mucronate to mucronulate, flat to ascendant, pilose, with malpighian trichomes, 6–13–veins evident but not prominent. Aerial stem 5–11 cm long, villous at leaves nodes, with white crooked trichomes. Inflorescences axillary to leaves. Spathes ca. 2.0 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute to obtuse, tip uncinated, margin entire, not involute, glabrous to glabrescent with capitate filamentous hairs in both surfaces. Scapes prostrate, 3–15 cm long, cream to whitish-colored, 3-costate, glabrescent to pilose with capitate hairs. Capitula 1.0–1.5(–3.0) mm in diameter, piryform when immature, it becomes radiated later. Involucral bracts in 1–sometimes 2–series, 1.65–2.2 × 0.85–1.3 mm, triangular to ovate, apex acute to acuminate, white to cream-colored, glabrous, almost equaling the flower height; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 10–40 per capitulum, the staminate and pistillate generally equal in number. Staminate flowers 1.5–2.3 mm long including pedicels; pedicels 0.2–0.5 mm long with filamentous trichomes at insertion with receptacle; sepals 1.3–1.8 mm long, cream, shortly fused at base, concave, margin involute, membranous, lanceolate or elliptic, apex acuminate, glabrous; corolla 0.6–1.4 mm long, fleshy, fused, tubular, lobes obtuse to rounded, involute after anthesis, glabrous; stamens adnate to the petals, anthers 0.2–0.35 mm long, cream to yellowish; anthophore ca. 0.2 mm long; pistillodes 3, ca. 0.25 mm long, clavate, papillose at apex. Pistillate flowers 1.2–2.0 mm long including pedicels; pedicels 0.2–0.3 mm long with filamentous hairs at insertion with receptacle; sepals 1.0–1.75 mm long, oblong to lanceolate, concave, apex acute, white to hyaline, adaxially glabrous, abaxially pilose with simple filamentous hairs in central portion; petals 0.85–1.05 mm long, oblong with apex acute, fused at the upper half, free at base and at the very top, membranous, white to hyaline when hydrated, glabrescent to pilose with simple filamentous hairs abaxially, gabrous adaxially; gynoecium 1.1–2.0 mm long; ovary 0.3–075 mm long; style column ca. 0.15–0.3 mm long, cream-colored to castaneous; appendages ca. 0.2 mm long, the glandular apex capitate; stigmatic branches simple, 0.25–1.0 mm long. Seeds not observed.

Phenology— The single collection of *S. cachimboensis* was made in December. This period coincides with the flowering of most Eriocaulaceae that occur in the equatorial region. The holotype contains buds and flowers. No data are available about fruiting.

Habitat and Distribution— The species is restricted to Serra do Cachimbo (Amazonian region of Pará - Brazil) and occurs on the rocks next to waterfalls.

Conservation status— According to IUCN 2014, when a taxon does not have direct or indirect information about possible threats or very little information about the taxon it is considered Data Deficcient (DD) following criteria by IUCN 2014. Serra do Cachimbo is a military area and probably should be a protected area but the data are very uncertain about this situation.

Commentaries— *Syngonanthus cachimboensis* is a very distinctive species that shows unique floral traits and morphological characters among all species included in *Syngonanthus* sect. *Carphocephalus*. Unfortunatelly, just one collection was observed in herbaria, represented by the holotype deposited on NY and isotype in R.

Contrary to the original description, there are some divergences in length of scapes, pilosity and number of costae (three not two as in the original description). Pistillate flowers are not glabrous therefore contain trichomes (sepals pilose and petals glabrescent) and floral bracts are absent.

Syngonanthus cachimboensis is most similar morphologically to *S. caulescens* and *S. anomalus*, but previously we discuss about phylogenetic placement of *S. anomalus* and these arguments exclude a closer relationship with *S. cahimboensis* (see chapter 2). Additionally, *S. cachimboensis* differs from *S. caulescens* by the decumbent/prostrate habit with growth in clumps and congested leaves on aerial stem, which make the verification of lateral branches and their ramification a little difficult. Aerial stem and scapes are cream to whitish-colored, although that coloration is not usual for scapes in the genus. The capitulum is the smallest among all species included in the *S.* sect. *Carphocephalus* and the immature capitulum is pyriform-shaped. There are few flowers, no more than 40 per capitulum. This species has wider leaves than any other species of *S.* sect. *Carphocephalus.*

TYPE!

Syngonanthus cachimboensis Moldenke

Verified by H. N. MOLDENKE
November 1975

INSTITUTO AGRONÔMICO DO NORTE
PLANTAS DA AMAZONIA
Estado do Pará
(Eriocaul.)

Serr$_{a}$ do Cachimbo, 425 m. de altitude.
Na chuva da cachoeira, sôbre pedras.

J.M.Pires,G.A.Black,J.J.Wurdack & N.T.Silva 6168
12-Dez., 1956

Figure 09. Holotype of *Syngonanthus cachimboensis* deposited in NY herbarium.[†]

[†] Available at https://plants.jstor.org/stable/10.5555/al.ap.specimen.ny00103618 [Accessed April 29, 2015]

Syngonanthus caulescens (Poir.) Ruhland in Engler, Pflazenr. 13 (IV. 30): 267. 1903. *Eriocaulon caulescens* Poir., Encycl. (J. Lamarck et al.) Suppl. 3: 162. 1813. *Paepalanthus caulescens* (Poir.) Kunth, Enum. Pl. (Kunth) 3: 537. 1841. *Dupatya caules*cens (Poir.) Kuntze, Revis. Gen Pl. 2: 745. 1891. Type: Guyane. Cayenne. In herb. Poiret n.n. (Lectotype: photo P! [162057], designated by Trovó et al. 2015; Isolectotype: photo P! [162058]).

Eriocaulon plantaginioides Desv. ex Ham., Prodr. Pl. Ind. Occid.: 16. 1825. *Paepalanthus plantaginioides* (Desv. ex Ham.) Koern., Fl. Bras. (Martius) 3(1): 470. 1863. *Dupatya plantaginioides* (Desv. ex Ham.) Kuntze, Revis. Gen. Pl. 2: 746. 1891. Type: Guyane. In herb. Desvaux s.n. (Holotype: photo P!).

Eriocaulon splendens Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math.1: 633, t. 66. 1831. *Paepalanthus splendens* (Bong.) Mart. ex Koern., Fl. Bras. (Martius) 3(1): 466. 1863, nom illeg. Type: Brazil. Minas Gerais: Habitat in humidis graminosis inter Barbacena et St. João, Jun 1824, Riedel 291 (Holotype: photo LE!).

Paepalanthus surinamensis Miq., Linnaea 19: 126. 1847. *Eriocaulon surinamense* (Miq.) Steud., Syn. Pl. Glumac. 2(10): 275. 1855. Type: Suriname. n.d., A. Kappler 1002 (Holotype: U; Isotypes: photo B!, S).

Eriocaulon geraense Steud., Syn. Pl. Glumac. 2(10): 276. 1855. Type: Brazil. Minas Gerais: n.d., P. Claussen 1173 (Holotype: photo P [1879408]!; Isotypes: G, photo P [1879409]!).

Eriocaulon simillimum Steud., Syn. Pl. Glumac. 2(10): 277. 1855. Type: Brazil. Bahia: *s.d.*, P. Salzmann *s.n.* (Holotype: photo P!; Isotype: LE).

Eriocaulon subuncinatum Steud., Syn. Pl. Glumac. 2(10): 277. 1855. Type: Brazil. G. Gardner 2959 (Holotype: photo P!; Isotype: OXF).

Syngonanthus llanorum Ruhland in Engler, Pflanzenr. 13 (IV.30): 265. 1903. Syntypes: Colombia. Norte de Santander: Prov. de Ocaña, Nlle. Grenade, 1200 m alt., Oct. 1850, L. Schlim 193 (G, photo K!); Meta: Llanos of Villavicencio, n.d., H. Karsten n.n. in Hb. Vienna (W, destroyed). Syntype excluded [= *Syngonanthus davidsei* Huft]: Llanos of Villavicencio, *s.d.*, H. Karsten n.n. (photo B!).

Syngonanthus planus Ruhland in Engler, Pflanzenr. 13 (IV.30): 265. 1903. Type: Brazil. Minas Gerais: Barbacena, 23 Jun 1879, A. Glaziou 11634 (Holotype: photo B!; Isotype: photo K!; LL!).

Syngonanthus glandulosus Gleason, Bull. Torrey Bot. Club 56: 394. 1929. Type: Guyana. Mount Roraima, Philipp Swamp, at 5100–5200 feet, 11 Nov 1927, G.H.H. Tate 345 (Holotype: NY!; Isotype: photo K!).

Paepalanthus mellii Moldenke, N. Amer. Fl. 19(1): 41. 1937. Type: Mexico. Veracruz. Minatitlan, 28 Nov 1928, C.D. Mell n.n. (Holotype: NY!).

Syngonanthus caulescens var. *bellohorizontinus* Silveira, Floral. Mont.: 358. 1928. Type: Brazil. Minas Gerais: In humidis prope Belo Horizonte, 1903 [*sphalm.* "Set. 1899" in the sheet], A. Silveira 219 (Holotype: R!).

Syngonanthus caulescens var. *obtusifolius* Silveira, Floral. Mont.: 358. 1928. Type: Brazil. In humidis in Chapada do Couto inter Serrina et Itacambira, 1918 e 1926 [*sphalm.* "Bahia, 1912; prope Rio Preto, Goyaz, 1912" in the sheet], Lützelburg in herb. Silveira 613 (Holotype: R!).

Syngonanthus caulescens var. *angustifolius* Moldenke, Bull. Torrey Bot. Club 68: 70. 1941. Type: Colombia. Los Llanos: Metá, in a bog 20 km south and 30° west of Orocué, about 150 m alt., 9 Apr 1939, O. Haught 2747 (Holotype NY!; Isotype F!).

Syngonanthus caulescens var. *proliferus* Moldenke, Phytologia 21(6): 418. 1971. Type: Brazil. Santa Catarina: Porto União, fazenda Frei Rogério, 12 km southeast of Porto União, about 750 m alt., 18 Dec 1956, *L. B. Smith & Reitz 8681* (Holotype: photo US!).

Syngonanthus glandulosus var. *epapillosus* Moldenke, Phytologia 26(3): 177. 1973. *Syngonanthus glandulosus* f. *epapillosus* (Moldenke) Moldenke, Phytologia 44: 384. 1979. Type: Venezuela. Bolívar: Rocky edge of river at Salto Acarima, rio Urimán, 393 m alt., 9 Jan 1955, *Steyermark & Wurdack 45A* (Holotype: NY!; Isotype: F!, photo G!).

Syngonanthus caulescens var. *hatschbachii* Moldenke, Phytologia 31(2): 233. 1975. Type: Brazil. Mato Grosso: Alto Araguaia, córrego do Sapo, 21 Set 1974, G. Hatschbach & R. Kummrow 35037 (Holotype: LL!; Isotype: MBM!, C).

Syngonanthus caulescens f. *longipes* Moldenke, Phytologia 32(4): 336. 1975. Type: Brazil. Distrito Federal: creek bank, burned-over cerrado, near Sobradinho, 27 Sep 1965, *H. S.* Irwin et al. 8730 (Holotype: NY!; Isotype: MO!).

Syngonanthus leprieurii f. *viviparus* Moldenke, Phytologia 41(1): 10. 1978. Type: Brazil. Pará: Serra do Cachimbo, BR 163, Cuiabá Santarém Highway, Cachoeira de Curuá, north slope of Serra Cachimbo, 300 m alt., 4 Nov 1977, G.T. Prance et al. P.24837 (Holotype: NY!; Isotype: K!, L).

Syngonanthus caulescens f. *longifolius* Moldenke, Phytologia 51(4): 245. 1982. Type: Guyane. SE of Cayenne, Toulouse savanna, road to Tour de l'Ile, 4 Jul 1977, G. Cremers 4833 (Holotype: CAY; Isotype: photo P!).

Syngonanthus caulescens var. *gardnerianus* Moldenke, Phytologia 53(5): 367. 1983. Type: Brazil. Minas Gerais: Diamantina, n.d., *G. Gardner 5253* (Holotype: NY!; isotype: BM, OXF).

Syngonanthus caulescens var. *hirsutus* Moldenke, Phytologia 53(5): 367. 1983. Type: Venezuela. Bolívar: Southwest face of Cerro Altamira, 10 Km east of Ciudad Pilar, 21 Out 1953, B. Maguire et al. 35909 (Holotype: photo US!).

Caulescent herbs, 4–60 cm tall, erect, occasionally branching at base. Roots white, 0.20–0.55 mm in diameter, spongy. Rosette absent. Aerial stem sometimes very short, with leaves congested at base, 0.2–31.0 cm long, villous or woolly with white crooked trichomes, sometimes branched, bearing an umbel of 5-75 inflorescences at the apex. Leaves oblique/patent to ascending, equally distributed over the stem, densely or sparsely distributed, slightly congested at the apex near synflorescence, 0.4–4.0 × 0.1–0.7 cm, linear, narrowly lanceolate, elliptic or oblong, apex acute, mucronate or acuminate, pilose or glabrescent with simple filamentous hairs or adpressed trichomes on both surfaces, veins 7–12 prominent. Spathes 0.7–4.2 cm long, chartaceous, cylindrical, erect, obliquely opened, apex obtuse or acuminate, enlarged, tip uncinate, margin entire, not involute, glabrous or pilose only at apex adaxially, pilose abaxially with simple filamentous hairs and adpressed trichomes. Scapes erect to flexuous, 2.7–34.0 cm long, green or straw-colored with age, 3-costate, glabrescent or pilose with simple filamentous hairs and adpressed trichomes. Capitula 2.0–7.5 mm in diameter. Involucral bracts in 3–4 series, glabrous, those of the external series 1.4–2.5 × 0.65–0.90 mm, ovate to oblong, apex acute, white to cream-colored, those of the internal series progressively longer 2.0–2.4 × 0.65–1.00 mm, surpassing the flower height, linear, elliptic or lanceolate, apex acute, acuminate or apiculate, cream to white-colored; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 35–230 per capitulum, the staminate and pistillate similar in number. Staminate flowers 1.7–2.0 mm including pedicels; pedicels 0.4–0.7 mm long with filamentous trichomes at insertion with receptacle; sepals 1.4–1.8 mm long, cream, shortly fused at base, cymbiform, chartaceous, upper part white, bottom part hyaline when hydrated, elliptic, apex acuminate, margin involute, glabrous abaxially, pilose adaxially, especially at central part, with simple filamentous hairs; corolla 0.7–1.0 mm long, fleshy, fused ca. 1/3 their length, urceolate, usually free at base, lobes acute, involute after anthesis, glabrous; filaments adnate to the petals in the lower half , anthers 0.1–0.3 mm long, cream to whitish; pistillodes 3, ca. 0.15 mm long, clavate, papillose at apex. Pistillate flowers 1.85–2.65 mm including the short pedicels (sub-sessile); pedicels 0.20–0.25 mm long with filamentous hairs at insertion with receptacle; sepals 1.75–2.5 mm long, elliptic, cymbiform, margin involute, white to hyaline, chartaceous, pilose adaxially with simple filamentous hairs, abaxially glabrous; petals 0.7–1.5 mm long, oblanceolate, spatulate, connate at the upper margin, free at base and apex very top, apex acute, lower half of petal fleshy, upper half membranous, cream-colored, pilose or pubescent abaxially with simple filamentous hairs, glabrous adaxially; gynoecium 1.4–2.0 mm long; ovary 0.5–0.8 mm long; style column 0.20–0.35 mm long, cream-colored to castaneous; appendages 0.25–0.35 mm long, the glandular apex capitate; style branches simple, 0.5–1.5 mm long. Seeds about 0.4 × 0.3 mm, ovoid, brown-colored, striate with very short pseudotrichomes.

Phenology— There are records for flowering and fruiting collections of *S. caulescens* throughout all the year.

Habitat and Distribution— *Syngonanthus caulescens* is the species with the widest geographical distribution in the genus, occurring broadly in South America (Argentina, Bolivia, Brazil, Colombia, French Guiana, Guyana, Paraguay, Peru, Suriname, Uruguay and Venezuela) Costa Rica and Mexico. It occurs in the most diverse ecological domains, commonly in riverbanks, wetlands and even in open sewers.

Conservation status—"*The category Least Concern is applied to taxa that do not qualify (and are not close to qualifying) as threatened or Near Threatened. It is important to emphasize that "least concern" simply means that, in terms of extinction risk, these species are of lesser concern than species in other threat categories. It does not imply that these species are of no conservation concern*" (IUCN 2014:9). *Syngonanthus caulescens* has a very extensive geographical distribution and innumerable populations in the nature, so it is not considered threatened.

Commentaries— *Syngonanthus caulescens* is the most morphologically variable and widespread species in *Syngonanthus*. Sometimes, the aerial stem is very short, the leaves becoming very congested near the roots, which makes them be confused with rosettes. This species can also show ramification at the base or apex of the aerial stem. Sometimes, the corolla of staminate flowers is not completely fused, a characteristic observed in the "*Philodice* group" (see Chapter 2).

The lectotype of *S. caulescens* was recently designated by Trovó et al. (2015). Poiret (1813) described *Eriocaulon caulescens* based on a material from Cayenne (Guyane). There are two sheets containing the same information cited in the protologue in the P herbarium, which housed the Poiret herbarium. The exsiccate number P162057 was chosen as lectotype because the original label from Poiret herbarium is attached (Trovó et al. 2015).

The enormous morphological variability of *S. caulescens* boosted several descriptions of species and infraspecific categories, many of which are synonyms of *S. caulescens,* generating a proliferation of names associated with this taxon. A recent example was the synonymization of *S. caulescens* var. *angustifolius* with the typical variety (Trovó et al. 2014). The concept of *S. caulescens* var. *angustifolius* adopted by Moldenke (1941) encompassed a large geographical distribution, habit and floral traits. In the protologue, he emphasized the width of the leaves, a character extremely variable in this taxon. Sheets of the most diverse locations were cited as belonging to this taxon (paratypes), for example in Brazil (in Santa Catarina [*Reitz 5343*, NY], Minas Gerais [*Davidse & Ramamoorthy 10572*, NY] and Paraná [*Hatschbach 1761*, NY]). The overlapping characters and an unclear definition of this taxon justifies the synonymy.

There is no evidence of the association of morphological variation with geographic distribution in this taxon. In the same population can be observed plants with or without ramification on the aerial stem; or plants with aerial stem elongated or very short. In general, this species can be associated with involucral bracts with apex very acute or acuminate and leaves usually lax and equally distributed on the erect aerial stem.

The species more similar to *S. caulescens* are *S. ruhlandii* and *S. cachimboensis*. *S. ruhlandii* is differentiated by decumbent habit and senescent leaves in the base of aerial stem and congested in the apex (*vs*. usually uniform distribution of the leaves and habit erect) and *S. cachimboensis* by the clump-forming habit and the leaves oblong to obovate, elliptic or lanceolate (*vs.* usually solitary plants with leaves narrowly lanceolate or linear). It is not incorrect to claim that *S. caulescens* does not have a robust taxonomic identity. The confirmation of specimens as *S. caulescens* is based on contraposition and exclusion of other taxa.

Specimens examined—**ARGENTINA. Corrientes**: Concepción, estancia Tranquera de Hierro, 66 km al NE de Chavarría, 03 Dec 1996, *Arbo et al. 6992* (HUEFS, NY), estancia Santa Rosalia, 03 Jan 1955, *Pedersen 3088* (MO); Ituzaingó, ruta 39, 10 km de ruta 14, 24 Sep 1974, *Krapovickas et al. 26426* (LL); Paso de los Libres, alrededores, 01 Nov 1973, *Schinini 7682* (LL, MO); SE de Saladas, pasando el arroyo de Santa Lucia, 14 Oct 1983, *Beck & Liberman 9512* (MO); San Martin, reserva natural Provincial del Ibera, costa W de la laguna Ibera, 09 Dec 1992, *Tressens et al. 4307* (NY), San Miguel, 12 km NE de San Miguel Ea. Toro-y, 1 Mar 1990, *Vanni et al. 1590* (LL);

BOLIVIA. La paz: Iturralde, Ixiamas, a lado de la pista de aterrizaje, 04 Jun 1990, *Beck 18470* (MO); Santa Cruz: Andres Ibañez, road to Lomas de Arena c. 4 km SSW of Palma de Oratorio, 22 May 1991, *Proctor & Nee 46904* (MO), idem, El Mangue community, near cerro “la capilla”, 28 km W of Santa Cruz on road to Terravinto community, 30 Apr 1995, *Abbott et al. 16689* (MO), idem, Curichi N.W. of the río Piray, adjacente to the gaseoducto, 06 May 1995, *Ritter & Nash 1986* (MO), idem, pampas del Urubo, caminho a Terebinto, 12 Apr 2001, *Catari et al. 12* (MO), Nuflo de Chavez, sudoeste de Concepión, ca. 78 km nordeste de San Ramón, 14 Mar 2002, *Churchill et al. 21306* (MO); Buena vista, 25 Mar 1921, *Steinbach 5446* (NY), Ichilo, along road to Palacios, 2.5 km NNW of Montero-Buena Vista highway, 11 Jun 1998, *Nee 49735* (MO, NY), road to Laguna Madrejón, c. 3 km N of Buena Vista, 19 May 1991, *Proctor 46842* (MO), along highway from Portachuelo to Buena Vista, 3.1 km E of La Arboleda, 17º24’02”S 63º35’04”W, 28 Apr 2007, *Nee et al. 55179* (MO, NY), 3 km N of Buena vista, on road to Laguna Madrejón, 19 May 1991, *Nee et al. 40463* (MO, NY), Andres Ibanez, 16 km, SSE of Santa cruz, Lomas de Arena, 18 Jan 1987, *Nee & Killeen 33639* (MO, NY), Santa Cruz, Parque Nacional Noel Kempff Mercado, lago Caiman, 13º38’19”S 60º53’56”W, 05 Apr 1996, *Garvizu & Ritter 121* (MO), Velasco, caminho a Cerro Pelao, 14º36’13”S 61º29’28”W, 19 Mar 1997, *Guzmán et al. 447* (MO).

BRAZIL. **Acre:** Rio Branco, igarapé do Caxangá, 18 Aug 1951, *Black 51-12673* (NY); **Amapá:** Macapá, estrada Ciapoque – campo de aviação, 30 Sep 1949, *Black 49-8204* (NY); rio Oiapoque, on large granitic outcrop, 04 Oct 1960, *Irwin et al. 48645* (NY); **Amazonas:** Fortaleza savana, rio Puciari tributary of rio Ituxi, 30 Jun 1971, *Prance et al. 13822* (NY); Humaitá, fazenda Flávio ao sul da BR 319, km 658, 17 Apr 1980, *Janssen 1981* (LL); **Bahia**: Abaíra, estrada Catolés-Ribeirão, próximo ao escorregador, 10 Sep 1992, *Ganev 1060* (HUEFS, NY); Barra do Choça, fazenda Santa Clara, 22 Jun 1987, *Guedes 1270* (ALCB); Barreiras, cachoeira acaba vida, 14 Jul 1983, *Guedes 820* (ALCB), idem, 14 Jul 1984, *Guedes 815* (ALCB), Palmeiral, 12º30’59”S 45º05’42”W, 16 Jun 2007, *Cotrim et al. 506* (HUEFS); Correntina, fazenda

Jatobá, 08 Aug 1992, *Aparecida da Silva et al. 1596* (MO), velha da galinha, 13º31'24"S 45º22'24"W, 25 Aug 1995, *Mendonça et al. 2347* (IBGE), idem, 26 Aug 1995, *Fonseca et al. 526* (RB); Érico Cardoso, margem de um tributário do rio do Pires, 13º15'25"S 42º07'56"W, 23 Jul 2009, *Fraga et al. 2762* (RB); Itaparica, 15 Jul 1951, *Pires 3408* (ALCB, NY); Jaborandi, rio Pratudão, estrada Posse – Jaborandi, 14º08'45"S 45º41'36"W, 18 May 2001, *França et al. 3735* (HBR, HUEFS); Livramento do Brumado, km 5 da rodovia Liv. do Brumado – Rio de Contas, 19-20 Jul 1979, *Mori et al. [12254]* (LL, RB); Mucugê, estrada Mucugê-Guiné, a 28 km de Mucugê, 07 Sep 1981, *Furlan et al. [CFCR 2041]* (RB, SPF); Palmeiras, Pai Inácio, 12º27'17"S 41º28'05"W, 26 Sep 1994, *Giulietti et al. [PCD 0785]* (ALCB); Piatã, estrada Inúbia – Piatã, três morros, 08 Sep 1992, *Ganev 1036* (HUEFS); Rio de Contas, rio da água suja, caminho Jaqueiro, passagem de Arapiranga, 28 Aug 1993, *Ganev 2142* (HUEFS, NY); São Desidério, Manoel de Souza, 12º31'01"S 45º05'49"W, 21 Jul 2007, *Cotrim et al. 836* (HUEFS), Umburanas, estrada de Umburanas para Delfino, ca. 31.3 km, ramal à esquerda, 10º24'11"S 41º19'21"W, **Distrito Federal:** Brasília, bacia do rio São Bartolomeu, 10 Apr 1980, *Heringer et al. 4300* (NY), EEJBB, 16 Nov 2006, *Paiva 355* (HEPH, HUEFS), EEJB, Mata do Taquara, divisa com a cerca do IBGE e FAL, 21 NOV 2007, *Chacon et al. 223* (HEPH), UnB, abaixo do marco Zanata, 28 Nov 1977, *Heringer et al. 291* (MO, NY, RB), lago Paranoá, confluência do córrego Mata-Gado, 23 Mar 1982, *Heringer et al. 7420* (NY), lago Norte, 20 Apr 1982, *Mendonça & Pereira 180* (MO, NY); Guará, 2 km to S, 19 Mar 1968, *Irwin et al. [21424]* (LL, NY, UB); Paratinga, APA Cabeça de Veado, córrego do Cedro, 15º54'03"S 47º56'43"W, *Fonseca & Alvarenga 3957* (F, IBGE, SPF); Sobradinho, 27 Sep 1965, *Irwin et al. 8730* (LL); **Goiás:** Alto Paraíso de Goiás, 27 km to S, 23 Mar 1968, *Irwin et al. [21630]* (LL, NY, UB), Parque Nacional da Chapada dos Veadeiros, 24 May 1993, *Lima 112* (HEPH, UB), idem, Cruzeiro, 28 Sep 1995, *Filgueiras & Oliveira 3289* (IBGE, RB, SPF), em direção a Teresina, Fazenda Água Fria, 14º04'21.7"S 47º30'33.6"W, 02 Feb 2000, *Munhoz et al. 1924* (IBGE), idem, 08 May 2000, *Munhoz et al. 1263* (IBGE), idem, 03 Jun 2000, *Munhoz et al. 1516* (IBGE), idem, 17 Jun 2000, *Munhoz et al. 1626* (IBGE), idem, 01 Jul 2000, *Munhoz et al. 1756* (IBGE), rio dos Couros, 13º46'S 47º30'W, 31 Jul 1994, *Munhoz & Ribeiro 181* (UB), fazenda Água Fria, próximo da sede, 14º04'21"S 47º30'33"W, 24 Apr 1998, *Munhoz et al. 677* (HEPH, UB), fazenda Portal da Chapada, 14º09'48"S 47º35'35"W, 09 Oct 2004, *Chaves 46* (UB); Caiapônia, gallery forest about 25 km SW, 01 May 1973, *Anderson 9564* (NY); Caldas Novas, 11 Jul 1987, *Tsugaru & Sano B-93* (MO); Cavalcante, caminho para cachoeira Santa Bárbara, 07 Mar 2003, *Pastore & Suganuma 381* (CEN); Cristalina, creek margin about 6 km S of Cristalina, 02 Nov 1965, *Irwin et al. 9757* (NY); Ivolândia, bacia do rio Caiapó, fazenda Campo Redondo, 16º28'42"S 51º21'26"W, 12 Oct 2007, *Aparecida da silva et al. 6346* (IBGE); Minaçu, 10 Mar 1992, *Cavalcanti et al. 1087* (CEN, RB); Montes Claros de Goiás, bacia do rio Caiapó, Fazenda Bandeirantes, 15º53'40"S 51º50'46"W, 16 October 2007, Aparecida da silva et al. 6463 (IBGE); Niquelândia, região da Serra negra, 15 Apr 1992, *Walter et al. 1342* (CEN, RB), km 20 da estrada para CODEMIN, 14º17'02"S 48º20'02"W, 28 May 1996, *Fonseca et al. 939* (HUEFS, IBGE, RB, SP), estrada Niquelândia-CODEMIM, 14º15'38"S 48º20'04"W, 02 Jun 1998, *Walter et al. 4159* (CEN, HUEFS); Pirenópolis, Serra dos Pirineus, estrada principal para a serra, primeira estrada a esquerda chegando até Salto do Lajeado, 15º50'17"S 48º55'10"W, 26 May 2007, *Delprete & Gomes-Klein 10171* (HUEFS); Serra Negra, margem esquerda do rio bagagem, 15 Apr 1992, *Walter et al. 1342* (CEN); Posse, 6 km to S, Rio da Prata, 05 Apr 1966, *Irwin et al. [14410]* (MO, NY, UB); São Domingos, estrada da gruta Terra Rouca para São Domingos, 13º39'21"S 46º18'56"W, 29 Oct 2000, *Oliveira et al. 1147* (CEN, IBGE, F, SPF); Uruaçu, 7 km do vilarejo Água Branca, 21 km da BR-153, 06 Aug 1992, *Walter et al. 1948* (CEN, HUEFS, RB); **Maranhão:** Gerais de Balsas, Vila Nova de Carli, área de monitoramento ambiental, 09 Mar 1998, *Oliveira & Silva 980* (HUEFS); **Mato Grosso:** Alta Floresta, parque estadual do Cristalino, próximo a base do Limão, 25 Jan 2007, *Sasaki et al. 1417* (INPA, NY); Bandeirantes, Jatoba, 26 Aug 1973, *Hatschbach 32338* (LL); Barra do Garças, about 3.5 km West of main road on path R-10, 15 Sep 1968, *Eiten & Eiten 8768* (LL, NY), 9 km to NE, 05 May 1978, *Anderson 9760* (UB), 12º51'S, 51º48'W, 15 Sep 1968, *Eiten & Eiten 8768* (UB); Cuiabá, BR-384, km 71, 11 Feb 1975, *Hatschbach et al. 36052* (LL, NY); Chapada dos Guimarães, vicinity of Buriti, 21 Oct 1973, *Prance et al. 19232* (MO); Garapú, disturbed area, 30 Sep 1964, *Irwin & Soderstrom 6478* (NY); Nova Xavantina, fazenda Brasil, estrada para a serra Azul em direcnao a Fazenda Ouro e Prata, 14º53'32"S 52º30'15"W 28 Mar 1997, *Árbocz et al. 3710* (ESA), Km 246.5 of Xavantina-Cachimbo road, c. 0.5 km E, 06 Dec 1967, *Philcox et al. 3411* (UB); Rio Verde de Mato Grosso, ca. 30 km da cidade, fazenda Mirante, rodovia Sete Quedas-Rio Negro, 07 Sep 1993, *Silva & Rodrigues 1165* (MO); São Félix do Araguaia, estrada para Luciara, fazenda Buritizal, 11º30'5.8"S 50º56'32.7"W, 20 Mar 1997, *Souza et al. 14655* (ESA); Terenos, Cachoeirão, 09 Aug 1970, *Hatschbach 24562* (LL, MO, NY); Vila Bela da Santíssima Trindade, córrego da Cascata, 18 Aug 1997, *Hatschbach et al. 66998* (LL, NY); **Mato Grosso do Sul:** Amambai, rio Pandui, 12 Feb 1983, *Hatschbach*

46170 (LL); Bataguaçú, várzea do Rio Pardo, 22 Oct 1981, Dambrós 200 (HBR); Camapuã, Fazenda Império, 02 Nov 1979, *Silva 104* (IBGE); Pedro Gomes, córrego Catingueiro, a 50 m do rio Taqueri, fazenda Azanha, 17º58'05"S 54º02'49"W, 03 Mar 2002, *Pott & Pott 5166* (HUEFS); São Gabriel do Oeste, estrada do assentamento campanário, próximo ao Pontilhnao da nascente do rio Coxim, 19º16'50.4"S 54º35'59.7"W, 16 Sep 2002, *Pott et al. 5809* (HUEFS); **Minas Gerais:** Barão de Cocais, serra do Garimpo, 10 km by road NW of Barão de Cocais, 04 May 1982, *Hensold 782* (NY), serra do Caraça, 22 Jan 1971, *Irwin et al. 28843* (NY); Belo Horizonte, brejo, ressaca, 26 Jul 1934, *Mello-Barreto 2587* (ESA); Cambuí, 8 km Ne, 25 Feb 1976, *Davidse & Ramamoorthy 10572* (LL, MO, NY); Coromandel, margem de rio, 7 Jun 1940, Oliveira 67 (ESA); Conceição do Mato Dentro, 06 Nov 1981, *F.C.F. da Silva 104* (HRB); Diamantina, 15 km to E, 18 Mar 1970, *Irwin et al. [27824]* (NY, UB), Palmital, 29 Apr 1942, *Magalhães 2091* (NY), margem da estrada Diamantina-Conselheiro Mata, 12 km da cidade, 30 Aug 1981, *Giulietti et al. [CFCR 1879]* (NY); Formosa, córrego Bezerrinha na estrada entre Formosa e Cabeceiras, 02 Nov 1997, *Alvarenga & Lopes 926* (F, IBGE, SPF); Gouveia, km 243 on MG-259, 02 Feb 1972, *Anderson et al. [35146]* (NY, UB); Grão-Mogol, Lagoa Nova, 16º19'01"S 43º01'45"W, 27 May 2005, *Sevilha et al. 4578* (CEN); Itacambira, alto da serra de Itacambira, 27 Jul 1987, *Saturnino 1381* (PAMG), idem, *Saturnino 1384* (PAMG) idem, *Saturnino 1391* (PAMG); Joaquim Felício, serra do Cabral, estrada Joaquim Felício – Várzea da Palma, ca. 26 km de Joaquim Felício, 17º41'58"S 44º18'57"W, *Souza et al. 25610* (ESA); Lavras, sítio Três Barros, 16 Mar 1985, *Gavilanes 2178* (PAMG); Medina, 21 km N of highway BR-116, 30 Mar 1976, *Davidse et al. 11590* (LL, MO, NY); Ouro Preto, Chapada Clube, 24 May 1979, *Mautone et al. 841* (RB), serra das Andorinhas, 10 Mar 1982, *Hensold 552* (NY); Poços de Caldas, 01 Jul 1942, *Oliveira 933* (NY), 30 Nov 1982, Leitão et al. [1707] (RB), fazenda da família Carvalho Dias, 11 Dec 2001, *Fraga et al. 878* (RB); Rio Vermelho, Pedra Menina, morro do Ambrósio, 14 Jul 1984, *Giulietti et al. [CFCR 4466]* (RB, SPF), idem, morro da Virada do Mato Virgem, 31 Jul 1985, *Pirani et al. [CFCR 7806]* (NY); Rio Preto, Funil, serra da caveira D'anta, 23 Feb 2004, *Valente et al. 356* (HUEFS); Santana do Riacho, km 129 ao longo da rodovia Belo Horizonte – Conceição do Mato Dentro, 22 Aug 1972, *Joly & Semir [CFSC 3268]* (RB, SPF), idem, km 120, 18 Oct 1973, *Joly et al. [CFSC 4497]* (RB, SPF), margem da estrada no caminho da represa da usina, 27 Feb 1973, *Giulietti & Menezes [CFSC 4043]* (RB, SPF); São João d'el Rey, Água geral, serra do Lenheiro, 08 Jul 1936, *Mello Barreto 4674* (NY); Serra Azul, serra do Gavião, a margem do riacho, 02 Aug 1987, *Pereira 11310* (HUEFS); Três Marias, Serra do Bari, *Ferreira 5352* (PAMG); **Pará:** Alta Floresta, serra dos Carajás, scrubby vegetation on ferric rock outcrops, 13 May 1982, *Sperling et al. 5640* (MO, NY); Ilha de Marajó, rio Camará, 08 Jul 1950, *Black 50-9906* (NY); Itaiatuba, arredores da base aérea do Cachimbo, 25 Apr 1983, *Silva et al. 67* (MO, NY, RB); Oriximiná, rio Peru do Oeste, entre cachoeira Pancada e rio Trombetas, 08 Sep 1980, *Cid et al. 2303* (LL, NY, RB), cachoeira de Curuá, north slope of Serra do Cachimbo, 04 Nov 1977, *Prance et al. 24837* (MO); **Paraná:** Balsa Nova, São Luiz de Purunã, 8 Nov 1977, *Dombrowski & Scherer Neto 328* (LL); Clevelândia, N of rio Chopim, ca. 20 km N, 1 May 1966, *Linderman & Hess 1122* (LL); Curitiba, estrada Curitiba-Atuba, 04 Apr 1950, *Hertel 04* (NY); Guarapuava, 10 km a oeste, 14 Dec 1965, *Reitz & Klein 17620* (NY); Irani, 28 Dec 1963, *Reitz & Klein 16405* (LL); Imbituva, rio Imbituvinha, 20 Oct 1969, *Hatschbach 22504* (LL, MO, NY); Jaguariaiva, BR- 151, estrada Jaguaraiaiva-Castro, 24º22'52"S 49º51'13"W, 26 Nov 2005, *Cavalcanti et al. 3682* (CEN, HUEFS); Palmeira, fazenda Santa Rita, 15 Jan 1951, Mattos *4365* (NY), idem, 25 Jan 1983, *Kummrow 2179* (LL, NY), recanto dos Papagaios, 28 Oct 1996, *Ribas & Luz 1592* (ALCB); Pinhais, brejo, 18 Oct 1971, Hatschbach 27661 (LL); Piraquara, about 22 km E of Curitiba, 14 Jan 1949, Tessmann 3784a (NY); Ponta Grossa, 25 km W, just W of the intersection of highway BR-373 and rio Tabagi, 15 Mar 1976, *Davidse et al. 11352* (LL, MO); Porto Amazonas, fazenda São Roque, 3 Feb 1972, *Kummrow 1065* (LL); São José dos Pinhais, 22 Jan 1950, *Hatschbach 1761* (NY); São José dos Pinhais, Guaricana, 6 Feb 1976, *Hatschbach 38054* (LL); Sengés, fazenda Morungave, rio do Funil, 15 Dec 1958, Hatschbach & Lange 5316 (VIC); Tibagi, fazenda Monte Alegre, salto Conceição, as margens do rio Tibagi, 3 May 1958, *Hatschbach 4955* (LL); Tijucas do Sul, rincão, 21 Oct 1977, *Hatschbach 40434* (LL); **Pernambuco:** Pambos, in marsh, Jan 1931, *Pickel s.n.* (MO); **Rio de Janeiro:** Teresópolis, Serra dos Órgãos, 08 Jun 1951, *Rizzini 702* (RB); **Rio Grande do Sul:** Bom Jesus, fazenda Bernardo Velho, 13 Jan 1947, *Rambo 34685* (NY), Cambará do Sul, Aparados da Serra, 15 Feb 1947, *Rambo 35244* (NY); São Francisco de Paula, Vila Oliva, 03 Jan 1946, *Rambo 30865* (NY), 17 Feb 1998, Diesel 1191 (NY); arredores de São Leopoldo, Dec 1941, *Eugênio 433* (NY); Taquari, 12 Dec 1957, *Camargo [61599]* (LL); Tramandaí, 06 Mar 1950, *Rambo 46178* (MO); **Rondônia:** Porto Velho – Guajará-Mirim, estrada do Palheta, 23 Apr 1976, *Cordeiro 838* (LL); **Rorraima:** Alto Alegre, serra do Tepequém, South and West side of plateau, 23 Dec 1987, *Hopkins et al. 1015* (NY), Amajari, serra de Tepequém, plateau, 18 Feb 1967, *Prance et al. 4488* (NY), idem, southeast escarpment, 29 Nov 1954, *Maguire & Maguire 40100* (NY); Boa

Vista, reserva ecológica de Maracá, 07 Mar 1987, *Harley 24729* (NY); Ilha de Maracá, on the road to the ecological station on the SE end oh the island., 09 Oct 1987, *Pruski et al. 3439* (NY); **Santa Catarina:** Água Doce, 8 km South of the turn to the South in road east Palmas, 6 Dec 1971, *Smith et al. 15694* (LL); Caçador, fazenda dos carneiros, 07 Dez 1962, *Klein 3470* (NY); Curitibanos, 10 Jan 1962, *Reitz & Klein 11982* (LL); Lages, 10 Jan 1951, *Rambo s.n.* (NY [538204]); Mafra, 26 Jan 1953, *Reitz 5343* (NY); Porto União, fazenda Frei Rogério, 06 Jan 1962, *Reitz & Klein 11593* (LL, NY); São Joaquim, bog 10 km South of São Joaquim, 05 Jan 1965, *Smith & Reitz 14314* (NY); **São Paulo:** Águas de Santa Bárbara, SP 280 Castelo Branco, brejo localizado na fazenda Prata, 1 Nov 1997, *Aona et al. N.97/263* (ESA); Águas de São Pedro, barranco, beira de estrada, 4 Dec 1993, *Souza et al. 4866* (ESA); Campinas, estrada Campinas-Jaguariúna, primeiro lago após o posto rodoviário, lado direito da pista, 21 Jun 1996, *Amaral et al. 96/31* (HUEFS); Itaberá, beira do rio Verde, rodovia Itararé-Itapeva, 16 Feb 2006, *Souza et al. 32109* (ESA); Itararé, Banhado, brejo do horto florestal, 08 Feb 1991, *Scaramuzza 2708* (HUEFS); Itirapina, border between Itirapina and Brotas, 10.1 km along Itirapina-Brotas road, 30 Nov 1961, Eiten & Freitas Campos 3426 (NY); Mogi Guaçu, fazenda Campininha, 4.1 km NNW of Pádua Sales, 17 Dec 1959, *Eiten & Eiten 1631* (NY), fazenda Campininha, 3.7 km NNW of Pádua Sales, 22 Apr 1960, *Eiten & Eiten 1985* (NY); *Paulo de Faria*, Oct 1994, *Sanches et al. 103* (ESA); Pedregulho, distrito Estreito, margem de riacho, 21 Apr 1997, *Amaral et al. 97/114* (ESA); Pindamonnhangaba, margens do Ribeirão Grande, 05 Sep 1992, *Carvalho 138* (HUEFS); Praia Grande, rodovia SP 055, km 288, sentido Praia Grande – Cubatão, 24°00'34"S 46°30'02"W, 25 Oct 2007, *Monteiro et al. 190* (RB); Ribeirão Pires, 1 km nw of Campo Grande railway station, 28 Oct 1962, *Fosberg 43331* (LL); Santa Olívia, fazenda Santa Albertina, Jan 1944, *Pickel 539* (NY); São José dos Campos, parte interior da encosta leste do vale do Córrego da Ressaca, 6.5 km SW da saída para São José, 17 Oct 1961, *Minura 32* (NY); São Paulo, brejos do Butantã, 20 Dec 1948, Joly [16617] (RB, SPF), in marah at edge of lake, Interlagos, 25 Sep 1948, *Moldenke & Moldenke 19907* (NY), Brooklyn, 30 Sep 1948, *Moldenke & Moldenke 19671* (NY), road from Presidente Venceslau to Campinas, 23 Feb 1970, *Koyama et al. 13761* (MO, NY); Sengés, rio Funil, rodovia Itararé-Sengés a 5 km de Itararé, 03 Apr 1996, *van den Berg 178* (ESA); Zacarias, rodovia Planalto até entroncamento com a SP-425, fazenda santa Irene, 01 Jun 1995, *Nonato et al. 118* (HUEFS); **Tocantins:** Mateiros, Parque Estadual do Jalapão, comunidade da Mumbuca, 10°22'17"S 46°34'58"W, 17 Jun 2002, *Cavalcanti et al. 2907* (CEN), ribeirão do Porco Podre, 14 Aug 2005, *Rezende et al. 972* (CEN); Natividade, início da subida da serra da Natividade em direção, à antena, 11°39'39"S 47°42'24"W, 17 Jul 2000, Souza et al. 24051 (ESA); Paranã, fazenda Petrolina, 12°51'49"S 47°13'12"W, 14 Sep 2003, *Sevilha et al. 3592* (CEN); Pedro Afonso, 08°13'473"S 48°18'632"W, 19 Jan 2001, *Lolis et al. 447* (SPF).

COLOMBIA. **Boyacá**: cordillera oriental, entre Charalá y Tunja, 19 Jun 1966, *Schulz et al. 465* (LL); **Casarane**: Tauramena, Apr 1965, *Uribe 5180* (NY); **Cundinamarca**: Melgar, 4-5 Dec 1917, *Francis & Pennell 2888* (MO, NY), Mesa negra, Gazaguan valley, 6 km NW of Medina, 07 Oct 1944, *Grant 10458* (NY); **El Magdalena**: La Jagua, 40 km NE of Chiriguana, 22 Sep 1938, *Haught 2355* (MO); Llanos region: Orocué, Bog about 20 km S and 30° W of Orocué, 09 Apr 1939, *Haught 2747* (RB); **Meta**: La Macarena, reserva de La Macarena, 20 km No vía Los Conejos, 07 August 1988, *Callejas & Marulanda 6923A* (MO), S. Juan de Arama, caminho desde La Curia hasta carretera de Mesetas, 6 Sep 1987, *Fuertes et al. 434* (HUEFS); **Villavicencio**, 26-31 Aug 1917, *Pennell 1411* (MO); **Vaupés**: Yuruparí, 24 Sep 1939, *Cuatrecasas 6981* (NY); **Santander**: north slope of Mesa de los Santos, 11-15 Dec 1926, *Killip & Smith 15031* (NY), Charalá, corregimiento de Virolín, 06 May 1986, *Moreno & Mendez 05* (NY), Charalá, Virolín, Feb 1992, *Ohba & Barbosa 31* (MO); La Jague, Madalena valley, 10 Sep 1924, *Allen 649* (MO), idem, 17 Sep 1924, *Allen 707* (MO); la serranía entre los ríos Ariari y Meta, mata de San Vicente, 22 Nov 1939, *Cuatrecasas 7823* (NY).

COSTA RICA. Puntarenas, marshy área at upper N fork of Río Sabalito, just N of San Joaquín de Coto Brus, 13 Sep 1985, *Grayum et al. 5995* (MO)

GUYANA. Essequibo, nr. Ireng R. at Orinduik falls, 15 Jan 1956, *Irwin 775* (LL); Kaieteur plateau, bottom of Potaro Gorge near Kaieteur falls to western rim of splash-basin of falls, 13 Mar 1962, *Cowan & Soderstrom 2154* (NY); Marais à env. 2.5 km à 1'E de Roura, 25 km S de Cayenne, 25 Feb 1978, *Raynal-Roques 20121* (MO); upper Mazaruni river basin, 22 Oct 1960, *Tillett & Tillett 45741* (NY); Ayanganna Plateau, on Haieka savannah, E side of Haieka river, 2 mi E of Chinowieng Village, 21 Aug 1960, *Tillett & Tillett 45216* (NY); Corossony, savana, région littorale, 14 Feb 1978, *Raynal-Roques 20057* (MO, NY); Rupununi, 02 Nov 1957, *Cook 83* (NY), Kuyuwini landing, Kuyuwini river, 09 Oct 1992, *Jansen-Jacobs et al. 2801* (MO, NY), S Rupununi savanna, Wakadanawa savanna, 06 Sep 1997, *Jansen-Jacobs et al. 5383* (NY), Shea village, 09 Feb 1994, *Jansen-Jacobs et al. 3649* (MO, NY);

GUYANE. Cayenne, tige courte, 13 Jan 1974, *Halle 2223* (LL); Mataroni river, savanne de

Virginie, 04 May 2001, *Mori et al. 25269* (NY); Iracoubo, savane en contre bas de la route entre PK 20 et 21 a l'Est d'Iracoubo, 23 Mar 1979, *Cremers 5495* (LL); Mont Saint-Marcel, zone sud-est du massif, 18 Jul 2002, *De Granville et al. 15304* (MO); Savane roche du quatorze Juillet, basin du Bas-Oyapock, 15 Apr 1991, *Cremers 12125* (NY); savanne de sable blanc prés de Sinnamary, 02 Aug 1962, *Halle 511* (NY).

PARAGUAY. Alto Parana: reserva Itabó de Itaipu Binacional, 16 Oct 1984, *Brunner et al. 938* (MO); Amanbay: Bella Vista, 15 Jul 1983, *Vanni et al. 280* (LL, NY), 34 km S de Bella Vista, 26 Oct 1994, *Krapovickas et al. 46084* (NY), parque nacional Cerro Corá, open campos, South side of Cerro Tujá-og, 20 Feb 1982, *Solomon et al. 7111* (MO, NY); Caaguazú: entre Yhú y San Blas, 23 Sep 1980, *Casas 3872* (NY), cerca y al Sur de Yhú, 22 Feb 1982, *Casas & Molero 6434* (MO, NY), 22 km S de Caaguazú, est. Itá Carú, en campos de Yatay, a orillas del arroyo, 29 Dec 1972, *Schinini 5803* (LL); Caazapa: Tavai, en el estero seco, 05 Dec 1988, *Mereles 2004* (MO), idem, caminho a Castor Cue, 09 Dec 1989, *Degen 1740* (MO); Canindeyú: 15 km SE of Katueté, 15 Feb 1984, *Hahn 2082* (MO, NY), Carpa cue, pastizal sur, 05 Dec 1996, *Jiménez 1750* (MO); Cordillera: Piribebuy, cercanias del Arroyo, 10 Jan 1987, *Mereles 785* (MO), 1 km E of Nueva Colombia on road to Atyra, on a hill, inundated savana, 09 June 1990, *Zardini & Velázquez 20916* (MO), Tobati, Ybytú Silla mesa, 23 Feb 1991, *Zardini & Velázquez 26534* (MO); Guairá: colônia Independencia, 29 Mar 1972, *Pedersen 76 [10095]* (MO, NY); Missiones: reserva del Yabebyry, estancia Santa Ana, bosque del Mbaepu, 21 Feb 1993, *Florentín et al. 893* (MO); **Paraguari**: parque nacional Ybycui, 02 Dec 1983, *Hahn 1833* (LL, MO, NY), idem, northwestern of park, 11 Nov 1989, *Zardini & Velásquez 15938* (MO), Chololó, 16 Oct 1994, *Krapovickas et al. 45668* (NY); San Pedro: Alto Paraguay, Dec 1916, *Rojas 2032A* (MO), idem, Primavera, 21 Feb 1960, *Woolston 1187* (NY), Colonia 8 de diciembre, borde Arroyo Mboi, 01 Oct 1987, *Zardini & Benítez 3274* (MO); Lima, Carumbé, 26 Nov 1969, *Pedersen 76 [9399]* (MO, NY);

PERU. Amazonas: Mendoza, 17 Aug 1963, *Woytkowski 8133* (LL, MO); Loreto: balsapuerto, Jan 1933, *Klug 2866* (MO, NY), idem, 28-30 Aug 1929, *Killip & Smith 28683* (NY); Madre de Dios: Tambopata, parque nacional Bahuaja-Sonere, ex santuário nacional Pampas del Heath, estación guarda parques Juliaca, quebrada Shuyo, 04 Jun 1997, *Diaz & Pereira 8951* (NY); San Martín: Zepelacio, near Moyobamba, Oct 1933, *Klug 3270* (MO, NY); Rioja, logging road to Nof carretera marginal, km 431, 56 km W of Rioja, 2 km E of Naranjos, 01 Jun 1986, *Knapp et al. 7440* (MO), along road Rioja-Yorongos-La Florida, 30 Mar 2001, *van der Werff et al. 16506* (NY)

SURINAME. Eilerts de Haan Mts., 12 Aug 1963, *Linderman 1964* (NY); Sipaliwini, wet sand-savanna in the upper part, 04 Sep 1966, *Wildschut 1967* (NY); Wilhelmina Gebergte: Zuid River, 3.5 km E of Kayser Airstrip, 45 km above confluence with Lucie Rivier, 28 Aug 1963, *Irwin et al. [55265]* (RB, NY), 7 km S.S.W. of Juliana top, 12 km north of Lucie rivier, 01 Sep 1963, *Irwin et al. 55312a* (MO, NY).

VENEZUELA. **Amazonas:** Atabapo, between Caño Cotúa and W base Cerro Yapacana, 10 Aug 1983, *Kral & Huber 70702* (LL, MO, NY), río Ocamo, cerro Mawedi, Jan 1990, *Fernandez 6837* (MO), Alto río Orinoco, caño Soromoni, bosques médios en rebalse de aguas negras (Igapô), 15 km al W de La Esmeralda, 28 Feb 1990, *Aymard & Delgado 8347* (MO), Atures, a 8 km de Pavón, 16 Sep 1988, *Colella et al. 1261* (NY), Caño Yutaje at S base of Serranía de Yutaje, 17 Feb 1987, *Liesner & Horst 21212* (MO, NY), serranía Yutaje, cerro Coro-Coro, 02 Mar 1953, *Maguire & Maguire 35435* (NY), Puerto Ayacucho, ca. 56 km NE, 22 Nov 1984, *Kral et al. 71773* (MO, NY); **Anzoátegui:** Miranda, morichal Agua Clarita, 06 Mar 1985, *Figueiros 103* (NY); **Apure**: Muñoz, módulos "Fernando Corrales" de la UNELLEZ, 63 km al W de Mantecal, 09 Dec 1986, *Aymard et al. 5042* (MO), Pedro Camejo, E side of the Galeras de Cinaruco, 6 km N of southernmost tip, 21 Feb 1979, *Davidae & González 15557* (MO); San Fernando, ca. 4.5 miles ESE of San Carlos del Meta along the banks of the río Meta, 9-11 Feb 1978, *Davidse & González 13908* (LL, MO); **Bolívar:** Cedeño, Morichal el Caballo, ca. 225 km S of Caicara del Orinoco by road, 04 Nov 1985, *Holst & van der Werff 2557* (MO, NY), idem, Caño Aguas Negras, 4 km al NW del passo de Chalana sobre el río Guaniamito, Apr 1989, *Fernandez 5560* (MO, NY), idem, in morichal, 14 km S of Caicara de L'Orinoco, 07 Nov 1985, *van der Werff & Holst 7811* (MO, NY), caño Villaca, alrededores, carretera Caicara – El Burro, selva de galería, drenaje del escudo Guayanés, 18 Apr 1984, Stergios & Stergios 8424 (MO), idem, Foráneo La Urbana, bosque de galería con Morichales del caño "El Garzón", en las inmediaciones del cerro "El Gavilan", 06°13'38''N 67°12'42''W, 23 Jan 1989, *Cuello 515* (MO), Cerro Altamira, 10 km east of ciudad Piar, 21 Oct 1953, *Maguire et al. 35909* (NY), Chimantá Massif, vicinity of Techiné-Merú, along río Aparurén, between mouth of río Aparurén an Kon-quén, 08 Jul 1953, *Steyermark [76055]* (RB), El Puajl, 3 km S, 19 Oct 1985, Liesner & Holst 18800 (MO), Gran sabana, ca. 10 km SW of Karaurin tepui at junction of río Karaurin and río Asadon, 23 Apr 1988, *Liesner 23692* (MO), Piar, alti-planicies ubicadas entre la punta meridional del Auyan-tepui al Norte y el Uaipán-tepui al Sur, 11 dec 1984, *Huber et al. 9902* (NY), idem, región del Alto Arabopó, aprox. 10

km al SW del Uei-tepui, 21 Jan 1985, *Huber 9967* (NY), idem, Amaruay-tepui, West side, steep slope to base of wall, 02 May 1986, *Liesner & Holst 20507* (MO), alrededores de Ciudad Piar, Apr 1954, *Aristeguieta 2248* (NY), between Ciudad Piar and South base of Cerro Bolívar, 01 May 1953, *Maguire & Wurdack 35752* (NY), Auyantepui, en los alrededores del campamento de Guayaraca, Apr 1956, *Vareschi & Foldats 4743* (NY), Gran sabana, ca. 2 km NW of Kamarata, 23 Feb 1967, *Koyama & Agostini 7285* (NY), Gran sabana, Ilu tepui, drainage of the rio Kamarang, northwest of San Raphael, 26 Mar 1952, *Maguire 33613* (NY), between Divina Pastora on rio Kukenán and Santa Elena, S of mount Roraima, 03 Oct 1944, *Steyermark 59308* (NY), El Dorado – Sta. Elena road, km 1212, 16 Nov 1978, *Luteyn et al. 6263* (NY), Raudal Maraca, about 110 km to river from mouth, 31 Dec 1955, *Wurdack & Monachino 41048* (NY), Raul Leoni, alrededores del Cerro Pelon, 14 km al SW de El Pao de la Fortuna, Mar 1987, *Fernandez 4168* (MO, NY), represa Guri, east of Ciudad Piar, 07 Apr 1981, *Liesner & González 11312* (MO, NY), Roscio, largo de la Quebrada del Jaspe, aprox. 8 km al SE de San Ignacio de Yuruaní, 20 Jun 1983, *Huber 7530* (LL, NY), Salto de Pacairao in vicinity bordering río Pacairao, about 3 km east to northeast of Santa Teresita de Kavanayén, 24 Nov 1944, *Steyermark 60494* (NY), mount Roraima, Emerald swamp, SW facing slopes, 25 Sep 1944, *Steyermark 58621* (MO, NY), between Hato de Nuria and Cerro de Rancho Carata, 23 Jan 1961, *Steyermark 88759* (NY); **Guárico:** Calabozo, ca. 32 km SSE, on Finca Becerra, 06 Nov 1973, *Davidse 3771* (LL, MO, NY), Morichal El Recreo, 5 km sur dela estación biologica de Los Llanos, 17 Dec 1982, *Montes 1409* (MO); Infante, parque nacional Aguaro-Guariquito, sabanas de Juan Paulino, via Los Arroyuelos, Dec 1981, *Delascio et al. 11104* (LL, MO), Morichal Becerra, via Cazorla al sur de Calabozo, 05 Nov 1988, *Ramires 2589* (NY), idem, 5 km sur de la estación biológica de Los Llanos, 17 May 1982, *Montes 1069* (MO) idem, via Cazorla al sur de Calabozo, 05 Nov 1988, *Ramirez 2591* (MO); Miranda: pântanos de rio Aguaro, Jan 1971, *Brücher 10452* (NY); **Portuguesa:** Guanare, terrenos de la UNELLEZ, 17 Sep 1982, *Aymard 1274* (NY), idem, 30 Sep 1983, *Stergios & Aymard 6401* (NY).

Figure 09.

Figure 09. *Syngonanthus caulescens*. **A.** Habit: individual with aerial stem reduced; **B-C.** Capitulum; **D.** Involucral bracts; **E.** Staminate flower; **F.** Staminate flower dissected showing pistillodes; **G-H.** Pistillate flower; **I.** Fruit with calyx and corolla persistent; **J.** Petal of pistillate flower showing upper half membranous and lower half fleshy; **K.** Sepals of the pistillate flowers; **L.** Gynoecium.

Figure 10. Lectotype of *Syngonanthus caulescens* deposited in P herbarium.[‡]

[‡] Available at http://dsiphoto.mnhn.fr/sonnera2/LAPI/scanK/K20100414/P00162057.jpg [Accessed April 28, 2015]

Syngonanthus discretifolius (Moldenke) M.T.C.Watan. ***stat. nov.*** *Syngonanthus caulescens* var. *discretifolius* Moldenke, Phytologia 35(5): 364. 1977. Type: Brazil. Pará: Serra dos Carajás, 28 Jun 1976, Ribeiro 1397 (Holotype: LL!).

Caulescent herbs, 24–36 cm tall, rarely branching at base to form clumps up to two stems. Roots white, 0.1–0.3(–1.0) mm in diameter, spongy. Rosette absent. Aerial stem 6–13 cm long, villous, with white crooked trichomes, bearing an umbel of 2-20 inflorescence at the apex. Leaves patent to oblique, equally distributed along the stem, slightly congested at the apex near synflorescence, 7.0–26.0 × 0.5–4.0 mm, linear or linear triangular, apex acute, pubescent with capitated filamentous trichomes, latter glabrescent, veins 5–10, prominent. Spathes 1.2–4.1 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute to obtuse, tip uncinated, margin entire, not involute, glabrous adaxially, pubescent abaxially with capitate filamentous hairs, latter glabrescent. Scapes erect, 5–27.5 cm long, green or straw-colored with age, 3-costate, pilose, pubescent near the apex with capitate hairs and adpressed trichomes. Capitula 3–7 mm in diameter, radiate. Involucral bracts in 2–4 series, those of the external series 1.3–1.8 × 0.6–1 mm, triangular-ovate to oblong, apex obtuse mucronate, golden to cream-colored, glabrous, those of the internal series progressively longer 2.0–2.6 × 0.8–1.0 mm, almost equaling the flowers, oblanceolate, apex obtuse, cream to white-colored; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 80–160 per capitulum, the staminate slightly more numerous than pistillate. Staminate flowers 1.65–2.0 mm including pedicels; pedicels 0.45–0.6 mm long with filamentous trichomes at insertion with receptacle and bottom part of pedicel; sepals 1.3–1.9 mm long, cream, shortly fused at base, cymbiform, hyaline when hydrated, chartaceous, upper part slightly thickened and white, oblanceolate or elliptic, apex acute, margin involute, glabrous adaxially, pilose abaxially, especially at central part, with simple filamentous hairs; corolla 0.8–1.05 mm long, fleshy, fused ca. 4/5 of its length, tubular, lobes obtuse to rounded, involute after anthesis, glabrous; filaments adnate to the petals, anthers 0.1–0.3 mm long, cream to whitish; pistillodes 3, ca. 0.15 mm long, clavate, papillose at apex. Pistillate flowers 1.1–1.8 mm including the very short pedicels (sub-sessile); pedicels 0.15–0.2 mm long with filamentous hairs at insertion with receptacle; sepals 1.1–1.8 mm long, oblanceolate, cymbiform, white to hyaline, chartaceous, pubescent adaxially, especially at upper part, with adpressed trichomes, abaxially glabrous, hyaline when hydrated, white in the upper part; petals 0.95–1.3 mm long, oblong, fused at the upper margin, free at base and the apex, thick, the upper part membranous, lobes oblong, acute, glabrous adaxially, pilose abaxially with simple filamentous hairs; gynoecium 1.4–1.9 mm long; ovary 0.6–0.7 mm long; style column 0.4–0.5 mm long, cream-colored to castaneous; unappendaged or very short appendages; style branches simple, 0.55–0.95 mm long. Seeds 0.55–0.65 × 0.25–0.3 mm, ovoid, brown-colored, striate with very short pseudotrichomes.

Phenology—Flowers and fruit were observed in all herbarium specimens. All collections for this taxon were made in May.

Habitat and Distribution— Restricted to Pará state (Brazil) in Serra dos Carajás region, an area characterized by soils with rich ferriferous component with peculiar "canga" vegetation and intensive mining activity. This vegetation is characterized by "campo rupestre" vegetation on Cenozoic ferruginous rocks composed by fragments of hematite cemented by limonite (Rizzini 1979).

Conservation status— Based on criteria B2ab of geographic range (IUCN 2014), this taxon is categorized as critically endangered. This species occurs in a critical area with intensive mining exploitation, in which the area, extend and quality of habitat is considered severely fragmented and continuing decline is observed.

Commentaries— Moldenke described *S. caulescens* var. *discretifolius* based on morphological differences in the habit of the plant as transcribed here: "*this variety differs from the typical form of the species in having its stem-leaves distinctly alternate, conspicuously and rather widely separated from each other, ascending-spreading, and sharply acute apically*" (Moldenke 1977:364). In fact, there is a notable separation among the leaves on the aerial stem but orientation slightly adpressed and the capitate trichomes concentrated near the apex of the scapes make it more similar morphologically to *S. appressus*.

Enormous morphological variability is a notable characteristic of *S. caulescens* but it is speculated that this variation is restricted to habit and vegetative characters, rather than in floral traits. *S. caulescens* var. *discretifolius* has its status changed here because it combines characteristics that we consider enough to distinguish it as species. Consistently, *S. caulescens* has involucral bracts with acute apex and pistillate flowers show robust and well-developed appendages unlike *S. discretifolius*, which has involucral bracts with obtuse-mucronate apex and unappendaged gynoecia or when they are present, can be much reduced (incomplete development). *S. discretifolius* and *S. caulescens* occur sympatrically in the Serra dos Carajás region.

Because morphological characteristics are similar, we suppose that *S. discretifolius* belongs to core *Carphocephalus*. The evidence is the staminate flower with fleshy tubular corolla and very short membranous lobes. Additionally, the pistillate flowers have carnose petals in the lower half, and membranous in the upper half. Another characteristic is the texture of sepals in both pistillate and staminate flowers. They have a thickened upper part (white) and hyaline bottom portion when hydrated, likely a synaphomorphy for this group.

The material *Cavalcante 2101* shows narrower less congested leaves, but their distribution on aerial stem is similar to the other material. This could be an indication that this taxon may also be susceptible to striking vegetative variations.

Specimens examined—**BRAZIL**. **Pará**: Marabá, platô a 700 m de alt., rocha de minério de ferro, 21 May 1969, *Cavalcante 2101* (NY, RB), 2 km West of AMZA camp N-5, 13 May 1982, *Sperling et al. 5640* (F, LL, MO), arredores do lago, em canga, 14 May 1982, *Secco et al. 161* (F, MG, MO, NY), Serra Norte, margem do lago, 27 May 1983, *Silva et al. 1695* (HUEFS); Parauapebas, Serra Sul, Floresta Nacional de Carajás, 29 Jul 2007, *Nunes & Ferreira Júnior s.n.* (SPF, VIC); Serra Norte, Carajás, 31 May 1986, *Lima et al. 58* (HRB, RB); idem, 4 Jul 1987, *Silva 1346* (MBM);

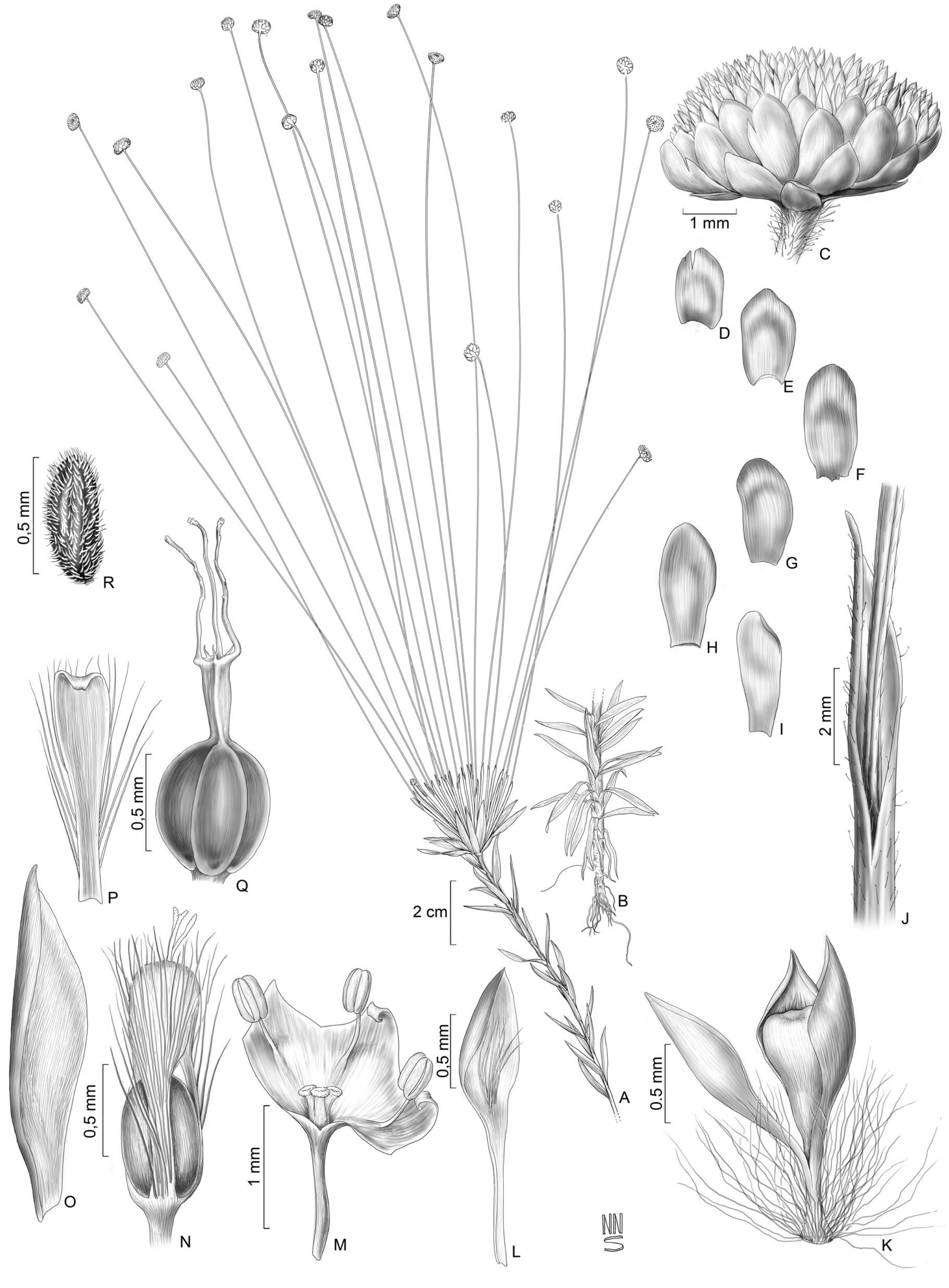
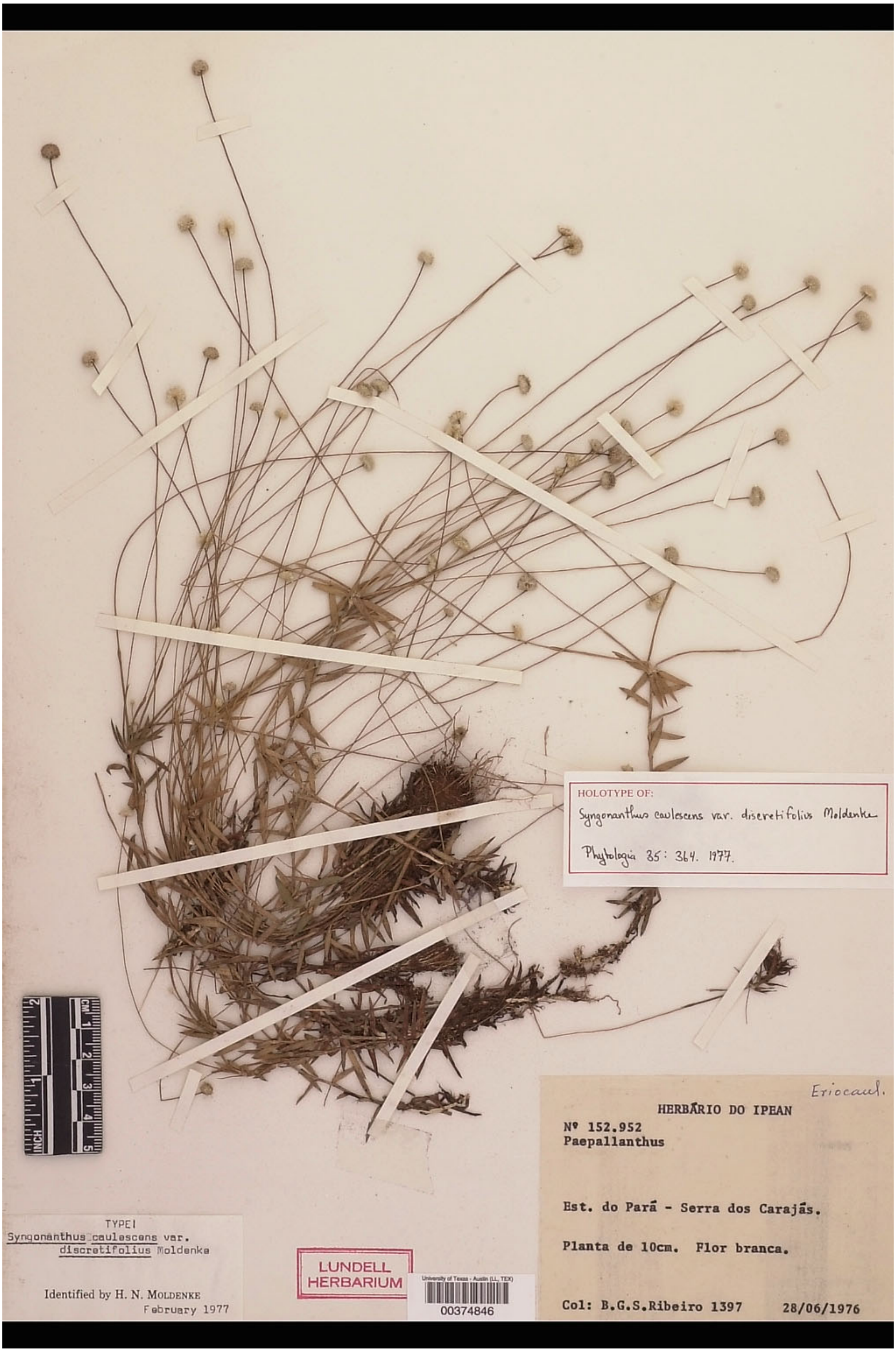


Figure 11–*Syngonanthus discretifolius* (based on *Irwin et al. 58*). **A-B.** Habit; **C.** Capitulum detail; **D–I.** From outermost to innermost series of involucral bracts; **J.** Spathe detail. **K.** Staminate flower; **L.** Detail of sepal of staminate flower; **M.** Staminate flower dissected showing pistillodes; **N.** Pistillate flower with sepals removed; **O.** Sepal of pistillate flower; **P.** Petal of pistillate flower; **Q.** Gynoecium; **R.** Seed.



HOLOTYPE OF:
Syngonanthus caulescens var. discretifolius Moldenke
Phytologia 35: 364. 1977.

TYPE!
Syngonanthus caulescens var. discretifolius Moldenke
Identified by H. N. MOLDENKE
February 1977

Eriocaul.
HERBÁRIO DO IPEAN
Nº 152.952
Paepallanthus
Est. do Pará - Serra dos Carajás.
Planta de 10cm. Flor branca.
Col: B.G.S.Ribeiro 1397 28/06/1976

Figure 12. Holotype of *Syngonanthus discretifolius* deposited in LL herbarium[§]

[§] Available at http://orchid.biosci.utexas.edu/pics/ready/00374846.JPG [Accessed September 23, 2014]

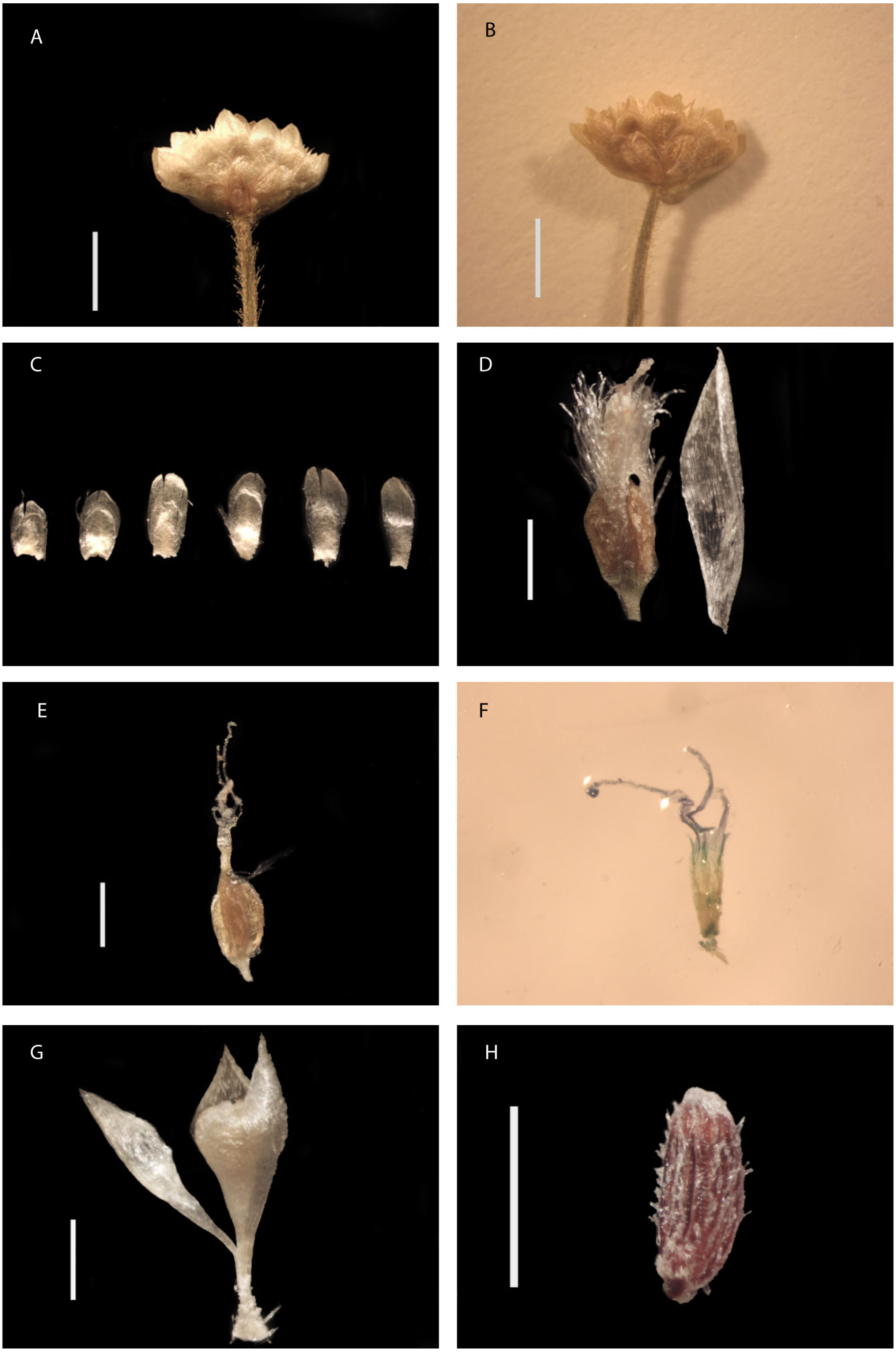


Figure 13. *Syngonanthus discretifolius*. A-B. Capitulum. C. Series of involucral bracts. D. Pistillate flower and one dissected sepal. E. Gynoecium. F. Very short appendages. G. Staminate flowers. H. Seed. Scales: A-C: 2mm; D-E,G: 0.5 mm; H: 1mm. Based on *Sperling et al. 5640*.

Syngonanthus fischerianus (Bong.) Ruhland in Engler, Pflanzenr. 13 (IV.30): 256. 1903. *Eriocaulon fischerianum* Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 6, Sci. Math. 1:627. 1831. *Paepalanthus fischerianus* (Bong.) Koern., Fl. Bras. (Martius) 3(1):455. 1863. Dupatya fischeriana (Bong.) Kuntze, Revis. Gen. Pl. 2:745. 1891. Lectotype: Brazil. Minas Gerais: G.H. von Langsdorff n.n. (Lectotype designated here: LE! [1074]).

Paepalanthus nardifolius Kunth, Enum. Pl. (Kunth) 3:532. 1841. *Eriocaulon nardifolium* (Kunth) Steud., Syn. Pl. Glumac. 2:281. 1855. Type: Brazil. Brasilia meridionalis, Dec 1836, Sellow 4957 (Holotype: photo B!; Isotype: photo P!).

Syngonanthus breviramosus Diogo, Bol. Mus. Nac. Rio de Janeiro 1:28. 1923. Type: Brazil. Santa Catarina: In campis Curitybanus, Müller 36 (Holotype: R!).

Syngonanthus ferrensis Silveira, Floral. Mont.: 355, fig. 224. 1928. Type: Brazil. Minas Gerais: In vicina urbis Patrocínio, in humidis prope Lagoa do Ferro, 1050 m alt., Sep 1924; in humidis prope Milho Verde, in Serra do Espinhaço, Jun 1925, Silveira 736 (Holotype: R!).

Syngonanthus micropus Silveira, Floral. Mont.: 314, fig. 199. 1928. Type: Brazil. São Paulo: In campis humidis prope Campo Grande, ad Alto da Serra do Cubatão, Oct 1892, Edwall in herb. A. Silveira 419 (Holotype: R!; Isotypes: SP!, RB!).

Syngonanthus fischerianus var. *hatschbachii* Moldenke, Phytologia 28(4): 403. 1974. Type: Brazil. Paraná: Curitiba, Rio Atuba, 30 Oct 1973, Hatschbach 32760 (Holotype: LL!).

Herbs, sometimes short caulescent, 10–55 cm tall. Roots white, 0.05–0.75 mm in diameter, spongy. Rosette present. Leaves 1.0–5.5 cm × 0.05–1.00 mm, linear, apex round to truncate, with 3–7 veins prominent, scarcely pilose to glabrescent on both surfaces, with simple filamentous hairs, adpressed trichomes and small glandular trichomes, with villous hairs at the insertion of the leaves on the rosette. Synflorescences with a primary axis bearing only one inflorescence at the apex. Synflorescence axis 0.15–1.00 cm long, emerging from the center of the rosette, erect, straw-colored, pubescent with adpressed trichomes and filamentous hairs. Bracts of synflorescence axis restricted to the apex, 0.6–2.5 cm × 0.1–0.8 mm, whorled, progressively elongating from the outer toward the inner series, ascending, paleaceous to membranous, linear-lanceolate or linear-triangular, apex acuminate, scarcely pilose to glabrescent on both surface with simple filamentous hairs and adpressed trichomes. Inflorescences composed of a closed spathe subtending a scape with a capitulum at the apex. Spathes 3.5–7.0 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute, usually lacerate, margin entire, not involute, glabrous or scarcely pilose to glabrescent on both surfaces with simple filamentous hairs and adpressed trichomes. Scapes erect, 8.0–47.5 cm long, greenish to straw-colored with age, costae 3–5, pilose with simple filamentous hairs, sometimes a collar of trichomes near the apex. Capitula 3–8 mm in diameter. Involucral bracts in 3–6 series, glabrous, white to cream or golden colored, those of the external series 1.4–2.0 × 0.6–0.8 mm, ovate-triangular or obovate, apex acuminate, those of the internal series progressively longer 2.2–3.0 × 0.5–0.9 mm, oblanceolate, apex obtuse or acuminate; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 70–250 per capitulum, the staminate and the pistillate similar in number, or depending on phenophase the pistillate can be twice the staminate. Staminate flowers 2.5–3.2 mm including pedicels; pedicels 0.5–0.8 mm long with filamentous trichomes at insertion with receptacle; sepals 1.6–2.8 mm long, cream, shortly fused at base, cymbiform, chartaceous, elliptic, lanceolate or rhombic, apex acuminate, margin involute, glabrous or glabrescent, sometimes pilose with simple filamentous hairs, only adaxially; corolla 1.0–2.1 mm long, partly fleshy with membranous lobes and fleshy base of the corolla, fused ca. 4/5 of its length, tubular, lobes obtuse, involute after anthesis, glabrous; filaments free, anthers 0.3–0.4 mm long, cream to whitish; pistillodes 3, 0.2–0.4 mm long, clavate, papillose at apex. Pistillate flowers 2.4–2.9 mm long including the pedicel; pedicels 0.2–0.7 mm long with filamentous hairs at insertion with receptacle and bottom part of pedicel; sepals 2.0–2.4 mm long, shortly fused at base, cymbiform, chartaceous, hyaline, white at the apex, elliptic, apex acuminate, glabrous; petals 1.2–1.8 mm long, spatulate, fused at the upper margin, free at base and the apex, lobes obtuse, membranous, white in central portion, hyaline when hydrated at base and apex, glabrous adaxially, glabrous to glabrescent or sparsely pilose abaxially with simple filamentous hairs; gynoecium 1.7–2.6 mm long; ovary 0.5–0.7 mm long; style column 0.3–0.5 mm long, cream-colored to castaneous; appendages 0.25–0.40 mm long; style branches simple, 0.8–1.2 mm long. Seeds 0.6–0.7 × 0.3 mm, ellipsoid, brown-colored with very short pseudotrichomes.

Phenology— Flowers and fruit were collected in February, April, May and from September to December.

Habitat and Distribution— There are records for this taxon from Minas Gerais, São Paulo, Paraná and Santa Catarina. Ruhland (1903) cited materials from Goiás belonging to *S. fischerianus* in his revision, but the exsiccata corresponds to another taxon, as explained below. There is also a historical record for its occurrence in Rio de Janeiro, *Glaziou 7997*. In some cases, Glaziou's collection series have misrepresented collection data, including changes in localities (Wurdack 1970). For Minas Gerais, there are only old collections, including the lectotype designated here. *Syngonanthus fischerianus* occurs near border of rivers and wetlands in the Cerrado vegetation.

Conservation status— Although this species has been evaluated against the criteria of IUCN (2014) but does not qualify in critical categories, we considered close to an imminent risk, so we propose it as near threatened. This category may also be used if a taxon nearly qualifies as Vulnerable (IUCN 2014). This taxon occurs in a large territorial extension, but several risks including pastures could be a real danger in a few years.

Commentaries— When Bongard (1831) described *Eriocaulon fischerianum*, he did not mention on which material he based the description of the species. The protologue described the species as acaulescent with spathe trifid, occurring in Minas Gerais. There is only one material corresponding to this description, locality, with personal notes on the sheet, in the LE herbarium, where probably Bongard observed this material. This exsiccate is deposited under the herbarium number [LE1074], without collector name. Actually, this species has spathe with apex lacerate and short synflorescence axis, a morphological description adopted by Ruhland (1903) when he transferred this taxon to *Syngonanthus*. Ruhland cited some additional specimens observed in his revision as representing *S. fischerianus*. One of them was the specimen *Glaziou 22298* collected in Goiás (deposited in G), which in fact corresponds to *S. philcoxii*, a plant with aerial elongated non-fertile stem and without synflorescence axis.

Syngonanthus fischerianus, *S. hygrotrichus* and *S. philcoxii* are very similar species and may be considered a complex of species within *S.* sect. *Carphocephalus*. The differences between these three species reside in the linear leaves of *S. fischerianus* (vs. capillaceous in *S. philcoxii* and *S. hygrotrichus*) and synflorescence axis present (vs. absent in *S. philcoxii*). The floral traits are variable but expected in *S.* sect. *Carphocephalus* species concept: staminate flowers with corolla, at least partly, fleshy and involute after anthesis; sepals slightly thickened in the upper half in both flowers; pistillate flowers with petals slightly thickened in the lower half.

Specimens examined—**BRAZIL**. **São Paulo**: Itirapina, estação ecológica de Itirapina, em lagoa alagada junto a ponte do rio do Lobo, 7 Apr 2005, *Trovó et al. 171* (SPF); Itararé, estrada Itararé-Bonsucesso, fazenda Ibiti (Ripasa), campo alagável, beira do rio Verde, 26 Nov 1993, *Souza et al. 4824* (ESA, SPF); São José do Barreiro, serra da Bocaína, brejo, May 1951, *Brade 21081* (SPF); São Paulo, campos Congonhas, 4 Nov 1941, *Hoehne 758* (SPF), butantan, brejos, instituto de Butantan − horto Oswaldo Cruz, 14 Sep 1922, Gehrt [100877] (SPF); Taubaté, *Riedel 1478* (photo, G, K, LE, M, P); **Paraná:** Balsa Nova, São Luiz do Purunã, 8 Nov 1977, *Dombrowski & Scherer Neto 329* (LL); Guarapuava, passo do Jacu, 12 Dec 1973, *Hatschbach 33474* (LL); Palmas, leste Palmas e Ponte Serrada, 5 Nov 1971, *Hatschbach et al. 28247* (LL); São José dos Pinhais, brejo, 18 Oct 1980, *Hatschbach 43215* (LL); Tijucas do Sul, rincão, 14 Dec 1972, *Hatschbach 30989* (LL); **Santa Catarina:** Bituruna, fazenda Etienne, 12 Feb 1948, *Mello Filho 682* (LL); Curitibanos, between Ponte Alta and Curitibanos, 4 Dec 1956, *Smith & Klein 8260* (LL); Matos Costas, 9 Dec 1962, *Klein 3612* (LL); Santa Cecília, campo alto, 19 Dec 1962, *Reitz & Klein 14230* (LL).

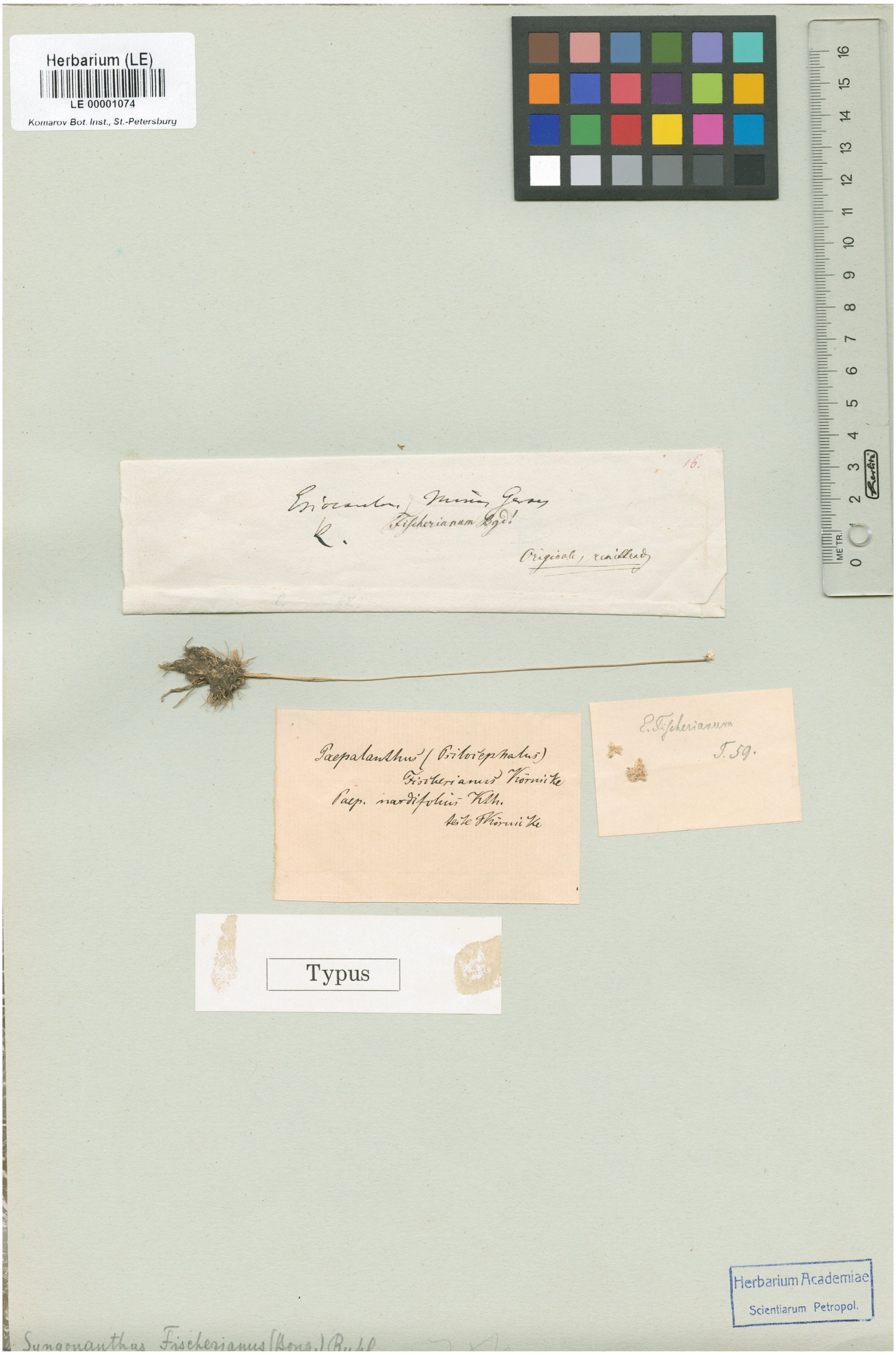


Figure 14. Lectotype of *Syngonanthus fischerianus* deposited in LE herbarium[**]

[**] Available at http://plants.jstor.org/stable/10.5555/al.ap.specimen.le00001074 [Accessed April 28, 2015]

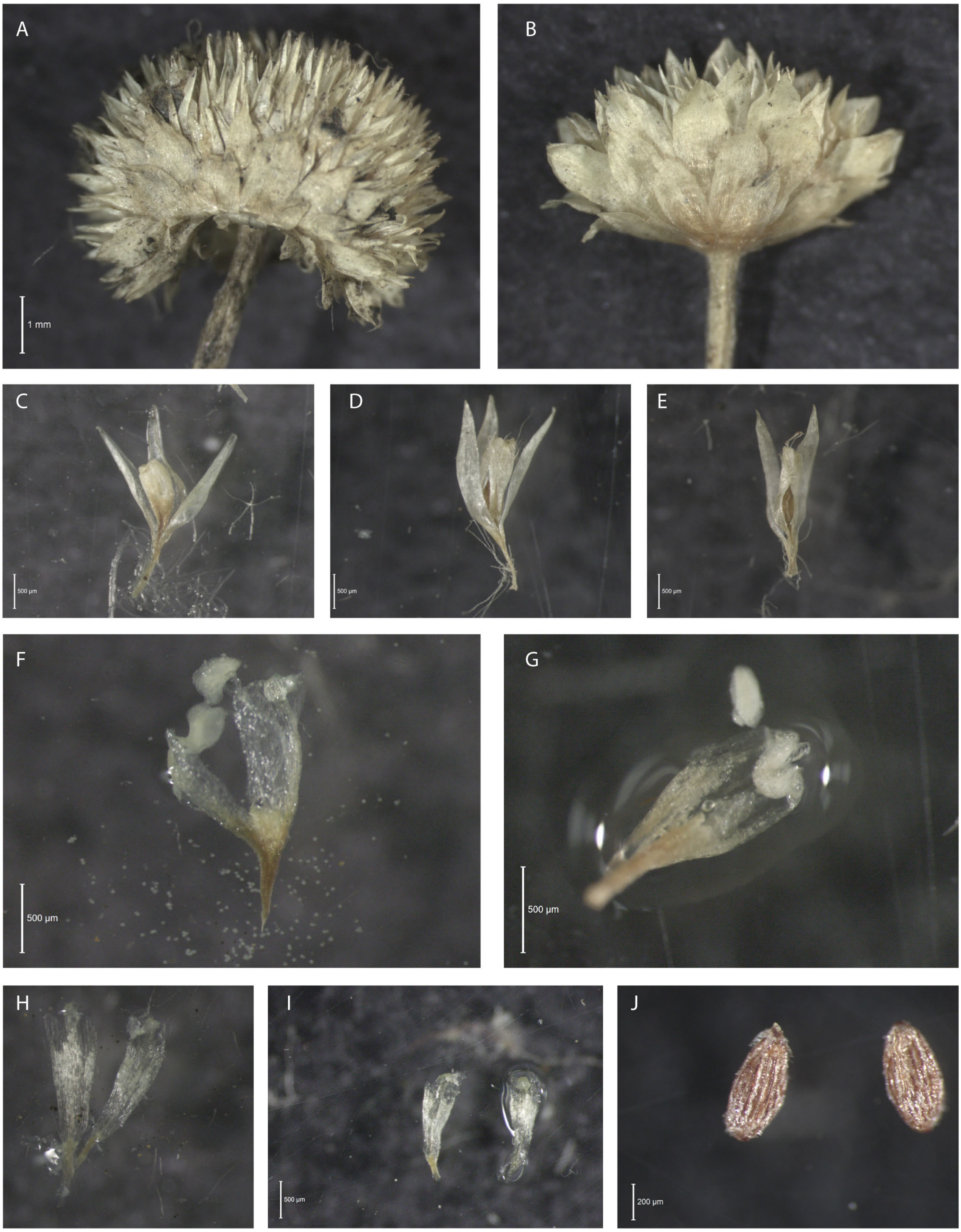


Figure 14. *Syngonanthus fischerianus*. **A-B.** Capitulum; **C-E.** Pistillate flowers; **F-G.** Corolla of staminate flower dissected showing texture partly fleshy; **H-I.** Petals of pistillate flower showing lobes membranous and lower half slightly thickned; **J.** seeds.

Syngonanthus hygrotrichus Ruhland in Engler, Pflanzenr. 13 (IV.30): 246. 1903. Type: Brazil. Minas Gerais: Biribiry, dans l'eau des rapides sur le rocher, 29 Mar 1892, Glaziou 19998 (Lectotype: P [742566] *pro parte*, designated by Parra & Giulietti, 1997; Isolectotypes: B, BM, BR, C *pro parte*, F, G, LE, K, NY!, P [742564 and 742565]).

Syngonanthus aquaticus Silveira, Fl. Serr. Min.: 74, fig. 29. 1908. Type: Brazil. Minas Gerais: Serra do Cipó, in stagnis perenibus prope Capão Redondo, Apr 1905, Silveira 213 (Holotype: R!; Isotype: B, LL fragm.!, SPF!).

Aquatic herbs, short caulescent, 15–33 cm tall. Roots white, 0.15–0.50 mm in diameter, spongy. Rosette present with aerial stem undeveloped, or axillary stem without inflorescences rarely developed. Leaves 2.5–11.0 cm × 0.05–0.35 mm, capillaceous, apex round to truncate, with 2–3 prominent veins, ciliate, scarcely pilose to glabrescent on both surfaces, with simple filamentous hairs, adpressed trichomes and small glandular trichomes. Synflorescences with a primary axis bearing only one inflorescence at the apex. Synflorescence axis 0.1–1.55 cm long, emerging from the center of the rosette, erect, straw-colored, pubescent with adpressed trichomes and filamentous hairs. Bracts of synflorescence axis restricted to the apex, 0.4–2.5 cm × 0.05–0.5 mm, whorled and numerous, progressively elongating from the outer toward the inner series, ascending, paleaceous to membranous, linear-lanceolate or linear-triangular, apex acuminate, scarcely pilose to glabrescent on both surface with simple filamentous hairs and adpressed trichomes. Inflorescences composed of a closed spathe subtending a scape with a capitulum at the apex. Spathes 3–7 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute, usually lacerate, margin entire, not involute, glabrous or scarcely pilose to glabrescent on both surfaces with simple filamentous hairs and adpressed trichomes. Scapes erect, 8.0–28.5 cm long, greenish to straw-colored with age, costae 4–8, pilose with simple filamentous hairs, with a collar of trichomes near the apex. Capitula 3.5–8.0 mm in diameter. Involucral bracts in 3–6 series, those of the external series 1.25–1.45 × 0.7–0.8 mm, obovate, oblong, apex mucronate, golden to cream-colored, glabrous, those of the internal series progressively longer 1.9–2.45 × 0.5–0.7 mm, surpassed by the flowers in anthesis, oblanceolate, apex acute, cream to white-colored; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 40–140 per capitulum, the staminate and the pistillate similar in number. Staminate flowers 1.8–2.5 long mm including pedicels; pedicels 0.3–0.9 mm long with filamentous trichomes at insertion with receptacle; sepals 1.5–2.3 mm long, cream, shortly fused at base, cymbiform, chartaceous, elliptic, apex acuminate, pilose adaxially with simple filamentous hairs, glabrous abaxially; corolla 1.0–1.5 mm long, slightly spongy, fused ca. 4/5 of its length, tubular, lobes obtuse, involute after anthesis, glabrous; filaments free, anthers 0.15–0.35 mm long, cream to whitish; pistillodes 3, about 0.25 mm long, clavate, papillose at apex. Pistillate flowers 1.6–2.8 mm long including the pedicel; pedicels 0.2–0.5 mm long with filamentous hairs at insertion with receptacle; sepals 1.4–2.3 mm long, shortly fused at base, cymbiform, chartaceous, hyaline, white at the apex, elliptic or rhombic, apex acuminate, pilose adaxially with simple filamentous hairs, glabrous abaxially; petals 1.0–1.9 mm long, spatulate, obtrullate, fused at the upper margin, free at base and the apex, lobes obtuse, membranous, white to hyaline when hydrated, glabrous adaxially, pilose abaxially with simple filamentous hairs; gynoecium 1.3–1.8 mm long; ovary 0.4–0.7 mm long; style column 0.25–0.50 mm long, cream-colored to castaneous; appendages 0.3–0.4 mm long; style branches simple, 0.3–0.8 mm long. Seeds about 0.6 × 0.3 mm, ellipsoid, brown-colored with very short pseudotrichomes.

Phenology— There are records for blooming of *S. hygrotrichus*, with mature flowers abundant, between February and November.

Habitat and Distribution— *Syngonanthus hygrotrichus* is a submerged aquatic plant and occurs only in Minas Gerais state (Brazil) in campo rupestre phytophysiognomy.

Conservation status— The endemism and records for only two plateaus, Diamantina and Serra do Cipó, make this species rare and locally spread. It occurs outside National Park in Diamantina with only two rare records for Serra do Cipó, including the lectotype and a recent collection by Kew Botanical Garden expedition in 2009. Following the criteria B1 and B2ab of IUCN Red List categories and criteria (IUCN 2014), this taxon is categorized as endangered.

Commentaries— *Syngonanthus hygrotrichus* was described by Ruhland (1903) based on the syntypes *Glaziou 19998*, *Schwacke 8479* and *Schwacke 14553*. Actually, Parra & Giulietti (1997) noticed that the material *Schwacke 8479* corresponds to another taxon, *Leiothrix fluitans* (Mart.) Ruhland, a species with convergent habit and similar vegetative morphology. According to these authors, the material *Schwacke 14553* was not found in any representative herbaria and so the collection *Glaziou 19998* was chosen as lectotype. It is morphologically similar to *S. fischerianus*, a Brazilian cerrado species, with which it shares the evident synflorescence axis. Only these two species have this structure developed in *S.* sect. *Carphocephalus*. It is speculated that *S. peruvianus* and *S. philcoxii* have this structure poorly developed, but plant anatomy and ontogeny studies are necessary to confirm this. The specific boundaries between *S. hygrotrichus* and *S. fischerianus* are obscure because the floral traits overlap and only few characteristics are contrasting. In comparison, *S. hygrotrichus* has smaller staminate flowers (up to 2.5 mm long *vs.* at least 2.5 mm long) and glabrous sepals in the staminate flowers (*vs.* pilose sepals with filamentous simple trichomes on the adaxial surface). Except for those differences, floral traits are very similar. Other slight differences are the very capillary leaves of the rosette in *S. hygrotrichus*, the habit exclusively aquatic and the restricted geographical distribution.

Some specimens in the holotype of *S. hygrotrichus* shows capitula with and without vivipary. This is not usual in this species, and probably is the result of an abnormality. Some specimens also have an axillary aerial stem developed without inflorescences, a peculiar characteristic also observed in *S. philcoxii*, another species which shares similar floral traits. Complementary studies involving population genetics may provide a more accurate decision about the identities of species in this complex including *S. hygrotrichus*, *S. fischerianus* and *S. philcoxii*. For the moment we prefer not to synonymize the taxa because there is no superposition in the geographical distribution (There is no record for *S. fischerianus* in Serra do Cipó and Diamantina). They might also be the result of a recent isolation and diversification.

Additional specimens examined—**BRAZIL**. **Minas Gerais**: Diamantina, Biribiri. Alto da cachoeira da sentinela, campo rupestre, 18°11'6.7"S 43°36'55.8"W, 09 Sep 2012, *Watanabe et al. 313* (F, SPF), estrada para Conselheiro Mata, km 185, campo limpo, no leito do córrego seco, 26 Jul 1986, *Giulietti et al. CFCR 9958* (HUEFS, SPF), idem, em brejo, 17 Apr 1987, *Zappi et al. CFCR 10589* (SPF), estrada Diamantina - Conselheiro Mata, km 185, próximo à grande inselberg, 23 Feb 1986, *Mello Silva et al. CFCR 9515* (SPF, UEC), margem da estrada Corinto – Conceição da Mata, 03 Apr 1980, *Giulietti 937-80* (SPF), estrada para Milho Verde, campo arenoso, 13 Feb 1998, *Sano et al. 896* (SPF); Santana do Pirapama, Serra do Cipó, capela de São José, trilha da Senhorinha, caminho a Congonhas do Norte, 18°57'30.79"S 43°44'17.96"W 1422m alt., 25 Nov 2009, *Zappi et al. 2589* (SPF).

HERB. MUS. PARIS.

Syngonanthus hygrotrichus Ruhl.

Croît dans les rapides & l'eau courante
Biribiry 29-30 mars 1892

BRÉSIL Minas
n. 19998

Herbier de A. GLAZIOU
donné par Mme SIMARD, sa fille, en 1907.

Herbier Muséum Paris
P00742566

Eriocaulaceae
Syngonanthus hygrotrichus Ruhland
SYNTYPUS
Det. Livia Echternacht (SPF & P)

Figure 15. Lectotype of *Syngonanthus hygrotrichus* deposited in P herbarium††

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†† Available at http://dsiphoto.mnhn.fr/sonnera2/LAPI/scanK/K20110411/P00742566.jpg [Accessed April 26, 2015]

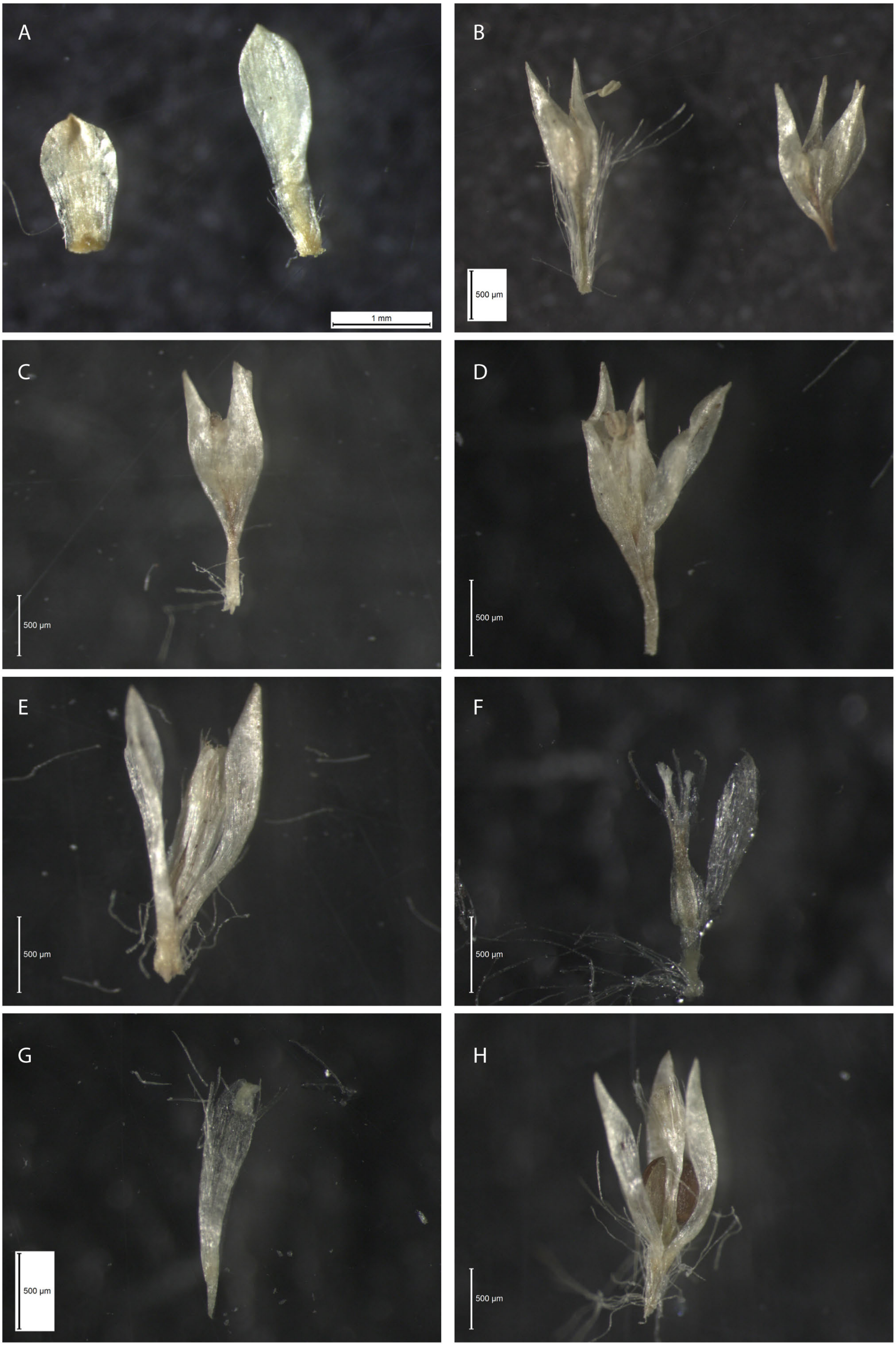

Figure 16. *Syngonanthus hygrotrichus*.**A.** Involucral bracts; **B-D.** Staminate flowers; **E.** Pistillate flower; **F.** Pistillate flower dissected showing gynoecium; **G.** Petal of pistillate flower; **H.** Fruit with calyx and corolla persistent.

Syngonanthus mollis M.T.C. Watan. ***sp. nov.*** Type: Bolivia, Velasco, Estación Flor de Oro, Margen del Rio Iténez (Guaporé), frontera con Rondonia; aprox. 20 km norte del Serrania de Huanchaca; aprox. 85 km este del Rio Paragua. 23 May 1991, M. Peña & R. Foster 165 (Holotype: SPF; Isotypes: F, USZ).

Caulescent herbs, 13.5–46.5 cm tall. Roots white, 0.1–0.3 mm in diameter, spongy. Rosette absent. Aerial stem 6–19 cm long, villous, with white crooked trichomes, bearing an umbel of 4-20 inflorescences at the apex. Leaves patent to oblique, equally distributed along the stem or slightly congested at the base near roots or apex, 10–40 × 0.5–1.5 mm, linear or filiform, apex retuse, round or obtuse, pubescent with adpressed trichomes and rare simple filamentous hairs, later glabrescent, veins 4–7, prominent. Spathes 2.8–6.8 cm long, chartaceous, cylindrical, erect, obliquely opened, apex retuse, tip uncinate, margin entire, not involute, pilose adaxially and abaxially with capitate filamentous hairs and adpressed trichomes. Scapes erect, 7–26 cm long, green or straw-colored with age, 3-costate, pilose with simple filamentous hairs and capitate trichomes near the apex. Capitula 3–5 mm in diameter, radiate. Involucral bracts in 4–6 series, those of the external series 1.2–1.8 × 0.5–0.7 mm, triangular-oblong, apex mucronate, golden to cream-colored, glabrous, those of the internal series progressively longer 2.4–2.8 × 0.7–1.0 mm, almost equaling the flowers, oblanceolate or elliptic, apex mucronate or retuse, cream to white-colored; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 30–60 per capitulum, the staminate slightly more numerous than pistillate. Staminate flowers 1.8–2.5 mm long including pedicels; pedicels 0.25–0.50 mm long with filamentous trichomes at insertion with receptacle; sepals 1.5–2.3 mm long, cream, shortly fused at base, cymbiform, chartaceous, lanceolate or elliptic, apex acute, margin involute, glabrous adaxially, pilose abaxially, especially below the apex, with simple filamentous hairs; corolla 1.0–1.4 mm long, fleshy below the lobes, the lobes membranous, fused ca. 4/5 of its length, tubular, lobes obtuse to rounded, involute after anthesis, glabrous; filaments adnate to the petals, anthers 0.2–0.4 mm long, cream to whitish; pistillodes 3, 0.25–0.35 mm long, clavate, papillose at apex. Pistillate flowers 1.9–2.5 mm long including the very short pedicels (sub-sessile); pedicels 0.10–0.25 mm long with filamentous hairs at insertion with receptacle; sepals 1.8–2.3 mm long, lanceolate, cymbiform, white to hyaline, chartaceous, glabrescent adaxially, especially at upper part, with adpressed hairs, abaxially glabrous; petals 1.1–1.7 mm long, oblanceolate, fused at the upper margin, free at base and the apex, lobes obtuse, thick, the upper part membranous (usually only the lobes), white to hyaline when hydrated, glabrous adaxially, pubescent abaxially with simple filamentous hairs; gynoecium 1.1–1.7 mm long; ovary 0.40–0.55 mm long; style column 0.2–0.4 mm long, cream-colored to castaneous; appendages 0.15–0.30 mm long, clavate; style branches simple, 0.4–0.9 mm long. Seeds not seen.

Phenology—Only flowers were observed in the herbarium specimens. They were collected in May and June.

Habitat and Distribution— *Syngonanthus mollis* was registered in Bolivia and Peru. Occurs in the pampas, particularly in floodplains along the rivers Heath and Iténez.

Conservation status— The disjunct distribution and lack of knowledge about other areas of occurrence for *S. mollis* allow categorizing this species as endangered following the criterion B (geographic range) of IUCN 2014. Area of occupancy probably < 500 km^2, number of locations = 2, complying with the requirements of criterion B2ac.

Commentaries— *Syngonanthus mollis* is a distinct new species from *Syngonanthus* sect. *Carphocephalus*. The specific epithet refers to the soft aspect of the capitulum when compared to similar species of *Carphocephalus*, such as *S. caulescens* and *S. rhizonema*. Although floral traits do not help to easily differentiate these taxa, vegetative characters are informative and easy to compare. *Syngonanthus mollis* has linear leaves similar to *S. rhizonema* but these leaves are thinner than the latter, most often filiform. In addition, *S. mollis* does not show viviparous capitula as observed in *S. rhizonema* and the pistillate flowers have petals narrower than in *S. rhizonema* and *S. caulescens*. A notable difference between *S. mollis* and *S. caulescens* resides in involucral bracts. Usually the apex of involucral bracts in *S. caulescens* is markedly acute but the apex of involucral bracts in *S. mollis* is mucronate, sometimes retuse. Another important difference is the shape of the appendages in the gynoecium. *S. caulescens* has well-defined capitate appendages but in *S. mollis* these appendages appear to be clavate. Furthermore, only a small portion of the petals in the pistillate flowers is membranous (only the lobes), compared to other species that belong to the core *S.* sect. *Carphocephalus* (chapter 2), which have approximately half of the petals membranous as observed in *S. weddelli*, *S. rhizonema*, among others.

Another differentiating characteristic of the leaves in *Syngonanthus mollis* is the apex, which may be retuse instead of acute as observed in *S. caulescens* and *S. discretifolius*. The apex of spathe and some internal bracts can also be retuse. *S. mollis* has leaves on the aerial stem more congested near the base and at the apex, just below the inflorescences. However, the leaves of young individuals are evenly distributed throughout the length of the stem. *S. mollis* also has some vegetative similarities with *Syngonanthus surinamensis*. However, *S. surinamensis* does not belong to *Syngonanthus* sect.

Carphocephalus, since it does not have staminate flowers with thick petals; therefore these similarities only represent convergence of habits. *Syngonanthus surinamensis* still has axillary inflorescences but *S. mollis* has only terminal inflorescences.

The collection *Albán & Foster 6968* is a mixture of two species, one corresponding to *S. androgynus*, a new species also described for this section. The other is *S. mollis*, with leaves smaller than specimens from northeastern Bolivia.

Specimens examined—PERU. Madre de Dios; Río Heath, Santuario Nacional de las Pampas del Heath, lado este de la Pampa, 3-4 km oeste del río, camino del Refugio Juliaca, hasta el bosque de galería y campamento Aguas Claras, 15 Jun 1992, *J. Albán C. & R. Foster 6968* (F).

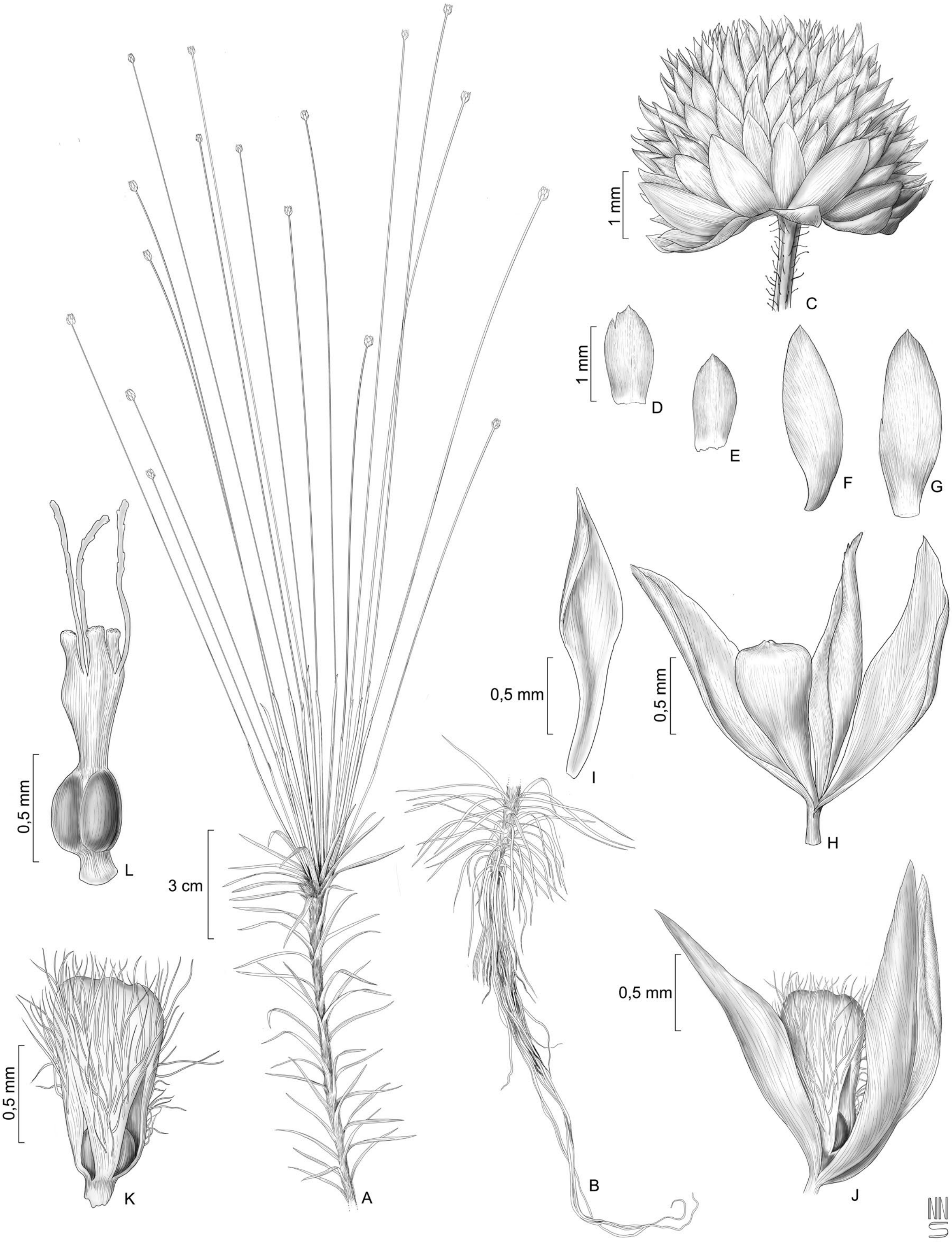

Figure 17–*Syngonanthus mollis* (based on *Pena & Foster 165*). **A-B.** Habit; **C.** Capitulum detail; **D**–**G.** From outermost to innermost series of involucral bracts; **H.** Staminate flower; **I.** Detail of sepal of staminate flower; **J.** Pistillate flower **K.** Pistillate flower with sepals removed; **L.** Gynoecium.

BOLIVIA
Dpto. de Santa Cruz

ERIOCAULACEAE

Syngonanthus inundatus (Koern.) Ruhl.
det. N. Hensold '91

Prov. Velasco: Estación Flor de Oro.
Margen del Rio Iténez (Guaporé); frontera con Rondonia; ~ 20 km norte del Serrania de Huanchaca; ~ 85 km este del Rio Paragua.

61°00' W, 13°33' S
Pampa inundada de hierbas, con islas termiteros cubierto con arbustos y arbolitos. Libre de inundación hace 2 semanas.
Alt. 200m

Hierba; cabezas blancas.

Marielos Peña **165** 23 Mayo 1991
Robin Foster

Museo de Historia Natural - Santa Cruz (SCZ)

Figure 18. Holotype of *Syngonanthus mollis* deposited in SPF herbarium.

Figure 19. *Syngonanthus mollis*. **A-B.** Capitula. **C.** Involucral bracts. **D.** Pistillate flowers. **E.** Pistillate flowers with sepals removed. **F.** Gynoecium. **G.** Staminate flower and sepals dissected. **H.** Staminate flower. Scale bars. A-B= 2 mm; C= 1 mm; D-H= 0.5 mm. Based on *Pena 165* and *Castillo & Foster 6968*.

Syngonanthus peruvianus Ruhland in Engler, Pflanzenr. 13 (IV.30): 253. 1903. *Paepalanthus peruvianus* (Ruhland) J.F.Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 11:8. 1931. Type: Peru. Amazonas: Excursion de Pacasmayo a Moyobamba, cuesta de Léjia cerca de Molinobamba, 4 Jun 1875, Stübel 19b (Lectotype designated here: photo B! [100250262]; Isolectotype: photo B! [100250264]).

Syngonanthus yacuambensis Moldenke, Phytologia 4:182. 1953. Type: Ecuador. Azuay, between Oña and the río Yacuambi, on the Eastern Cordillera, 10-19 Sep 1945, Pietro P.197 (Holotype: NY!; Isotypes: G, MO!, P).

Herbs, sometimes short caulescent, 4–27.5 cm tall. Roots white, 0.5–1.0 mm in diameter, spongy. Rosette present. Leaves 1.2–6.2 cm × 0.75–4.50 mm, fenestrate at the base, linear-lanceolate, apex acute or mucronate, uncinate, with 5–9 veins prominent, pilose to glabrescent on both surfaces, with simple filamentous hairs and adpressed trichomes, villous hairs in the insertion of the leaves on the rosette. Synflorescences with very short primary axes bearing up to 15 inflorescences per individual. Synflorescence axis covered by leaves, emerging from the center of the rosette. Bracts of synflorescence axis 8–12 × 0.25–1.00 mm, whorled, progressively elongating from the outer toward the inner series, ascending, paleaceous to membranous, linear-lanceolate, apex acuminate, ciliate, scarcely pilose to glabrescent on both surface with simple filamentous hairs and adpressed trichomes. Inflorescences composed by a closed spathe subtending a scape with a capitulum at the apex. Spathes 1.5–4.0 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute, margin entire, not involute, glabrescent or scarcely pilose abaxially with simple filamentous hairs and adpressed trichomes, glabrous adaxially. Scapes erect, 2.5–25.5 cm long, green or straw-colored with age, costae 3–5, twisted, pilose with simple filamentous hairs and adpressed trichomes, a collar of trichomes near the apex. Capitula 4–7 mm in diameter. Involucral bracts in 3–4 series, glabrous, white to cream or golden colored, those of the external series 2.50–3.15 × 1.2–1.3 mm, ovate-triangular, oblong, apex acuminate or round, those of the internal series slightly longer 2.60–3.35 × 1.00–1.45 mm, oblanceolate, obovate, apex obtuse; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 30–80 per capitulum, the staminate twice more numerous than pistillate. Staminate flowers 2.8–3.3 mm including pedicels; pedicels 0.7–1.0 mm long with filamentous trichomes at insertion with receptacle; sepals 2.0–2.7 mm long, cream, shortly fused at base, cymbiform, chartaceous, elliptic or lanceolate, apex acuminate, margin involute, hyaline, white at the apex, glabrescent, sometimes pilose with simple filamentous hairs, only adaxially; corolla 1.4–2.2 mm long, membranous, sometimes carnose in the basal portion of the tube, fused ca. 3/4 of its length, tubular, lobes acute, involute after anthesis, glabrous; filaments adnate only in the base, anthers 0.30–0.45 mm long, cream to whitish; pistillodes 3, 0.25–0.35 mm long, clavate, papillose at apex. Pistillate flowers 2.6–3.4 mm long including the pedicel; pedicels 0.2–0.5 mm long with filamentous hairs at insertion with receptacle and bottom part of pedicel; sepals 2.2–2.7 mm long, shortly fused at base, cymbiform, chartaceous, hyaline, white at the apex, elliptic, apex acuminate, glabrous; petals 1.60–2.35 mm long, elliptic, fused at the upper margin, free at base and the apex, lobes acute, membranous, hyaline when hydrated, glabrous; gynoecium 1.2–2.7 mm long; ovary 0.4–1.0 mm long; style column 0.2–0.5 mm long, cream-colored; appendages 0.25–0.40 mm long; style branches simple, 0.5–1.0 mm long. Seeds about 0.75 × 0.55 mm, ovoid, brown-colored with very short pseudotrichomes.

Phenology— Flowers and fruit from March to October.

Habitat and Distribution— Occurs from Southern Ecuador to Northern Peru, in elevations between 2000 - 4000 m. There is one record further North of Ecuador in Napo. It inhabits open areas and grass páramos near the montane forest. Some notes in exsiccates indicated that specimens were collected in pastures or disturbed areas.

Conservation status— Although this species has been evaluated against the criteria of IUCN (2014) but does not qualify in critical categories, we considered close to an imminent risk, so we propose it as near threatened. This taxon occurs in a large territorial extension, but several risks including pastures could be a real danger in few years.

Commentaries— It is one of the few species that does not occur in Brazil, the center of diversity of this group. This is also the early divergent species in the clade involving *S.* sect *Carphocephalus*. It shares more characteristics with a group including *S. fischerianus*, *S. philcoxii* and *S. hygrotrichus,* in which rosettes are always present, than with the "core group" (*S.* sect. *Carphocephalus s. s.*). This species has short synflorescence axes, a character shared with *S. hygrotrichus* and *S. fischerianus*. Sometimes it is very hard to observe this because its very short axes are covered by leaves of the rosette. The only evidence is the presence of thin leaves (or bracts) present around the inflorescences. The staminate flowers do not have an urceolate corolla, like most species of *S.* sect. *Carphocephalus*, and only a small part of the corolla is spongy (above the anthophore). Both staminate and pistillate flowers have petals slightly thickened in the upper half and lower half hyaline. All species in *S.* sect. *Carphocephalus* share this character and it is necessary to verify accurately whether this is an exclusive character of this group.

Syngonanthus peruvianus was described by Ruhland (1903) based on material from Molinopampa, Peru. The material observed by Ruhland to describe this species probably is housed at B. There are two sheets of *S. peruvianus* with the same information as the protologue, the collection *Stübel 19b*. We designate the sheet B 100250262 as lectotype because there are original notes of Ruhland on the sheet and there is more than one specimen on the sheet (the other sheet has only one specimen).

Specimens examined— **ECUADOR**. **Azuay**: "oriente" border, eastern Cordillera, between Oña and the río Yacuambi, 10-19 Sep 1945, *Prieto P-197* (MO, NY); **Loja**: between Urdaneta and Puente León, 6 Oct 1955, *Asplund [17993]* (LL), Loja-Saraguro, km 18, pastures and partially cut, montane forest, 3º54'8"S 79º14'54"W, 21 Apr 1994, *Jørgensen et al. 449* (MO); **Napo**, closest town, Cuyuja, hacienda Antisana, along banks of Rio Quijos (northside), sotuhwest of Quito-Baeza road, 29 Aug 1980, *Sobel & Strudwick 2522* (SPF); **PERU**. **Amazonas**: Chachapoyas, cerros Calla Calla 19 km above Leymebamba, road to Balsas, 6 Jun 1964, *Hutchison & Wright 5556* (LL, MO), distrito de Leymebamba, ruta laguna de los Cóndores, entre la Fila y Toronjil, borde de camino, 19 Aug 1998, *Quipuscoa et al. 1361* (MO), road Chachapoyas-Mendoza, a little past Molinopampa, 6º14'11"S 77º35'49"W, 15 Mar 1998, *Henk van der Werff et al. 15070* (MO), Chachapoyas-Cajamarca road, between Leimebamba and Calla-Calla, 12-15km from Leimebamba, 4 Sep 1983, *Smith & Vasquez 5006* (MO), Leimebamba-Lajasbamba trail, 28 Jun 1977, *Boeke 2034* (MO), idem, 28 May 1977, *Boeke 1977* (MO);

Figure 20. *Syngonanthus peruvianus*. **A.** Rosette showinng tiny leaves in the center with the inflorescence; **B.** Capitulum; **C.** Involucral bracts; **D.** Staminate flower senescent; **E.** Staminate flower in pre-anthesis; **F.** Corolla of staminate flower dissected showing lower part fleshy; **G.** Gynoecium; **H.** Pistillate flower; **I.** Seed.

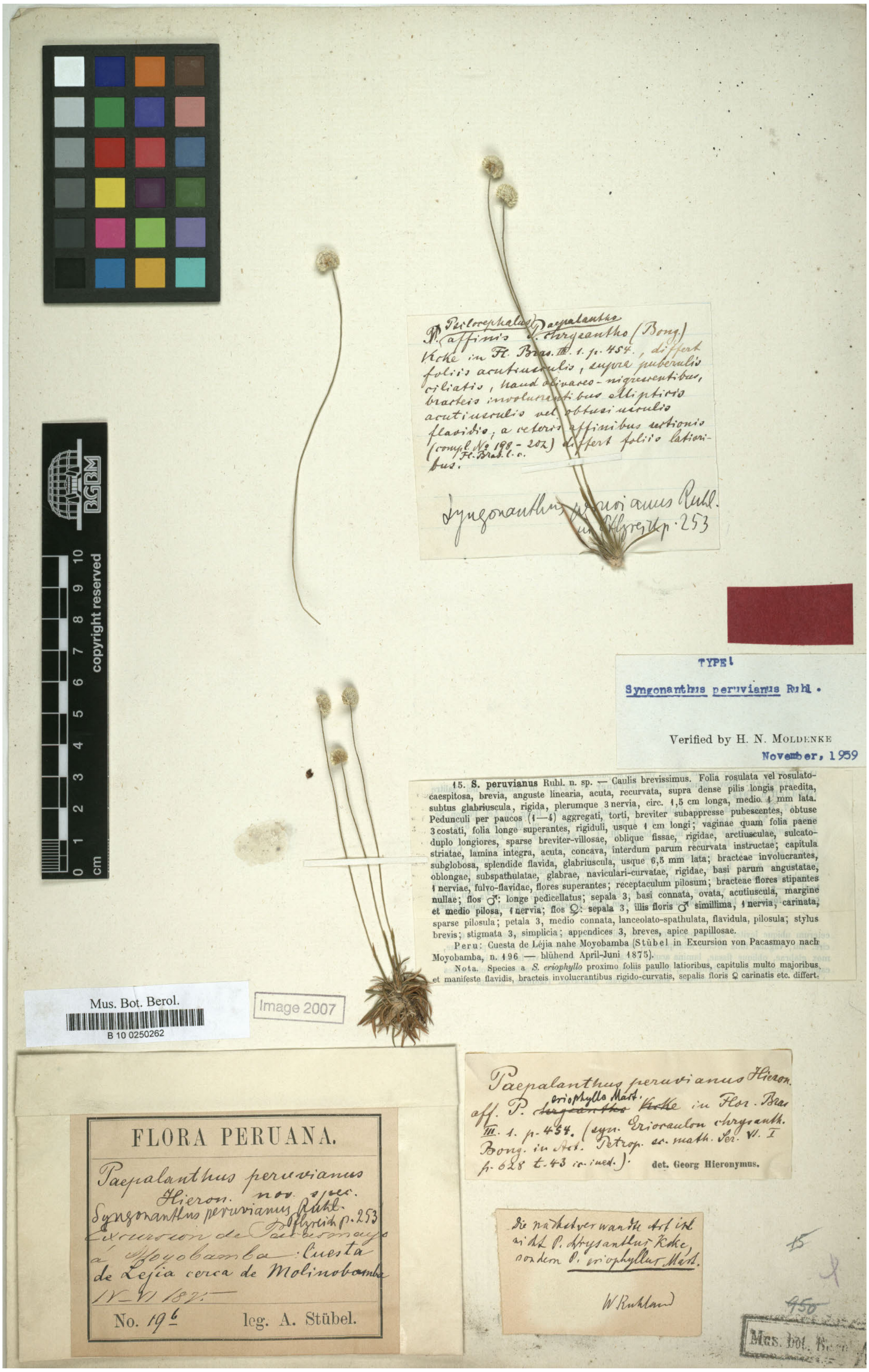

Figure 21. Lectotype of *Syngonanthus peruvianus* deposited in B herbarium*

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* Available at http://herbarium.bgbm.org/object/B100250262 [Accessed April 26, 2015]

Syngonanthus philcoxii Moldenke, Phytologia 26(3): 178. 1973. Type: Brazil. Mato Grosso: Central Brazilian Plateau. Xavantina – Cachimbo road, 3 km W of km 259, in mud between grass tussocks in wet campo, 30 Nov 1967, Philcox et al. 3316 (Holotype: K; Isotypes: UB!, LL fragm!).

Caulescent herbs, 9–25 cm tall. Roots white, 0.15–0.45 mm in diameter, spongy. Rosette present, inflorescences emerging from the center. Leaves of the rosette 0.8–2.5 cm × 0.05–0.4 mm, capillaceous, apex round, base truncate, veins 1-3, prominent, pilose with simple filamentous hairs and adpressed trichomes, when older glabrescent on both surfaces. Vegetative aerial stem 0.8–9.5 cm, decumbent, without inflorescences, pilose with villous trichomes mainly concentrated at apex. Cauline leaves 0.6–1.7 cm × 0.05–0.45 mm, capillaceous, occasionally linear, pilose with simple filamentous hairs and adpressed trichomes, when older glabrescent on both surfaces. Inflorescences composed by a closed spathe subtending a scape with a capitulum at the apex. Spathes 2.0–3.5 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute, tip uncinate, margin entire, not involute, glabrous adaxially, pilose abaxially with capitate filamentous hairs and adpressed trichomes. Scapes erect to slightly flexuous, 2.5–24.0 cm long, white to cream-colored, 3 or 4-costate, pilose with simple and adpressed filamentous hairs, mainly concentrated at apex. Capitula 3.5–5.5 mm in diameter, radiate. Involucral bracts about 5 series, glabrous, those of the external series 1.1–1.6 × 0.55–0.70 mm, oblong to obovate or elliptic to lanceolate, apex acute or mucronate, white to cream-colored, those of the internal series progressively longer 1.65–2.30 × 0.55–0.80 mm, almost equaling the flowers, oblanceolate, lanceolate or obovate, apex mucronate or round, white to cream-colored; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 35–60 per capitulum, the staminate twice as numerous as the pistillate. Staminate flowers 1.5–2.0 mm long including pedicels; pedicels 0.25–0.5 mm long with filamentous trichomes at insertion with receptacle; sepals 1.2–1.6 mm long, cream, shortly fused at base, usually two sepals similar in form, and the third different, cymbiform, membranous, lanceolate, oblanceolate or elliptic, apex acute, margin involute, glabrous abaxially, pilose adaxially, especially at upper part, with simple filamentous hairs; corolla 0.75–1.35 mm long, partly fleshy, lobes membranous, or sometimes exclusively membranous, fused ca. 4/5 of its length, tubular, lobes rhomboidal, involute after anthesis, glabrous; filaments adnate to the petals, anthers 0.2–0.3 mm long, cream; pistillodes 3, ca. 0.2 mm long, clavate, papillose at apex. Pistillate flowers 1.5–2.0 mm long including the very short pedicels (sub-sessile); pedicels 0.1–0.25 mm long with filamentous hairs at insertion with receptacle; sepals 1.45–1.85 mm long, lanceolate to elliptic, cymbiform, white to hyaline, membranous, pilose adaxially, especially at upper part, with simple filamentous hairs, abaxially glabrous; petals 0.7–1.6

mm long, oblanceolate, fused at the upper margin, free at base and the apex, lobes obtuse, membranous, white to hyaline when hydrated, glabrous adaxially, pilose abaxially with simple filamentous hairs; gynoecium 1.45–2.70 mm long, considering the style branches unrolled; ovary 0.40–0.55 mm long; style column 0.15–0.25 mm long, cream-colored to castaneous; appendages 0.15–0.4 mm long; style branches simple, 0.55–2.00 mm long. Seeds 0.4–0.5 × 0.20–0.25 mm, ellipsoid, brown-colored, with very short pseudotrichomes.

Phenology— Specimens with flowers and fruits were collected from July to October and January.

Habitat and Distribution— There are records for *Syngonanthus philcoxii* occurring only in the edge of Brazilian gallery forest, on wet mud. This species is known only from Distrito Federal in the municipalities of Brasília and Planaltina, and to the type locality in Mato Grosso state, next to the road interconnecting Xavantina and Serra do Cachimbo.

Conservation status— *Syngonanthus philcoxii* could be categorized as endangered following the criterion B1 and B2ac of IUCN 2014. The disjunct distribution and lack of knowledge about other areas of occurrence for *S. philcoxii*, with concomitant occurrence in degraded areas and deforestation activities can put this species in imminent danger. Its geographical distribution is only covered by two protected areas: Jardim Botânico de Brasília and Estação Ecológica de Águas Emendadas.

Commentaries— This is a very distinctive species of *S.* sect. *Carphocephalus*. Clonal propagation is an unusual characteristic among species in that section but it is observed in *S. philcoxii*. When present in the section, it is observed as an exception (some specimens of *S. appressus*) or an anomalous condition.

It was thought that this species was only known by the holotype, but detailed examination of unidentified material from Distrito Federal (Central Brazil) allowed us to come to the conclusion that these specimens belong to the same taxon as *S. philcoxii*. The remarkable characteristic of this species is the axillary aerial stem, purely vegetative, without inflorescences at the apex. Some specimens of *S. hygrotrichus* share this character, but they are extremely rare. The specimens observed in herbaria have a considerable morphological variation and some specimens do not show that modified aerial stem.

Syngonanthus fischerianus and *S. hygrotrichus* are the most morphologically similar species to *S. philcoxii*. The floral traits among these three species almost completely overlap. The basic differences reside in the capitate filamentous hairs found in the abaxial surface of the spathe and the seeds slightly smaller than the other two. Other difference among *S. philcoxii*, *S. fischerianus* and *S.*

hygrotrichus is the absence of an evident synflorescence axis in *S. philcoxii*, present in the two remaining.

Syngonanthus fischerianus and *S. philcoxii* are sister species, forming a clade, which is sister to *S. hygrotrichus* (see chapter 2). These three species have variable texture of the corolla in the staminate flowers, sometimes membranous, sometimes carnose or corolla partly carnose with lobes and upper portion of the tube membranous. They also share the style branches very delicate and involucral bracts with outer series obovate and inner series oblanceolate.

The holotype of *S. philcoxii* is partly damaged and there are not many capitula available on the sheet. The specimens in this collection have capitula with involucral bracts with acute apex and longitudinal stramineous band, characteristics somewhat different from the Distrito Federal populations analyzed (*vs.* homogeneous bracts with mucronate apex). Botanical expeditions to the original area of the type collection would be required for a more robust study about morphological variation of this taxon.

Specimens examined—**BRAZIL**. **Distrito Federal**: Brasília, fazenda Água Limpa, borda de mata de galeria, 11 Oct 2006, *Amaral & Munhoz 282* (SPF), Jardim Botânico, anexo, campo úmido, na margem de um lago pequeno dentro d'água, 24 Aug 1990, *Splett 22* (HEPH), Reserva Ecológica do IBGE, brejo próximo ao córrego Taquara, 20 Aug 1985, *Mendonça & Alvarenga 502* (IBGE); Planaltina, Estação ecológica Águas Emendadas, próximo ao marco divisor de águas, 15º33'25.6"S 47º35'48.1"W, 27 Jul 2012, *Watanabe & Watanabe 391* (SPF), idem, após o divisor de águas, campo úmido, área muito perturbada, 4 km depois da porteira, próximo à mata de galeria, 15 Jan 1998, *Oliveira & Meireles 947* (HEPH, MBM).

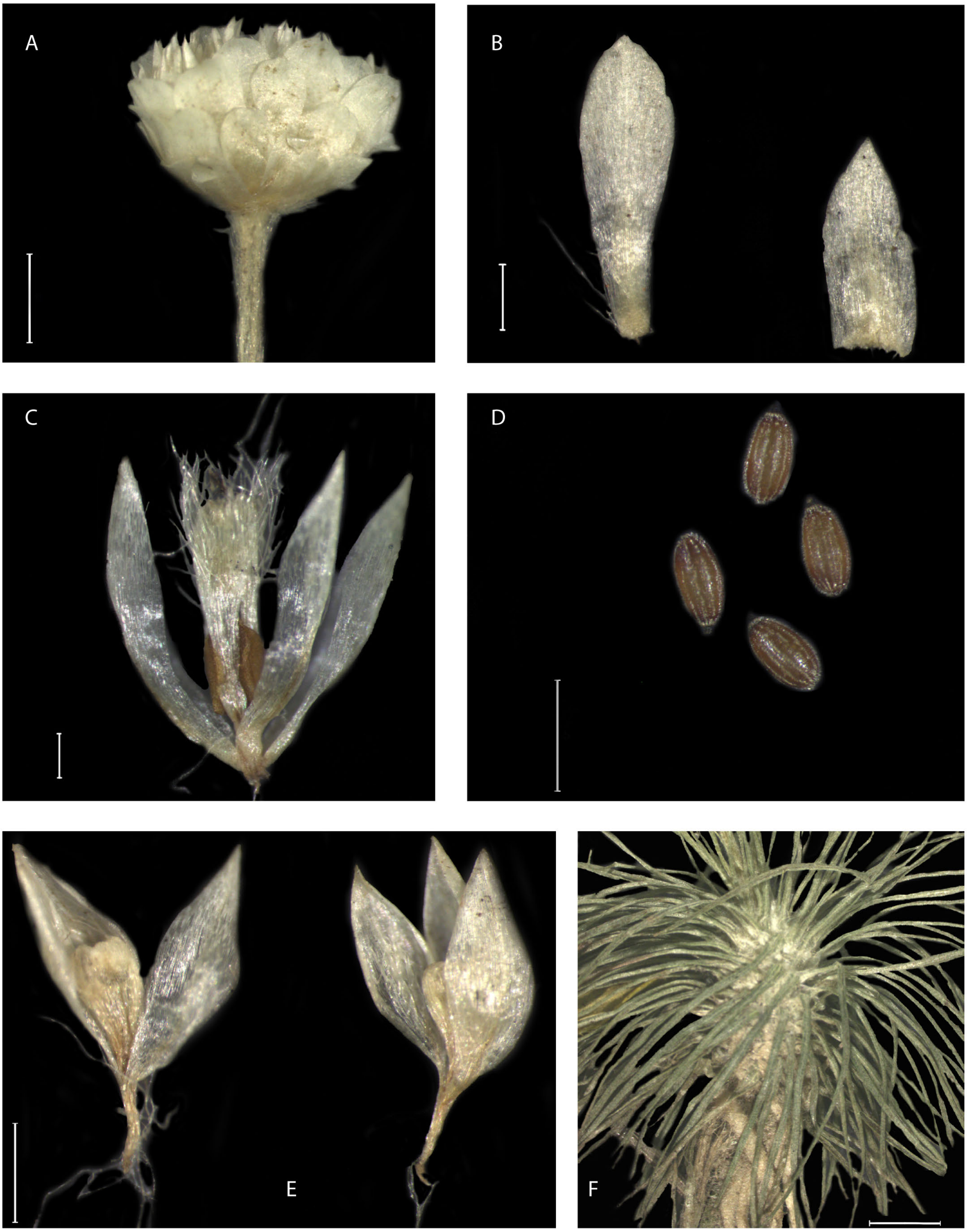

Figure 22. *Syngonanthus philcoxii*. **A.** Capitulum; **B.** Involucral bracts; **C.** Pistillate flowers; **D.** seeds; **E.** Staminate flowers; **F.** Leaves congests in the base. Scale bars.A= 1 mm; B,D-E= 500 µm; C= 200 µm; F= 2 mm.

TYPE
of Syngonanthus philcoxii Moldenke

Field Museum of Natural History
HOLOTYPE: Syngonanthus philcoxii Mold.
Phytologia 26: 178. 1973.

TYPE!
Syngonanthus philcoxii Moldenke

Identified by H. N. Moldenke
May 1973

HERB. HORT. BOT. REG. KEW.

HERBARIUM KEWENSE
ROYAL SOCIETY/ROYAL GEOGRAPHICAL SOCIETY EXPEDITION 1967-1969
CENTRAL BRAZILIAN PLATEAU
State of Mato Grosso. Expedition Base Camp: 12° 49′ S., 51° 46′ W.
Syngonanthus cf. indet.

c. 3 Km. W. of km. 259. Xavantina - Cachimbo Road. Edge of gallery forest, in mud between grass tussocks in wet campo.
D. Philcox, A. Fereira & J. Bertoldo 3316
30th November, 1967

Figure 23. Holoype of *Syngonanthus philcoxii* deposited in K herbarium†

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† http://apps.kew.org/herbcat/getImage.do?imageBarcode=K000640309 [Accessed April 26, 2015]

Syngonanthus rhizonema Ruhland in Engler, Pflanzenr. 13 (IV.30): 269. 1903. Type: Brazil. São Paulo. 29 Apr. 1881, A. Glaziou 13284 (Lectotype designated here: photo B!; Isolectotype: BR, G, photo LE!, NY!, photo P!).

Syngonanthus surinamensis Moldenke, Bull. Torrey Bot. Club 75: 202 (1948). Type: Suriname. Tafelberg, west of Grace Falls, 200 m alt., 26 Aug. 1944, B. Maguire 24502 (Holotype: NY!; Isotype: photo K!, L). ***syn. nov.***

Syngonanthus lanatus var. *glabrescens* Moldenke, Phytologia 46: 155. 1980. Type: Brazil. Mato Grosso: Sararé, 4 Ago 1978, J. M. Pires & M.R. Santos 16392 (Holotype: NY!; Isotype: F!). ***syn. nov.***

Caulescent herbs, 17.5–42 cm tall, viviparous. Roots white, elongate, and spongy. Rosette absent. Aerial stem 3.0–26.5 cm long, villous, with white crooked trichomes, bearing an umbel of 1-20 inflorescences at the apex. Leaves ascendant to lax, equally distributed along the stem, slightly congested at the apex near synflorescence, 2.5–6.0 × 0.01–0.03 cm, linear or narrowly lanceolate, apex acute, sometimes slightly uncinate, pilose to glabrescent, with adpressed trichomes and simple filamentous hairs, veins 5–9 prominent. Spathes 1.4–4.6 cm long, chartaceous, cylindrical, erect, obliquely opened, apex acute to obtuse, tip uncinate, margin entire, not involute, glabrous adaxially, pilose abaxially with capitate filamentous hairs. Scapes erect to flexuous, 2.8–16.1 cm long, green or straw-colored with age, 2–3-costate, pilose with capitate and simple filamentous hairs and adpressed trichomes. Capitula 2–5 mm in diameter, radiate to hemi-spherical. Involucral bracts in 4–5 series, glabrous abaxially, pilose adaxially with simple filamentous hairs, those of the external series 0.8–1.2 × 0.45–0.6 mm, obovate to oblong, apex rounded, cream-colored, those of the internal series progressively longer 1.0–1.5 × 0.4–0.6 mm, almost equaling the flower height, lanceolate, apex acute, cream to white-colored; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 40–60 per capitulum, the staminate and pistillate generally equal in number. Staminate flowers 1.3–1.5 mm long including pedicels; pedicels 0.3–0.5 mm long with filamentous trichomes at insertion with receptacle; sepals 0.75–1.45 mm long, cream, shortly fused at base, cymbiform, chartaceous, oblanceolate or elliptic, apex acute, margin involute, both surfaces glabrous; corolla 0.5–1.0 mm long, fleshy, only the lobes membranous, fused ca. ½ their length, tubular, lobes obtuse to rounded, involute after anthesis, glabrous; filaments partially adnate to the petals, anthers 0.15–0.2 mm long, cream to whitish; pistillodes 3, ca. 0.3 mm long, clavate, papillose at apex. Pistillate flowers 1.3–1.8 mm long including the very short pedicels (sub-sessile); pedicels 0.2–0.3 mm long with filamentous hairs at insertion with receptacle; sepals 1.1–1.8 mm long, obovate to oblong, cymbiform, white to hyaline, chartaceous, pubescent adaxially with capitate filamentous hairs, abaxially glabrous; petals 0.8–1.1 mm long, oblanceolate, lower half of petal fleshy, upper half membranous, fused at the upper margin, free at base and the apex, lobes oblong, acute, cream to whitish, glabrous adaxially, scarcely pilose abaxially with rare simple filamentous hairs at the upper surface; gynoecium 1.0–1.3 mm long; ovary 0.4–0.6 mm long; style column 0.2–0.4 mm long, cream-colored to castaneous; appendages about 0.15 mm long, the glandular apex capitate; style branches simple, about 0.35 mm long. Seeds 0.45–0.5 × 0.25–0.3 mm, ovoid to elliptic, brown-colored, striate with very short pseudotrichomes.

Phenology— The holotype of *Syngonanthus rhizonema* is dated from April and it shows flowers in mature stage (anthesis) and fruit. However, the legitimacy of the data is in doubt as explained below. There are also records to August.

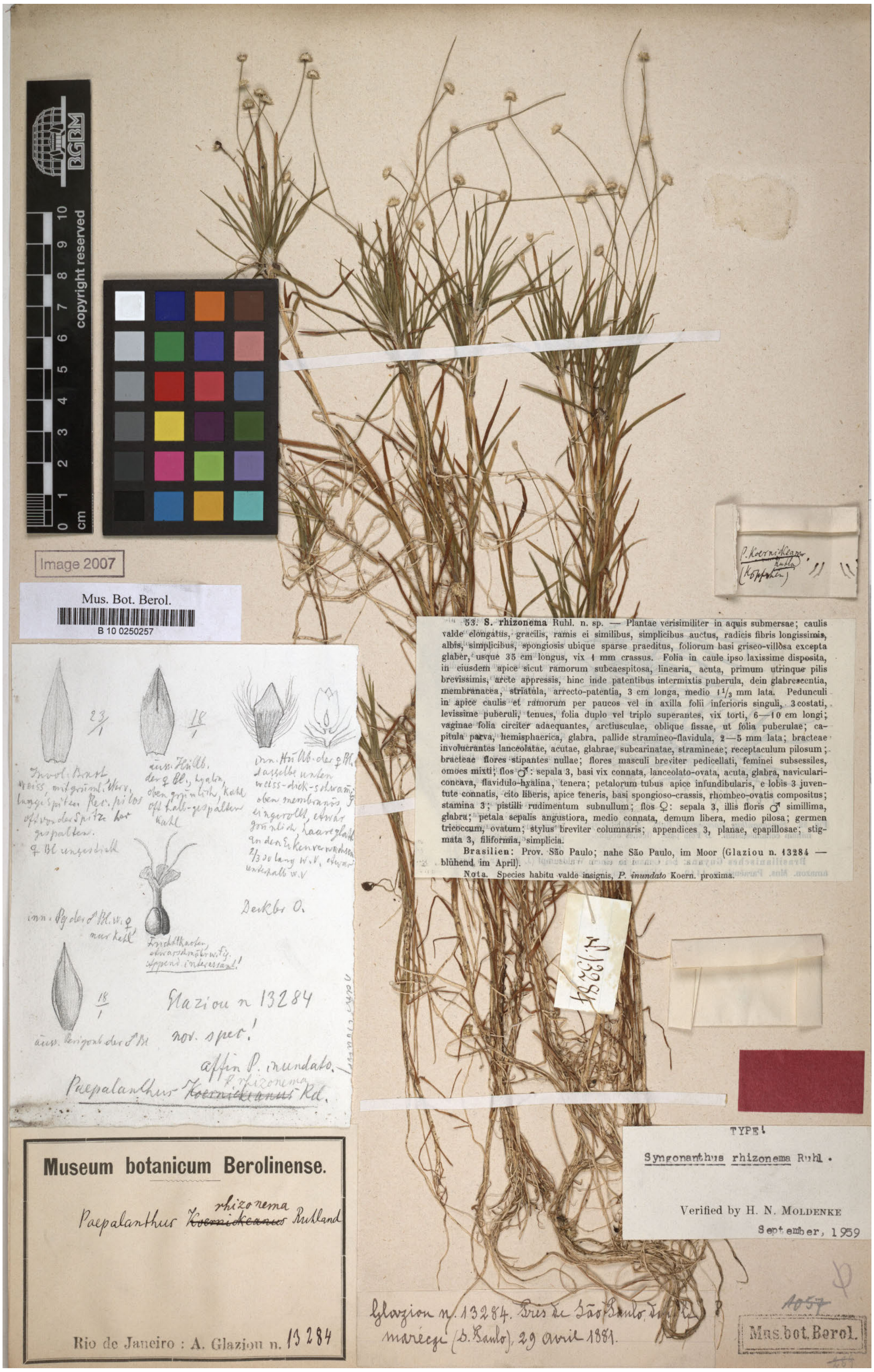
Habitat and Distribution— This species was only known by the holotype. The type locality is São Paulo, a locality with nowaday low probability for occurrence for this taxon. There is no additional information about the locality, the label info only mentions São Paulo state, near city of São Paulo, in swamp. Glaziou's collection data are considered to be questionable or doubtful. A considerable number of Glaziou's collection series appear to have misrepresented collection data, including changes in the name of original collectors, localities, and date of collection (Wurdack 1970). Due to this inaccuracy, it is not possible to be confident about geographical distribution, but probably this taxon is endemic to an unknown area and inhabits very wet soils or even may be aquatic. How we decided to synonymize *S. surinamensis* and *Syngonanthus lanatus* var. *glabrescens* in *S. rhizonema*, now we have a basic notion of the occurrence of this taxon: Mato Grosso (Brazil) and Guiana highlands.

Conservation status— The type of *Syngonanthus rhizonema* was collected two centuries ago and there has not been noted any record for this species in São Paulo or any other region around. São Paulo municipality is highly urbanized, and areas further inland are threatened by industrial farming. Uncertainties surround the real collection locality of the holotype confusing considerations about conservation status for this taxon but much time has passed without new records, and this taxon could well be extinct.

Commentaries— Ruhland described *Syngonanthus rhizonema* based on Glaziou 13284 from a doubtful locality as described above. This species is very peculiar among all *S.* sect. *Carphocephalus* because the type includes viviparous individuals. In addition, the involucral bracts are pilose inside and glabrous outside; and sepals of pistillate flowers have capitate hairs on inside. Its vegetative axis shows elongate and filiform leaves. These leaves are lax and among the largest observed of all species of the section. The aerial stem produces roots throughout its length, which may indicate this species as aquatic or living on riverbanks.

Syngonanthus rhizonema is most similar to *S. caulescens*. This similarity can mainly be attributed to the elongate axis observed in some specimens of *S. caulescens*. However *S. rhizonema* has a receptacle less pilose (vs. usually densely pilose), smaller capitula and leaves filiform (*vs.* lanceolate). Some individuals bear inflorescences laterally from the aerial stem (axillary), a characteristic observed in *S. anomalus*, a species excluded from sect. *Carphocephalus*. Because morphological characteristics are similar, we suppose that *S. rhizonema* also belongs to core *S.* sect. *Carphocephalus*. The evidence is the staminate flowers with fleshy corolla and membranous lobes. Additionally, the pistillate flowers have carnose petals in the lower half, and membranous in the upper half. *S. rhizonema* shares with *S. caulescens*, *S. ruhlandii*, *S. appressus*, *S. androgynus*, *S. mollis, S. discretifolius* and *S. weddellii* this set of characters, potential synapomorphies of this minor group of *S.* sect. *Carphocephalus* (see chapter 2).

The Glaziou collection (number 13284) has multiple materials distributed in some European and American herbaria (B, BR, G, LE, NY, P - syntypes). Echternacht (2012) elected as lectotype the material deposited in Herbarium Berolinense (B), but this information has not been formally published; then, this lectotypification has not been effected, yet. Our opinion is in accordance, because this material has more individuals on the sheet, with vegetative and reproductive structures well developed. Furthermore, that institution provides free access to check the digital collection-type in the website. Since Ruhland worked at B and the sheet was seen and annotated by him, this is another criterion for type selection.



53. **S. rhizonema** Ruhl. n. sp. — Plantae verisimiliter in aquis submersae; caulis valde elongatus, gracilis, ramis ei similibus, simplicibus auctus, radicis fibris longissimis, albis, simplicibus, spongiosis ubique sparse praeditus, foliorum basi griseo-villosa excepta glaber, usque 35 cm longus, vix 1 mm crassus. Folia in caule ipso laxissime disposita, in eiusdem apice sicut ramorum subcaespitosa, linearia, acuta, primum utrinque pilis brevissimis, arcte appressis, hinc inde patentibus intermixtis puberula, dein glabrescentia, membranacea, striatula, arrecto-patentia, 3 cm longa, medio $1\frac{1}{3}$ mm lata. Pedunculi in apice caulis et ramorum per paucos vel in axilla folii inferioris singuli, 3 costati, levissime puberuli, tenues, folia duplo vel triplo superantes, vix torti, 6—10 cm longi; vaginae folia circiter adaequantes, arctiusculae, oblique fissae, ut folia puberulae; capitula parva, hemisphaerica, glabra, pallide stramineo-flavidula, 2—5 mm lata; bracteae involucrantes lanceolatae, acutae, glabrae, subcarinatae, stramineae; receptaculum pilosum; bracteae flores stipantes nullae; flores masculi breviter pedicellati, feminei subsessiles, omnes mixti; flos ♂: sepala 3, basi vix connata, lanceolato-ovata, acuta, glabra, naviculari-concava, flavidulo-hyalina, tenera; petalorum tubus apice infundibularis, e lobis 3 juventute connatis, cito liberis, apice teneris, basi spongioso-crassis, rhombeo-ovatis compositus; stamina 3; pistilli rudimentum subnullum; flos ♀: sepala 3, illis floris ♂ simillima, glabra; petala sepalis angustiora, medio connata, demum libera, medio pilosa; germen tricoccum, ovatum; stylus breviter columnaris; appendices 3, planae, epapillosae; stigmata 3, filiformia, simplicia.

Brasilien: Prov. São Paulo; nahe São Paulo, im Moor (Glaziou n. 13284 — blühend im April).

Nota. Species habitu valde insignis, *P. inundato* Koern. proxima.

Museum botanicum Berolinense.

Paepalanthus ~~Koernickeanus~~ rhizonema Ruhland

Rio de Janeiro : A. Glaziou n. 13284

TYPE!

Syngonanthus rhizonema Ruhl.

Verified by H. N. Moldenke
September, 1959

Glaziou n. 13284. Près de São Paulo, dans le marécage (S. Paulo), 29 avril 1881.

Figure 24. Lectotype of *Syngonanthus rhizonema* deposited in herbarium B.‡‡

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‡‡ Röpert D. (ed.) 2000+ [continuously updated]: Digital specimen images at the Herbarium Berolinense. - Published at http://ww2.bgbm.org/herbarium/ (Barcode: B 10 0250257 / ImageId: 255853) [accessed 24 Sep 2014].

Syngonanthus ruhlandii M.T.C.Watan., ***sp. nov.*** Type: Brazil. Bahia: Luís Eduardo Magalhães, 30 km em direção a Brasília, Rio de Ondas, na beira do córrego, 12º22’38’’S 45º51’55’’W, 28 July 2012, *M. Watanabe & W. Watanabe 394* (Holotype SPF!; Isotypes ALCB!, F!).

Caulescent herbs, 22–37(–55) cm tall, decumbent, ocasionally branching at base. Roots white, 0.05–0.25 mm in diameter, spongy. Rosette absent. Aerial stem 7–26(–33) cm long, villous, with white crooked trichomes, sometimes branched, bearing an umbel of 2-14(–30) inflorescences at the apex. Leaves oblique to adpressed, unequally distributed through the stem, scarce near the roots, congested at the apex near synflorescence, 3–20 × 0.1–1.9 mm, linear or narrowly lanceolate, apex acute, glabrescent or pilose with simple filamentous hairs or adpressed trichomes, veins 5–10 prominent. Spathes 1.2–3.2(–3.8) cm long, chartaceous, cylindrical, erect, obliquely opened, apex obtuse, enlarged, tip uncinate, margin entire, not involute, glabrous adaxially, pilose abaxially with capitate filamentous hairs and adpressed trichomes. Scapes erect to flexuous, 3–26 cm long, green or straw-colored with age, 3-costate, pilose, pubescent near the apex with simple and capitate filamentous hairs and adpressed trichomes. Capitula 3.0–6.5 mm in diameter, radiate. Involucral bracts in 3–5 series, those of the external series 1.7–2.2 × 0.6–0.9 mm, ovate-lanceolate, triangular-ovate, apex acute, white to cream-colored, glabrous, those of the internal series progressively longer 2.3–3.0 × 0.7–0.9 mm, almost equaling the flower height, elliptic, apex acute, white-colored; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 60–130 per capitulum, the staminate three times more numerous than pistillate. Staminate flowers 2.0–2.7 mm long including pedicels; pedicels 0.3–0.6 mm long with filamentous trichomes at insertion with receptacle and bottom part of pedicel; sepals 2.0–2.7 mm long, cream, shortly fused at base, cymbiform, chartaceous, upper part white, lower part hyaline, lanceolate to elliptic, apex acuminate, margin involute, glabrous adaxially, pilose abaxially with simple filamentous hairs; corolla 1.15–1.85 mm long, fleshy, fused ca. 4/5 their length, tubular, lower half fleshy, upper half membranous, lobes obtuse, involute after anthesis, glabrous; filaments adnate to the petals, anthers 0.20–0.35 mm long, cream to whitish; pistillodes 3, 0.3–0.5 mm long, clavate, papillose at apex. Pistillate flowers 2.5–2.9 mm long including the short pedicels, frequently sub-sessile; pedicels 0.15–0.4 mm long with filamentous hairs at insertion with receptacle; sepals 2.0–2.5 mm long, lanceolate, cymbiform, upper part white, lower part hyaline, chartaceous, glabrous; petals 1.4–2.6 mm long, obtrullate, fused at the upper margin, free at base and the apex, lobes obtuse, lower half of petal fleshy, upper half membranous, glabrous adaxially, pilose abaxially with simple filamentous hairs; gynoecium 1.3–2.0 mm long; ovary 0.4–0.8 mm long; style column 0.2–0.35 mm long, cream-colored to castaneous;

appendages 0.2–0.4 mm long; style branches simple, 0.6–1.0 mm long. Seeds 0.5–0.7 × 0.25–0.40 mm, ovoid or elliptic, dark brown-colored, striate with very short pseudotrichomes.

Phenology— *Syngonanthus ruhlandii* has been found blooming from July to September. Mature fruits also were observed in the same period.

Habitat and Distribution— This new species is restricted to Luís Eduardo Magalhães (municipality of Bahia state, Brazil), occurring along riverbanks in the Cerrado vegetation. This area is threatened by the extensive soy crops. One population was collected near the highway, in a place that frequently suffers anthropic activities (casual tourism).

Conservation status— Following the criterion B2ab of IUCN (2014), *S. ruhlandii* could be considered as critically endangered. This species is represented by endemic populations in unprotected areas.

Commentaries— *Syngonanthus ruhlandii* is a new species based on molecular sequences and morphological characters. It is named in honor of Wilhelm Otto Eugen Ruhland, a noteworthy German botanist, for his significant contributions to Eriocaulaceae in the last century. He did the last worldwide revision for the family, and one of his main contributions was to describe new species and genera, including *Syngonanthus*.

Syngonanthus caulescens is characterized by extensive morphological variability and probably is the most related species to *Syngonanthus ruhlandii.* Maybe this is the reason that it had previously been identified in herbaria as *S. caulescens*. A notable difference between them resides in habit. *Syngonanthus caulescens* stands upright, whereas *Syngonanthus ruhlandii* is decumbent.

The new taxon is characterized by a large number of leaves on aerial stem, mainly concentrated at top just below the insertion of inflorescence (spathes and scapes), giving a robust appearance to this region. Leaves are short and sparse near the roots, frequently deciduous, gradually becoming more congested toward the apex, unlike *S. caulescens* with leaves more evenly distributed. The disposition of leaves is ascending, but not completely adpressed as observed in *Syngonanthus appressus*. Some lateral branches can grow from aerial stem, especially when parts of the prostrate stem are submerged in water or covered up by soil.

Floral traits overlap those of *Syngonanthus caulescens* except for thinner appendages (nectariferous portion of style). Petals of pistillate flowers are carnose in the lower half, and membranous in the upper half, a character shared with other *Carphocephalus* species such as *S. appressus*, *S. caulescens* and *S. weddellii*. Sometimes, staminate flowers have a membranous corolla (usually observed in younger flowers). This fact reveals that the condition of thickened corolla may depend on phenological phase or might be an intrinsic morphological variation, something similar with other species in the section (*S. fischerianus*, *S. hygrotrichus*).

Phylogenetic analysis of molecular data of *Syngonanthus* (see chapter 2) demonstrates considerable changes of base pairs in the five molecular markers tested. The differences involve duplication in one stretch of the sequence generated by *trn*L–*trn*F plastidial marker. The mentioned part is deleted in sampled species of the *Syngonanthus* sect. *Carphocephalus*, although is present in most species of the genus. Other differences include simple changes of base pairs for ITS, ETS, *rps*16 and *psb*A-*trn*H. For futher details, see below the comparison between sequences of *S. ruhlandii* and *S. caulescens*, the most phylogenetically related species.

Nucleotide differences in the sequence for *trn*L-F marker:

85 89 171 524 542 572 575 826 830 875 882 1020 1022 1071 1077
AAAAA...A...CAGTTATTCCATAGTTTGA...GGAT...TCTTT...CAAAATGG...TGC...AATAAAG ***S. ruhlandii*** AACAA...G...CCGTTATTACAGAGTTTTA...GGAG...TATTT...AAAAATGA...TTC...———AAG ***S. caulescens***

Nucleotide differences in the sequences for *psb*A-*trn*H, ITS and ETS markers, respectively:

108 121 | 88 95 144 145 335 337 631 635 683 687 469 | 477
TTGAGTCAGCCCAA | CCCGCGAA...CT...CCC...CGTTA...GGTGG | TCCGTAGGG ***S. ruhlandii***
TTGAGCCAGCCCAA | CCCGTGAA...CC...–CC...CGTGA...GGCGG | TCCGCAGGG ***S. caulescens***

Nucleotide differences in the sequence for *rps*16 marker:

21 25 58 62 110 115 128 132 197 200 278 280 318 327 371 373 481 494 516 518 564 567
TTGGC...TGTGC...TATTAT...TACAA...GATC...AGT...TCAGTTTTCG...TGA...GAAACACTTTTTAA...CCC...CCGC...
TTAGC...TGGGC...TAATAT...TAAAA...GACC...ATT...GCAGTTTTCT...TAA...AAAAGACTTTTTTT...CTC...CTGC...

576 579 600 604 619 622 760 764 803 807 848 852
TTTA...GAAA...GATT...AATAA...TTTTT...TACAT ***S. ruhlandii***
TTGA...G–AA...GACT...AATCA... TTGTT...TATAT ***S. caulescens***

Specimens examined: **BRAZIL**. **Bahia**: Luís Eduardo Magalhães, BR-020, próximo ao Rio de Ondas, ca. 30 km de Luís Eduardo Magalhães em direção a Brasília, buritizal degradado com cerrado adjacente, 12º22'38"S 45º51'55"W, 21 Jul 2000, *Souza et al. 24414* (ESA, SPF), idem, 12º18'28"S, 45º43'06"W, 21 Sep 2003, *Xavier et al. 76* (ALCB).

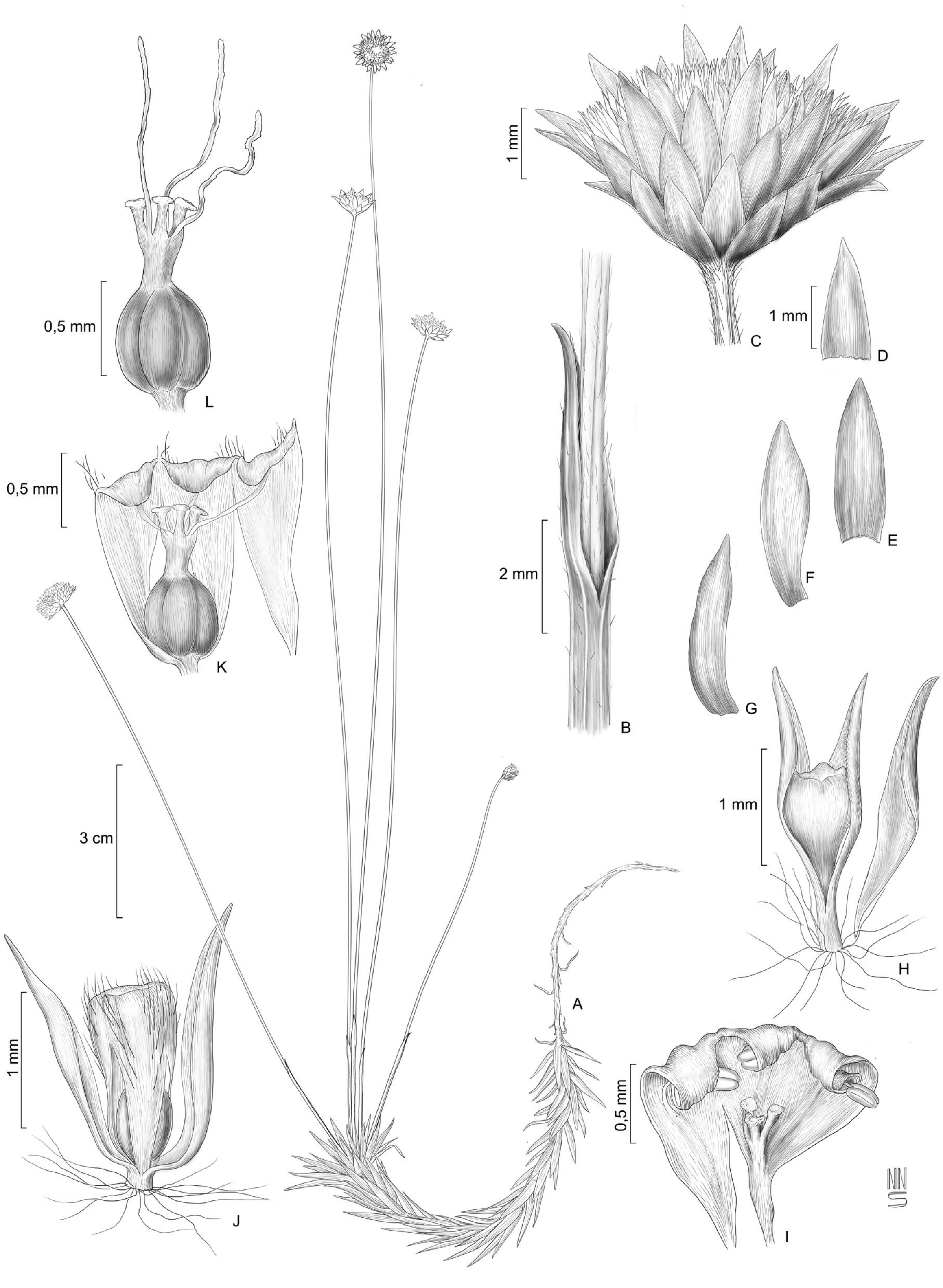

Figure 25–*Syngonanthus ruhlandii* (based on *Watanabe & Watanabe 394*). **A.** Habit; **B.** Spathe detail; **C.** Capitulum detail; **D**–**G.** From outermost to innermost series of involucral bracts; **H.** Staminate flower; **I.** Staminate flower dissected showing pistillodes; **J.** Pistillate flower with one sepal removed; **K.** Pistillate flower dissected; **L.** Gynoecium.

UNIVERSIDADE DE SÃO PAULO
Escola Superior de Agricultura "Luiz de Queiroz"
HERBÁRIO ESA

ESA 66956

ERIOCAULACEAE

Syngonanthus

Det.:

BRASIL. Estado de Bahia. Município de Barreiras. BR-020, próximo ao Rio de Ondas, ca. de 30 km do Distrito de Luis Eduardo Magalhães em direção a Brasília. 12o22'38"S, 45o51'55"W. Buritizal degradado com cerrado adjacente.

Obs.: Erva; capítulos alvos.

Col.: V.C.Souza, J.P.Souza, G.O.Romão 24414

Data: 21/Jul/00

Prensado em álcool

Figure 26: Paratype of *Syngonanthus ruhlandii* deposited in SPF herbarium.

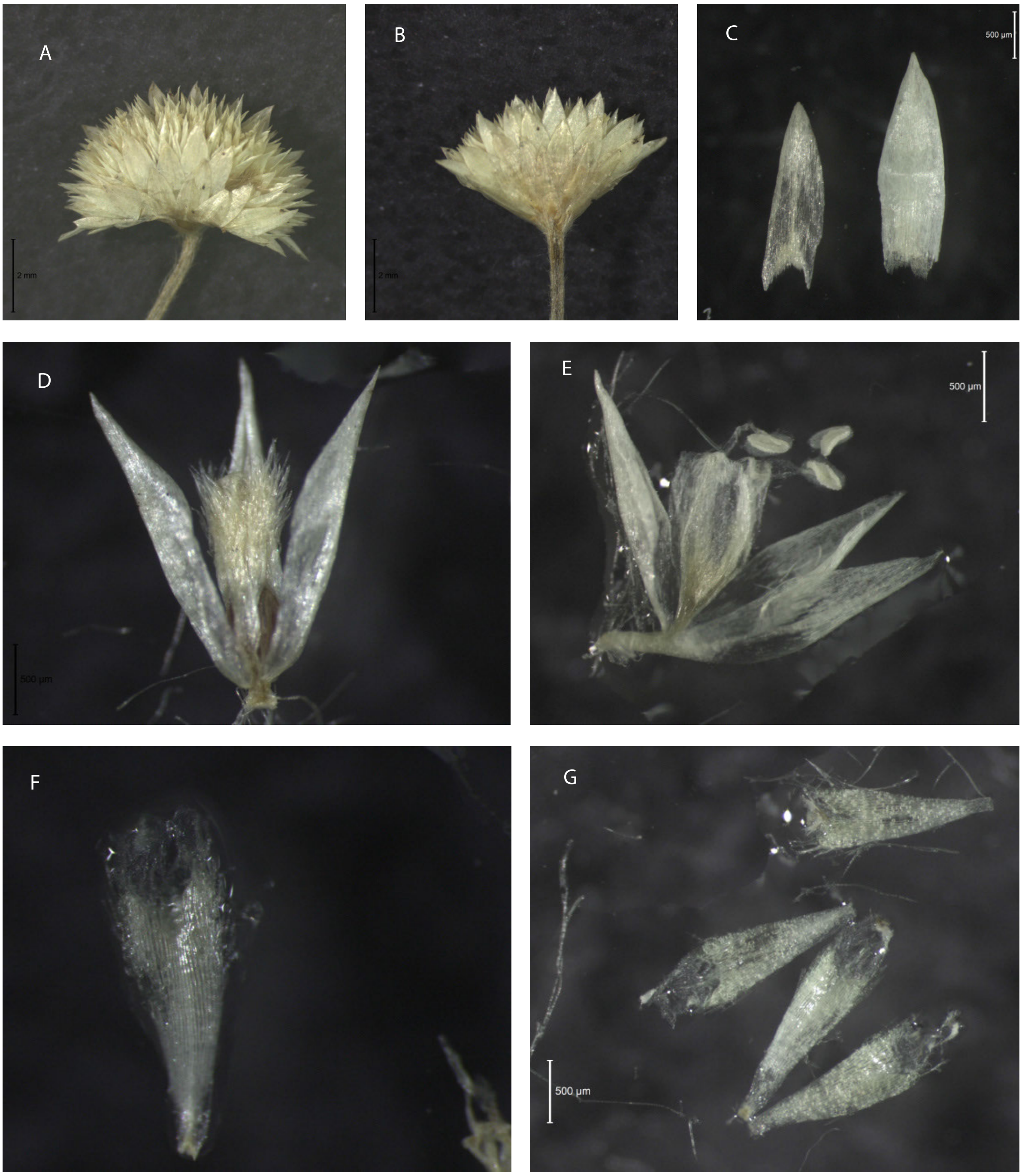

Figure 27. *Syngonanthus ruhlandii*. **A-B.** Capitulum; **C.** Involucral bracts; **D.** Pistillate flower; **E.** Staminate flower showing corolla partly membranous and sepals slightly thickened in the upper half. **F-G.** Carnose petals of pistillate flower showing lobes membranous.

Syngonanthus weddellii Moldenke, Phytologia 3(8): 425. 1951. Type: Brazil. Goiás: Amaro Leite, dans le marais, Sept-Oct 1844, *H.A. Weddell 17, cat. n. 2725* (Holotype: BR; Isotype: P, NY fragm!)

Caulescent herbs, 27.5–62.5 cm tall, sometimes branching at the apex. Roots white, spongy. Rosette absent. Aerial stem 12.5–17.5 cm long, villous, with white crooked trichomes, bearing an umbel of 13-35 inflorescences at the apex. Leaves patent to slightly oblique, equally distributed through the stem, 0.5–2.3 × 0.1–0.3 cm, linear-lanceolate, acute, pilose with capitate filamentous hairs and adpressed trichomes, veins 3–7 prominent. Spathes 2.5–5 cm long, chartaceous, cylindrical, erect, obliquely opened, apex obtuse, tip uncinate, margin entire, not involute, glabrous adaxially, glabrescent abaxially with capitate filamentous hairs and adpressed trichomes. Scapes erect, 8.5–36.5 cm long, green or golden/straw-colored with age, 3-costate, pilose, pubescent near the apex with capitate and simple filamentous hairs and adpressed trichomes. Capitula 4–6 mm in diameter, radiate. Involucral bracts in 4–6 series, glabrous adaxially, pilose abaxially, with adpressed trichomes, those of the external series 1.5–1.8 × 0.6 mm, triangular-ovate to oblong, apex acute or obtuse, cream-colored, golden at base, those of the internal series progressively longer 2.6–3,3 × 0.7–0.8 mm, almost equaling the flower height, oblanceolate, apex acute, cream-colored; receptacle obconic, pilose. Floral bracts absent. Flowers 3-merous, 45–85 per capitulum, the staminate slightly more numerous than pistillate. Staminate flowers 1.6–2.2 mm long including pedicels; pedicels 0.3–0.6 mm long, filamentous trichomes at insertion with receptacle and bottom part of pedicel; sepals 1.5–2.3 mm long, cream, shortly fused at base, cymbiform, chartaceous, lanceolate or elliptic, apex acute, margin involute, pilose adaxially especially at central part, with adpressed trichomes, glabrous abaxially; corolla 0.85–1.5 mm long, thick, fused, tubular, lobes obtuse to rounded, involute after anthesis, glabrous; stamens adnate to the petals, anthers 0.2–0.3 mm long, cream to whitish; pistillodes 3, ca. 0.4 mm long, clavate, papillose at apex. Pistillate flowers 1.8–2.2 mm long including pedicels; pedicels 0.25–0.35 mm long, filamentous hairs at insertion with receptacle; sepals 1.6–2.1 mm long, lanceolate, cymbiform, chartaceous, white to hyaline, pubescent adaxially, especially at upper part, with adpressed trichomes, abaxially glabrous; petals 1.15–1.45 mm long, oblanceolate, connate at the upper margin, free at base and apex very top, apex acute to obtuse, lower half of petal fleshy, upper half membranous, cream-colored, pilose abaxially with simple filamentous hairs, glabrous adaxially; gynoecium 0.9–1.6 mm long; ovary 0.5–0.8 mm long; style column 0.25–0.5 mm long, castaneous; appendages 0.15–0.25 mm long; stigmatic branches simple, ca. 0.3 mm long. Seeds about 0.5 × 0.3 mm, ovoid, brown-colored, striate with very short pseudotrichomes.

Phenology— *Syngonanthus weddellii* was previously only known by the type collection and there is no precise indication about date (between September and October). A recent new collection of this species found plants with flowers in mature stage and fruit in July.

Habitat and Distribution— Although there is no precise localization in the holotype, the expedition in which Dr. Hugh Algernon Weddell participated went down the Rio Araguaia until it joined the Rio Tocantins (Goodman 1972). *S. weddellii* was recently recollected in Tocantins state (Brazil) in Cerrado phytophysiognomy, specifically in *Campo limpo* with "buritis" and next to margin of Rio Tocantins.

Conservation status— *S. weddellii* could be considered an endangered species. Only two collections are known at the moment. This species falls within B1 (extent of occurrence $< 5,000$ km^2) and B2a (number of locations ≤ 5) criteria according to IUCN 2014.

Commentaries—The petals of the pistillate flowers of *S. weddellii* Moldenke are similar to the petals of *S. caulescens*, *S. appressus* and *S. ruhlandii*, and also similar to the petals of bisexual flowers of *S. androgynus*. These species have the same texture and form of petals: connate at the upper margin, free at base and apex very top, lower half of petal fleshy, upper half membranous. Vegetatively, *S. weddellii* is differentiated from these species by more congested and patent leaves on the aerial stem.

The most recent material collected of *S. weddellii* (*Watanabe & Watanabe 381*) is slightly different from the holotype. Mainly, these differences are represented by the short aerial stem and smaller capitula in the specimens from Ipueiras – Tocantins state (the recent collection). The type collection is represented by taller and robust plants with many scapes in the same individual. However, floral traits are very similar and there is no difference in pistillate and staminate flowers between these collections.

Specimens examined—**BRAZIL**. **Tocantins**: Ipueiras, Pântano do Papagaio. Fazenda Ouro Verde, divisa com a fazenda União, campo limpo próximo a buritis, em área com gado, 11°05'46.5"S 48°31'22.8"W , 22 Jul 2012, *Watanabe & Watanabe 381* (F, SPF).

Figure 28. Isotype of *Syngonanthus weddellii* deposited in P herbarium.[§§]

[§§] Available at http://dsiphoto.mnhn.fr/sonnera2/LAPI/scanE/E20140120/P01827914.jpg [Accessed September 24, 2014]

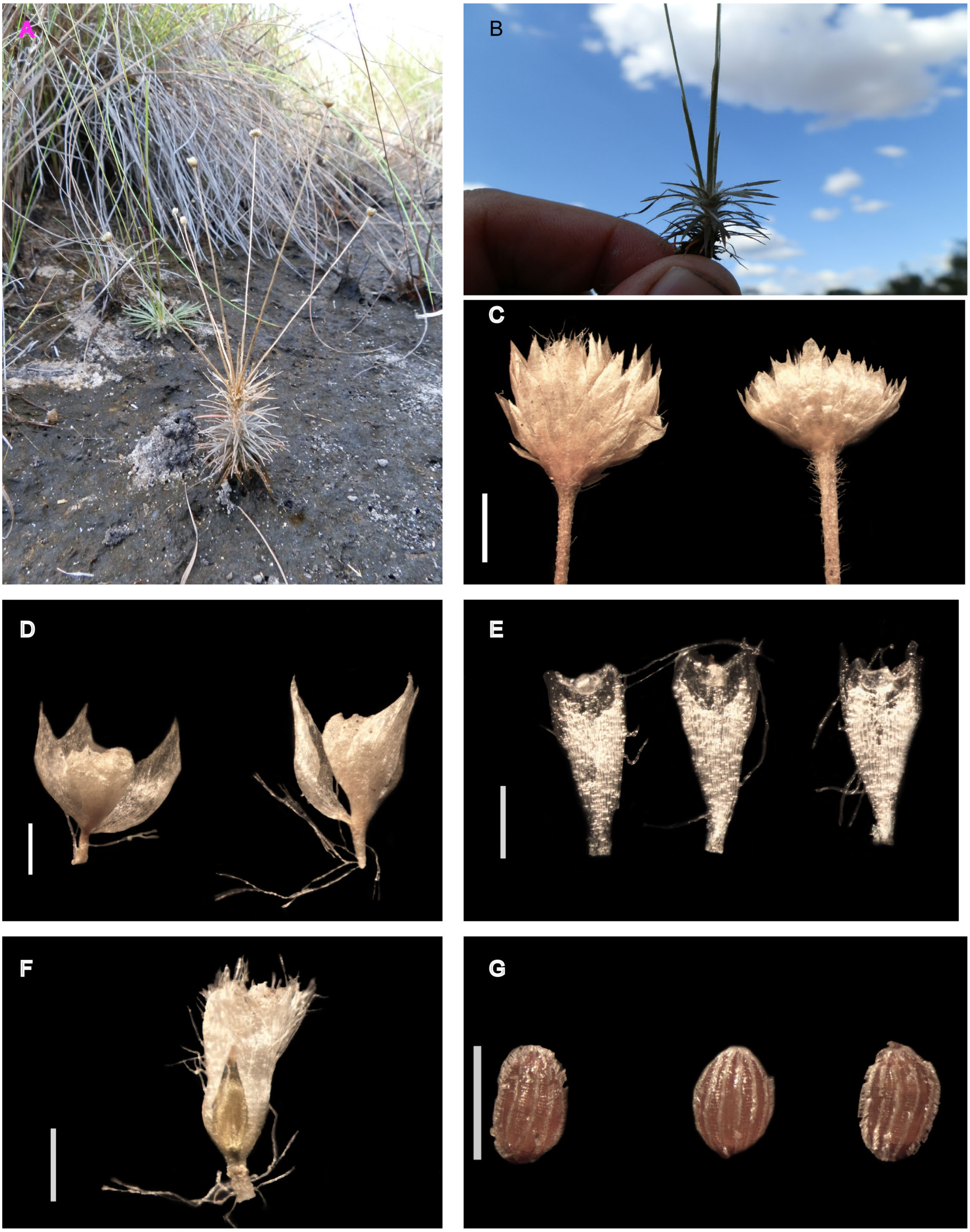

Figure 29. *Syngonanthus weddellii*. **A-B**. Habit of *S. weddellii* showing aerial stem with patent leaves. **C.** Capitula. **D.** Staminate flowers. **E.** Petals of pistillate flowers showing thick and membranous parts. **F.** Pistillate flower with sepals removed. **G.** Seeds. Scale bars: C= 2 mm; D-G= 0.5 mm. Based on *Watanabe & Watanabe 381*.

Incertae Sedis

Syngonanthus caulescens var. ***douradensis*** Moldenke, Phytologia 21(6): 418. 1971. Type: Brazil. Goiás: Serra Dourada, in shallow water in an area of campo and cerrado on the sandstone summit, 800 m alt., about 20 km southeast of Goiás Velho, 18 Jan. 1966, Irwin et al. 11753 (Holotype: NY!).

The holotype of *Syngonanthus caulescens* var. *douradensis* has capitula very young, with immature flowers. However, the roots are not similar to *S. caulescens*. Probably it is a *Paepalanthus* species but botanical field trips to the original area of the holotype may be necessary to confirm it.

Excluded taxa

Syngonanthus appressus var. ***chapadensis*** Moldenke, Phytologia 25(3): 118. 1973. Type: BRAZIL. Goiás, Chapada dos Veadeiros, gallery forest and adjacent wet campo (brejo), ca. 20 km N of Alto do Paraíso, elev. ca. 1250m, 19 Mar 1971, Irwin et al. 32203 (Holotype: LL!).

Notes: Echternacht 2012 detected this taxon as belonging to *Paepalanthus*. A taxonomic treatment has been prepared for this taxon, by Echternacht & Watanabe, involving a new name, a new combination and a new status. This plant was recently rediscovered by Watanabe in 2012 near the Chapada dos Veadeiros region.

Syngonanthus anomalus (Koern.) Ruhland in Engler, Pflanzenr. 13 (IV.30): 267. 1903. *Paepalanthus anomalus* Koern., i*n* Fl. Bras. (Martius) 3(1): 469. 1863. *Dupatya anomala* (Koern.) Kuntze, Revis. Gen. Pl. 2: 745. 1891. Type: Brazil. Amazonas. Crescit secundum fluvium Rio Negro inter Barcellos et S. Gabriel, Dec 1851, Spruce 2039 (Syntypes: C, LE, K, P)

Notes: The phylogenetic placement of *S. anomalus* always was controversial. It can be attributed to the polyphyletic condition of *Syngonanthus* sect. *Carphocephalus*, when included *S. anomalus* as representative taxon of this section (Andrade et al. 2010; Echternacht et al. 2014). Our results corroborated the placement of *S. anomalus* outside of the group considered as *S.* sect. *Carphocephalus* in our circumscription. *S. anomalus* does not share characteristics of *S.* sect. *Carphocephalus*, especially those of the "core group", as petals of pistillate flowers carnose in the lower half, exclusively terminal inflorescences and sepals slightly thickened in the upper half. The corolla of staminate flower is rigid, not spongy. The convergence of characteristics is homoplastic for many characters in *Syngonanthus* and it may be an example of this.

Syngonanthus philodicoides (Koern.) Ruhland in Engler, Pflanzenr. 13 (IV.30): 266. 1903. *Paepalanthus philodicoides* Koern., *in* Fl. Bras. (Martius) 3(1): 469. 1863. *Dupatya philodicoides* (Koern.) Kuntze, Revis. Gen. Pl. 2: 746. 1891. Type: Brazil. Goiás: In prov. Goyazensis campis arenosis humidis prope Salinas, H.A. Weddell 2126 (Syntypes: P BR, P, NY!).

Notes: Koenicke (1863) described this species and *S. anomalus* in *Paepalanthus* subg. *Carphocephalus* because these taxa have staminate flowers with a carnose corolla. Ruhland (1903) transferred these species to *Syngonanthus* in *S.* sect. *Carphocephalus*, basically following the concepts adopted by Koernicke (1863). *Syngonanthus philodicoides* is morphologically similar to species belonging to a new emergent clade in our phylogenetic study (see chapter 2), the "*Philodice* group". Species in this clade have flowers with corolla not involute after anthesis and petals of pistillate flowers with lower half membranous and upper half carnose.

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Conclusões

As espécies descritas no primeiro capítulo foram de fundamental importância para o estudo taxonômico do grupo e entendimento de padrões no gênero. *Syngonanthus androgynus*, a nova espécie descrita no capítulo 1.2, foi a primeira espécie com flores exclusivamente trímeras e bissexuais na família, o que nos levou a concluir que a evolução de flores bissexuais no gênero ocorreu, pelo menos, mais de uma vez. A filogenia de *Syngonanthus* com uma amostragem expandida, abrangendo uma maior variabilidade morfológica e geográfica do gênero (capítulo 2), alterou o cenário até então desenhado recentemente para Eriocaulaceae. Neste estudo, *Syngonanthus* emergiu como um gênero monofilético e em uma linhagem completamente diferente dos demais gêneros de Paepalanthoideae, sendo grupo-irmão dos demais gêneros reunidos. Este estudo também mostrou que classificações infragenéricas históricas não se sustentam e novas circunscrições são necessárias. Por fim (capítulo 3), uma dessas propostas é posta em prática, com uma delimitação mais precisa para *Syngonanthus* sect. *Carphocephalus*, numa tentativa de reestabelecer a condição monofilética do grupo. Nesta revisão, duas novas espécies são apresentadas e um táxon tem seu status alterado. Também são apresentados novos sinônimos e lectotipificações.