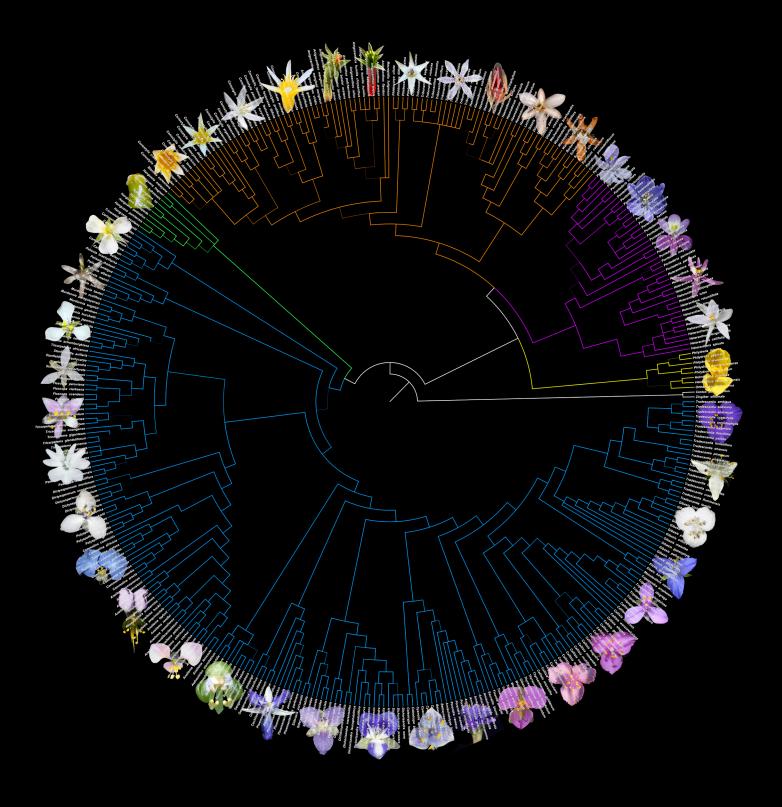
Sistemática de Commelinales com ênfase em linhagens Neotropicais

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

Orientador: Dr. Jefferson Prado

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Prof.(a) Dr.(a)	Prof.(a) Dr.(a)	

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memoriam), e minha afilhada, Roberta de Oliveira Giardini Preisner. Vocês são as
luzes que me guiam, sempre fazendo eu me esforçar para ser a melhor versão de mim
mesmo.

EPÍGRAFE

I don't need you to respect me, I respect me
I don't need you to love, I love me
But I want you to know you could know me
If you change your mind
If you change your mind...

Rebecca Sugar, Steven Universe

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RESUMO

Commelinales é uma pequena e bem sustentada ordem de monocotiledôneas, atualmente posicionada no clado das Commelinídeas, juntamente com Zingiberales (seu grupo-irmão), Poales, Arecales e Dasypogonales. A ordem é composta por Commelinaceae, Haemodoraceae, Hanguanaceae, Philydraceae e Pontederiaceae, e compreende 60 gêneros e ca. 1080 espécies. Apesar do seu relativamente pequeno número de gêneros e espécies, Commelinales é geografica-, ecológica- e morfologicamente bastante diversa. A ordem apresenta uma distribuição Pantropical, mas alcança regiões temperadas em algumas partes do mundo. A relação entre as cinco famílias de Commelinales é atualmente bem compreendida e fortemente sustentada. Entretanto, Commelinales é a ordem menos estudada dentre as monocotiledôneas do ponto de vista evolutivo e taxonômico. Em sua circunscrição atual, a ordem é exclusivamente circunscrita com base em caracteres moleculares, carecendo de qualquer tipo de suporte morfológico. Assim, no presente trabalho foi realizado um estudo abrangente da morfologia da ordem e suas famílias, visando: (1) apresentar uma nova hipótese filogenética para Commelinales com base em dados combinados; (2) circunscrever morfologicamente Commelinales; e (3) revisitar sua classificação. Como resultado desse estudo são apresentados trabalhos de cunho taxonômico e sistemático para as três famílias ocorrentes no Neotrópico, que também representam as três maiores famílias da ordem (i.e., Commelinaceae, Haemodoraceae e Pontederiaceae), assim como é proposta uma nova classificação para Commelinales com base na combinação de dados moleculares com uma grande matriz morfológica.

Palavras-chave. Commelinídeas, filogenia, monocotiledôneas, morfologia, taxonomia

ABSTRACT

Commelinales is a small and well-supported monocot order, currently placed in the commelinid monocots, together with Zingiberales (its sister-group), Poales, Arecales, and Dasypogonales. The order is composed of Commelinaceae, Haemodoraceae, Hanguanaceae, Philydraceae, and Pontederiaceae, and comprises 60 genera and ca. 1,080 species. Despite its relatively small number of genera and species, Commelinales is geographically, ecologically and morphologically very diverse. The order presents a Pantropical distribution, but also reaching temperate regions in some parts of the globe. The relationship between its five families is currently wellunderstood and statistically well-supported. Nonetheless, Commelinales is the least studied monocot order from evolutionary and taxonomic points of view. In its current circumscription, it is solely circumscribed by molecular data, lacking any kind of morphological support. Thus, in the present thesis a comprehensive study of the morphology of the order and its families was carried out, with the aim: (1) presenting a new phylogenetic hypothesis for Commelinales, based on the combination of molecular and morphological data; (2) morphologically circumscribe Commelinales; and (3) revisit its classification. As a result, I provide taxonomic and systematic studies for the three families recorded for the Neotropics, which are also the largest in the order (i.e., Commelinaceae, Haemodoraceae, and Pontederiaceae), together with a new classification for Commelinales, based on the combination of molecular data and an extensive morphological matrix.

Keywords. Commelinid, monocots, morphology, phylogeny, taxonomy

INTRODUÇÃO GERAL

Commelinales é uma pequena e bem sustentada ordem de monocotiledôneas, atualmente posicionada no clado das Commelinídeas, juntamente com Zingiberales (seu grupo-irmão), Poales, Arecales e Dasypogonales (Hertweck et al. 2015; Givnish et al. 2018). A ordem é composta pelas famílias Commelinaceae, Haemodoraceae, Hanguanaceae, Philydraceae e Pontederiaceae (Givnish et al. 1999, 2006, 2018; Chase et al. 2000, 2006; Savolainen et al. 2000; Soltis et al. 2000; Graham et al. 2002, 2006; Davis et al. 2004; Saarela et al. 2008; Hertweck et al. 2015; APG IV 2016), compreendendo 60 gêneros e ca. 1080 espécies (Hamann 1966, 1998; Simpson 1990, 1998b; Faden & Hunt 1991; Bayer et al. 1998; Faden 1998; Leong-Škorničková & Boyce 2015; Pellegrini 2017a, 2017b; Pellegrini et al. 2018; presente estudo). Apesar do seu relativamente pequeno número de gêneros e espécies, comparado a outras ordens monocotiledôneas. Commelinales é geografica, ecológica morfologicamente bastante diversa (Saarela et al. 2008). A ordem apresenta uma distribuição Pantropical, alcançando regiões temperadas em algumas partes do mundo, especialmente devido a ampla distribuição de suas três maiores famílias, Commelinaceae, Haemodoraceae e Pontederiaceae (Stevens 2001-em diante). Em relação às famílias, a Australásia representa o centro de diversidade de Hanguanaceae, Haemodoraceae e Philydraceae (Hamann 1966, 1998; Simpson 1990, 1998b; Bayer et al. 1998). Por outro lado, Pontederiaceae tem os Neotrópicos como centro de diversidade, especialmente o Brasil (Pellegrini & Horn 2017; Pellegrini et al. 2018). Por último, Commelinaceae apresenta dois centros de diversidade Neotropicais (i.e., México e Brasil; Hunt 1983; Aona 2008; Pellegrini 2017b) e dois Paleotropicais (i.e., África e Ásia; Faden 1991, 2012; Nandikar & Gurav 2015; Pellegrini et al. 2016).

Commelinales é a ordem menos estudada dentre as monocotiledôneas do ponto de vista evolutivo e taxonômico, tendo sofrido as mudanças mais marcantes em sua composição entre os diferentes sistemas de classificação (Givnish et al. 1999; Chase 2004; Wilkin et al. 2005; Saarela et al. 2008). A única família consistentemente associada à Commelinales foi a sua família-tipo, Commelinaceae, juntamente com Mayacaceae. A maioria das famílias, tradicionalmente posicionadas em Commelinales (i.e., Eriocaulaceae, Mayacaceae, Rapateaceae, Restionaceae e Xyridaceae), está atualmente posicionada em Poales sensu APG (Givnish et al. 1999; Chase 2004; APG

IV 2016), enquanto Dasypogonaceae é posicionada em Arecales (Hertweck et al. 2015; APG IV 2016) ou aceita em sua própria ordem, Dasypogonales (Givnish et al. 1999, 2018). Por outro lado, as famílias atualmente incluídas em Commelinales foram raramente consideradas como proximamente relacionadas à Commelinaceae (Givnish et al. 1999; Chase 2004). Haemodoraceae, Philydraceae e Pontederiaceae foram geralmente consideradas como, mais ou menos, proximamente relacionadas, apesar de terem sido posicionadas em diferentes ordens ao longo dos vários sistemas de classificação propostos (Simpson 1990; Chase 2004). Além disso, Hanguanaceae foi historicamente considerada uma família de posicionamento incerto dentre as monocotiledôneas (Rudall et al. 1999). Entretanto, a relação entre as cinco famílias de Commelinales é atualmente bem entendida e fortemente sustentada, baseada em vários marcadores nucleares e plastidiais (Chase et al. 2006; Graham et al. 2006; Saarela et al. 2008; Hertweck et al. 2015) e, mais recentemente, com base no genoma completo de cloroplasto (Givnish et al. 2018).

Em sua circunscrição atual, Commelinales era exclusivamente circunscrita com base em caracteres moleculares, carecendo de qualquer tipo de suporte morfológico (Chase 2004; Judd et al. 2008; Saarela et al. 2008; Takhtajan 2009; Soltis et al. 2018), até o presente trabalho. Apesar de alguns estudos sistemáticos terem apontado sinapomorfias morfológicas para famílias individuais Commelinales em (Haemodoraceae: Simpson 1983, 1989, 1990, 1998a; Philydraceae: Simpson 1985, 1990; Pontederiaceae: Simpson 1987, 1990, Simpson & Burton 2006, Pellegrini et al. 2018), poucos estudos apontaram sinapomorfias para agrupamentos suprafamiliares (i.e., Givnish et al. 1999; Prychid & Rudall 1999; Saarela et al. 2008; Pellegrini et al. 2018). Ainda, apenas um único estudo anterior a esse apontou uma sinapomorfia morfológica para a ordem (Givnish et al. 1999). Os dois estudos mais abrangentes e importantes sobre a filogenia da ordem são Jesson & Barrett (2003) e Saarela et al. (2008). Jesson & Barrett (2003) apresentam uma super-árvore para monocotiledôneas, com ênfase na ordem Commelinales (Fig 1). A árvore apresentada pelos autores foi construída com base em hipóteses filogenéticas disponíveis na época, tanto para as monocotiledôneas quanto para a ordem

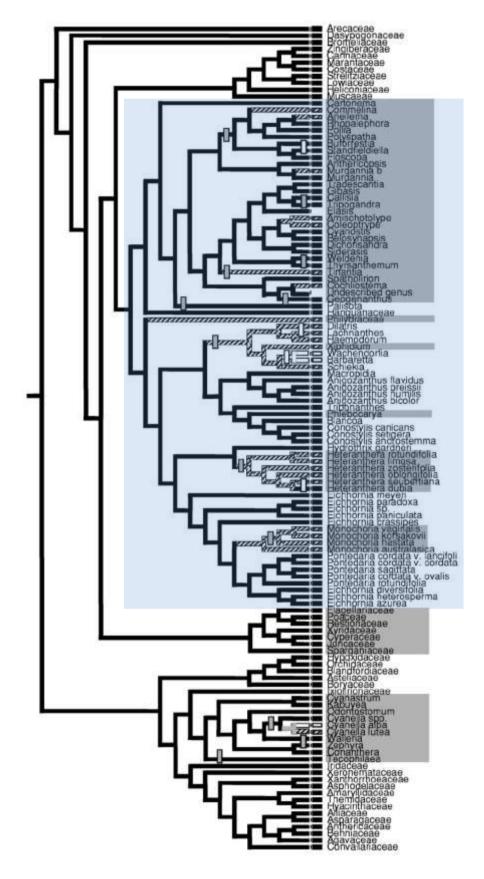


Figura 1. Super-árvore das monocotiledôneas detalhando as relações dentro de Commelinales, mostrando a reconstrução mais parcimoniosa para a perda de nectários, surgimento de heteranteria, e o surgimento de enantiostilia. Commelinales destacada no retângulo azul. Modificado de Jesson & Barrett (2003).

Commelinales. Devido à metodologia utilizada, a árvore apresentada não possui valores de suporte estatístico para seus agrupamentos. Mesmo assim, é a hipótese filogenética com a amostragem mais ampla até o momento. Já o trabalho de Saarela et al. (2008) se propôs em apresentar uma filogenia para Commelinales, resolvendo, com grande suporte estatístico, o posicionamento incerto de Philydraceae (Fig 2). Assim, a ordem Commelinales apresenta duas hipóteses filogenéticas baseadas em metodologias distintas. A primeira foi baseada em uma ampla amostragem de táxons dentro da ordem, mas não apresentou suporte estatístico, devido à natureza do método utilizado. Enquanto a segunda apresentou uma topologia com base em vários marcadores moleculares, robustamente sustentada, mas com poucos terminais por família, produzindo assim apenas uma hipótese de *backbone* ou relações em nível de família, para a ordem.

Objetivos

Assim, a presente tese teve como objetivos principais: (1) apresentar uma nova hipótese filogenética para Commelinales com base na combinação de dados moleculares e uma extensa matriz morfológica; (2) circunscrever morfologicamente Commelinales; e (3) revisitar a classificação de Commelinales com base nos resultados obtidos, propondo uma nova classificação, composta por grupos monofiléticos e com coerência morfológica. Para isso, foi necessário um amplo e aprofundado estudo de todas as famílias e suas principais linhagens. Os objetivos específicos dessa tese, estão relacionados com os problemas taxonômicos dentro das famílias de Commelinales e foram: (1) refinar a filogenia e apresentar a primeira hipótese biogeográfica para Commelinaceae; (2) revisar alguns gêneros com posicionamento chave dentro de Commelinaceae (i.e., *Gibasoides* D.R.Hunt., *Thyrsanthemum* Pichon, *Rhopalephora*

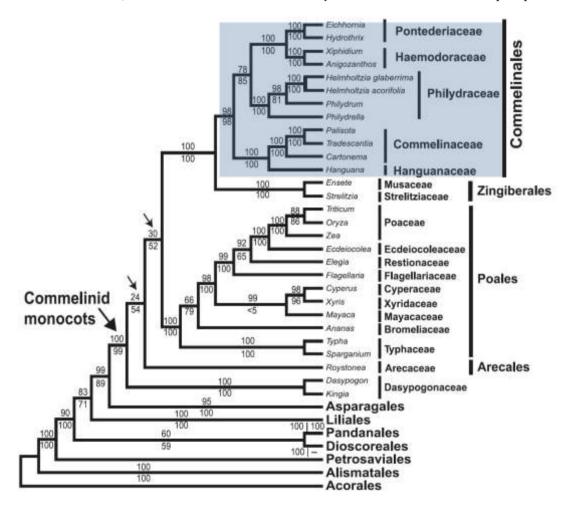


Figura 2. Filogenia para as monocotiledôneas com base em 17 loci plastidiais e regiões não-codificantes associadas. Valores acima dos ramos apresentam o valor de suporte (*bootstrap*) da análise de Parcimônia, enquanto abaixo representam o valor de suporte (*bootstrap*) da análise de Máxima Verossimilhança. Ramos com setas colapsaram no consenso estrito. Commelinales destacada no retângulo azul. Modificado de Saarela et al. (2008).

Hassk., *Siderasis* Raf. e *Weldenia* Schult.f.) e grupos de espécies dentro de gêneros (i.e., *Commelina* L., *Dichorisandra* J.C.Mikan, e *Murdannia* Royle); (3) revisitar a taxonomia das Haemodoraceae Neotropicais; (4) nova circunscrição para os gêneros de Pontederiaceae, com base em dados morfológicos e moleculares; e (5) descrever os novos táxons encontradas ao longo da elaboração do tratamento taxonômico para Commelinales.

Organização da tese

A tese está organizada em quatro seções, cada uma subdividida em um ou mais capítulos:

- Seção 1. Commelinales— Essa seção encontra-se dividida em apenas um capítulo, intitulado "An updated classification of Commelinales (Monocotyledonae) based on molecular and morphological data". Este capítulo está diretamente relacionado aos objetivos principais dessa tese, representando a compilação de todos os estudos realizados durante o desenvolvimento dessa tese.
- Seção 2. Commelinaceae— Essa seção encontra-se dividida em oito capítulos, que abordam problemas taxonômicos dentro das duas principais linhagens de Commelinaceae (i.e., tribos Commelineae e Tradescantieae), assim como apresentam uma nova hipótese filogenética para a família, datada e calibrada, juntamente com sua primeira hipótese biogeográfica. Os gêneros *Rhopalephora* e *Siderasis* foram revisados, assim como as espécies Neotropicais de *Murdannia*, enquanto para os gêneros *Gibasoides*, *Thyrsanthemum* e *Weldenia* são apresentadas sinopses. Para o gênero *Commelina* é apresentada uma sinopse para o estado do Rio de Janeiro, com a descrição de uma nova espécie. Enquanto para *Dichorisandra*, o grupo de espécies acaules foi investigado, com ênfase na sua morfologia e variação floral, dentro do contexto da revisão de seu grupo-irmão (i.e., *Siderasis*).
- Seção 3. Haemodoraceae— Essa seção encontra-se dividida em apenas um capítulo, intitulado "Revisiting the taxonomy of the Neotropical Haemodoraceae (Commelinales)". Este capítulo revisita a taxonomia das Haemodoraceae Neotropicais, solucionando problemas que ficaram pendentes desde o tratamento da família para a obra *Flora Neotropica*.

• Seção 4. Pontederiaceae— Essa seção encontra-se dividida em três capítulos, abordando os limites genéricos e arquitetura de inflorescência em Pontederiaceae. No primeiro capítulo, o gênero *Heteranthera* Ruiz & Pav. é expandido para incluir *Hydrothrix* Hook.f. e *Scholleropsis* H.Perrier. No segundo capítulo, a arquitetura de inflorescência de Pontederiaceae é revisitada, dentro do contexto da descrição de duas espécies peculiares para o Brasil. Por último, o terceiro capítulo conclui e re-delimitação genérica de Pontederiaceae, com base em análise combinada de dados morfológicos e moleculares. Nesse contexto, *Pontederia* L. é expandida para incluir *Eichhornia* Kunth e *Monochoria* C.Presl.

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SECTION 1- COMMELINALES MIRB. EX BERCHT. & J.PRESL

Chapter 1.1. A revisited classification for Commelinales (Monocots) based on total evidence genus-level phylogeny

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Abstract

Despite being strongly recovered as monophyletic by molecular studies, Commelinales completely lacks any morphological support and circumscription. It is also the order that suffered the most striking changes across different classification systems, with its type-family, Commelinaceae, being the only one placed in it since its proposition. The order is currently of Commelinaceae. Haemodoraceae. Hanguanaceae. Philvdraceae. Pontederiaceae, presenting a Pantropical distribution and great ecological and morphological diversity. Based on our combined efforts, and extensive herbarium, field, botanical illustration, and morphological molecular phylogenetic research, we provide total evidence analysis of Commelinales, based on available and new molecular data, plus an extensive 570character morphological matrix, sampling almost a third of the species in the order. Based on the recovered topology and relationships, we revisited the classification of Commelinales and proposed an updated classification, recognizing 60 genera and ca. 1,080 species, arranged in five families, supported by molecular data and each by extensive morphological synapomorphies. As part of our taxonomic results we propose the recognition of a new subfamily in Commelinaceae (Palisotoideae), three new subtribes (Cochliostematinae, Floscopinae, and Murdanniinae), two new genera (Brachyphyllum and Campylonanthus), several infrageneric taxa. Haemodoraceae and Pontederiaceae, together with many generic and specific updates.

Keywords

Commelinaceae, commelinid monocots, Haemodoraceae, Hanguanaceae, Philydraceae, Pontederiaceae

Introduction

Commelinales is a small and well-supported monocot order, currently understood as belonging to the commelinid monocots (Hertweck et al. 2015; Givnish et al. 2018). This group also includes the Commelinales' sister group, the order Zingiberales, together with Poales, Arecales, and Dasypogonales (Hertweck et al. 2015; Givnish et al. 2018). The order is Commelinaceae. Haemodoraceae. Hanguanaceae. Philvdraceae. Pontederiaceae (Givnish et al. 1999, 2006, 2018; Chase et al. 2000, 2006; Savolainen et al. 2000; Soltis et al. 2000; Graham et al. 2002, 2006; Davis et al. 2004; Saarela et al. 2008; Hertweck et al. 2015; APG IV 2016), and includes a total of ca. 65 genera and 900 species (Commelinaceae: Faden and Hunt 1991, Faden 1998; Haemodoraceae: Simpson 1990, 1998b; Hanguanaceae: Bayer et al. 1998, Leong-Škorničková and Boyce 2015; Philydraceae: Hamann 1966, 1998; Pontederiaceae: Pellegrini 2017, Pellegrini et al. 2018). Despite its relatively reduced number of genera and species, Commelinales is geographically, ecologically, and morphologically very diverse (Saarela et al. 2008). The order is Pantropical in distribution reaching temperate areas in some parts of the world, especially due to the wide distribution of Commelinaceae, Haemodoraceae, and Pontederiaceae (Stevens 2001onwards). Regarding the individual families, Australasia represents the diversity centers of Haemodoraceae, Hanguanaceae, and Philydraceae (Hamann 1966, 1998; Simpson 1990, 1998b; Bayer et al. 1998). Alternatively, Pontederiaceae has the Neotropics as its diversity center, especially in the Brazilian territory (Pellegrini and Horn 2017; Pellegrini et al. 2018). Finally, Commelinaceae possesses two Neotropical (i.e., Mexico and Brazil; Hunt 1983, 2004; Aona 2008; Pellegrini 2017) and two Paleotropical (i.e., Africa and Asia; Faden 1991, 2012; Nandikar and Gurav 2015; Pellegrini et al. 2016) diversity centers.

Commelinales is probably the least studied monocot order from an evolutionary and taxonomic point of view, having suffered the most striking changes in its circumscription between different classification systems (Givnish et al. 1999; Chase 2004; Wilkin et al. 2005; Saarela et al. 2008). The only family consistently associated with Commelinales since its beginning to modern times being its type of family, Commelinaceae. Most families historically placed in previous circumscriptions of Commelinales (i.e., Eriocaulaceae, Mayacaceae, Rapateaceae, Restionaceae, and Xyridaceae) are currently placed in Poales (Givnish et al. 1999; Chase 2004; APG IV 2016), while Dasypogonaceae is either placed in Arecales (Hertweck et al. 2015; APG IV 2016) or in Dasypogonales (Givnish et al. 1999, 2018). On the other hand, the families currently placed in Commelinales have rarely been considered to be closely related to Commelinaceae (Givnish et al. 1999; Chase 2004). Haemodoraceae, Philydraceae, and Pontederiaceae have generally been considered to be more or less closely related to each other, despite being placed in different orders depending on the author and classification (see below the History and classification of Commelinales section for further details and references). Alternatively, Hanguanaceae has consistently been considered a family of uncertain affinity amongst the monocots (Rudall et al. 1999). Nonetheless, the relationships between the families of Commelinales are now well-understood and supported, based on several nuclear and plastidial markers (Chase et al. 2006; Graham et al. 2006; Saarela et al. 2008; Hertweck et al. 2015), and more recently based on complete chloroplast genome (Givnish et al. 2018).

As currently accepted, Commelinales is circumscribed based exclusively on molecular characters, lacking any kind of morphological support (Chase 2004; Judd et al. 2008; Saarela et al. 2008; Takhtajan 2009; Soltis et al. 2018). Despite some systematics studies having recovered morphological synapomorphies for the individual families in Commelinales (Haemodoraceae: Simpson 1983, 1989, 1990, 1998a; Philydraceae: Simpson 1985, 1990; Pontederiaceae: Simpson 1987, 1990, Simpson and Burton 2006, Pellegrini et al. 2018), very

few studies have recovered synapomorphies for suprafamilial groupings in the order (i.e., Givnish et al. 1999; Prychid and Rudall 1999; Saarela et al. 2008; Pellegrini et al. 2018). While only a single study has ambiguously recovered one morphological synapomorphy for the order (Givnish et al. 1999). Intending to retrieve unambiguous morphological synapomorphies for Commelinales, we present a total evidence phylogeny for the order based on combined molecular, macromorphological, palynological, anatomical, cytological, and phytochemical characters. Furthermore, based on all previous studies focusing on the individual families of the order, plus our current and ongoing contributions, we propose the revised classification for Commelinales, summarizing all accepted families, infrafamiliar groups, and genera. The present work is the first finer-scale study on the phylogenetics and evolution of Commelinales.

Methods

Taxon sampling

The molecular sampling was initially based on previous studies regarding the families of the order and the availability of sequences for the regions *matK*, *trnK-psbA*, *rbcL*, and *trnL-trnF* on GenBank. It was posteriorly complemented aiming to fill in all remaining generic gaps on the molecular dataset. The final molecular dataset is represented by 395 taxa of Commelinales, with Zingiberales represented by two taxa, one of *Zingiber L.* (Zingiberaceae) and one of *Costus L.* (Costaceae), as outgroups.

The morphological sampling was initially correspondent to the molecular dataset. Posteriorly, based on the elevated congruence between both datasets, the morphological dataset was increased to properly access the morphological diversity and variation within each genus and lineage. Finally, types of all infrafamilial ranks currently accepted in Commelinales were sampled. Thus, the present study samples 393 taxa of Commelinales (ca. 37% of ca. 1,080), including all 52 genera currently accepted for the order. Out of the total, the ingroup is represented by ca. 30% (236 spp. out of ca. 800) of Commelinaceae, ca. 61% (160 spp. out of ca. 120) of Haemodoraceae, ca. 20% (10 spp. out of estimated ca. 50) of Hanguanaceae, 100% (i.e., eight spp.) of Philydraceae, and 100% (i.e., 42 spp.) of Pontederiaceae (Table 1).

Morphology and taxonomy

Specimens from the following herbaria were analyzed: AD, AAU, ALCB, ASU, B, BA, BAF, BHCB, BHZB, BKL, BLH, BM, BOL, BOTU, BR, BRIT, C, CAL, CANB, CAS, CBG, CEN, CEPEC, CESJ, CGE, CGMS, CLF, CM, CNMT, COL, COR, CORD, CTES, CVRD, DR, DS, E, EA, EAC, ESA, F, FCAB, FCQ, FLOR, FURB, G, GBH, GH, GMUF, GOET, GUA, HAL, HAMAB, HAS, HB, HBR, HDCF, HEM, HERBAM, HNMN, HRB, HRCB, HSTM, HUAP, HUCS, HUEFS, HUFSJ, HURB, IAC, IAN, IBE, ICN, INPA, IPA, JOI, K, KANU, KYO, L, LE, LG, LIL, LL, LP, M, MA, MBM, MBML, MEL, MEXU, MICH, MIN, MG, MO, MVM, MY, NBG, NBYC, NDG, NO, NSW, NY, OS, P, PACA, PERTH, PH, PMSP, PR, PRC, PRE, R, RB, RFA, RFFP, S, SCP, SMU, SP, SPF, SPSF, SRGH, TEX, U, UAMI, UC, UEC, UFRN, UMO, UNA, UPCB, US, USF, VDB, VIC, VT, W, WAG, and WU (herbaria acronyms according to Thiers, continuously updated). The authors gathered fresh specimens, spirit samples, field notes, photographs, and specimens for cultivation during several field trips around the globe, from 1970 to 2018. The indumentum and shape terminology follow Radford et al. (1974); inflorescence terminology and morphology follow Weberling (1965, 1989), Panigo et al. (2011), and Pellegrini and Horn (2017); fruit terminology follows Spjut (1994); seed terminology follows Faden (1991); and general morphology for each of the families follows Faden (1991, 1998) and Pellegrini (2017) for Commelinaceae, Simpson (1990, 1998b) for Haemodoraceae, Bayer et al. (1998) for Hanguanaceae, Hamann (1966, 1998) for Philydraceae, and Pellegrini et al. (2018) Pontederiaceae.

Character selection and coding

Characters were scored mainly from living specimens in the field and specimens in cultivation and later complemented by spirit and herbarium samples from the aforementioned herbaria. When no living or herborized specimens were available for examination, information was taken from published literature. We have studied at least two specimens for each taxon, with the most representative specimen chosen as the voucher for the morphological matrix (Table 1). Some characters were chosen based on previous studies, with most characters being scored for the present study. Character coding followed the recommendations of Sereno (2007) for morphological phylogenies. Primary homology hypotheses (De Pinna 1991) were proposed for root, stem, leaf, inflorescence architecture, floral, fruit, seed, seedling, palynological, anatomical, cytological, and phytochemical characters. A total of 555 discrete macro- and micromorphological characters were scored, being treated as unordered and equally weighted. Out of 555, 396 were macromorphological, 31 were palynological, 15 were for seedling morphology, 96 were anatomical, four were cytological, and 13 were phytochemical (Appendix 1). The complete morphological matrix is provided in Appendix 2.

Morphological analyses

Data were entered into a matrix of characters per taxa using the software Mesquite 3.20 (Maddison and Maddison 2017; Appendix 2). All characters were treated as unweighted and unordered. Maximum Parsimony (MP) analysis was performed using PAUP* 4 (Swofford 2003), with a heuristic search with 1000 random taxon additions and tree bisectionreconnection (TBR) branch swapping. Consistency index (CI) and retention index (RI) were used to assess the degree of homoplasy in the dataset and using character optimization of ACCTRAN (accelerated transformation optimization; Swofford and Maddison 1987). Statistical support for each branch of the cladogram was evaluated with bootstrap support (BS) analyses with 1000 random addition replication. The search parameters used to estimate the bootstrap values were the same as the initial heuristic search. A Bayesian Analysis (BA) was conducted with mixed models and unlinked parameters, using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). The Markov Chain Monte Carlo (MCMC) was performed using two simultaneous independent runs with four chains each (one cold and three heated), saving one tree every 1,000 generations, for a total of ten million of generations. We excluded as 'burnin' trees from the first two million generations, and tree distributions were checked for a stationary phase of likelihood. The posterior probabilities (PP) of clades were based on the majority-rule consensus, using the remaining trees, calculated with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Posteriorly, Mesquite 3.20 was used to reconstruct the ancestral character states, while WinClada ver. 1.0000 (Nixon 2002) was used to trace the synapomorphic characters on the strict consensus tree.

Molecular analyses

All sequences were aligned using Muscle (Edgar 2004) implemented on Geneious software (Kearse *et al.* 2012), with subsequent adjustments in the preliminary matrices made by eye. Combined analyses of the plastid regions and plastid + morphology datasets were performed. Before combining our data, we performed the incongruence length-difference (ILD) test (Farris *et al.* 1994) to investigate incongruence between DNA data sets. Analyses using maximum parsimony (MP) on both matrices were conducted with PAUP* 4 (Swofford 2003). A heuristic search was performed using TBR swapping (tree-bisection reconnection) and

1,000 random taxon-addition sequence replicates with TBR swapping limited to 15 trees per replicate to prevent extensive searches (swapping) in suboptimal islands, followed by TBR in the resulting trees with a limit of 1,000 trees. In all analyses, the characters were equally weighted and unordered (Fitch 1971). Relative support for individual nodes was assessed using non-parametric bootstrapping (Felsenstein 1985), with 1000 bootstrap pseudoreplicates, TBR swapping, simple taxon addition and a limit of 15 trees per replicate. For the model-based approach, we selected the model using hierarchical likelihood ratio tests (HLRT) on J Modeltest 2 (Darriba et al. 2012). For the morphological partition, the standard discrete Markov model (Mkv) was used following Lewis (2001) with rates set to equal. A Bayesian Analysis (BA) was also conducted for the molecular and combined datasets, using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003; see details in the section above).

Analyses of the combined datasets

Combined analyses of the plastid + morphology datasets were performed for MP and BA following the procedures from the abovementioned section.

Results

Morphological analyses

The MP retrieved seven equally parsimonious trees with 4911 steps, Consistency Index (CI) of 0.2179, Homoplasy Index (HI) of 0.7821, Retention Index (RI) of 0.9028, and Rescaled Consistency Index (RC) of 0.1967. The BA retrieved a consensus tree with all families to subgenera recovered as well-supported (Figs 1–3). Out of the 570 coded characters, 553 were parsimony informative. Almost no incongruence was observed between the MP and the BA topologies. Thus, the BA majority-rule tree (Figs 1–3) is presented and discussed below showing BS (below the branches) and PP (above the branches) support values.

Suprafamilial relationships. In both the MP and BA topologies, Commelinales is recovered organized in two well-supported clades (Figs 1-3): (1) Commelinaceae + Hanguanaceae (PP= 1; BS= 80); and (2) Philydraceae (Haemodoraceae + Pontederiaceae) (PP= 1; BS= 100). The order as a whole is supported by 27 characters (Fig 4): plants aquatic or growing in damp environments (character 5), ligule absent (character 27), immature blades flat (character 42, homoplastic), blades abaxially green (character 56, homoplastic), buds of the inflorescence producing inflorescence primordia (character 84), secondary inflorescence branches pedunculate (character 94, homoplastic), bract subtending the secondary inflorescence branch bracteose (character 105, homoplastic), flowers 3 to several per secondary branch (character 127, homoplastic), perianth persistent to slightly accrescent in fruit (character 192), petals cuneate to obtuse at base (characters 223 and 232), outer antesepalous stamens present (character 238, homoplastic), filaments of the anterior stamens equal in length to the posterior (character 261), pollen grains released with adhering raphides (character 327) and tectate-columellate (character 348), pistil 1/2 times longer than the stamens (character 370, homoplastic), ovary superior (character 373), stigma capitate or subtrilobed to trilobed (character 390, homoplastic), fruits ellipsoid to oblongoid (character 400, homoplastic), dull-colored (character 405, homoplastic) and 3-valved (character 408), seedlings with rhizoids (character 440), stomata with terminal and lateral neighboring cells equal in size (character 483), perianth with tannin cells (character 505), tapetum ameboid (character 517), seed coat bitegmic (character 541), and endosperm copious (character 549). The Commelinaceae + Hanguanaceae clade is supported by 10 characters (Fig 5): bracts subtending the secondary branches of the inflorescence flat (character 108, homoplastic), flowers non-resupinate (character 135, homoplastic), flower flat (character 154), filaments

free from the perianth (Character 245, homoplastic), antepetalous stamens with filaments of the same length (character 258, homoplastic), seedlings with cotyledon lacking chlorophyll (character 444), at least the first primary leaf modified into a cataphyll (character 450), silica bodies present in the leaves (character 452), ovules orthotropous (character 532, homoplastic), and seed coat sclerified (character 543). The Philydraceae (Haemodoraceae + Pontederiaceae) clade is supported by 21 characters (Fig 4): ptyxis conduplicate (Character 25), leaves unifacial (character 26, homoplastic), blades ribbon-like or linear (Character 40, homoplastic) with truncate base (character 44, homoplastic) and acute apex (character 53, homoplastic), floral buds ellipsoid or fusiform or oblongoid (character 130, homoplastic), perianth whorls basally fused (character 156, homoplastic) and petaloid (character 158, homoplastic), seeds fusiform to barrel-shaped (character 415), testa reticulate to foveolate (character 423, homoplastic), cotyledon assimilating (character 445) with a long middle part (character 449, homoplastic), primary leaves bifacial and ribbon-like (character 451), bean-shaped starch grains present (character 453), stomata with 2 neighboring cells (character 482, homoplastic), xylem and phloem alternate or circular phloem with central xylem (character 489), styloid crystals present (character 495), placental sclereids present (character 530), and presence of pro-anthocyanins (character 555, homoplastic), diferulic acids (character 558) and p-coumaric acids (character 570). Finally, the Haemodoraceae + Pontederiaceae clade is well-supported (PP= 1; BS= 62) by 9 characters (Fig 4): presence of an hypanthium (character 152), perianth homochlamydeous (character 157, homoplastic), pollen wall with a papillate or baculate inner layer (character 343), lacking an infratectum (character 347) and tectum baculate (character 348), sulcal membrane verrucate (character 357), neighboring cells of the stomata with oblique division (character 481), seed coat with calcium oxalate (character 544), and the presence of phenylphenalenones (character 560).

Family level relationships. All five families of Commelinales are recovered as monophyletic, with high statistical support (Figs 1–3): (1) Commelinaceae (PP=1; BS=91); (2) Hanguanaceae (PP=1; BS=100); (3) Philydraceae (PP=1; BS=99); (4) Haemodoraceae (PP=1; BS=85); and (5) Pontederiaceae (PP=1; BS=100). The synapomorphies for each family are described below.

The monophyly of Commelinaceae is supported by 14 synapomorphic characters, half of which are exclusive (Fig 5): internodes with a leaf-opposite line of uniseriate hairs (character 21), internodes swollen (character 22), leaf sheaths closed and asymmetric (character 29), sepals free (character 206, homoplastic), filaments slender (character 248, homoplastic), inner antepetalous stamens with basifixed anthers (character 304, homoplastic), seedlings with a collar (character 441, homoplastic), cotyledonary sheath with a coleoptile (character 447, homoplastic), vessels in the roots and stems (character 454, homoplastic), presence of a nodal vascular plexus (character 457), presence of raphide canals in the leaves (493), if present perianth tannin cells moderate (character 509, homoplastic), outer tegmen of the seed coat thin and sloughing off during development (character 542), inner layer with silica crystals (character 544), and embryo of the *Xyris/Scirpus*- or grass-type (character 546).

Hanguanaceae is recovered as monophyletic and supported by 29 synapomorphic characters, 13 of which are exclusive (Fig 5): plants dioecious (character 4), stems fibrous (character 18, homoplastic), leaf margins scarious (character 30), immature leaves subpetiolate (character 37, homoplastic), variable number of secondary branches per node of the inflorescence (character 92, homoplastic), flowers forming clusters in the secondary branches of the inflorescence (character 128, homoplastic), floral buds globose (character 130, homoplastic) and erect (character 144, homoplastic), perianth homochlamydeous (character 157, homoplastic), inner perianth whorl sepaloid (character 159), as wide as the outer whorl (Character 190, homoplastic) and herbaceous (character 191), and anthers latrorse

(Characters 319–322, homoplastic), pistillate flowers with nectariferous scales (character 358), staminate flowers with nectariferous pistillode (character 369), locules 1-ovulate (characters 378 and 379, homoplastic), style absent (character 380), fruits subglobose to globose (character 400, homoplastic) and indehiscent (character 408, homoplastic), seedlings with primary roots brown (character 439), absence of uniseriate macrohairs *sensu* Tomlinson (1966) (character 464, homoplastic), multiseriate fruticose hairs (character 472), ovary locules with mucilage secreting hairs (character 525), placenta globose (character 528), seed coat with two layers of crossing fibers (character 545), and seeds tenuinucellate (character 550).

Philydraceae is supported as monophyletic by eight synapomorphic characters, three of which are exclusive (Fig 4): inflorescences with elongate secondary branches (character 98, homoplastic), flowers with a pseudotetramerous perianth (character 173), outer antepetalous stamen absent (character 240, homoplastic), filaments fused only to the inner tepals (character 245, homoplastic), antesepalous filament longer (character 260, homoplastic), seeds with an enlarged chalazal cap (character 427), perianth with abundant tannin cells (character 509, homoplastic), and a glandular tapetum (character 517).

Haemodoraceae recovered as monophyletic, supported by nine synapomorphic characters, with six of them exclusive (Fig 4): fibrous and coriaceous leaf blades (character 41), secondary inflorescence branch a branched cyme (character 88), perianth lobes equal to subequal to each other (character 197, homoplastic), seedlings lacking rhizoids (character 440, reversion), primary leaves unifacial (character 451), root pith with a sclerified pith (character 456), absence of uniseriate macrohairs (character 464, homoplastic), presence of tapering hairs (character 470), and the presence of chelidonic acid (character 557).

Pontederiaceae is recovered as monophyletic, being supported by 28 synapomorphic characters, 12 of which are exclusive (Fig 4): dimorphic leaves (character 24), ptyxis conduplicate-involute, enclosing the petiole of the preceding leaf (character 25), leaves late bifacial (character 26), leaves ligulate (character 27, homoplastic), early deciduous (character 33), submerged (character 36, homoplastic) and patent immature leaves (character 38, homoplastic), mature leaves always produced (character 57), basal bract spathaceous (character 77, homoplastic) and basally connate (character 79, homoplastic), inflorescence peduncle lacking accessory bracts (character 83, homoplastic), secondary branches lacking subtending bracts (character 102, homoplastic), bracteoles absent (character 118, homoplastic), perianth connate forming a conspicuous tube (character 156, homoplastic), perianth ranging from blue to lilac to purple (character 169, homoplastic), perianth lobes longer than the fruit (character 193, homoplastic), posterior lobes with a nectar guide (character 202), outer antesepalous stamen with glandular macrohairs (characters 269, homoplastic), inner antesepalous stamens pubescent (character 272, homoplastic) with glandular macrohairs (character 274, homoplastic), pollen grains bisulcate (character 339), presence of an anthocarp originated from a superior ovary (character 394), seeds longitudinally winged or crested (character 423, homoplastic), cotyledonary sheath ligulate (character 447), with xylem abaxial and phloem adaxial near the margins of the blades, plus xylem and phloem alternate near the center of the blade (character 489), leaf mesophyll with aerenchyma (character 496, homoplastic), and floral receptacle (character 502, homoplastic), and perianth (character 510) and ovary wall (character 521) with aerenchyma.

Infrafamiliar relationships. Infrafamiliar relationships and exclusive synapomorphies for each of the five families of Commelinales are briefly described below. We focus on higher hierarchical relationships and will be dealing only with infrageneric relationships when they are related to previous, present or putative infrageneric classifications for that genus.

Commelinaceae— The family is divided into four main lineages (Figs 5–6), the last two representing subfamily Commelinoideae: (1) subfamily Cartonematoideae; (2) *Palisota* Rchb.

ex Endl.; (3) tribe Commelineae; and (4) tribe Tradescantieae, excluding subtribe Palisotinae. Cartonematoideae is recovered as monophyletic with high statistical support (PP=1; BS=100; Fig 2) and supported by 21 synapomorphies, five of them exclusive (Fig 5): sepals with membranous margins which are much thinner than the remaining of the sepal (character 209), seedlings with inconspicuous collar (character 442), presence of a mesocotyl (character 443), presence of clavate uniseriate macrohairs (character 464), and mesophyll with elaborately-lobed palisade cells (character 491). Cartonema R.Br. and Triceratella Brenan (and consequently tribes Cartonemateae and Triceratelleae) are differentiated by several morphological characters, but each one is supported by a sole non-homoplastic synapomorphy (Fig 5). Cartonema is characterized by its laterally compressed seeds (character 416), while Triceratella is supported by its dorsally conical seeds (character 419) (Fig 5).

The clade consisting of *Palisota* + Commelinoideae is statistically mildly-supported (PP=0.65; Fig 2) and morphologically supported by two exclusive synapomorphies (Fig 5): stems with cortex expanded and with vascular tissue (character 458), and by the presence of glandular microhairs *sensu* Tomlinson (1966) (character 461). On the other hand, *Palisota* itself is statistically strongly-supported (PP=1; BS=100; Fig 2), and morphologically characterized by six exclusive synapomorphies (Fig 5): pollen grains dimorphic in the same whorl of polliniferous anthers (character 337), ovary (character 374) and style pubescent with rugose hairs (character 386), roots with mucilage canals (character 455), and uniseriate hairs of the rugose (character 464) and branched types (character 466). Two clades are recovered in *Palisota*: (1) supported by cincinni with swollen axis (character 97); and (2) supported by pedicels spirally-coiled at post-anthesis (character 145).

Subfamily Commelinoideae is statistically well-supported (PP=0.92; BS=91; Fig 2), being morphologically supported by a sole exclusive synapomorphy (Fig 5), seedlings with an umbrella-like collar (character 442). It is divided into two clades (Figs 2, 3): (1) the strongly supported tribe Commelineae (PP=1; BS=100); and (2) the strongly-supported tribe Tradescantieae s.str. (PP=1; BS=73). Tribe Commelineae is morphologically supported by 17 characters, six of which are exclusive (Fig 5): petals deliquescent (character 216), seeds with light brown to tan lateral appendages (character 433), cotyledonary sheath inconspicuous (character 446), presence of macrohairs of the papillae type (character 469), stomata with six neighboring cells with the terminal smaller than the laterals (character 482), and presence of 3-glycoside anthocyanin (character 556). Commelineae is divided into three well-supported lineages (Fig 2): (1) the Murdannia clade (PP=1; BS=100); (2) the Floscopa clade (PP=0.99; BS=66); and (3) the Commelina clade (PP=1; BS=96). The Murdannia and Floscopa clades are sister to each other (PP=0.89; BS=64), being supported by four exclusive synapomorphies (Fig 5): pollen grains with tectal elements closer to each other in the transitional zone (character 341), exine tuberculate (character 350), tectum with sparse microperforations (character 355), and glandular microhairs with basal cells lenticular and not wedged between epidermal cells (character 462). The Murdannia clade is supported by four exclusive synapomorphies (Fig 5): antherodes 3-lobed (character 363), glandular microhairs with ellipsoid medial cell (character 463), cuticle of the leaf epidermis striated to ridged (character 476), and leaf mesophyll with marginal mechanical tissue (character 500). The Floscopa clade is supported by three exclusive synapomorphies (Fig 5): posterior stamens producing sterile pollen (characters 330 and 336), and the presence of star-shaped idioblasts (character 467). The Floscopa clade is represented by five genera, out of which Tricarpelema J.K.Morton is paraphyletic due to the placement of T. africanum Faden as sister to Stanfieldiella Brenan (Fig 2). The clade composed of Stanfieldiella s.lat. and Floscopa Lour. is supported by characters such as seed with embryotega much lighter than the testa or white (character 431) (Fig 5). Stanfieldiella (incl. T. africanum) is supported by characters such as pedicels oblique at post-anthesis (character 145), glandular microhairs with basal cell

lenticular and wedged between regular epidermal cells (character 462), and chromosomes ≤ 2 µm long (character 552) (Fig 5). *Floscopa* is supported as monophyletic by the posterior stamens with connectives obdeltoid or dumbbell-shaped (characters 290 and 296), and capsules subcordate to cordate (character 400) (Fig 5). The clade composed of *Tricarpelema* s.str., *Buforrestia* C.B.Clarke, and *Pseudoparis* H.Perrier is supported by the presence of star-shaped idioblasts in the leaf margins (character 52) (Fig 5). *Tricarpelema* s.str. is supported as monophyletic by anterior stamens with connectives ob-saddle-shaped (characters 294 and 296) (Fig 5). *Buforrestia* is supported as monophyletic by the anterior stamens held throughout the anthesis inside the cup-shaped medial petal (character 256) (Fig 5). Finally, *Pseudoparis* is supported as monophyletic by its trilobed petals (characters 224 and 233) (Fig 5).

The Commelina clade is supported by (Fig 5): glandular microhairs with clavate medial cell (character 463), and by the presence of hook-like uniseriate macrohairs (character 464). It is represented by six genera, viz., Aneilema R.Br., Commelina L., Dictyospermum Wight, Pollia Thunb., Polyspatha Benth., and Tapheocarpa Conran, out of which the two largest genera (i.e., Aneilema and Commelina) are paraphyletic (Fig 2). The morphologically isolated Dictyospermum is strongly supported as monophyletic by (PP=1; BS=100): descendingfalcate filaments (characters 262–264) and style (character 384). The remaining genera of the Commelina clade are supported by filaments coiled at post-anthesis (character 266) (Fig 5). The clade composed of *Pollia*, *Aneilema brasiliense* C.B.Clarke, and *Polyspatha* is statistically well-supported (PP=1; BS=81; Fig 2) and morphologically supported by (Fig 5): pedicels lignified at post-anthesis (character 140), paired petals cucullate-spathulate to cucullate-obovate (character 222), and stigma pointing downwards (character 389). Pollia is strongly recovered as monophyletic (PP=1; BS=100; Fig 2), supported by (Fig 5): pseudopetiole repandous (character 47), and fruits with brilliant structural coloration (character 406). Aneilema brasiliense and Polyspatha are strongly supported as sister taxa (PP=1; BS=100; Fig 2) by their zig-zag inflorescence main axis (character 86), while A. brasiliense is supported as distinct by its geniculate pedicels at anthesis (character 144), and Polyspatha is strongly supported as monophyletic by antherodes V-shaped with ellipsoid lobes (character 365) (Fig 5). The sister relationship between Aneilema s.str. (excl. A. brasiliense) and Commelina s.lat. (incl. Tapheocarpa) is supported by stigmatic papillae with the folded epidermis (character 537) (Fig 5). Aneilema s.str. is well-supported as monophyletic (PP=1; BS=80; Fig 2) by its sepals with apical or subapical glands (character 207) (Fig 5). Most of the sections proposed by Faden (1991), the reduction of Rhopalephora to a section of Aneilema, as well as the transfer of Floscopa yunnanensis D.Y.Hong to Aneilema (Pellegrini et al., in prep.) are monophyletic in the present analysis. The exception is A. sect. Amelina, which is polyphyletic due to the position of A. johnstonii K.Schum. as sister to A. yunnanense (D.Y.Hong) M.Pell., and due to A. gillettii Brenan being sister to A. sect. Pedunculosa (Fig 2). Finally, Commelina s.lat. is strongly-supported as monophyletic (PP=1; BS=100; Fig 2) by the presence of papillae-like uniseriate macrohairs at the margins of the leaf blades (character 51), presence of minute pollen sacs (character 362) in the X-shaped antherodes (character 363), and the occurrence of a unique anthocyanin called commelinin (character 556) (Fig 5).

Tribe Tradescantieae is morphologically supported by 12 synapomorphies, five of which are exclusive (Fig 6): lower leaves of the stem reduced to bladeless sheaths (character 39), stamens barbate with moniliform hairs (characters 269–284), and leaf epidermis with domed cells (character 477). The tribe is divided in five, well-supported, main lineages (Fig 2, 3): (1) subtribe Streptoliriinae (PP=1; BS=100); (2) the *Cochliostema* clade (PP=1; BS=100); (3) the *Dichorisandra* clade (PP=1; BS=73); (4) the *Cyanotis* clade (PP=1; BS=99); and (5) subtribe Tradescantiinae *sensu* Pellegrini (2017) (PP=1). Subtribe Streptoliriinae is supported by (Fig

6): lower 1(-2) cincinni with bisexual flowers and remaining cincinni only with staminate flowers (Character 131), and petals narrower than the sepals (character 190). All three genera of Streptolirinae are recovered as monophyletic, with *Aëtheolirion* Forman recovered as sister to *Streptolirion* Edgew., supported by leaves with posterior divisions (character 46), and basal 1(-2) cincinni brats spathaceous and the remaining bracteose (character 105) (Fig 6). We have been unable to recover any exclusive synapomorphy for *Streptolirion*, while *Aëtheolirion* is supported by its pedicels becoming pendulous at post-anthesis (character 145) (Fig 6). *Spatholirion* is supported by basal 1(-2) cincinni brats spathaceous and the remaining cincinni ebracteate (character 102). The remaining four lineages are supported (PP=0.97) by the presence of an epicuticular wax layer in the young petals (character 512) (Fig 6).

The Cochliostema clade is supported by (Fig 6): pedicels reflexed at pre-anthesis (character 143), petal margins barbate with moniliform hairs (character 218), and inner antepetalous stamens with strongly curved to spirally-coiled anther sacs (character 315). It is composed of the three Amazonian genera of subtribe Dichorisandrinae sensu Faden and Hunt (1991). Geogenanthus Ule is supported by the presence of a unique type of uniseriate glandular macrohairs (character 142), whereas Cochliostema Lem. is characterized by its seeds with a mucilaginous testa that becomes sticky when hydrated (character 426), and Plowmanianthus Faden & C.R.Hardy is supported by stigmas with marginal papillae moniliform (character 538) (Fig 6). The remaining three lineages of Tradescantieae are wellsupported (PP=0.98; Fig 3) by cell walls of the leaf epidermis with lenticular thickenings (character 479) and petals with striate cuticle (character 513) (Fig 6). The Dichorisandra clade (Fig 6) is supported by: anther walls with more than 2 layers at maturity (character 515), and a spirally-thickened endothecium (character 516). This clade represents Dichorisandrinae sensu Pellegrini and Faden (2017). Dichorisandra J.C.Mikan (Fig 6) is supported by: bracteoles that become brown and scarious during the early stages of cincinni development (character 121), anther 3-4 times longer than the filaments (character 297), and stigma composed solely by multicellular papillae (character 538). On the other hand, Siderasis Raf. emend. M.Pell. & Faden is supported exclusively pollen grains with fossulate exine (character 352) (Fig 6).

The Cyanotis clade + subtribe Tradescantiinae is well-supported (PP=1; Fig 3) by the presence of silica crystal in specialized epidermal cells of the leaves (character 484), and chromosomes longer than 5 µm and shorter than 10 µm (character 552) (Fig 6). The Cyanotis clade is supported by (Fig 6): basal bract bracteose and bicarinate and/or bidentate (character 77), and bracteoles leaf-like and equal to the cincinni bracts (character 118). This clade consists of the paraphyletic subtribe Coleotrypinae, plus the monogeneric subtribe Cyanotinae. This clade is a victim of persistent generic problems, with Cyanotis D.Don recovered as paraphyletic without the inclusion of *Belosynapsis* Hassk., and *Amischotolype* Hassk, being also non-monophyletic without the inclusion of *Porandra D.Y. Hong (Fig 6)*. Coleotrype C.B.Clarke is recovered as monophyletic, being strongly-supported (PP=1; BS=99; Fig 3) by (Fig 6): its capsules with ejaculatory dehiscence (character 408), and stigma with only the marginal papillae multicellular, the central ones unicellular (character 538). Amischotolype (incl. Porandra) is supported (PP=0.98; BS=90; Fig 3) by (Fig 6): secondary inflorescence branches modified into a dichasium (character 88), and leaf epidermis with specialized cells containing silica crystals deep and wedged between regular epidermal cells (character 486). Finally, Cyanotis (incl. Belosynapsis) is strongly-supported (PP=1; BS=100; Fig 3) by (Fig 6): filaments apically inflated (character 250), anther basally poricidal (character 324), style apically inflated (character 383), apical embryotega (character 428), presence of flagelliform hairs (character 464), ovules campylotropous (character 532), and stigmatic papillae of the G type sensu Owens and Kimmins (1981) (character 536).

Subtribe Tradescantiinae sensu Pellegrini (2017) (Fig 6) is recovered as monophyletic, being supported by: bracteoles tightly imbricate arranged in 1 whorl (character 119), sepals with margins hyaline and as thick as the remaining sepal (character 210), pollen grains with exine areolate to rugose (character 352), and sulcal membrane granular or coarsely granularinsulate or coarsely granular-ridged (character 357). The subtribe is recovered by us organized in four main lineages (Fig 3): (1) the strongly supported (PP=1; BS=99) Tinantia clade, composed of Sauvallia C.Wright ex Hassk. and Tinantia Scheidw.; (2) the strongly-supported (PP=1; BS=99) Weldenia clade, composed of Gibasoides D.R.Hunt, Thyrsanthemum Pichon, and Weldenia Schult.f.; (3) the well-supported (PP=1; BS=89) Tradescantia clade, composed of Elasis D.R.Hunt, Gibasis Raf., Matudanthus D.R.Hunt, and Tradescantia L. emend M.Pell.; and (4) the mildly-supported (PP=0.99; BS=75) Callisia/Tripogandra generic complex, composed of several lineages of Callisia Loefl. sensu Hunt (1986) and Tripogandra Raf. Subtribe Tradescantiinae sensu Faden and Hunt (1991) is non-monophyletic due to Elasis and Matudanthus (previously members of subtribe Thyrsantheminae) being nested within it (Fig 3). The *Tinantia* clade is supported by pollen grains with the ornamentation of the sulcal membrane obviously different from the ornamentation of the exine (character 356) (Fig 6). Unsurprisingly, we have been unable to recover any exclusive synapomorphies for Sauvallia, while Tinantia is supported as monophyletic by cincinnus bract fused to the axis of the cincinnus (Character 110), and pollen grains with coarsely areolate exine (Character 352) (Fig 6). The remaining lineages of Tradescantiinae are mildly supported (PP= 0.96; BS= 87; Fig 3) by connectives ranging from rhomboid to sagittate (characters 290, 292, 294, and 296) (Fig 6). The Weldenia clade (Fig 6) is supported by: presence of an underground and tuberized stem (character 15), leaf blades cannulate (character 42) with repandous margins (character 47), and filaments becoming flaccid and pointing outwards at post-anthesis (character 266). Gibasoides is recovered as sister to Thyrsanthemum, supported by becoming stout and fibrous at post-anthesis (character 140), sepals striated (character 212), and pollen grains with sulcal membrane coarsely granular-ridged (character 357) (Fig 6). Nonetheless, neither of them alone is supported by even a single exclusive synapomorphy (Fig 6). On the other hand, Weldenia is supported by a long underground and tuberized stem (Character 16), spathaceous sepals (character 158), and by the presence of a petalo-staminal tube (character 248) (Fig 6).

The sister relationship between the Tradescantia clade and the Callisia/Tripogandra generic complex is strongly-supported (PP=1; BS=95; Fig 3) by hyaline and tubular basal bract (character 77), and main florescence with opposite (character 93), fused back-to-back cincinni (character 99 and 101), and elliptic anther sacs (characters 312-315) (Fig 6). In the Tradescantia clade, Elasis recovered as sister to Matudanthus is strongly supported (PP=1; BS=99; Fig 3) by their geniculate anthers that point outwards to the flower (character 300) (Fig 6). Both genera can be uniquely differentiated by the insertion of their anthers (characters 301–304) (Fig 6), which in *Elasis* are versatile and articulated at mid-length, while in Matudanthus they are versatile but articulate from the base. The placement of Gibasis is still uncertain in our analysis. In the Parsimony-based tree, Gibasis is recovered as sister of Elasis + Matudanthus, low statistical support (BS=68; Fig 3), while in the Bayesian topology Gibasis is recovered as sister to Tradescantia with strong statistical support (PP=0.97;Fig 6). In this scenario, Elasis + Matudanthus is, in turn, recovered as sister to Gibasis + Tradescantia (Fig 3). The clade Gibasis (Elasis + Matudanthus) (Fig 6) from the Parsimonybased tree is morphologically supported by: pedicels laterally spreading at post-anthesis (character 145), leaf epidermis with silica crystals in thin-walled specialized cells (character 485), these cells arranged in longitudinal bands or solitary and wedged at the same level as regular epidermal cells (character 486), and leaf mesophyll with fibrous extensions (character 499). Alternatively, the clade Gibasis + Tradescantia from the Bayesian tree is

morphologically supported by no exclusive synapomorphy (Fig 6). Gibasis is recovered for the first time as monophyletic, strongly-supported in the Bayesian tree (PP=1; Fig3) by its geniculate cincinni (character 96), connectives trapezoid to V-shaped (characters 290, 292, 294 and 296), and stigma with a combination of papillae of the types C and E sensu Owens and Kimmins (1981) (character 536). Nonetheless, Gibasis is still internally poorly resolved and requires further studies (Fig 3). On the other hand, Tradescantia is once again recovered as monophyletic with moderate statistical support (PP=1; BS=69; Fig 3) and morphologically supported by (Fig 6): bracteoles with erose margins (character 124), pollen wall internally striate-rugulate (character 344), glandular microhairs with medial cell cylindrical, wider and with thicker wall than the distal (character 463), and the presence of hidroxiluteolin (character 565) and 6-hidroxiluteolin (character 568). All five subgenera proposed by Pellegrini (2017) with the same relationships (Fig recovered monophyletic Callisia/Tripogandra generic complex, unsurprisingly, almost all genera are recovered as paraphyletic. Callisia sensu Hunt (1986) is recovered in five main lineages, with Tradescantia triandra Kunth (≡ Callisia ciliata Kunth, nom. illeg.), C. filiformis (M.Martens & Galeotti) D.R.Hunt, and C. gracilis (Kunth) D.R.Hunt sister to Tripogandra (Fig 3). The first two lineages of Callisia form a well-supported (PP=1; BS=92; Fig 3) clade, which is morphologically supported by its apically cleft or lobed cincinni bracts (character 113) (Fig 6). The first Callisia lineage has moderate statistical support (PP=0.97; BS=68; Fig 3), corresponds to C. sect. Brachyphylla, and consists of C. hintoniorum B.L.Turner, C. laui (D.R.Hunt) D.R.Hunt, C. micrantha (Torr.) D.R.Hunt, and C. navicularis (Ortgies) D.R.Hunt. It is morphologically supported by its inflorescence with a 90° torsion causing the bracts of the double-cincinni to the decussate (character 86), and somewhat succulent bracteoles (character 121) (Fig 6). The second Callisia lineage, sister to C. sect. Brachyphylla, is the strongly supported (PP=1; BS=99; Fig 3) Cuthbertia Small. It is morphologically supported by its lanate roots (character 12), and petals with crenulate margins (character 219) (Fig 6). Callisia sect. Brachyphylla and Cuthbertia are, together, sister to the remaining lineages of the Callisia/Tripogandra generic complex, being statistically well-supported (PP=0.99; BS=91; Fig 3) but lacking the support of any exclusive synapomorphy (Fig 6). The following lineage corresponds to Aploleia Raf. [incl. C. cordifolia (Sw.) E.S.Anderson & Woodson, as suggested by Pellegrini (2017)]. It is statistically strongly supported (PP=1; BS=99; Fig 3), being morphologically supported by its inconspicuous to very short styles (character 380), lacking a stylar canal (character 534) (Fig 6). The next three lineages form a mildly supported clade (PP=0.93; BS=51; Fig 3), supported morphologically by the presence of type 2 silica crystals sensu Tomlinson (1966) (character 487) (Fig 6). Nonetheless, the relationship between these three lineages is still poorly resolved, with the lineage representing Hadrodemas H.E.Moore being either recovered as sister to Callisia s.str. or to Tripogandra s.lat. (Fig 3). Both possible relationships lack the support of any exclusive synapomorphy, with both of them being supported by the same number of homoplastic characters (Fig 6). Hadrodemas is supported as monophyletic by its cincinni only basally fused (character 101) (Fig 6). Callisia s.str. strongly supported (PP=1; BS=100; Fig 3) as monophyletic by its paleaceous bracteoles (character 121) and sepals (character 191) (Fig 6). Finally, Tripogandra s.lat. is strongly supported (PP=1; BS=100; Figs 3, 6) by its cincinni bracts which are vestigial (character 105), fused and cup-shaped (character 111), with erose margins (character 113).

Hanguanaceae— As aforementioned, Hanguanaceae is monogeneric and, thus, infrafamiliar relationships in this group are resumed to species-level relationships. The position of *H. malayana* (Jack) Merr. is still unresolved, being either recovered in a polytomy with two clades (Fig 2) or poorly supported as sister to these two clades. The first of these two unnamed clades are represented by *H.* Siti Nurfazilah et al. and *H. bogneri* Tillich & E.Sill, being supported by prominent stigmas in fruit (character 412) (Fig 5). The other clade is

composed of *H. exultans* Siti Nurfazilah et al., *H. loi* Mohd Fahmi et al., *H. major* Airy Shaw, *H. nitens* Siti Nurfazilah et al., *H. pantiensis* Siti Nurfazilah et al., *H. podzolica* Siti Nurfazilah et al., and *H. stenopoda* Siti Nurfazilah et al. This clade is supported by nectariferous scales of the pistillate flowers with hyaline margins (character 359) (Fig 5). Finally, a sub-clade composed of *H. pantiensis*, *H. podzolica*, and *H. stenopoda* is supported by the oblique insertion of the stigmas in the ovary and fruit (Fig 5). This peculiar character has been included in the present analysis as independent to enantiostyly due to the lack of studies investigating the possible correlation of these features.

Philydraceae- The genus-level relationships recovered by us have been somewhat inconsistent throughout the different analyses. Philydrella Caruel and Philydrum Banks & Sol. ex Gaertn. are generally recovered sister to each other, but with medium statistical support (PP=1; BS=65; Fig 1), and morphologically supported by no exclusive synapomorphy (Fig 4). Orthothylax (Hook.f.) Skottsb. was also generally recovered sister to Helmholtzia F.Muell. s.str., with low statistical support (PP=0.59; Figs 1, 4), and morphologically supported by: narrowly ovoid floral buds (character 130), and outer perianth lobes with involute margins (character 176) and deflexed (character 177). The most common topology recovered for Philydraceae had the reverse generic sequence of the topology recovered by (Saarela et al. (2008), with Helmholtzia s.str. diverging first, followed by Orthothylax, and Philydrum sister to Philydrella (Fig 1). Finally, we have also recovered the same topology recovered by Saarela et al. (2008). Regardless, all aforementioned topologies seem to be equally poorly supported. Philydrella is robustly supported as monophyletic (PP=1; BS=100; Figs 1, 4) by: rhomboid outer perianth lobes (character 175), and filaments fused for the basal third or half of the inner perianth lobes (character 246). Philydrum is strongly recovered as monophyletic (PP=1; BS=96; Fig 1, 4) and supported by: outer perianth lobes plicate (character 176), and spirally striate-tuberculate seeds (character 423). Finally, Helmholtzia s.lat. is only sometimes recovered as monophyletic, and when so, only with very low statistical support (PP=0.59; Fig 1). Orthothylax is supported as distinct from Helmholtzia s.str. by its perianth becoming succulent at post-anthesis (character 166), broadly oblong outer perianth lobes (character 175), and flattened (character 381) (Fig 4). Finally, Helmholtzia s.str. is robustly-supported as monophyletic (PP=1; BS=100; Figs 1, 4) by: outer perianth lobes basally connate (character 174), inner perianth lobes oblong to rectangular (character 180) with tridentate apex (character 183), and filament fused to the posterior outer perianth lobe and to the inner lobes (character 246).

Haemodoraceae- The family is divided into two main lineages, corresponding to its two accepted subfamilies (Fig 1). Subfamily Haemodoroideae is statistically strongly-supported (PP=1; BS=94; Fig 1), being morphologically supported by (Fig 4): plantlets with primary roots vellow or orange or red or violet (character 439), cotyledonary sheaths lobed (character 447), presence of multiseriate pilate hairs (character 474), and hairs with a basal cell-rosette (character 475). Haemodoroideae is divided into two clades (Fig 1): (1) the strongly supported (PP=1; BS=93) Haemodorum clade; and (2) the well-supported (PP=1; BS=88) Wachendorfia clade. The Haemodorum clade is currently represented by three genera, Dilatris P.J.Bergius s.lat. (PP=1; BS=99), Haemodorum Sm. (PP=1; BS=100), and the monospecific Lachnanthes Elliott (Fig 1). Dilatris s.lat. is morphologically supported exclusively by the presence of mucilage cells in the leaf mesophyll (character 498) (Fig 4), being organized in two wellsupported clades (PP=1; BS=96; Fig 1): (1) the yellow-flowered clade, consisting of D. paniculata L.f. and D. viscosa L.f. and supported by aristate capsules (character 401) (Fig 4); and (2) the mauve-flowered clade (i.e., Dilatris s.str.), consisting of D. corymbosa P.J.Bergius, D. ixioides Lam., and D. pillansii W.F.Barker., and morphologically supported by tuberculate stigma (character 390), the presence of an anthocarp originated from an inferior ovary (character 394), and septifragal (i.e., 6-valved) capsules (character 408) (Fig 4).

The sister relationship between Lachnanthes and Haemodorum (PP=1; BS=93; Fig 1) is morphologically supported by (Fig 4): coriaceous perianth lobes (character 191), style remaining intact in fruit at the columella (character 387), and strongly trilobed capsules (character 400). Lachnanthes is supported by anthers coiled at post-anthesis rimose anthers dehiscing from the base to apex (character 318), and denticidal capsules (character 408) (Fig 4). On the other hand, *Haemodorum* is morphologically supported by (Fig 4): the presence of a bulb (character 15), perianth remaining coriaceous at post-anthesis (character 166), and seedlings with turnip-shaped primary root (character 438). Haemodorum is recovered by us in two clades (Fig 1): (1) the strongly supported (PP=1; BS=100) paired-flowered clade, represented by H. brevisepalum Benth. and H. spicatum R.Br., and morphologically supported by their pedicels basally fused (character 138) (Fig 4); and (2) Haemodorum s.str. clade (PP=0.53; BS=57), represented by the remaining species sampled by us, and morphologically supported by the bracteoles with densely crispate margins (character 122) (Fig 4). The Wachendorfia clade is morphologically supported by (Fig 4): non-resupinate flowers (character 135, reversion), infralocular septal nectaries (character 149), and nectar guides orange to red (character 204) and consisting of three spots (Character 205). It is divided into two statistically well-supported sub-clades (Fig 1): (1) the Neotropical clade (PP=1; BS=83), consisting of Cubanicula Hopper et al., Pyrrorhiza Maguire & Wurdack, and Xiphidium Aubl.; and (2) the Afro-American clade (PP=1; BS=94), represented by Schiekia Meisn., Barberetta Harv., and Wachendorfia Burm. The Neotropical clade is morphologically characterized by (Fig 4): upper three tepals basally to medially fused (character 156), all darkmucronate at apex (character 199), ovary with pilate hairs (character 375) restricted to the septal ridges (character 376), and seeds with dactyliform projections restricted to the margins (character 425). The relationship between its genera is poorly-resolved, with all three genera recovered either: (1) in a polytomy; (2) Cubanicula recovered sister to Xiphidium and Pyrrorhiza as their sister; (3) Pyrrorhiza sister to Xiphidium and Cubanicula sister to them; or (4) Cubanicula sister to Pyrrorhiza and Xiphidium sister to them. Nonetheless, all three genera are supported by exclusive synapomorphies (Fig 4). Cubanicula is supported by unequal anther sacs (character 307), Pyrrorhiza is supported by foliaceous and leaf-like bracteoles (character 121), while Xiphidium is strongly supported (PP=1; BS=98; Fig, 1) by cuboid seeds (character 415) with verrucose to tuberculate testa (character 423) (Fig 4). The Afro-American clade is morphologically characterized by (Fig 4): the presence of commissure slits connecting the septal nectaries to the perianth (character 150), bilabiate perianth (character 155) with the upper five tepals basally to medially fused (character 156) and two lateral apertures that hold and present the nectar to pollinators (character 165), and trigonous capsules (character 400). Schiekia is strongly supported as monophyletic (PP=1; BS=100; Figs 1, 4) by: paired stamens with caducous anthers (character 316), pollen grains with 3layered walls (character 342), and the presence of two filiform staminode-like projections in the inner paired tepals (character 360). *Barberetta* is strongly recovered (PP=1; BS=94; Fig 1) as sister to Wachendorfia, supported by (Fig 4): unifacially plicate leaves (character 42) and leaves with bulliform cells in their mesophyll (character 488). Barberetta is supported on its own by its emarginate-mucronate tepals (character 224), and the presence of a blanket-like placenta surrounding the sole ovule/seed (character 528) (Fig 4). On the other hand, Wachendorfia is poorly supported as monophyletic (PP=0.93; BS=51; Fig 1), being morphologically supported by no exclusive character (Fig 4). Furthermore, only two homoplastic characters unambiguously supporting it as distinct from Barberetta: perianth lobes with a 5+1 arrangement (character 185) and lobes of different shapes in the same whorl (character 197) (Fig 4).

Subfamily Conostylidoideae is statistically well-supported (PP=1; BS=89; Fig 1, 4) and morphologically (Fig 4) supported by: porate pollen grains (character 338), and presence of

multiseriate branched hairs (character 471). The first lineage of Conostylidoideae represents the robustly supported Tribonanthes Endl. (PP=1; BS=100; Fig 1), which is supported as monophyletic by (Fig 4): filaments with flat and thickened dorsal appendages (character 252), pollen grains 5-7-porate (character 340), and hypanthium pubescent with branched multiseriate hairs (character 375). Internally, Tribonanthes is recovered in our analysis as poorly resolved, with most species in a polytomy (Fig 1). Nonetheless, on some trees the genus is internally resolved with very low statistical support. In this scenario, the subgenera proposed by Hickman and Hopper (2019) are recovered as monophyletic, except T. subg. Tribonanthes, which is paraphyletic due to the placement of T. brachypetala Lindl. as sister to T. minor M.Lyons & Keighery (i.e., T. subg. Salina). The clade composed of Anigozanthos Labill. (incl. Macropidia J.Drumm. ex Harv.), Conostylis R.Br. s.lat. (incl. Blancoa Lindl.), and Phlebocarya R.Br., is statistically well-supported (PP=1; BS=85; Fig 1), being morphologically (Fig 4) corroborated by: equitant leaves (character 35), hypanthium with a supra-ovarian constriction (character 153), pollen grains with hemispheric aperture walls (character 345), and the presence of multiseriate dendritic hairs (character 473). *Phlebocarva* is strongly recovered as monophyletic (PP=1; BS=100; Fig 1), but poorly-supported (PP=0.72; BS=72; Fig 1) as sister to Anigozanthos and Conostylis, lacking any exclusive synapomorphies (Fig 4). Phlebocarya is morphologically supported by (Fig 4): extrorsely rimose anthers (character 319–322), hemispheric aperture walls of the pollen grains pollen with flattened with scattered exine elements (character 346), and pleurotropous ovules (character 533). Anigozanthos s.lat. is strongly recovered as monophyletic (PP=1; BS=94; Fig 1), supported by (Fig 4): perianth with longitudinal splitting (character 164), perianth lobes internally pubescent with dendritic hairs (character 217), and straight-peltate placentae (character 528). Macropidia is either recovered as sister to A. flavidus DC. or in a basal polytomy with it and the remaining species of Anigozanthos (Fig 1). No morphological character supports Macropidia as sister to Anigozanthos s.str. Aside from that, the infrageneric classification proposed by Hopper (1987) was not corroborated by our analysis. Finally, Conostylis s.lat. is statistically strongly-supported by us as monophyletic (PP=1; BS=76; Fig 1) with the inclusion of *Blancoa*, supported by (Fig 4): leaf epidermis with evenly thickened cell walls (character 479) and paradermic invaginations (character 480), and pendulous-peltate or inclinate-peltate placentation (character 528). Several of the infrageneric taxa proposed for Conostylis by Hopper et al. (1987) are recovered as non-monophyletic in the present study. Blancoa is recovered nested deep inside Conostylis, and when it is recovered as sister to Conostylis s.str., then Conostylis is morphologically supported exclusively by its placenta morphology. On the other hand, the internal relationships recovered by us in the present analysis are greatly convergent with the one recovered by Hopper et al. (2006), based on molecular data (Fig 1).

Pontederiaceae— Heteranthera sensu Pellegrini (2017a), is once again recovered as monophyletic with high statistical support (PP=1; BS=96; Fig 1). It is morphologically supported by (Fig 4): water-binding/mucilaginous roots (character 11), ligules bidentate (character 28), filaments obliquely inserted (character 242), unevenly trilobed stigma (character 390), sparse aerenchymatous tissue in the perianth (character 503), and axileparietal placentation (character 527). Within Heteranthera we recover three main clades (Fig 1): (1) the H. limosa group (PP=1; BS=99), composed of H. limosa (Sw.) Willd., H. lutea (H.Perrier) M.Pell., and H. rotundifolia (Kunth) Griseb.; (2) an expanded H. dubia group (PP=1), composed of H. dubia (Jacq.) MacMill., H. gardneri (Hook.f.) M.Pell., H. oblongifolia Mart. ex Schult. & Schult.f., H. seubertiana Solms, and H. zosterifolia Mart.; and (3) the H. reniformis group (PP=1; BS=99), composed of H. callifolia Rchb. ex Kunth, H. catharinensis C.N.Horn & M.Pell., H. longirachilla D.J.Sousa & Giul., H. multiflora (Griseb.) C.N.Horn, H. peduncularis Benth., H. pumila M.Pell. & C.N.Horn, H. reniformis

Ruiz & Pav., and *H. spicata* C.Presl. The *H. limosa* group is morphologically supported by (Fig 4): central posterior perianth lobe flanged at base (character 200), pollen grains with heterogenous tectal elements (character 353), and the presence of apigenin (character 563). The *H. dubia* group is morphologically supported exclusively by its slightly 2-flanged placentation (character 529) (Fig 4). Finally, the *H. reniformis* group is supported by: blade at the petiole insertion conspicuously discolorous (character 61), and central anterior perianth lobe with a basal fold (character 200) (Fig 4).

Pontederia sensu Pellegrini et al. (2018) is also recovered as monophyletic with robust statistical support (PP=1; BS=100; Figs 1, 4) being supported by: ligules truncate (character 28), petiolate leaves pulvinate (character 62) and with chartaceous to coriaceous blades (character 63), main axis of the inflorescence fistulose (character 87), tristylous flowers (character 134), perianth coiled at post-anthesis (character 166), anthocarp with longitudinal ridges (character 397), and perianth with dense aerenchymatous tissue (character 511). Pontederia is recovered arranged in five clades, corresponding to the subgenera proposed by (Pellegrini et al. 2018), each of them monophyletic and with the exact same composition as proposed by Pellegrini et al. (2018) (Fig 1). Pontederia subg. Cabanisia group is the first lineage of the genus, being statistically highly supported (PP=0.99; BS=99; Fig 1) and morphologically supported by the anthocarp tightly involving and fused to the fruit (character 396) (Fig 4). It is sister to the remaining subgenera, which are supported (PP=0.62; Fig 1) by (Fig 4): anthocarp tightly involving but free from the fruit (character 396), and the presence of eichhornin (character 556) and cyanogenic compounds (character 559). Pontederia subg. Oshunae is morphologically supported by (Fig 4): its free-floating habit (character 6), and flabellate ligules (character 28). It is recovered as sister to P. subg. Monochoria, P. subg. Eichhornia, and P. subg. Pontederia poorly-supported (PP=0.65; Fig 1) by crested anthocarp (character 397) and by the presence of epithelial cells in the ovary septae (character 523) (Fig 4). Pontederia subg. Monochoria is recovered with high statistical support (PP=1; BS=99; Fig 1) and morphologically (Fig 4) supported by: presence of a tepalo-staminal tube (character 247), stamens connivent or pointing towards the center of the flower, except for an odd straight stamen (character 299), and chromosome number of n=14 (character 551). Pontederia subg. Eichhornia and P. subg. Pontederia are recovered as sister with medium-statistical support (PP= 1; BS= 70; Fig 1) and morphologically supported by coiled perianth at postanthesis with involute apex (character 167) (Fig 4). Pontederia subg. Eichhornia is recovered with medium-statistical support (PP=0.89; BS=83; Fig 1), morphologically supported solely by (Fig 4): morphologically supported by the anthocarp loosely enclosing the fruit (character 396), perianth with fibrillar tannin cells (character 508, reversion), and ovary walls lacking aerenchymatous tissue (character 521, reversion). Finally, P. subg. Pontederia is as monophyletic with good statistical support (PP=1; BS=80; Fig, 1), being morphologically supported by (Fig 4): pseudomonomerous ovary (character 377), echinate anthocarp (character 398), fruit an achene (character 409), and pendulous placentation (character 527).

Plastid and combined analyses

The *matK* characters represented 866 characters of the plastid dataset, with GTR+G+I as the nucleotide model selected. The *ndhF* characters represented 1992 characters of the plastid dataset, with GTR+G+I as the nucleotide model selected. The *rbcL* characters represented 1283 characters of the plastid dataset, with GTR+G+I as the nucleotide model selected. The *psbA-trnK* characters represented 1310 characters of the plastid dataset, with GTR+G+I as the nucleotide model selected. The *trnL-F* characters represented 822 characters of the plastid dataset, with GTR+G+I as the nucleotide model selected. The plastid dataset represented 6273 characters, of which 4241 characters were variable. The plastid Bayesian analysis recovered a mostly resolved tree with all studied taxa well supported (>PP 95%). The

congruence between the plastid and morphological datasets is illustrated in Figures 1–3 and 7–9. Topologies produced by MP and BI analyses, based on the combined plastid + morphology datasets, were highly congruent and provided higher support for more clades than the results based on independent datasets (Figs 7–9). Thus, based on the combined plastid + morphological datasets (6843 analyzed characters, of which 353 were variable and 140 parsimony-informative), the combined Bayesian analysis recovered a fully resolved tree with Commelinales, all families to subgenera ranks in well-supported clades (>PP 95%) (Figs 7–9). The topology recovered for the Bayesian combined analysis (Figs 7–9) is almost identical to the one recovered for the morphological dataset (Figs 1–3), differing in only very small details.

Discussion

History and classification of Commelinales

The circumscription and characterization of Commelinales has varied greatly throughout the years, according to the author, their interpretation of morphology, and more recently, on the data used to define it. In some instances, aside from its inconsistent circumscription and characterization, the order has also been treated under different descriptive ordinal names. The number of included families has also varied greatly, ranging from one to 11, depending on the author. Furthermore, the order has been historically associated with several monocot orders (e.g., Bromeliales, Typhales, Velloziales, etc.), but is currently placed in the commelinids, sister to Zingiberales (Givnish et al. 1999, 2006, 2018; Chase et al. 2000, 2006; Savolainen et al. 2000; Soltis et al. 2000; Graham et al. 2002, 2006; Davis et al. 2004; Saarela et al. 2008; Hertweck et al. 2015; APG IV 2016).

Commelinales was originally described by Berchtold and Presl (1820: 267), based on Mirbel's concept of Commelinaceae, composed solely by this family, which at the time also included the Mayacaceae (Tables 2 & 3). Only a few years later, Reichenbach (1828) proposed that Commelinaceae (which included under the tribe Restioneae, the families Anarthriaceae, Centrolepidaceae, Rapateaceae, and Restionaceae; under Xyrideae the families Eriocaulaceae pro parte, Xyridaceae; and under Commelineae the families Commelinaceae, Eriocaulaceae pro parte, Flagellariaceae, Haemodoraceae pro parte, Mayacaceae, Philydraceae, and Pontederiaceae) was to be included in his order Caulo-Acroblastae, suborder Glumaceae (Tables 2 & 3). This order also included several other broadly circumscribed families, such as Bromeliaceae, Cyperaceae, Iridaceae, and Poaceae, but the author provided no characterization or rationale for the order and the circumscription of each family. For these reasons, this work has been greatly ignored by most botanists throughout the years. In the following year, Dumortier (1829) provided a rearrangement of Commelinales (as "Commelinariae"), characterizing it as containing families with deliquescent petals, superior ovary, and dehiscent fruits. It included the families Commelinaceae (incl. Mayacaceae), Dasypogonaceae, Eriocaulaceae, and Xyridaceae (Tables 2 & 3). Dumortier's publication is considered the most relevant of the previous circumscriptions of the order, since it was, until very recently, believed to be the original place of publication of the name Commelinales (Reveal 1993; APG III 2009). Endlicher (1836) described the "class" Enantioblastae (which had its rank posteriorly corrected to order; Turland et al. 2017, Art. 16.3 and 32.3) characterized by its heterochlamydeous flowers, dehiscent fruits, and orthotropous ovules. The order was composed of Centrolepidaceae, Commelinaceae, Eriocaulaceae, Restionaceae, and Xyridaceae (incl. Mayacaceae) (Tables 2 & 3). The circumscription and composition of Endlicher's Enantioblastae were considerably similar to the concept of Commelinales adopted by Dumortier (1829), which was faithfully followed by Eichler (1890), in his classification system. Lindley (1846), deviated from previous authors in adopting the name Xyridales

instead of Commelinales. His new order was composed of Commelinaceae, Mayacaceae, Philydraceae, and Xyridaceae (incl. Dasypogonaceae and Rapateaceae) (Tables 2 & 3), and was characterized by presenting trimerous and heterochlamydeous flowers, superior ovaries, and copious albumen. Furthermore, the author mentioned the similarity between Eriocaulaceae and Xyridaceae, despite treating them in different orders. Engler (1886) proposed the order Farinosae, which was characterized by plants that presented a mealy endosperm, as the name suggests. Aside from that, the Farinosae were further characterized by presenting deliquescent corolla, superior ovary, and dehiscent fruits (Engler 1886). The order was composed of 11 families, some of which were rarely considered to be closely related: Bromeliaceae, Centrolepidaceae, Commelinaceae, Eriocaulaceae, Flagellariaceae, Mayacaceae, Philydraceae, Pontederiaceae, Rapateaceae, Restionaceae, and Xyridaceae (Tables 2 & 3). This concept of Farinosae was also followed in detail by Rendle (1904).

Between 1930–2000, several classification systems were proposed, and consequently, a great disagreement erupted regarding the circumscription of Commelinales, as well as several other plant families and orders. Hutchinson (1934) proposed the reduction of Commelinales, accepting only three families: Commelinaceae, Flagellariaceae, and Mayacaceae (Tables 2 & 3). In this circumscription, the Dasypogonaceae are sunk into Xanthorrhoeaceae and placed in the order Agavales, the Eriocaulaceae are placed in the monofamilial Eriocaulales, while Xyridaceae and Rapateaceae are placed in Xyridales (Table 2). After a hiatus of over three decades, a myriad of classification systems, and their versions, were proposed by different authors (e.g., Cronquist 1968, 1981; Dahlgren 1980, Dahlgren and Clifford 1982; Dahlgren and Rasmussen 1983; Dahlgren et al. 1985; G. Dahlgren 1989; Goldberg 1989; Takhtajan 1969, 1980; Thorne 1992a, 1992b; Table 2 & 3). According to the author and version of each classification system, Commelinales was composed of (Tables 2 & 3): (1) Commelinaceae and Mayacaceae (Dahlgren 1980; Dahlgren and Clifford 1982; Dahlgren and Rasmussen 1983); (2) Commelinaceae, Mayacaceae, Rapateaceae, and Xyridaceae (Cronquist 1968, 1981; Takhtajan 1969, 1980, 1997); or (3) Commelinaceae, Eriocaulaceae, Mayacaceae, Rapateaceae, and Xyridaceae (Dahlgren et al. 1985; G. Dahlgren 1989; Goldberg 1989; Thorne 1992a, 1992b). Cronquist (1968, 1981) considered Commelinales to be closely related to Bromeliales and Liliales (the later including Haemodoraceae, Philydraceae, and Pontederiaceae). He characterized Commelinales as possessing paracytic stomata with four or six subsidiary cells, nuclear endosperm generally starchy with some protein, and embryo capped at the micropylar end. This circumscription of Commelinales including Commelinaceae, Mayacaceae, Rapateaceae, and Xyridaceae, was followed by Takhtajan (1969, 1980), since it appeared to him to represent a "morphologically cohesive group". Nonetheless, the morphological similarities between Eriocaulaceae, Mayacaceae, and Xyridaceae was observed by other systems at the time (Dahlgren 1980; Dahlgren and Clifford 1982; Dahlgren and Rasmussen 1983), which questioned its naturality. The last exclusively morphological circumscription for Commelinales was proposed by Dahlgren et al. (1985), which was updated by Dahlgren (1989), and modified by Goldberg (1989) and Thorne (1992a, 1992b). It was characterized by a tendency to a rosette habit, closed leaf-sheaths, showy and insect-pollinated flowers, deliquescent petals (generally yellow, purple, pink or blue), and the absence of septal nectaries. Commelinales sensu Dahlgren et al. (1985) included Commelinaceae, Eriocaulaceae, Mayacaceae, Rapateaceae, and Xyridaceae, being accepted by most botanists until the advent of molecular phylogenetics (Givnish et al. 1999).

With the dawn of the molecular era, our knowledge and understanding of the phylogenetic relationships in plants drastically changed and increased (APG 1998; APG II 2003; APG III 2009; APG IV 2016). Similarly, the concept of Commelinales was completely changed, grouping families which were rarely considered to be closely related (Givnish et al. 1999). All families previously placed, at some point, in Commelinales (i.e., Anarthriaceae,

Bromeliaceae, Centrolepidaceae, Cyperaceae, Eriocaulaceae, Flagellariaceae, Joinvilleaceae, Mayacaceae, Poaceae, Rapateaceae, Restionaceae, and Xyridaceae are currently placed in different lineages of Poales sensu APG; Givnish et al. 1999, 2018; Chase 2004; Bouchenak-Khelladi et al. 2014; Hertweck et al. 2015; APG IV 2016; Table 2). The only exceptions being its type family (i.e., Commelinaceae), Iridaceae, and Dasypogonaceae. Iridaceae, was only once placed in the same order as Commelinales (Reichenbach 1828), being posteriorly associated with other lilioid monocots in all morphological systems, and currently placed in Asparagales sensu APG (APG 1998; APG II 2003; APG III 2009; APG IV 2016). On the other hand, Dasypogonales was generally associated with Juncaceae and/or Xyridaceae (Table 2), or sometimes sunk into Xanthorrhoeaceae and placed with other lilioid monocots (Table 2). Currently, it is either placed in Arecales (Hertweck et al. 2015; APG IV 2016) or in its own order, Dasypogonales (Givnish et al. 1999, 2018; Table 2). Especially surprising was the placement of Mayacaceae in Poales (Givnish et al. 1999, 2018; Chase 2004; Bouchenak-Khelladi et al. 2014; Hertweck et al. 2015; APG IV 2016; Table 2), since it was always considered to be either sister to Commelinaceae or included in it (Pellegrini and Carvalho 2016).

Commelinales sensu APG is monophyletic and composed of Commelinaceae, Haemodoraceae, Hanguanaceae, Philydraceae, and Pontederiaceae (Givnish et al. 1999, 2006, 2018; Chase et al. 2000, 2006; Savolainen et al. 2000; Soltis et al. 2000; Graham et al. 2002, 2006; Davis et al. 2004; Saarela et al. 2008; APG IV 2016; Hertweck et al. 2015; Table 3). Out of these families, Haemodoraceae, Philydraceae, and Pontederiaceae were generally considered as closely related to each other (Simpson 1990). They were generally placed in: (1) Liliales (Lindley 1846, Hutchinson 1934, Goldberg 1989, only Pontederiaceae; Cronquist 1968, 1981; Takhtajan 1969, 1980); (2) each in its monofamilial order (Dahlgren 1980, Dahlgren and Clifford 1982, Dahlgren et al. 1985, G. Dahlgren 1989); (3) Haemodorales (Hutchinson 1934, only Haemodoraceae and Philydraceae); (4) Bromeliales (Thorne 1992b); (5) Iridales (Goldberg 1989, only Haemodoraceae and Philydraceae); or (6) all in Philydrales (Thorne 1992a) (Table 3). Rarely, Haemodoraceae was placed in Narcissales/Amaryllidales (Lindley 1846), while Philydraceae was placed in Xyridales (Lindley 1846). On the other hand, Hanguanaceae was always considered as a family of uncertain affinity (Rudall et al. 1999) and has commonly been left unplaced in several classification systems (Table 3). It was historically considered to be morphologically similar to several genera and families of monocots (Maury 1888), such as: Amaryllidaceae (Crinum L.), Arecaceae (Chamaedorea Liebm. ex Mart., Pinanga Blume, and Morenia Ruiz & Pav.; also suggested by Airy Shaw 1965), Asparagaceae (Dracaena L. and Lomandra Labill.), Asteliaceae (Astelia Banks & Sol. ex R.Br.), Cyclanthaceae (Carludovica Ruiz & Pav.), Juncaceae, Melanthiaceae (Veratrum L.), Rapateaceae, and Smilacaceae (Smilax L.), and finally as part of the exceedingly broad concept of Liliaceae (as several other genera and families of flowering plants have; Table 3). Nonetheless, the most widely accepted grouping was proposed by Backer (1951), in which Hanguana Blume was placed as a genus of Flagellariaceae (incl. Joinvilleaceae). Regarding ordinal placement, Hanguanaceae has been tentatively placed in: (1) Coronariae (Endlicher 1836; Eichler 1890); (2) Juncales (Lindley 1846); (3) Commelinales (Hutchinson 1934); (4) Liliales (Cronquist 1968, 1981; Takhtajan 1969, 1980); (5) Asparagales (Dahlgren 1980; Dahlgren and Clifford 1982; Dahlgren and Rasmussen 1983; Dahlgren et al. 1985; Thorne 1992a, 1992b); (6) Poales (Dahlgren and Clifford 1982; Dahlgren and Rasmussen 1983); and (7) Hanguanales (G. Dahlgren 1989). Hanguana has also been associated with Arales, Arecales, Asparagales, Xyridales, and Zingiberales, but never formally placed in these orders. The final ordinal association, based solely on morphology, was made by Rudall et al. (1999). These authors suggested an association with Zingiberales, despite Hanguanceae presenting unisexual and actinomorphic (questionably) flowers, superior ovary, and lacking septal

nectaries. The morphological hypothesis that seemed to the least likely to be natural, was the one proposed by Tillich (1996) and Tillich and Sill (1999). They suggested, based on fruits, seeds, and seedlings characters that Hanguanaceae might be closely related to Commelinaceae, with a basal position [sic] in Commelinales. Nonetheless, this hypothesis has been confirmed over and over and over by different molecular studies, with Hanguanaceae strongly recovered in a sister position to Commelinaceae (Givnish et al. 1999, 2018; Chase et al. 2006; APG II 2003; Saarela et al. 2008; APG III 2009; Hertweck et al. 2015; APG IV 2016).

Congruence between morphology and molecular data in Commelinales

Despite the already known elevated degree of homoplasy in morphological datasets for the order (Evans and Faden 1998; Graham et al. 1998; Evans et al. 2000, 2003; Pellegrini 2017; Pellegrini et al. 2018), they are still congruent with the molecular dataset, and therefore, informative and relevant for phylogenetic inference. The topology recovered by us based exclusively on morphology, and thus also on combined data, is highly congruent with the available hypotheses available for each family and Commelinales as a whole. The familylevel relationships recovered by us are an exact match to the ones presented by Chase et al. (2006), Saarela et al. (2008) and Givnish et al. (2018) with low to medium statistical support. These relationships are robustly supported in our analysis, resolving the position of Philydraceae as sister to Haemodoraceae + Pontederiaceae, of Hanguanaceae as sister to Commelinaceae, and of Commelinaceae + Hanguanaceae as sister to Philydraceae (Haemodoraceae + Pontederiaceae). The apparent incongruence observed by our molecular analysis is a result of the great amount of missing data of our combined dataset, and future molecular studies sequencing the needed markers for all five families should address this issue. The small degree of incongruence observed between the morphological/combined and previously published molecular datasets is limited to some smaller generic relationships, such as: (1) the position of Elasis, Gibasis, Matudanthus, and Tradescantia in the Tradescantia clade (Commelinaceae); (2) the internal relationship of Plowmanianthus; (3) the position of Phlebocarya in relation to Anigozanthos and Conostylis (Haemodoraceae); (4) the position of the monospecific Blancoa to Conostylis and of the also monospecific Macropidia to Anigozanthos (Haemodoraceae); (5) the relationship between Cubanicula, Pyrrorhiza and Xiphidium (Haemodoraceae); (6) the internal relationships for Anigozanthos s.lat.; and (7) the relationship between the four genera of Philydraceae. Aside from that, some of the specieslevel relationships also differ from the recovered in molecular-based topologies. One interesting increase of congruence between datasets can be observed in Pontederiaceae, where the morphologically-topology recovered by Pellegrini et al. (2018) was considerably different from the molecular one. Nonetheless, in the present study, the topology recovered by us is completely congruent with the one recovered by Pellegrini et al. (2018), based on molecular data. Increase of congruence between datasets was also observed in: (1) Commelinaceae as a whole, where the morphology-based topology presented by Evans et al. (2000) was consistently different from the molecular-based one presented by Evans et al. (2003); (2) subtribe Tradescantiinae (Commelinaceae), where the relationships recovered by us are much closer to the ones recovered by Hertweck and Pires (2014), than the ones recovered by Pellegrini (2017); and (3) Haemodoraceae as a whole, with most of the genus-level incongruence observed between Simpson (1999; morphological) and Hopper et al. (1999, 2009, in prep.; molecular) having been resolved.

Several groups in Commelinales had, until now, only molecular-based phylogenetic hypotheses. *Palisota* had a preliminary molecular phylogeny based solely on *rbcL* (Zuiderveen et al. 2011) in which the authors recovered the genus organized in two clades. The same topology was recovered by us in the present study, giving not only morphological

support for these clades but also supporting the proposition of a much needed infrageneric classification for this complicated group. The phylogenetic relationships within Aneilema had only been investigated based on molecular data. Kelly and Evans (2014) recovered a paraphyletic Aneilema, due to A. brasiliense being recovered sister to Polyspatha and due to the inclusion of Rhopalephora in Aneilema s.str. Furthermore, of the sections proposed by Faden (1991), A. sect. Amelina was recovered as polyphyletic due to A. johnstonii being recovered sister to all species of Aneilema s.str., and A. gillettii being nested in A. sect. Pedunculosa. Aneilema sect. Lamprodithyros is also rendered as paraphyletic due to A. indehiscens subsp. keniense Faden being nested in A. sect. Brevibarbata. Added to that, none of the recovered relationships between the proposed sections of Aneilema were deemed by Kelly and Evans (2014) to make any morphological sense. The present morphology-based hypothesis for Aneilema is not only the first but also lends morphological support for the results of Kelly and Evans (2014). Our analysis is almost completely congruent, being further resolved and more statistically well-supported than the molecular one. A molecular phylogeny for Conostylis s.lat. was presented by Hopper et al. (2006), where most of the infrageneric classification proposed by Hopper et al. (1987) was recovered as non-monophyletic. According to the authors, they were unable to give any morphological support for the recovered topology. Nonetheless, the morphology-based topology recovered by us is considerably similar to the one recovered by Hopper et al. (2006). We have recovered the same four main lineages, despite some minor incongruences. These results point towards the changes and updates that need to be done to allow a monophyletic and morphologically cohesive classification for *Conostylis*. For instance, despite the strong statistical support for Blancoa as sister to Conostylis in the molecular analysis, our morphological analysis does not support that relationship. In the few trees where Blancoa is recovered in this position, Conostylis s.str. is supported by a single exclusive synapomorphy (i.e., character 528: pendulous-peltate placenta). This strongly argues against maintaining both genera as an independent. The case of Anigozanthos s.lat. is similar to that of Conostylis s.lat. Our morphological analysis does not support the recognition of *Macropidia* as independent from Anigozanthos s.str. Nonetheless, in the case of Anigozanthos, Macropidia is recovered in a basal polytomy together with A. flavidus, plus a clade with the remaining species of Anigozanthos. Added to that, in the trees, Macropidia is recovered as sister to Anigozanthos s.str. not even a single character supports that relationship. Regarding the incongruence of the species-level relationships between the morphological and molecular datasets, it seems to be small. Interestingly, neither datasets support the infrageneric classification proposed by Hopper (1987).

Until the present study, no phylogenetic hypothesis of any kind was available for Hanguanaceae. In this study, we provided not only a molecular-based hypothesis, but also a highly congruent morphology-based one, and consequently a robust combined hypothesis. Nonetheless, we have only sampled a third of the currently accepted species, plus the many still undescribed. Despite our sampling problem, our results are encouraging since they indicate a strong correlation between morphology, molecular data, and the group's evolutionary history. Further studies are surely needed in Hanguanaceae, especially regarding macro- and micro-morphology. The taxonomy of the group is still exceedingly reliant on characters that are either difficult or impossible to observe in herbarium specimens, added to the fact that most taxonomically informative characters are found only in female, mostly fruiting specimens.

Monophyly and systematics of Commelinales

The monophyly and composition of Commelinales have been the focus of much debate since its recognition. The current circumscription of Commelinales was, until now, supported exclusively by molecular data and, thus, was the focus of much criticism in the botanical community. Despite the order being statistically robustly supported, its generally poorlyresolved internal relationships prevented any acceptable subdivision of the group. Furthermore, all clades recovered with medium to high statistical support lacked compelling synapomorphies. Among the 16 morphological synapomorphies recovered by us for Commelinales, some are recovered as non-homoplastic exclusively due to the limited sampling of closely related orders of commelinid monocots. These characters are: plants aquatic or growing in damp environments (character 5), ligule absent (character 27), petals cuneate to obtuse at base (characters 223 and 232, filaments of the anterior stamens equal in length to the posterior (character 261), pollen grains released with adhering raphides (character 327) and tectate-columellate (character 348), superior ovary (character 373), fruits 3-valved (character 408), seedlings with rhizoids (character 440), tapetum ameboid (character 517), bitegmic seed coat (character 541), and endosperm copious (character 549). This leaves us with actually only four putatively non-homoplastic characters. The development of synflorescence/inflorescence buds (character 84) is a character that to our knowledge has never been investigated in monocots. Thus, we cannot affirm with certainty that it is indeed an exclusive synapomorphy for Commelinales and further studies on monocots lineages are needed to investigate this character. Persistent to slightly accrescent perianth (character 192) is somewhat an uncommon, but widespread feature in angiosperms (Spjut 1994). Based on this wide distribution is several very distantly related families, we can assume it has evolved independently several times, and are thus, homoplastic. Stomata are incredibly variable structures, found in most land plants. Their morphology and evolution were recently reviewed for the monocots (Rudall et al. 2017), emphasizing the number of neighboring cells and type of cell division. Nonetheless, the size, shape and general morphology of the neighboring cells was not addressed. Thus, for the time being, stomata with terminal and lateral neighboring cells equal in size (character 483) are to be considered restricted to Commelinales. Finally, perianth with tannin cells (character 505) seems to be uncommon in angiosperms, being recorded for only a few families but mostly in eudicots (e.g., Dilleniaceae, Anandakumar et al. 1986; Urticaceae, Kravtsova et al. 2003; Balsaminaceae, Marcgraviaceae and Tetrameristaceae, Von Balthazar & Schönenberger 2013; Melastomataceae, Robil & Tolentino 2015; Adoxaceae, Konarska 2017), being otherwise found in the monocots only in Arecales (Uhl & Moore 1977; Castaño et al. 2011) and Commelinales (Simpson 1990; Simpson & Burton 2006; Pellegrini 2017; Pellegrini et al. 2018; this study). Nonetheless, further studies are necessary to properly compare the morphology of these perianth tannin cells, especially between Arecales and Commelinales, and address their homology.

Despite the gross morphological differences, the Commelinaceae + Hanguanaceae clade is supported by four non-homoplastic synapomorphies, being also extensively supported by molecular data (Givnish et al. 1999, 2018; Chase et al. 2006; APG II 2003; Saarela et al. 2008; APG III 2009; Hertweck et al. 2015; APG IV 2016). Out of these, only two are truly non-homoplastic. Flat flowers (i.e., non-tubular; Character 154) are known to be plesiomorphic in angiosperms (Sauquet et al. 2017). Nonetheless, tubular flowers seem to become the rule, starting at the ancestral of the lilioid monocots (excl. Petrosaviales) (Pellegrini, pers. observ.). Flowers seem to have shifted from tubular to flat flowers independently several times in families such as Triuridaceae (Pandanales), Nartheciaceae (Dioscoriales), Smilacaceae (Liliales), Hypoxidaceae (Asparagales), Arecaceae (Arecales), Mayacaceae (Poales), and several other families. Nonetheless, tubular flowers are indisputably much more frequent in the monocots as a whole. In Zingiberales and most Commelinales, the flowers are tubular, either as a result of perianth fusion or perianth posture. A marking exception is the Commelinaceae + Hanguanaceae clade, in which tubular flowers are found again in genera nested deed within Commelinaceae (i.e., subtribe Coleotrypinae +

Cyanotinae, *Weldenia*, some species of *Tradescantia*, two lineages of the polyphyletic *Callisia*, and some species of *Pollia*). Thus, despite being homoplastic, this character is of clear systematic relevance. Seedling morphology has only been superficially studied in the monocots as a whole by Tillich (1995). Thus, the true systematic relevance of its morphology is still not well-understood. Nonetheless, Tillich (1995, 1996) clearly states the uniqueness of the complete absence of chlorophyll in the cotyledons of Commelinaceae and Hanguanaceae and the fact that at least the first primary leaf is modified into a cataphyll. Further studies on the seedling morphology of the monocots are essential to investigate the putative exclusiveness of these characters and their phylogenetic relevance for the Commelinaceae + Hanguanaceae clade. Regardless, this is the first study empirically recover any kind of morphological synapomorphies for this clade.

The Philydraceae (Haemodoraceae + Pontederiaceae) clade is morphologically much more easily recognized that the Commelinaceae + Hanguanaceae clade, having been recovered or suggested based on morphological data alone by several authors (e.g., Simpson 1990, 1993; Kress 1995; Linder and Kellogg 1995). It is also strongly supported by molecular data (Graham et al. 2003; Chase et al. 2006; Saarela et al. 2008; Givnish et al. 2018). Out of the 11 exclusive synapomorphies recovered by us as supporting this clade, ptyxis conduplicate, leaves unifacial with xylem and phloem alternate or circular phloem with central xylem, seeds fusiform to barrel-shaped, cotyledon assimilating are homoplastic with the inclusion of further outgroups, and the presence of diferulic acids and p-coumaric acids. Primary leaves bifacial and ribbon-like were recorded by Tillich (1994, 1995) in other monocot families with primarily aquatic species, and thus seems to be part of the aquatic syndrome. The presence of bean-shaped starch grains was suggested by Givnish et al. (1999) as an exclusive synapomorphy for this clade, and we haven't been able to find any evidence that would indicate otherwise. Finally, the morphology and distribution of calcium oxalate crystals in monocots were reviewed by Prychid and Rudall (1999), and showed that styloid crystals are widespread in monocots, but notably absent in almost all commelinids, except for this clade and few records in Zingiberaceae. Thus, despite being homoplastic, this character is still phylogenetically relevant. Prychid et al. (2003) investigated the systematic significance of cell inclusions in Commelinales but failed to observe the presence or absence of placental sclereids in the order, added to not sampling any representatives of Hanguanaceae. For this reason, the only available reference for this character is the one provided by Simpson (1990), where the author records the presence of placental sclereids for Haemodoraceae, Philydraceae, and Pontederiaceae for the first time. Thus, this character is considered, for the time being, an exclusive synapomorphy for this clade. Finally, the Haemodoraceae + Pontederiaceae clade recovered in the present study is consistent with several morphological (Simpson 1987, 1990, 1993; Simpson and Burton 2006; Pellegrini et al. 2018) and molecular studies (Graham et al. 2003; Chase et al. 2000, 2006; Givnish et al. 2006, 2018; Saarela et al. 2008; APG IV 2016; Hertweck et al. 2015). Out of the seven exclusive synapomorphies recovered by us, sulcal membrane verrucate and neighboring cells of the stomata with the oblique division are homoplastic with the inclusion of further outgroups. The presence of phenylphenalenones was originally regarded by Simpson (1990) as a synapomorphy for Haemodoraceae. Nonetheless, further phytotaxonomic studies have shown phenylphenalenones to be also present in Pontederiaceae and the distantly related Musaceae and Strelitziaceae (Otálvaro et al. 2002; Hölscher and Schneider 2005). Thus, this character is now to be regarded as a homoplastic synapomorphy for the Haemodoraceae + Pontederiaceae clade. We also recover the seed coat with calcium oxalate as a non-homoplastic synapomorphy for this clade. Nonetheless, studies focusing on the macromicromorphology of monocot seeds are sparse and much needs to test the exclusivity of this feature. Finally, the palynological characters reported by Simpson (1983, 1987, 1990) are exclusive to the Haemodoraceae + Pontederiaceae clade.

Enantiostyly in Commelinales

Enantiostyly is a type of floral asymmetry that is caused by the reciprocal deflection of the style either to the left (left-styled) or right (right-styled) side of a flower. In case the enantiostyly is reciprocal, it will produce mirror-image flowers, where the left- and rightstyled morphs are a perfect reflection of each other (Barrett et al. 2002; Jesson and Barrett 2003). Like several other types of stylar polymorphisms, enantiostyly has the primary function of reducing the geitonogamous selfing, and thus, improving proficient crosspollination (Jesson and Barrett 2002c, 2005; Barrett 2010). The occurrence of these mirrorimage flowers in at least a dozen unrelated families indicates that enantiostyly has originated independently on numerous occasions in flowering plants (Jesson and Barrett 2003). As noted by Givnish et al. (1999) and Rudall and Bateman (2004), enantiostyly seems to be the dominant feature, and most likely, also the ancestral state of Commelinales sensu APG. The only other monocot family with known records of enantiostyly is the distantly related Tecophilaeaceae (Asparagales) (Jesson and Barrett 2003). It had previously been widely reported for Haemodoraceae (subfamily Haemodoroideae: Ornduff 1974; Ornduff and Dulberger 1978; Simpson 1990; Jesson and Barrett 2002a), Philydraceae (the whole family: Simpson 1990; Graham and Barrett 1995), and Pontederiaceae (Heteranthera and Pontederia subg. Monochoria: Iyengar 1923; Graham and Barrett 1995; Wang et al. 1995: Pellegrini et al. 2016), Nonetheless, reports of enantiostyly in Commelinaceae have been sparse and inconsistent. This feature has been recorded for Aneilema (Faden 1991; Jesson and Barrett 2003), Amischotolype, Coleotrype and Porandra (Evans et al. 2000; Jesson and Barrett 2003), and Cochliostema (Hardy 2001; Jesson and Barrett 2003), Commelina (Jesson and Barrett 2003), Murdannia (Evans et al. 2000; Jesson and Barrett 2003; Pellegrini et al. 2016), and Tinantia (Jesson and Barrett 2003). Nonetheless, previous studies have failed to observe the enantiostyly in the flowers of Cartonema, Dictyospermum, Floscopa, Pollia, and Stanfieldiella, which are reported here for the first time. The only family of Commelinales never investigated for this feature was the poorly understood Hanguanaceae.

Hanguanaceae are peculiar in that they are dioecious, with pistillate flowers completely lacking a style (Bayer et al. 1998). As aforementioned, and also made obvious by its name, enantiostyly seems to be inherently depended on the presence of a developed style (Barrett et al. 2002; Jesson and Barrett 2003), but not necessarily its length. Thus, due to the absence of a style, the flowers of Hanguana could never be classified as enantiostylic. Furthermore, the fact that the flowers of Hanguana are unisexual creates unique scenery, since enantiostyly would completely lose its function of reducing the geitonogamous selfing, due to the impossibility of self-pollination in such a flower. Nonetheless, flowers of several species of Murdannia are still classified as enantiostylic (Evans et al. 2000; Jesson and Barrett 2003), even though the deflection is done exclusively by the filaments, being accompanied by a deflection in the style only by few species. Thus, the definition of enantiostyly needs to be broadened and clarified. Furthermore, several species of Hanguana present non-terminal stigmas (Leong-Škorničková and Boyce 2015), which creates the same floral asymmetry as enantiostyly. These stigmas are oblique to laterally inserted in the ovaries, and observable even in herbarium specimens. Thus, our working hypothesis is that this feature in *Hanguana* is homologous to, but more precisely derived from, an enantiostylic ancestor. Unisexual flowers are often associated with miniaturization, as observed in several groups of aquatic plants (e.g., Araceae, Ceratophyllaceae, and Hydatellaceae) or terrestrial plants (e.g., Casuarinaceae, several Eriocaulaceae, Moraceae, Urticaceae. Amborellaceae. Nonetheless, exceptions are as common, and a direct correlation cannot be properly made. On

the other hand, the occurrence of style polymorphisms seems to be directly limited by floral size, with small and large flowers rarely presenting any kind of style polymorphism (Richards and Barrett 1992). As already stated, unisexual flowers are not known to present any type of style polymorphisms. Furthermore, the loss of the style might also be explained by miniaturization, since most diminutive flowers seem to completely lack or present extremely reduced styles (e.g., Acoraceae, Araceae, Pandanaceae, Poaceae, etc.). Thus, it seems most likely that the loss of the style occurred concomitantly with floral miniaturization, the appearance of the dioecy, or at least with the appearance of unisexual flowers, all of them leading to a secondary loss of the enantiostyly in Hanguanceae. Floral ontogeny might be key to understand and properly address enantiostyly in *Hanguana*.

In our morphological dataset, Hanguanaceae was coded as "?" for the presence of enantiostyly. This caused the ancestral state reconstruction to recover a non-enantiostylic ancestral for Commelinales (Fig 10A). Nonetheless, based on our aforementioned hypothesis, we have also made an ancestral state reconstruction considering Hanguanaceae to possess enantiostylic pistillate flowers. In this second scenario, the ancestral for Commelinales is recovered with a high probability of being enantiostylic (Fig 10B), supporting the hypothesis of Givnish et al. (1999) and Rudall and Bateman (2004). Finally, based on the rarity of enantiostyly in the monocots (Jesson and Barrett 2003), it would make much more evolutionary sense for the ancestral of the order being enantiostylic, with posterior reversions to non-enantiostylic flowers in several of its lineages, including Hanguanaceae.

Tapetal raphides and styloid crystals

Prychid et al. (2003) investigated the systematic significance of cell inclusions in Commelinales. Nonetheless, the group was called "Haemodoraceae and allied families" by the authors due to them excluding Hanguanaceae from it since they believed the family was to be positioned in the Zingiberales (Rudall et al. 1999). This study gave special focus to the presence of tapetal raphides, which were sometimes accompanied by tapetal styloid crystals (Prychid et al. 2003). Tapetum producing raphides and occasional styloid crystals is a unique character reported for Commelinaceae (Mepham and Lane 1969; Tiwari and Gunning 1986; Hardy and Stevenson 2000; Prychid et al. 2003), Haemodoraceae (Simpson 1983, 1988, 1990; Prychid et al. 2003), Philydraceae (Hamman 1966; Prychid et al. 2003), and Pontederiaceae (Prychid et al. 2003; Simpson and Burton 2006). This character has the potential of being an exclusive synapomorphy for Commelinales, but further studies are needed increasing the sample in Commelinaceae (several genera not sampled) and also including Hanguanaceae. Due to the uncertainty regarding the presence of tapetal raphides and styloid crystals in Hanguanaceae and most of the genera in Commelinaceae, we are presently unable to confirm this character as synapomorphic for the order. Future studies decreasing the amount of missing data for this character might improve the quality of ancestral character state reconstruction.

Systematics and infrafamilial classification of Commelinales

Being a small order, composed of small to medium-sized families, it is not surprising that only Commelinaceae and Haemodoraceae make use of an infrafamilial classification (below family, but above the rank of genera). In Commelinaceae, a lot of attention was historically given to the group's infrafamilial classification. The most recent system was proposed by Faden and Hunt (1991) and is supported, in most part, by the available phylogenies. Exceptions are tribe Tradescantieae (due to the position of subtribe Palisotinae), subtribe Dichorisandrinae, and subtribe Coleotrypinae. Aside from that, all currently accepted infrafamilial ranks are supported as monophyletic. In the infrafamilial classification of Commelinaceae, different sets of characters are associated with the support of different ranks.

For instance, the three recognized subfamilies (i.e., Cartonematoideae, the herein recognized Palisotoideae, and Commelinoideae) are mainly supported by anatomical characters, coupled with hair and seed morphology. The tribes are also supported by anatomical characters, plus hair and seed morphology, but are further supported by pollen morphology. Finally, subtribes are generally supported by a combination of inflorescence architecture, pollen morphology, anatomical characters, and hair and seed morphology. Nonetheless, the big and morphologically diverse tribe Commelineae is not further divided into subtribes, due to the lack of systematically informative characters (Faden and Hunt 1991). The recognition of subtribes in Commelineae seem warranted, due to the groups' complexity and difficulty to study. The recognition of these subtribes would greatly help future studies by recognizing monophyletic and morphologically cohesive assemblages of genera. The three subtribes proposed in the present study make use of the same set of characters used by Faden and Hunt (1991) to recognize subtribes in Tradescantieae, plus our subtribes of Commelineae are further supported by androecium characters.

The infrafamilial classification of Haemodoraceae has received little attention over the years, with the only its subdivision in two subfamilies being widely accepted. Nonetheless, tribes have been historically proposed, with tribe Tribonantheae being the most recently described (Macfarlane and Hopper 1987). Our results are almost completely congruent with the available molecular data, and allow us to, once again, recognize tribes in Haemodoraceae. Both subfamilies seem to be easily further divided into two morphologically cohesive tribes. Haemodoroideae can be divided into Haemodoreae and Wachendorfieae, while Conostylidoideae can be divided into Tribonantheae and Conostylideae.

Generic limits in Commelinales

Out of all currently recognized genera of Commelinales, most of them (57 out of 63) where recovered by us supported by at least one exclusive synapomorphy (Figs 4-6). Striking examples were: Anigozanthos without the inclusion of Macropidia (Haemodoraceae), Wachendorfia without the inclusion of Barberetta (Haemodoraceae), Commelina without the inclusion of Tapheocarpa (Commelinaceae), Murdannia without the inclusion of Anthericopsis (Commelinaceae), Stanfieldiella without the inclusion of Tricarpelema africanum (Commelinaceae), and Streptolirion (Commelinaceae). The excessive recognition of monospecific genera has been a historical issue in the order, with genera such as Hydrothrix Hook.f., Eurystemon Small, Scholleropsis H.Perrier, and Zosterella Small making Heteranthera (Pontederiaceae) hopelessly polyphyletic (Pellegrini 2017b; Pellegrini et al. 2018). The successive pulverization of *Tradescantia* into a myriad of small to monospecific genera has also caused the paraphyly of the latter, and the recognition of a broader sense was necessary to maintain its monophyly and to facilitate the circumscription of genera to nonspecialists (Pellegrini 2017a). Thus, aside from cases where the recognition of a monospecific genus causes the obvious non-monophyly of a larger genus, the recognition of monospecific genera should be carefully contemplated. In cases where there is a clear incongruence between morphological and molecular data regarding the recognition of such genera, the most conservative approach should be taken to assure that the larger genus will remain monophyletic, regardless of the dataset, approach or method used. Thus, the recognition of Macropidia as independent from Anigozanthos, Blancoa as independent from Conostylis, Hydrothrix as independent from Heteranthera, Anthericopsis as independent from Murdannia is not warranted, since their recognition affects the consistency of the monophyly of a larger genus. Furthermore, the recognition of these genera also impairs, or completely prevents, a larger genus to be defined by observable morphological synapomorphies. For instance, the recognition of Barberetta as independent from Wachendorfia does not affect its monophyly. Barberetta + Wachendorfia is morphologically supported by two exclusive characters, while

Barberetta is supported by one. Nonetheless, Wachendorfia is not supported by a single exclusive character, being defined solely by the arrangement of the perianth lobes and their similarity to each other. Thus, the recognition of Barberetta directly prevents Wachendorfia of being properly circumscribed by observable morphological characters. A similar situation occurs with Gibasoides and Thyrsanthemum (Commelinaceae), with the difference that neither genera is recognized as independent, being supported by a single exclusive morphological character. Furthermore, they are solely differentiated from each other by the degree of elongation of the main axis of the inflorescence, which is extremely variable in the tribe they are placed. With the recognition of Thyrsanthemum s.lat., the genus is now supported by three exclusive characters, and readily differentiated from its sister-genus, Weldenia.

On the other hand, the recognition of Lachnanthes and Haemodorum is supported in the present study. Firstly, Haemodorum is unambiguously supported as monophyletic based o morphological and molecular data, added that both genera are readily distinguishable and each of them supported by more than one exclusive morphological character. Furthermore, Lachnanthes is restricted to the Americas, while Haemodorum is Australasian in distribution and thus, provide relevant information about phylogenetic relationships and the biogeography of the family. The same scenario is observed in Commelinaceae for Cartonema and Triceratella, Aëtheolirion and Streptolirion, Sauvallia and Tinantia, and Aneilema brasiliense and Polyspatha, which are also recognized as independent from each other by us. Another peculiar situation is regarding the recognition of Orthothylax as independent from Helmholtzia (Philydraceae). In this case, Helmholtzia s.lat. is not consistently recovered as monophyletic, and when it is, it is generally with low statistical support (see Results). In case Orthothylax is accepted it is supported by two exclusive characters, while Helmholtzia s.str. is supported by three. On the other hand, Helmholtzia s.lat. is defined by a sole exclusive morphological character. Finally, the number of morphological characters differentiating Orthothylax from Helmholtzia s.str. is equivalent to the ones differentiating Orthothylax from Philydrella and Philydrum. Thus, Orthothylax is accepted by us as distinct from Helmholtzia.

Taxonomy

In the present study we recognize five families in Commelinales: Commelinaceae, Haemodoraceae, Hanguanaceae, Philydraceae, and Pontederiaceae. We adopt a phylogenetic classification for Commelinales, in which only monophyletic groups are recognized (Hennig 1966; Wiley et al. 1991; de Queiroz and Gauthier 1994). Each recognized group should be consistent in all equally parsimonious trees, defined by observable morphological synapomorphies, and preferably statistically well-supported. Thus, each recognized family is easily diagnosable and supported by both molecular and morphological data. Monogeneric families and monospecific genera have been avoided whenever possible, since they provide little information about phylogenetic relationships, making the classification redundant (Hennig 1966; Wiley et al. 1991; de Queiroz and Gauthier 1994). In the same way, infrafamilial taxa (e.g., subfamilies, tribes, subtribes, genera, etc.) are generally recognized by us if they represent stable and well-supported clades, also composed of more than one subordinate taxon. This is done to facilitate the application and recognition of names above the species level, making the groups taxonomy and classification more accessible to non-specialists.

Taxa are presented in a phylogenetic sequence, being secondarily arranged in alphabetical order. We provide identification keys to all accepted relevant taxonomic ranks, namely family, subfamily, tribe, subtribe, genus, subgenus, and section. We also provide a

complete list of all species accepted in each of the 60 genera recognized by us in Commelinales.

Commelinales Mirb. ex Bercht. & J.Presl, Přir. Rostlin: 267. 1820, as "*Commelinariae*". Type. Commelinaceae Mirb., nom. cons. (*Commelina* L.).

Commelinales Dumort., Anal. Fam. PI.: 54. 1829, isoym. Type. Commelinaceae Mirb., nom. cons. (*Commelina* L.).

Enantioblastae Mart. ex Endl., Gen. Pl.: 119. 1836. Type (designated here). Commelinaceae Mirb., nom. cons. (*Commelina* L.).

Farinosae Engl., Bot. Gart. Breslau: 23: 1886. Type (designated here). Commelinaceae Mirb., nom. cons. (*Commelina* L.).

Haemodorales Mart., Consp. Regn. Veg.: 9. 1835. Type. Haemodoraceae R.Br., nom. cons. (*Haemodorum* Sm.).

Hanguanales R.Dahlgren ex Reveal, Novon 2: 239. 1992. Type. Hanguanaceae Airy Shaw (*Hanguana* Blume).

Philydrales Dumort., Anal. Fam. Pl.: 62. 1829. Type. Philydraceae Link, nom. cons. (*Philydrum* Banks & Sol. ex Gaertn.).

Pontederiales Mart., Consp. Regn. Veg.: 7. 1835. Type. Pontederiaceae Kunth, nom. cons. (*Pontederia* L.).

Description. Herbs monoecious, rarely dioecious, perennial or annual, aquatic or growing in damp environments, sometimes terrestrial or rupicolous, rarely epiphytic; vegetative organs generally variously covered by different types of uniseriate or multiseriate hairs. Roots generally thin and fibrous, but sometimes tuberous or spongy, glabrous to shortly pilose, sometimes arachnoid, rarely lanate, sand-binding or not, lacking a rhizosheath or not. Underground stem absent or a corm or a rhizome, sometimes a bulb. Stems submerged or floating or aerial, trailing, ascending, erect or twining, herbaceous or succulent, sometimes fibrous, variously branched, sometimes rooting at the basal nodes and/or along the whole stem; internodes contracted to elongate, secondary branches sometimes present producing stolon-like structures. Leaves monomorphic, rarely dimorphic; ptyxis involute or convolute or conduplicate, rarely conduplicate-involute and enclosing the petiole of the preceding leaf; sheaths open or closed, margins entire, sometimes marcescent; ligule generally absent, but present in Pontederiaceae. Immature leaves persistent throughout the plant's life, rarely deciduous, distichously- or spirally-alternate, unifacial or bifacial, pseudopetioles present or not, when present conspicuous to indistinct; blades generally flat, sometimes falcate to conduplicate, rarely twisted or plicate or bullate or cannulate or acicular or subterete to terete or conduplicate-keeled, membranous to chartaceous or succulent, abaxially green, sometimes white or ranging from pink to red to purple to vinaceous to maroon; venation parallel, midvein evident or not, secondary veins evident or not. Mature leaves rarely produced; if produced petiolate, rarely subsessile, pulvinate or not; blades with posterior divisions or not. Synflorescence composed of a solitary main florescence or by 1-several coflorescences. Main florescences (inflorescences) terminal or axillary or leaf-opposed, consisting of a sessile or pedunculate, few-many-branched thyrse, sometimes reduced to solitary cincinnus; basal bract leaf-like to bracteose or spathaceous or bracteose and bicarinate/bidentate or reduced hyaline and tubular; accessory bracts present or not, buds generally producing inflorescence primordia, sometimes simple; main axis developed or not; secondary branch's bract present or not, bracteose, sometimes vestigial or frondose; secondary branch generally a cincinnus, sometimes a branched cyme, rarely a dichasium, 1-many per thyrse, alternate or opposite to subopposite or verticillate to subverticillate or fasciculate or glomerulate, 1-many-flowered,

generally pedunculate, sometimes sessile, internodes contracted or elongated; bracteoles present or not, vestigial or reduced or conspicuous. Flowers resupinate or not, all bisexual or a mixture or bisexual and staminate and/or pistillate or staminate and pistillate in different individuals, sessile to pedicellate, chasmogamous, rarely cleistogamous, homostylous, sometimes tristylous, rarely pseudomonostylous, generally enantiostylous, actinomorphic or zygomorphic or asymmetric due to the position of the filaments or style, hypanthium absent or present, perianth homo- or heterochlamydeous, variously colored but generally white or blue or lilac to purple or pink to mauve or yellow to orange to red, generally black-, brown- or red-dotted (tannin cells), persistent and slightly accrescent in fruit, rarely obviously accrescent and involving the fruit; outer whorl with (2–)3 lobes, sepaloid or petaloid, free or connate, equal or unequal, membranous or chartaceous, sometimes coriaceous or paleaceous or succulent; inner whorl with (2-)3 lobes, petaloid, rarely sepaloid, free or connate, equal or unequal, sessile or clawed, membranous, sometimes chartaceous or coriaceous or slightly succulent; stamens (1–)3–(5–)6, equal or dimorphic or unequal, filaments straight or variously curved, terete, sometimes flattened or inflated, glabrous to variously pubescent or barbate, anthers basifixed or dorsifixed, rarely medifixed, versatile or not, rimose or poricidal, when rimose introrse or introrse and functionally poricidal or latrorse or extrorse, connective inconspicuous or not, when expanded variously shaped and colored, anther sacs parallel or divergent, variously shaped, rarely anthers hidden by a hood-like structure made by the fusion of filament hairs, pollen grains tectate-columellate or non-tectate-columellate, released with adhering raphides or not; pistil 1/2 times longer than the stamens, ovary superior or inferior or half-inferior, sessile or stipitate, (1–)2–3-locular, locules all fertile or posterior abortive, rarely posterior fertile and anterior ones abortive, placentation axile, ovules 1-many per locule, style present or not, when present generally elongated, sometimes short, rarely very short to vestigial, stigma generally capitate or subtrilobed to trilobed, sometimes truncate to capitulate or unevenly trilobate or trifid, rarely tuberculate or punctate or penicilliform. Fruit a generally capsule, sometimes a berry or an achene, rarely a coccarium, capsules (2-)3-valved, sometimes indehiscent or partially dehiscent, generally ellipsoid to oblongoid, sometimes obovoid or dolabriform or ovoid or lageniform or subglobose to globose, rarely linearoblongoid to linear to cylindrical or cordate trigonous or strongly trilobed, generally dullcolored, sometimes brightly-colored, 1-many-seeded, generally apiculate due to persistent style base. Seeds variously shaped, commonly arillate, sometimes exarillate, aril generally consisting of a hyaline membrane covering the seed, sometimes aril thick and spongy and also brightly-colored, appendaged or not, testa variously ornamented, with farinose granules or not, rarely mucilaginous and becoming sticky when hydrated; chalazal cap inconspicuous, rarely conspicuous; hilum punctate to elliptic or linear or C-shaped; embryotega dorsal to semidorsal or lateral to semilateral, rarely apical, conspicuous or not.

Distribution and habitat. The Pantropical distribution of Commelinales and its lineages is probably explained by a Gondwanan origin between 124 to 86 million years before present (mybp) (Givnish et al. 1999; Janssen and Bremer 2004; Bremer and Janssen 2006; Kress and Specht 2006; Anderson and Janssen 2009; Magallón and Castillo 2009; Bell et al. 2010; Hertweck et al. 2015; Pellegrini et al., unpublished data). Previous ancestral area reconstructions based on a dispersal-vicariance analysis, suggested that the common ancestor of the order originated in Australasia ca. 110 Mya (Bremer and Janssen 2006). Nonetheless, recent analyses based on our combined Commelinales dataset do not corroborate this hypothesis (Pellegrini et al., unpublished data). Between 120–100 mybp, Gondwana was still extant (Jokat et al. 2003) and ancestral area reconstructions (Pellegrini et al., unpublished data) indicate that the common ancestor of Commelinales is likely to have originated and diversified in this paleocontinent, as suggested by Givnish et al. (1999).

Circumscription and classification. The circumscription adopted by us for Commelinales is equivalent to the one adopted by most molecular-based systems in the last 20–30 years (Givnish et al. 2006, 2018; Chase et al. 2000, 2006; Savolainen et al. 2000; Soltis et al. 2000; Graham et al. 2002, 2006; Davis et al. 2004; Saarela et al. 2008; Hertweck et al. 2015; APG IV 2016), recognizing five families: Commelinaceae, Haemodoraceae, Hanguanaceae, Philydraceae, and Pontederiaceae. Nonetheless, this is the first time the order is reviewed and characterized as a whole. Commelinales is composed mainly by aquatic or paludal plants, perianth with tannin cells, persistent in fruit, stamens dimorphic, tapetum amoeboid, pollen grains released with adhering raphides, with a columellate tectum, superior ovary, fruits 2-valved, bitegmic seeds, starchy endosperm, and seedlings with rhizoids. We recognize a total of 60 genera and ca. 1,080 species.

Key to the families of Commelinales

- 1. Leaves bifacial, distichously or spirally-alternate; flowers heterochlamydeous or homochlamydeous sepaloid, lacking styloid crystals, sepals free from the petals, ovules uni- or biseriate, placental sclereids absent; seed coat sclerified; embryo shorter than 1/2 the length of the seed, endosperm nuclear; cotyledon non- chlorophyllate and haustorial, at least the first primary leaf reduced to a cataphyll, the subsequent bifacial and leaf-like... 2
- Leaves unifacial (if bifacial, leaves ligulate), equitant; flowers homochlamydeous petaloid, styloid crystals present, sepals partially to completely fused to the petals, ovules multiseriate, placental sclereids present; seed coat not sclerified; embryo ca. as long as the seed, endosperm helobial; cotyledon chlorophyllate and assimilating, primary leaves all expanded, unifacial or bifacial and ribbon-like... 3
- 2. Plants monoecious; internodes generally with a leaf-opposed line of uniseriate hairs, nodes swollen; leaf-sheaths closed, margin entire; inner whorl of the perianth petaloid, deliquescent at post-anthesis, absence of any kind of nectar-producing organ, ovaries internally glabrous; seeds variously shaped, but never bowl-shaped, seed coat lacking layers of crossing fibers, outer tegmen thin and sloughing off; crassinucellate; hairs uniseriate... Commelinaceae (Figs 11–13)
- Plants dioecious; internodes lacking a line of uniseriate hairs, nodes not swollen; leaf-sheaths open, margin scarious; inner whorl of the perianth sepaloid, herbaceous at pos-anthesis, staminodes with nectariferous scales and pistilode with nectariferous lobes, ovary internally covered by mucilage hairs; seeds bowl-shaped, seed coat with two layers of crossing fibers, outer tegmen thick and persistent; tenuinucellate; hairs multiseriate...
 Hanguanaceae (Fig 14)
- 3. Flowers pseudo-tetramerous (lateral outer tepals fused to the medial inner tepal, producing a labellum-like lobe), lacking septal nectaries, lacking a hypanthium; endothecium not thickened, tapetum glandular, pollen with exine tectate-columellate, sulcal membrane granular; chalazal cap enlarged; neighboring cells of the stomata with parallel division; phenylphenalenones absent... **Philydraceae (Fig 15)**
- Flowers hexamerous, rarely trimerous or tetramerous, generally presenting septal nectaries (secondarily lost in some genera), presenting a hypanthium; endothecium with a basal thickening, tapetum amoeboid, pollen with exine papillate or baculate (i.e., non-tectate-columellate), sulcal membrane verrucate; chalazal cap diminute; neighboring cells of the stomata with oblique division; phenylphenalenones present... 4

- 4. Roots with a sclerified endodermis; ptyxis conduplicate, leaves monomorphic, lacking a ligule, leaf blades fibrous and coriaceous; secondary branches of the main florescence a branched cyme (secondarily lost in some species); anthocarp generally absent, rarely present and then derived from an inferior ovary and anemochoric; pollen monosulcate or bi–many-porate, ovary wall lacking aerenchyma; multiseriate hairs generally present... **Haemodoraceae (Fig 16)**
- Root with endodermis not sclerified; ptyxis conduplicate-involute, enclosing the petiole of the preceding leaf, leaves dimorphic (juvenile leaves sessile, mature leaves petiolate), ligulate, leaf blades membranous or chartaceous; secondary branches of the main florescence an unbranched cincinnus; anthocarp invariably present, derived from a superior ovary and hydrochoric, pollen bisulcate, ovary wall with aerenchyma; hairs uniseriate... Pontederiaceae (Fig 17)
- **1. Commelinaceae Mirb.**, Hist. Nat. Pl. 8: 177. 1804, nom. cons. Type genus. *Commelina* L. Figs 11–13
- Ephemeraceae Batsch, Tab. Affin. Regni Veg.: 125. 1802, as "*Ephemera*", nom. rej., non Ephemeraceae Hampe in Flora 20: 285. 1837, nom. cons., Bryopsida. Type genus. *Ephemerum* Mill. (= *Tradescantia* L. emend. M.Pell.).
- Tradescantiaceae Salisb., Trans. Linn. Soc. London 8: 9. 1834, as "*Tradescanteae*". Type genus. *Tradescantia* L. emend. M.Pell.
- Cartonemataceae Pichon, Notul. Syst. (Paris) 12: 219. 1946, nom. cons. Type species. *Cartonema* R.Br.

Description. Herbs monoecious, perennial or annual, terrestrial, sometimes rupicolous aquatic, amphibious or paludal, rarely epiphytic; vegetative organs generally covered by uniseriate glandular microhairs, lacking in subfamily Cartonematoideae. Roots generally thin and fibrous, but sometimes tuberous or spongy, tuberous roots evenly thickened and fusiform or only distally thickened with conspicuous fusiform or ellipsoid or subglobose tubers, glabrous to shortly pilose, rarely lanate, sand-binding or not, lacking a rhizosheath or not. *Underground stem* absent or a corm or a rhizome, if present rhizome generally short. Stems aerial or submerged, trailing, ascending, erect or twining, herbaceous or succulent, rarely fibrous, unbranched to branching only at the base to branched throughout, sometimes rooting at the basal nodes and/or along the whole stem; internodes contracted to elongate, secondary branches sometimes present producing stolon-like structures. Immature leaves persistent throughout the plant's life, distichously- or spirally-alternate, bifacial, evenly distributed or congested at the apex of the stem; ptyxis involute or convolute; sheaths closed, tubular, asymmetric due to a conspicuous suture scar, margins entire and non-marcescent, sheaths generally persistent and papyraceous in old stems; ligule absent; pseudopetioles present or not, when present conspicuous to indistinct; blades linear or loriform or oblong to elliptic to lanceolate to ovate or obovate, sometimes orbicular or cordate, flat or falcate to conduplicate or bullate, base cuneate or obtuse to round or truncate to amplexicaulous, apex obtuse to acute or acuminate or mucronate to cuspidate to caudate, membranous to chartaceous or succulent; midvein evident, rarely inconspicuous, adaxially impressed, abaxially prominent, secondary veins evident or not. Mature leaves never produced. Synflorescence composed of a solitary main florescence or by 1-several coflorescences; synflorescence leaves equal to the regular leaves or not. Main florescences (inflorescences) terminal or axillary or leaf-opposed, consisting of a sessile or pedunculate, few-many-branched thyrse, sometimes reduced to solitary cincinnus; basal bract leaf-like to bracteose or spathaceous or bracteose and bicarinate/bidentate or reduced hyaline and tubular; accessory bracts present or not, buds simple or producing inflorescence primordia; main axis developed or not; cincinnus' bract present or not, vestigial or bracteose or frondose, rarely basal frondose and apical bracteose; cincinni 1-many per thyrse, alternate or opposite to subopposite or verticillate to subverticillate or fasciculate or glomerulate, 1-many-flowered, sessile or pedunculate, internodes contracted or elongated; bracteoles present or not, vestigial or reduced or conspicuous. Flowers non-resupinate, bisexual, staminate or pistillate, sessile to pedicellate, chasmogamous, rarely cleistogamous, homostylous, enantiostylous or not, actinomorphic or zygomorphic or asymmetric due to the position of the filaments or style, hypanthium absent, perianth heterochlamydeous; sepals (2-)3, sepaloid, free to connate, equal to unequal, membranous or chartaceous, sometimes paleaceous or succulent, cymbiform to cucullate, generally green, sometimes white or purple to vinaceous or pink, rarely hyaline or yellow, persistent and slightly accrescent in fruit, rarely obviously accrescent or fleshy and involving the fruit; petals (2–)3, petaloid, sometimes black-, brown- or red-dotted (tannin cells), free to connate, equal to unequal, sessile to clawed, membranous, sometimes slightly succulent, generally white or blue or lilac to purple or pink to mauve to vinaceous, sometimes creamcolored to yellow to orange to apricot, rarely hyaline or green or red; stamens (1-)3-5-6, equal or dimorphic or unequal, filaments straight or variously curved, terete, sometimes flattened or inflated, glabrous to variously pubescent or barbate, anthers basifixed or dorsifixed, rarely medifixed, versatile or not, rimose or poricidal, when rimose introrse or introrse and functionally poricidal or latrorse or extrorse, connective inconspicuous or not, when expanded variously shaped and colored, anther sacs parallel or divergent, linear to elongate to oblong or elliptic or round or reniform to C-shaped, rarely spirally-coiled or dripshaped, rarely anthers hidden by a hood-like structure made by the fusion of filament hairs; ovary superior, sessile or stipitate, 2–3-locular, locules all fertile or posterior abortive, rarely posterior fertile and anterior ones abortive, placentation axile, ovules 1-many per locule, style present, generally elongated, sometimes short, rarely very short to vestigial, stigma truncate to capitulate or capitate to trilobed, rarely punctate or penicilliform. Fruit a capsule, rarely a berry, capsules 2-3-valved, sometimes indehiscent or partially dehiscent, variously shaped and colored, 1-many-seeded, generally apiculate due to persistent style base. Seeds circular or elliptic to oblong or rectangular or triangular or tetrahedral or kidney-shaped or polygonal, commonly arillate, sometimes exarillate, aril generally consisting of a hyaline membrane covering the seed, sometimes aril thick and spongy and also brightly-colored, appendaged or not, testa variously ornamented, with farinose granules or not, rarely mucilaginous and becoming sticky when hydrated; chalazal cap inconspicuous; hilum punctate to elliptic or linear or C-shaped; embryotega dorsal to semidorsal or lateral to semilateral, rarely apical, conspicuous or not.

Comments. Commelinaceae is the largest family of the order, with 40 genera and ca. 810 species, and also the most widely distributed. It is easily differentiated from the remaining families of Commelinales by their tendency to succulence, internodes with a leafopposite line of uniseriate hairs, internodes swollen, bifacial leaves, closed and asymmetric leaf-sheaths, heterochlamydeous perianth, and absence of a hypanthium and of nectaries of any kind. Furthermore, the family is anatomically well-supported, presenting a nodal vascular plexus, and supported by two anatomical synapomorphies, the presence of raphide canals and outer tegmen of the seed coat thin and sloughing off during development. Some authors have proposed in the past that subfamily Cartonematoideae is different enough to be recognized as an independent family. Nonetheless, the differences are exclusively anatomical and the recognition of Cartonemataceae greatly impairs the recognition of Commelinaceae based on easily observable characters. The family is currently divided into three subfamilies, supported by molecular and morphological data (this study): Cartonematoideae, Palisotoideae, and Commelinoideae. Cartonematoideae and Commelinoideae are each divided into two tribes, but subtribes are only recognized in Commelinoideae. Tribe Commelineae (subfamily Commelinoideae) is here divided by us into three subtribes, while only five subtribes accepted in Tradescantieae, as opposed to the seven subtribes accepted by Faden and Hunt (1991).

Phylogeny. The relationships within Commelinaceae are well-understood, with several morphological, molecular, and combined phylogenies available for the group (Bergamo 2003; Evans et al. 200, 2003; Wade et al. 2006; Burns et al. 2011; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini 2017; this study). Despite initial assumptions (Evans and Faden 1998; Evans et al. 2000, 2003), morphological and molecular data show great congruence, despite the high degree of homoplasy (Pellegrini 2017; this study).

Distribution. Cosmopolitan, but with four primary diversity centers, two Paleotropical and two Neotropical: (1) Africa, due to *Aneilema* and *Commelina*; (2) Asia, due to *Cyanotis* and *Murdannia*: (3) eastern Brazil, due to *Dichorisandra*; and (4) North America, especially Mexico, due to *Tradescantia* and other members of Tradescantiinae.

Key to the subfamilies of Commelinaceae

- 1. Plants with glandular microhairs absent, stems and/or leaves with clavate macrohairs; stems with cortex expanded and with vascular tissue, raphide-canals absent or next to the veins of the leaf blades, palisade cells elaborately-lobed; embryotega lacking a micropillar collar; seedlings with collar inconspicuous, mesocotyl present... Cartonematoideae Faden ex G.C.Tucker (Fig 11A)
- Plants with glandular microhairs present, stems and/or leaves variously pubescent but never with clavate macrohairs; stems with a narrow cortex and lacking vascular tissue, raphide-canals present and between the veins of the leaf blades, palisade cells unlobed; embryotega with a micropillar collar; seedlings with collar a thick ring or umbrella-like, mesocotyl absent... 2
- 2. Roots with mucilage canals; leaves with branched and rugose macrohairs; sepals petaloid, outer whorl of the androecium staminodial, staminodes barbate with dumbbell-shaped hairs, lacking antherodes; pollen grains dimorphic in the same polliniferous stamen, ornamentation of the sulcal membrane almost indistinguishable from the tectum; fruit a berry; seedling collar a thick ring... Palisotoideae M.Pell. & Faden (Fig 11B)
- Roots lacking mucilage canals; leaves with unbranched and smooth macrohairs; sepals sepaloid, outer whorl of the androecium various, but never like that, pollen grains monomorphic or dimorphic between anthers of different polliniferous stamens,

ornamentation of the sulcal membrane clearly distinct from the tectum; fruit a capsule; seedling collar umbrella-like... **Commelinoideae Eaton (Figs 11C–13)**

1.1. Subfamily Cartonematoideae Faden ex G.C.Tucker, J. Arnold Arbor. 70: 99. 1989. Type genus. *Cartonema* R.Br. Fig 11A

Cartonematoideae Faden & D.R.Hunt, Taxon 40: 22. 1991, isonym.

Distribution. Restricted to Australia and New Guinea (*Cartonema*), and Zimbabwe (*Triceratella*).

Comments. This small subfamily is morphologically peculiar when compared to the rest of the family in which it presents several plesiomorphic characters, such as the absence of glandular microhairs, enantiostylous and yellow flowers (rarely white or pink to purple), perianth with tannin cells, and dorsal embryotega. These characters have led the segregation of *Cartonema* into a distinct family, Cartonematoideae, but its recognition seems systematically uninformative and morphologically unnecessary since *Cartonema* and *Triceratella* share several synapomorphies with Palisotoideae and Commelinoideae. The division of Cartonematoideae in two tribes is questionable, but since *Triceratella* has never been sampled in molecular analysis, we believe that it is best to recognize it in a separate tribe, for the time being.

Key to the tribes of Cartonematoideae

- 1. Plants perennial, cormose; inflorescences terminal or apparently so; filaments glabrous, anther poricidal; capsules with persistent valves straight or almost so; seeds uniseriate, 2 per locule, kidney-shaped, laterally compressed; raphide canals absent, stomata with 2–4 subsidiary cells... Cartonemateae Faden & D.R.Hunt (Fig 11A)
- Plants annual, lacking an underground system; inflorescences leaf-opposed; filaments minutely pubescent, anthers rimose; capsules with persistent valves strongly deflexed; seeds biseriate, many per locule, conical, not laterally compressed; raphide canals next to the veins, stomata with 2 subsidiary cells... Triceratelleae Faden & D.R.Hunt
- **1.1.1. Tribe Cartonemateae Faden & D.R.Hunt**, Taxon 40: 23. 1991. Type genus. *Cartonema* R.Br.

Distribution. Australia and New Guinea.

Comments. Cartonemateae is a monogeneric tribe describe to accommodate *Cartonema* due to its morphological differences from *Triceratella* and marking geographic disjunction.

1.1.1.1. *Cartonema* **R.Br.**, Prodr.: 271. 1810. Type species. *Cartonema spicatum* R.Br. Fig 11A

Distribution and ecology. Cartonema is endemic to Australia (Northern Territory, Queensland, and Western Australia) and New Guinea, growing in sandy soils, sometimes with gravel or over laterite, in seasonally inundated lowlands, along watercourses, and other moist sites.

Comments. A genus of seven described species with further species awaiting description, with a total of ca. 11 species. It desperately urges for a complete taxonomic revision, a molecular phylogeny, coupled with the description of the needed new species, reevaluation of some species boundaries, and anatomy, pollen, and floral biology studies. A better understanding of *Cartonema* is key for a better understanding of the evolution of morphological characters in the family.

Accepted species. A total of seven species: *Cartonema baileyi* F.M.Bailey, *C. brachyantherum* Benth., *C. parviflorum* Hassk., *C. philydroides* F.Muell., *C. spicatum* R.Br., *C. tenue* Caruel, and *C. trigonospermum* C.B.Clarke

1.1.2. Tribe Triceratelleae Faden & D.R.Hunt, Taxon 40: 23. 1991. Type species. *Triceratella* Brenan.

Distribution. Zimbabwe and Mozambique.

Comments. Triceratelleae is a monogeneric tribe described to accommodate the peculiar *Triceratella*. The tribe and its sole genus are poorly understood, know from only a handful of collections.

1.1.2.1. *Triceratella* **Brenan**, Kirkia 1: 14. 1961. Type species. *Triceratella drummondii* Brenan.

Distribution and ecology. *Triceratella* is restricted to Zimbabwe and Mozambique, growing in sandy and seasonally inundated soils.

Comments. The genus is monospecific and poorly understood. Field efforts with the aim to recollect this extremally rare species are pressing.

Accepted species. Triceratella drummondii Brenan.

1.2. Subfamily Palisotoideae M.Pell. & Faden, comb. et stat. nov. Fig 11B

Palisotinae Faden & D.R.Hunt, Taxon 40: 23. 1991. Type genus. *Palisota* Rchb. ex Endl., nom. cons.

Distribution. Endemic to continental Africa.

Commets. Palisota was originally included by Faden and Hunt (1991) as the sole member of subtribe Palisotinae, which was included in tribe Tradescantieae, subfamily Commelinoideae. Nonetheless, the first molecular phylogenies for the family which sampled Palisota (Evans et al. 2003; Wade et al. 2006; Burns et al. 2011; Zuiderveen et al. 2011; Hertweck and Pires 2014) indicated the paraphyly of Tradescantieae due to the position of Palisotinae. Palisota has either been recovered as sister of the remaining Tradescantieae, to Commelineae, as sister to Commelineae + Tradescantieae, and even in a trichotomy with Commelineae and Tradescantieae, but all with low statistical support. In the present study, Palisota is recovered with strong statistical support as sister to Commelineae + Tradescantieae, which supports the recognition of the new subfamily proposed here. The subfamily is composed solely by the morphologically deviant Palisota.

1.2.1. *Palisota* **Rchb. ex Endl.**, Gen. Pl.: 125. 1836, nom. cons. Type species. *Palisota ambigua* (P.Beauv.) C.B.Clarke. Fig 11B

Duchekia Kostel., Allg. Med.-Pharm. Fl. 1: 213. 1831. Type species. Duchekia hirsuta (Thunb.) Kostel. [≡ Palisota hirsuta (Thunb.) K.Schum.].

Distribution and ecology. *Palisota* is endemic to continental Africa, more precisely Angola (incl. Cabinda), Benin, Burundi, Cameroon, Central African Republic, Chad, Congo, Equatorial Guinea (incl. Annobón, Bioko, Corisco, Elobey Chico, and Elobey Grande), Gabon, Ghana (incl. Bobowasi Island), Guinea, Guinea-Bissau, Ivory Coast, Liberia, Nigeria, Rwanda, São Tomé and Príncipe, Senegal, Sierra Leone, Sudan, Tanzania, Togo, Uganda, Zaire, and Zambia. They grow in a myriad of primary, secondary and disturbed forested environments, generally in shaded conditions.

Comments. A genus of ca. 30 species, which need taxonomic revision, a molecular phylogeny, anatomy of pollen, and floral biology studies. Species are very difficult to identify based on herbarium specimens and intense fieldwork is key to solve the genus' current issues. The genus is currently being studied by Bidault and Burg (pers. com.), which indicates the existence of several still undescribed species, several taxonomic and nomenclatural issues.

Accepted species. Currently, about 30 species are accepted for *Palisota*. Further taxonomic studies are sure to increase this number (Pellegrini and Bidault, pers. observ.).

Infrageneric classification. The only infrageneric classification for *Palisota* was proposed by Clarke (1881a), where he recognized two sections: (1) P. sect. Monostichos, which was characterized by uniseriate ovules, and berries with 1-3 seeds per locule; (2) P. sect. Distichos, which was characterized by biseriate ovules, and berries with 6-8 seeds per locule. Only two studies, so far, sampled more than one species of *Palisota* (Zuiderveen et al. (2011), based on molecular data; this study, based on morphological and combined data). Both studies recovered two well-supported clades: (1) the rosette species with erect or prostrate stems, pseudopetiolate leaves, thin cincinni, and pubescent, ovoid to lageniform berries; and (2) the erect or climbing, long-stemmed species with sessile leaves, stout to swollen cincinni, and glabrous, globose to subglobose or obovoid to ellipsoid berries. Clarke's groups mostly match the recovered clades, with some minor changes in composition and circumscription. As stated by Faden (1999), the seed/ovule arrangement only partially fits Clarke's sections, since species such as P. bogneri, P. flagelliflora Faden and P. satabiei Brenan that would be included in P. sect. Monostichos have 5–7 biseriate ovules, which can produce 1–4 uni- or biseriate seeds in the berries. Nonetheless, P. flagelliflora lacks the stout to swollen cincinni, and presents rosette habit, subpetiolate leaves, and ovoid, pubescent, and red berries, which would place it in our clade 1. Regarding berry coloration, blue, purple or black berries are restricted to our clade 2. Nonetheless, orange and red berries are not exclusive to clade 1, being also found in *P. brachythyrsa* (clade 2) and other morphologically closely related species not sampled in this study. Alternatively, the pubescens of the berries is the one character that seems to be constant in both clades. Clade 1 always presents at least sparsely pubescent berries, while in clade 2 berries are always glabrous and sometimes also glaucous.

We have chosen to propose a new classification system for *Palisota* due to great confusion in Clarke's system regarding the morphology and placement of *P. ambigua*, the

type of the genus. In his treatment for *Palisota*, Clarke (1881a) recognized *P. ambigua* as the type of the genus and by placing it in his new *P. sect. Monostichos*, automatically typifies the section and creates the name *P. sect. Palisota* for it (Turland et al. 2018, Art. 22.1). Nonetheless, *P. ambigua* has 6–8 biseriate seeds per locule and should not be placed here, based on Clarke's circumscription. This misplacement of *P. ambigua* is critical, since it makes both sections nomenclaturally equivalent to our clade 2. Thus, our clade 1 is left without any prior infrageneric names. Thus, it is described here as a new subgenus for *Palisota*.

Key to the subgenera of Palisota

- 1. Rosette herbs; stems completely prostrate or prostrate with only and erect apex, unbranched, internodes very short to inconspicuous; leaves spirally- or distichously-alternate, rarely pseudowhorled, pseudopetiolate, rarely with short pseudopetiole; cincinni with slender axis; pedicels spirally-coiled and slender at post-anthesis and in fruit; berries ovoid to lageniform, slightly to densely pubescent; seeds completely to partially uniseriate, 1–4 per locule... *Palisota* subg. *Brenania* M.Pell. & E.Bidault
- Caulescent herbs or vines; stems erect or twining, generally freely branching, internodes elongate; leaves pseudowhorled, sessile or almost so; cincinni with stout to swollen axis; pedicels erect and stout at post-anthesis and in fruit; berries globose to subglobose or obovoid to ellipsoid, glabrous; seeds biseriate, 6–8 per locule... *Palisota* Rchb. ex Endl. subg. *Palisota*

1.2.1.1. *Palisota* **subg.** *Brenania* **M.Pell.** & E.Bidault, **subg. nov.** Type species. *Palisota barteri* Hook.f.

Fig 11B

Description. Herbs rosetted. Stems prostrate or prostrate with erect apex, unbranched. Leaves spirally- or distichously-alternate, rarely pseudowhorled, clearly pseudopetiolate, rarely with short pseudopetioles. Main florescences (inflorescences) terminal or axillary, pedunculate, many-branched or reduced to a solitary cincinnus; cincinni with slender axis. Flowers long-pedicellate, pedicels spirally-coiled and slender at post-anthesis and in fruit. Berries ovoid to lageniform, slightly to densely pubescent. Seeds 1–4 per locule, completely to partially uniseriate.

Distribution and ecology. Widespread throughout the genus distribution, but centered in Cameroon, Congo, Equatorial Guinea, and Gabon.

Accepted species. A total of 17 species: *Palisota akouangoui* E.Bidault & Burg, *P. albertii* L.Gentil, *P. alboanthera* Burg & E.Bidault, *P. barteri* Hook.f., *P. bogneri* Brenan, *P. bracteosa* C.B.Clarke, *P. cristalensis* E.Bidault & Burg, *P. ebo* Cheek, *P. flagelliflora* Faden, *P. lagopus* Mildbr., *P. laurentii* De Wild., *P. leewhitei* Burg et al., *P. mannii* C.B.Clarke, *P. plicata* E.Bidault & Burg, *P. pynaertii* De Wild., *P. repens* E.Bidault & Burg, and *P. satabiei* Brenan.

Etymology. The name of this new subgenus honors the late Dr. John Patrick Micklethwait Brenan (b. 19 June 1917, d. 26 Sept. 1985), former director of the Royal Botanical Gardens, Kew (1976–1981), renowned Commelinaceae specialist, and an important contributor to the knowledge of the African flora.

- **1.2.1.2.** *Palisota* **Rchb. ex Endl. subg.** *Palisota*. Type species. *Palisota ambigua* (P.Beauv.) C.B.Clarke.
- Palisota Rchb. ex Endl. sect. Palisota ≡ Palisota sect. Monostichos C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 131. 1881, nom. superfl. Type species. Palisota ambigua (P.Beauv.) C.B.Clarke.
- Palisota sect. Distichos C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 131. 1881, **Syn. nov.** Type species (designated here). Palisota thyrsiflora Benth. [= Palisota hirsuta (Thunb.) K.Schum.].

Description. Herbs or vines, caulescent. Stems erect, densely branched. Leaves pseudowhorled or pseudo-opposite, sessile or almost so. Main florescences (inflorescences) terminal, pedunculate, many-branched; cincinni with stout to swollen axis. Flowers subsessile to shortly-pedicellate, pedicels erect and stout at post-anthesis and in fruit. Berries globose to subglobose or obovoid to ellipsoid, glabrous. Seeds 6–8 per locule, biseriate.

Distribution and ecology. Widespread throughout the genus distribution, but centered in Cameroon, Central African Republic, Congo, Equatorial Guinea (incl. Gulf of Guinea Islands), Gabon, and Zaire.

Accepted species. A total of 14 accepted species: *Palisota alopecurus* Pellegr., *P. ambigua* (P.Beauv.) C.B.Clarke, *P. brachythyrsa* Mildbr., *P. fadenii* Burg & E.Bidault, *P. gracilior* Mildbr., *P. hirsuta* (Thunb.) K.Schum., *P. laxiflora* C.B.Clarke, *P. myriantha* K.Schum., *P. orientalis* K.Schum., *P. pedicellata* K.Schum., *P. preussiana* K.Schum. ex C.B.Clarke, *P. schweinfurthii* C.B.Clarke, *P. stevartii* Burg & E.Bidault, and *P. thollonii* Hua.

1.3. Subfamily Commelinoideae Eaton, Bot. Dict., ed. 4: 27. 1836, as "Commelineae". Type genus. Commelina L.

Figs 11C-13

Tradescantioideae G.Brückn., Bot. Jahrb. Syst. 61(Beibl. 137): 56. 1927, as "*Tradescantieae*". Type genus. *Tradescantia* L. emend. M.Pell.

Distribution. Cosmopolitan, but not naturally reaching Europe.

Comments. In our present circumscription, subfamily Commelinoideae excludes *Palisota* (now placed in subfamily Palisotoideae) and represents what could be treated as "core Commelinaceae". It includes the largest and most morphologically and ecologically genera in the family, such as *Aneilema*, *Commelina*, *Cyanotis*, *Dichorisandra*, *Murdannia*, and *Tradescantia*. Commelinoideae can be differentiated from Palisotoideae by its roots lacking mucilage canals, the absence of unbranched and smooth macrohairs, ornamentation of the sulcal membrane distinct from the tectum, and seedling with and umbrella-like collar. Its two tribes, Commelineae and Tradescantieae, have been accepted since the first infrafamilial classifications for Commelinaceae, despite considerable changes in the genera included in each of them (Faden and Hunt 1991).

Key to the tribes of Commelinoideae

1. If present floral hairs non-moniliform, medial sepal shorter than the laterals; pollen tectal elements acute (spinulose, spinulose-rugose or tuberculate), closer to each other in the transitional zone, tectum perforate; leaf epidermis leaf epidermis with flattened cells,

- papillate, stomata with 6 subsidiary cells, the terminal pair smaller than the second lateral pair; cotyledonary sheath inconspicuous... **Commelineae Dumort.** (**Fig 11C–T**)
- If present floral hairs moniliform, medial sepals equal or longer than the laterals; pollen tectal elements rounded, not closer to each other in the transitional zone, tectum lacking perforations; leaf epidermis with domed cells, lacking papillae, stomata with (2–)4 subsidiary cells, if 6 then the terminal pair equal to or larger than the second lateral pair; cotyledonary sheath conspicuous... Tradescantieae Meisn. (Figs 12 & 13)

1.3.1. Tribe Commelineae Dumort., Anal. Fam. Pl.: 55. 1829. Type genus. *Commelina* L. Fig 11C–T

Pollieae C.B.Clarke, J. Bot. 18: 127. 1880. Type genus. *Pollia* Thunb.

Anthericopsideae Pichon, Notul. Syst. (Paris) 12: 237. 1946. Type genus. *Anthericopsis* Engl.

Pseudoparideae Pichon, Notul. Syst. (Paris) 12: 240. 1946. Type genus. *Pseudoparis*H.Perrier

Distribution. Mainly Paleotropical and centered in Africa and Australasia, but with some genera also reaching the Neotropics.

Comments. Tribe Commelineae sensu Faden and Hunt (1991) was robustly circumscribed and has invariably been recovered as monophyletic in phylogenetic studies. Nonetheless, it was considered still inappropriately understood to allow its further division into subtribes. This was due to lack of known phylogenetically informative characters, with most characters being either autapomorphic or homoplastic (Faden and Hunt 1991). The present study presents a strongly supported phylogeny for the group, which is also congruent with previous molecular-based phylogenies. Commelineae is organized in three main groups, which coincide with the three floral Bauplans known for the group. Additionally, these three groups are further supported by a series of macro- and micromorphological characters and are thus recognized here as subtribes. The first group comprises Murdannia (incl. Anthericopsis) and is characterized by a unique set or floral and micromorphological characters (Faden and Hunt 1991; Faden and Inman 1994; Faden 1998). The second group has been informally recognized by the first author as the "Floscopa group", and comprises Buforrestia, Floscopa, Pseudoparis, Tricarpelema, and Stanfieldiella. It was first recovered by Evans et al. (2003) but lacked morphological support. The final group represents the bulk of species richness and morphological diversity of the tribe. It comprises Aneilema (incl. Rhopalephora, and excl. Campylonanthus brasiliense), Commelina (incl. Tapheocarpa), Dictyospermum, Pollia, Polyspatha, and the new Campylonanthus.

Key to the subtribes of Commelineae

- 1. Androecium actinomorphic, outer whorl fertile, inner whorl staminodial, outer filaments longer than inner, antherodes trilobed; leaf mesophyll with marginal mechanical tissue... Murdanniinae M.Pell. & Faden (Fig 11C & D)
- Androecium zygomorphic (stamens posterior + anterior), if present staminodes posterior, fertile stamens anterior, outer and inner whorls with filaments of different sizes and thus not comparable; leaf mesophyll lacking marginal mechanical tissue... 2
- 2. Filaments straight at post-anthesis, if present posterior stamens polliniferous, rarely staminodial, if staminodial antherodes unlobed, pollen sterile, pollen grains tuberculate, microperforations sparse; leaf epidermis with star-shaped idioblasts, hook-shaped hairs absent... Floscopineae M.Pell. & Faden (Fig 11E–J)

- Filaments coiled at post-anthesis, posterior stamens staminodial, antherodes bilobed and not polliniferous or X-shaped and polliniferous with food-pollen, pollen grains spinulose or spinulose-rugose, microperforations dense; leaf epidermis lacking star-shaped idioblasts, hook-shaped hairs generally present, especially in inflorescence axis... Commelinineae Engl. (Fig 11K-T)
- **1.3.1.1. Subtribe Murdanniinae M.Pell. & Faden, subtrib. nov.** Type genus. *Murdannia* Royle, nom. cons.

Fig 11C & D

Description. Herbs perennial or annual, paludal to aquatic, sometimes terrestrial or rupicolous. Roots tuberous or not. Rhizomes short. Stems prostrate to erect, branched or not. Leaves spirally- or distichously-alternate, sessile; mesophyll with tannin cells, marginal mechanical tissue present. Synflorescence composed of a solitary main florescence or by 1several coflorescences, synflorescence leaves equal to the regular leaves, reduced in size or reduced to bladeless sheaths. Main florescences (inflorescences) terminal or axillary, sessile or pedunculate, many-branched or reduced to a solitary cincinnus; cincinni 1-many-flowered; bracteoles flat or canaliculate or tubular or cup-shaped. Flowers enantiostylous, sometimes not, actinomorphic, rarely zygomorphic; petals 3, sessile, equal to subequal, free, deliquescent, glabrous or with minute glandular hairs at base or medially bearded with hairs with dumbbell-shaped cells on the adaxial surface; androecium actinomorphic, rarely zygomorphic, filaments free, rarely connate at base with only 1 staminode free, stamens (2–)3, equal, antesepalous, filaments longer than the antepetalous, anthers dorsifixed, rimose; staminodes 3(-4), antepetalous (if 4 staminodes are present, the outer antesepalous staminodial), antherodes dorsifixed, 3-lobed; pollen with tuberculate exine; ovary sessile or stipitate, 3-locular, locules equal, style tapering at base, erect or gently curved at the apex, stigma truncate to capitate. Capsules loculicidal, 3-valved. Seeds 1-many per locule, uni- or biseriate, appendaged or not; hilum linear; embryotega lateral to semilateral or semidorsal.

Distribution. Mainly Asian, but with a secondary diversity center in Africa, with some species reaching Australia and the Neotropics.

Comments. Due to the morphological peculiarities of *Murdannia* and its size (it has more species than all the genera of Floscopineae combined), it seems to suit to place it in its own subtribe. Aside from that, the placement of the genus has been uncertain, being either placed sister to the remaining members of tribe Commelineae (Evans et al. 2003; Zuiderveen et al. 2011) or as sister to Floscopineae (Pellegrini et al., in prep.; this study).

- **1.3.1.1.** *Murdannia* **Royle**, Ill. Bot. Himal. Mts. 1: 403, pl. 95, f. 3. 1839, nom. cons. Type species. *Murdannia scapiflora* (Roxb.) Royle [= *Murdannia edulis* (Stokes) Faden]. Fig 11C & D
- Aphylax Salisb., Trans. Hort. Soc. London 1: 271. 1812, nom. nud. Type species. Aphylax spiralis (L.) Salisb. [≡ Murdannia spirata (L.) G.Brückn.].
- Dilasia Raf., Fl. Tellur. 4: 122. 1836[1838], nom. rej. Type species. Dilasia vaginata (L.) Raf. [≡ Murdannia vaginata (L.) G.Brückn.].
- Ditelesia Raf., Fl. Tellur. 3: 69. 1836[1838], nom. rej. Type species. Ditelesia nudiflora (L.) Raf. [≡ Murdannia nudiflora (L.) Brenan].

- Talipulia Raf., Fl. Tellur. 2: 17. 1836[1838], nom. rej. Type species. Talipulia malabarica (L.) Raf. [= Murdannia nudiflora (L.) Brenan].
- Streptylis Raf., Fl. Tellur. 4: 122. 1836[1838], nom. rej. Type species. Streptylis bracteolata Raf. [= Murdannia spirata (L.) G.Brückn.].
- Dichoespermum Wight, Icon. Pl. Ind. Orient. 6: 31. 1853, as "Dichaespermum". Type species. Dichoespermum lanceolatum Wight [≡ Murdannia lanceolata (Wight) Kammathy].
- *Prionostachys* Hassk., Flora 49: 212. 1866. Type species. *Prionostachys ensifolia* Hassk. *ex* C.B. Clarke [= *Murdannia gigantea* (Vahl) G.Brückn.].
- Anthericopsis Engl., Pflanzenw. Ost-Afrikas C: 139. 1895, **Syn. nov.** Type species. Anthericopsis fischeri Engl. [≡ Murdannia sepalosa (C.B.Clarke) M.Pell.].
- Gillettia Rendle, J. Bot. 34: 55. 1896, **Syn. nov.** Type species. Gillettia sepalosa (C.B.Clarke) Rendle [≡ Murdannia sepalosa (C.B.Clarke) M.Pell.].
- Baoulia A.Chev., Bull. Soc. Bot. France 8d: 217. 1912. Type species. Baoulia tenuissima A.Chev. [≡ Murdannia tenuissima (A.Chev.) Brenan].
- *Phaeneilema* G.Brückn., Bot. Jahrb. Syst. 61(Beibl. 137): 63. 1926, nom. illeg. Type species. *Phaeneilema sinicum* (Ker Gawl.) G.Brückn. [=*Murdannia simplex* (Vahl) Brenan].

Distribution and ecology. *Murdannia* is Pantropical, centered in the Paleotropics, and only eight species are currently recognized for the Neotropics (Pellegrini et al. 2016). Its species are mainly associated with permanently or seasonally flooded environments across the genus distribution range.

Comments. Anthericopsis has been historically recognized as distinct from Murdannia and more commonly associated with the distantly related Aneilema (Faden 1998). Nonetheless, Anthericopsis is undisputedly closely related to Murdannia, being either recovered sister to one another or with Anthericopsis nested within Murdannia. In the case of retaining Anthericopsis as distinct from Murdannia, the latter would have no morphological synapomorphy. For these reasons, Anthericopsis is here reduced to a synonym of Murdannia.

Infrageneric classification. Murdannia was divided by Brückner (1930) is four sections, based on inflorescence morphology: (1) M. sect. Pauciflorae, with few-flowered axillary inflorescences; (2) M. sect. Intermediae, with terminal and axillary few-branched inflorescences; (3) M. sect. Terminatae, with exclusively terminal and many-branched inflorescences; and (4) M. sect. Murdannia (called by him M. sect. Scapiflorae), with scapose inflorescences. Fifty years later, Faden (1980) described a fifth section, M. sect. Vaginatae, which was characterized by scapose synflorescences, with florescences restricted to bladeless leaf sheaths. Murdannia sect. Terminatae was further divided into three series, based on the number of ovules per locule, i.e., M. ser. Pluriovulatae, M. ser. Diovulatae, and M. ser. Monoovulatae. Murdannia sect. Pauciflorae and M. sect. Intermediae were only informally subdivided, with any proposed names and some of them even lack a diagnosis. Currently, this same classification system is accepted, despite not being used in any of the major recent works for the genus (Ancy 2014; Ancy and Nampy 2014; Nandikar and Gurav 2015; Pellegrini et al. 2016). Also, it hasn't been critically tested in a molecular study,

morphological or molecular. The present results give us a hint that this classification might represent a natural assemblage. Nonetheless, our sampling is insufficient to test the current classification system due to it being: (1) too sparse when taking into account the total number of accepted species in the genus (11 out of 68 species); (2) not morphologically inclusive with several morphologically critical species not represented; (3) sectionally incomplete, since we have not sampled species of M. sect. *Intermediae* and sect. *Vaginatae*; and (4) biogeographically biased, with all Neotropical species sampled, but only with three Asian species, one African, and the widespread M. *nudiflora*. It is our opinion that, as stated by Pellegrini et al. (2016), *Murdannia* requires a robust phylogenetic sampling before any changes can be made to its infrageneric classification.

Accepted species. A total of 68 accepted species, but with some still undescribed totaling ca. 70 species: Murdannia acutifolia (Lauterb. & K.Schum.) Faden, M. allardii (De Wild.) Brenan, M. assamica Nampy & Ancy, M. audreyae Faden, M. axillaris Brenan, M. blumei (Hassk.) Brenan, M. bracteata (C.B.Clarke) J.K.Morton ex D.Y.Hong, M. brownii Nandikar & Gurav, M. burchellii (C.B.Clarke) M.Pell., M. citrina D.Fang, M. clandestina (Ridl.) Faden, M. clarkeana Brenan, M. crocea (Griff.) Faden, M. cryptantha Faden, M. dimorpha (Dalzell) G.Brückn., M. dimorphoides Faden, M. divergens (C.B.Clarke) G.Brückn., M. edulis (Stokes) Faden, M. engelsii M.Pell. & Faden, M. esculenta (Wall. ex C.B.Clarke) Abeyw., M. fadeniana Nampy & Joby, M. fasciata (Warb. ex K.Schum. & Lauterb.) G.Brückn., Murdannia flavanthera (Nandikar & Gurav) M.Pell., M. gardneri (Seub.) G.Brückn., M. gigantea (Vahl) G.Brückn., Murdannia glabrisepala (Faden) M.Pell., M. glauca (Thwaites ex C.B.Clarke) G.Brückn., M. graminea (R.Br.) G.Brückn., M. hookeri (C.B.Clarke) G.Brückn., M. japonica (Thunb.) Faden, M. juncoides (Wight) R.S.Rao & Kammathy, M. kainantensis (Masam.) D.Y.Hong, M. keisak (Hassk.) Hand.-Mazz., M. lanceolata (Wight) Kammathy, M. lanuginosa (Wall. ex C.B.Clarke) G.Brückn., M. loriformis (Hassk.) R.S.Rao & Kammathy, M. macrocarpa D.Y.Hong, M. medica (Lour.) D.Y.Hong, M. nampyana Joby et al., M. nudiflora (L.) Brenan, M. ochracea (Dalzell) G.Brückn., M. paraguayensis (C.B.Clarke ex Chodat) G.Brückn., Murdannia parviflora (Faden) M.Pell., M. pauciflora (G.Brückn.) G.Brückn., Murdannia perennis (Faden) M.Pell., M. saddlepeakensis M.V.Ramana & Nandikar, M. sahyadrica Ancy & Nampy, M. sanjappae M.C.Nafik & B.R.P.Rao, M. satheeshiana Joby et al., M. schomburgkiana (Kunth) G.Brückn., M. semifoliata (C.B.Clarke) G.Brückn., M. semiteres (Dalzell) Santapau, M. sepalosa (C.B.Clarke) M.Pell., M. simplex (Vahl) Brenan, M. spectabilis (Kurz) Faden, M. spirata (L.) G.Brückn., M. stenothyrsa (Diels) Hand.-Mazz., M. stictosperma Brenan, M. striatipetala Faden, M. stricta Brenan, M. tenuissima (A.Chev.) Brenan, M. triquetra (Wall. ex C.B.Clarke) G.Brückn., M. ugemugei R.B.Kamble et al., M. undulata D.Y.Hong, M. vaginata (L.) G.Brückn., M. versicolor (Dalzell) G.Brückn., M. yunnanensis D.Y.Hong, and M. zeylanica (C.B.Clarke) G.Brückn.

New combinations. *Murdannia flavanthera* (Nandikar & Gurav) M.Pell., **stat. nov.** ≡ *Murdannia* var. *flavanthera* Nandikar & Gurav, Phytodiversity 2(1): 93. 2015.

Murdannia glabrisepala (Faden) M.Pell., **stat. nov.** ≡ *Murdannia vaginata* var. *glabrisepala* Faden, Novon 11(1): 27. 2001.

Murdannia parviflora (Faden) M.Pell., **stat. nov.** \equiv *Murdannia spirata* var. *parviflora* Faden, Novon 11(1): 25. 2001.

Murdannia perennis (Faden) M.Pell., **stat. nov.** ≡ *Murdannia dimorphoides* subsp. *perennis* Faden, Novon 11(1): 24. 2001.

Murdannia sepalosa (C.B.Clarke) M.Pell., **comb. nov.** ≡ *Anthericopsis sepalosa* (C.B.Clarke) Engl., Nat. Pflanzenfam. Nachtr. 1: 69. 1897 ≡ *Aneilema sepalosum* C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 202 1881.

1.3.1.2. Subtribe Floscopineae M.Pell. & Faden, subtrib. nov. Type genus. *Floscopa* Lour. Fig 11E–J

Description. *Herbs* perennial or annual, paludal to aquatic or terrestrial, rarely rupicolous. *Roots* tuberous or not. *Rhizomes* absent. *Stems* prostrate to erect, branched or not. *Leaves* spirally-alternate, rarely distichously-alternate, sessile or pseudo petiolate; epidermis with star-shaped idioblasts. *Synflorescence* composed of a solitary main florescence or by 1–several coflorescences, synflorescence leaves equal to the regular leaves, reduced in size or reduced to bladeless sheaths. *Main florescences* (*inflorescences*) terminal or axillary, sessile or pedunculate, many-branched or reduced to a solitary cincinnus; cincinni 1–many-flowered; bracteoles flat or cup-shaped. *Flowers* enantiostylous or not, zygomorphic; petals 3, sessile, subequal to unequal; androecium zygomorphic, filaments free, sometimes the anterior basally connate at base, straight at post-anthesis, stamens (1–3–5–)6, equal or dimorphic, posterior filaments shorter than the anterior, posterior anthers basifixed, anterior dorsifixed; staminodes if present posterior, antherodes unlobed; pollen with tuberculate exine, pollen of the posterior anthers sterile; ovary sessile or stipitate, 2–3-locular, locules equal, style abrupt or tapering at base, gently curved at the apex, stigma truncate to capitate. *Capsules* loculicidal, 3-valved. *Seeds* 1–many per locule, uniseriate; hilum linear; embryotega lateral to semilateral or dorsal.

Distribution. Mainly African, but with one genus restricted to Australasia, two genera reaching the Neotropics, and one also reaching Australasia.

Comments. The genera included in subtribe Floscopineae have rarely been associated to each other. *Tricarpelema* has long been associated with *Aneilema* due to overall gross and plesiomorphic morphology. On the other hand, *Stanfieldiella* was segregated from *Buforrestia*, but is more closely related to *Floscopa*. Finally, *Floscopa* and *Pseudoparis* have generally been treated as more or less systematically isolated, and either included in their own tribe or broader, and generally polyphyletic, concept of other tribes.

Key to the genera of Floscopineae

- 1. Rhizome absent; leaves lacking star-shaped idioblast at the margins; bracteoles diminute, membranous, flat; pedicels erect at pre-anthesis; capsules stipitate; embryotega white or lighter than the rest of the seed... 2
- Rhizome present; leaves with star-shaped idioblast at the margins; bracteoles conspicuous, chartaceous, cup-shaped; pedicels deflexed at pre-anthesis; capsules sessile; embryotega concolorous with the rest of the seed... 3
- 2. Aquatic or paludal herbs; bracteoles rhomboid; pedicels obliquely-decurved at post-anthesis, ovary 2-carpellate; capsules cordate to subcordate, locules 1-seeded; seeds costate, rarely smooth; chromosomes $> 3\mu m \le 5\mu m \log ...$ Floscopa Lour. (Fig 11G)
- Terrestrial or rupicolous herbs; bracteoles triangular to ovate to broadly ovate; pedicels oblique at post-anthesis, ovary 3-carpellate; capsules cylindrical, locules many-seeded; seeds scrobiculate or reticulate; chromosomes ≤ 2μm long... Stanfieldiella Brenan (Fig 11E & F)

- 3. Herbs sympodial; inflorescences terminal, not perforating the leaf sheaths, cincinni bracts and bracteoles caducous; petals longer than wide, filaments slender, posterior connectives butterfly-shaped, medial anterior connective ob-saddle-shaped... *Tricarpelema* **J.K.Morton** (Fig 11H)
- Herbs monopodial; inflorescences axillary or basal, perforating the leaf sheaths, cincinni bracts and bracteoles persistent; petals wider than long, filaments inflated, connectives oblong or slightly curved... 4
- 4. Roots thin; petals with obtuse apex, medial petal cup-shaped, holding the anterior stamens at the beginning of anthesis, golden-yellow on the basal half, latero-anterior stamens present, filaments sigmoid or J-shaped... *Buforrestia* C.B.Clarke (Fig 11I)
- Roots tuberous; petals with trilobed apex, medial petal equal to the lateral ones, not cupshaped or holding the stamens, concolorous, latero-anterior stamens absent, filaments straight... *Pseudoparis H.Perrier* (Fig 11J)
- **1.3.1.2.1.** *Floscopa* Lour., Fl. Cochinch. 1: 189, 192. 1790. Type species. *Floscopa scandens* Lour.

Fig 11G

Dithyrocarpus Kunth, Ber. Bekanntm. Verh. Königl. Preuss. Akad. Wiss. Berlin: 245. 1841. Type species. *Dithyrocarpus paniculatus* (Roxb.) Kunth. (= *Floscopa scandens* Lour.).

Distribution and ecology. Pantropical, found in Central and South America, Africa (incl. Madagascar), and Australasia. This is the only non-monospecific genus in the Commelinaceae, which is exclusively aquatic or paludal. Species of *Floscopa* can be found growing in open water bodies, shaded water bodies, or flooded forest understories.

Comments. With the recent transfer of *Floscopa yunanensis* to *Aneilema*, *Floscopa* is now a morphologically well-circumscribed and easily recognizable genus. On the other hand, its species are of difficult identification and delimitation, due to their plasticity and the poorly understood variation floral characters. Taxonomy of the genus has been historically exceedingly reliant on vegetative characters and a reinterpretation of the group taxonomy is urgently necessary. A taxonomic revision for *Floscopa* is urgently necessary and has been initiated by the first author (Pellegrini, in prep.).

Accepted species. Currently with 24 accepted species: Floscopa africana (P.Beauv.) C.B.Clarke, F. aquatica Hua, F. axillaris (Poir.) C.B.Clarke, F. clarkeana Kuntze, F. confusa Brenan, F. elegans Huber, F. flavida C.B.Clarke, F. glabrata (Kunth) Hassk., F. glomerata (Willd. ex Schult. & Schult.f.) Hassk., F. gossweileri Cavaco, F. hirsuta (Kunth) Hassk., F. leiothyrsa Brenan, F. majuscula (C.B.Clarke) M.Pell., F. mannii C.B.Clarke, F. petrophila (Gilg & Ledermann ex J.K.Morton) M.Pell., F. perforans Rusby, F. peruviana Hassk. ex C.B.Clarke, F. polypleura Brenan, F. rivularioides T.C.E.Fr., F. scandens Lour., F. schweinfurthii C.B.Clarke, F. sprucei (C.B.Clarke) M.Pell., F. tanneri Brenan, and F. tuberculata C.B.Clarke.

New combinations. Floscopa majuscula (C.B.Clarke) M.Pell., **stat. nov.** \equiv Floscopa africana var. majuscula C.B.Clarke, Fl. Trop. Afr. 8: 85. $1901 \equiv$ Floscopa africana subsp. majuscula (C.B.Clarke) Brenan, Kew Bull. 22: 387. 1968.

Floscopa petrophila (Gilg & Ledermann ex J.K.Morton) M.Pell., **stat. nov.** ≡ Floscopa africana subsp. petrophila Gilg & Ledermann ex J.K.Morton, J. Linn. Soc., Bot. 60: 200. 1967.

Floscopa sprucei (C.B.Clarke) M.Pell., **stat. nov.** ≡ *Floscopa robusta* var. *sprucei* C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 271. 1881.

1.3.1.2.2. *Stanfieldiella* **Brenan**, Kew Bull. 14: 283. 1960. Type species. *Stanfieldiella imperforata* (C.B.Clarke) Brenan. Fig 11E & F

Tricarpelema subg. *Keatingia* Faden, Novon 17(2): 166. 2007, **Syn. nov.** Type. *Tricarpelema* africanum Faden [≡ Stanfieldiella africana (Faden) M.Pell.].

Distribution and ecology. Australasia, from northeastern India to the Philippines and Borneo, usually in the forest understory.

Comments. *Stanfieldiella* is currently understood as a small genus of seven species. A new taxonomic revision is necessary due to the great number of new specimens collected since the genus was described, the inclusion of *S. africana*, and the general short diagnosis provided in its first revision.

Accepted species. A total of seven species: *Stanfieldiella africana* (Faden) M.Pell., *S. axillaris* J.K.Morton, *S. brachycarpa* (Gilg & Ledermann ex Mildbr.) Brenan, *S. glabrisepala* (De Wild.) M.Pell., *S. hirsuta* (Brenan) M.Pell., *S. imperforata* (C.B.Clarke) Brenan, and *S. oligantha* (Mildbr.) Brenan.

New combinations. *Stanfieldiella africana* (Faden) M.Pell., **comb. nov.** \equiv *Tricarpelema africanum* Faden, Novon 17(2): 160–163, f. 1. 2007.

Stanfieldiella glabrisepala (De Wild.) M.Pell., **stat. nov.** ≡ Stanfieldiella imperforata var. glabrisepala (De Wild.) Brenan, Kew Bull. 14: 285. 1960 ≡ Buforrestia glabrisepala De Wild., Pl. Bequaert. 5: 224. 1931.

Stanfieldiella hirsuta (Brenan) M.Pell., **stat. nov.** ≡ *Stanfieldiella brachycarpa* var. *hirsuta* (Brenan) Brenan, Kew Bull. 14: 286. 1960 ≡ *Buforrestia brachycarpa* var. *hirsuta* Brenan, Kew Bull. 7: 455. 1953.

1.3.1.2.3. *Tricarpelema* **J.K.Morton**, J. Linn. Soc., Bot. 59(380): 436. 1966. Type species. *Tricarpelema thomsonii* (C.B.Clarke) J.K.Morton [= *Tricarpelema giganteum* (Hassk.) H.Hara.]

Fig 11H

Distribution and ecology. Australasia (from northeastern India to the Philippines) and Borneo, usually in the forest understory.

Comments. *Tricarpelema* was recently revised by Faden (2007), where he presented valuable information on the genus, with an identification key and the description of two new species. Aside from *T. africanum*, which is here transferred to *Stanfieldiella*, we accept all species recognized by Faden (2007).

Accepted species. A total of seven species: *Tricarpelema brevipedicellatum* Faden, *T. chinense* D.Y.Hong, *T. giganteum* (Hassk.) H.Hara, *T. glanduliferum* (J.Joseph & R.S.Rao)

R.S.Rao, *T. philippense* (Panigrahi) Faden, *T. pumilum* (Hallier f.) Faden, and *T. xizangense* D.Y.Hong.

1.3.1.2.4. *Buforrestia* **C.B.Clarke** in Candolle & Candolle, Monogr. Phan. 3: 120, 233. 1881. Type species. *Buforrestia mannii* C.B.Clarke. Fig 11I

Distribution and ecology. Disjunctly distributed between continental Africa and South America, growing in the understory of rainforests.

Comments. *Buforrestia* is a small genus with four species, two of them African and two Neotropical, one of them still undescribed (Faden and Pellegrini, in prep.). The genus has seldom been collected in both continents and its floral morphology is not completely understood. It is in need of an updated taxonomic revision based on field data and new floral data.

Accepted species. *Buforrestia candolleana* C.B.Clarke, *B. mannii* C.B.Clarke, and *B. obovata* Brenan.

1.3.1.2.5. *Pseudoparis* **H.Perrier**, Notul. Syst. (Paris) 5(3): 176. 1936. Type species. *Pseudoparis cauliflora* H.Perrier. Fig 11J

Distribution and ecology. Endemic to Madagascar, growing in understory of seasonally dry forests.

Comments. *Pseudoparis* is a small genus with five species, two of them still undescribed (Pellegrini, in prep.). The genus has not been critically reviewed since it was first described and no identification key with all currently accepted species is available. A taxonomic revision for the genus is being prepared (Pellegrini, in prep.). Its flowers are peculiar due to their trilobed petals not found anywhere else in the order, only one anterior fertile stamen, with two or three stamens, which only produced sterile pollen.

Accepted species. *Pseudoparis cauliflora* H.Perrier, *P. monandra* H.Perrier, and *P. tenera* (Baker) Faden

1.3.1.3. Subtribe Commelinineae Engl., Syllabus, ed. 2: 87. 1898. Type genus. Commelina L.Fig 11K-T

Distribution. Pantropical, but most centered in Africa, with some genera reaching Australasia, and North, Central and South America.

Comments. Subtribe Commelinineae was the only group within tribe Commelineae that was previously suggested to represent a monophyletic assemblage (Faden 1975; Faden and Hunt 1991). This was due to the presence of glandular microhairs with clavate medial cell and of peculiar hook-like uniseriate macrohairs. Of the accepted genera, *Dictyospermum* is the most morphologically and phylogenetically isolate of them, with a unique floral Bauplan. The *Pollia* clade is peculiar in producing stolon-like flagelliform-shoots, aside from their cucullate

petals. Finally, the *Commelina* clade is composed of two of the family's largest genera, *Aneilema* and *Commelina*, being characterized by stigmatic papillae with folded epidermis.

Key to the genera of Commelinineae

- 1. Cincinni bracts present, caducous, bracteoles caducous; filaments and style descending-falcate, filaments curved at post-anthesis, style tapered at base; capsules with locules equal, 1-seeded... *Dictyospermum* Wight (Fig 11K)
- Cincinni bracts present or not, if present persistent, bracteoles persistent; filaments and style variously curved but never that way, filaments coiled at post-anthesis, style abruptly-cylindrical at base; capsules with locules unequal or equal, (1–)2–many-seeded, if 1-seeded capsules 2-valved or 3-valved with an aborted or reduced posterior locule... 2
- 2. Herbs never producing stolons; pedicels herbaceous at post-anthesis, petals generally patent, if deflexed also flat, paired petals with auriculate base, style with almost straight or apically decurved with stigma pointing upwards, stigmatic papillae with folded cuticle...
- Herbs stoloniferous; pedicels fibrous at post-anthesis, petals deflexed and cucullate or erect with revolute apex, paired petals with cuneate to obtuse base, style apically decurved with stigma pointing downwards, stigmatic papillae lacking folded cuticle... 4
- 3. Herbs sympodial; inflorescences terminal or axillary, basal bract leaf-like or bracteoles, cincinni bracteate; sepals apically or subapically glandular, antherodes 2-lobed, lacking pollen-sacs... *Aneilema* **R.Br.** (**Fig 110–Q**)
- Herbs monopodial; inflorescences leaf-opposite, basal bract spathaceous, rarely absent, cincinni ebracteate; sepals eglandular, antherodes X-shaped, with reduced pollen-sacs...
 Commelina L. (Fig 11R-T)
- 4. Main axis of the inflorescence straight or almost so, cincinni bracts patent to ascending, bracteoles perfoliate; petals equal to subequal, lateral petals sessile to obscurely clawed, medial equal to subequal to the laterals; fruits indehiscent, coloration structural, metallic; seeds with dorsal embryotega... *Pollia* Thunb. (Fig 11L)
- Main axis of the inflorescence in zig-zag, cincinni bracts deflexed, bracteoles non-perfoliate; lateral petals conspicuously clawed, medial much smaller than the laterals; capsules dehiscent, dull-colored; seeds with semilateral embryotega... 5
- 5. Annual herbs; cincinni bracts bracteose, patent, cincinni long-pedunculate; pedicels geniculate at anthesis, petals lilac, antherodes hourglass-shaped, lobes transversally broadly ellipsoid; capsules 3-capellate, posterior locule reduced and 1-seeded, anterior locules 2-seeded; seeds rugose... *Campylonanthus* Faden & M.Pell. (Fig 11M)
- Perennial herbs; cincinni bracts spathaceous, generally deflexed, sometimes patent, cincinni sessile or almost so; pedicels straight at anthesis, petals white, antherodes V-shaped, lobes longitudinally ellipsoid; capsules 2-carpellate, locules 1-seeded; seeds costate to costate-tuberculate... *Polyspatha* Benth. (Fig 11N)

1.3.1.3.1. Dictyospermum Wight, Icon. Pl. Ind. Orient. 6: 29. 1853
 = Aneilema sect.
 Dictyospermum (Wight) C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 196.
 1881. Types species. Dictyospermum montanum Wight.
 Fig 11K

Distribution and ecology. Southern Asia and the Malay Archipelago, found growing in the understory of rainforests.

Comments. The circumscription of *Dictyospermum* was the subject of much debate through the years. These problems in circumscription are greatly caused by misinterpretation of floral characters, i.e., floral display angle and androecium morphology, but also due to the lack of access of previous workers to fresh or preserved flowers. *Dictyospermum* is florally quite unique in the family and the order, and thus, well-circumscribed. The current circumscription for the genus is monophyletic, with the exclusion of some species, which are currently placed in *Aneilema*, *Murdannia*, and *Tricarpelema*.

Dictyospermum has never been taxonomically reviewed and no identification key for its species is available. This is the first phylogenetic hypothesis for the genus, but molecular phylogeny would certainly be welcome.

Accepted species. A total of five species: *Dictyospermum conspicuum* (Blume) J.K.Morton, *D. humile* (Warb.) J.K.Morton, *D. montanum* Wight, *D. ovalifolium* Wight, and *D. ovatum* Hassk.

- **1.3.1.3.2.** *Pollia* **Thunb.**, Nov. Gen. Pl. 1: 11. 1781. Type species. *Pollia japonica* Thunb. Fig 11L
- Dirtea Raf., Fl. Tellur. 3: 69. 1836[1837], nom. illeg., **Syn. nov.** Type species. Dirtea japonica (Thunb.) Raf. (≡ Pollia japonica Thunb.).
- Aclisia E.Mey. ex C.Presl, Reliq. Haenk. 1: 137. 1827. Type species. Aclisia sorzogonensis E.Mey. ex C.Presl. [= Pollia secundiflora (Blume) Bakh.f.].
- *Lamprocarpus* Blume ex Schult. & Schult.f., Syst. Veg. (ed. 15 bis) 7(2): 1615, 1726. 1830. Type species. *Lamprocarpus* thyrsiflorus (Blume) Blume ex Schult. & Schult.f. [≡ *Pollia thyrsiflora* (Blume) Steud.].

Distribution and ecology. Africa (incl. Madagascar) and Australasia, with a sole species (i.e., *P. americana* Faden) in Central America (Panama), all found growing in the understory of rainforests.

Comments. *Pollia* is monophyletic, with several unique or peculiar morphological characters circumscribing it. Nonetheless, *Pollia* was traditionally split by several authors into two genera, based on androecium morphology (*Aclisia* with posterior stamens staminodial *vs. Pollia* with posterior stamens fertile). Nonetheless, this character does not seem to be strong enough to recognize two genera. Added to that, since both genera are virtually identical when in fruit, with the recognition of two genera most herbarium specimens would remain unidentified, since most specimens of *Pollia* are collected only with fruits. Thus, it seems unpractical to recognize *Aclisia* as distinct from *Pollia*. *Pollia* urges for further taxonomic studies and fieldwork. Its species are very difficult to differentiate, and floral morphology is

poorly recorded for most species. A taxonomic revision on a global scale has never been done and is long overdue.

Infrageneric classification. *Pollia* was divided by Clarke (1881a) in three sections: (1) *P.* sect. *Pollia*, with 6 subequal and fertile stamens, fruits 5–8-seeded, and polygonal seeds; (2) *P.* sect. *Aclisia*, with posterior stamens reduced to staminodes, fruits 5–8-seeded, and polygonal seeds; and (3) *P.* sect. *Phaeocarpa*, with posterior stamens reduced to staminodes, fruits with 2-seeded locules, and elliptic seeds. Nonetheless, this classification was never used in subsequent works and has never been tested. Thus, we refrain from accepting any formal infrageneric classification for *Pollia* without the support of a phylogeny.

Accepted species. A total of ca. 20 species: *Pollia americana* Faden, *P. bracteata* K.Schum., *P. condensata* C.B.Clarke, *P. crispata* (R.Br.) Benth., *P. gracilis* C.B.Clarke, *P. hasskarlii* R.S.Rao, *P. ×horsfieldii* C.B.Clarke, *P. japonica* Thunb., *P. macrobracteata* D.Y.Hong, *P. macrophylla* (R.Br.) Benth., *P. mannii* C.B.Clarke, *P. miranda* (H.Lév.) H.Hara, *P. papuana* Ridl., *P. pentasperma* C.B.Clarke, *P. sambiranensis* H.Perrier, *P. secundiflora* (Blume) Bakh.f., *P. subumbellata* C.B.Clarke, *P. sumatrana* Hassk., *P. thyrsiflora* (Blume) Steud., *P. verticillata* Hallier f., and *P. × zollingeri* (Hassk.) C.B.Clarke.

1.3.1.3.3. Campylonanthus Faden & M.Pell., gen. nov. Type species. Campylonanthus brasiliense (C.B.Clarke) Faden & M.Pell. (≡ Aneilema brasiliense C.B.Clarke). Fig 11M

Description. Herbs perennial, with a definite base, terrestrial or rupicolous. Roots thin and fibrous. Stolons absent, rarely produced. Stems erect, unbranched to sparsely branched on the upper third, rooting at the basal nodes; internodes puberulous with hook-hairs, the lower ones glabrescent at age. Leaves subpetiolate, sessile towards the apex of the stem, spirallyalternate, congested at the apex of the stem; sheaths puberulous with hook-hairs, margins ciliate; lamina flat, smaller towards the apex of the stems, membranous, sparsely to densely puberulous with hook-hairs on both sides, abaxial side scabrid with prickle-hairs near the margins, sometimes also with eglandular uniseriate hairs, base symmetrical, cuneate, margins scabrid with prickle-hairs, apex acuminate; midvein conspicuous, adaxially impressed, abaxially very prominent, secondary veins inconspicuous. Synflorescence composed of a solitary main florescence or with 1–few coflorescences. *Main florescences (inflorescences)* terminal or axillary in the in the uppermost nodes, not perforating the leaf-sheaths; main florescence a many-branched, pedunculate, lax thyrse; basal bract reduced to leaf-like; peduncle densely puberulous with hook-hairs; peduncle bracts (sterile bracts) absent; main axis elongated, in zig-zag, puberulous with hook-hairs; cincinni bracts persistent, flat, decreasing in size towards the apex of the main florescence, almost glabrous or puberulous with a mixture of hook-hairs and uniseriate eglandular hairs; cincinni alternate, longpedunculate, peduncles decreasing in length towards the apex, puberulous with hook-hairs, axis elongated, ascending to erect, rarely patent, sinuate, puberulous with hook-hairs; bracteoles cup-shaped, non-perfoliate, herbaceous, apex eglandular, persistent, puberulous with a mixture of hook-hairs and uniseriate eglandular hairs. Flowers hermaphrodite or staminate (the staminate ones with a reduced or completely aborted gynoecium), zygomorphic, non-enantiostylous, chasmogamous, flat (not tubular); pedicels deflexed at preanthesis, geniculate at anthesis, erect at post-anthesis; pedicels stout, not gibbous at apex, slightly elongated and lignified at post-anthesis and in fruit; sepals 3, unequal, free, cucullate, membranous, dorsally not keeled, sparsely with a mixture of hook-hairs and uniseriate eglandular hairs, margins hyaline, apex eglandular, slightly accrescent and persistent in fruit;

petals 3, unequal, free, deliquescent, glabrous, medial one discolorous, light blue to pale lilac to lilac, paired petals clawed, held upwards to deflexed, claws glabrous, lighter than the limb, limb concave, the medial sessile, held downwards to strongly deflexed, white, limb linear, flat; staminodes 0-3, if present subequal, posterior, filaments glabrous, medial staminode sometimes with an unlobed antherode, lateral staminodes free from the stamens, antherodes bilobed, lobes sessile, lobes transversally ellipsoid, lilac; stamens 3, unequal, anterior, filaments free, glabrous, anthers versatile, dehiscence rimose, introrse, lateral filaments initially horizontal, straight but sharply recurved near apex, then arcuate-descending, anthers with an inconspicuous connective, medial filament initially arcuate-ascending, then arcuatedescending, anther with a conspicuous connective, of a different size, shape and color, its pollen also different in color; ovary sessile, glabrous, apex truncate, 3-locular, ovules uniseriate, dorsal locule reduced, 1-ovulate, ventral locules 2-ovulate, style elongate, gently arcuate-descending but sharply recurved at apex, then arcuate-descending, not spirally-coiled at post-anthesis, stigma capitate. Capsules loculicidal, 2-valved, sessile, smooth, glabrous, apex emarginate, valves slightly spreading, persistent, dorsal locule empty, ventral locules 2seeded. Seeds monomorphic, exarillate, unappendaged, non-farinose, uniseriate, rectangular, not cleft towards the embryotega, ventrally flattened, testa rugose, tan, spotted with dark brown, especially on the bumps, with a very low, fine, irregular, colorless reticulum on the surface; hilum linear, prominent, raised in a shallow groove, slightly extended onto apical and basal surfaces; embryotega lateral.

Etymology. The name of the new genus derives from the Greek "καμπύλος" + "άνθος", meaning curved flowers, in reference to the peculiar geniculate pedicels.

Distribution and ecology. South America (in Brazil and Venezuela), it grows in the understory of rainforests or seasonally dry forests.

Comments. Campylonanthus brasiliense has long been considered a species of uncertain generic placement, as well as of uncertain systematic affinity (Clarke 1881a, b; Faden 1975, 1991). Due to the lack of obvious morphological differences from Aneilema, Faden (1975, 1991) felt it was best to keep it in Aneilema and await further phylogenetic data. Kelly and Evans (2014) recovered C. brasiliense in an averagely supported clade with Pollia, and strongly supported as sister to Polyspatha. This relationship was deemed as morphologically surprising, but our morphological dataset recovers this exact relationship, with strong statistical support. At this time, the only synapomorphy for the genus seems to be its geniculate pedicels. Nonetheless, Campylonanthus is macromorphologically very different from its sister group, Polyspatha, which in turn is very distinct from Pollia. Thus, the recognition of a new genus is necessary.

Accepted species and new combination. *Campylonanthus brasiliense* (C.B.Clarke) Faden & M.Pell., **comb. nov.** ≡ *Aneilema brasiliense* C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 225. 1881.

1.3.1.3.4. *Polyspatha* **Benth.**, Niger Fl.: 543. 1849. Type species. *Polyspatha paniculata* Benth. Fig 11N

Distribution and ecology. Continental Africa, growing understory in rainforests.

Comments. *Polyspatha* was recently revised by Faden (2011), where he described a third species for the genus. In the present study, we have sampled all species of the genus and provide the first phylogenetic hypothesis for the group.

Accepted species. *Polyspatha hirsuta* Mildbr., *P. oligospatha* Faden, and *P. paniculata* Benth.

1.3.1.3.5. *Aneilema* **R.Br.**, Prodr.: 270. 1810 ≡ *Aneilema* R.Br. subg. *Aneilema* ≡ *Aneilema* subg. *Dicarpellaria* C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 196. 1881. Type species. *Aneilema biflorum* R.Br. Fig 11O–O

Perosanthera Fend, Sitzungsb. Akad. Wien. 50: 353. 1864, nom. nud.

Distribution and ecology. Mainly Paleotropical and centered in Africa, but extending to Australasia, and a sole species reaching the Neotropics (Pellegrini et al., in prep.). Its species are can be found growing from open and dry environments to shady and moist environments and forest understories.

Comments. With the exclusion of *Camplylonanthus brasiliense*, the reduction of *Rhopalephora* to a section, and the inclusion of *A. yunnanense*, *Aneilema* is finally rendered monophyletic. It is currently represented by 80 species.

Infrageneric classification. Aneilema is currently divided into eight sections (Pellegrini et al., in press): (1) A. sect. Aneilema, characterized by petals equal to subequal, ovaries and capsules glabrous, seeds rugose-tuberculate; (2) A. sect. Amelina, characterized by medial antherode larger than the laterals; (3) A. sect. Brevibarbata, characterized by lateral filaments bearded in the upper half with short and hyaline uniseriate hairs, and seeds with the coat of fused farinose granules; (4) A. sect. Lamprodithyros, characterized by lower stamens initially held inside the cup-shaped medial petal, and dimorphic seeds; (5) A. sect. Pedunculosa, characterized by cincinni bracts with a filiform apical gland, and lateral filaments bearded in the upper half with brightly-colored uniseriate hairs; (6) A. sect. Rendlei, antherodes with lobes reniform, and medial connective strongly convex and maroon-spotted; (7) A. sect. Rhopalephora, flowers with a 60° torsion, sepals deflexed in fruit, and gynoecium puberulous with a mixture of hook and minute glandular hairs; and (8) A. sect. Somaliensia, characterized by cincinni detaching at the end of the flowering season. Nonetheless, as recovered by Kelly and Evans (2014) and in the present study, A. sect. Amelina is polyphyletic, with A. gilletti Brenan grouping with A. sect. Pedunculosa, and A. johnstonii K.Schum. being recovered sister to the rest of the genus (in our case, A. johnstonii K.Schum. is sister to A. yunnanense and both are sister to the rest of Aneilema). Thus, the infrageneric classification of Aneilema requires further amendments, aside from the recognition of Rhopalephora as a new section. Based on morphological peculiarities, a new subgenus is described below to accommodate A. johnstonii and A. yunnanense.

Key to the subgenera and sections of Aneilema

- 1. Lateral petals with claw darker than blade, blade cucullate-reniform, medial petal sessile, antherodes upside-down horseshoe-shaped; pollen with sulcal membrane coarsely spinulate... *Aneilema* subg. *Pristiniflora* M.Pell. & Faden (Fig 110)
- Lateral petals with claw lighter or concolorous to the blades, blades variously shaped but never as above, medial petal shortly-clawed; antherodes variously shaped but never

upside-down horseshoe-shaped; pollen with sulcal membrane spinulate... 2 (Aneilema R.Br. subg. Aneilema, Fig 11P & Q)

- 2. Petals equal to subequal, staminodes equal to subequal, medial connective oblong to elliptic to ovate; seeds rugose-tuberculate, not-farinose... *Aneilema* **R.Br. sect.** *Aneilema*
- Petals unequal, if subequal medial petal cucullate or boat-, slipper-, or cup-shaped, staminodes unequal, medial connective strongly convex or obdeltoid or dumbbell-shaped or saddle-shaped; seeds smooth to alveolate, shallowly foveolate, reticulate-foveolate or scrobiculate, generally farinose... 3
- 3. Cincinni long-pedunculate, mostly subopposite or subverticillate, bracteoles eglandular; lateral filaments straight to undulate, not geniculate... 4
- Cincinni medium to shortly-pedunculate, alternate, bracteoles glandular; lateral filaments J-S-shaped, slightly geniculate to geniculate... 5
- 4. Flowers not twisted, sepals patent in fruit, medial antherode absent or equal to the laterals, filaments of the stamens connate up to half their length, medial antherode than the laterals, medial filament strongly ascending at apex, gynoecium puberulous with uniseriate eglandular hairs... *Aneilema* sect. *Amelina* (C.B.Clarke) C.B.Clarke
- Flowers with a 60° torsion in floral display, sepals deflexed in fruit, medial antherode lacking or the same size as the laterals, medial filament almost straight, gynoecium puberulous with a mixture of hook and minute glandular hairs... Aneilema sect. Rhopalephora (Hassk.) M.Pell. & Nandikar (Fig 11P)
- 5. Flowers scented, medial petal cucullate, apex acute, claw concolorous to the blade, gynoecium stipitate, stigma truncate; seeds scrobiculate... 6
- Flowers unscented, medial petal boat-, slipper-, or cup-shaped, apex acuminate, claw hyaline or lighter than the blade, gynoecium sessile, stigma capitate; seeds reticulate to foveolate... 7
- 6. Cincinni persistent; filament of the lateral staminodes thickened basally, antherode lobes reniform, lateral stamens dimorphic in hermaphrodite and staminate flowers, medial connective strongly convex... *Aneilema* sect. *Rendlei* Faden
- Cincinni detaching at the end of the flowering season; filaments of the lateral staminodes slender, antherode lobes globose to sub-globose or obovoid or transversally ellipsoid, lateral stamens monomorphic, medial connective saddle-shaped... Aneilema sect. Somaliensia Faden
- 7. Thyrsi lax to moderately lax; petals subequal, lower stamens initially held by the medial petal, filaments basally connate, glabrous; seeds dimorphic... *Aneilema* sect. *Lamprodithyros* (Hassk.) C.B.Clarke
- Thyrsi moderately dense to dense; petals unequal, lower stamens not held by the medial petal, filaments free, barbate on the upper half, rarely on the basal half; seeds monomorphic... 8
- 8. Roots tuberous or fibrous; bracteoles cup-shaped, generally perfoliate, lacking a linear apex; lateral stamens sparsely and inconspicuously bearded, hairs hyaline... *Aneilema* sect. *Brevibarbata* Faden (Fig 11Q)

- Roots fibrous; bracteoles neither cup-shaped nor perfoliate, often with a linear gland-tipped apex; lateral stamens densely and conspicuously bearded, hairs brightly-colored...
 Aneilema sect. Pedunculosa Faden
- **1.3.1.3.5.1.** *Aneilema* **subg.** *Pristiniflora* **M.Pell. & Faden, subg. nov**. Type species. *Aneilema johnstonii* K.Schum. Fig 110

Description. Stems prostrate with erect apex. Leaves spirally-alternate, with short pseudopetioles. Main florescences (inflorescences) terminal pedunculate, many-branched; cincinni alternate. Flowers non-enantiostylic, lateral petals with claw darker than blade, blade cucullate-reniform, medial petal sessile, elliptic; antherodes upside-down horseshoe-shaped; pollen with sulcal membrane coarsely spinulate.

Distribution and ecology. With a disjunctive distribution between continental Africa and the province of Yunnan, China, growing in forested areas.

Accepted species. A total of two species: *Aneilema johnstonii* K.Schum. and *A. yunnanense* (D.Y.Hong) M.Pell.

Etymology. The name of this new subgenus derives from the Latin, meaning "old flower" in reference to this subgenus being the first lineage to diverge in *Aneilema*.

1.3.1.3.5.2. *Aneilema* **R.Br. subg.** *Aneilema* ≡ *Aneilema* subg. *Dicarpellaria* C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 196. 1881. Type species. *Aneilema biflorum* R.Br.

Fig 11P & Q

Description. Stems various. Leaves spirally- or distichously-alternate, sessile or pseudopetiolate. Main florescences (inflorescences) terminal or axillary, sessile or pedunculate, few-many-branched; cincinni alternate or subopposite or subverticillate to verticillate. Flowers enantiostylic or not, lateral petals with claw lighter or concolorous to the blades, blades variously shaped but never cucullate-reniform, medial petal shortly-clawed, elliptic; antherodes variously shaped but never upside-down horseshoe-shaped; pollen with sulcal membrane spinulate.

Distribution and ecology. Pantropical, but centered in continental Africa, found mainly in non-forested habitats.

1.3.1.3.5.2.1. *Aneilema* **R.Br. sect.** *Aneilema*. Type species. *Aneilema biflorum* R.Br.

Distribution and ecology. Australasia, growing in forest understories.

Accepted species. A total of seven species: *Aneilema acuminatum* R.Br., *A. aparine* H.Perrier, *A. biflorum* R.Br., *A. neocaledonicum* Schltr., *A. papuanum* Warb., *A. sclerocarpum* F.Muell., and *A. siliculosum* R.Br.

1.3.1.3.5.2.2. *Aneilema* **sect.** *Amelina* (C.B.Clarke) C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 197. 1881 ≡ *Amelina* C.B.Clarke, Commelyn. Cyrtandr. Bengal: 38. 1874. Type species. *Amelina wallichii* C.B.Clarke [= *Aneilema aequinoctiale* (P.Beauv.) Loudon].

Distribution and ecology. Widespread in continental Africa, except for the extreme north and northeastern, found growing in open environments or understory in seasonally dry forests.

Accepted species. A total of six species: *Aneilema aequinoctiale* (P.Beauv.) G.Don, *A. ephemerum* Faden, *A. hockii* De Wild., *A. longirrhizum* Faden, *A. nyasense* C.B.Clarke, and *A. plagiocapsa* K.Schum.

- **1.3.1.3.5.2.3.** *Aneilema* **sect.** *Rhopalephora* (Hassk.) **M.Pell. & Nandikar**, in prep. ≡ *Rhopalephora* Hassk., Bot. Zeitung (Berlin) 22: 58. 1864a. Type species. *Rhopalephora blumei* Hassk., nom. illeg. [≡ *Aneilema micranthum* (Vahl) Kunth]. Fig 11P
- *Piletocarpus* Hassk., Flora 49: 212. 1866. Type species. *Piletocarpus protensus* (Wall. ex Wight) Hassk. [= *Aneilema protensum* (Wall. ex Wight) Thwaites].

Distribution and ecology. Madagascar and Australasia, growing in the understory of rainforests.

Accepted species. A total of five species: *Aneilema micranthum* (Vahl) Kunth, *A. protensum* (Wall. ex Wight) Thwaites, *A. rugosum* H.Perrier, *A. scaberrimum* (Blume) Kunth, and *A. vitiense* Seem.

1.3.1.3.5.2.4. *Aneilema* sect. *Rendlei* Faden, Smithsonian Contr. Bot. 76: 62. 1991. Type species. *Aneilema* rendlei C.B.Clarke.

Distribution and ecology. Southwestern Ethiopia to Northeastern Tanzania, growing in partially shaded to shaded rocky environments or at the margins of seasonally to permanently dry forests.

Accepted species. A total of four species: *Aneilema brenanianum* Faden, *A. rendlei* C.B.Clarke, *A. taylorii* C.B.Clarke, and *A. usambarense* Faden.

1.3.1.3.5.2.5. *Aneilema* **sect.** *Somaliensia* **Faden**, Smithsonian Contr. Bot. 76: 77. 1991. Type species. *Aneilema somaliense* C.B.Clarke.

Distribution and ecology. Somali Republic, Somaliland, eastern Ethiopia, and southern to central Kenya. It grows in full sun to partial shade in bushlands, shrublands, woodlands, or rocky slopes.

Accepted species. A total of eight species: *Aneilema grandibracteolatum* Faden, *A. gypsophilum* (Faden) M.Pell., *A. longicapsa* Faden, *A. obbiadense* Chiov., *A. pusillum* Chiov., *A. somaliense* C.B.Clarke, *A. thulinii* (Faden) M.Pell., and *A. variabile* (Faden) M.Pell.

New combinations. *Aneilema gypsophilum* (Faden) M.Pell., **stat. nov.** ≡ *Aneilema pusillum* subsp. *gypsophilum* Faden Smithsonian Contr. Bot. 76: 88. 1991.

Aneilema thulinii (Faden) M.Pell., **stat. nov.** ≡ *Aneilema pusillum* subsp. *thulinii* Faden Smithsonian Contr. Bot. 76: 89. 1991.

Aneilema variabile (Faden) M.Pell., **stat. nov.** ≡ *Aneilema pusillum* subsp. *variabile* Faden Smithsonian Contr. Bot. 76: 88. 1991.

- **1.3.1.3.5.2.6.** *Aneilema* **sect.** *Lamprodithyros* (Hassk.) C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 196. 1881 ≡ *Lamprodithyros* Hassk., Flora 46: 388. 1863. Type species. *Lamprodithyros* petersii Hassk. [≡ *Aneilema* petersii (Hassk.) C.B.Clarke.].
- Ballya Brenan, Kew Bull. 19: 63. 1964. Type species. Ballya zebrina (Chiov. ex Chiarugi) Brenan (≡ Aneilema zebrina Chiov. ex Chiarugi).
- Aneilema sect. Pseudo-axillares C.B.Clarke in Thiselton-Dyer, Fl. Trop. Africa 8: 63. 1901, pro. syn.

Distribution and ecology. Red Sea Hills of northeastern Sudan and southern Arabian Peninsula to southern Zimbabwe, Swaziland, and South Africa. It grows in grassland with scattered shrubs, bushland, thicket margins, wooded grassland, woodland, lowland forest margins, roadsides, occasionally in damp situations, rarely in rocky places.

Accepted species. A total of 16 species: Aneilema benadirense Chiov., A. calceolus Brenan, A. clarkei Rendle, A. forskalii Kunth, A. indehiscens Faden, A. lamuense Faden, A. lilacinum (Faden) M.Pell., A. pallidiflorum (Faden) M.Pell., A. petersii (Hassk.) C.B.Clarke, A. recurvatum Faden, A. sebitense Faden, A. succulentum Faden, A tanaense Faden, A. trispermum Faden, A. woodii Faden, and A. zebrinum Chiov.

New combinations. *Aneilema lilacinum* (Faden) M.Pell., **stat. nov.** \equiv *Aneilema indehiscens* subsp. *lilacinum* Faden Bothalia 15(1-2): 97. 1984.

Aneilema pallidiflorum (Faden) M.Pell., **stat. nov.** ≡ Aneilema petersii subsp. pallidiflorum Faden, Smithsonian Contr. Bot. 76: 97. 1991.

- **1.3.1.3.5.2.7.** *Aneilema* sect. *Brevibarbata* Faden, Smithsonian Contr. Bot. 76: 143. 1991. Type species. *Aneilema beniniense* (P.Beauv.) Kunth. Fig 11Q
- Bauschia Seub. ex Warm., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1872: 123. 1872. Type. Bauschia bracteolata (Mart.) Seub. ex Warm. (≡ Aneilema bracteolatum Mart.).

Distribution and ecology. West Africa, eastern to southern Sudan, southwestern Ethiopia, western Kenya, eastern Tanzania, Angola, Zambia, Zimbabwe, Swaziland, and South Africa (East Cape Province), with *A. bracteolatum* occurring in the Neotropics, from Panama to Bolivia and Northern Brazil. Found growing in understory in rainforests and seasonally dry forests, woodlands, and savannas.

Accepted species. A total of 22 species: *Aneilema angolense* C.B.Clarke, *A. arenicola* Faden, *A. beniniense* (P.Beauv.) Kunth, *A. bracteolatum* Mart., *A. brunneospermum* Faden, *A. dispermum* Brenan, *A. dregeanum* Kunth, *A. homblei* De Wild., *A. keniense* (Faden) M.Pell., *A. lanceolatum* Benth., *A. luteum* (C.B.Clarke) M.Pell., *A. macrorrhizum* T.C.E.Fr., *A.*

- mortonii Brenan, A. ovato-oblongum P.Beauv., A. paludosum A.Chev., A. pomeridianum Stanf. & Brenan, A. schlechteri K.Schum., A. setiferum A.Chev., A. silvaticum Brenan, A. subnudum A.Chev., A. umbrosum (Vahl) Kunth, and A. welwitschii C.B.Clarke.
- **New combinations.** *Aneilema keniense* (Faden) M.Pell., **stat. nov.** ≡ *Aneilema indehiscens* subsp. *keniense* Faden, Smithsonian Contr. Bot. 76: 104. 1991.
- Aneilema luteum (C.B.Clarke) M.Pell., et stat. nov. ≡ Aneilema angolense var. luteum (C.B.Clarke) Faden in Figueiredo & Smith, Strelitzia 22: 176. 2008 ≡ Aneilema pedunculosum var. luteum C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 228. 1881.
- **1.3.1.3.5.2.8.** *Aneilema* sect. *Pedunculosa* Faden, Smithsonian Contr. Bot. 76: 146. 1991. Type species. *Aneilema pedunculosum* C.B.Clarke.
- **Distribution and ecology.** Southeastern Sudan and western Ethiopia, Namibia (Caprivi Strip), Botswana, Zimbabwe, and Mozambique. It grows on the understory of rainforests.
- Accepted species. A total of 10 species: Aneilema chrysopogon Brenan, A. gillettii Brenan, A. hirtum A.Rich., A. leiocaule K.Schum., A. minutiflorum Faden, A. nicholsonii C.B.Clarke, A. pedunculosum C.B.Clarke, A. richardsiae Brenan, A. spekei C.B.Clarke, and A. termitarium Faden.
- **1.3.1.3.6.** *Commelina* L., Sp. Pl. 1: 40. 1753. Type species. *Commelina communis* L. Fig 11R–T
- Erxlebia Medik., Hist. & Commentat. Acad. Elect. Sci. Theod.-Palat. 6(Phys.): 494. 1790. Type species. Erxlebia fusiformis Medik. (= Commelina tuberosa L.).
- Hedwigia Medik. Hist. & Commentat. Acad. Elect. Sci. Theod.-Palat. 6(Phys.): 495. 1790, nom. rej., non Hedwigia P.Beauv. Type species. Hedwigia africana (L.) Medik. (≡ Commelina africana L.).
- *Lechea* Lour., Fl. Cochinch.: 34, 60, 1790, nom. illeg., non *Lechea* L. Type species. *Lechea chinensis* Lour. (≡ *Commelina loureiroi* Kunth).
- *Ananthopus* Raf., Fl. Ludov.: 20–22. 1817. Type species (designated here). *Ananthopus clandestinus* Raf. (= *Commelina virginica* L.).
- Allotria Raf., Fl. Tellur. 3: 70. 1836[1837]. Type species. Allotria scabra Raf. (= Commelina virginica L.).
- Eudipetala Raf., Fl. Tellur. 3: 68. 1836 [1837]. Type species. Eudipetala deficiens (Hook.) Raf. (= Commelina erecta L.).
- Larnalles Raf., Fl. Tellur. 3: 70. 1836[1837]. Type species (designated here). Larnalles dichotoma Raf. (= Commelina erecta L.).
- Nephralles Raf., Fl. Tellur. 3: 70. 1836[1837]. Type species. Nephralles parviflora Raf. (= Commelina diffusa Burm.f.).

- Ovidia Raf., Fl. Tellur. 3: 68. 1836[1837]. Type species. Ovidia gracilis (Ruiz & Pav.) Raf. (= Commelina diffusa Burm.f.).
- Allosperma Raf., Fl. Tellur. 4: 122. 1836[1838]. Type species. Allosperma tuberosa (L.) Raf. (≡ Commelina tuberosa L.).
- Isanthina Rchb. ex Steud., Nomencl. Bot. ed. 2, 1: 400. 1840, pro. syn.
- Heterocarpus Wight, Icon. Pl. Ind. Or. 6: 29. 1853. Type species (designated here). Heterocarpus glaber Wight (≡ Commelina wightii Raizada).
- Athyrocarpus Schltdl. ex Hassk., Flora 49: 212. 1866. Type species. Athyrocarpus leiocarpus (Benth.) Benth. & Hook.f. ex Hemsl. (= Commelina leiocarpa Benth.).
- Disecocarpus Hassk., Flora 49: 211. 1866. Type species. Disecocarpus polygamus (Roth) Hassk. (= Commelina communis L.).
- Omphalotheca Hassk., Bull. Congr. Int. Bot. Hort. Amsterdam 1865: 103. 1866. Type species Not designated.
- Phaeosphaerion Hassk., Flora 49: 212. 1866. Type species. Phaeosphaerion leiocarpum (Benth.) Hassk. (≡ Commelina leiocarpa Benth.).
- Spathodithyros Hassk., Flora 49: 211. 1866. Type species. Spathodithyros suffruticosus (Blume) Hassk. (≡ Commelina suffruticosa Blume).
- *Trithyrocarpus* Hassk., Flora 49: 211. 1866. Type species (designated here). *Trithyrocarpus paleatus* (Hassk.) Hassk. (≡ *Commelina paleata* Hassk.).
- Commelinopsis Pichon, Notul. Syst. (Paris) 12: 227. 1946. Type species. Commelinopsis persicariifolia (Delile) Pichon [= Commelina rufipes var. glabrata (D.R.Hunt) Faden & D.R.Hunt].
- Tapheocarpa Conran, Austral. Syst. Bot. 7: 585. 1994, **Syn. nov.** Type species. Tapheocarpa calandrinioides (F.Muell.) Conran [≡ Commelina calandrinioides (F.Muell.) M.Pell. & Faden].

Distribution and ecology. Cosmopolitan, but centered in Africa, found growing in a myriad of environments, especially dry, but seldom in forests.

Comments. Tapheocarpa was described to accommodate the peculiar A. calandrinioides, which clearly does not fit in Aneilema (Faden 1975, 1991). It was defined by its inflorescences reduced to a solitary flower, echinate, indehiscent, and geocarpic fruits (Conran 1994). At the time of the description of the genus, its antherodes were misinterpreted as 2-lobed, but a careful dissection of flowers in herbarium specimens show the presence of X-shaped antherodes, which can appear 2-lobed when folded in half during pressing and drying of specimens. This character alone would be enough to safely place Tapheocarpa in Commelina. On the light of antherode morphology and phylogenetic placement, the inflorescence of Tapheocarpa can be easily reinterpreted as an extreme reduction of the Commelina-type inflorescence, which is already greatly reduced on its own merit. The

inflorescences of typical *Commelina* already lack a developed main axis, cincinni bracts, with bracteoles generally so minute they are virtually invisible to the naked eye. Thus, the inflorescence of *Tapheocarpa* would only need to lose its basal bract, abort the upper cincinnus (which is commonly observed in several species of *Commelina*), and have the lower cincinnus reduced to become 1-flowered (also not uncommon in *Commelina*). Finally, inflorescences of *Commelina* are always leaf-opposed, even when they appear terminal (e.g., *C. erecta* L.). This can only be confirmed by dissecting the apex of the flowering branches, or if they posteriorly elongate, revealing such a pattern. Nonetheless, as it happens with several species of *Commelina* with apparently terminal inflorescences, that flowering branch does not continue its growth after flowering (Panigo et al. 2011). Based on morphological evidence, *C. calandrinioides* seems to be closely related to other aquatic Australian species with floating stems, linear and succulent leaves, reduced spathes, aborted upper cincinni, 1–few-flowered lower cincinni, and very broad and subequal petals (e.g., *C. agrostophylla* F.Muell.; Fig 11R).

Infrageneric classification. Commelina was divided by Clarke (1881) in two subgenera: (1) Commelina subg. Commelina (erroneously named C. subg. Didymoon), characterized by ventral locules of the ovary 2-ovullate; and (2) C. subg. Monoon, characterized by ventral locules 1-ovullate. Furthermore, each subgenus was subdivided into three sections each: (1) Commelina subg. Commelina- C. sect. Eucommelina (nom. illeg.), C. sect. Commelina (erroneously named C. sect. Heterocarpus), and C. sect. Disecocarpus; and (2) C. subg. Monoon- C. sect. Trithyrocarpus, C. sect. Heteropyxis, and C. sect. Spathodithyros. Nonetheless, Burns et al. (2011) have already evidenced the two subgenera to be non-monophyletic, while the independent sections have not been tested. Ongoing phylogenetic studies in Commelina have recovered some medium- to well-supported clades, but in a mostly unresolved backbone (Faden et al., unpubl. data). Thus, we refrain from accepting any formal infrageneric classification for Commelina at this moment, pending further phylogenetic studies combining molecular and morphological data.

Accepted species. A total of 198 species, but with several undescribed worldwide: Commelina acutispatha De Wild., C. acutissima Urb., C. africana L., C. agrostophylla F.Muell., C. albescens Hassk., C. albiflora Faden, C. amplexicaulis Hassk., C. andamanica S.M.Joseph & Nampy, C. appendiculata C.B.Clarke, C. arenicola Faden, C. ascendens J.K.Morton, C. aspera G.Don ex Benth., C. attenuata J.Koenig ex Vahl, C. aurantiiflora Faden & Raynsf., C. auriculata Blume, C. avenifolia J.Graham, C. bambusifolia Matuda, C. barbata Lam., C. beccariana Martelli, C. bella Oberm., C. benghalensis L., C. bequaertii De Wild., C. boissieriana C.B.Clarke, C. bracteosa Hassk., C. bravoa Matuda, C. calandrinioides (F.Muell.) M.Pell. & Faden, C. cameroonensis J.K.Morton, C. capitata Benth., C. caroliniana Walter, C. catharinensis Hassemer et al., C. chamissonis Klotzsch ex C.B.Clarke, C. chayaensis Faden, C. ciliata Stanley, C. clarkeana K.Schum., C. clavata C.B.Clarke, C. clavatoides Nampy & S.M.Joseph, C. communis L., C. congesta C.B.Clarke, C. congestipantha López-Ferr. et al., C. corbisieri De Wild., C. corradii Chiov. ex Chiarugi, C. crassicaulis C.B.Clarke, C. cufodontii Chiov., C. cyanea R.Br., C. dammeriana K.Schum., C. dekindtiana Fritsch, C. demissa C.B.Clarke, C. dianthifolia Redouté, C. dielsii Herter, C. diffusa Burm.f., C. disperma Faden, C. droogmansiana De Wild., C. eckloniana Kunth, C. efoveolalta (C.B.Clarke) M.Pell., C. elliptica Kunth, C. ensifolia R.Br., C. erecta L., C. fluviatilis Brenan, C. foliacea Chiov., C. forskaolii Vahl, C. frutescens Faden, C. gambiae C.B.Clarke, C. gelatinosa Edgew., C. geniculata Desv., C. giorgii De Wild., C. gourmaensis A.Chev., C. grandis Brenan, C. grossa C.B.Clarke, C. haitiensis Urb. & Ekman, C. heterosperma Blatt. & Hallb., C. hirsuta (Wight) Bedd., C. hispida Ruiz & Pav., C. hockii De Wild., C. holubii C.B.Clarke, C. homblei De Wild., C. huillensis Welw. ex C.B.Clarke, C.

humblotii H.Perrier, C. huntii M.Pell., C. imberbis Ehrenb. ex Hassk., C. indehiscens E.Barnes, C. irumuensis De Wild., C. jaliscana Matuda, C. jamesonii C.B.Clarke, C. kapiriensis De Wild., C. kilanga De Wild., C. kisantuensis De Wild., C. kitaleensis Faden, C. kituloensis Faden, C. kotschyi Hassk., C. lanceolata R.Br., C. latifolia Hochst. ex A.Rich., C. leiocarpa Benth., C. longicapsa C.B.Clarke, C. longicaulis Jacq., C. longifolia Lam., C. loureiroi Kunth, C. lukei Faden, C. lukonzolwensis De Wild., C. luteiflora De Wild., C. luzonensis Elmer, C. macrospatha Gilg & Ledermann ex Mildbr., C. macrosperma J.K.Morton, C. maculata Edgew., C. madagascarica C.B.Clarke, C. major H.Perrier, C. martyrum H.Lév., C. mascarenica C.B.Clarke, C. melanorrhiza Faden, C. membranacea Robyns, C. mensensis Schweinf., C. merkeri K.Schum., C. microspatha K.Schum., C. milneredheadii Faden, C. modesta Oberm., C. montigena H.Perrier, C. mwatayamvoana P.A.Duvign. & Dewit, C. neurophylla C.B.Clarke, C. nigritana Benth., C. nivea López-Ferr. et al., C. nyasensis C.B.Clarke, C. obliqua Vahl, C. oligotricha Miq., C. orchidophylla Faden & Layton, C. paleata Hassk., C. pallida Willd., C. pallidispatha Faden, C. paludosa Blume, C. petersii Hassk., C. phaeochaeta Chiov., C. platyphylla Klotzsch ex Seub., C. polhillii Faden & M.H.Alford, C. pseudopurpurea Faden, C. pseudoscaposa De Wild., C. purpurea C.B.Clarke, C. pycnospatha Brenan, C. pynaertii De Wild., C. quarrei De Wild., C. queretarensis López-Ferr. et al., C. quitensis Benth., C. ramosissima López-Ferr. et al., C. ramulosa (C.B.Clarke) H.Perrier, C. reflexa Rusby, C. reptans Brenan, C. reticulata Stanley, C. reygaertii De Wild., C. rhodesica Norl., C. robusta Kunth, C. robynsii De Wild., C. roensis M.D.Barrett & R.L.Barrett, C. rogersii Burtt Davy, C. rosulata Faden & Layton, C. ruandensis De Wild., C. rufipes Seub., C. rupicola Font Ouer ex Emb. & Maire, C. rzedowskii López-Ferr. et al., C. saxatilis H.Perrier, C. saxosa De Wild., C. scabra Benth., C. scandens Welw. ex C.B.Clarke, C. scaposa C.B.Clarke ex De Wild. & T.Durand, C. schinzii C.B.Clarke, C. schliebenii Mildbr., C. schweinfurthii C.B.Clarke, C. shinsendaensis De Wild., C. sikkimensis C.B.Clarke, C. socorrogonzaleziae Espejo & López-Ferr., C. somalensis Chiov., C. spectabilis C.B.Clarke, C. sphaerorrhizoma Faden & Layton, C. standleyi Steyerm., C. stefaniniana Chiov., C. subcucullata C.B.Clarke, C. subscabrifolia De Wild., C. subulata Roth, C. suffruticosa Blume, C. sulcatisperma Faden, C. sylvatica De Wild., C. texcocana Matuda, C. trachysperma Chiov., C. transversifolia De Wild., C. triangulispatha Mildbr., C. tricarinata Stanley, C. tricolor E.Barnes, C. trilobosperma K.Schum., C. tuberosa L., C. umbellata Schumach. & Thonn., C. undulata R.Br., C. ussilensis Schweinf., C. velutina Mildbr., C. vermoesenii De Wild., C. virginica L., C. welwitschii C.B.Clarke, C. wightii Raizada, C. zambesica C.B.Clarke, C. zanzibarica (Faden) M.Pell., C. zenkeri C.B.Clarke, C. zeylanica Falkenb., and C. zigzag P.A.Duvign. & Dewit.

New combinations. Commelina calandrinioides (F.Muell.) M.Pell. & Faden, **comb. nov.** ≡ Aneilema calandrinioides F.Muell., Fragm. 9: 191. 1875 ≡ Tapheocarpa calandrinioides (F.Muell.) Conran, Austral. Syst. Bot. 9: 659. 1996.

Commelina efoveolalta (C.B.Clarke) M.Pell., **comb. nov.** ≡ Phaeosphaerion efoveolaltum C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 136. 1881.

Commelina zanzibarica (Faden) M.Pell., **stat. nov.** ≡ *Commelina africana* subsp. *zanzibarica* Faden, Fl. Trop. E. Africa Commelinaceae: 148. 2012.

1.3.2. Tribe Tradescantieae Meisn., Pl. Vasc. Gen.: Tab. Diagn. 406. 1842. Type genus. *Tradescantia* L. emend M.Pell.

Figs 12 & 13

Dichorisandreae Dumort., Anal. Fam. Pl.: 55. 1829. Type genus. *Dichorisandra* J.C.Mikan, nom. cons.

Callisieae Pichon, Notul. Syst. (Paris) 12: 236. 1946. Type genus. Callisia Loefl.

Cyanoteae Pichon, Notul. Syst. (Paris) 12: 242. 1946. Type genus. *Cyanotis* D.Don, nom. cons.

Geogenantheae Pichon, Notul. Syst. (Paris) 12: 240. 1946. Type genus. *Geogenanthus* Ule. Zebrineae Small, Man. S.E. Fl.: 259. 1933. Type genus. *Zebrina* Schnizl.

Zebrineae Pichon in Notul. Syst. (Paris) 12: 241. 1946, isonym. Type genus. Zebrina Schnizl.

Distribution. Mainly Neotropical and centered in Central and North America, but with two subtribes exclusively Paleotropical.

Comments. The tribe Tradescantieae sensu Faden and Hunt (1991) was circumscribed in opposition to tribe Commelineae, following the principle that if one of the groups was monophyletic, then the other one must also be. This has resulted in the obvious paraphyly of Tradescantieae, due to the position of Palisota, and the complete lack of a single synapomorphy. In the present study, we have recovered the basal leaf with reduced blades or modified into bladeless sheaths, leaf epidermis with domed cells, and the presence of floral moniliform hairs as exclusive synapomorphies. The hairs of Palisota (now, subfamily Palisotoideae) and Murdannia (tribe Commelineae, subtribe Murdanniinae) were previously misinterpreted as being moniliform, when they are composed of dumbbell-shaped cells, instead of globose or ellipsoid cells. Differently, from Commelineae, Tradescantieae was readily divided by Faden and Hunt (1991) into seven subtribes. Nonetheless, Palisotinae is here excluded from Tradescantieae, Dichorisandrinae is paraphyletic, Cyanotinae is nested Thyrsantheminae made Coleotrypinae, and Tradescantiinae paraphyletic. Thyrsantheminae was synonymized under Tradescantiinae by Pellegrini (2017). The paraphyly of Dichorisandrinae was addressed by Faden and Pellegrini (2017), which suggested the recognition of a new subtribe to accommodate the Amazonian members of the subtribe, but no formal proposition was made. Finally, Coleotrypinae sensu Faden and Hunt (1991) lacked any kind of synapomorphy, which is supported both by morphological and molecular data. Thus, the needed changes are implemented here, with the description of the new subtribe Cochliostematinae, and the expansion of Cyanotinae to include Coleotrypinae.

Key to the subtribes of Tradescantieae

- 1. Leaf blades commonly with posterior divisions; bracteoles absent; floral buds obpyriform, flowers of the lower 1–2 cincinni hermaphrodite, remaining cincinni with staminate flowers, petals covered in bud by a mucilage layer, narrower than the sepals... **Streptoliriinae Faden & D.R.Hunt (Fig 12A–C)**
- Leaf blades lacking posterior divisions; bracteoles present; floral buds ovoid to ellipsoid or fusiform or oblongoid, rarely obovoid, flowers all hermaphrodite or staminate, rarely pistillate flowers randomly distributed, petals covered in bud by an epicuticular layer of wax, as broad or broader than the sepals... 2
- 2. Pedicels reflexed at pre-anthesis, petals with margins bearded with moniliform hairs, epicuticular wax layer smooth, anther sacs strongly curved to spirally-coiled... Cochliostematinae M.Pell. & Faden (Fig 12D-F)
- Pedicels erect or patent at pre-anthesis, petals with margins glabrous, rarely ciliate with non-moniliform hairs, epicuticular wax layer striate, anther sacs round or elliptic to reniform or oblong to linear, when C-shaped anther sacs not appressed to each other... 3
- 3. Leaf epidermis lacking silica crystals in specialized cells; pedicels and filaments stout, petals generally with basal third with a white band, anther walls with more than 2 layers at

- maturity, endothecium spirally thickened; seeds biseriate to partially biseriate... **Dichorisandrinae Faden & D.R.Hunt (Fig 12G-N)**
- Leaf epidermis generally with silica crystals in specialized cells; pedicels and filaments slender, petals lacking a white band, anther walls 2-layered at maturity, endothecium basally thickened; seeds uniseriate... 4
- 4. Basal bract bracteose and bicarinate and bidentate, bracteoles herbaceous, leaf-like and equal to the cincinni bracts, not tightly imbricate; sepals with opaque margins... Cyanotinae Faden & D.R.Hunt (Fig 120–T)
- Basal bract leaf-like or spathaceous or tubular and hyaline, if bracteose not bicarinate and bidentate, bracteoles membranous or chartaceous, distinct from the cincinni bracts, tightly imbricate; sepals with hyaline margins... Tradescantiinae Rohw. (Fig 13)
- **1.3.2.1. Subtribe Streptoliriinae Faden & D.R.Hunt**, Taxon 40: 25. 1991. Type genus. *Streptolirion* Edgew.

Fig 12A-C

Distribution. Asia, reaching the Malay Archipelago.

Comments. Subtribe Streptoliriinae was circumscribed by Faden and Hunt (1991) as comprising scandent plants in which the lower 1–2 cincinni of the inflorescence were subtended by a spathaceous bracts. Nonetheless, the authors failed to notice the absence of bracteoles, obpyriform floral buds, inflorescence with flowers of the lower 1–2 cincinni hermaphrodite, while the remaining cincinni produced only staminate flowers, and petals linear to oblong, much narrower than the sepals. Faden and Hunt (1991) also misinterpreted the sepals as being petaloid, due to they sometimes being brightly-colored. Nonetheless, they are obviously distinct from the petals, presenting a distinct consistency of that of the true petals. Thus they are reinterpreted by us as being sepaloid.

Key to the genera of Streptoliriinae

- 1. Leaf blades lacking posterior divisions; inflorescences leaf-opposed, basal 1(-2) cincinni subtended by spathaceous bracts, remaining ones ebracteate... *Spatholirion* Ridl. (Fig 12A)
- Leaf blades with posterior divisions; inflorescences axillary, basal 1(-2) cincinni subtended by spathaceous bracts, remaining ones subtended by bracteose cincinni bracts... 2
- 2. Pedicels pendulous at post-anthesis and in fruit, stamens 3–5, when 5 unequal, connectives inconspicuous; capsules linear; seeds winged, exarillate... *Aëtheolirion* Forman (Fig 12B)
- Pedicels upright to erect at post-anthesis and in fruit, stamens 6, equal, connectives expanded; capsules ovoid or ellipsoid to oblongoid; seeds not winged, arillate...
 Streptolirion Edgew. (Fig 12C)
- **1.3.2.1.1.** *Spatholirion* **Ridl.**, J. Bot. 34: 329. 1896. Type species. *Spatholirion ornatum* Ridl. Fig 12A

Distribution and ecology. From Thailand to China, reaching the Malay Archipelago, and found growing in the understory of rainforests.

Comments. Spatholirion is the largest genus of Streptoliriinae, with ca. 10 species that can range from vines to trailing plants or rosette herbs. The genus is in much need of a taxonomic revision, especially of an identification key. This study presents the first phylogenetic hypothesis for the genus, where we show that the rosette and prostrate species form a basal grade in the genus. Nonetheless, further and more refined phylogenetic studies are necessary for the genus and subtribe Streptoliriinae for us to better understand the evolution of growth form in this group.

Accepted species. A total of six accepted species, and at least two still undescribed: *Spatholirion calcicola* K.Larsen & S.S.Larsen, *S. decumbens* Fukuoka & N.Kurosaki, *S. elegans* (Cherfils) C.Y.Wu, *S. longifolium* (Gagnep.) Dunn, *S. ornatum* Ridl., and *S. puluongense* Aver.

1.3.2.1.2. Aëtheolirion Forman, Kew Bull. 16: 209. 1962. Type species. Aëtheolirion stenolobium Forman. Fig 12B

Distribution and ecology. Endemic to Thailand and found growing in the understory of rainforests.

Comments. Aëtheolirion is a monospecific genus characterized by its dimorphic flowers, in which the hermaphrodite flowers have 3 stamens, while the staminate have 5 stamens, linear capsules, and winged seeds.

Accepted species. Aëtheolirion stenolobium Forman.

1.3.2.1.3. *Streptolirion* **Edgew.**, Proc. Linn. Soc. Lond. 1: 254. 1845. Type species. *Streptolirion volubile* Edgew. Fig 12C

Distribution and ecology. Japan to the Himalayas and Indo-China, found growing in the understory of rainforests.

Comments. Despite its reduced size, *Streptolirion* needs a taxonomic revision since the taxonomic status of most of its species has historically been questioned. Based on the specimens seen during the development of this study, the reestablishment of *S. lineare* is needed, together with a new combination.

Accepted species. A total of three species: *Streptolirion khasianum* (C.B.Clarke) M.Pell., *S. lineare* Fukuoka & N.Kurosaki, and *S. volubile* Edgew.

New combination. *Streptolirion khasianum* (C.B.Clarke) M.Pell., **stat. nov.** ≡ *Streptolirion volubile* var. *khasianum* C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 262. 1881 ≡ *Streptolirion volubile* subsp. *khasianum* (C.B.Clarke) D.Y.Hong, Acta Phytotax. Sin. 12(4): 463. 1974.

1.3.2.2. Subtribe Cochliostematinae M.Pell. & Faden, comb. et stat. nov. Fig 12D–F

Cochliostemateae Pichon, Notul. Syst. (Paris) 12: 240. 1946. Type genus. Cochliostema Lem.

Distribution. Central and Northern South America.

Comments. As stated by Pellegrini and Faden (2017), the need to recircumscribe subtribe Dichorisandrinae and to recognize an independent subtribe for the genera allied to *Cochliostema* is pressing. Aside from chromosome morphology, no macro- or micromorphological synapomorphies are known for Dichorisandrinae *sensu* Faden and Hunt (1991). On the other hand, both lineages are morphologically well-circumscribed and thus more easily recognizable.

Key to the genera of Cochliostematinae

- 1. Dracaenoid herbs; roots with terminal tubers; shoots determinate; inflorescences borne at the lower nodes below the leaves; pedicel with glandular hairs, stamens 5–6, all fertile, stigmas never fringed with moniliform hairs... *Geogenanthus* Ule (Fig 12D)
- Rosette herbs; roots without terminal tubers; shoots indeterminate; inflorescences borne among the leaves; pedicels with eglandular hairs, fertile stamens 3, on the upper half of the flower, staminodes 3 (sometimes microscopic), on the lower half of the flower, stigmas commonly marginally fringed with moniliform hairs... 2
- 2. Tank-forming or creeping rosettes, epiphytes, rarely terrestrial; inflorescence a many-branched thyrse, with alternate or verticillate cincinni, cincinni bracts showy; fertile anthers spirally-coiled, hidden within a hood-like structure; testa smooth, sticky when hydrated... *Cochliostema* Lem. (Fig 12E)
- Rosettes not tank-forming, terrestrial; inflorescence reduced to a solitary pedunculate cincinnus, cincinnus bract inconspicuous; fertile anthers semicircular, not hidden within a hood-like structure; testa rugose to foveolate, farinose... *Plowmanianthus* Faden & C.R.Hardy (Fig 12F)
- **1.3.2.2.1.** *Geogenanthus* **Ule**, Repert. Spec. Nov. Regni Veg. 11: 524. 1913. Type species. *Geogenanthus wittianus* (Ule) Ule [= *Geogenanthus poeppigii* (Miq.) Faden.]. Fig 12D
- Chamaeanthus Ule, Verh. Bot. Vereins Prov. Brandenburg 50: 71. 1908, nom. illeg., non Chamaeanthus Schltr. ex J.J.Sm. Type species. Chamaeanthus wittianus Ule [= Geogenanthus poeppigii (Miq.) Faden.].
- *Uleopsis* Fedde, Just's Bot. Jahresber. 37(2): 77. 1911, nom. superfl. Type species. *Uleopsis* wittianus (Ule) Fedde [= Geogenanthus poeppigii (Miq.) Faden.].

Distribution and ecology. From Central to northern South America. It can be found growing understory in rainforests.

Comments. Geogenanthus has rarely been confused with other genera in the family, except for *Dichorisandra*. Nonetheless, its floral morphology differs greatly from the latter, and their similarity can be resumed to maculated leaves and basal inflorescences, found only in few species of *Dichorisandra*. A taxonomic revision with the description of the three new species is in the works (Hardy and Faden, in prep.).

Accepted species. A total of six species, three of them still undescribed (Hardy and Faden, pers. comm.): *Geogenanthus ciliatus* G.Brückn., *G. poeppigii* (Miq.) Faden, and *G. rhizanthus* (Ule) G.Brückn.

1.3.2.2.2. *Cochliostema* **Lem.**, Ill. Hort. 6: Misc. 70. 1859. Type species. *Cochliostema odoratissimum* Lem. Fig 12E

Distribution and ecology. From Nicaragua to Colombia and Ecuador. It grows growing in the understory of rainforests.

Comments. Cochliostema is a morphologically isolated genus, with a unique floral morphology. The hood-like structure that encloses the three corkscrew-shaped anthers makes them functionally poricidal, which coupled with moniliform hairs in the petals and androecium, and strongly scented flowers seem to suggest pollination by big orchid bees. But as most of the Commelinaceae, reproductive studies are scarce. A yet unpublished taxonomic revision of *Cochliostema* was done by Hardy (2001).

Accepted species. A total of two species: *Cochliostema odoratissimum* Lem. and *C. velutinum* Read.

1.3.2.2.3. *Plowmanianthus* Faden & C.R.Hardy in Hardy & Faden, Syst. Bot. 29(2): 316–318. 2004. Type species. *Plowmanianthus perforans* Faden & C.R.Hardy. Fig 12F

Distribution and ecology. Panama to Peru, Colombia, Ecuador and Northern Brazil, found growing in the understory of rainforests.

Comments. *Plowmanianthus* was recently described by Hardy and Faden (2004), based on extensive studies on micro- and macromorphological characters, added to a still unpublished combined phylogeny (Hardy 2001).

Accepted species. A total of six species: *Plowmanianthus dressleri* Faden & C.R.Hardy, *P. grandifolius* Faden & C.R.Hardy, *P. panamensis* Faden & C.R.Hardy, *P. perforans* Faden & C.R.Hardy, *P. peruvianus* C.R.Hardy & Faden, and *P. robustus* (C.R.Hardy & Faden) M.Pell.

New combination. *Plowmanianthus robustus* (C.R.Hardy & Faden) M.Pell., **stat. nov.** ≡ *Plowmanianthus grandifolius* subsp. *robustus* C.R.Hardy & Faden, Syst. Bot. 29(2): 323–324, f. 4C–D, 6B,D–F, 11B, 12E. 2004.

1.3.2.3. Dichorisandrinae Faden & D.R.Hunt, Taxon 40: 25. 1991. Type genus. *Dichorisandra* J.C.Mikan, nom. cons. Fig 12G–N

Distribution. Neotropical (from Mexico to Argentina), but centered in eastern Brazil.

Comments. With the recognition of subtribe Cochliostematinae, Dichorisandrinae becomes a morphologically cohesive and consistently monophyletic group. A good overview

of the subtribe is given by Pellegrini and Faden (2017), where they recircumscribe and revise *Siderasis*. The two accepted genera, *Dichorisandra* and *Siderasis*, can be easily differentiated based on androecium and gynoecium characters.

Key to the genera of Dichorisandrinae

- 2. Stamens 5–6, staminodes sometimes present; anthers basifixed, anthers sacs parallel, elongate, 3 to 4 times longer than the filaments, connectives inconspicuous, dehiscence poricidal or introrsely rimose, but functionally poricidal; stigmatic papillae multicellular, completely concealing the stylar canal... *Dichorisandra* J.C.Mikan (Fig 12G–L)
- Stamens 6, staminodes absent; anthers dorsifixed, anther sacs divergent, semicircular, 3 to 4 times shorter than the filaments, connectives expanded, dehiscence extrorsely rimose; stigmatic papillae unicellular, restricted to margins of the stigma and leaving the stylar canal evident... *Siderasis* Raf. emend. M.Pell. & Faden (Fig 12M & N)
- **1.3.2.3.1.** *Dichorisandra* **J.C.Mikan,** Del. Fl. Faun. Bras.: pl. 3. 1820. Type species. *Dichorisandra thyrsiflora* J.C.Mikan Fig 12G–L
- Stickmannia Necker ex A.H.L.Jussieu, Dict. Sci. Nat. (ed. 2) 51: 1. 1827. Type species. Stickmannia hexandra (Aubl.) Kuntze [≡ Dichorisandra hexandra (Aubl.) C.B.Clarke].
- Petaloxis Raf., Fl. Tellur. 2: 83. 1836[1837]. Type species. Petaloxis purpurea Raf., nom. superfl. (≡ Dichorisandra oxypetala Hook.).

Distribution and ecology. Mexico to Argentina, but centered in the Atlantic Forest of coastal Brazil, and generally found growing in the understory of rainforests, but sometimes also found growing in rocky outcrops.

Comments. Dichorisandra is one of the largest genera in the family, with most of the species being endemic to Brazil. The genus was revised by Aona (2008) on a yet unpublished taxonomic revision, which recognizes ca. 30 new species. The present study provides the first phylogenetic hypothesis for the genus, where the clades recovered by us are equivalent to morphological groups proposed by Pellegrini and Faden (2017). Nonetheless, not all groups were sampled by us and some were represented by a sole species. Thus, their monophyly could not be properly tested.

Infrageneric classification. No infrageneric was ever proposed for *Dichorisandra*. Despite the congruence of our topology to the morphological groups proposed by Pellegrini and Faden (2017), we refrain from recognizing any sections or subgenera, since our sampling is far from optimal in this large and complex genus. Future studies sampling a greater number of taxa might shed some light on the internal relationships in *Dichorisandra* and allow the proposition of a much-needed classification system for the genus.

Accepted species. A total of 49 accepted species, but with several still undescribed (ca. 70 species): Dichorisandra acaulis Cogn., D. albomarginata Linden ex Regel, D. amabilis J.R.Grant, D. bahiensis Aona & M.C.E.Amaral, D. bonitana Philipson, D. conglomerata Aona & M.C.E.Amaral, D. densiflora Ule, D. diederichsanae Steyerm., D. fluminensis Brade, D. gaudichaudiana Kunth, D. glabrescens (Seub.) Aona & M.C.E.Amaral, D. glaziovii Taub., D. hexandra (Aubl.) C.B.Clarke, D. hirtella Mart., D. incurva Mart., D. interrupta Mart., D. jardimii Aona & M.C.E.Amaral, D. leonii Aona & M.C.E.Amaral, D. leucophthalmos Hook.,

- D. leucosepala Aona & M.C.E.Amaral, D. marantoides Aona & Faden, D. micans C.B.Clarke, D. mosaica Linden ex K.Koch, D. nana Aona & M.C.E.Amaral, D. neglecta Brade, D. nutabilis Aona & M.C.E.Amaral, D. odorata Aona & M.C.E.Amaral, D. ordinatiflora Aona & Faden, D. oxypetala Hook., D. paranaënsis D.Maia et al., D. penduliflora Kunth., D. perforans C.B.Clarke, D. picta Lodd., D. procera Mart., D. puberula Nees & Mart., D. pubescens Mart., D. radicalis Nees & Mart., D. reginae (L.Linden & Rodigas) H.E.Moore, D. rupicola Aona & M.C.E.Amaral, D. sagittata Aona & M.C.E.Amaral, D. saundersii Hook.f., D. saxatilis Aona & M.C.E.Amaral, D. subtilis Aona & M.C.E.Amaral, D. tejucensis Mart. D. thyrsiflora J.C.Mikan, D. ulei J.F.Macbr., D. variegata Aona & Faden, D. velutina Aona & M.C.E.Amaral, and D. villosula Mart.
- **1.3.2.3.2.** *Siderasis* **Raf.**, Fl. Tellur. 3: 67. 1837, **emend. M.Pell. & Faden**, PhytoKeys 83: 6. 2017. Type species. *Siderasis acaulis* Raf. [≡ *S. fuscata* (Lodd.) H.E.Moore]. Fig 12M & N
- *Pyrrheima* Hassk., Flora 52: 366. 1869, nom. illeg. Type species. *Pyrrheima loddigesii* Hassk., nom. illeg. [≡ *S. fuscata* (Lodd.) H.E.Moore].

Distribution and ecology. Endemic to coastal Brazil, found growing in the understory of the Atlantic Rainforest.

Comments. Siderasis was recently revised by Pellegrini and Faden (2017), who recognized six species, four of them were new. Despite its small size, Siderasis presents considerable diversity in growth forms and floral morphology.

Accepted species. A total of six species: *Siderasis albofasciata* M.Pell., *S. almeidae* M.Pell. & Faden, *S. fuscata* (Lodd.) H.E.Moore, *S. medusoides* M.Pell. & Faden, *S. spectabilis* M.Pell. & Faden, and *S. zorzanellii* M.Pell. & Faden.

1.3.2.4. Subtribe Cyanotinae Faden & D.R.Hunt, Taxon 40: 24. 1991. Type genus. *Cyanotis* D.Don, nom. cons. Fig 12O–T

Coleotrypinae Faden & D.R.Hunt, Taxon 40: 25. 1991, **Syn. nov.** Type genus. *Coleotrype* C.B.Clarke.

Distribution. Paleotropical, from Africa to Asia, but centered in Asia.

Comments. Subtribe Coleotrypinae is here treated as a synonym of Cyanotinae, due to it being inconsistently recovered as monophyletic, and when recovered as monophyletic with low statistical support and no morphological synapomorphy. Alternatively, Cyanotinae s.lat. is consistently monophyletic, with high statistical support, and supported by at least two unambiguous synapomorphies.

Key to the genera of Cyanotinae

1. Flowers large, corolla hypocrateriform, filaments epipetalous, stigmatic papillae longer than 1µm; capsules ca. as long as the persistent sepals, ejaculatory, with aril retained during expulsion of the seeds... *Coleotrype* C.B.Clarke (Fig 12O & P)

- Flowers diminute, corolla infundibuliform, filaments free, stigmatic papillae equal or shorter than $0.5\mu m$; capsules shorter than the persistent sepals, not mechanically releasing the seeds... 2
- 2. Leaves membranous or chartaceous, rarely coriaceous, hairs acicular, epidermis with specialized cells silica crystals deep and wedged between regular epidermal cells; inflorescences perforating the leaf sheaths, secondary branches dichasial; filaments and style not inflated, anthers rimose or poricidal, if poricidal pores apical, ovules hemianatropous; seeds arillate, aril orange, embryotega semidorsal... *Amischotolype* Hassk. (Fig 12Q & R)
- Leaves crass, hairs flagelliform, epidermis with specialized cells silica crystals enlarged; inflorescences never perforating the leaf sheaths, secondary branches monochasial; filaments and style generally apically inflated, anthers rimose or poricidal, when poricidal pores basal, ovules campylotropous; seeds exarillate, embryotega apical... *Cyanotis* D.Don (Fig 12S & T)
- **1.3.2.4.1.** *Coleotrype* **C.B.Clarke** in Candolle & Candolle, Monogr. Phan. 3: 120, 238. 1881. Type species. *Coleotrype natalensis* C.B.Clarke. Fig 12O & P

Distribution and ecology. Continental Africa and Madagascar. It can be found growing in the understory of rainforests.

Comments. Coleotrype is in desperate need of a taxonomic revision, since species identification is very complicated, especially using herbarium specimens, and several specimens don't fit perfectly to any of the available names. Furthermore, morphological (Pellegrini, pers. observ.) and molecular evidence (Faden and Wurdack, unpublish. data) seem to indicate the non-monophyly of the genus. Floral morphology is extremally variable between the three species groups, with petals ranging from all equal to the medial strongly differentiated, the stamens might be free from each other to connate, filaments might be glabrous or barbate, a hood-like structure involving the anthers (somewhat similar to the one found in Cochliostema) might be present or not, connectives might be expanded or not, and anthers range from rimose to poricidal. Further studies focusing on the group are necessary to elucidate this situation.

Accepted species. A total of 10 species: *Coleotrype baronii* Baker, *C. brueckneriana* Mildbr., *C. goudotii* C.B.Clarke, *C. laurentii* K.Schum., *C. lutea* H.Perrier, *C. madagascarica* C.B.Clarke, *C. natalensis* C.B.Clarke, *C. synanthera* H.Perrier, *C. udzungwaensis* Faden & Layton, and *C. vermigera* H.Perrier.

1.3.2.4.2. *Amischotolype* **Hassk.**, Flora 46: 391. 1863. Type species. *Amischotolype glabrata* Hassk.

Fig 12Q & R

- Forrestia A.Rich., Voy. Astrolabe 2: 1. 1834, nom. illeg., non Forrestia Raf. Type species. Forrestia hispida A.Rich. [≡ Amischotolype hispida (A.Rich.) D.Y.Hong].
- *Porandra* D.Y.Hong, Acta Phytotax. Sin. 12(4): 462, f. 1–8. 1974, **Syn. nov.** Type species. *Porandra ramosa* D.Y.Hong [≡ *Amischotolype ramosa* (D.Y.Hong) M.Pell.].

Distribution and ecology. Disjunctive between western tropical continental Africa, tropical and subtropical Asia. It grows in the understory of rainforests.

Comments. As stated by Duistermaat (2012), the boundaries between *Amischotolype* and *Porandra* are blurred by the recognition of species of *Amischotolype* with scandent habit and/or poricidal anthers. This is supported by our analysis, in which the three species of *Porandra* are nested within *Amischotolype* s.lat.

Accepted species. A total of accepted 26 species, but with some yet undescribed species: Amischotolype barbarossa Duist., A. divaricata Duist., A. dolichandra Duist., A. glabrata Hassk., A. gracilis (Ridl.) I.M.Turner, A. griffithii (C.B.Clarke) I.M.Turner, A. hirsuta (Hallier f.) Duist., A. hispida (A.Rich.) D.Y.Hong, A. hookeri (Hassk.) H.Hara, A. irritans (Ridl.) I.M.Turner, A. laxiflora (Merr.) Faden, A. leiocarpa (Hallier f.) Duist., A. lobata Duist., A. marginata (Blume) Hassk., A. microphylla (Y.Wan) M.Pell., A. mollissima (Blume) Hassk., A. monosperma (C.B.Clarke) I.M.Turner, A. parvifructa Duist., A. pedicellata Duist., A. ramosa (D.Y.Hong) M.Pell., A. rostrata (Hassk.) Duist., A. scandens (D.Y.Hong) M.Pell., A. sphagnorrhiza Cowley, A. strigosa Duist., A. tenuis (C.B.Clarke) R.S.Rao, and A. welzeniana Duist.

New combinations. *Amischotolype microphylla* (Y.Wan) M.Pell., comb. nov. \equiv *Porandra microphylla* Y.Wan, Bull. Bot. Res., Harbin 6(4): 153–155, f. 1. 1986.

Amischotolype ramosa (D.Y.Hong) M.Pell., **comb. nov.** ≡ *Porandra ramosa* D.Y.Hong, Acta Phytotax. Sin. 12(4): 462, pl. 89, f. 1–5. 1974.

Amischotolype scandens (D.Y.Hong) M.Pell., **comb. nov.** ≡ *Porandra scandens* D.Y.Hong, Acta Phytotax. Sin. 12(4): 462–463, pl. 89, f. 6–8. 1974.

1.3.2.4.3. *Cyanotis* **D.Don**, Prodr. Fl. Nepal.: 45. 1825, nom. cons. Type species. *Cyanotis barbata* D.Don.

Fig 12S & T

- *Tonningia* Neck., Elem. Bot. 3: 165. 1790, nom. not validly publ., published in opera utiq. oppr.; Neck. ex A.Juss., Dict. Sci. Nat. (ed. 2) 54: 505. 1829. Type species (designated here). *Tonningia axillaris* (L.) Raf. [≡ *Cyanotis axillaris* (L.) D.Don *ex* Sweet].
- *Zygomenes* Salisb., Trans. Hort. Soc. London 1: 271. 1812. Type species. *Zygomenes axillaris* (L.) Salisb. [= *Cyanotis axillaris* (L.) D.Don ex Sweet].
- Etheosanthes Raf., Neogenyton 3. 1825, **Syn. nov.** Type species. Etheosanthes ciliata (Blume) Raf. [= Cyanotis ciliata (Blume) Bakh.f.,].
- Siphostigma Raf., Fl. Tellur. 2: 16. 1836[1837]. Type species. Siphostigma cristata (L.) Raf. [≡ Cyanotis cristata (L.) D.Don].
- Dalzellia Hassk., Flora 48: 593. 1865. Type species. Dalzellia vivipara (Dalzell) Hassk. (≡ Cyanotis vivipara Dalzell).
- Belosynapsis Hassk., Flora 54: 259. 1871. Type species. Belosynapsis kewensis Hassk. [= Cyanotis beddomei (Hook.f.) Erhardt et al.].

- *Erythrotis* Hook.f., Bot. Mag. 101: t. 6150. 1875. Type species. *Erythrotis beddomei* Hook.f. [≡ *Cyanotis beddomei* (Hook.f.) Erhardt et al.].
- *Cyanopogon* Welw. ex C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 240, 258. 1881, pro. syn.
- Amischophacelus R.S.Rao & Kammathy, J. Linn. Soc., Bot. 59(379): 305–306. 1966. Type species. Amischophacelus axillaris (L.) R.S.Rao & Kammathy [≡ Cyanotis axillaris (L.) D.Don ex Sweet].

Distribution and ecology. Africa (incl. Madagascar), Asia and Oceania. It can be found generally growing in open areas, but also in the understory of rainforests, in dry or flooded environments.

Comments. Historically, *Belosynapsis* and *Cyanotis* were differentiated by cincinni elongation, petal connation, inflation of the filaments, and anther dehiscence. Nonetheless, molecular and morphological studies have shown *Belosynapsis* to be nested within *Cyanotis*. The genus needs a taxonomic revision, uniting the information gathered in the past years by floristic treatments and other local studies. The evolution and morphology of underground and storage organs in *Cyanotis* seem to be of systematic and taxonomic interest and should be studied soon. Finally, seed testa ornamentation is traditionally used in the taxonomy of Commelinaceae. Nonetheless, the complexity of the ornamentation patters in *Cyanotis* has precluded its proper use. Thus, studies focusing on these patterns might shed some much-needed light in the taxonomy of this complex group.

Accepted species. A total of 58 species, but some still undescribed: Cyanotis adscendens Dalzell, C. ake-assii Brenan, C. angusta C.B.Clarke, C. arachnoidea C.B.Clarke, C. arcotensis R.S.Rao, C. axillaris (L.) D.Don ex Sweet, C. barbata D.Don., C. beddomei (Hook.f.) Erhardt et al., C. burmanniana Wight, C. caespitosa Kotschy & Peyr., C. ceylanica Hassk.. C. ciliata (Blume) Bakh.f., C. cormosa M.Pell., C. cristata (L.) D.Don, C. cucullata (Roth) Kunth, C. cupricola J.Duvign., C. dybowskii Hua, C. epiphytica Blatt., C. fasciculata (B.Heyne ex Roth) Schult. & Schult.f., C. flexuosa C.B.Clarke, C. foecunda DC. ex Hassk., C. ganganensis Schnell, C. gracilis (Schnell) M.Pell., C. grandidieri H.Perrier, C. hepperi Brenan, C. homblei De Wild., C. karliana Hassk. C. kawakamii Hayata, C. lanata Benth., C. lanceolata Wight, C. lapidosa E.Phillips, C. longifolia Benth., C. loureiroana (Schult. & Schult.f.) Merr., C. lourensis Schnell, C. madagascarica (C.B.Clarke) M.Pell., C. moluccana (Roxb.) Merr., C. nyctitropa Deflers, C. obtusa (Trimen) Trimen, C. pachyrrhiza Oberm., C. paludosa Brenan, C. papyracea M.Pell., C. pedunculata Merr., C. pilosa Schult. & Schult.f., C. polyrrhiza Hochst. ex Hassk., C. racemosa B.Heyne ex Hassk., C. repens Faden & D.M.Cameron, C. reutiana Beauverd, C. robusta Oberm., C. rupicola Schnell, C. scaberula Hutch., C. somaliensis C.B.Clarke, C. speciosa (L.f.) Hassk., C. thwaitesii Hassk., C. tuberosa (Roxb.) Schult. & Schult.f., C. uda (C.B.Clarke) M.Pell., C. vaga (Lour.) Schult. & Schult.f., C. villosa (Spreng.) Schult. & Schult.f., and C. vivipara Dalzell.

New combinations. Cyanotis cormosa M.Pell., nom. nov. ≡ Cyanotis paludosa subsp. bulbifera Faden, Fl. Trop. E. Africa Commelinaceae: 19. 2012, non Cyanotis bulbifera Hutch. Cyanotis gracilis (Schnell) M.Pell., stat. nov. ≡ Cyanotis longifolia var. gracilis (Schnell) Schnell, Bull. Inst. Fondam. Afrique Noire, Sér. A, Sci. Nat. 19: 733 1957 ≡ Cyanotis lanata var. gracilis Schnell, Rev. Gén. Bot. 57: 287 1950.

Cyanotis madagascarica (C.B.Clarke) M.Pell., **stat. nov.** ≡ Cyanotis nodiflora var. madagascarica C.B.Clarke Monogr. Phan. 3: 258. 1881 ≡ Cyanotis nodiflora subsp. madagascarica (C.B.Clarke) H.Perrier, Fl. Madagasc. 37: 35. 1938 ≡ Cyanotis speciosa subsp. madagascarica (C.B.Clarke) Faden, Kew Bulletin 62(1): 140. 2007.

Cyanotis papyracea M.Pell., **nom. nov.** \equiv Cyanotis speciosa subsp. bulbosa Faden, Fl. Trop. E. Africa Commelinaceae: 31. 2012, non Cyanotis ulbosa H.Lév.

Cyanotis uda (C.B.Clarke) M.Pell., **stat. nov.** ≡ *Cyanotis somaliensis* var. *uda* C.B.Clarke, Ann. Mus. Congo Belge, Bot. sér. 1, V, 1: 223. 1906.

1.3.2.5. Subtribe Tradescantiinae Rohw., Abh. Auslandsk. 61, Reihe C, Naturwiss. 18: 144. 1956. Type genus. *Tradescantia* L. emend. M.Pell. Fig 13

Thyrsantheminae D.R.Hunt ex Faden & D.R.Hunt, Taxon 40: 23. 1991. Type genus. *Thyrsanthemum* Pichon.

Distribution. Tropical and subtropical New World, from Canada and USA to Argentina.

Comments. Subtribe Tradescantiinae was recently expanded to include the polyphyletic subtribe Thyrsantheminae (Pellegrini 2017). Prior to this expansion, both subtribes were consistently recovered as non-monophyletic (Bergamo 2003; Evans et al. 2003; Wade et al. 2006; Burns et al. 2011; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini 2017), but with both of them combined, Tradescantiinae *sensu* Pellegrini (2017) is finally rendered monophyletic. In its current sense, Tradescantiinae is the largest subtribe in the family concerning the number of included genera.

Key to the genera of Tradescantiinae

- 1. Basal bract spathaceous or leaf-like, cincinni bracts; flower zygomorphic, medial petal narrower than the laterals, ornamentation of the sulcal membrane obviously different from the one of the pollen wall... 2
- Basal bract tubular and hyaline or leaf-like, if leaf-like stamens equal; flowers actinomorphic or zygomorphic, when zygomorphic also with a 60° resupination, medial petal as wide as the laterals, ornamentation of the sulcal membrane slightly different from the one of the pollen wall... 3
- 2. Diminute prostrate herbs; cincinni bract free from the cincinnus, cincinnus contracted; medial petal as long as the laterals, gynoecium 2-locular, locules 2-seeded... *Sauvallia* C.Wright ex Hassk.
- Robust erect or ascending herbs; cincinni bract fused to the peduncle of the cincinnus, cincinni elongate; medial petal shorter than the laterals, gynoecium 3-locular, locules many-seeded... *Tinantia* Scheidw. (Fig 13A)
- 3. Stems tuberized and underground; leaves cannulate, margins repandous; basal bract leaf-like; filaments at post-anthesis becoming flaccid and pointing outwards of the flower... 4
- Stems herbaceous to succulent, aerial; leaves flat or conduplicate or falcate, margins flat;
 basal bract tubular and hyaline; stamens erect or curved, sometimes spirally-coiled at apex... 5

- 4. Underground stem short, aerial stem initially inconspicuous, but elongating during flowering season; flowers flat, sepals sepaloid, free, petals sessile, stamens dimorphic, filaments barbate with moniliform hairs, connective inconspicuous, rarely expanded, anther sacs C-shaped; ovules 2 per locule, ovaries and capsules subglobose to broadly ellipsoid, stigma truncate... *Thyrsanthemum* **Pichon** (**Fig 13B & C**)
- Underground stem elongate, aerial stems inconspicuous throughout the plant's life; flowers hypocrateriform, sepals spathaceous, connate, petals long-clawed, stamens equal, filaments glabrous, connective expanded, hastate, anther sacs elongate; ovules 6 per locule, ovaries and capsules cylindrical, stigma trilobed... Weldenia Schult.f. (Fig 13D)
- 5. Leaf epidermis with silica crystals in specialized thin-walled cells, longitudinal bundles with fibrous extensions; main florescence a umbelliform thyrse, cincinni pedunculate, free; pedicels laterally spreading at post-anthesis and in fruit, ovary generally glandular-pubescent, sometimes glabrous... 6
- Leaf epidermis with silica crystals in specialized thick-walled cells or lacking silica crystals, longitudinal bundles diffuse; main florescence a double-cincinni, cincinni sessile, fused back to back or rarely only basally fused; pedicels decurved or recurved at post-anthesis and in fruit, ovary glabrous or eglandular-pubescent... 8
- 6. Cincinni geniculate, pedunculate to long-pedunculate, verticillate or opposite, bracteoles tightly imbricate in 2 whorls; pedicels apically gibbous, anthers straight, connective expanded, anther sacs divergent... *Gibasis* Raf. (Fig 13E & F)
- Cincinni straight, sessile to short-pedunculate, fasciculate or solitary, bracteoles tightly imbricate in 1 whorl; pedicels lacking an apical gibbae, anthers geniculate pointing outwards of the flower, connective inconspicuous, anther sacs parallel... 7
- 7. Roots thin and fibrous; leaves membranous to chartaceous; cincinni subsessile; petals lacking tannin cells, anthers versatile articulate from the middle... *Elasis* **D.R.Hunt** (**Fig** 13G)
- Roots tuberous; cincinni sessile; leaves succulent; petals with tannin cells, anthers versatile articulated from the base... *Matudanthus* D.R.Hunt (Fig 13H)
- 8. Main florescence subtended by frondose cincinni bracts, bracts sometimes reduced (if reduced, inflorescences sessile and predominantly axillar), bracteoles with erose margins; pedicels decurved at post-anthesis and in fruit; seeds ellipsoid to reniform, hilum linear... *Tradescantia* L. emend. M.Pell. (Fig 13I–M)
- Main florescence subtended by bracteose or vestigial cincinni bracts; bracteoles with entire margins; pedicels recurved at post-anthesis and in fruit; seeds triangular to roundtriangular or tetrahedral, hilum punctiform to elliptic... 9
- 9. Roots tuberous; synflorescence composed of a solitary main florescence, cincinni bracts apically cleft or lobed; anther sacs C-shaped, connectives quadrangular... 10
- Root thin and fibrous; synflorescence composed of a main florescence plus 1-several
 coflorescences, cincinni bracts entire; anthers sacs oblong or elliptic or round, connectives
 hastate or flabellate or rhomboid, sometimes inconspicuous... 11
- 10. Roots glabrous to pilose; leaves ovate to lanceolate to elliptic, rarely acicular, succulent; cincinni bracts decussate to the leaves, bracteoles succulent; petals with entire margins... *Brachyphyllum** (D.R.Hunt) M.Pell. & Hertweck** (Fig 13N)

- Roots lanate; leaves linear to linear-elliptic, membranous or chartaceous; cincinni bracts distichous to the leaves, bracteoles chartaceous; petals with crenulate margins...
 Cuthbertia Small (Fig 130)
- 11. Specialized epidermal cells lacking type 2 silica; sepals completely hyaline, connectives inconspicuous, style inconspicuous to very short, solid; seeds striate... *Aploleia* Raf. (Fig 13P)
- Specialized epidermal cells with type 2 silica; sepals opaque with hyaline margins, connectives expanded, style elongate, with a stylar canal; seeds reticulate to foveolate...
 12
- 12. Synflorescence not thyrsoid, synflorescence leaves equal to the regular leaves, main florescence pedunculate, cincinni bracts vestigial, fused and cup-shaped, apex erose; flowers with a 60° resupination, pedicellate, flat, pollen verrucose-granulose... *Tripogandra* Raf. (Fig 13Q & R)
- Synflorescence thyrsoid, synflorescence leaves reduced to bladeless sheaths, main florescence sessile, rarely pedunculate, cincinni bracts bracteose, free, apex entire; flowers not resupinate, sessile to subsessile, tubular, pollen irregularly microclavate, rarely insulate-cerebroid... 13
- 13. Cincinni 2, fused back-to-back, bracteoles paleaceous; pedicels slender, sepals paleaceous, connectives flabellate or hastate, anther sacs round, stigma penicilliform, rarely trilobed... *Callisia* Loefl. (Fig 13S)
- Cincinni (1-)2-3, fused only at base; pedicels stout, sepals succulent, connectives rhomboid, anther sacs elliptic, stigma truncate... *Hadrodemas* H.E.Moore (Fig 13T)
- **1.3.2.5.1.** *Sauvallia* **C.Wright ex Hassk.**, Anales Acad. Ci. Med. Habana 7: 608. 1871. Type species. *Sauvallia blainii* C.Wright ex Hassk.

Distribution and ecology. Endemic to Cuba, probably growing in the understory of seasonally dry forests.

Comments. Sauvallia has long been considered a genus or uncertain systematic affinity (Faden and Hunt 1991; Faden 1998; Hunt and Arroyo-Leuenberger 2015; Pellegrini 2017), having been tentatively associated with Callisia s.lat., Cyanotis, and most recently with Tinantia (Pellegrini 2017). This association with Tinantia was based on Sauvallia's annual habit, spathaceous basal bract, conspicuous and persistent bracteoles, zygomorphic perianth and androecium. This hypothesis is here supported by our morphological analysis, with high statistical support. For this reason, Sauvallia should be investigated together with Tinantia, to give further support for our current phylogenetic association.

Accepted species. Sauvallia blainii C.Wright ex Hassk.

1.3.2.5.2. *Tinantia* **Scheidw.**, Allg. Gartenzeitung 7: 365. 1839, nom. cons., non *Tinantia* Dumort., nom. rej., nec *Tinantia* M.Martens & Galeotti, nom. illeg. Type species. *Tinantia fugax* Scheidw. [= *Tinantia erecta* (Jacq.) Fenzl]. Fig 13A

Commelinantia Tharp, Bull. Torrey Bot. Club 49: 272. 1922. Type species. Commelinantia anomala (Torr.) Tharp. [≡ Tinantia anomala (Torr.) C.B.Clarke].

Pogomesia Raf., Fl. Tellur. 3: 67. 1836[1837]. Type species. Pogomesia undata (Humb. & Bonpl. ex Willd.) Raf. [= Tinantia erecta (Jacq.) Fenzl].

Distribution and ecology. Tropical and subtropical, from Texas to Argentina and Brazil. It grows in the understory of seasonally dry forests or rainforests, sometimes also in open environments.

Comments. *Tinantia* is easily recognized, but its species are of very difficult identification. The plants are delicate in life and become even more so after pressed and dried, making generally awful herbarium specimens that tend to disintegrate with time and inappropriate handling. The genus needs a taxonomic revision coupled with intense fieldwork. *Tinantia erecta* is certainly a species complex that will represent the bulk of work in this revision, aside from some still undescribed new species (Pellegrini, pers. observ.).

Accepted species. A total of 13 species: *Tinantia anomala* (Torr.) C.B.Clarke, *T. caribaea* Urb., *T. erecta* (Jacq.) Fenzl, *T. glabra* (Standl. & Steyerm.) Rohweder, *T. leiocalyx* C.B.Clarke, *T. longipedunculata* Standl. & Steyerm., *T. macrophylla* S.Watson, *T. parviflora* Rohweder, *T. pringlei* (S.Watson) Rohweder, *T. sprucei* C.B.Clarke, *T. standleyi* Steyerm., *T. umbellata* (Vahl) Urb., and T. violacea Rohweder.

1.3.2.5.3. *Thyrsanthemum* **Pichon**, Notul. Syst. (Paris) 12: 224. 1946. Type species. *Thyrsanthemum floribundum* (M.Martens & Galeotti) Pichon. Fig 13B & C

Gibasoides D.R.Hunt, Kew Bull. 33(2): 331. 1978. Type species. Gibasoides laxiflora (C.B.Clarke) D.R.Hunt [≡ Thyrsanthemum laxiflorum (C.B.Clarke) M.Pell. & Espejo].

Distribution and ecology. Tropical and subtropical, from Texas to Argentina and Brazil. It can be found growing in understory in seasonally dry forests or rainforests, sometimes also in open environments.

Comments. Thyrsanthemum has recently received and updated synopsis, with the inclusion of Gibasoides (Pellegrini and Espejo-Serna, in prep.). Despite being a small genus, Thyrsanthemum would take great advantage of populational and morphometric studies to test the monophyly on its most plastic species, T. floribundum and T. longifolium.

Accepted species. A total of four species: *Thyrsanthemum floribundum* (M.Martens & Galeotti) Pichon, *T. goldianum* D.R.Hunt, *T. laxiflorum* (C.B.Clarke) M.Pell. & Espejo, and *T. longifolium* (M.Martens & Galeotti) M.Pell. & Espejo.

1.3.2.5.4. *Weldenia* **Schult.f.**, Flora 12: 1. 1829. Type species. *Weldenia candida* Schult.f. Fig 13D

Rugendasia Schiede ex Schltdl., Hort. Hal.: 14. 1841, pro. syn.

Lampra Benth., Pl. Hartw.: 95. 1842. Type species. Lampra volcanica Benth. [≡ Weldenia volcanica (Benth.) M.Pell. & Espejo].

Vibilia Sessé & Mociño, nom. nud.

Distribution and ecology. Tropica and subtropical, from Mexico to Guatemala. It grows in understory in temperate pine forests or in open ad rocky environments.

Comments. Weldenia has recently received and updated synopsis, with the recognition of a second species (Pellegrini and Espejo-Serna, in prep.).

Accepted species. A total of two species: *Weldenia candida* Schult.f. and *W. volcanica* (Benth.) M.Pell. & Espejo.

1.3.2.5.5. *Gibasis* **Raf.**, Fl. Tellur. 2: 16. 1836[1837]. Type species. *Gibasis pulchella* (Kunth) Raf. Fig 13E & F

Heterachthia Kunze, Bot. Zeitung (Berlin) 8: 1. 1850, nom. superfl. **Syn. nov.** Type species. *Heterachthia pulchella* (Kunth) Kunze [= *Gibasis pulchella* (Kunth) Raf.].

Distribution and ecology. From Mexico to Brazil, generally growing in open environments, but sometimes understory in seasonally dry forests or rainforests.

Comments. Gibasis was revised by Hunt (1986), but since that two new species have been described. Added to that, Hunt's broad of G. karwinskyana, G. linearis, and G. venustula seem too artificial and make species identification exceedingly difficult. A new taxonomic revision is much needed, with also a revision of the genus classification system (see below).

Infrageneric classification. Two classification systems were proposed for Gibasis: (1) describing G. sect. Stenygrophylla Reveal & W.J.Hess to accommodate G. linearis and related species, with the remainder lumped in G. sect. Gibasis (Reveal and Hess 1972); and (2) describing G. sect. Heterobasis D.R.Hunt, which based on a much wider set of characters proposed to accommodate G. geniculata and G. oaxacana in this new section, with the rest placed in the expanded G. sect. Gibasis (Hunt 1975, 1986). Nonetheless, neither systems are monophyletic in our analysis. Hunt's system is only poorly supported by our dataset, with its two sections being recovered as monophyletic in some analyses. Nonetheless, G. sect. Stenygrophylla proposed by Reveal and Hess (1972) is also recovered as monophyletic. Further studies might support the recognition of three infrageneric categories, but further morphological characters and further molecular data are necessary to propose any changes to the classification of Gibasis. For the time being, we do not accept any infrageneric classification for Gibasis.

Accepted species. A total of 17 species: Gibasis chihuahuensis (Standl.) Rohweder, G. consobrina D.R.Hunt, G. geniculata (Jacq.) Rohweder, G. gypsophila B.L.Turner, G. heterophylla (Brandegee) Reveal & W.J.Hess, G. hintoniorum B.L.Turner, G. karwinskyana (Schult. & Schult.f.) Rohweder, G. linearis (Benth.) Rohweder, G. matudae D.R.Hunt, G. oaxacana D.R.Hunt, G. pauciflora (Urb. & Ekman) D.R.Hunt, G. pellucida (M.Martens & Galeotti) D.R.Hunt, G. pulchella (Kunth) Raf., G. rhodantha (Torr.) Reveal & W.J.Hess, G. speciosa Reveal & W.J.Hess, G. triflora (M.Martens & Galeotti) D.R.Hunt, and G. venustula (Kunth) D.R.Hunt.

1.3.2.5.6. *Elasis* **D.R.Hunt**, Kew Bull. 33(2): 332. 1978. Type species. *Elasis hirsuta* (Kunth) D.R.Hunt.

Fig 13G

Tradescantia sect. Coholomia D.R.Hunt, Kew Bull. 35(2): 440. 1980. Type species. T. guatemalensis C.B.Clarke ex Donn.Sm. [≡ Elasis guatemalensis (C.B.Clarke ex Donn.Sm.) M.Pell.].

Distribution and ecology. Mexico to Guatemala and disjunctively found in Ecuador, growing understory in seasonally dry forests or rainforests.

Comments. *Elasis* is currently being revised, which will expand its distribution and the number of accepted species (Pellegrini and Hunt, in prep.).

Accepted species. A total of two accepted species, with further three undescribed species (Pellegrini and Hunt, in prep.): *Elasis guatemalensis* (C.B.Clarke ex Donn.Sm.) M.Pell. and *Elasis hirsuta* (Kunth) D.R.Hunt.

1.3.2.5.7. *Matudanthus* **D.R.Hunt**, Kew Bull. 33(2): 333. 1978. Type species. *Matudanthus nanus* (M.Martens & Galeotti) D.R.Hunt. Fig 13H

Distribution and ecology. Endemic to Mexico, growing in open environments or understory in seasonally dry forests.

Comments. *Matudanthus* is currently represented by a sole exceedingly plastic species. Nonetheless, ongoing studies seem to indicate the need to recognize at least a second taxon (Pellegrini and Espejo-Serna, in prep.).

Accepted species. Matudanthus nanus (M.Martens & Galeotti) D.R.Hunt.

1.3.2.5.8. *Tradescantia* L., Species Plantarum 1: 288. 1753, **emend. M.Pell.**, Phytokeys 98: 43. Type species. *Tradescantia virginiana* L. Fig 13I–M

Distribution and ecology. Tropical and subtropical New World, ranging from southern USA and Canada to Argentina and Brazil, but centered in southern USA, Mexico and Central America, and found growing in a myriad of environments.

Comments. A genus with ca. 90, several still undescribed. Due to the size and complexity of *Tradescantia*, its revision is better done in parts to allow a proper and careful study of all names, species complexes, and issues each subgenus presents.

Key to the subgenera of *Tradescantia* (from Pellegrini 2017)

- 1. Stems prostrate with ascending apex or erect; sepals generally all keeled, filaments densely bearded at the base with long moniliform hairs, stigma punctate; embryotega inconspicuous... *Tradescantia* subg. *Austrotradescantia* (D.R.Hunt) M.Pell. (Fig 13I)
- Stems erect, rarely prostrate with ascending apex; sepals rarely keeled, if present keel restricted to the dorsal sepal, filaments glabrous to sparsely bearded at mid-length, rarely

- at the base or apex with short moniliform hairs, stigma truncate to capitulate or capitate to trilobed; embryotega with a conspicuous apicule... 2
- 2. Roots thin and fibrous, rarely tuberous; inflorescence composed of the main florescence and generally 1-many coflorescences, peduncle bracts commonly present, cincinni bracts spathaceous; stamens subequal, connectives cordate to hastate to linear-tapered, rarely rhomboid, anther sacs globose, rarely ellipsoid, pollen white; embryotega semilateral... *Tradescantia* subg. *Campelia* (Rich.) M.Pell. (Fig 13J)
- Roots fleshy to tuberous; inflorescence composed only by the main florescence, peduncle bracts never present, cincinni bracts leaf-like or reduced; stamens equal, connectives quadrangular to rectangular, rarely slightly rhomboid to slightly hastate, anther sacs elliptic to curved, pollen yellow; embryotega dorsal... 3
- 3. Main florescences sessile, mainly axillary, cincinni bracts reduced; sepals chartaceous, filaments and style spirally-coiled at post-anthesis, style ½ longer than the stamens... *Tradescantia* subg. *Mandonia* (D.R.Hunt) M.Pell. (Fig 13K)
- Main florescences pedunculate, rarely sessile, terminal, cincinni bracts expanded and leaflike; sepals membranous, filaments and style straight at post-anthesis, style equal or shorter than the stamens... 4
- 4. Leaves lanceolate to ovate to rotund, rarely cylindrical, base obtuse to slightly cordate; pedicel apically gibbous, flowers tubular, stamens epipetalous, filaments glabrous or sparsely bearded, stigmatic papillae evenly distributed in the stigma... *Tradescantia* subg. *Setcreasea* (K.Schum. & Sydow) M.Pell. (Fig 13L)
- Leaves linear to acicular, base truncate to round; pedicels apically non-gibbous, flowers flat, stamens free, filaments densely bearded, stigmatic papillae restricted to the margins of the stigma... *Tradescantia L.* subg. *Tradescantia* (Fig 13M)
- **1.3.2.5.8.1.** *Tradescantia* **subg.** *Austrotradescantia* **(D.R.Hunt) M.Pell.**, Phytokeys 98: 47. 2017 ≡ *Tradescantia* sect. *Austrotradescantia* D.R.Hunt, Kew Bull. 35(2): 440. 1980. Type species. *Tradescantia fluminensis* Vell. Fig 13I
- *Tropitria* Raf., Fl. Tellur. 3: 68. 1836[1837]. Type species. *Tropitria crassula* (Link & Otto) Raf. (≡ *T. crassula* Link & Otto).

Distribution and ecology. Endemic to South American, found growing in the understory of rainforests in the Brazilian Atlantic Forest domain, open fields, rocky outcrops, being especially common in disturbed areas.

Accepted species. A total of 13 species: *Tradescantia atlantica* M.Pell., *cerinthoides* Kunth, *T. chrysophylla* M.Pell., *T. crassula* Link & Otto, *T. cymbispatha* C.B.Clarke, *T. decora* W.Bull., T. *fluminensis* Vell., *T. hertweckiae* M.Pell., *T. mundula* Kunth, *T. seubertiana* M.Pell., *T. tenella* Kunth, *T. tucumanensis* M.Pell., and *T. umbraculifera* Hand.-Mazz.

- **1.3.2.5.8.2.** *Tradescantia* **subg.** *Campelia* (**Rich.**) **M.Pell.**, Phytokeys 98: 51. 2017 ≡ *Campelia* Rich., Démonstr. Bot.: 46. 1808. Fig 13J
- Tradescantia sect. Campelia (Rich.) D.R.Hunt, Kew Bull. 41(2): 404. 1986.
- *Zanonia* Cramer., Disp. Syst.: 75. 1803, nom. illeg. Type species. *Zanonia bibracteata* Cramer., nom. illeg. [= *Tradescantia zanonia* (L.) Sw.].
- Sarcoperis Raf., Fl. Tellur. 2: 16. 1837. Type species. Sarcoperis bibracteata (Cramer) Raf. [= Tradescantia zanonia (L.) Sw.].
- *Zebrina* Schnizl., Bot. Zeitung (Berlin) 7: 870. 1849. Type species. *Zebrina pendula* Schnizl. (= *Tradescantia zebrina* Heynh. ex Bosse).
- Tradescantia sect. Zebrina (Schnizl.) D.R.Hunt, Kew Bull. 41(2): 404. 1986.
- Gonatandra Schltdl., Linnaea 24: 659. 1851. Type species. Gonatandra tradescantioides Schltdl. [= Tradescantia zanonia (L.) Sw.].
- Cymbispatha Pichon, Not. Syst. 12: 224. 1946. Type species. Tradescantia commelinoides Schult.f.
- Tradescantia sect. Cymbispatha (Pichon) D.R.Hunt, Kew Bull. 35(2): 440. 1980.
- Rhoeo Hance, Ann. Bot. Syst. 3: 659. 1852. Type species. Tradescantia discolor L'Hér. (= Tradescantia spathacea Sw.).
- Tradescantia sect. Rhoeo (Hance) D.R.Hunt, Kew Bull. 41(2): 401. 1986.
- Tradescantia sect. Corinna D.R.Hunt, Kew Bulletin 41(2): 405. 1986. Type species. Campelia standleyi Steyermark (= Tradescantia soconuscana Matuda).
- **Distribution and ecology.** Widespread in the Neotropics, ranging from Mexico to Argentina, but centered in Central America and northern South America, and found growing in the understory of seasonally dry forests and rainforests, or in elevated open areas.
- Accepted species. A total of 14 species, with some yet undescribed: *Tradescantia commelinoides* Schult. & Schult.f., *T. deficiens* Brandegee, *T. gracillima* Stand., *T. grantii* Faden, *T. huehueteca* (Standl. & Steyerm.) D.R.Hunt, *T. plusiantha* Stand., *T. poelliae* D.R.Hunt, *T. praetermissa* M.Pell., *T. schippii* D.R.Hunt, *T. soconuscana* Matuda, *T. spathacea* Sw., *T. standleyi* Steyerm., *T. zanonia* (L.) Sw., and *T. zebrina* Heynh. ex Bosse.

- **1.3.2.5.8.3.** *Tradescantia* **subg.** *Mandonia* (**D.R.Hunt**) **M.Pell.**, Phytokeys 98: 54. 2017 ≡ *Tradescantia* sect. *Mandonia* D.R.Hunt, Kew Bull. 35(2): 441. 1980. Type species. *Tradescantia ambigua* Mart. ex Schult. & Schult.f.
- Fig 13K
- Skofitzia Hassk. & Kanitz, Oesterr. Bot. Z. 22: 147. 1872.
- *Mandonia* Hassk., Flora 54: 260. 1871, nom. illeg, non *Mandonia* Wedd., Bull. Soc. Bot. France 11: 50–51, t. 1. 1864. Type species. *Tradescantia ambigua* Mart. ex Schult. & Schult.f.
- *Neomandonia* Hutch., Fam. Fl. Pl., Monocot. 2: 57. 1934. Type species. *Mandonia boliviana* Hassk. [= *Tradescantia boliviana* (Hassk.) J.R.Grant].
- Tradescantia sect. Parasetcreasea D.R.Hunt, Kew Bull. 30(3): 455. 1975. Type species. Tradescantia andrieuxii C.B.Clarke

Distribution and ecology. Widely but disjunctively distributed across the American continent, with species occurring in North America, Central America, and South America. Its species are restricted to seasonally dry forests or other dry biomes across the continent.

Included species. A total of 18 species, with some still undescribed (Pellegrini, Grant & Hunt, in prep.): *Tradescantia ambigua* Mart. ex Schult. & Schult.f., *T. andrieuxii* C.B.Clarke, *T. boliviana* (Hassk.) J.R.Grant, *T. burchii* D.R.Hunt, *T. crassifolia* Cav., *T. exaltata* D.R.Hunt, *T. gentryi* D.R.Hunt, *T. guiengolensis* Matuda, *T. iridescens* Lindl., *T. llamasii* Matuda, *T. masonii* Matuda, *T. mcvaughii* D.R.Hunt, *T. murilloae* Zamudio et al., *T. nuevoleonensis* Matuda, *T. peninsularis* Brandegee, *T. petricola* J.R.Grant, *T. tepoxtlana* Matuda, and *T. velutina* Kunth & C.D.Bouché.

1.3.2.5.8.4. *Tradescantia* **subg.** *Setcreasea* (**K.Schum. & Sydow**) **M.Pell.**, Phytokeys 98: 59. 2017 ≡ *Setcreasea* K.Schum. & Sydow, Just's Bot. Jahresber. 27(1): 452. 1901. Type. *Tradescantia brevifolia* (Torr.) Rose Fig 13L

Treleasea Rose, Contr. U.S. Natl. Herb. 5: 207. 1899, nom. illeg., non *Treleasia* Speg., Revista Fac. Agron. Univ. Nac. La Plata 2: 235. 1896. Type species. *Tradescantia leiandra* var. *brevifolia* Torr. [≡ *Tradescantia brevifolia* (Torr.) Rose].

Neotreleasea Rose, Contr. U.S. Natl. Herb. 8: 5. 1903, nom. superfl.

Tradescantia sect. Setcreasea (K.Schum. & Sydow) D.R.Hunt, Kew Bull. 30(3): 448. 1975.

Separotheca Waterf., Rhodora 61: 138. 1959. Type species. Zebrina pumila Greene (≡ Tradescantia pygmaea D.R.Hunt).

Tradescantia sect. Separotheca (Waterf.) D.R.Hunt, Kew Bull. 30(3): 454. 1975.

Tradescantia sect. Tradescantia ser. Orchidophyllae D.R.Hunt, Kew Bull. 35(2): 441. 1980. Type species. Tradescantia orchidophylla Rose & Hemsl.

Tradescantia sect. Tradescantia ser. Sillamontanae D.R.Hunt, Kew Bull. 35(2): 440. 1980. Type species. Tradescantia sillamontana Matuda.

Distribution and ecology. Restricted to southern USA and Mexico, generally found growing in rocky outcrops and open dry areas.

Accepted species. A total of 10 species: *Tradescantia brevifolia* (Torr.) Rose, *T. buckleyi* (I.M.Johnst.) D.R.Hunt, *T. hirta* D.R.Hunt, *T. leiandra* Torr., *T. mirandae* Matuda, *T. orchidophylla* Rose & Hemsl., *T. pallida* (Rose) D.R.Hunt, *T. pygmaea* D.R.Hunt, *T. rozynskii* Matuda, and *T. sillamontana* Matuda.

1.3.2.5.8.5. *Tradescantia* L. **subg.** *Tradescantia*. Type species. *Tradescantia virginiana* L. Fig 13M

Ephemerum Mill., Gard. Dict. Abr., ed. 4.: 462. 1754, nom. superfl. Type species. *Ephemerum virginianum* (L.) Mill. (≡ *Tradescantia virginiana* L.).

Tradescantia L. sect. Tradescantia sensu Hunt (1980), pro parte.

Tradescantia sect. *Tradescantia* ser. Virginianae D.R.Hunt, Kew Bull. 35(2): 440. 1980. Type species. *Tradescantia virginiana* L.

Knowlesia Hassk., Flora 49: 215. 1866. Type species. *Knowlesia spicata* (Knowles & Westc.) Hassk. (= *Tradescantia virginiana* L.).

Tradescantia sect. *Tradescantia* ser. *Tuberosae* D.R.Hunt, Kew Bull. 35(2): 441. 1980. Type species. *Tradescantia tuberosa* Greene (≡ *Tradescantia pinetorum* Greene)

Distribution and ecology. Restricted to Canada, USA and Mexico, but centered in the USA, and generally found growing in open grasslands, pine forests or open rocky areas.

Accepted species. A total of 25 accepted species, with some yet undescribed: Tradescantia bracteata Small ex Britton, T. cirrifera Mart., T. edwardsiana Tharp, T. ernestiana E.S.Anderson & Woodson, T. gigantea Rose, T. gypsophila B.L.Turner, T. hirsuticaulis Small, T. hirsutiflora Bush, T. humilis Rose, T. longipes E.S.Anderson & Woodson, T. monosperma Brandegee, T. occidentalis (Britton) Smyth, T. ohiensis Raf., T. ozarkana E.S.Anderson & Woodson, T. pedicellata Celarier, T. pinetorum Greene, T. reverchonii Bush, T. roseolens Small, T. stenophylla Brandegee, T. subacaulis Bush, T. subaspera Ker Gawl., T. subtilis Matuda, T. tharpii E.S.Anderson & Woodson, T. virginiana L., and T. wrightii Rose & Bush.

1.3.2.5.9. Brachyphyllum (D.R.Hunt) M.Pell. & Hertweck, comb. et stat. nov. ≡ Callisia sect. Brachyphylla D.R.Hunt., Kew Bull. 41(2): 409. 1986. Type. Callisia navicularis (Ortgies) D.R.Hunt [≡ Brachyphyllum naviculare (Ortgies) M.Pell. & Hertweck]. Fig 13N

Callisia sect. Lauia D.R.Hunt., Kew Bull. 41(2): 409. 1986, **Syn. nov.** Type species. Callisia laui (D.R.Hunt) D.R.Hunt [≡ Brachyphyllum laui (D.R.Hunt) M.Pell. & Hertweck].

Distribution and ecology. Endemic to the US, from Florida to Virginia, growing also in open environments.

Comments. Brachyphyllum is here proposed to accommodate the lineage sister to Cuthbertia. A close relationship between both genera is supported by their reduced and apically lobed cincinni bracts, which is further supported by B. hintoniorum (as Callisia hintoniorum) being described as a member of Callisia sect. Cuthbertia, and not of C. sect. Brachyphylla (Turner 1993). Despite a generic name having never been previously proposed for this lineage, Pichon (1946) had already indicated in his identification key the need to recognize Tradescantia navicularis as an independent genus. Nonetheless, the author never formalized this. Species of Brachyphyllum have flowers that mimic the ones of Tradescantia subg. Setcreasea.

Accepted species and new combinations. A total of four species: *Brachyphyllum hintoniorum* (B.L.Turner) M.Pell. & Hertweck, **comb. nov.** ≡ *Callisia hintoniorum* B.L.Turner, Phytologia 75(4): 277–279, f. 1. 1993.

Brachyphyllum laui (D.R.Hunt) M.Pell. & Hertweck, **comb. nov.** \equiv Phyodina laui D.R.Hunt, Kew Bull. 33(3): 404. 1979 \equiv Callisia laui (D.R.Hunt) D.R.Hunt, Kew Bull. 38(1): 131. 1983.

Brachyphyllum micranthum (Torr.) M.Pell. & Hertweck, **comb. nov.** \equiv Tradescantia micrantha Torr., Rep. U.S. Mex. Bound. 2(1): 224. 1859 \equiv Callisia micrantha (Torr.) D.R.Hunt, Kew Bull. 38(1): 131. 1983 \equiv Phyodina micrantha (Torr.) D.R.Hunt, Kew Bull. 33: 404. 1979.

Brachyphyllum naviculare (Ortgies) M.Pell. & Hertweck, **comb. nov.** \equiv *Tradescantia navicularis* Ortgies, Gartenflora 26: 130, t. 901. 1877 \equiv *Phyodina navicularis* (Ortgies) Rohweder, Abh. Auslandsk., Reihe C, Naturwiss. 61(18): 151 1956 \equiv *Callisia navicularis* (Ortgies) D.R.Hunt, Kew Bull. 38(1): 132. 1983.

1.3.2.5.10. *Cuthbertia* Small, Fl. S.E. U.S. 237, 1328. 1903 ≡ *Callisia* sect. *Cuthbertia* (Small) D.R.Hunt., Kew Bull. 41(2): 409. 1986. Type. *Callisia rosea* (Vent.) D.R.Hunt [≡ *Cuthbertia rosea* (Vent.) Small]. Fig 13O

Distribution and ecology. Endemic to the US, from Florida to Virginia, growing also in open environments.

Comments. Cuthbertia was reduced to section of Callisia by Hunt (1986) with the aim to make the genus monophyletic. Nonetheless, as showed by several molecular and morphological phylogenies (Burns et al. 2011; Hertweck and Pires 2014; Pellegrini 2017; this study), Hunt's expansion of Callisia made the genus paraphyletic, without the inclusion of the well-circumscribed Tripogandra. Cuthbertia is morphologically easily distinguished from the remaining genera of the Callisia/Tripogandra complex by its grass like habit and leaves, lobes and much reduced cincinni bracts, and flowers that mimic the ones of members Tradescantia subg. Tradescantia.

Accepted species. A total of four species: *Cuthbertia graminea* Small, *C. leucantha* (Lakela) M.Pell. & Hertweck, *C. ornata* Small, and *C. rosea* (Vent.) Small.

New combination. *Cuthbertia leucantha* (Lakela) M.Pell. & Hertweck, **comb. et stat. nov.** ≡ *Cuthbertia graminea* fo. *leucantha* Lakela, Sida 5: 28. 1972 ≡ *Callisia graminea* fo. *leucantha* (Lakela) G.C.Tucker, J. Arnold Arbor. 70(1): 118. 1989.

- **1.3.2.5.11.** *Aploleia* **Raf.**, Fl. Tellur. 2: 17. 1836[1837]. Type. *Aploleia diffusa* Raf., nom. superfl. [≡ *Aploleia monandra* (Sw.) H.E.Moore]. Fig 13P
- *Leiandra* Raf., Fl. Tellur. 2: 17. 1836[1837], **Syn. nov.** Type species (designated here). *Leiandra cordifolia* (Sw.) Raf. [≡ *Aploleia cordifolia* (Sw.) M.Pell. & Hertweck].
- Callisia sect. Leptocallisia Benth. & Hook.f., Gen. Pl. 3: 854. 1883. Type species. Callisia umbellata Lam. [= Aploleia monandra (Sw.) H.E.Moore].
- Leptocallisia (Benth. & Hook.f.) Pichon, Notul. Syst. (Paris) 12: 225, 237. 1946, nom. superfl.
- Tradescantella Small, Fl. S.E. U.S.: 237–238, 1328. 1903, **Syn. nov.** Type species. Tradescantella floridana (S.Watson) Small [= Aploleia cordifolia (Sw.) M.Pell. & Hertweck].
- **Distribution and ecology.** From the US to Argentina and Brazil, but with *A. cordifolia* and *A. multiflora* restricted to North America, Central America, and the Antilles. It can be found growing in the understory of seasonally dry forests or rainforests, sometimes also in open environments.
- **Comments.** Aploleia has been revised by Moore (1961), but with the present inclusion of A. cordifolia, the genus would benefit of an undated account making use of the information made available in the recent years, together with new data and fieldwork.
- **Accepted species.** A total of three species: *Aploleia cordifolia* (Sw.) M.Pell. & Hertweck, *A. monandra* (Sw.) H.E.Moore, and *A. multiflora* (M.Martens & Galeotti) H.E.Moor.
- **New combination.** *Aploleia cordifolia* (Sw.) M.Pell. & Hertweck, **comb. nov.** ≡ *Tradescantia cordifolia* Sw., Prodr.: 57. 1788 ≡ *Leiandra cordifolia* (Sw.) Raf., Fl. Tellur. 2: 17. 1836[1837] ≡ *Callisia cordifolia* (Sw.) E.S.Anderson & Woodson, Contr. Arnold Arbor. 9: 117. 1935 ≡ *Phyodina cordifolia* (Sw.) Rohweder, Abh. Auslandsk., Reihe C, Naturwiss. 18: 151. 1956 ≡ *Tripogandra cordifolia* (Sw.) Aristeg., Bol. Acad. Ci. Fís. 25(68): 125. 1965.
- **1.3.2.5.12.** *Tripogandra* Raf., Fl. Tellur. 2: 16. 1836[1837]. Type species. *Tripogandra multiflora* (Sw.) Raf.

Fig 13Q & R

- Heminema Raf., Fl. Tellur. 2: 17. 1836[1837], nom. superfl. Type species. Heminema multiflora (Sw.) Raf. [≡ Tripogandra multiflora (Sw.) Raf.].
- Descantaria Schltdl., Linnaea 26: 140. 1853[1854]. Type species. Descantaria cumanensis (Kunth) Schltdl. [= Tripogandra multiflora (Sw.) Raf.].
- *Disgrega* Hassk., Flora 49: 215. 1866. Type species. *Disgrega mexicana* Hassk. ex C.B.Clarke, pro syn. [≡ *Tripogandra disgrega* (Kunth) Woodson].
- Donnellia C.B.Clarke, Bot. Gaz. 33(4): 261. 1902, nom. illeg., non Donnellia Austin. Type species. Donnellia grandiflora (Donn. Sm.) C.B.Clarke [≡ Tripogandra grandiflora (Donn.Sm.) Woodson].

- Neodonnellia Rose, Proc. Biol. Soc. Washington 19(22): 96. 1906. Type species. Neodonnellia grandiflora (Donn.Sm.) Rose [≡ Tripogandra grandiflora (Donn.Sm.) Woodson].
- Leptorhoeo C.B.Clarke, Diagn. Pl. Nov. Mexic. 3: 55. 1880, **Syn. nov.** Type species. Leptorhoeo filiformis (M.Martens & Galeotti) C.B.Clarke [≡ Tripogandra filiformis (M.Martens & Galeotti) M.Pell. & Hertweck].
- *Phyodina* Raf., Fl. Tellur. 2: 16. 1836[1837], **Syn. nov.** Type species. *Phyodina gracilis* (Kunth) Raf. [≡ *Tripogandra gracilis* (Kunth) M.Pell. & Hertweck].

Distribution and ecology. From Mexico to Argentina and Brazil, generally growing in open, dry or flooded environments, but sometimes also found in the understory of seasonally dry forests or rainforests.

Comments. Christenhusz et al. (2018) proposed the inclusion of *Tripogandra* in *Callisia* s.lat., due to it being nested in the later. Nonetheless, this decision greatly hampers the taxonomy of this unnecessarily complicated group. As stated by Pellegrini (2017) and reinforced here, *Tripogandra* is easily diagnosable, even with the inclusion of *Callisia filiformis*, *Callisia gracilis*, and *Tradescantia triandra* Kunth (≡ *Callisia ciliata* Kunth, nom. illeg.). Furthermore, the remaining lineages of the *Callisia/Tripogandra* generic complex are also easily diagnosable, and thus recognized by us as distinct genera. If *Callisia sensu* Christenhusz et al. (2018) is accepted, the genus would only be differentiated based on two seed characters, which are most commonly absent in several herbarium specimens. This way, the recognition of this unnecessarily broad and morphologically hyper-variable *Callisia* goes against the "practical and usable" requirements that the authors themselves affirmed to be the base of their changes. With the circumscription accepted here for the lineages of the *Callisia/Tripogandra* generic complex, all six genera are easily differentiated from one another and other genera of Commelinaceae, and also supported by at least one easily observable synapomorphy.

Accepted species. A total of 26 species: *Tripogandra amplexans* Handlos, *T. amplexicaulis* (Klotzsch ex C.B.Clarke) Woodson, *T. angustifolia* (B.L.Rob.) Woodson, *T. australis* (Handlos) M.Pell., *T. brasiliensis* Handlos, *T. disgrega* (Kunth) Woodson, *T. diuretica* (Mart.) Handlos, *T. elata* D.R.Hunt, *T. encolea* (Diels) J.F.Macbr., *T. filiformis* (M.Martens & Galeotti) M.Pell. & Hertweck, *T. glandulosa* (Seub.) Rohweder, *T. gracilis* (Kunth) M.Pell. & Hertweck, *T. grandiflora* (Donn.Sm.) Woodson, *T. guerrerensis* Matuda, *T. ionantha* (Diels) J.F.Macbr., *T. kruseana* Matuda, *T. montana* Handlos, *T. multiflora* (Sw.) Raf., *T. neglecta* Handlos, *T. palmeri* (Rose) Woodson, *T. purpurascens* (Schauer) Handlos, *T. saxicola* (Greenm.) Woodson, *T. serrulata* (Vahl) Handlos, *T. silvatica* Handlos, *T. triandra* (Kunth) M.Pell. & Hertweck, and *T. warmingiana* (Seub.) Handlos.

New combinations. *Tripogandra australis* (Handlos) M.Pell., **stat. nov.** ≡ *Tripogandra purpurascens* subsp. *australis* Handlos, Rhodora 77(810): 297–298. 1975.

Tripogandra filiformis (M.Martens & Galeotti) M.Pell. & Hertweck, **comb. nov.** ≡ *Tradescantia filiformis* M.Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 9(2): 376. 1842 ≡ *Leptorhoeo filiformis* (M.Martens & Galeotti) C.B.Clarke, Diagn. Pl. Nov. Mexic. 3: 55. 1880 ≡ *Callisia filiformis* (M.Martens & Galeotti) D.R.Hunt, Kew Bull. 41(2): 410. 1986.

Tripogandra gracilis (Kunth) M.Pell. & Hertweck, **comb. nov.** \equiv *Tradescantia gracilis* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 261–262. 1815[1816] \equiv *Phyodina gracilis* (Kunth) Raf.,

Fl. Tellur. 2: 16. $1836[1837] \equiv Aneilema\ gracile\ (Kunth)\ Steyerm.$, Fieldiana, Bot. 28(1): 152. 1951, nom. illeg., as "gracilis" $\equiv Callisia\ gracilis\ (Kunth)\ D.R.Hunt,\ Kew\ Bull. 38(1): 131. 1983.$

Tripogandra triandra (Kunth) M.Pell. & Hertweck, **comb. nov.** \equiv *Tradescantia triandra* Kunth, Enum. Pl. 4: 93. $1843 \equiv$ *Tradescantia elongata* var. *triandra* (Kunth) C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 304. $1881 \equiv$ *Callisia ciliata* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 261. 1815[1816], nom. illeg., non *Callisia ciliata* Pers.

1.3.2.5.13. Callisia Loefl., Iter Hispan.: 305–306. 1758. Type species. Callisia repens (Jacq.)L.Fig 13S

Hapalanthus Jacq., Enum. Syst. Pl. 1, 12. 1760, nom. superfl. Type species. Hapalanthus repens Jacq. [≡ Callisia repens (Jacq.) L.].

Spironema Lindl., Edwards's Bot. Reg. 26: Misc. 26. 1840, nom. illeg., non Spironema Raf. Type species. Spironema fragrans Lindl. [≡ Callisia fragrans (Lindl.) Woodson]. Rectanthera O.Deg., Fl. Hawaiiensis 1: Fam 62. 1932. Type species. Rectanthera fragrans (Lindl.) O.Deg. [≡ Callisia fragrans (Lindl.) Woodson].

Distribution and ecology. Neotropical, ranging from Texas to Argentina and Brazil, but centered in Mexico. It can be found growing in open and generally rocky environments, also in the understory of seasonally dry forests, or sometimes of rainforests.

Comments. *Callisia* has been revised by Moore (1958), with further updates done by Hunt (1986). Nonetheless, the infraspecific taxa proposed by Hunt (1986) are far too different from each other and are once again treated at the species rank. Furthermore, some names from Matuda that had been reduced to synonyms (Moore 1958; Hunt 1986) are here reestablished since they are clearly different. A taxonomic revision for *Callisia* s.str. is also needed.

Accepted species. A total of nine species: *Callisia fragrans* (Lindl.) Woodson, *C. elegans* Alexander ex H.E.Moore, *C. gentlei* Matuda, *C. guerrerensis* Matuda, *C. insignis* C.B.Clarke, *C. macdougallii* Miranda, *C. nizandensis* Matuda, *C. repens* (Jacq.) L., *C. soconuscensis* Matuda, and *C. tehuantepecana* Matuda.

1.3.2.5.14. *Hadrodemas* **H.E.Moore**, Baileya 10: 134. 1963. Fig 13T

Callisia sect. Hadrodemas (H.E.Morre) D.R.Hunt., Kew Bull. 41(2): 409. 1986. Type species. Callisia warszewicziana (Kunth & C.D.Bouché) D.R.Hunt. [≡ Hadrodemas warszewiczianum (Kunth & C.D.Bouché) H.E.Moore].

Distribution and ecology. Restricted to Mexico and Guatemala, found growing in open environments, especially rocky outcrops.

Comments. *Hadrodemas* has been carefully addressed by Moore (1963) at the time of its description.

Accepted species. Hadrodemas warszewiczianum (Kunth & C.D.Bouché) H.E.Moore.

2. Hanguanaceae Airy Shaw, Kew Bull. 18: 260. 1964. Type genus. *Hanguana* Blume. Fig 14

Description. Herbs dioecious, perennial, aquatic, amphibious or paludal, rarely truly terrestrial; young organs covered by multiseriate fruticose hairs with a base uniseriate, caducous at age. Roots thin and fibrous, glabrous to pilose, not sand-binding, lacking a rhizosheath. Underground stem a rhizome, short and generally inconspicuous or long and trailing. Stems aerial or floating or submerged, erect or trailing, fibrous, unbranched to branching only at the base, sometimes rooting at the basal nodes, rarely along the whole stem; internodes contracted to elongate, secondary branches sometimes present producing stolonlike structures. Immature leaves persistent throughout the plant's life, spirally-alternate, bifacial, congested at the apex of the stem; ptyxis involute; sheaths open, margins earlymarcescent, sheaths generally persistent and marcescent in old stems; ligule absent; pseudopetioles conspicuous, rarely indistinct, canaliculate; blades elliptic to lanceolate or ovate, flat or plicate, base cuneate or obtuse to round, apex acute or acuminate, chartaceous to coriaceous; midvein evident, adaxially impressed, abaxially prominent, secondary veins evident or not. Mature leaves never produced. Synflorescence apparently composed of a solitary main florescence (but see comment below); synflorescence leaves equal to the regular leaves or not, but generally reduced in size and lacking a pseudopetiole. Main florescences (inflorescences) terminal, consisting of a pedunculate, many-branched thyrse; basal bract leaflike; cincinnus' bract present, leaf-like, reducing in size towards the apex of the main florescence; main axis developed; accessory bracts present or not, buds producing inflorescence primordia; cincinni many per thyrse, alternate or fasciculate, many-flowered, sessile, internodes elongate; bracteoles present, much reduced. Flowers non-resupinate, staminate or pistillate, solitary or arranged in clusters along the secondary branches, sessile, chasmogamous, homostylous, enantiostylous?, actinomorphic or pistillate asymmetric due to the position of the stigma, hypanthium absent, perianth homochlamydeous, sepaloid, flat to somewhat campanulate, yellowish green to medium green, sometimes red-dotted (tannin cells), persistent in fruit, lobes 6 (3 outer and 3 inner), 3 superior and 3 inferior, outer whorl basally connate, shorter than the inner whorl, cucullate, inner whorl free, not prominently cucullate; staminate flowers with stamens 6, equal, ca. as long or longer than the inner tepals, filaments straight, terete, broader at base, glabrous, anthers basifixed, rimose, introrse, connective inconspicuous, anther sacs elongate; pistillode present, rudimentary, basally 6lobed, nectariferous; pistillate flowers with 6 filiform staminodes, lacking antherodes, outer ones minute, inner ones larger, with a basal scale, nectariferous, margins hyaline or opaque, ovary superior, ca. as long to much longer than the inner tepals, 3-locular, all fertile, placentation axile, ovules 1 per locule, style absent, stigma entire or trilobed or triparted. Fruit a berry, variously shaped and colored, 1(-3)-seeded, persistent stigma elevated or not. Seeds bowl-shaped or hemispherical or ³/₄ globose, exarillate?, testa smooth, margin of the seed with a circular or wedge-shaped rim, with projections or not; chalazal cap inconspicuous; hilum punctate; embryotega dorsal, inconspicuous.

Comments. Hanguanaceae is the second smallest family in the order, with a sole genus and over 50 species (most still undescribed) and is by far the least understood (Leong-Škorničková and Boyce 2015). It is easily distinguished from the remaining members of Commelinales by its habit resembling a miniature, dioecious palm tree, completely sepaloid perianth (unique in the order), the presence of nectariferous scales and pistilodes, sessile stigmas, brightly-colored berries, and bowl-shaped seeds. Its sister relationship with Commelinaceae is supported by its flowers sepaloid outer perianth whorl, sclerified seed coat, embryos shorter than 1/2 the length of the seed, nuclear endosperm, cotyledon non-

chlorophyllate and haustorial, and seedlings with at least the first primary leaf reduced to cataphyll. Their palm-like leaves are generally conspicuously pseudopetiolate, with the base of the blade being greatly constricted and canaliculate, resembling a true petiole.

Phylogeny. This study presents the first phylogenetic hypothesis for the family and supports it as monophyletic and monogeneric. Further studies are still needed, with improved sampling and further morphological studies to properly understand the evolution of morphological characters in the family (Pellegrini & Niissalo, pers. observ.).

Distribution. Restricted to Australasia.

2.1. *Hanguana* Blume, Enum. Pl. Javae: 15. 1827. Type species. *Hanguana kassintu* Blume. Fig 14

Susum Blume ex Schult. & Schult. f., Syst. Veg. (ed. 15 bis) 7(2): XCV. 1830. Type species. Susum anthelminthicum Blume ex Schult. & Schult. f. [≡ Hanguana anthelminthica (Blume ex Schult. & Schult. f.) Masam.].

Veratronia Miq., Fl. Ned. Ind. 3: 553 1859, nom. illeg. Type species. Veratronia malayana (Jack) Miq. [≡ Hanguana malayana (Jack) Merr.].

Distribution and ecology. Known to occur in Australia (Northern Territory and Queensland), Borneo, Java, Malaysia, Micronesia, Myanmar, New Guinea, Palau, Philippines, Sri Lanka, Sulawesi, Sumatra, Thailand, and Vietnam. Species of *Hanguana* are commonly found in permanently humid, ever-wet, and fresh-water swamp forests in Australasia, with some species growing as emergent aquatics.

Comments. The species diversity of *Hanguana* is still incompletely known, with 19 currently accepted species (POWO 2019), but with an estimation of a total of over 50 extant species (Leong-Škorničková and Boyce 2015). The taxonomy of the group is greatly impaired by the lack of properly prepared herbarium vouchers of the few collected specimens, the lack of field annotations and observations describing relevant morphological and ecological characters (Siti Nurfazilah et al. 2011), and also by the still incompletely understood variation in the relevance of several morphological characters (Pellegrini & Niissalo, pers. observ.). A need to standardize species descriptions in *Hanguana* is pressing, with each of the newly described species so far providing morphological descriptions with very little comparable characters. Aside from the commonly described ecological and morphological characters (e.g., habitat, stolon production, stigma morphology, mature fruit's size, shape and coloration, etc.), descriptions should also provide thorough descriptions of the: staminate and pistillate flowers, nectariferous scales, and seeds (especially the shape of the margin rim and the presence or absence of projections in them).

Future studies on Hanguanaceae should also investigate the ontogeny of inflorescences in the group. The inflorescences are thyrsoid, but the observed degree and patterns of branching indicate that they might represent complex synflorescences. For instance, the flowers can be solitary or arranged in "clusters" along the branches, possibly indicating that these "clusters" represent the actual partial florescences (i.e., secondary branches) and that each branch actually represents a highly modified thyrse (i.e., the main florescence). Floral ontogeny also seems to be key to understand and properly address the possible presence of enantiostyly in *Hanguana* (see Discussion). Furthermore, anatomical, palynological, phytochemical and cytological studies are almost non-existent in the family and might provide useful taxonomically relevant characters. Also, the reproductive biology of the group

is completely unknown, with no information available of floral visitors, putative pollinators, pollination mechanisms, and putative fruit/seed dispersers. Finally, a complete taxonomic revision for the family is much needed.

Infrageneric classification. To this date, no infrageneric classification was ever proposed for *Hanguana*. This can be easily explained by the complete lack of taxonomic attention the group received until very recently (Siti Nurfazilah et al. 2011). As the taxonomy of *Hanguana* continues to develop and species continue to be described, the need for an infrageneric classification begins to become evident. In our current phylogenetic study, we have sampled 10 out of the 19 currently accepted species. Nonetheless, since estimates are that over 30 species are still awaiting formal description (Leong-Škorničková and Boyce 2015), it seems extremally premature to interpret these results and propose any classification at all. Further morphological and molecular studies are still needed before such system can be properly proposed.

Accepted species. A total of 19 accepted species, but with many new species still undescribed, totaling ca. 50 spp. (Leong-Škorničková and Boyce 2015): Hanguana anthelminthica (Blume ex Schult. & Schult.f.) Masam., H. bakoensis Siti Nurfazilah et al., H. bogneri Tillich & E.Sill, H. corneri Škorničk. & P.C.Boyce, H. exultans Siti Nurfazilah et al., H. fraseriana Škorničk. & Kiew, H. kassintu Blume, H. loi Mohd Fahmi et al., H. major Airy Shaw, H. malayana (Jack) Merr., H. minor (Miq.) Škorničk. & Niissalo, H. neglecta Škorničk. & Niissalo, H. nitens Siti Nurfazilah et al., H. pantiensis Siti Nurfazilah et al., H. podzolica Siti Nurfazilah et al., H. rubinea Škorničk. & P.C.Boyce, H. stenopoda Siti Nurfazilah et al., H. thailandica Wijedasa & Niissalo, and H. triangulata Škorničk. & P.C.Boyce.

3. Philydraceae Link, Enum. Hort. Berol. Alt. 1: 5. 1821, nom. cons. Type genus. *Philydrum* Banks & Sol. ex Gaertn.Fig 15

Description. Herbs monoecious, perennial, aquatic, amphibious or paludal. Roots thin, fibrous or spongy, glabrous or pilose, not sand-binding, lacking a rhizosheath. Underground stem a rhizome or a corm. Stems aerial or submerged, erect, herbaceous, unbranched to branching only at the base, sometimes rooting at the basal nodes; internodes contracted. Immature leaves persistent throughout the plant's life, equitant, unifacial, congested at the apex of the stem; ptyxis conduplicate; sheaths open, margins non-marcescent; ligule absent; pseudopetioles absent; blades ensiform to linear to terete, base truncate, apex acute or acuminate, membranous, coriaceous or spongy; midvein inconspicuous. Mature leaves never produced. Synflorescence composed of a solitary main florescence or by 1-several coflorescences, synflorescence leaves equal to the regular leaves or not, but generally reduced in size and becoming bifacial towards the apex. Main florescences (inflorescences) terminal, consisting of a pedunculate, many-branched thyrse or reduced to a solitary cincinnus; basal bract leaf-like; accessory bracts present or not, buds producing inflorescence primordia; main axis developed; cincinnus' bract present, bracteose, reducing in size towards the apex of the main florescence; cincinni many per thyrse, alternate, 2-many-flowered, sessile to subsessile, internodes contracted or elongate; bracteoles present, bracteose or spathaceous. Flowers resupinate, hermaphrodite, sessile or shortly-pedicellate, chasmogamous, homostylous, enantiostylous, asymmetric due to the position of the style, hypanthium absent, perianth homochlamydeous, petaloid, somewhat campanulate to infundibuliform, white or light pink or yellow to lemon-yellow, persistent in fruit, the paired outer anterior tepals fused to the

medial inner tepal, forming a labellum-like lobe, lobes 4 (2 external and 2 internal), the external free or basally connate, longer and wider than the internal, patent or involute, the internal free or connate to the stamen, straight or curved inwards; stamen 1, ca. as long or longer than the inner lobes, filaments straight, terete, medially inflated or not, glabrous, anthers basifixed, rimose, introrse, connective inconspicuous, anther sacs elongate, spirally-coiled or C- or hook-shaped; ovary superior, 1–3-locular, all fertile, placentation axile or intrusive-parietal, ovules many per locule, style elongate, stigma truncate or capitate. *Fruit* a capsule or berry, many-seeded. *Seeds* oblongoid or ellipsoid, exarillate, testa reticulate or striate or spirally-striate or striate with short dactyliform projections; chalazal cap prominent; hilum punctate; embryotega dorsal, inconspicuous.

Comments. Philydraceae is the smallest family in Commelinales, being composed of four genera and eight species (Pellegrini, in prep.). It is micro- and macromorphologically, taxonomically and phylogenetically well-understood, having been the focus of several studies (Skottsberg 1932, 1934; Hamann 1966; Simpson 1985; Adams 1987; Prychid and Rudall 1999; Saarela et al. 2008). It is recovered as sister to Haemodoraceae + Pontederiaceae, being supported by unifacial and equitant leaves, flowers resupinate and homochlamydeous petaloid, styloid crystals present, sepals partially to completely fused to the petals, multiseriate ovules, the presence of placental sclereids, and seedling with primary leaves all expanded, unifacial or bifacial and ribbon-like. Philydraceae can be easily recognized by its unifacial equitant leaves, flowers pseudotetramerous, posterior perianth lobe formed by the fusion of two members of the outer whorl to one member of the inner whorl, one stamen, ameboid tapetum, and seeds with enlarged chalazal cap.

Phylogeny and generic limits. The present study provides the second phylogenetic hypothesis for Philydraceae, the first one having been proposed by Saarela et al. (2008). The topology produced by us differs from the one by Saarela et al. (2008) in the backbone but highlights the relevance of morphological characters when interpreting molecular-base topologies. In Saarela et al. (2008), *Philydrella* is sister to the remainder of Philydraceae, subsequently followed by the monospecific *Philydrum*, sister to *Helmholtzia* and *Orthothylax*. In our analysis, *Helmholtzia* is sister to *Orthothylax*, but with low statistical support, while *Philydrella* is sister to *Philydrum*, also with low statistical support. The strict consensus of our analysis recovers all four genera in a polytomy, and thus, *Helmholtzia* s.lat. is paraphyletic, and *Orthothylax* must be reestablished. Nonetheless, in the topology recovered by Saarela et al. (2008) *Orthothylax* is sister to *Helmholtzia*, which makes its recognition optional. When the morphology of the whole family is put into perspective, it is clear that the morphological differences between *O. glaberrimus* and the two species of *Helmholtzia* is equivalent to the difference between any other genera. Thus, we reestablish *Orthothylax* as distinct from *Helmholtzia*, in order to maintain morphologically cohesive genera.

Distribution. Restricted to Australasia.

Key to the genera of Philydraceae (modified from Pellegrini in prep.)

- 1. Flowers sessile, perianth basally connate (urceolate), inner perianth lobes apically tridentate, stamen basally adnate to the posterior outer perianth lobe, anther 3 times longer than the filament, gynoecium synseptalous; fruit a berry, sometimes partially dehiscent; seeds testa with short dactyliform projections... *Helmholtzia* F.Muell. (Fig 15A)
- Flowers shortly pedicellate, perianth free, inner perianth lobes apically entire, stamen free from the posterior outer perianth lobe, anther ca. the same length or shorter than the

- filament, gynoecium hemiseptalous or aposeptalous; fruit a loculicidal capsule; seeds testa lacking dactyliform projections... 2
- 2. Leaves flat, evenly green; thyrsi many-branched, bracteoles bracteose; perianth fleshy, pale to medium pink, stamen free from the inner perianth lobes, anthers sacs straight, ovary anterior locule reduced or aborted, style flattened, with an abruptly-conical base; capsules subglobose, with a sunken apex... *Orthothylax* (Hook.f.) Skottsb. (Fig 15B)
- Leaves sub-terete to terete, generally partially or completely flushed with red or maroon; thyrsi reduced to a solitary cincinnus, bracteoles spathaceous; perianth membranous, yellow to lemon-yellow, stamen adnate at base up to 2/3 of the inner perianth lobes, anther sacs curved or spirally-coiled, ovary with evenly developed locules, style cylindrical, with a tapered base; capsules ellipsoid, with a apiculate apex... 3
- 3. Plants diminute, cormose; leaves 1–2, dyeing off during the dry season, solid and lacking aerenchyma; flowers with receptacle lacking aerenchyma, outer perianth lobes rhomboid, flat to slightly repandous, filament thin, curved, connective expanded, pollen released in monads, tectum verrucose; seeds testa reticulate... *Philydrella* Caruel (Fig 15C)
- Plants robust, rhizomatous; leaves many, perennial, fistulose with aerenchyma; flower with receptacle aerenchymatous, outer perianth lobes ovate to broadly ovate, plicate, filament stout and medially broadened, straight, connective inconspicuous, pollen release in tetrads, tectum foveolate; seeds testa spirally-striate... *Philydrum* Banks & Sol. ex Gaertn. (Fig 15D)
- **3.1.** *Helmholtzia* **F.Muell.**, Fragm. 5: 202. 1866 ≡ *Philydrum* sect. *Helmholtzia* (F.Muell.) Baill., Hist. Pl. 13: 234. 1894. Type species. *Helmholtzia acorifolia* F.Muell. Fig 15A

Distribution and ecology. Restricted to northwestern Australia, Indonesia and Papua New Guinea. The type, *H. acorifolia*, is endemic to the Queensland territory, Australia, while *H. novoguineensis* is endemic to the New Guinea island. Both species are found growing in rainforest gullies and vegetation along streams.

Comments. *Helmholtzia* can be easily differentiated from the closely related *Orthothylax* by its urceolate flowers, inner perianth lobes apically tridentate, stamen basally adnate to the posterior outer perianth lobe, and fleshy fruits.

Accepted species. A genus of two morphologically very similar species, differentiated by minor floral characters and their allopatric distribution: *Helmholtzia acorifolia* F.Muell. and *H. novoguineensis* (K.Krause) Skottsb.

3.2. Orthothylax (Hook.f.) Skottsb., Bot. Jahrb. Syst. 65: 264. 1932 ≡ Philydrum sect. Orthothylax Hook.f., Bot. Mag. 99: t. 6056. 1873. Type species. Philydrum glaberrimum Hook.f. [≡ Orthothylax glaberrimus (Hook.f.) Skottsb.]. Fig 15B

Distribution and ecology. Endemic to Australia, more precisely to the New South Wales and Queensland territories, found growing in rainforest gullies and vegetation along streams.

Comments. Orthothylax has recently been treated as a synonym of Helmholtzia. Nonetheless, O. glaberrimus presents more differences with the latter than similarities, and thus is here reestablished.

Accepted species. Orthothylax glaberrimus (Hook.f.) Skottsb.

3.3. Philydrella Caruel, Nuovo Giorn. Bot. Ital. 10: 91. 1878. Type species. Philydrella pygmaea (R.Br.) Caruel.Fig 15C

- Hetaeria Endl. Gen. Pl.: 133. 1836, nom, illeg. non Hetaeria Blume, Bijdr. Fl. Ned. Ind. 8: 409. 1825. Type species. Hetaeria pygmaea (R.Br.) Endl. [≡ Philydrella pygmaea (R.Br.) Caruel].
- Pritzelia F.Muell. Descr. Notes Papuan Pl. 1: 13. 1875, nom. illeg. non Pritzelia Walp.,
 Repert. 2: 428. 1843, nec Pritzelia Schauer Flora 26: 407. 1843. Type species. Pritzelia pygmaea (R.Br.) F.Muell. ex Benth. [≡ Philydrella pygmaea (R.Br.) Caruel].
- Philydrum sect. Pritzelia Baill., Hist. Pl. 13: 234. 1894. Type species. Philydrum pygmaeum R.Br. [≡ Philydrella pygmaea (R.Br.) Caruel].

Distribution and ecology. Endemic to Western Australia, growing in freshwater swamps, seasonally flooded white-sand formations, and seepage areas.

Comments. *Philydrella* can be easily differentiated from the other three genera of Philydraceae by its diminute cormose habit, rhomboid outer perianth lobes, thin filament, expanded connective, pollen grains with, tectum verrucose, and seeds with reticulate testa.

Accepted species. A small genus represented by three morphologically similar species: *Philydrella drummondii* L.G.Adams, *P. minima* (L.G.Adams) M.Pell., and *P. pygmaea* (R.Br.) Caruel.

3.4. *Philydrum* Banks & Sol. ex Gaertn., Fruct. Sem. Pl. 1: 62. 1788 ≡ *Philydrum* Banks & Sol. ex Gaertn. sect. *Philydrum*. Type species. *Philydrum lanuginosum* Banks & Sol. ex Gaertn.

Fig 15D

Garciana Lour., Fl. Cochinch.: 14. 1790. Type species. Garciana cochinchinensis Lour. [≡ Philydrum cochinchinense (Lour.) M.Pell.].

Philydrum sect. Garciana (Lour.) Baill., Hist. Pl. 13: 233. 1894.

Distribution and ecology. Known to occur in Australia (New South Wales, Northern Territory, Queensland, Victoria, Western Australia), Southeast China, India (Andaman Islands), Japan (Ryukyu Islands), Malaysia, Myanmar, Micronesia, New Guinea, Palau, Taiwan, Thailand, and Vietnam. It grows in freshwater swamps and drainage areas.

Comments. *Philydrum* is unique in possessing spongy and fistulose leaves, plicate outer perianth lobes, filament stout and medially broadened, inconspicuous connective, pollen release in tetrads with foveolate tectum, and seeds testa spirally-striate.

Accepted species. A total of two species: *Philydrum cochinchinense* (Lour.) M.Pell. and *P. lanuginosum* Banks & Sol. ex Gaertn.

4. Haemodoraceae R.Br., Prodr.: 299. 1810, nom. cons. Type genus. *Haemodorum* Sm. Fig 16

Wachendorfiaceae Herb., Amaryllidaceae: 48. 1837. Type genus. *Wachendorfia* Burm. Dilatridaceae M.Roem., Handb. Allg. Bot. 3: 476. 1840, as "Dilatrideae". Type genus. *Dilatris* P.J.Bergius.

Conostylidaceae Takht., Sist. Magnoliof. [Syst. Magnolioph.]: 313. 1987. Type genus. *Conostylis* R.Br.

Description. Herbs monoecious, perennial, terrestrial, or paludal. Roots thin and fibrous, arachnoid, sometimes glabrous or pilose, sand-binding or not, rhizosheath present or not. Underground stem a rhizome or a corm, sometimes a bulb. Stems aerial, erect, herbaceous, unbranched to branching only at the base, sometimes rooting at the basal nodes; internodes contracted. Immature leaves persistent throughout the plant's life, equitant, unifacial, congested at the base or apex of the stem; ptyxis conduplicate; sheaths open, margins non-marcescent; ligule absent; pseudopetioles absent; blades ensiform to linear, falcate or subterete to terete, rarely twisted or plicate or conduplicate-keeled, base truncate, apex acute or acuminate, coriaceous, rarely spongy; midvein inconspicuous. Mature leaves never produced. Synflorescence composed of a solitary main florescence or by 1-several coflorescences, synflorescence leaves equal to the regular leaves or not, but generally reduced in size and becoming bifacial towards the apex. Main florescences (inflorescences) terminal, consisting of a pedunculate, many-branched thyrse or reduced to a solitary cincinnus or branched cyme; basal bract leaf-like; accessory bracts present or not, buds producing inflorescence primordia; main axis developed or not; secondary branch's bract present or not, when present bracteose, reducing in size towards the apex of the main florescence; cincinni or branched cymes many per thyrse, alternate, 1-many-flowered, sessile to pedunculate, internodes contracted or elongate; bracteoles present, inconspicuous or bracteose or leaf-like but distinct from the cincinni bracts or spathaceous. Flowers resupinate, rarely nonresupinate, hermaphrodite, sessile or shortly-pedicellate, chasmogamous, cleistogamous, homostylous, enantiostylous, asymmetric due to the position of the style, hypanthium absent, perianth homochlamydeous, petaloid, infundibuliform or tubular or urceolate, sometimes bilabiate or campanulate, rarely rotate, yellow or orange or red, sometimes green or white or purple to vinaceous or maroon or black, rarely mauve, persistent in fruit, lobes 6 (3 outer and 3 inner), 3 superior + 3 inferior or 5 superior + 1 inferior, anterior lobes sometimes with a nectar guide, consisting of 3 spots, spots orange to red to maroon, rarely green, rarely surrounded by a dark purple to maroon line; stamens (1-)3-6, epipetalous, monomorphic or dimorphic, filaments straight or curved, rarely twisted, terete, glabrous, rarely eglandular-pubescent, anthers basifixed or dorsifixed, rarely medifixed, versatile or not, rimose, introrse, sometimes extrorse, rarely introrse but functionally poricidal, connective inconspicuous, sometimes expanded, anther sacs elongate; ovary inferior, sometimes half-inferior or superior, (1–)3-locular, (1–)3 fertile, placentation axile, rarely central, ovules (1-)many per locule, septal nectaries present, rarely absent or nonfunctional, when present 2-3, infra- or inter- or supralocular, style elongate, straight or curved, rarely spirally-coiled, stigma triparted or capitate or trilobed to subtrilobed or truncate to capitulate, rarely tuberculate. Fruit a capsule with loculicidal dehiscence or sometimes septifragal, sometimes and achene, rarely a coccarium or a berry, (1–)many-seeded; anthocarp present only in *Dilatris*, thin and papery, crowned by 6 persistent perianth lobes, adnate to the

fruit due to its inferior ovary origin. *Seeds* globose to subglobose or lenticellate or ovoid or fusiform to barrel-shaped, sometimes irregular and angled, rarely elliptic to oblong or deltoid or cuboid, exarillate, testa generally longitudinally striated or scabrid, sometimes covered with dactyliform projections, reticulate to foveolate or rugose or tuberculate, rarely smooth; chalazal cap inconspicuous; hilum punctate; embryotega dorsal, inconspicuous.

Comments. Haemodoraceae is the second largest family in Commelinales, with 13 genera and ca. 160 species, taking into account all the still undescribed species (Pellegrini and Hopper, pers. observ.). It is micro- and macromorphologically, taxonomically and phylogenetically well-understood, having been the focus of several studies (Aerne-Hains and Simpson 2017; Hopper et al. 1999, 2009, in prep., Pellegrini et al., in prep.; Prychid and Rudall 1999; Simpson 1990). It is recovered as sister to Pontederiaceae, being supported by flowers with a hypanthium, the presence of septal nectaries (secondarily lost in some genera), endothecium with a basal thickening, pollen with exine non-tectate-columellate, sulcal membrane verrucate, neighboring cells of the stomata with oblique division, and the presence of phenylphenalenones. Haemodoraceae can be easily recognized by its roots with a sclerified endodermis, conduplicate ptyxis, monomorphic leaves, ligule absent, blades fibrous and coriaceous, secondary branches of the main florescence a branched cyme (secondarily lost in some genera/species), anthocarp absent, if present derived from a inferior ovary and anemochoric, pollen monosulcate or bi–many-porate, ovary wall lacking aerenchyma, and multiseriate hairs generally present.

Distribution. Disjunctive among Australasia, Cape Region (Africa), and the American continent.

Key to the subfamilies of Haemodoraceae

- 1. Hairs branched and/or dendritic; roots and stems internally pale; leaves with tannin cells; flowers non-enantiostylous, perianth with valvate aestivation (except for *Phlebocarya*), stamens 6, pollen grains porate; cotyledonary sheath lacking any kind of projection... **Conostylidoideae Lindl.** (Fig 16A–I)
- Hairs pilate with a basal cell-rosette; roots and stems internally yellow to orange to red to purple; leaves lacking tannin cells; flowers enantiostylous, perianth with imbricate aestivation, stamens (1–)3, pollen grains sulcate; cotyledonary sheath with a pair of lobes... Haemodoroideae Arn. (Fig 16J-T)
- 4.1. Subfamily Conostylidoideae Lindl., Veg. Kingd.: 153. 1846, as "Conostyleae". Type genus. Conostylis R.Br.
 Fig 16A–I

Distribution. Endemic to Australia.

Comments. The largest subfamily, due to the great number of species in *Conostylis*. Generic limits have been controversial, due to the recognition of monospecific genera, such as *Blancoa* and *Macropidia*. We currently accept only four genera in Conostylidoideae, since the recognition of the two aforementioned monospecific genera is of no evolutionary value, and morphologically, there is no justification for recognizing them (see morphologically-based topologies in Results). The subfamily is further divided into two tribes.

Key to the tribes of Conostylidoideae

- 1. Plants lacking dendritic hairs; flowers lanate with branched hairs, rarely glabrous, filaments with a dorsal appendage, anthers medifixed... **Tribonantheae T.D.Macfarl. & Hopper (Fig 16A)**
- Plants with dendritic hairs; flowers glabrous or tomentose with dendritic hairs, filaments lacking a dorsal appendage, anthers basifixed... Conostylideae Benth. (Fig 16B–I)
- **4.1.1. Tribe Tribonantheae T.D.Macfarl. & Hopper**, Fl. Australia 45: 454. 1987. Type genus. *Tribonanthes* Endl. Fig 16A

Distribution. Endemic to Australia.

Comments. Tribonantheae is monogeneric and described to accommodate the peculiar *Tribonanthes*. It can be differentiated from tribe Conostylideae by the lack of dendritic hairs, only presenting simple branched hairs, flowers with lanate perianth, the presence of a dorsal filament appendage, and medifixed anthers.

4.1.1.1. *Tribonanthes* Endl., Nov. Stirp. Dec.: 27. 1839. Type species. *Tribonanthes australis* Endl.

Fig 16A

Distribution and ecology. *Tribonanthes* is most diverse in higher rainfall provinces of the SWAFR (Gioia and Hopper 2017), with a few species penetrating further inland in locally mesic habitats afforded by granite outcrops or seasonal damplands. Endemic to Western Australia, growing in dry or seasonally wet sand (Hickman and Hopper 2019).

Comments. A genus of 12 species (Hickman and Hopper 2019).

Infrageneric classification. The infrageneric classification follows the one proposed by Hickman and Hopper (2019), which recognize three subgenera, based on a yet unpublished molecular phylogeny for *Tribonanthes*. It is not supported by our morphological analysis, but further morphological studies are necessary to test the morphological support for this classification.

Key to the subgenera of *Tribonanthes* **(modified from Hickman and Hopper 2019)**

- 1. Perianth purplish pink, tube long, lobes erect, apex with glandular papillae... *Tribonanthes* subg. *Boya* E.J.Hickman & Hopper
- Perianth white to purple, rarely green or vinaceous, tube inconspicuous, lobes patent to slightly recurved or deflexed, apex lacking glandular papillae... 2
- 2. Aerial stems up to 3 cm tall; flowers zygomorphic due to lateral compression of the perianth tube, patent, perianth adaxially glabrous... *Tribonanthes* subg. *Salina* E.J.Hickman & Hopper
- Aerial stems longer than 5 cm tall; flowers actinomorphic, erect or pendulous, perianth adaxially pubescent... *Tribonanthes* Endl. subg. *Tribonanthes* (Fig 16A)

4.1.1.1. *Tribonanthes* **subg.** *Salina* **E.J.Hickman** & **Hopper**, Nuytsia 30: 144. 2019. Type species. *Tribonanthes minor* M.Lyons & Keighery.

Characterization. *Tribonanthes* subg. *Salina* is characterized by its minute stature, zygomorphic flowers, and perianth lobes, green to vinaceous, triangular, and deflexed.

Circumscription. Monospecific, composed solely by *T. minor*. Nonetheless, in our morphological analysis, *T. brachypetala* is recovered as sister to *T. minor*, supported by globose floral buds, flower not erect (either patent or pendulous), and perianth lobes, green to vinaceous, triangular and deflexed. Further studies are needed in order to properly place *T. brachypetala*.

Distribution and ecology. Known from scattered populations from the Meckering area south to the Lake King area. Populations are located in the Wongan District of the Transitional Rainfall Province and Maalak District of the Southeast Coastal Province of south-west Western Australia (Gioia and Hopper 2017; Hickman and Hopper 2019). It grows on seasonally wet, low sandy rises on the margins of naturally saline lakes (Hickman and Hopper 2019).

Accepted species. *Tribonanthes minor* M.Lyons & Keighery.

4.1.1.1.2. *Tribonanthes* **subg.** *Boya* **E.J.Hickman** & **Hopper**, Nuytsia 30: 145. 2019. Type species. *Tribonanthes purpurea* T.D.Macfarl. & Hopper.

Characterization. *Tribonanthes* subg. *Boya* is morphologically peculiar due to its purplish pink and glabrous flowers, long perianth tube, erect perianth lobes, lobes apically with glandular papillae, reduced dorsal filament appendage, and long style.

Distribution and ecology. Known from the Mt Dale area in the Darling Range to the Porongurup Range, and east to Varley. Populations are located within the Jarrah and Narrogin Districts of the Bibbulmun Province, the Hyden District of the Transitional Rainfall Province, and the Maalak and Fitzgerald-Stirling Districts of the Southeast Coastal Province of Western Australia (Gioia and Hopper 2017; Hickman and Hopper 2019). It mostly grows on brown sandy loam associated with granite outcrops but has also been found growing on grey sandy clays of winter wet flats (Hickman and Hopper 2019).

Accepted species. *Tribonanthes purpurea* T.D.Macfarl. & Hopper.

4.1.1.13. *Tribonanthes* **Endl. subg.** *Tribonanthes*. Type species. *Tribonanthes australis* Endl.

Fig 16A

Characterization. *Tribonanthes* subg. *Tribonanthes* is characterized by its erect and star-shaped flowers, perianth ranging from white to purple, densely covered by lanate, white, branched hairs, and perianth lobes patent to slightly recurved.

Distribution and ecology. Western Australia, growing on granite outcrops or seasonal damplands or in shallow pools.

Accepted species. It is composed of 10 species, but *T. brachypetala* does not seem to completely fit here (see comment above): *Tribonanthes australis* Endl., *T. brachypetala* Lindl., *T. elongata* E.J.Hickman & Hopper, *T. keigheryi* E.J.Hickman & Hopper, *T. longipetala* Lindl., *T. monantha* E.J.Hickman & Hopper, *T. porphyrea* E.J.Hickman & Hopper, *T. uniflora* Lindl., *T. variabilis* Lindl., and *T. violacea* Endl.

4.1.2. Tribe Conostylideae Benth., Fl. Austral. 6: 417. 1873, as "Conostyleae". Type genus. Conostylis R.Br.

Fig 16B–I

Phlebocaryeae Meisn., Pl. Vasc. Gen.: tab. diagn. 396, comm. 299. 1842, **Syn. nov.** Type genus. *Phlebocarya* R.Br.

Distribution. Endemic to Australia.

Comments. Conostylideae is currently composed of three genera, being characterized by the presence of dendritic hairs, flowers generally tomentose with dendritic hairs, filaments lacking a dorsal appendage, and anthers basifixed.

Key to the genera of Conostylideae

- 1. Floral buds obovoid, flowers zygomorphic, perianth longitudinally split, lacking a supraovarian constriction, internally pubescent with dendritic hairs, style tapering at base... *Anigozanthos* Labill. (Fig 16B–D)
- Floral buds ellipsoid, flowers actinomorphic, perianth not longitudinally split, with a supraovarian constriction, internally glabrous, style conic-dilatated at base... 2
- 2. Flowers glabrous, lacking a perianth tube, ovules epitropous... *Phlebocarya* R.Br. (Fig 16E)
- Flowers pubescent, generally with a short to conspicuous perianth tube, rarely lacking a perianth tube, ovules hypotropous... *Conostylis* **R.Br.** (Fig 16F-H)
- **4.1.2.1.** *Anigozanthos* Labill., Voy. Rech. Pérouse 1: 410. 1800. Type species. *Anigozanthos rufus* Labill.

Fig 16B-D

- Anigosia Salisb., Trans. Hort. Soc. London 1: 327. 1812. Type species. Anigosia flavida (DC.) Salisb. (≡ Anigozanthos flavidus DC.).
- *Schwaegrichenia* Spreng. Pl. Pugil. 2: 58. 1815, nom. superfl. Type species (designated here). *Schwaegrichenia flavida* (DC.) Spreng. (≡ *Anigozanthos flavidus* DC.).
- Macropidia J.Drumm. ex Harv., Hooker's J. Bot. Kew Gard. Misc. 7: 57. 1855. Type species. Macropidia fumosa J.Drumm. ex Harv., nom. superfl. (≡ Anigozanthos fuliginosus Hook.).

Distribution and ecology. *Anigozanthos* is endemic to Western Australia, growing in dry or seasonally wet sand.

Comments. *Anigozanthos* would greatly benefit from a modern taxonomic revision. Furthermore, based on available molecular and morphological data, all accepted infraspecific taxa should be recognized at the specific rank.

Infrageneric classification. The infrageneric classification proposed by Hopper (1987), recognizes two subgenera, with the first one being further divided into three sections. Nonetheless, all infrageneric ranks are recovered as non-monophyletic in all molecular (Hopper et al. 1999, 2009, in prep.) and morphological (Simpson 1990; present study) phylogenetic studies. Thus, we do not accept any infrageneric classifications for *Anigozanthos* in the present study. The apparent incongruence between the morphological and molecular phylogenies might be due to the lack of informative taxonomic characters for the group. Further morphological studies, especially regarding vegetative and floral anatomy, might help solve this incongruence between datasets and propose a new classification system for *Anigozanthos*.

Accepted species. A total of 17 species: Anigozanthos bicolor Endl., A. chrysanthus (Hopper) M.Pell. & Hopper, A. decrescens (Hopper) M.Pell. & Hopper, A. exstans (Hopper) M.Pell. & Hopper, A. flavidus Redouté, A. gabrielae Domin, A. humilis Lindl., A. kalbarriensis Hopper, A. manglesii D.Don, A. minor (Benth.) M.Pell. & Hopper, A. onycis A.S.George, A. preissii Endl., A. pulcherrimus Hook., A. quadrans (Hopper.) M.Pell. & Hopper, A. rufus Labill., A. terraspectans (Hopper.) M.Pell. & Hopper, and A. viridis Endl.

New combinations. *Anigozanthos chrysanthus* (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Anigozanthos humilis* subsp. *chrysanthus* Hopper, Fl. Australia 45: 456. 1987.

Anigozanthos decrescens (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Anigozanthos bicolor* subsp. *decrescens* Hopper, Fl. Australia 45: 455. 1987.

Anigozanthos exstans (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Anigozanthos bicolor* subsp. *exstans* Hopper, Fl. Australia 45: 455. 1987.

Anigozanthos minor (Benth.) M.Pell. & Hopper, **stat. nov.** \equiv Anigozanthos bicolor var. minor Benth., Fl. Austral. 6: 446. $1873 \equiv$ Anigozanthos bicolor subsp. minor (Benth.) Hopper, Fl. Australia 45: 455. 1987.

Anigozanthos quadrans (Hopper.) M.Pell. & Hopper, **stat. nov.** ≡ *Anigozanthos manglesii* subsp. *quadrans* Hopper, Fl. Australia 45: 456. 1987.

Anigozanthos terraspectans (Hopper.) M.Pell. & Hopper, **stat. nov.** ≡ *Anigozanthos viridis* subsp. *terraspectans* Hopper, Fl. Australia 45: 456. 1987.

4.1.2.2. *Conostylis* **R.Br.**, Prodr.: 300. 1810. Type species. *Conostylis aculeata* R.Br. Fig 16F–H

Distribution and ecology. *Conostylis* is endemic to Western Australia, growing in dry or seasonally wet sand.

Comments. Conostylis needs a taxonomic revision focusing on poorly explored characters in the genus. As evidenced by our analyses, anatomical characters are promising and should be further explored.

Accepted species. Based on available molecular and morphological data, it seems that most accepted infraspecific taxa should be recognized at the specific rank since several don't coalesce either in molecular or morphologic phylogenies. With the necessary changes, *Conostylis* has a total of 69 species.

Infrageneric classification. The infrageneric classification proposed by Hopper et al. (1987), recognizes five subgenera, with *C.* subg. *Pendula* being further divided into three sections. Nonetheless, molecular data recover all non-monospecific subgenera as non-

monophyletic (Hopper et al. 2006). Conostylis subg. Conostylis is rendered monophyletic with the transfer of C. lepidospermoides Hopper to C. subg. Pendula. Conostylis subg. Pendula sect. Appendiculae is monophyletic, but recovered as sister to C. subg. Conostylis (Hopper et al. 2006), and thus is here recognized as a subgenus. Conostylis subg. Pendula sect. Catosporae is paraphyletic due to C. subg. Androstemma, subg. Greenia, C. neocymosa (subg. Pendula sect. Divaricatae), and C. lepidospermoides being nested within it (Hopper et al. 2006). With the inclusion of these taxa, the section is rendered monophyletic and is treated by us at the subgeneric rank as C. subg. Pendula. Conostylis subg. Brachycaulon is recircumscribed to include C. subg. Bicolorata and the type of C. subg. Pendula sect. Divaricata. Finally, Blancoa is here recognized as a subgenus. Thus, we recognize five subgenera and, for the time being, no sections in Conostylis.

Key to the subgenera of Conostylis

- 1. Flowers pendulous, perianth tubular, orange to red, with supra-ovarian nectar pockets... *Conostylis* subg. *Blancoa* (Lindl.) M.Pell. & Hopper (Fig 16F)
- Flowers erect to upright, perianth campanulate or urceolate, rarely rotate or tubular, yellow (at anthesis), rarely white, lacking supra-ovarian nectar pockets... 2
- 2. Connectives inconspicuous, anther sacs parallel, ovules many over a hemispheric placenta... *Conostylis* **R.Br. subg.** *Conostylis*
- Connectives expanded at least at base, anther sacs divergent at base or from the middle downwards, apex connivent, ovules few and pendulous from a peltate placenta, rarely several on the lateral and lower sides of a more or less hemispheric placenta... 3
- 3. Inflorescences terminal, erect; flowers sessile, perianth urceolate, connectives dorsally decurrent from middle upwards, with two horn-like appendages... *Conostylis* subg. *Appendiculae* (Geer.) M.Pell. & Hopper
- Inflorescences axillary, prostrate; flowers short-pedicellate, perianth campanulate or tubular, rarely rotate, connectives dorsally decurrent from base upwards, lacking appendages... 4
- 4. Flowers concolorous at post-anthesis, anthers geniculate... *Conostylis* subg. *Brachycaulon* (Benth.) Hopper (Fig 16I)
- Flowers becoming red or flushed with red at post-anthesis, anthers erect... *Conostylis* subg. *Pendula* Hopper (Fig 16G & H)
- **4.1.2.2.1.** Conostylis subg. Blancoa (Lindl.) M.Pell. & Hopper, comb. et stat. nov. ≡ Blancoa Lindl., Edwards's Bot. Reg.: 45. 1840 ≡ Styloconus Baill., Hist. Pl. 13: 75. 1894, nom. superfl. ≡ Conostylis sect. Blancoa (Lindl.) Kuntze in von Post & Kuntze, Lex. Gen. Phan.: 1903. Type species. Blancoa canescens Lindl. [≡ Conostylis canescens (Lindl.) F.Muell.].

Fig 16F

Characterization. Conostylis subg. Blancoa is characterized by its terminal and decumbent inflorescence, pendulous flowers with orange to red, tubular, and concolorous at post-anthesis perianth, straight anthers, and by the peculiar septa which partially fuses the perianth to the pistil, producing supra-ovarian nectar pockets.

Distribution and ecology. Endemic to the northern sandplains and Perth regions of Western Australia.

Accepted species. Conostylis canescens (Lindl.) F.Muell.

4.1.2.2.2. Conostylis R.Br. subg. Conostylis ≡ Conostylis sect. Euconostylis Benth., Fl. Austral. 6: 429. 1873. Type species. Conostylis aculeata R.Br.

Characterization. *Conostylis* subg. *Conostylis* is characterized by its terminal and erect inflorescences, sessile flowers, perianth generally urceolate, concolorous at post-anthesis, anther straight, connectives inconspicuous, anther sacs parallel, many ovules over a hemispheric placenta.

Circumscription. Its composition is the same as the one adopted by Hopper et al. (1987), with the exception of *C. lepidospermoides*, which is here transferred to *C.* subg. *Pendula*.

Distribution and ecology. Widespread in Western Australia.

Accepted species. A total of 29 species: Conostylis aculeata R.Br., C. bracteata Endl., C. breviflora (Hopper) M.Pell. & Hopper, C. bromelioides Endl., C. calcicola (Hopper) M.Pell. & Hopper, C. candicans Endl., C. cygnorum (Hopper) M.Pell. & Hopper, C. echinissima (Hopper) M.Pell. & Hopper, C. echinissima (Hopper) M.Pell. & Hopper, C. festucacea Endl., C. filifolia F.Muell., C. flavifolia (Hopper) M.Pell. & Hopper, C. gracilis (Hopper) M.Pell. & Hopper, C. juncea Endl., C. laxiflora Benth., C. longissima (Hopper) M.Pell. & Hopper, C. misera Endl., C. pauciflora Hopper, C. preissii Endl., C. procumbens (Hopper) M.Pell. & Hopper, C. prolifera Benth., C. rhipidion (J.W.Green) M.Pell. & Hopper, C. robusta Diels & E.Pritz., C. seorsiflora F.Muell., C. septentrionora (Hopper) M.Pell. & Hopper, C. serrulata R.Br., C. spinuligera F.Muell. ex Benth., C. stylidioides F.Muell., and C. trichophylla (Hopper) M.Pell. & Hopper,

New combinations. *Conostylis breviflora* (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis aculeata* subsp. *breviflora* Hopper, Nuytsia 2: 261. 1978.

Conostylis calcicola (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis candicans* subsp. *calcicola* Hopper, Fl. Australia 45: 459. 1987.

Conostylis cygnorum (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis aculeata* subsp. *cygnorum* Hopper, Fl. Australia 45: 457. 1987.

Conostylis echinissima (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ Conostylis aculeata subsp. echinissima Hopper, Fl. Australia 45: 458. 1987.

Conostylis euryrhipis (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis pauciflora* subsp. *euryrhipis* Hopper, Fl. Australia 45: 461. 1987.

Conostylis flavifolia (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis candicans* subsp. *flavifolia* Hopper, Fl. Australia 45: 459. 1987.

Conostylis gracilis (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis aculeata* subsp. *gracilis* Hopper, Fl. Australia 45: 458. 1987.

Conostylis longissima (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis scorsiflora* subsp. *longissima* Hopper, Fl. Australia 45: 462. 1987.

Conostylis procumbens (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis candicans* subsp. *procumbens* Hopper, Fl. Australia 45: 459. 1987.

Conostylis rhipidion (J.W.Green) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis aculeata* subsp. *rhipidion* J.W.Green, Proc. Linn. Soc. New South Wales 85: 348. 1961.

Conostylis septentrionora (Hopper) M.Pell. & Hopper, stat. nov. \equiv Conostylis aculeata subsp. septentrionora Hopper, Fl. Australia 45: 458. 1987.

Conostylis trichophylla (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis scorsiflora* subsp. *trichophylla* Hopper, Fl. Australia 45: 462. 1987.

4.1.2.2.3. Conostylis subg. Appendiculae (Geer.) M.Pell. & Hopper, stat. nov. ≡ Conostylis sect. Appendiculae Geer., Bull. Jard. Bot. État. 39: 64. 1969. Type species. Conostylis aurea Lindl.

Characterization. *Conostylis* subg. *Appendiculae* is characterized by its erect and terminal inflorescences, sessile flowers, perianth urceolate, connectives dorsally decurrent from the middle upwards, with two horn-like appendages, and ovules few and pendulous from a peltate placenta.

Distribution and ecology. Widespread in Western Australia, growing in seasonally or permanently wet sands.

Accepted species. Its composition is the same as the one adopted by Hopper et al. (1987), composed of six species: *Conostylis angustifolia* Hopper, *C. aurea* Lindl., *C. hiemalis* Hopper, *C. resinosa* Hopper, *C. seminuda* Hopper, and *C. tomentosa* Hopper.

4.1.2.2.4. Conostylis subg. Brachycaulon (Benth.) Hopper, Fl. Australia 45: 457. 1987 ≡ Conostylis sect. Brachycaulon Benth., Fl. Austral. 6: 428. 1973. Type species. Conostylis breviscapa R.Br.

Fig 16I

Conostylis subg. Bicolorata Hopper, Fl. Australia 45: 456. 1987, **Syn. nov.** Type species. Conostylis vaginata Endl.

Conostylis subg. Pendula sect. Divaricata Hopper, Fl. Australia 45: 457. 1987, **Syn. nov.** Type species. Conostylis plathyrantha Diels.

Characterization. Conostylis subg. Brachycaulon is characterized by its axillary and prostrate inflorescences, short-pedicellate flowers, perianth campanulate, concolorous at post-anthesis, anthers geniculate, connectives dorsally decurrent from base upwards, lacking appendages, and ovules few and pendulous from a peltate placenta.

Distribution and ecology. Endemic to southern Western Australia, growing in dry sand in heath and mallee heath.

Accepted species. A total of 3 species: *Conostylis breviscapa* R.Br., *C. plathyrantha* Diels., and *C. vaginata* Endl.

4.1.2.2.5. *Conostylis* **subg.** *Pendula* **Hopper**, Fl. Australia 45: 457. 1987. Type species. *Conostylis setigera* R.Br.

Fig 16G & H

Conostylis subg. Pendula sect. Catospora Benth., Fl. Austral. 6: 428. 1873, **Syn. nov.** Type species. Conostylis setigera R.Br.

Androstemma Lindl., Edwards's Bot. Reg. 23 App. (Swan River): xlvi. 1840, **Syn. nov.** Type species. Androstemma junceum Lindl. (≡ Conostylis androstemma F.Muell.).

Conostylis sect. Androstemma (Lindl.) Benth., Fl. Austral. 6: 430. 1873.

Conostylis subg. Androstemma (Lindl.) Hopper Fl. Australia 45: 456. 1987.

Conostylis sect. Greenia Geer., Bull. Jard. Bot. État. 39: 65. 1969, **Syn. nov.** Type species. Conostylis bealiana F.Muell.

Conostylis subg. Greenia (Geer.) Hopper, Fl. Australia 45: 457. 1987.

Characterization. Conostylis subg. Pendula is characterized by its axillary and prostrate inflorescences, short-pedicellate flowers, perianth campanulate or tubular, becoming completely red or flushed with red at post-anthesis, anthers straight, connectives dorsally decurrent from the base upwards, lacking appendages, and ovules few and pendulous from a peltate placenta.

Distribution and ecology. Endemic to southern Western Australia, growing in dry, generally gravelly sand, in woodland, heath, low heath, or mallee heath.

Accepted species. A total of 28 species: Conostylis absens (Hopper) M.Pell. & Hopper, C. albescens Hopper, C. androstemma F.Muell., C. argentea (J.W.Green) Hopper, C. bealiana F.Muell., C. canteriata Hopper, C. caricina Lindl., C. crassinerva J.W.Green, C. dasys (Hopper) M.Pell. & Hopper, C. deplexa J.W.Green, C. dielsii W.Fitzg., C. drummondii Benth., C. elachys (Hopper) M.Pell. & Hopper, C. latens Hopper, C. lepidospermoides Hopper, C. micrantha Hopper, C. neocymosa Hopper, C. petrophiloides F.Muell. ex Benth., C. planescens (Hopper) M.Pell. & Hopper, C. pusilla Endl., C. rogeri Hopper, C. setigera R.Br., C. setosa Lindl., C. teres (Hopper) M.Pell. & Hopper, C. teretifolia J.W.Green, C. teretiuscula F.Muell., C. villosa Benth., and C. wonganensis Hopper.

New combinations. *Conostylis absens* (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis crassinerva* subsp. *absens* Hopper, Fl. Australia 45: 460. 1987.

Conostylis dasys (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis setigera* subsp. *dasys* Hopper, Fl. Australia 45: 463. 1987.

Conostylis elachys (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis caricina* subsp. *elachys* Hopper, Fl. Australia 45: 460. 1987.

Conostylis planescens (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis teretifolia* subsp. *planescens* Hopper, Fl. Australia 45: 463. 1987.

Conostylis teres (Hopper) M.Pell. & Hopper, **stat. nov.** ≡ *Conostylis dielsii* subsp. *teres* Hopper, Fl. Australia 45: 460. 1987.

4.1.2.3. *Phlebocarya* **R.Br.**, Prodr.: 301. 1810. Type species. *Phlebocarya ciliata* R.Br. Fig 16E

Distribution and ecology. *Phlebocarya* is endemic to southern Western Australia, and grows in well-drained to swampy sandy soils, in heath and woodland.

Comments. *Phlebocarya* has rarely been the aim of any taxonomic study and has only been addressed in floristic studies. Thus, it would greatly benefit of a taxonomic revision.

Accepted species. A total of four species: *Phlebocarya ciliata* R.Br., *P. filifolia* (F.Muell.) Benth., *P. pilosissima* (F.Muell.) Benth., and *P. teretifolia* (T.D.Macfarl.) M.Pell.

New combination. *Phlebocarya teretifolia* (T.D.Macfarl.) M.Pell., **stat. nov.** ≡ *Phlebocarya pilosissima* subsp. *teretifolia* T.D.Macfarl., Fl. Australia 45: 465. 1987.

4.2. Subfamily Haemodoroideae Arn., Botany: 133. 1832, as "*Haemodoreae*". Type genus. *Haemodorum* Sm.

Fig 16J-T

Wachendorfioideae Arn., Botany: 133. 1832, as "Wachendorfieae". Type genus. Wachendorfia Burm.

Distribution. Australia, New Guinea, southern Africa and the American continent (from Canada to Florida and Cuba, reaching Central-Western Brazil).

Comments. A much smaller subfamily, but also with controversial generic limits. We currently accept eight genera in Haemodoroideae, with the recent description of two new genera (i.e., *Cubanicula* and *Paradilatris*) and the present synonymization of *Barberetta* under *Wachendorfia*. The subfamily is further divided into two tribes.

Key to the tribes of Haemodoroideae

- 1. Flowers resupinate, septal nectaries 3, inter- or supralocular, nectar guides absent, ovary inferior; fruits lacking thickened septal ridges; seeds winged, cleft towards the embryotega, testa smooth to scabrid... **Haemodoreae Dumort.** (Fig 16J–N)
- Flowers non-resupinate, when present septal nectaries 2, infralocular, nectar guides generally present (composed of 3 orange to red spots), ovary superior; fruits with thickened septal ridges; seeds not winged, not cleft towards the embryotega, testa generally with coarse hairs, sometimes reticulate or verrucose... Wachendorfieae Dumort. (Fig 16O-T)
- **4.2.1. Tribe Haemodoreae Dumort.**, Anal. Fam. Pl.: 62. 1829. Type genus. *Haemodorum* Sm.

Fig 16J-N

Dilatrideae M.Roem., Handb. Allg. Bot. 3: 476. 1840. Type genus. Dilatris P.J.Bergius.

Distribution. Disjunctively distributed in North and Central America (including the Antilles), southern Africa (Cape Region), and Australia and New Guinea.

Comments. Haemodoreae is composed of four genera, with *Haemodorum* restricted Australasia, *Dilatris* and *Paradilatris* restricted to the Cape Region (Africa), and *Lachnanthes* restricted to the American continent. It can be differentiated from tribe Wachendorfieae by the presence of three inter- or supralocular septal nectaries, winged seeds with a scrobiculate testa, cleft towards the embryotega.

Key to the genera of Haemodoreae

- 1. Leaves with mucilage cells; perianth lobes patent, membranous or succulent, filaments curved, gynoecium with 1 ovule per locule; capsules unlobed, persistent style splitting together with the valves... 2
- Leaves lacking mucilage cells; perianth lobes erect, coriaceous, filaments straight, gynoecium with 2-many ovules per locule; capsules strongly trilobed, persistent style remaining intact at the top of the columella... 3

- 2. Plants growing in rocky areas; floral buds erect; perianth mauve to lilac, lobes wider than long, with apical or subapical gland-dots; anthocarp present; capsules septifragal, subglobose, apex apiculate... *Dilatris* P.J.Bergius (Fig 16J)
- Plants growing in seasonally marshy areas; floral buds recurved; perianth yellow to orange, lobes longer than wide, lacking apical or subapical gland-dots; anthocarp absent; capsules loculicidal, oblongoid, apex aristate... *Paradilatris* (Hopper ex J.C.Manning) Hopper et al. (Fig 16K)
- 3. Plants bulbous; leaves coriaceous, solid; perianth glabrous, anthers dehiscent from base to apex, straight at post-anthesis, ovary with locule 2-ovulate, ovules hypotropous; vessels restricted to the roots... *Haemodorum* Sm. (Fig 16M & N)
- Plants rhizomatous; leaves spongy, fistulose; perianth lanate, anthers dehiscent from apex to base, coiled at post-anthesis, ovary with locules 5-7-ovulate, ovules pleurotropous; vessels at the roots and stem... *Lachnanthes* Elliot (Fig 16L)
- **4.2.1.1.** *Dilatris* **P.J.Bergius**, Descr. Pl. Cap.: 9. 1767. Type species. *Dilatris corymbosa* P.J.Bergius. Fig 16J

Distribution and ecology. Restricted to rocky outcrops of the Cape Region, Africa.

Comments. *Dilatris* is the only genus of Haemodoraceae to present and anthocarp and mauve to lilac flowers.

Accepted species. A total of three species: *Dilatris corymbosa* P.J.Bergius, *D. ixioides* Lam., and *D. pillansii* W.F.Barker.

4.2.1.2. Paradilatris (Hopper ex J.C.Manning) Hopper et al., unpublished ≡ Dilatris subg. Paradilatris Hopper ex J.C.Manning, S. African J. Bot. 113: 104. 2017. Type species. Paradilatris viscosa (L.f.) Hopper et al. Fig 16K

Distribution and ecology. Restricted to seasonally wet areas of the Cape Region, Africa.

Comments. *Paradilatris* is distinct from *Dilatris* s.str. due to the posture of the pedicels in pre-anthesis, perianth coloration, perianth lobes shape, the lack of an anthocarp, fruit dehiscence, and the presence of an apical arista in the capsules. All these characters support their segregation from *Dilatris*.

Accepted species. A total of two species: *Paradilatris viscosa* (L.f.) Hopper et al., and *P. paniculata* (L.f.) Hopper et al.

4.2.1.3. *Haemodorum* Sm., Trans. Linn. Soc. London 4: 213. 1798. Type. *Haemodorum corymbosum* Vahl.

Fig 16M & N

Distribution and ecology. Restricted to Australia, Tasmania and New Guinea.

Comments. A genus of ca. 30 species, that urges for a taxonomic revision.

Infrageneric classification. No classification was ever formally proposed for *Haemodorum*. Nonetheless, due to its size, an infrageneric classification should facilitate its taxonomy. Based on our present results, we only propose the recognition of two subgenera. The further division might prove to be necessary in *H.* subg. *Haemodorum*, but further studies are needed.

Key to the subgenera of *Haemodorum*

- 1. Bulbs partially above the soil; bracteoles diminute, flat; pedicels joined at base; perianth lobes connivent, filaments stout, curved, anthers basifixed, connective expanded... *Haemodorum* subg. *Geminiflorum* M.Pell. & Hopper
- Bulbs underground; bracteoles frondose, with crispate margins; pedicels free; perianth lobes erect, filaments slender, straight, anthers versatile, connective inconspicuous...
 Haemodorum Sm. subg. Haemodorum (Fig 16M & N)

4.2.1.3.1. *Haemodorum* **subg.** *Geminiflorum* **M.Pell.** & **Hopper, subg. nov.** Type species. *Haemodorum spicatum* R.Br.

Description. Herbs perennial, paludal. Bulbs partially above the soil. Stems unbranched. Leaves terete or sub-terete. Synflorescence composed of a main florescence with 1–several coflorescences; synflorescence (cauline) leaves becoming gradually smaller towards the apex. Main florescences (inflorescences) pedunculate, many-branched, main axis elongate; basal bract bracteose; cincinni alternate, 2-flowered, sessile, internodes contracted; bracteoles flat, diminute. Flowers sessile, pedicels joined at base, perianth lobes connivent; stamens dimorphic, filaments stout, curved, J-shaped, anthers basifixed, connective expanded.

Distribution and ecology. Restricted to southwestern Western Australia, growing in eucalypt and banksia woodlands, mallee and heathland, in seasonally wet sandy or sand over clay soil, rarely overlying granite and laterite.

Accepted species. A total of two species, plus a third undescribed species (Hickman and Hopper, pers. comm.): *Haemodorum brevisepalum* Benth. and *H. spicatum* R.Br.

Etymology. The subgeneric name of this new subgenus derives from the Latin, meaning twin-flowered.

4.2.1.3.2. *Haemodorum* **Sm. subg.** *Haemodorum*. Type species. *Haemodorum corymbosum* Vahl.

Fig 16M & N

Characterization. Herbs perennial, terrestrial. Bulbs underground. Stems unbranched. Leaves flat or terete or sub-terete. Synflorescence composed of a main florescence with 1–several coflorescences, sometimes solitary; synflorescence (cauline) leaves becoming gradually smaller towards the apex or all bracteose. Main florescences (inflorescences) pedunculate, few- or many-branched, main axis generally contracted, sometimes elongate; basal bract bracteose; cincinni alternate or glomerulate, many-flowered, pedunculate, internodes contracted or elongate; bracteoles with crispate margins, conspicuous. Flowers sessile or pedicellate, pedicels free, perianth lobes erect; stamens monomorphic, filaments slender, straight, anthers versatile, connective contracted.

Distribution and ecology. Widely distributed in Australia, Tasmania and New Guinea, growing in eucalypt and banksia woodlands, mallee and heathland, in seasonally wet sandy or sand over clay soils, rarely overlying granite and laterite.

Accepted species. A total of 25, plus two undescribed (Hickman and Hopper, pers. comm.): Haemodorum austroqueenslandicum Domin, H. basalticum R.L.Barrett et al., H. brevicaule F.Muell., H. capitatum R.L.Barrett & Hopper, H. coccineum R.Br., H. condensatum Hopper & R.L.Barrett, H. corymbosum Vahl, H. discolor T.D.Macfarl., H. distichophyllum Hook., H. ensifolium F.Muell., H. gracile T.D.Macfarl., H. griseofuscum R.L.Barrett et al., H. interrex R.L.Barrett & M.D.Barrett, H. laxum R.Br., H. loratum T.D.Macfarl., H. macfarlanei R.L.Barrett, H. paniculatum Lindl., H. parviflorum Benth., H. planifolium R.Br., H. simplex Lindl., H. simulans F.Muell., H. sparsiflorum F.Muell., H. tenuifolium A.Cunn. ex Benth., H. thedae R.L.Barrett, and H. venosum T.D.Macfarl.

- **4.2.1.4.** *Lachnanthes* Elliott, Sketch Bot. S. Carolina 1: 47. 1816. Type species. *Lachnanthes tinctoria* (Walter *ex* J.F.Gmel.) Elliott [= *Lachnanthes caroliniana* (Lam.) Dandy]. Fig 16L
- Heritiera J.F.Gmel., Syst. Nat. (ed. 13) 2(1): 113. 1791, nom. illeg., non Heritiera Aiton, nec Heritiera Retz. Type species. H. tinctorum Walter ex J.F.Gmel. [= Lachnanthes caroliniana (Lam.) Dandy].
- Gyrotheca Salisb., Trans. Hort. Soc. London 1: 327. 1812, nom. nud. Type species. G. tinctorum (Walter ex J.F.Gmel.) Salisb. [= Lachnanthes caroliniana (Lam.) Dandy].
- Camderia Dumort., Anal. Fam. Pl.: 80. 1829, nom. superfl. Type species. Heritiera tinctorum Walter ex J.F.Gmel. [= Lachnanthes caroliniana (Lam.) Dandy].

Anonymos Walter, Fl. Carol.: 37. 1788, nom. not val. publ.

Distribution and ecology. Known to occur from Nova Scotia (Canada) to Florida (USA), reaching Cuba. It grows in marshy and acidic environments, swampy grasslands, and moist pine forests throughout its range, generally producing extensive clonal populations.

Comments. Despite the strong statistical support as sister to *Haemodorum*, its Neotropical distribution (*vs.* Australasian) and morphological differences support its recognition as an independent genus.

Accepted species. *Lachnanthes caroliniana* (Lam.) Dandy.

4.2.2. Tribe Wachendorfieae Dumort., Anal. Fam. Pl.: 61. 1829, "Wachendorfiaceae". Type genus. Wachendorfia Burm.Fig 16O-T

Xiphidieae Dumort., Anal. Fam. Pl.: 61. 1829, as "Xiphideae". Type genus. Xiphidium Aubl.

Distribution. Cape Region and Neotropics.

Comments. Wachendorfieae is composed of five genera, being almost exclusively Neotropical, except for *Wachendorfia* which is restricted to Africa. It can be differentiated from tribe Haemodoreae by its non-resupinate flowers, the 2 infralocular septal nectaries (when present), perianth with nectar guides generally present (composed of 3 orange to red

spots), ovary superior, fruits with thickened septal ridges, seeds not winged, not cleft towards the embryotega, and testa generally with coarse hairs, sometimes reticulate or verrucose

Key to the genera of Wachendorfieae

- 1. Roots lacking a rhizosheath, not sand-binding; flowers bilabiate, perianth aperturate (forming 2 nectar pouches), upper 5 lobes basally to medially fused, lobes lacking a black mucron at apex, septal nectaries functional, with commissure slits, ovary glabrous; coarse hair of the seed testa evenly distributed... 2
- Roots with a rhizosheath, sand-binding; flowers campanulate, perianth inaperturate, upper 3 lobes basally to medially fused, lobes with a black mucron at apex, septal nectaries absent or non-functional, lacking commissure slits, ovary with hairs restricted to the septal ridges; coarse hairs of the seed testa restricted to the margins... 3
- 2. Plants rhizomatous; leaves flat, bulliform cells absent; lateral stamens with caducous anthers, pollen wall 3-layered, 2 staminode-like filiform projections adnate to the inner paired tepals, medial filament spirally-coiled; seeds deltoid, testa reticulate... *Schiekia* **Meisn.** (Fig 16O)
- Plants cormose; leaves plicate, with bulliform cells; lateral stamens with persistent anthers; pollen wall 2-layered, staminodes absent, medial filaments curved; seeds polygonal to subglobose, testa with coarse hairs or smooth... *Wachendorfia* Burm. (Fig 16P & Q)
- 3. Stems elongate; anthers introrsely rimose but functionally poricidal; septal nectaries absent; capsules subglobose to globose, indehiscent, somewhat fleshy at maturity; seeds cuboid, testa tuberculate... *Xiphidium* **Aubl.** (**Fig 16T**)
- Stems contracted; anthers rimose, septal nectaries present but vestigial; capsules trigonous,
 3-valved, dry at maturity; seeds lenticellate, testa covered with coarse hairs... 4
- 4. Plants rhizomatous; thyrsi composed of 9–27, 1–2-branched cincinni; flowers enantiostylous, upper tepals with three orange-yellow to orange nectar guides, stamens 3, lateral filaments twisted, central filament bent upwards, anther sacs asymmetric, staminodes absent... *Cubanicula* Hopper et al. (Fig 16R)
- Plants cormose; thyrsi composed of 2–4, unbranched cincinni; flowers non-enantiostylous, upper tepals lacking nectar guides, stamen 1, filament straight, anther sacs symmetric, staminodes 2, filiform... *Pyrrorhiza* Maguire & Wurdack (Fig 16S)
- **4.2.1.1.** *Schiekia* Meisn., Pl. Vasc. Gen. 2(12): 300. 1842. Type species. *Schiekia orinocensis* (Kunth) Meisn.

Fig 160

Troschelia Klotzsch & M.R.Schomb. *in* Schomburgk MR, Reis. Br.-Guiana: 1066. 1849, nom. nud. Type species. *Troschelia orinocensis* (Kunth) Klotzsch & M.R.Schomb. [≡ *Schiekia orinocensis* (Kunth) Meisn.].

Distribution and ecology. Restricted to South America, growing in seasonally flooded rocky outcrops in tepuis, savanna grasslands and forests.

Comments. *Schiekia* is vegetatively similar to *Xiphidium* in several aspects while being florally similar to *Wachendorfia*. Nonetheless, it is unique due to the presence of two filiform staminode-like structure in the inner perianth lobes, and its spirally-coiled filament of the medial stamen.

Accepted species. A total of three species: *Schiekia orinocensis* (Kunth) Meisn., *S. silvestris* (Maas & Stoel) Hopper et al., and *S. timida* M.Pell. et al.

4.2.1.2. *Wachendorfia* **Burm.**, Wachendorfia: 2. 1757. Type species. *Wachendorfia paniculata* Burm.

Fig 16P & Q

Pedilonia C.Presl, Pedilonia Nov. Pl. Gen.: 1. 1829, nom. superfl. Type species. Pedilonia violacea C.Presl (= Wachendorfia paniculata Burm.).

Barberetta Harv., Gen. S. Afr. Fl. Pl. (ed. 2): 377. 1868, **Syn. nov.** Type species. Barberetta aurea Harv. [≡ Wachendorfia aurea (Harv.) M.Pell. & Hopper].

Distribution and ecology. Restricted to seasonally wet areas of the Cape Region, Africa.

Accepted species. A total of six, with one still undescribed (Hopper, pers. observ.): *Wachendorfia aurea* (Harv.) M.Pell. & Hopper, *W. brachyandra* W.F.Barker, *W. multiflora* (Klatt) J.C.Manning & Goldblatt, *W. paniculata* Burm., and *W. thyrsiflora* Burm.

New combination. *Wachendorfia aurea* (Harv.) M.Pell. & Hopper, **comb. nov.** ≡ *Barberetta aurea* Harv., Gen. S. Afr. Fl. Pl. (ed. 2): 377. 1868.

4.2.1.3. *Cubanicula* **Hopper et al.**, unpublished. Type species. *Cubanicula xanthorrhiza* (C.Wright *ex* Griseb.) Hopper et al. Fig 16R

Distribution and ecology. *Cubanicula* is endemic to western Cuba and restricted to the Province of Pinar del Rio and the Special Municipality of Isla de la Juventud. It is found in pinelands or open, anthropogenic tropical savanna, on deep, acidic, quartzitic sand, with some organic matter and quartzite/laterite gravel at the surface.

Comments. *Cubanicula* is only superficially similar to *Xiphidium*, being differentiated by anther symmetry and dehiscence, fruit consistency, and seed morphology.

Accepted species. Cubanicula xanthorrhiza (C.Wright ex Griseb.) Hopper et al.

4.2.1.4. *Pyrrorhiza* **Maguire & Wurdack**, Mem. New York Bot. Gard. 9(3): 318. 1957. Type species. *Pyrrorhiza neblinae* Maguire & Wurdack. Fig 16S

Distribution and ecology. *Pyrrorhiza* is only known to occur at the Venezuelan side of the Cerro de la Neblina. It grows in open, acidic and swampy savannas or along streams.

Comments. *Pyrrorhiza* is peculiar in its foliaceous bracteoles distinct from the cincinnus bract, free perianth lobes, 1 stamen, and 2 staminodes.

Accepted species. Pyrrorhiza neblinae Maguire & Wurdack.

4.2.1.5. *Xiphidium* **Aubl.**, Hist. Pl. Guiane 1: 33, pl. 11. 1775. Type species. *Xiphidium caeruleum* Aubl.

Fig 16T

Tonduzia Boeckeler *ex* Tonduz, Bull. Herb. Boissier 3: 464. 1895, nom. nud. Type species. *Tonduzia macrophylla* Boeckeler *ex* Tonduz (= *X. caeruleum* Aubl.).

Durandia Boeckeler, Allg. Bot. Z. Syst. 2: 160, 173. 1896. Type species. Durandia macrophylla Boeckeler (= X. caeruleum Aubl.).

Distribution and ecology. Widely distributed in the Neotropics, ranging from Mexico to northern Brazil, growing in permanently or seasonally wet, open or forested environments.

Comments. *Xiphidium* is unique in the Haemodoraceae due to its functionally poricidal anthers, fleshy fruits, and cuboid seeds.

Accepted species. A total of two species: *Xiphidium caeruleum* Aubl. And *X. pontederiiflorum* M.Pell.

5. Pontederiaceae Kunth, Nov. Gen. Sp. (quarto ed.) 1: 265. 1815[1816], nom. cons. Type genus. *Pontederia* L. Fig 17

Heterantheraceae J.Agardh, Theoria Syst. Pl.: 36. 1858. Type genus. Heteranthera Ruiz & Pay

Description. Herbs monoecious, perennial or annual, aquatic to amphibious, erectemergent, procumbent-emergent or free-floating. Roots thin, fibrous or spongy, glabrous or pilose, not sand-binding, lacking a rhizosheath, but sometimes with covered by mucilage. Underground stem a rhizome, generally short and generally inconspicuous. Stems submerged or floating or aerial, trailing or erect, herbaceous or spongy, unbranched to branching only at the base or branched throughout, sometimes rooting at the basal nodes or along the whole stem; internodes contracted or elongate, secondary branches sometimes present producing stolons. Immature leaves distichously- or spirally-alternate, congested at the apex of the stem or evenly distributed along the stem, submerged, deciduous or persistent in mature plants, ligulate, sessile; ptyxis conduplicate-involute, enclosing the petiole of the preceding leaf; sheath open, margins non-marcescent; ligule truncate, flabellate or with 2-many projections; blades linear to linear-obovate, membranous, rarely chartaceous; midvein inconspicuous, rarely conspicuous. Mature leaves distichously- or spirally-alternate, congested at the apex of the stem or evenly distributed along the stem, floating or emergent; ptyxis conduplicateinvolute, enclosing the petiole of the preceding leaf; sheath open, margins non-marcescent; ligule truncate, flabellate or with 2-many projections; petioles present or not, when present conspicuous, rarely indistinct, inflated or not; blades acicular to filiform, elliptic to lanceolate or ovate to cordate to reniform or obovate to rounded, membranous or chartaceous to coriaceous; venation acrodromous, midvein generally absent, rarely inflated. Synflorescence composed of a solitary main florescence, synflorescence leaf generally equal to the regular leaves or not, generally petiolate and with a developed, leaf-sheath inflated or not. Main florescences (inflorescences) axillary or apparently terminal, consisting of a pedunculate, rarely sessile, many-branched thyrse, sometimes reduced to a solitary cincinnus; basal bract flat or tubular; accessory bracts absent; main axis developed or not; cincinnus' bract absent; cincinni 1-many per thyrse, alternate or fascicle-like, 1-many-flowered, sessile or

pedunculate, internodes contracted, rarely elongate; bracteoles absent, rarely present. Flowers resupinate, hermaphrodite, sessile or pedicellate, chasmogamous, rarely cleistogamous, homostylous or pseudo-homostylous or tristylous, enantiostylous or not, zygomorphic or asymmetric, rarely actinomorphic, hypanthium present, perianth fused generally forming a conspicuous tube, rarely only basally fused, campanulate or infundibuliform or hypocrateriform, white to light pink to pink to mauve to pale lilac to lilac to bluish lilac to purple, sometimes yellow, spirally-coiling or revolute at post-anthesis, deliquescent or not, persistent in fruit, lobes 6 (3 outer and 3 inner), 3 superior + 3 inferior or 5 superior + 1 inferior, rarely (1–)3 superior + 2 lateral + 1 inferior, anterior lobes generally with a nectar guide, consisting of 1-2 spots or a transverse band, spots yellow to green, generally surrounded by a dark purple to bluish purple line, rarely white blur, bands yellow or mauve to purple or maroon, sometimes surrounded by a white line or blur; stamens (1-)3-6, epipetalous, monomorphic or dimorphic (3 stamens, the medial longer and stouter or 6 stamens, the superior 3 shorter than the inferior 3) or unequal (6 stamens, 1 inferior longer, sometimes with a differently colored anther), filaments straight or J-shaped or recurveddecurved, terete or medially inflated, glabrous or eglandular-pubescent or glandular-pubescent or bearded with long hairs with dumbbell-shaped cells, anthers basifixed or dorsifixed, rimose, introrse, sometimes poricidal, connective inconspicuous, anther sacs elongate; ovary superior, 1–3-locular, (1–)3 fertile, placentation axile or intrusive-parietal, rarely pendulous, ovules (1–)many per locule, septal nectaries present or not, when present 3, interlocular, style elongate, straight or J-shaped, stigma asymmetrically trilobed or capitate to trilobed, rarely trifid. Fruit a capsule with loculicidal or irregular dehiscence, rarely an achene, (1-)manyseeded; anthocarp present, thin or hardened, loosely or tightly involving the fruit, free or adnate to the fruit. Seeds oblongoid or ellipsoid or subglobose to broadly oblongoid or ovoid or curved narrowly ovoid, exarillate, testa conspicuously to inconspicuously longitudinally winged, rarely smooth, when present wings membranous and testa also transversally striated between each wing; chalazal cap inconspicuous; hilum punctate; embryotega dorsal, inconspicuous.

Comments. Pontederiaceae is a small family, composed of two genera and ca. 50 species (Pellegrini 2017; Pellegrini et al. 2018). It is micro- and macromorphologically, taxonomically and phylogenetically well-understood, having been the focus of several studies (Eckenwalder and Barrett 1986; Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011; Pellegrini et al. 2018). It is recovered as sister to Haemodoraceae, being supported by several morphological characters (see above under Results or at the Haemodoraceae taxonomic section). Pontederiaceae can be easily recognized by its late-bifacial leaves, xylem and phloem alternate at the center of the leaf, but xylem abaxial and phloem adaxial at the margins, ptyxis conduplicate-involute (enclosing the petiole of the preceding leaf), leaves dimorphic, ligulate, presence of an anthocarp, pollen bisulcate, and ovary wall with aerenchymatous tissue.

Phylogeny and generic limits. Pontederiaceae was one of the first angiosperm families to be the focus of studies dealing with its phylogenetic history, based on morphological, molecular, and combined data (Eckenwalder and Barrett 1986; Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011; Pellegrini et al. 2018). With the adoption of a phylogenetic classification for Pontederiaceae by Pellegrini et al. (2018), each recognized group is easily diagnosable and supported by both molecular and morphological data. The implementation of these ideals has generated not only monophyletic genera but has considerably facilitated the taxonomy of the group.

Distribution. Pantropical, but with diversity center in Brazil.

Key to the genera of Pontederiaceae (modified from Pellegrini et al. 2018)

- 1. Immature leaves spirally-alternate, mature leaves sometimes produced, when produced non-pulvinate, blade membranous; inflorescence reduced to a solitary cincinnus; stamens (1–)3, obliquely inserted, staminodes sometimes present, septal nectaries absent, stigma unevenly trilobed... *Heteranthera* Ruiz & Pav. (Fig 17A–C)
- Immature leaves distichously-alternate, mature leaves always produced, pulvinate, blade chartaceous to coriaceous; inflorescence a 2-many branched thyrsi (rarely reduced to a solitary flower); stamens 6, parallelly inserted, staminodes absent, septal nectaries present (if absent than flowers pedicellate and anthers poricidal), stigma capitate or trilobed, rarely trifid... *Pontederia* L. (Fig D-H)
- 5.1. Heteranthera Ruiz & Pav., Fl. Peruv. Prodr.: 9. 1794. Type species. Heteranthera reniformis Ruiz & Pav.Fig 17A-C

Distribution and ecology. *Heteranthera* has a Pantropical distribution, but most of its species concentrated in the Neotropical region, especially in Brazil (Horn 1985; Pellegrini 2017; Pellegrini & Horn 2017). Its species are found growing in permanent or seasonal freshwater environments, with some species also commonly found growing as weeds in rice, and other flooded plantations.

Comments. Heteranthera (incl. Hydrothrix and Scholleropsis) is easily differentiated from Pontederia by leaf morphology, inflorescence architecture, and floral morphology. A much-needed comprehensive taxonomic revision for the genus is underway (Horn and Pellegrini, in prep.).

Infrageneric classification. Heteranthera was traditionally divided into sections by previous authors, but this classification was abandoned by Horn (1985), in his taxonomic revision for the genus, in which he accepted Hydrothrix Hook.f., Scholleropsis H.Perrier, and Zosterella Small as distinct from Heteranthera. Rosatti (1987), disagreed with Horn's circumscription and reduced Zosterella to a subgenus of Heteranthera. Pellegrini (2017), reduced Hydrothrix and Scholleropsis to synonyms of Heteranthera, but made no combinations either for the subgeneric or sectional ranks. With the present study sampling all species of Heteranthera recognized so far, it seems convenient to propose a new infrageneric classification, based on monophyletic and morphologically well-defined groupings.

Accepted species. *Heteranthera* is a small genus with ca. 20 species, some still undescribed.

Key to the subgenera of *Heteranthera*

- 1. Plants with a definite base, stems of mature plants contracted; mature leaves distichously-alternate; perianth lacking tannin cells, medial outer tepal with basal flanges, gynoecium hemiseptalous... *Heteranthera* subg. *Leptanthus* (Michx.) M.Pell. & C.N.Horn (Fig 17A)
- Plants with an indefinite base, stems of mature plants elongate; mature leaves spirallyalternate; perianth with tannin cells, outer medial tepals lacking basal flanges, gynoecium aposeptalous... 2

- 2. Mature leaves always produced, blades reniform, conspicuously lighter at the petiole insertion; perianth tube with a collar-like base, outer medial tepal basally convolute, placenta 2-flanged... *Heteranthera* Ruiz & Pav. subg. *Heteranthera* (Fig 17B)
- Mature leaves sometimes produced, blades acicular to linear or ovate, concolorous at the petiole insertion; perianth tube lacking a collar-like base, outer medial tepal basally flat, placenta slightly 2-flanged... *Heteranthera* subg. *Zosterella* (Small) Rosatti (Fig 17C)
- **5.1.1.** Heteranthera subg. Leptanthus (Michx.) M.Pell. & C.N.Horn, comb. et stat. nov. ≡ Leptanthus Michx. subg. Leptanthus ≡ Leptanthus Michx., Fl. Bor.-Amer. 1: 24. 1803. Type species (designated here). Leptanthus ovalis Michx., nom. superfl. [≡ Heteranthera limosa (Sw.) Willd.].

Fig 17A

- Lunania Raf., Med. Fl. 2: 106. 1830, nom. illeg. non Lunania Hook., London J. Bot. 3: 317. 1844. Type species. Lunania uniflora Raf., nom. superfl. [≡ Heteranthera limosa (Sw.) Willd.].
- Triexastima Raf., Fl. Tellur. 4: 121. 1836 [1838]. Type species. Triexastima uniflora Raf., nom. superfluous [≡ Heteranthera limosa (Sw.) Willd.].
- Phrynium Loefl. ex Kuntze, Revis. Gen. Pl. 3(3): 318. 1898, nom. illeg., non Phrynium Willd., Sp. Pl. Editio quarta 1: 1, 17. 1797. Type species (designated here). Phrynium limosum (Sw.) Kuntze [≡ Heteranthera limosa (Sw.) Willd.].
- Scholleropsis H.Perrier, Notul. Syst. (Paris) 5: 158. 1936. Type species. Scholleropsis lutea H.Perrier [≡ Heteranthera lutea (H.Perrier) M.Pell.].

Characterization. Heteranthera subg. Leptanthus is characterized by its definite base, stems of mature plants contracted, long-lived immature leaves, mature leaves distichously-alternate, blades oblong to elliptic or ovate or rotund, concolorous at the petiole insertion, perianth lacking tannin cells, perianth tube without a collar-like base, medial outer tepal with basal flanges, gynoecium hemiseptalous, and placenta 2-flanged.

Distribution and ecology. This subgenus has an interestingly disjunct distribution, with two species restricted to the Neotropics (i.e., *H. limosa* and *H. rotundifolia*), and the third one (i.e., *H. lutea*) restricted to Madagascar and continental Africa. All three species are found growing in seasonal floodplains, with the two Neotropical species also being found growing like a weed.

Accepted species. A small subgenus composed of three species: *Heteranthera limosa* (Sw.) Willd., *H. lutea* (H.Perrier) M.Pell., and *H. rotundifolia* (Kunth) Griseb.

5.1.2. Heteranthera Ruiz & Pav. subg. Heteranthera. Type species. Heteranthera reniformis Ruiz & Pav.Fig 17B

- Leptanthus subg. Heteranthera (Ruiz & Pav.) Pers., Syn. Pl. 1: 56. 1805. Type species. Leptanthus peruvianus Pers., nom. superfl. (= Heteranthera reniformis Ruiz & Pav.).
- Heterandra P.Beauv., Trans. Amer. Philos. Soc. 4: 175. 1799. Type species. Heterandra reniformis P.Beauv. (= Heteranthera reniformis Ruiz & Pav.).

Buchosia Vell., Fl. Flumin.: 33. 1829. Type species. Buchosia aquatica Vell. (= Heteranthera reniformis Ruiz & Pav.).

Characterization. *Heteranthera* subg. *Heteranthera* is characterized by its indefinite base, stems of mature plants elongate, immature leaves short-lived, mature leaves always produced and spirally-alternate, blades reniform, conspicuously lighter at the petiole insertion, perianth with tannin cells, perianth tube with a collar-like base, outer medial tepal basally convolute, gynoecium aposeptalous, and placenta 2-flanged.

Distribution and ecology. This subgenus is mainly Neotropical, with the exception of the African *Heteranthera callifolia*. Its species are known to be weedy, growing in almost any open, damp or aquatic environments.

Accepted species. It is composed of eight species, with some species related to *H. multiflora* still undescribed (Horn and Pellegrini, in prep.): *Heteranthera callifolia* Rchb. *ex* Kunth, *H. catharinensis* C.N.Horn & M.Pell., *H. longirachilla* D.J.Sousa & Giul., *H. multiflora* (Griseb.) C.N.Horn, *H. peduncularis* Benth., *H. pumila* M.Pell. & C.N.Horn, *H. reniformis* Ruiz & Pav., and *H. spicata* C.Presl.

- **5.1.3.** *Heteranthera* **subg.** *Zosterella* (Small) **Rosatti**, J. Arnold Arbor. 68(1): 59. 1987 ≡ *Zosterella Small*, Fl. Lancaster Co.: 68. 1913. Type species. *Zosterella dubia* (Jacq.) Small [≡ *Heteranthera dubia* (Jacq.) MacMill.]. Fig 17C
- Schollera Schreb., Gen. Pl. 785. 1791, nom. illeg., non Schollera Roth, Tent. Fl. Germ. 1: 165, 170. 1788. Type species (designated here). Schollera graminea (Michx.) Willd. ex A.Gray [= Heteranthera dubia (Jacq.) MacMill.].
- *Eurystemon* Alexander, N. Amer. Fl. 19: 55. 1937. Type species. *Eurystemon mexicanum* (S.Watson) Alexander (≡ *Heteranthera mexicana* S.Watson).
- Hookerina Kuntze, Revis. Gen. Pl. 2: 718. 1891, nom. superfl. Type species. Hookerina gardneri (Hook.f.) Kuntze [≡ Heteranthera gardneri (Hook.f.) M.Pell.].
- *Hydrothrix* Hook.f., Ann. Bot. (Oxford) 1: 89. 1887. Type species. *Hydrothrix gardneri* Hook.f. [≡ *Heteranthera gardneri* (Hook.f.) M.Pell.].

Characterization. Heteranthera subg. Zosterella is characterized by its indefinite base, stems of mature plants elongate, immature leaves long-lived, mature leaves sometimes produced, blades acicular to linear or ovate, concolorous at the petiole insertion; perianth tube lacking a collar-like base, outer medial tepal basally flat, gynoecium aposeptalous, and placenta slightly 2-flanged.

Distribution and ecology. This subgenus is exclusively Neotropical, with is species ranging from the USA to Argentina. Its species are generally found in perennial freshwater bodies, rarely on seasonal ones, also associated with open environments.

Accepted species. It is composed of six species, plus a yet undescribed species from Brazil (Pellegrini & Horn, in prep.): *Heteranthera dubia* (Jacq.) MacMill., *H. gardneri* (Hook.f.) M.Pell., *H. mexicana* S.Watson, *H. oblongifolia* Mart. *ex* Schult. & Schult.f., *H. seubertiana* Solms, and *H. zosterifolia* Mart.

5.2. *Pontederia* L., Sp. Pl. 1: 288. 1753. Type species. *Pontederia cordata* L. Fig 17D–H

Distribution and ecology. *Pontederia* is Pantropical, with half of its species exclusive to the Neotropical region, while the remaining ones are restricted to the Paleotropics. Species in *Pontederia* can range from paludal to free-floating plants, thus occurring in a wide range of water bodies, from perennial to temporary, but most commonly in open environments with slow or stagnated water (Pellegrini et al. 2018).

Comments. A genus of 26 species. Almost all Paleotropical species belong to *P.* subg. *Monochoria*, except for *P. natans* P.Beauv. (*P.* subg. *Eichhornia*), which is restricted to Africa (Pellegrini et al. 2018).

Infrageneric classification. The infrageneric classification of *Pontederia* follows the one proposed by Pellegrini et al. (2018), where five monophyletic subgenera are accepted. To facilitate the identification and to maintain the formatting adopted by us throughout the Taxonomy section, we reproduced the identification key for the subgenera. Nonetheless, comments, composition, distribution, illustrations, etc. are omitted here, since we would need to reproduce a considerable portion of their text.

Key to the subgenera of *Pontederia* (from Pellegrini et al. 2018)

- 1. Basal bract commonly with a caudate apex, rarely leaf-like; flowers pedicellate, enantiostylous, perianth only basally connate, campanulate; stamens with filaments connate forming a petalo-staminal tube, anthers basifixed, poricidal; septal nectaries absent... *Pontederia* subg. *Monochoria* (C.Presl.) M.Pell. & C.N.Horn (Fig 17F)
- Basal bract with an acute to acuminate to aristate apex, rarely caudate; flowers sessile, non-enantiostylous, perianth connate forming a conspicuous tube, infundibuliform or hypocrateriform; stamens with free filaments, anthers dorsifixed, rimose; septal nectaries present... 2
- 2. Ovary 1-locular by abortion, fertile locule 1-ovulate, placentation pendulous; fruit an achene, anthocarp hardened, ridges sinuate, toothed or echinate; seeds smooth... *Pontederia* L. subg. *Pontederia* (Fig 17H)
- Ovary 3-locular, locules many-ovulate, placentation axial; fruit a capsule, anthocarp thin to thickened, if thickened ridges smooth; seeds longitudinally winged... 3
- 3. Herbs procumbent-emergent, stems elongate; sessile leaves late deciduous, rarely persistent in mature plants, petiolate leaves distichously-alternate, evenly distributed along the stem; perianth infundibuliform, style glabrous... *Pontederia* subg. *Eichhornia* (Kunth) M.Pell. & C.N.Horn (Fig 17G)
- Herbs erect emergent or free-floating, stems inconspicuous; sessile leaves early deciduous, petiolate leaves spirally-alternate, congested at the apex of the stem; perianth hypocrateriform, style glandular-pubescent... 4

- 4. Herbs stoloniferous; ligule flabellate, petioles generally inflated; inflorescences deflexed post-anthesis and in fruit, emerging from a non-inflated leaf-sheath, basal bract tubular; flowers ca. 4–6 cm diam., perianth loosely enclosing the developing fruit; seeds oblongoid... *Pontederia* subg. *Oshunae* M.Pell. & C.N.Horn (Fig 17E)
- Herbs never producing stolons; ligule truncate, petioles never inflated; inflorescences erect at post-anthesis, emerging from an inflated leaf-sheath, basal bract flat; flowers ca. 2–3 cm diam., perianth tightly enclosing the developing fruit; seeds subglobose to broadly oblongoid... *Pontederia* subg. *Cabanisia* (Klotzsch ex Schltdl.) M.Pell. & C.N.Horn (Fig 17D)
- **5.2.1.** *Pontederia* **subg.** *Cabanisia* (**Klotzsch ex Schltdl.**) **M.Pell. & C.N.Horn**, PhytoKeys 108: 50. 2018 ≡ *Cabanisia* Klotzsch ex Schltdl., Abh. Naturf. Ges. Halle 6: 176. 1862. Type species. *Cabanisia caracasana* Klotzsch ex Schltdl., nom. illeg. (≡ *Pontederia paniculata* Spreng.).

Fig 17D

Distribution and ecology. Mainly Central-West and Northeastern Brazil (reaching Argentina and Paraguay), growing in temporary water bodies in the Caatinga, Cerrado and Chaco domains. However, two species have very peculiar disjunctions in their distributions, also occurring in northwestern South America (Colombia, Ecuador, Guyana and Venezuela), Central America (Costa Rica, Guatemala and Nicaragua), Antilles (Jamaica), and North America (Mexico).

Accepted species. A total of three accepted species: *Pontederia meyeri* (A.G.Schulz) M.Pell. & C.N.Horn, *P. paniculata* Spreng., and *P. paradoxa* Mart.

5.2.2. *Pontederia* **subg.** *Oshunae* **M.Pell. & C.N.Horn**, PhytoKeys 108: 61. 2018. Type species. *Pontederia crassipes* Mart. Fig 17E

Piaropus Raf., Fl. Tellur. 2: 81. 1837, nom. rej. Type species. Piaropus mesomelas Raf., nom. illeg. (≡ Pontederia crassipes Mart.).

Distribution and ecology. Widespread throughout South America, growing in a myriad of freshwater bodies.

Accepted species. *Pontederia crassipes* Mart.

- **5.2.3.** *Pontederia* **subg.** *Monochoria* (C.Presl) **M.Pell. & C.N.Horn**, PhytoKeys 108: 54. 2018 ≡ *Monochoria* C.Presl, Reliq. Haenk. 1(2): 127. 1827. Type species. *Monochoria hastifolia* C.Presl., nom. illeg. (≡ *Pontederia hastata* L.). Fig 17F
- Calcarunia Raf., Med. Fl. 2: 106. 1830. Type species. Calcarunia hastata (L.) Raf., nom. inval. (≡ Pontederia hastata L.).
- Carigola Raf., Fl. Tellur. 2: 10. 1837. Type species. Carigola hastata (L.) Raf. (≡ Pontederia hastata L.).
- Gomphima Raf., Fl. Tellur. 2: 10. 1837. Type species. Gomphima vaginalis (Burm.f.) Raf. (≡ Pontederia vaginalis Burm.f.).

- *Kadakia* Raf., Fl. Tellur. 2: 9. 1837. Type species. *Kadakia dilatata* (Buch.-Ham.) Raf. (= *Pontederia hastata* L.).
- *Limnostachys* F.Muell., Fragm. 1: 24. 1858. Type species. *Limnostachys cyanea* F.Muell. [≡ *Pontederia cyanea* (F.Muell.) M.Pell. & C.N.Horn].

Distribution and ecology. Exclusively Paleotropical, with two species native to Africa, four to Australia (two of them endemic), and six to Asia. They are found growing in seasonal or perennial freshwater bodies.

Accepted species. A total of 10 accepted species: *Pontederia africana* (Solms) M.Pell. & C.N.Horn, *P. australasica* (Ridl.) M.Pell. & C.N.Horn, *P. brevipetiolata* (Verdc.) M.Pell. & C.N.Horn, *P. cyanea* (F.Muell.) M.Pell. & C.N.Horn, *P. elata* (Ridl.) M.Pell. & C.N.Horn, *P. hastata* L., *P. korsakowii* (Regel & Maack) M.Pell. & C.N.Horn, *P. plantaginea* Roxb., *P. vaginalis* Burm.f., and *P. valida* (G.X.Wang & Nagam.) M.Pell. & C.N.Horn.

5.2.4. *Pontederia* **subg.** *Eichhornia* (**Kunth**) **M.Pell. & C.N.Horn**, PhytoKeys 108: 64. 2018 ≡ *Eichhornia* Kunth, Enum. Pl. 4: 129. 1843. Type species. *Eichhornia azurea* (Sw.) Kunth. (≡ *Pontderia azurea* Sw.). Fig 17G

Leptosomus Schltdl., Abh. Naturf. Ges. Halle 6: 174. 1862. Type species. *Leptosomus natans* (P.Beauv.) Schltdl. (≡ *Pontederia natans* P.Beauv.).

Distribution and ecology. Mainly Neotropical, except for *Pontederia natans*, which is restricted to continental Africa and Madagascar. It is found growing in seasonal or perennial freshwater bodies.

Accepted species. A total of four accepted species: *Pontederia azurea* Sw., *P. diversifolia* (Vahl) M.Pell. & C.N.Horn, *P. heterosperma* (Alexander) M.Pell. & C.N.Horn, and *P. natans* P.Beauv.

5.2.5. *Pontederia* L. **subg.** *Pontederia*. Type species. *Pontederia cordata* L. Fig 17H

Pontederas Hoffmanns., Verz. Pfl.: 137. 1824, orth. var.

Pontederaea Kuntze, Revis. Gen. Pl. 2: 718. 1891, orth. var.

Michelia Adans., Fam. Pl. 2: 201. 1763, nom. superfl. Type species. Pontederia cordata L. Narukila Adans., Fam. Pl. 2: 54. 1763, nom. superfl. Type species. Narukila cordata (L.) Nieuwl. (≡ Pontederia cordata L.).

Unisema Raf. Med. Repos. 5: 352. 1808, nom. superfl. Type species. *Unisema obtusifolia* Raf. (≡ *Pontederia cordata* L.).

Umsema Raf. Med. Repos. 5: 352 1808, orth. var.

Unisemma D.A.Godron, in Orbigny CVD, Dict. Univ. Hist. Nat.: 761. 1848, orth. var.

Reussia Endl., Gen. Pl.: 139. 1836. Type species. Reussia triflora Endl. ex Seub. [≡ Pontederia triflora (Endl. ex Seub.) G.Agostini et al.].

Distribution and ecology. Exclusively Neotropical. It can be found growing in perennial freshwater bodies.

Accepted species. A total of seven accepted species: *Pontederia cordata* L., *P. ovalis* Mart. ex Schult. & Schult.f., *P. parviflora* Alexander, *P. rotundifolia* L.f., *P. sagittata* C.Presl, *P. subovata* (Seub.) Lowden, and *P. triflora* (Endl. ex Seub.) G.Agostini et al.

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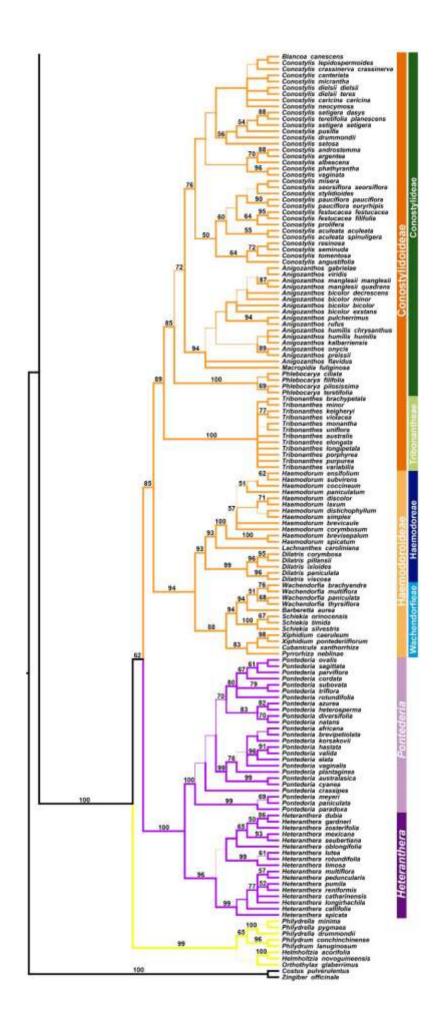


Figure 1. Morphology-based Bayesian consensus tree with posterior probability values expressed through branch thickness (thick branches $PP \ge 0.95$ and thin branches PP < 0.95). Bootstrap values of the Parsimony tree depicted above the branches when recovered by the analysis. Yellow branches representing Philydraceae, purple branches representing Pontederiaceae, and orange branches representing Haemodoraceae. Lateral bars highlighting relevant infrafamilial taxa.

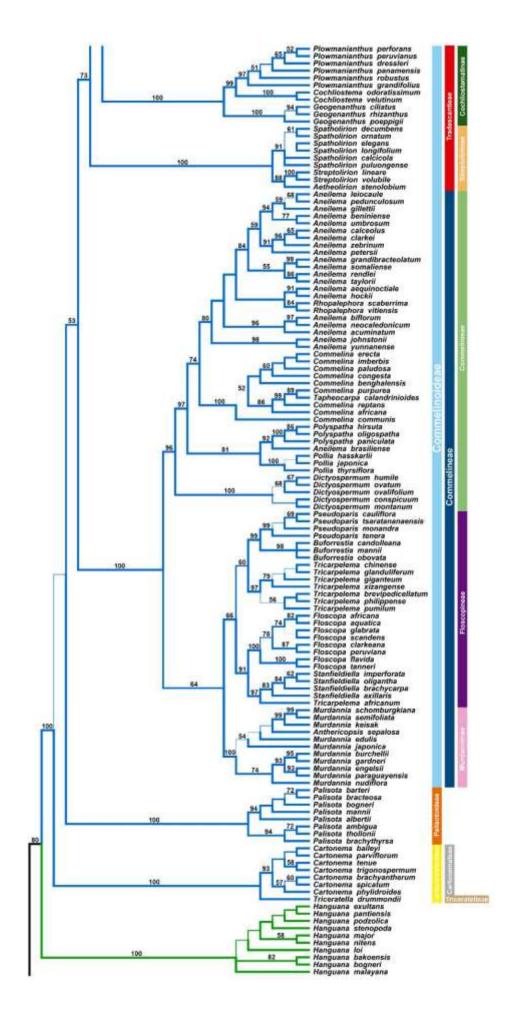


Figure 2. Continuation of the morphology-based Bayesian consensus tree with posterior probability values expressed through branch thickness (thick branches $PP \ge 0.95$ and thin branches PP < 0.95). Bootstrap values of the Parsimony tree depicted above the branches when recovered by the analysis. Green branches representing Hanguanaceae, and blue branches representing Commelinaceae. Lateral bars highlighting relevant infrafamilial taxa.

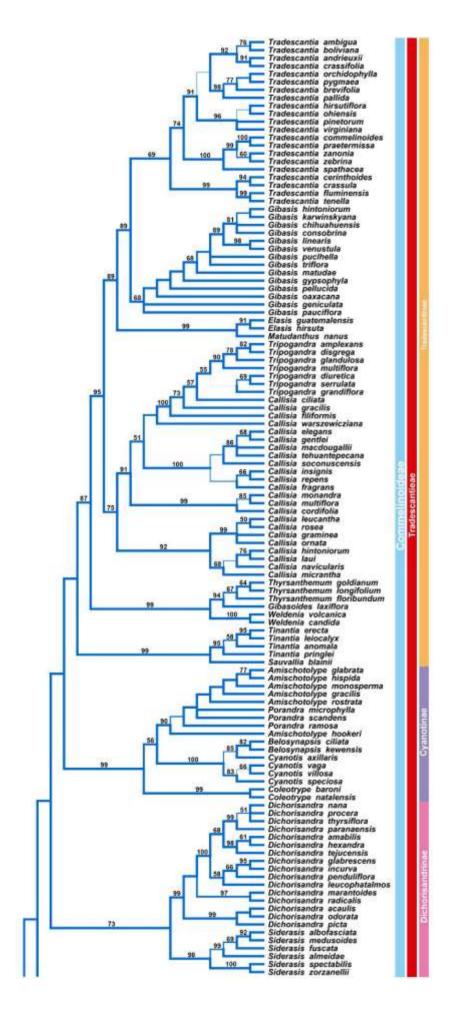


Figure 3. Continuation of the morphology-based Bayesian consensus tree with posterior probability values expressed through branch thickness (thick branches $PP \ge 0.95$) and thin branches PP < 0.95). Bootstrap values of the Parsimony tree depicted above the branches when recovered by the analysis. Blue branches representing Commelinaceae. Lateral bars highlighting relevant infrafamilial taxa.

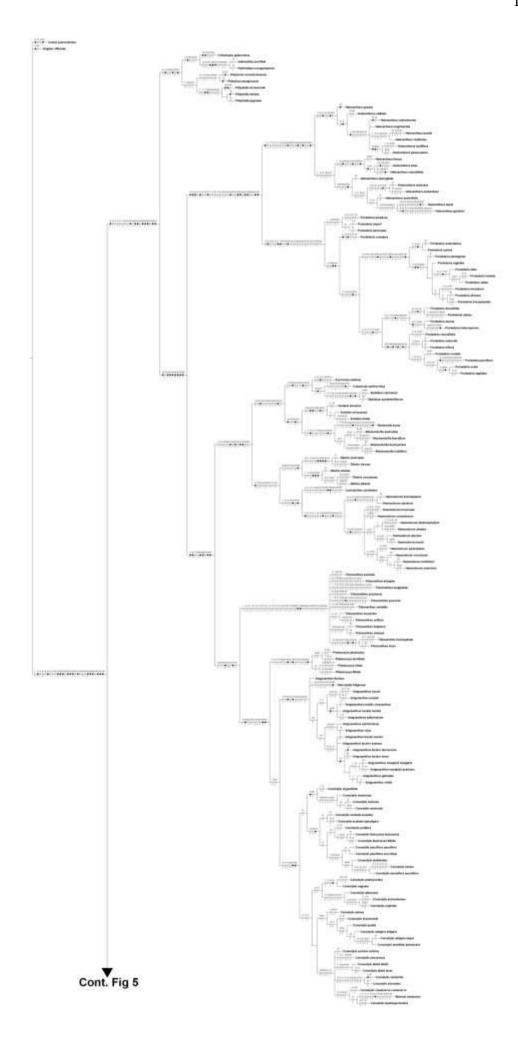


Figure 4. Morphology-based Bayesian consensus tree, showing the character state optimizations at each node of the cladogram, represented by circles. In each circle, the numbers above and below represent the character and character state numbers, respectively (as presented in Appendix 1).

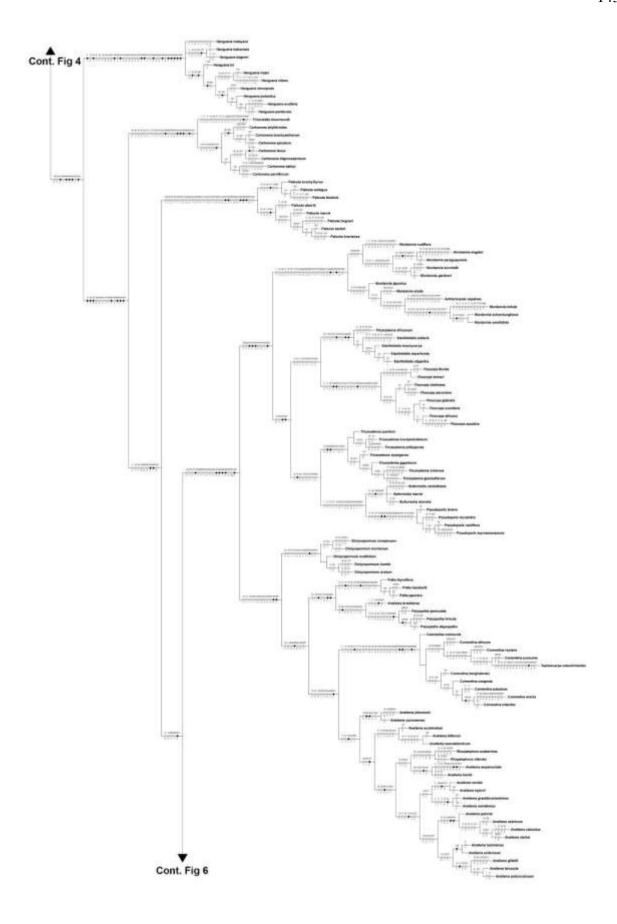


Figure 5. Continuation of the morphology-based Bayesian consensus tree, showing the character state optimizations at each node of the cladogram, represented by circles. In each circle, the numbers above and below represent the character and character state numbers, respectively (as presented in Appendix 1).

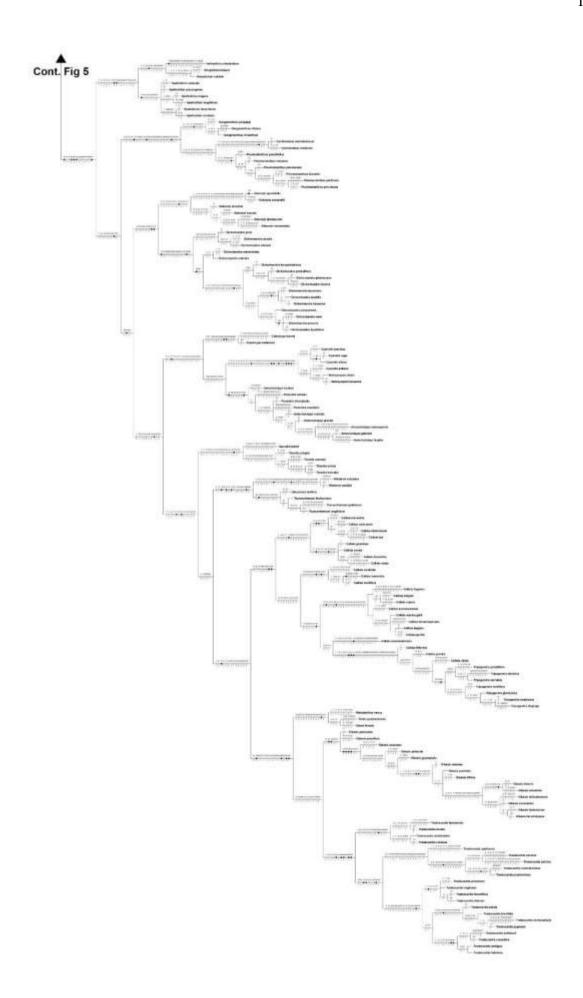


Figure 6. Continuation of the morphology-based Bayesian consensus tree, showing the character state optimizations at each node of the cladogram, represented by circles. In each circle, the numbers above and below represent the character and character state numbers, respectively (as presented in Appendix 1).

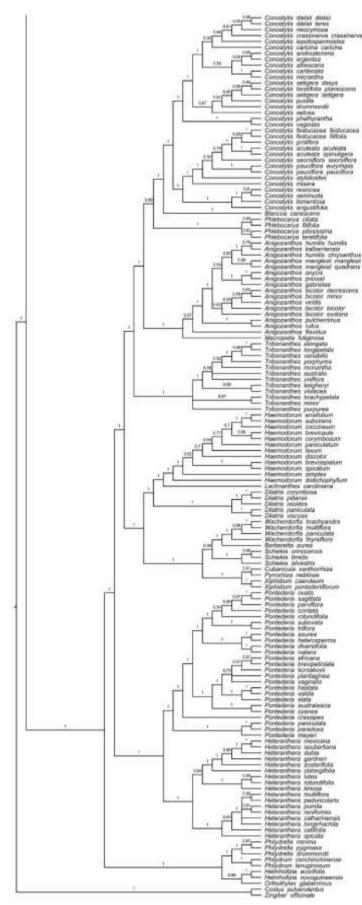


Figure 7. Bayesian consensus tree of the combined molecular and morphological datasets. Posterior probability values depicted above the branches.

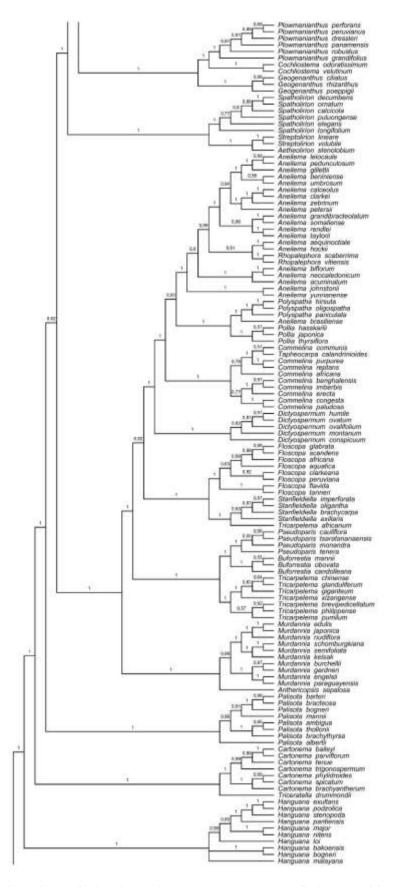


Figure 8. Continuation of the Bayesian consensus tree of the combined molecular and morphological datasets. Posterior probability values depicted above the branches.

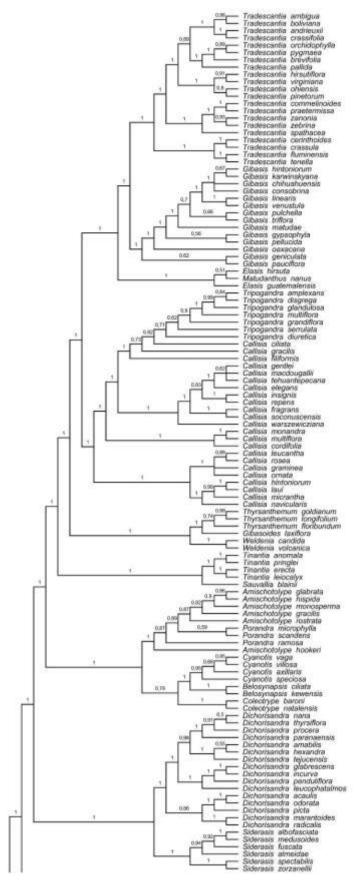


Figure 9. Continuation of the Bayesian consensus tree of the combined molecular and morphological datasets. Posterior probability values depicted above the branches.

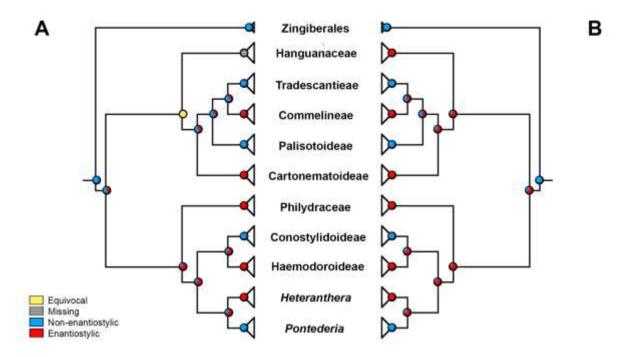


Figure 10. Simplified Bayesian consensus tree of the combined molecular and morphological datasets for Commelinales showing the ancestral state reconstruction of enantiostyly. **A,** Mapping with Hanguaceae left with mssing data. **B,** Mapping with Hanguanaceae treated as enantiostylic.

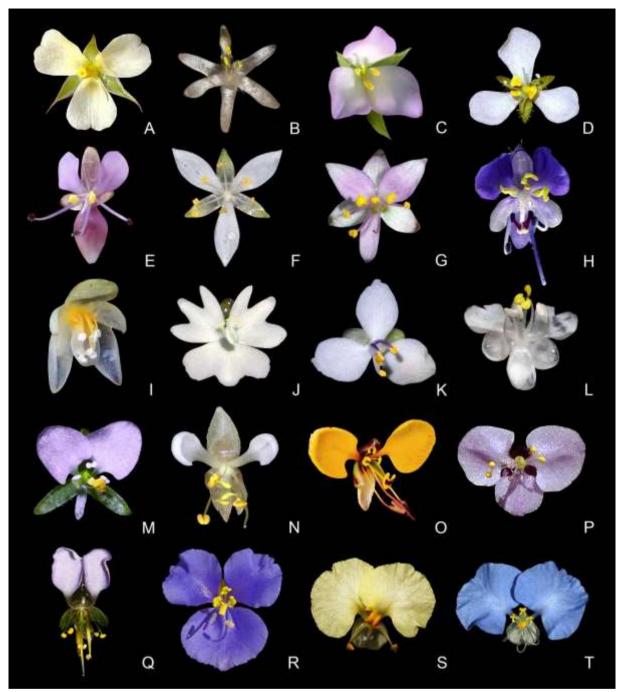


Figure 11. Floral morphology of Commelinaceae. A, subfamily Cartonematoideae: Cartonema trigonospermum C.B.Clarke. B, subfamily Palisotoideae: Palisota barterii Hook. C-D, subfamily Commelinoideae, tribe Commelineae, subtribe Murdanniinae: C, Murdannia sepalosa (C.B.Clarke) M.Pell.; D, Murdannia engelsii M.Pell. & Faden. E-J, subfamily Commelinoideae, tribe Commelineae, subtribe Floscopineae: E, Stanfieldiella africana (Faden) M.Pell.; F, Stanfieldiella imperforata (C.B.Clarke) Brenan; G, Floscopa hirsuta (Kunth) Hassk.; H, Tricarpelema chinense D.Y.Hong; I, Buforrestia sp. nov. Faden & M.Pell. ined.; J, Pseudoparis cauliflora H.Perrier. K-T, subfamily Commelinoideae, tribe Commelineae, subtribe Commelinineae: K, Dictyospermum montanum Wight; L, Pollia secundiflora (Blume) Bakh.f.; M, Campylonanthus brasiliense (C.B.Clarke) Faden & M.Pell.; N, Polyspatha paniculata Benth.; O, Aneilema johnstonii K.Schum.; P, Aneilema protensum (Wall. ex Wight) Thwaites; Q, Aneilema beniniense (P.Beauv.) Kunth; R, Commelina agrostophylla F.Muell.; S, Commelina catharinensis Hassemer et al.; T, Commelina erecta L.

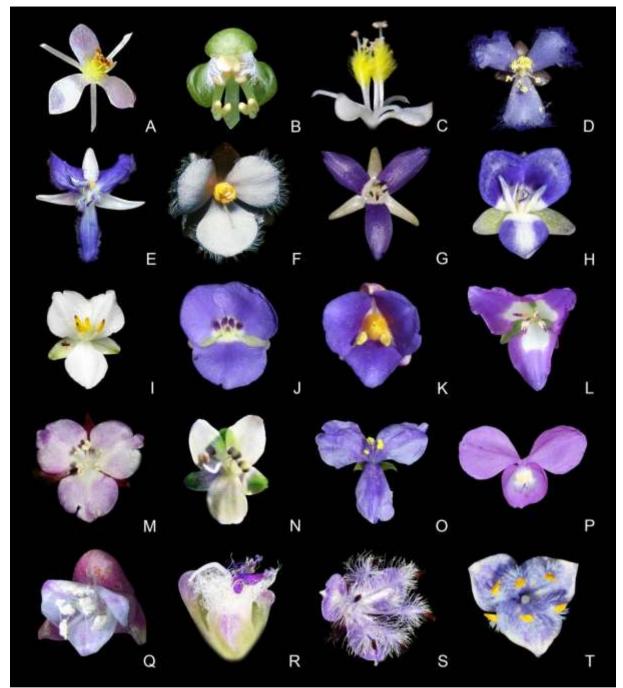


Figure 12. Floral morphology of Commelinaceae. A–C, subfamily Commelinoideae, tribe Tradescantieae, subtribe Streptoliriinae: A, Spatholirion calcicola K.Larsen & S.S.Larsen; B, Aëtheolirion stenolobium Forman; C, Streptolirion volubile Edgew. D–F, tribe Tradescantieae, subtribe Cochliostematinae: D, Geogenanthus rhizanthus (Ule) G.Brückn; E, Cochliostema odoratissimum Lem.; F, Plowmanianthus panamensis Faden & C.R.Hardy; G–N, tribe Tradescantieae, subtribe Dichorisandrinae: G, Dichorisandra acaulis Cogn.; H, Dichorisandra hexandra (Aubl.) C.B.Clarke; I, Dichorisandra incurva Mart.; J, Dichorisandra penduliflora Kunth; K, Dichorisandra thyrsiflora J.C.Mikan; L, Dichorisandra radicalis Nees & Mart.; M, Siderasis fuscata (Lodd.) H.E.Moore; N, Siderasis zorzanellii M.Pell. & Faden. O–T, tribe Tradescantieae, subtribe Cyanotinae: O, Coleotrype natalensis C.B.Clarke; P, Coleotrype baronii Baker; Q, Amischotolype hispida (A.Rich.) D.Y.Hong; R, Amischotolype microphylla (Y.Wan) M.Pell.; S, Cyanotis ciliata (Blume) Bakh.f.; T, Cyanotis repens Faden & D.M.Cameron.

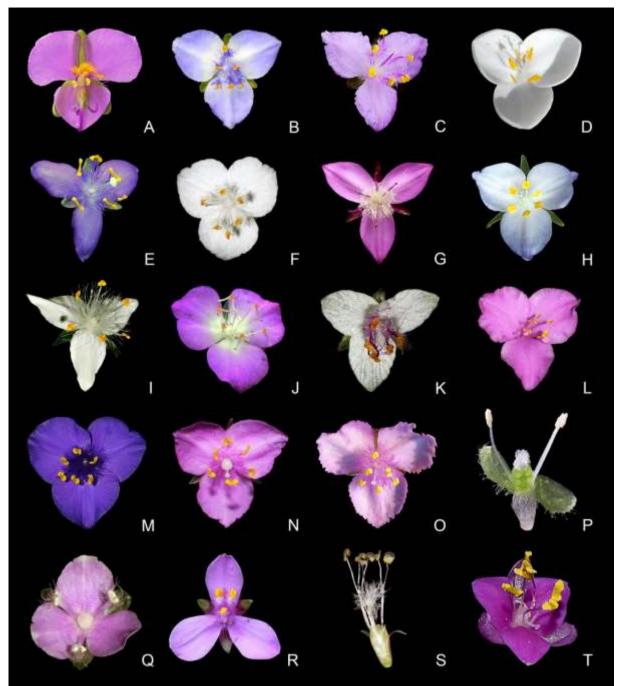


Figure 13. Floral morphology of Commelinaceae. A–T, subfamily Commelinoideae, tribe Tradescantieae, subtribe Tradescantiinae: A, Tinantia erecta (Jacq.) Fenzl; B, Thyrsanthemum laxiflorum (C.B.Clarke) M.Pell. & Espejo; C, Thyrsanthemum floribundum (M.Martens & Galeotti) Pichon. D, Weldenia candida Schult.f.; E, Gibasis matudae D.R.Hunt; F, G. pellucida (M.Martens & Galeotti) D.R.Hunt; G, Elasis hirsuta (Kunth) D.R.Hunt; H, Matudanthus nanus (M.Martens & Galeotti) D.R.Hunt; I, Tradescantia fluminensis Vell.; J, Tradescantia commelinoides Schult.f.; K, Tradescantia ambigua Mart. ex Schult. & Schult.f.; L, Tradescantia sillamontana Matuda; M, Tradescantia ohiensis Raf.; N, Brachyphyllum naviculare (Ortgies) M.Pell. & Hertweck. O, Cuthbertia ornata Small; P, Aploleia monandra (Sw.) H.E.Moore; Q, Tripogandra triandra (Kunth) M.Pell. & Hertweck; R, Tripogandra diuretica (Mart.) Handlos; S, Callisia repens (Jacq.) L.; T, Hadrodemas warszewiczianum (Kunth & C.D.Bouché) H.E.Moore.

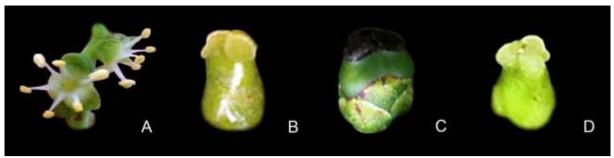


Figure 14. Floral morphology of Hanguanaceae. **A,** staminate flower of *Hanguana sp.* **B,** pistillate flower of *H. anthelmica* (Blume *ex* Schult. & Schult. f.) Masam. **C,** pistillate flower of *H. anthelmica* starting fruit development. **D,** pistillate flower of *H. neglecta* Škorničk. & Niissalo.



Figure 15. Floral morphology of Philydraceae. **A,** *Helmholtzia acorifolia* F.Muell. **B,** *Orthothylax glaberrimus* (Hook.f.) Skottsb. **C,** *Philydrella pygmaea* (R.Br.) Caruel. **D,** *Philydrum cochinchinense* (Lour.) M.Pell.

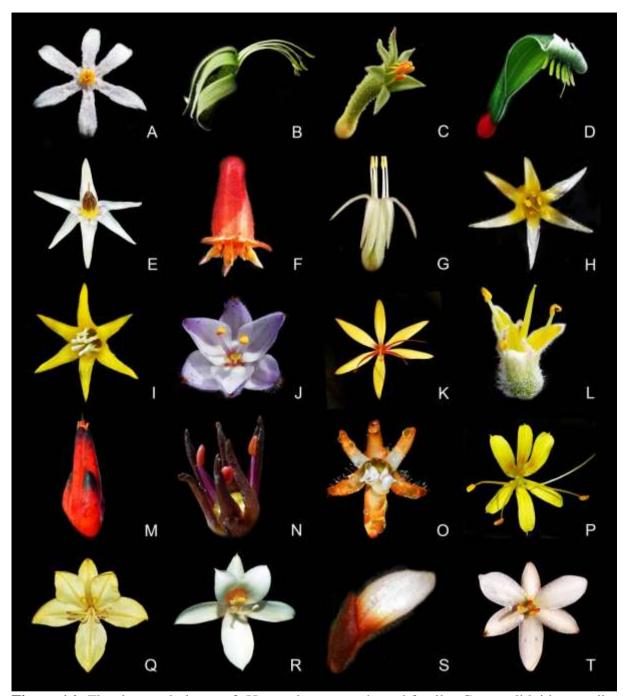


Figure 16. Floral morphology of Haemodoraceae. A, subfamily Conostylidoideae, tribe Tribonatheae: *Tribonanthes longipetala* Lindl. B–I, subfamily Conostylidoideae, tribe Conostylideae: B, *Anigozanthos fuliginosus* Hook.; C, *Anigozanthos flavidus* DC.; D, *Anigozanthos manglesii* D.Don; E, *Phlebocarya ciliata* R.Br.; F, *Conostylis canescens* (Lindl.) F.Muell.; G, *Conostylis androstemma* F.Muell.; H, *Conostylis setigera* R.Br.; I, *Conostylis vaginata* Endl. J–N, subfamily Haemodoroideae, tribe Haemodoreae: J, *Dilatris ixioides* Lam.; K, *Paradilatris viscosa* (L.f.) Hopper et al.; L, *Lachnanthes caroliniana* (Lam.) Dandy; M, *Haemodorum coccineum* R.Br.; N, *Haemodorum simplex* Lindl. O–T, subfamily Haemodoroideae, tribe Wachendorfieae: O, *Schiekia silvestris* (Maas & Stoel) Hopper et al.; P, *Wachendorfia aurea* (Harv.) M.Pell. & Hopper; Q, *Wachendorfia paniculata* Burm.; R, *Cubanicula xanthorrhiza* (C.Wright *ex* Griseb.) Hopper et al.; S, *Pyrrorhiza neblinae* Maguire & Wurdack; T, *Xiphidium caeruleum* Aubl.

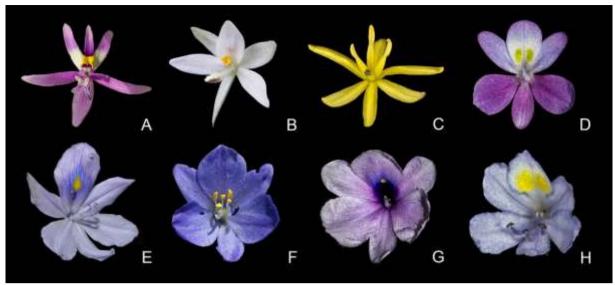


Figure 17. Floral morphology of Pontederiaceae. **A–C,** *Heteranthera* Ruiz & Pav.: **A,** *H. rotundifolia* (Kunth) Griseb.; **B,** *H. reniformis* Ruiz & Pav.; **C,** *H. dubia* (Jacq.) MacMill. **D–H,** *Pontederia* L.: **D,** *P. paniculata* Spreng.; **E,** *P. crassipes* Mart.; **F,** *P. korsakowii* (Regel & Maack) M.Pell. & C.N.Horn; **G,** *Pontderia azurea* Sw.; **H,** *P. ovalis* Mart. ex Schult. & Schult.f.

Tables

Table 1. List of voucher specimens for the morphological matrix

Taxa	Voucher
Costus pulverulentus C.Presl	Donnell 4973 (US)
Zingiber officinale Roscoe	Canfield 290 (US)
Hanguana bakoensis Siti Nurfazilah et al.	Malcom S.100599 (SAR)
Hanguana bogneri Tillich & E.Sill	Bogner 94/2211 (M)
Hanguana exultans Siti Nurfazilah et al.	Siti Nurfazilah HA-55 (KEP)
Hanguana loi Mohd Fahmi et al.	Chai S34089 (K)
Hanguana major Airy Shaw	Chew RSNB4233 (K)
Hanguana malayana (Jack) Merr.	Curtis s.n. (SING 0203818)
Hanguana nitens Siti Nurfazilah et al.	Siti Nurfazilah HA-48 (KEP)
Hanguana pantiensis Siti Nurfazilah et al.	Siti Nurfazilah HA-56 (KEP)
Hanguana podzolica Siti Nurfazilah et al.	Siti Nurfazilah HA-50 (KEP)
Hanguana stenopoda Siti Nurfazilah et al.	Siti Nurfazilah HA-60 (KEP)
Aëtheolirion stenolobium Forman	Thitimetharoch 579 (US)
Amischotolype glabrata Hassk.	Cameron s.n. (US 00520209)
Amischotolype gracilis (Ridl.) I.M.Turner	Bartlett 7312 (US)
Amischotolype hispida (Less & A.Rich.) D.Y.Hong	Robinson 1831 (US)
Amischotolype hookeri (Hassk.) H.Hara	Kress 98-6247 (US)
Amischotolype monosperma (C.B.Clarke) I.M.Turner	Bogner 1811 (US)
Amischotolype rostrata (Hassk.) Duist.	Hallier 533/71 (L)
Aneilema acuminatum R.Br.	Faden 1/94 (US)
Aneilema aequinoctiale (P.Beauv.) G.Don	Faden 290 (US)
Aneilema beninense (P.Beauv.) Kunth	Faden 87/2 (US)
Aneilema biflorum R.Br.	Pellegrini 218 (RB)
Aneilema brasiliense C.B.Clarke	Amaral 7/99 (US)
Aneilema calceolus Brenan	Faden 77/565 (US)
Aneilema clarkei Rendle	Faden 77/629 (US)
Aneilema gillettii Brenan	Friis 1044 (US)
Aneilema grandibracteolatum Faden	Glover 408 (K)
Aneilema hockii De Wild.	Faden 96/9 (US)
Aneilema johnstonii K.Schum.	Faden 97/8 (US)
Aneilema leiocaule K.Schum.	Bidgood 440 (US)
Aneilema neocaledonicum Schltr.	MacKee 2170 (US)
Aneilema pedunculosum C.B.Clarke	Bidgood 4196 (US)
Aneilema petersii (Hassk.) C.B.Clarke	Luke 2495 (US)
Aneilema rendlei C.B.Clarke	Faden 27/85 (US)
Aneilema somaliense C.B.Clarke	Faden 74/939 (US)
Aneilema taylorii C.B.Clarke	Faden 74/371 (US)
Aneilema umbrosum (Vahl) Kunth	Faden 74/2 (US)
Aneilema yunnanense (D.Y.Hong) M.Pell.	Wang 80888 (A)
Aneilema zebrinum Chiov.	Faden 77/311 (US)
Anthericopsis sepalosa Engl.	Faden 74/504 (US)
Belosynapsis ciliata (Blume) R.S.Rao	Merrill 8154 (US)
Belosynapsis kewensis Hassk.	Cultivated (US 01276642)
Buforrestia candolleana C.B.Clarke	Pires 52215 (US)
Buforrestia mannii C.B.Clarke	Faden 87/5 (US)
Buforrestia obovata Brenan	Straub 145 (US)
Callisia ciliata Kunth	Prance 16762 (US)

Callisia cordifolia (Sw.) E.S.Anderson & Woodson

Callisia elegans Alexander ex H.E.Moore

Callisia filiformis (M.Martens & Galeotti) D.R.Hunt

Callisia fragrans (Lindl.) Woodson

Callisia gentlei Matuda

Callisia gracilis (Kunth) D.R. Hunt

Callisia gracilis (Kunth) D.R. Hunt

Callisia gracilis (Kunth) D.R. Hunt

Dorr 8571 (US)

Callisia gracilis (Kunth) D.R.HuntDorr 8571 (US)Callisia gramínea (Small) G.C.TuckerNash 879 (US)Callisia insignis C.B.ClarkeMoore 1516 (US)Callisia hintoniorum B.L.TurnerHinton 25725 (US)Callisia laui (D.R.Hunt) D.R.HuntLau s.n. (K 000434009)Callisia graminea fo. leucantha (Lakela) G.C.TuckerLakela 32048 (USF)

Callisia macdougallii Miranda McDougal s.n. (US no. 1981074)

Callisia micranta (Torr.) D.R.HuntTraverse 1016 (US)Callisia monandra (Sw.) Schult. & Schult.f.Pellegrini 430 (RB)Callisia multiflora (M.Martens & Galeotti) Standl.Matuda 1992 (US)

Callisia navicularis (Orteges) D.R.Hunt Hinton 18492 (US)
Callisia ornata (Small) G.C.Tucker Small 9054 (US)
Callisia repens (Jacq.) L. Pellegrini 284 (RB)

Callisia repens (Jacq.) L.Pellegrini 284 (RB)Callisia rósea (Vent.) D.R.HuntHarper 1314 (US)Callisia soconuscensis MatudaHinton 11587 (US)Callisia tehuantepecana MatudaTores 1021 (US)

Callisia warszewicziana (Kunth & C.D.Bouché) D.R.HuntKnunth BH 60-511 (US)Cartonema baileyi F.M.BaileyBailey s.n. (BRI-AQ0512720)Cartonema brachyantherum Benth.Fitzalan s.n. (K 000854172)

Cartonema brachyantherum Benth. Fitzalan s.n. (K 000854172 Cartonema parviflorum Hassk. s.leg. s.n. (L 0041670) Cartonema phylidroides F.Muell. Preiss 2228 (P)

Cartonema spicatum R.Br. Brown s.n. (K 000854169)

Cartonema tênue CaruelDixon 1085 (US)Cartonema trigonospermum C.B.ClarkeFryxell 4122 (US)Cochliostema odoratissimum Lem.Knapp 1834 (US)Cochliostema velutinum ReadCuatrecasas 21438 (US)Coleotrype baronii BakerNusbaumer 926 (US)

Coleotrype natalenses C.B.Clarke

Commelina africana L.

Commelina benghalensis L.

Commelina communis L.

Faden 77/287 (US)

Pellegrini 233 (RB)

Faden 76/29 (US)

Commelina congesta C.B.Clarke

Porembski 1154 (US)

Commelina erecta L.

Pellegrini 471 (RB)

Commelina imberbis Ehrenb. ex Hassk. Faden 2003/024 (US) Faden 76/206 (US) Commelina paludosa Blume Commelina purpurea C.B.Clarke Faden 94/1 (US) Faden 94/2 (US) Commelina reptans Brenan Cyanotis axillaris (L.) D.Don Faden 76/196 (US) Faden 97/3 (US) Cyanotis speciosa (L.f.) Hassk. Cyanotis vaga (Lour.) Schult.f. Gajurel 301 (US) Cyanotis villosa Schult. Faden 76/267 (US) Dichorisandra acaulis Cogn. Pellegrini 328 (RB) Dichorisandra amabilis J.R.Grant Funk 10992 (US)

Dichorisandra hexandra (Aubl.) C.B.ClarkePellegrini 484 (RB)Dichorisandra glabrescens (Seub.) Aona & M.C.E.AmaralForzza 5514 (RB)Dichorisandra incurva Mart.Wängler 1598 (RB)

Dichorisandra leucophatalmos Hook.	Pellegrini 458 (RB)
Dichorisandra marantoides Aona & Faden	Pellegrini 492 (RB)
Dichorisandra nana Aona & M.C.E.Amaral	Jardim 4220 (RB)
Dichorisandra odorata Aona & M.C.E.Amaral	Santos-Lima 14183 (RB)
Dichorisandra paranaënsis D.Maia et al.	Pellegrini 469 (RB)
Dichorisandra penduliflora Kunth	Pellegrini 375 (RB)
Dichorisandra procera Mart.	Pellegrini 464 (RB)
Dichorisandra picta Lodd.	Costa 284 (RB)
Dichorisandra tejucensis Mart.	Forzza 2722 (RB)
Dichorisandra thyrsiflora J.C.Mikan	Pellegrini 219 (RB)
Dichorisandra radicalis Nees & Mart	Pellegrini 459 (RB)
Dictyospermum conspicuum (Blume) Hassk.	Thitimetharoch 568 (US)
Dictyospermum humile (Warb.) J.K.Morton	Merrill 10459 (US)
Dictyospermum montanum Wight	Faden 76/210 (US)
Dictyospermum ovalifolium Wight	Faden 76/474 (US)
Dictyospermum ovatum Hassk.	Thitimetharoch 426 (US)
Elasis guatemalensis (C.B.Clarke ex Donn. Sm.) M.Pell.	Heyde 3519 (US)
Elasis hirsuta (Kunth) D.R.Hunt	Bonpland (2160) (P)
Floscopa africana (P.Beauv.) C.B.Clarke	Faden 87/11 (US)
Floscopa aquática Hua	Fosberg 40431 (US)
Floscopa clarkeana Kuntze	Schunke 8578 (US)
Floscopa flavida C.B.Clarke	Faden 96/188 (US)
Floscopa glabrata (Kunth) Hassk.	Pellegrini 450 (RB)
Floscopa peruviana Hassk. ex C.B.Clarke	Medeiros 20176 (RB)
Floscopa tanneri Brenan	Bidgood 2590 (US)
Floscopa scandens Lour.	Faden 76/447 (US)
Geogenanthus ciliatus G.Brückn.	Killip 29347 (US)
Geogenanthus poeppigii (Miq.) Faden	Daly 7921 (US)
Geogenanthus rhizanthus (Ule) G.Brückn.	Plowman 4076 (US)
Gibasis chihuahuensis (Standl.) Rohweder	Hinton 13944 (US)
Gibasis consobrina D.R.Hunt	Pringle 6723 (US)
Gibasis geniculata (Jacq.) Rohweder	Pellegrini 338 (RB)
Gibasis gypsophyla B.L.Turner	Hinton 22082 (GBH)
Gibasis hintoniorum B.L.Turner	Hinton 23013 (GBH)
Gibasis karwinskyana (Schult. & Schult.f.) Rohweder	Pringle 9250 (US)
Gibasis linearis (Benth.) Rohweder	Palmer 319 (US)
Gibasis matudae D.R.Hunt	Smith 3913 (US)
Gibasis oaxacana D.R.Hunt	Hunt 8175 (K)
Gibasis pauciflora (Urb. & Ekman) D.R.Hunt	Eggers 7361 (US)
Gibasis pellucida (M.Martens & Galeotti) D.R.Hunt	Pellegrini 5 (RFA)
Gibasis puclhella (Kunth) Raf.	Matuda 21459 (US)
Gibasis triflora (M.Martens & Galeotti) D.R.Hunt	Hunt 8130 (K)
Gibasis venustula (Kunth) D.R.Hunt	Gaona 436 (US)
Gibasoides laxiflora (C.B.Clarke) D.R.Hunt	Smith 3818 (US)
Matudanthus nanus (M.Martens & Galeotti) D.R.Hunt	Frame 259 (US)
Murdannia burchellii (C.B.Clarke) M.Pell.	Burchell 8165 (K)
Murdannia edulis (Stokes) Faden	Faden 2009/013 (US)
Murdannia engelsii M.Pell. & Faden	Engels 3474 (RB)
Murdannia gardneri (Seub.) G.Brückn.	Gardner 4021 (K)
Murdannia japônica (Thunb.) Faden	Ramamoorthy 335 (US)
Murdannia keisak (Hassk.) HandMazz.	Faden 1/04 (US)

Faden 77?151 (US) Murdannia nudiflora (L.) Brenan Murdannia paraguayensis (C.B.Clarke ex Chodat) G.Brückn. Hassler 5083 (G) Murdannia schomburgkiana (Kunth) G.Brückn. Schomburgk 842 (B) Murdannia semifoliata (C.B.Clarke) G.Brückn. Moore 541 (BM) Palisota albertii L.Gentil SI Greenhouse (US no. 1991-071x) Palisota ambígua (P.Beauv.) C.B.Clarke Faden 87/10 (US) Palisota barteri Hook. Faden 86/57 (US) Palisota bogneri Brenan Le Testu 7520 (US) Palisota brachythyrsa Mildbr. Harris 2433 (US) Palisota bracteosa C.B.Clarke Faden 86/48 (US) Palisota mannii C.B.Clarke Faden 86/16 (US) Palisota thollonii Hua Harris 5616 (US) Plowmanianthus dressleri Faden & C.R.Hardy Hardy 236 (US) Plowmanianthus grandifolius Faden & C.R.Hardy Hardy 140 (US) Plowmanianthus panamensis Faden & C.R.Hardy Hardy 243 (US) Plowmanianthus perforans Faden & C.R.Hardy Vásquez 34244 (US) Plowmanianthus peruvianus C.R.Hardy & Faden Hardy 122 (US) Plowmanianthus robustus (C.R.Hardy & Faden) M.Pell. Hardy 200 (US) Thitimetharoch 411 (US) Pollia hasskarlii R.S.Rao Pollia japônica Thunb. Charette 1837 (US) Pollia thyrsiflora (Blume) Steud. Merrill 9268 (US) Polyspatha hirsuta Mildbr. Faden 87/13 (US) Polyspatha oligospatha Faden Poulsen 1275 (US) Polyspatha paniculata Benth Faden 86/32 (US) Porandra microphylla Y.Wan Thitimetharoch 458 (US) Henry 12204a (US) Porandra ramosa D.Y.Hong Thitimetharoch 410 (US) Porandra scandens D.Y.Hong Pseudoparis cauliflora H.Perrier Perrier de la Bâthie 16764 (P) Pseudoparis monandra H.Perrier Gautier 4179 (US) Pseudoparis tenera (Baker) Faden Humbert 48416 (P) Perrier de la Bâthie 7296 (P) Pseudoparis tsaratananaensis H.Perrier ex M.Pell. sp. nov. ined. Rhopalephora scaberrima (Blume) Faden Reinwardt s.n. (L 0820741) Seemann 643 (K) Rhopalephora vitiensis (Seem.) Faden Sauvallia blainii Wright ex Hassk. Wright 3729 (US) Siderasis albofasciata M.Pell. Pellegrini 337 (RB) Siderasis almeidae M.Pell. & Faden Pellegrini 493 (RB) Siderasis fuscata (Lodd.) H.E.Moore Pellegrini 217 (RB) Siderasis medusoides M.Pell. & Faden Fiaschi 3489 (SPF) Siderasis spectabilis M.Pell. & Faden Melo-Filho 1172 (R) Siderasis zorzanellii M.Pell. & Faden Zorzanelli 969 (RB) Spatholirion calcícola K.Larsen & S.S.Larsen Larsen 43586 (US) Fukuoka T-96210 (KYO) Spatholirion decumbens Spatholirion elegans (Cherfils) C.Y.Wu Pételot 4829 (P) Spatholirion longifolium (Gagnep.) Dunn Bartholomew 948 (US) Spatholirion ornatum Ridl. Kerr 3617 (P) Spatholirion puluongense Aver. Averyanov 3957 (LE) Stanfieldiella axillaris J.K.Morton Slayback 94-8 (US)

Hall 091/93 (US)

Faden 86/39 (US)

Faden 97/14 (US)

Peng 20537 (US)

Stanfieldiella brachycarpa (Gilg & Ledermann ex Mildbr.) Brenan

Stanfieldiella imperforata (C.B.Clarke) Brenan

Stanfieldiella oligantha (Mildbr.) Brenan

Streptolirion lineare Fukuoka & N.Kurosaki

Streptolirion volubile Edgew. Henry 4170 (US) Tapheocarpa calandrinioides (F.Muell.) Conran Guliver s.n. (K 000854161) Thyrsanthemum floribundum (M.Martens & Galeotti) Pichon Galeotti 4952 (K) Thyrsanthemum goldianum D.R.Hunt Hinton 13082 (K) Thyrsanthemum longifolium (M.Martens & Galeotti) M.Pell. & Espejo Galeotti 4942a (BR) Tinantia anomala C.B.Clarke Tharp 44104 (US) Tinantia erecta (Jacq.) Fenzl Pellegrini 315 (RB) Hinton 12227 (US) Tinantia leiocalyx C.B.Clarke Tinantia pringlei (S.Watson) Rohweder Bartlett 10462 (US) Pellegrini 445 (RB) Tradescantia cerinthoides Kunth Tradescantia crassula Link & Otto Pellegrini 439 (RB) Tradescantia fluminensis Vell. Pellegrini 48 (RB) Tradescantia tenella Kunth Pellegrini 431 (RB) Tradescantia commelinoides Schult. & Schult.f. Breedlove 12239 (US) Tradescantia praetermissa M.Pell. Mandon 1237 (K) Tradescantia spathacea Sw. Pellegrini 499 (RB) Tradescantia zanonia (L.) Sw. Pellegrini 412 (RB) Tradescantia zebrina Heyhn. ex Bosse Pellegrini 406 (RB) Fraga 3654 (RB) Tradescantia ambígua Mart. Tradescantia andrieuxii C.B.Clarke Tores 132 (US) Tradescantia boliviana (Hassk.) J.R.Grant Mandon 1239 (K) Tradescantia crassifólia Cav. Rose 216 (US) Tradescantia brevifolia (Torr.) Rose Bigelow 1500-a (NY) Tradescantia orchidophylla Rose & Hemsl. Jones 467 (US) Tradescantia pallida (Rose) D.R.Hunt Palmer s.n. (US 00091625) Rose 2095 (US) Tradescantia pygmaea D.R.Hunt Tradescantia hirsutiflora Bush Faden 76/21 (US) Tradescantia ohiensis Raf. Pellegrini 512 (RB) Tradescantia pinetorum Greene Greene s.n. (US 00044946) Tradescantia virginiana L. Faden 87/1a (US) Keating 90-11 (US) Tricarpelema africanum Faden Evrard 1178 (P) Tricarpelema brevipedicellatum Faden Tang 23593 (PE) Tricarpelema chinense D.Y.Hong Tricarpelema giganteum (Hassk.) H.Hara Long 1110 (US) Tricarpelema glanduliferum (J.Joseph & R.S.Rao) R.S.Rao Harder 5415 (US) Tricarpelema philippense (Panigrahi) Faden Ramos 22082 (US) Tricarpelema pumilum (Hallier f.) Faden Poulsen 187 (K) Tricarpelema xizangense D.Y.Hong Tibet-MacArthur 2050 (US) Triceratella drummondii Brenan Drummond 5780 (K) Hinton 9260 (US) Tripogandra amplexans Handlos Tripogandra disgrega (Kunth) Woodson Sanders 11287 (US) Tripogandra diurética (Mart.) Handlos Pellegrini 4 (RFA) Tripogandra glandulosa (Seub.) Rohweder Pellegrini 298 (RB) Tripogandra grandiflora (Donn. Sm.) Woodson Sanders 9829 (US) Tripogandra multiflora (Sw.) Raf. Swartz s.n. (BM 000578859) Tripogandra serrulata (Vahl) Handlos Faden 76/181 (US) Hartweg s.n. (K 000363199) Weldenia volcanica (Benth.) M.Pell. & Espejo Weldenia candida Schult.f. Karwinsky 272 (M 0244244)

Helmholtzia acorifolia F.Muell.Kress 92-3505 (US)Helmholtzia novoguineensis (K.Krause) Skottsb.Hoogland 11068 (US)Orthothylax glaberrimus (Hook.f.) Skottsb.Constable 22483 (US)

Philydrella drummondii L.G.Adams Morrison s.n. (CANB 139276) Philydrella minima (L.G.Adams) M.Pell. comb. ined. Orchard 4341 (CANB) Philydrella pygmaea (R.Br.) Caruel Pritzel 471 (US) Fosberg 37834 (US) Philydrum conchinchinense (Lour.) M.Pell. comb. ined. Philydrum lanuginosum Banks & Sol. ex Gaertn. Johnson 20418 (US) Anigozanthos bicolor Endl. subsp. bicolor Preiss 1417 (P) Anigozanthos bicolor subsp. decrescens Hopper Hopper 773 (PERTH) Hopper 4169 (PERTH) Anigozanthos bicolor subsp. exstans Hopper Anigozanthos bicolor subsp. minor (Benth.) Hopper Hopper 2510 (PERTH) Hopper 809 (PERTH) Anigozanthos flavidus DC. Anigozanthos gabrielae Domin Hopper 806 (PERTH) Anigozanthos humilis subsp. chrysanthus Hopper Hopper 2612 (PERTH) Anigozanthos humilis Lindl. subsp. humilis Hopper 749 (PERTH) Anigozanthos kalbarriensis Hopper George 9604 (PERTH) Anigozanthos manglesii D.Don subsp. manglesii Hopper 757 (PERTH) Anigozanthos manglesii subsp. quadrans Hopper Hopper 1393 (PERTH) Anigozanthos onycis A.S.George Hopper 4241 (PERTH) Anigozanthos preissii Endl. Preiss 1413a (P) Anigozanthos pulcherrimus Hook. George 3221 (PERTH) Anigozanthos rufus Labill. Hopper 819 (PERTH) Anigozanthos viridis Endl. Preiss 1415 (P) Barberetta aurea Harv. Bolus 8709 (K) Blancoa canescens Lindl. Spjut 6992 (US) Conostylis aculeata R.Br. subsp. aculeata Hopper 703 (PERTH) Conostylis aculeata subsp. Spinuligera (F.Muell. ex Benth.) Hopper Hopper 1177 (PERTH) Hopper 1247 (PERTH) Conostylis albescens Hopper Crisp 6709 (US) Conostylis androstemma F.Muell. Conostylis angustifolia Hopper Hopper 276 (PERTH) Conostylis argentea (J.Green) Hopper Hopper 66 (PERTH) Conostylis canteriata Hopper Hopper 5185 (PERTH) Conostylis caricina Lindl. subsp. caricina Green 488 (US) Conostylis crassinerva J.Green. subsp. crassinerva Hopper 388 (PERTH) Hopper 430 (PERTH) Conostylis dielsii W.Fitzg. subsp. dielsii Conostylis dielsii subsp. teres Hopper Hopper 442 (PERTH) Conostylis drummondii Benth. Hopper 55 (PERTH) Conostylis festucacea Endl. subsp. festucacea Hopper 19 (PERTH) Conostylis festucacea subsp. filifolia (F.Muell.) Hopper Hopper 458 (PERTH) Conostylis lepidospermoides Hopper Hopper 1149 (PERTH) Conostylis micrantha Hopper Hopper 2468 (PERTH) Hopper 129 (PERTH) Conostylis misera Endl. Conostylis neocymosa Hopper Hopper 445 (PERTH) Conostylis pauciflora Hopper subsp. pauciflora Hopper 131 (PERTH) Conostylis pauciflora subsp. Euryrhipis Hopper Hopper 4894 (PERTH) Conostylis phathyrantha Diels Hopper 568 (PERTH) Conostylis prolifera Benth. Pritzel 634 (US) Conostylis pusilla Endl. Hopper 473 (PERTH) Conostylis resinosa Hopper Hopper 318 (PERTH) Conostylis seminuda Hopper Hopper 2621 (PERTH) Conostylis seorsiflora F.Muell. subsp. seorsiflora Hopper 79 (PERTH) Conostylis setigera subsp. dasys Hopper Hopper 4707 (PERTH)

Pritzel 790 (US)

Conostylis setigera R.Br. subsp. setigera

Green 1726 (US) Conostylis setosa Lindl. Conostylis stylidioides F.Muell. Green 428 (US) Conostylis teretifolia subsp. planescens Hopper Hopper 27 (PERTH) Conostylis tomentosa Hopper Hopper 5184 (PERTH) Conostylis vaginata Endl. Hopper 679 (PERTH) Cubanicula xanthorrhiza (C.Wright ex Griseb.) Hopper Wright 3259 (US) Dilatris corymbose P.J.Bergius Manning 3129 (NBG) Dilatris ixioides Lam. Barker 3318 (NBG) Dilatris paniculata L.f. Bolus 8389 (BOL) Dilatris pillansii W.F.Barker Pillans 3701 (BOL) Dilatris viscosa L.f. Barker 690 (NBG) Haemodorum brevicaule F.Muell. Chippendale NT 4477 (PERTH) Haemodorum brevisepalum Benth. Koch N69 (PERTH) Haemodorum coccineum R.Br. White 8715 (US) Haemodorum corymbosum Vahl MacKee 8276 (US) Haemodorum discolor T.D.Macfarl. Macfalane 1658 (PERTH) Haemodorum distichophyllum Hook. Davis 1440 (MEL) Haemodorum ensifolium F.Muell. Gardner 1374 (PERTH) Haemodorum laxum R.Br. Morrison s.n. (US 00592008) Haemodorum paniculatum Lindl. Spjut 7192 (US) Haemodorum simplex Lindl. Pritzel 840 (US) Morrison s.n. (US 00592017) Haemodorum spicatum R.Br. Haemodorum subvirens F.Muell. Mueller s.n. (K 000846218) Lachnanthes caroliniana (Lam.) Dandy Cronquist 5446 (US) Macropidia fuliginosa (Hook.) Druce Pritzel 443 (US) Pritzel 99 (US) Phlebocarya ciliata R.Br. Cranfield 1668b (PERTH) Phlebocarya filifolia (F.Muell.) Benth. Phlebocarya pilosissima (F.Muell.) Benth. Pritzel 15 (US) Phlebocarya teretifolia (T.D.Macfarl.) M.Pell. Gardner 9394 (PERTH) Pyrrorhiza neblinae Maguire & Wurdack Maguire 37108 (US) Schiekia orinocensis (Kunth) Meisn. Humboldt 843 (P) Schiekia silvestris (Maas & Stoel) Hopper et al. Prance 15864 (US) Forzza 8562 (RB) Schiekia timida M.Pell. et al. sp. nov. ined. Tribonanthes australis Endl. Hickman 2067 (PERTH) Tribonanthes brachypetala Lindl. Hickman 2022 (PERTH) Tribonanthes elongate E.J.Hickman & Hopper Hickman 2073 (PERTH) Tribonanthes keigheryi E.J.Hickman & Hopper Hickman 2065 (PERTH) Tribonanthes longipetala Lindl. Hickman 2021 (PERTH) Tribonanthes monantha E.J.Hickman & Hopper Hickman 2048 (PERTH) Hickman 2079 (PERTH) Tribonanthes minor M.Lyons & Keighery Tribonanthes porphyria E.J.Hickman & Hopper Hickman 2025 (PERTH) Tribonanthes purpurea T.D.Macfarl. & Hopper Hickman 2083 (PERTH) Tribonanthes uniflora Lindl. Hickman 2084 (PERTH) Tribonanthes variabilis Lindl. Hickman 2053 (PERTH) Tribonanthes violacea Endl. Hickman 2090 (PERTH) Wachendorfia brachvandra W.F.Barker Barker 1096 (NBG) Wachendorfia multiflora (Klatt) J.C.Manning & Goldblatt Barker 4600 (NBG) Wachendorfia paniculata Burm. Pillans 9138 (BOL) Wachendorfia thyrsiflora Burm. Pillans 8086 (BOL)

Perdiz 2376 (RB)

Daly 5142 (US)

Xiphidium caeruleum Aubl.

Xiphidium pontederiiflorum M.Pell. sp. nov. ined.

Heteranthera callifolia Rchb. ex Kunth

Heteranthera catharinensis C.N.Horn & M.Pell.

Heteranthera dubia (Jacq.) MacMill. Heteranthera gardneri (Hook.f.) M.Pell. Heteranthera limosa (Sw.) Willd.

Heteranthera longirachilla D.J.Sousa & Giul.

Heteranthera lutea (H.Perrier) M.Pell. Heteranthera mexicana S.Watson

Heteranthera multiflora (Griseb.) C.N.Horn

Heteranthera oblongifolia Mart. ex Schult & Schult.f.

Heteranthera peduncularis Benth. Heteranthera pumila M.Pell. & C.N.Horn Heteranthera reniformis Ruiz & Pav. Heteranthera rotundifolia (Kunth) Griseb.

Heteranthera seubertiana Solms Heteranthera spicata C.Presl Heteranthera zosterifolia Mart.

Pontederia meyeri (A.G.Schulz) M.Pell. & C.N.Horn

Pontederia paniculata Spreng. Pontederia paradoxa Mart. Pontederia crassipes Mart. Pontederia azurea Sw.

Pontederia diversifolia (Vahl) M.Pell. & C.N.Horn

Pontederia heterosperma (Alexander) M.Pell. & C.N.Horn

Pontederia natans P.Beauv.

Pontederia africana (Solms) M.Pell. & C.N.Horn Pontederia australasica (Ridl.) M.Pell. & C.N.Horn Pontederia brevipetiolata (Verdc.) M.Pell. & C.N.Horn Pontederia cyanea (F.Muell.) M.Pell. & C.N.Horn Pontederia elata (Ridl.) M.Pell. & C.N.Horn

Pontederia hastata L.

Pontederia korsakovii (Regel & Maack) M.Pell. & C.N.Horn

Pontederia plantaginea Roxb. Pontederia vaginalis Burm.f.

Pontederia valida (G.X.Wang & Nagam.) M.Pell. & C.N.Horn

Pontederia cordata L.
Pontederia ovalis Mart.
Pontederia parviflora
Pontederia rotundifolia L.f.
Pontederia sagittata C.Presl

Pontederia subovata Pontederia triflora Hepper 3683 (K) Smith 13919 (US) Horn 410 (UNA) Gardner 1863 (K) Assunção 721 (RB) Hage 1438 (MBM)

Perrier de la Bâthie 7178 (P)

Palmer 1324 (K)
Lorentz 310 (UNA)
Araújo 38 (RB)
Hartweg 226 (K)
Pellegrini 495 (RB)
Pellegrini 457 (RB)
Walter 6644 (RB)
Horn 525 (UNA)
Haynes 8618 (UNA)
Fontana 8316 (RB)
Prance 26220 (NY)
Machado 574 (RB)
Harley 21401 (K)
Martius 60 (M)

Martinelli 18669 (RB) Harley 10248 (RB) Smith 2290 (NY)

s.leg. s.n. (US 00763681) Schweinfurth 2296 (K)

Allen 81 (K)

Espírito Santo 2777 (K) Leichhardt s.n. (K 000873493)

Haniff 1208 (K)

Hermann s.n. (BM 000621681) Maack s.n. (K 000873544)

Wallich 5096 (K) Boeea 8471 (US) Wong 901001 (KYO) Barton s.n. (PH 00038346)

Pellegrini 474 (RB) Forzza 8440 (RB) Alvarenga 952 (RB) Catharino 342 (RB) Table 2- Ordinal placement of main families historically placed in Commelinales, but currently placed elsewhere.

Reference	Bromeliaceae	Dasypogonaceae	Eriocaulaceae	Flagellariaceae	Mayacaceae	Rapateaceae	Restionaceae	Xyridaceae
Berchtold and Presl (1820)	Alliales	Juncales (included in Juncaceae)	Restionales (included in Restionaceae)	Unplaced	Commelinales (included in Commelinaceae)	Unplaced	Restionales	Restionales (included in Restionaceae)
Reichenbach (1828)	Caulo- Acroblastae	Phyllo-Acroblastae (included in Sarmentaceae/ Asparagaceae)	Caulo- Acroblastae (included in Commelinaceae)	Caulo- Acroblastae (included in Commelinaceae)	Caulo- Acroblastae (included in Commelinaceae)	Caulo- Acroblastae (included in Commelinaceae)	Caulo- Acroblastae (included in Commelinaceae)	Caulo- Acroblastae (included in Commelinaceae)
Dumortier (1829)	Bromeliales	Commelinales	Commelinales	Liliales	Commelinales (included in Commelinaceae)	Juncales	Juncales	Commelinales
Endlicher (1836)	Ensatae	Coronariae (included in Juncaceae)	Enantioblastae	Coronariae (included in Juncaceae)	Enantioblastae (included in Xyridaceae)	Coronariae (included in Juncaceae)	Enantioblastae	Enantioblastae
Eichler (1890)	Ensatae	Coronariae (included in Juncaceae)	Enantioblastae	Coronariae (included in Juncaceae)	Enantioblastae (included in Xyridaceae)	Coronariae (included in Juncaceae)	Enantioblastae	Enantioblastae
Lindley (1846)	Narcissales	Xyridales (included in Xyridaceae)	Glumales	Xyridales (included in Commelinaceae)	Xyridales	Part in Xyridales (included in Xyridaceae) and part in Juncales (included in Juncaceae)	Glumales	Xyridales
Engler (1886)	Farinosae	Liliiflorae (included in Liliaceae)	Farinosae	Farinosae	Farinosae	Farinosae	Farinosae	Farinosae
Rendle (1904)	Farinosae	Liliiflorae (included in Liliaceae)	Farinosae	Farinosae	Farinosae	Farinosae	Farinosae	Farinosae
Hutchinson (1934)	Bromeliales	Agavales (included in Xanthorrhoeaceae)	Eriocaulales	Commelinales	Commelinales	Xyridales	Juncales	Xyridales

Cronquist (1968)	Bromeliales	Liliales (included in Xanthorrhoeaceae)	Eriocaulales	Restionales	Commelinales	Commelinales	Restionales	Commelinales
Thorne (1968)	Commelinales	Liliales (included in Liliaceae)	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales
Takhtajan (1969)	Bromeliales	Liliales (included in Liliaceae)	Eriocaulales	Restionales	Commelinales	Commelinales	Restionales	Commelinales
Thorne (1976)	Commelinales	Liliales (included in Liliaceae)	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales
Dahlgren (1980)	Bromeliales	Asparagales	Eriocaulales	Poales	Commelinales	Eriocaulales	Poales	Eriocaulales
Takhtajan (1980)	Bromeliales	Liliales (included in Xanthorrhoeaceae)	Eriocaulales	Restionales	Commelinales	Commelinales	Restionales	Commelinales
Cronquist (1981)	Bromeliales	Liliales (included in Xanthorrhoeaceae)	Eriocaulales	Restionales	Commelinales	Commelinales	Restionales	Commelinales
Dahlgren and Clifford (1982)	Bromeliales	Asparagales	Eriocaulales	Poales	Commelinales	Eriocaulales	Poales	Eriocaulales
Dahlgren and Rasmussen (1983)	Bromeliales	Asparagales	Eriocaulales	Poales	Commelinales	Eriocaulales	Poales	Eriocaulales
Dahlgren et al. (1985)	Bromeliales	Asparagales	Commelinales	Poales	Commelinales	Commelinales	Poales	Commelinales
G. Dahlgren (1989)	Bromeliales	Asparagales	Commelinales	Poales	Commelinales	Commelinales	Poales	Commelinales
Goldberg (1989)	Bromeliales	Liliales (included in Xanthorrhoeaceae)	Commelinales	Juncales	Commelinales	Commelinales	Juncales	Commelinales
Thorne	Bromeliales	Asparagales	Commelinales	Poales	Commelinales	Commelinales	Poales	Commelinales

(1992a)								
Thorne (1992b)	Bromeliales	Liliales	Commelinales	Poales	Commelinales	Commelinales	Poales	Commelinales
Takhtajan (1997)	Bromeliales	Xanthorrhoeales	Eriocaulales	Flagellariales	Mayacales	Rapateales	Restionales	Xyridales
Kubitzki (1998)	Bromeliales	Dasypogonales	Xyridales	Poales	Xyridales	Xyridales	Poales	Xyridales
APG (1998)	Poales	Unplaced	Poales	Poales	Poales	Poales	Poales	Poales
APG II (2003)	Poales	Unplaced	Poales	Poales	Poales	Poales	Poales	Poales
Thorne & Reveal (2007)	Bromeliales	Dasypogonales	Xyridales	Poales	Xyridales	Bromeliales	Restionales	Xyridales
APG III (2009)	Poales	Unplaced	Poales	Poales	Poales	Poales	Poales	Poales
Takhtajan (2009)	Bromeliales	Dasypogonales	Xyridales	Restionales	Xyridales	Xyridales	Restionales	Xyridales
APG IV (2016)	Poales	Arecales	Poales	Poales	Poales	Poales	Poales	Poales
Givnish et al. (2018)	Poales	Dasypogonales	Poales	Poales	Poales	Poales	Poales	Poales

Table 3- Ordinal placement of families currently accepted in Commelinales.

Commelinaceae	Haemodoraceae	Hanguanaceae	Philydraceae	Pontederiaceae
Commelinales	Alliales	Unplaced	Unplaced	Unplaced
Caulo-Acroblastae	Part in Caulo-Acroblastae (part included in Commelinaceae and part in Narcissaceae)	Unplaced	Caulo- Acroblastae (included in Commelinaceae)	Caulo- Acroblastae (included in Commelinaceae)
Commelinales	Part in Narcissales (included in Agavaceae) and part in Liliales (included in Xiphidiaceae)	Unplaced	Philydrales	Liliales
Enantioblastae	Ensatae	Coronariae (included in Juncaceae)	Coronariae	Coronariae
Enantioblastae	Ensatae	Coronariae (included in Juncaceae)	Coronariae	Coronariae
Xyridales	Narcissales	Juncales (included in Juncaceae)	Xyridales	Liliales
Farinosae	Liliiflorae	Unplaced	Farinosae	Farinosae
Farinosae	Liliiflorae	Unplaced	Farinosae	Farinosae
Commelinales	Haemodorales	Commelinales (included in Flagellariaceae)	Haemodorales	Liliales
Commelinales	Liliales	Liliales	Liliales	Liliales
Commelinales	Liliales (included in Liliaceae)	Liliales (included in Liliaceae)	Commelinales	Commelinales
Commelinales	Liliales	Restionales	Liliales	Liliales
Commelinales	Liliales (included in	Liliales (included	Commelinales	Commelinales
	Commelinales Caulo-Acroblastae Commelinales Enantioblastae Enantioblastae Xyridales Farinosae Farinosae Commelinales Commelinales Commelinales Commelinales	Commelinales Caulo-Acroblastae Caulo-Acroblastae Caulo-Acroblastae Part in Caulo-Acroblastae (part included in Commelinaceae and part in Narcissaceae) Commelinales Part in Narcissales (included in Agavaceae) and part in Liliales (included in Xiphidiaceae) Enantioblastae Ensatae Enantioblastae Ensatae Xyridales Narcissales Farinosae Liliiflorae Farinosae Liliiflorae Commelinales Liliales	Commelinales Alliales Unplaced Caulo-Acroblastae Part in Caulo-Acroblastae (part included in Commelinaceae and part in Narcissaceae) Commelinales Part in Narcissales (included in Agavaceae) and part in Liliales (included in Xiphidiaceae) Enantioblastae Ensatae Coronariae (included in Juncaceae) Enantioblastae Ensatae Coronariae (included in Juncaceae) Xyridales Narcissales Juncales (included in Juncaceae) Farinosae Liliiflorae Unplaced Farinosae Liliiflorae Unplaced Commelinales Haemodorales Commelinales (included in Flagellariaceae) Commelinales Liliales Liliales Commelinales Liliales (included in Liliaceae) Commelinales Liliales Restionales	Commelinales Alliales Unplaced Unplaced Caulo-Acroblastae (part in Caulo-Acroblastae (part included in Commelinaceae and part in Narcissaceae) Commelinales Part in Narcissales (included in Agavaceae) and part in Liliales (included in Xiphidiaceae) Enantioblastae Ensatae Coronariae (included in Juncaceae) Enantioblastae Ensatae Coronariae Coronariae (included in Juncaceae) Xyridales Narcissales Juncales (included in Juncaceae) Farinosae Liliiflorae Unplaced Farinosae Commelinales Haemodorales Commelinales (included in Flagellariaceae) Commelinales Liliales (included in Liliaceae) Commelinales Liliales (included in Liliaceae) Commelinales Liliales Restionales Liliales Commelinales Liliales Liliales Restionales Liliales

		Liliaceae)	in Liliaceae)		
Dahlgren (1980)	Commelinales	Haemodorales	Asparagales	Philydrales	Pontederiales
Cronquist (1981)	Commelinales	Liliales	Liliales	Liliales	Liliales
Takhtajan (1980)	Commelinales	Liliales	Liliales	Liliales	Liliales
Dahlgren and Clifford (1982)	Commelinales	Haemodorales	Asparagales	Philydrales	Pontederiales
Dahlgren and Rasmussen (1983)	Commelinales	Haemodorales	Asparagales or Poales	Philydrales	Pontederiales
Dahlgren et al. (1985)	Commelinales	Haemodorales	Asparagales	Philydrales	Pontederiales
G. Dahlgren (1989)	Commelinales	Haemodorales	Hanguanales	Philydrales	Pontederiales
Goldberg (1989)	Commelinales	Iridales	Liliales (Included in Liliaceae)	Iridales	Liliales
Thorne (1992a)	Commelinales	Philydrales	Asparagales	Philydrales	Philydrales
Thorne (1992b)	Commelinales	Bromeliales	Liliales	Bromeliales	Bromeliales
Takhtajan (1997)	Commelinales	Haemodorales	Hanguanales	Philydrales	Pontederiales
Kubitzki (1998)	Commelinales	Commelinales	Unplaced	Commelinales	Commelinales
APG (1998)	Commelinales	Commelinales	Unplaced	Commelinales	Commelinales
APG II (2003)	Commelinales	Commelinales	Unplaced	Commelinales	Commelinales
Thorne & Reveal (2007)	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales
APG III (2009)	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales
Takhtajan (2009)	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales
APG IV (2016)	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales
Givnish et al. (2018)	Commelinales	Commelinales	Commelinales	Commelinales	Commelinales

Appendix 1- List of characters from the morphological dataset

- 1. Plant, life cycle, duration: perennial (0); annual (1)
- **2.** Plant, life cycle, perennial, duration of aerial shoots: overwintering (0); dying off during the dry/cold/fire season (1)
- **3.** Plant, clonal reproduction: absent (0); present (1)
- **4.** Plants, sexual expression: monoicous (0); dioicous (1)
- **5.** Habitat, substrate: aquatic or growing in damp environments (0); terrestrial (1); rupicolous (2); epiphytic (3)
- **6.** Habitat, aquatic, emergence: paludal or emergent (0); mostly to completely submersed or rooted-floating (1); free-floating (2)
- **7.** Habit, growth, branching, type: sympodial (0); monopodial (1)
- **8.** Habit, growth type: herb (0); vine (1)
- **9.** Habit, growth form: solitary (0); mat/cluster/clump-forming (1)
- **10.** Habit, base: definite (0); indefinite (1)
- **11.** Roots, surface: non-binding (0); sand-binding (1); water-binding/mucilaginous (2)
- **12.** Roots, pubescence: glabrous to pilose (0); lanate (1); arachnoid (2)
- **13.** Roots, type: thin (0); tuberous (1); stilt (2)
- **14.** Roots/Stems, internal coloration: pale (0); yellow to orange to red to maroon to vinaceous (1)
- **15.** Stems, underground system: absent (0); rhizome (1); corm (2); tuberized stem (3); bulb (4)
- **16.** Stems, underground system, crass or tuberized stem, development: short (0); elongate (1)
- 17. Stems, posture: prostrate (0); erect to fruticose (1)
- **18.** Stems, consistency: fibrous (0); herbaceous (1); crass (2)
- **19.** Stems, branching: unbranched or branched only at base (0); branched throughout (1)
- **20.** Stems, internodes, elongation: elongated (0); contracted (1)
- **21.** Stems, internodes, leaf-opposite line of uniseriate hairs, presence: absent (0); present (1)

- **22.** Stems, node, swelling: slender (0); swollen (1)
- **23.** Stems, secondary branches, flagelliform-shoots, presence: absent (0); present (1)
- **24.** Leaves, dimorphic: absent (0); present (1)
- **25.** Leaves, ptyxis: supervolute to convolute (0); involute (1); conduplicate (2); conduplicate-involute, enclosing the petiole of the preceding leaf (3)
- **26.** Leaves, blade: bifacial (0); unifacial (1); late bifacial (2)
- **27.** Leaves, sheath, projection (ligule): absent (0); present (1)
- **28.** Leaves, sheath, projection (ligule), shape: truncate (0); bidentate (1); flabellate (2); filiform (3)
- **29.** Leaves, sheaths, type: open (0); closed symmetric (1); closed asymmetric (2)
- **30.** Leaves, sheaths, margins: entire (0); scarious (1)
- **31.** Leaves, sheaths, closed, suture scar, presence: absent (0); present (1)
- **32.** Leaves, sheaths, closed, splitting open at maturity: absent (0); present (1)
- **33.** Leaves, immature, duration: early deciduous (0); late deciduous (1); persistent (2)
- **34.** Leaves, immature, phyllotaxy: distichously-alternate (0); spirally-alternate/rosette (1); equitant (2); pseudo-whorled (3)
- **35.** Leaves, immature, distribution: evenly distributed (0); congested at base/apex (1); equitant (2)
- **36.** Leaves, immature, environment: submerged (0); floating or emerse (1)
- **37.** Leaves, immature, insertion: sessile (0); subpetiolate (1)
- **38.** Leaves, immature, blade, posture: pendulous (0); patent to slightly recurved (1); ascending to erect (2); apressed to the soil (3)
- **39.** Leaves, immature, blade, development, lower leaves on the stem: scale-like, sometimes with an open sheath (0); reduced (1); expanded (2)
- **40.** Leaves, immature, blade, shape: ribbon-like or linear to ensiform or loriform (0); oblong to elliptic (1); lanceolate to ovate (2); spathulate to obovate to rotund or cordate (3)
- **41.** Leaves, immature, blade, consistency: membranous (0); chartaceous (1); crass (2); fibrous and coriaceous (3); spongy (4)
- **42.** Leaves, immature, blade, architecture: flat (0); falcate to conduplicate (1);

- bifacial plicate (2); unifacial plicate (3); bullate (4); cannulate (5); acicular or subterete to terete (6); twisted (7); conduplicate-keeled (8)
- **43.** Leaves, immature, blade, fistulous, presence: absent (0); present (1)
- **44.** Leaves, immature, blade, base, shape: amplexicaulous to truncate (0); cuneate (1); obtuse to rounded to cordate (2)
- **45.** Leaves, immature, blade, base, symmetry: symmetric (0); asymmetric (1)
- **46.** Leaves, immature, blade, base, posterior divisions: absent (0); present (1)
- **47.** Leaves, immature, blade, margins, architecture: flat (0); repandous (1); only the pseudopetiole repandous (2)
- **48.** Leaves, immature, blade, margins, prickle hairs, presence: absent (0); present (1)
- **49.** Leaves, immature, blade, margins, Conostylis-type hairs, type: absent (0); stiff, rigid or tooth-like, patent or upright bristles (1); fine or soft apressed bristles or simple hairs (2); fine and patent bristles (3); stiff bristles enclasping the blade (4); plumose (5); papillose (6)
- **50.** Leaves, immature, blade, margins, uniseriate hairs, presence: absent (0); present (1)
- **51.** Leaves, immature, blade, margins, papillae, presence: absent (0); present (1)
- **52.** Leaves, immature, blade, margins, star-shaped idioblast, presence: absent (0); present (1)
- **53.** Leaves, immature, blade, apex, shape: round to obtuse (0); acute (1); acuminate or apiculate to mucronate (2); caudate (3)
- **54.** Leaves, immature, blade, adaxial side, secondary veins, impression: inconspicuous (0); conspicuous (1)
- **55.** Leaves, immature, blades, adaxial side, variegation, presence: absent (0); longitudinal silver/white/light green stripes (1); brown to vinaceous blotches (2)
- **56.** Leaves, immature, blades, abaxial side, coloration: white (0); green (1); vinaceous to purple to maroon (2)
- **57.** Leaves, mature, production: never or rarely produced (0); always produced (1)
- **58.** Leaves, mature, phyllotaxy: distichously-alternate (0); spirally-alternate (1)
- **59.** Leaves, mature, distribution: distributed along the stem (0); congested (1)
- **60.** Leaves, mature, environment: floating (0); emerse (1)
- **61.** Leaves, mature, petiole, insertion, coloration in relation to the rest of the blade:

- concolorous (0); conspicuously discolorous (1)
- **62.** Leaves, mature, pulvinus: absent (0); present (1)
- **63.** Leaves, mature, blade, consistency: membranous (0); chartaceous to coriaceous (1)
- **64.** Leaves, mature, blade, overall shape: linear to tapered (0); elliptic to ovate (1); obovate (2); cordate to reniform (3); hastate to sagittate (4); rotund (5)
- **65.** Leaves, mature, blade, posture: pendulous (0); patent or floating (1); erect (2)
- **66.** Leaves, mature, blade, base, posterior divisions: absent (0); present (1)
- **67.** Leaves, mature, blade, base, posterior divisions, apex: round (0); acuminate (1)
- **68.** Leaves, mature, blade, venation, thickened midvein: absent (0); present (1)
- **69.** Synflorescence, leaves, dimorphism, presence: absent (0); present (1)
- **70.** Synflorescence, leaves, sheath: inflated (0); not inflated (1); spliting open with the development of the inflorescence (2)
- **71.** Synflorescence, composition: solitary main florescence (0); main florescence with 1-several coflorescences (1)
- **72.** Synflorescence, structure: terminal or restricted to the apex of the stem (0); mainly axillary to spike-like or at the base of the plant (1)
- **73.** Synflorescence, vivipary, presence: absent (0); present (1)
- **74.** Inflorescence, position: terminal or apparently so (0); axillary or at the base of the plant (1); leaf-opposed (2)
- **75.** Inflorescence, at anthesis, posture: erect (0); pendulous (1); prostrate (2)
- **76.** Inflorescence, post-anthesis/in fruit, posture: the same as during anthesis (0); deflexed (1)
- **77.** Inflorescence, basal bract, development: leaf-like or bracteose (0); vestigial and tubular (1); spathaceous (2); bracteose and bicarinate/bidentate (3)
- **78.** Inflorescence, basal bract, spathaceous, shape: cordate (0); ovate to triangular to broadly ovate to depressed ovate (1)
- **79.** Inflorescence, basal bract, base, connation: free (0); connate (1)
- **80.** Inflorescence, basal bract, apex, posture: straight (0); revolute (1)
- **81.** Inflorescence, emergence: not perforating the leaf-sheath (0); perforating the leaf-sheath (1)
- **82.** Inflorescence, peduncle, development: sessile to subsessile (0); obviously

- pedunculate (1)
- **83.** Inflorescence, peduncle, accessory bracts: absent (0); present (1)
- **84.** Inflorescence, peduncle, accessory bracts, bud, development: simple buds (0); primordial inflorescence buds (1)
- **85.** Inflorescence, main axis, development: abreviated (0); basally elongated, apically abbreviated (1); elongated (2)
- **86.** Inflorescence, main axis, developed, architecture: straight (0); zig0zag (1); with a 90° torsion (2)
- 87. Inflorescence, main axis, internal consistency: solid (0); fistulose (1)
- **88.** Inflorescence, secondary branches, type: monochasium (0); dichasium (1); branched cyme (2)
- **89.** Inflorescence, secondary branches, branched cyme, number of branches: bifurcate (0); trifurcate (1)
- **90.** Inflorescence, secondary branches, persistency: persistent (0); detaching at the end of the flowering season (1)
- **91.** Inflorescence, secondary branches, number per main florescence: one (0); two (1); three to several or variable (2)
- **92.** Inflorescence, secondary branches, number per node of the main florescence: one (0); two to several or variable (1)
- **93.** Inflorescence, secondary branches, arrangement: alternate (0); subopposite to opposite (1); subverticillate to verticillate (2); fasciculate to glomerulate (3)
- **94.** Inflorescence, secondary branches, peduncle, development: sessile (0); pedunculate (1)
- **95.** Inflorescence, secondary branches, peduncle, pedunculate, length: short (0); long (1); very long (2)
- **96.** Inflorescence, secondary branches, posture: straight (0); geniculate (1)
- **97.** Inflorescence, secondary branches, axis, thickness: thin (0); stout to greatly swollen (1)
- **98.** Inflorescence, secondary branches, axis, internodes, development: contracted (0); elongate (1); medial internode contracted, remaining ones elongate (2)
- **99.** Inflorescence, secondary branches, fusion, to the main axis of the inflorescence: free (0); fused (1)
- **100.** Inflorescence, secondary branches, fusion, to the peduncle of the cincinnus: free (0); fused (1)

- **101.** Inflorescence, secondary branches, fusion, to each other: free (0); fused (1); partially fused (2)
- **102.** Inflorescence, secondary branches, bracts, presence: absent (0); present (1); present only on lower cincinnus of the thyrse, remaining cincinni ebracteate (2)
- **103.** Inflorescence, secondary branches, bracts, persistency: caduceus (0); persistent (1)
- **104.** Inflorescence, secondary branches, bracts, posture: patent to ascending (0); deflexed (1)
- **105.** Inflorescence, secondary branches, bracts, development: vestigial (0); bracteose (1); frondose (2); basal frondose, apical bracteose (3)
- **106.** Inflorescence, secondary branches, bracts, frondose, aspect: leaf-like (0); spathaceous (1)
- **107.** Inflorescence, secondary branches, bracts, similarity to each other: equal (0); subequal to unequal (1)
- **108.** Inflorescence, secondary branches, bracts, architecture: flat (0); complicate or canaliculate to folded (1)
- **109.** Inflorescence, secondary branches, bracts, overlap: not overlaping (0); overlaping one another (1)
- **110.** Inflorescence, secondary branches, bracts, fusion, to the secondary branch axis: free (0); fused (1)
- **111.** Inflorescence, secondary branches, bracts, fusion, to each other: free (0); fused only at the base (1); completely fused/cup-shaped (2)
- **112.** Inflorescence, secondary branches, bracts, base, inflation: non-saccate (0); saccate (1)
- **113.** Inflorescence, secondary branches, bracts, apex: acute (0); with an apical gland (1); cleft or lobed (2); erose (3)
- **114.** Inflorescence, secondary branches, bracts, apex, with an apical gland, shape: acute (0); filiform (1)
- **115.** Inflorescence, secondary branches, bracts, supernumerary bracts: absent (0); present (1)
- **116.** Inflorescence, secondary branches, anthesis pattern, direction: basal brachhes first (0); apical branches first (1)
- **117.** Inflorescence, secondary branches, anthesis pattern, flowers: sequential (0); simultaneous (1)
- 118. Bracteoles, development: absent to vestigial (0); inconspicuous (1);

- conspicuous (2); leaf-like and equal to the cincinni bracts (3); leaf-like but distinct from the cincinni bracts (4); spathaceous (5)
- **119.** Bracteoles, arrangement: zig-zag (0); tightly imbricate in 1 whorl (1); tightly imbricate in 2 whorls (2); spirally-alternate or one-sided (3)
- **120.** Bracteoles, persistency: caduceous (0); persistent (1)
- **121.** Bracteoles, consistency: membranous (0); herbaceous (1); paleaceous (2); scarious (3); crass (4); chartaceous to coriaceous (5); papyraceous (6)
- **122.** Bracteoles, architecture: flat (0); complicate or canaliculate (1); cup-shaped (2); cucullate (3); tubular (4); envolving the cincinnus (5); margins crispate (6)
- **123.** Bracteoles, base, conation: free (0); perfoliate (1)
- **124.** Bracteoles, margins: entire (0); erose (1)
- **125.** Bracteoles, aspect: hyaline (0); center opaque, margins translucent (1); opaque (2)
- **126.** Flowers, number, per main florescence: one to two (0); three to several (1)
- **127.** Flowers, number, per secondary branch: one to two (0); three to several (1)
- **128.** Flowers, arrangement, in the cincinnus: solitary (0); clustered (1)
- **129.** Flowers, scent, presence: scentless (0); scented (1)
- **130.** Flowers, buds, shape: globose (0); ovoid (1); ellipsoid or fusiform or oblongoid (2); obovoid (3); obpyriform (4); narrowly ovoid (5)
- **131.** Flowers, sexual expression: all bisexual (0); occasionally unisexual randomly distributed (1); lower cincinnus with bisexual remaining cincinni staminate (2); all unisexual (3)
- **132.** Flowers, cleistogamy: absent (0); present (1)
- **133.** Flowers, heterostyly, enantiostyly: absent (0); present (1)
- **134.** Flowers, heterostyly, tristylous: monostylous (0); pseudomontylous (1); tristylous (2)
- 135. Flowers, display angle: without torsion (0); with 60° torsion (1); resupinate (2)
- **136.** Flowers, overall symmetry: actinomorphic (0); zygomorphic or asymmetric (1)
- **137.** Flowers, pedicel, length: sessile to subsessile (0); ca. 1/2 the length of the floral bud or around the same length as the floral bud (1); longer than the floral bud (2); more than three times longer than the floral bud (3)

- **138.** Flowers, pedicel, fusion to each other: free (0); fused (1)
- **139.** Flowers, pedicel, thickness: thin (0); stout (1)
- **140.** Flowers, pedicel, consistency, at post-anthesis: herbaceous (0); lignified (1); stout and fibrous (2)
- **141.** Flowers, pedicel, apical gibbae, presence: absent (0); present (1)
- **142.** Flowers, pedicel, pubescence, long hairs: absent (0); setose and eglandular (1); glandular (2); Geogenathus-type glandular hair (3)
- **143.** Flowers, pedicel, posture at pre-anthesis: upright to erect (0); patent (1); deflexed (2); reflexed (3)
- **144.** Flowers, pedicel, posture at anthesis: upright to erect (0); patent (1); geniculate (2); pendulous (3); geniculate (4)
- **145.** Flowers, pedicel, posture at post-anthesis: decurved (0); upright to erect (1); recurved (2); laterally spreading (3); spirally-coiled (4); oblique (5); pendulous (6)
- **146.** Flowers, pedicel, in fruit: persistent (0); persistent and greatly elongate (1); deciduous (2)
- **147.** Flowers, septal nectaries, presence: absent (0); present (1)
- **148.** Flowers, septal nectaries, number: two (0); three (1)
- **149.** Flowers, septal nectaries, position: infralocular (0); interlocular (1); supralocular (2)
- **150.** Flowers, septal nectaries, commissure slits, prsence: absent (0); present (1)
- **151.** Flowers, septal nectaries, supra-ovarian nectar pockets, presence: absent (0); present (1)
- **152.** Flowers, hypanthium, presence: absent (0); present (1)
- **153.** Flowers, hypanthium, supra-ovarian constriction, presence: absent (0); present (1)
- **154.** Flowers, shape: flat (0); tubular (1)
- **155.** Perianth, shape, tubular, type: infundibuliform (0); tubular (1); bilabiate (2); campanulate (3); hypocrateriform (4); rotate (5); urceolate (6)
- **156.** Perianth, whorls, fusion: free from each other (0); basally fused (1); forming a conspicuous tube (2); the upper three tepals basally to medially fused (3); the upper five tepals basally to medially fused, the remaining one free (4)
- **157.** Perianth, whorls, similarity to each other: homochlamydeous (0);

- heterochlamydeous (1)
- **158.** Perianth, whorls, outer, aspect: sepaloid (0); petaloid (1); spathaceous (2)
- **159.** Perianth, whorls, inner, aspect: sepaloid (0); petaloid (1)
- **160.** Perianth, tube, curvature: straight (0); falcate (1)
- **161.** Perianth, tube, collar-like base, presence: absent (0); present (1)
- **162.** Perianth, tube, medial or sub-apical constriction, presence: absent (0); present (1)
- **163.** Perianth, aestivation: imbricate (0); valvate (1)
- **164.** Perianth, longitudinal splitting, presence: absent (0); present (1)
- **165.** Perianth, apertures, presence: absent (0); present (1)
- **166.** Perianth, at post-anthesis: coiled but apex withering or deliquescent (0); marcescent (1); entire inner whorl withering or deliquescent, outer whorl variable (2); herbaceous (3); coriaceous (4); succulent (5)
- **167.** Perianth, at post-anthesis, coiling, type: slightly spirally-coiled to patent (0); strongly spirally-coiled (1); involute (2)
- **168.** Perianth, at post-anthesis, marcescent, lobes, becoming tooth-like, presence: absent (0); present (1)
- **169.** Perianth, overall color: green to yellow to orange (0); white to cream to grey or hyaline (1); pink to mauve (2); blue to lilac to purple (3); red to vinaceous to maroon or black (4)
- **170.** Perianth, red or suffused with red at post-anthesis, presence: absent or perianth already red at anthesis (0); present (1)
- **171.** Perianth, hypanthium/ovary, coloration in relation to the remaining of the perianth: equal to similar (0); different (1)
- **172.** Perianth, hypanthium/ovary, coloration in relation to the remaining of the perianth, different, specific coloration: orange (0); red (1); vinaceous (2)
- **173.** Perianth, merosity: dimerous (0); tetramerous (1); pseudotetramerous (2); hexamerous (3)
- **174.** Perianth, pseudotetramerous, outer lobes, connation: free (0); basally connate (1)
- **175.** Perianth, pseudotetramerous, outer lobes, shape: broadly oblong (0); lanceolate or ovate (1); rhomboid (2)
- **176.** Perianth, pseudotetramerous, outer lobes, architecture: flat (0); plicate (1);

- margins involute (2)
- **177.** Perianth, pseudotetramerous, outer lobes, posture: patent (0); oblique (1); deflexed (2)
- **178.** Perianth, pseudotetramerous, outer lobes, margin: entire (0); crenulate (1); erose (2)
- **179.** Perianth, pseudotetramerous, outer lobes, pubescence: glabrous (0); pubescent (1)
- **180.** Perianth, pseudotetramerous, inner lobes, shape: oblong to rectangular (0); linear-spathulate (1); spathulate to obovate (2); widely obtrullate (3)
- **181.** Perianth, pseudotetramerous, inner lobes, architecture: straight or curved outwards (0); curved inwards (1); repandous (2)
- **182.** Perianth, pseudotetramerous, inner lobes, margins: entire (0); dentate (1)
- **183.** Perianth, pseudotetramerous, inner lobes, apex, shape: obtuse (0); tridentate (1)
- **184.** Perianth, pseudotetramerous, inner lobes, pubescence: glabrous (0); basally pubescent (1)
- **185.** Perianth, lobes, overall arrangement: 3+3 (0); 5+1 (1); 3+1 or 3+2+1 (2)
- **186.** Perianth, lobes, posture: erect (0); patent (1); apex revolute to slightly decurved (2); deflexed (3); connivent (4); incurved (5)
- **187.** Perianth, lobes, outer whorl, lenght, relative to each other: medial lobe shorter than the laterals (0); all equal (1); medial lobe longer then the laterals (2)
- **188.** Perianth, lobes, outer whorl, width, relative to each other: medial sepal narrower than the laterals (0); all equal to subequal (1); medial sepal broader then the lateral (2)
- **189.** Perianth, lobes, outer whorl, size, length relative to the inner whorl: outer shorter than the inner (0); equal to subequal (1); outer longer than the inner (2)
- **190.** Perianth, lobes, outer whorl, width, relative to the inner whorl: outer narrower than the paired inner lobes (0); outer equal or subequal to the paired inner lobes (1); outer broader than the paired inner lobes (2)
- **191.** Perianth, lobes, outer whorl, consistency: membranous (0); chartaceous (1); succulent or fleshy (2); herbaceous (3); paleaceous (4); coriaceous (5)
- **192.** Perianth, lobes, outer whorl, in fruit, development: persistent to slightly accrescent (0); obviously accrescent (1); caduceous (2)
- 193. Perianth, lobes, outer whorl, in fruit, size relative to the fruit (superior

- ovary): smaller than the fruit (0); same size as the fruit (1); longer than the fruit (2)
- **194.** Perianth, lobes, inner whorl, length, relative to each other: medial lobe shorter than the laterals (0); equal to subequal (1); medial lobe longer then the laterals (2)
- **195.** Perianth, lobes, inner whorl, width, relative to each other: medial lobe narrower than the laterals (0); equal to subequal (1); medial lobe broader then the laterals (2)
- **196.** Perianth, lobes, gland-dots, presence: absent (0); 2-3 apical dots (1); several distal dots (2)
- **197.** Perianth, lobes, shape, between one another: all equal or subequal (0); equal to subequal in the same whorl (1); different in the same whorl (2)
- **198.** Perianth, lobes, apex, glandulose-papillae, presence: absent (0); present (1)
- **199.** Perianth, lobes, apex, dark-mucronate, presence: absent (0); present (1)
- **200.** Perianth, lobes, central anterior lobe, base: flat, lacking projections or folds (0); with a basal fold (1); basal flanges (2)
- **201.** Perianth, lobes, nectar guide, presence: absent (0); present (1)
- **202.** Perianth, lobes, nectar guide, location: anterior lobes (0); posterior lobes (1)
- **203.** Perianth, lobes, nectar guide, morphology: bands (0); spots (1)
- **204.** Perianth, lobes, nectar guide, coloration: maroon to atro-vinaceous to black (0); mauve to purple or blue (1); green (2); yellow (3); orange to red (4); lighter than the remaining lobe or white (5)
- **205.** Perianth, lobes, nectar guide, spots, number: one (0); two (1); three (2)
- **206.** Sepals, connation: free (0); connate in at least one point (1)
- **207.** Sepals, subapical gland, presence: absent (0); present (1)
- **208.** Sepals, symmetry: actinomorphic (0); zygomorphic (1)
- **209.** Sepals, margins, thickness: as thick as the remaining sepal (0); margin hyaline but as thick as the remaining sepal (1); membranous and much thinner than the remaining sepal (2)
- **210.** Sepals, transparency: opaque (0); completely hyaline (1)
- **211.** Sepals, ornamentation: absent (0); dorsal keel present in one sepal (1); dorsal keel present in all sepals (2); striated (3)
- **212.** Sepals, medial sepal, shape: elliptic to broadly elliptic (0); lanceolate to ovate to triangular (1); obovate to spatulate (2); rhomboid to orbicular (3); linear to

- oblong (4)
- **213.** Sepals, lateral sepals, shape: elliptic to broadly elliptic (0); lanceolate to ovate to triangular (1); obovate to spatulate (2); rhomboid (3); linear to oblong (4)
- **214.** Petals, symmetry: actinomorphic (0); zygomorphic (1)
- **215.** Petals, connation: free (0); fused in at least one point (1)
- **216.** Petals, senescence: withering (0); deliquescent (1)
- **217.** Petals, indumentum, adaxial side: glabrous (0); only base with glandular macrohairs (1); completely glandular macrohairs (2); base bearded with non-moniliform uniseriate hairs (3); with branched multiseriate hairs (4); with dendritic hairs (5)
- **218.** Petals, margin: glabrous or entire (0); barbate with moniliform hairs (1); fimbriate to erose (2); cilliate with non-moniliform hairs (3); crenulate (4)
- **219.** Petals, paired petals, claw, presence: absent (0); present (1)
- **220.** Petals, paired petals, claw, lenght: short (0); medium-sized (1); longer than the blade (2)
- **221.** Petals, paired petals, claw, color compared to the blade: concolorous (0); lighter or hyaline (1); darker (2)
- **222.** Petals, paired petals, blade, ovarall, shape: elliptic (0); lanceolate to ovate or triangular (1); rhomboid to orbicular or reniform (2); spatulate to obovate (3); linear to oblong (4); cucullate-spathulate to cucullate-obovate (5); cucullate-reniform (6)
- **223.** Petals, paired petals, blade, base, shape: cuneate to obtuse (0); rounded or auriculate (1); truncate (2)
- **224.** Petals, paired petals, blade, apex, shape: obtuse to rounded (0); acute (1); acuminate (2); emarginate-mucronate (3); trilobed (4)
- **225.** Petals, paired petals, blade, overall color: white to cream to grey or hyaline (0); blue (1); lilac to purple or pink to mauve (2); yellow (3); green (4); orange to apricot (5); red (6); vinaceous to maroon (7); black (8)
- **226.** Petals, paired petals, color, base: concolorous (0); white basal third (1); red to orange base (2)
- **227.** Petals, medial petal, claw: absent (0); present (1)
- **228.** Petals, medial petal, claw, color compared to the blade: concolorous (0); lighter or hyaline (1)
- **229.** Petals, medial petal, blade, architecture: similar to the paired petals (0);

- different from the paired petals (1)
- **230.** Petals, medial petal, blade, architecture, different from the paired petals: involute (0); cucullate (1); cup- to boat- to slipper-shaped (2); revolute (3); flat (4)
- **231.** Petals, medial petal, blade, ovarall, shape: elliptic to trullate (0); lanceolate to ovate (1); rhomboid to orbicular or reniform (2); spatulate to obovate (3); linear to oblong (4); cucullate-spathulate to cucullate-obovate (5)
- 232. Petals, medial petal, blade, base, shape: cuneate to obtuse (0); truncate (1)
- **233.** Petals, medial petal, blade, apex, shape: obtuse to rounded (0); acute (1); acuminate (2); emarginate-mucronate (3); trilobed (4)
- **234.** Petals, medial petal, blade, overall color: white to cream to grey or hyaline (0); blue (1); lilac to purple or pink to mauve (2); yellow (3); green (4); orange to apricot (5); red (6); vinaceous to maroon (7); black (8)
- **235.** Petals, medial petal, color, base: concolorous (0); white basal third (1); medially extending towards the apex of the petal (2); red to orange base (3)
- **236.** Androecium, symmetry: actinomorphic (0); zygomorphic (1); asymmetric (2)
- **237.** Androecium, stamens, diversity: monomorphic (0); dimorphic (1); unequal (2)
- **238.** Androecium, stamens, outer antesepalous, presence: absent or microscopic (0); present (1)
- **239.** Androecium, stamens, inner antesepalous, presence: absent or microscopic (0); present (1)
- **240.** Androecium, stamens, outer antepetalous, presence: absent or microscopic (0); present (1)
- **241.** Androecium, stamens, inner antepetalous, presence: absent or microscopic (0); present (1)
- **242.** Androecium, filaments, insertion, position: straight (0); oblique (1)
- **243.** Androecium, filaments, insertion, levels: one (0); two (1); three (2)
- **244.** Androecium, filaments, connation: all free (0); inner antepetalous stamens conate with anterior ones or anterior conate (1); anterior connate (2); all connate (3)
- **245.** Androecium, filaments, fusion to the perianth: free (0); epitepalous (1); fused only to the inner tepals (2); fused to the posterior outer perianth lobe and to the inner lobes (3)
- **246.** Androecium, filaments, fusion to the inner perianth lobes

- (pseudotetramerous), degree of fusion: basally fused (0); fused for the basal third or half (1)
- **247.** Androecium, filaments, perianth-filament tube, presence: absent (0); tepalostaminal (1); petalo-staminal (2)
- **248.** Androecium, filaments, thickness: thin (0); stout (1)
- **249.** Androecium, filaments, shape, trasverse section: cylindrical throughout (0); basally inflated (1); medially inflated (2); apically inflated (3); flattened (4); medially concave (5)
- **250.** Androecium, filaments, hood-like structure, presence: absent (0); present (1)
- **251.** Androecium, filaments, hood-like structure, apex, shape: truncate (0); tubular (1)
- **252.** Androecium, filaments, appendage, presence: absent (0); tooth-shaped (1); flat and thickened (2)
- **253.** Androecium, filaments, appendage, flat and thickened, apex, shape and size: small and bifid (0); medium-sized and dactyliform to slightly petaloid (1); large and dentate/crested (2)
- **254.** Androecium, filaments, appendage, flat and thickened, coloration: white to cream (0); yellow to orange (1)
- **255.** Androecium, filaments, appendage, flat and thickened, projection in relation to the anther: below the anther (0); at the same level as the anther (1); above the anther (2)
- **256.** Androecium, filaments, lower stamens held inside the cup-shaped medial petal: not held by the medial petal (0); only during the beginning of the anthesis (1); throughout the anthesis (2)
- **257.** Androecium, filaments, relative size, within the same whorl, antesepalous: outer filament shoter, inner longer (0); equal (1); outer filament longer, inner shorter (2)
- **258.** Androecium, filaments, relative size, within the same whorl, antepetalous: outer filament shoter, inner longer (0); equal (1); outer filament longer, inner shorter (2)
- **259.** Androecium, filaments, relative size, between whorls: outer whorl shorter, inner whorl longer (0); equal (1); outer whorl longer, inner whorl shorter (2); whorls with heteromorphic stamens, thus not comparable (3)
- **260.** Androecium, filaments, relative size, posterior stamens: antesepalous shorter, antepetalous longer (0); equal (1); antesepalous longer, antepetalous shorter (2)
- **261.** Androecium, filaments, relative size, anterior stamens: antesepalous longer, antepetalous shorter (0); equal (1); antesepalous shorter, antepetalous longer

- **262.** Androecium, filaments, outer antesepalous stamen, curvature, at anthesis: straight (0); curved (1); descending-falcate (2)
- **263.** Androecium, filaments, inner antesepalous stamens, curvature, at anthesis: straight (0); curved (1); twisted (2); descending-falcate (3)
- **264.** Androecium, filaments, outer antepetalous stamen, curvature, at anthesis: straight (0); curved (1); descending-falcate (2); spirally-coiled (3)
- **265.** Androecium, filaments, inner antepetalous stamens, curvature, at anthesis: straight (0); curved (1); twisted (2)
- **266.** Androecium, filaments, curvature, at post-anthesis: straight (0); curved (1); coiled (2); apex spirally-coiled (3); flaccid and pointing outwards (4)
- **267.** Androecium, filaments, outer antesepalous stamen, indumentum: absent (0); present (1)
- **268.** Androecium, filaments, outer antesepalous stamen, indumentum, density: sparse (0); dense (1)
- **269.** Androecium, filaments, outer antesepalous stamen, indumentum, hair, type: glandular macrohair (0); simple macrohair (1); hook hair (2); moniliform hair (3); uniseriate hairs with dumbbell-shaped cells (4)
- **270.** Androecium, filaments, outer antesepalous stamen, indumentum, distribution: basal (0); up to the middle of the filament (1); apical (2); tuffed at based and apex (3); the whole filament (4)
- **271.** Androecium, filaments, outer antesepalous stamen, indumentum, length of the hair: shorter than 1/2 the length of the filament (0); ca. 1/2 the length of the filament (1); ca. as long as the filament (2)
- **272.** Androecium, filaments, inner antesepalous stamens, indumentum: absent (0); present (1)
- **273.** Androecium, filaments, inner antesepalous stamens, indumentum, density: sparse (0); dense (1)
- **274.** Androecium, filaments, inner antesepalous stamens, indumentum, hair, type: glandular macrohair (0); simple macrohair (1); hook hair (2); moniliform hair (3); uniseriate hairs with dumbbell-shaped cells (4); brightly-colored macrohair (5)
- **275.** Androecium, filaments, inner antesepalous stamens, indumentum, distribution: basal (0); up to the middle of the filament (1); apical (2); tuffed at based and apex (3); the whole filament (4); upper half (5)
- **276.** Androecium, filaments, inner antesepalous stamens, indumentum, length of the hair: shorter than 1/2 the length of the filament (0); ca. 1/2 the length of the

- filament (1); ca. as long as the filament (2)
- **277.** Androecium, filaments, outer antepetalous stamen, indumentum: absent (0); present (1)
- **278.** Androecium, filaments, outer antepetalous stamen, indumentum, density: sparse (0); dense (1)
- **279.** Androecium, filaments, outer antepetalous stamen, indumentum, hair, type: glandular macrohair (0); simple macrohair (1); hook hair (2); moniliform hair (3); uniseriate hairs with dumbbell-shaped cells (4); brightly-colored macrohair (5)
- **280.** Androecium, filaments, outer antepetalous stamen, indumentum, distribution: basal (0); up to the middle of the filament (1); apical (2); tuffed at based and apex (3); the whole filament (4); upper half (5)
- **281.** Androecium, filaments, outer antepetalous stamen, indumentum, length of the hair: shorter than 1/2 the length of the filament (0); ca. 1/2 the length of the filament (1); ca. as long as the filament (2)
- **282.** Androecium, filaments, inner antepetalous stamens, indumentum: absent (0); present (1)
- **283.** Androecium, filaments, inner antepetalous stamens, indumentum, density: sparse (0); dense (1)
- **284.** Androecium, filaments, inner antepetalous stamens, indumentum, hair, type: glandular macrohair (0); simple macrohair (1); hook hair (2); moniliform hair (3); uniseriate hairs with dumbbell-shaped cells (4)
- **285.** Androecium, filaments, inner antepetalous stamens, indumentum, distribution: basal (0); up to the middle of the filament (1); apical (2); tuffed at based and apex (3); the whole filament (4)
- **286.** Androecium, filaments, inner antepetalous stamens, indumentum, length of the hair: shorter than 1/2 the length of the filament (0); ca. 1/2 the length of the filament (1); ca. as long as the filament (2)
- **287.** Androecium, connectives, fertile stamens, appendages, dorsal horn-like, presence: absent (0); present (1)
- **288.** Androecium, connectives, fertile stamens, appendages, apical, presence: absent (0); eglandular (1); glandular (2)
- **289.** Androecium, connectives, fertile stamens, development, outer antesepalous stamen: contracted (0); expanded (1)
- **290.** Androecium, connectives, fertile stamens, shape, outer antesepalous stamen: oblong to elliptic (0); quadrangular to slightly curved (1); flabellate (2); rhomboid or sagittate (3); obdeltoid or dumbbell-shaped (4); saddle-shaped (5); cordate to hastate to linear-tappered (6); shield-shaped (7); trapezoid to V-

- shaped (8)
- **291.** Androecium, connectives, fertile stamens, development, inner antesepalous stamens: contracted (0); expanded (1)
- **292.** Androecium, connectives, fertile stamens, shape, inner antesepalous stamens, shape: oblong to elliptic (0); quadrangular to slightly curved (1); flabellate (2); rhomboid or sagittate (3); obdeltoid or dumbbell-shaped (4); saddle-shaped (5); cordate to hastate to linear-tappered (6); shield-shaped (7); trapezoid to V-shaped (8)
- **293.** Androecium, connectives, fertile stamens, development, outer antepetalous stamen: contracted (0); expanded (1)
- **294.** Androecium, connectives, fertile stamens, shape, outer antepetalous stamen: oblong to elliptic (0); quadrangular to slightly curved (1); flabellate (2); rhomboid or sagittate (3); obdeltoid or dumbbell-shaped (4); saddle-shaped (5); cordate to hastate to linear-tappered (6); shield-shaped (7); trapezoid to V-shaped (8); ob-saddle-shaped (9); strongly convex and maroon-spotted (11)
- **295.** Androecium, connectives, fertile stamens, development, inner antepetalous stamens: contracted (0); expanded (1)
- **296.** Androecium, connectives, fertile stamens, development, inner antepetalous stamens: oblong to elliptic (0); quadrangular to slightly curved (1); flabellate (2); rhomboid or sagittate (3); obdeltoid or dumbbell-shaped (4); saddle-shaped (5); cordate to hastate to linear-tappered (6); shield-shaped (7); trapezoid to V-shaped (8); butterfly-shaped (9)
- **297.** Androecium, anthers, size, relative to the filaments: 3-6 times shorter than the filaments (0); ca. the same length as the filaments (1); ca. 1-3 times longer than the filaments (2); 3-4 times longer than the filaments (3); anthers sessile to subsessile (4)
- **298.** Androecium, anthers, 3-4 times longer than the filaments, overall color: white to cream, with anther sacs apically pink to purple to blue (0); yellow (1)
- 299. Androecium, anthers, posture: connivent or all pointing towards the center of the flower (0); all straight, pointing upwards or pointing outwards of the flower (1); 4 pointing towards the center of the flower + 2 lower pointing outwards (2); posterior +/- straight, paired anterior curved inwards, medial anterior curved towards the center of the flower (3); pointing downwards (4); connivent or pointing towards the center of the flower, except for an odd straight stamen (5); reclined against the perianth lobes (6)
- **300.** Androecium, anthers, insertion, angle: straight (0); upwards-geniculate (1); outwards-geniculate (2)
- **301.** Androecium, anthers, insertion, position, outer antesepalous stamen: basifixed (0); dorsifixed (1); verstile (2); medifixed-versitile (3); basifixed-versitile (4)

- **302.** Androecium, anthers, insertion, position, inner antesepalous stamens: basifixed (0); dorsifixed (1); verstile (2); medifixed-versitile (3); basifixed-versitile (4)
- **303.** Androecium, anthers, insertion, position, outer antepetalous stamen: basifixed (0); dorsifixed (1); verstile (2); medifixed-versitile (3); basifixed-versitile (4)
- **304.** Androecium, anthers, insertion, position, inner antepetalous stamens: basifixed (0); dorsifixed (1); verstile (2); medifixed-versitile (3); basifixed-versitile (4)
- **305.** Androecium, anthers, curvature, at anthesis: straight (0); falcate (1)
- **306.** Androecium, anthers, curvature, at post-anthesis: straight (0); falcate to coiled (1)
- **307.** Androecium, anthers, anther sacs, symmetry: symmetric (0); asymmetric (1)
- **308.** Androecium, anthers, fertile stamens, anther sacs, position, outer antesepalous stamen: parallel (0); divergent (1); base divergent, apex connivent (2)
- **309.** Androecium, anthers, fertile stamens, anther sacs, position, inner antesepalous stamens: parallel (0); divergent (1); base divergent, apex connivent (2)
- **310.** Androecium, anthers, fertile stamens, anther sacs, position, outer antepetalous stamen: parallel (0); divergent (1); base divergent, apex connivent (2)
- **311.** Androecium, anthers, fertile stamens, anther sacs, position, inner antepetalous stamens: parallel (0); divergent (1); base divergent, apex connivent (2)
- **312.** Androecium, anthers, fertile stamens, anther sacs, shape, outer antesepalous stamen: linear to elongate (0); elliptic (1); round (2); spirally-coiled (3); reniform to C-shaped (4); drip-shaped (5); hook-shaped (6)
- **313.** Androecium, anthers, fertile stamens, anther sacs, shape, inner antesepalous stamens: linear to elongate (0); elliptic (1); round (2); spirally-coiled (3); reniform to C-shaped (4); drip-shaped (5)
- **314.** Androecium, anthers, fertile stamens, anther sacs, shape, outer antepetalous stamen: linear to elongate (0); elliptic (1); round (2); spirally-coiled (3); reniform to C-shaped (4); drip-shaped (5)
- **315.** Androecium, anthers, fertile stamens, anther sacs, shape, inner antepetalous stamens: linear to elongate or drip-shaped (0); elliptic (1); round (2); spirally-coiled (3); reniform to C-shaped (4); drip-shaped (5)
- **316.** Androecium, anthers, persistency: all persistent (0); at least two consistently

- caduceous (1)
- **317.** Androecium, anthers, dehiscence: rimose (0); functionally poricidal or truly poricidal (1)
- **318.** Androecium, anthers, dehiscence, rimose and rimose but functionally poricidal, opening direction: base to apex (0); apex to base (1)
- **319.** Androecium, anthers, dehiscence, rimose and rimose but functionally poricidal, slit position, outer antesepalous stamen: latrorse (0); introrse (1); extrorse (2)
- **320.** Androecium, anthers, dehiscence, rimose and rimose but functionally poricidal, slit position, inner antesepalous stamens: latrorse (0); introrse (1); extrorse (2)
- **321.** Androecium, anthers, dehiscence, rimose and rimose but functionally poricidal, slit position, outer antepetalous stamen: latrorse (0); introrse (1); extrorse (2)
- **322.** Androecium, anthers, dehiscence, rimose and rimose but functionally poricidal, slit position, inner antepetalous stamens: latrorse (0); introrse (1); extrorse (2)
- **323.** Androecium, anthers, dehiscence, trully poricidal, pore, number: one (0); two (1)
- **324.** Androecium, anthers, dehiscence, trully poricidal, pore, position: basal (0); apical (1)
- **325.** Androecium, anthers, dehiscence, trully poricidal, pore, ornamentation: absent (0); one-sided wedge-like projection (1); two revolute projections, forming a rim around the pore (2)
- **326.** Androecium, anthers, pollen, release, number of grains: monads (0); tetrads (1)
- **327.** Androecium, anthers, pollen, release, raphides: absent (0); with raphides adhering (1)
- **328.** Androecium, anthers, pollen, color: white to cream or similar to the petals (0); yellow to orange (1)
- **329.** Androecium, anthers, pollen, production, outer antesepalous stamen: no pollen production (staminodial) (0); present (1)
- **330.** Androecium, anthers, pollen, fertility, outer antesepalous stamen: sterile (0); fertile (1)
- **331.** Androecium, anthers, pollen, production, inner antesepalous stamens: no pollen production (staminodial) (0); present (1)

- **332.** Androecium, anthers, pollen, fertility, inner antesepalous stamens: sterile (0); fertile (1)
- **333.** Androecium, anthers, pollen, production, outer antepetalous stamen, pollen production: no pollen production (staminodial) (0); present (1)
- **334.** Androecium, anthers, pollen, fertility, outer antepetalous stamen: sterile (0); fertile (1)
- **335.** Androecium, anthers, pollen, production, inner antepetalous stamens: no pollen production (staminodial) (0); present (1)
- **336.** Androecium, anthers, pollen, fertility, inner antepetalous stamens: sterile (0); fertile (1)
- **337.** Androecium, anthers, pollen, dimorphism: absent (0); in different whorls of polliniferous anthers (1); in the same whorl of polliniferous anthers (2)
- **338.** Androecium, anthers, pollen, aperture, type: inaperturate (0); sulcate (1); porate (2)
- **339.** Androecium, anthers, pollen, aperture, sulcate, number: monosulcate (0); monosulcate with acessory apertures (1); bisulcate (2)
- **340.** Androecium, anthers, pollen, aperture, porate, number: 2-3-porate (0); 5-7-porate (1)
- **341.** Androecium, anthers, pollen, aperture, transitional zone, ornamentation: elements equal (0); elements reduced (1); elements larger (2); elements closer to each other (3); apertural border (4)
- **342.** Androecium, anthers, pollen, wall, structure: 1-layered (0); 2-layered (1); 3-layered (2)
- **343.** Androecium, anthers, pollen, wall, inner layer, papillate or baculate: absent (0); present (1)
- **344.** Androecium, anthers, pollen, wall, inner surface, striate-rugulate: absent (0); present (1)
- **345.** Androecium, anthers, pollen, wall, hemispheric aperture walls, presence: absent (0); present (1)
- **346.** Androecium, anthers, pollen, wall, hemispheric aperture walls, exine development: devoid of exine (0); flattened with scattered exinous elements (1)
- **347.** Androecium, anthers, pollen, infratectum, presence: absent (0); present (1)
- **348.** Androecium, anthers, pollen, tectum, structure: tectate-columellate (0); baculate (1); channeled-tectate (2)
- **349.** Androecium, anthers, pollen, tectum, tectal elements: acute (0); rounded (1)

- **350.** Androecium, anthers, pollen, tectum, tectal elements, acute, ornamentation, type: spinulose (0); spinulose-rugose (1); tuberculate (2)
- **351.** Androecium, anthers, pollen, tectum, tectal elements, acute, ornamentation, spinulose or spinulose-rugose, spacing: regular (0); irregular (1)
- **352.** Androecium, anthers, pollen, tectum, tectal elements, rounded, ornamentation, type: areolate-rugulate (0); micro clavate (1); coarsely areolate (2); rugulose to coarsely rugulose (3); insulate-cerebroid (4); verrucose-granulose (5); verrucate (6); reticulate to foveolate (7); micro verrucate (8); fossulate (9); domed areolate (10); irregularly microclavate (11)
- **353.** Androecium, anthers, pollen, tectum, tectal elements, rounded, ornamentation, homogenity: homogeneous (0); heterogenous (1)
- **354.** Androecium, anthers, pollen, tectum, microperforations, presence: absent (0); present (1)
- **355.** Androecium, anthers, pollen, tectum, microperforations, density: sparse (0); dense (1)
- **356.** Androecium, anthers, pollen, sulcal membrane, ornamentation, distinguishability from the tectum: equal (0); slightly different (1); obviously different (2)
- **357.** Androecium, anthers, pollen, sulcal membrane, ornamentation, type: granular (0); coarsely granular-insulate (1); coarsely granular-ridged (2); tuberculate (3); spinulate (4); coarsely spinulate (5); verrucate (6)
- **358.** Androecium, staminodes, nectariferous scales, presence: absent (0); present (1)
- **359.** Androecium, staminodes, nectariferous scales, margins: opaque (0); hyaline (1)
- **360.** Androecium, staminodes, filiform staminodes adnate to the lower inner tepals, presence: absent (0); present (1)
- **361.** Androecium, staminodes, antherodes, presence: all staminodes with antherodes (0); medial staminode with an enlarged antherode (1); medial staminode lacking the antherode or antherode much reduced (2); all staminodes lacking antherodes (3)
- **362.** Androecium, staminodes, antherodes, reduced anther scas, presence: absent (0); present (1)
- **363.** Androecium, staminodes, antherodes, lobes, number: 2-lobed (0); 3-lobed (1); 4-lobed/X-shaped (2)
- **364.** Androecium, staminodes, antherodes, lobes, insertion: sessile (0); stipitate (1)

- **365.** Androecium, staminodes, antherodes, lobes, 2-lobed, shape: scarsely lobed (0); globose to sub-globose or obovoid or transversally ellipsoid (1); ellipsoid, antherode V-shaped (2); horseshoe-shaped to curved (3); reniform (4); C-shaped (5)
- **366.** Androecium, staminodes, antherodes, lobes, 3-lobed, shape: cordate (0); clove-shaped (1); sagittate to hastate (2)
- **367.** Androecium, staminodes, antherodes, lobes, 4-lobed/X-shaped, shape: upper lobes larger (0); all lobes equal to subequal (1); lower lobes larger (2)
- **368.** Gynoecium, pistilode, presence in staminate flowers: absent (0); present (1)
- **369.** Gynoecium, pistilode, nectariferous lobes, presence: absent (0); present (1)
- **370.** Gynoecium, pistil, relative length: shorter than the stamens (0); ca. the same length as the stamens (1); 1/2 times longer than the stamens (2); 1-2 times longer than the stamens (3)
- **371.** Gynoecium, epigynial nectaries, presence: absent (0); present (1)
- **372.** Gynoecium, stipe, presence: absent (0); present (1)
- **373.** Gynoecium, ovary, position: inferior (0); superior (1); half-inferior (2);
- **374.** Gynoecium, ovary/hypanthium (inferous ovary), indumentum, uniseriate, macrohairs: absent (0); eglandular simple (1); glandular (2); hook (3); rugose (4); clavate (5)
- **375.** Gynoecium, ovary/hypanthium (inferous ovary), indumentum, multiseriate, macrohairs: absent (0); tapering (1); dendritic (2); fruticose (3); pilate (4); branched (5)
- **376.** Gynoecium, ovary/hypanthium (inferous ovary), indumentum, distribution: evenly distributed (0); restricted to or concentrated at the apex (1); restricted to septal ridges (2)
- **377.** Gynoecium, ovary, locules, number: one (0); two (1); three (2); posterior locule recuded or aborted (3); pseudomonomerous (4)
- **378.** Gynoecium, ovary, posterior locule, ovules, number: empty (0); one (1); two (2); three (3); four to several (4)
- **379.** Gynoecium, ovary, anterior locules, ovules, number: empty (0); one (1); two (2); three (3); four to several (4)
- **380.** Gynoecium, style, development: absent (0); inconspicuous to very short (1); short to elongate (2)
- **381.** Gynoecium, style, thickness: slender (0); stout (1); flattened (2)
- **382.** Gynoecium, style, base: conic-inflate (0); tappered (1); abrut-cylindrical (2);

- abrut-obconic (3)
- **383.** Gynoecium, style, inflation: not inflated (0); inflated (1)
- **384.** Gynoecium, style, curvature, at anthesis: straight (0); curved (1); descending-falcate (2)
- **385.** Gynoecium, style, curvature, at post-anthesis: straight (0); curved (1); spirally-coiled (2)
- **386.** Gynoecium, style, indumentum, uniseriate, macrohairs: absent (0); eglandular simple (1); glandular (2); clavate (3); branched (4); apically moniliform (5)
- **387.** Gynoecium, style, in fruit: spliting with the valves (0); remaining intact at the columella (1)
- **388.** Gynoecium, stigma, position: terminal (0); oblique (1)
- **389.** Gynoecium, stigma, posture: pointing upwards or straight (0); pointing downwards (1)
- **390.** Gynoecium, stigma, shape: triparted (0); capitate or trilobed to subtrilobed (1); punctate (2); truncate to capitulate (3); peniciliform (4); cup- or funnel-shaped (5); unevenly trilobed (6); trifid (7); tuberculate (8)
- **391.** Gynoecium, stigma, apex, tuff of silky hairs, presence: absent (0); present (1)
- **392.** Gynoecium, stigma, apex, three protuberances, presence: absent (0); present (1)
- **393.** Gynoecium, stigma, sessile, projection: same level as the ovary (0); prominent (1)
- **394.** Fruit, anthocarp, presence: absent (0); present, ovary superior (1); present, ovary inferior (2)
- **395.** Fruit, anthocarp, superior ovary, development: thin (0); thickened to hardened (1)
- **396.** Fruit, anthocarp, superior ovary, coiled, enclosing the fruit: loosely (0); tightly but free from the fruit (1); tightly and fused to the fruit (2)
- **397.** Fruit, anthocarp, superior ovary, longitudinal projections: absent (0); ridges (1); crests (2)
- **398.** Fruit, anthocarp, superior ovary, ornamentation, type: smooth (0); sinuate (1); thoothed (2); echinate (3)
- **399.** Fruits, consistency: fleshy (0); dry (1)
- **400.** Fruits, outline shape: ellipsoid to oblongoid (0); obovoid or dolabriform (1); subglobose to globose (2); cordate (3); linear-oblongoid to linear to cylindrical

- (4); trigonous (5); ovoid or lageniform (6); strongly trilobed (7)
- **401.** Fruits, apex: sunken (0); emarginate to truncate or round to slightly apiculate (1); rostrate (2); aristate (3)
- **402.** Fruits, wall, thickness: thin (0); thick and hardened (1)
- **403.** Fruits, wall, ornamentation: smooth (0); tuberculate (1); echinate (2)
- **404.** Fruit, septal ridges, thickening: thin (0); thickened (1)
- **405.** Fruits, overall color: dull-colored (0); bright-colored (1)
- **406.** Fruits, coloration, type: chemical (0); structural (1)
- **407.** Fruits, surface: opaque (0); lustrous (1)
- **408.** Fruits, dehiscence: indehiscent or irregular (0); 2-valved (1); partially 3-valved (2); 3-valved (3); lateral (4); 6-valved (5); denticidal (6); ejaculatory (7)
- **409.** Fruits, dry, type: achene (0); capsule (1); cocccarium (2)
- **410.** Fruits, dry, constriction between the seeds: not constricted (0); constricted (1)
- **411.** Fruits, fleshy, color: white to pale yellow to light green (0); pink to red to orange (1); blue to purple to black (2)
- **412.** Fruits, fleshy, stigma, sessile, projection: same level as the ovary (0); prominent (1)
- **413.** Seeds, dimorphism, presence: absent or all subequal (0); present in the same locule (1); seeds from the dorsal locule different from the ventral locules (2)
- **414.** Seeds, overall shape: longer than wide (0); wider than long or as wide as long (1); ca. as long as wide (2)
- **415.** Seeds, outline, shape: circular (0); elliptic to oblong or rectangular (1); triangular or tetrahedral (2); kidney-shaped (3); polygonal (4); ovoid or fusiform to barrel-shaped (5); cuboid (6); bottle-shaped (7); irregular and angled (8); deltoid (9)
- **416.** Seeds, outline, compression: absent (0); lateral (1); dorsi-ventral (2)
- **417.** Seeds, lateral wings, presence: absent (0); present (1)
- **418.** Seeds, lateral wings, distribution: radiate (0); restricted to the margins of the longer axis of the seed (1)
- **419.** Seeds, dorsal side, shape: flattened (0); rounded or acute (1); conical (2)
- **420.** Seeds, ventral side, shape: flattened (0); rounded to acute (1); ridged (2); depressed (3); concave or wedge-shaped (4)

- **421.** Seeds, ventral side, concave or wedge-shaped, pojection, shape: absent (0); 1-lobed (1)
- **422.** Seeds, lateral side: uncleft (0); cleft towards the embryotega (1)
- **423.** Seeds, testa, ornamentation, type: smooth (0); reticulate to foveolate (1); scrobiculate (2); rugose (3); ridged to costate (4); striate (5); longitudinally winged or crested (6); verrucose to tuberculate (7); spirally striate-tuberculate (8); with dactyliform projections (9); scabrid (10); rugose-tuberculate (11)
- **424.** Seeds, testa, ornamentation, longitudinally winged, ornamentation between the longitudinal wings: transversally striate (0); reticulate (1); foveolate (2)
- **425.** Seeds, testa, ornamentation, with dactyliform projections, distribution: evenly distributed (0); restricted to the margins (1); arranged in longitudinal striae with short dactyliform projections (2)
- **426.** Seeds, testa, deposition: absent (0); farinose (1); sticky/mucilaginous (2); coat of fused farinose granules (3)
- **427.** Seeds, chalazal cap, development: reduced (0); enlarged (1)
- **428.** Seeds, embryotega, position: dorsal (0); semidorsal to semilateral to lateral (1); apical (2)
- **429.** Seeds, embryotega, development: inconspicuous (0); prominent (1); prominent but obscured by a deep depression (2)
- **430.** Seeds, embryotega, micropillar scar: absent (0); present (1)
- **431.** Seeds, embryotega, color, relative to the remaining testa: evenly colored (0); distinctively lighter than the testa or white (1)
- **432.** Seeds, accessory tissues, presence: none (0); aril (1); lateral appendage (2)
- **433.** Seeds, accessory tissues, aril, coloration: hyaline (0); white (1); orange to red (2); tan to light brown (3)
- **434.** Seeds, accessory tissues, aril, development: covering only its seed (0); expanded fused to the neighbouring seed's aril, forming a sole dispersal unit per locule (1)
- **435.** Seeds, hilum, shape: punctate to elliptic (0); linear (1); C-shaped (2)
- **436.** Seeds, hilum, length, relative to 1/2 of the seed's total length: shorter (0); equal (1); slightly longer (2); ca. the same length as the seed (3)
- **437.** Seedlings, primary root, branching: unbranched (0); freely-branching (1)
- **438.** Seedlings, primary root, shape: straight (0); turnip-shaped (1); sinuate to spirally-coilled (2)

- **439.** Seedlings, primary root, coloration: white (0); brown (1); yellow or orange or red or violet (2)
- **440.** Seedlings, rhizoids, presence: absent (0); present (1)
- **441.** Seedlings, collar, presence: absent (0); present (1)
- **442.** Seedlings, collar, morphology: inconspicuous (0); thick ring (1); umbrellalike (2)
- **443.** Seedlings, mesocotyl, presence: absent (0); present (1)
- **444.** Seedlings, cotyledon, chlorophyll production: chlorophyllate (0); non-chlorophyllate (1)
- **445.** Seedlings, cotyledon, function: haustorial (0); assimilating (1)
- **446.** Seedlings, cotyledon, sheath, development: inconspicuous (0); conspicuous (1)
- **447.** Seedlings, cotyledon, sheath, projection: absent (0); coleoptile (1); lobes (2); ligule (3)
- **448.** Seedlings, cotyledon, hyperphyll, morphology: cylindrical (0); bifacial (1); leaf-like with an apical ventral cone (2)
- **449.** Seedlings, cotyledon, middle part, presence: absent (0); short (1) long (2)
- **450.** Seedlings, primary leaves, development: all blade expanded (0); at lest the first modified into a cataphyll (1)
- **451.** Seedlings, primary leaves, type: unifacial (0); bifacial leaf-like (1); bifacial ribbon-like (2)
- **452.** Anatomy, silica bodies, in the leaves, presence: absent (0); present (1)
- **453.** Anatomy, bean-shaped starch grains, presence: absent (0); present (1)
- **454.** Anatomy, vessels, distribution: restricted to the roots (0); roots and stems (1)
- **455.** Anatomy, roots, mucilage canals, presence: absent (0); present (1)
- **456.** Anatomy, roots, pith, sclerification: non-sclerified (0); sclerified (1)
- **457.** Anatomy, stems, nodal vascular plexus, presence: absent (0); present (1)
- **458.** Anatomy, stems, cortex, morphology: narrow and lacking vascular tissue (0); expanded and with vascular tissue (1)
- **459.** Anatomy, stems, vascular bundles, fibrous layer, presence: absent (0); present (1)
- **460.** Anatomy, stems, vascular bundles, fibrous layer, development: partially

- enclosing the bundles (0); completely enclosing the bundles (1)
- **461.** Anatomy, hairs, uniseriate, glandular microhairs, presence: absent (0); present (1)
- **462.** Anatomy, hairs, uniseriate, glandular microhairs, basal cell, morphology: lenticular and not wedged between epidermal cells (0); lenticular and wedged (1); with a short neck (2); with a conspicuous neck (3)
- **463.** Anatomy, hairs, uniseriate, glandular microhairs, medial cell, morphology: cylindrical and narrower than the distal (0); cylindrical and as wide as the distal (1); cylindrical, wider and with thicker wall than the distal (2); barrel-shaped (3); ellipsoid (4); fusiform (5); clavate (6)
- **464.** Anatomy, hairs, uniseriate, macrohairs, type: absent (0); exclusively simple uniseriate or glandular (1); flagelliform (2); hook (3); clavate (4); rugose (5)
- **465.** Anatomy, hairs, uniseriate, macrohairs, moniliform, presence: absent (0); present (1)
- **466.** Anatomy, hairs, uniseriate, macrohairs, branched (Palisota type), presence: absent (0); present (1)
- **467.** Anatomy, hairs, uniseriate, macrohairs, star-shaped idioblasts, presence: absent (0); present (1)
- **468.** Anatomy, hairs, uniseriate, macrohairs, star-shaped idioblasts, arm, morphology: long with rounded apex (0); short with acute apex (1)
- **469.** Anatomy, hairs, uniseriate, macrohairs, papillae: absent (0); present (1)
- **470.** Anatomy, hairs, multiseriate, tapering, presence: absent (0); present (1)
- **471.** Anatomy, hairs, multiseriate, branched (Conostylidoideae type), presence: absent (0); present (1)
- **472.** Anatomy, hairs, multiseriate, fruticose (Hanguana type), presence: absent (0); present (1)
- **473.** Anatomy, hairs, multiseriate, dendritic, presence: absent (0); present (1)
- **474.** Anatomy, hairs, multiseriate, pilate, presence: absent (0); present (1)
- **475.** Anatomy, hairs, multiseriate, basal cell-rosette, presence: absent (0); present (1)
- **476.** Anatomy, leaf epidermis, cuticle, ornamentation: smooth (0); striated to ridged (1)
- **477.** Anatomy, leaf epidermis, surface, cell, morphology: not-domed (0); domed (1)
- **478.** Anatomy, leaf epidermis, cell layer, number: one (0); two or more (1); two

- layers at margin (2)
- **479.** Anatomy, leaf epidermis, cell wall, thickness: thin (0); evenly thick (1); lenticular thickened (2)
- **480.** Anatomy, leaf epidermis, cell wall, morphology: absent (0); paradermic invaginations (1); transverselly lobed (2)
- **481.** Anatomy, leaf epidermis, stomata, neighboring cells, division: oblique (0); parallel (1)
- **482.** Anatomy, leaf epidermis, stomata, neighboring cells, number: 2-celled (0); 4-celled (1); 6-celled, terminal cells small (2); 6-celled, terminal cells large (3)
- **483.** Anatomy, leaf epidermis, stomata, neighboring cells, terminal cells, size in comparison to the lateral cells: smaller (0); equal (1); larger (2)
- **484.** Anatomy, leaf epidermis, silica crystals, in specialized cells, presence: absent (0); present (1)
- **485.** Anatomy, leaf epidermis, silica crystals, in specialized cells, cell walls: thin (0); thickened (1)
- **486.** Anatomy, leaf epidermis, silica crystals, in specialized cells, cell morphology: enlarged (0); deep and wedged between regular epidermal cells (1); arranged in longitudinal bands or solitary and wedged, but at the same level as regular epidermal cells (2)
- **487.** Anatomy, leaf epidermis, silica crystals, in specialized cells, silica type 2, presence: absent (0); present (1)
- **488.** Anatomy, leaf epidermis, bulliform cells, presence: absent (0); present (1)
- **489.** Anatomy, leaf, vascular bundles, organization: xylem abaxial, plhoem adaxial (0); xylem and phloem alternate or circular phloem with central xylem or xylem abaxial (1); xylem abaxial and phloem adaxial near the margins of the blades plus xylem and phloem alternate near the center of the blade (2)
- **490.** Anatomy, leaf, vascular bundles, contact with the epidermis: absent (0); present (1)
- **491.** Anatomy, leaf, mesophyll, palisade cells, shape: unlobed (0); elaborately-lobed (1)
- **492.** Anatomy, leaf, mesophyll, calcium oxalate raphids, presence: absent (0); present (1)
- **493.** Anatomy, leaf, mesophyll, calcium oxalate raphids, inside raphid canals, presence: absent (0); present (1)
- **494.** Anatomy, leaf, mesophyll, calcium oxalate raphids, inside raphid canals, distribution: evenly distribuded throughout the blades (0); restricted to along

- the veins of the blades (1)
- **495.** Anatomy, leaf, mesophyll, styloid crystals, presence: absent (0); present (1)
- **496.** Anatomy, leaf, mesophyll, aerenchyma, presence: absent (0); present (1)
- **497.** Anatomy, leaf, mesophyll, tannin cells, presence: absent (0); present (1)
- **498.** Anatomy, leaf, mesophyll, mucilage cells, presence: absent (0); present (1)
- **499.** Anatomy, leaf, mesophyll, longitudinal bundles: diffuse (0); with fibrous extensions (1)
- **500.** Anatomy, leaf, mesophyll, marginal mechanical tissue, presence: absent (0); present (1)
- **501.** Anatomy, leaf, mesophyll, marginal fiber caps, presence: absent (0); present (1)
- **502.** Anatomy, flower, receptacle, aerenchyma, presence: absent (0); present (1)
- **503.** Anatomy, flower, receptacle, aerenchyma, concentration: sparse (0); dense (1)
- **504.** Anatomy, flower, perianth, tube, epidermal unicellular gland, presence: absent (0); present (1)
- **505.** Anatomy, flower, perianth, tannin cells: absent (0); present (1)
- **506.** Anatomy, flower, perianth, tannin cells, homogeneous, presence: absent (0); present (1)
- **507.** Anatomy, flower, perianth, tannin cells, granular, presence: absent (0); present (1)
- **508.** Anatomy, flower, perianth, tannin cells, fibrillar, presence: absent (0); present (1)
- **509.** Anatomy, flower, perianth, tannin cells, distribution: sparse (0); moderate (1); abundant (2)
- **510.** Anatomy, flower, perianth, aerenchyma, presence: absent (0); present (1)
- **511.** Anatomy, flower, perianth, aerenchyma, density: sparse (0); dense (1)
- **512.** Anatomy, flower, perianth, inner whorl/petals, cuticular surface, deposition, type: mucilage (0); epicuticular layer of wax (1)
- **513.** Anatomy, flower, perianth, inner whorl/petals, cuticular surface, deposition, ornamentation: smooth (0); striate (1)
- **514.** Anatomy, flower, androecium, stamens primordia, ontogeny, origin: same as

- the petals (0); distinct (1)
- **515.** Anatomy, flower, androecium, anthers, wall, at maturity: 2-layered (0); more than 2 layers (1)
- **516.** Anatomy, flower, androecium, anthers, endothecium, type: not thickened (0); basally thickened (1); spirally thickened (2); medially thickened (3)
- **517.** Anatomy, flower, androecium, anthers, tapetum, type: glandular (0); amoeboid (1); invasive non-syncytial (2)
- **518.** Anatomy, flower, androecium, anthers, tapetum, raphides: absent (0); present (1)
- **519.** Anatomy, flower, gynoecium, ovary, wall, silica crystals: absent (0); present (1)
- **520.** Anatomy, flower, gynoecium, ovary, wall, tannin cells: absent (0); present (1)
- **521.** Anatomy, flower, gynoecium, ovary, wall, aerenchyma: absent (0); present (1)
- **522.** Anatomy, flower, gynoecium, ovary, septae, conation: aposeptalous (0); hemiseptalous (1); synseptalous (2)
- **523.** Anatomy, flower, gynoecium, ovary, septae, epithelial cells: absent (0); present (1)
- **524.** Anatomy, flower, gynoecium, ovary, septae, tannin cells: absent (0); present (1)
- **525.** Anatomy, flower, gynoecium, ovary, locules, mucilage hairs, presence: absent (0); present (1)
- **526.** Anatomy, flower, gynoecium, ovary, placenta, ovules, arrangement: uniseriate (0); partially biseriate to biseriate (1); multiseriate (2)
- **527.** Anatomy, flower, gynoecium, ovary, placenta, position: axile (0); pendule (1); intrusive-parietal (2); axile-parietal (3); basal (4)
- **528.** Anatomy, flower, gynoecium, ovary, placenta, shape: linear (0); clavate (1); pendulous-peltate or inclinate-peltate (2); straight-peltate (3); hemispheric (4); globose (5); blanket-like (6); ribbon-like (7)
- **529.** Anatomy, flower, gynoecium, ovary, placenta, flanges: unflanged (0); slightly 2-flanged (1); 2-flanged (2)
- **530.** Anatomy, flower, gynoecium, ovary, placenta, sclereids: absent (0); present (1)
- **531.** Anatomy, flower, gynoecium, ovary, placenta, tannin cells: absent (0);

- present (1)
- **532.** Anatomy, flower, gynoecium, ovary, ovule, orientation: orthotropous (0); hemianatropous to anatropous (1); campylotropous (2)
- **533.** Anatomy, flower, gynoecium, ovary, ovule, non-orthotropous, position: epitropous (0); hypotropous (1); pleurotropous (2)
- **534.** Anatomy, flower, gynoecium, style, stylar canal, presence: absent (0); present (1)
- **535.** Anatomy, flower, gynoecium, stigma, surface: dry (0); wet (1)
- **536.** Anatomy, flower, gynoecium, stigma, papillae, type: A (0); B or B+E (1); C (2); D (3); E (4); F (5); G (6); C+E (7)
- **537.** Anatomy, flower, gynoecium, stigma, papillae, epidermis, folded, presence: absent (0); present (1)
- **538.** Anatomy, flower, gynoecium, stigma, papillae, cell number: unicellular (0); all multicellular (1); only the marginal multicellular (2); the marginal moniliform (3)
- **539.** Anatomy, flower, gynoecium, stigma, papillae, distribution: evenly distributed across (0); restricted to the margins (1)
- **540.** Anatomy, flower, gynoecium, stigma, papillae, length: longer than $1\mu m$ (0); equal or shorter than $1\mu m$ (1); equal or shorter than $0.5\mu m$ (2)
- **541.** Anatomy, seed, coat, type: testal (0); bitegmic (1)
- **542.** Anatomy, seed, coat, outer tegmen: thick and persistent (0); thin and sloughing off (1)
- **543.** Anatomy, seed, coat, sclerified, presence: absent (0); present (1)
- **544.** Anatomy, seed, coat, crystals, presence: absent (0); silica (1); calcium oxalate (2)
- **545.** Anatomy, seed, coat, two layers of crossing fibers, presence: absent (0); present (1)
- **546.** Anatomy, seed, embryo, type: Trillium (0); Xyris-Scirpus or grass (1)
- **547.** Anatomy, seed, embryo, relative size: shorter than 1/2 the length of the seed (0); ca. 1/2 the length of the seed (1); ca. as long as the seed (2)
- **548.** Anatomy, seed, endosperm, type: nuclear (0); helobial (1); helobial-chalazal (2)
- **549.** Anatomy, seed, endosperm, concentration/amount: scanty (0); copious (1)

- **550.** Anatomy, seed, nucellus, parietal layer: crassinucellate (0); tenuinucellate (1)
- **551.** Chromosomes, number: n= 4–5 (0); n= 6 (1); n=7 (2); n= 8 (3); n= 9 (4); n= 10 (5); n= 11 (6); n= 14 (7); n= 15 (8); n= 16 (9); n= 17 (10); n= 19 (11); n= 29 (12); n= ca. 85 (13); n= variable due to Robertsonian Translocations (14)
- **552.** Chromosomes, size: $\leq 2\mu m$ (0); ca. $3\mu m$ (1); $> 3\mu m \leq 5\mu m$ (2); $> 5\mu m < 10\mu m$ (3); $\geq 10\mu m$ (4)
- **553.** Chromosomes, karyotype, homogeneity: unimodal (0); bimodal (1)
- **554.** Chromosomes, complements, symmetry: symmetric (0); at least some asymmetric (1)
- **555.** Phytochemistry, pro-anthocyanins, presence: absent (0); present (1)
- **556.** Phytochemistry, anthocyanin, type: acylated cyanidin 3,7,3'-triglycoside (0); commelinin (1); 3-glycoside (2); eichhornin (3); delphinidin (4)
- **557.** Phytochemistry, acids, chelidonic acid, presence: absent (0); present (1)
- **558.** Phytochemistry, acids, presence: absent (0); diferulic acids (1); syringic acids (2)
- **559.** Phytochemistry, cyanogenic compounds, presence: absent (0); present (1)
- **560.** Phytochemistry, phenylphenalenones, presence: absent (0); present (1)
- **561.** Phytochemistry, C-glycosides, presence: absent (0); present (1)
- **562.** Phytochemistry, flavonols, presence: absent (0); present (1)
- **563.** Phytochemistry, flavonoids, apigenin, presence: absent (0); present (1)
- **564.** Phytochemistry, flavonoids, luteolin, presence: absent (0); present (1)
- **565.** Phytochemistry, flavonoids, hidroxiluteolin, presence: absent (0); present (1)
- **566.** Phytochemistry, flavonoids, isorhamnetin, presence: absent (0); present (1)
- **567.** Phytochemistry, flavonoids, quercetin, presence: absent (0); present (1)
- **568.** Phytochemistry, flavones, 6-hidroxiluteolin, presence: absent (0); present (1)
- **569.** Phytochemistry, phenolic and sulphate derivates, presence: absent (0); present (1)
- **570.** Phytochemistry, p-coumaric acids, presence: absent (0); present (1)

SECTION 2— COMMELINACEAE MIRB.

Chapter 2.1. Wandering from Down Under: Late Cretaceous origin of Commelinaceae (Commelinales) in Australian rainforests and the tropical conquering by five major dispersal events

Running tittle Biogeography of Commelinaceae

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Abstract We investigated the timing of the origin and ancestral area reconstructions for Commelinaceae, a family of commelinid monocots widespread in the tropics worldwide. We used a time-calibrated phylogenetic tree based on two cpDNA (*rbcL* and *trnL-F*) and a single nDNA (AT103) regions, including 37 out of the 41 currently accepted genera of Commelinaceae for ancestral area reconstructions. Our results show that the ancestor of Commelinaceae originated in Australian rainforests around 80 Mya, and five major dispersal events shaped the intercontinental diversification of this family: (1) the first dispersal event occurred from Australian to African rainforests ca. 63 Mya; (2) the second dispersal event occurred from African to Asian rainforests ca. 61 Mya; (3) the third dispersal event occurred from Asian rainforests back to African seasonal biomes ca. 40 Mya; (4) the fourth dispersal event occurred from Asian to the Neotropical rainforests ca. 32 Mya. Additionally, 11 colonization events from rainforests to seasonal biomes, such as kwongans, savannas, and seasonally dry forests occurred from 37 to 10 Mya.

Keywords ancestral area reconstruction; biogeography; Commelinid Monocots; Hanguanaceae; molecular clock

INTRODUCTION

Commelinaceae Mirb. is an herbaceous family of pantropical commelinid monocots currently comprising 41 genera and ca. 730 species, that occur in moist and seasonal habitats worldwide (Faden & Hunt, 1991; Faden, 1998; POWO, 2019). The family is easily recognized by its swollen internodes, closed and tubular leaf-sheaths, thyrsoid inflorescences, ephemerous flowers, generally with deliquescent petals, and seeds with an embryotega (Faden & Hunt, 1991; Faden, 1998; Pellegrini, 2017). Its monophyly has been consistently corroborated in the past few years based on different datasets (Evans & al., 2000, 2003; Burns & al., 2011; Zuiderveen & al., 2011). As a result, four main lineages have consistently been recovered (i.e., Cartonematoid, Palisotoid, Commelinoid, and Tradescantoid) (Evans & al., 2000, 2003; Burns & al., 2011; Zuiderveen & al., 2011). Commelinaceae is a member of Commelinales, consistently recovered in a clade of Australasian origin (i.e., Commelinaceae + Hanguanaceae) (Givnish & al., 1999, 2006, 2018; Chase & al., 2006; Saarela & al., 2008; Hertweck & al., 2015; APG IV, 2016).

The Cartonematoid lineage corresponded to subfamily Cartonematoideae and comprises *Cartonema* R.Br. and *Triceratella* Brenan, two small genera with 12 species

altogether, confined to Mediterranean vegetation in Southwestern Australia and Southeastern Africa (Faden & Hunt, 1991; Faden, 1998; Evans & al., 2003). The Palisotoid lineage comprises a single genus, Palisota Rchb. ex Endl., with 30 species confined to rainforests of Western Africa (Faden & Hunt, 1991; Faden, 1998; Evans & al., 2003). This lineage is to be recognized as a new subfamily soon (Pellegrini & al., in prep.). Together, lineages Commelinoid and Tradescantoid represent subfamily Commelinoideae (Pellegrini & al., in prep.). The Commelinoid lineage represents tribe Commelineae, and comprises 14 genera (i.e., Aneilema R.Br., Anthericopsis Engl., Buforrestia C.B.Clarke, Commelina L., Dictyospermum Wight, Floscopa Lour., Murdannia Royle, Pollia Thunb., Polyspatha Benth., Pseudoparis H.Perrier, Rhopalephora Hassk., Stanfieldiella Brenan, Tapheocarpa Conran, and Tricarpelema J.K.Morton). It is most diversified in rainforests and savannas of tropical Africa and Australasia, but with few species reaching the Neotropics (Faden & Hunt, 1991; Faden, 1998; Evans & al., 2003). Finally, the Tradescantoid lineage represents tribe Tradescantieae, excluding *Palisota*, and comprises 24 genera (i.e., Aëtheolirion Forman, Amischotolype Hassk., Belosynapsis Hassk., Callisia Loefl., Cochliostema Lem., Coleotrype C.B.Clarke, Cyanotis D.Don, Dichorisandra J.C.Mikan, Elasis D.R.Hunt, Geogenanthus Ule, Gibasis Raf., Gibasoides D.R.Hunt, Matudanthus D.R.Hunt, Plowmanianthus Faden & C.R.Hardy, Porandra D.Y.Hong, Sauvallia C.Wright ex Hassk., Siderasis Raf. emend. M.Pell. & Faden, Spatholirion Ridl., Streptolirion Edgew., Thyrsanthemum Pichon, Tinantia Scheidw., Tradescantia L. emend. M.Pell., Tripogandra Raf., and Weldenia Schult.f.). It is mostly diversified in rainforests, savannas, and seasonally dry forests of the Neotropics (Faden & Hunt, 1991; Faden, 1998; Evans & al., 2003). Despite few authors having suggested Commelinaceae might have originated somewhere in Eastern Gondwana (Givnish & al., 1999; Evans & al., 2003), no biogeographical analyses have already been done to properly test this hypothesis.

In this study, we generated a new time-calibrated phylogeny sampling 37 out of 41 currently accepted genera of Commelinaceae. We used this new time-calibrated phylogenetic framework for Commelinaceae as the basis to further understanding patterns of historical biogeography among commelinid herbs. More specifically, we: (1) reconstructed a new molecular phylogeny for Commelinaceae including most currently accepted genera; (2) time-calibrated the phylogenetic tree of Commelinaceae; and (3) estimated the ancestral areas of Commelinaceae. This was done to answer the following questions: "What's the age and place of origin of the ancestor of Commelinaceae?" and "How many times have Commelinaceae lineages dispersed intercontinental over the geological time?"

MATERIAL AND METHODS

Taxon sampling and plant material. — We sampled a total of 63 taxa representing 37 out of 41 genera of Commelinaceae, including two representatives from the genus *Hanguana* as outgroup (according to Givnish & al., 2018). For DNA extraction, we used mainly silica-gel dried leaves (12–80 mg), and herbarium materials when necessary. All specimens used in this study are listed in Table 1.

Molecular protocols. — Genomic DNA was extracted using the CTAB 2× protocol, modified from Doyle & Doyle (1987). Fragments were amplified by PCR (Polymerase Chain Reaction). Two plastids (*rbcL* and *trnL-F*) and a single nuclear region (AT103) were selected based on their variability and number of parsimony-informative characters on previous studies in Commelinaceae. Protocols to amplify and sequence the plastid regions *rbcL* and *trnL-F* followed Evans & al. (2003), and Hertweck & Pires (2014). To amplify the AT103 region, we followed Li & al. (2008). PCR products were purified using PEG 11% (polyethylene glycol) and were sequenced directly with the same primers used for the PCR amplification. Sequence electropherograms were produced in an automatic sequencer (ABI 3130XL Genetic Analyzer) using Big Dye Terminator 3.1 (Applied Biosystem). Additional sequences for *rbcL* and *trnL-F* regions were retrieved from GenBank (Table 1). Newly generated sequences were edited using Geneious (Kearse & al., 2012), and all sequences were aligned using Muscle (Edgar, 2004), with subsequent adjustments in the preliminary matrices made manually by eye.

Phylogenetic analyses. – All trees were rooted in representatives of *Hanguana* according to Givnish & al., 2018). The model was selected using hierarchical likelihood ratio tests, using JModeltest 2 (Darriba & al., 2012): AT103 (HKY+G), *rbcL* (GTR+G+I), and *trnL-F* (GTR+G). The Bayesian inference analysis (BI) was conducted with a mixed model and unlinked parameters, using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). The Markov Chain Monte Carlo (MCMC) was run using two simultaneous independent runs with four chains each (one cold and three heated), saving one tree every 1,000 generations, for a total of ten million of generations. We excluded 20% of retained trees as 'burn-in', and checked for a stationary phase of likelihood, checking for ESS values higher than 200 for all parameters on Tracer 1.6 (Rambaut & al., 2014). The posterior probabilities (PP) of clades were based on the majority rule consensus, using the stored trees, and calculated with MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003).

Calibration. – Estimates were conducted using BEAST 1.8.4 (Drummond & al., 2012) based on an ultrametric Bayesian combined tree generated by the Bayesian analysis in MrBayes. This analysis used a relaxed uncorrelated lognormal clock and Yule process speciation before inferring trees (Drummond & al., 2012). The calibration parameters were based on previous estimates derived from comprehensive studies of Monocots (Hertweck & al., 2015; Givnish & al., 2018). We opted for calibrating at the root, using a normal prior with mean initial values of 103.0 Mya (representing the age estimated for the MRCA of the Commelinaceae + Hanguanaceae clade) according to Givnish & al. (2018), and the MRCA of Commelinaceae with mean initial values of 80.0 Mya according to Hertweck & al. (2015). We used three fossils as priors for calibration: (1) a fossil flower of Pseudohaplocricus hexandrus Poinar & K.L.Chambers from Dominican amber (Poinar & Chambers, 2015) of 40.0 Mya representing the MRCA of Dichorisandrinae + Cyanotinae + Tradescantiinae clade; (2) a fossil flower of *Commelinacites dichorisandroides* Caspary from Baltic amber (Caspary 1880) of ~40.0 Mya also representing the MRCA of Dichorisandrinae + Cyanotinae + Tradescantiinae clade; and (3) fossil leaves and fruits of *Pollia* from the Ngorora Formation in Kenya, Africa of 12.2 Mya representing the MRCA of *Pollia* (Jacobs, 1989). Two separate and convergent runs were conducted, with 10,000,000 generations, sampling every 1,000 steps and 2,000 trees as burn-in. We checked for ESS values higher than 200 for all parameters on Tracer 1.6 (Rambaut & al., 2014). Tree topology was assessed using TreeAnnotator and FigTree 1.4.0 (http://tree.bio.ed.ac.uk/software/figtree/).

Ancestral area reconstruction. — Species distribution data regarding continental and seasonal/rainforest environments were compiled from the taxonomic literature of Commelinaceae (Pellegrini & al., unpublished data), and Hanguanaceae (Pellegrini & al., unpublished data), besides herbarium collections from several herbaria worldwide (BR, K, MO, NY, P, and US; acronyms according to Thiers, continuously updated). Occurrences were categorized according to a modified version of the biogeographic areas adopted by WWF (2019). Ancestral areas were estimated using a maximum likelihood analysis of geographic range evolution using the Bayesian Binary MCMC (BBM) implemented in RASP 3.2 (Yu & al., 2015) using default parameters, the exceptions being that the maximum number of unit areas was set to five for both analyses and the number of BBM runs was set to 1.0×10^6 generations. Initial BBM runs assumed a null distribution for the outgroup.

RESULTS

Phylogenetic analyses. – The nuclear characters represented 59 taxa and 711 characters of the dataset, the plastid characters represented 65 taxa and 2,042 characters, and the combined plastid + nuclear dataset included 65 taxa and 2,753 analyzed characters. The plastid dataset recovered a well-supported and almost fully resolved topology, while the nuclear dataset recovered most relationships between the analyzed species, but a backbone with major relationships was not recovered (Fig. 1). Topologies produced by BI analyses, based on the nuclear and plastid datasets, did not exhibit major incongruences among the topologies produced (Fig. 1). Combined plastid + nuclear datasets provided higher support for more clades than the results based on independent plastid or nuclear datasets. The Bayesian analysis recovered an almost fully resolved tree with 61 well-supported clades (>PP95%) (Fig. 2).

Divergence time estimation. — Our divergence time analysis (Fig. 3) suggests that the most recent common ancestor (MRCA) of Commelinaceae (clade A) arose during the Late Cretaceous [95% highest posterior density (HPD) (81.96—) 79.98 (—78.04) Mya]. The first lineage to diverge in the family was the subfamily Cartonematoideae (clade B) in which its MRCA diversified only around Early Miocene [95% highest posterior density (HPD) (42.48—) 20.12 (—4.54) Mya]. The second lineage to diverge was the subtribe Palisotinae (clade C) with its MRCA arising around Early Paleocene [95% highest posterior density (HPD) (73.79—) 63.53 (—52.86) Mya]. The third lineage to diverge was subfamily Commelinoideae *s.str.* (clade D) with its MRCA arising around Late Paleocene [95% highest posterior density (HPD) (70.06—) 61.14 (—50.37) Mya]. The fourth lineage to diverge was tribe Commelineae (clade E) with its MRCA arising around Early Eocene [95% highest posterior density (HPD) (61.63—) 50.41 (—38.15) Mya]. And the fifth lineage to diverge was tribe Tradescantieae *s.str.* (clade F) with its MRCA arising around mid-Eocene [95% highest posterior density (HPD) (60.37—) 50.7 (—41.89) Mya].

Within tribe Commelineae, two major clades were recovered, the *Commelina* and *Floscopa* clades. The *Commelina* clade comprises three major clades, the *Dictyospermum*, *Aneilema* + *Rhopalephora* + *Pollia* + *Polyspatha* (herein called *Aneilema* clade, but in the Bayesian inference from Mr.Bayes it was recovered as a grade) and *Commelina* + *Tapheocarpa* (herein called *Commelina s.l.* clade) clades. The MRCA of the *Dictyospermum* clade arose in mid-Eocene [95% highest posterior density (HPD) (57.76–) 45.8 (–34.24) Mya], the MRCA of the *Aneilema* clade arose in Late Oligocene [95% highest posterior density (HPD) (19.93–) 10.42 (–2.53) Mya], and the MRCA of *Commelina s.l.* arose in Late

Eocene [95% highest posterior density (HPD) (47.12–) 36.53 (–24.24) Mya]. On the other hand, the *Floscopa* clade comprises two internal clades, the *Anthericopsis + Murdannia* clade (herein called *Murdannia s.l.* clade) and the *Buforrestia + Floscopa + Tricarpelema + Stanfieldiella* clade (herein called core *Floscopa* clade). The MRCA of the *Murdannia s.l.* arose in mid-Oligocene [95% highest posterior density (HPD) (43.05–) 29.89 (–17.54) Mya]. While the MRCA of the core *Floscopa* clade arose in Late Eocene [95% highest posterior density (HPD) (52.13–) 39.13 (–26.06) Mya].

Within tribe Tradescantieae, the MRCA of subtribe Streptoliriinae arose in Late Oligocene [95% highest posterior density (HPD) (41.14–) 25.89 (-11.18) Mya], and the MRCA of Aëtheolirion + Spatholirion clade arose in Early Miocene [95% highest posterior density (HPD) (30.15–) 17.54 (–5.08) Mya]. In subtribe Dichorisandrinae, two major clades were recovered in our analysis, Siderasis + Dichorisandra (herein called Dichorisandra clade) and Cochliostema + Geogenanthus + Plowmanianthus (herein called Cochliostema clade) clades. The MRCA of subtribe Dichorisandrinae arose in mid-Oligocene [95% highest posterior density (HPD) (40.1–) 28.74 (–15.8) Myal, while the MRCA of *Dichorisandra* clade arose in Late Miocene [95% highest posterior density (HPD) (16.69–) 8.57 (-2.26) Mya], and the MRCA of the Cochliostema clade arose in mid-Miocene [95% highest posterior density (HPD) (29.4–) 16.48 (–5.27) Mya]. Subtribes Coleotrypinae and Cyanotinae were recovered in a well-supported clade and are herein called Cyanotinae s.l., with three major lineages recovered Coleotrype, Amischotolype + Porandra clade (herein called Amischotolype s.l.), and Cyanotis + Belosynapsis clade (herein called Cyanotis s.l.). The MRCA of Cyanotinae s.l. arose in Late Oligocene [95% highest posterior density (HPD) (33.18–) 26.07 (–18.85) Mya], while the MRCA of Amischotolype s.l. arose in Late Miocene [95% highest posterior density (HPD) (13.97–) 6.35 (-1.22) Mya], and the MRCA of Cyanotis s.l. arose in mid-Miocene [95% highest posterior density (HPD) (23.71–) 16.54 (– 9.29) Mya]. Finally, subtribe Tradescantiinae was recovered with three major clades, Tinantia + Thyrsanthemum + Weldenia clade (herein called Tinantia clade, but recovered as a grade in the Bayesian inference from MrBayes analysis), Elasis + Gibasis + Tradescantia clade (herein called *Tradescantia* clade), and the *Callisia* + *Tripogandra* clade (herein called Callisia clade). The MRCA of subtribe Tradescantiinae arose in Early Oligocene [95%] highest posterior density (HPD) (37.1-) 32.12 (-26.33) Myal, while the MRCA of the Tinantia clade arose in Early Miocene [95% highest posterior density (HPD) (32.38–) 21.32 (-9.05) Mya]. The MRCA of the *Tradescantia* clade arose in Late Oligocene [95% highest posterior density (HPD) (29.93–) 23.26 (–17.23) Mya], and the MRCA of the *Callisia* clade arose in Early Miocene [95% highest posterior density (HPD) (25.75x-) 22.73 (-12.26) Mya].

Ancestral area reconstruction. – The BBM reconstruction suggests that the MRCA of Commelinaceae (clade A) arose in Australian rainforests around 80 Mya (Figs. 3, 4). A vicariance event in Australia was recorded, splitting the populations of the MRCA of Commelinaceae from the MRCA of the subfamily Cartonematoideae (clade B) (Figs. 3, 4). The latter colonized and remained associated with seasonal biomes, such as dunes and kwongans, in South Western Australia since the Late Cretaceous, giving rise to extant species of Cartonema ca. 20 Mya. Then, a dispersal event occurred from Australian to African rainforests ca. 63 Mya, followed by a vicariance event, splitting the MRCA of tribe Palisotinae (clade C) from the MRCA of Commelinoideae s.str. (clade D) (Figs. 3, 4). Another dispersal event from Africa to Asian rainforests occurred in the MRCA of Commelinoideae s.str. ca. 61 Mya (clade D). The latter remained widespread in Southeast Asian rainforests for ca. 10 Mya (Figs. 3, 4), when the MRCA of tribes Commelineae and Tradescantieae arose in Southeastern Asian rainforests ca. 50 Mya (Figs. 3, 4). In tribe Commelineae, a second dispersal event from Southeastern Asian back to African rainforests took place ca. 39 Mya, in the MRCA of the *Floscopa* clade, followed by a vicariance event that colonized the African seasonal biomes, such as the savannas, in the MRCA of Murdannia s.l. ca. 30 Mya (Figs. 3, 4). The MRCA of the Commelina clade remained in Southeastern Asian rainforests and diversified into its extant genera in the past 45 Mya (Figs. 3, 4). In tribe Tradescantieae, its MRCA remained distributed in Southeast Asian rainforests, giving rise to the MRCA of subtribe Streptoliriinae and the MRCA of the Dichorisandrinae + Cyanotinae + Tradescantiinae clade ca. 50 Mya (Figs. 3, 4). The MRCA of subtribe Streptoliriinae arose ca. 26 Mya still in Southeast Asian rainforests, giving rise to the extant genera in this tribe ca. 17 Mya (Figs. 3, 4). The MRCA of the Dichorisandrinae + Cyanotinae + Tradescantiinae clade remained distributed in Southeast Asian rainforests, giving rise to the MRCA of subtribe Dichorisandrinae and the MRCA of Cyanotinae + Tradescantiinae ca. 40 Mya. The MRCA of tribe Dichorisandrinae dispersed from Southeast Asian rainforests to Neotropical rainforests ca. 40 Mya, latter colonizing both the Amazon and the Atlantic rainforests from 16 to 8 Mya (Figs. 3, 4). Then, the MRCA of the Cyanotinae + Tradescantiinae still in Southeastern Asian rainforests gave rise to the MRCA of subtribes Cyanotinae and Tradescantiinae ca. 36 Mya (Figs. 3, 4). The MRCA of subtribe Cyanotinae remained distributed in Southeast Asian rainforests, giving rise to the extant genera in this clade ca. 26 Mya (Figs. 3, 4). Finally, the MRCA of subtribe Tradescantiinae accounts for the second dispersal event from Southeast Asia rainforests to Neotropical rainforests ca. 32 Mya (Figs. 3, 4).

Additionally, the MRCA of Commelinaceae (clade A) arose in rainforests, with seven colonization events to seasonal biomes in the Paleotropics starting ca. 40 Mya, and four colonization events to seasonal biomes in the Neotropics starting ca. 23 Mya. In other words, a total of 11 biome shifts from rainforests to different types of seasonal biomes, such as kwongans, savannas and seasonal dry forests, occurred throughout the diversification of Commelinaceae' lineages (Fig. 4): 1. from Asian rainforests to Australian kwongans in Cartonema, 2. from Asian rainforests to African savannas in Murdannia s.l., 3. from Asian rainforests to African savannas in Tricarpelema africanum Faden, 4. From Asian rainforests to African and Neotropical savannas and seasonally dry forests in species of Floscopa, 5. from Asian rainforests to African and Neotropical savannas or seasonally dry forests in some species of Aneilema, 6. from Asian rainforests to African and Neotropical savannas or seasonally dry forests in Commelina s.l., 7. from Asian rainforests to Asian seasonally dry forests in Cyanotis speciosa, 8. from Neotropical rainforests to seasonally dry forests in the Thyrsanthemum + Weldenia clade, 9, from Neotropical rainforests to seasonally dry forests in the Tradescantia ohiensis + T. hirsutiflora + T. virginica clade, 10. from neotropical rainforests to seasonally dry forests in Tradescantia spathacea, and 11. from Neotropical rainforests to seasonally dry forests in the MRCA of the Callisia clade (Fig. 4).

DISCUSSION

Phylogenetics of Commelinaceae. — The current classification system of Commelinaceae is divided into two subfamilies, Cartonematoideae Faden *ex* G.C.Tucker and Commelinoideae Eaton, both subdivided into several tribes and/or subtribes (Faden & Hunt, 1991). The subfamily Cartonematoideae is divided into two small tribes, Cartonemateae Faden & D.R.Hunt and Triceratelleae Faden & D.R.Hunt, while the subfamily Commelinoideae is divided into two tribes, Commelineae Dumort. and Tradescantieae Meisn. (Faden & Hunt, 1991). The latter is divided into six subtribes: Coleotrypinae Faden & D.R.Hunt, Cyanotinae Faden & D.R.Hunt, Dichorisandrinae Faden & D.R.Hunt, Palisotinae Faden & D.R.Hunt, Streptolirinae Faden & D.R.Hunt, and Tradescantiinae Rohw. (Faden & Hunt, 1991). The topology resulted from the combined dataset analysis recovered most of the current infrafamiliar ranks of Commelinaceae as monophyletic, except for tribe Tradescantieae, in which Palisotinae was recovered as an early-diverging lineage of Commelinaceae, sister to

core Commelinoideae. These results also corroborate previous phylogenetic hypothesis made for Commelinaceae based on molecular and morphological data (Evans & al., 2000, 2003).

Few genera were recovered as non-monophyletic, such as Callisia, Commelina, and Stanfieldiella. Callisia sensu D.R.Hunt (1986) is only monophyletic with the inclusion of the morphologically cohesive *Tripogandra*. Commelina is only monophyletic with the inclusion of Tapheocarpa, a monospecific Australian endemic. Stanfieldiella is only monophyletic with the inclusion of Tricarpelema africanum. The combinations for Commelina and Stanfieldiella will soon be proposed in a new classification system for the family (Pellegrini & al., unpublished data). On the other hand, the combinations for Callisia have already been made by Christenhusz & al. (2018). Nonetheless, Callisia sensu Christenhusz & al. (2018) is not morphologically cohesive, lacking any morphological character to properly circumscribe this genus, and a recircumscription for this generic complex based on the combination of morphological and molecular data will also soon be proposed (Pellegrini & al., in prep.). On the other hand, Belosynapsis was recovered by our analysis as monophyletic, while in previous studies by Hertweck & Pires (2014), which made Cyanotis paraphyletic, leading Christenhusz & al. (2018) to sink Belosynapsis into Cyanotis. Recognizing Belosynapsis as an independent genus will depend on sampling additional species from it and Cyanotis in future phylogenetic studies. However, unpublished data by Pellegrini & al. suggests the recognition of *Cyanotis s.l.* in a new classification system for the family.

Divergence times of Commelinaceae. — The calibration points in our analysis comprehended two divergence times estimates, the first for the MRCA of the Commelinaceae + Hanguanaceae clade of 103 Mya from Givnish & al. (2018), and the second for the MRCA of Commelinaceae of 80 Mya from Hertweck & al. (2015). Most calibrated phylogenies for Commelinid Monocots recovered similar divergence times estimates for this clade (Janssen & Bremer, 2004; Anderson & Janssen, 2009; Bell & al., 2010; Eguchi & Tamura, 2016). Additionally, we used three fossils as calibration points, two of them in the MRCA of the Dichorisandrinae + Coleotrypinae + Cyanotinae + Tradescantiinae clade dating from ca. 40 Mya, and the other on the MRCA of *Pollia* dating from ca. 12 Mya. Monocot fossils are rarely recorded in the literature since herbaceous structures do not usually preserve in the fossilization process, making it very difficult to generate calibrated phylogenies for this group (Iles & al., 2015). All fossils used in this study are undoubtfully placed in Commelinaceae based on several morphological characters described in their protologues (Caspary, 1880; Jacobs, 1989; Poinar & Chambers, 2015). Furthermore, what makes them quite impressive is that they fossil flowers or fruits of a family in which, as stated by Faden & Hunt (1991), these

characters are key in circumscribing its tribes and subtribes. This fact makes us quite confident about the divergence times estimates for tribes and subtribes in Commelinaceae. However, there is great uncertainty in the calibration of the whole monocot phylogenetic tree, due to the lack of fossils as calibration points. This leaves us wondering whether the age of the MRCA of Commelinaceae might reveal, in future studies, to be older than estimated by us.

Continental diversification of Commelinaceae. – Our results evidence that the continental conquering by Commelinaceae was shaped by five major intercontinental dispersals and three main vicariance events since 80 Mya. Our results evidenced that the MRCA of Commelinaceae arose in Australian rainforests in the Late Cretaceous, at the same time as most of flowering plant families (Couvreur & al., 2010; Davis & al., 2014; Weeks & al., 2014; Berger & al., 2016). The diversity centers for other families of Commelinales, such as Haemodoraceae, Hanguanaceae, and Philydraceae, are currently found in Australia or the Malay Archipelago (Hopper & al., 2009; Pellegrini & al., unpublished data). However, the MRCA of Commelinales arose ca. 118 Mya (Givnish & al., 2018), likely having a Gondwanan origin, since this supercontinent only started to break up ca. 90 Mya (Givnish & Renner, 2004). A vicariance event then split the MRCA of Commelinaceae into the MRCAs of Cartonematoideae and Commelinoideae, with the first group colonizing the dune vegetation and kwongans from South Western Australia ca. 20 Mya, and the latter remaining in Australian rainforests. This vicariance event might be explained by the aridification of Australia, a well-documented event that started ca. 33 Mya and reshaped the vegetation cover of this continent (Owen & al., 2016). In the Early Paleogene water was widely available throughout Australia, but throughout the last 60 Mya, the majority of inland surface water has been lost (Mabbutt, 1977). This dramatic reduction in surface water has been caused by several factors. First, Australia has little vertical relief of ca. 330 m above sea level (Goudie, 2002). This coupled with its northward migration and prevailing winds dramatically desiccated the interior of Australia (Owen & al., 2016). The transition of the earth's climate from the greenhouse to ice ages at 33 Mya coincided with a drop in global CO2 levels, the establishment of the Antarctic Circumpolar Current (ACC), and the glaciation of Antarctica (DeConto & Pollard, 2003; McGowran & al., 2004). The last 30 Mya has seen three major bursts of cooling and drying in Australia with concomitant biotic transitions (Crisp & al., 2004). This scenario is supported by Eocene fossil floras from southern Australia, that bear a striking similarity in community structure and taxonomic composition to the present-day wet tropics of north Queensland (Christophel & Greenwood, 1988). The Early Miocene diversification of Cartonematoideae in seasonal biomes of Australia is supported by taxa that now characterize the sclerophyll communities of Australia, which radiated rapidly during the period of climatic change, ca. 25–10 Mya (Crisp & al., 2004).

The first major dispersal event out of Australia rainforests took place at ca. 63 Mya in the MRCA of the Palisotinae + Commelinoideae s.str. clade, which dispersed and colonized the African rainforests. Since the breakup of Gondwana started ca. 90 Mya, Australia, Antarctica, and Africa were long isolated from each other with the opening of the Indian sea (Morley, 2003). In this scenario, there would be only two hypotheses that would explain this long-distal dispersal event: 1. a dispersal event from Australia to Africa through sub-Antarctic islands; or 2. a dispersal event by birds. The dispersal, via sub-Antarctic islands, would have happened through a group of scattered islands, remnants from the Gondwana breakup, and mostly placed on the Kerguelen Plateau (Frey & al., 2003). This plateau is a microcontinent, from a large igneous province (LIP) located on the Antarctic Plate, which supported conifer forests ca. 100 Mya, but submerged ca. 90 Mya in the southern Indian Ocean (Frey & al., 2003). Since the MRCA of Commelinaceae arose ca. 80 Mya, the Kerguelen Plateau was long submerged in the Indian ocean, making the long-distant dispersal through birds from Australia to Africa the most probable explanation. The extant species of Palisotinae are the only lineage of Commelinaceae to show berries as dispersal units (Faden & Hunt, 1981), most probably as a symplesiomorphy, since all extant species of the sistergroup of Commelinaceae, Hanguanaceae, show berry fruits (Niissalo & al., 2014; Pellegrini & al., unpublished data). According to Claramunt & Cracraft (2015), the diversification of the main lineages of modern birds took place after the Cretaceous/Tertiary boundary, ca. 66 Mya. And within core Passeriformes, a dispersion event from Australia to Africa is recovered by these authors from 55–47 Mya, perfectly matching the ages from the confidence interval of our results for the MRCA of the Palisotinae + Commelinoideae s.str. clade.

The second dispersal event occurred only 3 Mya latter in the MRCA of Commelinoideae *s.str.*, that dispersed from African to Southeast Asian rainforests, colonizing Eurasia for the first time and giving rise to the MRCAs of Commelineae and Tradescantieae ca. 50 Mya. The time of diversification bursts in plant lineages of Southeast Asian rainforests seems to agree with our results. According to Wang & al. (2012), the MRCA of Menispermaceae arose ca. 100 Mya in Southeast Asia rainforests, and dispersal events from Asia to elsewhere only started to took place ca. 60 Mya. The MRCA of Sapindaceae arose ca. 100 Mya in Southeast Asian rainforests while most of its main lineages just started to diversify after 60 Mya (Buerki & al., 2010). The same pattern was recovered for the MRCA

of Anacardiaceae, which arose ca. 65 Mya in Southeastern Asian rainforests and dispersed out of Eurasia ca. 50 Mya (Weeks & al., 2014).

The third dispersal event occurred from Southeast Asian rainforests back to Africa, but now in seasonal environments, such as savannas as seasonal dry forests, in the MRCA of the *Floscopa* clade ca. 39 Mya. The savanna flora, which has grasses as its key element, evolved in the Miocene (ca. 23 Mya), while in the Eocene no grass pollen was found in Africa (Utescher & Mosbrugger, 2007). From the Early Miocene, there are increasing proportions of grass pollen in the fossil record (Morley & Richards, 1993; Jacobs & al., 1999; Dupont & al., 2013; Feakins & al., 2013; Hoetzel & al., 2013), with indications of a dominance of characteristic savannas' C4 grasses dating only from the Late Miocene/Pliocene (Dupont & al., 2013; Feakins & al., 2013; Hoetzel & al., 2013). Many of the woody Leguminosae genera associated with African savannas also contain rainforest species (e.g. *Brachystegia* Benth., *Isoberlinia* Craib & Stapf *ex* Holland, and *Acacia* Mill.) (Linder, 2014). This same pattern was recovered for clade 3 of Anacardiaceae, in which its MRCA dispersed from Asia to Africa ca. 65 Mya, but only diversified ca. 40 Mya in the African savanna (Weeks & al., 2014).

The fourth dispersal event occurred from Southeast Asian forests to South American rainforests ca. 40 Mya in the MRCA of the Dichorisandrinae + Coleotrypinae + Cyanotinae + Tradescantiinae clade. The fossil record most strongly supports an origin of rainforests at equatorial latitudes around the Cretaceous-Tertiary mass extinction event ca. 66 Mya (Jaramillo & al., 2010; Couvreur & al., 2011). Major modern angiosperm families typical of multilayered, closed canopy rainforests become dominant in Neotropical and Southeast Asian palaeofloras ca. 66-60 Mya (Morley, 2000; Burnham & Johnson, 2004; Jacobs, 2004; Jaramillo & al., 2006, 2010; Wing & al., 2009; Jacobs & al., 2010; Wolf & al., 2017). This evidence is consistent with the appearance of typical rainforest morphologies such as large seeds and angiosperm wood structures at the start of the Cenozoic (Tiffney, 1984; Wheeler & Baas, 1993; Wing & Boucher, 1998). Recent calibrated molecular trees show that colonization events from Northwestern and Mesoamerican rainforests to the Atlantic rainforests might have started ca. 30 Mya in the MRCA of Eugenia L. (Myrtaceae) (Mazine & al., 2018). The same pattern is recorded for Myrcia DC. (Myrtaceae) in which the MRCA of the genus colonized the Atlantic rainforest from the Amazon + Mesoamerican rainforests ca. 31 Mya (Staggemeier & al., 2015). Our results show that the MRCA of Dichorisandrinae arose ca. 28 Mya in Mesoamerican rainforests and colonized the Amazon rainforest ca. 16 Mya in the MRCA of the Cochliostema + Geogenanthus + Plowmanianthus clade. Then ca. 9 Mya the MRCA of *Siderasis* + *Dichorisandra* colonized the Atlantic rainforest from the Amazon rainforest.

Finally, the fifth dispersal event occurred from Southeast Asian rainforests to Neotropical rainforests again in the MRCA of Tradescantiinae ca. 32 Mya. The MRCA of Tradescantiinae colonized the South America rainforest in multiple dispersal events within *Tinantia, Tradescantia*, and *Gibasis*. On the other hand, at least four biome shifts from Mesoamerican rainforests to Mesoamerican seasonally dry forests took place in the Miocene in the MRCAs of *Thyrsanthemum* + *Weldenia, Tradescantia spathacea, Tradescantia ohiensis* + *T. hirsutiflora* + *T. virginiana*, and the *Callisia* clade. Mesoamerican seasonally dry forests might have already been well stablished around Early Eocene according to a calibrated phylogeny elaborated by De-Nova & al. (2012) for the genus *Bursera* Jacq. *ex* L. (Burseraceae). The MRCA of *Bursera* arose ca. 50 Mya in seasonally dry forests of Mesoamerica, but only in the Early Miocene, ca. 23 Mya, that most lineages on this genus diversified. This date perfectly matches the first Tradescantiinae radiation in Mesoamerican seasonally dry forests that started ca. 23 Mya in the MRCA of the *Callisia* clade, with the last radiation taking place ca. 5 Mya in the MRCA of the *Tradescantia spathacea*, *Tradescantia ohiensis* + *T. hirsutiflora* + *T. virginiana* clade.

Timing the Boreotropical migration route. – Several studies indicate that the Boreotropical migration route would have been well-established for few plant lineages since the mid-Cretaceous (ca. 100 Mya) (Morley, 2003; Buerki & al., 2010; Wang & al., 2012; Baker & Couvreur, 2013). Nonetheless, it seems that most diversification and dispersal events in flowering plants via the Boreotropics took place from the Cretaceous/Tertiary boundary (66 Mya) to mid-Miocene (10 Mya) (Davis & al., 2002, 2014; Morley, 2003; Specht, 2006; Chen & al., 2012; Baker & Couvreur, 2013; Viruel & al., 2016). This timeframe is similar to estimates for epiphytic ferns, which have a niche entirely dependent on the presence of a developed rainforest biome and which diversified most markedly in the Cenozoic (Schuettpelz & Pryer, 2009). Several key angiosperm elements of modern tropical rainforests, such as Sapindales (Wang & al., 2009; Weeks & al., 2014), Fabaceae (Lavin & al., 2005), Malpighiaceae (Davis & al., 2014), and Rubiaceae (Antonelli & al., 2009), also appear to have diverged or radiated at or near the Cretaceous/Tertiary boundary. Our results corroborate these studies since dispersal events via the Boreotropics in Commelinaceae ranged from 61 to 36 Mya, and two Commelinaceae fossils validate this past distribution, being reported from Germany and Costa Rica, both dating from ca. 40 Mya. Several other lineages of flowering plants also show fossils validating this past distribution, such as the Malpighiaceae, with a fossil from ca. 33 Mya Hungary (Hably & Manchester, 2000).

Conclusions. – The biogeographic history of Commelinaceae revealed to be more complex than previously hypothesized. The East Gondwanan origin of the family was not corroborated by our analyses, with the MRCA of Commelinaceae arising in Australian rainforests 80 Mya, when Gondwana was long broke up. Additionally, five major intercontinental dispersal events were recovered from 64–32 Mya, seven shifts to seasonal biomes took place in the Paleotropics starting 40 Mya, and four shifts to seasonal biomes in the Neotropics starting 23 Mya. A generic molecular phylogeny for Commelinaceae allied to new divergence time estimates from future robust phylogenomic studies might push back the age of the MRCA of Commelinaceae and help elucidate the complex biogeographic history of this ancient Commelinid monocot.

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AUTHOR CONTRIBUTIONS

MOOP designed, collected data, performed data analysis, interpreted and wrote part of the research and manuscript; RBF, TME, and KJW collected data and wrote part of the manuscript; and RFA designed, performed data analysis, interpreted and wrote part of the research and manuscript.

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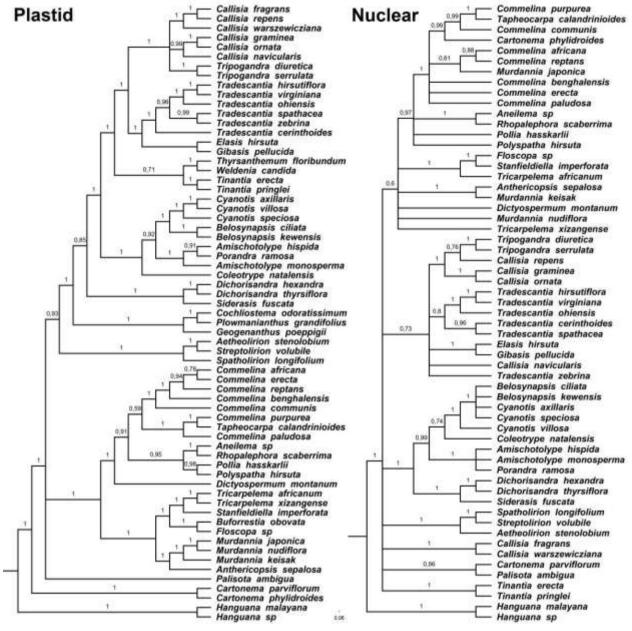


Fig. 1. Phylogenetic trees from the Bayesian inference analyses for separate datasets: the plastid tree, based on *rbcL* and trn*L-F*, is presented on the left, while the nuclear tree, based on AT103, is presented on the right. Posterior probability values are presented above the branches.

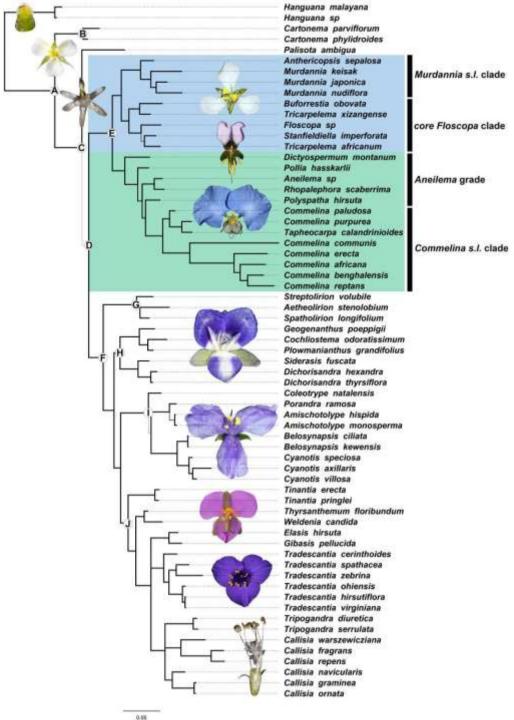


Fig. 2. Phylogram resulted from the Bayesian analysis of the combined plastid + nuclear datasets. Support values from the posterior probabilities are represented by the thickness of branches: thin branches < 0.95 posterior probabilities, and thick branches ≥ 0.95 posterior probabilities. A= Commelinaceae, B = Cartonematoideae, C = Palisotinae + Commelinoideae s.str., D = Commelinoideae s.str., E = Commelineae, F = Tradescantieae, G = Streptoliriinae, H = Dichorisandrinae, I = Coleotrypinae + Cyanotinae, and J = Tradescantiinae. Green= Floscopa clade and Blue = Commelina clade.

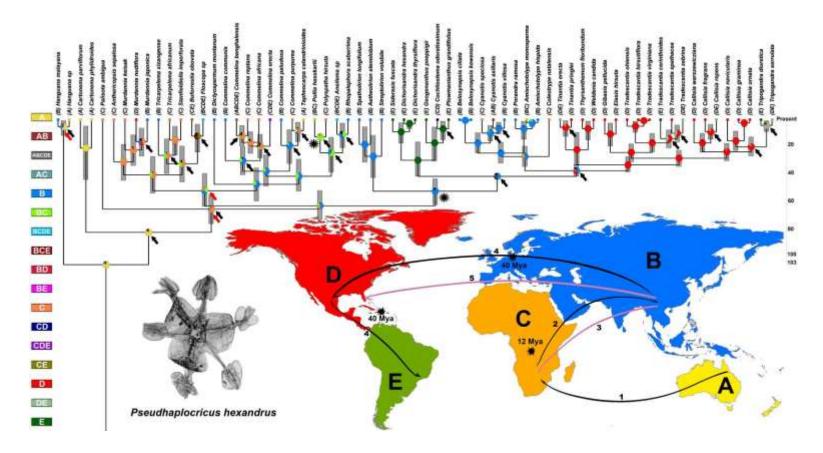


Fig. 3. Maximum clade credibility tree for Commelinaceae. Branch lengths are proportional to time, with grey bars indicating 95% highest posterior densities and mean heights for each node. Biogeographic areas adopted in this study. **A**, Australia; **B**, Laurasia; **C**, Africa; **D**, North and Central America and; **E**, South America. Asterisk represents the location of fossils used in the calibrated tree, being one of them the fossil species *Pseudohaplocricus hexandrus* Poinar & J.L.Chambers. Black setae in the tree represent dispersal events and red setae in the tree represent vicariance events recovered by the BBM analysis. Long setae represent main dispersal events recovered by the BBM analysis, and the numbers on them represent the order of events.

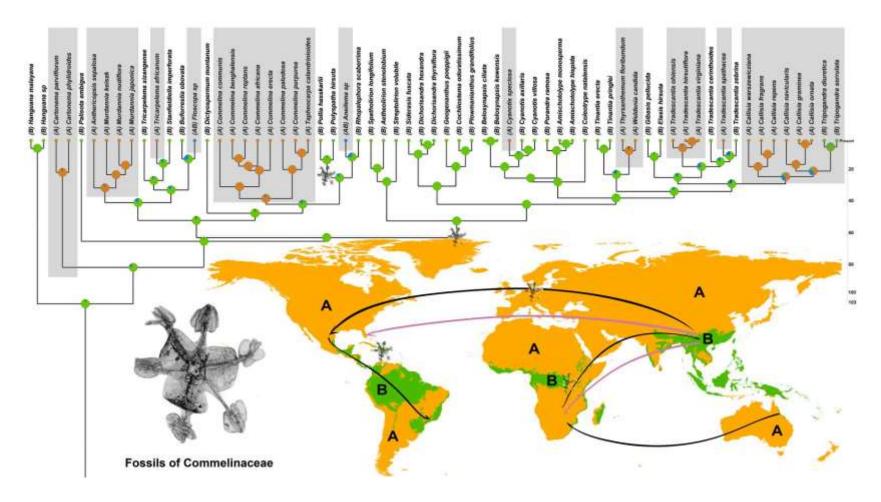


Fig. 4. Biome areas adopted in this study. **A**, Seasonal environments (i.e., kwongans, savannas, and seasonally dry forests); **B**, Rainforests. Grey flowers represent the location of fossils used in the calibrated tree, being one of them the fossil species *Pseudohaplocricus hexandrus* Poinar & J.L.Chambers. Grey bars represent the 11 niche changes, with colonization events from rainforests to seasonal environments. Long setae represent main dispersal events recovered by the BBM analysis, and the numbers on them represent the order of events.

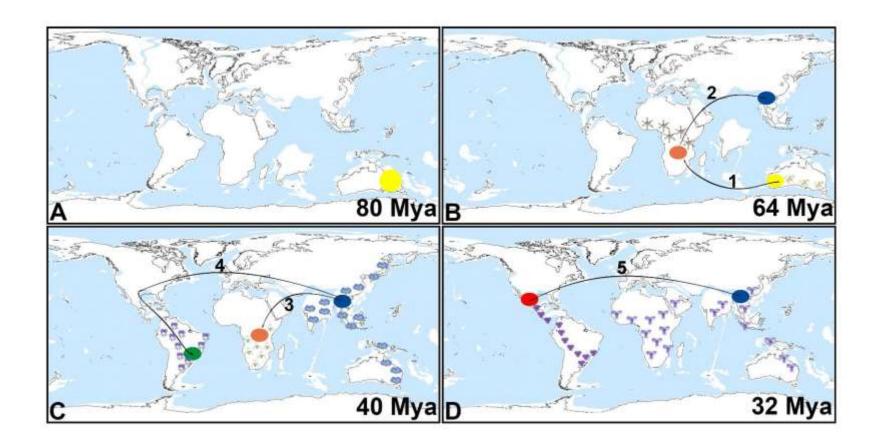


Fig. 5. Time slices representing major dispersal events recovered in the BBM analysis for Commelinaceae. Yellow circles represent the MRCA of Commelinaceae; Orange circles represent the MRCA of Palisotinae + Commelinaceae *s.str.*; Blue circles represent the MRCA of Commelinaceae *s.str.*; Green circles represent the MRCA of Dichorisandrinae; Red circles represent the MRCA of Tradescantiinae. Long setae represent main dispersal events recovered by the BBM analysis, and the numbers on them represent the order of events.

Table 1. Species and GenBank accessions from all DNA regions used in this study.

Species	AT103	rbcL	trnL-F
Hanguana malayana (Jack) Merr.		MH141088.1	
Hanguana sp.	Wurdack	FJ861125.1	KF933756.1
Aëtheolirion stenolobium Forman	Wurdack	Wurdack	Wurdack
Amischotolype hispida (Less. & A.Rich.) D.Y.Hong	Wurdack	AB586259.1	KC512030.1
Amischotolype monosperma (C.B.Clarke) I.M.Turner	Wurdack	AF312239.1	Wurdack
Aneilema sp.	Wurdack	KU564757.1	Wurdack
Anthericopsis sepalosa (C.B.Clarke) Engl.	-	AF312259.1	Wurdack
Belosynapsis ciliata (Blume) R.S. Rao	-	HQ182418.1	KC512031.1
Belosynapsis kewensis Hassk.	-	AF312257.1	Wurdack
Buforrestia obovata Brenan	-	AF036886.1	Timothy
Callisia fragrans (Lindl.) Woodson	Wurdack	MH549760.1	EF092890.1
Callisia graminea (Small) G.C.Tucker	Wurdack	KJ773330.1	EF092887.1
Callisia navicularis (Ortgies) D.R.Hunt	Wurdack	AF312248.1	EF092888.1
Callisia ornata (Small) G.C.Tucker	Wurdack	KX397720.1	KC512042.1
Callisia repens (Jacq.) L.	Wurdack	AF312247.1	EF092886.1
Callisia warszewicziana (Kunth & C.D.Bouché) D.R.Hunt	Wurdack	AY298821.1	KC512046.1
Cartonema parviflorum Hassk.	Wurdack	FN870780.1	Wurdack
Cartonema phylidroides F.Muell.	Wurdack	AF036890.1	Wurdack
Cochliostema odoratissimum Lem.	-	AF312244.1	-
Coleotrype natalensis C.B.Clarke.	Wurdack	MF349710.1	KC512047.1
Commelina africana L.	Wurdack	JQ025036.1	KR738448.1
Commelina benghalensis L.	Wurdack	L05033.2	KR738678.1
Commelina communis L.	Wurdack	AY298825.1	EF092868.1
Commelina erecta L.	Wurdack	MK525585.1	KR737593.1
Commelina paludosa Blume	Wurdack	JF941295.1	EF092862.1
Commelina purpurea C.B.Clarke	Wurdack	EF590514.1	EF092870.1
Commelina reptans Brenan	-	KR736847.1	KR738044.1
Cyanotis axillaris (L.) D.Don ex Sweet	Wurdack	KY018933.1	EF092878.1
Cyanotis speciosa (L.f.) Hassk.	-	JQ025038.1	EF092879.1
Cyanotis villosa (Spreng.) Schult.f.		MF349754.1	EF092877.1
Dichorisandra hexandra (Aubl.) C.B.Clarke		MF349483.1	EF092883.1
Dichorisandra thyrsiflora J.C.Mikan		AY298828.1	EF092884.1
Dictyospermum montanum Wight.	Wurdack	-	Wurdack
Elasis hirsuta (Kunth) D.R.Hunt	-	AF312251.1	KC512055.1
Floscopa sp.	-	KF724345.1	Timothy
Geogenanthus poeppigii (Miq.) Faden	-	AF312261.1	KC512056.1
Gibasis pellucida (M.Martens & Galeotti) D.R.Hunt		AF312250.1	EF092891.1
Murdannia japonica (Thunb.) Faden		KT067728.1	EF092843.1
Murdannia keisak (Hassk.) HandMazz.		KX527291.1	EF092848.1
Murdannia nudiflora (L.) Brenan	Wurdack	KJ773694.1	EF092844.1

Palisota ambigua (P.Beauv.) C.B.Clarke.	Wurdack	FJ861122.1	EF092882.1
Plowmanianthus grandifolius Faden & C.R.Hardy	-	AF312258.1	-
Pollia hasskarlii R.S.Rao	Wurdack	AF312262.1	EF092873.1
Polyspatha hirsuta Mildbr.	Wurdack	AF312263.1	Wurdack
Porandra ramosa D.Y.Hong.	-	KX527511.1	-
Rhopalephora scaberrima (Blume) Faden	-	AF312264.1	Wurdack
Siderasis fuscata (Lodd.) H.E.Moore	Wurdack	AF312254.1	EF092885.1
Spatholirion longifolium (Gagnep.) Dunn	-	AF036887.1	AJ387744.1
Stanfieldiella imperforata (C.B.Clarke) Brenan.	Wurdack	AF312265.1	Timothy
Streptolirion volubile Edgew.	Wurdack	KF724346.1	Wurdack
Tapheocarpa calandrinioides (F.Muell.) Conran		Wurdack	Wurdack
Thyrsanthemum floribundum (M.Martens & Galeotti) Pichon	-	AF312246.1	AJ387745.1
Tinantia erecta (Jacq.) Schltdl.	-	KM281436.1	KC512090.1
Tinantia pringlei (S.Watson) Rohweder	Wurdack	MF349369.1	EF092881.1
Tradescantia cerinthoides Kunth	Wurdack	GU135256.1	EF092896.1
Tradescantia hirsutiflora Bush		KX397989.1	EF092910.1
Tradescantia ohiensis Raf.	Wurdack	HQ644075.1	EF092907.1
Tradescantia spathacea Sw.	Wurdack	JQ734524.1	EF092901.1
Tradescantia virginiana L.	-	MG225893.1	KC512073.1
Tradescantia zebrina Heynh. ex Bosse	Wurdack	L05042.2	EF092898.1
Tricarpelema africanum Faden	Wurdack	-	Timothy
Tricarpelema xizangense D.Y.Hong	Wurdack	MF786660.1	Timothy
Tripogandra diuretica (Mart.) Handlos	Wurdack	AF312249.1	KC512103.1
Tripogandra serrulata (Vahl) Handlos	Wurdack	KF724347.1	EF092880.1
Weldenia candida Schult.f.	-	AF312245.1	AJ387746.1

Table 2. Divergence time estimates and ancestral area reconstructions for all clades. HPD = highest posterior density. Continental ancestral area reconstruction: A = Australia, B = Eurasia, C = Africa + Madagascar, D = América Central e do Norte, E = América do Sul. Niche ancestral area reconstruction A = Seasonal environments, B = Rainforests.

Clade	Higher (Mya)	Mean (Mya)	Lower (Mya)	Continent's AAR	Niche's AAR
Root	104.79	102.9	100.84	A: 0.41	B: 0.78
Hanguanaceae	11.21	4.96	0.73	A: 0.61	B: 1.0
Commelinaceae	81.96	79.98	78.04	A: 0.58	B: 0.76
Subfamily Cartonematoideae	42.48	20.12	4.54	A: 1.0	A: 0.97
Subtribe Palisotinae + Subfamily Commelinoideae s.str. clade	73.79	63.53	52.86	C: 0.33	B: 0.98
Subfamily Commelinoideae s.str.	70.96	61.14	50.37	B: 0.16	B: 0.95
Tribe Commelineae	61.63	50.41	38.15	B: 0.17	B: 0.79
Commelina clade/Dictyospermum clade	57.76	45.8	34.24	B: 0.40	B: 0.82
Pollia + Polyspatha + Aneilema + Rhopalephora + Commelina s.l. clade	50.71	40.16	28.1	BC: 0.26	B: 0.70
Aneilema clade	37.25	23.47	12.56	BC: 0.24	B: 0.66
Pollia + Polyspatha clade	14.06	12.15	10.26	BC: 0.84	B: 0.98
Aneilema + Rhopalephora clade	19.93	10.42	2.53	BC: 0.44	B: 0.75
Commelina s.l. clade	47.12	36.53	24.94	B: 0.38	A: 0.91
Floscopa clade	52.13	39.13	26.06	C: 0.31	B: 0.67
core Floscopa clade	44.18	31.18	18.69	C: 0.12	B: 0.55
Buforrestia + Floscopa clade	23.12	11.63	3.32	CE: 0.45	B: 0.70
Murdannia s.l. clade	43.05	29.89	17.54	C: 0.86	A: 0.92
Tricarpelema s.str. + Stanfieldiella s.l. clade	38.25	25.25	13.67	C: 0.50	B: 0.81
Stanfieldiella s.l. clade	25.22	14.42	4.73	C: 0.95	B: 0.88
Tribe Tradescantieae	60.37	50.7	41.89	B: 0.44	B: 0.99
Subtribe Streptoliriinae	41.14	25.89	11.18	B: 0.99	B: 1.0
Spatholirion + Aëtheolirion clade	30.15	17.54	5.08	B: 1.0	B: 1.0
Dichorisandrinae + Cyanotinae + Tradescantiinae clade	42.11	40.18	38.31	B: 0.20	B: 0.99

Subtribe Dichorisandrinae	40.1	28.74	15.8	E: 0.97	B: 1.0
Cochliostema clade	29.4	16.48	5.27	E: 0.94	B: 1.0
Cochliostema + Plowmanianthus clade	14.24	6.51	1.1	E: 0.95	B: 1.0
Dichorisandra clade	16.69	8.57	2.26	E: 1.0	B: 1.0
core <i>Dichorisandra</i> clade	6.38	2.78	0.32	E: 1.0	B: 1.0
Cyanotinae + Tradescantiinae clade	40.25	36.25	31.85	B: 0.23	B: 0.90
Subtribe Cyanotinae/Coleotrype clade	33.18	26.07	18.85	B: 0.53	B: 1.0
Amischotolype s.l. clade	13.97	6.35	1.22	B: 0.86	B: 1.0
Cyanotis s.l. clade	23.71	16.54	9.29	B: 0.85	B: 0.92
Amischotolype s.l. + Cyanotis s.l. clade	30.83	23.67	16.14	B: 0.88	B: 0.99
Subtribe Tradescantiinae	37.1	32.12	26.33	D: 0.92	B: 0.57
Tinantia clade	32.38	21.32	9.05	D: 0.87	B: 0.77
core Tinantia clade	11.88	5.38	0.73	D: 0.90	B: 0.99
Weldenia + Thyrsanthemum clade	14.42	6.4	1.08	D: 1.0	A: 0.96
Tradescantia clade	29.93	23.26	17.23	D: 0.94	B: 0.59
Elasis + Gibasis clade	18.74	10.13	2.43	D: 1.0	B: 0.98
core Tradescantia clade	22.85	16.47	9.76	D: 0.56	B: 0.55
Callisia clade	25.75	22.73	12.26	D: 0.79	A: 0.26
Tripogandra clade	8.46	4.02	0.84	DE: 0.81	B: 0.95

SECTION 2- COMMELINACEAE MIRB.

Chapter 2.2. Taxonomic revision of Neotropical *Murdannia* Royle (Commelinaceae)

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Abstract

This study provides a taxonomic revision for the Neotropical species of the genus *Murdannia*. Six species are recognized as native, including a new species and a new combination, while two Asian species are recognized as invasive. We present an identification key, a table summarizing the morphologic differences among the species, a new synonym, six lectotypifications, a distribution map, and descriptions, comments and photographic plates for each species. We also provide comments on the morphology of the Neotropical species of *Murdannia*, comparing them with the Paleotropical species, and a discussion of inflorescence architecture in the genus as a whole.

Keywords

Aquatic plants, Brazil, Commelinales, Commelineae, dewflower, Neotropical flora, spiderwort

Introduction

Murdannia Royle is one of the largest genera in Commelinaceae, comprising ca. 60 species (Faden 1998; eMonocot 2010; The Plant List 2013; Govaerts & Faden 2015). It was described by Royle (1840), based on Aneilema scapiflorum Roxb. [= M. edulis (Stokes) Faden], and was named after Murdan Ali, the keeper of the Saharanpur Botanic Garden herbarium at India. Unware of Royle's name, Brückner (1926) described Phaeneilema G.Brückn., and transferred several species from Aneilema to his new genus (Brückner 1926, 1927). A few years later, in his treatment for Commelinaceae in Engler's Natürlichen Pflanzenfamilien, Brückner (1930) realized that Phaeneilema and Murdannia were congeneric and made the required combinations. Pichon (1946) pointed out the existence of two names prior to Murdannia (i.e. Dilasia Raf. and Streptylis Raf.), both published by Rafinesque (1838) in his Flora Telluriana. Since both names were published in the same work and none had priority over the other, Dilasia was adopted by Pichon (1946) as the accepted name. Nevertheless, Brenan (1952), noted that most of the necessary combinations in Murdannia had already been made by Brückner (1930). Thus, the author proposed to conserve Murdannia against Dilasia and Streptylis, to avoid the unnecessary creation of about 30 new combinations in the monospecific Dilasia (Brückner 1930; Merrill 1937).

Murdannia nom. cons. is currently placed in subfamily Commelinoideae, tribe Commelineae, together with Aneilema R.Br., Buforrestia C.B.Clarke, Commelina L., Floscopa Lour., Pollia Thunb., and Stanfieldiella Brenan, among others (Faden & Hunt 1991; Evans et al. 2003; Burns et al. 2011; Faden 1998). As aforementioned, Murdannia species have been historically treated under Aneilema by several authors (e.g. Brown 1810; Clarke 1881; Bentham & Hooker 1883; Woodson 1942), and sometimes also under Commelina. Nevertheless, Murdannia can be easily differentiated from Aneilema and Commelina by its flowers commonly enantiostylous, petals sessile and equal to subequal, three antesepalous stamens (one sometimes staminodial), three antepetalous staminodes, 3-lobed antherodes, capsules always equally 3-locular, and 3-valved (Brenan 1952, 1966; Faden 1998). The genus has a Pantropical and Warm Temperate distribution, being especially diverse in Asia, where most (more than 50%) of the accepted species and morphological diversity are known to occur (Nandikar 2013; Ancy 2014; Ancy & Nampy 2014; Nandikar & Gurav 2015). Most recent studies on Murdannia have focused on the Paleotropical species, especially the Asian (e.g. Faden 2001; Nandikar 2013; Ancy 2014; Ancy & Nampy 2014; Nandikar & Gurav 2015) and the African (Faden 2012) members of the genus. Nevertheless, very little is known about the Neotropical species of the genus (Pellegrini et al. 2013). A total of four Neotropical species of *Murdannia* were accepted in the most recent account on the group (Barreto 1997; eMonocot 2010), with the occurrence of *M. schomburgkiana* (Kunth) G.Brückn. in Brazil being considered doubtful. Barreto (1997), in her unpublished Ph.D. thesis and based on the limited material she had available, also considered the *M. gardneri* (Seub.) G.Brückn. species complex to be composed of a sole and widely polymorphic and distributed species. In the most recent checklist for the Brazilian Flora (BFG 2015), Barreto's taxonomic viewpoints were followed in detail, with the sole addition of *M. nudiflora* (L.) Brenan as an invasive species.

Recent field and herbaria studies have shed some light in this neglected group. As a first attempt to clarify the taxonomy and systematics of Neotropical Commelinaceae, the present study provides a revision of the Neotropical species of *Murdannia*, with the description of a new species (endemic to Central-Western Brazil), and a new combination. We also provide a detailed taxonomic treatment on the group and comments on the morphology and systematics of *Murdannia* as a whole.

Methods

The descriptions and phenology of the species were based on herbaria, spirit, fresh material and literature. Descriptions of M. engelsii M.Pell. & Faden sp. nov., M. nudiflora and M. paraguayensis (C.B.Clarke ex Chodat) G.Brückn. were complemented, using spirit samples kindly provided by the collectors, and living samples. Specimens from the following herbaria were also analyzed: ALCB, B, BHCB, BHZB, BM, BRIT, C, CEPEC, CESJ, CNMT, CVRD, ESA, F, FCAB, FLOR, FURB, G, GH, GUA, HAMAB, HAS, HB, HBR, HERBAM, HRB, HSTM, HUEFS, HURB, IAC, ICN, INPA, K, MBM, MBML, MG, MO, MY, NY, P, PORT, R, RB, RFA, RFFP, SP, SPF, TANG, TCD, UEC, UPCB and US (herbaria acronyms according to Thiers, continuously updated). The distribution of the species is based on herbarium materials, field data and literature. The classification of the vegetation patterns follows IBGE (2012). The indumenta and shapes terminology follows Radford et al. (1974); the inflorescence terminology and morphology follows Weberling (1965, 1989) and Panigo et al. (2011); the fruit terminology follows Spjut (1994) and Ancy & Nampy (2014); and seeds terminology follows Faden (1991) and Ancy & Nampy (2014). The conservation statuses were proposed following the recommendations of IUCN Red List Categories and Criteria, Version 3.1 (IUCN 2001). GeoCAT (Bachman et al., 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). The generic description of Murdannia presented in this work applies only to the Neotropical region, and is not meant to reflect the entire morphological diversity of this widespread and diverse genus.

Results

In the present work, we accept six species native to the Neotropical region, with a new combination and a new species, and recognize two invasive Asian species. We present below descriptions for all native species, detailed diagnosis for the two invasive species, and a table summarizing the morphologic differences between all species found in the Neotropical region (Table 1). We also provide comments on the morphology of the Neotropical species of *Murdannia*, comparing them with the Paleotropical species, and a discussion of inflorescence architecture in the genus as a whole.

Murdannia Royle, Ill. Bot. Himal. Mts. 1: 403, pl. 95, f. 3. 1839.

Type species. *Murdannia scapiflora* (Roxb.) Royle [= *Murdannia edulis* (Stokes) Faden].

Aphylax Salisb., Trans. Hort. Soc. London 1: 271. 1812, nom. nud. Type species. Aphylax spiralis (L.) Salisb. [≡ Murdannia spirata (L.) G.Brückn.].

Baoulia A.Chev., Bull. Soc. Bot. France 58 (8): 217. 1912. Type species. *Baoulia tenuissima* A.Chev. [≡ *M. tenuissima* (A.Chev.) Brenan].

Dichaespermum Wight, Icon. Pl. Ind. Orient. 6: 31. 1853. Type species (designated here). *Dichaespermum lanceolatum* Wight [≡ *M. lanceolata* (Wight) Kammathy].

Dilasia Raf., Fl. Tellur. 4: 122. 1838, nom. rej. Type species. Dilasia vaginata (L.) Raf. [≡ M. vaginata (L.) G.Brückn.].

Ditelesia Raf., Fl. Tellur. 3: 69. 1837 nom. rej. Type species. Ditelesia nudiflora (L.) Raf. [≡ Murdannia nudiflora (L.) Brenan].

Phaeneilema G.Brückn., Bot. Jahrb. Syst. Beibl. 137: 63. 1926, nom. illeg. Type species. *Phaeneilema sinicum* (Ker Gawl.) G.Brückn. [=*M. simplex* (Vahl) Brenan]

Prionostachys Hassk., Flora 49: 212. 1866. Type species (designated here). *Prionostachys ensifolia* Hassk. *ex* C.B. Clarke [= *M. gigantea* (Vahl) G.Brückn.].

Streptylis Raf., Fl. Tellur. 4: 122. 1838, nom. rej. Type species. Streptylis bracteolata Raf. [= M. spirata (L.) G.Brückn.].

Talipulia Raf., Fl. Tellur. 2: 17. 1837, nom. rej. Type species. Talipulia malabarica (L.) Raf. [= Murdannia nudiflora (L.) Brenan].

Description. Herbs, perennial or annual, rhizomatous or not, with a definite or indefinite base, terrestrial to paludal to rooted emergent aquatics. Roots thin and fibrous or tuberous and fusiform. Rhizomes short to elongate. Stems trailing and ascending at the apex or erect, unbranched to densely branched, rooting in the rhizome and at the basal nodes, rarely at the distal ones when they touch the substrate. *Leaves* sessile; distichously or spirally-alternate, congested at the apex of the stem or evenly distributed along the stem; lamina flat to slightly falcate to falcate and/or conduplicate, base symmetrical, midvein inconspicuous to conspicuous, adaxially impressed or not, abaxially prominent or not, secondary veins conspicuous to inconspicuous. Synflorescence composed of a solitary main florescence or with 1-several coflorescences. Main florescences (inflorescences) terminal or axillary in the in the uppermost nodes, not perforating the leaf-sheaths; main florescence a thyrse, composed of 1-many cincinni; basal bract reduced to leaf-like; peduncle bracts (sterile bracts) absent; cincinni bracts persistent; cincinni, sessile to pedunculate, contracted to elongate, bracteoles flat or tubular, persistent or caducous. Flowers bisexual or male (the male ones with a reduced gynoecium), actinomorphic, zygomorphic or enantiostylous, chasmogamous, flat (not tubular); pedicels erect at anthesis and pre-anthesis, erect or deflexed at post-anthesis; sepals 3, equal, free, cucullate, membranous to chartaceous, dorsally not keeled, margins hyaline, accrescent and persistent in fruit; petals 3, sessile, equal to subequal, free, deliquescent, glabrous or with minute glandular hairs at base or medially bearded with moniliform hairs on the adaxial surface; stamens (2–)3, equal, antesepalous, filaments bent ca. 30° either to the left or to the right, free, glabrous or with minute glandular hairs or medially bearded with moniliform hairs, anthers dorsifixed, rimose, connective narrow, anther sacs parallel, elongate; staminodes 3–(4), antepetalous (if 4 staminodes are present, than 1 antesepalous to the lower sepal), filaments free, glabrous, minutely glandular-puberulous basally or medially bearded with moniliform hairs, antherodes dorsifixed, 3-lobed, indehiscent, connective expanded, golden yellow or mauve to purple; ovary sessile, bent ca. 30° on the opposite direction as the stamens, smooth, glabrous or glandular-puberulous, 3-locular, locules equal, locule 1–2–(6)-ovulate, style erect or gently curved at the apex, stigma truncate to capitate,

papillate. *Capsules* loculicidal, 3-valved, apiculate due to persistent style base, smooth, glabrous or glandular-puberulous. *Seeds* exarillate, farinose, uniseriate, 1–2–(6) per locule, reniform to broadly ellipsoid or cuboid to polygonal, slightly to strongly cleft towards the embryotega, ventrally flattened or not, testa costate to slightly rugose or shallowly scrobiculate to scrobiculate to foveolate, with ridges radiating from the embryotega, appendaged or not, hilum elliptic or linear, embryotega lateral to semilateral or semidorsal.

Ecology and habitat. As with most aquatic plants, Neotropical *Murdannia* are seldom collected throughout their distribution range. Despite that, the species seem to be locally common or uncommon, depending on the species. They all seem to be intimately related to permanent and seasonal water bodies of drier domains and vegetation, such as flooded grasslands in the Cerrado, Chaco and Pantanal domains, or the white sand formations in the Amazon basin.

Morphological relationships among the Neotropical species and within the genus. Murdannia is one of the six (i.e. Aneilema, Buforrestia, Commelina, Floscopa and Pollia) out of 41 genera of Commelinaceae distributed in the Neotropics and Paleotropics (Faden 1998). Although few in number, the Neotropical species of Murdannia exhibit all the extremes in inflorescence morphology found in *Murdannia* as a whole. The terminal thyrse consisting of well-spaced whorls of cincinni, present in M. gardneri and M. paraguayensis, is elsewhere present only in the rare Central African M. allardii (De Wild.) Brenan, and in the Asian species M. divergens (C.B.Clarke) G.Brückn, and M. juncoides (Wight) R.S.Rao & Kammathy (Ancy 2014; Faden & Pellegrini pers. obs.). Glandular-pubescent sepals and pedicels, present in M. burchellii (C.B.Clarke) M.Pell. comb. et stat. nov., M. englesii, M. gardneri, and M. paraguayensis, are otherwise known only from the Asian species M. medica (Lour.) D.Y.Hong (usually present) and M. spectabilis (Kurz) Faden. Moniliform hairs on the upper surface of the petals, present in M. schomburgkiana (Kunth) G.Brückn. and M. semifoliata (C.B.Clarke) G.Brückn., are recorded only in the Asian and African M. simplex (Vahl) Brenan. One-seeded capsule locules, which characterize M. burchellii, M. engelsii and M. gardneri, are known only in the Asian/Malaysian M. vaginata (L.) G.Brückn., and in the Indian M. assamica Nampy & A.Ancy (Ancy & Nampy 2014). Finally, characters present in one or more Neotropical species that are not recorded elsewhere in the genus, include: (1) inflorescences with whorls of 1-flowered cincinni (present in M. paraguayensis); (2) the presence of glandular hairs on the inflorescence axis, cincinnus peduncles and axes (present in M. burchellii, M. englesii, M. gardneri, and M. paraguayensis); (3) petals with minute glandular hairs at base on the adaxial surface (present in M. engelsii and M. paraguayensis); (4) the presence of glandular hairs on the filaments, ovaries and capsules (present in M. engelsii and M. paraguayensis); (5) long moniliform hairs on the petals and not confined to the petal bases (present in M. schomburgkiana and M. semifoliata); and (6) appendages on the seeds (present in M. burchellii, M. engelsii, M. gardneri and M. paraguayensis).

Inflorescence architecture in *Murdannia*. Brenan (1966) has shown a great diversity of inflorescence architecture in *Murdannia*, with variations in the position of the main florescence, total number of cincinni, number of nodes with cincinni, number of cincinni per node, and degree of development of each cincinnus. According to Panigo *et al.* (2011), the basic inflorescence pattern for Commelinaceae is a many-branched, pedunculate and terminal thyrse, with verticillate cincinni, each cincinnus multi-flowered. Based on Brenan (1966) and Panigo *et al.* (2011), we could also infer that the plesiomorphic inflorescence architecture for *Murdannia* would correspond to the basic inflorescence pattern for Commelinaceae. Brenan (1966) indicates that most of the variation in inflorescence architecture could be derived from

this basic type, as exemplified by the Asian *M. divergens*, by only three changes. On the other hand, Panigo *et al.* (2011) states that additional changes would be necessary to express all the known variation in the inflorescence morphology for *Murdannia*, as: (1) the production of coflorescences, in addition to the main florescence; (2) variation in the length of the peduncle and internodes of the main florescence; (3) variation in the number of cincinni per node; (4) variation in the arrangement of cincinni on each node of the main florescence; (5) variation in the length of the cincinnus peduncle; and (6) variation in the total flower number per cincinnus. These changes can occur separately or in different combinations. In the most extreme cases, the inflorescences are mainly axillary, with each inflorescence being fascicle-like, and composed of a few 1-flowered cincinni.

If we were to consider this stepwise change a possible evolutionary sequence within Murdannia, then the South American species with the most plesiomorphic inflorescence type would be M. gardneri. By its reduced number of cincinni per node and change in their arrangement, the inflorescence of M. burchellii could be morphologically derived from M. gardneri. Murdannia paraguayensis, shares the numerous verticillate cincinni of M. gardneri, but each cincinnus is reduced to a single flower. Murdannia engelsii has terminal or terminal and axillary inflorescences, that are reduced to single cincinni, but the cincinnus is 2-severalflowered. The most reduced inflorescences, and perhaps the ones that accumulated the greatest number of stepwise changes, can be observed in M. schomburgkiana and M. semifoliata, in which most inflorescences are fascicle-like, axillary in the distal leaves, and with all cincinni 1-flowered. Species with similarly reduced inflorescences are numerous in Asia [e.g. M. blumei (Hassk.) Brenan, M. crocea (Griff.) Faden, M. keisak (Hassk.) Hand.-Mazz., M. lanuginosa (Wall. ex C.B.Clarke) G.Brückn., M. pauciflora (Wight) G.Brückn., M. triquetra (Wall. ex C.B.Clarke) G.Brückn., and M. versicolor (Dalzell) G.Brückn.], and represented in Africa by M. axillaris Brenan (Faden 2012; Ancy 2014). Nonetheless, some of them show characters not present in any of the Neotropical species, such as annual habit, biseriate seeds and yellow to orange flowers. Thus, in the absence of a well sampled molecular phylogeny it would be impossible to state whether the Neotropical species represent one or several distinct lineages in Murdannia.

Key to the native and invasive species of Murdannia in the Neotropics

- 1. Inflorescences composed of 2-several verticillate or alternate to subopposite cincinni, rarely composed of a solitary cincinnus, bracteoles persistent; flowers enantiostylous, sepals with glandular hairs or with a mixture of glandular and eglandular hairs, androecium glabrous or with minute glandular hairs; seeds with a ventri-lateral appendage... 2
- 1'. Inflorescences composed of a solitary cincinnus or fascicle-like, bracteoles caducous; flowers non-enantiostylous, sepals glabrous, androecium medially bearded with moniliform hairs; seeds without a ventri-lateral appendage... 5
- 2. Bracteoles cup-shaped; pedicels erect at post-anthesis and in fruit; petals glabrous, filaments, ovaries and capsules glabrous; hilum in a deep depression... 3
- 2'. Bracteoles flat; pedicels deflexed at post-anthesis and in fruit; petals with minute glandular hairs at base on the adaxial surface, filaments, ovaries and capsules with glandular hairs; hilum in a shallow depression...4
- 3. Cincinni alternate, rarely subopposite, sinuate; plants generally delicate; stems prostrate, thin, delicate to fibrous, densely branched at the base; leaves chartaceous, conduplicate, linear to linear-oblong; main axis of inflorescence with sparse eglandular and glandular

- hairs; cincinnus bracts with caudate apex; seeds densely farinose, the testa costate to slightly rugose... *M. burchellii* (C.B.Clarke) M.Pell. (Fig. 1)
- 3'. Cincinni verticillate, straight; plants generally robust; stems ascending to erect, succulent, little branched at base to unbranched; leaves succulent, canaliculate, linear-lanceolate to lanceolate; main axis of inflorescence with dense glandular and sparse eglandular hairs; cincinnus bracts with acuminate apex; seeds farinose, the testa scrobiculate to foveolate... *M. gardneri* (C.B.Clarke) G.Brückn. (Figs. 3–4)
- 4. Inflorescence reduced to a solitary cincinnus (but sometimes several clustered in a synflorescence near towards the shoot apex), peduncles with a mixture of eglandular (scabrid) and glandular to densely glandular hairs, cincinni 2–7-flowered; plants without a definite base; leaves distichously-alternate; flowers buds ovoid; capsules broadly ovoid to broadly ellipsoid, locules 1-seeded... *M. engelsii* M.Pell. & Faden (Fig. 2)
- 4'. Inflorescence a terminal thyrse composed of several whorls of 1-flowered cincinni, peduncles with glandular to densely glandular hairs, cincinni 1-flowered; plants with a definite base; leaves spirally-alternate; flower buds ellipsoid to narrowly ellipsoid; capsules oblongoid to broadly oblongoid, locules 2-seeded... *M. paraguayensis* (C.B.Clarke *ex* Chodat) G.Brückn. (Fig. 6)
- 5. Leaves distichously-alternate; inflorescences long-pedunculate, exerted from the leaf-sheaths, cincinni 2–12-flowered, pendent; flowers zygomorphic, stamens 2, staminodes 4 (1 staminode antesepalous, sometimes lacking the antherode), antherodes white to cream; capsules ovoid to subglobose... *M. nudiflora* (L.) Brenan (Fig. 5)
- 5'. Leaves spirally-alternate; inflorescences sessile, enclosed by the leaf-sheaths; cincinni 1-flowered, erect; flowers actinomorphic, stamens 3, staminodes 3, antherodes yellow (flowers uncertain in *M.* aff. *triquetra*); capsules oblongoid to ellipsoid... 6
- 6. Annuals without a definite base; roots thin; stems trailing, apex ascending, densely branched; petals glabrous; capsules with 3-seeded locules; seeds transversely ellipsoid... *M.* aff. *triquetra* (Wall. *ex* C.B.Clarke) G.Brückn. (Fig. 9)
- 6'. Perennials with a definite base; roots tuberous; stems erect (only the short rhizome prostrate), unbranched; petals medially bearded with moniliform hairs on the adaxial surface; capsules with 6-seeded locules; seeds cuboid to polygonal... 7
- 7. Leaf-blades margins glabrous throughout, inflorescences-bearing leaves with expanded blades (2.2–13.6 cm long); anthers brown... *M. schomburgkiana* (Kunth) G.Brückn. (Fig. 7)
- 7'. Leaf-blades margins ciliate at least at base, inflorescences-bearing leaves reduced to bladeless sheaths or with much reduced blades (0.2–1.8 cm long); anthers purple... *M. semifoliata* (C.B.Clarke) G.Brückn. (Fig. 8)

1. Murdannia burchellii (C.B.Clarke) M.Pell., comb. et stat. nov.

Figs 1 & 10

- Aneilema gardneri var. burchellii C.B.Clarke, Monogr. Phan. 3: 217. 1881. Lectotype (designated here): BRAZIL. s.loc., fl., fr., s.dat., W.J. Burchell 8165 (K barcode K000363240!; isolectotypes: GH barcode GH00415446!, P barcode P02088020!).
- Aneilema gardneri var. glabrior C.B.Clarke, Monogr. Phan. 3: 217. 1881. Lectotype (designated here): BRAZIL. Goyaz, fl., fr., 1841, G. Gardner 4020 (P barcode

P02088023!; isolectotypes: BM not found, G barcode G00098263!, NY barcode NY00247402!). Syn. nov.

Description. Herbs ca. 14.0–55.0 cm tall., perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in flooded fields. Roots thin, fibrous, brown to darkbrown, densely to sparsely pilose with medium to dark brown hairs, emerging from the rhizome and from the basal most nodes. *Rhizomes* short, light to medium brown, buried in the sand or ground. Stems trailing with ascending apex, thin, densely branched or branched only at the base; internodes 1.8–8.4 cm long, green to vinaceous to reddish brown, sparsely pilose to hispid with hyaline hairs, becoming glabrous with age, with a line of eglandular hyaline hairs opposite the leaf above. Leaves spirally-alternate, evenly distributed along the stems, the distal ones gradually smaller than the proximal ones; sheaths 0.3–1.3 cm long, vinaceous to reddish brown, sparsely pilose to hispid with hyaline hairs, becoming glabrous with age, hairs hyaline, margins setose, with a line of eglandular hairs opposite to the leaf above; lamina 2.7– 13 × 0.3–0.6 cm, linear to linear oblong, membranous, conduplicate, slightly falcate, light green to greyish green on both sides, drying light brown to olive-green on both sides, sparsely pilose to hispid, becoming glabrous with age, rarely glabrous, base truncate, margins green, ciliate to setose throughout or only at base, apex acuminate to mucronate; midvein conspicuous, impressed adaxially, prominently acute abaxially, secondary veins 2–(3) pairs, adaxially inconspicuous to slightly conspicuous, dark green, abaxially somewhat conspicuous, dark green. Inflorescences 1–2–(4) thyrsi, terminal or axillary in the uppermost nodes, thyrse with (1–)2–16, alternate to subopposite cincinni; peduncles 2.3–7.6 cm, with a sparse mixture of eglandular (scabrid) and glandular, hyaline hairs; basal bract reduced or leaf-like, 1.4–5.1 × 0.1–0.3 cm, lanceolate to linear, sparsely pilose to hispid, rarely glabrous, base truncate, margins ciliate to setose, apex acuminate, veins inconspicuous, concolorous or green; cincinni bracts ca. 0.2–1.1 × 0.1–0.4 cm, triangular to broadly triangular, cup-shaped, light green to lilac, glabrous to pilose at base, base amplexicaul, non-perfoliate, margins glabrous to sparsely ciliate, apex caudate; cincinni 2–9-flowered, erect, sinuate, cincinnus peduncle 0.4– 2.2 cm, green to vinaceous to purple, with a mixture of sparse eglandular (scabrid) and sparse or more numerous glandular, hyaline hairs, cincinnus internodes 0.2-1.1 cm long, green to vinaceous to purple, with a mixture of sparse eglandular (scabrid) and sparse or more numerous glandular, hyaline hairs; bracteoles ca. $1.8-3.7 \times 0.9-1$ mm, persistent, triangular to broadly triangular, cup-shaped, light green to lilac, glabrous to sparsely pilose, base amplexicaul, non-perfoliate, margins glabrous or rarely sparsely ciliate, apex acuminate. Flowers bisexual or male, enantiostylous, ca. 0.5–1.2 cm diameter; floral buds narrowly ovoid to ovoid, 2.1-4 × 1-2 mm, green to lilac; pedicels 0.3-1 cm long, green to vinaceous to purple, with a mixture of sparse eglandular (scabrid) and sparse or more numerous glandular, hyaline hairs, erect and elongate in fruit; sepals $3.2-5 \times 1.5-2$ mm, triangular to ovatetriangular, cucullate, green, glandular to densely glandular, hyaline hairs, apex acuminate, margins hyaline light green to hyaline lilac; petals equal, 4-6.3 × 3-4.2 mm, obovate to narrowly obovate, slightly cucullate, pale lilac to lilac to pink, rarely white, glabrous, base cuneate, margins entire, apex obtuse to rounded; stamens 3, equal, filaments glabrous, gently curved at the apex, 3.8-5.2 mm long, pale lilac to lilac or white, anthers narrowly elliptic to narrowly oblong, $0.8-1.0 \times 0.3-0.7$ mm, connective lilac, anthers sacs white, pollen white; staminodes 3, equal, filaments glabrous, straight, 1.6-2.1 mm long, pale lilac to white, antherodes sagittate, 0.8–0.9 × 0.9–1.0 mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to oblongoid, 0.9–1.8 × 0.6–0.8 mm, 3-locular, white to light green, smooth, glabrous, style gently curved at the apex, ca. 1.8–3.6 mm, pale lilac to lilac or white, stigma truncate, white to lilac. Capsules 2.8-4.4 × 3-4.8 mm, subglobose to globose, apiculate due to persistent style, 3-locular, 3-valved, light brown when mature, glabrous, smooth. Seeds 1 per locule, $1.9-2.8 \times 1.3-2.1$ mm, reniform to broadly ellipsoid, cleft towards the embryotega, ventrally flattened, testa dark brown to greyish brown, densely farinose, costate to slightly rugose, with ridges radiating from the embryotega, with a tan appendage that extends ventri-laterally to the embryotega and basally into the hilum; embryotega semilateral, relatively inconspicuous, generally covered by a cream farina, without a prominent apicule; hilum linear, approximately the same length as the seed, in a deep depression.

Specimens seen. BOLIVIA. Santa Cruz: San Ignacio de Velasco, 30 km acia S, 12 Apr 1988, B. Bruderreck 310 (LPB, US). BRAZIL. Goiás: Provincia Goyaz, Salinas, May-Jul 1844, M.A. Weddell 2103 (P); loc. cit., May-Jul 1844, M.A. Weddell 2106 (P); s.loc., 1841, G. Gardner 3481 (K); Colinas do Sul, Vila Borba, 15 Jun 1993, G. Hatschbach et al. 59587 (MBM, MO, USU); Formoso, arredores de Formoso, 3 May 2012, R.J.V. Alves 8898 (R); Paraíso, ca. 27 km sul de Paraíso, 23 Mar 1968, H.S. Irwin et al. 21659 (K, NY, UB); loc. cit., 23 Mar 1968, H.S. Irwin et al. 21717 (NY, UB); Maranhão: Carolina, 1 Jun 1950, J.M. Pires & G.A. Black 2564 (UFMA, US); **Pará:** Ilha do Marajó, 15 Aug 1901, fl, fr., M. Guedes 2314 (BM); Serra do Cachimbo, Jun 1955, M. Alvarenga s.n. (RB 90541); loc. cit., 12 Dec 1956, J.M. Pires et al. 6104 (NY, UFMA); Itaituba, arredores da base aérea do Cachimbo, 25 Apr 1983, M.N. Silva et al. 90 (INPA, K, MG, NY, US); loc. cit., 26 Apr 1983, M.N. Silva et al. 118 (INPA, MG, NY, US); Piauí: Piauhy, Parnaguá, marshy places, Aug-Sep 1839, fl., fr., G. Gardner 2743 (BM, K); Tocantins: Araguaina, 20 km ao Sul, 26 Mar 1976, G. Hatschbach & R. Kummrow 38378 (MBM, US). VENEZUELA. Apure: Departamento Muñoz, módulos F. Corrales de la UNELLEZ, entre los caños Guaritico y Caicara, 25 Oct 1980, B. Stergios 2379 (PORT, US); loc. cit., 10 Sep 1981, fr., G. Aymard 466 (PORT); loc. cit., 13 Sep 1981, B. Stergios et al. 9568 (PORT, US); loc. cit., 9 Dec 1986, G. Aymard & R. Schargel 5017 (PORT, US); loc. cit., 12 Dec 1986, G. Aymard & R. Schargel 5071 (PORT, US); Cojedes: San Carlos, en extremo Sur del Hato "El Laurel", mas o menos km. 17 al sur de San Carlos, 21 Aug 1976, fl., fr., B. Trujillo 13843 (MY); Guárico: Calabozo, ca. 39 km SSW of Calabozo on Hato Masaguaral, 17 Sep 1983, R. Rondeau 469 (US); Portuguesa: Guanare, terrenos de la UNELLEZ, Mesa de Cavacas, 6 Sep 1986, fl., fr., B. Stergios 7151 (PORT).

Distribution and habitat. *Murdannia burchellii* has a very fragmented distribution, probably due to lack of collections, being known to occur in Bolivia, Brazil (in the states of Goiás, Maranhão, Pará, Piauí and Tocantins), and Venezuela (Fig. 10). It grows in shady to open sandy river banks of the Amazon and Cerrado domains.

Phenology. It was found in bloom and fruit from October to July.

Conservation status. Murdannia burchellii possesses a wide EOO (ca. 3,513,319.273 km²), but due to the few and scattered collections known for this species, its AOO is considerably smaller (ca. 22,500.000 km²). Thus, following the IUCN recommendations (IUCN 2001), M. burchellii should be considered Least Concern. Nonetheless, it is important to highlight the small number of collections and how fragmented the distribution of M. burchellii is. Also, the most recent collection was made in 1993. Which may indicate an ongoing decrease of size of the subpopulations and the loss of habitat for this species.

Nomenclatural notes. When describing *Aneilema gardneri* var. *burchelli*, Clarke (1881) lists two collections (*W.J. Burchell 8165* and *M.A. Weddell 2106*). Since the name of Clarke's new variety honors W.J. Burchell, it seems logical to designate his collections as the

lectotype. Aside from that, this collection is well distributed in several herbaria around the world. Furthermore, the specimen from K herbarium matches Clarke's description and has hand annotations made personally by Clarke. Thus, we designate this specimen as the lectotype for *Aneilema gardneri* var. *burchelli*.

When describing Aneilema gardneri var. glabrior, Clarke (1881) cites three collections by G. Gardner (2743, 3481, 4020). The specimen of at K Gardner 4020 is mounted on the same sheet as Gardner 3481, and both being annotated by Clarke as A. gardneri var. glabrior. Gardner 4020 is also the most well distributed of the three collections. Nonetheless, the specimen of at K represents M. gardneri, so it cannot be designated as the type of A. gardneri var. glabrior. Thus, the specimen at K is not considered part of the original material. One of us (RBF) examined and recorded a specimen of Gardner 4020 at BM in 1993, with the following data on the label: "Moist campos between Natividade and Conceição, Feby 1840, Herb. Gardner." While this would appear to be the most logical choice for a lectotype, the specimen was not photographed when other types were photographed at BM, and it cannot be found today. Therefore, the specimen at P is here designated as the lectotype. This specimen also bears an identification in Clarke's handwriting.

Discussion. Murdannia burchellii is morphologically similar to M. gardneri due to the general aspect of the plants, indumentum and by the presence of a ventri-lateral appendage in the seeds. It was traditionally treated as part of M. gardneri s.l. due to the number of cincinni per inflorescence, the posture of the pedicels at post-anthesis and in fruit, general floral and capsule morphology, and due to the hilum being positioned in a deep depression (Table 1). Nevertheless, both species can be readily differentiated by the stature and robustness of the plants, the insertion of the cincinni in the main axis of the inflorescence and testa ornamentation. Furthermore, the cincinni in M. burchellii are conspicuously sinuate, while the cincinni in M. gardneri are straight. After analyzing the syntypes for Aneilema gardneri var. glabrior, it became clear that they were conspecific with M. burchellii. All specimens possess the characteristic alternate to subopposite cincinni, being differentiated only from M. burchellii by sparser eglandular and glandular hairs in the inflorescence. All the analyzed specimens possessed some type of indumentum in the inflorescence, despite Clarke's description (1881) stating they were completely glabrous.

Some young specimens of *Murdannia burchellii* with inflorescences reduced to a solitary cincinnus, can be confused with specimens of *M. engelsii*. Nevertheless, these can be differentiated by their glabrous stems, leaf-blades with truncate base, sinuate cincinni, cupshaped bracteoles, and glabrous androecium and gynoecium (vs. stems with glandular hairs, leaf-blades with an amplexicaul base, straight cincinni, flat bracteoles and minutely glandular-pubescent androecium and gynoecium in *M. engelsii*) (Table 1).

2. *Murdannia engelsii* **M.Pell. & Faden, sp. nov.** Figs 2 & 10

Diagnosis. Similar to *M. paraguayensis* due to its deflexed pedicels at post-anthesis and when fruiting; petals with minute glandular hairs at base on the adaxial surface; filaments, ovaries, styles and capsules with minute glandular hairs, and capitate stigma. It can be differentiated by its trailing stems, distichously-alternate leaves, inflorescence reduced to a solitary cincinnus, peduncles with a mixture of eglandular and glandular hairs, cincinni 2–7-flowered, capsules broadly ovoid to broadly ellipsoid, and 1-seeded locules.

Type. BRAZIL. Mato Grosso: Itaúba, Resgate de Flora da UHE Colíder, lote G de supressão, 260 m, floresta do Planalto dos Parecís, prainha arenosa no rio Teles Pires, fl., fr.,

27 May 2015, M.E. Engels et al. 3474 (RB!; isotypes: CNMT!, HERBAM!, MBM!, US!, TANG!).

Description. Herbs ca. 10.0–36.0 cm tall, perennial, rhizomatous without a definite base, terrestrial to paludal in river banks. Roots thin, fibrous, brown, densely to sparsely pilose with hyaline hairs, emerging from the basalmost nodes and rhizome. Rhizomes long, trailing, light brown to light green, shallowly buried in the sand. Stems ascending to erect, thin, herbaceous to slightly succulent, usually densely branched or branched only at the base, sometimes branching from the upper nodes; internodes 1.3-3.5 cm long, green, with a mixture of eglandular (scabrid) and glandular hairs, becoming glabrous with age, with a line of eglandular hairs opposite the leaf above, hairs hyaline. Leaves distichously-alternate, evenly distributed along the stems, rarely somewhat congested at the apex of the stems, the distal ones gradually smaller than the proximal ones; sheaths 2-2.5 mm long, green, with glandular hairs, becoming glabrous with age, hairs hyaline, margins sparsely ciliate, with a line of eglandular hairs opposite the leaf above, hairs hyaline; lamina $(0.5-)1.6-6 \times 0.3-1$ cm. membranous, generally conduplicate, rarely flat, slightly falcate to falcate, green on both sides, drying olive-green on both sides, narrowly elliptic to narrowly lanceolate or narrowly ovate, glabrous on both sides or the uppermost usually with glandular hairs at least basally, base amplexicaul, margins green, ciliate to setose at base or the uppermost sometimes with glandular hairs, apex acuminate; midvein slightly conspicuous, slightly impressed adaxially, prominently acute abaxially, secondary veins 2(-3) pairs, inconspicuous to slightly conspicuous on both sides, dark green. *Inflorescences* 1–2–(5), terminal or axillary from the uppermost nodes, consisting of a solitary cincinnus; peduncles 1-1.4 cm, with a mixture of eglandular (scabrid) and glandular to densely glandular hyaline hairs; basal bract reduced, 5- 5.5×4 –4.5 mm, lanceolate to ovate, adaxially glabrous, abaxially glabrous or with glandular hairs, base amplexicaul, margins ciliate at base, apex acute, veins inconspicuous on both sides, dark green; cincinni 2–7-flowered, erect, straight, peduncle 3.5–8 mm long, green, with glandular to densely glandular, hyaline hairs, cincinnus internodes 4.5-8 mm long, green, with glandular to densely glandular hyaline hairs; cincinnus bract and bracteoles ca. $1-1.5 \times$ 0.9–1 mm, persistent, ovate, flat, light green, with a sparse mixture of eglandular (scabrid) and glandular hairs near the base, base amplexicaul, non-perfoliate, margins glabrous, apex acute. Flowers bisexual or male, enantiostylous, 1–1.4 cm diam.; floral buds ovoid, 2.8–3.1 × 2.5-3 mm, green; pedicels 1-6 mm long, green, with glandular to densely glandular, hyaline hairs, deflexed and slightly elongate in fruit; sepals $3-3.5 \times 0.5-0.8$ mm, triangular to ovatetriangular, cucullate, green, with glandular to densely glandular, hyaline hairs, apex acute, margins hyaline light green; petals equal, 4.5–7.3 × 2.5–4.5 mm, obtrullate, rarely obovate, slightly cucullate, pale lilac to lilac, mauve or pink, rarely white, with minute glandular hairs at the base on the adaxial surface, base cuneate, margins entire, apex obtuse to rounded; stamens 3, equal, filaments basally with minute glandular hyaline hairs, gently curved in the middle, 4.1–5.9 mm long, pale lilac to lilac or white, anthers elliptic, $0.6-0.7 \times 0.3-0.7$ mm, connective white to lilac, anthers sacs white to pale lilac, pollen white; staminodes 3, equal, filaments with minute glandular hyaline hairs, straight, 1.3–1.7 mm long, white to pale lilac, antherodes subsagittate to subcordate, $0.9-1.0 \times 0.9-1.0$ mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ovoid to ellipsoid, 0.9× 0.7–0.8 mm, 3locular, white to light green, smooth, with minute glandular hyaline hairs, style curved at the apex, ca. 3.6-8 mm, white to pale lilac or lilac, stigma capitate, white to lilac. Capsules 3locular, 3-valved, 3.2-4.5 × 2-2.5 mm, broadly ovoid to broadly ellipsoid, apiculate due to persistent style, light brown when mature, with minute glandular hyaline hairs, sometimes glabrescent with age, smooth. Seeds 1 per locule, 1.8–2.0 × 1–1.2 mm, reniform to broadly ellipsoid, cleft towards the embryotega, ventrally flattened, testa medium to dark brown,

sparsely farinose, scrobiculate to shallowly scrobiculate, with ridges radiating from the embryotega, sometimes with 4–7 ventral furrows, with a tan appendage that extends ventrilaterally to the embryotega and basally into the hilum; embryotega semilateral to semidorsal, relatively inconspicuous, generally covered by a cream farina, without a prominent apicule; hilum linear, approximately the same length as the seed, in a shallow depression.

Specimens seen (paratypes). BRAZIL. Mato Grosso: Itaúba, resgate de Flora da UHE Colíder, Lote G de supressão, floresta do Planalto dos Parecís, região de ecótono entre a Floresta Amazônica e Cerrado, 3 Jun 2016, M.E. Engels & A.S. Bezerra 4510 (HERBAM, MBM, RB); Poconé, rodovia Transpantaneira, 17 May 1983, J. Barcia et al. 1560 (R); loc. cit., Fazenda Nova Berlim, Transpantaneira highway, km 85, 3 May 1992, M. Schessl 2602b (CH, UFMT, ULM, US); loc. cit., highway Poconé-Porto Cercado, 30 May 1992, M. Schessl 2631g (CH, CPAP, UFMT, ULM, US); loc. cit., estrada para Porto Cercado, km 18, 22 Apr 1993, A.L. Prado 2017 (UEC, UFMT); loc. cit., Fazenda Ipiranga, 8 May 1993, A.L. Prado & R. Ribeiro 2045 (HURB, UEC, UFMT); loc. cit., Fazenda Ipiranga, Pousada Piuvial, vazante da sede, km 11 da rodovia Transpantaneira, 20 May 1996, V.J. Pott et al. 3186 (CPAP, US); Vila Bela da Santíssima Trindade, Parque Estadual Serra de Ricardo Franco, margem do rio Guaporé, 23 May 1978, P.G. Windisch 1863 (RB); Mato Grosso do Sul: Corumbá, Fazenda Caceres, próximo da sede de Nhecolândia, 12 Aug 1988, V.J. Pott et al. 595 (CPAP, MBM, US); loc. cit., Fazenda Alegria, Nhecolândia, 30 Jul 1989, A. Pott et al. 4912 (CPAP, MBM, US); loc. cit., próximo ao mata burro na divisa com Retiro Mandovi, Nhecolândia, 3 Aug 1999, V.J. Pott & A. Rodrigues 3993 (CPAP, US); Tocantins: Pium, Ilha do Bananal, Parque Nacional do Araguaia, base física do rio Javaés, antigo acampamento do Projeto Quelônios do Amazônia, 27 Mar 1999, M. Aparecida da Silva et al. 4167 (IBGE, RB).

Etymology. The epithet honors the collector of the holotype, the Brazilian botanist Mathias Erich Engels, Orchidaceae taxonomist and dear friend of the authors.

Distribution and habitat. *Murdannia engelsii* is endemic to Brazil, being known from the states of Tocantins, Mato Grosso and Mato Grosso do Sul (Fig. 10). It grows in shady to open sandy river banks of the Amazon, Cerrado and Pantanal domains. Its prostrate stems produce dense mats, generally near rocks and grasses.

Phenology. It was found in bloom and fruit from March to August.

Conservation status. *Murdannia engelsii* possesses both a wide EOO (ca. 514,893.048 km²) and a wide AOO (ca. 15,000.000 km²). Following the IUCN recommendations (IUCN 2001), *M. englesii* should be considered Least Concern. Nevertheless, most of the known populations of *M. engelsii* are in areas currently being deforested and turned into pasture sites for cattle. We believe that this species is highly affected by human activity and should be considered Vulnerable [VU, A2cd+ B2ab(ii, iii,v)+D2].

Discussion. Murdannia engelsii is morphologically similar to M. burchellii, M. gardneri and M. paraguayensis due to indumentum and flower morphology, and also similar to M. paraguayensis due to the deflexed pedicels in fruit. However, M. engelsii can be easily differentiated by its inflorescence reduced to a solitary cincinnus (vs. thyrsi with several, verticillate or alternate to subopposite cincinni). It can be easily differentiated from M. burchellii and M. gardneri by inflorescence morphology, position of the pedicels at postanthesis and in fruit, by the indumentum of the filaments, gynoecium and capsules, and seed morphology. Murdannia engelsii is much more similar to M. paraguayensis, due to several

key characters. These are the only species in the genus to have an androecium and gynoecium with glandular hairs, and the only Neotropical species to have pedicels deflexed post-anthesis and in fruit. Nevertheless, *M. engelsii* can be differentiated by its trailing habit (*vs.* erect in *M. paraguayensis*), leaves distichously-alternate (*vs.* spirally-alternate), inflorescence reduced to a solitary cincinnus (*vs.* inflorescence with several verticillate cincinni), cincinni 2–7-flowered (*vs.* 1-flowered), capsules broadly ovoid to broadly ellipsoid (*vs.* oblongoid to broadly oblongoid), and locules 1-seeded (*vs.* 2-seeded). *Murdannia engelsii* can also be confused with *M. nudiflora*, due to their small stature, phyllotaxy and inflorescence morphology. However, they can be easily differentiated by its erect cincinni (*vs.* pendulous), persistent bracteoles (*vs.* caducous), corolla actinomorphic (*vs.* zygomorphic), three stamens and three staminodes (*vs.* two stamens and four staminodes), filaments with minute glandular hairs (*vs.* bearded with moniliform hairs), and locules 1-seeded (*vs.* locules 2-seeded) (Table 1). One of the most striking features of *M. engelsii* would be occasional production of several inflorescences clustered towards the apex of a shoot, forming a synflorescence. This synflorescence resembles a single inflorescence with several alternate cincinni.

3. *Murdannia gardneri* (**Seub.**) **G.Brückn.**, Nat. Pflanzenfam. (ed. 2)15a: 173. 1930. Figs 3–4 & 10

Phaeneilema gardneri (Seub.) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10 (91): 56. 1927.

Aneilema gardneri Seub., in Martius, Fl. Bras. 3 (1): 259. 1855. Lectotype (designated here): BRAZIL. Goyaz, moist places near Villa de Arrayal, fl., fr., April 1841, G. Gardner 4021 (K barcode K000363236!; isolectotypes: B barcode B100367834!, BM barcodes BM001172132!, BM001172133!, G barcodes G00098261!, G00098262!, G00165012!, K barcode K000363237!, NY barcodes NY00247400!, NY00247401!, P barcode P02088022!, US barcode US00091574!).

Description. Herbs ca. 30.0–150.0 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in flooded fields. Roots thin, fibrous, medium to dark brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the short rhizome and from the basalmost nodes. Rhizomes short, light to medium brown, buried in the sand or ground. Stems prostrate, with erect to ascending apex, succulent, unbranched to littlebranched at the base; internodes 1.9–10.7 cm long, green to vinaceous, glabrous to sparsely pilose or hispid, becoming glabrous with age, with a line of eglandular hairs opposite the leaf above, hairs hyaline. Leaves spirally-alternate, evenly distributed along the stems, sessile, the distal ones gradually reduced; sheaths 0.5–3.2 cm long, green to vinaceous, sparsely pilose to hispid, becoming glabrous with age, hairs hyaline, margins ciliate to hispid, with a line of eglandular hairs opposite the leaf above, hairs hyaline; lamina $4.2-17.4 \times 0.7-1.3$ cm, chartaceous, conduplicate, slightly falcate to falcate, green on both sides, drying light brown to olive-green on both sides, linear-lanceolate to lanceolate, sparsely pilose to hispid, becoming glabrous with age, rarely glabrous, base truncate to rounded, margins light green, ciliate to setose only at base, apex acuminate; midvein inconspicuous, slightly impressed adaxially, slightly obtuse abaxially, secondary veins 3–4(–5) pairs, adaxially inconspicuous to slightly conspicuous, light green, abaxially somewhat conspicuous. Inflorescences 1–(3) thyrsi, terminal or axillary from the uppermost nodes, thyrse with 16–38 verticillate cincinni, arranged in 2-9 whorls; peduncles 2.7-8.4 cm, with a mixture of eglandular (scabrid) and glandular, hyaline hairs; basal bract leaf-like, 2.4–7.2 × 0.3–0.9 cm, linear-lanceolate to lanceolate, sparsely pilose to hispid, rarely glabrous, base rounded, margins ciliate to setose only at base, apex acuminate, veins inconspicuous, concolorous to light green; cincinni bracts

ca. $0.4-0.8 \times 0.1-0.3$ cm, ovate to broadly ovate, cup-shaped, light green to lilac, glabrous to pilose, base truncate, margins glabrous to sparsely ciliate, apex acuminate; cincinni 2-11flowered, ascending, straight, peduncle 0.5–1.3 cm, light green to vinaceous to purple, with a mixture of eglandular (scabrid) and glandular or all glandular hyaline hairs, internodes 0.9-5.2 mm long, light green to vinaceous to purple, with a mixture of eglandular (scabrid) and glandular or all glandular, hyaline hairs; bracteoles ca. 1.8–4.1 × 2.8–4.2 mm, persistent, broadly ovate to depressed ovate, cup-shaped, light green to lilac or pink, sparsely pilose, base amplexicaul, non-perfoliate, margins glabrous to ciliate, apex acuminate. Flowers bisexual or male, enantiostylous, ca. 1.4–2.3 cm diam.; floral buds narrowly ovoid to ovoid, 2.6–5.3 × 1.2-2.4 mm, light green to pink to vinaceous; pedicels 2.2-7.3 mm long, light green to vinaceous to purple, with a mixture of eglandular (scabrid) and glandular or all glandular, hyaline hairs, erect and elongate in fruit; sepals 3.6-6.1 × 3.2-4.8 mm, triangular to ovatetriangular, cucullate, green to lilac to vinaceous to purple, with glandular to densely glandular, hyaline hairs, apex acuminate, margins hyaline light green to hyaline pink; petals equal, 0.7– 1.2 × 0.6–0.8 cm, obovate to elliptic-obovate, slightly cucullate, pale lilac to lilac, purple or pink, rarely white, glabrous, base cuneate, margins entire, apex acute to obtuse; stamens 3, equal, filaments glabrous, gently curved at the apex, 6.2-9.4 mm long, pale lilac to lilac or white, anthers elliptic, $0.7-0.9 \times 0.3-0.4$ mm, connective lilac to white, anthers sacs white to lilac, pollen white; staminodes 3, equal, filaments glabrous, straight, 3.1-5.3 mm long, pale lilac to white, antherodes cordate, $0.7-0.9 \times 0.8-0.9$ mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to broadly ellipsoid, $0.6-0.8 \times 10^{-2}$ 0.4–0.6 mm, 3-locular, white to light green, smooth, glabrous, style gently curved at the apex, ca. 4.8–6.2 mm, pale lilac to lilac or white, stigma truncate, white to lilac. Capsules $3.6-4.5 \times$ 3.4–4.2 mm, 3-locular, 3-valved, subglobose to globose, apiculate due to persistent style, light brown when mature, glabrous, smooth. Seeds 1 per locule, 1.9–2.6 × 1.2–1.8 mm, reniform to broadly ellipsoid, strongly cleft towards the embryotega, ventrally flattened, testa dark brown to grevish brown, sparsely farinose, scrobiculate to foveolate, with ridges radiating from the embryotega, with a tan appendage that extends ventri-laterally to the embryotega and basally into the hilum; embryotega semilateral, relatively inconspicuous, without a prominent apicule; hilum linear, approximately the same length as the seed, in a deep depression.

Specimens seen. BRAZIL. Bahia: Correntina, Chapadão Ocidental da Bahia, Islets and banks of the rio Corrente, 23 Apr 1980, R.M. Harley et al. 21668 (CEPEC, HRB, K, MBM, US); loc. cit., 21 Jan 1997, G. Hatschbach et al. 66044 (MBM); Goiás: Cavalcante, estrada rio Trairas/rio Custódio, km 2, 28 Nov 2006, G. Pereira-Silva & G.A. Moreira 11159 (CEN, RB); Colinas do Sul, fazenda Saracura, estrada de manutenção das novas linhas de transmissão Minacu/Niquelândia, 8 Sep 1995, B.M.T. Walter et al. 2604 (CEN, RB); Goyaz, 1841, G. Gardner 4020 (K barcode K000363238, US barcode US00160560); Itumbiara, rodovia Itumbiara-Rio Verde, a 31 km de Itumbiara, 18 Apr 1978, G.J. Shepherd et al. 7415 (F ex UEC); Niquelândia, 27 km de Colinas em direção a Niquelândia, próximo ao rio Tocantinzinho, 6 May 1998, M.A. Silva et al. 3772 (IBGE, RB, US); Teresina de Goiás, km 12 da estrada GO-118, sentido Nova Roma, 29 April 1996, B.A.S. Pereira & D. Alvarenga 3027 (IBGE, RB); Mato Grosso: Novo Mundo, Parque Estadual do Cristalino, entrada para Fazenda J.J., 26 January 2008, D. Sasaki et al. 1934 (HERBAM, HURB, SPF); Minas Gerais: Ituiutaba, 26 May 1946, A. Macedo 760 (US); Tocantins: Conceição do Tocantins, rodovia TO-050, km 375, fazenda São José, próximo do rio Santa Isabel, 11 May 2000, G. Hatschbach et al. 70903 (MBM); Gurupi, próximo à Gurupi, 20 Apr 1978, R.P. Orlandi 73 (HRB, RB).

Distribution and habitat. *Murdannia gardneri* is endemic to Brazil, being known from the states of Bahia, Goiás, Mato Grosso, Minas Gerais and Tocantins (Fig. 10). It grows in open sandy river banks or flooded grass fields, of the Cerrado domain.

Phenology. It was found in bloom and fruit throughout the year.

Conservation status. *Murdannia gardneri* possesses a EOO of ca. 497,658.992 km² and a AOO of ca. 20,000.000 km². Most of the known collections are concentrated in central Brazil, where the native vegetation is commonly removed to give place to livestock. This is especially common in the Cerrado domain, due to its savanna vegetation being easier to remove than the dense rainforests of the Amazon and Atlantic Forest domains. Thus, we believe that *M. gardneri* should be considered Nearly Threatened.

Nomenclatural notes. When describing *Aneilema gardneri*, Seubert (1855) lists two collections from G. Gardner (4020 and 4021). As aforementioned, *Gardner* 4020 consists of a mixture of *M. burchellii* and *M. gardneri*. Fortunately, the same is not true for *Gardner* 4021. Furthermore, the *Gardner* 4020 specimen at P was designated by us as the lectotype for *A. gardnei* var. *glabrior*. Thus, we designate a specimen at K as the lectotype for *A. gardneri*.

Discussion. Murdannia gardneri is morphologically similar to M. burchellii and M. paraguayensis due to their phyllotaxy and by the number of cincinni per inflorescence. It is morphologically more similar to M. burchellii due to the posture of the pedicels at postanthesis and when fruiting, general floral and capsule morphology, and due to the hilum being positioned in a deep depression. Nevertheless, both species can be easily differentiated based on the insertion of the cincinni in the main axis of the inflorescence (alternate to subopposite in M. burchellii vs. verticillate in M. gardneri), the ornamentation of the testa (costate to slightly rugose vs. scrobiculate to foveolate), robustness of the plants (delicate vs. robust, branching pattern (densely branched at base vs. unbranched to little-branched), leaf-blade consistency (chartaceous vs. succulent), and some indumentum differences. On the other hand, M. paraguayensis can be readily differentiated from M. gardneri by its 1-flowered cincinni (vs. many-flowered in M. gardneri), deflexed pedicels post-anthesis and when fruiting (vs. erect), filaments with minute glandular hairs (vs. glabrous), gynoecium and capsules with glandular hairs (vs. glabrous), capsule oblongoid to broadly oblongoid (vs. subglobose to globose), locules 2-seeded (vs. 1-seeded), and hilum in a shallow depression (vs. in a deep depression) (Table 1).

4. *Murdannia nudiflora* (**L.**) **Brenan**, Kew Bull. 7(2): 189. 1952. Fig 5

Phaeneilema nudiflorum (L.) G.Brückn., Notizbl. Bot. Gart. Berlin-Dahlem 10 (91): 56. 1927.

Ditelesia nudiflora (L.) Raf., Fl. Tellur. 3: 69. 1837.

Aneilema nudiflorum (L.) R.Br., Prodromus Florae Novae Hollandiae: 271. 1810.

Commelina nudiflora L., Sp. Pl. 1: 41. 1753. Lectotype (designated by Merrill 1937): INDIA. s.loc., fl., fr., s.dat., P. Osbeck s.n. (LINN barcode LINN-HL65-12!).

Diagnosis. Herbs annual, with a definite base, terrestrial to paludal to rooted emergent in flooded fields. Roots thin, fibrous, brown, densely to sparsely pilose, emerging from the basal most nodes. Rhizomes absent. Stems prostrate, erect to ascending apex, unbranched or branched at the base, glabrous. Leaves distichously-alternate, distributed along the stems, rarely 1–2 congested at base, the distal ones gradually smaller than the basal ones; lamina membranous, conduplicate, linear to linear-lanceolate or lanceolate-oblong, glabrous or with eglandular hairs. Inflorescences 1-(2), terminal or axillary from the uppermost node, longpedunculate, exerted from the leaf-sheaths, consisting of a solitary cincinnus; basal bract inconspicuous; cincinni bracts cup-shaped; cincinni 2–12-flowered, pendent, bracteoles cupshaped, caducous. Flowers bisexual or male, zygomorphic due to the position of the lateral petals; pedicels erect and elongate in fruit; sepals ovate-elliptic to ovate-triangular, cucullate, glabrous; petals subequal, obovate to spatulate to obtrullate, slightly cucullate, pale lilac to purple or mauve, glabrous; stamens 2 (opposite to the lower petals), equal, filaments gently sigmoid, closely parallel to each other, white at the base, lilac at the middle, purple at the apex, densely bearded with moniliform, purple hairs, anthers elliptic to oblong, connective bluish lilac to white, anthers sacs purple to dark purple, pollen white; staminodes 4, 1 staminode antesepalous, opposite to the lower sepal, filament white to lilac, medially bearded with moniliform, purple hairs, antherode small, white, sometimes lacking, 3 antepetalous, filaments straight, pale lilac to white, glabrous or sparsely medially bearded with moniliform, purple hairs, antherodes hastate, white to cream; ovary ellipsoid to oblongoid, 3-locular, light green smooth, glabrous, style strongly curved at the apex, white to pale lilac, glabrous, stigma capitate, lilac. Capsules 3-locular, 3-valved, ovoid to subglobose, apiculate due to persistent style, light brown when mature, smooth, glabrous. Seeds 2 per locule, broadly ellipsoid to oblongoid, not cleft towards the embryotega, ventrally ridged, testa yellowish brown to brown, foveolate-reticulate, with pale warts around depressions, farinose, appendage absent; embryotega semilateral, relatively inconspicuous, without a prominent apicule; hilum elliptic, approximately ½ the length of the seed, on a weak ridge.

Distribution and habitat. Native to Tropical Asia to Malaysia and naturalized in West Africa, North America, Mexico, Central America, the West Indies and South America; in the New World ranging from the southeastern United States to Argentina. In Brazil it is known to occur in the states of Acre, Alagoas, Amazonas, Bahia, Ceará, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo and Tocantins, in disturbed vegetation, roadsides and near rice crops.

Phenology. It was found in bloom and fruit throughout the year.

Discussion. *Murdannia nudiflora* can be easily recognized by its caduceus bracteoles, single terminal cincinni, two fertile stamens and four staminodes, and capsules with 2-seeded locules (Table 1).

5. *Murdannia paraguayensis* (C.B.Clarke *ex* Chodat) G.Brückn., Nat. Pflanzenfam. (ed. 2)15a: 173. 1930.

Figs 6 & 10

Phaeneilema paraguayensis (C.B.Clarke ex Chodat) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10 (91): 56. 1927.

Aneilema paraguayense C.B.Clarke ex Chodat, Bull. Herb. Boissier, sér. 2, 1: 437. 1901. Lectotype (designated here): PARAGUAY. Departamento de Canindeyú: Sierra de Maracayú, fl., fr., Oct 1898–1899, E. Hassler 5083 (G barcode G00195432!; isolectotypes: BM barcode BM000526690!; G barcode G00009034!, NY barcode NY00247403!).

Description. Herbs ca. 20.0–150.0 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in flooded fields. Roots thin, rarely thick, fibrous, medium to dark brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the short rhizome and from the basalmost nodes. Rhizomes short, light to medium brown, buried in the sand or ground. Stems prostrate, with erect to ascending apex, succulent, unbranched or only branched at the base; internodes 3.4–13.0 cm long, green to vinaceous, glabrous to sparsely pilose, becoming glabrous with age, with a line of eglandular hyaline hairs opposite the leaf above. Leaves spirally-alternate, sometimes becoming distichouslyalternate at apex, evenly distributed along the stems, the distal ones gradually smaller than the basal ones; sheaths 1.2-3.3 cm long, green to vinaceous, glabrous to pilose along the fused edge, sometimes with a few scattered long, glandular hairs, margins ciliate to sparsely setose at base, hairs hyaline; lamina $2.5-23.6 \times 0.4-1.2$ cm, succulent, canaliculate, slightly falcate to falcate, green on both sides, drying light brown to olive-green or light green on both sides, linear-lanceolate to linear-elliptic or linear-oblong, glabrous, base truncate to rounded, margins light green to pink or vinaceous, ciliate to sparsely setose only at base, apex acute to acuminate; midvein conspicuous or inconspicuous, slightly impressed adaxially, slightly obtuse abaxially, secondary veins 2-3(-4) pairs, adaxially inconspicuous or slightly conspicuous, light green, abaxially slightly conspicuous. Inflorescences 1-(2), thyrsi, terminal or axillary from the uppermost node, thyrse with 9–24 verticillate cincinni, arranged in 3–9 whorls; peduncles 1.2-7.5 cm, with glandular to densely glandular, hyaline hairs; basal bract leaf-like, 2.1-3.2 × 0.9-1.2 cm, lanceolate, glabrous, base rounded, margins ciliate to setose only at base, apex acute to acuminate, veins inconspicuous or slightly conspicuous, concolorous to light green; cincinni bracts ca. 1.4-5.1-(10.0) × 1.0-1.6 mm, lanceolate to ovate, light green to pink or vinaceous, glandular-pubescent to glabrous, base truncate, margins glabrous, sometimes with a tooth at the base in each side, apex acute; cincinni 1flowered, patent to erect, straight, peduncle inconspicuous, internodes absent; bracteoles ca. 0.8–1.2 × 0.3–0.6 mm, persistent, triangular, flat, light green to pink, glabrous, base truncate, margins glabrous, apex acute. Flowers bisexual or male, enantiostylous, ca. 1.3–2.5 cm diam.; floral buds narrowly ovoid, 5.3–6.2 × 2.6–3.2 mm, light green to pink; pedicels 1.0–5.2 mm long, light green to pink or vinaceous, with glandular to densely glandular, hyaline hairs, deflexed and elongate in fruit; sepals 5.3–8.0 × 1.8–4.7 mm, triangular to ovate-triangular, cucullate, light green to pink to vinaceous, with glandular to densely glandular, hyaline hairs, apex acuminate, margins hyaline light green to hyaline pink or vinaceous; petals equal, 0.8- 1.3×0.5 –0.7 cm, obovate to narrowly obovate, slightly cucullate, white to lilac to purple or mauve, with minute glandular hairs at base on the adaxial surface, base cuneate, margins entire to erose at the apex, apex acute to obtuse; stamens 3, equal, filaments gently curved at the apex, 6.0–9.6 mm long, pale lilac to lilac or purple, with minute glandular, hyaline hairs,

anthers elliptic to oblong, $0.9-2.0 \times 0.4-0.7$ mm, connective purple to bluish purple, anthers sacs lilac to purple, pollen white; staminodes 3, equal, filaments straight, 3.1-5.3 mm long, pale lilac to white, with minute glandular, hyaline hairs, antherodes sagittate, $0.8-2.3 \times 0.8-1.1$ mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to oblongoid, $1.5-3.5 \times 0.7-1.3$ mm, 3-locular, light green to green, smooth, with densely glandular, hyaline hairs, style gently curved at the apex, ca. 3.5-8.0 mm, pale lilac to lilac, with minute glandular, hyaline hairs, stigma capitate, lilac to purple. *Capsules* $5.1-9.8 \times 3.2-5.0$ mm, 3-locular, 3-valved; oblongoid to broadly oblongoid, apiculate due to persistent style, light brown when mature, smooth, with sparse glandular, hyaline hairs, sometimes becoming glabrous with age. *Seeds* 2 per locule, $3.4-4.2 \times 1.7-2.1$ mm, reniform to broadly ellipsoid, strongly cleft towards the embryotega, ventrally flattened, testa dark brown to greyish brown, sparsely farinose, scrobiculate, with ridges radiating from the embryotega, with a tan appendage that extends ventri-laterally to the embryotega and basally into the hilum; embryotega semilateral, relatively inconspicuous, without a prominent apicule; hilum linear, approximately the same length as the seed, in a shallow depression.

Specimens seen. BRAZIL. Distrito Federal: Brasília, immediately N of Brasília, rio Torto, 18 Sep 1965, H.S. Irwin et al. 8425 (NY, RB, US); Mato Grosso: Santa Cruz Do Xingu, Parque Estadual do Xingu, limite norte do parque, 6 Mar 2011, D.C. Zappi et al. 3166 (K, RB, UNEMAT); São Félix do Araguaia, estrada entre a vila Pontinópolis e a Serra dos Magalhães, 21 Mar 1997, V.C. Souza et al. 14814 (ESA, RB); Sinop, estrada para Porto dos Gaúchos, ca. 500 km leste do rio Teles Pires, 22 Oct 2004, V.C. Souza 30056 (ESA); Xavantina, Camp B of Base Camp, 10 Jan 1968, D. Philcox & A. Ferreira 3958 (K); loc. cit., 10 km E from base, ca. 270 km from Xavantina, 6 Mar 1968, fl, D.R. Gifford RG76 (K); loc. cit., s.dat., fl., fr., G.R.D. Smith 43 (K); loc. cit., Oct-Nov 1967, fl., J. Ramos & R. Sousa R7 S30 (K); loc. cit., 1 km S of base camp, 14 Mar 1968, D. Philcox & A. Ferreira 4539 (K, NY, P, UB); loc. cit., Xavantina-Cachimbo road, 1 km E of km 244, 15 Mar 1968, D. Philcox & A. Ferreira 4550 (K, NY, P, RB, UB); loc. cit., close to the Xavantina-São Félix do Araguaia road, 11 Apr 1968, J.A. Ratter et al. 992 (K, NY, P, UB); loc. cit., córrego do Porco, 240 km N of Xavantina, 7 May 1968, J.A. Ratter et al. 1339 (K, NY, P, RB, UB); loc. cit., 5 Oct 1968, R.M. Harley 10489 (K, NY, P, RB, UB); loc. cit., 10 Oct 1968, R.M. Harley et al. 10591 (K, NY, P, RB); loc. cit., arredores do acampamento da expedição inglesa até o córrego do Surucucu, 10 Oct 1968, Sidney & Onishi 1356 (RB, UB); Mato Grosso do Sul: Indaiá do Sul/Chapéu Azul, cachoeira aos fundos da cidade, 18 Feb 1996, M.R. Pietrobom da Silva et al. 2923 (MBM); Sidrolândia, fazenda Olho D'água, km 392 da Estrada Campo Grande-Sidrolândia, 19 Apr 2013, S.N. Moreira et al. 1451 (BHCB); Minas Gerais: Araxá, próximo a Araxá, vale do rio Araguarí, 1 Nov 1970, A.P. Duarte 13912 (HB, MBM). PARAGUAY. Amambay: Sierra de Amambay, April 1912–1913, E. Hassler 11347 (BM, K, P).

Distribution and habitat. *Murdannia paraguayensis* occurs in Paraguay and central Brazil, being known from the states of Distrito Federal, Goiás, Mato Grosso, Mato Grosso do Sul and Minas Gerais (Fig. 10). It grows in open flooded grass fields, of the Amazon, Cerrado, Chaco and Pantanal domains.

Phenology. It was found in bloom and fruit throughout the year.

Conservation status. *Murdannia paraguayensis* possesses one of the widest distribution ranges among Neotropical *Murdannia*, with a EOO of ca. 886,876.606 km² and a AOO of ca. 22,500.000 km². Thus, following the IUCN recommendations (IUCN 2001), *M. paraguayensis* should be considered Least Concern.

Nomenclatural notes. When describing *Aneilema paraguayensis*, Chodat (1901) only mentions "Ipé-hu, Oct., 5083", at the end of his brief diagnosis. According to Stafleu & Cowan (1979), Hassler's Paraguayan collections are generally housed at G. After consulting several herbaria, we found a specimen at NY herbarium, two specimens at G, and one at BM that matched the protologue. Thus, we selected as the lectotype the specimen at G which shows the typical deflexed pedicel characteristic of this species.

Discussion. Murdannia paraguayensis has been historically confused with M. gardneri s.l., due to the verticillate cincinni in the inflorescence. For differences between M. burchellii, M. gardneri and M. paraguayensis, see the comments on those species above and Table 1. Despite this historic confusion, M. paraguayensis is morphologically very similar to M. engelsii, due to its petals, androecium and gynoecium with glandular hairs, pedicels deflexed postanthesis and in fruit, and capitate stigma. Nevertheless, M. paraguayensis can be differentiated by its erect habit (vs. trailing in M. engelsii), leaves spirally-alternate (vs. distichously-alternate), much larger inflorescences with several whorls of cincinni (vs. consisting of a solitary cincinnus), peduncle solely with glandular hairs (vs. with a mixture of eglandular and glandular hairs), cincinni 1-flowered (vs. 2–7-flowered), capsules oblongoid to broadly oblongoid (vs. broadly ovoid to broadly ellipsoid), and locules 2-seeded (vs. locules 1-seeded).

The specimen *H.S. Irwin et al.* 8425 looks very distinctive from the other analyzed specimens due to its: apparently creeping habit, leaves distichously-alternate at apex, sheaths with a few scattered long glandular hairs, blades with strongly undulate margins, short congested inflorescence, and very short pedicels. Nevertheless, it possesses the same inflorescence architecture, capsules with glandular hairs, and seeds 2-locules. We believe that the blades with strongly undulate margins may be a result of the drying process. Thus, we consider that these collections don't merit any taxonomic recognition.

6. *Murdannia schomburgkiana* (Kunth) G.Brückn., Nat. Pflanzenfam. (ed. 2)15a: 173. 1930.

Figs 7 & 10

Phaeneilema schomburgkiana (Kunth) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10 (91): 56. 1927.

Aneilema schomburgkianum Kunth, Enum. Pl. 4: 661. 1843. Lectotype (designated here): GUYANA. s.loc., fl., fr., Oct 1841, R.H. Schomburgk 842 (B barcode B100367820!; isolectotypes: 2 ex BM not found, G barcodes G00176335!, G00176336!, G00176337!, P barcodes P02088026!, P02088027!, TCD barcode TCD0008088!).

Description. Herbs ca. 30.0–65.0 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in open flooded savannas. Roots tuberous, thick and fusiform, medium to dark brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the short rhizome and from the basal nodes. Rhizomes short, brown, buried in the sand or soil. Stems erect, succulent, unbranched; internodes 1.0–11.5 cm long, green to vinaceous, glabrous, sometimes with a line of hyaline eglandular hairs opposite the leaf above. Leaves spirally-alternate, evenly distributed along the stems, sessile, the distal ones gradually smaller than the basal ones; sheaths 0.8-2.2 cm long, green to vinaceous, glabrous, with a line of hyaline, eglandular hairs opposite the leaf above; lamina $2.2-14 \times 0.4-1.0$ cm, membranous to succulent, canaliculate, slightly falcate, green on both sides, glaucous, drying olive-green to light green on both sides, linear-elliptic to linear-lanceolate, glabrous, base

truncate to rounded, margins light green, glabrous, apex acuminate; midvein slightly conspicuous to inconspicuous, slightly impressed adaxially, slightly obtuse abaxially. secondary veins 2–3–(4) pairs, adaxially inconspicuous to slightly conspicuous, light green, abaxially slightly conspicuous. Inflorescences 1-4, terminal or axillary in the uppermost nodes, fascicle-like, composed of 1–2–(3) verticillate cincinni; peduncles absent; basal bract inconspicuous; cincinni bracts 1.6–1.8 × 0.3–0.4 cm, tubular, amplexicaul; cincinni 1flowered, erect, straight, peduncle 1.0–1.9 cm long, light green to pink or vinaceous, glabrous; bracteoles inconspicuous, generally caducous. Flowers bisexual or male, actinomorphic, ca. 1.3–2.3 cm diam.; floral buds ellipsoid, $5.0–5.8 \times 1.5–1.8$ mm, light green to pink; pedicels 0.6-1.1 cm long, light green to pink to vinaceous, glabrous, erect and elongate in fruit; sepals 6.5–10.0 × 3.2–4.1 mm, triangular to ovate-triangular, cucullate, pink to pinkish brown, glabrous, apex acute, margins hyaline pink to hyaline vinaceous; petals equal, $0.8-1.3 \times 0.8-$ 1.0 cm, obovate to broadly obovate, slightly cucullate, lilac to purple, medially bearded with lilac to purple, moniliform hairs on the adaxial surface, base cuneate, margins entire, apex acute to obtuse; stamens 3, equal, filaments gently curved at the apex, 4.4–5.2 mm long, lilac to purple, densely bearded with moniliform, lilac to purple hairs, hairs slightly shorter than the filaments, anthers elliptic to oblong, $1.7-2.4 \times 0.6-1.0$ mm, connective brown, anthers sacs brownish lilac, pollen brownish lilac; staminodes 3, equal, filaments straight, 4.1–5.0 mm long, pale lilac to lilac, densely bearded with moniliform, lilac to purple hairs, hairs slightly shorter than the filaments, antherodes hastate, $0.9-1.7 \times 1.3-1.7$ mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to oblongoid, 1.9- $3.1 \times 0.7 - 1.3$ mm, 3-locular, light green to green, smooth, glabrous, style gently curved at the apex, ca. 4.1–5.4 mm, lilac to purple, stigma capitate, lilac to purple. Capsules 5.9–8.5 × 2.8– 4.6 mm, 3-locular, 3-valved, oblongoid to broadly oblongoid, apiculate due to persistent style. light brown when mature, smooth, glabrous. Seeds (immature) 6 per locule, $2.7-3.3 \times 2.6-3.1$ mm, cuboid to polygonal, slightly cleft towards the embryotega, testa dark brown to greyish brown, densely farinose, scrobiculate, with ridges radiating from the embryotega; embryotega semilateral, relatively inconspicuous, without a prominent apicule, generally covered by a cream farina; hilum linear, ½ the length of the seed or smaller, on a weak ridge.

Specimens seen. BRAZIL. Amazonas: Provincia do Rio Negro, Rio Madeira, fl., s.dat., s.leg. s.n. (P barcode P03653202); s.loc., fl., Oct 1894, A.R. Ferreira 755 (K). **GUYANA. Rupununi District:** foot of Mount Shiriri, fl., 19 Jun 1995, M.J. Jansen-Jacobs et al. 4175 (P, U, US); loc. cit., Manari, Takatu river, fl., 5 Aug 1995, M.J. Jansen-Jacobs et al. 4764 (U, US); loc. cit., upper Rupununi river, fl., *Appun 2361* (K).

Distribution and habitat. *Murdannia schomburgkiana* is known from only four collections from Guyana (including the type) and perhaps only one collection from Brazil (in the state of Amazonas) (Fig. 10). It grows in open flooded grass fields and savannas in the Amazon domain. The distance between the Rio Madeira specimen and the other specimens collected in Guyana, make clear how poorly collected this species is. It is widely possible that field trips focusing on the group or in the white sand formations in the state of Amazonas will fill this distribution gap.

It is interesting to highlight that both specimens from Brazil might represent different sheets of the same collection. Firstly, it is known that Dr. Alexandre Ferreira collected exclusively in Brazilian territory. Thus, despite the locality not being clearly stated in the label of the specimen at Kew, this is the only possible option. Secondly, the specimen at Paris was collected in Brazil, Provincia Rio Negro, at the margins of Rio Madeira (currently state of Amazonas). This was one of the most important areas collected by Ferreira, during his philosophical travels, and probably the longest part of this fieldtrip. Also, it is widely known

that many specimens collected by Friar Vellozo, Dr. Vellozo de Miranda and Dr. Alexandre Ferreira, were taken from Lisbon to Paris, during the Napoleonic Wars. Finally, the labels of both specimens possess complementary information, where the locality in the label of the Paris' specimen is one of locations where Ferreira collected, and the date is congruent with this specific fieldtrip. Moreover, the specimens on both sheets are very similar in appearance.

Phenology. It was found in bloom from June to October, and in fruit in October.

Conservation status. *Murdannia schomburgkiana* is only known from five (or at most six) collections, including the type species. Furthermore, the last known collections for this species are 11 years old, and the AOO of *M. schomburgkiana* is of only ca. 12.000 km². Following the IUCN recommendations (IUCN 2001), *M. schomburgkiana* should be considered Endangered [EN, B1a+C2a(ii)+D1].

Nomenclatural notes. When describing *Aneilema schomburgkiana*, Kunth (1843) mentions "Rob. Schomburgk misit sub. no. 842". According to Stafleu & Cowan (1985), Robert Schomburgk's collections are generally housed at BM or K. Despite having found two specimens at BM, the specimen at B (B100367820) possesses the annotation "Ex. herb. Kunth misit. 1841.", made in Kunth's handwriting and matching the protologue, and it is widely known that Kunth's herbarium was part of B (Stafleu & Cowan 1979). Thus, it was the obvious choice for a lectotype. The two sheets at BM were observed and described in detail by one of us (RBF) in 1993. However, they were not photographed when other types at BM were photographed, and the specimens cannot currently be located. If found they should be treated as isolectotypes.

Discussion. Murdannia schomburgkiana can be easily confused with M. semifoliata (C.B.Clarke) G.Brückn., due to their tuberous roots, reduced inflorescences enclosed by the leaf-sheaths, cincinni bracts tubular, petals medially bearded with moniliform hairs on the adaxial surface, filaments densely bearded with moniliform hairs, the number of seeds per locule of the capsule, and seed morphology. Their petals medially bearded with moniliform hairs on the adaxial surface, are quite unique within Murdannia. As aforementioned, this character is otherwise only known in Commelinaceae in M. simplex (in which the hairs are tiny and only present at the petal, being fundamentally different), and in the distantly related genera Cochliostema Lem. and Geogenanthus Ule (Tribe Tradescantieae, subtribe Dichorisandrinae; Hardy & Faden 2004; Pellegrini in press). Nevertheless, the distribution of both species does not overlap and they grow in different environments (white sand formations vs. flooded grass fields). Murdannia schomburgkiana can be differentiated by its 2.2–13.6 cm long blades of the leaves bearing inflorescences (vs. 0.2–1.8 cm long), leaf-blades margins glabrous (vs. ciliate), cincinni bracts 1.6–1.8 cm long (vs. 0.4–1.3 cm long), and brown anthers (vs. purple) (Table 1).

Despite the few collections known for this species, it is the authors' opinion that the morphological, geographical and environmental factors are enough to differentiate both species. *Murdannia schomburgkiana* and *M. semifoliata* are very similar to each other, and quite distinct from the remaining Neotropical species of the genus. They are morphologically similar to some Asian and African species with fascicle-like, mainly axillary inflorescences, and 1-flowered cincinni, such as *M. axillaris* and *M. triquetra*.

7. Murdannia semifoliata (C.B.Clarke) G.Brückn., Nat. Pflanzenfam. (ed. 2)15a: 173. 1930.

Figs 8 & 10

Phaeneilema semifoliata (C.B.Clarke) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10 (91): 56. 1927.

Aneilema semifoliatum C.B.Clarke, C.B.Clarke in Moore, Trans. Linn. Soc. London, Bot. 4: 498. 1895. Lectotype (designated here): BRAZIL. Mato Grosso: Santa Cruz [do Xingú], fl., Oct 1891–1892, S.M. Moore 541 (BM barcode BM000938202!; isolectotypes: B barcode B100367821!, NY barcode NY00247404!).

Description. Herbs ca. 20.0–70.0 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal to rooted emergent in open flooded fields. Roots tuberous, thick and fusiform, medium to dark brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the short rhizome and from the basal nodes. *Rhizomes* short, brown, buried in the sand or soil. Stems erect, succulent, unbranched; internodes 1.2–13.3 cm long, green to vinaceous, glabrous, with a line of hyaline, eglandular hairs opposite to the leaf above. Leaves spirally-alternate, evenly distributed along the stems, the distal ones much smaller than the basal ones (which are generally bladeless sheaths with lamina no longer than 1.8 cm); sheaths 0.5-2.3 cm long, green to vinaceous, glabrous, with a line of hyaline, eglandular hairs opposite to the leaf above, margins setose to ciliate; lamina $0.2-8.9 \times 0.2-0.7$ cm, succulent, canaliculate, slightly falcate, green on both sides, glaucous, drying olive-green on both sides, linear-triangular to triangular, glabrous, base truncate, margins light green, setose at the base, ciliate at the middle, glabrous at the apex, apex acuminate; midvein inconspicuous on both sides, rarely slightly obtuse abaxially, secondary veins inconspicuous. *Inflorescences* (1–)2–6, terminal and axillary from the uppermost nodes, fascicle-like, composed of 1-2-(3) verticillate cincinni; peduncles absent; basal bract inconspicuous; cincinni bracts 0.4–1.3 × 0.1-0.3 cm, tubular, amplexicaul; cincinni 1-flowered, erect, straight, peduncle 0.8-4.2 mm long, light green to pink to vinaceous, glabrous, internodes inconspicuous; bracteoles inconspicuous, generally caducous. Flowers bisexual or male, actinomorphic, ca. 0.6–2.3 cm diam.; floral buds ellipsoid, 4.9–7.2 × 1.7–2.2 mm, light green to pink; pedicels 1.4–1.1 mm long, light green to pink to vinaceous, glabrous, erect and elongate in fruit; sepals 4.8–8.0 × 1.8–3.3 mm, triangular to ovate-triangular, cucullate, pink to pinkish brown, glabrous, apex acute, margins hyaline pink to hyaline vinaceous; petals equal, $0.5-1.2 \times 0.3-0.8$ cm, obovate, slightly cucullate, lilac to purple or mauve, rarely white, medially bearded with moniliform hairs on the adaxial surface, hairs lilac to purple, base cuneate, margins entire, apex acute to obtuse; stamens 3, equal, filaments gently curved at the apex, 3.2-5.0 mm long, lilac to purple, densely bearded with moniliform, lilac to purple hairs, hairs slightly shorter than the filaments, anthers linear-oblong to oblong, $2.0-3.5 \times 0.4-0.7$ mm, connective purple, anthers sacs lilac to purple, pollen lilac; staminodes 3, equal, filaments straight, 3.1–4.3 mm long, pale lilac to lilac, densely bearded with moniliform, lilac to purple hairs, hairs slightly shorter than the filaments, antherodes hastate, $0.7-2.0 \times 0.5-1.2$ mm, connective golden yellow, lobes conspicuous, cream-colored to pale yellow; ovary ellipsoid to oblongoid, 1.5–3.3 × 0.5–1.0 mm, 3-locular, light green to green, smooth, glabrous, style gently curved at the apex, ca. 3.2– 4.5 mm, lilac to purple, stigma capitate, lilac to purple. Capsules 5.8–1.2 × 3.3–5.6 mm, 3locular, 3-valved; oblongoid to broadly oblongoid, apiculate due to persistent style, light brown when mature, smooth, glabrous. Seeds 6 per locule, 2.2-3.1 × 2.0-2.8 mm, cuboid to polygonal, slightly cleft towards the embryotega, testa dark brown to greyish brown, densely farinose, scrobiculate, with ridges radiating from the embryotega; embryotega semilateral, relatively inconspicuous, without a prominent apicule, generally covered by a cream farina; hilum linear, less than ½ the length of the seed, on a weak ridge.

Specimens seen. BOLIVIA. Santa Cruz: San Ignacio de Velasco, Oct 1958, M. Cardenas 5629 (BOLV, US). BRAZIL. Mato Grosso: Bananalzinho, Nov 1914, J.G. Kuhlmann 89 (R, SP); Braco, rio Arinos, 26 Sep 1943, J.T. Baldwin Jr. 3097 (US); Cuiabá, entre Cuiabá e Goyaz, Nov-Dec 1844, M.A. Weddell 3018 (P); loc. cit., rodovia MT-364, 35 km S de Cuiabá, 13 Nov 1975, G. Hatschbach 37491 (K, MBM); Nova Olímpia, Chapada dos Guimarães, 10 Oct 1995, J.H.A. Dutilh 199 (UEC); Poconé, 50 km S of Poconé on Transpantaneira highway to Porto Jofre, 27 Oct 1985, W. Thomas et al. 4641 (INPA, NY, US); loc. cit., highway Poconé-Porto Cercado, ca. km 21, 17 Feb 1992, M. Schessl 100/1-10 (UFMT, US); loc. cit., about 21 km S of Poconé, 7 Oct 1992, M. Schessl 071092-1-1 (UFMT, US); loc. cit., fazenda Ronco Bugiu, ca. 6-8 km à esquerda da rodovia Transpantaneira Poconé-P. Jofre, km 36, 31 Oct 1992, A.L. Prado et al. 3218 (HURB, UEC, UFMT); loc. cit., 22 Nov 1992, A.L. Prado et al. 2736 (HURB, UEC, UFMT); Rosário Oeste, ca. 2 km de Marzagão em direção à Planalto da Serra, 7 Oct 1997, V.C. Souza et al. 20255 (ESA, UFMT, UEC); Santo Antônio de Leverger, Barão do Melaço, km 30 of Leverger highway, 5 Nov 1991, M. Schessl 2421 (CH, UFMT, US); Mato Grosso do Sul: Aquidauana, entre as fazendas São Salvador e Costa Rica, 19 Nov 1995, A. Pott et al. 7628 (CGMS, CPAP, US); loc. cit., rodovia Taunay, fazenda Santa Cruz, próximo da aldeia indígena Ipegue, 20 Nov 2002, G. Hatschbach et al. 74377 (MBM).

Distribution and habitat. *Murdannia semifoliata* occurs mainly in Brazil (in the states of Mato Grosso and Mato Grosso do Sul) and in Bolivia (Fig. 10). It grows in open flooded grass fields in the Amazon, Cerrado and Chaco domains.

Phenology. It was found in bloom and fruit from September to February.

Conservation status. Murdannia semifoliata possesses a EOO of ca. 298,091.226 km² and a AOO of ca. 22,500.000 km². Despite the relatively great number of collections, most of them are in the state of Mato Grosso, with only one known collection on the state of Mato Grosso do Sul and another one from Bolivia. This whole region is under great treat due to the constant deforestation for cattle ranching. Thus, we believe that following the IUCN recommendations (IUCN 2001), M. semifoliata should be considered Nearly Threatened.

Nomenclatural notes. When describing *Aneilema semifoliatum*, Clarke (1895) mentions "Crescit ad Santa Cruz, ubi mens. Oct. floret. (N. 541)". The specimen at BM matched the protologue perfectly. Furthermore, it possesses a detailed description and was identified by Clark himself. Thus, it is here designated as the lectotype of *A. semifoliatum*.

Discussion. Murdannia semifoliata, as aforementioned, is morphologically similar to M. schomburgkiana. They share a peculiar vegetative morphology, inflorescence architecture, and petals medially bearded with moniliform hairs on the adaxial surface, not similar to any other Neotropical species. Murdannia semifoliata is especially distinctive due to its extremely reduced blades of the leaves bearing inflorescences, produced during the flowering period (Table 1). In most individuals, the blades are so reduced that the whole plant seems to be aphyllous. Furthermore, M. semifoliata and M. schomburgkiana are the only Neotropical species to possess more than two seeds per locule, which gives the seeds a peculiar cuboid to polygonal shape.

8. Murdannia aff. triquetra (Wall. ex C.B.Clarke) G.Brückn., Nat. Pfl.-Syst. (ed. 2) 15a: 173. 1930.

Fig 9

Phaeneilema triquetrum (Wall. *ex* C.B.Clarke) G.Brückn., Notizbl. Bot. Gart. Berlin–Dahlem 10: 56. 1927.

Aneilema triquetra Wall. ex C.B.Clarke, Monogr. Phan. 3: 208. 1881. Lectotype (designated by Ancy et al. 2015): BANGLADESH. India Orientalis, in Prov. Sylhet, fl., fr., s.dat., N. Wallich 5220 (B barcode B100367814!: isolectotypes: E barcode E00393352!, GDC barcode GDC00489348!; K n.v.).

Diagnosis. Herbs ca. 10.0–20.0 cm tall, annual, without a definite base, rooted emergent in flooded fields. Roots thin, fibrous, medium to dark brown, densely to sparsely pilose with medium to dark brown hairs, emerging from the basalmost nodes. Rhizomes absent. Stems trailing, floating on water with ascending apex, succulent, densely branched at the base, glabrous or with minute eglandular hairs. Leaves spirally-alternate, evenly distributed along the stems; sheaths 0.7–1.0 cm long, glabrous; lamina $2.0-4.5 \times 0.6$ cm, narrowly lanceolate to lanceolate-oblong, glabrous membranous, slightly canaliculate, green on both sides, base rounded to amplexicaul, margins glabrous, sometimes undulate, apex acute to acuminate. Inflorescences 1-3, terminal or axillary in the distalmost (up to 4) nodes, fascicle-like, sessile, enclosed by the leaf-sheaths, composed of 1–2–(3) verticillate cincinni; peduncle absent; basal bract inconspicuous; cincinni bracts absent; cincinni 1-flowered, erect, straight, peduncle ca. 3.0 mm long, glabrous, internodes inconspicuous; bracteoles absent. Flowers male or bisexual, actinomorphic, barely exserted from the sheath; floral buds ellipsoid, light green; pedicels ca. 3 mm long, erect and elongate in fruit; sepals 4.0-5.5 mm long, linear-elliptic, cucullate, light green to pale pink, glabrous; petals equal, elliptic, slightly cucullate, white to pale lilac or pale pink, glabrous; androecium not determinable; ovary ellipsoid, tapering into the style, 3-locular, light green, smooth, glabrous, style straight, 1.7 mm long, glabrous, stigma capitate. Capsules 4.5–5.5 × 2.0–2.5 mm, oblongoid to ellipsoid, 3-locular, 3-valved, apiculate due to persistent style, light brown when mature, smooth, glabrous, locules 3-seeded (only 1 counted). Seeds (only 1 mature seed seen) transversely ellipsoid, ca. 1.5×0.9 mm, testa brown, with deep dorsal pits and longitudinal furrows, farinose only around the embryotega, appendage absent; embryotega lateral, inconspicuous, without a prominent apicule; hilum linear, less than ½ the length of the seed, borne on a ridge.

Specimen seen. VENEZUELA. Tachira. Distr. Liberatador: 10 km S of El Piñal, 71° 55' W, 7° 27' N, alt. 250 m, 7 Nov. 1982, G. Davidse & A. C. González 21663 (US).

Distribution and habitat. Known for certain only from this collection. The general habitat was recorded as "partially inundated forest remnant with slow stream and pools of standing water" and for this collection as "stems floating in pool of creek." A photograph of a plant from Colombia, which may or may not be the same species, was sent to the first author, but without a corroborating specimen, so it has not been considered for this description. However, we have illustrated it in Fig. 9 to encourage collectors to look for it.

The *M. keisak* complex is widespread in Asia, ranging from India to China and Japan, growing in flooded grasslands and disturbed areas. In South America, it is known from only two collections, one from Venezuela and one from Colombia. Unfortunately, it seems that the specimen from Colombia went astray during shipping, since it was never received by the first author.

Phenology. It was found in bloom and fruit in November.

Conservation status. Following the IUCN recommendations (IUCN 2001), this species should be considered Data Deficient. Correspondence by the second author with the collector Gerrit Davidse, indicated that this was not a disturbed habitat in which one would expect to find introduced weeds. However, the habitat was under great pressure and possibly no longer exists.

Nomenclatural notes. Nandikar & Gurav (2015) designated the specimen at CAL (CAL0000025807) as the lectotype for *A. triquetrum*. Nevertheless, after analyzing the specimen, comparing it to the protologue and to the remaining specimens, it became clear that the specimen at CAL is not conspecific to the specimens at B, E and GDC. Ancy *et al.* (2015), unaware of the article published just few months earlier by Nandikar & Gurav (2015), designate the specimen at B (B100367814) as the lectotype for *A. triquetrum*. Their choice matches perfectly the protologue, and thus should be followed instead of the lectotypification made by Nandikar & Gurav (2015). Nonetheless, if ever found, the specimen at K would make a much better choice of a lectotype. At the time of the description of *A. triquetrum* and the completion of his monograph (i.e. 1881), Clarke was working at K, and would had access to a possible specimen in the Wallich Herbarium, housed at Kew.

Discussion. This is a widely distributed species complex, being very common and well collected in Asia. Nevertheless, the morphologic limits between M. keisak and M. triquetra, as well as the application of these names, varies greatly according to each author. In Flora of China (Hong & DeFilipps 2000), both species are accepted, although somewhat tentatively, and are separated by the length of the sepals, shape and size of the capsule, and number and shape of the seeds. The authors also state that the morphologic differences seem to be associated with the geographic distribution of the taxa. Nevertheless, both descriptions overlap with the description presented by Faden (2000) for M. keisak, in North America. Ancy (2014), in her unpublished Ph.D. thesis, presents a thorough taxonomic account on Murdannia from India. Her description of M. triquetra matches very closely the two specimens known for South America, in sepal, petal and fruit morphology. Nonetheless, Ancy (2014) describes the filaments as being glabrous, contrary to the bearded filaments known for the South American specimens. The author also omits the description of the antherodes, which in the South American specimens are yellow and cordate. Nevertheless, some young flower buds dissected by the second author lacked hairs on the filaments of the stamens and completely lacked staminodes, but that might have been a developmental stage and thus may not be a discrepancy. This could be related to the extremely immature state of the dissected buds, and could explain the discrepancy of our description and the description presented by Ancy (2014). Nandikar & Gurav (2015) published a second account on the Indian species of Murdannia. In their treatment, M. triquetra differs greatly from the South American specimens. However, it matches very closely the description presented by Hong & DeFilipps (2000), Faden (2000) and Chowdhury et al. (2015) for M. keisak. In these descriptions, the antherodes are described as sagittate and ranging from lilac to purple, and clearly do not match the South American specimens.

It is the authors opinion that a study focusing on the specific boundaries between these taxa is necessary. Nevertheless, since this species complex is only invasive in the New World, we also believe that the required investigation should be carried out in the plants native range. It is also possible that these Neotropical collections represent a distinct taxon, not closely related to the other native South American species. But a much better South American sampling for comparison and a much more detailed would be required. Field work, better

sampling of herbaria specimens, detailed study of reproductive morphology, analysis of the protologues, and population studies might shed a light on the issue.

Conclusions

Neotropical *Murdannia* is represented by six native species confined to South America, mostly in Brazil. The species can be distinguished from one another by growth habit, branching pattern of the stems, phyllotaxy, indumentum type, inflorescence morphology, indumentum on the petals, androecium and gynoecium, capsule morphology, seed shape, and by the ornamentation of the testa. Two invasive species, native to Asia, are found in the Neotropics. *Murdannia* aff. *triquetra* is recorded for the first time in South America. Despite being rarely collected, the known South American populations seem to be well-established and should be monitored to avoid the dispersal of yet another invasive species of Commelinaceae. It may be mentioned, for the sake of completeness, that the only other *Murdannia* species recorded from the Western Hemisphere is the Asian taxon *M. spirata* (L.) G.Brückn., which in naturalized in southern Florida, United States (Faden 2000).

Despite being seldom collected, Neotropical *Murdannia* are generally described in labels as forming large populations. It is possible that the lack of collections for the group is connected to: (1) the difficulty to access the areas where they occur (e.g. Amazonian river banks); (2) general neglect of aquatic flora, due to logistic difficulties in field work; (3) the difficulty to preserve Commelinaceae flowers in dried specimens, discouraging botanists to collect them; (4) and lack of field work focusing on herbaceous plants. The authors hope that the present work will encourage field workers to collect Commelinaceae specimens in the Amazon, Cerrado, Chaco and Pantanal domains. Furthermore, the increase of collections will enable researchers to monitor these species' populations in order to update and provide more precise conservation assessments for them, and monitor the need for biological control of the known invasive species.

Although several studies focusing on morphology, anatomy and cytology of Murdannia are available in the literature, no comprehensive phylogenetic study has been presented up to date. Burns et al. (2011) were the first to sample more than one species of Murdannia in a phylogenetic analysis. However, all of the five sampled species were Asian and none represented the type-species. Thus, the monophyly of Murdannia is still to be tested in future studies. Ancy (2014) presented a morphological phylogeny, sampling exclusively the species native to India. In her analysis, the clades are supported by characters like inflorescence architecture, and androecium, capsule and seed morphology. As aforementioned, the Neotropical species of Murdannia are extremely peculiar in a considerable number of morphological characters, and nothing is known regarding their phylogenetic relationships, anatomy or even their cytology. Thus, three important questions about the Neotropical species are: (1) how are they related to one another; (2) what is the relationship between the Neotropical species and the rest of the genus; and (3) how many dispersal events the Neotropical lineages of *Murdannia* would represent. In a more general sense, it would also be important to understand the evolution of morphological characters in the genus on a phylogenetic framework, such as the inflorescence and androecium morphology.

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Figure 1. *Murdannia burchellii* (C.B.Clarke) M.Pell. Lectotype of *Aneilema gardneri* var. *burchellii* (K barcode K000363240). Photograph courtesy of Royal Botanic Gardens, Kew, London.

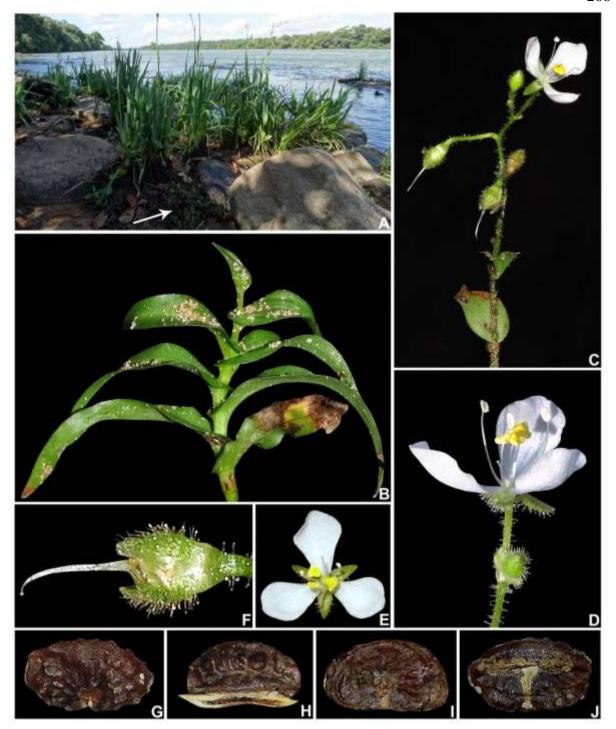


Figure 2. *Murdannia engelsii* M.Pell. & Faden. **A,** Sandy banks of rio Teles Pires, white arrow showing a subpopulation of *M. engelsii*. **B,** detail of the stem, showing the conduplicate and falcate leaves, with amplexicaul bases. **C,** detail of the inflorescence, showing the deflexed pedicels at post-anthesis. **D,** side view of a male flower, showing the short and bent style. **E,** front view of a bisexual flower, showing the long curved style. **F,** detail of a young fruit, showing the pedicel and sepals with glandular hairs, gently curved style and capitate stigma. **G–J,** seeds: **G,** dorsal view of a seed, showing the scrobiculate and cleft testa, and the semilateral embryotega. **H,** ventral view of the same seed, showing the ventral furrows and tan appendage surrounding the hilum. **I,** dorsal view of another seed, showing the shallowly scrobiculate and slightly cleft testa, and the semidorsal embryotega. **J,** ventral view of the same seed, with the appendage removed, showing the linear hilum in a shallow depression. K, dorsal view of a seed, showing the smooth testa. Photographs A–F by M.E. Engels, G–J by R.F. Almeida.

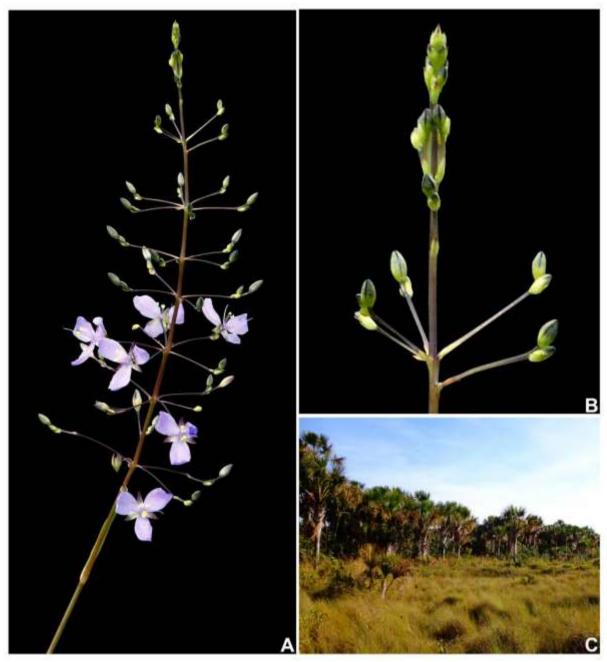


Figure 3. *Murdannia gardneri* (Seub.) G.Brückn. **A,** Inflorescence, showing the verticillate cincinni and open lilac flowers. **B,** detail of the inflorescence, showing the ascending and straight cincinni. **C,** flooded grassland in the state of Minas Gerais. Photographs A–B by W. Milliken, C by I.L.M. Resende.

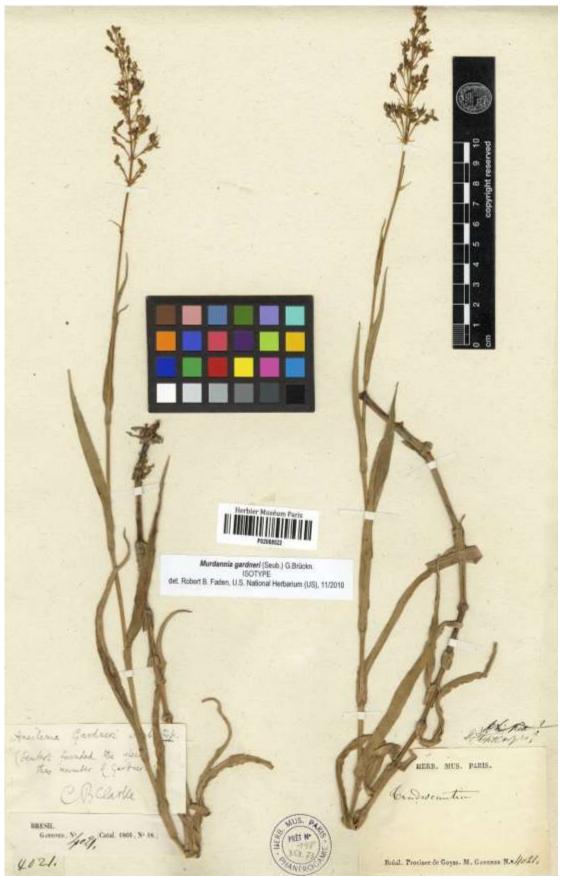


Figure 4. *Murdannia gardneri* (Seub.) G.Brückn. Isolectotype of *Aneilema gardneri* (P barcode P02088022). Photograph courtesy of the Muséum National d'Histoire Naturelle, Paris.



Figure 5. *Murdannia nudiflora* (L.) Brenan. **A,** Habit. **B,** detail of a stem, showing the apical and long-pedunculate inflorescence. **C,** front view of a bisexual flower. Photograph A by A. Cardoso, B by M.E. Engels and C by W. Vargas.

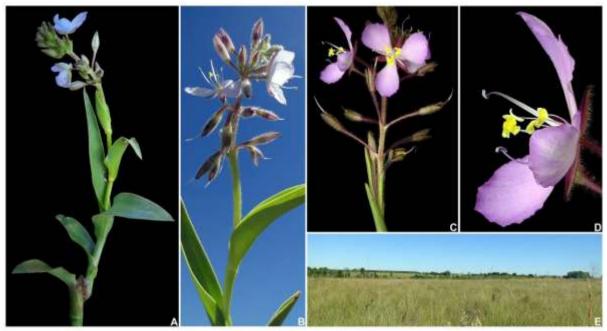


Figure 6. *Murdannia paraguayensis* (C.B.Clarke) G.Brückn. **A,** Detail of a flowering shoot, showing the succulent stem, succulent, canaliculate and falcate leaves, and an inflorescence with lilac flowers. **B,** Detail of the apex of a flowering shoot, showing a terminal inflorescence with white flowers, and pedicels deflexed post-anthesis. **C,** Inflorescence showing the 1-flowered verticillate cincinni and open mauve flowers. **D,** Side view of a male flower, showing the sepals with glandular hairs. **E,** flooded grassland in Sidrolândia, Mato Grosso do Sul. Photograph A by I.L.M. Resende, B & E by S.N. Moreira and C–D by V.C. Souza.



Figure 7. *Murdannia schomburgkiana* (Kunth) G.Brückn. Isolectotype of *Aneilema schomburgkianum* (P barcode P02088026). Photograph courtesy of the Muséum National d'Histoire Naturelle, Paris.

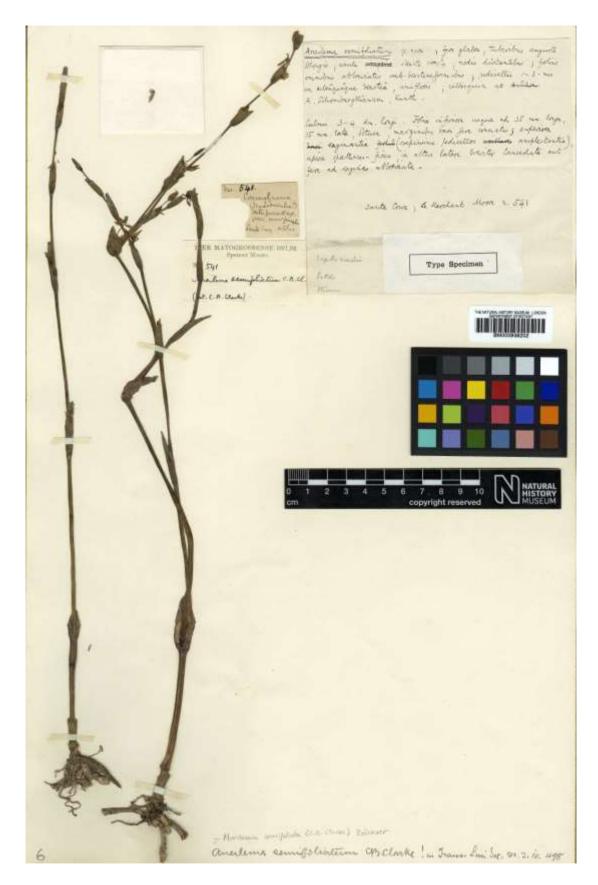


Figure 8. *Murdannia semifoliata* (C.B.Clarke) G.Brückn. Lectotype of *Aneilema semifoliatum* (BM barcode BM000938202). Photograph courtesy of The Natural History Museum of London.



Figure 9. *Murdannia* aff. *triquetrum* (Wall. *ex* C.B.Clarke) G.Brückn., from Esteros de Arauca, Colombia. **A,** Detail of a stem, showing an apical fruit. **B,** detail of an internode, showing a side view of a male flower. Photographs by M. Fernández.

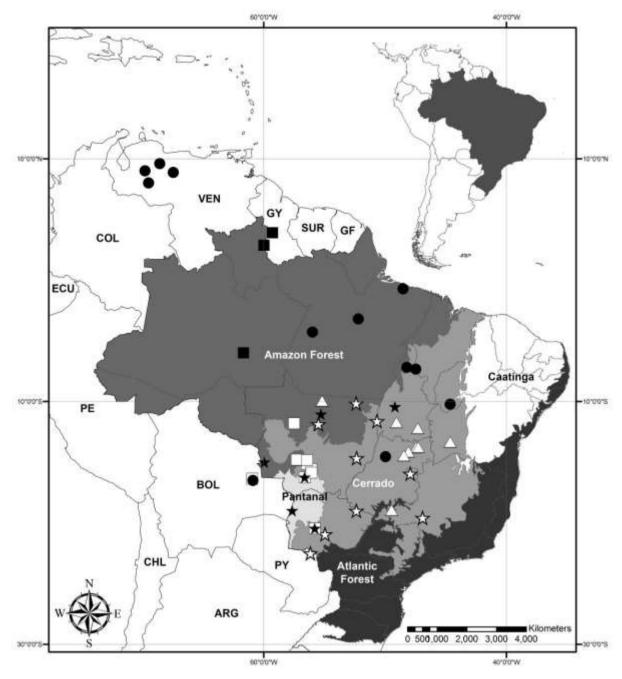


Figure 10. Distribution map of Neotropical *Murdannia* Royle. **Full circles**– *M. burchellii*; **Full stars**– *M. engelsii*; **Triangles**– *M. gardneri*; **Stars**– *M. paraguayensis*; **Full squares**– *M. schomburgkiana*; **Squares**– *M. semifoliata*.

Table 1- Morphologic characters differentiating the species of Murdannia known for the Neotropical region.

Characters	M. burchellii	M. engelsii	M. gardneri	M. nudiflora	<i>M</i> .	<i>M</i> .	M. semifoliata	M. aff.
DI 11 4	C : 11	D' (' 1 1	C : 11	D' 4' 1 1	paraguayensis	schomburgkiana	0 : 11	triquetra
Phyllotaxy	Spirally- alternate	Distichously- alternate	Spirally- alternate	Distichously- alternate	Spirally- alternate, sometimes becoming distichously- alternate at	Spirally-alternate	Spirally- alternate	Spirally- alternate
Inflorescence	Terminal or axillary in the uppermost nodes; pedunculate	Terminal or axillary in the uppermost nodes; pedunculate	Terminal or axillary in the uppermost nodes; pedunculate	Terminal or axillary in the uppermost nodes; pedunculate	apex Terminal or axillary in the uppermost nodes; pedunculate	Mainly axillary; sessile	Mainly axillary; sessile	Mainly axillary; sessile
Cincinnus bracts	Cup-shaped, apex caudate	Flat, apex acute	Cup-shaped, apex acuminate	Cup-shaped, apex acute	Flat, apex acute	Tubular, apex truncate	Tubular, apex truncate	Not observed
Cincinni	(1–)2–16, alternate to sub-opposite, 2–9-flowered	1, solitary, 2– 7-flowered	16–38, verticillate, 2– 11-flowered	1, solitary, 2– 12-flowered	9–24, verticillate, 1- flowered	1–2(–3), fascicle-like, 1- flowered	1–2(–3), fascicle-like, 1-flowered	1–2(–3), fascicle-like, 1- flowered
Floral buds	Narrowly ovoid to ovoid	Ovoid	Narrowly ovoid to ovoid	Ellipsoid to oblongoid	Narrowly ovoid	Ellipsoid	Ellipsoid	Ellipsoid
Flower symmetry	Enantiostylous	Enantiostylous	Enantiostylous	Zygomorphic	Enantiostylous	Actinomorphic	Actinomorphic	Actinomorphic?
Petals pubescence	Glabrous	With minute glandular hairs at base on the adaxial surface	Glabrous	Glabrous	With minute glandular hairs at base on the adaxial surface	Densely bearded with moniliform hairs on the adaxial surface	Densely bearded with moniliform hairs on the adaxial surface	Glabrous
Filaments	Glabrous	With	Glabrous	Bearded with	With	Bearded with	Bearded with	Not observed

pubescence		glandular hairs		moniliform hairs	glandular hairs	moniliform hairs	moniliform hairs	
Anthers	Narrowly elliptic to narrowly oblong, connective lilac, anthers sacs white	Elliptic, connective white to lilac, anthers sacs white to light- lilac	Elliptic, connective lilac to white, anthers sacs white to lilac	Elliptic to oblong, connective bluish-lilac to white, anthers sacs purple to dark-purple	Elliptic to oblong, connective purple to bluish-purple, anthers sacs lilac to purple	Elliptic to oblong, connective brown, anthers sacs brownish- lilac	Linear-oblong to oblong, connective purple, anthers sacs lilac to purple	Not observed
Antherodes	Sagittate, golden yellow	Subsagittate to subcordate, golden-yellow	Cordate, golden yellow	Hastate, white to cream	Sagittate, golden yellow	Hastate, golden yellow	Hastate, golden yellow	Not observed
Gynoecium pubescence	Glabrous	With glandular hairs	Glabrous	Glabrous	With glandular hairs	Glabrous	Glabrous	Glabrous
Fruiting pedicel	Erect	Deflexed	Erect	Erect	Deflexed	Erect	Erect	Apparently erect
Capsules	Subglobose to globose	Broadly ovoid to broadly ellipsoid	Subglobose to globose	Ovoid to subglobose	Oblongoid to broadly oblongoid	Oblongoid to broadly oblongoid	Oblongoid to broadly oblongoid	Oblongoid to ellipsoid
Seeds	1 per locule, reniform to broadly ellipsoid, ventri-lateral appendage present	1 per locule, reniform to broadly ellipsoid, ventri-lateral appendage present	1 per locule, reniform to broadly ellipsoid, ventr -lateral appendage present	2 per locule, broadly ellipsoid to oblongoid, ventri-lateral appendage absent	2 per locule, reniform to broadly- ellipsoid, ventri-lateral appendage present	6 per locule, cuboid to polygonal, ventri-lateral appendage absent	6 per locule, cuboid to polygonal, ventri-lateral appendage absent	3 per locule, transversely ellipsoid, ventri-lateral appendage absent

SECTION 2— COMMELINACEAE MIRB.

Chapter 2.3. Taxonomic revision of *Aneilema* sect. *Rhopalephora* (Hassk.) M.Pell. & Nandikar, and comments on *Aneilema* R.Br. s.l. (Commelinaceae)

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Abstract

Rhopalephora has hitherto been considered a small genus restricted to Madagascar, Asia, and Oceania, segregated from Aneilema. Nonetheless, recent phylogenetic analyses have recurrently recovered Rhopalephora nested within Aneilema, with high statistical support. In order to retain Aneilema monophyletic, we propose Rhopalephora to be reduced to sectional rank. We present a taxonomic revision for the group, with the needed typifications, descriptions, comments, photo plates, illustrations, conservation assessments, and distribution maps for all the species. Furthermore, with the return of Rhopalephora to Aneilema, we update the genus' current sectional classification, provide a new identification key for the accepted sections, and present comments on the genus. Finally, we address the enigmatic Floscopa yunnanensis, which has been suggested as a member of Rhopalephora, being herein excluded from A. sect. Rhopalephora but transferred to Aneilema s.l. with uncertain sectional placement. We also provide an updated description and comments regarding the species' putative taxonomical affinities within Aneilema s.l.

Keywords

Aneilema, Commelinaes, dayflower, Dictyospermum, Floscopa, Piletocarpus, spiderwort.

Introduction

Rhopalephora Hassk. (Commelinaceae) has hitherto been considered a small genus restricted to Africa, Madagascar, Asia, and Oceania (Faden 1975, 1977, 1998). It was segregated from Aneilema R.Br., as a monospecific genus, based on its stipitate capsules with one seed per locule (Hasskarl 1864a). Both genera are currently placed in tribe Commelineae, alongside the morphologically and phylogenetically related *Dictyospermum* Wight, and *Tricarpelema* J.K.Morton (Faden 1975, 1977, 1991; Faden and Hunt 1991; Evans et al. 2003). Depending on the author, Rhopalephora was either treated as a synonym of, or at the infrageneric rank within either Aneilema (Clarke 1881; Hooker 1894; Brückner 1930) or Dictyospermum (Wight 1853; Morton 1966). Nonetheless, recent phylogenetic studies have shown that Aneilema and Rhopalephora are more closely related to each other than to Dictyospermum and Tricarpelema (Evans et al. 2003; Zuiderveen et al. 2011; Kelly and Evans 2014; Pellegrini et al., in prep.). Ongoing phylogenetic studies in Commelinaceae (Pellegrini et al., in prep.), consistently recover Aneilema (including Rhopalephora) in a well-supported clade together with Commelina L., Dictyospermum, Pollia Thunb., Polyspatha Benth., and Tapheocarpa Conran. This clade is recovered as sister to a well-supported clade, consisting of two inner clades, the Floscopa clade (i.e., Buforrestia C.B.Clarke, Floscopa Lour., Stanfieldiella Brenan, and Tricarpelema), and the Murdannia clade (i.e., Murdannia Royle and Anthericopsis Engl.) (Pellegrini et al., in prep.).

Faden (1977), on his synopsis for *Rhopalephora*, considered the genus to comprise four very ill-defined species, differentiated from each other largely based on capsule morphology. Nonetheless, no identification key or comments on how to differentiate the species were presented by the author, with problems on species delimitation persisting until this day, especially regarding the *R. scaberrima* species complex. A significant part of the taxonomical instability that revolves around *Rhopalephora*, results from its poorly-defined generic limits. It is similar to *Aneilema* due to the presence of hook hairs, its perfoliate and cup-shaped

bracteoles, clawed petals, three posterior staminodes with bilobed antherodes, three anterior fertile stamens, and 2-locular or unequally 3-locular, 2-valved capsules (Faden 1975, 1977, 1991, 1998). According to Faden (1975, 1991), both genera are so similar that Rhopalephora must be defined by a combination of characters, none of which is unique to it; except for the basic chromosome number x=29. Thus, Faden (1975, 1977, 1991, 1998) differentiated Rhopalephora from Aneilema based on the following combination of characters: thyrsi with elongate cincinni and shortened main axis (i.e., corymb-like), central staminode commonly lacking the antherode, gynoecium stipitate and covered with a mixture of hook and glandular hairs (making it sticky to touch), and by the number of ovules per locule. Added to that, Faden (1975, 1991) found no anatomical difference between them, and their distributions are complementary, with almost no overlap between both genera (Faden 1975, 1991; eMonocot 2010; Fig. 1). Alternatively, Aneilema sensu Faden (1991) is one of the biggest genera in the family (ca. 65 species), being extremely morphologically and cytogenetically diverse (Faden 1975, 1991, 1998; eMonocot 2010). Most of the morphological diversity currently accepted for Aneilema already overlaps with the delimitation of Rhopalephora proposed by Faden (1977); which added to the available phylogenetic evidence (Evans et al. 2003; Zuiderveen et al. 2011; Kelly and Evans 2014; Pellegrini et al., in prep.), gives strong support against maintaining both genera as independent.

This way, in order to retain a monophyletic and morphologically cohesive *Aneilema*, it is necessary that the generic status of *Rhopalephora* be overruled, and its species are once again treated under *Aneilema s.l.* Nonetheless, it seems suiting for *Rhopalephora* to be recognized at the sectional rank, since it can be readily differentiated from the remaining sections of *Aneilema* (Faden 1977, 1991, 1998). Thus, the present study recognizes *Rhopalephora* as a new section for *Aneilema*, emending the current sectional treatment for the genus (i.e., Faden 1991). Furthermore, we present the taxonomic revision and the needed typifications for *A.* sect. *Rhopalephora*, as suggested by Faden (1975). Finally, the enigmatic *Floscopa yunanensis* is herein excluded from *Floscopa*, and also transferred to *Aneilema s.l.*, with comments on its systematic placement.

Methods

The descriptions and phenology of the species were based on herbaria, spirit, fresh material, and literature. Specimens of *A. protensum* (Wall. *ex* Wight) Thwaites and *A. scaberrimum* (Blume) Kunth were kept in cultivation in order to observe, photograph, and analyze fresh flowers, fruits and seeds, as well as other phenological data. Descriptions of *A. protensum*, *A. scaberrimum*, and *A. vitiense* Seem. were complemented using spirit samples and field photos kindly provided by the collectors. Specimens from the following herbaria were also analyzed: ASSAM, B, BK, BLAT, BM, BO, BSI, C, CAL, CMU, DD, E, G, GZU, HE, GH, K, KUN, L, MH, MICH, NGCPR, P, PCM, PNH, RB, SUK, U, UPS, US, and W (herbaria acronyms according to Thiers, continuously updated). The distribution of the species is based on herbaria specimens, literature, and fieldwork data. The indumentum and shapes terminology follow Radford et al. (1974); the inflorescence terminology and morphology follows Weberling (1965, 1989) and Panigo et al. (2011); the fruit terminology follows Spjut (1994) and Faden (1991); seed terminology follows Faden (1991); and general terminology follows Faden (1991).

Results

In the present work we recognize five species under A. sect. Rhopalephora (Hassk.) M.Pell. & Nandikar. This section is morphologically well-defined and possesses a relatively restricted distribution, mainly in southern Asia and Oceania, with only one species reaching Madagascar. Below we present an identification key for the species, together with descriptions, illustrations, comments, conservation assessments, and distribution maps. Finally, we provide an updated description for Aneilema s.l., encompassing the variation observed in A. sect. Rhopalephora and A. yunnanense (D.Y.Hong) M.Pell. An updated key to the sections of Aneilema s.l. is also provided, together with some comments on the morphological patterns of the genus as a whole

Taxonomic treatment

Aneilema R.Br., Prodr.: 270. 1810.

Type species (designated by Brückner 1927). Aneilema biflorum R.Br.

Anilema Kunth, Enum. Pl. 4: 64. 1843, orth. var.

- Aneilema R.Br. subg. Aneilema ≡ Aneilema subg. Dicarpellaria C.B.Clarke in De Candolle & De Candolle, Monogr. Phan. 3: 196. 1881. Type species (designated here). Aneilema biflorum R.Br.
- Aneilema sect. Pseudo-axillares C.B.Clarke in Thiselton-Dyer, Fl. Trop. Africa 8: 63. 1901, pro. syn. Type species (designated by Faden 1991). Aneilema clarkei Rendle.
- Ballya Brenan, Kew Bull. 19: 63. 1964. Type species. Ballya zebrina (Chiov. ex Chiarugi) Brenan (≡ Aneilema zebrina Chiov. ex Chiarugi).
- Bauschia Seub. ex Warm., Vidensk. Meddel. Naturhist. Foren. Kjøbenhavn 1872: 123. 1872. Type species. Bauschia bracteolata (Mart.) Seub. ex Warm. (≡ Aneilema bracteolatum Mart.).
- Lamprodithyros Hassk., Flora 46: 388. 1863 ≡ Aneilema sect. Lamprodithyros (Hassk.) C.B.Clarke in De Candolle & De Candolle, Monogr. Phan. 3: 196. 1881. Type species (designated by Faden 1991). Lamprodithyros petersii Hassk. [≡ Aneilema petersii (Hassk.) C.B.Clarke.].
- Amelina C.B.Clarke, Commelyn. Cyrtandr. Bengal: 38. 1874 ≡ Aneilema sect. Amelina (C.B.Clarke) C.B.Clarke in De Candolle & De Candolle, Monogr. Phan. 3: 197. 1881. Type species. Amelina wallichii C.B.Clarke [= Aneilema aequinoctiale (P.Beauv.) Loudon].

Perosanthera Fend, Sitzungsb. Akad. Wien. 50: 353. 1864, nom. nud.

Description. Herbs perennial or annual, with or without a definite base, terrestrial or rupicolous. Roots thin and fibrous or thick and tuberous. Rhizomes present or not. Stems

trailing to ascending at the apex or erect, unbranched to little branched or densely branched, rooting in the rhizome and at the basal nodes, rarely at the distal ones when they touch the substrate. Leaves sessile or subpetiolate; spirally- or distichously-alternate, evenly distributed or congested at the base or apex of the stem; sheaths usually with ciliate to setose margins, rarely glabrous; lamina flat or conduplicate to falcate, membranous to chartaceous, rarely succulent, base symmetrical to slightly asymmetrical or asymmetrical to strongly asymmetrical, midvein conspicuous, adaxially impressed, abaxially prominent, secondary veins conspicuous or not. Synflorescence composed of a solitary main florescence or with 1several coflorescences. Main florescences (inflorescences) terminal or axillary in the in the uppermost nodes, not perforating the leaf-sheaths; main florescence a variously looking thyrse, composed of 1-many, alternate or subopposite or verticillate cincinni; basal bract reduced to leaf-like; peduncle bracts (sterile bracts) absent, sometimes present; main axis abbreviated or elongated; cincinni bracts persistent, flat; cincinni sessile to pedunculate, contracted to elongate, patent to erect, straight to sinuate; bracteoles cup-shaped, perfoliate or not, herbaceous or membranous, apex generally glandular, rarely also with a filiform apex, persistent. Flowers bisexual or staminate (the staminate ones with a reduced or completely aborted gynoecium), rarely pistillate, zygomorphic, enantiostylous or not, chasmogamous, rarely cleistogamous, flat (not tubular), with a 60° torsion in the floral display or not; pedicels patent to erect or deflexed at anthesis and pre-anthesis, patent or erect or deflexed or reflexed at post-anthesis; pedicels gibbous or not at apex, sometimes elongated in post-anthesis and in fruit; sepals 3, unequal, free, cucullate, membranous, dorsally not keeled, glabrous to sparsely pubescent, margins hyaline, each with a subapical gland, accrescent or not, persistent in fruit, sometimes also and deflexed in fruit; petals 3, unequal, rarely subequal, free, deliquescent, glabrous or pubescent, concolorous or the medial one discolorous or hyaline, generally white to light blue to pale lilac to lilac, sometimes pale pink to pink to pinkish red to red to coral to orange to orange-yellow to yellow to pale yellow, paired petals clawed, held upwards or oblique to lateral, sometimes slightly deflexed, claws glabrous, rarely sparsely pubescent, concolorous or discolorous with the limb, limb flat to slightly concave to concave, the medial sessile to shortly clawed, rarely clawed, held downwards, sometimes slightly to strongly deflexed, base or claw concolorous or discolorous with the limb, glabrous, rarely puberulous basally, limb flat to slightly convexo-concave or convexo-concave, cup-, boat- or slippershaped; staminodes (2–)3, equal to subequal, posterior, filaments glabrous, medial staminode sometimes lacking or greatly reduced with the antherode completely lacking, lateral staminodes free or basally connate with the stamens, antherodes bilobed, rarely unlobed, lobes sessile or shortly stipitate to stipitate, lobes curved to C-shaped or ellipsoid or globose to subglobose to transversally ellipsoid or reniform, yellow, sometimes white or lilac to purple or pink, rarely maroon; stamens 3, unequal, anterior, filaments free or connate basally to half their length, glabrous or the laterals sparsely to densely bearded with uniseriate, nonmoniliform, hyaline to brightly-colored hairs, anthers basifixed, dorsifixed or versatile, dehiscence rimose, usually introrse, rarely latrorse or extrorse, lateral anthers with an inconspicuous connective, medial anther with a conspicuous connective, usually different in size and/or shape from those of the lateral stamens, its pollen often also different in color and sometimes sterile; ovary sessile to shortly-stipitate or stipitate, glabrous or puberulous with glandular hairs, occasionally mixed with few to many hook-hairs, hook hairs often of two lengths, 2–3-locular, ovules uniseriate, dorsal locule developed or not, rarely prominent, (0–)1(-6)-ovulate, ventral locules 1-6-ovulate, style elongate, not spirally-coiled at post-anthesis, generally persistent in fruit, stigma truncate or capitate, papillate. Capsules loculicidal, 2(-3)valved, rarely indehiscent, sessile to subsessile or shortly-stipitate to stipitate, apiculate or not due to persistent style base, smooth, glabrous or puberulous, dorsal valve deciduous or persistent, ventral valve deciduous or persistent, dorsal locule (0-)1-seeded, ventral locules

(0–)1–6-seeded. *Seeds* monomorphic, sometimes dimorphic, exarillate, farinose or not, uniseriate, variously shaped, not cleft or slightly to strongly cleft towards the embryotega, ventrally flattened, testa variously ornamented, rarely smooth, unappendaged, hilum linear; embryotega semilateral or lateral.

Distribution. Pantropical, ranging from Central and South America to Africa, Madagascar, Asia, and Oceania (Fig 1). Distribution for each of the seven previously accepted sections can be found in Faden (1991).

Phylogeny and classification. Kelly and Evans (2014), in a preliminary molecular phylogeny for Aneilema based on four markers, were able to sample all sections of Aneilema s.l. currently accepted by us. The authors recovered A. sect. Amelina as polyphyletic, arranged in three different lineages; and A. sect. Lamprodithyros as paraphyletic, due to A. indehiscens var. keniense Faden being nested within A. sect. Brevibarbata. Nonetheless, A. sect. Aneilema was recovered as monophyletic with medium statistical support. The remaining sections (i.e., A. sect. Pedunculosa, A. sect. Rendlei, A. sect. Rhopalephora, and A. sect. Somaliensia) could not have their monophyly tested, since they were represented by a sole species. From a morphological point of view, the placement of A. gilletti Brenan (A. sect. Amelina) as sister to A. leiocaule K.Schum. (A. sect. Pedunculosa) is not surprising since A. gilletti seems to be the only species in A. sect. Amelina to possess non-perfoliate and membranous bracteoles. On the other hand, all species of A. sect. Pedunculosa consistently present non-perfoliate and membranous bracteoles (Faden 1991). With the transfer of A. gilletti to A. sect. Pedunculosa, the section would still retain its peculiar and cohesive morphology, as described by Faden (1991). Nonetheless, A. sect. Amelina would still be paraphyletic due to the placement of A. johnstonii K.Schum. as sister to the remaining species of Aneilema s.l. Aneilema johnstonii is peculiar in A. sect. Amelina due to its completely glabrous inflorescences and filaments, medium to dark vinaceous inflorescences and sepals, orange-yellow to orange petals, medial petal with a dark red to vinaceous spot at base, equal staminodes, and ovary and capsules puberulous only with glandular microhairs. Added to that, its antherodes which are shaped like upside-down horseshoes, are considered to be unique in Aneilema s.l. (Faden 1991, 2012). Nonetheless, they are quite similar in shape to the ones observed in Floscopa yunnanensis D.Y.Hong (see below). It is most likely that a new section might need to be proposed to accommodate A. johnstonii (and maybe F. yunnanensis, see section below). Nonetheless, further phylogenetic studies (both molecular and morphological) are still needed before a complete review of the sectional classification of *Aneilema s.l.* can be properly done.

Fruit dispersal and geographical patterns in Aneilema. As with most Commelinaceae, Aneilema spp. in general show no specialization regarding fruit dispersal, with seeds being most probably dispersed by chance (i.e., autochory; Faden 1991, 1992). However, in A. sect. Lamprodithyros and A. sect. Rhopalephora the capsules are 2-valded, with a prominent, indehiscent and persistent dorsal locule, probably working as a disseminule; which is also commonly accompanied by strong seed dimorphism in A. sect. Lamprodithyros (Faden 1991; this study). Furthermore, in A. sect. Lamprodithyros and A. sect. Rhopalephora the gynoecium is peculiarly covered by a mixture of glandular and hook hairs (Faden 1977, 1991, 1998; this study). When the capsules are mature, these hairs make the fruits characteristically sticky to touch, and they easily adhere to fabric, and most likely also animal fur and feathers. A similar sticky to touch aspect is also observable in the leaf-sheaths and internodes of some scrambling species of A. sect. Amelina [e.g., A. aequinoctiale (P.Beauv.) Loudon], which greatly helps them to climb surrounding shrubs (Faden 1991, 2012). This is a unique type of vector-mediated dispersal in the family (Pellegrini and Faden 2017) and is

analogous to the zoochoric dispersal mechanism used by many species of tribe Coreopsidae (Asteraceae). This vector-mediated dispersal could help explain, by long distance dispersal, the obvious disjunction between the Madagascar endemic *A. rugosum* and the remaining species of *A.* sect. *Rhopalephora* (Sri Lanka, India to Southeastern Asia, Malesia, and the Western Pacific).

Emended key to the sections of *Aneilema* (based on Faden 1991)

- 1. Thyrsi lax to moderately lax, if contracted inflorescence with an inconspicuous main axis (umbel-like) or all inflorescences axillary and fascicle-like, cincinni elongate; filaments connate, rarely free... 2
- Thyrsi moderately dense to dense, cincinni contracted; filaments free... 5
- 2. Cincinni mostly subopposite or subverticillate; staminodes equal or medial staminode with a comparatively larger antherode, medial stamen strongly ascending at apex... *Aneilema* sect. *Amelina* (C.B.Clarke) C.B.Clarke
- Cincinni mostly alternate; medial staminode smaller than the laterals or lacking, medial stamen almost straight... 3
- 3. Medial petal reduced, filaments free, antherodes-lobes reniform, filament of the lateral staminodes thickened basally, strongly deflexed, then strongly recurved towards the apex, lateral stamens dimorphic in bisexual and staminate flowers, pollen differently in colored in the medial and lateral anthers, medial anther similar in shape and size to the laterals, ovary and capsules sessile, stigma truncate... *Aneilema* sect. *Rendlei* Faden
- Medial petal equal to subequal to the paired petals, filaments connate, antherodes-lobes globose to ellipsoid, filament of the lateral staminodes thin basally, nearly straight, lateral stamens monomorphic in bisexual and staminate flowers, pollen of the same color in the medial and lateral stamens, medial anther bigger and of a different shape to the lateral, ovary and capsules stipitate, rarely sessile, stigma capitate... 4
- 4. Inflorescence commonly a regular looking thyrse, rarely umbel- or fascicle-like; flowers straight (i.e., without a 60° torsion in the floral display), sepals loosely enclosing the capsule to patent, medial petal boat-, slipper-, or cup-shaped, antherode-lobes sessile, filaments of the stamens only basally connate, gynoecium sessile, glabrous to puberulous with glandular hairs; mature capsules without persistent style or just apiculate; seeds of the ventral and dorsal locules dimorphic... *Aneilema* sect. *Lamprodithyros* (Hassk.) C.B.Clarke
- Inflorescence a corymb- or umbel-like thyrse; flowers with a 60° torsion in the floral display, sepals deflexed in fruit, medial petal flat to slightly concave, antherode-lobes stipitate to shortly stipitate, filaments of the stamens connate up to half their length, gynoecium stipitate, puberulous with a mixture of hook and minute glandular hairs; mature capsules with persistent elongated style; seeds monomorphic... Aneilema sect. Rhopalephora (Hassk.) M.Pell. & Nandikar
- 5. Medial petal equal to subequal to the paired petals, filaments of the lateral stamens straight or undulate, not geniculate, all anthers well developed, antherodes unlobed to bilobed, sessile, yellow or white to violet... *Aneilema* **R.Br. sect.** *Aneilema*
- Medial petal reduced (if subequal, then lateral stamen filaments bearded and medial anther reduced), filaments of the lateral stamens S-shaped and +/- geniculate, medial anther smaller to bigger than the laterals, antherodes bilobed, stipitate, yellow... 6

- 6. Perennial herbs, tuberous-rooted, growing in dry bushlands; flowering shoots often disarticulating at the nodes at the end of the growing season; filaments of the stamen glabrous, medial anther saddle-shaped... *Aneilema* sect. *Somaliensia* Faden
- Perennial or annual herbs, fibrous-rooted, rarely tuberous-rooted, growing in grasslands or forests, rarely in bushlands; flowering shoots not disarticulating at the nodes; filaments of the stamen bearded, medial anther dumbbell-shaped or subequal to the laterals... 7
- 7. Roots tuberous or fibrous; bracteoles cup-shaped, generally perfoliate, lacking a linear apex; lateral stamens sparsely and inconspicuously bearded, hairs hyaline... *Aneilema* sect. *Brevibarbata* Faden
- Roots fibrous; bracteoles neither cup-shaped nor perfoliate, often with a linear gland-tipped apex; lateral stamens densely and conspicuously bearded, hairs brightly-colored...
 Aneilema sect. Pedunculosa Faden

Aneilema sect. Rhopalephora (Hassk.) M.Pell. & Nandikar, comb. et stat. nov.

Rhopalephora Hassk., Bot. Zeitung (Berlin) 22: 58. 1864a. Type species (designated by Faden 1977). Rhopalephora blumei Hassk., nom. illeg. [≡ Aneilema micranthum (Vahl) Kunth].

Piletocarpus Hassk., Flora 49: 212. 1866. Type species (designated here). Piletocarpus protensus (Wall. ex Wight) Hassk. [= Aneilema protensum (Wall. ex Wight) Thwaites], Syn. nov.

Description. Herbs perennial or annual, with or without a definite base, terrestrial. Roots thin and fibrous. Rhizomes absent. Stems trailing and ascending at the apex or erect, unbranched to little branched or densely branched, rooting at the basal nodes, rarely at the distal ones when they touch the substrate. Leaves sessile or subpetiolate; spirally-alternate, rarely distichously-alternate, evenly distributed along the stem; sheaths pubescent with a mixture of hook hairs and eglandular hairs; lamina flat, base symmetrical to slightly asymmetrical or asymmetrical to strongly asymmetrical, midvein conspicuous, adaxially impressed, abaxially prominent, secondary veins conspicuous. Synflorescence composed of a solitary main florescence or with 1-several coflorescences. Main florescences (inflorescences) terminal or axillary in the in the uppermost nodes, not perforating the leafsheaths; main florescence a corymb-like thyrse, composed of 1-many, alternate cincinni (but apparently verticillate due to the reduced main axis); basal bract reduced to leaf-like; peduncle bracts (sterile bracts) absent; main axis abbreviated, much shorter than the cincinni; cincinni bracts persistent, flat; cincinni pedunculate, elongate, of different sizes (the basal longer than the terminal), erect, straight to sinuate; bracteoles cup-shaped, perfoliate, herbaceous, persistent. Flowers bisexual or staminate (the staminate ones with a reduced to completely aborted gynoecium), zygomorphic, non-enantiostylous, chasmogamous, flat (not tubular), with a 60° torsion in the floral display; pedicels patent at anthesis and pre-anthesis, erect at post-anthesis, rarely deflexed at anthesis, pre-anthesis and post-anthesis; floral buds obovoid to broadly obovoid, apex round; pedicels not gibbous at apex, much elongated in post-anthesis and in fruit, erect; sepals 3, unequal, free, cucullate, membranous, dorsally not keeled, sparsely pubescent with hook hairs to glabrous, margins hyaline, accrescent, persistent and deflexed in fruit; petals 3, unequal, rarely subequal, free, deliquescent, glabrous, concolorous, white to light blue to pale lilac to lilac, paired petals clawed, flat, the medial shortly-clawed or sessile, flat or slightly concave; staminodes 2(-3), subequal, posterior, filaments glabrous, medial staminode generally lacking, sometimes present and greatly reduced, with the antherode completely lacking, lateral staminodes connate only basally to a third of their length with the stamens, filaments straight pointing downward or slightly decurved to undulate pointing upward, antherodes bilobed, lobes stipitate to shortly stipitate, ellipsoid or globose, yellow; stamens 3, unequal, anterior, filaments connate only basally to half their length, glabrous, lateral stamens with filaments gently sigmoid to sigmoid to J-shaped or slightly decurved pointing upward, glabrous, anthers elliptic, connective inconspicuous, medial stamen shorter than the laterals, filament straight or slightly decurved pointing upward, anther bigger than the laterals, saddle-shaped, connective expanded; ovary shortlystipitate, densely puberulous with a mixture of hook and minute glandular hairs, hook hairs often of two lengths, 3-locular, dorsal locule prominent, 1-ovulate, ventral locules 0-1(-2)ovulate, style gently straight or gently curved at the apex to sigmoid, usually recurved towards the apex, persistent in fruit, stigma capitate, papillate. Capsules loculicidal, 2-valved, shortlystipitate to stipitate, rarely subsessile to sessile, apiculate or not due to persistent style base, smooth, sticky to touch, puberulous with a mixture of hook and minute glandular hairs, dorsal valve extremely prominent, persistent, ventral valve deciduous, sometimes persistent, dorsal locule (0-)1-seeded, ventral locules slightly concave to flat or slightly prominent, much smaller than the dorsal, (0-)1(-2)-seeded. Seeds monomorphic, farinose or not, reniform to elliptic to rectangular, slightly to strongly cleft towards the embryotega, ventrally flattened, testa scrobiculate or foveolate, rarely rugulose to rugulose-foveolate, with pits or ridges radiating or not from the embryotega, hilum ca. the same length as the seed, on a weak ridge, rarely in a deep groove; embryotega semilateral or lateral.

Distribution. Madagascar, Sri Lanka, India to Southeastern Asia, Malesia, and the Western Pacific (Fig 1).

Etymology. From the Greek "rhopalon" (ροπαλον) + "phorein" (φορειν), in reference to the club-shaped fruits of the section. On the other hand, the name *Piletocarpus* derives from the Greek "pilètos" (πιλητος) + "carpos" (καρπος), making reference to the sections' villose fruits.

Ecology, habitat and conservation. The species belonging to A. sect. Rhopalephora are intimately related to shady and moist understory environments across their distribution range. Nonetheless, they can also be found growing in dry or flooded grasslands, forest margins and disturbed areas. The section as a whole seems to be in need of conservationist attention. Two out of the five species accepted by us are known from a handful of collections, with the Madagascar endemic A. rugosum H.Perrier being known by only three collections. Aneilema micranthum is known from a considerably greater number of collections, nonetheless its distribution clearly indicates that this species might occur or might have occurred in other countries and areas of Malesia. Finally, A. vitiense has its distribution greatly extended in the present study, rendering it as Least Concern (LC) and with no need of current conservationist attention.

Taxonomical notes. *Piletocarpus* has hitherto been considered as a synonym of *Dictyospermum*, because of *D. protensum* Wight (eMonocot 2010; The Plant List 2013; Tropicos.org 2016). *Dictyospermum protensum* was described by Wight (1853), who mentioned it was a synonym of the unpublished *A. protensum* Wall. The name was later combined by Hasskarl (1863) into his new genus *Lamprodithyros* Hassk. (currently treated as a section of *Aneilema*; Faden 1991). When Hasskarl (1864a) described *Piletocarpus*, he assigned no species to his new genus. Six years later, Hasskarl (1870) combined *D. protensum* and *A. vitiense* into *Piletocarpus*. Nonetheless, many authors still follow Kunth's

misinterpretation of *D. protensum* in which he also included specimens of *D. ovalifolium* Wight. This tortuous taxonomic history revolving around *D. protensum* made most Commelinaceae specialists erroneously treat *Piletocarpus* under the synonymy of *Dictyospermum*. Since *D. protensum* is accepted by us as a synonym of *A. protensum*, and *D. vitiense* is accepted by us as a synonym of *A. vitiense* (see taxonomic treatment below), all names ever associated to *Piletocarpus* are currently treated under a broader concept of *Aneilema s.l.*, more precisely under *A.* sect. *Rhopalephora*. Thus, *Piletocarpus* is here considered a synonym to *A.* sect. *Rhopalephora*.

Nomenclatural notes. Lauterbach (1905) incorrectly designated A. vitiense as the type species of Rhopalephora. However, this species was not included by Hasskarl (1864a) in the genus' original description. Thus, the valid typification of Rhopalephora was only later accomplished by Faden (1977), when he designated R. blumei Hassk. [$\equiv A$. micranthum (Vahl) Kunth] as the type of the genus.

Morphology. The species of A. sect. Rhopalephora possess unusual leaf, inflorescence, floral, and fruit morphologies. The leaves are peculiarly subpetiolate, a character also present in various species of A. sect. Amelina, A. sect. Aneilema, A. sect. Brevibarbata, A. sect. Lamprodithyros, A. sect. Pedunculosa, and A. sect. Rendlei. This character seems to be closely related to the understory habit of some species of Aneilema s.l., being especially striking in A. sect. Rhopalephora, due to the length of the subpetiolate and the abrupt basal constriction of the leaf blade of most species. The main florescence in A. sect. Rhopalephora in a pedunculate, terminal, many-branched thyrse, with alternate cincinni, as in most species of Aneilema (Faden 1991; Panigo et al. 2011). Nonetheless, the main florescence in A. sect. Rhopalephora tends to present a characteristic lax corymb- to umbel-like appearance. This is due to the reduction of the main axis, combined to the gradual reduction in the length of the cincinni internodes, and the decrease in the number of flowers per cincinni towards the apex of the main florescence.

Floral morphology in A. sect. Rhopalephora is very characteristic for some reasons: (1) they possess relatively big flowers (i.e., much bigger than most species of Aneilema); (2) the flowers possess a 60° torsion in the floral display, which is only similar to the one observed in Dictyospermum and Murdannia (tribe Commelineae), and Cochliostema Lem. and Tripogandra Raf. (tribe Tradescantieae); (3) the sepals are deflexed at post-anthesis and in fruit; (4) the medial petal is generally flat or just slightly concave; (5) the filaments of the stamens are connate at least basally, but generally up to half their length, and also generally basally connate with the filaments of the staminodes; (6) the antherodes possess stipitate lobes; (7) and the gynoecium is stipitate and puberulous with a mixture of minute glandular and 2-lenghted hook hairs. Furthermore, the dorsal locule is peculiarly prominent, giving the capsules of most species a very characteristic humpbacked appearance. It is worth highlighting that aside from the 60° torsion in the floral display, none of the aforementioned characters is exclusive to A. sect. Rhopalephora, inside Aneilema s.l. Nonetheless, this combination of characters is exclusively found in members of this section (Faden 1977, 1991, 1998; present study). Aneilema sect. Rhopalephora seems to be morphologically and phylogenetically related to A. sect. Lamprodithyros, with high statistical support (Kelly and Evans 2014; Evans et al., in prep.). Both sections share the medial petal equal or subequal to the paired petals, filaments of the stamens at least basally connate, antherodes-lobes stipitate and globose to ellipsoid, filaments of the lateral staminodes basally not thickened and generally straight, lateral stamens monomorphic in bisexual and staminate flowers, pollen of the same color in the medial and lateral anthers, medial anther bigger and of a different shape than the lateral ones, ovary and capsules stipitate commonly covered with a mixture of

glandular and hook hairs, and capitate stigma. Furthermore, both sections possess adjacent distributions, being separated by a small geographic area.

Key to the species of Aneilema sect. Rhopalephora

- 1. Herbs annual; leaf blades puberulous with hook hairs; medial petal sessile; mature capsules trigonal obconic, apex truncate; seeds rectangular to narrowly rectangular, testa rugulose to rugulose-foveolate, embryotega lateral... *Aneilema rugosum* H.Perrier (Figs 2C & 10–11)
- Herbs perennial; leaf blades glabrous or pubescent with simple hairs; medial petal shortly-clawed; mature capsules broadly trigonal ellipsoid or dolabriform or globose to subglobose, apex acute to acuminate or round; seeds slightly reniform to elliptic to broadly elliptic to broadly oblong, testa slightly costate or scrobiculate or foveolate, embryotega semilateral... 2
- 2. Leaves distichously-alternate; medial petal trullate, staminodes with filaments almost straight and pointing downwards, antherode-lobes ellipsoid; mature capsules shortly-stipitate, ellipsoid to broadly ellipsoid; seeds deeply foveolate... *Aneilema vitiense* Seem. (Figs 2E & 16–18)
- Leaves spirally-alternate; medial petal broadly ovate to reniform, staminodes with filaments slightly curved and pointing upwards, antherode-lobes globose to subglobose; mature capsules stipitate or sessile, dolabriform or globose to subglobose; seeds with shallow pits and foveolas... 3
- 3. Herbs delicate, with a definite base; leaves membranous, blade ovate, base obtuse to round, smooth; thyrsi with 1–2 cincinni; flowers with pedicels deflexed at anthesis, pre-anthesis and post-anthesis, staminodes with filaments only basally connate with the stamens; testa slightly costate with ridges generally terminating in a small furrow... *Aneilema micranthum* (Vahl) Kunth (Figs 2A & 3–4)
- Herbs robust, with an indefinite base; leaves chartaceous, blade lanceolate to elliptic, base cuneate, rarely obtuse, scabrid; thyrsi with (2–)3–8 cincinni; flowers with pedicels patent at anthesis and pre-anthesis, erects at post-anthesis, staminodes with filaments connate ca. 1–2 mm to the stamens; testa scrobiculate or foveolate... 4
- 4. Leaf-blades abaxially sparsely pubescent to pubescent with uniseriate hairs; cincinni sparsely puberulous with a mixture of eglandular and hook hairs; mature capsules stipitate, dolabriform, persistent style not sunken into the capsule apex; seeds broadly oblong to rectangular, foveolate, testa strongly cleft towards the embryotega, grey to greyish brown, not farinose, hilum in a deep groove.... *Aneilema scaberrimum* (Blume) Kunth (Figs 2D, Fxxii & 13–14)
- Leaf-blades abaxially glabrous; cincinni sparsely puberulous with eglandular hairs; mature capsules sessile to subsessile, globose to subglobose, persistent style slightly sunken into the capsule apex; seeds broadly elliptic to slightly reniform, scrobiculate, testa slightly cleft towards the direction of the embryotega, light grey to light greyish brown, farinose with the white farinae accumulating in the pits, hilum in a weak ridge... Aneilema protensum (Wall. ex Wight) Thwaites (Figs 2B, Fxxi & 6-8)

1. *Aneilema micranthum* (Vahl) Kunth, Enum. Pl. 4: 70. 1843. Figs 2A & 3–4

Rhopalephora micrantha (Vahl) Faden, Phytologia 37(5): 479. 1977.

Commelina micrantha Vahl, Enum. Pl. 2: 178. 1805. Lectotype (designated by Faden 1977): INDONESIA: Java, s.loc., fl., s.dat., F. Lahaie 3207 (P-JU barcode P00668941!).

Commelina conspicua Zoll., Syst. Verz.: 64. 1854, nom. illeg. non Commelina conspicua Blume. Lectotype (designated here). INDONESIA. s.loc., fl., fr., May 1843, H. Zollinger 1251 (G-DC barcode G00357404!; isolectotypes: B†, P barcode P06869579!; the L barcode L002509104 specimen is a Syzygium sp.).

Commelina monadelpha Blume, Enum. Pl. Javae 1: 4. 1827.

Aneilema monadelphum (Blume) Kunth, Enum. Pl. 4: 70. 1843.

Rhopalephora blumei Hassk., Bot. Zeitung (Berlin) 22: 59. 1864, nom. superfl.

Aneilema scaberrimum var. monadelphum (Blume) R.S.Rao, Notes Roy. Bot. Gard. Edinburgh 25: 183. 1964.

Dictyospermum monadelphum (Blume) Panigrahi, Phytologia 29: 338. 1975[1974]. Lectotype (designated here): INDONESIA. East Java: Salak, Apr 1784, fl., fr., C.L. Blume 1784 (L barcode L0041722!; isolectotype: L barcode L0820851!).

Commelina trifida Thunb., Thunberg [Nensén], Mus. Nat. Acad. Upsal., App. 18: 3. 1809, nom. nud.

Commelina triflora Thunb., Thunberg [Winberg], Fl. Jav.: 6. 1825, nom. nud. Voucher. INDONESIA: Java, Herb. Thunberg 7882 (UPS, IDC microfiche 1036 "trifida").

Commelina pulchra Blume, pro. syn. Voucher. INDONESIA. Java, Blume s.n. (L barcodes L001433162!, L001433178!, L001433179!).

Description. Herbs 20–36 cm tall, perennial, with a definite base, terrestrial. Stems prostrate with ascending apex, little branched or branched only at the base; internodes 0.5-1 cm long, green, sparsely puberulous to puberulous with hook hairs. Leaves spirally-alternate, subpetiolate; sheaths 0.6–1.8 cm long, green to reddish, sparsely puberulous to puberulous with hook hairs, becoming glabrous with age, margins setose, hairs hyaline; petiole 0.2-1 cm long, rarely inconspicuous in the upper leaves; lamina $2.3-13.5 \times 0.8-3.5$ cm, ovate to ovate oblong, membranous, light to medium green, drying greyish green to olive-green on both sides, glabrous on both sides, base symmetric, rarely slightly asymmetric, round to obtuse, margins green, glabrous, sometimes sparsely ciliolate at base, apex acute; midvein impressed adaxially, obtuse abaxially, secondary veins 2–4 pairs. *Inflorescences* 1–4, terminal or axillary in the uppermost nodes, with 1–2 cincinni; peduncles 2.5–4.6 cm, puberulous with hook hairs; basal bract reduced or leaf-like, $0.6-1.2 \times 0.1-3.1$ cm, elliptic to ovate, glabrous, base obtuse to cuneate, margins glabrous, apex acuminate; cincinni bracts ca. 1.3–2.6 × 0.7–2.4 cm, triangular to broadly triangular, minutely puberulous at base with a mixture of glandulous and hook, margins glabrous, apex acute; cincinni 3-6-flowered, cincinnus peduncle 1.2-2.6 cm, green to vinaceous to purple, with a mixture of sparse eglandular (scabrid) and sparse or more numerous glandular, hyaline hairs, cincinnus internodes 0.2–2.1 cm long, glabrous to sparsely puberulous with hook hairs; bracteoles $1.3-2.4 \times 2.6-4$ mm, glabrous, margins glabrous, apex acute. Flowers 1.2–1.6 cm diameter; floral buds $1.5-2.1 \times 1-1.9$ mm, green; pedicels deflexed at anthesis, pre-anthesis and post-anthesis, 2.6–7.4 mm long, green, glabrous, 1.3–1.7 cm long in fruit; sepals green, upper sepal $2.4-3.2 \times 0.9-1.4$ mm, ovate, apex round, lower sepals 2.1- $2.6 \times 1-1.2$ mm, obovate, apex round; petals white to pale lilac, paired petals $6.8-8.1 \times 4.3-$ 5.8 mm, limb reniform, $5.9-6.7 \times 4.3-5.8$ mm, base cordate, apex round, claw 1.8-2.4 mm long, medial petal $4.5-5.9 \times 3.9-5.4$ mm, shortly-clawed, claw 1.4-2 mm long, limb 3.2-3.9× 3.9–5.4 mm, rhomboid reniform, base cordate, apex round; staminodes with filaments 4.6– 5.8 mm long, only basally connate with the filaments of the stamens, slightly decurved to undulate pointing upward, white, antherodes $0.2-0.3 \times 0.7-1.2$ mm, lobes globose; stamens with filaments connate for ca. 3–4 mm, lateral stamens with filaments 6.2–7.7 mm long, slightly decurved pointing upward, white, anthers $0.3-0.5 \times 0.3-0.4$ mm, ovate to broadly ovate, connective pale yellow, anther sacs brown to vinaceous; medial stamen with filament 6.1-6.8 mm long, slightly decurved pointing upward, white, anther $0.4-0.5 \times 0.3-0.5$ mm. held near the antherodes, connective light pink to pale lilac, anther sacs cream; ovary subglobose, 2.1–2.8 × 1.7–2.5 mm, green, style 6–7.4 mm, not sunken into the ovary, gently curved at the apex, white, stigma white. Capsules 5.4–7.6 × 2.2–4.4 mm, stipitate, stipe 1.9– 2.6 mm long, dolabriform, green when immature, light brown when mature, apex acute, dorsal locule 0(-1)-seeded, ventral locules slightly concave to flat, (0-)1-seeded. Seeds 3.4-3.9 × 1.7–2.2 mm, slightly reniform to elliptic, slightly cleft towards the embryotega, testa light grey, sparsely farinose, slightly costate, with ridges radiating from the embryotega and generally terminating in a small furrow; hilum on a weak ridge; embryotega semilateral.

Specimens seen. INDONESIA. Without province: Java, fl., s.dat., s.leg., s.n. (L barcode L1433162); Java, fl., fr., s.dat., s.leg., s.n., (L barcode L1433179); fl., fr., 31 May 1894, H. Raap 134 (BO, GE, L); Java, fl., s.dat., s.leg., s.n. (L barcode L1433178); st., Sep 1794, F. Lahaie 2255 (P). Aceh [Atjeh]: Sumatra Island, Gunong Kemiri, fl., 27 Aug 1971, K. Iwatsuki et al. 828 (K). Bali: Java Island, Kleine Soenda Eilanden, N Bali Gitgit, fl., 5 Apr 1936, C.G.G.J. van Steenis 7785 (K); fl., 11 Apr 1936, C.G.G.J. van Steenis 8123 (K). Banten: Java Island, Sadjira, fl., fr., 28 Jun 1911, C.A. Baker 2103 (BO, L). Maluku [Moluccas]: Boano Island, near Ceram, fl., 12 May 1918, Kornassi s.n. (L barcode L0614591). North Maluku [North Moluccas]: Bucan Island, Gunung Sibela near Waiaua, fl., 1 Oct 1974, E.F. Vogel 3798 (K). Central Java: Dårå en Josoredjo, fl., fr., 18 Sep 1914, C.A. Baker 16284 (BO, L); Semarang, Rararoea, Zhellin bij Banoe, fl., fr., 22 Jun 1930, C.A. Backer 36345 (BO, L). East Java: Banggil, Tjoereh Pedang, fl., 7 Jun 1931, E.H.H. Clason-Laarman F16 (L); Helling Smeroe, Ranoe Daronga, fl., fr., 27 Jul 1932, Kleinhoonte 288 (L); Besoeki, Jang Plateau East, Ravine of Djeloewang, fl., fr., 18 Jun 1938, C.G.G.J. van Steenis 11084 (BO, L); Madiun Regency, Ngebel District, fl., fr., 25 May 1896, S.H. Koorders 23220B (K, L); Kediri, Gadoengan-Pare, fl., fr., 11 May 1905, S.H. Koorders 42521B (BO, L); Meru Betiri Nature Reserve, SE of Djember, fl., Jul 1975, R. van der Veen s.n. (L barcode L1433170); Situbondo Regency, Besuki, Gunung Ringgit, fl., 8 Mar 1940, P. Buwalda 7494 (BO, K, L). Special Capital Region of Jakarta: Island of Java, Jakarta [Batavia], Gunung Salak, fl., fr., 5 Jan 1919, C.A. Baker 26441 (L); fl., 2 May 1920, B van den Brink 3602 (K). West Java: Dajo (omgeving waterval), fl., fr., 10 May 1949, S.M. Popta 791/81 (L); Prope Saka, fl., s.dat., C.L. Blume s.n. (L barcode L1433165); Mt. Gede, au bord du lac Talaga Warna, prés du Poentjak, de Sindanglaya, 23 May 1904, B.P.G. Hochreutiner 1190 (G, L); ad groote Tjikideng, 2 May 1920, R.C. Bakhuizen van den Brink Jr. 3602 (BO, L); Tjibodas river, fl., 21 Jun 1931, W.A. Visser D40102 (L); Bandung, Dennenkust, fl., fr., 29 May 1950, S.M. Popta 791 (L).

Distribution and habitat. Endemic to Indonesia, more specifically to the islands of Sumatra, Java, Lombok, Flores, and Boano (Fig 5). Found in shaded areas understory or along margins of forests at 50–1300 m alt.

Phenology. It was found in bloom from January to October and fruit from January to September but peaking between April and June.

Conservation status. Aneilema micranthum possesses a wide EOO (ca. 2,578,719.079 km²), but a considerably narrow AOO (ca. 96.000 km²). Since it is only known from few collections and endemic to four Indonesian islands, but mostly concentrated in Java, following the IUCN (2001) recommendations, *A. micranthum* should be considered Endangered [EN, A2cde+B2b(ii, iii, iv)+D2].

Etymology. The epithet derives from the Greek "*mikros*" (μικρς) + "*anthos*" ('ανθος) presumably due to this species small flowers.

Nomenclatural notes. According to the label on the type of *Commelina micrantha* in P-JU, the specimen was collected in India by a naturalist named "Lahaye". Faden (1977) interpreted to represent a collection by Abbé Lahaye (?–1802). Nevertheless, Lahaye worked in the West Indies (Haiti) around 1796, and never collected in the Paleotropics (Chaudhri et al. 1972). It is far more likely for the "Lahaye" on the label represents a misspelling of Félix De Lahaie's name (1767–1829). At the time, De Lahaie was living in the Pacific and Malesia region, and lived in Java from October 1793 and January 1797 (Van Steenis-Kruseman 1950) and, as written in the label, the specimen was received by Thullier in 1800. Thus, the correct collector of the type of *C. micrantha* is "*F. Lahaie 3207*", with no specified collection date.

Blume (1827), when describing *Commelina monadelpha*, only mentions "*Crescit ad montem Salak Javae insulae*", making no reference to the collection number and where the specimen was deposited. Faden (1977), after visiting L found only one specimen matching the protologue and thus treated it as the holotype. However, after a more thorough search we found a second specimen also matching the protologue. Thus, we designate the specimen L0041722 as the lectotype of *C. monadelpha*.

In Thunberg's herbarium, you can find a specimen from Java under the name *Commelina trifida* Thunb. This name was only mentioned in a checklist by Nensén (1809), thus being considered a *nomen nudum*. It was once again mentioned in a checklist by Winberg (1825), as "*C. triflora* Thunb.", which clearly represents a transcription error by the author (Juel 1918).

Affinities. Aneilema micranthum is similar to A. scaberrimum due to its stipitate dolabriform capsules, commonly with empty dorsal locules. Nevertheless, it can be easily differentiated by its prostrate stems (vs. erect in A. scaberrimum), leaves membranous, glabrous and smooth, with obtuse to round bases, and glabrous margins (vs. chartaceous, scabrid and hispid, cuneate, rarely obtuse, and ciliate margins), and inflorescences composed of 1–2 cincinni (vs. 3–8 cincinni). Dried specimens of A. micranthum can be similar to specimens of A. vitiense due to their reduced stature, membranous leaves with obtuse to round bases, and few-branched inflorescences. Both species can be differentiated by their phyllotaxy (spirally-alternate in A. micranthum vs. distichously-alternate in A. vitiense), the morphology of the medial petal (shortly-clawed and broadly ovate to reniform vs. sessile and trullate), staminode morphology and posture (slightly curved and pointing upwards, with globose antherode-lobes vs. straight and pointing downwards, with ellipsoid antherode-lobes), and shape of the mature capsules (dolabriform vs. ellipsoid to broadly-ellipsoid). Finally, A. micranthum can be confused with some flowering specimens of A. protensum that possess a reduced stature, and ovate leaves. Nonetheless, both species can be distinguished by the number of cincinni, posture of the flowers at anthesis and pre-anthesis, and the degree of connation of the filaments.

2. *Aneilema protensum* (Wall. *ex* Wight) Thwaites, Enum. Pl. Zeyl.: 322. 1864. Figs 2B, Fxxi & 6–8

Dictyospermum protensum Wall. ex Wight, Icon. Pl. Ind. Orient. 6: 30, t. 2071. 1853. Lamprodithyros protensus (Wall. ex Wight) Hassk., Flora 46: 389. 1863. Piletocarpus protensus (Wall. ex Wight) Hassk., Commelin. Ind.: 15. 1870. Piletocarpus protensus var. intermedius Hassk., Commelin. Ind.: 17. 1870.

Aneilema protensum (Wall. ex Wight) C.B.Clarke, Commelyn. & Cyrtandr. Bengal.: t. 24. 1874; C.B.Clarke in De Candolle & De Candolle, Monogr. Phaner. 3: 219, t. 4, f., 1881, isonyms. Lectotype (designated by Panigrahi 1975). NEPAL. India orient., fl., fr., 1821, N. Wallich 5218 (K barcode K000854140!; isolectotypes: B barcode B100367823!, E barcode E00179399!, G-DC barcode G00489387!, GZU barcode 000282990!, K barcode K001120173!, P barcode P02197259!, P-JU barcode P06869580!, W n.v.).

Aneilema protensum Wall. ex Wight, Icon. Pl. Ind. Orient. 6: 30, t. 2071. 1853, pro. syn. Aneilema protensum Wall., Numer. List: [182] # 5218. 1831–1832, "protensa", nom. nud. Commelina protensa Wall. ex Steud., Nomencl. Bot., ed. 2, 1: 402. 1840, nom. nud.

Piletocarpus protensus var. angustifolius Hassk., Commelin. Ind.: 17. 1870. Lectotype (designated here). INDIA. Meghalaya: Khasia regione tropica, fl., fr., s.dat., J.D. Hooker & T. Thomson s.n. (L barcode L0820737!; isolectotypes: G-DC barcode G00489385!, K n.v., L barcode L0820738!, P barcodes P02197255!, P02197257!, P02197258!, P02197260!, P02197261!, U barcode U0282855!), Syn. nov.

Piletocarpus protensus var. latifolius Hassk., Commelin. Ind.: 15. 1870. Lectotype (designated here). INDONESIA. Sumatra, fl., s.dat., P.W. Korthals s.n. (L barcode L0820736!; isolectotypes: L barcodes L0820734!, L0820735!, L0820740!), Syn. nov.

Floscopa bambusifolia H.Lév., Repert. Spec. Nov. Regni Veg. 9(196–198): 20–21. 1910. Pollia bambusifolia (H.Lév.) H.Lév., Fl. Kouy-Tchéou: 77. 1914. Lectotype (designated here). CHINA. Kouy-Tchéou: Lo-Fou, fl., fr., 8 Oct 1908, J. Cavalerie 3471 (E barcode E00386732!; isolectotypes: E barcodes E00386733!, E00386734!, P barcodes P02197252!, P02197253!, P06869584!, US barcode US00091579!). Syn. nov.

Description. Herbs 0.5–2 m tall, perennial, with an indefinite base, terrestrial. Stems with a short prostrate base, ascending to erect apex, densely branched or branched only at the base; internodes 0.8–14.6 cm long, green, sparsely pubescent with uniseriate hairs, becoming glabrous with age. Leaves spirally-alternate, sessile to subpetiolate; sheaths 0.5-4 cm long, green to reddish, puberulous with uniseriate hairs, margins setose, hairs hyaline; petiole 0.3– 0.8 cm long, sometimes inconspicuous; lamina $1.5-15.2(-17) \times 0.5-4.2$ cm, linear elliptic to elliptic to lanceolate, rarely ovate, chartaceous, dark to medium green, drying olive-green to light brown on both sides, adaxially scabrid and pubescent with uniseriate hairs, abaxially scabrid and glabrous, base symmetric, cuneate, margins green, ciliate, apex acuminate to caudate, sometimes acute in young leaves; midvein impressed adaxially, obtuse abaxially, secondary veins 2-3 pairs. *Inflorescences* 1-5, terminal or axillary in the uppermost nodes, with 2-8 cincinni; peduncles 1.8-7.3 cm long, densely puberulous with uniseriate hairs; basal bract reduced or leaf-like, 1.1-2.6 × 1.2-1.9 cm, elliptic to ovate, adaxially scabrid and sparsely pubescent with uniseriate hairs, abaxially glabrous, rarely sparsely pubescent with uniseriate hairs, base obtuse to cuneate, margins ciliate, apex acute; cincinni bracts 2.3–4.2 × 1.2-3.3 mm, ovate to broadly ovate, glabrous, margins glabrous, apex acute; cincinni 4-6flowered, cincinnus peduncle 1.1–3.1 cm, green to vinaceous to purple, sparsely pubescent with eglandular, hyaline hairs, cincinnus internodes 4.2–15.4 mm long, glabrous to sparsely pubescent with eglandular, hyaline hairs; bracteoles $0.8-2.5 \times 2.2-3.7$ mm, glabrous, margins glabrous, apex acute. Flowers 1.1–1.9 cm diameter; floral buds 1.9–3.8 × 1.4–2 mm, green to vinaceous to purple; pedicels patent at anthesis, pre-anthesis and post-anthesis, 0.1–1 cm long, green, glabrous, 1.2–2.7 cm long in fruit; sepals green to vinaceous to purple, upper sepal 2.8– $3.5 \times 1.3 - 2.5$ mm, ovate, apex round, lower sepals $1.8 - 3.2 \times 1.2 - 1.9$ mm, obovate, apex round; petals pale lilac to lilac to light blue, paired petals 5.6-8.8 × 5.5-6.8 mm, limb triangular reniform to reniform to rhomboid reniform, $4.8-7.2 \times 5.5-6.8$ mm, base truncate to cordate, apex round to obtuse, sometimes acute, claw 0.8-1.6 mm long, medial petal 3.2-4.1 \times 2.6–4.2 mm, shortly-clawed, claw 0.4–1 mm long, limb 2.8–3.1 \times 2.6–4.2 mm, rhomboid reniform to rotund, base cordate to truncate, apex obtuse to round; staminodes with filaments 4.2–5.6 mm long, connate for ca. 1–2 mm with the filaments of the stamens, straight pointing downward, white to pale lilac, antherodes 0.2–0.4 × 0.7–1 mm, lobes globose; stamens with filaments connate for ca. 3–4 mm, lateral stamens with filaments 6.8–9.2 mm long, sigmoid to J-shaped, white to pale lilac to lilac, anthers $0.6-0.8 \times 0.2-0.4$ mm, ovate to elliptic, connective pale lilac to lilac, anther sacs lilac to purple, rarely vinaceous; medial stamen with filament 4.7–7.1 mm long, slightly decurved pointing upward, white to pale lilac, anther 0.9– 1.1×0.4 –0.7 mm, not held near the antherodes, connective pale yellow or light pink to pale lilac, anther sacs yellow; ovary subglobose, $1.8-2.1 \times 2-2.2$ mm, light to medium green, style 6.2–8.2 mm, not sunken into the ovary, gently sigmoid, white to lilac, stigma yellow or white to lilac. Capsules $3.3-4 \times 2.5-3.5$ mm, subsessile to sessile, if present stipe 0.1-0.3 mm long, globose to subglobose, green with 3 longitudinal atro-purpureus stripes when immature, light brown with 3 longitudinal black stripes when mature, apex round, dorsal locule (0-)1-seeded, ventral locules slightly prominent, 1-seeded. Seeds 2.5–3.8 × 1.8–3 mm, broadly elliptic to slightly reniform, light grey to light grayish brown, slightly cleft towards the embryotega, testa scrobiculate, with ridges radiating from the embryotega, farinose, with the white farinae accumulating in the pits; hilum on a weak ridge; embryotega semilateral.

Specimens seen. INDIA. Assam: Dalawade, fl., fr., Nov 1848, M.A. Hock 437 (P, US); Jungali Kam/ Bam Garden, fl., fr., Oct 1848, M.A. Hock 175 (CAL, L, P); Tirap River Valley, 12.4-mile mark on Ledo Road, fl., fr., 24 Oct 1945, R.O. Belcher 896 (K). East Bengal: s.loc., fl., s.dat., K.D. Griffith 5490 (CAL, K, P). Karnataka: Sollekolli forest, along Barpole river bank, frequent, Coorg Dist., fl., fr., 29 Oct 1963, A.S. Rao 95293 (BSI, L). Kerala: Palakkad, Dhoni, fl., 27 Mar 1910, C.E.C. Fischer 1840 (K). Manipur: Barak River, fl., fr., Nov 1907, A.E. Meebold 6217 (K); Karong, fl., fr., 16 Oct 1950, W.N. Koelz 26622 (L. MICH). Meghalava: East Khasi Hills, Shillong, fl., fr., 16 Nov 1887, s.leg. s.n. (K); fl., fr., 14 Aug 1886, C.B. Clarke 44514B (K); 11 Nov 1872, C.B. Clarke 18155 (CAL, K); Guwahati road, 6-7 miles from Shillong, 14 Oct 1930, P.C. Kanjilal 8678 (ASSAM); Khasia Hills, Burnihat, fl., fr., 30 May 1949, T.R. Chand 1595 (L, MICH); Mawryngkneng, fl., fr., 20 Sep 1951, T.R. Chand 4763 (L, MICH); fl., fr., 1 Oct 1951, T.R. Chand 4931a (L, MICH); Shillong, fl., fr., 17 Sep 1954, T.R. Chand 8217 (L, MICH). Mizoran: Lushai Hills, fl., fr., 2 Sep 1831, M.L. Wenger 330 (K). Nagaland: Naga Hills, fl., fr., 5 Sep 1935, N.L. Bor 6287 (K); Kohima, fl., fr., 16 Sep 1950, W.N. Koelz 26198 (L, MICH). **Odisha:** Koraput, Medeng Gandi, near Pottangi, bank of stream under slight shade, 11 Oct 1950, H. F. Mooney 4102 (K, L); Waltair to Jeypore, 23 Nov 1956, H. Santapau 21374 (BLAT); 23 Nov 1956, H. Santapau 21375 (BLAT). Tamil Nadu: Chennai [Madras], fl., fr., s.dat., R. Wight s.n. (K); fl., fr., 1849, N. Wallich 5223 (K); Pulney Hills, Periyar Shola, fl., fr., 13 Jul 1898, A.G. Bourne & Lady Bourne 127 (K); on the way to Ootacamund from Gudalur, 22 Nov 2010, M.D. Nandikar R10 (BSI, CAL, NGCPR, RB, SUK, US). West Bengal: Kandra, Bardhaman, fl.,

Feb 1908, A.E. Meebold 9106 (K); Seshachal Wildlife Sanctuary, Darjeeling, 20 Oct 2008, A.K. Ghosh & B. Raj 41559 (CAL). INDONESIA. Without province: Java, fl., fr., s.dat., J.-P.L.C.T. Leschenault s.n. (P barcode P06869581!); Sumatra, G. Merapi, fl., fr., 13 Sep 1918, H.A.B. Bünnemeijer 4510 (BO, K, L); Sumatra, Midden Habinsaran, fl., 14 Nov 1920, J.A. Lörzing 7855 (L); Eil. Sipora, omgeving van Sioban, fl., fr., 14 Oct 1924, Iboet 396 (BO, L); Uluan Hills, between Perapat and Porsea, east of Lake Toba, fl., fr., 21 Dec 1925, J.A. Lörzing 14876 (L); East Coast, Déléng Singkoet, north of Bérastagi, Karo Plateau, fl., fr., 1 Feb 1927, H.H. Bartlett 6563 (K, L, MICH, US); E. Mount Sibajak, upper Petani valley, fl., fr., 23 Apr 1929, J.A. Lörzing 15722 (BO, K, L, P, US). North Sumatra: Gunung Batu Lopang, ca. 10 km ESE of Prapat, Lake Toba, fl., fr., 8 Jul 1972, W.J.J.O. de Wilde & B.E.E. de Wilde-Duyfjes 13524 (K); Karo Regency, Berastagi, fl., fr., 5 Feb 1921, H.N. Ridley s.n. (K). South Sumatra: Sungai Kumbang River, fl., fr., 31 Mar 1914, H.C. Robinson & C.B. Kloss 4500 (K). Sulawesi: North Sulawesi, Minahasa Regency, fl., fr., 1897, S.H. Koorders 17800B (BO, L). West Java: Dago Waterval, Bandoeng, fl., fr., 11 Mar 1940, C. Holstvoogd 384C (L); Lembangweg, fl., 25 Jun 1951, S.M. Popta s.n. (L barcode L1433120); Preanger, Tjibodas, fl., 13 Jul 1913, S.H. Koorders 42057B (BO, L); Telagá Warna bij de Poentjak, fl., 14 Feb 1895, H. Hallier 1918 (L); Tjibodas, fl., fr., May 1937, P.J. Eyma 91 (BO, L); Tiibodas (area II), fl., 24 May 1948, D.R. Pleyte 85 (BO, K, L); Telagá Warna prope Poentjak, fl., 24 Feb 1914, H. Hallier 13 (BO, L). West Nusa Tenggara: Sumbawa Island, W Sumbawa, Mt. Batulanteh, N of Batudulang, fl., 2 May 1961, Kostermans 18653 (BO, K, L, P, US). LAOS. Without province: Entre B. Poi et Hong Bok Kao, peo Banac plateau des Boloven, fl., 5 Oct 1928, M.E. Poilane 15810 (P). MALAYSIA. Sabah: Mount Kinabalu, fl., fr., 14 May 1932, J. Clemens & M.S. Clemens 29682 (K). SRI LANKA. Without province: Ceylon, fl., fr., 1836, R. Wight 2844 (K); fl., fr., 1868, G.H.K. Thwaites 3026 (P barcode P02197262); fl., fr., 28 May 1913, M. Walker s.n. (L barcode L1433100). TAIWAN. Without province: Bumkiko, fl., Dec 1914, U. Faurie1501 (P), THAILAND, Without province: Siam, fl., fr., 14 Sep 1922, A.F.G. Kerr 6500 (K). Chiang Mai: Doi Intanond, fl., 13 Sep 1974, K. Larsen & S.S. Larsen 34442 (AAU, L); fl., fr., 13 Sep 1974, K. Larsen & S.S. Larsen 34469 (K); Mae Ditang, Mawn Nga (Hmong) village, Muang Guy subdistrict, fl., fr., 3 Dec 2001, J.F. Maxwell 01-703 (CMU, L); Mae Rim, above Mae Sa Mai village, Mae Sa Gow village, Bong Yaeng subdistrict, fl., fr., 18 Nov 2001, J.F. Maxwell 01-617 (L); Mae Wang, Jet Lahng village, below Pah Ngaem limestone cliffs, Mae Win subdistrict, fl., fr., 6 Oct 2004, J.F. Maxwell 04-568 (L); Muang, Doi Suthep, fl., 3 May 1958, F. Floto 3212 (L); fl., fr., 11 Sep 1958, F. Floto 4920 (L 2ex); fl., fr., 10 Oct 1958, F. Floto 5574 (C, L); Doi Sutep, east side, Pah Laht Falls, fl., 1 Oct 1987, J.F. Maxwell 87-1101 (CMU, L). Chiang Rai: Mae Sai, Doi Dtung, east slope of Doi Chang Moop above Wat Noi, Huay Cry subdistrict, off highway 1149, 26 Sep 2006, J.F. Maxwell 06-671 (CMU, L). Chonburi: Chundaten Falls, fl., 16 Nov 1974, J.F. Maxwell 74-981 (BK, L). Kew Kieo: Siricha District, Chonburi, fl., fr., 22 Dec 1974, J.F. Maxwell 74-1117 (BK, L). Payao: Muang, Dei Luang National Park, Jahm Bah Tawng Falls, fl., fr., 21 Nov 1997, O. Petrmitr 169 (CMU, L). Yala: Betong district, Boon Jeen Falls, Tana Merah subdistrict, fl., fr., 16 Dec 1986, J.F. Maxwell 86-1070 (CMU, L). VIETNAM. Without province: s.loc., fl., s.dat., A.L. Takhtajan s.n. (US barcode US1998278); fl., fr., Nov 1930, M. Pételot 5307 (P); Tonkin, fl., fr., Oct 1887, B. Balansa 4107 (P). Lào Cai: Sa Pa, Khoang Village, fl., 11 Sep 2005, V.X. Phuong et al. HNK 88 (K). Son La: Bac Yen, Ta Sua, Chu Village, fl., fr., 8 Oct 2008, N.V. Du et al. HNK 2723 (K); Ngoc Chien, Ban Chomkhon, fl., fr., 2 Oct 2008, N.V. Du et al. HNK 2248 (K, US).

Distribution and ecology. Known to occur in India (Assam, Karnataka, Manipur, Meghalaya, Nagaland, Odisha, Tamil Nadu, and West Bengal), Indonesia (Java, Sulawesi and Sumatra), Malaysia, Sri Lanka, Taiwan, Thailand (Chiang Mai, Chiang Rai, Chonburi, Kew

Kieo, Payao, and Yala), and Vietnam (Fig 9). Nonetheless, it is likely that with further field and herbaria studies, this species distribution will prove to be much wider than herein described. Found growing along roadsides and forests understory.

Etymology. It derives from the Latin "protensus", meaning extended, and probably makes reference to this species' elongated stems.

Phenology. Flowering and fruiting year-round but peaking between September and November. Flowers open around 10:00 AM and begin fading around 12:30 AM.

Conservation status. *Aneilema protensum* possesses wide EOO (ca. 15,521,685.917 km²) and AOO (ca. 360.000 km²). Thus, following the IUCN (2001) recommendations, *A. protensum* should be considered Least Concern (LC).

Nomenclatural notes. Much widespread in Southeast Asia was a species long known as Aneilema protensum Wall., a nomen nudum that appeared in Wallich's List of dried plants (1832–1833), based on a collection from Nepal. Although by present rules most of the names in this List are invalid as no descriptions or references to these are given, it was considered as an authorial work in Southeastern Asia, and the names in it were adopted by Cherfils (1937) and possibly still are today, as they are included in IPNI usually without any comments. Thus, they were often inadvertently effectively validated by later authors, like Thwaites (1864), who effectively proposed A. protensum as a new combination based on Dictyospermum protensum Wall. ex Wight. This species had, for a long time, a controversial generic placement. Steudel (1840) placed it in Commelina, while Wight (1853) was the first to validly publish a name for this taxon under the genus Dictyospermum. Hasskarl also included it in Dictyospermum (1864a), but almost simultaneously, also in Lamprodithyros Hassk. (Hasskarl 1863, 1864b), and later in Piletocarpus Hassk. (Hasskarl 1866, 1870). Hasskarl (1870) accepted three varieties for P. protensus, noting that there were intermediate forms between them, with Blume's C. scaberrima being intermediate between P. protensus var. intermedius and P. protensus var. angustifolius, based on leaf shape. Piletocarpus protensus var. intermedius is not an invalid or illegitimate name, although the autonym P. protensus var. protensus should have been used after the lectotypification by Panigrahi (1975). Aside from that, since Hasskarl (1870) cited C. scaberrima, the earliest valid epithet for his taxonomic concept, he should have placed his newly proposed varieties under that name. However, the *Code* is lenient: the combinations are legitimate, but incorrect (Turland et al. 2018, Art. 55.2). Rao (1964), after analyzing the type specimens in L, concluded that these varieties were just different ecoforms of the same species, and thus didn't merit any taxonomical recognition. He also regarded C. scaberrima (\equiv A. scaberrimum) and C. monadelpha (\equiv A. micranthum) as varieties of the same species and proposed a varietal name for the latter.

When describing *Piletocarpus protensus* var. *angustifolius* Hasskarl (1870) made reference to a Hooker & Thomson specimen, without details on its collector's number and herbaria where it is housed. After carefully analyzing G, K, L, P, and U we came across several specimens that matched the protologue. One of the specimens housed at L (i.e., L0820737) is in great conditions and bears both flowers and matures capsules. Furthermore, it is annotated in Hasskarl's handwriting, making it the obvious choice for a lectotype.

Léveillé (1910) described *Floscopa bambusifolia* from China and mentioned only "Kouy-Tcheou: Lo-Fou, oct. 1908 (Jul. Cavalerie, 3471)", making no reference to which herbarium the specimen was housed. After analyzing the collections of E, P, and US, we came across six specimens that matched the protologue. Since Léveillé's herbarium was purchased

in 1919 by E (Stafleu and Cowan 1979), we chose the specimen E00386732 as the lectotype, since it bears the original label with Léveillé handwriting.

A worth-mentioning herbarium name is *Aneilema sessile* Nandikar et al. During late 2017 the authors of this study erroneously believed the name *A. protensum* to be unavailable, due to a misinterpretation of the *Code* (Turland et al. 2018). This misinterpretation led us to believe a replacement name had to be proposed for this taxon. This name was used to name several herbarium specimens of *A. protensum* at K, L, P, W, and U. However, since we are now aware that *A. protensum* is indeed available for use, the name *A. sessile* will never be published by us in the same concept and circumscription as originally conceived.

Affinities. Aneilema protensum is similar to A. scaberrimum in gross morphology, due to their similar habit, leaf morphology, inflorescence architecture, and floral features. However, it differs from A. scaberrimum by its abaxially glabrous leaf-blades, medial petal concave, capsules globose to subglobose with persistent style slightly sunken into the capsule apex, seeds broadly elliptic to slightly reniform, testa scrobiculate, slightly cleft in the direction of the embryotega, farinose with the white farinae accumulating in the pits, and hilum on a weak ridge. Aneilema protensum can also be confused with A. micranthum due to its inflorescence architecture, but can be differentiated by leaf morphology, flower posture, and capsule morphology. Aneilema protensum, A. scaberrimum, and A. micranthum are morphologically very similar, and compose what is treated by us as the A. scaberrimum species complex. Species belonging to this complex are extremely hard to identify based solely on dried specimens lacking fruits and seeds.

Piletocarpus protensus var. angustifolius was distinguished by Hasskarl (1870) from P. protensus var. intermerdius and P. protensus var. latifolius based exclusively on leaf-blade shape. Based on our herbarium, field and cultivation studies, we have observed that variation leaf blade shape seems to be environmentally related, and so does not merit any taxonomic recognition. Thus, we reduce Piletocarpus protensus var. angustifolius, P. protensus var. imtermedium ($\equiv P$. protensus var. protensus), and P. protensus var. latifolius to mere synonyms of A. protensum.

3. *Aneilema rugosum* H.Perrier, Notul. Syst. (Paris) 5(3): 195. 1936. Figs 2C & 10–11

Rhopalephora rugosa (H.Perrier) Faden, Phytologia 37(5): 480. 1977. Type. MADAGASCAR. Diana [Antsiranana]: Montagnes du Sambirano, fl., fr., Mar 1909, J.M.H.A. Perrier de la Bâthie 7297 (holotype: P barcode P02088085!).

Description. Herbs 1–2 m tall, annual, with an indefinite base, terrestrial. Stems prostrate with ascending apex, branched only at the base; internodes 3.1–8.3 cm long, green, sparsely puberulous to puberulous with hook hairs. Leaves spirally-alternate, subpetiolate; sheaths 0.9-2.8 cm long, green, sparsely pubescent with hook long, 2-celled hairs, margins setose, hairs hyaline; petiole 1–5.2 mm long to inconspicuous; lamina $4.8-12 \times 1.2-2$ cm, narrowly elliptic to elliptic to narrowly ovate, membranous, drying greyish green to olivegreen on both sides, puberulous to densely puberulous with hook hairs, base symmetric, cuneate, margins ciliolate, apex acute to acuminate; midvein impressed adaxially, obtuse abaxially, secondary veins 2–3 pairs. Inflorescences a solitary thyrse, terminal, with 3–8 cincinni; peduncle 1.2-5.1 cm long, puberulous with hook hairs; basal bract reduced or leaf-like, $0.7-3.1 \times 0.2-0.9$ cm, elliptic to ovate, glabrous, base obtuse to cuneate, margins glabrous, apex acuminate; cincinni bracts $2.1-3.4 \times 1.2-1.8$ mm, ovate, minutely puberulous at base with hook hairs, apex acute; cincinni 5-7-flowered, cincinnus peduncle 1.3-2.2 cm,

puberulous with hook hairs, cincinnus internodes 0.5–2.1 cm long, glabrous to sparsely puberulous with hook hairs; bracteoles $1.3-1.7 \times 3.2-4.6$ mm, sparsely puberulous with hook hairs to glabrous, apex acute. Flowers ca. 1 cm diameter; floral buds 2.4–3.7 × 1.7–2.1 mm, green; pedicels patent at anthesis and pre-anthesis, erect at post-anthesis, 0.2–0.6 cm long, green, glabrous to sparsely puberulous with hook hairs, 1.2–1.7 cm long in fruit; sepals green, upper sepal $2.9-3.4 \times 1.4-1.8$ mm, elliptic, apex round, lower sepals $3.2-4.6 \times 2.1-2.6$ mm, obovate, apex round; petals white to pale lilac to light blue, paired petals $5.2-6.1 \times 4.1-5.5$ mm, limb obovate to broadly obovate, 4.6-5.8 × 4.1-5.5 mm, base cuneate to round to cordate, apex obtuse to acute, claw 0.6-1.3 mm long, medial petal 3.4-5.2 × 1.9-2.3 mm, sessile, base cuneate to obtuse, apex acute, broadly elliptic to obovate; staminodes with filaments 1.1–1.7 mm long, only basally connate with the filaments of the stamens, straight, white, antherodes with lobes ellipsoid; stamens with filaments only basally connate, lateral stamens with filaments 2.3–3.1 mm long, white, anthers $1-1.2 \times 0.9-1$ mm, elliptic, white; medial stamen with filament 1.4–2.2 mm long, white, anther $1.8-3.1 \times 1-1.5$ mm, white; ovary oblongoid, $0.8-1.2 \times 0.6-0.8$ mm, light green, style 4.5-8 mm long, not sunken into the ovary, gently curved at the apex, white to pale lilac to light blue, stigma white to lilac. Capsules 5.8–10 × 2.6–4.5 mm, stipitate, stipe 1.2–2.1 mm long, trigonal obconic, green when immature, light brown when mature, apex truncate, dorsal locule 0(-1)-seeded, ventral locules slightly convex to flat, (0-)1(-2)-seeded. Seeds $2.9-5.3 \times 1.7-2.5$ mm, rectangular to narrowly rectangular, strongly cleft towards the embryotega, testa light grey, rugulose to rugulose-foveolate, sparsely farinose; hilum on a weak ridge; embryotega lateral.

Specimens seen. MADAGASCAR. Itasy [Antananarivo]: bois humides, sur des gneiss, bassin de l'Andranomalaza, près de Bezofo, fl., fr., Oct 1908, J.M.H.A. Perrier de la Bâthie 7299 (P barcode P00446385!). **Atsimo-Andrefana [Toliara]:** Ankaizina, vers 1000 m d'alt., fl., fr., 27 Apr 1923, M.R. Decary 2083 (P barcode P02200183!)

Distribution and ecology. Endemic to Madagascar (Fig 12). In dense shade of humid forests, on gneiss, 100–1000 m alt. It is only known from the type and paratype specimens, despite the intense taxonomic activity in Madagascar.

Phenology. It was found in bloom and fruit from October to April.

Conservation status. *Aneilema rugosum* possesses a wide EOO (ca. 45,937.971 km²), but a considerably narrow AOO (ca. 12.000 km²). Since it is only known from three collections, endemic to Madagascar, and not collected in the past 95 years, following the IUCN (2001) recommendations, *A. rugosum* should be considered Critically Endangered [CR, A2cde+B2b(ii, iii, iv)+D2].

Etymology. From the Latin "rugosus", meaning wrinkled, and makes allusion the ornamentation of the seed testa.

Phenology. It was collected in bloom in March, April and October, and in fruits in April and October.

Affinities. Aneilema rugosum is a quite distinctive species, being easily distinguished from the remaining species of A. sect. Rhopalephora by its leaf blades puberulous with hook hairs, sessile medial petal, mature capsules trigonal obconic with a truncate apex, seeds with rugulose to rugulose-foveolate testa, and lateral embryotega. Based of inflorescence architecture and capsule morphology, A. rugosum seems to be more closely related to A. vitiense. Nonetheless, the evident geographic disjunction, coupled with the peculiar

morphology, makes it risky to infer any relationship with the remaining species of the section. On the other hand, *A. rugosum* is morphologically deviant from the other Madagascan species, *A. aparine* H.Perrier, and all the remaining *Aneilema* species from continental Africa. Despite possessing some peculiar morphological features, its overall morphology is coherent with the circumscription of *A.* sect. *Rhopalephora* proposed by us, thus being retained as a member of the section. In case this species is ever recollected, fresh samples should improve our understanding of its floral morphology, and it should also be sample in a molecular phylogeny. This should allow us to confirm the placement of *A. rugosum* in *A.* sect. *Rhopalephora*, to better understand the evolution of morphological features in the section, and its peculiar Madagascan distribution.

4. *Aneilema scaberrimum* (Blume) Kunth, Enum. Pl. 4: 69. 1843. Figs 2D, Fxxii & 13–14

Commelina scaberrima Blume, Enum. Pl. Javae 1: 4. 1827.

Tradescantia scaberrima (Blume) Hassk., Tijdschr. Nat. Geschied. 10: 120. 1843.

Phaeneilema scaberrimum (Blume) Raizada, J. Bombay Nat. Hist. Soc. 48: 677. 1950.

Dictyospermum scaberrimum (Blume) J.K.Morton, J. Linn. Soc. Soc., Bot. 59(480): 435. 1966, nom. not val. publ., sine ref.

Dictyospermum scaberrimum (Blume) J.K.Morton ex D.Hong, Acta Phytotax. Sin. 12(4): 476. 1974; ex Panigrahi, Phytologia 29(5): 338. 1975[1974]; ex H.Hara, Enum. Fl. Pl. Nepal 1: 82. 1978, isonyms.

Rhopalephora scaberrima (Blume) Faden, Phytologia 37(5): 480. 1977. Lectotype (designated here). INDONESIA. Java, crescit in Javae sylvis montanis, fl., s.dat., C.G.C. Reinwardt s.n. (L barcode L0820741!).

Rhopalephora scaberrima var. subfruticosa C.B.Clarke ex Vrinda & Panikkar., J. Econ. Taxon. Bot. 23: 670. 1999, nom. not val. publ.

Description. Herbs 0.4–1.5 m tall, perennial, with an indefinite base, terrestrial. Stems with a short prostrate base, ascending to erect apex, densely branched or branched only at the base; internodes 1.9-12.7 cm long, green, pubescent with a mixture of hook, glandular an eglandular hairs, becoming glabrous with age. Leaves spirally-alternate, subpetiolate; sheaths 0.6-4.8 cm long, green to reddish, puberulous with uniseriate hairs, margins setose, hairs hyaline; petiole 0.3–1.8 cm long, sometimes inconspicuous; lamina $(1.6-4.8-)9.2-18.7 \times 0.4-$ 4.5 cm, linear ovate to ovate oblong to elliptic, rarely ovate, chartaceous, medium to dark green, drying greyish green to olive-green on both sides, adaxially scabrid and sparsely pubescent to pubescent with uniseriate hairs, abaxially scabrid, sparsely pubescent to pubescent with uniseriate hairs, base symmetric, cuneate, rarely round to obtuse, margins green, ciliate or ciliate only at base, apex acuminate to caudate; midvein impressed adaxially, obtuse abaxially, secondary veins 2-3 pairs. Inflorescences 1-4, terminal or axillary in the uppermost nodes, with 3–8 cincinni; peduncles 2.7–6.7 cm long, puberulous with uniseriate hairs; basal bract reduced, 3.1-21.6 × 1.3-3.9 mm, elliptic to ovate, adaxially scabrid and pubescent with uniseriate hairs, abaxially sparsely pubescent with uniseriate hairs, base obtuse to cuneate, margins ciliate, apex acute; cincinni bracts 1.4–4.4 × 0.9–5.4 mm, ovate to oblong to obovate, glabrous to sparsely puberulous with a mixture of eglandular and hook hairs, margins glabrous, apex obtuse; cincinni (1-)4-6-flowered, cincinnus peduncle 0.9-4.2 cm, green to vinaceous to purple, sparsely puberulous with a mixture of eglandular and hook hairs, cincinnus internodes 1.5-12.3 mm long, sparsely puberulous with a mixture of eglandular and hook hairs; bracteoles 0.9–2.6 × 2.6–2.8 mm, glabrous, margins glabrous,

apex acute. Flowers 1.2–2 cm diameter; floral buds 1.9–2.7 × 1.4–1.9 mm, green to vinaceous to purple; pedicels deflexed at anthesis, pre-anthesis and post-anthesis, 0.2–1.1 mm long, green to vinaceous to purple, glabrous to sparsely puberulous with hook hairs, 1–2.2 cm long in fruit; sepals green to vinaceous to purple, upper sepal $2.2-3.5 \times 1-2.3$ mm, ovate, apex obtuse to acute, lower sepals $1.8-3.4 \times 1.2-1.9$ mm, obovate, apex obtuse to acute; petals white to pale lilac to lilac, paired petals $6.2-9.5 \times 6.8-7.6$ mm, limb triangular reniform to reniform to rhomboid reniform, 5.2–7.8 × 5.9–7.6 mm, base cordate, apex round to obtuse to acute, claw 1–1.8 mm long, medial petal 3.8–5.8 × 2.4–4.3 mm, shortly-clawed, claw 0.7–1.5 mm long, limb 3.1–4.3 × 2.4–4.3 mm, triangular reniform to rhomboid reniform, base cordate to truncate, apex obtuse to acute; staminodes with filaments 4.5-6.8 mm long, connate for ca. 1–2 mm with the filaments of the stamens, slightly decurved to undulate pointing upward, white, antherodes $0.2-0.4 \times 8.2-1.3$ mm, lobes globose, when present medial staminode free, opposed to the dorsal sepal, antherode globose; stamens with filaments connate for ca. 3-4 mm, lateral stamens with filaments 7.2–9.4 mm long, slightly decurved pointing upward, white, anthers $0.4-0.9 \times 0.3-0.5$ mm, ovate to elliptic, connective pale lilac to light blue. anther sacs lilac to purple or blue, rarely vinaceous; medial stamen with filament 5.4–7.8 mm long, slightly decurved pointing upward, white to light pink to pale lilac, anther $0.5-1 \times 0.5-$ 0.8 mm, held near the antherodes, connective pale yellow or light pink to pale lilac, anther sacs yellow; ovary subglobose, 1.8–2.6 × 1.5–2.2 mm, light to medium green, style 3.6–8.7 mm, not sunken into the ovary, gently sigmoid, white to lilac, stigma yellow. Capsules 5.2- 7.8×3.3 –4.8 mm, stipitate, stipe 1.2–3.3 mm long, dolabriform, entirely green or green with 3 longitudinal atro-purpureus stripes when immature, entirely light brown or light brown with 3 longitudinal black stripes when mature, apex acute, dorsal locule 0(-1)-seeded, ventral locules slightly concave to flat, 1(-2)-seeded. Seeds $2.5-3.9 \times 1.8-2.3$ mm, broadly elliptic to broadly oblong, strongly cleft towards the embryotega, testa grey to greyish brown, not farinose, shallowly foveolate, with pits radiating from the embryotega; hilum in a deep groove; embryotega semilateral.

Specimens seen. BANGLADESH. Without province: East Bengal, fl., fr., s.dat., s.leg. 5490 (K, L). CHINA. Yunnan: s.loc., fl., s.dat., A. Henry 11381 (K); s.loc., fl., s.dat., A. Henry 13177 (US); Longchuan, nearby the generator on Husa River, between Mangxian and Husa, Yingjiang, fl., 27 Aug 2001, Y.M. Yuan CN2k1-58 (US); between Husa and Zhangfeng, fl., 27 Aug 2001, Y.M. Yuan CN2k1-64 (US); Nujiang Lisu, Bao shan, off Provincial Road 230 at Gang dand, Bai hua ling, Han long zhai, fl., 22 Jul 2010, Zhang Ting et al. 10CS 2023 (K). INDIA. Andhra Pradesh: Vishakhapatannam, forest near Sunkarimetta, fl., 29 Aug 1960, N.P. Balakrishnan 10925 (MH); Sunkarimetta, fl., 14 Oct 1964, R.V. Kammathy 41229 (MH). Assam: Assam, 1893, fl., King 72636 (MH); Dalawade, fl., s.dat., Masters s.n. (CAL, L barcode L1433098, P barcode P06869585). Goa: Poinguinam, South Goa, 12 Oct 1964, R.S. Rao 103528 (CAL). Karnataka: Coorg, Bhimagundi, fl., 18 Feb 1963, A.S. Rao 85687 (BSI); Perambadi Ghat, fl., fr., 19 Oct 191, A.G. Bourne & Lady Bourne 6255 (K); Hassan, Kenchankumri state forest, fl., 15 Aug 1971, T.P. Ramamoorthy 2032 (US); Middle Shiradi chat, Kenchankumri, fl., fr., 1 Nov 1976, R.B. Faden et al. 76/209 (F, K, U); fl., fr., 1 Nov 1976, R.B. Faden et al. 76/213 (F, US); Jog Falls, Hegni Forest, 30 Nov 1961, Ansari & Kammathy 78698 (BSI); Mysore, Maranahalli, fl., fr., 22 Aug 1969, C.J. Saldanha 14068 (K); Nikund Ghat, North Kanara, 5 Dec 1883, Talbot 367 (BSI). Kerala: Calicut, Peruvannamzhy, fl., fr., 28 Sep 2001, S. Nampy 137 (US); Chenath Nair, fl., fr., 8 Dec 1920, C.E.C. Fischer 4561 (K); Kollam, Travancore, Thenmala, near Tirtakarai Falls, fl., fr., Dec 1933, E. Barnes 704 (K); Palaruvi Hill, Travancore, 10 Sep 1913, C.C. Calder & M.S. Ramaswami 782 (MH); Orkuomalan, 19 Sep 1958, E. Govindaragalu & B.G.L. Swamy 2630 (MH); Munnar, Oct 1938, T. Ekambaram 160 (PCM); Palaruvi Side, Tenamalai, 10 May

1961, K.N. Subramnaiyan 71560 (MH); Bal-mora track, Tenamalai, 04 May 1961, K.N. Subramnaiyan 70895 (MH); Ammanar state, Tennamalai, 21 Nov 1962, K.N. Subramnaiyan 77030 (BSI); Palavuri [Kuttalum], fl., fr., 28 Nov 1961, K.N. Subramnaiyan 77195 (K); Nedumgayam to Meenmutty, Malappuram, 13 Mar 1984, N.C. Nair 81221 (MH); Mukkali forests, 22 Dec 2009, M.D. Nandikar MDN125 (SUK). Odisha: Shrikuti, Ranapur State, 5 Oct 1942, H.F. Mooney 2106 (DD). Tamil Nadu: at the foot of Bonda, 16 May 1964, G.V. Subbarao 37902; Chennai [Madras], Nilgiris, fl., fr., Nov 1884, J.I. Gamble et al. 15702 (K); Gale Bonda, 16 May 1964, G.V. Subbarao 37903 (MH); Paringal, 26 Nov 1957, G.S. Puri 15953; Gokulmalai, Gudalaur, 07 Jan 1963, K.N. Subramnaiyan 82660 (MH); Waterfall state, Annamalai, 13 Sep 1961, K.N. Subramnaiyan 73948 (MH). INDONESIA. Without province: Java, fl., fr., s.dat., S.J. van Ooststroom 14070 (BO, L); Meduce, fl., s.dat., s.leg., s.n. (L barcode L1433114); Sumatra, fl., fr., s.dat., F.A.C. Waitz (L barcode L1433161); fl., fr., Sep 1794, F. Lahaie 2163 (P); fl., 1861, Forbes 2202 (BO, L); NW Helling, G. Malintang, fl., fr., 17 Jul 1918, H.A.B. Bünnemeijer 3541 (BO, L); Bt. nan Tigo, G. Malintang, fl., 20 Jul 1918, H.A.B. Bünnemeijer 3738 (BO, L); G. Merapi, fl., 23 Sep 1918, H.A.B. Bünnemeijer 4860 (BO, L); Karohoogvlakte bij Kabandjahe, fl., fr., 20 Jan 1919, J.A. Lörzing 6201 (BO, L); Midden Habinsaran, fl., 14 Nov 1920, J.A. Lörzing 7855 (BO, L); Uluan Hills between Perapat and Porsea, east of Lake Toba, fl., fr., 21 Dec 1925, J.A. Lörzing 14876 (BO, L); vicinity of Taloen na Oeli, Toba, east of Dolok Si Manoek-manoek, near headwaters of Aek Mandosi, fl., fr., 28 Sep 1936, R.S. Boeea 10104 (US); Taloen Na Oeli, fl., 17 Oct 1936, R.S. Boeea 10670 (US). East Java: Kediri, G. Wilis, fl., fr., 11 Feb 1914, C.A. Backer 11468 (BO, L). West Java: Preanger, Tjibodas, fl., 1919, Sapiin 2201 (BO, L); Tjibodas, fl., fr., May 1937, P.J. Eyma 91 (L); Tjisaroea-Zuid, fl., fr., 26 Feb 1950, Z.O. van Buitenzorg & S.J. van Ooststroom 12823 (BO, L). West Nusa Tenggara: Sumbawa Island, W Sumbawa, Pernek, Olat Seli, fl., fr., 20 May 1961, K. Kuswata 258 (K, L, P, US), fl., 2 May 1961, Kostermans 18653 (BO, K, L, P, US). Lesser Sunda Islands: Flores, Endeh, Roga, fl., 8 Feb 1910, J. Endert 4345 (L); near Endeh, fl., fr., 8 Apr 1965, Kostermans & Wirawan 2 (K, L); Watokobu, Nagawutung, Lowolaba, fl., 1 May 1984, J.J. Afriastini 1658 (BO, K, L). MALAYSIA. Sabah: Borneo, Mount Kinabalu, Kiau, fl., fr., 31 Oct 1915, D.L. Topping 1530 (US). Pahang: s.loc., fl., fr., 30 Mar 1909, s.leg. 13806 (K); Peninsular Malaysia, Cameron highlands, fl., 3 May 1937, s.leg. 32974 (US). MYANMAR. Chin: between Kanpetlet and Yelong Pan Village, fl., 15 Sep 2011, H. Funakoshi et al. 085365 (US); Natmsa Taung National Park, fl., 4 Sep 2012, L.S. Man 091656 (US). Magway: s.loc., fl., 13 Nov 2004, W.J. Kress et al. 04-7749 (US). SRI LANKA. Without province: Ceylon, fl., fr., s.dat., M. Walker s.n. (K). North Central: Anuradhapura, Ritigala Strict Natural Reserve, fl., 21 Jan 1973, A.H. Jayasuriya 1089 (US); fl., 18 Feb 1973, A.H. Jayasuriya & B.L. Burtt 1161 (US); fr., 2 Jun 1974, A.H. Jayasuriya 1743 (US). Sabaragamuwa: Ratnapura, SE of Godakewala, fl., fr., 24 Nov 1974, G. Davidse & D.B. Sumithraarachchi 8795 (US). Western: Kalutara, Pahingala, fl., fr., 5 Nov 1975, S.H. Sohmer & S. Waas 10232 (US). TAIWAN. Kaohsiung: Kaohsiung Hsien, between Shanping and Nanfengshan, fl., 19 Sep 1991, W.L. Wagner 6614 (US). Taipei: Taipei hsien, Sanhsia, Manyuehyuan Forest recreation area, fl., 20 Sep 1997, Y.C. Kao & C.N. Wang 6101 (US). THAILAND. Without province: Siam, fl., 3 Oct 1910, A.F.G. Kerr 1508 (K, L, P). Chiang Mai: Mae Rim, above Mae Sa Mai village, Mae Sa Gow village, Bong Yaeng subdistrict, fl., fr., 18 Nov 2001, J.F. Maxwell 01-617 (L); Me Raming, south of Chiang Dao, fl., fr., 9 Dec 1957, F.R. Fosberg 39166 (US); road Doi Sutep, fl., fr., 1 Nov 1969, H.P. Nooteboom et al. 722 (L); Doi Sutep-Pui National Park, east side of Doi Pui, upper Chang Kian Valley, fl., fr., 11 Dec 1996, C. Tiyayon 7 (CMU, L); Valley of Hue Me Nai, Doi Sutep Mountains, fl., fr., 2 Nov 1920, J.F. Rock 1143 (US). Chonburi: Si Racha, fl., fr., 10 Nov 1926, D.J. Collins 1358 (US). East Nusa Tenggara: West Timor, Putain, fl., fr., 29 Jun 1964, C.W. Kooy 177 (L).

Distribution and ecology. Widespread throughout Asia, occurring in Bangladesh, Bhutan, Brunei, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Sri Lanka, Taiwan, and Thailand (Fig 15). It mainly occurs in forest margins, understory, and riverbanks, from 250 to 2000 m above the sea level.

Etymology. The Latin derived epithet "scaberrimus" makes reference to the species leaf blade being very scabrous on both sides.

Phenology. Flowering and fruiting year-round, but peaking between August and December, with flowers opening between 10:00 and 13:30h.

Conservation status. *Aneilema scaberrimum* possesses wide EOO (ca. 14,746,787.575 km²) and AOO (ca. 712.000 km²). Thus, following the IUCN (2001) recommendations, *A. scaberrimum* should be considered Least Concern (LC).

Nomenclatural notes. Blume (1827) described *Commelina scaberrima* form Java, brought to *Tradescantia* L. by Hasskarl (1843) with a suggestion that it might perhaps belong to *Dithyrocarpus* Kunth (= *Floscopa* Lour.). Perhaps a little later Kunth himself placed it in *Aneilema* (1843, as "*Anilema*"), a century later Raizada (1949) thought it was a *Phaeneilema* G.Brückn., a synonym of *Murdannia* Royle (Pellegrini et al. 2016).

Morton's (1966) new combinations in *Dictyospermum* for the Blume names were not validly published, because there are no full and direct references in the text nor in the bibliography to the original publications. Morton was followed by Hong (1974), who without realizing it, validated the combination *D. scaberrimum*. Panigrahi (1975) and Hara (1978) intentionally proposed to validate the same combination, unaware of Hong's publication. Morton's other combinations in *Dictyospermum* are valid, as the references are included in his article's bibliography (see Turland et al. 2018, Rec. 33.A.1), even when the page is incorrectly cited (Turland et al. 2018, Art. 33.5).

Rhopalephora scaberrima var. subfruticosa C.B.Clarke ex Vrinda & Panikkar represents a rather remarkable and unique nomenclatural situation. Vrinda and Panikkar (1999) studied two accessions: (1) one collected in Kallar and Palaruvi; (2) and another one collected in Idukki, Kerala, later cultivated by them in the garden of the Department of Botany, Sree Narayana College, Kollam, Kerala. The authors concluded that these specimens represented two different infraspecific taxa: (1) one being Aneilema scaberrimum s.s.; (2) and the other one what they regarded as Aneilema scaberrimum var. fruticosum C.B.Clarke (in Hooker 1892). Nonetheless, Vrinda and Panikkar (1999) did not realize that Hooker (1892) followed the formatting used by Linnaeus in many of his publications, with each taxon organized in a paragraph, with the diagnosis in a following paragraph containing additional notes (Stearn 1957). The diagnosis and the description belong to the same taxon and no infraspecific taxon was ever proposed by Clarke or Hooker. Although the authors didn't realize it, they actually described a new taxon, instead of proposing a new combination. However, the combination proposed by Vrinda and Panikkar (1999) was not validly published, since there is no reference to one Latin diagnosis that valid the name (Turland et al. 2018, Art. 36.1), added to the fact that the type and is also not indicated (Turland et al. 2018, Art. 37.1, 6, 7). Finally, no voucher specimens appear to be housed in the Sree Narayana College herbarium, the collection where both botanists were known to work.

Affinities. Aneilema scaberrimum can easily be confused with A. micranthum and A. protensum, especially when mature capsules are not available. These species share a very

similar vegetative morphology and inflorescence architecture, with largely overlapping floral features. *Aneilema scaberrimum* can be differentiated from *A. micranthum* based on growth form (herbs erect and robust in *A. scaberrimum vs.* prostrate and delicate in *A. micranthum*), leaf morphology (blades chartaceous, scabrid to hispid, base cuneate, rarely obtuse *vs.* membranous, glabrous, obtuse to round), number of cincinni per inflorescence (3–8 cincinni *vs.* 1–2), pedicel posture (patent at anthesis and pre-anthesis, erects at post-anthesis *vs.* deflexed at anthesis, pre-anthesis and post-anthesis), and connation of the staminodes (filaments connate ca. 1–2 mm to the stamens *vs.* basally connate with the stamens). Furthermore, *A. scaberrimum* is the only specie in the section to present the hilum placed in a deep groove.

While Aneilema scaberrimum and A. protensum can be easily differentiated largely based on fruit and seed morphology (Fig 9), with distinction between both species based exclusively on flowering and/or vegetative specimens is extremely difficult. Since flowers are poorly preserved in dried specimens of Commelinaceae (Faden 1991), they are of little use in differentiating both species, especially since most of the useful floral characters (e.g., petal shape, filaments position and curvature, anthers coloration) are almost invariably lost during the drying process. In case only flowers are available in dried specimens, leaf and cincinni pubescence can be useful in differentiating both species.

5. *Aneilema vitiense* Seem., Bonplandia (Hannover) 9: 260. 1861, "*vitiensis*"; Viti: 443. 1862; Fl. Vit.: 314, t. 96. 1868. Figs 2E & 16–18

Dictyospermum vitiense (Seem.) J.K.Morton ex Panigrahi, Phytologia 29: 338. 1975. Dictyospermum vitiense (Seem.) J.K.Morton, J. Linn. Soc., Bot. 59: 436, 471. 1966, nom. not val. publ.. sine ref.

Piletocarpus vitiensis (Seem.) Hassk., Flora 49: 212. 1866.

Rhopalephora vitiensis (Seem.) Faden, Phytologia 37(5): 480. 1977. Lectotype (designated here). FIJI. Viti Levu, fl., fr., 1860, B.C. Seemann 643 (K barcode K000854139!; isolectotypes: B, BM barcode BM000990699!, CAL, G barcode G00176317!, G-DC barcode G00489388!, GH barcode GH00415436!, W n.v.).

Aneilema keyense Warb., Bot. Jahrb. Syst. 13: 269. 1891[1890].

Dictyospermum keyense (Warb.) J.K.Morton, J. Linn. Soc. Bot. 59: 436, 471. 1966, nom. not val. publ., sine ref.

Dictyospermum keyense (Warb.) J.K.Morton ex Panigrahi, Phytologia 29: 338. 1975. Type (not found). INDONESIA. Maluku [Moluccas]: Key Island, Warburg 21078 (B?).

Aneilema vitiense var. petiolatum C.B.Clarke in De Candolle & De Candolle, Monogr. Phan. 3: 220. 1881, "petiolata". Lectotype (designated here). PHILIPPINES. Palawan: Manila, fl., 1840, J.M.M. Callery 52bis (P barcode P02088015!; isolectotype: P barcode P06836929!), Syn. nov.

Description. Herbs 40–60 cm tall, perennial, with a definite base, terrestrial. Stems prostrate with ascending apex, densely branched or branched only at the base; internodes 2.6–5.2 cm long, green, glabrous. Leaves distichously-alternate, subpetiolate; sheaths 0.4–1.6 cm long, green to reddish, scabrid to pubescent with eglandular hairs, margins setose, hairs hyaline; petiole 0.5–1.3 cm long, rarely inconspicuous in the upper leaves; lamina $1.7–9.8 \times 1.3–4.5$ cm, ovate to ovate oblong, membranous, to medium green, drying greyish green to olive-green on both sides, glabrous to scabrid on both sides, base symmetric to asymmetric,

round to obtuse, margins green, glabrous to sparsely ciliolate, apex acuminate; midvein impressed adaxially, obtuse abaxially, secondary veins 2–3(–4) pairs. *Inflorescences* a solitary thyrse, terminal, with 1-4 cincinni; peduncles 2.5-8 cm, puberulous with a mixture of hook and minute eglandular hairs; basal bract reduced or leaf-like, 0.4–1.8 × 0.1–0.5 mm, linear ovate to ovate, glabrous to scabrid on both sides, base obtuse to cuneate, margins glabrous to sparsely ciliolate, apex acuminate; cincinni bracts 2-2.6 × 0.6-1 mm, oblong triangular to oblong, puberulous with a mixture of hook and minute eglandular hairs, margins glabrous, apex acute; cincinni 5–10-flowered, cincinnus peduncle 1.5–2.6 cm, green, sparsely minutely puberulous with a mixture of hook and eglandular hairs, cincinnus internodes 0.7-1.9 cm long, glabrous to sparsely minutely puberulous with a mixture of hook and eglandular hairs; bracteoles 1-1.5 × 2-2.4 mm, glabrous, margins glabrous, apex acute. Flowers 1.2-1.6 cm diameter; floral buds 1.7-2.3 × 1.5-1.9 mm, green; pedicels patent at anthesis and preanthesis, erects at post-anthesis, 5.6–7 mm long, green, glabrous, 0.9–1.3 cm long in fruit; sepals green, upper sepal $2-3.1 \times 2.2-2.9$ mm, ovate, apex round, lower sepals $1.8-2.5 \times 1.2-$ 1.8 mm, obovate, apex round; petals white to pale lilac to light blue, paired petals $5.6-8 \times 10^{-8}$ 4.1-6.4 mm, limb obovate to broadly obovate, 4.8-6.3 × 4.1-6.4 mm, base cuneate to round to cordate, apex obtuse to acute, claw 0.8-1.7 mm long, medial petal $3.5-5.6 \times 2-2.7$ mm, shortly-clawed, claw 0.6–1.4 mm long, limb $2.9-4.2 \times 2-2.7$ mm, base cuneate, apex acute, broadly elliptic to obovate; staminodes with filaments 2.3–3.5 mm long, only basally connate with the filaments of the stamens, straight pointing downward, white, antherodes $0.1-0.2 \times$ 0.8-1.4 mm, lobes ellipsoid; stamens with filaments basally connate, lateral stamens with filaments 5.4–7.6 mm long, gently sigmoid, geniculate distal to the middle, white to pale lilac, anthers 0.3–0.4 × 0.3–0.4 mm, elliptic to oblong elliptic, connective white to lilac to blue, anther sacs white to pale lilac to light blue; medial stamen with filament 2.8–3.7 mm long, straight or arcuate-decurved, decurved at the apex, white to pale lilac, anther $0.3-0.5 \times 0.3-$ 0.4 mm, connective white to pale yellow, anther sacs pale yellow; ovary ellipsoid to broadly ellipsoid, $1.7-3.1 \times 1-1.5$ mm, light to medium green, style 5.3-7.2 mm, not sunken into the ovary, straight, white to pale lilac, green at base, stigma white to pale lilac to lilac. Capsules $5.5-7.5 \times 1.9-3.2$ mm, shortly-stipitate, stipe 0.8-1.4 mm long, ellipsoid to broadly ellipsoid, green with vinaceous apex when immature, light brown when mature, apex acuminate, dorsal locule 0(-1)-seeded, ventral locules slightly concave to flat, (0-)1(-2)-seeded. Seeds 2.5-4.2 × 1.5–2.1 mm, elliptic to broadly elliptic, cleft to strongly cleft towards the embryotega, testa light grey, sparsely farinose, deeply foveolate, with pits radiating from the embryotega; hilum on a weak ridge; embryotega semilateral.

Specimens seen. AMERICAN SAMOA. Eastern District: Tutuila Island, Fagafue Bay, fl., fr., 10 Mar 1996, A. Whistler W9920 (K). Manu'a District: Ta'ū Island, Sani Ridge, Fitiuta, fl., fr., 9 Aug 1921, D.W. Garber 588 (K). FIJI. Without province: s.loc., fl., fr., 1877–1878, J. Horne 111 (K); Viti Levu Island, fl., Jul 192, A.E. Meebold 16505 (K). Central Division: Viti Levu Island, Tailevu, Wailotue Cave, fl., 11 Aug 1955, D. Koroiveibav 9405 (K); Rewa, near Suva, fl., 1927, J.D. Tothill 911 (K). Northern Division: Vanua Levu Island, Thakaundrove, Sava Sava bay, Mt. Uluinabathi, fl., fr., 26 Dec 1940, O. Degener & E. Ordonez 13929 (K, US). INDONESIA. Maluku [Moluccas]: Amboina Island, Kaju Poeti, roadside, fl., Jul 1913, C.B. Robinson 408 (US); Coran, Kiandarat, fl., 8 Sep 1938, P. Buwalda 5967 (BO, K, L). North Maluku [North Moluccas]: Ternate, Baku Gunung Tègètègè, fl., fr., 2 Mar 1938, Anang 6 (K, L). North Sumatra: Atjeh, Gunung Leuser Nature Reserve, Ketambe, valley of Lau Alas, near tributary of Lau Ketambe, ca. 35 km NW of Kutatjane, 24 May 1972, fl., fr., W.J.J.O. De Wilde & B.E.E. De Wilde-Duyfies 12322 (K, US). Sulawesi: Kolaka, Tirawuta, Kecamatan, Desa Lalingato, Hutan Ulu Simbune, fl., fr., 23 May 2008, A. Hidayat AH 3658 (BO, K); North Sulawesi, Minahasa

Regency, fl., Jul 1876, M. Savinierre 57 (P); fl., fr., 5 Sep 1876, M. Savinierre 182 (P). West Papua: Western New Guinea [Netherlands New Guinea], Vogelkop Peninsula [Bird's Head Peninsula], Nettoti Range, fl., fr., 10 Oct 1961, P. van Roven & H. Sleumer 6821 (K, L). MALAYSIA. Sabah: Borneo, Kota Marudu, Kampung Monggis, fl., 10 May 1996, M. Rumuton 247 (K). MICRONESIA. Kosrae: Kusaie, Mt. Iyawoe, fl., 29 Jul 1938, T. Hosokawa 9439 (US); Lela harbor, fl., 21 Aug 1946, F.R. Fosberg 26658 (US); Loal, fl., fr., Apr 1988, J.V. Ward 200 (US); Yela River Valley, fl., fr., 31 Jan 2005, T.W. Flynn et al. 7198 (US). Pohnpei: Mt. Tolotom, fl., 11 Aug 1949, S.F. Glassman 2846 (US). PAPUA NEW GUINEA. Without province: fl., fr., Jan 1962, R. Schlechter 14131 (K). Manus: Wylli valley to the west of Mt. Dremsel and to the east of Watani River, ca. 6 km from the south coast, fl., fr., 5 Mar 1970, M.J.S. Sands 964 (K), Morobe: Lae, Botanical Gardens of Lae, fl., fr., 22 Oct 1957, E. Henty 9821 (K, L). Milne Bay: Biniguni camp, Gwariu river, fl., 5 Aug 1953, L.J. Brass 23825 (K, US). Northern Province [Oro]: Kokoda, fl., s.dat., C.E. Carr 16442 (K); Soputa, fl., 23 May 1943, R. Dekalle s.n. (US barcodes US00161487, US00161488). Sandaun: Sepik, Aitape, near Mori Village, on Piore River, fl., 6 Jul 1961, P.J. Darbyshire & R.D. Hoogland 8084 (K, US); West Sepik, Vanimo, Ossima, fl., fr., 28 Jan 1969, H. Streimann & A. Kairo 9214 (K). West New Britain: New Britain, West Nakanai, near Cape Hoskins, Koimumu Village, fl., fr., 6 Aug 1954, A. Floyd 6487 (K). PHILIPPINES. Without province: s.loc., fl., 1838, s.leg., s.n. (US barcodes US00161480, US00161481). Abra: Luzon Island, Plobacion Gangal, Sallapadan, fr., 14 Nov 1996, D.A. Madulid & S.H. Sohmer 38587 (BRIT, K, PNM). Agusan del Norte: Mindanao Island, Cabadbaran, Mt. Urdaneta, fl., Aug 1912, s.leg. 13557 (US); Butuan, fl., s.dat., C.M. Weber 1022 (US). Benguet: Luzon Island, Bued river, fl., Oct 1905, E.D. Merrill 4862 (L, P, US). Cagavan: Luzon Island, fl., Mar 1909, M. Ramos 7497 (P). Cebu: Kantipla, fl., Aug 1995, C. Bicknell 882 (L, US). Greater Manila: Manila-Palawan, fl., fr., 1840, M. Calléry s.n. (P barcode P06836929). Iloilo: Panay Island, fl., 27 Dec 1912, C.B. Robinson 18081 (US). Laguna: Luzon Island, Calauan, fl., fr., Nov-Dec 1910, R.C. McGregor 12409 (K); Los Baños, fl., 17 Mar 1906, E.D. Merrill 5119 (US); Mt. Maquiling, fl., Jun 1917, s.leg., 18053 (US). Leyte: Ormoc, Lake Danao, fl., fr., Mar 1950, G.E. Edaño 14238 (L, PNH); Mt. Janagdan, fl., Apr 1950, G.E. Edaño 14237 (L, PNH); Southern Leyte, fl., fr., 1 Jun 1913, C.A. Wenzel 4 (US). Negros Oriental: Island of Negros, Dumaguete (Cuernos Mts.), fl., fr., Jun 1908, A.D.E. Elmer 10344 (L, P, US); Valencia, Talinis, Maeti Dam, fl., fr., 26 May 1991, Reynoso et al. 1129 (K). Palawan: Point Leparacion, fl., 20 Feb 1903, E.D. Merrill 812 (US). Quezon: Luzon Island, Mt. Banahao, Tayabas, fl., Oct 1904, H.N. Whitford 973 (US); Lucban, fl., May 1907, A.D.E. Elmer 7802 (US); Umiray, fr., May 1917, M. Ramos & G.E. Edaño 29057 (US). Sorsogon: Luzon Island, Irosin, Mt. Bulusan, fl., Nov 1915, A.D.E. Elmer 15366 (L, US); central area, fl., s.dat., A. Loher 1937 (US); Mt. Juban, fr., 20 Jun 1956, G.E. Edaño 56725 (L, PNH); Mt. Salikan, fl., fr., 26 May 1957, G.E. Edaño & H.G. Gutiérrez 371 (L, PNH). SAMOA. Manu'a: Ta'u Island, south of Fagamalo Cove, fr., 8 Jan 1991, W.A. Whistler 7960 (US). Tuamasaga: Upolu Island, Vaisingano river, Malololelei, fl., 7 Aug 1929, E. Christophersen 107 (K, US); Apia, Alaoa Falls, fl., fr., 26 Dec 1971, A. Whistler W2415 (K); towards Lake Lanoto'o, fl., 25 Jul 1973, W.A. Whistler W402 (US). SOLOMON ISLANDS. Guadalcanal: NW Guadalcanal, White [Ta'utu] River, fr., 26 Aug 1867, A. Nakisi 8055 (K). Western Province: Kolombangara Island, 1 mile E of Kuzi village, fl., 26 Aug 1965, E.J.H. Corner 2439 (K, P); SW Kolombangara, Shoulder Hill Area, fl., fr., 12 Jun 1968, R. Mauriasi et al. 11401 (K); New Georgia Island, fl., fr., 1 Jul 1929, J.H.L. Waterhouse 182 (K). TIMOR-LESTE [E. TIMOR]. Manatuto: Manatuto, Laclo, estrada Metinaro-Manatuto, em Beheda, fl., 26 Feb 2005, J.A.R. Paiva et al. T680 (L). VANUATU [NEW HEBRIDES]. Without province: s.loc., fl., fr., 15 Sep 1936, A. de la Rüe s.n. (P barcode P06836789). Sanma: Espiritu Santo Island, Big Bay [Malao], fl., 12 Sep

1971, H.S. McKee 24252 (K). **Tafea:** Tanna, Vallú de Fekal, fl., fr., 24 Mar 1936, A. de la Rüe s.n. (P barcode P06836790).

Distribution and ecology. *Aneilema vitiense* is known to occur in American Samoa, Indonesia (Maluku Islands), Fiji, Mariana Islands, Malaysia, Micronesia, Papua New Guinea, Philippines, Samoa, Solomon Islands, Timor-Leste, Tonga, and Vanuatu (Fig 19). Cleared pastured areas, forests, swampy pastures, open grassy areas, roadsides, 1–100 m alt.

Phenology. It was found in bloom and fruit from March to December.

Conservation status. *Aneilema vitiense* possesses a wide EOO (ca. 21,003,380.945 km²), but a proportionally narrow AOO (ca. 300.000 km²). Nonetheless, it is our opinion that our limited sampling most likely affected the AOO for this species. Thus, following the IUCN (2001) recommendations, *A. vitiense* should be considered Least Concern (LC).

Etymology. The epithet "vitiense" makes reference to the species type locality (i.e., Fiji).

Nomenclatural notes. Aneilema vitiense was published twice by Seemann (i.e., in 1861 and in 1862) prior to what is generally regarded as its valid publication (i.e., Seemann 1868). Thus, both citations of A. vitiense have been regarded as nomina nuda, despite the statement "(sp. nov.) florib. pallide coeruleis" (i.e., new species: flowers pale blue). This statement is regarded by us as a diagnosis, and thus enough to validate the publication of A. vitiense in Seemann (1861), and prior to (Seemann 1868). We are well-aware that for a Commelinaceae, these words generally do not amount to much, and could easily be applied to more than 50% of the species in the family. Nonetheless, it also should be pointed out that Seemann listed only four species under his "Commelynaceae": (1) Commelina communis L. (with sky blue flowers); (2) Flagellaria indica L. and Joinvillea elegans Gaudich. ex Brongn. & Gris (with greenish yellow flowers); (3) and Aneilema vitiense. Therefore, in this context of Seemann (1861), "florib. pallide coeruleis" can be regarded as a perfect diagnosis, easily differentiating his new species from the other three species listed by him. Furthermore, there is no prescription in the Code on the quality of a diagnosis, only that there should be one in order to validly publish a name. Thus, A. vitiense was validly published in 1861, cited once again in 1862, and finally, Seemann (1868) provides a more detailed and unambiguous description of A. vitiense, together with a beautiful watercolor illustrating his previously published new species (Fig 17).

Seemann (1868) depicts 6 perfect stamens (Fig 10), but states: "the stamens... not quite reliable, as the specimen was imperfect" (note the singular). This might mean that Seemann distributed the duplicates before he was able to complete the more detailed description and conclude the illustration of *Aneilema vitiense*. Thus, it would be rather surprising that Hasskarl, back in 1866, knew that *A. vitiense* had persistent cup-shaped bracteoles, 3 sterile stamens, and stipitate sticky fruits; while dubiously placing it (note the question mark in Hasskarl's publication) under his new genus *Piletocarpus*. These characters were never mentioned by Seemann (1861, 1862, 1868), in any of his publications dealing with *A. vitiense*. The mystery comes to an end in 1870, when Hasskarl makes no citation to any of Seemann's publications (i.e., Seemann 1861, 1862, 1868), but states that he had seen herbarium specimens in B, G-DC, and W, where he probably saw the name *A. vitiense* on the labels. However, it is curious that he stated that the flowers he saw were insufficient, and that he had only seen immature fruits. At first sight, *A. vitiensis* Seem. and *P. vitiensis* Hassk. are taxonomic, and not nomenclatural synonyms as they appear to have been based on specimens

in different institutes (Seemann's Fiji specimens are housed at K), and *P. vitiensis* is not cited as a new combination, but as a new species. Nonetheless, according to the *Code* (Turland et al. 2018, Art. 9. Note 2c), isotypes not seen by the author are still to be considered original material. Furthermore, Art. 33.3 (Turland et al. 2018) states that when in a presumed new combination, no reference is given to the basionym, but the epithet of a previously and validly published name that applies to the same taxon (a taxonomic decision!) is adopted, the new combination is validly published, if and only if, it was a validly published name. Therefore, the correct author for *P. vitiensis* is to be regarded as *P. vitiensis* (Seem.) Hassk.

Taxonomical notes. Plants from the Philippines were described as *Aneilema vitiense* var. *petiolatum* by C.B.Clarke (1881). After analyzing two of the syntypes and a number of specimens from the Philippines, we found no difference between these plants and *A. vitiense* var. *vitiense*. Thus, we reduce *A. vitiense* var. *petiolatum* to a synonym of *A. vitiense* var. *vitiense*, accepting no infraspecific taxa for this species.

Warburg (1890) described *Aneilema keyense* Warb. from the Kai (Kei) Islands, but it was soon reduced to a synonym of *A. vitiense* by Lauterbach (1905, 1913), who also recorded it for Kaiser Wilhelmsland (former Territory of New Guinea, now Papua New Guinea). This was followed by Faden (1977) and is ultimately accepted by us. *Aneilema vitiense* is apparently rare on mainland New Guinea.

Affinities. Aneilema vitiense seems to be a species with ambiguous morphological affinities. It is vegetatively similar to A. micranthum, due to its definite base, evidently petiolate, membranous leaves, and filaments only basally connate. It also shares with A. micranthum and A. scaberrimum the stipitate capsules. On the other hand, it seems to be more closely related to A. rugosum, due to its staminodes with straight filaments pointing downwards, and ellipsoid antherode-lobes. Nonetheless, it is unique in the section due to its distichously-alternate phyllotaxy and ellipsoid to broadly ellipsoid capsules with acuminate apex. The shape of its petals is also quite deviant from the petal morphology of the A. scaberrimum species complex, being probably similar to the petal morphology of the poorly-known A. rugosum.

Excluded name

Floscopa yunnanensis D.Y.Hong is a Chinese endemic species of ambiguous generic placement, known exclusively by its type collection. Different hypotheses of generic placement for this species were proposed over the years, with the most recent one (Wu Zhengyi, in Hong and DeFilipps 2000) suggesting it might be better accommodated in the genus Rhopalephora. Floscopa yunnanensis was originally described by Hong (1974). but hesitantly placed in *Floscopa* due to available specimens possessing only few and poorly preserved, exclusively staminate flowers and mostly dehisced capsules with few seeds. Thus, Hong (1974) felt it was better to maintain his new species in Floscopa, until more information became available. In order for F. yunnanensis to be safely placed in Floscopa, it would need to completely lack hook hairs (a character restricted to Commelina and allied genera), the synflorescence would commonly be composed of the main florescence plus several coflorescences, bracteoles caduceus, minute and rhomboid, sepals eglandular, sessile petals, 6 dimorphic stamens (arranged in upper and lower stamens), a 2-locular and stipitate gynoecium, seeds generally with costate testa, and a white, dorsal embryotega (Fig 20). Nonetheless, F. yunnanensis differs from the remaining species of Floscopa due to the presence of hook hairs, synflorescence composed of a solitary main florescence, cup-shaped and perfoliate bracteoles, sepals with a subapical gland, clawed petals, 3 upper staminodes

with bilobed antherodes, 3 lower unequal fertile stamens, 3-locular capsules, seeds with scrobiculate testa, and a concolorous semilateral embryotega. Faden (1975), as part of his systematic revision of *Aneilema*, analyzed the isotype of *F. yunnanensis* housed at the A herbarium, and confirmed that the species did not belong in *Floscopa*. The author suggested that the species might be better placed in a new, monospecific genus (Faden 1975, 1991, pers. comm.), without providing any justification for that. Nonetheless, the aforementioned characters would comfortably place *F. yunnanensis* under *Aneilema sensu* Faden (1991).

As aforementioned, Wu Zhengyi suggested in an editor note at the Flora of China's treatment for Commelinaceae (in Hong and DeFilipps 2000: 26) that *F. yunnanensis* might actually represent a species of *Rhopalephora*. Nonetheless, *F. yunnanensis* has a very dense and regular-looking thyrse (i.e., with elongated main axis), sepals not deflexed in fruit, apparently free filaments, central staminode with a perfect antherode, and shortly-stipitate capsules completely lacking either hook or glandular hairs. Thus, it is highly unlikely for *F. yunnanensis* to represent a member of *A.* sect. *Rhopalephora*, as currently defined by us. On the other hand, with *Rhopalephora* being once again treated under a broader sense of *Aneilema*, *F. yunnanensis* can be undoubtably placed under *Aneilema s.l.* based on the available information. Morphologically, *F. yunnanensis* is strikingly similar to *A. johnstonii* (currently a member of *A.* sect. *Amelina*), members of *A.* sect. *Aneilema* and *A.* sect. *Brevibarbata*, and superficially similar to members of *A.* sect. *Lamprodithyros*, based on ecological, vegetative, inflorescence and floral characters (Pellegrini, pers. observ.). Thus, we provide below the needed new combination, together with an updated description of the species, and comments regarding its possible affinities within *Aneilema s.l.*

Aneilema yunnanense (D.Y.Hong) M.Pell., comb. nov.

Fig 21

Floscopa yunnanensis D.Y.Hong, Acta Phytotax. Sin. 12: 464–465, pl. 93, f. 1. 1974. Type. CHINA. Yunnan: Meng-nün, Jenn-yeh Hsien, fr., Nov 1936, C.W. Wang 80888 (holotype: KUN barcode KUN00032801!; isotypes: A barcode A00415435!, KUN barcode KUN00032802!).

Description. Herbs ca. 30–40 cm, probably perennial, with a definite base, terrestrial. Roots not seen. Stems probably trailing with ascending apex, thin, unbranched to little branched; internodes 0.9–10 cm long, green, sparsely puberulous to puberulous with hook hairs, glabrescent with age. Leaves subpetiolate, spirally-alternate; sheaths 1.8–3.2 cm long, green with brown longitudinal striations, sparsely puberulous to puberulous with hook hairs, glabrescent with age, margins sparsely setose, hairs light brown; petioles 1.2–1.9 cm long; lamina 4.6–18.5 × 0.9–4.5 cm, narrowly elliptic to elliptic, membranous, adaxially dark to medium green, abaxially medium to greyish green, drying greyish green to olive-green on both sides, adaxially puberulous with hook hairs, abaxially with hook hairs restricted to the veins, base symmetric, cuneate, margins green, ciliate, apex acuminate; midvein impressed adaxially, obtuse to acute abaxially, secondary veins 2-3 pairs. Inflorescences a solitary thyrse, terminal, with 40–60, alternate to subverticillate cincinni; peduncle 2–5.6 cm, densely puberulous with hook hairs; basal bract reduced or leaf-like, 1.1–1.8 × 0.1–0.3 cm, linear triangular, puberulous with hook hairs, base truncate, margins ciliate, apex acuminate; cincinni bracts $0.6-2.5 \times 1-1.6$ mm, triangular to broadly triangular, glabrous to minutely puberulous with hook hairs, margins scarious, apex acute; cincinni 5–10-flowered, cincinnus peduncle 2.4-10.2 mm, green, minutely puberulous with hook hairs, cincinnus internodes 1.9–9.3 mm long, sparsely puberulous with hook hairs; bracteoles $1-1.7 \times 2.4-3.2$ mm, cupshaped, perfoliate, herbaceous, persistent, secundly arranged in the cincinnus, glabrous to sparsely puberulous with hook hairs near the base, glandular-pubescent at the apex, apex acute, eglandular. Flowers poorly preserved in the available specimens, staminate or bisexual, secund, without a 60° torsion in the floral display; floral buds $0.9-1.5 \times 0.6-1.1$ mm, broadly ellipsoid; pedicels 1.8–2.9 mm long, sparsely puberulous with hook hairs, 6.3–8 mm long in fruit, ascending at anthesis and post-anthesis; sepals 3, free, with a subapical gland, persistent in fruit, glabrous, upper sepal 1.7–2 × 0.8–1.1 mm, ovate, strongly cucullate, lower sepals 2– 2.5 × 1.2–1.6 mm, broadly elliptic to obovate, cucullate; petals lilac, paired petals clawed, limb apparently reniform, cucullate, medial petal sessile, elliptic, cucullate; staminodes 3, filaments free, slender, glabrous, antherodes 0.2–0.4 × 0.2–0.3 mm, bilobed, sessile, medial antherode saddle- to horseshoe-shaped, lateral antherodes subobcordate to horseshoe-shaped, lobes curved; stamens 3, filaments apparently free, thicker than the filaments of the staminodes, glabrous, medial stamen shorter than the laterals, probably held near the antherodes, anther 0.7-0.8 × 0.3-0.4 mm, saddle-shaped, falcate, lateral stamens with filaments thicker than the medial, anthers 0.5–0.6 × 0.2–0.3 mm, ellipsoid; gynoecium not seen. Capsules 3-4.2 × 1-2.7 mm, broadly ellipsoid to broadly obovoid, shortly-stipitate, light brown when mature, sparsely puberulous only with glandular microhairs, otherwise glabrous, lustrous, apex rounded to emarginate, loculicidal, 3-locular, 2-valved, 1-2(-3)-seeded, dorsal locule 0(-1)-seeded, ventral locules 0-1-seeded. Seeds 1.4- 2.5×1.9 -2 mm, ellipsoid to broadly ellipsoid, ventrally flattened, slightly cleft towards the embryotega, testa dark brown to greyish brown, scrobiculate, ridges radiating from the embryotega, not-farinose; embryotega semilateral, dark brown; hilum linear, on a weak ridge, ca. the same length as the seed.

Distribution, ecology and conservation. Aneilema yunnanense is endemic to China, more specifically, restricted to the Yunnan district (Fig 22), probably growing in dense, moist forests near water bodies, 800 meters above sea level. It is exclusively known from the type specimens, being probably extremely rare, or currently extinct in nature. Field efforts focusing on the recollection of this neglected species are necessary so its taxonomic problems and systematic position can be solved, and a proper conservation assessment can be done.

Etymology. The epithet "yunnanense" refers to the species type locality, the Yunnan Province, China.

Affinities. Due to the complete lack of well-preserved flowers (especially bisexual ones), and almost complete lack of fruits and seeds, it is extremely hard to properly access the affinities of A. yunnanense. Nonetheless, A. yunnanense seems somewhat morphologically related to species of A. sect. Aneilema, especially A. aparine (from Madagascar) and A. sclerocarpum F.Muell. (from Australia), mainly due to their forest habit, prominent subpetiolate leaves, antherode morphology, and its distribution, which would also perfectly fit in A. sect. Aneilema wide geographical distribution. Furthermore, as aforementioned, A. yunnanense can also be compared with A. johnstonii, due to their unique upside-down horseshoe-shaped antherodes (Pellegrini, pers. observ.). The antherode morphology shared by both species seems to be only superficially similar to the one observed in A. sect. Aneilema. Thus, a phylogenetic relation between A. sect. Aneilema, A. johnstonii and A. yunnanense could also be postulated, based on antherode morphology. This hypothesis seems congruent with the preliminary molecular phylogeny for Aneilema s.l., presented by Kelly and Evans (2014).

Alternatively, the inflorescence architecture of *A. yunnanense* is also reminiscent of members of *A.* sect. *Brevibarbata*, such as *A. beniniense* (P.Beauv.) Kunth and *A. dispermum* Brenan, restricted to continental Africa, and *A. umbrosum* (Vahl) Kunth, which extends from

continental Africa to South and Central America. Subpetiolate leaves are also known for many species belonging to A. sect. Brevibarbata, which contains most of the forest species in the genus (Faden 1991). Aneilema sect. Brevibarbata is characterized by its small to mediumsized flowers, the distal half of the lateral stamen filaments being minutely and inconspicuously bearded with hyaline hairs, and by the medial anther of similar size to the lateral anthers but differing in shape (Faden 1991). According to Faden (1991), the section is morphologically and cytologically diverse and mainly centered in western Africa. It comprises four species groups, one of them being a western African forest group, composed exclusively by forest species (i.e., A. beniniense, A. silvaticum Brenan, A. umbrosum, and A. dispermum). Thus, it might also be possible for A. yunnanense to be more closely related to, or even a member of A. sect. Brevibarbata, despite the geographic gap between them. The inflorescence architecture of A. yunnanense is especially similar to the one of A. beniniense, with capsule and seed morphology also being analogous. Nonetheless, due to the poor preservation of the flowers in the type specimens we have been unable to confirm the presence of short hyaline hairs in the medial portion of the filaments. Further collections of flowering specimens and/or sampling A. yunnanense in a phylogenetic study might help to solve this species' infrageneric placement in Aneilema s.l.

Final remarks

The present study recognizes eight sections in *Aneilema s.l.*, one of the five largest genera in Commelinaceae. These sections consist of the same seven recognized by Faden (1991; i.e., *A. sect. Aneilema*, *A. sect. Amelina*, *A. sect. Brevibarbata*, *A. sect. Lamprodithyros*, *A. sect. Pedunculosa*, *A. sect. Rendlei*, and *A. sect. Somaliensia*), added to the herein proposed section (i.e., *A. sect. Rhopalephora*). With *Rhopalephora* reduced to the sectional rank, *Aneilema s.l.* shows a continuous Pantropical distribution, ranging from Central and South America, to Africa, Madagascar, Asia, and Oceania (Fig 1), being represented by ca. 75 species (Pellegrini, pers. observ.). Despite our present contribution, added to the previous contributions to the taxonomy of the genus (e.g., Faden 1975, 1991), *Aneilema* remains a taxonomically challenging group, and better sampled phylogenetic studies are pressing to better understand it (Faden 1991). Furthermore, several taxonomic problems persist in larger sections (e.g., *A. sect. Amelina* and *A. sect. Brevibarbata*) with a considerable number of widespread and/or morphologically variable, or in sections not represented in Africa (i.e., *A. sect. Aneilema*) (Faden 1991; Pellegrini, pers. observ.).

With the transfer of *Floscopa yunnanensis* to *Aneilema*, *Floscopa* is currently represented in Asia and Oceania solely by *F. scandens* Lour. Furthermore, with this transfer, *Floscopa* finally seems to be morphologically cohesive, and most likely monophyletic. Nonetheless, the genus still represents a major taxonomic gap in the family, with the main contributions to its taxonomy being part of floristic studies or outdated family compendia (e.g., Hasskarl 1870; Clarke 1881; Brenan 1961, 1968; Morton 1967; Faden 1998). If in one hand the genus morphological limit is currently clean-cut (Fig 20), its species are extremely difficult to differentiate, especially based on herbaria specimens. This has prompted many names to be wrongly applied to a wide range of specimens, resulting in the recognition of ill-defined and highly morphologically variable species (Pellegrini, pers. observ.). Aside from that, studies combining morphological and molecular data are essential for circumscribing problematic genera in Commelinaceae and understanding the evolution of morphological characters in the family. Such studies are underway (Pellegrini et al., in prep.), and hopefully will address the aforementioned issues, not only in *Floscopa* and related genera, but for the family as whole. Furthermore, studies focusing on the taxonomy, nomenclature and

systematics of the *Floscopa* clade are currently being carried out by the first author and hope to deal with the most pressing issues in this intricate group.

Acknowledgements

The authors would like to thank to the staff and curators of the visited herbaria, who have kindly allowed us to examine the needed specimens and literature. MOOP would like to especially thank Maria Cândida H. Mamede, curator of SP herbarium, and the staff for kindly receiving loans and allowing us to examine the needed specimens and literature. The authors would also like to thank Timothy M. Evans for the discussion on Aneilema phylogeny, the placement of Rhopalephora, and suggestions on the best way to retain a monophyletic Aneilema; Jefferson Prado for his invaluable help and insights on nomenclature, especially regarding the name A. protensum; Rafael Felipe de Almeida, for comments on an initial version of the manuscript and graphical support; and Andrew Paget, Anurag N. Sharma, Bart Wursten, Daniel J. Layton, Ehoarn Bidault, Eric Barbier, Hai Le, LiChieh Pan, Michael Kesl, Pieter Pelser, Prashant Awale, Robert V. Blittersdorff, Saroj Kumar Kasaju, Steven & Alison Pearson, and Tariq Stévart for the beautiful field images. We also would like to thank the staff of Naturalis Biodiversity Center, who kindly sent the Aneilema specimens to MOOP, enabling us to finish and publish this study. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001, through the PhD fellowship granted to MOOP, besides Fundação Flora de Apoio à Botânica and Smithsonian Institution for his REFLORA grant. MDN thanks Vijay M. Crishna (NGCPR Director) for research support and encouragement; and the Department of Botany and Physics, Shivaji University, Kolhapur, for providing laboratory and SEM facilities during the development of his PhD thesis. This study was carried out as part of MOOP's PhD degree in Botany at Programa de Pós-Graduação em Botânica, Instituto de Biociências, Universidade de São Paulo — USP; and partially carried out as part of MDN's PhD thesis on Indian Commelinaceae. Finally, MOOP, MDN and RVG would like to thank and dedicate this publication to our late coauthor Dr. JeF Veldkamp, who greatly contributed to the completion of this study, but was unfortunately unable to see it published before his passing.

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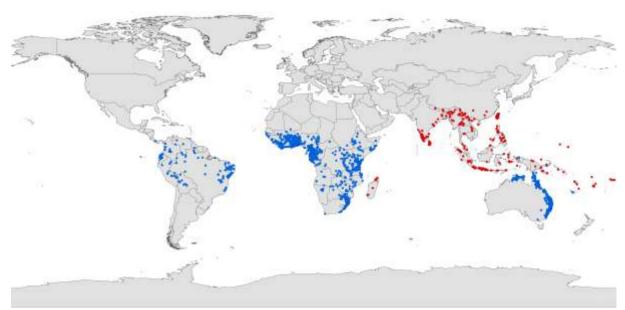


Figure 1. Distribution of *Aneilema R.Br. s.l.* Blue dots represent *Aneilema sensu* Faden (1991) and red dots represent *A.* sect. *Rhopalephora* (Hassk.) M.Pell. & Nandikar

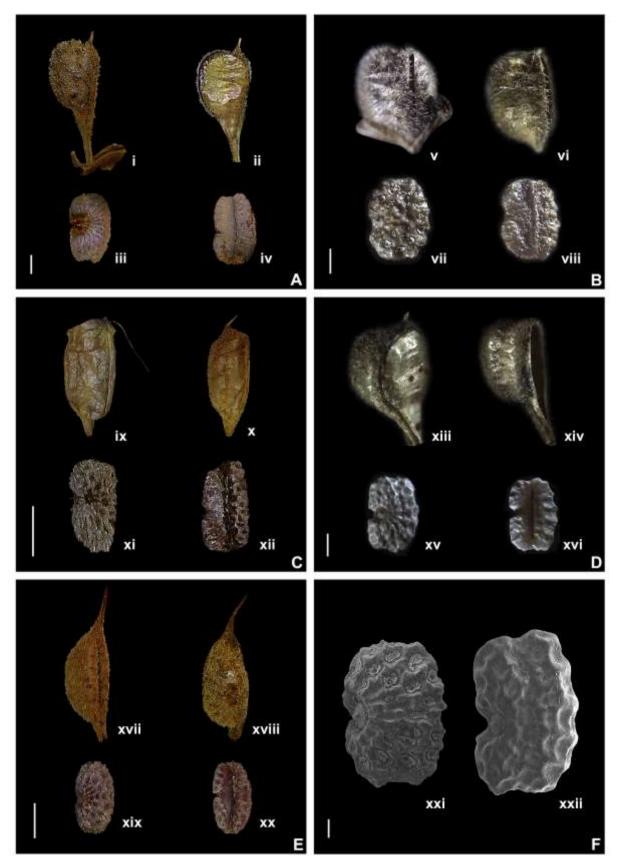


Figure 2. Comparative capsule and seed morphology of *Aneilema* sect. *Rhopalephora* M.Pell. & Nandikar. **A**, *Aneilema micranthum* (Vahl) Kunth: **i**, side view of a mature capsule; **ii**, side view of the dorsal valve of a mature capsule; **iii**, dorsal view of a seed, showing slightly cleft testa towards the embryotega; **iv**, ventral view of a seed, showing the hilum on a

weak ridge (scale bar = 1.5 mm). **B**, Aneilema protensum (Wall. ex Wight) Thwaites: **v**, side view of a mature capsule; vi, side view of the dorsal valve of a mature capsule; vii, dorsal view of a seed, showing slightly cleft testa towards the embryotega; viii, ventral view of a seed, showing the hilum on a weak ridge (scale bar = 0.5 mm). C, Aneilema rugosum H.Perrier: ix, side view of a mature capsule; x, side view of the dorsal valve of a mature capsule; xi, dorsal view of a seed, showing the lateral embryotega, strongly cleft testa towards the embryotega; xii, ventral view of a seed, showing the hilum on a weak ridge (scale bar = 2) mm). **D,** Aneilema scaberrimum (Blume) Kunth: **xiii**, side view of a mature capsule; **xiv**, side view of the dorsal valve of a mature capsule; xv, dorsal view of a seed, showing strongly cleft testa towards the embryotega; xvi, ventral view of a seed, showing the hilum in a deep groove (scale bar = 0.6 mm). **E.** Aneilema vitiense Seem.: **xvii.** side view of a mature capsule: **xviii.** side view of the dorsal valve of a mature capsule; xix, dorsal view of a seed, showing slightly cleft testa towards the embryotega; xx, ventral view of a seed, showing the hilum on a weak ridge (scale bar = 2 mm). F, micrography of seeds on dorsal view, showing the presence or absence of farinose accumulations in the pits: xxi, A. protensum, showing the presence of farinose accumulations; xxii, A. scaberrimum, showing the lack of farinose accumulations (scale bar = 550 μm). A, C & E by M.O.O. Pellegrini, B, D & F by M.D. Nandikar.

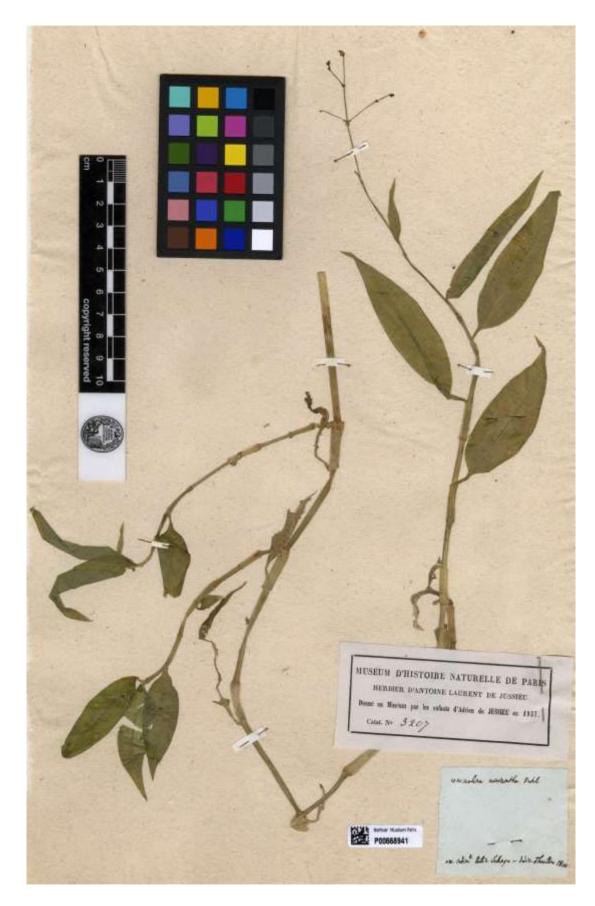


Figure 3. Aneilema micranthum (Vahl) Kunth. Lectotype of Commelina micrantha Vahl (P barcode P00668941). Photograph courtesy of the Muséum National d'Histoire Naturelle, Paris.

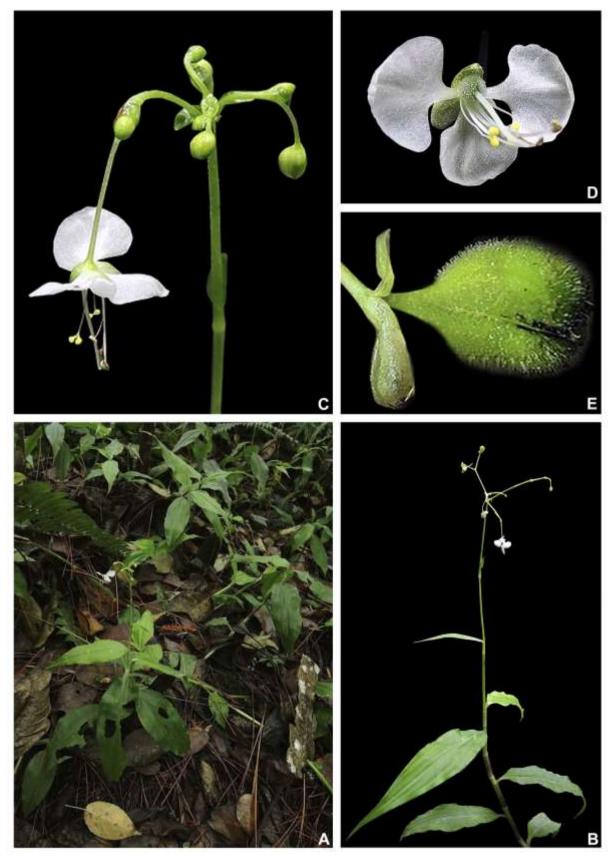


Figure 4. Aneilema micranthum (Vahl) Kunth. **A,** habit. **B,** fertile branch. **C,** detail of the inflorescence showing the pendulous flowers. **D,** front view of a bisexual flower. **E,** side view of an immature capsule. All photos by M. Kesl.

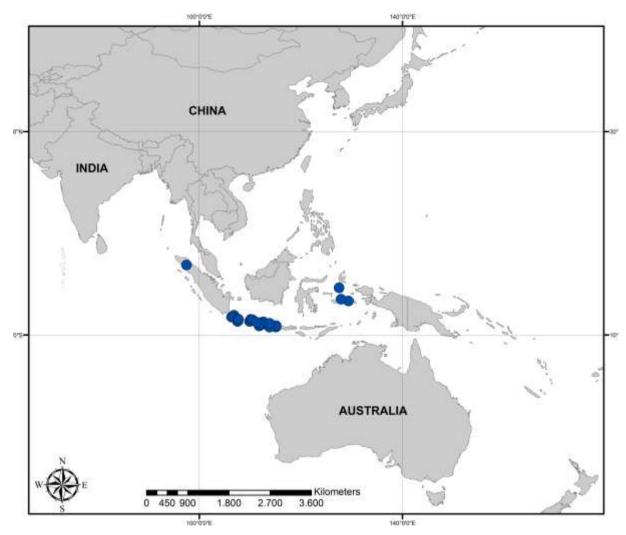


Figure 5. Distribution of *Aneilema micranthum* (Vahl) Kunth.

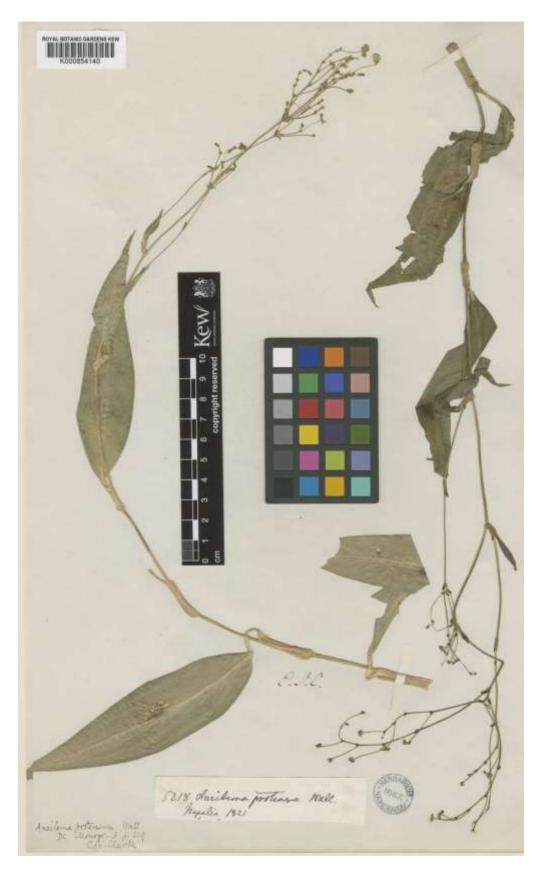


Figure 6. Aneilema protensum (Wall. ex Wight) Thwaites. Lectotype of Dictyospermum protensum Wall. ex Wight (K barcode K000854140). Photograph courtesy of The Royal Botanical Gardens, Kew.

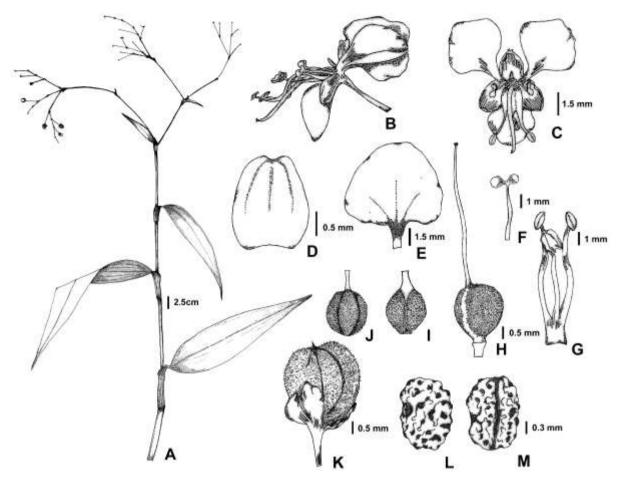


Figure 7. Aneilema protensum (Wall. ex Wight) Thwaites. **A,** fertile branch. **B–C,** bisexual flower: **B,** side view; **C,** front view. **D,** dorsal view of the upper sepal. **E,** paired petal. **F,** lateral staminode. **G,** fertile stamens. **H–J,** gynoecium: **H,** side view; **I,** ventral view of the ovary; **J,** dorsal view of the ovary. **K,** mature capsule. **L–M,** seed: **L,** dorsal view; **M,** ventral view. Line drawing by M.D. Nandikar.

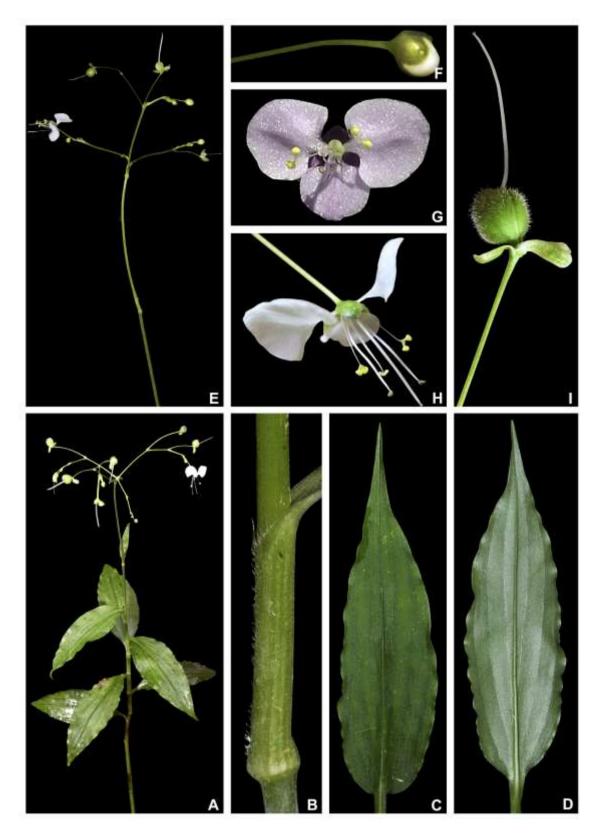


Figure 8. Aneilema protensum (Wall. ex Wight) Thwaites. **A,** fertile branch. **B,** detail of the leaf-sheath showing the pubescence restricted to the margin. **C–D,** leaf blade: **C,** adaxial side; **D,** abaxial side. **E,** inflorescence. **F,** floral bud. **G–H,** bisexual flower: **G,** frontal view of a lilac flower; **H,** upper view of a white flower. **I,** immature capsule. A, H & I by L.C. Pan, B–F by S.K. Kasaju, and G by P. Awale.

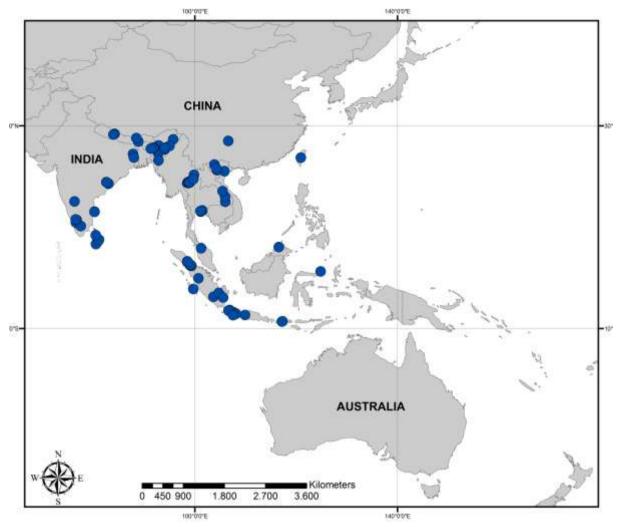


Figure 9. Distribution of *Aneilema protensum* (Wall. *ex* Wight) Thwaites.



Figure 10. *Aneilema rugosum* H.Perrier. Holotype of *A. rugosum* (P barcode P02088085). Photograph courtesy of the Muséum National d'Histoire Naturelle, Paris.

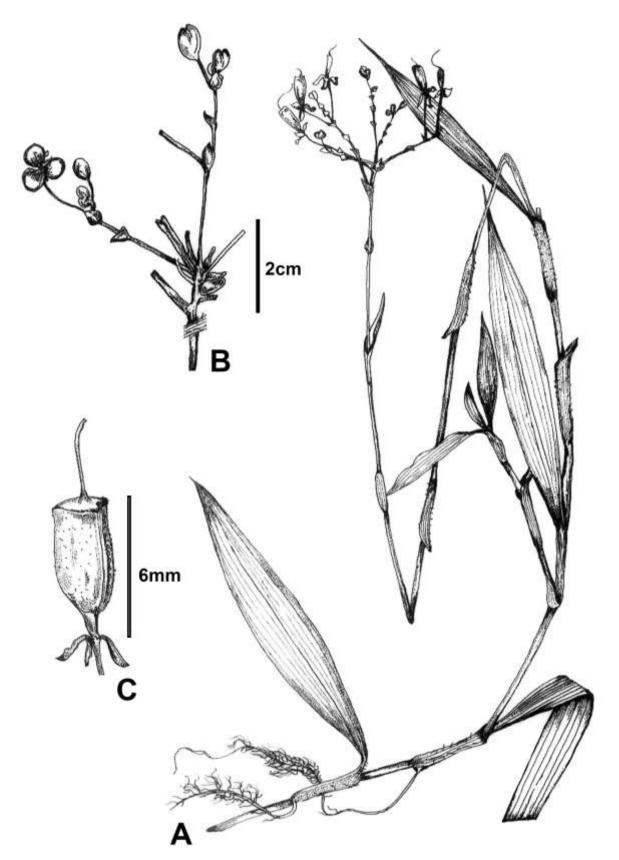


Figure 11. Aneilema rugosum H.Perrier. **A,** habit. **B,** detail of the inflorescence. **C,** mature capsule, showing the deflexed sepals. Line drawing by M.D. Nandikar, modified from the original (Perrier de la Bâthie 1938).

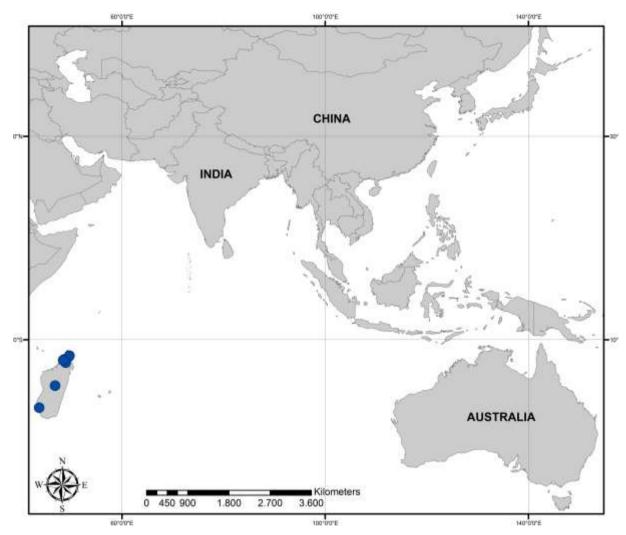


Figure 12. Distribution of *Aneilema rugosum* H.Perrier.



Figure 13. Aneilema scaberrimum (Blume) Kunth. Lectotype of *Commelina scaberrima* Blume (L barcode L0820741). Photograph courtesy of the Naturalis Biodiversity Center, Leiden, Netherlands.

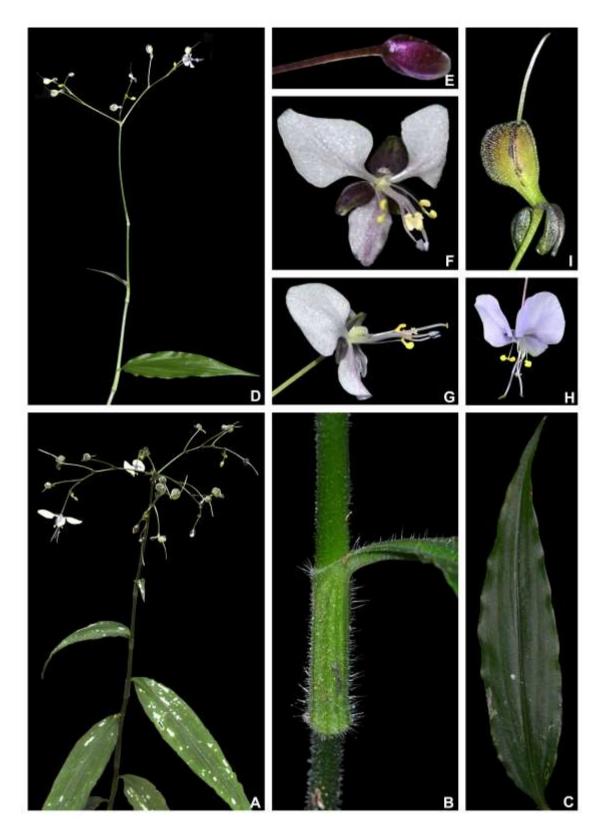


Figure 14. Aneilema scaberrimum (Blume) Kunth. **A,** habit. **B,** detail of the leaf-sheath showing it pubescence. **C,** adaxial side of the leaf blade. **D,** fertile branch showing the inflorescence. **E,** floral bud. **F–H,** flower: **F,** oblique view of a staminate flower; **G,** side view of a bisexual flower; **H,** upper view of a staminate flower, showing the connate stamens filaments. **I,** side view of a mature capsule. A by Hai Le, B–C, F & I by A.N. Sharma, D & G by M.D. Nandikar, and E & H by D.J. Layton.

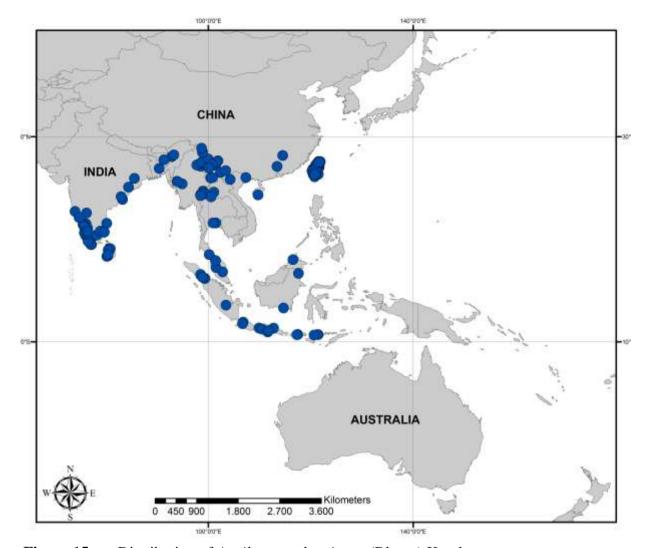


Figure 15. Distribution of *Aneilema scaberrimum* (Blume) Kunth.



Figure 16. Aneilema vitiense Seem. Lectotype of A. vitiense (K barcode K000854139). Photograph courtesy of The Royal Botanical Gardens, Kew.



Figure 17. *Aneilema vitiense* Seem. Original illustration of *A. vitiense* from Seemann (1868). Image available at Biodiversity Heritage Library.

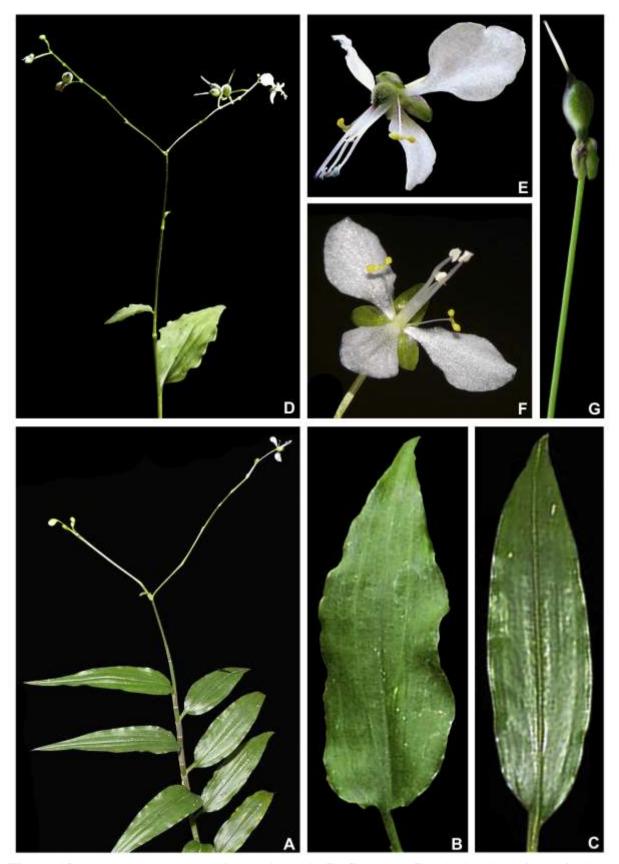


Figure 18. Aneilema vitiense Seem. **A,** habit. **B–C,** leaves: **B,** adaxial side of a leaf with a round base; **C,** adaxial side of a leaf with a cuneate base. **D,** fertile branch showing the inflorescence. **E–F,** flower: **E,** oblique view of a bisexual flower; **F,** ventral view of a staminate flower. **G,** mature capsule. A, C & F by P. Pelser, and B, D–E & G by M. Kesl.

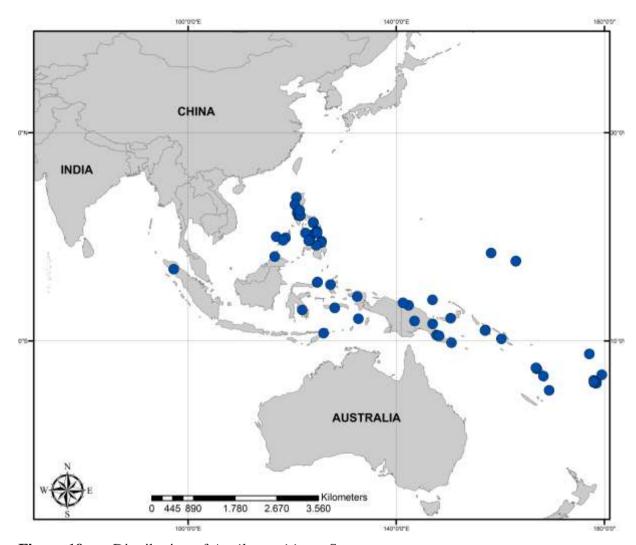


Figure 19. Distribution of *Aneilema vitiense* Seem.

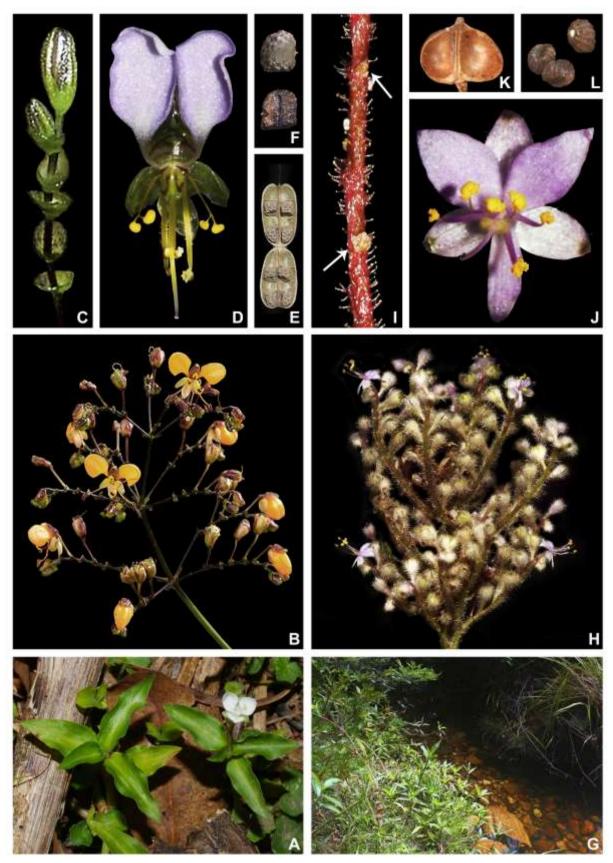


Figure 20. Morphological comparison between *Aneilema* R.Br. *s.l.* and *Floscopa* Lour. **A–F,** *Aneilema*: **A,** terrestrial and trailing habit of *A. biflorum* R.Br.; **B,** synflorescence of *A. johnstonii* K.Schum. composed by a solitary main florescence; **C,** cincinnus of *A. hockii* De Willd. showing the cup-shaped and perfoliate bracteoles; **D,** front view of a bisexual flower of

A. beniniense (P.Beauv.) Kunth; **E**, open capsule of A. paupanum Warb.; **F**, seeds of A. aequinoctiale (P.Beauv.) Loudon showing the lateral and concolorous embryotega and foveolate testa. **G–L**, Floscopa: **G**, aquatic and ascending habit of F. glabrata (Kunth) Hassk.; **H**, synflorescence of F. scandens Lour. composed by a main florescence plus several coflorescences; **I**, detail of the cincinnus of F. aquatica Hua showing the minute and rhomboid bracteoles; **J**, front view of a flower of F. hirsuta (Kunth) Hassk.; **K**, open capsule of F. glomerata (Willd. ex Schult. & Schult.f.) Hassk.; **L**, seeds of F. glabrata showing the dorsal and white embryotega and costate testa. A by A. Paget, B by B. Wursten, C by R.V. Blittersdorff, D, G, J & L by M.O.O. Pellegrini, E by Steven & Alison Pearson, F by E. Barbier, H by L.C. Pan, I by T. Stévart, and K by E. Bidault.



Figure 21. Aneilema yunnanense (D.Y.Hong) M.Pell. Isotype of *Floscopa yunnanensis* D.Y.Hong (A barcode A00415435). Photograph courtesy of the Herbarium of the Arnold Arboretum, Harvard University, USA.

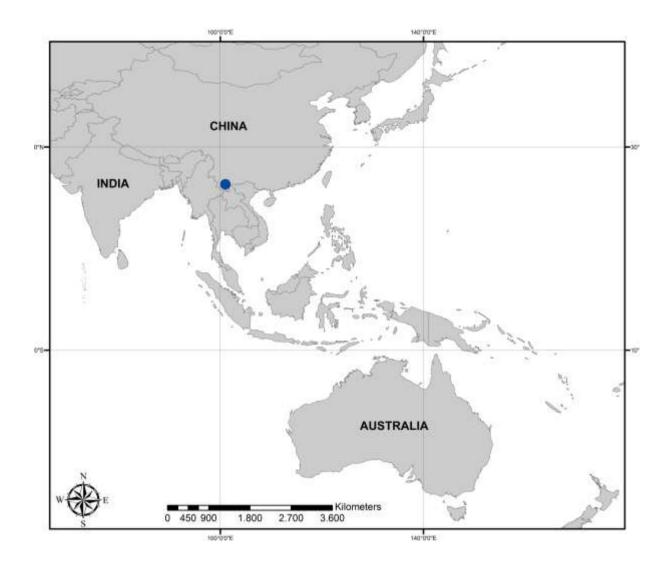


Figure 22. Distribution of *Aneilema yunnanense* (D.Y.Hong) M.Pell.

SECTION 2— COMMELINACEAE MIRB.

Chapter 2.4. Synopsis of *Commelina* L. (Commelinaceae) in the state of Rio de Janeiro, reveals a new white-flowered species endemic to Brazil

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Abstract

A synopsis for the genus *Commelina* in the state of Rio de Janeiro, Brazil, is presented here, including a new species, ten new synonyms, five designated lectotypes, two designated epitypes and an excluded name. *Commelina huntii*, a new species, is remarkable due to the combination of rusty to rusty-brown hairs at the margin of its leaf-sheaths, connate spathes, white flowers with auriculate medial petal, ovaries with sparse black papillae and dehiscent fruits. Additionally, we provide an identification key, illustrations, and conservation status for the species of *Commelina* recorded in the state of Rio de Janeiro.

Key words

Atlantic Forest, Commelineae, Commelinopsis, Neotropical flora, Phaeosphaerion

Introduction

Commelina L. is the largest genus of Commelinaceae, comprising between ca. 170 species (Faden 1998) and 205–215 species (Govaerts & Faden 2009; The Plant List 2013, respectively). It is one of the six genera of Commelinaceae (out of 42) to have a cosmopolitan distribution (Faden 1998), and one of the most complicated taxonomically. Commelina is easily differentiated from the remaining genera in the tribe by its inflorescences which are subtended by spathaceous basal bracts and reduced to (1–)2 fasciculate cincinni, zygomorphic flowers, petals clawed, unequal and mostly blue (but sometimes white or lilac, rarely yellow, apricot or orange), three posterior staminodes with 6-lobed cruciform antherodes, three anterior stamens, and 2-locular or unequally 3-locular and 2-valved capsules (Faden 1998).

The state of Rio de Janeiro is entirely placed within the Atlantic Forest domain (Veloso et al. 1991), being one of the four diversity centers of the family, and possessing 67 of the 96 accepted Commelinaceae species for Brazil (BFG 2015). With 1,109,546 ha of continuous forests, which represent 7% of what remains of the Atlantic Forest, Rio de Janeiro is also the state with the greatest amount of preserved forest remnants from this biome (Ribeiro et al. 2009). Nevertheless, the most recent published state flora is nearly two centuries old (i.e. Vellozo 1829) and no satisfactory taxonomic treatment for the Commelinaceae has been done since. As a first attempt to clarify the taxonomy of *Commelina* in the state of Rio de Janeiro, we describe a new species of *Commelina*, together with a synopsis for the genus in the state. This work includes an identification key, illustrations and an overview of some overlooked Brazilian *Commelina* names.

Methods

The descriptions and phenology of the species were based on herbaria, spirit, fresh material, field data, and literature. All species were studied in the field and had their descriptions complemented with field notes, photographs, and cultivated specimens, gathered between the years of 2010–2016. Live specimens collected by the authors were kept in cultivation at the greenhouse of the Jardim Botânico do Rio de Janeiro, in order to better observe, photograph and analyze fresh flowers, fruits and seeds, as well as other phenological data. Specimens from the following herbaria were also analyzed: ALCB, BHCB, BHZB, BM, BOTU, CEPEC, CESJ, CGE, CNMT, CVRD, ESA, FCAB, FLOR, FURB, GUA, HAMAB, HAS, HB, HBR, HRB, HSTM, HUEFS, HURB, IAC, ICN, JOI, K, MBM, MBML, PMSP, R, RB, RFA, RFFP, SP, SPF, UEC, UPCB, and US (herbaria acronyms according to Thiers, continuously updated). While specimens of the following herbaria were analyzed using high-resolution images available on-line: B, BRIT, C, CAL, F, INPA, L, MG, MO, MY, NY, P, U, and

WAG. The classification of the vegetation patterns follows IBGE (2012). The indumenta and shapes terminology follows Radford *et al.* (1974); the inflorescence terminology and morphology follows Weberling (1965, 1989) and Panigo *et al.* (2011); the fruit terminology follows Spjut (1994) and Joseph & Nampy (2012); and seeds terminology follows Faden (1991) and Joseph & Nampy (2012). The conservation statuses were proposed following the recommendations of *IUCN Red List Categories and Criteria, Version 3.1* (IUCN 2001). GeoCAT (Bachman *et al.*, 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). The typification of Vellozo's names for *Commelina* followed the same methodology used by Pellegrini (2015), Pellegrini *et al.* (2015) and Pellegrini & Carvalho (2016).

Results

Key to the species of *Commelina* in Rio de Janeiro state, Brazil

- 1. Inflorescences predominantly axillary and leaf-opposed, long pedunculate (peduncle the same length or longer than ½ length of the spathe); medial petal clawed... *Commelina diffusa* Burm.f.
- Inflorescences terminal or apparently so, short-pedunculate to sessile (peduncle shorter than ½ length of the spathe); medial petal sessile... 2
- 2. Spathe base free, *in vivo* much lighter than the leaves; capsules indehiscent, not constricted between the seeds, crustaceous, pearly-white to silvery; all seeds adhered to the capsule wall and septa, forming a dispersal unit... 3
- Spathe base connate, in vivo the same color as the leaves; capsules dehiscent, constricted between the seeds, green to light brown; dorsal seeds adhered to the capsule wall, ventral seeds free from each other, dispersed separately... 4
- 3. Leaf-sheaths hirsute throughout, hairs rusty to rusty-brown, blades lanceolate to elliptic-lanceolate, hispid on both sides, hairs hyaline, sparsely hirsute along the midvein and near base, hairs rusty to rusty-brown, base cuneate, apex acute... *Commelina rufipes* Seub. var. rufipes
- Leaf-sheaths glabrous, margin glabrous to setose, hairs rusty to rusty brown, blades ovateelliptic to ovate, glabrous, base round to obtuse, apex acuminate to caudate... Commelina rufipes var. glabrate (D.R.Hunt) Faden & D.R.Hunt
- 4. Leaf-sheaths with auriculate margin; upper cincinnus aborted, included; medial petal hyaline; capsules 3-seeded, dorsal locule commonly verrucous, rarely smooth; testa smooth... *Commelina erecta* L.
- Leaf-sheaths with patent and erect margin; upper cincinnus present, exerted; medial petal slightly paler to concolorous with the paired petals; capsules 5-seeded, dorsal locule smooth; testa ornate... 5
- 5. Leaves subpetiolate; spathe transversally rhomboid; cleistogamous subterraneous flowers present, medial petal trullate, ovary minutely pilose, stigma capitate; capsules ellipsoid; seeds black, testa shallowly reticulate... *Commelina benghalensis* L.
- Leaves sessile; spathe depressed ovate to subcordate; cleistogamous subterraneous flowers absent, medial petal obovate to oblong obovate, ovary glabrous, stigma trilobate; capsules obovoid; seeds dark-brown, testa shallowly foveolate, foveolate or rugose foveolate... 6

- 6. Leaf-sheath margin densely bearded with rusty to rusty brown hairs; petals white, paired petals broadly rhomboid to rhomboid-reniform, medial petal cucullate, biauriculate; ovary and capsules with black papillae, 1–2 capsules per spathe; seeds with peach-colored farina, dorsal locule seed testa shallowly foveolate... *Commelina huntii* M.Pell.
- Leaf-sheath margin with light to dark brown to atro-vinaceous hairs; petals blue to light-blue to lilac to pale lilac, paired petals broadly ovate to broadly ovate-reniform, medial petal involute, entire; ovary and capsules smooth, 5–7 capsules per spathe; seeds with white-farinose, dorsal locule seed testa rugose-foveolate... *Commelina obliqua* Vahl

1. Commelina benghalensis L., Sp. Pl. 1: 41. 1753, nom. cons. Fig 1A

Neotype (conserved and designated by Faden 1992). INDIA. Habitat in Benghala, s.dat., s.leg., Herb. Linn. 65.16 (LINN!).

Selected specimens seen. BRAZIL. Rio de Janeiro: Angra dos Reis, Ilha Grande, matas da praia de Abraão, 18 Apr 1987, L.C. Giordano 277 (RB). Armação de Búzios, 19 Aug 1998, D. Fernandes 19 (R). Cabo Frio, 22 Oct 2013, H.F. Uller s.n. (RB 612224). Campos dos Goytacazes, Morro do Itaoca, Pedra Negra ponto 1, 13 Oct 2009, L.P. Mauad & I.O.R. Areias 20 (RB). Casimiro de Abreu, Praião, Avenida Oceânica, 24 Jun 2012, A.J. Castelo 39 (RB). Iguaba Grande, Km 94, 1981, H. Barreto s.n. (RB 275353). Macaé, Córrego de Ouro, Fazenda Vitória, Morro do Oratório, 2 May 1971, J.P.P. Carauta 1364 (RB, U n.v.). Niterói, Itaipuaçu, próximo ao Canal da Costa, 18 Sep 2004, T.T. Carrijo 143 (RB). Resende, margem da rodovia Dutra, Km 302 sentido RJ, ao lado da Light, próximo ao Rio Paraíba do Sul, 9 Jun 2012, M.O.O. Pellegrini et al. 233 (RB). Rio de Janeiro, Morro do Rangel, Recreio dos Bandeirantes, 31 May 1973, D. Sucre 10005 (RB, US). São José de Ubá, 14 May 2014, T.M. Scarponi s.n. (RB 612228). Saquarema, Tingui em Sampaio Correia, 14 Apr 1995, J.A. Lira Neto 56 (RB). Silva Jardim, Próximo a sede da REBIO, 29 Oct 1997, J.A. Lira Neto 719 (RB).

Distribution and habitat. Tropical and subtropical regions of the world. In the state of Rio de Janeiro it is especially common in disturbed areas of drier regions inland or near the coast, being common in *restingas* (i.e. sandbank vegetation), and as a weed in agricultural fields (Fig. 2).

Phenology. Throughout the year, but especially in the rainy season.

Conservation status. It is a weed of worldwide distribution being very common in sunny disturbed areas and in agricultural fields. Following the IUCN recommendations (IUCN 2001), it should be considered as Least Concern (LC) in the state of Rio de Janeiro and worldwide.

Morphological and ecological notes. The underground cleistogamous flowers and fruits seem to be produced only in areas where the soil is soft. The flower morphology differs from the aerial chasmogamous in pigmentation (being paler), while the fruits are sub-globose (due to larger seeds).

2. Commelina diffusa Burm.f., Fl. Indica 18: pl. 7, f. 2. 1768. Fig 1B

Holotype. INDIA. Coromandel, s.dat., D. Outgaerden s.n. (G barcode G00360106!).

Commelina communis Vell., Fl. Flumin.: 30, 1829, nom. illeg. non *C. communis* L., Sp. Pl. 1: 40, 1753. Lectotype (designated here). [illustration] Original parchment plate of *Flora fluminensis* in the Manuscript Section of the Biblioteca Nacional do Rio de Janeiro [mss1095062_079] and later published in Vellozo, Fl. flumin. Icon. 1: t. 75. 1831. **Syn. nov.**

Selected specimens seen. BRAZIL. Rio de Janeiro: Arraial do Cabo, 24 Jul 1953, F. Segadas Vianna 1157 (R, US). Casimiro de Abreu, Barra de São João, 27 May 1953, F. Segadas Vianna 347 (R, US). Guapimirim, trilha das andorinhas, 20 Dec 1995, L.A. Lira Neto 161 (RB). Itaboraí, entre os rios Caceribu e Macacu, 10 Aug 2007, A. Rodarte 4Cf (RB). Itatiaia, Parque Nacional do Itatiaia, Hotel Repouso, 14 Dec 1997, J.M.A. Braga 4539 (RB). Mangaratiba, Reserva Ecológica Rio das Pedras, trilha para o mirante, 12 Jul 1997, J.A. Lira Neto 603 (RB). Niterói, Jurujuba, 16 Jan 1959, A. Castellanos 22336 (R). Petrópolis, Serra da Estrela, meio da Serra, antigo leito da estrada de ferro, próximo ao Poço do Cipó, 9 Mar 1978, P.P. Jouvin 121 (RB). Resende, margem da rodovia Dutra, Km 302 sentido RJ, ao lado da Light, próximo ao Rio Paraíba do Sul, 9 Jun 2012, M.O.O. Pellegrini et al. 232 (RB). Rio de Janeiro, Urca, 10 Jan2012, M.O.O. Pellegrini et al. 182 (RB). São João da Barra, 30 May 1953, F. Segadas Vianna 428 (R, US). Silva Jardim, próximo à sede da REBIO, 29 Oct 1997, J.A. Lira Neto 714 (RB). Teresópolis, Laje, estrada para Campo Limpo, Granja Mafra, 28 May 1977, L.D.A. Freire de Carvalho 600 (RB).

Distribution and habitat. Tropical and subtropical regions of the world, being very common in shady disturbed areas such as road sides, gardens and forest margins, and in agricultural fields. It is also found growing on the edge of wet paddy fields, ponds, ditches and stream sides (Fig. 2).

Phenology. Throughout the year, but especially in the rainy season.

Conservation status. Following the IUCN recommendations (IUCN 2001), it should be considered as Least Concern (LC) in the state of Rio de Janeiro and worldwide.

Morphological notes. The specimens from the state of Rio de Janeiro usually show a staminode malformation, i.e. the central antherode is lacking in most of the herbaria and living specimens examined.

Nomenclatural and taxonomical notes. *Commelina communis* Vell. is a later homonym of *C. communis* L. (the genus' type species), thus, rendering it illegitimate. Vellozo's description (1929) is little informative, especially for *Commelina*, lacking all the characters evidenced by Faden (2008) as important to delimitate species in the genus. Despite this, the spathe and flower details (Vellozo 1831: t. 75), along with the leaf shape and stem diagnosis (Vellozo 1929), make it possible to associate *C. communis* Vell. to *C. diffusa*, rather than to *C. deficiens* Herb. (= *C. erecta*), as pointed out in the *Index Methodicus* of *Flora fluminensis* (Vellozo 1831, v. 1).

3. *Commelina erecta* **L.**, Sp. Pl. 1: 41. 1753. Figs 1C–D

Lectotype (designated by Clarke 1881). "Commelina erecta, ampliore subcaeruleo flore" in Dillenius, Hort. Eltham. 1: 91, t. 77, f. 88. 1732.

- Commelina erecta var. angustifolia (Michx.) Fern., Rhodora 42(503): 439.1940. Syn. nov.
- Commelina virginica var. angustifolia (Michx.) C.B.Clarke, in De Candolle ALPP & De Candolle ACP Monogr. Phan. 3: 183. 1881. **Syn. nov.**
- Commelina angustifolia Michx., Fl. Bor.-Amer. 1: 24. 1803. Holotype. USA. Sabulosis in Carolinae, s.dat., A. Michaux 100 (P barcode P00680427!). **Syn. nov.**
- Eudipetala deficiens (Herb.) Raf., Fl. Tellur. 3: 68. 1837. Syn. nov.
- Commelina deficiens Herb., Bot. Mag. 53: t. 2644. 1826. Lectotype (designated here). [illustration] Original parchment plate of "Curtis's Botanical Magazine" at the Library of the Royal Horticultural Society, published in Hooker, Curtis's Bot. Mag. 53: t. 2644. 1826. **Syn. nov.**
- Commelina erecta f. villosa (C.B.Clarke) Stand. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23(2): 33. 1944. **Syn. nov.**
- Commelina villosa (C.B.Clarke) Chodat & Hassl., Bull. Herb. Boissier, sér. 2, 1: 438. 1901. Syn. nov.
- Commelina virginica var. villosa C.B.Clarke, Monogr. Phan. 3: 183. 1881. Lectotype (designated here). BRAZIL. Rio Grande do Sul: "provincia de Rio Grande do Sul", 1816–1821, A. St.-Hilaire 2598 (P barcode P01742038!; isolectotype: P barcode P01742041!). Syn. nov.

Selected specimens seen. BRAZIL. Rio de Janeiro: Araruama, 20 Apr 2008, A.C.S. Cavalcanti 139 (SPF). Armação de Búzios, loteamento de João Fernandes, quadra A, rua I, lote 10, 27 Jul 2013, M. Furtado 28 (RB). Arraial do Cabo, Praia do Pontal, 31 Jul 1953, F. Segadas Vianna s.n. (US barcode US 2283943.2455262). Cabo Frio, Peró, Sítio Guriri, 21 Jul 2003, G.S.Z. Rezende 191 (RB). Campos dos Goytacazes, Feb 1918, A.J. Sampaio 2813 (R). Carapebus, 23 Mar 1996, V. Esteves 947 (R). Macaé, Parque Nacional da Restinga de Jurubatiba, margem da estrada principal, entre a praia e as moitas, próximo a Lagoa Cabiúnas, 23 Jun 2013, L.S.B. Calazans 219 (RB). Mangaratiba, Ilha da Marambaia, Praia Grande, 15 Jan 1986, E.M. Occhioni 484 (RB). Maricá, 16 Feb 2005, A.T.A. Rodarte 195 (RB). Niterói, Parque Estadual da Serra da Tiririca, Pedra de Itacoatiara, 16 Feb 2000, M.C.F. Santos 496 (RB, RFFP). Paraty, Parati Mirim, Fazenda Parati-Mirim, propriedade da Flumitur, s.dat., C. Almeida 1931 (RB). Rio de Janeiro, Urca, 10 Jan 2012, M.O.O. Pellegrini et al. 181 (RB). Santo Antônio de Pádua, Monte Alegre, Mar 1927, J. Vidal s.n. (R 205994). São Gonçalo, Paraíso, Faculdade Formação de Professores da Universidade do Estado do Rio de Janeiro, 20 Oct 2006, N. Coqueiro 297 (RB, RFFP). São João da Barra, Restinga de Iquipari, 11 Dec 2002, M.C. Gaglione 8 (RB). Saquarema, 21 Feb 1996, A.Q. Lobão 76 (RB).

Distribution and habitat. Tropical and subtropical regions of the world, being common in disturbed areas of drier regions inland or near the coast, commonly found in *restingas* or in urban areas (Fig. 2).

Phenology. Throughout the year, but especially in the rainy season.

Conservation status. Following the IUCN recommendations (IUCN 2001), it should be considered as Least Concern (LC) in the state of the Rio de Janeiro and worldwide.

Nomenclatural and taxonomical notes. Clarke (1881), in his revision of Commelinaceae, erroneously considered *C. erecta* as a synonym of *C. virginica* L., a species endemic to the USA (Faden 2000). Thus, some names currently placed under the synonymy of *C. erecta* were originally described under *C. virginica*, or transferred to it at some point.

According to Faden (1993, 2000), *Commelina erecta* can be differentiated by its leaf-sheaths with auriculate margins, medial petal linear and hyaline, and all locules 1-seeded (vs. leaf-sheaths not auriculate, medial petal blue and conspicuous, and dorsal locule 1-seeded and ventral locules 2-seeded, in *C. virginica*).

There seems to be some doubt regarding *C. deficiens* Herb. synonymy. According to Tropicos.org (2015), this species is considered a synonym of *C. erecta*. Nevertheless, eMonocot.org (2010) and The Plant List (2013) treat *C. deficiens* under the synonymy of *C. virginica*. As abovementioned, there is an historical confusion regarding *C. erecta* and *C. virginica*. If we exclusively take into account that *C. deficiens* was described by Herbert (1826) from the surrounding areas of Rio de Janeiro, it is impossible for *C. deficiens* to be conspecific to *C. virginica*. Added to that, the watercolour presented by the author perfectly illustrates the habit, flower morphology and the inflorescence characteristic of *C. erecta* (with the aborted upper cincinnus). Thus, there is little doubt that *C. deficiens* is a synonym of the latter. According to Stafleu & Cowan (1979), Herbert's type specimens were deposited at K, but no specimen corresponding to *C. deficiens* was found. Thus, in accordance to the *Code* (McNeill *et al.* 2012, Art. 9.12), in the absence of herbarium specimens, we designate this illustration as the lectotype for *C. deficiens*.

Commelina villosa (C.B.Clarke) Chodat & Hassl. has long been a name of dubious application. Clarke (1881) had already noticed that its morphological concept overlapped with the one of the highly variable C. erecta, and that the difference between them relied solely on the plant's indumenta. The observation of a great number of natural populations and specimens kept in greenhouses showed that most of the morphological variation known for C. erecta has an environmental background. Large flowered specimens developed into small flowered specimens after being transplanted from sunny to shady areas. The same thing happened to narrow-leafed and erect plants (which would represent C. erecta var. angustifolia), developing into creeping and small to wide-leafed plants. The indumenta also varied when specimens were transplanted from the field to the greenhouse. Regarding growth form and position of the stem of *C. erecta*, the plants can vary from creeping to sub-scandent (i.e. stems leaning generally on bushes or any other kind of support) to partially or completely erect. The only morphological characters, constant in all areas and environmental conditions were: the auriculate leaf-sheath margins; terminal to apparently terminal inflorescences (1–3 per stem), broadly sagittate to subcordate spathes with connate margin, aborted upper cincinnus (generally completely absent, but sometimes only vestigial); hyaline, linear and involute medial petal (almost invisible at blind sight); capsules with 1-seeded locules; and smooth seed testa.

After analyzing the original descriptions and the type specimens, it became clear that *C. villosa* and *C. erecta* var. *angustifolia* are conspecific to *C. erecta*. Thus, no varieties or subspecies are accepted in Brazil for *C. erecta*.

4. Commelina huntii M.Pell., sp. nov.

Figs 3–5

Diagnosis. Commelina rufipes Seub. affinis, sed ab ea spathis depressum-ovatum vel subcordato, basi adnata, petalo inferioris auriculata, ovarium sparse nigro-papillose, capsulae ellipsoide dehicens, parda, seminibus libera differt.

Holotype. BRAZIL. Rio de Janeiro: Itatiaia, Parque Nacional do Itatiaia, subida para o brejo da Lapa, beira de estrada, fl., fr., 24 January 2012, M.O.O. Pellegrini & L.S. Sylvestre 191 (RB!; isotypes: SPF!, US!).

Description. Herbs 15–35 cm tall, perennial, terrestrial. Roots thin, fibrous, cream colored to light yellow, glabrous or minutely pubescent with absorbent hairs. Stems decumbent, apex ascending, becoming trailing or straggling, rooting only near the base; internodes 2.2-11.1 cm long, green, minutely velutine to minutely pilose, with line of uniseriate hairs opposite to the leaves, hairs hyaline, Leaves distichously-alternate, distributed along the stem, sessile; sheaths 1.4–2.6 cm long, pilose, hairs hyaline, margins densely setose, with a line of setose hairs opposite to the leaves, hairs rusty to rusty-brown; blades $3.3-9.1 \times$ (0.9-)1.6-2.3(-3.3) cm, chartaceous, adaxially dark-green to green, abaxially light-green to light-green tinted vinaceous to completely vinaceous, drying olive-green on both sides, lanceolate to ovate lanceolate, rarely ovate, adaxially scabrous, abaxially minutely villous, pilose along the midvein, hairs hyaline, base obtuse, rarely cuneate, margins green, scabrous, apex acuminate; midvein conspicuous, impressed adaxially, prominently obtuse abaxially, secondary veins (2–)4–6 pairs, adaxially conspicuous, abaxially inconspicuous. *Inflorescences* 1–4, terminal or apparently so, peduncles 1.3–5.5 mm, rarely inconspicuous, puberulous with hook hairs throughout, hairs hyaline; spathes $0.7-2 \times 1.4-3.2$ cm, depressed ovate to subcordate, usually slightly falcate, base connate for 3-6 mm, cordate to truncate, margin green to vinaceous, minutely pilose along the edge, hairs hyaline, sometimes also ciliate, cilia rusty to rusty-brown, apex acute, internally light-green, glabrous, veins inconspicuous, externally green, minutely villous with eventual cilia, hairs hyaline, cilia rusty to rusty-brown, veins inconspicuous, becoming conspicuous when dry; upper cincinnus 2–5-flowered, flowers male, very rarely bisexual, peduncle (0.7–)1.7–2.4 cm long, exserted from the spathe, commonly arcuate at post-anthesis, sparsely to densely puberulous with hook hairs, sometimes of 2 heights, hairs hyaline; lower cincinnus 2–4-flowered, flowers mainly bisexual, sometimes male, peduncle 0.5–1 cm, glabrous or sparsely puberulous with minute hook hairs. Flowers bisexual or male, zygomorphic, 6.5–9 mm diam.; pedicel 1–4 mm long, light green, glabrous, reflexed and slightly elongate in fruit; sepals hyaline white to hyaline light-green, glabrous, persistent in fruit, upper sepal $3,4-4,2\times1,1-1,4$ mm, elliptic, cucullate, round apex, lower sepals $4.1-5.3 \times 2.2-2.6$ mm, obovate, cucullate, connate, round apex; paired petals $6.2-6.9 \times 4.9-5.4$ mm, clawed, limb broadly rhomboid to rhomboid-reniform, $4.7-5.3 \times 4.9-$ 5.4 mm, white, apex rounded, base cordate, claw 1.6–2 mm, white to tinted vinaceous, medial petal 3.1–4 × 1–1.4 mm, sessile, obovate to oblong-obovate, with 2 auricles near the middle, cucullate, concolorous with or slightly paler than the paired petals; staminodes 3, subequal, filaments 3–3.6 mm long, tinted vinaceous, antherodes 6-lobed, $1-1.2 \times 1.2-1.4$ mm, yellow with tiny light-yellow pollen sacs; lateral stamen filaments gently sigmoid, geniculate distal to the middle, 5.6–6.6 mm long, white, anthers elliptic to oblong-elliptic, $1.2-1.4 \times 0.9-1.2$ mm, yellowish-orange to cream-orange with margins tinted purple, pollen yellowish-orange to cream-orange; medial stamen filament straight or arcuate-decurved, decurved at the apex, 2.2–2.8 mm long, white to tinted vinaceous, anther 1.5–2.2 × 1–1.8 mm, broadly elliptic to broadly oblong-elliptic, strongly curved, held near the antherodes, yellow-orange to creamorange, connective purple to dark-purple, pollen yellowish-orange to cream-orange; ovary oblong-ellipsoid, ca. 1–1.3 × 0.6–0.7 mm, 5-ovulate, glabrous, sparsely papillose, papillae black, style exceeding or equaling the stamens, sigmoid, strongly recurved apically, 8–11.3 mm, white, stigma trilobate, white. *Capsules* 1–2 per spathe, 5.5–8.1 × 3.8–5 mm, obovoid, constricted between the seeds, brown to light brown, glabrous, sparsely papillose, papillae black, 3-locular, 2-valved, dorsal locule 1-seeded, indehiscent, ventral locules 2-seeded. *Seeds* slightly dimorphic, dark brown with orange-brown verrucae, farinose, farina peach-colored; dorsal locule seed strongly adhered to the capsule wall, ellipsoid, strongly dorsiventrally compressed, ventrally flattened, not cleft towards the embryotega, 3.4–4.2 × 2.8–3.3 mm, testa shallowly foveolate, embryotega semilateral, relatively inconspicuous, without a prominent apicule, hilum linear, ½ the length of the seed; ventral locule seeds free from the capsule wall, ellipsoid, truncate at one end, ventrally flattened, not cleft towards the embryotega, 2.7–3.4 × 2–2.4 mm, testa foveolate, embryotega semilateral, relatively inconspicuous, without a prominent apicule, hilum linear, ½ the length of the seed.

Specimens seen (paratypes). BRAZIL, Minas Gerais: Araponga, Parque Estadual Serra do Brigadeiro, Fazenda Neblina, 17 February 2005, L.S. Leoni et al. 6112 (RB, UEC); Camanducaia, Monte Verde, Serra da Mantiqueira, 11 December 2001, L.D. Meireles & R. Belinello 775 (HURB, UEC); Delfim Moreira, Fazenda da Onça, trilha de subida para o Pico do Carrasco, 17 March 2011, L.L. Giacomin et al. 1429 (BHCB, RB); Lima Duarte, Parque Estadual do Ibitipoca, Conceição do Ibitipoca, gruta da Cruz, 30 November 2004, E.V.S. Medeiros et al. 364 (RB); loc. cit., gruta do Cruzeiro, 20 January 2005, L.G. Temponi et al. 407 (RB, UEC); loc. cit., gruta do Pião, 18 January 2005, R.C. Forzza et al. 3926 (RB, UEC); loc. cit., gruta do Cruzeiro, 26 January 2010, J.C. Lopes et al. 76 (RB, SPF); Poços de Caldas, Fazenda Campo da Cachoeira, área destinada para a instalação do Jardim Botânico de Poços de Caldas, 12 December 2001, C.N. Fraga & F.M. Fernandez 864 (RB); loc. cit., 12 December 2001, F.M. Fernandez 151 (BHZB, RB). Rio de Janeiro: Nova Friburgo, Morro da Caledônia, 8 June 1977, G. Martinelli 2469 (BA, RB); loc. cit., Reserva Macaé de Cima, cerca de 900 m do Hotel São João, 19 January 1999, L. Anderson et al. 99/15 (UEC); loc. cit., Reserva Macaé de Cima, cerca de 900 m do Hotel São João, 19 January 1999, L. Anderson et al. 99/20 (UEC); loc. cit., Parque Estadual dos Três Picos, Vale dos Deuses, 28 January 2015, M.S. Wängler et al. 1565 (RB); Resende, Parque Nacional do Itatiaia, estrada BR-485, próximo ao km 02, 22 February 2014, L.S.B. Calazans et al. 242 (RB). São Paulo: Itararé, divisa entre as Fazendas Santa Andreia e Prieto, 14 May 1989, C.A.M. Scaramuzza & V.C. Souza 259 (ESA); Ribeirão Grande, Parque Estadual Intervales, 15 April 2003, R.A.G. Viani et al. 79 (ESA).

Etymology. This species is named after the British botanist Dr. David R. Hunt, in honor of his extensive contribution to Commelinaceae systematics worldwide, especially for his contributions to Tradescantieae and the "*Phaeosphaerion* group" of *Commelina*.

Distribution and habitat. *Commelina huntii* was collected in moist and shaded nebular forests, generally near water bodies, in the states of Minas Gerais, Rio de Janeiro, and São Paulo, in elevations from 800 to 1,700 m above sea level (Fig. 5). In very rare cases it can also be found in open sometimes disturbed areas.

Phenology. It was found in bloom from November to June and in fruit from December to March, rarely in June.

Conservation status. Despite the wide EOO (112,904.528 km²), the AOO (40.000 km²) is considerably small, since all known populations are significantly small and fragmented. Following the IUCN recommendations (IUCN 2001), *C. huntii* should be considered as Endangered [EN, B2b(ii, iii)c(iv)+C2a(i)] in its overall distribution.

Affinities. Commelina huntii can be recognized by its white flowers with auriculate medial petal and sparsely papillose ovary and capsule. It is similar to *C. rufipes* Seub. due to its white flowers and rusty hairs on the leaf-sheaths, but it can be readily distinguished from the latter by its connate spathe base (vs. free base); auriculate medial petal without medial constriction (vs. entire medial petal with medial constriction); light-brown, ellipsoid, dehiscent capsules (vs. pearly-white to silvery, globose, crustaceous capsules); and by its free, ornamented seeds (vs. seeds fused to the capsule septa, forming a dispersal unit, with smooth testa). The gross floral morphology of *C. rufipes* is much more similar to the *C. benghalensis* than the one of *C. huntii*, possessing only the white petals in common.

Commelina huntii is most similar to *C. obliqua* Vahl due to its oblique leaf blades, connate spathe base, dehiscent capsules, and ventral seeds free with foveolate testa. Despite this, *C. huntii* can be distinguished from *C. obliqua* by its densely setose leaf-sheath margins with rusty to rusty brown hairs (*vs.* leaf-sheath margins long-ciliate with light to medium to dark brown to atro-vinaceous hairs); petals white (*vs.* blue to light blue to lilac to pale lilac), paired petals broadly rhomboid to rhomboid reniform (*vs.* broadly ovate to broadly ovate reniform), medial petal cucullate and biauriculate (*vs.* involute and entire); anthers of the lateral stamens light-yellow to cream with margins tinted vinaceous (*vs.* completely orange); ovary and capsules sparsely black papillate (*vs.* smooth); 1–2 capsules per spathe (*vs.* 5–7); seeds with peach-colored farina (*vs.* seeds white farinose), and dorsal locule seeds with shallowly foveolate testa (*vs.* rugose foveolate testa).

5. *Commelina obliqua* **Vahl**, Enum. Pl. 2: 172. 1806. Fig. 1E–G.

Lectotype (designated by Hunt 1994). *s.loc.*, cultivated in France, ex horto Celsii, Ventenat s.n. (C barcode C10009563!).

Selected specimens seen. BRAZIL. Rio de Janeiro: Guapimirim, trilha das Andorinhas, 20 Dec 1995, J.A. Lira Neto 145 (RB). Itatiaia, Parque Nacional do Itatiaia, parte baixa, atrás da casa do pesquisador, 21 Jan 2012, M.O.O. Pellegrini & L.S. Sylvestre 188 (RB). Nova Friburgo, Macaé de Cima, Reserva Ecológica Municipal de Macaé de Cima, estrada de terra próximo ao Hotel São João, 19 Jan 1999, J. Anderson et al. 9912 (UEC). Nova Iguaçu, Serra do Tinguá, Reserva Biológica do Tinguá, 13 May 1943, Guerra s.n. (NY 498159). Paraty, Fazenda São Lourenço, 17 Nov 1993, E. Martins s.n. (UEC 29410). Petrópolis, Quitandinha, Pedra do Quitandinha, 2 May 2010, M.O.O. Pellegrini 2 (RFA). Resende, margem da rodovia Dutra, Km 302 sentido RJ, ao lado da Light, próximo ao Rio Paraíba do Sul, 9 Jun 2012, M.O.O. Pellegrini et al. 231 (RB). Silva Jardim, 31 Jan 2015, L.S.B. Calazans 485 (RB). Teresópolis, Serra dos Órgãos, 26 Oct 1949, E. Pereira 635 (RB, US).

Distribution and habitat. Mexico to Argentina being very common in shady disturbed areas such as road sides, gardens and forest margins, and in agricultural fields. It is less commonly found growing in drier regions and rocky outcrops (Fig. 2).

Phenology. Throughout the year, but especially in the rainy season.

Conservation status. Following the IUCN recommendations (IUCN 2001), as currently circumscribed, *C. obliqua* should be considered as Least Concern (LC) in the state of Rio de Janeiro and worldwide.

Morphological notes. A great deal of morphological variation can be observed in *C. obliqua* and in its current circumscription. It comprises plants from small to large stature (sometimes more than a 1.5 m high); stems from creeping with ascending apex to erect to subscandent, and thin and fibrous to robust and somewhat succulent stems. The leaves can vary from 4–20 cm long, from glabrous to scabrous to pilose, and from green to dark green to vinaceous abaxially. Flower size and color also vary, which as in *C. erecta* seems to be environmentally influenced, probably by differences in soil pH and light intensity (Pellegrini, pers. obs.). The petals of *C. obliqua* can range from intense blue to light blue, sometimes varying from lilac to pale lilac. *Commelina obliqua* likely represents a species complex and biosystematic studies are necessary in order to better understand and elucidate its boundaries. Until this is addressed we believe that a wide circumscription, as presented here, is currently the best way to deal with this taxon.

6. *Commelina rufipes* **Seub.**, in Martius Fl. Bras. 3(1): 265. 1855. Figs 1H–J

Distribution and habitat. Mexico to Southeastern Brazil, being found in the understory of preserved rainforests, in the Amazon and Atlantic domains, as well as in gallery forests in the Cerrado biome. It is a rare species in the Atlantic Forest and Cerrado biomes, with most of its collections being from the Amazon Forest.

Conservation status. As abovementioned, *C. rufipes* is locally rare in the state of Rio de Janeiro and not as frequent in the field as the blue flowered species of the genus. Despite its wide distribution, it seems to occur only in preserved rainforests, forming dense but isolated populations. Data regarding its reproductive cycle would be of great value for this species' conservation. Following the IUCN recommendations (IUCN 2001), *C. rufipes* as currently circumscribed should be considered as Least Concern (LC) in its worldwide distribution.

Taxonomical notes. We currently accept two varieties within this species (sensu Faden & Hunt 1987). The floral morphology of both varieties of *C. rufipes* is poorly understood as little reproductive material exists. However there seems to be no morphological overlap in vegetative characters and very little overlap in their distributions. Further biosystematic study, focusing especially on floral morphology, would be most useful in evaluating their boundaries and taxonomic status.

6a. Commelina rufipes var. glabrata (D.R.Hunt) Faden & D.R.Hunt, Ann. Missouri Bot. Gard. 74(1): 122. 1987. Fig 1H

Commelinopsis glabrata D.R.Hunt, (1981: 195). Holotype. TRINIDAD. Irois Forest district, 25 January 1928, Broadway 6716 (K barcode K 000363259!).

Specimens seen. BRAZIL. Rio de Janeiro: Cardoso Moreira, Fazenda Santa Rosa, 11 Jan 2014, I.G. Costa 319 (RB). Santa Maria Madalena, Parque Estadual do Desengano, Serra

da Agulha, Fazenda Agulha do Imbé, between Santa Maria Madalena and Santo Antônio do Imbé, 23 February 1983, T.C. Plowman & H.C. Lima 12933 (US).

Taxonomical notes. Few collections of this variety are known for the Southeastern region of Brazil, with several specimens previously identified as *C. rufipes* var. *glabrata* actually representing the herein described *C. huntii*.

6b. *Commelina rufipes* **Seub. var.** *rufipes*, in Martius Fl. Bras. 3(1): 265. 1855. Figs 1I–J

Lectotype (designated here). BRAZIL. São Paulo: s.loc., 1817, C.F.P. Martius 76 (M barcode M0210921!). Epitype (designated here). BRAZIL. São Paulo: Bertioga, estrada Bertioga/São Sebastião, bairro São Rafael, 25 Oct 2007, R.C. Forzza et al. 4823 (RB barcode RB00515585!)

Selected specimens seen. BRAZIL. Rio de Janeiro: Duque de Caxias, Reserva da Petrobrás, trilha para a barragem, 28 August 1997, J.A. Lira Neto et al. 696 (RB). Magé, 1 November 1983, R.R. Guedes et al. 537 (RB). Sapucaia, estrada que liga Sapucaia das Terras Frias até o Rio Vermelho, 13 March 1981, M.G.A. Lobo 223 (RB). Silva Jardim, Reserva Biológica de Poço das Antas, Juturnaíba, trilha Rodolfo Norte, caminho para a Pelonha, 18 August 1995, J.M.A. Braga et al. 2735 (RB). Teresópolis, Parque Nacional da Serra dos Órgãos, trilha para a Pedra do Sino, da entrada até a primeira cachoeira, 14 Jul 2011, J.A. Lombardi 8616 (HRCB, UPCB)

Nomenclatural notes. When describing *C. rufipes*, Seubert (1855) only mentions that his new species was based on a Martius specimen, at M. After searching the M collection, we found just two specimens from this collector — *Martius 76* (M0210921) and *Martius 77* (M0210920). Since the specimen *Martius 76* was clearly annotated in Seubert's handwriting it is the obvious choice for a lectotype. Nonetheless, Seubert's original description makes it clear that all available specimens had few if any flowers, which matches the specimens found by us at M. This has caused great taxonomic problems over the years, with this name being ascribed to a number of different genera (i.e. *Athyrocarpus* Schltdl., *Commelina*, *Commelinopsis* Pichon, and *Phaeosphaerion* Hassk.), and as either accepted or as a synonym by different authors (Faden & Hunt 1987). Thus, in accordance to the *Code* (McNeill *et al.*, 2012, Art. 9.8), we also designate a well-preserved flowering specimen as an epitype, to avoid further taxonomic and nomenclatural problems.

Taxonomical notes. Apart from the obvious difference in indumenta, the leaves of *C. rufipes* var. *rufipes* tend to be thinner (lanceolate to elliptic-lanceolate), with a cuneate base and acute apex, while the leaves of *C. rufipes* var. *glabrata* tend to be wider (ovate-elliptic to ovate), with a round to obtuse base and acuminate apex.

Excluded name

After a thorough analysis of Vellozo's description and original illustration for *C. singularis* Vell., it became clear that this species does not belong in the genus *Commelina*. This name is better placed under the synonymy of *Tripogandra diuretica* (Mart.) Handlos (**Syn. nov.**), and the necessary taxonomic and nomenclatural comments and typifications are made below.

Commelina singularis **Vell.**, Fl. Flumin.: 31. 1829. Fig 6

Lectotype (designated here). [illustration] Original parchment plate of Flora fluminensis in the Manuscript Section of the Biblioteca Nacional do Rio de Janeiro [mss1095062_080] and later published in Vellozo, Fl. flumin. Icon. 1: t. 76, pro parte, flowers and inflorescence only. Epitype (designated here). BRAZIL. Rio de Janeiro: Rio de Janeiro, Área do Jardim Botânico do Rio de Janeiro, fl., fr., 21 Dec 1995, J.A. Lira Neto 194 (RB 2ex, barcode RB00685321!).

Accepted name. Tripogandra diuretica (Mart.) Handlos.

Taxonomical notes. Vellozo's plate for *C. singularis* (1831: t. 76) shows a creeping plant with eudicot-like leaves (net-veined and a single apparently trifoliate leaf), not identifiable as any known species of Commelinaceae. Nevertheless, the inflorescence type (Fig 6A & C), details of the androecium (Fig 6B & D), and the morphological description of six dimorphic stamens, three of which are staminodial — "Stamina sex, quorum tria nectaria mentiuntur" — (Vellozo 1829), consistently allows this name to be associated to the genus *Tripogandra* Raf. Another remarkable feature of Vellozo's plate is the gynoecium, which is illustrated with a very short and slightly curved style (Fig. 6B). This feature distances *C. singulars* from the genus *Commelina* where the style is long and sigmoid, bringing it closer to *Tripogandra*. The leaves illustrated by Vellozo belong to the genus *Polygonum* Linnaeus (1753: 359) (Polygonaceae), which usually possesses white to pink to lilac flowers, and occurs in the same marshes as *T. diuretica*. This confusion is apparently common in Brazilian herbaria, where *Polygonum* specimens are commonly misidentified as commelinaceous taxa (Pellegrini pers. obs.).

Vellozo (1829: 31) also mentions that *C. singularis* is found growing in slow-water environments — "Aquis stagnantibus, et confluentibus habitat" —. Only *T. diuretica* and *T. warmingiana* (Seub. 1872: 126) Handlos (1975: 311) occur in the state of Rio de Janeiro; the first being very common, extremely variable in size and flower morphology, and normally occurring in marshy areas; the second being very rare, uniformly small in size and flower morphology, and occurring in drier areas (Pellegrini et al. 2013). Thus, *C. singularis* is here regarded as a synonym of *T. diuretica*. In accordance to the *Code* (McNeill et al., 2012, Art. 9.8), in order to avoid future confusions and to fix the application of this name, we herein designate an epitype.

Discussion

Our work has reaffirmed the importance of thorough descriptions, fieldwork, photographs, spirit collections, and cultivation of specimens to better understand the taxonomy and systematics of intricate genera such as *Commelina*. This genus in particular poses problems as floral characters are difficult to observe in dried specimens (e.g. Faden 1993, 2008, 2012; Nampy *et al.* 2013), which calls for particular attention to be paid to adequate description of these in any new species (Faden 2008). Historically there are examples where either floral,

fruit, or seed characters are only incompletely described, or even omitted. In some cases, the available specimens possess such strikingly different habit or vegetative characters, that the name can be easily applied (e.g. Faden *et al.* 2009). Nevertheless, in most cases, the lack of appropriately detailed description may cause confusion or prevent identification and the application of a correct name. Capturing the range of a species' phenotype is also important and population studies have shown to be of great use, especially in the Neotropical species, allowing us to record and compare wide ranges of morphology. The description of new taxa, based on few and odd specimens needs to be carefully considered, and is a strategy that tends to inflate the description of unnecessary or invalid new species and infraspecific taxa.

Characters such as inflorescence position and morphology, spathe shape and fusion, petal and fruit morphology, and seed ornamentation play important roles in species distinction and delimitation, in Commelina, Nevertheless, characters once thought to be useful in species delimitation such as indumenta and leaf shape have shown to be highly variable within the same species and thus not completely reliable. This is easily observed in all Neotropical species, and most of the wide-spread species (e.g. C. benghalensis, C. diffusa, and C. erecta). Growth-form and subterraneous system morphology are also potentially interesting for the taxonomy of *Commelina* worldwide. On the other hand, most of the morphological characters pointed out by previous authors (e.g. Faden 1993, 2008; Nampy et al. 2013) as key to the taxonomy of the genus are mostly difficult to observe in herbaria specimens, and work to expand and refine the morphological tools available to workers in this group should be ongoing. It is also apparent that some species still need further systematic study in order to clarify their boundaries. The Pantropical C. diffusa complex is poorly understood in the Neotropical region and is probable that more than one species, being treated under the widely polymorphic C. diffusa subsp. diffusa. The Commelina obliqua and C. rufipes complexes also need critical attention. The C. rufipes complex seems to be exclusively Neotropical, while the C. obliqua complex is here confirmed to be Pantropical. These two species groups are historically problematic and many names have been accommodated under one concept or another, depending on the author. It is very likely that both complexes will need to be studied concomitantly in order to fully understand their phylogenetic history, taxonomy and nomenclature.

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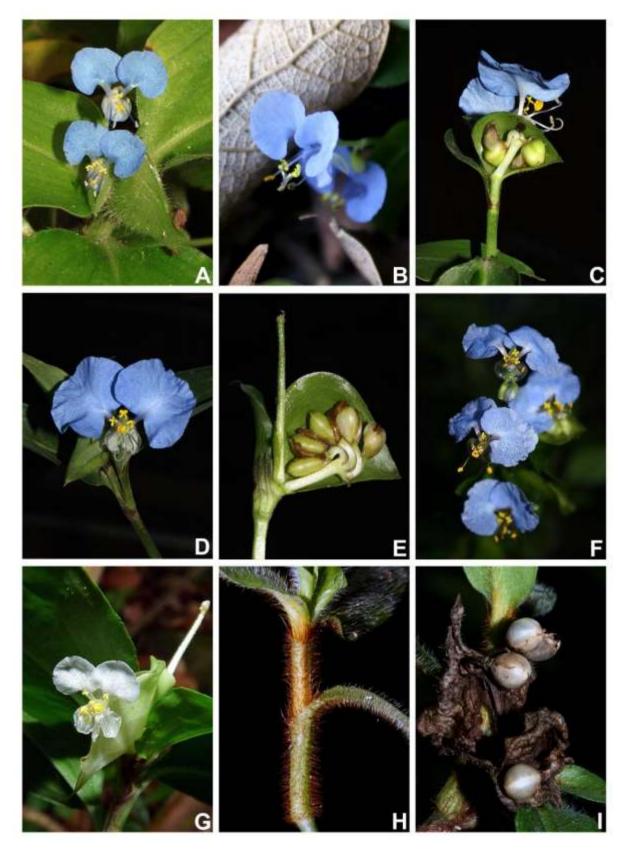


Figure 1. Commelina in the state of Rio de Janeiro. **A,** C. benghalensis L. **B,** C. diffusa Burm.f. **C–D,** C. erecta L.: **C,** detail of the inflorescence showing aborted upper cincinnus; **D,** flower. **E–F,** C. obliqua Vahl: **E,** detail of the inflorescence showing the two developed cincinni; **F,** flower. **G,** C. rufipes var. glabrata (D.R.Hunt) Faden & D.R.Hunt. **H–I,** C.

rufipes var. *rufipes* Seub.: **H,** detail of the leaf-sheaths, showing the hirsute rusty hairs. **I,** mature fruits. G by Flora Virtual Estación Biológica El Verde group, remaining field photos by M.O.O. Pellegrini.

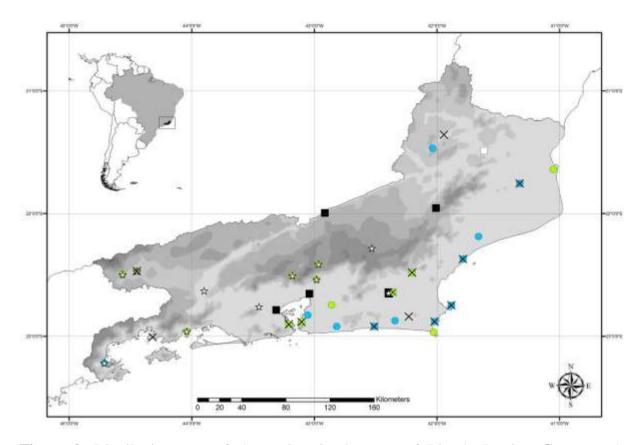


Figure 2. Distribution map of *Commelina* in the state of Rio de Janeiro. **Crosses**– *C. benghalensis*; **green dots**– *C. diffusa* var. *diffusa*; **blue dots**– *C. erecta*; **stars**– *C. obliqua*; **empty square**– *C. rufipes* var. *glabrata*; **full squares**– *C. rufipes* var. *rufipes*.

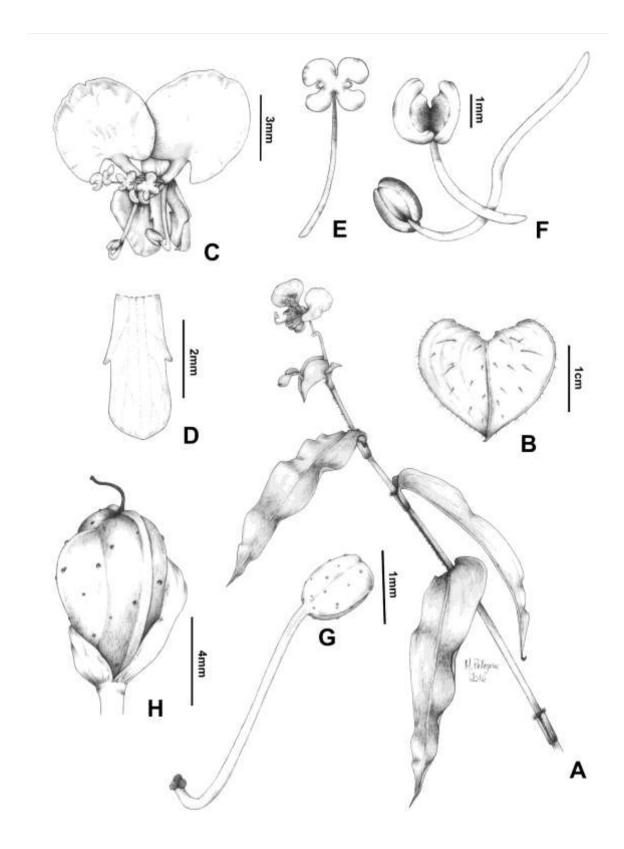


Figure 3. Commelina huntii M.Pell. **A,** habit. **B,** open spathe, showing eventual rusty cilia and villous margin. **C,** male flower. **D,** medial petal, showing auricles. **E,** staminode. **F,** lateral stamen and medial stamen. **G,** gynoecium, showing papillate ovary and trilobate stigma. **H,** capsule, showing the black papillae. Line drawings by M.O.O. Pellegrini, based on the holotype.

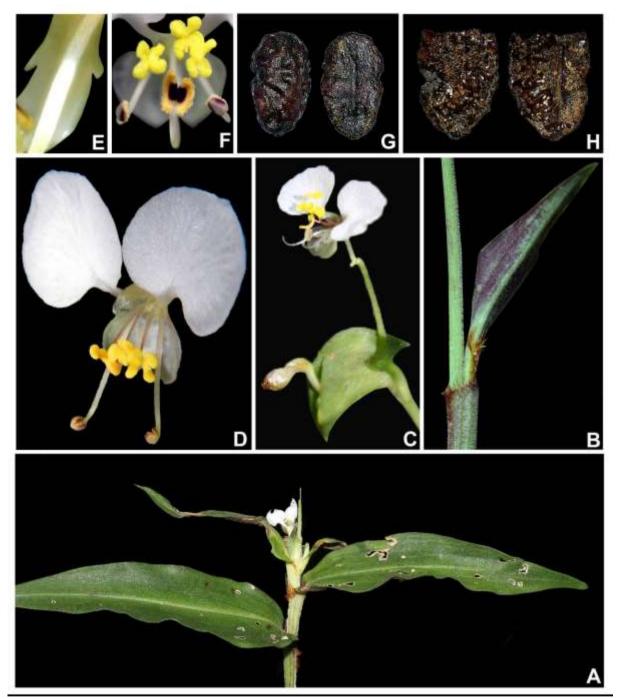


Figure 4. Commelina huntii M.Pell. **A,** apex of the stem, showing terminal inflorescence. **B,** detail of the densely setose leaf sheath margins, with rusty hairs. **C,** detail of the inflorescence, showing the fused spathe and developed upper and lower cincinni. **D,** detail of a male flower. **E,** detail of the medial petal, showing the two auricles. **F,** detail of the androecium. **G,** dorsal and ventral view of the seed of the dorsal locule. **H,** dorsal and ventral view of one of the seeds of the ventral locules. A by L.S.B. Calazans, B, C, E, G & H by M.O.O. Pellegrini, D by M.S. Wängler and F by R.S. Couto.

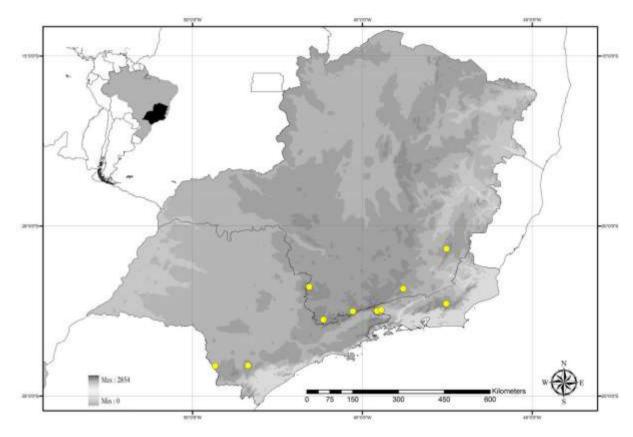


Figure 5. Distribution map of *Commelina huntii* M.Pell.

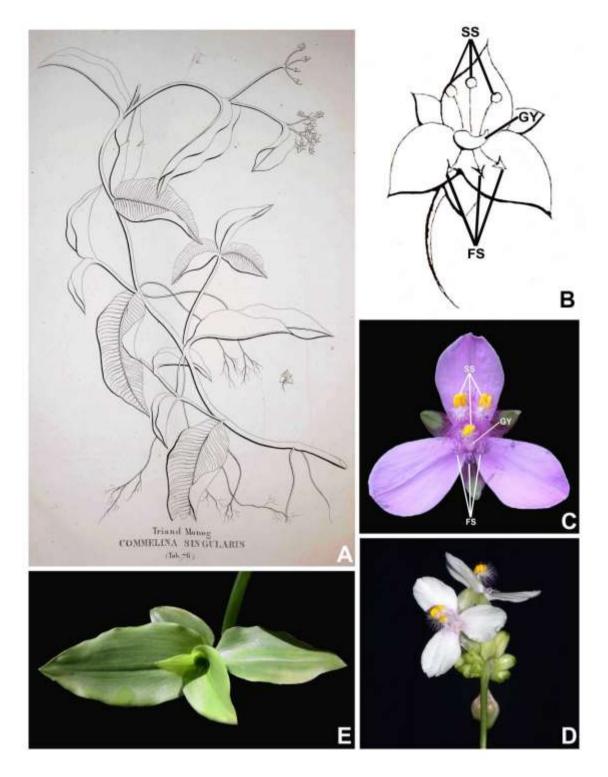


Figure 6. Commelina singularis Vell. **A--B**, Original plate of Vellozo's *C. singularis*: **A**, line drawings of habit, inflorescence and floral characters; **B**, detail of floral characters. **C**, photos of a natural population of *Tripogandra diuretica* from the Jardim Botânico Rio de Janeiro, RJ: detail of the inflorescence, showing flowers with white corolla; **D--E**, photos of *T. diuretica* from the municipality of Petrópolis, RJ: **D**, detail of floral characters of a flower with lilac corolla; **E**, detail showing the leaves (note the parallel venation characteristic of the species). **SS-** sterile stamens; **FS-** fertile stamens; **Gy-** gynoecium. Photo of *C. singularis* plate from Biodiversity Heritage Library; All field photos by M.O.O. Pellegrini.

SECTION 2— COMMELINACEAE MIRB.

Chapter 2.5. Rediscovery, identity and typification of *Dichorisandra picta* Lodd. (Commelinaceae) and comments on the short-stemmed *Dichorisandra* species

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Abstract

Dichorisandra picta has been considered a name of dubious application due to the lack of known herbarium specimens, and consequently lack of a type specimen, and information regarding its natural distribution. Recent field, herbaria and literature studies, focusing on the species of Commelinaceae from Rio de Janeiro state, shed new light on the identity and application of this enigmatic name. As a result, the typification of the names related to *D. picta* is presented, along with the first complete description for this species, field photos and a distribution map. Dichorisandra picta is also compared with the remaining species of the *D. acaulis* morphological group.

Key words

Atlantic Forest, Dichorisandrinae, endemism, IUNC Red List, Neotropical flora, Rio de Janeiro

Introduction

Dichorisandra J.C.Mikan (1820: 7) is one of the largest genera in Commelinaceae, comprising ca. 60 species mostly distributed throughout rainforests in the Neotropics and greatly diverse in the Atlantic Forest (Faden & Hunt 1991; Aona 2008). It can be characterized by truly poricidal to functionally poricidal anthers (i.e. introrsely rimose), anthers 3 to 4 times longer than the filaments, fruits with thickened walls, and arillate seeds (Faden 1998; Hardy & Faden 2004; Aona 2008). According to Faden (1995), the diversity of habits found in the species of *Dichorisandra* might only be compared to its Paleotropical counterpart, the much smaller and distantly related genus *Palisota* Reichenbach *ex* Endlicher (1836: 125). *Dichorisandra* has been recovered as monophyletic by different morphologic and phylogenetic studies. It is proximately related to *Siderasis* Rafinesque (1837: 67), a monospecific genus in the Brazilian Atlantic Forest (Evans *et al.* 2000; Hardy 2001; Evans *et al.* 2003; Wade *et al.* 2006; Burns *et al.* 2011; Hertweck & Pires 2014).

Commelinaceae is economically important due to the ornamental value of many genera, with its species being cultivated since early days due to their beautiful foliage and flowers (Hunt 2001). *Dichorisandra* is especially appealing because of its non-deliquescent and showy flowers, large leaves and for being easy to cultivate. For these reasons, during the 19th century, many specimens of *Dichorisandra* were introduced in greenhouses and Botanical

Gardens throughout Europe. Several new species were described, often solely based on sterile specimens, and sometimes without preparing herbarium specimens (e.g. Loddiges 1826, 1828, 1830; Hooker 1854; Koch 1866; Moore 1957). This situation is pointed as the probable origin of the misapplication of several names and the consequent exclusion of many of them (e.g. Aona 2008; Aona-Pinheiro *et al.* 2014).

Dichorisandra picta was described by Loddiges (1830: t. 1667) based on a cultivated specimen from Leyden Botanical Garden. The species was characterized by the brown macules in its young leaves, and said to be native from South America. Due to its obvious ornamental value, the species was distributed and commercialized throughout Europe. A specimen was eventually acquired by the Royal Botanical Gardens, Kew, and described by Hooker (1854). Unaware that the species had already been previously published, Hooker adopted the name used by the cultivator (Mr. Low, of the Clapton Nursery) and published the homonym *D. picta* Hooker f. (1854: t. 4760), saying the species was native to Brazil. After the description of both names, little attention was ever given to this enigmatic species, with the single known voucher for this species cited by Seubert in his Commelinaceae monograph for *Flora brasiliensis* (1855: 240). Nevertheless, this specimen was probably destroyed during the WWII, since it could not be found at B (Pellegrini pers. obs.). The name remained obscure in the absence of any herbarium collection.

The present work aims to report the recent rediscovery of *D. picta*, and provide a complete taxonomic treatment based on field studies, cultivated specimens, and on some recently collected specimens. Additionally, lectotypes for *D. picta* Lodd. and *D. picta* Hook.f. are here designated, and comments on the short-stemmed *Dichorisandra* morphological group, along with an identification key for the species, are presented.

Methods

Morphological descriptions and phenology of the five studied *Dichorisandra* species were based on herbaria (A, ALCB, BM, BHCB, BHZB, C, CEPEC, CESJ, CRVD, ESA, FCAB, FLOR, FURB, GUA, HAS, HB, HBR, HPL, HUEFS, HURB, HUSC, IAC, ICN, INPA, IPA, K, L, MBM, MBML, NY, P, R, RB, RFA, RFFP, SP, SPF, UEC, UPCB and US), spirit, fresh and cultivated specimens (herbaria acronyms according to Thiers, continuously updated). The indumenta and shapes terminology follows Radford *et al.* (1974); the inflorescence

terminology and morphology follows Weberling (1965, 1989) and Panigo *et al.* (2011), with some modifications; the fruit terminology follows Spjut (1994); and seed terminology follows Faden (1991). The conservation status was proposed following the recommendations of *IUCN Red List Categories and Criteria, Version 3.1* (IUCN 2001). GeoCAT (Bachman *et al.*, 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). Species distribution is based on herbaria specimens and field work data. The classification of the vegetation patterns follows Veloso *et al.* (1991).

Taxonomy

Dichorisandra picta Lodd., (1830: t. 1667) ≡ Stickmannia picta (Lodd.) Kuntze, (1891: 721).

Lectotype (designated here):—[illustration] Original parchment plate of "The Botanical Cabinet" at the British Museum Library and later published in Loddiges, Bot. Cab. 17: t. 1667. 1830. — For an image of the lectotype, see Fig. 1; for field photos, see Fig. 4.

= Dichorisandra picta Hook.f., (1854: t. 4760), nom. illeg. non D. picta Lodd., syn. nov. Lectotype (designated here):—SOUTH AMERICA. s.loc., June 1864, fl., R. Pearce s.n. (K000543688!).— For an image of the lectotype, see Fig. 2; for an image of the original illustration, see Fig. 3.

Herbs ca. 10–30 cm alt, perennial, terrestrial in understory. Roots thin, with terminal tubers, tubers fusiform. Stems erect, branched at base to unbranched, rooting only in underground nodes; internodes 1–4.5 cm long, vinous to brown with minute green dots or striations, minutely pilose, hairs hyaline. Leaves spirally-alternate, congested at the apex of the stem, subpetiolate; sheaths 1–3.2 cm long, pilose, rarely glabrous, margins setose, hairs hyaline; petiole 0.6–2.4 mm long to indistinct, canaliculated, densely lanate, green, margins green to vinous; lamina (6.1–)8.4–22.3 × 3–8.6 cm, slightly succulent, adaxially dark-green to green, with brown to vinous-brown macules and/or stripes when young, disappearing when mature, abaxially light-green to light-green tinted vinous to completely vinous, drying olive-green on both sides, elliptic to broadly elliptic to elliptic-ovate to obovate, adaxially glabrous to sparsely pilose, abaxially lanate, densely lanate along the midvein, hairs hyaline, base cuneate to rounded, margins vinous, rarely green, ciliate to lanate, apex acuminate; midvein adaxially conspicuous, impressed, abaxially prominently obtuse, secondary veins 4–6 pairs, adaxially conspicuous to inconspicuous, slightly impressed, abaxially inconspicuous. Thyrse terminal,

erect, pedunculate; basal bract leaf-like; peduncles 0.5–1.3 cm, densely lanate, hairs hyaline, internodes conspicuous, green, densely lanate, hairs hyaline; cincinni bracts $0.6-1.5 \times 0.2-0.3$ cm, reducing in size towards the apex of the cincinnus, parallel to the axis of the cincinnus, linear-triangular, apex acute to acuminate, brown, scarious, adaxially glabrous to sparsely pilose, abaxially lanate, margin ciliate to lanate; cincinni sessile to sub-sessile, peduncle 2–8 mm long to inconspicuous, 4–7 cincinni per inflorescence, each cincinnus 3–10-flowered, internodes 1–2 mm long, green, densely lanate, hairs hyaline; bracteoles 2–3 × 1.5–2 mm, reducing in size towards the apex of the cincinnus, broadly-triangular, apex acute, brown, scarious, adaxially glabrous to sparsely pilose, abaxially lanate, margin ciliate to lanate. Flowers bisexual or male, actinomorphic, 0.8-1.2 cm diam.; floral buds ellipsoid, $5-4 \times 2-3$ mm; pedicel 0.5-1 mm long, light green, sparsely lanate, reflexed and slightly elongate in fruit; sepals 6–7 × 2–3 mm, narrowly ovate, cucullate, white, sparsely lanate, apex round, margin purple, persistent and accrescent in fruit; petals $0.8-1.2 \times 5-6.5$ mm, elliptic to narrowly ovate, purple, proximal third white, apex acute; stamens 6, equal, erect to connivent, filaments 3–4.6 mm long, white, anthers 5–5.5 × 0.9–1.2 mm, linear-triangular, creamcolored, terminal half to two thirds purple to pinkish-purple, rarely completely cream-colored, base slightly sagitate, apex acute, dehiscent through one apical pore, anther-sacs parallel, connective inconspicuous, glabrous; ovary subglobose, 3–3.5 × 2.5–3 mm, smooth, lanate, hairs hyaline, 4–5 ovules per locule, style erect, 6–7 mm, white, terminal two thirds purple, stigma subtrilobate, purple. Capsules 3.2–4.4 × 3–4.3 mm, cylindrical, sometimes slightly curved, apiculate due to persistent style, light-green, smooth, glabrous to sparsely lanate. Seeds 5-6.5 × 2-3 mm, ellipsoid, ventrally flattened, testa rugose, dark brown to black; aril white, thin; embryotega semi-lateral, relatively inconspicuous, without a prominent apicule; hilum C-shaped, more than ½ the length of the seed.

Examined material:—BRAZIL. Rio de Janeiro: Cardoso Moreira, cultivada no Jardim Botânico Plantarum, 10 December 2011, fl., *A. Campos-Rocha 808* (HPL); *loc. cit.*, Morro Quindiba, 13 March 2013, fl., *M.G. Bovini et al. 3785* (RB); *loc. cit*, localidade de Vinhático, mata da Bicuíba, 26 December 2013, fl., fr., *I.G. Costa 284* (RB); *loc. cit*, localidade Silvado, em mata da Fazenda Santa Rosa, divisa com sítio Edvar Merlin, 28 December 2013, fl., fr., *I.G. Costa 292* (RB). Italva, localidade de Pão-de-Ló, Serra do Pão-de-Ló, 4 January 2014, fr., *I.G. Costa 311* (RB).

Distribution, habitat and ecology:—*Dichorisandra picta* is endemic to Rio de Janeiro state, Brazil, occurring in the understory of rainforest remnants in northern Rio de Janeiro

(Fig. 5). Its subpopulations are medium sized (ca. 10–15 mature individuals) and widely apart from each other, due to the reduction of habitats in this region by deforestation. Only few adult specimens were spotted in each of the known populations. Clonal reproduction is rather common, with new rosettes being produced from the short underground rhizome, and clones consequently growing very close to the mother plant.

Phenology:—It was found in bloom from December to March and in fruit from December to January.

Conservation status:—*Dichorisandra picta* is known from only five collections, all of them outside any conservation unit and in a highly deforested area. Added to that, the species possesses a considerably small EOO (53.46 km²) and AOO (3.53 km²), severally fragmented population, few mature individuals per subpopulation and is directly threatened by deforestation. Thus, following the IUCN recommendations (IUCN 2001), *D. picta* should be considered Critically Endangered [CR, B1ab(i,ii,iii,iv);C1+2a(i)] in its overall distribution.

Affinities and Morphological notes:—Dichorisandra picta is a member of the *D. acaulis* Cogniaux (1894: 297) morphological group, which is currently represented by *D. acaulis*, *D. nutabilis* Aona & M.C.E.Amaral (2012: 18), *D. odorata* Aona & M.C.E.Amaral (in Aona-Pinheito *et al.* 2014: 222), *D. picta* and *D. perforans* C.B.Clarke (1881: 281). Representatives of this group show small stature (i.e. short aerial stems), spirally arranged leaves, sessile to sub-sessile cincinni, ellipsoid floral buds, actinomorphic flowers, six equal erect to connivent stamens, cream colored anthers with pink to purple to blue anther sacs, dehiscent through 1–2 apical pores and cylindrical capsules.

Dichorisandra picta can be differentiated from D. acaulis and D. odorata by its pedunculate inflorescences with elongate main axis and pedicels much shorter than the floral buds (vs. sessile inflorescences with reduced main axis and pedicels much longer than or the same size as the floral buds in both species) (Fig. 4D & 6A, E). Dichorisandra picta can be differentiated from D. acaulis by its anthers dehiscing through one apical pore (vs. dehiscent through two apical pores). It can be differentiated from D. odorata by its leaves adaxially sparsely pilose and abaxially lanate, scentless flowers and stamens with glabrous connectives (vs. leaves densely pilose on both sides, scented flowers and stamens with pilose connectives). Dichorisandra picta is also similar to D. nutabilis and D. perforans, due to its pedunculate inflorescences with elongate main axis (Fig. 4D & 6C). However, it is readily differentiated from D. perforans by exclusively terminal inflorescences and anthers dehiscent

through an apical pore (vs. inflorescences either terminal or basal perforating the leaf-sheaths and anthers dehiscent through two apical pores). It is additionally similar to *Dichorisandra nutabilis* by its small stature, stems rarely branched, general floral morphology and anthers dehiscent through an apical pore. However, *D. picta* is readily distinguished from *D. nutabilis* by its young leaves with brown macules, leaves abaxially lanate, erect inflorescences completely covered with lanate indumenta and larger and imbricate bracteoles (vs. young leaves never maculated, leaves sparsely pilose, inflorescences pendulous and short pilose, and smaller and loose bracteoles) (Fig. 4A, D & 6C).

Nomenclatural notes:—When describing *D. picta*, Loddiges (1830) presented a beautiful watercolor illustration of a specimen he received at Harvard University (A), from Leyden Botanical Garden (L). Nevertheless, no specimen was found at A and L. Thus, the only original element left for a lectotype is the illustration presented by Loddiges (McNeill et al. 2012, Art. 9.12), which we designated here. The illustration is of great quality; nevertheless the depiction of the androecium lacks resolution, which led to Aona-Pinheiro et al. (2014) to believe that this species bares only five stamens. This assumption is clearly incorrect, since Loddiges classifies his new species using the Linnean Sexual System as a member of "Hexandria Monogynia". In order to be coherent in their assumption, Aona-Pinheiro et al. (2014) would have to assume the species possesses 4-6 stamens, since the other flower depicted by Loddiges bears only four stamens. From a systematic point of view, this assumption would also be highly unlikely, since the flower is clearly actinomorphic. Together with other morphological characters (e.g. plant stature, flower symmetry and stamen coloration) D. picta can be easily placed in the D. acaulis morphological group. All species within this group show actinomorphic flowers, with six equal, upright to connivent stamens (Fig. 6).

Hooker (1854), when describing *D. picta* Hook.f., mentions that he received this species from "Mr. Low, from the Clapton Nursery", and that the plant already came with the name *Dichorisandra picta*. However, since the author did not manage to find this name nor this species published anywhere else, he decided to publish it as new. This comment corroborates that this species was already in cultivation in England for quite some time. It also corroborates the hypothesis that Hooker and Loddiges species are conspecific, and that Hooker did intend to publish it as a new name, based on a different type. This makes Hooker's name (1854) a posterior homonym applied to the same biological entity as Loddiges' name (1830).

When describing his new species, Hooker (1854) presents an enlightening watercolor illustration that perfectly depicts the plant. In this illustration it is possible to observe the flowers with six equal and connivent stamens, anthers dehiscent through an apical pore, a terminal inflorescence, spiral phyllotaxy and the brown macules in the young leaves that characterize this species. According to Stafleu & Cowan (1979), Hooker's type specimens were generally deposited at BM, but no specimen corresponding to *D. picta* was found. Nevertheless, a specimen at K, identified as *D. picta* by C.B. Clarke, matches perfectly in the morphology the illustration presented by Hooker (1854). Added to that, the specimen was collected in the same year, but prior to, Hooker's publication.

Key to species of the *Dichorisandra acaulis* group

- 1. Inflorescences pedunculate, main axis elongate; pedicels much shorter than the floral buds...2
- Inflorescences sessile, main axis reduced; pedicels much longer than or the same size as the floral buds... 3
- 2. Stems unbranched; leaves adaxially glabrous, abaxially setose, hairs hyaline; flowers scentless, sepals externally glabrous, rarely sparsely setose at base, anthers dehiscent through two apical pores, connectives glabrous... *Dichorisandra acaulis* (Fig. 6A–B)
- Stems branched to unbranched; leaves pilose on both sides, hairs light-brown; flower scented, sepals externally pilose, anthers dehiscent through one apical pore, connectives pilose... *Dichorisandra odorata* (Fig. 6E–F)
- 3. Inflorescences either terminal or basal, perforating the leaf-sheaths; anthers dehiscent through two apical pores... *Dichorisandra perforans*
- Inflorescences exclusively terminal, not perforating the leaf-sheaths; anthers dehiscent through one apical pore... 4
- 4. Young leaves never maculated, leaves adaxially sparsely velutine, abaxially sparsely pilose; inflorescences pendulous, short pilose, bracteoles loose from the cincinnus; sepals externally glabrous... *Dichorisandra nutabilis* (Fig. 6C–D)

- Young leaves with brown macules, leaves adaxially glabrous, abaxially lanate; inflorescences erect, lanate, bracteoles imbricate; sepals externally sparsely lanate... *Dichorisandra picta* (Fig. 1–4)

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Fig. 1. Photo of the lectotype of *Dichorisandra picta* Lodd. Plate from the Biodiversity Heritage Library



Fig. 2. Photo of the lectotype of *Dichorisandra picta* Hook.f., *R. Pearce s.n.* (K000543688)



Fig. 3. Photo of the original illustration of *Dichorisandra picta* Hook.f. Plate from the Biodiversity Heritage Library

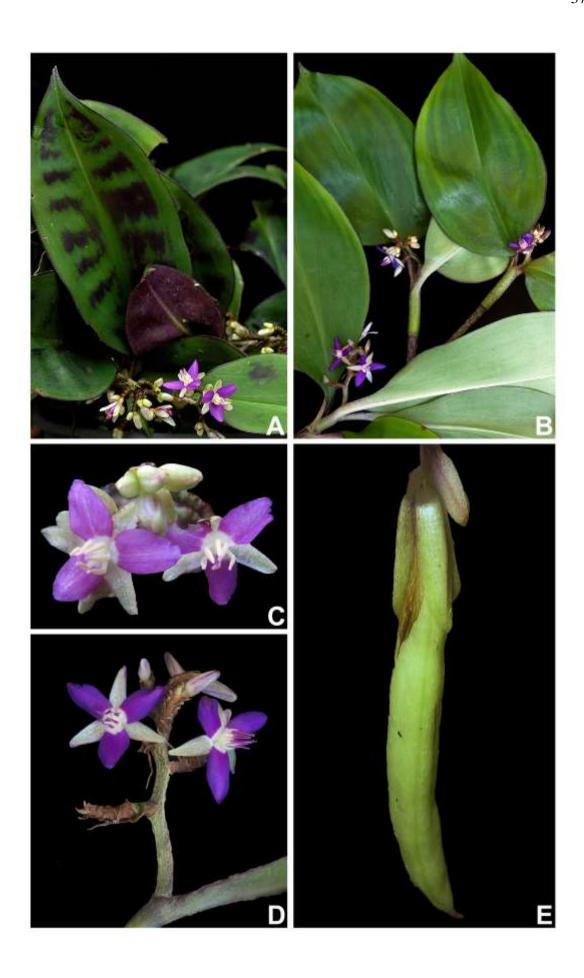


Fig. 4. *Dichorisandra picta* Lodd. **A–B,** habit: **A,** individuals in natural habitat, showing young leaves with brown macules; **B,** same individuals in cultivation at the Jardim Botânico Plantarum, showing mature leaves without brown macules. **C–D,** flowers and inflorescences: **C,** detail of the flowers, showing completely cream-colored anthers; **D,** detail of the inflorescence, showing the densely lanate peduncle, scarious bracts and bracteoles and flowers with anthers with purple apex. **E,** detail of the fruit. A–B & D by A. Campos-Rocha, C & E by I.G. Costa.

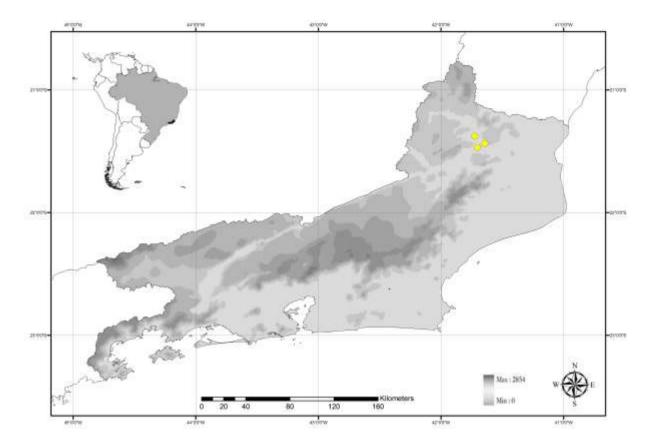


Fig. 5. Distribution map of *Dichorisandra picta* Lodd.

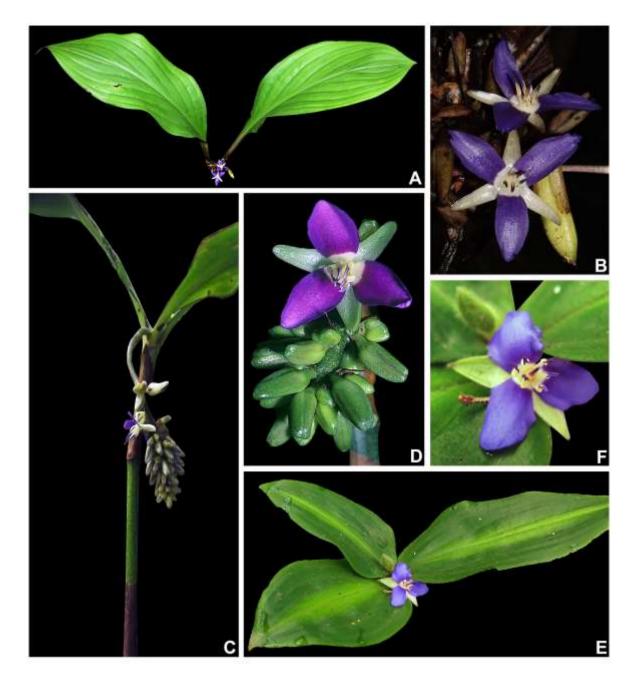


Fig. 6. *Dichorisandra acaulis* morphological group. **A–B,** *Dichorisandra acaulis* Cong.: **A,** habit, showing sessile inflorescence; **B,** detail of the flowers and fruits. **C–D,** *Dichorisandra nutabilis* Aona & M.C.E.Amaral: **C,** habit, showing pedunculate and pendulous inflorescence; **D,** detail of the flowers and fruits. **E–F,** *Dichorisandra odorata* Aona & M.C.E.Amaral: **E,** habit, showing sessile inflorescence; **F,** detail of the flower. A–B by M.O.O. Pellegrini, C by A. Tuler, D modified from Aona-Pinheiro & Amaral 2012, E–F by L. Kollmann.

Table 1. Comparison of diagnostic morphological characters between the species belonging to the *Dichorisandra acaulis* group.

Characters	Stem	Leaves indumenta	Inflorescence position	Inflorescence elongation	Inflorescence indumenta	Sepal indumenta	Anther's dehiscence	Connective indumenta
D. acaulis	Unbranched	Adaxially glabrous, abaxially setose, hyaline	Terminal, not perforating the leaf-sheaths	Sessile, main axis reduced, erect	Glabrous	Externally glabrous, rarely sparsely setose at base	Through two apical pores	Glabrous
D. nutabilis	Unbranched	Adaxially sparsely velutine, abaxially sparsely pilose, hyaline	Terminal, not perforating the leaf-sheaths	Pedunculate, main axis elongate, pendulous	Velutine	Externally glabrous	Through one apical pore	Glabrous
D. odorata	Branched	Densely pilose on both sides, light- brown	Terminal, not perforating the leaf-sheaths	Sessile, main axis reduced, erect	Pilose	Externally pilose	Through one apical pore	Pilose
D. picta	Branched	Adaxially glabrous, abaxially lanate, hyaline	Terminal, not perforating the leaf-sheaths	Pedunculate, main axis elongate, erect	Lanate	Externally sparsely lanate	Through one apical pore	Glabrous
D. perforans	Unbranched	Glabrous on both sides, rarely abaxially sparsely pilose, hyaline	Terminal or basal, perforating the leaf-sheaths	Pedunculate, main axis elongate, erect	Velutine	Externally pilose along the midvein and in the apical third	Through two apical pores	Glabrous

SECTION 2— COMMELINACEAE MIRB.

Chapter 2.6. *Siderasis albofasciata* sp. nov. (Commelinaceae), a new species endemic to the state of Espírito Santo, Brazil, and the typification of *S. fuscata*

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Abstract

A new species of *Siderasis* from the state of Espírito Santo is here described. This new species is readily differentiated from *S. fuscata* by its sessile to subpetiolate leaves covered by hyaline to light-brown indumenta, blades with a well-defined white stripe along the midvein on the adaxial side of the blade, main axis of the main florescence elongate, thyrsi reduced to one elongate cincinnus, bracteoles present, anthers purple to bluish-purple, filaments and style apically purple to bluish-purple, aril cream-colored and slightly hyaline and by the production of unique axillary flagelliform-shoots after its flowering period. I present a description of this new species, along with illustrations, a distribution map, comments on conservation assessment, ecology and taxonomy, and a table comparing the new species with the only accepted species in *Siderasis*. Furthermore, I designate a lectotype and an epitype for *S. fuscata*.

Key words

Atlantic Forest, Dichorisandrinae, IUNC Red List, Neotropics, Taxonomy, Tradescantieae

Introduction

Siderasis Raf. has hitherto been regarded as a monospecific genus of Commelinaceae, restricted to the Atlantic Forest from Southeastern Brazil. It is currently placed in subtribe Dichorisandrinae (sensu Faden and Hunt 1991, Pellegrini 2016), as sister-group to Dichorisandra J.C.Mikan. It differs from the later by the rusty to bright-red hirsute indumenta covering the entire plant (except the petals and androecium), its ebracteolate cincinni, filaments three to four times longer than the anthers, anthers with rimose dehiscence and exarillate seeds (Faden 1998, Hardy and Faden 2004). It can be easily distinguished from the remaining three genera of Dichorisandrinae (i.e. Cochliostema Lem., Geogenanthus Ule and Plowmanianthus Faden & C.R.Hardy) by its petals not fringed with moniliform hairs, all filaments glabrous, anther sacs divergent, capsules thick walled and embryotega semi-lateral (Pellegrini, unpublished data). As aforementioned, it is the least widespread genus of the subtribe, being endemic to the state of Rio de Janeiro, and possesses few published binomials (Barreto 1997, BFG 2015, Pellegrini 2016). In their revisited classification for the Commelinaceae, Faden and Hunt (1991) mention two species for *Siderasis*, while Faden (1998) mentions two to three species. Despite that, since Moore (1956) transferred Tradescantia fuscata Lodd. to Siderasis, no new names were published under this genus. Furthermore, Barreto (1997), in a survey of the Commelinaceae native to Brazil accepts only S. fuscata and reaffirms that Siderasis is indeed a monospecific genus. Thus, it seems clear that Siderasis remains poorly understood, especially regarding it circumscription, taxonomy and morphology, and that further studies are needed in order to elucidate this matter (Pellegrini et al. 2013).

I present the description of a new species for the genus, endemic to the Atlantic Forest from the of state Espírito Santo, Brazil. Altogether with the description of this new species I present a discussion on significant morphological characters that might shed some light in the evolution of morphological characters within subtribe Dichorisandrinae. Furthermore, I designate a lectotype and an epitype for *S. fuscata*, in order to fix the application of this name.

Methods

The terminology of indumenta and shapes follows Radford et al. (1974); inflorescence and morphology terminology follows Weberling (1965, 1989) and Panigo et al. (2011), with some modifications; fruit terminology follows Spjut (1994); and seed terminology follows Faden (1991). The conservation status was proposed following the recommendations and criteria of

IUCN Red List Categories and Criteria, Version 3.1 (IUCN 2001). GeoCAT (Bachman et al. 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). The map was elaborated using the software QGIS 2.6.1., data referring to the altitudinal gradient was taken from Worldclim (Hijmans et al. 2005) and the distribution records were taken from the analyzed herbaria material.

Specimens of *Siderasis albofasciata* M.Pell. *sp. nov.* and *S. fuscata* were kept in cultivation at the greenhouse of the Jardim Botânico do Rio de Janeiro, in order to observe, photograph and analyze fresh flowers, fruits and seeds as well as other phenological data. The description of the species, phenology and illustrations were based on herbaria, spirit, fresh and cultivated material. Fertile specimens were deposited in the herbarium RB. Additional specimens were analyzed, from both species, from the following herbaria: A, ALCB, BHCB, BHZB, BM, BRIT, CEPEC, CESJ, CGE, CVRD, ESA, FCAB, FLOR, FURB, GUA, HAMAB, HAS, HB, HBR, HSTM, HUEFS, HURB, IAC, ICN, INPA, K, MBM, MBML, MO, NY, P, R, RB, RFA, RFFP, SP, SPF, UEC, UPCB and US (herbaria acronyms according to Thiers, continuously updated). Furthermore, data on the distribution of *S. fuscata* was compiled based on literature and several field trips across the Brazilian Atlantic Forest, from the state of Sergipe to Rio Grande do Sul, between 2010–2016.

Taxonomy

Siderasis albofasciata M.Pell., sp. nov. (Figs. 1, 2B & 5)

Distinctissima in rami flageliformis axillaribus producendi, foliis sessile vel sub-sessile, medio albo-faciata, cum trichomatibus brunneis vel hyalinis, subtus hispidis, subter lanatis, cincinni bracteolati, staminibus et stylus apicem lilacs colorata, et semina cum aryl crassum cremeus.

Holotype: BRAZIL. Espírito Santo: Santa Teresa, Alto do Julião, Fazenda Novo Triunfo, property of Mrs. Florinda, gallery forest with rocky formations, above the dam, fl., fr., 18 April 2013, *M.O.O. Pellegrini et al. 337* (RB!; isotype US!).

Herbs ca. 10 cm alt, rhizomatous, terrestrial or rupicolous. Roots thin, fibrous, terminal tubers present, fusiform. Subterraneous stems buried deep in the soil, unbranched, produced directly from the short rhizome; internodes moderately elongate, vinaceous, sparsely lanate, hairs light-brown to hyaline. Aerial stems unbranched; internodes inconspicuous to weakly elongate, vinaceous, lanate, hairs light-brown to hyaline; flagelliform-shoots (ramets) axillar, unbranched, internodes elongate, produced after the fertile period, forming a new rosette at

the apex. Leaves spirally-alternate, congested at the apex of the aerial stems forming a rosette, sessile to subpetiolate; sheaths 0.7–1.3 cm long, vinaceous, with or without green spots, lanate, hairs light-brown to rusty; subpetiole 1–2.7 cm long to inconspicuous, D-shaped in cross section, canaliculated, dark green, hispid, hairs light-brown to hyaline; blade (4.5–4.8– $)10-15.8 \times (3.1-3.5-)4.4-7.2$ cm, succulent, elliptic to obovate, rarely lanceolate, base slightly subcordate to cuneate, vinaceous, margins vinaceous, slightly revolute, apex acute, curved to straight, adaxially dark green, with a thin white stripe along the midvein, hispid, hairs light-brown to hyaline, abaxially vinaceous to atro-vinaceous, lanate, hairs light-brown; midvein inconspicuous, slightly impressed adaxially, midvein prominent, obtuse abaxially, secondary veins inconspicuous in both faces. Synflorescence terminal or apparently so, composed of a main florescence with (1–)2 coflorescences; main florescence consisting of a pedunculate thyrse, reduced to a solitary pedunculate cincinnus; prophyll triangular, slightly cymbiform, amplexicaulous, 11.3–13.4 × 4.8–7.8 mm, vinaceous, hispid, hairs rusty, opaque at the base and margins. Thyrse terminal or apparently so, 1-2-(3) per rosette apex; inflorescence main axis 2.1–4.4 cm long, vinaceous, densely hispid, hairs rusty to brown; cincinni' bract triangular, amplexicaulous, 3.3–6.0 × 2.2–4.6 mm, vinaceous, hispid, hairs rusty; cincinni (3–)5–8-flowered, peduncles 0.8–1.6 cm long, vinaceous, densely hispid, hairs rusty to brown, reflexed in fruit; bracteoles broadly-ovate to depressed ovate, sessile, revolute, $2.9-4.4 \times 2.8-3.2$ mm, apex rounded to truncate, vinaceous to pinkish-purple, sparsely hispid, hairs rusty. Flowers bisexual, actinomorphic, 2.3–2.8 cm diameter; pedicel 1–7.2 mm long, white to light green, hispid, hairs rusty, reflexed and slightly elongate in fruit; floral buds ellipsoid to narrowly-obovoid, $0.7-1.6 \times 0.3-0.6$ cm, light green, apex obtuse; sepals narrowly-ovate to elliptic, cymbiform, $0.9-1.1 \times 0.4-0.7$ cm, unequal, the uppermost external and broader than the others, free, persistent and accrescent in fruit (½ as long to equaling the capsule in length), white to greenish, externally sparsely hispid, hairs hyaline to rusty, rusty in fruit, internally glabrous, margin hyaline, apex obtuse, slightly purple; petals broadly-ovate to broadly-elliptic, $1.3-1.6 \times 1.0-1.2$ cm, deliquescent, sub-equal, the lowermost usually broader than the others, bluish-lilac to bluish-purple, proximal third white, free, base cuneate, margin entire, apex obtuse to rounded, sometimes irregularly lacerated; stamens 6, equal, filaments 5– 7 mm long, straight, white, terminal third purple to bluish-purple, free, glabrous, anthers 1.5–2 × 1.3–2 mm, extrorsely rimose, dorsifixed, anther sacs semi-circular, divergent, purple to bluish-purple, connective expanded, quadrangular, purple; ovary globose, trigonous with obtuse angles, $1.5-2 \times 1.5-2$ mm, white, densely hispid, hairs hyaline, 3-locular, locules

equal, locule 3–4-ovulate, ovule uniseriate to partly biseriate, style 4–6 mm long, straight, white, terminal third purple to bluish-purple; stigma truncate, papillate. Capsules loculicidal, 3-valved, thick walled, subglobose to broadly-ellipsoid in outline, trigonous with round angles in cross-section, apiculate due to persistent style base, 1–1.3 × 0.7–0.9 cm, green, light-brown when mature, hispid, hairs rusty. Seeds obconic to ellipsoid, dorsoventrally compressed, ventrally slightly flattened, 3.3–5.2 × 2.4–2.9 mm, brown to dark-brown, testa rugose, ventral face slightly cleft on the side towards the embryotega; hilum C-shaped, approximately ½ the length of the seed, on a shallow ridge; embryotega semi-lateral, relatively inconspicuous, without a prominent apicule; aril cream-colored, slightly translucent, thick.

Additional specimens examined (Paratypes)

BRAZIL. Espírito Santo. Fundão: Alto Piaba, cultivated in the epiphyte greenhouse of the Museu de Biologia Mello Leitão, fl., 13 September 1989, *W. Boone 1349* (MBML); *loc. cit.*, A.P.A. do Goiapaba-açú, Piabas, property of Albino Casimiro, fl., 8 November 2007, *A.P. Fontana & K.A. Brahim 2827* (MBML, RB). Santa Teresa: Alto do Julião, property of João Luiz Rodrigues de Souza, fl., 23 February 2007, *A.P. Fontana & K.A. Brahim 2975* (MBML, RB); *loc. cit.*, 25 de Julho district, Julião, fl., 10 November 2007, *L. Kollmann et al. 11839* (MBML).

Etymology

The epithet means "white-striped", making reference to the persistent and well-defined white stripe along the midvein of this species' leaves.

Distribution and habitat

Siderasis albofasciata is known to occur exclusively at Alto do Julião, in the municipality of Santa Teresa, and Piabas, in the municipality of Fundão, both in the state of Espírito Santo (Fig. 5). It occurs on the understory of evergreen forests, in shady areas with shallow and rocky soil, with great leaf litter accumulation.

Phenology

Siderasis albofasciata can be found in bloom from November to June. This species was collected in fruit in April, where mature and immature capsules where seen.

Conservation status

The EOO (108.671 km²) and AOO (12.000 km²) are both very reduced, the subpopulations vary from small to medium-sized with many clones, but few mature individuals. All the four known subpopulations are strongly threatened by deforestation caused by coffee and eucalyptus crops, lumber exploration and human occupation. *Siderasis albofasciata* is also greatly threatened by illegal collections made by local horticulturists, because of the great ornamental value of its foliage and flowers, and for being very easy to cultivate. I estimate a total of ca. 2000 mature individuals for this species, but it seems doomed to decrease due to the abovementioned reasons. Also, only one, of the five known collections, was made inside a conservation unit. A very similar scenario can be observed for *S. fuscata*, endemic to the state of Rio de Janeiro (Fig. 5, Barreto 1997, Aona-Pinheiro et al. 2013, BFG 2015, Pellegrini 2016), where this species is also greatly threatened by deforestation and predatory collections (Aona-Pinheiro et al. 2013). Thus, following the IUCN recommendations (IUCN 2001), *S. albofasciata* should be considered as Critically Endangered [CR, B1ac(ii, iii, iv)+B2ab(ii, iii, iv)+C2a(i)].

Affinities

Siderasis albofasciata is similar to S. fuscata in its rosette habit, whole plant densely covered by conspicuous indumenta, leaves of a different color along the midvein, anthers with quadrangular connective and semi-circular anther sacs. However, S. albofasciata can be readily differentiated by its sessile to subpetiolate leaves covered by hyaline to light-brown indumenta (vs. petiolate leaves with bright-red to red indumenta, in S. fuscata), a well-defined white stripe along the midvein on the adaxial side of the blade (vs. sometimes blotched silver to metallic light-green), main axis of the synflorescence elongate (vs. inconspicuous), bracteoles present (vs. bracteoles absent), cincinni (3–)5–8-flowered [vs. 1–3–(4)-flowered], anthers purple, filaments and style apically purple (vs. androecium and gynoecium completely white), testa brown and rugose (vs. grey to light-grey and foveolate), and aril cream-colored, thick and slightly hyaline (vs. aril colorless and inconspicuous). Other morphological differences between both species can be seen in Table 1. Furthermore, S. albofasciata produces unique axillary flagelliform-shoots after its flowering period. Each flagelliformshoot is homologous to a daughter ramet. They consist of an extremely elongate stem, that may or not possess developed leaf-blades (sometimes the blades are very reduced or absent), and a terminal rosette that roots after it touches the soil. This clonal propagation strategy gives this species a chandelier appearance (Fig. 1A), similar to many epiphytic bromeliads. This clonal propagation strategy is also known in the Commelinaceae for some species of *Belosynapsis* Hassk. and *Cyanotis* D.Don (both members of subtribe Cyanotinae). Nevertheless, this is the first time it is recorded in Dichorisandrinae.

Siderasis fuscata (Lodd.) H.E.Moore (1956, p. 28). (Figs. 2C, 3, 4 & 5) Basionym: *Tradescantia fuscata* Lodd. (1820, t. 374).

Lectotype (**designated here**): [illustration] Original parchment plate of "The Botanical Cabinet" at the British Museum Library and later published in Loddiges, Bot. Cab. 4: t. 374. 1820.

Epitype (**designated here**): BRAZIL. Rio de Janeiro. Rio de Janeiro, Floresta da Tijuca, FEEMA, Parque Nacional da Tijuca, fl., fr., 7 November 2012, *M.O.O. Pellegrini* 217 (RB!).

Specimens examined

BRAZIL. Rio de Janeiro. Niterói: Itaipu, P.E. Serra da Tiririca, Itaipu, Alto Mourão, fl., 15 January 1982, V.F. Ferreira et al. 2104 (RB); boundary between the municipalities of Niterói and Maricá, between Itacoatiara and Itaipuaçu, Alto Mourão, fl., 11 September 2007, A.A.M. Barros & M. Pontes 3127 (RFFP). Rio de Janeiro: s.loc., fl., 1816-1821, A. Saint-Hilaire A/683 (P); s.loc., fl., fr., 1832, Riedel s.n. (P barcodes P01730357, P01730358); Corcovado, fl., fr., 1831–1833, C. Gaudichaud 337 (P 3 ex); loc. cit., Cova da Onça, fl., 15 August 1861, A.M. Glaziou 527 (NY, P); loc. cit., fl., 17 August 1869, A.M. Glaziou 4285 (P 2 ex); loc. cit., fl., July 1878, J. Miers 3534 (K, P); loc. cit., fl., 5 December 1889, P. Schwacke 6699 (RB); loc. cit., fl., 5 May 1892, A. Ducke s.n. (RB 64); loc. cit., sterile, 4 March 1943, A.P. Duarte & C.T. Rizzini 8 (RB); loc. cit., fl., 6 November 1944, P. Occhioni 50 (RB); Parque Natural da Tijuca, Matas do Pai Ricardo, fl., 29 October 1975, D.S. Araújo et al. 883 (GUA); loc. cit., fl., 30 October 2013, M.O.O. Pellegrini 404 (RB); loc. cit., fl., 15 November 2013, L.S.B. Calazans et al. 234 (RB); loc. cit., road to Vista Chinesa, next to the Biological Station, fl., 18 August 1960, C. Angeli 230 (GUA); loc. cit., Setor das Paineiras, next to Pedra do Beijo, fl., 15 November 1965, J.P.P. Carauta 286 (GUA); loc. cit., road to Vista Chinesa, fl., fr., 31 October 1969, J.P.P. Carauta 923 (GUA); loc. cit., Santa Cruz, fl., 6 July 1972, E. Lagasa s.n. (HB 71875); loc. cit., Pedra da Gávea, fl., 13 July 1966, D. Sucre 1304c (HB, RB); loc. cit., Alto da Boa Vista, Morro Queimado, next to the FEEMA biulding, fl., 26 October 2000, F. Pinheiro et al. 557 (HB); loc. cit., Estrada da Guanabara, Parque Lage, 25 January 1968, fl., *D. Sucre 2161* (RB); *loc. cit.*, Reserva Florestal do Jardim Botânico, fl., 19 January 1969, *D. Sucre & P.J.J. Braga 4472* (RB); *loc. cit.*, fl., 22 December 1971, *D. Sucre 8152* (RB); *loc. cit.*, Matas da Lagoinha, fl., 18 September 1946, *P. Occhioni 692* (RB); *loc. cit.*, fl., 6 March 1978, *V.F. Ferreira et al. 256* (RB); *loc. cit.*, fl., 11 November 1946, *P. Occhioni 781* (RFA); *loc. cit.*, brook trail between Paineiras and Jardim Botânico, fl., 4 December 1928, *L.B. Smith s.n.* (US barcode US1540545).

Distribution and habitat

Siderasis fuscata is endemic to the municipalities of Rio de Janeiro and Niterói, in the state of Rio de Janeiro (Fig. 5, Pellegrini 2016). It occurs on the understory of evergreen forests on mountainous formations, in shady areas with shallow and rocky soil, with great leaf litter accumulation.

Nomenclatural notes

When describing T. fuscata, Loddiges (1820) presented a beautiful watercolor illustration of a specimen he received. It is known that Loddiges specimens are generally distributed at Cambridge University (CGE) and Royal Botanic Gardens, Kew (K), and sometimes at the British Museum (BM) herbaria (Stafleu and Cowan 1981). Nevertheless, Loddiges (1820) gives no detailed information regarding which specimen(s) he studied when describing his new species. The only relevant detail given by the author is that his new species is native to South America. Due to the lack of information, I was unable to find any specimen that matched the protologue. One specimen at K (K001190685), is annotated as "T. fuscata Lodd., Bot. Cab. t. 374" in its original label. This specimen also bears great resemblance to the watercolor presented by Loddiges (1820, t. 374), due to the small stature, number of leaves, leaf shape and dense synflorescence. Nevertheless, it was collected by "Mr. Boag" and the label also states the specimen is original to Brazil (instead of the ambiguous South America origin, as stated in the protologue). Thus, due to the lack of specimens that can be undoubtedly considered as being part of Loddiges's original material, I designate here the original illustration, which is the only original element left (McNeill et al. 2012, Art. 9.12). The watercolor is of good quality, depicting the red indumenta on the whole plant, the acuminate sepals (seen in a flower bud), the rhomboid to broadly-rhomboid petals with generally lacerated margins, and the completely white androecium and gynoecium (Fig. 4). Nevertheless, due to the angle in which the plant was drawn, it fails to depict some important diagnostic features of this species such as: the petioles, the inflorescence morphology, the absence of bracteoles, and fruit and seed morphology. Thus, I designate an epitype for *T. fuscata*, in conformity to *The Code* (McNeill et al. 2012, Art. 9.8) and in order to fix the application of this name.

Discussion

Inflorescence morphology

The peculiar inflorescence architecture here described for *Siderasis* is similar to the one of *Plowmanianthus*. The main florescence is composed of a thyrse, reduced to a solitary cincinnus (in both *S. albofasciata* and *S. fuscata*). These reduced thyrsi are arranged into a synflorescence that may or not contain 1–2(–3) coflorescences (secondary thyrsi) in *S. albofasciata*, and (1–)2–6(–7) coflorescences *S. fuscata* (Fig. 2). Nevertheless, it differs from *Plowmanianthus*, in which the coflorescences only develop after the main florescence has failed to develop or set fruit (Hardy and Faden 2004). The coflorescences in *Siderasis* usually develop regardless of the reproductive success of the main florescence. Differently from *Plowmanianthus*, in which the cincinni from the primary and secondary thyrsi are morphologically different (Hardy and Faden 2004), the cincinni in *Siderasis* are always morphologically equal, regardless of being from the primary or any of the secondary thyrsi. The same can be said about the flowers in the primary and secondary thyrsi. Furthermore, the center of the mature *Siderasis* rosette may contain several terminal or apparently terminal synflorescences, instead of the always lateral synflorescences characteristic of *Plowmanianthus*, that may or not perforate the leaf-sheaths.

Seed morphology

Arillate seeds are uncommon in the Commelinaceae and recorded, until now, for only three genera: *Amischotolype* Hassk. (Duistermaat 2012), *Dichorisandra* (Aona 2008) and *Porandra* Hong (Faden 1998). This is the first time arillate seeds are reported for *Siderasis*. The inconspicuous aril from *S. fuscata*'s seeds has been completely neglected, while a thick aril (similar to the ones found in most *Dichorisandra* spp.) is described here for the first time (Fig. 1H–I). Arillate seeds are the only seeds with confirmed zoo-choric dispersion in the family (Faden 1992). The appendaged seeds of some *Commelina* L. and *Murdannia* Royle (Pellegrini et al. in prep.) species are also potentially dispersed by small insects (probably ants), and

further studies are still necessary. Nevertheless, there has been no further investigation regarding vector-mediated dispersion for these taxa and the evolutionary relevance of this character.

The present work sheds some light in the evolution of arillate seeds in Commelinaceae, in the systematics of subtribe Dichorisandrinae, and might give morphological support to the relation recovered by Evans et al. (2003) and Zuiderveen et al. (2011). Subtribe Dichorisandrinae is recovered as paraphyletic in most molecular and morphological phylogenies. The subtribe is generally recovered in two separate clades: the first composed by Dichorisandra and Siderasis; and the second composed by Cochliostema, Geogenanthus and Plowmanianthus (Evans et al. 2000, Hardy 2001, Evans et al. 2003, Wade et al. 2006, Zuiderveen et al. 2011 Hertweck and Pires 2014). In Evans et al. (2003) and Zuiderveen et al. (2011), Dichorisandra+Siderasis (i.e. subtribe Dichorisandrinae s.s.) is recovered as sister to subtribes Coleotrypinae and Cyanotinae. Whereas the well-supported Geogenanthus (Cochliostema+Plowmanianthus) is distantly related, recovered as one of the early diverging clades in tribe Tradescantieae. Most genera recovered in the Dichorisandrinae s.s.(Coleotrypinae+Cyanotinae) clade possess arillate seeds, with the exception of Coleotrype C.B.Clarke, Belosynapsis and Cyanotis. This could indicate two different scenarios for the origin of arillate seeds. The first one where arillate seeds evolved only once in Commelinaceae and would represent a synapomorphy for the Dichorisandrinae s.s.(Coleotrypinae+Cyanotinae) clade (with reversions in Coleotrype, Belosynapsis and Cyanotis). And the second where arillate seeds evolved independently in two separate lineages of Commelinaceae (i.e. in subtribes Dichorisandrinae s.s. and Coleotrypinae). Nevertheless, further phylogenetic studies are needed in order to better understand the evolution of this character in the family. Phylogenetic studies focusing on the systematic of Siderasis and the recircumscription of Dichorisandrinae are currently being carried out (Pellegrini et al. in prep.).

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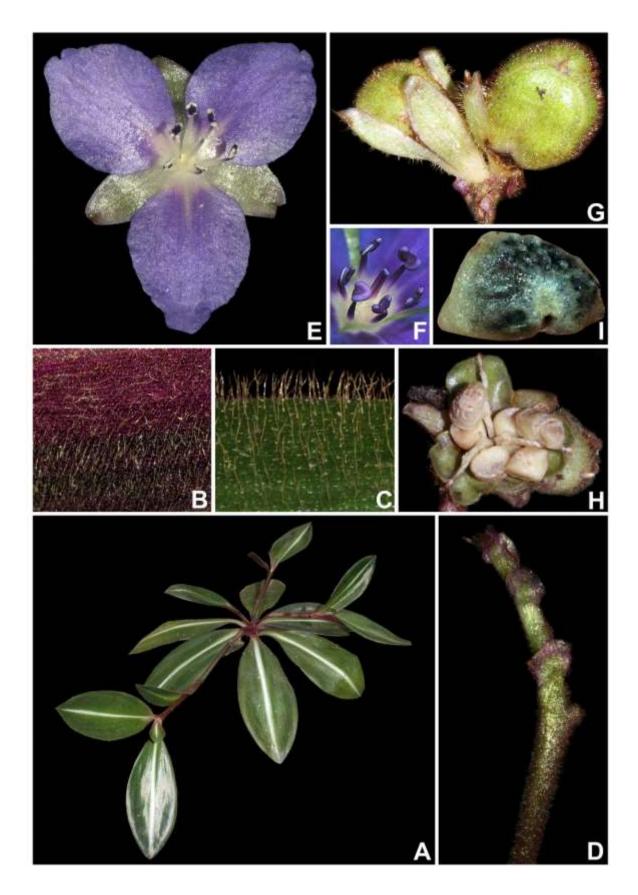


Fig. 1. *Siderasis albofasciata* M.Pell. **A,** habit, showing the well-defined white stripe along the midvein of the leaves and the flagelliform-shoots with terminal rosettes. **B,** detail of the

abaxial side of the leaf, showing the light-brown lanate indumenta. **C**, detail of the adaxial side of the leaf, showing the light-brown hispid indumenta. **D**, detail of the inflorescence, showing the solitary cincinnus. **E**, flower **F**, detail of the androecium and the gynoecium. **G**, detail of the capsules, the left one immature with evident accrescent sepals and the right one mature. **H**, detail of an open capsule, showing the uniseriate to partly biseriate arillate seeds. **I**, Dorsal view of a seed, showing the semi-lateral embryotega and the cream-colored, slightly translucent and thick aril. F by L. Kollmann (*L. Kollmann et al. 11839*, MBML), remaining photos by M.O.O. Pellegrini (*M.O.O. Pellegrini et al. 337*, RB, US).

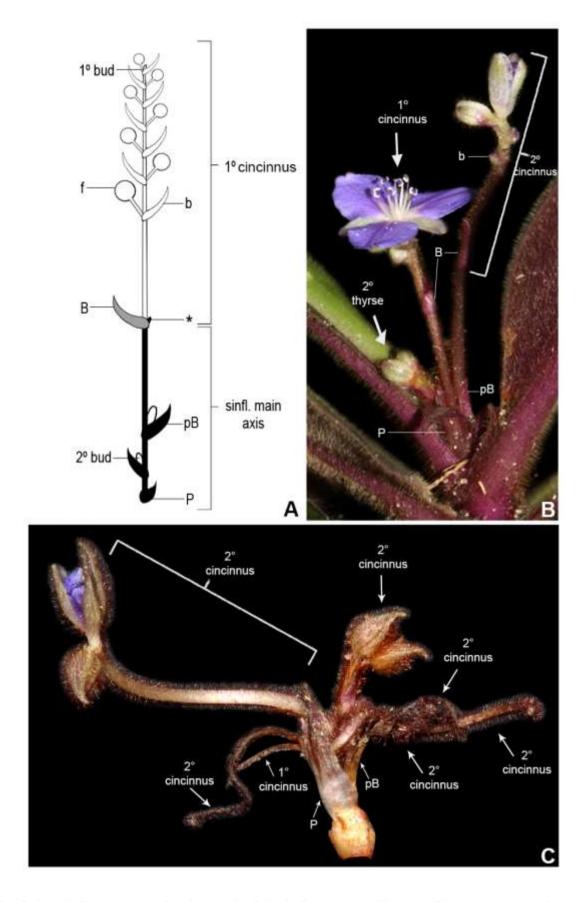


Fig. 2. The inflorescence of *Siderasis* Raf. **A,** inflorescence diagram. **B,** rosette apex of *S. albofasciata*, showing: the main florescence (primary thyrse) with a flower at post-anthesis

and a flower bud; the developed secondary thyrse with a flower at anthesis (arrow); and a young tertiary thyrse (arrow). **C**, synflorescence of *S. fuscata*, showing: the condensed synflorescence main axis and the long-pedunculate cincinni. **P**= prophyll; **pB**= peduncle bract on main synflorescence axis; *= aborted or dormant apex of main inflorescence axis (usually not observed); **B**= cincinnus bract; **b**= bracteole; **f**= flower; **1**° **bud**= bud terminating cincinnus; **2**° **bud**= bud in axil of peduncle bract with potential to develop into a secondary thyrse (coflorescence); **2**° **cincinnus**= cincinnus of the secondary thyrse (coflorescence). Modified from Hardy and Faden (2004).

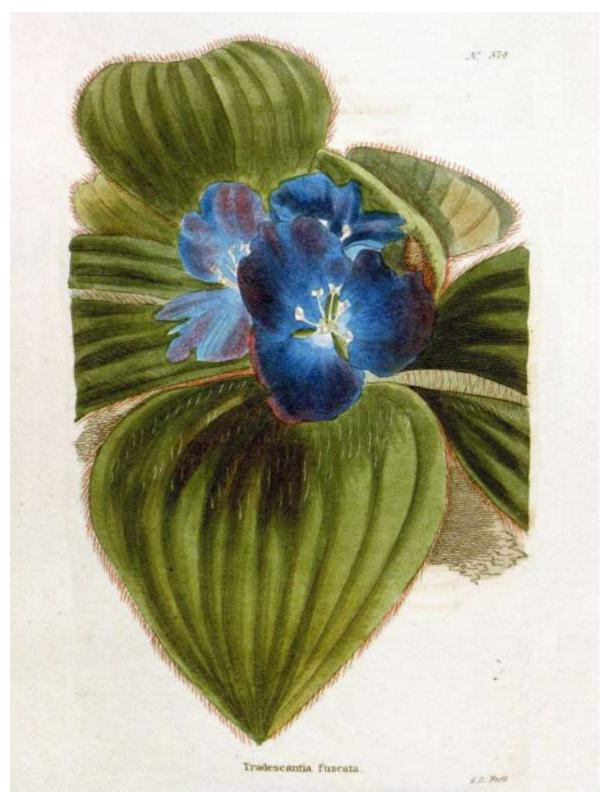


Fig. 3. Lectotype of *Tradescantia fuscata* Lodd. Photo courtesy of The Natural History Museum, London.

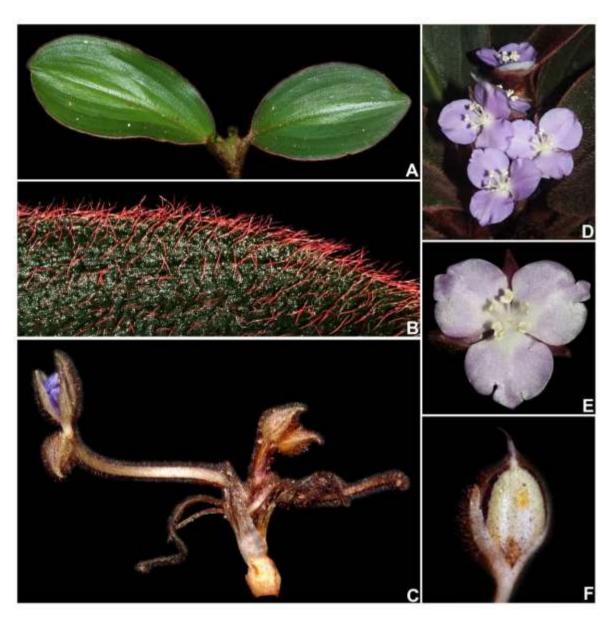


Fig. 4. *Siderasis fuscata* (Lodd.) H.E.Moore. **A,** habit, showing the petiolate leaves with silvery blotch along the midvein. **B,** detail of the bright-red hirsute indumenta. **C,** detail of the synflorescence detached from the rosette, showing the inconspicuous main axis and ebracteolate cincinni. **D,** upper view of a fertile rosette, showing many lilac flowers open at the same time. **E,** front view of a pale-lilac flower, showing the lacerated petals and completely white androecium and gynoecium **F,** detail of a mature capsule, showing the atrovinaceous longitudinal stripes. Photos by M.O.O. Pellegrini (*M.O.O. Pellegrini 217*, RB).



Fig. 5. Distribution map of *Siderasis* Raf. **Squares**– *Siderasis albofasciata* M.Pell.; **Circles**– *S. fuscata* (Lodd.) H.E.Moore.

Table 1. Comparison between *Siderasis albofasciata* and *S. fuscata*.

Characters	Siderasis albofasciata	Siderasis fuscata
Flagelliform-	Present	Absent
shoots		
Leaves	Sessile to subpetiolate, blades	Petiolate, blades blotched silver to
	white-striped, indumentum hyaline	metallic light-green, indumentum
	to light-brown, adaxially hispid,	bright-red to red, hirsute on both sides,
	abaxially lanate, secondary veins	secondary veins adaxially impressed,
	inconspicuous on both sides	abaxially slightly prominent (3–7
		pairs)
Inflorescence	Main axis elongate	Main axis inconspicuous
Bracteoles	Present	Absent
Cincinni	(3–)5–8-flowered	1–3–(4)-flowered
Sepals	Narrowly-ovate to elliptic, white to	Ovate to triangular, pink to vinaceous,
	greenish, apex obtuse	apex acuminate
Petals	Broadly-ovate to broadly-elliptic,	Rhomboid to broadly-rhomboid,
	bluish-lilac to bluish-purple,	entirely lilac to light-lilac, margin
	margin entire, apex obtuse to	irregularly lacerated towards the apex,
	rounded, sometimes irregularly	apex acute, sometimes irregularly
	lacerated	lacerated
Stamens	Filaments white with terminal third	Filaments and anthers entirely white
	purple to bluish-purple, anthers	
	purple to bluish-purple	
Gynoecium	Style white with terminal third	Style entirely white
	purple to bluish-purple	
Capsules	Subglobose to broadly-ellipsoid,	Ellipsoid to fusiform, cream with three
	entirely light-green	longitudinal atro-vinaceous stripes
Seeds	Testa brown to dark-brown,	Testa grey to light-grey, foveolate, aril
	rugose, aril cream-colored, slightly	colorless, hyaline and inconspicuous
	translucent and thick	-

SECTION 2— COMMELINACEAE MIRB.

Chapter 2.7. Recircumscription and taxonomic revision of *Siderasis*, with comments on the systematics of subtribe Dichorisandrinae (Commelinaceae)

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Abstract

A new circumscription and a total of six microendemic species, four of them new to science, are herein presented for *Siderasis*, based on field and herbaria studies, and cultivated material. We provide an identification key to the species and a distribution map, description, comments, conservation assessment, and illustration for each species. Also, we present an emended key to the genera of subtribe Dichorisandrinae, and comments on the morphology and systematics of the subtribe.

Keywords

Atlantic Forest, Brazil, Commelinales, Neotropical flora, spiderwort, Tradescantieae

Introduction

Siderasis Raf. is currently applied to a small genus of neotropical Commelinaceae, comprising only two microendemic species, restricted to the Atlantic Forest of Southeastern Brazil (Pellegrini 2017). It was originally described by Rafinesque (1836), together with several other small genera, in order to better organize the many species misplaced in Commelina L. and Tradescantia L. Rafinesque (1836) mentioned a possible affinity between Siderasis, Callisia Loefl. and Etheosanthes Raf. (= Belosynapsis Hassk.), and considered Siderasis not at all similar to *Tradescantia*; but gave no explanation for any of these statements. He also considered T. fuscata Lodd. a synonym of his newly described S. acaulis Raf., which was characterized by its rusty hirsute indumentum covering the entire plant, short stems, flowers emerging from the roots, petals basally connate, dimorphic stamens varying from four to six, and gynoecium 2–3locular [sic]. After Rafinesque's publication, Siderasis was completely overlooked by all Commelinaceae specialists for the next 120 years (Moore 1956). In the meantime, Hasskarl (1869) described the new genus Pyrrheima Hassk. following his discussions with Schlechtendal during the Botany Meeting in Amsterdam in April of 1865. Hasskarl and Schlechtendal believed that Pyrrheima diverged greatly from Tradescantia and Tinantia Scheidw. due to its non-tubular perianth, six equal and fertile stamens, and lunate anther sacs, and thus merited distinct generic status. Clarke (1881), in his monograph for Commelinaceae, accepted Pyrrheima, including only P. loddigesii Hassk., and reducing P. minus Hassk, to a variety of it. Brückner (1930), noticing that P. loddigesii was an unnecessary replacement name for T. fuscata, made the new combination P. fuscata (Lodd.) G.Brückn., but was unsure if Siderasis and Pyrrheima were indeed congeneric. This was later confirmed by Moore (1956), when he merged the two by transferring *P. fuscata* to *Siderasis*.

After further period of neglect, the genus was placed in subtribe Dichorisandrinae (Faden and Hunt 1991), along with its sister-genus *Dichorisandra* J.C.Mikan, *Cochliostema* Lem., *Geogenanthus* Ule, and *Plowmanianthus* Faden & C.R.Hardy (Faden and Hunt 1991; Hardy 2001; Evans et al. 2003; Hardy and Faden 2004). However, resolution of the relationships within the group remains elusive. While it appears certain that *Siderasis* is proximally related to *Dichorisandra*, the subtribe as a whole has been recovered as paraphyletic in most molecular and morphological phylogenies to date. Two separate clades are recovered with one containing *Dichorisandra* and *Siderasis* (i.e. subtribe Dichorisandrinae *s.s.*), while the remaining three genera (*Geogenanthus* and *Cochliostema+Plowmanianthus*) are recovered as one of the early-diverging clades in tribe Tradescantieae (Hardy 2001; Evans et al. 2003; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini 2017; Pellegrini et al., in prep.). *Siderasis* has hitherto been characterized by the rusty to bright red hirsute indumentum covering the entire plant (except the petals and androecium), its ebracteolate cincinni, filaments three to

four times longer than the anthers, anthers with rimose dehiscence (Hardy and Faden 2004), and exarillate seeds (Faden 1998).

Composition of the genus itself also remains unclear with Faden and Hunt (1991) mentioning two *Siderasis* species, while Faden (1998) mentions two to three species. Barreto (1997), in a survey of the Commelinaceae native to Brazil accepts only *S. fuscata* and reaffirmed *Siderasis* as a monospecific genus. Pellegrini (2017) recently described a new species of *Siderasis*, and provided important information regarding inflorescence and seed morphology in the genus. Clearly, further studies were still necessary to solve the ongoing issues (Pellegrini et al. 2013), and with this in mind recent field and herbaria studies have been undertaken to shed further light on this genus. In an attempt to clarify the taxonomy and systematics of neotropical Commelinaceae, and as part of the authors' ongoing studies in subtribe Dichorisandrinae (Hardy and Faden 2004; Aona et al. 2012; Aona et al. 2016; Pellegrini and Almeida 2016; Pellegrini 2017), we recircumscribe and revise *Siderasis*, with the description of four new species. We also provide detailed comments on the morphology and systematics of subtribe Dichorisandrinae *s.l.*

Methods

The description of the species, phenology and illustrations were based on herbaria (A, ALCB, B, BHCB, BHZB, BM, BOTU, BRIT, C, CAL, CEPEC, CESJ, CGE, CNMT, CVRD, ESA, F, FCAB, FLOR, FURB, G, GUA, HAMAB, HAS, HB, HBR, HRB, HRCB, HSTM, HUEFS, HUFSJ, HURB, IAC, ICN, INPA, K, L, MBM, MBML, MG, MO, MY, NY, P, PMSP, PORT, R, RB, RFA, RFFP, SP, SPF, U, UEC, UPCB, US, and WAG; herbaria acronyms according to Thiers, continuously updated), spirit, fresh, and cultivated material. Specimens of Siderasis albofasciata M.Pell., S. almeidae M.Pell. & Faden sp. nov., and S. fuscata were kept in cultivation at the greenhouse of the Jardim Botânico do Rio de Janeiro, in order to observe, photograph, and analyze fresh flowers, fruits, and seeds as well as other phenological data. Fresh specimens, field notes, photographs, and specimens for cultivation were gathered during several field trips across the Brazilian Atlantic Forest, from the states of Sergipe to Rio Grande do Sul, between 2008–2016. Field data and description of S. medusoides M.Pell. & Faden sp. nov., and S. zorzanellii M.Pell. & Faden sp. nov. were complemented with notes, photographs and spirit samples kindly provided by the collectors. Fertile specimens were deposited in RB, and whenever possible duplicates were sent to US. Indumentum and shape terminology follows Radford et al. (1974); the inflorescence and general morphology terminology follows Weberling (1965, 1989) and Panigo et al. (2011); the fruit terminology follows Spjut (1994); and the seed terminology follows Faden (1991). The conservation assessments followed the recommendations of IUCN Red List Categories and Criteria, Version 3.1 (IUCN 2001). GeoCAT (Bachman et al. 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). The distribution of the species is based on herbaria materials, field data, and literature. The classification of vegetation patterns follows IBGE (2012).

Results

In the present study, we accept six species of *Siderasis*, with four of them newly described here. All species in the genus are microendemics, restricted to the Atlantic Forest of eastern Brazil. Both *Dichorisandra* and *Siderasis* share considerable variation in growth form, inflorescence architecture and androecium arrangement, which may have hindered the emergence of a stable taxonomy. Due to the variation and peculiar morphology of the newly described species, especially the two climbing species, *Siderasis* is recircumscribed below. The genus can be distinguished from the remaining Dichorisandrinae *s.l.* based on floral morphology, especially

androecium and microstigmatic morphology. An updated identification key for the genera of Dichorisandrinae *s.l.* is presented, along with comments on the morphology of *Siderasis* compared to the remaining genera of the subtribe.

Emended key to the genera of Dichorisandrinae *s.l.* (modified from Hardy and Faden 2004)

- 1. Petals with glabrous margins, rarely ciliate with non-moniliform hairs; filaments glabrous, anther sacs not appressed to each other (if appressed, anther sacs not semicircular); capsules thick-walled; seeds arillate... 2
- Petals with margins fringed with moniliform hairs; filaments bearded with moniliform hairs, rarely glabrous, anther sacs appressed to each other; capsules thin-walled; seeds exarillate...
 3
- 2. Stamens 5–6, staminodes sometimes present; anthers basifixed, anthers sacs parallel, elongate, 3 to 4 times longer than the filaments, connectives inconspicuous, dehiscence poricidal or introrsely rimose, but functionally poricidal; stigmatic papillae multicellular, completely concealing the stylar canal... *Dichorisandra* J.C.Mikan (Fig. 1D–L)
- Stamens 6, staminodes absent; anthers dorsifixed, anther sacs divergent, semicircular, 3 to 4 times shorter than the filaments, connectives expanded, dehiscence extrorsely rimose; stigmatic papillae unicellular, restricted to margins of the stigma and leaving the stylar canal evident... *Siderasis* Raf. emend. M.Pell. & Faden (Fig. 1A-C)
- 3. Dracaenoid herbs; roots with terminal tubers; shoots determinate; inflorescences borne at the lower nodes below the leaves; pedicel with glandular hairs, stamens 5–6, all fertile, stigmas never fringed with moniliform hairs... *Geogenanthus* Ule (Fig. 1N)
- Rosette herbs; roots without terminal tubers; shoots indeterminate; inflorescences borne among the leaves; pedicels with eglandular hairs, fertile stamens 3, on the upper half of the flower, staminodes 3 (sometimes microscopic), on the lower half of the flower, stigmas commonly marginally fringed with moniliform hairs... 4
- 4. Tank-forming or creeping rosettes, epiphytes, rarely terrestrial; inflorescence a many-branched thyrse, with alternate or verticillate cincinni, cincinni bracts showy; fertile anthers spirally-coiled, hidden within a hood-like structure; testa smooth, sticky when hydrated... *Cochliostema* Lem. (Fig. 1M)
- Rosettes not tank-forming, terrestrial; inflorescence reduced to a solitary pedunculate cincinnus, cincinnus bract inconspicuous; fertile anthers semicircular, not hidden within a hood-like structure; testa rugose to foveolate, farinose... *Plowmanianthus* Faden & C.R.Hardy (Fig. 10)

Siderasis Raf., Fl. Tellur. 3: 67. 1837, emend. M.Pell. & Faden

Type species. *Siderasis acaulis* Raf. $[\equiv S. fuscata (Lodd.) H.E.Moore].$

Pyrrheima Hassk., Flora 52: 366. 1869, nom. illeg. Type species (designated here). *P. loddigesii* Hassk., nom. illeg. [≡ *S. fuscata* (Lodd.) H.E.Moore].

Description. Herbs or vines, perennial, with a definite base, terrestrial or rupicolous. Roots thin, fibrous, sometimes forming terminal, small, fusiform to oblongoid tubers. Rhizomes present or not, if present short, shallowly to deeply buried in the ground, rarely only covered by leaf litter. Subterraneous stems present or not, when present buried deep in the soil,

unbranched, produced directly from the short rhizome; internodes moderately elongate to elongate. Aerial stems with determinate or indeterminate growth, elongated or short to inconspicuous, densely branched or unbranched, when densely branched primary shoot determinate or not, when present secondary shoots determinate; internodes inconspicuous to weakly elongate, or elongate; flagelliform-shoots (ramets) present or not, if present produced after the fertile period, forming a new rosette at the apex, axillary, unbranched, internodes elongate. Leaves spirally-alternate or distichously-alternate, congested at the apex of the stems forming a rosette or evenly distributed along the secondary branches, sessile to subpetiolate or petiolate, sheathing at the base, ptyxis involute; blades membranous to chartaceous or succulent, base symmetric or slightly to completely asymmetric, margins slightly revolute to flat, apex curved or straight. Synflorescence composed of a solitary main florescence or with 1–7 coflorescences. *Main florescence (inflorescence)* a thyrse, terminal or apparently so, rarely axillary, a many-branched, pedunculate thyrse, with alternate cincinni or reduced to a solitary pedunculate cincinnus; basal bract sessile or amplexicaulous or sheathing; cincinni bracts sessile or amplexicaulous; cincinni pedunculate, 1-many-flowered; bracteoles present or not. Flowers bisexual or staminate, actinomorphic or zygomorphic, chasmogamous, flat, pedicellate or sessile; pedicels erect during pre-anthesis and anthesis, erect or deflexed post-anthesis, generally elongating in fruit; sepals 3, unequal, free, membranous or fleshy, persistent and accrescent in fruit, the uppermost external, broader than the others, sometimes also shorter than the others; petals 3, deliquescent, free, margins entire to irregularly lacerated, glabrous, rarely ciliated with non-moniliform hairs, apex entire to irregularly lacerated, subequal, the lowermost either broader or longer than the others; stamens 6, equal or unequal, straight or curved upwards, filaments free, glabrous, straight or sigmoid, anthers dorsifixed, extrorsely rimose, anther sacs semicircular, divergent, pollen white, connectives expanded, quadrangular to rectangular; ovary sessile, globose to broadly oblongoid to ellipsoid in outline, trigonous with obtuse to round angles in cross-section, densely hirsute or lanate or velutine, 3-locular, locules equal, 3-6ovulate, ovules hemianatropous, biseriate to partially uniseriate; style terminal, straight or curved upwards; stigma annular-truncate or annular-capitate, marginally papillate leaving the stylar canal evident, papillae unicellular. Capsules loculicidal, thick-walled, 3-valved, globose or subglobose to broadly ellipsoid to broadly oblongoid to oblongoid in outline, trigonous with obtuse to round angles in cross-section, smooth to sparsely reticulate, apiculate due to persistent style base. Seeds (1–)3–6 per locule, arillate, obconic to ellipsoid, dorsiventrally compressed, ventrally slightly flattened or with a mild ridge, testa foveolate or rugose; hilum C-shaped, in a shallow depression; embryotega semidorsal or semilateral, relatively inconspicuous, without a prominent apicule; aril cream-colored to hyaline, slightly to completely translucent, thick or inconspicuous.

Etymology. *Siderasis* was named in allusion to the peculiar red to bright-red hairs that cover almost the entire plant, but especially the leaves. However, only *S. fuscata* possesses the aforementioned hairs, and all of the remaining species possess leaf blades covered by hyaline to light brown, rarely rusty hairs.

Habitat, distribution and ecology. *Siderasis* is endemic to the Atlantic Forest domain in coastal Brazil, occurring in the states of Bahia, Espírito Santo, and Rio de Janeiro (Fig. 2). More specifically, *Siderasis* is restricted to the Central Corridor of the Atlantic Forest, growing in remnants of semideciduous forests associated with inselbergs, between 90–1350 m above sea level. The genus is composed exclusively by microendemic species distributed in very small and fragmented subpopulations, susceptible to deforestation and illegal collection of specimens for ornamental purposes.

Biogeography. Since most phylogenies for Commelinaceae corroborate the paraphyly of Dichorisandrinae (Evans et al. 2000, 2003; Hardy 2001; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini et al., in prep.), we can hypothesize on the independent diversification of these lineages from a biogeographical point of view. The clade composed by Cochliostema, Geogenanthus, and Plowmanianthus is consistently recovered as the second lineage to diverge in tribe Tradescantieae, following the diversion of subtribe Streptoliriinae (Evans et al. 2003; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini et al., in prep.). The ancestor of this lineage probably originated in the Amazon Basin, and posteriorly diversified in the Guyana Shield, northern Andes, and Central America reaching Costa Rica (Hardy 2001; Hardy and Faden 2004). On the other hand, the clade composed by Dichorisandra and Siderasis is recovered as the third lineage to diverge in Tradescantieae (Evans et al. 2003; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini et al., in prep.). The ancestor of this clade probably originated and diversified in the Atlantic Forest domain, since it is the center of diversity of both genera. Subsequently, the ancestors of various *Dichorisandra* lineages might have dispersed, more than once, diversifying in the Amazon Basin through gallery forests in the Cerrado domain.

Growth form and leaf morphology. Siderasis possesses two clearly differentiated growth patterns: (1) rosette herbs, generally with very short internodes, and spirally-alternate, symmetrical leaves (Fig. 3A-B); (2) climbing vines, with elongated internodes, and distichously-alternate, asymmetrical leaves (Fig. 3C-D). The rosette habit has hitherto been the only one recognized in the genus. Faden (1998) mentioned the existence of a climbing species in the genus, but due to the synoptic nature of that publication, no further remarks were made on the subject. The climbing habit is relatively uncommon in the family, but found in the closely related Dichorisandra. However, in Dichorisandra the plants tend to lean on nearby trees and shrubs, later producing pendant branches, or even growing completely intertwined with more robust shrubs (Fig. 3E-F). In Siderasis, the primary branch grows at the base of a tree (Fig. 3C), posteriorly spirally ascending around the trunk, and finally producing the flowering secondary branches (Fig. 3D). In the remaining genera of Dichorisandrinae, growth form is stable, with almost no variation within each genus. In Cochliostema, the plants tend to be tankforming rosette herbs, but creeping individuals are also known in C. velutinum Read (Hardy 2001). In Geogenanthus, the plants always possess a dracaenoid habit, with leaves congested at the apex (Hardy 2001). In *Plowmanianthus*, the plants are always rosette herbs with very short stems (Hardy and Faden 2004).

Considerable variation in leaf morphology occurs in *Siderasis*, with leaves ranging from: (1) sessile to subpetiolate (Fig. 3B–D); (2) truly petiolate, as in *S. fuscata* (Fig. 3A, 8C). Truly petiolate leaves are extremely rare in Commelinaceae, being recorded only in a handful of species restricted to the peculiar-looking subtribe Streptoliriinae, mostly comprised of vining plants (Pellegrini and Faden, pers. observ.). Phyllotaxy in *Siderasis* can range from distichous to spirally-alternate, the arrangement being correlated to symmetry of the leaf blades.

Inflorescence morphology. In all *Dichorisandra* and two species of *Siderasis* (i.e. *S. spectabilis* and *S. zorzanellii*), the main florescence is a many-branched, pedunculate, terminal or axillary thyrse with alternate cincinni, each cincinnus being multi-flowered. In the remaining species of *Siderasis* (i.e. *S. albofasciata*, *S. almeidae*, *S. fuscata* and *S. medusoides*), the main florescence is composed of a thyrse reduced to a solitary cincinnus, as described in Pellegrini (2017; Fig. 4A). These reduced thyrsi are arranged into a synflorescence that may contain up to seven coflorescences. The center of the mature *Siderasis* rosette may contain several terminal or apparently terminal synflorescences. In *Dichorisandra* and the two climbing species of *Siderasis*, the main axis of the inflorescence is usually well developed, thus producing a typical

looking thyrse (Fig. 4B). Nevertheless, the inflorescences may also be extremely reduced in some species (i.e. D. acaulis group), due to the shortening of the inflorescence's internodes (Pellegrini and Almeida 2016). The cincinni are also very short (i.e. sessile to subsessile), being enclosed by the leaf sheaths and not obvious at first glance (Pellegrini and Almeida 2016). The flowers are peculiarly long-pedicellate, giving the impression that all flowers emerge directly from the apex of the stems (Pellegrini and Almeida 2016; Fig. 4C). Despite the extreme reduction and superficial similarity, this inflorescence pattern differs from the one found in the rosette species of Siderasis, since it still is a many-branched thyrse. In Plowmanianthus the main florescence is also reduced to a solitary cincinnus. Nonetheless, coflorescences only develop after the main florescence has failed to develop or set fruit, and the cincinni from the primary and secondary thyrsi are morphologically distinct (Hardy and Faden 2004). In Geogenanthus the inflorescences are always born at the base of the plant, near the ground. Aside from that, the main florescence is a pedunculate, fascicle-like thyrse, with (1–)2–4–several alternate cincinni (Hardy 2001). Finally, in Cochliostema the main florescence is a manybranched, pedunculate, axillary thyrse, with alternate to verticillate cincinni, each cincinnus being multi-flowered and subtended by showy and cucullate spathaceous bracts (Hardy and Stevenson 2000; Hardy 2001).

Floral symmetry. Two distinct floral patterns can be observed in different species of Siderasis: (1) flowers are always bisexual, actinomorphic, having 6 equal stamens arranged cyclically around the ovary, with straight filaments (Fig. 1A-B); (2) flowers bisexual or staminate, zygomorphic, having 6 unequal stamens curved upwards, with sigmoid filaments (Fig. 1C). Furthermore, in the zygomorphic staminate flowers, the lower antepetalous stamen is longer, and is arranged and curved in the same way as the style in bisexual flowers. The first flower morph is very similar to that found in the D. acaulis group (Pellegrini and Almeida 2016; Fig. 1D), while the second is equivalent to that of the *D. hexandra* and *D. incurva* groups (Fig. 1E & I). In *Dichorisandra*, flower symmetry is generally influenced by the positioning of the stamens, rather than by the relationship of stamens and staminodes. Actinomorphic flowers can be found not only in the D. acaulis group (Fig. 1D), but also in a group of still-undescribed species from the Guyana Shield (Faden and Pellegrini, pers. observ.). In all remaining species groups in Dichorisandra, the flowers are clearly zygomorphic, either due to the number of stamens, their size and/or position. In the D. thyrsiflora group, the androecium is generally composed of six fertile stamens, four of them curved towards the center of the flower, and the two lower lateral ones curved towards their opposing sides (Fig. 1F). An exception can be noticed in D. paranaënsis D.Maia et al. (Fig. 1G) and D. nana Aona & M.C.E.Amaral (Fig. 1H). In D. paranaënsis the stamens are curved upwards, varying from five fertile stamens with a staminode (present or not) to six fertile stamens, and introrsely rimose anthers. On the other hand, in D. nana the six fertile stamens are curved upwards, and possess poricidal anthers. In the D. incurva (Fig. 1I), D. penduliflora (Fig. 1J), D. leucophthalmos (Fig. 1K), and D. radicalis groups (Fig. 1L), the androecium is composed of five stamens (generally with an upper staminode; notice the filiform staminode in Fig. 1L), rarely six fertile stamens, curved upwards, and with introrsely rimose anthers. In the *D. incurva* and *D. leucophthalmos* groups, the anthers are always yellow (Figs. 11 & K), while in the D. pendulifora and D. radicalis groups, the anthers are white, generally with the anther sacs partially to totally colored in blue, pink or purple (Figs. 1J & L). The remaining genera of Dichorisandrinae possess strongly zygomorphic flowers, especially due to the position and/or number of stamens: (1) 5-6 dimorphic, free and fertile stamens in Geogenanthus (Hardy 2001; Fig. 1N); (2) 3 stamens in the upper side of the flower, fused in a hood-like structure, and 3 lower staminodes (the middle one microscopic) in Cochliostema (Hardy 2001; Fig. 1M); (3) and 3 free to partially fused stamens in the upper side

of the flower, and 3 lower staminodes (generally all of them microscopic) in *Plowmanianthus* (Hardy and Faden 2004; Fig. 10).

Androecium and gynoecium morphology. The anthers in *Siderasis* are dorsifixed, with extrorsely rimose dehiscence, two times wider than long, three to four times shorter than the filaments, with semicircular, divergent anthers sacs, and expanded connectives (Fig. 1A–C). In *Dichorisandra* the anthers are basifixed, with poricidal or introrsely rimose (but functionally poricidal) dehiscence, three to four times longer than wide, and three to four times longer than the filaments, rarely equal to the filaments, with elongate, parallel anther sacs, and inconspicuous connectives (Aona 2008; Figs. 1D–L). In *Cochliostema*, *Geogenanthus* and *Plowmanianthus* the anthers vary from dorsifixed to basifixed, with extrorsely rimose dehiscence, as wide as long to two times shorter than the filaments, with semicircular to spirally-coiled, appressed anther sacs, and inconspicuous connectives (Hardy and Stevenson 2000; Hardy 2001; Hardy and Faden 2004; Figs. 1M–O).

The gynoecium is fairly homogeneous in Dichorisandrinae *s.l.*, with all genera having sessile, 3-locular ovaries, with all locules fertile, ovules hemianatropous, biseriate to partially uniseriate, style terminal, straight or bent at the apex, stigma annular-truncate to annular-capitate, peripherally ciliate with moniliform hairs (i.e. *Cochliostema* and *Plowmanianthus*) or not (i.e. *Dichorisandra*, *Geogenanthus* and *Siderasis*). In *Siderasis*, the stigmatic papillae are unicellular, and restricted to the margins of the stigma, leaving the stylar canal evident (Owens and Kimmins 1981). On the other hand, in *Dichorisandra*, the stigmatic papillae are multicellular, and evenly distributed on the stigma, completely concealing the stylar canal (Owens and Kimmins 1981).

Fruit and seed morphology. The capsules of Dichorisandra and Siderasis can be differentiated from capsules of other Commelinaceae by their thick and tough walls. In Commelinaceae the fruits are commonly (1–)2–3-locular, thin walled, septicidal capsules (Faden 1998). Dichorisandra and Siderasis possess 3-locular, 3-valvar capsules, and arillate seeds. The aril in *Dichorisandra* is generally opaque (rarely hyaline), usually thick (rarely inconspicuous), and colored from white to grayish or bright orange (rarely colorless) (Fig. 5A-B). Whereas the aril in Siderasis can be hyaline to slightly hyaline, inconspicuous or thick, and cream-colored to colorless (Fig. 5C-D). The seeds in both genera are very similar in gross morphology, varying in shape from obconic to ellipsoid to quadrangular; in ornamentation from foveolate to scrobiculate to rugose, with a semilateral to semidorsal embryotega, and with a Cshaped hilum. In Cochliostema, Geogenanthus and Plowmanianthus the capsules are thinwalled, 3-locular, 3-valvar, and with exarillate seeds. In Cochliostema the capsules are narrowly cylindrical, and the seeds vary from subcylindrical to narrowly oblongoid, with a smooth testa that becomes sticky when hydrated, semidorsal embryotega, and a linear hilum with curved edges. In Geogenanthus and Plowmanianthus the capsules are fusiform to ellipsoid, the seeds range from reniform to ellipsoid, with rugose to foveolate, farinose testa, lateral embryotega, and a C-shaped hilum (Hardy 2001; Hardy and Faden 2004).

In *Dichorisandra* and *Siderasis* capsule and seed morphology differences may have great taxonomic potential. In *Dichorisandra*, many of the aforementioned species groups display characteristic capsule and seed morphology, as exemplified in the *D. acaulis* group by Pellegrini and Almeida (2016). In the *D. thyrsiflora* group, capsule morphology can easily differentiate most known species, based on shape, coloration, texture and pubescence (Pellegrini, pers. observ.). In *Siderasis*, capsule morphology shows a similar potential, with the fruits of *S. zorzanellii* being completely deviant in shape, texture and pubescence from the remaining species. Unfortunately, since the fruits of *S. spectabilis* are still unknown, it is impossible to know if this change in capsule morphology is correlated to the change in habit

from rosette to vining herbs. *Siderasis fuscata* possesses unique seed morphology, being the only known species with an inconspicuous and hyaline aril, testa light gray to gray, and foveolate. Field expeditions focused on collecting fruit and seed samples of all species of *Siderasis* could be of great taxonomic value. It is possible that most, if not all, presently accepted species could be differentiated based exclusively on fruit and seed morphology.

Reproductive biology. Little is known regarding the floral biology of subtribe Dichorisandrinae, although this subtribe possesses the greatest range in inflorescence architecture and floral patterns in the family. In Siderasis the anthers are always extrorsely rimose, but apart from the floral specialization (i.e. zygomorphic, bisexual or staminate flowers, and unequal and sigmoid stamens) in the two climbing species and the petals with margins ciliated with non-moniliform hairs, a character unique in the family, in S. spectabilis, the flowers are relatively unspecialized. Dichorisandra possesses a wide variation in flower morphology and androecium arrangement. Its flowers can range from actinomorphic to zygomorphic, the stamens can vary from (5–)6, sometimes with the upper stamen reduced to a staminode in some species. The filaments can be either straight, slightly sigmoid or slightly twisted depending on their position in the flower, while the anthers can be introrsely rimose and functionally poricidal or truly poricidal (Aona 2008; Fig. 1D-L). On the other hand, in Cochliostema, Geogenanthus and Plowmanianthus, the flowers are highly specialized, being zygomorphic (in all genera), scented (in *Cochliostema*), with a high frequency of cleistogamous flowers (in *Plowmanianthus*), petals and stigma fringed with moniliform hairs (fringed petals in all genera, stigma fringed exclusively in Cochliostema and Plowmanianthus), filaments bearded with moniliform hairs (in all genera), functionally poricidal androecium (in Cochliostema, due to the hood-like structure enclosing the anthers), and curved to spirallycoiled anthers (in all genera) (Hardy and Stevenson 2000; Hardy 2001; Hardy and Faden 2004; Fig. 1M-O). Only three species of *Dichorisandra* have had their reproductive biology investigated, presenting typical buzz-pollination, performed by bumblebees (Apidae) and/or sweatbees (Halictidae) (D. thyrsiflora, Boaventura and Matthes 1987; D. hexandra and D. incurva, Sigrist and Sazima 2015). Information regarding flower visitation in Cochliostema, Geogenanthus, and Plowmanianthus is completely lacking from the available literature. During our field studies and while observing the Siderasis specimens grown at the greenhouse of Jardim Botânico do Rio de Janeiro, the first author has observed flowers of S. albofasciata, S. almeidae, and S. fuscata being visited by stingless honey bees (Apidae, tribe Meliponini). Siderasis medusoides was not seen in the field, but high-resolution photographs sent by one of the collectors clearly show several small ants walking around the flowers and cincinni (Fig. 9C). The bees might either represent pollen robbers or potential pollinators, but the presence of the ants is hard to explain, since nectaries are unknown for Commelinaceae (Faden 1992, 1998). Further studies on the reproductive biology of *Siderasis* are clearly needed.

Aside from the peculiar floral diversity, Dichorisandrinae *s.l.* has two genera (out of five) and the majority of species in the family with arillate seeds (Pellegrini 2017). Nonetheless, no study has ever focused on vector-mediated (i.e. zoo-choric) seed dispersal in the family. In *Dichorisandra*, the seeds in the *D. hexandra* group are most certainly dispersed by birds (Faden 1992), due to the plants vining habit (Fig. 3E), which help in displaying the seeds, covered by an orange to bright orange, thick and opaque aril (Fig. 5B). The seeds in the *D. thyrsiflora* group are covered by a thick and opaque, white to cream-colored aril (Fig. 5A), and are generally easy to see in the field, due to the plants high stature (Pellegrini pers. observ.). Nonetheless, these species lack the characteristic colors that are generally associated with bird pollination/dispersal (i.e. pink, red, orange and yellow; Fleming and Estrada 1993), always present in the *D. hexandra* group. The species in the *D. acaulis* group possess seeds also covered by a thick and opaque, white aril, lacking the visual attraction associated with bird dispersal, and also lack an

elevated display, since they are always shorter than 1 m long (Pellegrini and Almeida 2016). These seeds might be dispersed by ants, or by small terrestrial vertebrates (e.g. small rodents), instead of being dispersed by birds, as hypothesized for other species of *Dichorisandra*. The seeds from the rosette species of *Siderasis* have similar morphological and ecological features to the species from the *D. acaulis* group. These species also have small stature and seeds with hyaline and inconspicuous, or cream-colored, slightly translucent, thick arils (Fig. 5C–D), being most probably dispersed by animals similar to the ones dispersing the seeds of the species in the *D. acaulis* group.

From a phylogenetic point of view, it seems that vector-mediated seed dispersal has evolved several times in the family: (1) arillate seeds are recorded for *Dichorisandra* and *Siderasis* in Dichorisandrinae, Amischotolype Hassk., Coleotrype C.B.Clarke and Porandra Hong in Coleotrypinae (Pellegrini 2017), and Spatholirion Ridl. in Streptoliriinae (Thitimetharoch 2004); (2) appendaged seeds are recorded for at least two separate lineages in tribe Commelineae (i.e. some species of *Commelina* L. and *Murdannia* Royle; Pellegrini et al. 2016); (3) truly fleshy fruits are known only from Palisota Rchb. ex Endl. (Faden 1998); (4) in Tradescantia zanonia (L.) Sw. the fleshy sepals cover the indehiscent fruit at post-anthesis, producing a sweet and atro-vinaceous berry-like fruit, dispersed by birds (Pellegrini, obs. pers.); (5) in *Pollia* Thunb. the fruits are dry, crustaceous and indehiscent, and due to their vibrant colors (metallic blue to shiny black) mimic real berries (Faden 1978); (6) in some Commelina (i.e. the species originally placed under *Phaeosphaerion Hassk.* and *Commelinopsis Pichon*) the fruits are morphologically similar to those of Pollia, being also crustaceous, but either dehiscent or indehiscent (Faden and Hunt 1987); (7) and sticky capsules covered by a mixture of hook and minute glandular hairs, in Rhopalephora Hassk. (Pellegrini et al., in prep.). Nonetheless, further investigations are needed to better understand the ecology and evolution of vector-mediated seed dispersal in Commelinaceae.

Key to the species of Siderasis

- 1. Vining herbs; aerial stems spirally-twining, densely branched; leaves distichously-alternate, blades ±asymmetric at base; main florescence a many-branched thyrse, with alternate cincinni; flowers bisexual or staminate, zygomorphic, stamens unequal, curved upwards, filaments sigmoid, stigma annular-capitate; embryotega semidorsal... 2
- Rosette herbs; aerial stems inconspicuous or trailing, unbranched; leaves spirally-alternate, blades symmetric at base; main florescence reduced to a solitary cincinnus; flowers always bisexual, actinomorphic, stamens equal, directed towards the center of the flower, filaments straight, stigma annular-truncate; embryotega semilateral... 3
- 2. Inflorescences always terminal in the secondary branches; flowers 1–1.3 cm diameter, petals dark mauve to vinaceous, rarely light pink or white, margins ciliate with non-moniliform hairs; northern montane Rio de Janeiro state... *Siderasis spectabilis* M.Pell. & Faden (Fig. 10–11)
- Inflorescences axillary in older primary branches and/or terminal in the secondary branches;
 flowers 0.7–0.9 cm diameter, petals white, margins glabrous; southern montane Espírito
 Santo state... Siderasis zorzanellii M.Pell. & Faden (Fig. 1C, 3B–C & 12)
- 3. Leaves petiolate, indumentum bright red to red, hirsute on both sides; bracteoles absent; capsules ellipsoid to fusiform, greenish brown with 3 atro-vinaceous stripes; seeds grey to light grey, testa foveolate, aril hyaline and inconspicuous; coastal Rio de Janeiro state... *Siderasis fuscata* (Lodd.) M.E.Moore (Fig. 1A & 8)
- Leaves sessile to subpetiolate, indumentum rusty to light brown to hyaline, adaxially hispid, abaxially hispid to lanate; bracteoles present; capsules oblongoid to broadly oblongoid to

subglobose, green; seeds medium to dark brown, testa rugose, aril cream-colored, slightly translucent and thick; Bahia and Espírito Santo states... 4

- 4. Rosettes forming flagelliform-shoots; leaves adaxially dark green with a thin white to silvery line along the midvein; flowers pedicellate, petals with white proximal third, anthers purple to bluish purple; capsules with elongated pedicels up to 7.2 mm long; central montane Espírito Santo state... *Siderasis albofasciata* M.Pell. (Fig. 1B & 6)
- Rosettes not forming flagelliform-shoots; leaves adaxially uniformly green to dark green; flowers sessile, petals evenly colored, anthers white; capsules with elongated pedicels shorter than 2.2 mm long... 5
- 5. Aerial stems with elongate internodes; leaves covered with light brown to rusty hairs, midvein shallowly canaliculate; cincinni compact, straight; sepals fleshy, internally lilac to purple, petals rhomboid to broadly obtrullate, ovary densely lanate; southern Bahia state... *Siderasis almeidae* M.Pell. & Faden (Fig. 7)
- Aerial stems with inconspicuous internodes; leaves covered with hyaline hairs, midvein deeply canaliculate; cincinni elongated, tangled; sepals membranous, internally light green, petals obovate to spatulate, ovary hispid; northern lowland Espírito Santo state... Siderasis medusoides M.Pell. & Faden (Fig. 9)

1. Siderasis albofasciata M.Pell., Nordic J. Bot. 35(1): 30. 2017. Figs 1B, 2 & 6

Type. BRAZIL. Espírito Santo: Santa Teresa, Alto do Julião, Fazenda Novo Triunfo, property of Mrs. Florinda, gallery forest with rocky formations, above the dam, fl., fr., 18 Apr 2013, M.O.O. Pellegrini et al. 337 (holotype: RB barcode RB00813532!; isotype: US!).

Description. Herbs ca. 10 cm tall, rhizomatous, terrestrial or rupicolous. Roots with terminal tubers present. Rhizomes buried deep in the ground. Subterraneous stems with internodes moderately elongate, vinaceous, sparsely lanate, hairs light brown to hyaline. Aerial stems short to inconspicuous, unbranched; internodes inconspicuous to weakly elongate, vinaceous, lanate, hairs light brown to hyaline; flagelliform-shoots (ramets) present. Leaves spirally-alternate, forming a rosette at the apex of the aerial stems, sessile to subpetiolate; sheaths 0.7–1.3 cm long, vinaceous, with or without green spots, lanate, hairs light brown to rusty; subpetiole 1–2.7 cm long to inconspicuous, D-shaped in cross section, canaliculate, dark green to vinaceous, hispid, hairs light brown to hyaline; blade $(4.5-4.8-)10-15.8 \times (3.1-3.5-$)4.4–7.2 cm, elliptic to obovate, rarely lanceolate, succulent, adaxially dark green, with a thin white stripe along the midvein, hispid, hairs light brown to hyaline, abaxially vinaceous to atrovinaceous, lanate, hairs light brown, base slightly subcordate to cuneate, vinaceous, margins vinaceous, slightly revolute, apex acute, straight to curved downwards; midvein adaxially inconspicuous, slightly impressed, abaxially prominent, obtuse, secondary veins 3-5, inconspicuous in both faces, becoming more evident when dry. Synflorescence composed of a solitary main florescence with 1–2 coflorescences. Main florescence (inflorescence) reduced to a solitary pedunculate cincinnus, terminal or apparently so; basal bract 11.3-13.4 × 4.8-7.8 mm, triangular, slightly cymbiform, amplexicaulous, vinaceous, hispid, hairs rusty, opaque at the base and margins; inflorescence main axis 2.1–4.4 cm long, vinaceous, densely hispid, hairs rusty to brown; cincinni bract 3.3-6 × 2.2-4.6 mm, triangular, amplexicaulous, vinaceous, hispid, hairs rusty; cincinni (3–)5–8-flowered, peduncles 0.8–1.6 cm long, vinaceous, densely hispid, hairs rusty to brown, reflexed in fruit; bracteoles 2.9–4.4 × 2.8–3.2 mm, broadly ovate to depressed ovate, sessile, revolute, vinaceous to pinkish purple, sparsely hispid, hairs rusty,

apex rounded to truncate. Flowers bisexual, actinomorphic, 2.3–2.8 cm diameter, pedicellate; pedicel 1–7.2 mm long, white to light green, hispid, hairs rusty, reflexed and slightly elongate in fruit; floral buds 0.7–1.6 × 0.3–0.6 cm, ellipsoid to narrowly obovoid, light green, apex obtuse; sepals $0.9-1.1 \times 0.4-0.7$ cm, narrowly ovate to elliptic, membranous, white to light green on both sides, externally sparsely hispid, hairs hyaline to rusty, rusty in fruit, internally glabrous, margin hyaline, apex obtuse, slightly purple; petals $1.3-1.6 \times 1-1.2$ cm, broadly ovate to broadly elliptic, bluish lilac to bluish purple, proximal third white, base cuneate, margin entire, apex obtuse to rounded, sometimes irregularly lacerated; stamens equal, filaments 5–7.1 mm long, straight, white, terminal third purple to bluish purple, anthers $1.5-2.2 \times 1.3-2$ mm, anther sacs purple to bluish purple, connectives quadrangular, purple; ovary $1.5-2 \times 1.5-2$ mm, globose, white, densely hispid, hairs hyaline, style 4.1-6.3 mm long, straight, white, terminal third purple to bluish purple; stigma annular-truncate, purple to bluish purple, papillate. Capsules $1-1.3 \times 0.7-0.9$ cm, subglobose to broadly oblongoid in outline, smooth, green, when mature light brown, hispid, hairs rusty. Seeds 3.3-5.2 × 2.4-2.9 mm, obconic to ellipsoid, medium to dark brown, testa rugose; hilum approximately ½ the length of the seed; embryotega semilateral; aril cream-colored, slightly translucent, thick.

Specimens seen. BRAZIL. Espírito Santo: Fundão, Alto Piaba, cultivado na casa de epífitas do MBML, fl., 13 Sep 1989, W. Boone 1349 (MBML); A.P.A. do Goiapaba-açú, Piabas, propriedade de Albino Casimiro, fl., 8 Nov 2007, A.P. Fontana & K.A. Brahim 2827 (MBML, RB). Santa Teresa, Alto do Julião, propriedade de João Luiz Rodrigues de Souza, fl., 23 Feb 2007, A.P. Fontana & K.A. Brahim 2975 (MBML, RB); Cabeceira do 25 de Julho, Julião, fl., 10 Nov 2007, L. Kollmann et al. 11839 (MBML).

Etymology. The epithet means "white-striped", making reference to the thin and always present, white to silver stripe along the midvein of this species' leaves.

Distribution and habitat. *Siderasis albofasciata* is known exclusively from the municipalities of Santa Teresa and Fundão, state of Espírito Santo (Fig. 2). It occurs in the understory of evergreen forests, in shady areas with shallow and rocky soil, with great leaf-litter accumulation.

Phenology. It blooms from November to February. This species was collected in fruit in April, when mature and immature capsules were seen.

Conservation status. According to Pellegrini (2017), *S. albofasciata* should be considered as Critically Endangered [CR, B1ac(ii, iii, iv)+B2ab(ii, iii, iv)+C2a(i)].

Affinities. Siderasis albofasciata is similar to S. fuscata due to its leaves being of a different color along the midvein of the adaxial side, abaxially vinaceous, and inflorescences covered with rusty hairs. However, S. albofasciata can be readily differentiated by its sessile to subpetiolate leaves covered by hyaline to light brown indumentum (vs. petiolate leaves with bright red to red indumentum, in S. fuscata), a well-defined white stripe along the midvein on the adaxial side of the blade (vs. sometimes blotched silver to metallic light green), main axis of the synflorescence elongate (vs. inconspicuous), bracteoles present (vs. bracteoles absent), cincinni (3–)5–8-flowered [vs. 1–3(–4)-flowered], anthers purple, filaments and style apically purple (vs. androecium and gynoecium completely white), testa brown and rugose (vs. grey to light grey and foveolate), and aril cream-colored, thick and slightly hyaline (vs. aril colorless and inconspicuous). It is also similar to S. almeidae and S. medusoides due to the leaf blades adaxially hispid, abaxially lanate, and presence of bracteoles in the cincinni. Siderasis

albofasciata can be easily differentiated from all the accepted species in the genus by the peculiar coloration pattern in its androecium and gynoecium.

Furthermore, *S. albofasciata* produces unique axillary flagelliform-shoots after its flowering period. Each flagelliform-shoot is homologous to a daughter ramet, consisting of an extremely elongate stem, that may or not develop leaf blades (sometimes the blades are very reduced or absent), and a terminal rosette that roots after it touches the soil. This clonal propagation strategy gives this species a chandelier appearance, similar to many epiphytic bromeliads. This clonal propagation strategy is unique within subtribe Dichorisandrinae (Pellegrini 2017).

2. Siderasis almeidae M.Pell. & Faden, sp. nov. Figs 2 & 7

Diagnosis. Similar to *S. fuscata* due to its rusty indumentum in the leaves, lilac to purple rhomboid petals and white anthers. Also, similar to *S. albofasciata* due to its sessile to subpetiolate leaves, blades adaxially hispid and abaxially lanate, present bracteoles, and purple filaments and style. Nevertheless, *Siderasis almeidae* is peculiar in lacking terminal tubers in the roots, subterraneous stems, and having aerial stems elongate and trailing in the leaf litter, leaves entirely green, fleshy showy sepals, and a densely lanate ovary.

Type. BRAZIL. Bahia: Itamarajú, Fazenda Pau Brasil, caminho para o Monte Pescoço, fl., 19 Nov 2015, M.O.O. Pellegrini & R.F. Almeida 493 (holotype: RB barcode RB01132619!; isotype: US!).

Description. Herbs ca. 20–45 cm tall, terrestrial. Roots thin, fibrous, terminal tubers absent. Rhizomes only covered by leaf litter. Subterraneous stems absent. Aerial stems trailing, only covered by leaf litter, unbranched to little branched, produced directly from the short rhizome; internodes elongate, green, sparsely lanate, becoming glabrous at age, hairs light brown to rusty; flagelliform-shoots (ramets) absent. Leaves spirally-alternate, forming a rosette at the apex of the stems, sessile to subpetiolate; sheaths 1.5–3.2 cm long, green, lanate, margin densely lanate, hairs light brown to rusty; subpetiole 0.8-4.6 cm long to inconspicuous, D-shaped in cross section, canaliculate, green, hispid, margin densely lanate, hairs light brown to rusty; blades 12.6–25.7 × 4–9.1 cm, succulent, elliptic or narrowly obovate to obovate, base cuneate, margins green, slightly revolute, densely lanate, apex acute, curved downwards, adaxially green to dark green, hispid, hairs light brown to rusty, abaxially light green, lanate, light brown to hairs rusty; midvein adaxially inconspicuous to conspicuous, slightly impressed, abaxially prominent, obtuse, secondary veins 6–8 pairs, adaxially conspicuous, slightly impressed, abaxially slightly prominent, becoming more evident adaxially when dry. Synflorescence composed of a solitary main florescence, or with 1–3(–5) coflorescences. Main florescence (inflorescence) reduced to a solitary pedunculate cincinnus; basal bract triangular, 2.4-4.6 × 1.1-2.2 cm, slightly cymbiform, amplexicaulous, green, hispid, hairs rusty, opaque at the base and margins; inflorescence main axis 2.2–8.6 mm long, green, densely hispid, hairs rusty; cincinni bract 1.1– 3.6 × 0.4–1.4 cm, narrowly triangular, amplexicaulous, green, hispid, hairs rusty, apex acuminate; cincinni 5-11-flowered, peduncles 0.7-1.8 cm long, green, densely hispid, hairs rusty, reflexed in fruit; bracteoles $7.4-15.3 \times 3.8-7.4$ mm, broadly triangular, sessile, revolute, green at pre-anthesis, becoming purple at anthesis, hispid to densely hispid, hairs rusty, apex acuminate. Flowers bisexual, actinomorphic, 1.6-2.2 cm diameter, sessile; pedicel inconspicuous at anthesis, elongated in fruit, 0.8–2.2 mm long; floral buds 5.7–7.6 × 4.6–6.5 mm, broadly ellipsoid to broadly obovoid, green, apex obtuse to truncate; sepals 6.8–10.9 × 2.3-5.9 mm, ovate to broadly ovate, fleshy, externally green, densely hispid, hairs rusty,

internally lilac to purple, glabrous, margins hyaline to hyaline lilac, apex acute; petals 8–18.2 \times 6.4–8.1 mm, rhomboid to broadly obtrullate, purple to bluish purple, base cuneate, margin entire, rarely irregularly lacerated, apex obtuse to rounded; stamens equal, filaments 2.4–4.8 mm long, straight, lilac to purple, anthers 0.7–2.3 \times 0.7–1.9 mm, anther sacs white, connectives quadrangular, white; ovary 1.8–2.9 \times 1.2–2.1 mm, broadly oblongoid, white, densely lanate, hairs hyaline, style 3.6–4.8 mm long, straight, purple; stigma annular-truncate, purple, papillate. *Capsules* (immature) 5.7–6.8 \times 5.9–7.2 mm, subglobose to broadly oblongoid in outline, smooth, green, when mature light brown, hispid, hairs rusty. *Seeds* unknown.

Specimens seen (paratypes). BRAZIL. Bahia: Itamarajú, ca. 2 km da Estrada BR-101 ao S de Itamarajú, fl., 5 Apr 1971, T.S. Santos 1559 (CEPEC, K); Fazenda Pau Brasil, ca. 5 km ao NW de Itamarajú, 17° 1' S 39° 33' W, fl., fr., 19 Sep 1978, S.A. Mori et al. 10730 (CEPEC, K, NY, RB, US); fl., 31 Oct 1979, L.A. Mattos Silva & H.S. Brito 692 (CEPEC, K, US). Prado, rod. BA-001, a 61 km ao N de Alcobaça, fl., 19 Mar 1978, S.A. Mori et al. 9739 (CEPEC, RB); km 21 of road from Itamarajú to Prado, forest on N side near logging operation, fl., 9 Feb 1993, J.A. Kallunki & J.R. Pirani 474 (NY, SPF).

Etymology. The epithet honors Brazilian botanist Rafael Felipe de Almeida, a prominent specialist in Malpighiaceae, contributor in the studies of Commelinaceae, husband of the first author, and co-collector of the holotype, for his unmeasurable support in the field and in my research.

Distribution and habitat. *Siderasis almeidae* is confined to the municipalities of Itamarajú and Prado, Bahia (Fig. 2). It occurs in the "mata higrófila" vegetation with emerging rocky formations, in shady and moist areas. In the type locality, the subpopulations were found growing in great accumulations of leaf litter, among dense clusters of Marantaceae. The area is greatly disturbed, and within private property.

Phenology. It was found in bloom from September to April, beginning to fruit in September, but mature fruits are unknown.

Conservation status. Siderasis almeidae has considerably narrow EOO (ca. 180.390 km²) and AOO (ca. 2800 km²). Most of the known collections were made in the type locality, in a small forest patch inside a private cattle farm. None of the known subpopulations is protected by a conservation unit, and the southern region of Bahia has few undisturbed areas of Atlantic Forest, being subjected to ongoing deforestation, cattle breeding, and several crops. The subpopulations of S. almeidae are small to medium-sized (with ca. 20 individuals), but mainly composed of clonal individuals. Thus, following the IUCN (2001) criteria, we suggest S. almeidae to be considered Critically Endangered [CR, A2abcd+B2ab(i, ii, iii, iv, v)+C1].

Affinities. Siderasis almeidae is similar to S. fuscata due to their rusty indumentum covering the leaf blades, inflorescences and sepals, lilac to purple petals, and white anthers. It is also similar to S. albofasciata due to its sessile to subpetiolate leaves, present bracteoles, and purple filaments and style. Furthermore, S. almeidae is similar to S. medusoides, due to their sessile flowers, purple filaments and style, and white anthers.

3. Siderasis fuscata (Lodd.) H.E.Moore, Baileya 4: 28. 1956.

Figs 1A, 2 & 8

Pyrrheima fuscatum (Lodd.) Backer, Handb. Fl. Java 3: 37. 1924.

Pyrrheima loddigesii var. minus (Hassk.) C.B.Clarke in Candolle & Candolle, Monogr. Phan. 3: 272. 1881.

Pyrrheima loddigesii Hassk., Flora 52: 367. 1869, nom. illeg.

Pyrrheima minus Hassk., Flora 52: 368. 1869. Holotype. BRAZIL. Rio de Janeiro. Rio de Janeiro, Corcovado, fl., s.dat., C. Gaudichaud 137 (P barcode P01799823!).

Tradescantia hirsutissima Pohl *ex* Seub., *in* Martius, Fl. bras. 3(1): 254. 1855, pro. syn.

Siderasis acaulis Raf., Fl. Tellur. 3: 67. 1837, nom. illeg.

Tradescantia fuscata Lodd., Bot. Cab. 4: t. 374. 1820. Lectotype (designated by Pellegrini 2017). [illustration] Original parchment plate of "The Botanical Cabinet" at the British Museum Library and later published in Loddiges, Bot. Cab. 4: t. 374. 1820. Epitype (designated by Pellegrini 2017). BRAZIL. Rio de Janeiro. Rio de Janeiro, Floresta da Tijuca, FEEMA, Parque Nacional da Tijuca, fl., fr., 7 Nov 2012, M.O.O. Pellegrini 217 (RB barcode RB01093071!).

Description. Herbs ca. 20–30 cm tall, terrestrial. Roots thin, fibrous, terminal tubers present. Rhizomes buried deep in the ground. Subterraneous stems with internodes elongate, brownish vinaceous to vinaceous with white spots, hirsute, hairs reddish brown. Aerial stems short to inconspicuous, unbranched; internodes weakly to moderately elongate, vinaceous with white spots, hirsute, hairs reddish brown; flagelliform-shoots (ramets) absent. Leaves spirallyalternate, forming a rosette at the apex of the aerial stems, petiolate; sheaths 1–1.5 cm long, hirsute, hairs dark red; petiole 2.7–9.6(–11.4) cm long, terete, canaliculate, C-shaped in cross section, succulent, green to dark green with dense vinaceous spots, spots sometimes covering almost all the petiole, hirsute, hairs red to dark red; blade $(4.8-5.6-)7.8-21.1(-23.6) \times (2-)3-$ 9.6 cm, succulent, elliptic to obovate to broadly obovate, rarely lanceolate, base cuneate, margins green, flat, densely hirsute, apex acute to obtuse or rounded, slightly curved downwards, adaxially dark green, with a silver to light green, blotched silver to metallic light green along the midvein or not, abaxially light green, with dense vinaceous spots or not; midvein conspicuous, adaxially impressed, abaxially prominent, obtuse, secondary veins 3-6 pairs, adaxially conspicuous, impressed, abaxially inconspicuous, becoming more evident on both sides when dry. Synflorescence composed of a solitary main florescence, or with (1-)2-6(-7) coflorescences. Main florescence (inflorescence) reduced to a solitary pedunculate cincinnus; basal bract $1.5-2.2 \times 0.3-1$ cm, triangular, cymbiform, dorsally keeled, light pink, hirsute, hairs rusty to dark red, hyaline at the base and margins, apex acuminate; inflorescence main axis inconspicuous; cincinni bract $0.8-2 \times 0.2-0.9$ cm, triangular, slightly cymbiform, amplexicaulous, pink to vinaceous, hirsute along the midvein, hairs red, base hyaline, margins light brown to golden, glabrous, hyaline, apex acuminate; cincinni 1–3(–4)-flowered, peduncle 1.3–7.4 cm long, light brown, hirsute, hairs red, reflexed in fruit, more rarely also spirallycoiled in fruit; bracteoles absent. Flowers bisexual, actinomorphic, 2-2.8 cm diameter, pedicellate; pedicel 1-5.6 mm long, light brown, hirsute, hairs red, reflexed and elongate in fruit; floral buds $0.8-1.2 \times 0.4-0.6$ cm, ovoid, light brown to light pink, apex acuminate; sepals $0.8-1.4 \times 0.3-0.8$ cm, ovate to triangular, membranous, externally light brown, hirsute, hairs red, internally pink to vinaceous, glabrous, margin hyaline, apex acuminate; petals 1.2-1.6 × 1.2–1.5 cm, rhomboid to broadly obtrullate, rarely orbicular, pale lilac to lilac, proximal third gradually white, base cuneate, margin entire, sometimes irregularly lacerated, glabrous, apex obtuse to rounded, sometimes irregularly lacerated; stamens equal, filaments 3.5–6.3 mm long, straight, white, anthers $1.5-2.1 \times 3-4.2$ mm, anther sacs white, connectives quadrangular,

white; ovary globose, $2.9-3.7 \times 2.3-3.2$ mm, white, densely hirsute, hairs white at base, gradually becoming rusty, then dark red terminally, style 3.1-4.4 mm long, straight, white; stigma annular-truncate, white, papillate. *Capsules* ellipsoid to fusiform in outline, $1.1-1.6 \times 0.5-0.8$ cm, smooth, light greenish brown with minute purple spots near the base and 3 longitudinal atro-vinaceous stripes along the septa, when mature light brown with 3 longitudinal black stripes along the septa, hirsute, hairs red. *Seeds* obconic to ellipsoid, dorsoventrally compressed, ventrally slightly ridged, $2.9-4.4 \times 2.9-3.6$ mm, grey to light grey, testa foveolate, ventral face slightly cleft on the side towards the embryotega; hilum longer than ½ the length of the seed; embryotega semilateral; aril hyaline, inconspicuous.

Specimens examined. BRAZIL. Rio de Janeiro: Niterói, Itaipu, P.E. Serra da Tiririca, Alto Mourão, fl., 15 Jan 1982, V.F. Ferreira et al. 2104 (RB); divisa entre os municípios de Niterói e Maricá, entre Itacoatiara e Itaipuacu, Alto Mourão, fl., 11 Sep 2007, A.A.M. Barros & M. Pontes 3127 (RFFP). Rio de Janeiro, s.loc., fl., s.dat., Mr. Boag s.n. (K barcode K001190685); s.loc., fl., s.dat., Mrs. Graham s.n. (K barcode K001190684); s.loc., fl., 1816-1821, A. Saint-Hilaire A/683 (P); s.loc., fl., fr., 1832, Riedel s.n. (P barcodes P01730357, P01730358); Corcovado, fl., fr., 1831-1833, C. Gaudichaud 337 (P 3 ex); fl., Jul 1837, G. Gardner 847 (K barcode K001190683); Cova da Onça, fl., 15 Aug 1861, A.M. Glaziou 527 (NY, P); fl., 17 Aug 1869, A.M. Glaziou 4285 (P 2 ex); fl., Jul 1878, J. Miers 3534 (K, P); fl., fr., 5 Dec 1889, P. Schwacke 6699 (RB); fl., 5 May 1892, A. Ducke s.n. (RB 64); Tijuca, rio Trapicheiros (Fábrica da Cheetos), fl., Nov 1925, J.S. Kuhlmann s.n. (RB 19282, U barcode U1210766); fl., fr., 4 Mar 1943, A.P. Duarte & C.T. Rizzini 8 (RB); fl., 6 Nov 1944, P. Occhioni 50 (RB); Parque Natural da Tijuca, Matas do Pai Ricardo, fl., 29 Oct 1975, D.S. Araújo et al. 883 (GUA); fl., 30 Oct 2013, M.O.O. Pellegrini 404 (RB); fl., 15 Nov 2013, L.S.B. Calazans & R.T. Valadares 234 (RB); road to Vista Chinesa, next to the Biological Station, fl., 18 Aug 1960, C. Angeli 230 (GUA); Setor das Paineiras, next to Pedra do Beijo, fl., 15 Nov 1965, J.P.P. Carauta 286 (GUA); road to Vista Chinesa, fl., fr., 31 Oct 1969, J.P.P. Carauta 923 (GUA); Santa Cruz, fl., 6 Jul 1972, E. Lagasa s.n. (HB 71875); Pedra da Gávea, fl., 13 Jul 1966, D. Sucre 1304c (HB, RB); Alto da Boa Vista, Morro Queimado, next to the FEEMA building, fl., 26 Oct 2000, F. Pinheiro et al. 557 (HB); Estrada da Guanabara, Parque Lage, 25 Jan 1968, fl., D. Sucre 2161 (RB); Reserva Florestal do Jardim Botânico, fl., 19 Jan 1969, D. Sucre & P.J.J. Braga 4472 (RB); fl., 22 Dec 1971, D. Sucre 8152 (RB); Matas da Lagoinha, fl., 18 September 1946, P. Occhioni 692 (RB); fl., 6 Mar 1978, V.F. Ferreira et al. 256 (RB); fl., 11 Nov 1946, P. Occhioni 781 (RFA); brook trail between Paineiras and Jardim Botânico, fl., 4 Dec 1928, L.B. Smith s.n. (US barcode US1540545).

Specimens examined (cultivated). ENGLAND. Greater London: London, Royal Botanic Gardens, Kew, cultivated at the Nepenthes House, Kew, fl., 1908, s. leg. s.n. (K); fl., fr., Jun 1879, N.L. Brown s.n. (K); fl., 1967, Mason 458/61 (K); fl., 9 Jul 1974, Jodrell Laboratory s.n. (K 458-61-45801).

Etymology. The epithet "fuscata" means dark-colored, in allusion to the red to bright red hairs that cover almost the entire plant, in opposition to the normally hyaline hairs in most Commelinaceae.

Distribution and habitat. *Siderasis fuscata* is endemic to the municipalities of Rio de Janeiro (with several localities inside Floresta da Tijuca) and Niterói (with just one locality, Alto Mourão), in the Rio de Janeiro state (Fig. 2). It occurs in the vegetation on hillsides (mata de encosta) near the littoral, in shady areas with shallow and rocky soil.

Phenology. It blooms from August to May and fruits from January to May, although fructification seems to be an uncommon event since few fruiting specimens were seen or collected.

Common name. "violeta-silvestre", "orelha-de-urso", "pelo-de-urso", "trapoeraba-peluda", "brown spiderwort", "bear ears".

Conservation status. Siderasis fuscata is one of the few Commelinaceae included in the Lista da Flora Brasileira Ameaçada de Extinção (List of the Threatened Brazilian Flora; Fundação Biodiversitas 2009) and in the Lista Oficial das Espécies da Flora Brasileira Ameaçadas de Extinção (Official List of the Threatened Species of the Brazilian Flora; MMA 2008), at both lists classified as Data Deficient (DD). In the recently published Commelinaceae chapter of the Livro Vermelho da Flora do Brasil (Red Book of the Brazilian Flora; Aona-Pinheiro et al. 2013), S. fuscata is classified as Endangered (EN) by the authors, based on existing published data.

The subpopulation from Niterói is disjunct from the others in Rio de Janeiro, due to the urban area of both cities. It possesses a considerably small EOO (ca. 7000 km²), with the population being severely fragmented. Despite all the extant subpopulations being inside conservation units (i.e. Parque Nacional da Tijuca and Parque Estadual Serra da Tiririca), they are considerably small, composed mainly of clonal individuals, with no more than 30 mature individuals. Only a small number of fertile individuals can be found during the flowering season in each population, and very few fruits are produced. All these areas are extremely susceptible to real-estate development, deforestation, and have many invasive species, with areas like Parque Estadual Serra da Tiririca being especially affected by human-related forest fires. The subpopulations from Pedra da Gávea and Corcovado are probably extinct, or nearly so, since no recent collection in either areas is known by the authors. A total of 250 mature individuals is estimated for the overall population, based on our field observations. Added to the above factors, S. fuscata is appreciated as an ornamental plant all over the world due to its exotic foliage and beautiful flowers, so the few known extant subpopulations are also a target of illegal collection for exotic plant growers from all over the world. Thus, following the IUCN criteria (2001),suggest S. considered Critically Endangered we fuscata be [CR, A2abcde+B1ab(i,ii,iii,iv,v)+B2a(i,ii)+C2a(i)+D2].

Affinities. Siderasis fuscata is similar to S. albofasciata in their variegated leaf blades, and similar to S. almeidae and S. medusoides in their white anthers. Nevertheless, it can be readily distinguished from all species of Siderasis by its petiolate leaves, red to bright red indumentum covering almost the entire plant (vs. sessile to subsessile leaves, light brown to hyaline indumentum), cincinni without bracteoles (vs. bracteoles present), acuminate flower buds and sepals (vs. obtuse to rounded), androecium and gynoecium completely white (vs. androecium and gynoecium partially bluish, lilac or purple), ovary and capsules hirsute (vs. velutine, hispid or lanate), seeds with light grey to grey and foveolate testa (vs. medium to dark brown and rugose or scrobiculate testa), and hyaline and inconspicuous aril (vs. aril cream-colored, slightly translucent and thick).

4. Siderasis medusoides M.Pell. & Faden, sp. nov. Figs 2 & 9

Diagnosis. Similar to *S. almeidae* due to its sessile to subpetiolate, entirely green leaves, present bracteoles, sessile flowers, purple filaments and style combined with white anthers, and oblongoid to broadly oblongoid capsules. *Siderasis medusoides* is distinct due to its membranous leaves, elongate and tangled cincinni, small flowers, and purple to dark blue and elliptic to narrowly obovate or spatulate petals.

Type. BRAZIL. Espírito Santo: Marilândia, perímetro urbano, na Estrada para São Pedro, fragment de floresta junto a uma serraria de madeira, a ca. 100 m do portão da serraria, em encosta de morro, 19° 24' 30.5" S 40° 32' 1.8" W, fl., fr., 20 Jan 2011, P. Fiaschi et al. 3489 (holotype: SPF barcode SPF200900!; isotype: MBML barcode MBML42135!).

Description. Herbs ca. 5–10 cm tall, rhizomatous, terrestrial. Roots with terminal tubers present. Rhizomes shallowly buried in the ground. Subterraneous stems short to inconspicuous. unbranched, dark green to vinaceous to brown, sparsely lanate, hairs light brown to hyaline. Aerial stems short to inconspicuous, unbranched; internodes inconspicuous to weakly elongate, green, lanate, hairs light brown to hyaline; flagelliform-shoots (ramets) absent. Leaves spirallyalternate, forming a rosette; sheaths 0.8–1.4 cm long, hispid, hairs hyaline to light brown; subpetiole 0.4-4.6 cm long to inconspicuous, D-shaped in cross section, canaliculate, dark green to vinaceous, hispid, hairs light brown to hyaline; blades 10–24.4 × 5.9–11.2 cm, elliptic to broadly elliptic, membranous, adaxially dark green, hispid, hairs light brown to hyaline, abaxially green to vinaceous, hispid to lanate, hairs light brown to hyaline, base cuneate, margins green, revolute, lanate, hairs light brown to hyaline, apex obtuse, rarely acute, straight; midvein conspicuous, adaxially impressed, abaxially prominent, acute, secondary veins 2–7 pairs, inconspicuous on both sides, becoming more conspicuous on both sides when dry. Synflorescence composed of a solitary main florescence, or with 1–15 coflorescences. Main florescence (inflorescence) reduced to a solitary pedunculate cincinnus; basal bract 7.6–10.4 × 4.6–6.2 cm, broadly elliptic to broadly ovate, slightly cymbiform, amplexicaulous, green, sparsely hispid, hairs rusty, opaque at the base and margins; inflorescence main axis 2.3-4.8 cm long, green, densely hispid, hairs rusty; cincinni bract ovate, amplexicaulous, 2.4–4.9 × 1.5– 4 mm, green, hispid, hairs rusty, apex acute; cincinni (5–)8–26-flowered, peduncles 5.6–12.7 mm long, green, densely hispid, hairs rusty, reflexed in fruit; bracteoles $0.9-1.5 \times 0.8-1.3$ mm, broadly triangular, sessile, flat, green, hispid, hairs rusty, apex obtuse. Flowers bisexual, actinomorphic, 0.9–1.2 cm diameter, sessile; pedicel inconspicuous, elongate in fruit, 1–2.2 mm long, green, hispid, hairs light brown to rusty; floral buds 2.6–5.4 × 2–3.7 mm, broadly ellipsoid to broadly obovoid, light green, apex obtuse to truncate; sepals 3.7–6.7 × 2.2–3.6 mm, elliptic to obovate, the uppermost external and broader than the others, membranous, externally light green to green, sparsely hispid, hairs light brown to rusty, internally light green, purple towards the apex, glabrous, margin hyaline, apex obtuse; petals 4.4–10.1 × 1.9–6.7 mm, elliptic to narrowly obovate to spatulate, the lowermost usually broader than the others, bluish purple to dark blue, margin entire to irregularly lacerated, apex obtuse to round, irregularly lacerated; stamens 6, equal, filaments 2.6–3.4 mm long, bluish purple to dark purple, anthers 0.8–1 × 1– 1.3 mm, anther sacs semicircular, divergent, white, connectives quadrangular, white; ovary broadly oblongoid, $1.2-1.9 \times 1-1.5$ mm, white, densely hispid, hairs white; style 1.3-4.7 mm long, straight, bluish purple to dark blue, lilac at the terminal end; stigma annular-truncate, lilac to white, papillate. Capsules 6.8–9.4 × 6.7–7.8 mm, oblongoid to broadly oblongoid, smooth, green, hispid, hairs rusty. Seeds 3.6-4.1 × 2.6-3.2 mm, obconic to ellipsoid, medium to dark

brown, testa rugose; hilum longer than ½ the length of the seed; embryotega semilateral; aril cream-colored, slightly translucent, thick.

Specimens seen (paratypes). BRAZIL. Espírito Santo: Marilândia, rodovia Marilândia-Rio Bananal, ca. 1 km N de Marilândia, remanescente de floresta junto a Cerâmica Floresta, fl., 6 Dec 1994, J.R. Pirani et al. 3421 (NY, SPF); Liberdade, propriedade de Deoclécio Lorenccini, 19° 21' 7" S 40° 30' 51" W, fl., fr., 22 Mar 2007, V. Demuner et al. 3429 (HERB, MBML); propriedade de Sônia e Reinaldo Bautz, 19° 20' 8" S 40° 32' 8" W, fl., 10 Dec 2007, V. Demuner et al. 4682 (MBML). Santa Leopoldina, Colina Verde (Morro do Agudo), propriedade de Israel Elias Ramos, trilha da casa, 20° 6' 12" S 40° 26' 34" W, fl fr., 13 Mar 2007, V. Demuner et al. 3118 (MBML).

Etymology. The epithet alludes to the extremely elongated cincinni, common in mature individuals of this species, due to their resemblance to the snakes that composed the hair of Medusa, one of the three Gorgon sisters from Greek mythology.

Distribution and habitat. *Siderasis medusoides* is known from the municipalities of Marilândia and Santa Leopoldina, in the state of Espírito Santo (Fig. 2). It grows in lowland Atlantic Forest, in shady and moist areas with great leaf litter accumulation, 90–550 m above the sea level.

Phenology. It blooms from December to March and fruits between January and March.

Conservation status. *Siderasis medusoides* possesses narrow EOO (ca. 11037 km²) and AOO (ca. 2000 km²), and based solely on distribution data should be treated as Endangered (EN). Nonetheless, it is known from only five collections in three different localities. They were made within urban areas, and these localities have suffered greatly with direct anthropic influence and deforestation in recent years. We have made several attempts to recollect *S. medusoides*, but they were all unsuccessful. Thus, we suggest that *S. medusoides* be considered Critically Endangered [CR, A2abcd+B2ab(i, ii, iii, iv)+C1+C2b+D2].

Affinities. Siderasis medusoides is similar to S. almeidae and S. albofasciata, due to their sessile to subpetiolate leaves, inflorescence with elongate main axis, bracteolate cincinni, sessile flowers, and purple filaments and style combined with white anthers. Nevertheless, it can be easily differentiated from S. almeidae by its inconspicuous subterraneous and aerial stems (vs. subterraneous stems absent and aerial stems elongate, in S. almeidae), membranous leaves appressed against the soil (vs. succulent and ascending), membranous and internally light green sepals (vs. fleshy and internally lilac to purple), narrowly obovate to spatulate petals (vs. rhomboid to broadly obtrullate), and hispid ovary (vs. lanate). It can be differentiated from S. albofasciata by lacking flagelliform-shoots (vs. flagelliform-shoots produced after the fertile period, in S. albofasciata), concolorous and membranous leaves (vs. adaxially variegated, abaxially vinaceous, succulent leaves), petals entirely purple to bluish purple (vs. petals with white basal third), and white anthers (vs. anthers purple to bluish purple). Siderasis medusoides is peculiar due to its membranous leaves appressed to the soil, tangled and elongate cincinni, small flowers, and narrow petals.

5. Siderasis spectabilis M.Pell. & Faden, sp. nov. Figs 2, 10 & 11

Diagnosis. Very distinctive due to its vining habit, distichously-alternate leaves, blades asymmetric at base, main florescence a many-branched thyrse, with alternate cincinni, flowers zygomorphic, bisexual or staminate, stamens unequal, curved upwards, sigmoid filaments, and capsules globose and shallowly foveolate. It can be differentiated from *S. zorzanellii* by its membranous and velutine leaves, inflorescences always terminal in the secondary branches, petals dark mauve to vinaceous, rarely light pink or white, with margins ciliate with non-moniliform hairs.

Type. Brazil. Rio de Janeiro: Santa Maria Madalena, morro atrás do Horto Santos Lima (sede do Parque Estadual do Desengano), fl., 19 Jan 1957, L.E. Mello-Filho 1172 (holotype: R barcode R000103716!; isotypes: RB!, SPF!, US!).

Description. Vines ca. 0.5–3 m tall, terrestrial. Roots unknown. Rhizomes unknown. Subterraneous stems unknown. Aerial stems twining, primary stem indefinite, densely branched, internodes elongate, 2.2–6.5 cm long, green, minutely velutine on both sides, hairs hyaline to light brown; secondary branches definite, unbranched, ca. 17–25 cm long, internodes elongate, 1.1–2.3 cm long, green, minutely velutine on both sides, hairs hyaline to light brown. Leaves distichously-alternate, evenly distributed along the secondary branches, sessile; sheaths 0.7–2 cm long, green to vinaceous, minutely velutine, with a line of eglandular hairs opposite the leaf above, margins setose, hairs hyaline to light brown; subpetiole 1.1–3.3 mm long to inconspicuous, C-shaped in section, canaliculate, membranous, green to dark green, minutely velutine on both sides, hairs hyaline to light brown; blades $4.6-11.8 \times 1.6-2.5$ cm, linear elliptic or linear lanceolate or linear oblong, membranous, adaxially dark green to green, becoming dark brown when dry, abaxially light green to green, becoming greyish green to olive-green when dry, minutely velutine on both sides, hairs hyaline to light brown, base slightly asymmetric to asymmetric, cuneate to narrowly rounded, margins vinaceous, flat, minutely velutine, hairs hyaline to light brown, apex acuminate to caudate, straight; midvein conspicuous, impressed adaxially, prominent, obtuse abaxially, secondary veins (3–)4–5 pairs, slightly conspicuous on both sides, becoming more evident when dry. Synflorescence composed of a solitary main florescence. Main florescence (inflorescence) a pedunculate, many-branched thyrse, with alternate cincinni, terminal in the secondary branches; basal bract leaf-like, amplexicaulous to sheathing, sheaths 1.2–4.8 mm long, minutely velutine, margins of the sheaths densely setose, blades $3.9-6.7 \times 0.5-1.1$ cm, green to dark green, minutely velutine on both sides, base opaque, margins minutely velutine, apex acuminate to caudate, hairs hyaline to light brown; peduncle 1–1.3 cm long, green, minutely velutine, hairs hyaline to light brown; cincinni bract 3.2–10.6 × 0.8–1.2 mm, linear triangular, mauve to vinaceous, minutely velutine on both sides, base truncate, margin sparsely setose, apex acuminate to caudate, hairs hyaline to light brown; cincinni 14-17 per thyrse, 3-8-flowered, peduncles 1.4-7.2 mm long, light green to pink, minutely velutine, hairs hyaline to light brown, erect in fruit; bracteoles 1.8–2.2 × 0.8–1.2 mm, ovate to broadly ovate, flat, cream-colored densely covered with vinaceous to pinkish purple spots to completely mauve to vinaceous, minutely velutine on both sides or only along the midvein, base rounded, margin hyaline, sparsely ciliate, apex hyaline, acute to obtuse, hairs hyaline to light brown. Flowers bisexual or staminate, zygomorphic, 1–1.3 cm diameter, pedicellate; pedicel 0.5–0.7 mm long, medium to dark mauve, sparsely minutely velutine, hairs hyaline to light brown, patent and slightly elongate in fruit; floral buds $3.5-4.4 \times 2.4-3.8$ mm, broadly ellipsoid to broadly obovoid, vinaceous to dark vinaceous, apex truncate; sepals 4.8-5.2 × 2–2.6 mm, narrowly ovate to elliptic, cymbiform, unequal, the uppermost external,

broader and shorter than the others, fleshy, vinaceous to dark vinaceous, externally sparsely minutely velutine, hairs hyaline to light brown, internally glabrous, margin hyaline, glabrous to sparsely minutely velutine, hairs hyaline, apex obtuse, slightly purple; petals 5.1– 6.3×2.8 –3.6 mm, trullate to obovate, the lowermost narrower than the others, dark mauve to vinaceous, rarely light pink or white, base cuneate, margin entire, ciliate with dark mauve, eglandular, non-moniliform, uniseriate hairs, apex obtuse to rounded; stamens 6, unequal, the anterior longer than the posterior ones, curved upwards, filaments 1.8–4.6 mm long, sigmoid, white, terminal third dark mauve, anthers 1.2– 1.4×0.8 –1 mm, anther sacs dark mauve, connectives quadrangular in the shorter stamens and rectangular in the longer, dark mauve to purple; ovary 1.7– 1.9×1 –1.4 mm, ellipsoid to broadly ellipsoid, white, velutine, hairs hyaline, style 3.2–4 mm long, curved upward at the apex, white to pink, terminal third dark mauve; stigma annular-capitate, mauve to pink, papillate. *Capsules* and *Seeds* unknown.

Specimens seen (paratypes). BRAZIL. Rio de Janeiro: Santa Maria Madalena, morro atrás do Horto Santos Lima (sede do Parque Estadual do Desengano), fl., 19 Jan 1957, L.E. Mello-Filho 1162 (R, RB, US); fl., 19 Jan 1957, L.E. Mello-Filho 1171 (R, RB, US).

Etymology. The epithet means "admirable, remarkable, spectacular", in allusion to its distinctive growth form, small flowers with a peculiar coloration, and the unique petal margins ciliate with non-moniliform hairs.

Distribution and habitat. *Siderasis spectabilis* is confined to the type locality, in the native vegetation of the Horto Santos Lima (currently the headquarters of the Desengano State Park), in Santa Maria Madalena, state of Rio de Janeiro (Fig. 2). Nothing is known about this species habitat, since the original labels give no information on the area and all field expeditions to recollect this plant have been unsuccessful.

Phenology. Since all known collections were done on the same day, *S. spectabilis* is only known to bloom during January. Fruits and seeds are unknown for this species.

Conservation status. Due to the complete lack of information on the distribution, ecology and lack of any collections aside from the type specimens, according to the criteria proposed by IUCN (2001), *S. spectabilis* should be considered Data Deficient (DD), until new collections and data become available.

Affinities. Siderasis spectabilis is morphologically closely related to S. zorzanellii, but S. spectabilis can be easily differentiated due to its inflorescences being always terminal in the secondary branches (vs. axillary in the primary branches or terminal in the secondary branches, in S. zorzanellii), and petals dark mauve to vinaceous, rarely light pink or white, and margins ciliate with non-moniliform hairs (vs. white and glabrous margins). All studied specimens were in excellent condition, and color of most organs could be easily described. Regarding color pattern in the androecium and gynoecium, S. spectabilis is similar to S. albofasciata. These are the only two species in the genus to present the upper third of filaments and style, and the anthers in the same color as the petals, contrasting greatly with the white base of filaments and style, and the white ovary of other species. Nevertheless, both species can be easily differentiated using vegetative or reproductive characters. One specimen (L.E. Mello-Filho 1171) is peculiar in being the only specimen with light-colored flowers. In the label, it is described by the collector as possessing white flowers. Nonetheless, while analyzing the duplicates available at R, RB, SPF and US, we noticed that a few flowers possessed pale pink pigment (particularly noticeable in the petals and stamens). We believe that these specimens

might represent albino or semialbino individuals, and thus merit no taxonomic status, especially since they were collected at the same place and date as the remaining dark-flowered specimens.

Aona (2008), in her unpublished Ph.D. thesis, lists one of the paratypes of *S. spectabilis* under *Dichorisandra incurva* Mart. This is justified by her due to the specimens climbing habit, decumbent apical branches, distichously-alternate and sessile leaves, inflorescence composed of a pedunculate, many-branched thyrse, with alternate cincinni, and "white" [sic] flowers. Nevertheless, *S. spectabilis* can be easily differentiated by its erect inflorescences (*vs.* pendant to curved downwards, hence the name, in *D. incurva*), flower buds broadly ellipsoid to broadly obovoid, with truncate apex (*vs.* ellipsoid, with acute apex), sepals fleshy (*vs.* membranous), petals dark mauve to vinaceous, rarely light pink or white, with margins ciliate with nonmoniliform hairs (*vs.* white with glabrous margins), stamens 6, anthers dorsifixed, 3 to 4 times shorter than the filaments, dehiscent by extrorse slits, and anther sacs divergent, semicircular, and expanded connectives (*vs.* stamens 6 or 5 + the upper one modified into a staminode, anthers basifixed, 3 to 4 times longer than the filaments, dehiscent by introrse slits, but functionally poricidal, anthers sacs parallel, elongate, and inconspicuous connectives). All these floral characters can be easily observed with the dissection of mature flower buds in herbarium specimens. The floral morphology of *D. incurva* is illustrated in Fig. 1I.

6. Siderasis zorzanellii M.Pell. & Faden, sp. nov.

Figs 1A, 2, 3B-C & 12

Diagnosis. Similar to *S. spectabilis* due to its vining habit, distichously-alternate leaves, blades asymmetric at base, main florescence a many-branched thyrse, with alternate cincinni, flowers bisexual or staminate, zygomorphic, stamens unequal, curved upwards and sigmoid filaments. It can be differentiated from by its chartaceous and sparsely velutine leaves, inflorescences axillary in the primary branches or terminal in the secondary branches, and petals white with glabrous margins.

Type. Brazil. Espírito Santo: Iúna, Serra do Valentim, ao lado do transecto 1, 20.4989° S 41.4725° W, fl., 27 Mar 2014, J.P.F. Zorzanelli 969 (holotype: RB!; isotype: VIES!).

Description. Vines ca. 0.5–3 m tall, terrestrial. Roots thin, fibrous, terminal tubers present, fusiform. Rhizomes buried deep in the ground. Subterraneous stems inconspicuous. Aerial stems twining, primary stem indefinite, densely branched, internodes elongate, 4.3–10.6 cm long, green, minutely velutine on both sides, hairs hyaline to light brown; secondary branches definite, unbranched, (6.4-8-)15-34 cm long, internodes elongate, 2-2.3 cm long, green, minutely velutine on both sides, hairs hyaline to light brown. Leaves distichously-alternate, evenly distributed along the secondary branches, sessile; sheaths 2-2.7 cm long, green to brown, minutely velutine, with a line of eglandular hairs opposite the leaf above, margins setose to densely setose, hairs hyaline to light brown; subpetiole 2.9–3.5 mm long to inconspicuous, C-shaped in section, canaliculate, membranous, green to dark green, minutely velutine on both sides, hairs hyaline to light brown; blades 5.1–12.7 × 1.1–2.8 cm, linear elliptic to linear lanceolate, chartaceous, adaxially dark green to green, becoming dark brown when dry, abaxially light green to green, becoming greyish green to olive-green when dry, sparsely minutely velutine on both sides, hairs hyaline to light brown, base slightly asymmetric to asymmetric, cuneate to narrowly rounded, margins green to vinaceous, flat, glabrous, apex acuminate to caudate, straight; midvein conspicuous, impressed adaxially, prominent, obtuse abaxially, secondary veins 2-3 pairs, inconspicuous on both sides, becoming more evident when dry. Synflorescence composed of a solitary main florescence. Main florescence

(inflorescence) a pedunculate, many-branched thyrse, with alternate cincinni, axillary in the primary branches or terminal in the secondary branches; basal bract reduced, rarely leaf-like, sessile, 1.7–2 × 0.2–0.4 cm, green, minutely velutine on both sides, base opaque, margins minutely velutine, apex caudate, hairs hyaline; peduncle 0.9–1.2 cm long, light green to green, minutely velutine hairs hyaline; cincinni bract linear triangular, 3–15.3 × 1.4–1.8 mm, green to brown, minutely velutine on both sides, base truncate, margin velutine, setose only at base, apex acuminate to caudate, hairs hyaline; cincinni 14–19 per thyrse, (1–)2–5-flowered, peduncles 1.2–5.3 mm long, white to pink, minutely velutine, hairs hyaline, erect in fruit; bracteoles ovate to broadly ovate, flat, $1-1.7 \times 0.8-1.3$ mm, vinaceous to brown, minutely velutine, base rounded, margin hyaline, ciliate, apex hyaline, acute to obtuse, hairs hyaline. Flowers bisexual or staminate, zygomorphic, 0.7–0.9 cm diameter, pedicellate; pedicel 1.2–2.8 mm long, white, minutely velutine, hairs hyaline, patent and slightly elongate in fruit; floral buds 3.6–4.9 × 2.2– 4.1 mm, broadly obovoid to subglobose, white, apex truncate to rounded, green; sepals $3.6-4 \times 10^{-4}$ 1.5–2.1 mm, narrowly ovate to elliptic, cymbiform, unequal, the uppermost external, broader and shorter than the others, fleshy, white, externally minutely velutine, hairs hyaline, internally glabrous, margin hyaline, glabrous to sparsely velutine, hairs hyaline, apex obtuse, green; petals $3.7-4.5 \times 2.7-3.4$ mm, trullate to obovate, the lowermost narrower than the others, white, base cuneate, margin entire, glabrous, apex obtuse to rounded; stamens 6, unequal, the anterior longer than the posterior, curved upwards, filaments 1.3–4.2 mm long, sigmoid, white, anthers $0.7-0.9 \times 0.7-1$ mm, anther sacs white, connectives quadrangular in the shorter stamens and rectangular in the longer, white; ovary $1.5-1.7 \times 1.1-1.2$ mm, ellipsoid, white, velutine, hairs hyaline, style 2.7–3.2 mm long, curved upward at the apex, white; stigma annular-capitate, papillate, white. Capsules 0.9–1.3 × 0.8–1.2 cm, subglobose to globose, green, sparsely reticulate, sparsely velutine, hairs hyaline. Seeds 3.6–3.9 × 2.9–3.2 mm, obconic to ellipsoid, medium to dark brown, testa scrobiculate; hilum longer than ½ the length of the seed; embryotega semidorsal; aril cream-colored, slightly translucent, thick.

Specimens seen (paratypes). BRAZIL. Espírito Santo: Iúna, Serra do Valentim, trilha do Sr. Aristides, próximo à borda da mata, fl., 27 Jan 2012, J.P.F. Zorzanelli et al. 328 (VIES); floresta do Sr. Aristides, próximo à borda da vegetação, antes da primeira subida íngreme da trilha, fl., 15 Dec 2015, J.P.F. Zorzanelli 1391 (RB, VIES); floresta do Sr. Aristides, próximo ao início do zigue-zague da trilha, 20° 21' 56" S 41° 28' 26" W, fr., 31 Mar 2016, J.P.F. Zorzanelli 1505 (RB, VIES).

Etymology. The epithet honors the collector of the type specimens, João Paulo Fernandes Zorzanelli, Brazilian botanist and dear friend of the authors. JPFZ is an active and prominent collector in the state of Espírito Santo, with collections currently focused on Serra do Valentim, the type locality of *S. zorzanellii*.

Distribution and habitat. Siderasis zorzanellii is confined to the municipality of Iúna, Espírito Santo (Fig. 2). It occurs in the "Floresta Ombrófila Densa Montana" vegetation, at 1200–1350 m above the sea level, generally near disturbed sites, being less frequent in well-preserved areas. This could be related to its climbing habit and the need of more sunlight exposure then the rosette species of the genus. This pattern is common in other liana and vine groups, such as Bignoniaceae, Malpighiaceae, and Sapindaceae (Acevedo-Rodríguez, pers. comm.), especially evident in big families such as Asteraceae, where the primarily climbing genus Mikania Willd. is almost exclusively found at the edge of forests, along trails, and in disturbed areas (Oliveira 2015).

Phenology. It was found in bloom from December to March and in fruit in March.

Conservation status. *Siderasis zorzanellii* is very narrowly distributed, with an EOO of ca. 7.779 km² and an AOO of ca. 300 km². The subpopulations are small, with no more than 10 mature individuals each. Unlike for the rosette species in the genus, it is still uncertain if the two climbing species reproduce vegetatively through cloning. Flowering seems to be frequent, although fruits have been collected only once. Thus, following the recommendations from IUCN (2001), *S. zorzanellii* should be considered Critically Endangered [CR, A2abde+B1ab(iii, iv, v)+ B2ab(iii, iv, v)+C2a(ii)+D1+D2].

Affinities. Siderasis zorzanellii is morphologically similar to S. spectabilis. Nevertheless, both species can be differentiated based on consistency of the leaf blades (chartaceous in S. zorzanellii vs. membranous in S. spectabilis), density of their pubescence (sparsely minutely velutine vs. minutely velutine), position of the inflorescences (terminal in the secondary branches or axillary in the older nodes of the primary branches vs. exclusively terminal in the primary branches), floral morphology (flowers 0.7–0.9 cm diameter, petals white, margins glabrous vs. flowers 1–1.3 cm diameter, petals dark mauve to vinaceous, rarely light pink or white, margins ciliate with non-moniliform hairs), and by their disjunct distribution (southern montane Espírito Santo state vs. northern montane Rio de Janeiro state).

Final remarks

The present work adds four new species to Siderasis, along with the addition of new morphological characters that help clarify the circumscription of the group. Siderasis Raf. emend. M.Pell. & Faden may be uniquely characterized as comprising small perennial rosette herbs or robust perennial vines, with shoots determinate or indeterminate, leaves spirally- or distichously-alternate. The inflorescences are terminal or axillary, either a many-branched thyrse with alternate cincinni or reduced to a solitary cincinnus, cincinni always severalflowered. The flowers are chasmogamous, bisexual or male, actinomorphic or zygomorphic, and petals with glabrous margins or ciliated with non-moniliform hairs. The androecium is composed of 6 fertile stamens, filaments straight or sigmoid, anthers dorsifixed and extrorsely rimose, anther sacs semicircular, divergent, connectives expanded and quadrangular. In the gynoecium, the stigma is annular-truncate or annular-capitate, marginally papillate with unicellular papillae restricted to the margin of the stigmatic regions. Also, similar to Dichorisandra, the capsules are thick-walled, and the seeds are arillate, biseriate to partially uniseriate, with semidorsal or semilateral embryotega, and a C-shaped hilum. All species accepted by us are easily diagnosed by a unique and constant combination of morphological character states. Furthermore, each species can be easily separated based on their geographical distribution, since they are microendemics, with non-overlapping distribution areas (Fig. 2).

As indicated by several systematic studies in Commelinaceae (Evans et al. 2000, 2003; Hardy 2001; Wade et al. 2006; Zuiderveen et al. 2011; Hertweck and Pires 2014) and by the morphological evidence presented here and by Pellegrini (2017), the need to recircumscribe subtribe Dichorisandrinae is pressing. Aside from the cytological character of x=19 large chromosomes described by Jones and Jopling (1972) and hypothesized by Faden and Hunt (1991), no macro or micromorphological synapomorphies were found so far for subtribe Dichorisandrinae in its current circumscription. On the other hand, if subtribe Dichorisandrinae is recircumscribed to exclusively contain *Dichorisandra* and *Siderasis*, Dichorisandrinae s.s. can be easily morphologically characterized by its thick-walled capsules, the biseriate to partially uniseriate arillate seeds, semidorsal to semilateral embryotega, and C-shaped hilum. The lineage composed by *Geogenanthus*(*Cochliostema+Plowmanianthus*) needs to be formally recognized as a subtribe, and can be easily circumscribed by its petals with marginally fringed

with moniliform hairs, and anthers sacs curved to spirally-coiled and appressed to each other. Phylogenetic studies using both nuclear and chloroplast sequences seem promising in elucidating phylogenetic incongruences in Commelinaceae (e.g. Burns et al. 2011). However, most phylogenetic in the family so far completely disregard morphological data, with the exception of Evans et al. (2000, 2003). Studies focusing on the systematics and recircumscription of Dichorisandrinae are currently being conducted, combining morphological and molecular data (Pellegrini et al., in prep.), and should shed some light on the evolution of the reproductive biology in the family.

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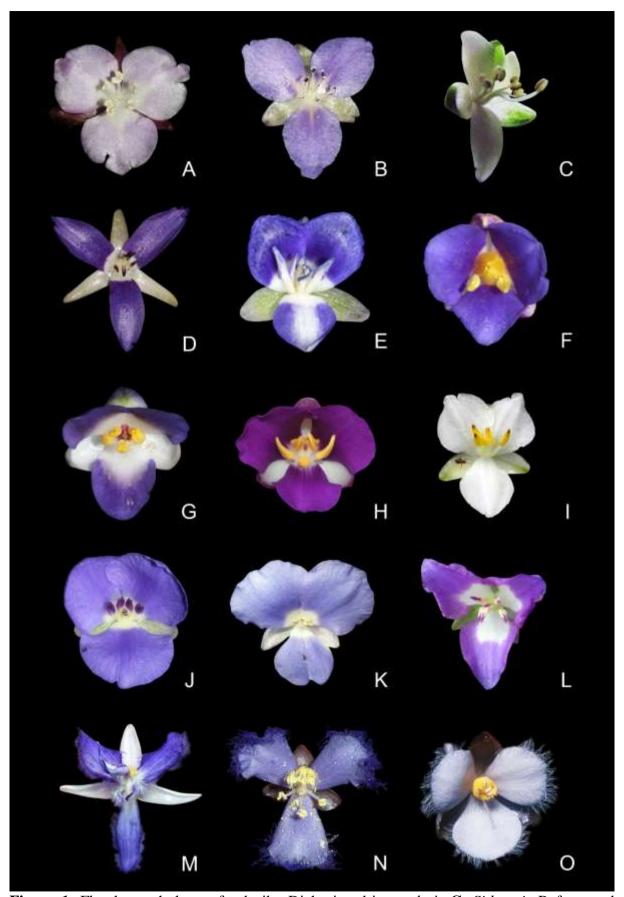


Figure 1. Floral morphology of subtribe Dichorisandrinae *s.l.* **A–C,** *Siderasis* Raf. emend M.Pell. & Faden: **A,** *S. fuscata* (Lodd.) H.E.Moore; **B,** *S. albofasciata* M.Pell.; **C,** *S. zorzanellii*

M.Pell. & Faden. **D–L**, *Dichorisandra* J.C.Mikan: **D**, *D. acaulis* Cogn.; **E**, *D. hexandra* (Aubl.) C.B.Clarke; **F**, *D. thyrsiflora* J.C.Mikan; **G**, *D. paranaënsis* D.Maia *et al.*; **H**, *D. nana* Aona & M.C.E.Amaral; **I**, *D. incurva* Mart.; **J**, *D. penduliflora* Kunth; **K**, *D. sagittata* Aona & M.C.E.Amaral; **L**, *D. radicalis* Nees & Mart. **M**, *Cochliostema odoratissimum* Lem. **N**, *Geogenanthus rhizanthus* (Ule) G.Brückn. **O**, *Plowmanianthus panamensis* Faden & C.R.Hardy. Photographs A–B, D–G & J by M.O.O. Pellegrini, C by J.P.F. Zorzanelli, H by V. Bittrich, I by G.H. Shimizu, K by J.L. Costa-Lima, L by M.A.N. Coelho, M by R. Moran, N by D. Scherberich, and O by C.R. Hardy.

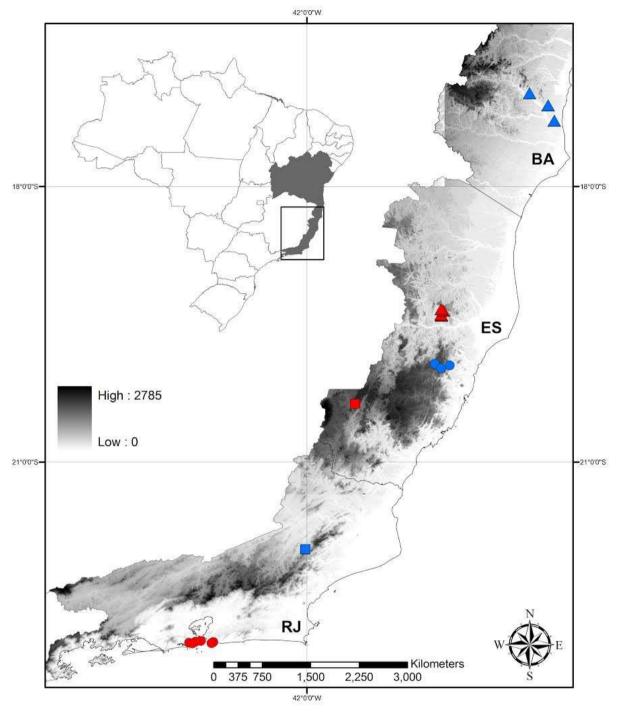


Figure 2. Distribution map of *Siderasis* Raf. *emend*. M.Pell. & Faden. **Blue circles**– *S. albofasciata*; **Blue triangles**– *S. almeidae*; **Red circles**– *S. fuscata*; **Red triangles**– *S. medusoides*; **Blue square**– *S. spectabilis*; **Red Square**– *S. zorzanellii*; **BA**– state of Bahia; **ES**– estate of Espírito Santo; **RJ**– estate of Rio de Janeiro.



Figure 3. Growth forms in Dichorisandrinae *s.s.* **A–D,** *Siderasis* Raf. emend. M.Pell. & Faden: **A,** rosette habit of *S. fuscata* (Lodd.) H.E.Moore; **B,** rosette habit with flagelliform-shoots of *S. albofasciata* M.Pell.; **C,** habit of an immature, still prostrate, individual of *S. zorzanellii* M.Pell. & Faden. **D,** habit of a mature individual of *S. zorzanellii* spirally ascending a tree. **E–F,** *Dichorisandra hexandra* (Aubl.) C.B.Clarke: **E,** intertwined habit; **F,** decumbent stem apex, bearing flowers and fruits. Photographs A–B & E–F by M.O.O. Pellegrini, C–D by J.P.F. Zorzanelli.

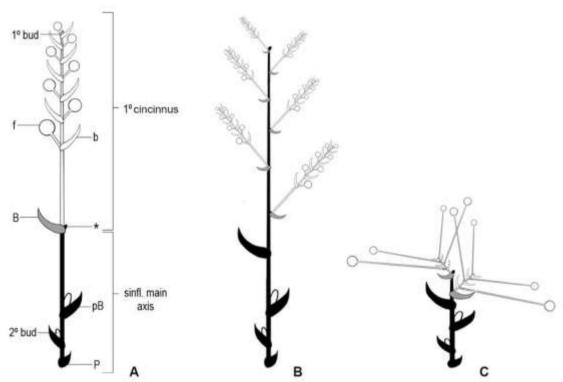


Figure 4. Inflorescence architecture in Dichorisandrinae *s.s.* **A**, diagram of the basic *Siderasis* Raf. emend M.Pell. & Faden inflorescence type, consisting of a thyrse reduced to a solitary cincinnus. **B**, diagram of the basic *Dichorisandra* inflorescence type (also characteristic of *S. spectabilis* and *S. zorzonellii*), consisting of a many-branched thyrse with alternate, many-flowered cincinni. **C**, diagram of the basic *D. acaulis* species group inflorescence type, where the main florescence axis and cincinni axis are greatly reduced, and the pedicels are peculiarly elongated. **P**= prophyll; **pB**= peduncle bract on main synflorescence axis; *= aborted or dormant apex of main inflorescence axis (usually not observed); **B**= cincinnus bract; **b**= bracteole; **f**= flower; **1° bud**= bud terminating cincinnus; **2° bud**= bud in axil of peduncle bract with potential to develop into a secondary thyrse (coflorescence); Modified from Pellegrini (2017).



Figure 5. Aril morphology in Dichorisandrinae *s.s.* **A–B,** *Dichorisandra* J.C.Mikan: **A,** *D. thyrsiflora* J.C.Mikan; **B,** *D. hexandra* (Aubl.) C.B.Clarke. **C–D,** *Siderasis* Raf. emend. M.Pell. & Faden: **C,** *S. fuscata* (Lodd.) H.E.Moore; **D,** *S. albofasciata* M.Pell. Photographs by M.O.O. Pellegrini.

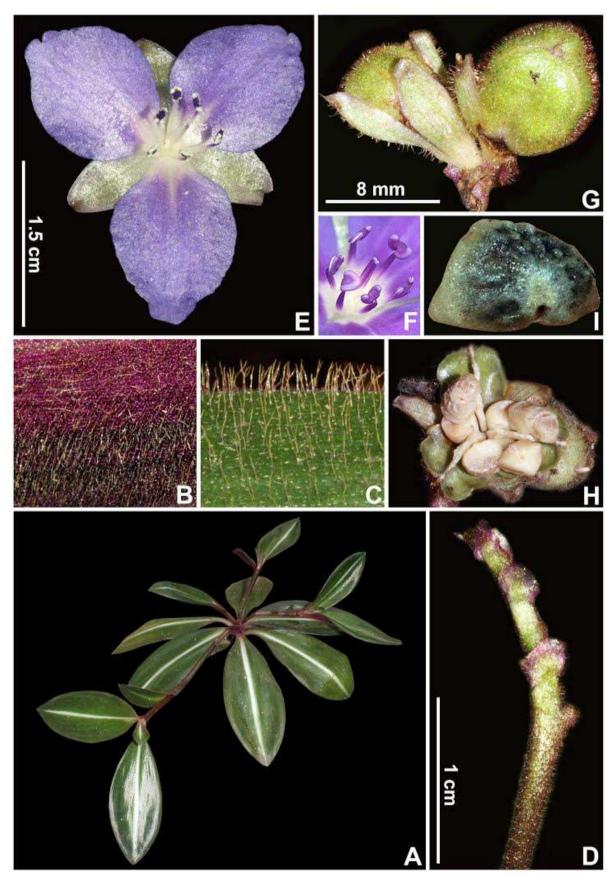


Figure 6. Siderasis albofasciata M.Pell. **A,** habit, showing the well-defined white stripe along the midvein of the leaves and the flagelliform-shoots with terminal rosettes. **B,** detail of the abaxial side of the leaf, showing the light-brown lanate indumentum. **C,** detail of the adaxial

side of the leaf, showing the light-brown hispid indumentum. **D**, detail of the inflorescence, showing the solitary cincinnus. **E**, flower **F**, detail of the androecium and the gynoecium. **G**, detail of the capsules, the left one immature with evident accrescent sepals and the right one mature. **H**, detail of an open capsule, showing the biseriate to partially uniseriate, arillate seeds. **I**, Dorsal view of a seed, showing the semi-lateral embryotega and the cream-colored, slightly translucent and thick aril. Photograph F by L. Kollmann, remaining by M.O.O. Pellegrini.

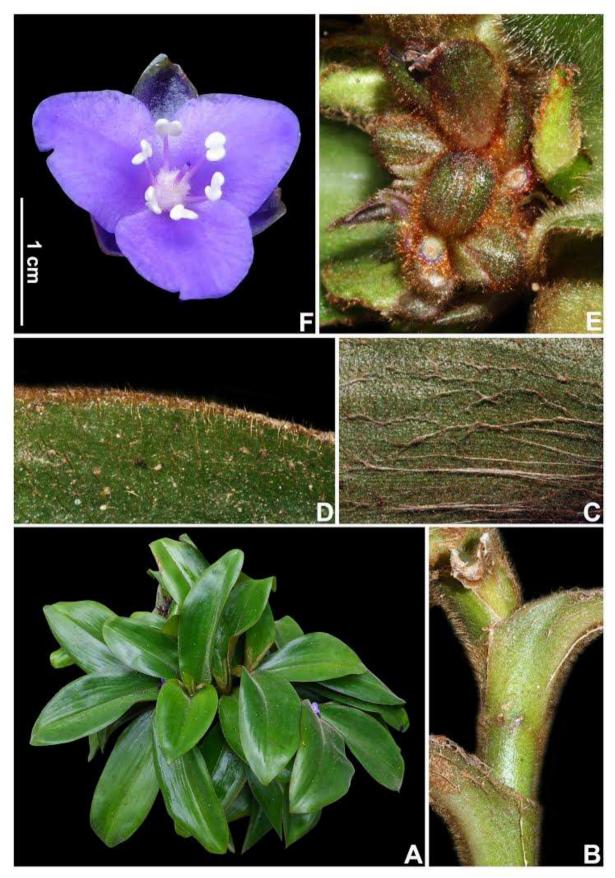


Figure 7. Siderasis almeidae M.Pell. & Faden. **A,** habit, showing a fertile rosette. **B,** detail of the elongated aerial stem, showing the rusty internodes and leaf-sheaths. **C,** detail of the lanate indumentum on the abaxial side of the leaf blade. **D,** detail of the hispid indumentum on the

adaxial side of the leaf blade. **E**, detail of the inflorescence, showing the contracted cincinnus and some floral buds. **F**, front view of a flower, showing the fleshy and internally purple sepals, and the lanate ovary. Photographs A & F by M.A.N. Coelho, remaining photographs by M.O.O. Pellegrini.

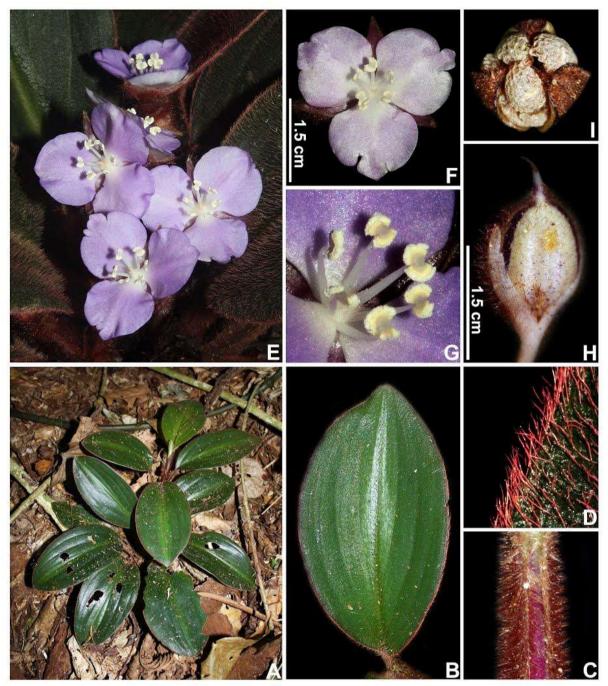


Figure 8. Siderasis fuscata (Lodd.) H.E.Moore. **A,** habit, showing a mature rosette and green leaves. **B,** detail of leaf with a silvery blotch along the midvein. **C,** detail of the canaliculate petiole, showing the rusty hairs. **D,** detail of the bright-red hirsute indumentum. **E,** upper view of a fertile rosette, showing many lilac flowers open at the same time. **F,** front view of a palelilac flower, showing the lacerated petals and completely white androecium and gynoecium. **G,** detail of the androecium and the gynoecium. **H,** detail of a mature capsule, showing the atrovinaceous longitudinal stripes. **I,** detail of an open capsule, showing the biseriate to partially uniseriate, inconspicuously arillate seeds, with grey foveolate testa. Photographs by M.O.O. Pellegrini.

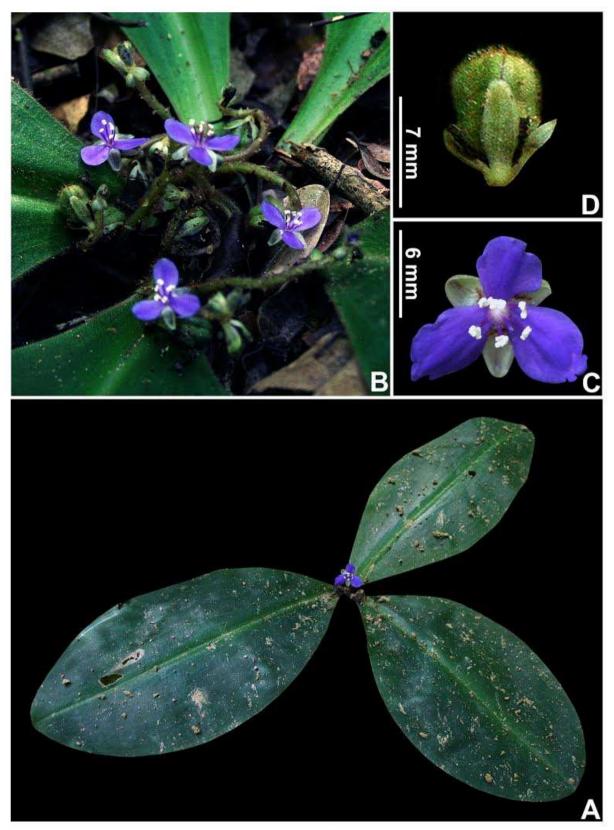


Figure 9. Siderasis medusoides M.Pell. & Faden. A, habit, showing a fertile rosette. B, detail of the synflorescence, showing the elongated and tangled cincinni. C, front view of a flower, showing small ants near the flower center. D, detail of the capsule. Photographs by P. Fiaschi.

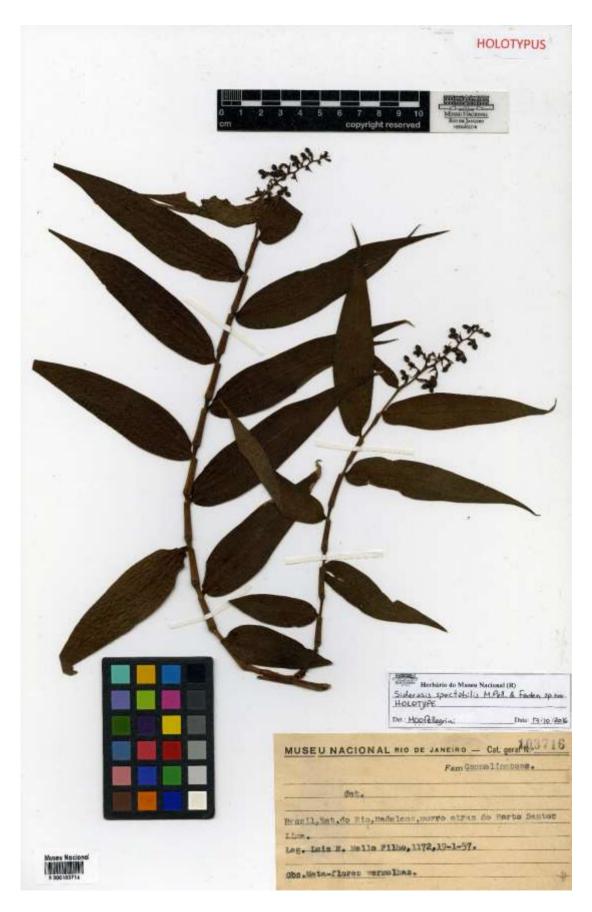


Figure 10. Holotype of *Siderasis spectabilis* M.Pell. & Faden. Image courtesy of the Museu Nacional, Rio de Janeiro, Brazil.

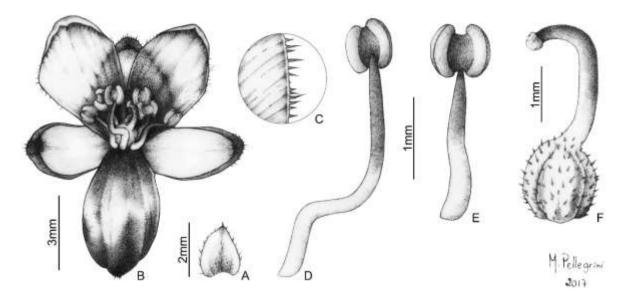


Figure 11. Line drawings of *Siderasis spectabilis* M.Pell. & Faden. **A,** bracteole. **B,** front view of a bisexual flower, showing the petals ciliate with non-moniliform hairs. **C,** detail of the petal margin, showing the non-moniliform hairs. **D,** lower stamen, showing the rectangular anther connective. **E,** upper stamen, showing the quadrangular anther connective. **F,** Detail of the gynoecium, showing the velutine ovary and bent style. Line drawings by M.O.O. Pellegrini.

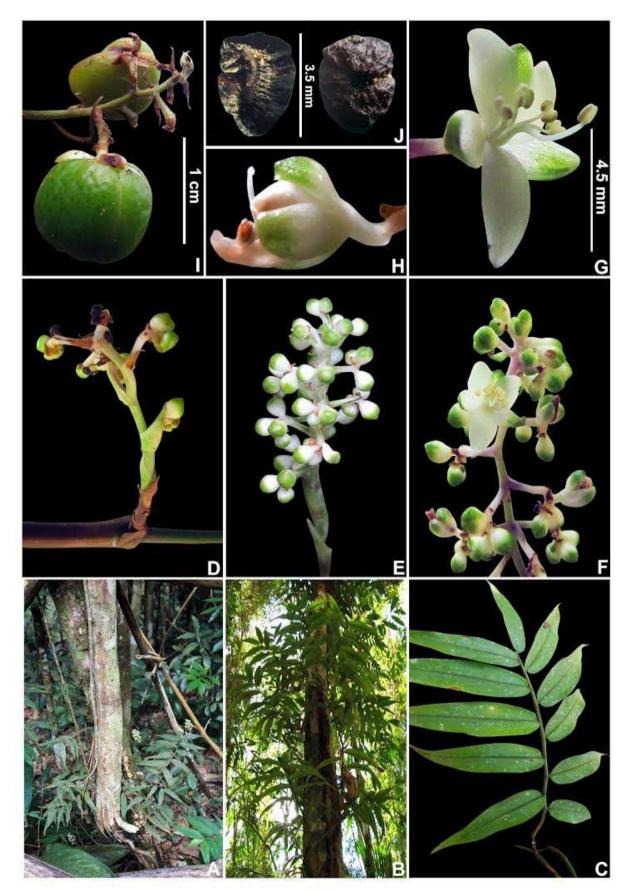


Figure 12. *Siderasis zorzanellii* M.Pell. & Faden. **A,** habit, showing an immature individual. **B,** habit, showing a mature individual spirally ascending a tree. **C,** detail of a secondary branch,

showing distichously-alternate, asymmetric leaves. **D**, detail of an axillary inflorescence, in the primary branch. **E**, detail of a terminal inflorescence, at pre-anthesis, in a secondary branch. **F**, detail of a terminal inflorescence, at anthesis, in a secondary branch, showing an open male flower. **G**, side view of a male flower, showing the unequal and sigmoid stamens. **H**, side view of a post-anthesis bisexual flower, showing the bent style. **I**, detail of the inflorescence bearing two mature capsules. **J**, dorsal and ventral view of the seeds, showing the rugose testa, cleft towards the semidorsal embryotega, and the C-shaped hilum. Photographs by J.P.F. Zorzanelli.

SECTION 2— COMMELINACEAE MIRB.

Chapter 2.8. Recircumscription and synopsis of Thyrsanthemum Pichon and Weldenia

Schult.f. (Commelinaceae), two narrow endemic genera from Mesoamerica

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Summary. A new circumscription and updated synopsis of *Thyrsanthemum*, together with a synopsis of *Weldenia*, are presented, with three new combinations, an identification key, and comments, distribution maps, and illustrations for all accepted species.

Key Words. Alpine flora, Commelinales, Guatemala, Mexico, Thyrsantheminae, Tradescantiinae

Introduction

Thyrsanthemum Pichon and Weldenia Schult. f. (Commelinaceae) are two narrow endemic genera to the cordilleras of Mesoamerica (Hunt 1976, 1983, 2015a, b). Those genera were previously placed in the subtribe Thyrsantheminae (Faden & Hunt 1991), which was recently reduced to a synonym of Tradescantiinae (Pellegrini 2017). Tradescantiinae s.l. is currently composed of 11 exclusively Neotropical genera (i.e., Callisia Loefl., Elasis D.R.Hunt, Gibasis Raf., Gibasoides D.R.Hunt, Matudanthus D.R.Hunt, Tinantia Scheidw., Thyrsanthemum, Tradescantia L. emend. M.Pell., Tripogandra Raf., Sauvallia C.Wright ex Hassk., and Weldenia; Pellegrini 2017). The subtribe is characterized by its succulent stems, tightly imbricate bracteoles, pollen grains released without adhering raphides, yellow to orange in vivo and with tectum rugose to rugose-insulate, cotyledons lacking a coleoptile, and the cotyledon hyperphyll with an elongate middle part (Pellegrini 2017; Pellegrini et al., unpublished data). Tradescantiinae is recovered organized in four main lineages: 1) *Tinantia* + *Sauvallia*; 2) Weldenia (Gibasoides + Thyrsanthemum); 3) Tradescantia (Gibasis (Elasis + Matudanthus)); and 4) the Callisia/Tripogandra generic complex (Bergamo 2003; Evans et al. 2003; Wade et al. 2006; Burns et al. 2011; Zuiderveen et al. 2011; Hertweck and Pires 2014; Pellegrini 2017; Pellegrini et al. unpublished data).

Hunt (1983) considers *Thyrsanthemum* and *Gibasoides* to be closely related, members of his still unpublished subtribe Thyrsantheminae, but excluded *Weldenia* from his concept of tribe Tradescantieae, altogether. The close relationship between *Thyrsanthemum* and *Weldenia* was

Despite lacking a phylogenetic approach, their concept of subtribe Thyrsantheminae was broader than originally idealized by Hunt (1983), also including *Weldenia* and *Tinantia*. Posteriorly, the close relationship between *Thyrsanthemum* and *Weldenia* was supported by several molecular studies (Evans et al. 2003; Wade et al. 2006; Burns et al. 2011; Zuiderveen et al. 2011; Hertweck & Pires 2014) but lacked morphological support (Pellegrini 2017). Despite the differences in reproductive gross morphology between *Gibasoides* + *Thyrsanthemum* and *Weldenia*, this clade is well-supported by vegetative morphology, some reproductive characters, and several non-conventional characters (e.g., karyotype morphology) (Pellegrini et al., unpublished data). It is characterized by its tuberous roots, presence of a succulent underground stem covered by scale-like leaves, aerial shoots dying off during the dry season, loriform and cannulate leaves with repandous margins, congested into an apical rosette, leaves dimorphic in the synflorescence, caducous cincinni bracts and bracteoles, sessile flowers, filaments flaccid at post-anthesis pointing outwards of the flower, versatile anthers, wet stigmas, and chromosomes larger than 5 μm but smaller than 10μm (Pellegrini et al., unpublished data).

During the first author's ongoing studies on the taxonomy and systematics of Neotropical Commelinaceae, it became clear that the monospecific *Gibasoides* is congeneric with *Thyrsanthemum*, and that two distinct entities should be recognized under *Weldenia* (Pellegrini 2017). Thus, we present below a new circumscription and updated synopsis of *Thyrsanthemum* and the synopsis for *Weldenia*, together with the needed new combinations and typifications, illustrations, distribution maps, comments on the systematic relationships of those genera, and an identification key to the genera and species of lineage two of subtribe Tradescantiinae.

Methods

The indumentum and shape terminology follow Radford *et al.* (1974); the inflorescence terminology and morphology follows Weberling (1965, 1989) and Panigo *et al.* (2011), with

some modifications; the fruit terminology follows Spjut (1994); seeds terminology follows Faden (1991); the general morphology and terminology follows Pellegrini (2017). The description of the species, phenology, and illustrations were based on herbaria material. Specimens from the following herbaria were analysed: ASU, B, BKL, BM, BR, CAS, CICY, CLF, CM, E, F, G, GH, GOET, HAL, HEM, HUAP, K, L, M, MA, MEXU, MICH, MIN, MO, NDG, NO, NY, OAX, P, PH, S, U, UAMIZ, UC, US, and VT (herbaria acronyms according to Thiers, continuously updated).

Taxonomic Treatment

With the present reduction of Gibasoides to a synonym of Thyrsanthemum, subtribe Tradescantiinae is now represented by 10 genera; with further generic rearrangements still needed in the *Callisia/Tripogandra* generic complex (Pellegrini 2017; Pellegrini *et al.* in prep.). Despite the inclusion of Gibasoides, the expanded Thyrsanthemum maintains its morphological cohesion, as accepted by Hunt (1976, 1983, 2015b). The dimorphic stamens cited by Hunt (1978) as diagnostic of *Gibasoides* are also observed in *Thyrsanthemum*, just not as pronounced. The degree of expansion of the connectives seems to be variable in the anthers of both genera and tend to be inconspicuous in most specimens. The same degree of variation can be observed in different Elasis and Matudanthus, and are not enough to segregate these specimens into different genera (Pellegrini, pers. observ.). Furthermore, Hunt (1978) mentions the seeds of Gibasoides as being "very different" from the ones of Thyrsanthemum, but gives no further explanation. After comparing the seeds of both genera, the only difference lies in the seeds of Gibasoides being slightly narrower than the ones from Thyrsanthemum. Thus, the distinction between both genera relies solely on the development of the main axis of the main florescence (Hunt 1983; Pellegrini 2017). This character is considered by us to be unsatisfactory for the recognition of Gibasoides as independent from Thyrsanthemum. Furthermore, its sole species is recovered as sister to *Thyrsanthemum* s.str., with strong statistical support (Pellegrini et al., unpublished data), and supports their close relationship.

As previously suggested by Hunt (1983, 2015a) and Pellegrini (2017), the degree of morphological variation between specimens of *Weldenia* warrants the recognition of two distinct entities. Thus, a new combination is herein presented to accommodate the blue- to lilacflowered specimens of *Weldenia*.

Key to the species of lineage two of subtribe Tradescantiinae

- 1. Underground stem elongate, aerial stems inconspicuous throughout the plant's life; flowers hypocrateriform, sepals spathaceous, connate, petals long-clawed, stamens equal, filaments glabrous, connective expanded, hastate, anther sacs elongate; ovules 6 per locule, ovaries and capsules cylindrical, stigma trilobate... 2
- 1'. Underground stem short, aerial stem initially inconspicuous, but elongating during flowering season; flowers flat, sepals sepaloid, free, petals sessile, stamens dimorphic, filaments barbate with moniliform hairs, connective inconspicuous, rarely expanded, anther sacs C-shaped; ovules 2 per locule, ovaries and capsules subglobose to broadly ellipsoid, stigma truncate... 3
- 2. Leaf blades with inconspicuous secondary veins, adaxially glabrous to sparsely floccose, abaxially glabrous except for the velutine hairs along the veins; calyx apically 3-dentate, glabrous or with an apical tuff of hairs, petals cucullate, white, pistil shorter to ca. as along as the stamens... 2.1. Weldenia candida (Fig. 2A–E)
- 2'. Leaf blades with conspicuous secondary veins, adaxially floccose, abaxially velutine with hairs congested along the veins; calyx apically entire, pilose along the dorsal keels, petals flat, blue to lilac, pistil longer than the stamens... 2.1. Weldenia volcanica (Fig. 2F–K)

- 3. Thyrsi few-branched and open, sparsely pubescent, lowermost cincinni bracts 1.5–3 cm long, persistent, chartaceous, cincinni long-pedunculate (5–45 mm long), stiff; style 3–5 mm long, exceeding the stamens... 4
- 3'. Thyrsi many-branched and dense, densely pubescent, lowermost cincinni bracts ca. 1 cm long, usually early deciduous, membranous, cincinni sessile to short-pedunculate, if present peduncle flexible; style 1–2 mm long, ca. the same length as or shorter than the stamens... 5
- 4. Leaves narrowly elliptic to lanceolate, base cuneate; main florescence with an elongated main axis (*i.e.*, thyrsiform), cincinni peduncles eglandular pubescent; flowers ca. 1 cm diam., pedicels shorter than 0.5 mm long, petals white, filaments strongly sigmoid... **1.2.** *Thyrsanthemum goldianum* (Fig. 1D–F)
- 4'. Leaves ovate-lanceolate to ovate to broadly ovate, base cordate to amplexicaulous; main florescence with an inconspicuous main axis (*i.e.*, umbelliform), cincinni peduncles glandular pubescent; flowers ca. 2 cm diam., pedicels 1.8–8 cm long, petals purple to bluish purple, filaments slightly sigmoid... **1.3.** *Thyrsanthemum laxiflorum* (Fig. 1G–I)
- 5. Leaves ovate-lanceolate to ovate to broadly ovate, base cordate to amplexicaulous; inflorescences densely pubescent with a mixture of glandular and eglandular hairs, cincinni peduncles 4–10 mm long; pedicels 1–2 mm long, flowers 1.4–1.6 cm diam., sepals eglandular-pubescent or with a mixture of glandular and eglandular hairs, petals 6–7.5 mm long... 1.1. Thyrsanthemum floribundum (Fig. 1A–C)
- 5'. Leaves narrowly elliptic to lanceolate, base truncate to cuneate; inflorescences densely pubescent with eglandular hairs, cincinni peduncles absent or shorter than 3 mm long; pedicels ca. 0.5 mm long to inconspicuous, flowers 1–1.2 cm diam., sepals densely glandular pubescent, petals 5–5.5 mm long... 1.4. Thyrsanthemum longifolium (Fig. 1J–M)

- **1. Thyrsanthemum** *Pichon* (1946: 224). Type species: *Tradescantia floridunda* M.Martens & Galeotti [≡ *Thyrsanthemum floribundum* (M.Martens & Galeotti) Pichon].
- = Gibasoides D.R.Hunt (1978: 331), **syn. nov.** Type species: Gibasoides laxiflora (C.B.Clarke)

 D.R.Hunt [≡ Thyrsanthemum laxiflorum (C.B.Clarke) M.Pell. & Espejo].

(Fig. 1)

Herbs geophytes, perennial, succulent, base definite, terrestrial or rupicolous. Roots tuberous, fusiform. *Underground stem* short, succulent, covered by small scales, sheaths open. Aerial stem inconspicuous, erect, succulent, unbranched, but becoming elongate during flowering season. Leaves sessile to subpetiolate; spirally-alternate, initially congested at the apex of the stem forming a rosette, but becoming more or less distributed along the elongated stem during flowering season; sheaths closed; ptyxis involute; blades cannulate, base symmetrical, amplexicaulous to cordate to cuneate, margins repandous, rarely flat, ciliate or glabrous, apex acuminate, midvein conspicuous or not, secondary veins conspicuous or not. Synflorescences terminal in the distal portion of the stem, main florescence with 1-several coflorescences. Inflorescences (main florescences) consisting of a pedunculate, many- to fewbranched thyrse, with an elongate main axis; inflorescence bract leaf-like; peduncle bracts present or not; supernumerary bracts absent; cincinni bracts bracteose, unequal to each other, persistent or not, not saccate at base, free from each other; cincinni short- to long-pedunculate, free, elongate, alternate, bracteoles present, generally deciduous, expanded, imbricate, lineartriangular to triangular, green or pink to mauve to red. Flowers bisexual, actinomorphic to slightly zygomorphic due to the curvature of the style, chasmogamous, scentless, flat; pedicel inconspicuous to short, not gibbous at apex, upright at pre-anthesis, anthesis and post-anthesis; sepals equal, free, membranous, dorsally striate, margin hyaline, apex obtuse to round, persistent in fruit; petals sessile, equal, free, flat; stamens 6, arranged in two series, dimorphic, outer stamens shorter than inner ones, filaments free, slightly to strongly sigmoid at anthesis, apex flaccid and pointing to the outside of the flower post-anthesis, medially sparsely barbate with moniliform hairs, hairs concolorous to the petals, anthers versatile, rimose, connective inconspicuous, yellow, anther sacs parallel, C-shaped, yellow, pollen yellow *in vivo*; ovary sessile, subglobose, green, glandular-pubescent, 3-locular, locules equal, locules 2-ovulate, ovules uniseriate, style slightly sigmoid at anthesis and post-anthesis, white to slightly darker than the petals, cylindrical throughout, stigma capitellate, white or yellow, pistil ca. the same length as or longer than the stamens. *Capsules* broadly ellipsoid to subglobose, thin-walled, light to medium brown when mature, loculicidal, 3-valved, apex rostrate due to persistent style base. *Seeds* exarillate, 1 or 2 per locule, ellipsoid to reniform, ventrally depressed, cleft towards the embryotega, testa rugose with ridges radiating from the embryotega, hilum C-shaped, embryotega semilateral, conspicuous, generally covered by a sparse cream farina, with a prominent apicule or not.

DIAGNOSTIC MORPHOLOGICAL CHARACTERS. Pedunculate inflorescence, elongate cincinni, striated sepals, dimorphic stamens, filaments slightly to strongly sigmoid, anther sacs C-shaped, pollen grains with reduced tectal elements in the transition zone with the sulcal membrane, the sulcal membrane coarsely granular-ridged, glandular-pubescent ovary, and rostrate capsules.

COMMENTS. Thyrsanthemum has been confused with Tradescantia due to its floral morphology and with Dichorisandra J.C.Mikan due to its stature and thyrsiform main florescence. In regards to its similarity with Tradescantia, Thyrsanthemum is most commonly confused with members of T. subg. Mandonia, since this group of Tradescantia is characterized by its thyrsiform synflorescences (Pellegrini 2017). Nonetheless, it can be easily differentiated from Tradescantia by its thyrsiform main florescence with free, alternate cincinni (vs. reduced to double-cincinni fused back to back in Tradescantia), by its caducous bracteoles (vs. persistent), pedicels erect at post-anthesis (vs. deflexed), slightly to strongly sigmoid filaments

(vs. straight), anthers with inconspicuous connectives (vs. expanded), sigmoid style (vs. straight), and seeds with semilateral embryotega and C-shaped hilum (vs. generally dorsal with linear hilum). Alternatively, *Thyrsanthemum* can be differentiated easily from *Dichorisandra* by its equal sepals (vs. unequal in *Dichorisandra*), petals lacking a white basal third (vs. almost invariably present), filaments thin and sigmoid (vs. stout and straight or twisted), anthers versatile and latrorsely rimose (vs. basifixed and poricidal or at least functionally poricidal), capsules thin-walled (vs. thick-walled), and seeds exarillate (vs. arillate).

HABITAT, DISTRIBUTION, AND ECOLOGY. *Thyrsanthemum* is endemic to Mexico, more precisely to central and southern Mexican cordilleras (Hunt 1976, 2015b). All species are geophytes, which perennate by clusters of fusiform tubers during the long winter drought where they occur. During a relatively short summer rainfall period, they initially produce acaulescent rosettes, which ultimately develop into erect or sprawling elongate stems, bearing a terminal synflorescence (Hunt 1976, 2015b). The genus seems to be ecologically associated with calcareous soils, including gypsum (Hunt 1976, 2015b).

1.1. Thyrsanthemum floribundum (M.Martens & Galeotti) Pichon (1946: 225).

- Tradescantia galeottiana Kunth (1843: 696), nom. superfl. = Tradescantia floribunda
 M.Martens & Galeotti (1842: 377). Lectotype (designated here): MEXICO. Oaxaca:
 Oaxaca de Juárez, Cordillera, Cerro San Felipe, June 1840, fl., fr., H.G. Galeotti 4952
 (BR barcode BR0000008577986!; isolectotypes: BR barcodes BR0000008577610!,
 BR0000008577658!, BR0000008577948!, K barcode K000363198!, P barcode P02173836!).
- = *Tradescantia holosericea* var. *purpusiana* G.Brückn. (1927: 59), **syn. nov.** Holotype: MEXICO. Puebla: Tlacuilotepec, s.dat., fl., *C.A. Purpus 3912* (B†). Lectotype (designated here): MEXICO. Cerro de la Yerba, July 1908, fl., fr., *C.A. Purpus 2754* (GH barcode GH01117811!; isolectotype: B†).

= Aneilema holosericeum (Kunth) Woodson (1942: 147) ≡ Tradescantia holosericea Kunth var.

holosericea ≡ Tradescantia holosericea Kunth (1843: 92). Holotype: MEXICO. Oaxaca:

Oaxaca de Juárez, Cerro San Felipe, s.dat., fl., W.F. von Karwinsky 169 (M barcode M0244250!).

(Fig. 1A–C)

NOMENCLATURAL NOTES. When describing *Tradescantia floribunda*, Martens & Galeotti (1842) designate the gathering "Galeotti 4952" as type. Nonetheless, after analysing specimens from several herbaria, we came across six specimens (syntypes), distributed in BR, K, and P, matching the protologue. It is widely known that Martens and Galeotti specimens were traditionally housed at LW, which was latter included in BR (Stafleu & Cowan 1976). Thus, we have selected the specimen BR0000008577986 as the lectotype, since it has three inflorescences (with buds, open flowers and immature fruits) and show the characteristic leaves with cordate to amplexicaulous base.

When describing *Tradescantia holosericea* var. *purpusiana*, Brückner (1927) designated the specimen "*Purpus 3912*" at B as type, which is understood by the Code as representing the designation of the holotype (Turland et al. 2018, Art. 9.1). Furthermore, Brückner (1927) also cites the specimen "*Purpus 2754*", which is to be treated as a paratype (Turland et al. 2018, Art. 9.7). Nonetheless, both specimens seem to have been destroyed during Second World War (Robert Vogt, pers. comm.). Luckily, a duplicate of "*Purpus 2754*", was located at GH (barcode GH01117811) and is here designated as the lectotype.

TAXONOMY. As the oldest name and types species of *Thyrsanthemum*, great confusion is associated with *T. floribundum*, having been applied to both *T. goldianum* and *T. longifolium* (= *T. macrophyllum*). *Thyrsanthemum floribundum* can be easily differentiated from *T. goldianum* and *T. longifolium* due to its lanceolate-ovate to ovate to broadly ovate leaves with cordate to amplexicaulous bases (vs. narrowly elliptic to lanceolate, cuneate), by its generally

pinkish purple petals (vs. always white in *T. goldianum*, generally white to light to medium pink in *T. longifolium*), and generally smaller stature. Alternatively, *T. floribundum* is vegetatively similar to *T. laxiflorum*, since both species present leaf blades, which have cordate to amplexicaulous bases and acuminate apexes. Furthermore, *T. floribundum* and *T. laxiflorum* are the only species in the genus that can present purple flowers (*T. goldianum* has white flowers, while in *T. longifolium* the flowers can range from white to pink).

The name *Tradescantia holosericea* var. *purpusiana* was never used in any relevant publication, were also overlooked by Hunt (1976, 1983, 2015b), in his studies on *Thyrsanthemum*. The diagnosis provided by Brückner (1927) provides no taxonomically relevant character to properly apply his name. Furthermore, the two specimens cited by him as holotype and paratype in B were supposedly destroyed during WWII (Robert Vogt, pers. comm.). Luckily, a duplicate of the paratype was located at GH, which allowed us to undoubtedly place it as a synonym of *T. floribundum*.

HABITAT, DISTRIBUTION, AND ECOLOGY. Thyrsanthemum floribundum is recorded from pine-oak forests, "bosques tropicales caducifolios" (i.e., seasonally dry tropical forests), and other semi-dry habitats, such as "matorral espinoso", "matorral xerófilo" (i.e., thorn scrubs), and "encinares", between 1350–2200 m. It is also found in secondary/disturbed vegetation. It is widespread in mountain areas of central and southwestern Mexico. It can be found with flowers and fruits from June to November.

CONSERVATION STATUS. *Thyrsanthemum floribundum* possesses a wide EOO (ca. 368,781.251 km²) and a wide AOO (ca. 592.000 km²). Thus, following the IUCN (2001) recommendations, *T. floribundum* should be considered Least Concern (LC), due to the lack of any imminent threats.

1.2. Thyrsanthemum goldianum *D.R.Hunt* (1976: 410).

Lectotype (designated here): MEXICO. Michoacán: Zitácuaro, Tuxantla-San Carlos, 1 Aug 1938, fl., fr., *G.B. Hinton & J.C. Hinton 13082* (K barcode K000363197!; isolectotypes: GH barcode GH00415464!, K barcode K000363196!, MEXU barcode MEXU01053710!, MO accession no. MO-206544!, US barcode 00091630!).

(Fig. 1D–F)

NOMENCLATURAL NOTES. When describing *Thyrsanthemum goldianum*, Hunt (1976) cites the holotype as being housed at K. After visiting the collection, I came across two sheets with the same collection number and marked as holotype. Since each sheet received its own barcode number, they were understood as representing distinct specimens, therefore representing syntypes, which requires the designation of a lectotype (Turland *et al.* 2018, Art. 9.11). Thus, we have chosen the specimen K000363197 as the lectotype, since it is better preserved than the other one.

TAXONOMY. Thyrsanthemum goldianum is morphologically similar to T. laxiflorum due to their fewer-branched, open and sparsely pubescent inflorescences, lowermost cincinni bracts 1.5–3 cm long, persistent, chartaceous, cincinni peduncle long and stiff, and styles 3–5 mm long, exceeding the stamens. Both species can be differentiated based on leaf morphology, inflorescence architecture, pedicel length, petal color, and filament curvature (see identification key). Alternatively, T. goldianum is easily confused with T. longifolium due to their robust size, similar leaf morphology, and generally white flowers. Nonetheless, T. goldianum is easily differentiated due to its long-pedunculate cincinni, larger, persistent and chartaceous cincinni bracts, and longer styles. Finally, degree of curvature of the filaments of T. goldianum is far greater than any species in the genus, rending its flowers unique. Based on autapomorphies, such as the ones used to stablish Gibasoides as a genus distinct from Thyrsanthemum s.s., T.

goldianum should also merit a distinct genus. This, of course, is untannable since it would render the taxonomy of the group unnecessarily complicated to any non-specialist.

HABITAT, DISTRIBUTION AND ECOLOGY. *Thyrsanthemum goldianum* is found in deciduous woodland in moist shady chaparral, between 600–1000 m. It is restricted to the semitropical zone of southeast Mexico. It can be found in flower and in fruit from August to September.

CONSERVATION STATUS. *Thyrsanthemum goldianum* possesses a wide EOO (ca. 153,247.645 km²) and a wide AOO (ca. 308.000 km²). Thus, following the IUCN (2001) recommendations, *T. goldianum* should be considered Least Concern (LC), due to the lack of any imminent threats.

1.3. Thyrsanthemum laxiflorum (C.B. Clarke) M.Pell. & Espejo, comb. nov.

≡ Tradescantia laxiflora C.B.Clarke in Candolle & Candolle (1881: 307) ≡ Descantaria laxiflora (C.B.Clarke) G.Brückn. (1927: 56) ≡ Gibasoides laxiflora (C.B.Clarke) D.R.Hunt (1978: 331). Lectotype (designated here): MEXICO. Oaxaca: Oaxaca de Juárez, Cerro San Felipe, June 1834, fl., G. Andrieux 51 (K barcode K000363194!; isolectotypes: G-DC barcode G00489705!, K barcode K000363195!, M barcode M0243776!, P barcode P00753048!).

(Fig. 1G-I)

NOMENCLATURAL NOTES. When describing the genus *Gibasoides*, Hunt (1978) did not designate a lectotype for *Tradescantia laxiflora* C.B.Clarke and, once again, overlooked it in the Flora del Valle de Tehuacán-Cuicatlán (Hunt & Arroyo-Leuenberger 2017). As it is widely known, Clarke was a researcher at Kew and thus, most of his type specimens are housed at K (Stafleu & Cowan 1976). After consulting the herbarium collection, one of us (MOOP) came across two specimens that perfectly matched the protologue. We have chosen the specimen

K000363194 as the lectotype since it is completer and more well-preserved and, thus, better represents the species.

TAXONOMY. Thyrsanthemum laxiflorum is morphologically close to T. goldianum based on inflorescence and floral morphology, as already pointed out by previous authors (Rohweder 1956; Hunt 1976, 1978, 2015b; Pellegrini 2017; see identification key). Alternatively, it is vegetatively similar to T. floribundum due to their ovate-lanceolate to ovate to broadly ovate blades, with cordate to amplexicaulous base, and acuminate apex. Furthermore, both species generally present purple flowers, while tending to blue in T. laxiflorum and pink in T. floribundum. Fig. 1B–C.

HABITAT, DISTRIBUTION, AND ECOLOGY. *Thyrsanthemum laxiflorum* is found in pine-oak forests, between 2000–2500 m, in the districts of Centro, Coixtlahuaca, Ixtlán, Miahuatlán, and Teotitlán (Oaxaca), being also found in the municipality of Coxcatlán (Puebla). It seems to be the most ecologically specialized species in the genus. It can be found with flowers and fruits from July to September.

CONSERVATION STATUS. *Thyrsanthemum laxiflorum* possesses a narrow EOO (ca. 26,563.046 km²) and an even narrower AOO (ca. 112.000 km²). Herbarium records for this species are considerably sparse, with even fewer made in the last 10 years. Thus, following the IUCN (2001) recommendations, *T. laxiflorum* should be considered Endangered [EN, A2cde+B2b(ii, iii, iv)+D2].

- 1.4. Thyrsanthemum longifolium (M.Martens & Galeotti) M.Pell. & Espejo, comb. nov.
- Dichorisandra longifolia M.Martens & Galeotti (1842: 378) = Tradescantia longifolia
 (M.Martens & Galeotti) Greenm. (1898: 471), nom. illeg., non T. longifolia Sessé & Moc.
 nec T. longifolia Small = Tradescantia holosericea var. dracaenoides C.B.Clarke in
 Candolle & Candolle (1881: 302) = Tradescantia dracaenoides (C.B.Clarke) Greenm.
 (1903: 70). Holotype: MEXICO. Hidalgo: Metztitlan, San Pedrito, 1840, fl., H.G. Galeotti
 4942a (BR barcode BR00000008577955!).
- = Tradescantia macrophylla Greenm. (1898: 472) = Thyrsanthemum macrophyllum (Greenm.) Rohweder (1956: 166) = Aneilema greenmanii Woodson, (1942: 147), non Aneilema macrophyllum R.Br. (1810: 270). Lectotype (designated here): MEXICO. Morelos: Cuernavaca, bluffs of barranca, 26 July 1896, fl., fr., C.G. Pringle 7224 (GH barcode GH00415467!). Remaining syntypes: MEXICO. Morelos: Cuernavaca, bluffs of barranca, 21 August 1897, fl., fr., C.G. Pringle 6695 (US barcode 00153017!; isolectotypes: AC barcode AC00319696!, BKL barcode BKL00000398!, BM barcode BM000938203!, BR barcode BR0000008577627!, E barcode E00373667!, F barcode barcode GH01117812!, **GOET** barcodes F0045348F!, GH GOET000948!, GOET000949!, **MEXU** barcodes MEXU00007017!, MEXU00007018!, MEXU00528886!, MIN barcode MIN1002644!, NDG barcode NDG10393!, NY barcode 00247505!, P barcodes P01730363!, P01730364!, P01730365!, P01730366!, PH barcode PH00027705!, S accession no. S-G-8057!, UC barcode UC119457!, US barcode 00091603!, VT barcode UVMVT024134!), syn. nov.
- Dichorisandra ehrenbergiana Klotzsch ex C.B.Clarke in De Candolle, A.L.P.P. & De Candolle, A.C.P., (1881: 302), pro. syn.

NOMENCLATURAL NOTES. It is known that Dr Pringle had the VT herbarium (Vermont University, USA) as his primary collection, with duplicates widely in several herbaria, including A and GH (Stafleu & Cowan 1983). Nonetheless, Dr Greenman worked at Harvard University, USA, and its associated herbaria (i.e., A and GH) but was not known for designating specimens from VT as types (Stafleu & Cowan 1976). The gathering *Pringle 6695* would seem like the most obvious choice of a lectotype, since it is represented by 25 duplicates in 18 herbaria around the globe. Nonetheless, the specimen at GH barely has any flowers, and it would be the only specimen that we could be certain that Greenman analyzed while describing *Tradescantia macrophylla*. Despite lacking any duplicates, the specimen *Pringle 7224* (GH00415467) seems to be the most obvious choice of a lectotype. It is the sole specimen to present a label identifying it as a new species, with Greenman's handwriting. All remaining specimens have a printed label which says "*Tradescantia macrophylla*, Greenman *n. sp.*", but no indisputable evidence that the specimens were analysed by Greenman before their distribution. Thus, we designate the specimen GH00415467 as the lectotype for *T. macrophylla*.

TAXONOMY. Despite the significant contributions by Hunt (1976, 1983, 2015b) to the knowledge of *Thyrsanthemum*, some issues persist to this day. For instance, the differentiation between *T. floribundum* and *T. macrophyllum* is problematic, especially due to an error on the author's identification key (Hunt 1976). The author describes *T. macrophyllum* as possessing densely eglandular-pubescent sepals, when in reality it has densely glandular-pubescent sepals, as stated by in the protologue (Greenman 1898) and as observed in the type specimens. Aside from that, both species differ greatly in leaf shape, inflorescence pubescence, the length of cincinnus peduncle, pedicel development, and flower and petal size (see identification key). Aside from that, another problem regarding this biological entity revolves around the names *Dichorisandra longifolia* M.Martens & Galeotti and *Tradescantia macrophylla* Greenm. *Dichorisandra longifolia* was first published by Martens & Galeotti (1842), in the same placed

they published *Tradescantia floribunda*. *Dichorisandra longifolia* was treated as a mere synonym of *Thyrsanthemum floribundum* by most authors (e.g., Hunt 1976, 1983, 2015b), but Clarke (1881) treated it at the variety rank, under the new name *Tradescantia holosericea* var. *dracaenoides* C.B.Clarke. Since names do not have priority outside of their original rank (Turland et al. 2018, Art. 11.2), *T. holosericea* var. *dracaenoides* is legitimate and the correct name for this taxon, at the variety level. Later, Greenman (1898), recognizes *D. longifolia* as distinct from *Tradescantia holosericea* (= *Thyrsanthemum floribundum*), and following the generic concept at the time, makes the new combination *Tradescantia longifolia*. Nonetheless, this name was previously occupied in *Tradescantia*, which rendered his new name illegitimate (Turland et al. 2018, Art. 53.1). Realizing this, Greenman (1903) proposed the new combination *Tradescantia draecenoides*, based on *T. holosericea* var. *draecenoides*, as the correct name for this taxon under *Tradescantia*.

Tradescantia draecenoides and T. macrophylla were considered by Greenman (1989, 1903) as distinct taxa, based exclusively on the dimension of their leaves (but with the same shape and pubescence) and coloration of their petals (white vs. pink). Due to a nomenclatural confusion, Hunt (1976) considered Tradescantia draecenoides to be heterotypic to Dichorisandra longifolia, treating the first name under the synonymy of Thyrsanthemum macrophyllum and the second under T. floribundum. This was aggravated by a taxonomic misconception that the specimens Ghiesbreght s.n. (K001129660; interpreted by Hunt 1976 as the "type" of Tradescantia holosericea var. dracaenoides) and Galeotti 4942a (BR0000008577955; the actual type of both names) were not conspecific. This can be refuted based on the characters used by Hunt (1976), since both specimens present leaves with cuneate bases and cincinni with peduncles not exceeding 0.5 cm long. Thus, based on these characters and the ones presented in our identification key, it is clear that Dichorisandra longifolia is conspecific with T. macrophyllum. Since D. longifolia has priority over Tradescantia

macrophylla (the basionym of *T. macrophyllum*), it is here transferred to *Thyrsanthemum* and treated as the correct name or this taxon.

HABITAT, DISTRIBUTION, AND ECOLOGY. *Thyrsanthemum longifolium* is found growing in oak, pine-oak and juniper forests, rocky slopes, roadside banks, etc. in the subtropical low deciduous woodland (*i.e.*, *selva baja caducifolia*) of the semitropical zone of southeast Mexico, between 1100–1800 m. It can be found with flowers and fruits from July to September.

CONSERVATION STATUS. *Thyrsanthemum longifolium* possesses a wide EOO (ca. 326,936.424 km²) and a wide AOO (ca. 244.000 km²). Thus, following the IUCN (2001) recommendations, *T. longifolium* should be considered Least Concern (LC), due to the lack of any imminent threats.

- **2.** Weldenia Schult. f., (1829: 1). Type species: Weldenia candida Schult.f.
- = Lampra Benth., (1842: 95). Type species: Lampra volcanica Benth. [≡ Weldenia volcanica (Benth.) M.Pell. & Espejo].
- Rugendasia Schiede ex Schltdl., (1841: 14), pro. syn. Type species: Rugendasia majalis
 Schiede ex Schltdl. (= Weldenia candida Schult.f.).
- Vibilia Sessé & Mociño, nom. nud.

(Fig. 2)

Herbs geophytes, perennial, succulent, base definite, terrestrial or rupicolous. Roots tuberous, fusiform. Underground stem elongate, succulent, covered by small scales, sheaths open. Aerial stem inconspicuous, erect, succulent, unbranched. Leaves sessile; spirally-alternate, congested at the apex of the stem forming a rosette; sheaths closed; ptyxis involute; blades cannulate, base symmetrical, truncate to cuneate, margins repandous, rarely flat, ciliate or glabrous, apex acute to acuminate, midvein conspicuous or not, secondary veins conspicuous

or not. Synflorescences terminal in the distal portion of the stem, main florescence with 1several coflorescences. Inflorescences (main florescences) consisting of a sessile, manybranched thyrse, with an inconspicuous main axis; inflorescence bract leaf-like; peduncle bracts present or not; supernumerary bracts absent; cincinni bracts bracteose, unequal to each other, persistent or not, not saccate at base, free from each other; cincinni sessile, free, contracted, alternate, bracteoles present or not, generally deciduous, reduced, imbricate, linear-triangular to triangular, green. Flowers bisexual or functionally staminate (due to the abortion of the gynoecium), actinomorphic to slightly zygomorphic due to the curvature of the corolla tube, chasmogamous, fragrant, long-tubular, hypocrateriform; pedicel inconspicuous, not gibbous at apex, upright at pre-anthesis, anthesis and post-anthesis; sepals unequal, conate forming a tubular and spathaceous structure, chartaceous, dorsally keeled, margin hyaline, apex entire to 3-dentate, persistent in fruit; petals long-clawed, equal, connate, blade flat or cucullate; stamens 6, arranged in two series, equal, filaments epipetalous, also connate to each other forming a short petalo-staminal tube, straight at anthesis, apex flaccid and pointing to the outside of the flower at anthesis and post-anthesis, glabrous, anthers versatile, rimose, connective expanded, hastate, yellow, anther sacs parallel, elongate, yellow, pollen yellow in vivo; ovary sessile, cylindrical, white, glabrous, 3-locular, locules equal, locules 6-ovulate, ovules uniseriate, style slightly sigmoid at anthesis and post-anthesis, white or pale blue to pale lilac, cylindrical throughout, stigma trilobate, white, pistil shorter or longer than stamens. Capsules cylindrical, thin-walled, light to medium brown when mature, loculicidal, 3-valved, sometimes apiculate due to persistent style base. Seeds exarillate, up to 6 per locule, ellipsoid to barrel-shaped, ventrally depressed, cleft towards the embryotega, testa rugose with ridges radiating from the embryotega, hilum C-shaped, embryotega semilateral, conspicuous, generally covered by a sparse cream farina, with a prominent apicule or not.

DIAGNOSTIC MORPHOLOGICAL CHARACTERS. Elongate underground stem, contracted aerial internodes, leaves loriform, sessile main florescence and cincinni, flowers bisexual and staminate, tubular with long floral tube, connate, zygomorphic and dorsally keeled spathaceous sepals, petals connate and long-clawed, filaments connate and epipetalous forming a petalo-staminal tube, pollen with domed areolate tectum, sulcal membrane coarsely granular-insulate, locules up to 6-ovulate, capsules cylindrical, seeds longer than wide, and hilum punctate.

COMMENTS. Weldenia has not been historically confused with any other genus of Commelinaceae, due to its unique and peculiar combination of morphological characters. Weldenia is so peculiar that in its protologue (Schultes 1829) the genus was only briefly compared with *Tradescantia*, while being compared to several other monocot families (e.g., Amaryllidaceae, Bromeliaceae, Iridaceae, and Melanthiaceae), having also been compared with the Pontederiaceae (Schlechtendal 1841).

HABITAT, DISTRIBUTION, AND ECOLOGY. Weldenia is endemic to Mexico and Guatemala, restricted to alpine and sub-alpine areas (Hunt 2015a). As in *Thyrsanthemum*, both species of *Weldenia* are geophytes, which perennate by clusters of fusiform tubers during the long winter drought where they occur. Nonetheless, the aerial stems of *Weldenia* are consistently inconspicuous, even during the flowering season, with only the leaves developing after the plant blooms.

2.1. Weldenia candida *Schult. f.* (1829: 3).

- ≡ Weldenia candida Schult.f. f. candida. Holotype: MEXICO. Mexico: Toluca, Nevado de Toluca, June 1827, fl., fr., W.F. von Karwinsky 272 (M barcode M0244244!).
- Rugendasia majalis Schiede ex Schltdl., (1841: 14), pro. syn.
- Rugendasia majalis Ehrenb. ex Hook.f., (1895: t. 7405), non R. majalis Schiede ex Schltdl.,
 pro. syn.

- Vibilia glabriflora Sessé & Mociño, nom. nud.
- Weldenia schultesii Schltdl., nom. nud.

(Fig. 2A–E)

NOMENCLATURAL NOTES. The specimen at W presents a label, which seems to indicate it is part of the original material of *Weldenia candida*. Nonetheless, the handwriting does not match the one from the specimen at M, and the label seems like an identification slip, rather than a collector's label. Furthermore, the specimen at W is morphologically deviant from the one at M, and represents *W. volcanica* (which is supported by its blue flowers). Thus, the blue-flowered specimen from W is here excluded from the original material, and the specimen at M is treated as the holotype.

The name *Weldenia schultesii* represents an interesting case of nomenclatural confusion. Schlechtendal (1841: 14) presents some taxonomic and morphological notes on *Weldenia*, with a new proto-synonym (i.e., *Rugendasia majalis* Schiede *ex* Schltdl.), further specimens, which were unknown to the botanical community, and an emended description of its sole species. The title of this note is "*Additamentum de Weldenia Schultesii*", and due to confusion while translating it, some databases (Tropicos.org 2019) have included the name *Weldenia schultesii* as a new species described by Schlechtendal (1841). Nonetheless, this name was never proposed by Schlechtendal (1841), it in fact, never existed anywhere outside plant name databases. Thus, it is here regarded as a *nomen nudum*.

TAXONOMY. Despite the recognition of two species, *Weldenia candida* is still a fairly plastic species. Great variation can be observed in the plants' overall size, size/shape of the leaves, number of flowers per rosette, size of the flowers, and shape of the corolla lobes. Nonetheless, most of the observed variation in *W. candida* (and also *W. volcanica*) is likely environmental, while variation in the number of flowers per rosette might also be related to the age of the plant.

This hypothesis seems to be further supported by the astonishing difference in the overall size of the rosette, size of the leaves, and number of flowers per rosette between cultivated and wild specimens (pers. observ.). Regardless, all specimens currently treated under the narrower circumscription of *W. candida* consistently present the leaves with inconspicuous secondary veins, calyx 3-dentate at the apex, petals white with cucullate blades, and stigma ca. the same length or shorter than the stamens.

HABITAT, DISTRIBUTION, AND ECOLOGY. Weldenia candida is generally found growing in open areas and grasslands with rocky soil found inside Abies sp. forests or Juniperus monticola woodlands, from central Mexico to Guatemala. It is also found in disturbed pine forests and pastures in alpine and sub-alpine areas. It can be found with flowers and fruits from May to September.

CONSERVATION STATUS. Weldenia candida possesses a wide EOO (ca. 942,769.592 km²) and a wide AOO (ca. 532.000 km²). Furthermore, W. candida forms dense patches on most subpopulations, efficiently reproducing sexually and asexually. Thus, following the IUCN (2001) recommendations, W. candida should be considered Least Concern (LC), due to the lack of any imminent threats.

2.2. Weldenia volcanica (Benth.) M.Pell. & Espejo, comb. nov.

- ≡ *Lampra volcanica* Benth., (1842: 95). Holotype: GUATEMALA. Sacatepéquez: crater of Volcán de Agua, s.dat., fl., *T. Hartweg s.n.* (K barcode K000363199!).
- = Weldenia candida f. caerulea Matuda, (1960: 112), **syn. nov.** Holotype: MEXICO. Durango: north slopes of Cerro Huehueto, south of Huachicheles, about 75 miles west of Ciudad de Durango, 2 July 1950, fl., fr., *J.H. Maysilles* 7280 (MICH barcode MICH1111101!).
- Vibilia pubiflora Sessé & Mociño, nom. nud.

(Fig. 2F-L)

TAXONOMY. After carefully examining the type specimens and protologues of *Lampra volcanica* and *Weldenia. candida* f. *caerulea*, it became clear that both names were conspecific. Bentham (1842) describes the petals of *L. volcanica* as "*cæruleæ*?", which added to the sepals being only scarcely 3-dentate confirms without a doubt they represent the same taxon. Since *L. volcanica* has priority over *W. candida* f. *caerulea*, it is here transferred to *Weldenia*.

As shown in the identification key, *Weldenia volcanica* can be differentiated from the more common *W. candida* based on leaves with conspicuous secondary veins, pubescence of the leaves and calyx, the shape of the apex of the calyx, architecture/colour of the corolla, and proportion between the androecium and the gynoecium. Interestingly, despite never publishing the name *Vibilia pubiflora* Sessé & Mociño, the authors recognized *W. volcanica* distinct from *W. candida*. As the name suggests, Sessé & Mociño considered the pubescence of the calyx to be more taxonomically important than the colour of the petals. The size of the plants, size and shape of leaves, length of the corolla tube, and shape/size of the corolla lobes are extremely variable and thus not useful for species delimitation. This variation also seems to be environmental, similarly to what is observed in *W. candida*.

HABITAT, DISTRIBUTION, AND ECOLOGY. *Weldenia volcanica* is commonly found in dense pine forests growing in humus-rich, deep, woodland soil, from central Mexico to northern Guatemala. Differently from *W. candida*, *W. volcanica* tends to prefer more shaded, moist and preserved environments, being also much less frequent. It can be found with flowers and fruits from April to November.

CONSERVATION STATUS. Weldenia volcanica possesses a wide EOO (ca. 357,493.005 km²), but a considerably narrower AOO (ca. 140.000 km²). Based on the available records, its subpopulations seem to be greatly fragmented, but with each one being considerably big, with individuals forming dense patches. Furthermore, these subpopulations seem to be affected by human activities, especially loss of quality (deforestation) and by livestock (grazing and

trampling). Thus, following the IUCN (2001) recommendations, *W. volcanica* should be considered Endangered [EN, A2cde+B2b(ii, iii, iv)+D2].

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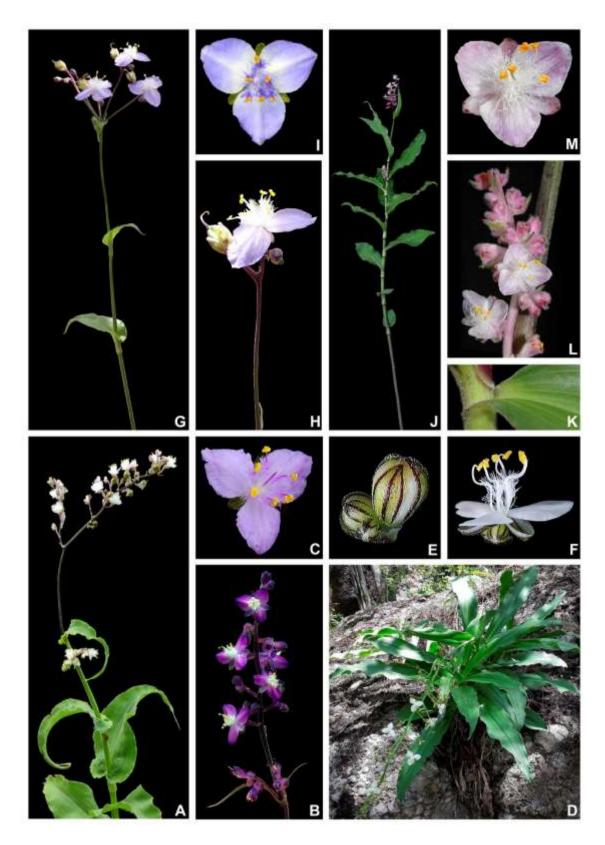


Fig. 1. *Thyrsanthemum* **Pichon. A–D,** *T. floribundum* (M.Martens & Galeotti) Pichon: **A,** young specimen, showing the rosette habit of the beginning of the flowering season; **B,** mature specimen, showing the elongate stems that generally develop during the flowering

season, plus the leaves with amplexicaulous bases; **C**, inflorescence, showing the short-pedunculate cincinni and peculiar purple-form flowers; **D**, oblique view of a flower, showing the slightly sigmoid filaments. **E**–**G**, *T. goldianum* D.R.Hunt: **E**, habit, showing a specimen growing over gypsum; **F**, floral buds, showing the characteristic atro-vinaceous striations; **G**, side view of a flower, showing the strongly sigmoid filaments. **H**–**K**, *T. longifolium* (M.Martens & Galeotti) M.Pell. & Espejo: **H**, habit; **I**, detail of the leaf bade, showing the cuneate base; **J**, inflorescence; **K**, front view of a flower, showing the slightly sigmoid filaments. A & C by M.B.N. Oberg, B by R.A. Torres, D by P. Acevedo-Rodríguez, E–G by L. Ramírez, H–K by P.T. Lezama.

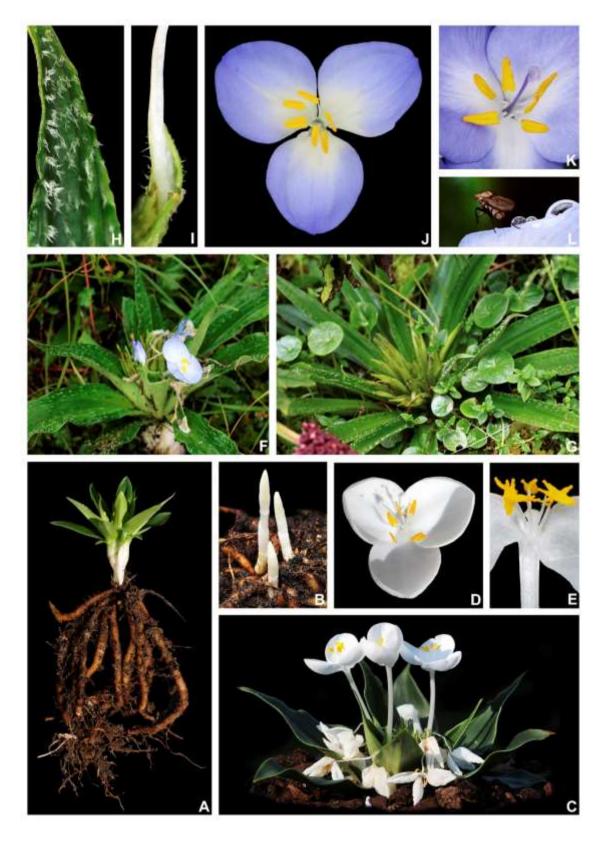


Fig. 2. *Weldenia* **Schult. f. A–E,** *W. candida* **Schult.** f.: **A,** habit, showing tuberous roots and terminal rosette; **B,** young shoots rising from the tuberous roots; **C,** side view of a flowering rosette, showing the congested inflorescence and long-tubular flowers; **D,** front view of a

bisexual flower, showing the cucullate petals; **E**, side view of a bisexual flower, showing the pistil shorter than the stamens. **F–L**, *W. volcanica* (Benth.) M.Pell. & Espejo: **F**, habit; **G**, habit, showing the congested inflorescence; **H**, detail of the leaf blade, showing the floccose pubescence; **I**, detail of the sepals, showing their pubescence; **J**, front view of a bisexual flower, showing the lilac and flat petals; **K**, detail of a bisexual flower, showing the pistil longer than the stamens; **L**, fly observed landing in the flowers. Photos A & B by H. Jans, C by B. Zaalberg, D by S. Cross, E by D. Stevenson, F–L by M. Egger.

SECTION 3— HAEMODORACEAE R.BR.

Chapter 3.1. Revisiting the taxonomy of the Neotropical Haemodoraceae (Commelinales)

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Abstract

On the basis of extensive herbarium, field, botanical illustration and molecular phylogenetic research, five genera and eight species are recognized in the Neotropical Haemodoraceae. New taxa include *Cubanicula* Hopper et al., *Xiphidium pontederiiflorum* M.Pell. et al., and *Schiekia timida* M.Pell. et al. Two new combinations are made, *Cubanicula xanthorrhizon* (C.Wright ex Griseb.) Hopper et al. and *Schiekia silvestris* (Maas & Stoel) Hopper et al. We also provide the necessary typifications, an updated identification key, comments, and photo plates for each species.

Keywords

Cubanicula, Haemodoreae, Haemodoroideae, Pontederiaceae, Philydraceae

Introduction

Haemodoraceae is a small monocot family of 14 genera and ca. 113 species currently recognized (Simpson 1998b; Hopper et al. 2009; eMonocot 2010; The Plant List 2013; Smith et al. 2011). The family is placed in the order Commelinales as the sister to Pontederiaceae, with both families having Philydraceae as their sister-group (Saarela et al. 2008; APG IV 2016; Pellegrini et al. 2018). All three families possess distichously-alternate and unifacial or cylindrical leaf-blades, with xylem and phloem alternate, or rarely phloem circular with central xylem (with a reversion to bifacial leaves in Pontederiaceae, and xylem and phloem alternate near the centre of the blades, plus xylem abaxial and phloem adaxial near the margins; Pellegrini et al. 2018); the presence of styloid crystals; perianth petaloid with the presence of tannin cells, flowers always bisexual and mainly zygomorphic and enantiostylous; pollen released with raphides, the presence of placental sclereid idioblasts; seeds longer than wide with longitudinal wings or striations (with a reversion in subfamily Haemodoroideae; Simpson 1990); and abundant helobial endosperm (Simpson 1985, 1987, 1990, 1993; Rudall 1997; Prychid et al. 2003; Simpson and Burton 2006). Furthermore, the relationship between Haemodoraceae and Pontederiaceae is morphologically supported by the presence of a hypanthium, endothecium with a basal thickening, non-columellate-tectate exine, septal nectaries, and phenylphenalenones (Simpson 1987, 1990, 1993; Pellegrini et al. 2018).

Haemodoraceae are clearly monophyletic, characterized by their vascular bundles enveloped by a fibrous layer and their peculiar inferior ovary, and classified into two subfamilies: Haemodoroideae and Conostylidoideae (Simpson 1990, 1998a; Hopper et al. 1999, 2009; Aerne-Hains and Simpson 2017; Pellegrini et al., unpubl. data). The Haemodoraceae are generally associated with semi-arid to temperate environments, due to the diversity of taxa in Australia (Macfarlane et al. 1987; Hopper et al. 2006, 2009; Smith et al. 2011). Nonetheless, most genera of Haemodoraceae possesses representatives that inhabit wetlands or swamps, with some genera being completely dependent on these aquatic environments (Simpson 1998b; Pellegrini et al., unpubl. data). The family possesses an unusual disjunct distribution, having Australia-New Guinea as its centre of diversity (Simpson 1998b; Hopper et al. 2009). Subfamily Conostylidoideae, with six genera and ca. 70 species, is endemic to Southwestern Australia, together with the species-rich genus *Haemodorum* Sm. from subfamily Haemodoroideae (Simpson 1998b; Hopper et al. 2009). The Americas and South Africa are secondary centres of diversity for Haemodoraceae, with nine small genera and ca. 20 species (Simpson 1998b; Hopper et al. 2009, in prep.; this study).

The Neotropical region was the focus of a comprehensive floristic study on the Haemodoraceae 25 years ago (Maas and Maas van de Kamer 1993). However, recent field, herbaria, and phylogenetic studies have shed some light on this still poorly understood group

and provide evidence the need for several taxonomic changes (Hopper et al. in prep.; Pellegrini pers. observ.). As an attempt to clarify the taxonomy and systematics of Neotropical Haemodoraceae, the present study revisits the Flora Neotropica Monograph for Haemodoraceae, with the description of a new genus, two species, and two new combinations. In addition, we provide an updated identification key, distribution maps, photo plates for each species, comments, and the necessary typifications.

Methods

The descriptions and phenology of the species were based on data from herbaria, spirit collections, fresh material, and literature. Specimens from the following herbaria were also analysed: AD, ALCB, B, BA, BHCB, BHZB, BM, BOTU, BRIT, C, CAL, CANB, CBG, CEN, CEPEC, CESJ, CGE, CGMS, CNMT, COL, COR, CORD, CVRD, DR, EAC, ESA, F, FCAB, FCQ, FLOR, FURB, GUA, HAMAB, HAS, HB, HBR, HDCF, HRB, HRCB, HSTM, HUCS, HUEFS, HUFSJ, HURB, IAC, IAN, ICN, INPA, JOI, K, L, MBM, MBML, MEL, MG, MO, MY, NBG, NSW, NY, P, PACA, PERTH, PMSP, R, RB, RFA, RFFP, SCP, SP, SPF, SPSF, U, UEC, UFRN, UPCB, US, USF, W, WAG, and WU (herbaria acronyms according to Thiers, continuously updated). All species of Neotropical Haemodoraceae, with the exception of Pyrrorhiza neblinae Maguire & Wurdack, were observed in the field by the authors through the course of several field trips across Central and South America, Cuba and the eastern USA, between 1990-2016 Indumentum and shape terminology follows Radford et al. (1974); the inflorescence and general morphology terminology follows Weberling (1965, 1989) and Panigo et al. (2011); the fruit terminology follows Spjut (1994); the seed terminology follows Faden (1991); and general morphology follow Simpson (1990, 1998). The conservation assessments follow the recommendations of the IUCN Red List Categories and Criteria, Version 3.1 (IUCN 2001). GeoCAT (Bachman et al. 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO). The distribution of the species is based on herbaria materials, field data, and literature.

Results

The current study recognizes five genera and eight species of Neotropical Haemodoraceae. This number differs from the previous study by Maas and Maas van de Kamer (1993; four genera and five species), due to the present description of a new genus (i.e., *Cubanicula* Hopper et al., *gen. nov.*), the description of a new species of *Xiphidium* and one of *Schiekia*, and the recognition of *S. orinocensis* subsp. *silvestris* Maas & Stoel at species rank. Thus, we present an updated identification key for the Neotropical Haemodoraceae, complete descriptions for the new genus and the two new species, as well as comments, illustrations and some nomenclatural updates for the remaining taxa.

Updated key to Neotropical Haemodoraceae

- 1. Inflorescences and flowers lanate; outer tepals ½ times shorter than the inner, ovary inferior; seeds minutely scabrid, winged... *Lachnanthes caroliniana* (Lam.) Dandy (Fig 3)
- Inflorescences and flowers tomentose, glandular-pubescent or glabrous; outer and inner tepals more or less equal to each other in length, ovary superior; seeds obviously ornate, not winged... 2
- 2. Roots lacking a rhizosheath, not sand-binding; flowers bilabiate, perianth basally aperturate, tepals lacking an apical black mucron, outer androecium whorl with two linear

- staminodes, lateral anthers with an apical connective appendage, anthers 3–4 times shorter than the filaments, stigma capitate; seeds deltoid, testa reticulate... 3
- Roots with a rhizosheath, sand-binding; flowers campanulate, perianth without basal apertures, tepals with an apical black mucron, outer androecium whorl undeveloped, lateral anthers lacking connective appendages, anthers as long as to ca. ½ times shorter than the filaments, stigma truncate; seeds lenticellate or cuboid, testa tuberculate or covered with coarse trichomes... 5
- 3. Rhizome long and trailing; stems elongate; leaves membranous, evenly distributed along the stem; thyrse corymb-like; flowers pendulous, stamens with apex decurved upwards, staminodes thick (0.4–0.6 mm wide), fusiform; capsules green when immature, becoming medium brown when mature... *Schiekia silvestris* (Maas & Stoel) Hopper et al. (Fig 9)
- Rhizome short; stems inconspicuous to short; leaves fibrous, congested forming a rosette;
 thyrse spike-like; flowers upright to patent, stamens with apex decurved downwards,
 staminodes thin (0.1 mm wide), filiform; capsules orange when immature, becoming
 medium to dark red when mature... 4
- 4. Cincinni bracts present; flowers chasmogamous, clearly bilabiate, 0.7–1.3 cm diam., tepals externally hirsutulous, reflexed apex, apricot to cream, upper tepals with three dark orange to orange-brown nectar guides, medial filament not inflated, staminodes almost as long as its subtending tepal; capsules broader than long... *Schiekia orinocensis* (Kunth) Meisn. (Fig 7)
- Cincinni bracts absent; flowers cleistogamous, narrowly tubular, 0.2–0.4 cm diam., tepals externally glandular-pubescent, apex straight, light to medium green, upper tepals lacking nectar guides, medial filament inflated, staminodes 1/3 to 2/3 the length of its subtending tepals; capsules slightly longer than broad or as broad as long... Schiekia timida M.Pell. et al. (Fig 11)
- 5. Stems elongate; anthers introrsely rimose but functionally poricidal; septal nectaries absent; capsules subglobose to globose, indehiscent, somewhat fleshy at maturity; seeds cuboid, testa tuberculate... 6
- Stems contracted; anthers rimose, septal nectaries present but vestigial; capsules trigonous,
 3-valved, dry at maturity; seeds lenticellate, testa covered with coarse trichomes... 7
- 6. Flower buds white to cream-colored, flowers 0.7–1.2 cm diam., perianth actinomorphic, inner lobes elliptic with acute apex, upper tepals only basally connate, basally green and without nectar guides; capsules 4.8–6.4 × 5.2–6.6 mm, orange to red when mature; seeds black... *Xiphidium caeruleum* **Aubl.** (**Fig 13**)
- Flower buds apricot to light orange, flowers 1.9–2.7 cm diam., perianth zygomorphic, inner lobes obovate with obtuse to round apex, upper tepals connate in the basal third or halfway through, with three orange-yellow to orange nectar guides; capsules 6.8–8.9 × 7.2–10.1 mm, dark red to vinaceous when mature; seeds dark reddish brown to reddish black... *Xiphidium pontederiiflorum* M.Pell. et al. (Fig 15)
- 7. Cormose herbs; thyrsi composed of 2–4, unbranched cincinni; flower non-enantiostylous, upper tepals lacking nectar guides, stamen 1, filament straight, anther sacs symmetric, staminodes 2, filiform... *Pyrrorhiza neblinae* Maguire & Wurdack (Fig 5)
- Rhizomatous herbs; thyrsi composed of 9–27, 1–2-branched cincinni; flower enantiostylous, upper tepals with three orange-yellow to orange nectar guides, stamens 3, lateral filaments

twisted, central filament bent upwards, anther sacs asymmetric, staminodes absent... *Cubanicula xanthorrhiza* (C.Wright ex Griseb.) Hopper et al. (Fig 1)

1. Cubanicula Hopper, J.E.Gut., E.J.Hickman, M.Pell. & Rhian J.Sm., gen. nov. Type species. Cubanicula xanthorrhiza (C.Wright ex Griseb.) Hopper et al. (≡ Xiphidium xanthorrhizon C.Wright ex Griseb.). Fig 1

Diagnosis. Similar to *Xiphidium* Aubl. in inflorescence and floral morphology, differing due to its contracted stems, leaves congested into an apical rosette, 1–2-branched cincinni, extrorsely rimose anthers, the presence of two vestigial infralocular septal nectaries, capsules trigonous, 3-valved, with thickened and tomentose septal ridges, and dry at maturity, dehiscence loculicidal, lenticellate, with coarse trichomes on margins and outer testa.

Etymology. Named for Cuba, in which the genus is narrowly endemic.

Comments. Cubanicula is recovered with strong bootstrap support in a clade with Xiphidium s.str. and Pyrrorhiza Maguire & Wurdack, sister to the latter genus, not Xiphidium in which the species of Cubanicula was originally placed. (Hopper et al., in prep). This clade can be morphologically supported by the presence of sand-binding roots, campanulate and pollen rewarding flowers, tepals with an apical black mucron, anthers as long as to ca. ½ times shorter than the filaments, vestigial septal nectaries, truncate stigmas, and enlarged placental attachments subtending the ovules and seed (Pellegrini et al., unpubl. data). Cubanicula can be differentiated from Pyrrorhiza by its rhizomatous underground system (vs. cormose in Pyrrorhiza), thyrsi 1–2-branched cincinni (vs. always unbranched), flower enantiostylous (vs. non-enantiostylous), upper tepals with three orange-yellow to orange nectar guides (vs. lacking nectar guides), stamens 3 (vs. one), lateral filaments twisted and central filament bent upwards (vs. filament straight), staminodes absent (vs. staminodes 2, filiform), and circular seed glabrous on the hilar testa. The difference between Cubanicula and Xiphidium s.str. is especially evident in capsule and seed characters, as well as floral size. These genera can be differentiated by the characters summarized in Table 1.

Table 1. Morphological differences between *Cubanicula* Hopper et al. and *Xiphidium* Aubl. s.str.

Character	Cubanicula	Xiphidium s.str.
Stems	Contracted	Elongated
Leaves	Congested at the apex of the stems forming a rosette	Evenly distributed along the stems
Cincinni	1–2-branched	Unbranched
Flowers	Bicolored	Uniformly coloured, rarely bicolored
Stamens	Dimorphic, anthers extrorsely rimose, anther sacs asymmetric	Monomorphic, anthers, introrsely rimose but functionally poricidal, anther sacs symmetric
Septal nectaries	Two and infralocular, vestigial	Absent
Enlarged placental attachment	Capitate, vertically compressed, red	Cylindrical, truncate, green
Capsules	Trigonous, loculicidal 3-valved, dry at maturity, septal ridges tomentose at maturity	Subglobose to globose, indehiscent, somewhat fleshy at maturity, septal ridges glabrous at maturity
Seeds	Lenticellate	Cuboid
Testa	Coarse trichomes on margins and outer surface, glabrous on hilar surface	Tuberculate

1.1. Cubanicula xanthorrhiza (C.Wright ex Griseb.) Hopper, J.E.Gut., E.J.Hickman, M.Pell. & Rhian J.Sm., comb. nov.

Fig 1

Xiphidium xanthorrhizon C.Wright ex Griseb., Cat. Pl. Cub. 1: 252. 1866. Lectotype (designated by Maas & Maas van de Kamer 1993). CUBA. Artemisia: Pinar del Río, San Cristóbal, La Palma, fl., fr., 1860–1864, C. Wright 3259 (GOET barcode GOET004074!; isolectotypes: G barcode G00098226!, GH barcode GH00030236!, K barcode K000574288!, NY barcodes 00073224!, 00073225!, P barcodes P04457878!, P00643765!, S accession no. S-R-6536!, US barcodes US00092055!, US00092056!).

Description. Herbs ca. 50–180 cm tall, perennial, rhizomatous with a definite base, terrestrial in white sand. Roots slightly tuberous, densely tomentose with long light brown to grey hairs forming a rhizosheath, sand-binding. Rhizomes underground, short, externally light to medium brown, internally yellow to orange. Stems inconspicuous, fibrous, unbranched. Leaves distichously-alternate, equitant, congested at the apex of the stems forming a rosette, sessile, the apical ones gradually smaller than the basal ones; sheaths 8.6-15.2 cm long, glabrous; blades $(5-)15.7-60.3-(85) \times 0.3-3.4$ cm, coriaceous, unifacial, medium green, drying yellowish green to olive-green, linear-elliptic to narrowly elliptic, slightly ensiform,

glabrous, base sheathing, margins green, glabrous to sparsely ciliate, apex acuminate; midvein inconspicuous, secondary veins inconspicuous to slightly impressed, becoming prominent when dry. Inflorescences terminal or apparently so, consisting of a pedunculate manybranched thyrse, sometimes with ones to several coflorescences; peduncles 43.7–75.2 cm, densely tomentose, hairs pilate, light brown; basal bract 5.1–7.8 × 0.5–1.5 cm, leaf-like, linear-elliptic, slightly ensiform to ensiform, glabrous or sparsely tomentose at base, hairs pilate, white, base truncate to slightly sheathing, margin ciliate at apex, apex acuminate, secondary veins inconspicuous; cincinnus bract 0.8-6 × 0.1-0.4 cm, linear-lanceolate to lanceolate, green, glabrous to sparsely tomentose, hairs pilate, white, base truncate, margin ciliate, apex acuminate; cincinni 9-27 per thyrse, 1-2-branched, alternate, 3-19-flowered, peduncle 0.2–3.4 cm long, green, sparsely tomentose to densely tomentose, hairs pilate, white; bracteoles $2.8-6.3 \times 1.3-2$ mm, elliptic to ovate, green, glabrous to sparsely tomentose, hairs pilate, white, base truncate, margin glabrous, apex acute. Flowers 1.3-2.6 cm diam., bisexual, chasmogamous, enantiostylic, campanulate, asymmetric due to the position of the style; floral buds $3.2-8.2 \times 1.5-3.5$ mm, narrowly ovoid, white to apricot; pedicels 1.4-5.6mm long, green, tomentose to densely tomentose, hairs pilate, white, upright and slightly elongate in fruit; perianth zygomorphic, lobes free, except for the upper 3 lobes which are conate on the basal third to mid-length, nectar guide yellow with reddish orange spots, on the basal third of the conate lobes, outer lobes $7.3-13.2 \times 2.5-5.6$ mm, subequal, the upper slightly shorter, elliptic to narrowly obovate, externally white to apricot, glabrous to sparsely tomentose, hairs pilate, white, internally white, glabrous, base cuneate, margins glabrous, apex acute to obtuse, inner lobes $9.5-14.5 \times 4.8-8.6$ mm, subequal, the upper two slightly shorter and deflexed, obovate to broadly oblong, externally white to apricot, rarely light orange, glabrous, internally white, glabrous, base cuneate, margins glabrous, apex obtuse to rounded, greenish yellow to apricot; stamens 3, lateral stamens with filaments 1.5-3.5 mm long, slightly twisted, basally cream to apricot, apically white, glabrous, anthers $1.8-2.8 \times 1.8$ 0.6-1 mm, dorsifixed, rimose, oblongoid, thecae unequal, light yellow, central stamen with filament 4.2–5.6 mm long, bent upwards, basally cream to apricot, apically white, glabrous, anthers $0.9-2.2 \times 0.3-0.7$ mm, dorsifixed, rimose, broadly oblongoid, white; ovary $0.8-1 \times 0.00$ 0.6-0.7 mm, broadly ellipsoid, 3-loculate, reddish orange green, smooth, densely tomentose along the septal ridges, style 5.8–7.3 mm, bent upwards, basally cream to apricot, apically white, glabrous, stigma truncate-trilobate, white, papillose. Capsules 6-8.1 × 6.4-9.8 mm, subglobose to depressed ovoid, 6-winged, medium green when immature, dark brown when mature, glabrous, 3-valved. Seeds 1.9–3 × 1.7–3.2 mm, lenticellate, testa dark brown to black, covered with finger-like hairs on the dorsal surface, hairs concentrated to the margins on the ventral side, sparser in the centre, orange to red; embryotega dorsal, relatively inconspicuous, without a prominent apicule; hilum punctate.

Specimens seen. CUBA. Isla de la Juventud: near Managua, fl., 11 Jul 1900, W. Palmer & J.H. Riley 1101 (US); near km 7 of the road between Nueva Genova and Santa Fé, fl., fr., 27 Oct 1920, E.L. Ekman 11940 (NY, US); east of Los Indios, fl., 17 May 1910, O.E. Jennings 315 (BM, GB, NY, US, USF); fl., 17 May 1910, O.E. Jennings 668 (NY, US); vicinity of San Pedro, fl., 15–17 Feb 1916, N.L. Britton et al. 14341 (F, GH, MO, NY, US); Santa Bárbara, fl., fr., 9 Feb 1953, E.P. Killip 42656 (US); along road from Nueva Gerona to Santa Bárbara, fl., fr., 19 Nov 1955, E.P. Killip 45173 (US); Reserva Natural Los Indios Norte, arenas brancas com pinar, fl., fr., 27 Feb 2002, W. Greuter et al. 25923 (NY); Siguanea region, fl., 19 Apr 1954, E.P. Killip 44041 (P, US); fl., 20 Nov 1955, E.P. Killip & H.S. Cunniff 45185 (US); in white sands near San Pedro, fl., fr., 8 Feb 1956, C.V. Morton 10028 (US). Pinar del Río: Arroyo del Sumidero, fr., 7–9 Aug 1912, J.A. Shafer & B. Léon 13576 (BM, F, NY, US); Guane, Los Ocujes, 1.6 km along track leading north from the road to

Mantua at the W extent of Guane, fr., 17 Apr 2010, R.J. Smith et al. RJS290 (HAJB, K); Laguna Santa Maria, fl., fr., 8 Sep 1910, N.L. Britton et al. 7119 (NY); mountains near El Guama, fr., 25 Mar 1900, W. Palmer & J.H. Riley 423 (US); Ovas, El Punto, fl., fr., 29 Apr 1989 A. Urquiola 5392 (NY); Pinar del Río, pinelands 12 km of the highway to Coloma, fl., 28 Oct 1923, E.L. Ekman 17802 (K, S); Sandino, 4 km NE of Sandino adjacent to old Air Base of San Julian, 100 m S of main road, fl., fr., 19 Apr 2010, R.J. Smith et al. RJS292 (HAJB, K).

Distribution and ecology. Cubanicula xanthorrhiza is endemic to western Cuba and restricted to the Province of Pinar del Río and the Special Municipality of Isla de la Juventud (known until 1978 as Isla de Pinos) (Fig 2). It is found in pinelands or in open, anthropogenic tropical savanna, on deep, acidic, quartzitic sand, with some organic matter and quartzite/laterite gravel at the surface. Such habitats qualify as old, climatically-buffered infertile habitats (OCBIL sensu Hopper 2009).

Cubanicula habitats surveyed as part of the collection of specimens by some of the authors in 2010 included pine woodland edge, open anthropogenic savannah with scattered trees, open lakeside vegetation and a seasonally dry lake basin with open vegetation. In the pineland habitat, Cubanicula was found at the woodland edge, bordering a road cutting, occurring under a canopy of Xylopia aromatica (Lam.) Mart. (Annonaceae), Tabebuia lepidophylla (A.Rich.) Greenm. (Bignoniaceae), and Acoelorraphe wrightii (Griseb. & H.Wendl.) H.Wendl. ex Becc. (Arecaceae), at the edge of *Pinus caribaea* Morelet (Pinaceae) woodland. Other components of the vegetation included Alibertia edulis (Rich.) A.Rich. and Roigella correifolia (Griseb.) Borhidi (Rubiaceae), Brya microphylla Bisse (Fabaceae), Byrsonima crassifolia (L.) Kunth (Malpighiaceae), Casearia spinescens (Sw.) Griseb. (Salicaceae), Cassytha filiformis L. (Lauraceae), Cecropia peltata L. (Urticaceae), Cochlospermum vitifolium (Willd.) Spreng. (Bixaceae), Croton cerinus Müll.Arg. (Euphorbiaceae), Davilla rugosa Poir. and Doliocarpus dentatus (Aubl.) Standl. (Dilleniaceae), Didymopanax morototoni (Aubl.) Decne. & Planch. (Araliaceae), Lantana involucrata L. (Verbenaceae), Ouratea nitida (Sw.) Engl. (Ochnaceae), and Pachyanthus mantuensis Britton & P.Wilson (Melastomataceae).

In the open anthropogenic savannah habitat (a degraded pineland with adjacent *Eucalyptus* spp. plantation and scattered *Pinus caribaea* and *Eucalyptus* trees), *Cubanicula* was found in full sun in a grassy sward with *Angelonia pilosella* J.Kickx f. and *Bacopa longipes* (Pennell) Standl. (Plantaginaceae), *Cassytha filiformis*, *Chamaecrista diphylla* (L.) Greene and *Mimosa pudica* L. (Fabaceae), *Diodia* sp. (Rubiaceae), Eriocaulaceae, *Hypericum styphelioides* A.Rich. (Hypericaceae), *Melochia savannarum* Britton and *Waltheria indica* L. (Malvaceae), *Paspalum notatum* Flüggé (Poaceae), *Phyllanthus* sp. (Phyllanthaceae), *Scirpus* sp. (Cyperaceae), *Stachytarpheta* sp. (Verbenaceae), *Tetramicra eulophiae* Rchb.f. ex Griseb. (Orchidaceae), *Tetrazygia discolor* (L.) DC. (Melastomataceae), and *Xyris* spp. (Xyridaceae).

In the lakeside vegetation, *Cubanicula* was found in a range of microhabitats from sparse grass/sedgeland to the shallow slopes of wet seeps, with abundant *Drosera* spp. (Droseraceae). The main associated grassland species were *Blechnum serrulatum* Rich. (Blechnaceae), *Cassytha filiformis*, *Chamaecrista* sp. and *Desmodium* sp. (Fabaceae), *Drosera intermedia* Hayne, *Hypericum styphelioides*, *Lycopodiella* sp. and *Lycopodium* sp. (Lycopodiaceae), *Polygala squamifolia* C.Wright ex Griseb. (Polygalaceae), *Rhexia* sp. (Melastomataceae), *Scirpus* sp., *Spiranthes* sp. (Orchidaceae), and *Xyris* sp., with occasional shrubs including *Byrsonima crassifolia*, *Pachyanthus* sp., and *Tetrazygia discolor*.

Finally, in the lake basin habitat, *Cubanicula* was found on sandy soils with a higher organic matter content at the surface than in the other habitats. The population was scattered through dense tussock sedges and growing through dense leaf litter in association with

Telmatoblechnum serrulatum (Rich.) Perrie et al. (Blechnaceae), Centella asiatica (L.) Urb. (Apiaceae), Chamaecrista diphylla, and Rhynchospora sp. (Cyperaceae), with occasional Chrysobalanus icaco L. (Chrysobalanaceae).

The altitudinal range of these sites was from 3 m a.s.l. in the lake basin to 54 m a.s.l. in the pinelands.

Phenology. Flowering and fruiting between October and February.

Conservation status. *Cubanicula xanthorrhiza* possesses a narrow EOO (10,132.599 km²) and AOO (ca. 96.000 km²), being endemic to western Cuba. Thus, following IUCN (2001) recommendations *C. xanthorrhiza* should be considered as Endangered [EN, A2ac+B2b(ii, iii)+C1].

2. *Lachnanthes* **Elliott**, Sketch Bot. S. Carolina 1: 47. 1816. Type species. *Lachnanthes tinctoria* (Walter ex J.F.Gmel.) Elliott [= *Lachnanthes caroliniana* (Lam.) Dandy]. Fig 3

Camderia Dumort., Anal. Fam. Pl.: 80. 1829, nom. illeg. Type species. Heritiera tinctorum Walter ex J.F.Gmel. [= Lachnanthes caroliniana (Lam.) Dandy].

Heritiera J.F.Gmel., Syst. Nat. (ed. 13) 2(1): 113. 1791, nom. illeg., non Heritiera Aiton, nec Heritiera Retz. Type species. Heritiera tinctorum Walter ex J.F.Gmel. [= Lachnanthes caroliniana (Lam.) Dandy].

Gyrotheca Salisb., Trans. Hort. Soc. London 1: 327. 1812, nom. nud.

Comments. Lachnanthes is morphologically and phylogenetically related to Dilatris P.J.Bergius s.str., an undescribed genus, and Haemodorum, due to their red to orange roots, branched cincinni, upright tepals, three fertile stamens, inferior ovary, and lenticellate and winged seeds (Simpson 1990, 1998b; Hopper et al. 1999, 2009, in prep.). Lachnanthes can be differentiated from *Haemodorum* based on their roots being sand-binding or not (roots lacking a rhizosheath and not sand-binding in Lachnanthes vs. with a rhizosheath and sand-binding in almost all Haemodorum), pubescence (present vs. absent), on the presence of enantiostyly (present vs. absent), the consistency of the tepals (fleshy vs. coriaceous), and number of ovules per carpel (5-7 vs. 2) (Pellegrini et al., unpubl. data). On the other hand, Lachnanthes can be differentiated from Dilatris s.str. by its roots lacking a rhizosheath and not sandbinding (vs. with a rhizosheath and sand-binding in Dilatris s.str.), outer tepals ½ times shorter than the inner tepals (vs. outer and inner tepals equal), tepals erect and lacking apical glands (vs. tepals patent, with apical glands), monomorphic stamens (vs. dimorphic), septal nectaries interlocular (vs. supralocular), 5-7 ovules per locule (vs. one), the absence of an anthocarp (vs. anthocarp present), and loculicidal capsules (vs. septifragal) (Pellegrini et al., unpubl. data). The differences between Lachnanthes and the undescribed genus will be posteriorly discussed (Hopper et al. in prep.).

2.1. Lachnanthes caroliniana (Lam.) Dandy, J. Bot. 70: 329. 1932. Fig 3

Dilatris caroliniana Lam., Tabl. encycl. 1: 127. 1791, as "Caroliana". Holotype. UNITED STATES. North Carolina: s.loc., fl., fr., s.dat., Fraser s.n. (P-LA barcode P00382893!). Heritiera tinctorium Walter ex J.F.Gmel., Syst. Nat. 2: 113. 1791, nom. superfl. Heritiera gmelinii Michx., Fl. Bor.-Amer. 1: 21, pl. 4. 1803, as "Gmelini", nom. superfl.

Dilatris heritiera Pers., Syn. Pl. 1: 54. 1805, nom. superfl.

Gyrotheca tinctoria Salisb., Trans. Hort. Soc. London 1: 327. 1812; Gyrotheca tinctoria W.Stone, Pl. S. New Jersey 1: 354. 1911[1912], isonym.

Dilatris tinctoria Pursh, Fl. Amer. Sept. 1: 30–31. 1813[1814].

Lachnanthes tinctoria Elliott, Sketch Bot. S. Carolina 1(1): 47. 1816.

Lachnanthes tinctoria var. major C.Wright ex Griseb., Cat. Pl. Cub.: 252. 1866. Lectotype (designated by Maas & Maas van de Kamer 1993). CUBA. s.loc., fl., fr., 1860–1864, C. Wright 3270 (GOET barcode GOET004073!; isolectotypes: BM barcode BM000923988!; G barcode G00098220!, K barcode K000574289!, MO accession no. MO-202080!, NY barcodes 00073226!, 00073227!, P barcodes P00753470!, P00753471!, S accession no. S-R-3123!).

Anonymos tinctoria Walter, Fl. Carol.: 68. 1788, nom. rej.

Distribution and habitat. *Lachnanthes caroliniana* is known to occur from Nova Scotia (Canada) to Florida (USA), reaching Cuba (Fig 4). It grows in marshy and acidic environments, swampy grasslands, and moist pine forests throughout its range, generally producing extensive clonal populations.

Phenology. Flowers and fruits from April to November.

Conservation status. *Lachnanthes caroliniana* possess a wide EOO (1,886,962.465 km²) but a narrow AOO (ca. 616.000 km²). Nonetheless, as aforementioned, *L. caroliniana* is listed as Endangered in four USA states, Threatened in Rhode Island, of Special Concern in Massachusetts (USDA-NRCS 2013), and as Threatened in Canada (COSEWIC 2009). Thus, following IUCN (2001) recommendations *L. caroliniana* should be considered as Vulnerable (VU).

Comments. Lachnanthes caroliniana is morphologically variable regarding stature and coloration, with much of this variation being related to environmental conditions. The roots and underground organs can range from a yellowish orange to a dark red, the leaves, peduncles, bracts, and outsides of the tepals can range from light to dark green to bluish green, and the tepals can be internally light green to yellowish green to bright yellow. Aside from that, plants can range from 10 cm to over 100 cm tall.

Lachnanthes caroliniana is commonly considered a widespread weed in blueberry and cranberry crops (Meggitt and Aldrich 1959; Robertson 1976; Meyers et al. 2013), pastures (Ferrell et al. 2009), and to form extensive clonal populations followed by feral swine rooting disturbance (Boughton et al. 2016). Nonetheless, L. caroliniana is known to be an important nectar source for many insects (Hopper unpubl.) and a pollen source for bees and certain flies. It is viewed as an important "bridge species" supporting flower visitors in summer until fall composites begin to bloom (Boughton et al. 2016). Its seeds also constitute an important food source for sandhill cranes (Valentine and Noble 1970). And although generally abundant within its native range, L. caroliniana is listed as Endangered in four USA states (i.e., Connecticut, Maryland, New York, and Tennessee), Threatened in Rhode Island, and of Special Concern in Massachusetts (USDA-NRCS 2013), and Threatened in Canada (COSEWIC 2009).

3. *Pyrrorhiza* **Maguire & Wurdack**, Mem. New York Bot. Gard. 9(3): 318. 1957. Type species. *Pyrrorhiza neblinae* Maguire & Wurdack. Fig 5

Comments. Pyrrorhiza was originally described as being closely related to Schiekia Meisn. (Maguire and Wurdack 1957), a view supported by the morphological phylogeny of Simpson (1990), but not supported by the anatomical studies of Aerne-Hains and Simpson (2017) and the molecular phylogeny of Hopper et al. (in prep.). As currently understood, Pyrrorhiza is sister to Xiphidium s.str., with both being sister to the Cubanicula. The supposed relation between Pyrrorhiza and Schiekia was thought to be supported by zygomorphic perianth, dimorphic stamens, and the discontinuous subexterior exine wall (Simpson 1983, 1990), but the first two characters are clearly homoplastic in Haemodoroideae, while the second seems to be a convergence between Pyrrorhiza and Schiekia (Pellegrini et al., unpubl. data). Pyrrorhiza shares with Cubanicula the dry capsules with thickened septal ridges, and peculiar lenticellate seeds with the margin of the testa covered with coarse trichomes (Pellegrini et al., unpubl. data).

3.1. Pyrrorhiza neblinae Maguire & Wurdack, Mem. New York Bot. Gard. 9(3): 318, fig. 63a-g. 1957.Fig 5

Holotype. VENEZUELA. Amazonas: Río Yatua, Cerro de la Neblina, locally frequent in open savanna, 5 km SW of cumbre camp, alt. 1900 m, fl., fr., 6 January 1954, B. Maguire et al. 37108 (NY barcode 00247967!; isolectotypes: COL barcode COL000000167!, F barcode V0045883F!, GH barcode GH00030234!, IAN barcode IAN091102!, K barcode K000574291!, MICH barcode MICH1192344!, MO barcode MO-202079!, NY barcode 00247968, P barcode P00753469, S accession no. S-R-5402!, U barcode U0002447!, UC barcode UC1035482!, US barcode US00092054!, VEN barcode VEN39086!, W n.v.).

Distribution and habitat. *Pyrrorhiza neblinae* is until this moment only known to occur at the Venezuelan side of the Cerro de la Neblina (Fig 6). It grows in open, acidic and swampy *Heliamphora* Benth. (Sarraceniaceae) and *Bonnetia maguireorum* Steyerm. (Bonnetiaceae) savannas with *Euterpe* Mart. (Arecaceae), along streams, between 1800–2100 m. Due to its cormose underground system, *P. neblinae* forms dense clonal clusters. Its pollination syndrome is unknown but based on the vestigial pair of septal infralocular nectaries, it is most likely that *P. neblinae* is a pollen rewarding, self-compatible species.

Phenology. It was found in bloom and fruit from November to February.

Conservation status. As aforementioned, *Pyrrorhiza neblinae* is only known from a sole locality. It possesses very narrow EOO (20.126 km²) and AOO (ca. 12.582 km²), and thus, following IUCN (2001) recommendations *P. neblinae* should be considered as Critically Endangered [CR, B1a+C2a(ii)+D2].

Comments. *Pyrrorhiza neblinae* is still poorly known, with only a handful of collections. Nonetheless, it is known that *P. neblinae* is restricted to swampy savanna. The peculiar cormose underground system of *P. neblinae* is only comparable to those of *Barberetta* Harv., *Wachendorfia* Burm. (both Haemodoroideae), and *Tribonanthes* Endl. (Conostylidoideae) (Simpson 1998b). The seeds covered with coarse trichomes might also be an adaptation to hydric stress. These projections might help the seed to quickly absorb and

store water, which could come in handy in such an inconstant environment such as the tepuis (i.e., *Pyrrorhiza*), the white sand savannas (i.e., *Cubanicula*), and seasonally dry fynbos from South Africa (i.e., *Wachendorfia*).

4. *Schiekia* **Meisn.**, Pl. Vasc. Gen. 2(12): 300. 1842. Type species. *Wachendorfia orinocensis* Kunth. [≡ *Schiekia orinocensis* (Kunth) Meisn.]. Figs 7, 9 & 11

Troschelia Klotzsch & M.R.Schomb. in Reisen, Br.-Guiana: 1066. 1849, nom. nud.

Comments. Schiekia is indisputably closely related to Wachendorfia (Hopper et al. 1999, 2009, in prep.; Pellegrini et al., unpubl. data), which is shown by its taxonomic history and due to several morphological characters. Schiekia and Wachendorfia share some unique floral traits, such as the perianth apertures (produced by the connation of five tepals, giving the flowers a bilabiate appearance, and producing two basal pouches; Simpson 1990), and the infralocular septal nectaries with commissure slits which channel the nectar to the perianth apertures (Simpson 1993; Pellegrini et al., unpubl. data). These features serve as strong morphological synapomorphies that support the clade composed Schiekia+(Wachendorfia+Barberetta), with a posterior loss of the perianth apertures in Barberetta (Pellegrini et al., unpubl. data). Nonetheless, the nectary apparatus in Barberetta is extremely similar to that of Wachendorfia and Schiekia, only lacking the ducts that would carry the secreted nectar to the perianth apertures (Simpson 1993). Furthermore, Schiekia and Wachendorfia share the presence of tapering trichomes and dimorphic stamens, while Barberetta and Wachendorfia share the unique plicate leaves (Simpson 1990).

4.1. *Schiekia orinocensis* (Kunth) Meisn., Pl. Vasc. Gen. 2(12): 300. 1842. Fig 7

- Wachendorfia orinocensis Kunth, Nov. Gen. Sp. (quarto ed.) 1(3): 319. 1816. Lectotype (designated here). VENEZUELA. Isla de Pararuma, in humidis, in ripa Orinoco propter confluentem Sinaruci et in insula Pararuma, fl., fr., May, F.W.H.A. Humboldt & A.J.A. Bonpland 843 (P barcode P00669614!; isolectotype: P barcode P00669615!).
- Xiphidium angustifolium Willd. ex Link, Jahrb. Gewächsk. 1(3): 73. 1820, nom. superfl., Syn nov.
- Troschelia orinocensis (Kunth) Klotzsch & M.R.Schomb., Reis. Br.-Guiana 1066, 1120. 1849.
- Schiekia flavescens Maury, J. Bot. (Morot) 3: 269. 1889. Lectotype (designated here). VENEZUELA. Upper Río Orinoco, Atures, Salvajito, fl., 3 Apr 1887, M. Gaillard 52 (P barcode P06891121!, pro parte, the two specimens on the sides).
- Schiekia congesta Maury, J. Bot. (Morot) 3: 269, f. 12. 1889, nom. nud.
- Schiekia orinocensis subsp. savannarum Maguire & Wurdack, Mem. New York Bot. Gard. 9(3): 320. 1957. Holotype. VENEZUELA. Amazonas: Cerro Yapacana, Río Orinoco, in savanna no. 1, northwest base of the mountain, fl., fr., 31 Dec 1950, B. Maguire et al. 30496 (NY barcode 00214486!; isotypes: F barcode V0045884F!, K barcode K000574294!).

Nomenclatural notes. When describing *Wachendorfia orinocensis*, Kunth (1816) mentions a collection made in Isla de Pararuma, Río Orinoco, but makes no reference to collector, collection number, or herbarium. During a visit to P herbarium, we came across two specimens in which the labels matched the locality in the protologue, and also had a label indicating it had been part of the Bonpland & Humboldt herbarium. The specimen P00669614 is clearly where the majority of the original illustration was based upon, while P00669615 was only used to illustrate the fruits. Thus, since the specimen P00669614 possesses well-preserved leaves and stems, floral buds, and mature flowers, it is here designated as the lectotype.

When describing *Schiekia flavescens*, Maury (1889) mentions two collections, *Gaillard* 52 and *Chaffanjon 185*. During a visit to P, we were unable to locate the collections *Chaffanjon 185*, but managed to find *Gaillard 52*. The later was cited by Maury as a mixed gathering, with two specimens of his *S. flavescens* and a central specimen of *S. orinocensis*. Thus, we designate the two lateral specimens (right and left) as the lectotypes for *S. flavescens*.

Distribution and habitat. *Schiekia orinocensis*, in its current circumscription, is a much more geographically restricted taxon, than traditionally accepted. It is known to occur in Colombia, Guyana, Venezuela, and Brazil (states of Amazonas, Pará, Roraima) (Fig 8), in tepuis and other montane formations in the Guyana Shield, in seasonally flooded environments.

Phenology. It was found in flower and fruit from June to October but during the dry season.

Conservation status. Schiekia orinocensis possesses a wide EOO (1,193,173.154 km²), but a relatively narrow AOO (ca. 224.000 km²). This narrow AOO might be related to the relatively reduced number of collections, especially when compared to *S. timida*. This might be due to the difficulty to reach and collect specimens in tepui and other mountainous formations in the Amazon region. Nonetheless, field observations by one of us (EJH) indicate that *S. orinocensis* forms considerably smaller and more restricted subpopulations than *S. timida*, which might indicate it is ecologically more demanding. Thus, following IUCN (2001) recommendations *S. orinocensis* should be considered as Vulnerable [VU, A2ab+C2a(i).

Comments. Schiekia has consistently been treated as a monospecific genus until the present study since S. flavescens has been considered a synonym of S. orinocensis since very early days. Nonetheless, previous studies such as Maguire and Wurdack (1957) and Maas and Maas van de Kamer (1993) have treated the polymorphism observed in herbarium specimens by the recognition of different subspecies. Both previous attempts to divide S. orinocensis were almost entirely based on vegetative morphology, with the second one relying also on the proportion between the leaves and the inflorescences (Maas and Maas van de Kamer 1993). The observed variation in plant stature, and leaf length and width, which was used by previous authors to recognize subspecies (Maguire and Wurdack 1957; Maas and Maas van de Kamer 1993), seems to be purely environmental and thus disregarded as taxonomically relevant. Our present treatment is based on extensive field and herbaria studies and suggests that three species can be recognized, based on ecological preferences, underground system morphology, leaf morphology, tepal arrangement and coloration, the width of the filiform staminodes, and capsules morphology and coloration. Schiekia orinocensis s.str. is morphologically similar to S. timida due to its rhizome morphology, leaf arrangement and

consistency, inflorescence architecture, upright to patent flowers, and filiform staminodes, differing mainly due to floral morphology. *Schiekia orinocensis s.str.* can be differentiated by its chasmogamous and bilabiate flowers (*vs.* cleistogamous and narrowly tubular in *S. timida*), tepals externally hirsutulous (*vs.* glandular-pubescent), apex reflexed and apricot to cream (*vs.* straight and light to medium green), upper tepals with three dark orange to orange-brown nectar guides (*vs.* lacking nectar guides), medial filament not inflated (*vs.* inflated), staminodes almost as long as its subtending tepal (*vs.* 1/3 the length of its subtending tepals), and capsules broader than long (*vs.* slightly longer than broad or as broad as long). *Schiekia orinocensis s.str.* and *S. silvestris* share the chasmogamous flowers and upper tepals with nectar guides and capsules slightly longer than broad or as broad as long. Nonetheless, they can be easily differentiated based on vegetative morphology, flower orientation, shape and thickness of the filiform staminodes, and capsule coloration.

4.2. Schiekia silvestris (Maas & Stoel) Hopper, E.Hickman, Rhian J.Sm. & M.Pell., comb. et stat. nov.

Fig 9

Schiekia orinocensis subsp. silvestris Maas & Stoel in Maas PJM & Maas van de Kamer H, Fl. Neotrop. Monogr. 61: 21. 1993. Holotype. BRAZIL. Amazonas: Rio Negro, road from Camanaus to Vaupés airport, fl., 30 Oct 1971, G.T. Prance et al. 15864 (INPA barcode INPA34082!; isotypes: F, K barcode K000574292!, MG n.v., MO n.v., NY barcode NY00247969!, S barcode S06-6076!, U barcode U0002448!, US barcode US00592174!).

Distribution and habitat. Brazil (states of Amazonas, Pará, and Roraima), Colombia, French Guiana, Surinam, and Venezuela (Fig 10). Found growing in seasonally flooded forest understory, near rivers.

Phenology. It was found in flower and fruit from January to November but peaking during the dry season.

Conservation status. Schiekia silvestris possesses a wide EOO (1,634,289.582 km²), but a relatively narrow AOO (ca. 392.000 km²). This narrow AOO might, once again, be related to difficulty to collect in the Amazon region. Nonetheless, the number of known collections is relatively big, which leads us to believe this species might be much more common than Maas and Maas van de Kamer (1993) were led to believe. Thus, following IUCN (2001) recommendations S. silvestris should be considered as Least Concern (LC).

Comments. Schiekia silvestris is by far the easiest species to differentiate from the three accepted by us in the present study. It is the only species to exclusively inhabit understory and other mesic habitats and has a growth form similar to the one of *X. caeruleum*, with its long and trailing rhizomes and leaves evenly distributed along the stem. Aside from that, the leaves are considerably more delicate and broader, and several herbarium specimens of *S. silvestris* are commonly misidentified as *X. caeruleum* in Brazilian herbaria. Furthermore, the inflorescences of *S. silvestris* generally possess a corymb-like appearance, added to the diminutive and strongly bilabiate, pendulous, apricot to orange-yellow flowers, with tepals reflexed at the apex, and thick staminodes. The capsules of *S. silvestris* also tend to be much broader than those of *S. orinocensis* and *S. timida*, ranging from green when immature to chocolate brown when mature.

4.3. *Schiekia timida* M.Pell., E.J.Hickman, Rhian J.Sm. & Hopper, sp. nov. Fig 11

Diagnosis. Similar to *Schiekia orinocensis* (Kunth) Meisn. in rhizome morphology, leaf arrangement and consistency, inflorescence architecture, floral orientation, and filiform staminode, but differs due to its inflorescences lacking cincinni bracts, narrowly tubular and cleistogamous flowers, tepals externally glandular-pubescent, apex straight, light to medium green, upper tepals lacking nectar guides, medial filament inflated, staminodes 1/3 the length of its subtending tepals, and capsules slightly longer than broad or as broad as long.

Type. BRAZIL. Tocantins: Natividade, Serra da Natividade, fl., fr., 6 Mar 2015, R.C. Forzza et al. 8562 (RB!; isotypes: CEPEC!, HTO!, UPCB!).

Description. Herbs ca. 40–100 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal in boggy areas. Roots thick, fibrous, orange to red, sand-binding, emerging from the rhizome. Rhizomes underground, short, new shoots externally reddishorange to red, older shoots externally brown to reddish-brown, internally orange to reddishorange to red. Stems inconspicuous to short, ascending to erect, fibrous, unbranched; internodes inconspicuous when sterile, 2.5-7.9 cm long when fertile, green to orange to reddish orange, glabrous to tomentose, hairs pilate, light to medium brown. Leaves distichously-alternate, equitant, congested at the apex of the stem when sterile, some evenly distributed along the elongated stem when fertile, sessile, the apical ones gradually smaller than the basal ones; sheaths 2.2–14.8 cm long, light green, glabrous to sparsely tomentose, margin glabrous to ciliate, hairs pilate, light to medium brown; blades 1.7–29.2 × 0.4–1 cm, fibrous to coriaceous, unifacial, yellowish green to medium green to bluish green, drying olive-green to brown, linear to linear-elliptic, slightly ensiform to ensiform, glabrous to tomentose, hairs pilate, light to medium brown, base sheathing, margins green, glabrous to ciliate, apex acuminate; midvein inconspicuous, secondary veins 4-6, slightly impressed, becoming prominent when dry. Inflorescences terminal, solitary, consisting of a pedunculate many-branched thyrse; peduncles 7.7-38.8 cm, tomentose to densely tomentose, with a mixture of pilate glandulous hairs, light to medium brown; basal bract $1.8-7.3 \times 0.1-0.4$ cm, leaf-like, linear to linear-elliptic, straight to slightly ensiform, glabrous to tomentose, with a mixture of pilate glandulous hairs, light brown, base truncate to slightly sheathing, margin ciliate, apex acuminate, secondary veins inconspicuous; cincinnus bract absent; cincinni 6–28 per thyrse, alternate, 1-6-flowered, sessile, bright orange to reddish orange, tomentose to densely tomentose, hairs glandulous, light brown; bracteoles 4.6-8.8 × 1.4-3.1 mm, lanceolate to elliptic to broadly elliptic, bright orange to reddish orange, apex sometimes green to yellowish green, tomentose, hairs glandulous, light brown, base cuneate, margin glabrous, hyaline, apex acute. Flowers 0.2-0.4 cm diam., bisexual, cleistogamous, enantiostylic, campanulate, asymmetric due to the position of the style; floral buds 4.2–8.2 × 2–2.9 mm, ovoid, orange to reddish orange, base generally white to cream, apex light green; pedicels 2.3-7.2 mm long, orange to reddish orange, densely tomentose with a mixture of pilate and glandular hairs, white to light brown, upright to patent and elongate in fruit; perianth zygomorphic, upper lobes connate to 2/3 of their length, upper and lower lateral lobes basally conate forming two lateral perianth pouches, nectar guide absent, outer lobes $8.3-10.1 \times 1.8-2.3$ mm, subequal, the upper slightly broader and longer, the lateral ones asymmetric, elliptic to spathulate or lanceolate, externally white to cream, base apricot to bright orange to reddish orange, apex medium to light green, rarely completely apricot to bright orange to reddish orange, tomentose to densely tomentose, hairs glandulous, white to light brown, internally white to cream, base light orange to apricot, apex medium to light

green, rarely completely light orange to apricot, glabrous, base truncate or cuneate, symmetric in the upper, asymmetric in the lateral ones, margins glabrous, apex obtuse, inner lobes 7.2– $10.2 \times 4.8 - 7.3$ mm, subequal, the lower slightly broader, the upper ones asymmetric, elliptic to spathulate, externally white to cream, base apricot to bright orange to reddish orange, apex medium to light green, rarely completely apricot to bright orange to reddish orange, glabrous, tomentose along the midvein, hairs glandulous, white to light brown, internally white to cream, base light orange to apricot, apex medium to light green, rarely completely light orange to apricot, glabrous, base cuneate, the upper ones asymmetric, the lower one symmetric, margins glabrous, apex obtuse to slightly emarginate; staminodes 2, 3.5–3.7 × 0.1-0.2 mm, adnate to the base of the lateral outer perianth lobes, thin, filiform, white; stamens 3, lateral stamens with filaments 4.4–5.1 mm long, slender, slightly sigmoid, apex filiform, decurved downwards, cream, basally apricot, apically white, glabrous, anthers 0.5– 0.6 × 0.4–0.6 mm, basifixed, deciduous, extrorsely rimose, broadly oblongoid to broadly ellipsoid, with an apical connective appendage, cream, central stamen with filament 5.1–5.8 mm long, sigmoid, slightly spirally coiled either to the left or to the right, apex decurved downwards, cream, basally apricot, apically white, glabrous, anthers $1.1-1.4 \times 0.6-0.8$ mm, dorsifixed, extrorsely rimose, broadly oblongoid to broadly ovoid, cream; ovary 1.4–1.7 × 1.5-1.8 mm, broadly ovoid to subglobose, slightly trigonous, 3-loculate, apricot to bright orange, smooth, glabrous, style 3.4–3.8 mm, slightly sigmoid, apex decurved downwards, white, basally cream to apricot to light orange, glabrous, stigma capitate, white, papillose. Capsules 6.4–7.1 × 4.6–5.7 mm, broadly ellipsoid in outline, trigonous, dry, thick-walled, orange when immature, becoming medium to dark red when mature, loculicidal, 3-valved. Seeds 1.6–2.2 × 1.3–1.7 mm, deltoid, each face sunken, testa medium to dark brown, reticulate; embryotega dorsal, relatively inconspicuous, without a prominent apicule; hilum punctate.

Specimens seen (paratypes). BRAZIL. Amazonas: Rio Negro, across Comunidade Aparecida, 1 km up from Rio Taurí, fl., fr., 7 Nov 1987, D.W. Stevenson et al. 890 (K, NY). Goiás: Salinas, fl., Mar-Jul 1844, M.A. Weddell 2087 (P); Caiapônia, 46 km N de Caiapônia, fl., fr., 23 Feb 1982, P.I. Oliveira & W.R. Anderson 425 (MBM, MICH, MO, NY). Maranhão: Carolina, Cachoeira do Garrote, margem esquerda do Rio Garrote, ca. 4.3 km W da estrada, fl., 24 Feb 2005, G. Pereira-Silva et al. 9624 (CEN); Parque Nacional da Chapada das Mesas, Gleba II, fl., fr., 9 Apr 2016, A.C. Sevilha et al. 5742 (CEN); perto de Carolina, fl., 26 May 1950, J.M. Pires & G.A. Black 2262 (IAN); BR-010, Transamazônica, Pedra Caída, fr., 13 Apr 1983, M.F.F. Silva et al. 1084 (IAN, INPA, MG, MO, NY); Vereda do Seu Zico, ca. 3.5 km do asfalto, fl., fr., 27 Feb 2005, G. Pereira-Silva et al. 9702 (CEN); estrada Carolina/Babaculândia, km 8.2, margem direita do Rio Tocantins, kms marcados da Igreja São Francisco, Bairro Brejinho, fr., 22 May 2010, G. Pereira-Silva et al. 15292 (CEN); Riachão, estrada Riachão/Vila Nova de Carli, Proceder III, ca. 30 km S de Riachão, fl., 21 Mar 2000, B.M. Walter et al. 4426 (CEN); rodovia Vila Gerais das Balsas/Riachão, km 153, fl., 24 Mar 1999, G. Pereira-Silva et al. 4140 (CEN). Mato Grosso: Canabrava do Norte, Serra do Roncador, ca. 60 km N of Xavantina, fr., 25 May 1966, H.S. Irwin et al. 16002 (K, MO, NY, RB, U, UB, US); Cataqui-imaúi, Campos dos Urupós, Cab. do Cantário, fl., Dec 1918, J.G. Kuhlmann 1647 (RB); Rio Turvo, ca. 210 km N of Nova Xavantina, fr., 29 May 1966, H.S. Irwin et al. 16283 (K, NY, RB, UB, US); Nova Canaã do Norte, resgate de flora da UHE Colider, estrada de acesso à UHE, fl., fr., 26 Feb 2015, M.E. Engels & M. Lautert 2839 (CNMT, HERBAM, MBM, RB, TANG); fr., 27 Apr 2016, H.R.W. Zanin 373 (CNMT, HERBAM, RB); Nova Xavantina, Km 85 from Nova Xavantina-Cachimbo road, fr., 31 May 1966, D.R. Hunt & J.F. Ramos 5695 (K, NY, UB); Serra do Roncador, ca. 84 km N of Nova Xavantina, fr., 6 Jun 1966, H.S. Irwin et al. 16454 (MO, NY, RB, UB, UMO, US); 60 km

from Nova Xavantina, fl., fr., 6 Jun 1966, D.R. Hunt & J.F. Ramos 5835 (K, NY, UB); 20 km NE of Base Camp of the Expedition, fl., fr., 4 Mar 1968, D.R. Gifford 2657 (K, NY, UB); Km 57 N from Nova Xavantina-Cachimbo road, fl., 16 Jan 1968, D. Philcox & A. Ferreira 4080 (K, UB); Km 241 from Nova Xavantina-Cachimbo road, fl., fr., 16 Mar 1968, D. Philcox & A. Ferreira 4563 (K); ca. 1 km E from Km 242 from Nova Xavantina-Cachimbo road, fl., fr., 18 Mar 1968, D. Philcox & A. Ferreira 4567 (K, MO, NY, P, RB, S, UB); ca. 15 km S of Base Camp of the Expedition, Lagoa do Sucuri, close to the Nova Xavantina-São Felix road, fr., 13 Jun 1968, R.R. Santos et al. 1767 (IAN, K, NY, P, UB); 270 km N of Nova Xavantina, Lagoa do Leo, 8 km SW of Base Camp of the Expedition, fl., fr., 8 May 1968, J.A. Ritter et al. 1362 (K, NY, UB); Santa Cruz do Xingu, Parque Estadual do Xingu, limite norte do parque, fl., fr., 4 Mar 2011, D.C. Zappi et al. 3091 (K, RB, UNEMAT); Vila Bela da Santíssima Trindade, topo da Cachoeira do Jatobá, fl., fr., 17 May 2013, J.E.O. Faria et al. 3508 (CEN, RB, SP, UB). Pará: Belém do Pará, Ariramba, igarapé Quebra-Dente, fl., 30 May 1957, G.A. Black et al. 57-19801 (IAN); Itaituba, arredores da base Aérea do Cachimbo, próximo ao destacamento Km 6 da estrada para o Aeroporto, Km 794, fr., 25 Apr 1983, M.N. Silva et al. 73 (INPA, K, RB). Roraima: Boa Vista, estrada do Cantá, fl., 31 Jul 1986, J.A. Silva et al. 539 (MO, NY, UB); estrada para Serra Grande, fl., 4 Aug 1986, E.L. Sette-Silva et al. 665 (K, MIRR, MO, NY); Ilha de Maracá, sandy savanna at Santa Rosa, at the E side of the island, fl., fr., 8 Oct 1987, J. Pruski et al. 3417 (INPA, K, MG, MO, NY); Caracaraí, estrada Perimetral Norte [BR-210], 9 km do entroncamento com as estrada Manaus/Caracaraí [BR-174], próximo a Novo Paraíso, fl., fr., 28 Aug 1987, C.A. Cid Ferreira et al. 9210 (INPA, NY, U). Tocantins: [Govaz] between Natividade and Conceição, fl., Feb 1866, G. Gardner 4014 (BM, G, K, NY, P); Almas, RPPN Fazenda Minnehaha, campo úmido limpo bordeado pelo Cerrado que desce a barra do Rio Lapa com o Rio Laurentino, fr., 21 Apr 2004, J.M. Felfili et al. 522 (RB); Barra do Ouro, margem direita do Rio Tauá, ca. 12 km de Barra do Ouro, ponte suspensa, fl., 15 Jan 2010, G. Pereira-Silva et al. 14926 (CEN); Centenário, Bacia do Tocantins, Sub-bacia do Rio Manuel Alves Pequeno, fl., fr., 27 Mar 2010, M.L. Fonseca et al. 6494 (IBGE, RB); Goiatins, Área Indígena Krahô, Aldeia Nova, fr., 8 Mar 2000, E. Rodrigues 695 (PMSP); estrada Aldeia Indígena Krahô Santa Cruz/Itacajá, km 10, margem direita do Riozinho, próximo a Kapey, fr., 27 Apr 2009, G. Pereira-Silva et al. 14314 (CEN); estrada Goiatins/Itacajá, margem esquerda do Ribeirão Cartucho, fr., 4 May 2009, G. Pereira-Silva et al. 14391 (CEN); Reserva Indígena Krahô, Aldeia Pedra Branca, fl., fr., 6 May 2000, A.A. Santos et al. 659 (CEN); Guaraí, margem esquerda da Ferrovia Norte Sul, estrada vicinal Guaraí/Itupiratins, fl., fr., 24 Apr 2009, G. Pereira-Silva et al. 14217 (CEN); Gurupi, rodovia Belém/Brasilia, 5 km S de Gurupi, fl., fr., 24 Mar 1976, G. Hatschbach & R. Kummrow 38313 (MBM, MO, NY); Itapiratins, Bacia do Tocantins, Sub-bacia do Rio Tocantins, fl., fr., 24 Mar 2010, F.C.A. Oliveira et al. 1834 (IBGE, RB); Kraolandia, próximo a cidade de Peritoró, fl., 20 Mar 1974, J.S. Assis 26 (RB); Lagoa da Confusão, Bacia do Araguaia, Subbacia Rio Formoso, fr., 22 Mar 2010, F.C.A. Oliveira et al. 1666 (IBGE, RB); Mateiros, fr., 3 May 2001, R. Farias et al. 363 (CEN, UB); entorno do Parque Estadual do Jalapão, estrada Mateiros/Ponte Alta, ca. 2 km do Rio Novo, fr., 15 Jun 2002, T.B. Cavalcanti et al. 2831 (CEN); margem esquerda do Rio Novo, fl., fr., 8 May 2001, C.E.B. Proença et al. 2523 (UB); estrada Mumbuca/Boa Esperança, Vereda do Bebedouro, fl., fr., 8 Mar 2006, G.H. Rua et al. 787 (CEN); Parque Estadual do Jalapão, Vereda do Porco Podre, fl., fr., 15 Feb 2005, J.M. Rezende et al. 1019 (CEN); Pindorama do Tocantins [Pindorama de Goiás], fl., fr., 21 Apr 1978, R.P. Orlandi 78 (RB). BOLIVIA. Santa Cruz: Velasco, Parque Nacional Noel Kempff Mercado, Campamento Huanchaca II, fl., 8 Mar 1997, S. Jiménez et al. 1254 (MO, U); Campamento Las Torres, margen del Río Iténez [Guaporé], frontera con Mato Grosso, lado noreste del Serrania Huanchaca, 24 km S Flor de Oro, fr., 24 May 1991, M. Peña & R. Foster 222 (U); Lago Caimán, fl., 15 Jan 1997, T. Killeen et al. 8151 (U, USZ). COLOMBIA. Guainia: Casuarito, immediately S of Casuarito, lajas along the Río Orinoco, fl., 22 Jun 1984, G. Davidse & J.S. Miller 26411 (MO, U). Guajira: Barrancas, Río Quatiquia, fl., 16 Jul 1897, Lehmann 8841a (K); llanos on Río Meta and Río Quatiquia, fl., fr., 16 Jul 1897, Lehmann 8841b (K). GUYANA. Rupununi: Manari, fl., 24 Jul 1995, M.J. Jansen-Jacobs et al. 4621 (K, P, U). VENEZUELA. Amazonas: Atures, alrededores de Puerto Ayacucho, ca. 4 km SE, sabana de los alrededores del vivero de MARNR, alto Caño Carinagua, fl., 17 Jun 1977, O. Huber 841 (MO, U, VEN); Carretera Coromoto, along Río Coromoto, Tobogán de la Selva, 35 km SE of Puerto Ayacucho, fl., 14 May 1980, J.A. Steyermark et al. 122561 (F, U, VEN); Oripopos, 7 km N of Puerto Ayacucho on the road to El Burro, fl., 22 Jun 1984, J.S. Miller 1608 (MO, U); San Juan de Manapiare, sobanas sobre los cerros de arenisca al Norte del Cerro Movocoy, arriba del sitio llanado "Pazo de la Carlina" a unos 12 km al Oeste de San Juan de Manapiare, fl., fr., 16 Oct 1977, O. Huber 1205 (MO, U).

Etymology. The epithet means "shy" and makes reference to the cleistogamous flowers, which open only a few millimetres. This is the first record of cleistogamy in the Haemodoraceae.

Distribution and habitat. Currently known for Brazil (states of Amazonas, Pará, Roraima, Tocantins, Maranhão, Goiás, and Mato Grosso), Colombia, Guyana, and Venezuela (Fig 12). Found growing in seasonally flooded grasslands.

Phenology. It was found in flower and fruit from November to June, rarely during July and August, but peaking during the rainy season.

Conservation status. *Schiekia timida* possesses wide EOO (5,598,458.893 km²) and AOO (ca. 580.000 km²). Thus, following IUCN (2001) recommendations *S. timida* should be considered as Least Concern (LC).

Vernacular name and use. Called "ahtu" in the language spoken by the native Brazilian Krahô tribe. *Schiekia timida* seems to be used in some religious ceremonies, together with some confirmedly psychoactive plants.

Comments. Schiekia timida is morphologically similar to S. orinocensis due to its rhizome morphology, leaf arrangement and consistency, inflorescence architecture, floral orientation, and filiform staminodes, but differs due to its inflorescence lacking cincinni bracts, narrowly tubular and cleistogamous flowers, tepals externally glandular-pubescent, apex straight, light to medium green, upper tepals lacking nectar guides, medial filament inflated, staminodes 1/3 the length of its subtending tepals, and capsules slightly longer than broad or as broad as long. Until the present work, both species were treated under a broad concept of S. orinocensis subsp. orinocensis, as proposed by Maas and Maas van de Kamer (1993). However, as noticed by the authors during fieldwork, S. timida seems to be a cleistogamous species, with flowers never opening more than a few millimetres.

5. Xiphidium Aubl., Hist. Pl. Guiane 1: 33, pl. 11. 1775. Type species. Xiphidium caeruleum Aubl.

Figs 13 & 15

Tonduzia Boeckeler ex Tonduz, Bull. Herb. Boissier 3: 464. 1895, nom. nud.

Durandia Boeckeler, Allg. Bot. Z. Syst. 2: 160, 173. 1896, **Syn. nov.** Type species. Durandia macrophylla Boeckeler (= Xiphidium caeruleum Aubl.).

Comments. Xiphidium has traditionally been considered an ill-circumscribed genus, lacking any obvious synapomorphy (Simpson 1990, 1993, 1998b). However, with the transfer of X. xanthorrhizon to Cubanicula, Xiphidium s.str. easily can be defined by its introrsely rimose but functionally poricidal anthers (an adaptation to buzz-pollination; Buchmann 1980), the complete loss of septal nectaries (also an adaptation to buzz-pollination), capsules brightcoloured, indehiscent, lacking thickened septal ridges, and somewhat fleshy at maturity (a possible adaptation to zoochory), and cuboid seeds (Pellegrini et al., unpubl. data). All these characters are unique in the family and observed on the two species of *Xiphidium* accepted by us in the present study. The anther morphology of Xiphidium and its floral biology are reminiscent of some species of *Dichorisandra* J.C.Mikan (Commelinaceae, Commelinales) that also possess introrsely rimose but functionally poricidal anthers (Pellegrini and Faden 2017). However, studies on the reproductive biology of Xiphidium are almost non-existent, save that by Buchmann (1980). Further studies focusing on effective pollination and seed dispersal should be investigated. The genus is well documented as a medicine for snake bite (Odonne et al. 2013), as well as having antimalarial and leishmanicidal properties (Valadeau et al. 2009). Xiphidium caeruleum also shows the greatest levels of genetic divergence for any species of Haemodoraceae amongst populations across its wide Neotropical range. Further detailed taxonomic study is recommended.

5.1. *Xiphidium caeruleum* **Aubl.**, Hist. Pl. Guiane 1: 33, pl. 11. 1775. Fig 13

Xiphidium floribundum var. caeruleum (Aubl.) Hook., Bot. Mag. 84: t. 5055. 1858. Lectotype (designated by Maas & Maas van de Kamer 1993). [Illustration] Original parchment plate of Histoire des Plantes de la Guiane Françoise and later published in Aublet, Hist. Pl. Guiane 1: 33, pl. 11. 1775.

Ixia xiphidium Loefl., Iter Hispan.: 179. 1758. Type: VENEZUELA. Macarapa, s.dat., P. Loefling s.n. (LINN? not found).

Xiphidium floribundum Sw., Prodr.: 17. 1788.

Xiphidium albidum Lam., in Lamarck & Poiret Tabl. Encycl. 1: 131. 1791, nom. superfl.

Xiphidium album Willd., Sp. Pl. Editio quarta 1(1): 248. 1798.

Xiphidium floribundum var. *albiflorum* Hook., Bot. Mag. 84: t. 5055. 1858, nom. superfl. (≡ *X. floribundum* Sw. var. *floribundum*).

Xiphidium caeruleum var. albidum (Lam.) Backer, Handb. Fl. Java 3: 80. 1924.

Xiphidium loeflingii Mutis, Diario 2: 51. 1958, nom. nud.

Eccremis scabra Kuntze, Revis. Gen. Pl. 3(3): 316. 1898. Holotype. B†. Lectotype (designated here). BOLIVIA. Cochabamaba: Chapare, Río Juntas, fr., 13–21 Apr 1892, C.E.O. Kuntze 461 (NY barcode 00841967!), **Syn. nov.**

Xiphidium giganteum Lindl., Edwards's Bot. Reg. 32: under t. 66. 1846. Type. (K?, not

found).

- Xiphidium fockeanum Miq., Linnaea 17: 63. 1843. Lectotype (designated by Maas & Maas van de Kamer 1993). SURINAM. prope Paramaribo, fl., April 1654, H.C. Focke 293 (U barcode U0002449!; isolectotype: P barcodes P00753474!, P02188828!).
- *Xiphidium rubrum* D.Don, Edinburgh New Philos. J. 13: 235. 1832. Lectotype (designated here). PERU. s.loc., fl., s.dat., J.A. Pavón 358 (BM barcode BM000923989!; isolectotype: MA barcode MA810534!).
- Ornithogalum rubrum Ruiz & Pavón ex D.Don, Edinburgh New Philos. J. 13: 235. 1832, nom. not val. publ., pro. syn.
- Durandia macrophylla Boeckeler, Allg. Bot. Z. Syst. 2: 173. 1896. Holotype. COSTA RICA. s.loc., fl., Nov 1893, A. Tonduz 8402 (B barcode BR0000006885779!), **Syn. nov.** *Tonduzia macrophylla* Boeckeler ex Tonduz, Bull. Herb. Boissier 3: 464. 1895, nom. nud.

Nomenclatural notes. The taxonomic circumscription of *Xiphidium caeruleum* is greatly impaired by lack of knowledge of the current whereabouts of several of its associated synonyms. Types for the names *X. caeruleum* and *X. fockeanum* were successfully located and designated by Maas and Maas van de Kamer (1993); while types for the names *X. rubrum*, *Eccremis scabra*, and *Durandia macrophylla* were located by us, and had types designated when necessary. Nonetheless, we have been unable to locate the type specimens of *X. giganteum* and *Ixia xiphidium*.

Maas and Maas van de Kamer (1993) erroneously designate plate 66 from Lindley (1846) as the lectotype of *Xiphidium giganteum*. Nonetheless, the indicated plate actually depicts *Swainsona greyana* Lindl. (Fabaceae), and obviously cannot be the type for *X. giganteum*. Lindley mentions that a live specimen was brought from Caraccas and flowered in Syon [Park], London. After searching for specimens that matched these data at K herbarium, we were unable to locate any. I also searched for a possible unpublished illustration that might serve as the type for *X. giganteum*, but were also unlucky. Thus, we currently are unable to designate a lectotype for *X. giganteum*, and choose to retain it under the synonym of *X. caeruleum*.

Ixia xiphidium was described by Loefling (1758) from Macarapa, Venezuela, without any mention of specimens or herbaria. After searching for specimens on several herbaria, we were unable to any specimens that matched the protologue.

When describing *X. rubrum*, Don (1832) mentions his new species is based on a Ruiz & Pavón collections, but without collection number or herbarium information. During a visit to BM we came across a specimen that matched the protologue in which it presented a label in Pavón's handwriting saying "Ornithogalum rubrum sp. n., Fl. Per.". This is specimen is here selected as the lectotype.

Kuntze (1898), described *Eccremis scabra* based on a collection from Río Juntas, Bolivia. The author mentions a specimen at B, but we were unable to locate it and it might have been lost during WWII. Luckily, we were able to locate a duplicate at NY, which is designated here as the lectotype.

Distribution and habitat. *Xiphidium caeruleum* is widely distributed in the Neotropics, ranging from Mexico, through the Antilles, reaching northern South America (Fig 14). It can be found growing in permanently or seasonally wet environments, more rarely in dry and rocky environments.

Phenology. It was found in bloom and fruit throughout the year.

Conservation status. As currently circumscribed, *Xiphidium caeruleum* is widely distributed, with equally wide EOO (14,922,958.926 km²) and AOO (ca. 3,056.000 km²). Thus, following IUCN (2001) recommendations *X. caeruleum* should be considered as Least Concern (LC).

Comments. Xiphidium caeruleum is a widely distributed species and even in our present circumscription, still a variable species. Despite our best efforts, we have been unable to undoubtedly correlate any of the observed morphological variability to any of the previously proposed names in Xiphidium. After careful study of protologues, we concluded that X. loeflingii Mutis, X. caeruleum var. albidum (Lam.) Backer, X. floribundum var. albiflorum Hook., X. album Willd., X. albidum Lam., X. floribundum Sw., and Ixia xiphidium Loefl., actually represent homotypic synonyms, and are unambiguously conspecific to the type of X. caeruleum. Alternatively, Durandia macrophylla Boeckeler, Eccremis scabra Kuntze, X. fockeanum Mig., and X. rubrum D.Don are all heterotypic synonyms. However, all diagnostic characters provided by the original authors in their respective protologues are easily observed in the typical morph of X. caeruleum. Some peculiar specimens of X. caeruleum are recorded for French Guiana (in which the specimens seem to present peculiarly large, red, crustose and trigonous fruits), Costa Rica (where some specimens possess flowers with three inconspicuous light green nectar guides at the base of the upper tepals), and Mexico (where specimen inner tepals much longer than the outer tepals, and perianth generally with apricot to pinkish hue). Furthermore, it is also known for berries of X. caeruleum to range from yellowish orange to orange with reddish-orange spots, or completely red. We were also unable to find any obvious correlation between the different colours of berries, geographical distribution, and any of the observed genetic diversity. Nonetheless, due to limited access to such morphs, and to herbarium specimens in *Xiphidium* being generally poorly preserved, we consider it premature to recognize or propose any taxonomic status to any of these morphs. Thus, we propose that studies focusing on population genetics and reproductive biology, associated with a morphometric study and intense field studies, are necessary to properly deal with the issue.

5.2. Xiphidium pontederiiflorum M.Pell., Hopper & Rhian J.Sm., sp. nov. Fig 15

Diagnosis. Similar to *Xiphidium caeruleum* Aubl. in habit and inflorescence morphology, differing due to its leaves marginally ciliate at apex, apricot to light orange flower buds, bigger and zygomorphic flowers, inner lobes obovate with obtuse to rounded apex, upper tepals connate in the basal third or halfway through with three orange-yellow to orange nectar guides, dark red to vinaceous mature capsules, and dark reddish brown to reddish black seeds.

Type. ECUADOR. Esmeraldas: Lita, Río Lita and tributaries, 120 km NW of Ibarra, 14 km of Lita, fl., fr., 7 May 1987, D.C. Daly & P. Acevedo-Rodríguez 5142 (US!; isotype: NY!).

Description. *Herbs* ca. 35–185 cm tall, perennial, rhizomatous with a definite base, terrestrial to paludal in boggy areas. *Roots* thin, fibrous, brown, sand-binding, emerging from the rhizome. *Rhizomes* underground, long, trailing, externally brown to reddish-brown, internally reddish-orange to red. *Stems* ascending to erect, fibrous, unbranched; internodes 4.3–7 cm long, green, glabrous to sparsely tomentose, hairs pilate, white. *Leaves* distichously-

alternate, equitant, evenly distributed along the stems, sessile, the apical ones gradually smaller than the basal ones; sheaths 0.6–2.2 cm long, light green, glabrous to sparsely tomentose, margin ciliate, hairs pilate, white; blades $18.7-47.3 \times (0.9-1.6-)2.4-5$ cm, fibrous, succulent, unifacial, medium green, drying olive-green to brown, linear-elliptic to narrowly elliptic, slightly ensiform to ensiform, glabrous, base sheathing, margins green, glabrous to ciliate at the apex, apex acuminate; midvein inconspicuous, secondary veins 5-8, slightly impressed to impressed, becoming more prominent when dry. Inflorescences terminal, solitary, consisting of a pedunculate many-branched thyrse; peduncles (1.5–)2.4–7.8 cm, sparsely tomentose to densely tomentose, hairs pilate, white; basal bract $5-5.7 \times 0.4-0.5$ cm, leaf-like, linear-elliptic, slightly ensiform to ensiform, glabrous or sparsely tomentose at base, hairs pilate, white, base truncate to slightly sheathing, margin ciliate at apex, apex acuminate, secondary veins inconspicuous; cincinnus bract 2.8–4.4 × 1.2–4 mm, broadly triangular to narrowly triangular, green, glabrous to sparsely tomentose, hairs pilate, white, base truncate, margin ciliate, apex acuminate; cincinni (9-)12-41 per thyrse, alternate, 3-18-flowered, peduncle 0.3–1.7 cm long, green, sparsely tomentose to densely tomentose, hairs pilate, white; bracteoles $0.8-1.3 \times 0.6-1$ mm, broadly triangular to broadly depressed ovate, green, glabrous to sparsely tomentose, hairs pilate, white, base amplexicaulous, non-perfoliate, margin glabrous, apex acute. Flowers 1.9-2.7 cm diam., bisexual, chasmogamous, enantiostylic, campanulate, asymmetric due to the position of the style; floral buds $4.8-6 \times$ 2.2–3 mm, ovoid, apricot to light orange; pedicels (2–)5.1–7.3 mm long, green, tomentose to densely tomentose, hairs pilate, white, upright and slightly elongate in fruit; perianth zygomorphic, lobes free, except for the upper 3 lobes which are conate on the basal third to mid-length, nectar guide orange-yellow to orange on the basal third of the conate lobes, outer lobes $8.5-13.1 \times 3.5-4.7$ mm, subequal, the upper slightly shorter, narrowly obovate to obovate, externally apricot to light orange, rarely white, glabrous to sparsely tomentose, hairs pilate, white, internally white, glabrous, base cuneate, margins glabrous, apex acute to obtuse, dark brown to black, inner lobes $9.7-13.2 \times 4.8-7.3$ mm, subequal, the lower slightly narrower and cucullate, obovate to broadly obovate to broadly obtrullate, externally white to apricot, rarely light orange, glabrous, internally white, glabrous, base cuneate, margins glabrous, apex obtuse to rounded, greenish yellow to apricot; stamens 3, lateral stamens with filaments 1.6-1.8 mm long, straight, basally cream to apricot, apically white, glabrous, anthers 1.4–1.7 × 0.6–0.9 mm, dorsifixed, introrsely rimose but functionally poricidal, broadly oblongoid to sagittate, yellow, central stamen with filament 3.7-4.3 mm long, bent upwards, basally cream to apricot, apically white, glabrous, anthers $2-2.4 \times 0.7-1.1$ mm, dorsifixed, introrsely rimose but functionally poricidal, broadly oblongoid to sagittate, yellow; ovary 1.8–2.2 × 1.7–2 mm, broadly ellipsoid to globose, 3-loculate, green to red to vinaceous, smooth, densely tomentose between the locules, style 5.6-8.3 mm, bent upwards, basally cream to apricot to light orange, apically white, glabrous, stigma truncate-trilobate, white, papillose. Capsules 5.2–7.4 × 5.8–8 mm, subglobose to globose, somewhat fleshy, medium green to dark red when immature, dark red to vinaceous when mature, glabrous, indehiscent. Seeds $0.78-0.84 \times 0.65-0.67$ mm, cuboid to polygonal, each face sunken, testa dark reddish brown to reddish black, tuberculate; embryotega dorsal, relatively inconspicuous, without a prominent apicule; hilum punctate.

Specimens seen (paratypes). COLOMBIA. Antioquia: Frontino, km 23 of road Nutibara/La Blanquita, region of Murrí, fl., fr., 4 Nov 1988, J.L. Zarucchi et al. 7140 (MO, US). Guarira: Sierra Nevada de Santa Marta, entre Riohacha y Pueblo Viejo, fr., 7 Feb 1959, H.G. Barclay & P. Juajibioy 6838 (US). Putamayo: road from Sibundoy to Mocoa, fl., fr., 15 Mar 1953, R.E. Schultes & I. Cabrera 18823 (GH, U, US); Intendencia of Putamayo, steep roadside slopes along road from Mocoa towards Sibundoy, fl., fr., 27 Jan 1976, J.L. Luteyn et

al. 5062 (F, NY, US). Valle del Cauca: km 100, on Cali/Buena-Ventura highway, fl., fr., 5 Dec 1946, O. Haught 5324 (US). Vaupés: Puerto Hevea, confluence of Macaya and Ajaju rivers, fl., Jul 1943, R.E. Schultes 5654 (GH, US). ECUADOR. El Oro: 11 km West of Pinas, on the new road to Santa Rosa, fl., fr., 8 Oct 1979, C.H. Dodson et al. 9012 (SEL, US); Pichincha: virgin forest along Río Toachi near Santo Domingo, fr., 3 Aug 1962, C. Jativa & C. Epling 322 (US). PANAMA. Colón: Canal Zone, Las Cascadas Plantation, near Summit, fr., 2 Dec 1923, P.C. Standley 25671 (US); hills north of Frijoles Station, fr., 19 Dec 1923, P.C. Standley 27414 (US); Gamboa, fr., 26 Dec 1923, P.C. Standley 28397 (US); near Fort Randolph, fr., 28 Dec 1923, P.C. Standley 28734 (US). Darien: Cerro Pirre, fr., 9–10 Aug 1967, J.A. Duke & T.S. Elias 13747 (GH, US); Río Chico, from Yaviza at junction with Río Chucunaque to ca. 1 hour by outboard from junction, fr., 19 Dec 1966, D. Burch et al. 1096 (GH, K, NY, UC, US). Panamá: Río La Maestra, fr., 4 Dec 1936, P.H. Allen 67 (MO, US). Panamá Oeste: Capira, about 50 km southwest of Panama City, fl., fr., Sep 1932, B. Paul 141 (US).

Etymology. The epithet refers to the similarity between the floral morphology of our new species and of some species of *Pontederia s.l.* (Pellegrini et al. 2018).

Distribution and habitat. *Xiphidium pontederiiflorum* is known to occur in Colombia, Ecuador and Panama (Fig 16), in the understory in rainforests, generally near rivers, along streams, and other water bodies.

Phenology. Blooms and fruits from March to August.

Conservation status. *Xiphidium pontederiiflorum* possesses a relatively narrow EOO (849,855.988 km²) and AOO (ca. 132.000 km²). Thus, following IUCN (2001) recommendations *X. pontederiiflorum* should be considered as Endangered [EN, A2ac+C2a(i).

Comments. Xiphidium pontederiiflorum is morphologically similar to X. caeruleum in overall habit and inflorescence morphology. However, X. pontederiiflorum can be differentiated by its leaves marginally ciliate at apex (vs. glabrous in X. caeruleum), apricot to light orange flower buds (vs. white to cream, rarely apricot in some Mexican populations), bigger and zygomorphic flowers (vs. smaller and actinomorphic flowers), inner lobes obovate with obtuse to rounded apex (vs. elliptic with acute apex), upper tepals connate in the basal third or halfway through with three orange-yellow to orange nectar guides (vs. only basally connate and lacking nectar guides), capsules dark red to vinaceous mature when mature (vs. orange to medium red), and dark reddish brown to reddish black seeds (vs. black). Added to that, X. pontederiiflorum is generally a more robust plant, growing erect up to 2 m tall, while X. caeruleum generally reaches up to 1 m tall and its stems tend to lean due to the plant's weigh, especially when in bloom or fruit.

Xiphidium pontederiiflorum was first collected in 1923 in Panama by the pioneering Neotropical botanist P.C. Standley (1884–1963) from the United States (Williams 1963). Reference was included to it under *X. caeruleum* in Standley's (1928) *Flora of the Panama Canal Zone*.

Conclusion

The Neotropical species of Haemodoraceae represent morphological outliers in the family, that remained poorly studied for far too long; despite previous comprehensive studies dealing

with macro- and micromorphology, and the systematics of the Haemodoraceae (Simpson 1985, 1987, 1990, 1993, 1998a, 1998b; Hopper et al. 2006, 2009; Smith et al. 2011; Aerne-Hains and Simpson 2017). Furthermore, most of its species dwell deep in the Amazon Forest, and key and enigmatic taxa, like *Pyrrorhiza neblinae*, are restricted to almost impossible to reach tepuis. This paper is the result of the combined efforts and collaboration of the authors, in hopes that this new data will update our current knowledge on the Haemodoraceae and encourage further studies on the family.

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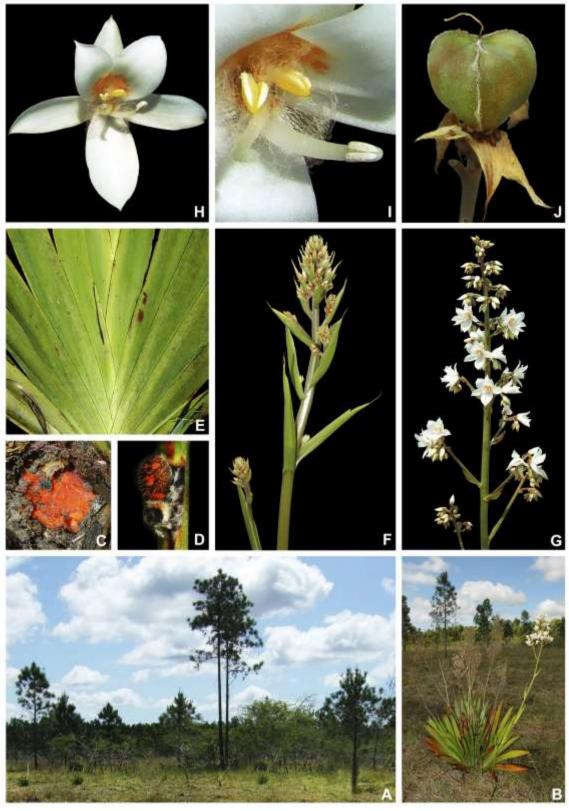


Figure 1. Cubanicula xanthorrhiza (C.Wright ex Griseb.) Hopper et al. **A,** habitat. **B,** habit. **C,** cross-section of the stem showing the bright orange coloration. **D,** spider that camouflages using the plant as a background. **E,** detail of the equitant leaves. **F–G,** inflorescences: **F,** immature inflorescence; **G,** mature inflorescence. **H,** flower. **I,** detail of the androecium and gynoecium. **J,** immature capsule showing the persistent hairs along the septal ridges.

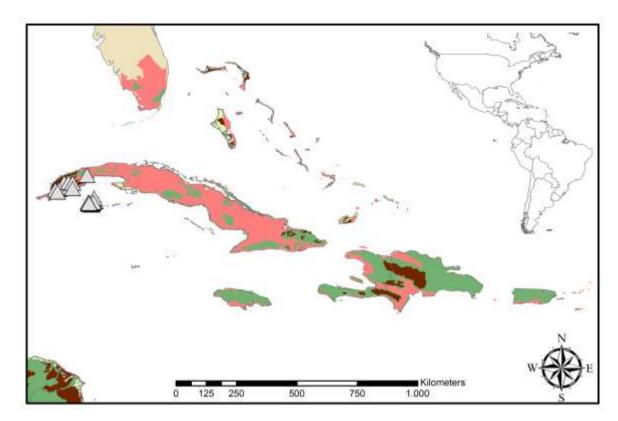


Figure 2. Distribution of *Cubanicula xanthorrhiza* (C.Wright ex Griseb.) Hopper et al. Beige— Temperate Coniferous Forests and Boreal Forests; Light Green— Subtropical Coniferous Forests; Red— Deserts, Xeric Shrublands and Tropical Coniferous Forests; Maroon— Dry Broadleaf Forests; Green— Moist Broadleaf Forests.

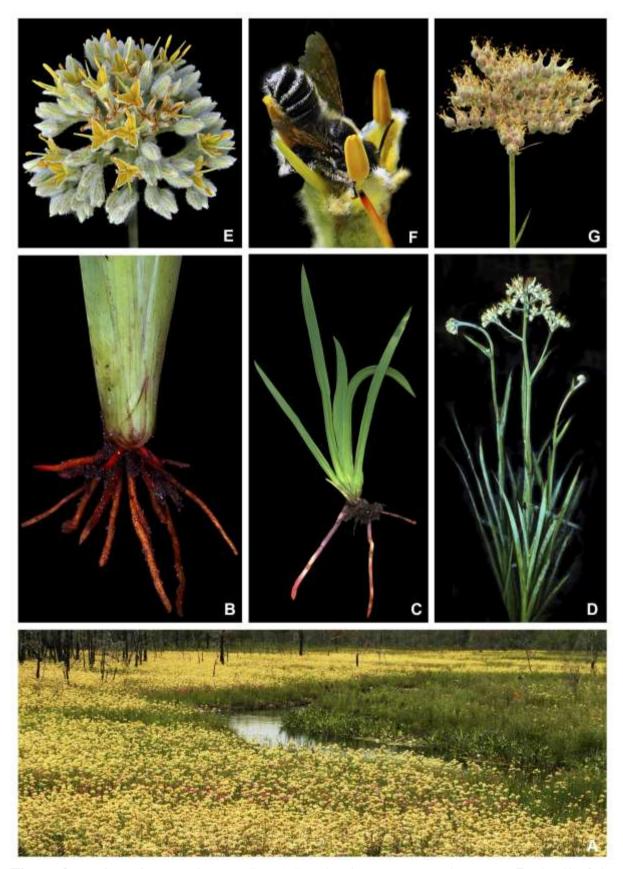


Figure 3. Lachnanthes caroliniana (Lam.) Dandy. **A,** swampy environment. **B,** detail of the red roots. **C,** habit showing flagelliform-shoots. **D,** habit of an adult flowering specimen. **E,** inflorescence showing externally lanate and internally glabrous and yellow perianth. **F,** detail of a flower being visited by a bee. **G,** fruiting inflorescence.

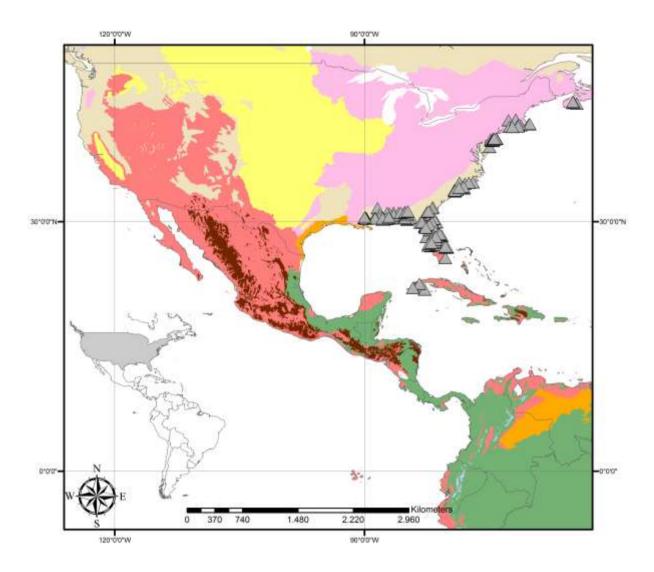


Figure 4. Distribution of *Lachnanthes caroliniana* (Lam.) Dandy. Beige—Temperate Coniferous Forests and Boreal Forests; Yellow—Temperate Grasslands, Savannas and Shrublands; Pink—Temperate Broadleaf and Mixed Forests; Light Green—Subtropical Coniferous Forests; Red—Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange—Tropical/Subtropical Grasslands, Savannas and Shrublands; Maroon—Dry Broadleaf Forests; Green—Moist Broadleaf Forests; Lilac—Montane Grasslands and Shrublands.

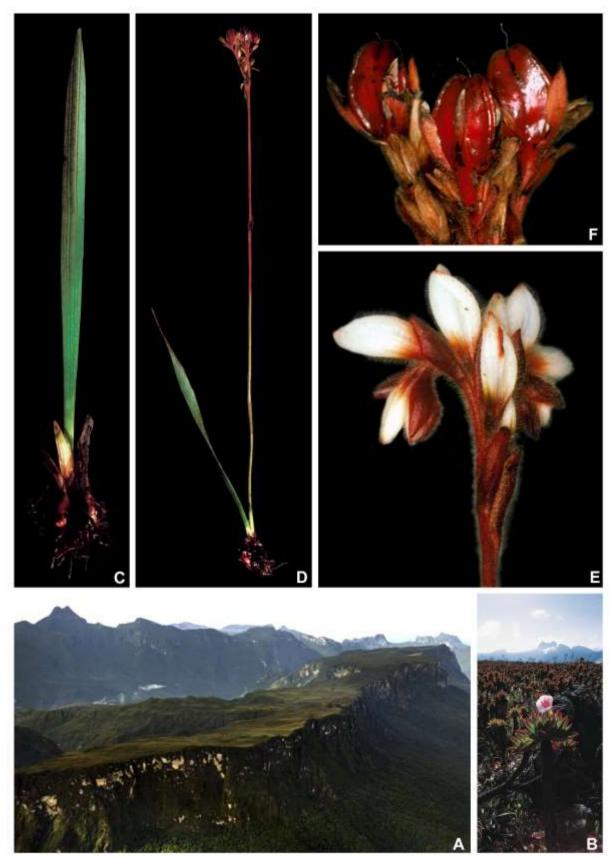


Figure 5. *Pyrrorhiza neblinae* Maguire & Wurdack. **A,** Cerro de la Neblina. **B,** detail of the vegetation at the top of the Cerro de la Neblina. **C,** habit. **D,** flowering habit. **E,** inflorescence showing the spathaceous bracteoles and floral buds. **F,** inflorescence bearing immature capsules.

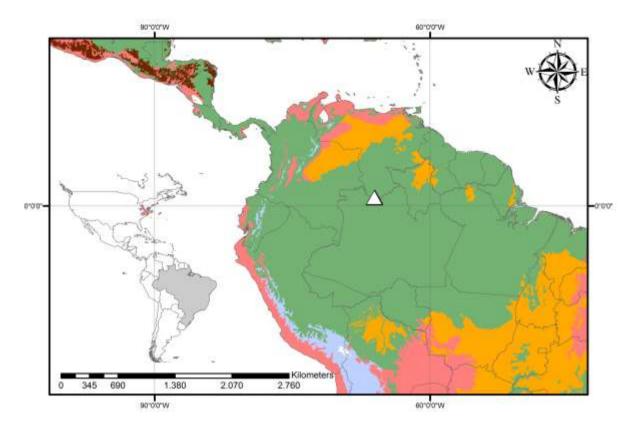


Figure 6. Distribution of *Pyrrorhiza neblinae* Maguire & Wurdack. Light Green—Subtropical Coniferous Forests; Red—Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange—Tropical/Subtropical Grasslands, Savannas and Shrublands; Maroon—Dry Broadleaf Forests; Green—Moist Broadleaf Forests; Lilac—Montane Grasslands and Shrublands.



Figure 7. *Schiekia orinocensis* (Kunth) Meisn. **A,** habitat. **B,** habit, showing an inflorescence from this flowering season and an old one from the previous year. **C,** inflorescence. **D,** flower. **E,** dissected flower showing the androecium and gynoecium.

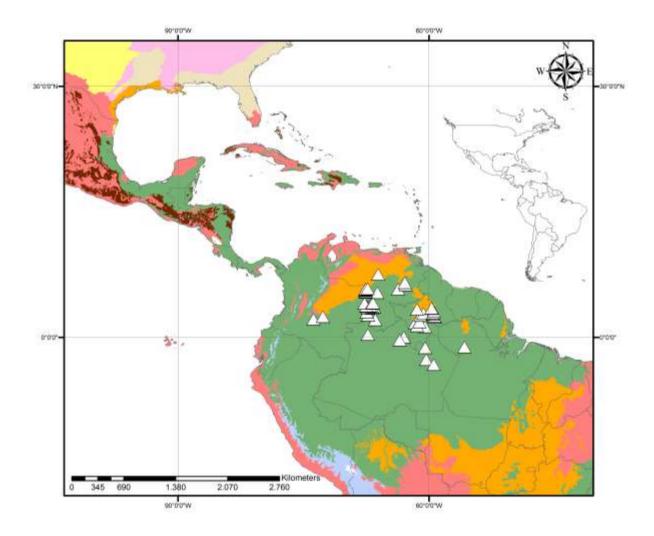


Figure 8. Distribution of *Schiekia orinocensis* (Kunth) Meisn. Beige– Temperate Coniferous Forests and Boreal Forests; Yellow– Temperate Grasslands, Savannas and Shrublands; Pink– Temperate Broadleaf and Mixed Forests; Light Green– Subtropical Coniferous Forests; Red– Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange– Tropical/Subtropical Grasslands, Savannas and Shrublands; Maroon– Dry Broadleaf Forests; Green– Moist Broadleaf Forests; Lilac– Montane Grasslands and Shrublands.



Figure 9. Schiekia silvestris (Maas & Stoel) Hopper et al. **A,** habit of two flowering specimens. **B,** habit of a fruiting specimen. **C–D,** inflorescences: **C,** inflorescence with flowers at anthesis; **D,** inflorescence with flowers at post-anthesis. **E–F,** flowers: **E,** side view of a flower showing the nectar drop (arrow) in the perianth aperture; **F,** front view of a flower. **G,** inflorescence bearing last few flowers and several capsules. **H,** detail of the cincinnus showing immature capsules.

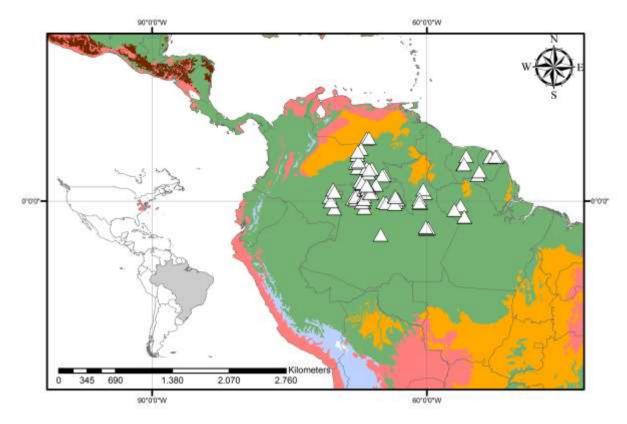


Figure 10. Distribution of *Schiekia silvestris* (Maas & Stoel) Hopper et al. Light Green–Subtropical Coniferous Forests; Red– Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange– Tropical/Subtropical Grasslands, Savannas and Shrublands; Maroon– Dry Broadleaf Forests; Green– Moist Broadleaf Forests; Lilac– Montane Grasslands and Shrublands.

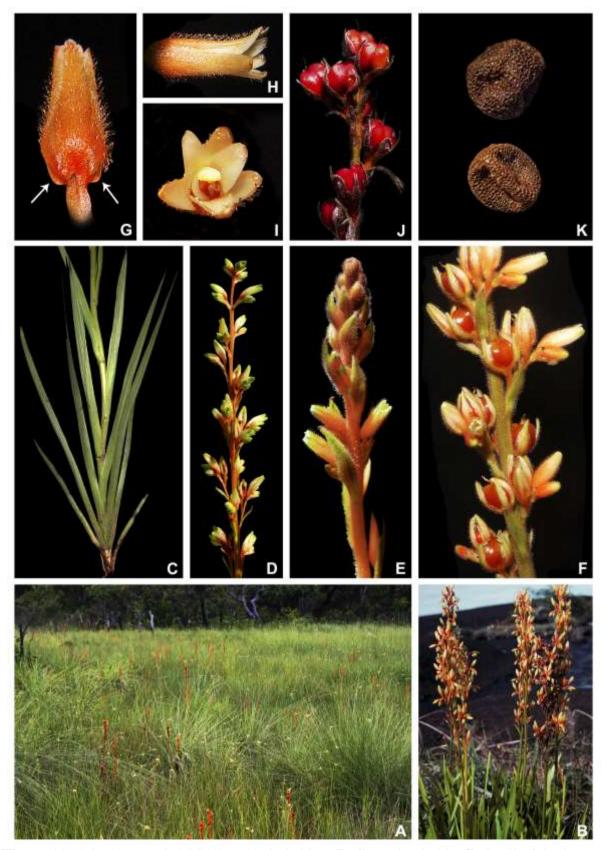


Figure 11. *Schiekia timida* M.Pell. et al. **A**, habitat. **B**, flowering habit. **C**, detail of the leaves. **D**–**E**, inflorescences: **D**, inflorescence with cincinni many-flowered; **E**, inflorescence with cincinni 1-flowered. **F**, inflorescence bearing young capsules. **G**–**I**, flowers: **G**, upper view of a flower showing both perianth apertures and their respective nectar drops (arrows); **H**, side view of a flower; **I**, front view of a flower. **J**, mature capsules before opening. **K**, seeds.

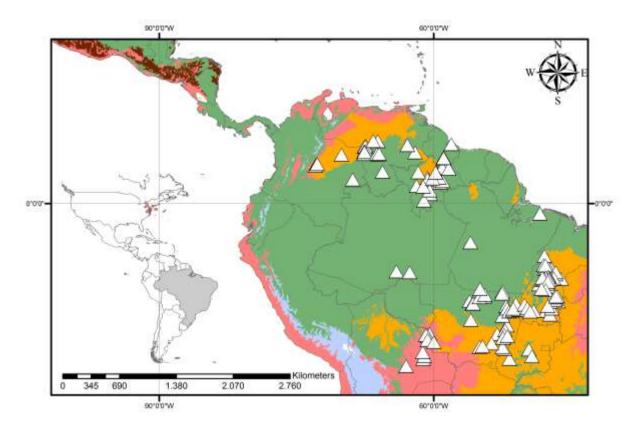


Figure 12. Distribution of *Schiekia timida* M.Pell. et al. Light Green– Subtropical Coniferous Forests; Red– Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange– Tropical/Subtropical Grasslands, Savannas and Shrublands; Maroon– Dry Broadleaf Forests; Green– Moist Broadleaf Forests; Lilac– Montane Grasslands and Shrublands.

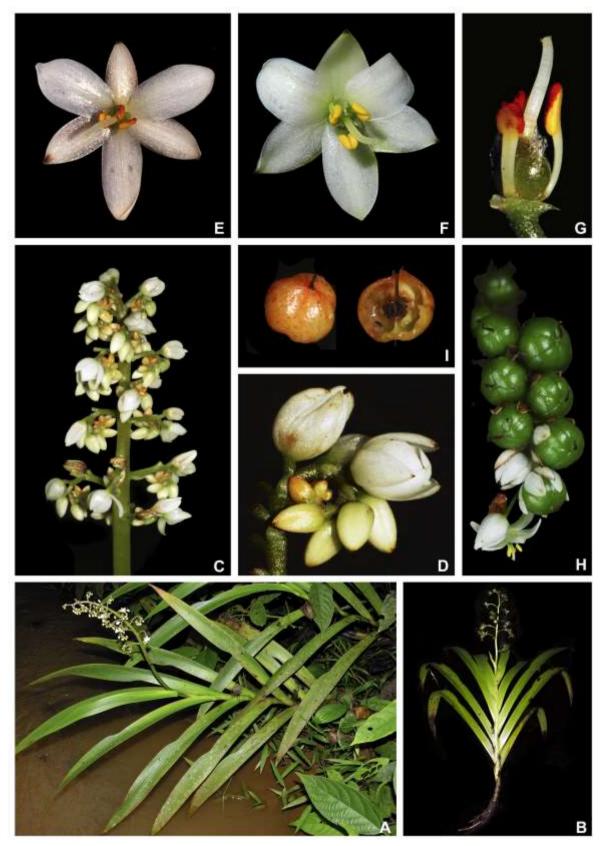


Figure 13. *Xiphidium caeruleum* Aubl. **A,** specimen growing in flooded forest. **B,** habit. **C,** inflorescence. **D,** cincinnus. **E–F,** flowers: **E,** flowers with subequal, narrow and pale apricot perianth lobes; **F,** flowers with equal, broad and white perianth lobes. **G,** flower with perianth removed showing androecium and gynoecium with ovary pubescent long the septal ridges. **H,** cincinnus with immature berries. **I,** mature berries.

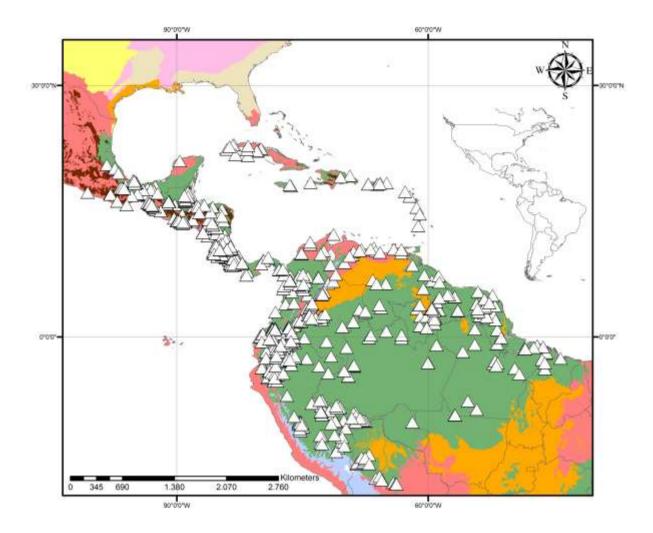


Figure 14. Distribution of *Xiphidium caeruleum* Aubl. Beige—Temperate Coniferous Forests and Boreal Forests; Yellow—Temperate Grasslands, Savannas and Shrublands; Pink—Temperate Broadleaf and Mixed Forests; Light Green—Subtropical Coniferous Forests; Red—Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange—Tropical/Subtropical Grasslands, Savannas and Shrublands; Maroon—Dry Broadleaf Forests; Green—Moist Broadleaf Forests; Lilac—Montane Grasslands and Shrublands.

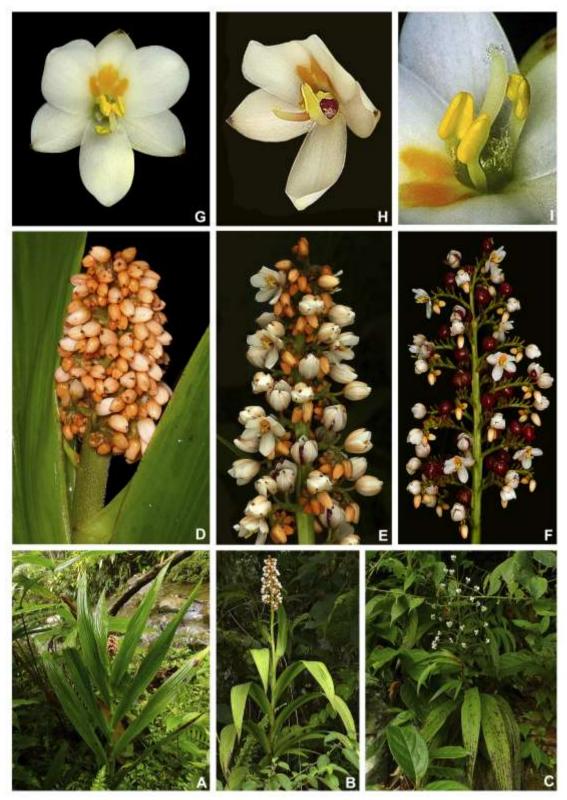


Figure 15. Xiphidium pontederiiflorum M.Pell. et al. **A–C**, habit: **A**, vegetative habit; **B**, flowering habit with a young inflorescence; **C**, flowering habit with an older inflorescence. **D–F**, inflorescences: **D**, very young inflorescence showing apricot floral buds; **E**, inflorescence with open flowers; **F**, inflorescence with open flowers and mature berries. **G–H**, flowers: **G**, white flower with green ovary; **H**, pale apricot flower with vinaceous ovary. **I**, detail of the androecium and the gynoecium showing the ovary pubescent along the septal ridges.

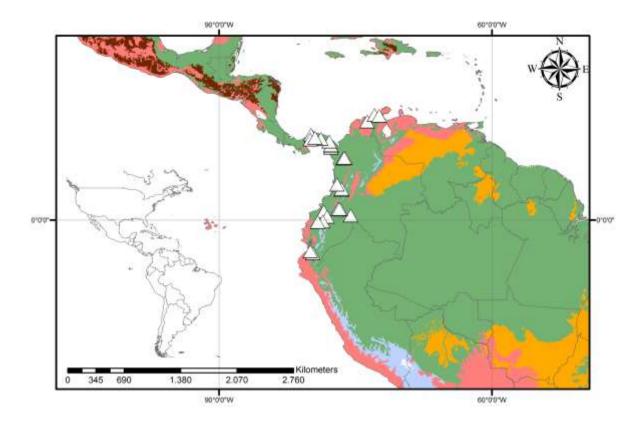


Figure 16. Distribution of *Xiphidium pontederiiflorum* M.Pell. et al. Light Green–Subtropical Coniferous Forests; Red– Deserts, Xeric Shrublands and Tropical Coniferous Forests; Orange– Tropical/Subtropical Grasslands, Savannas and Shrublands; Maroon– Dry Broadleaf Forests; Green– Moist Broadleaf Forests; Lilac– Montane Grasslands and Shrublands.

SECTION 4—PONTEDERIACEAE KUNTH

Chapter 4.1. Two new synonyms for *Heteranthera* Ruiz & Pavón (Pontederiaceae)

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Abstract

Hydrothrix and Scholleropsis, two segregate monospecific genera placed within Heteranthera s.l. clade, are here transferred to Heteranthera based on phylogenetic and morphological data. A brief discussion on Heteranthera s.l. morphology and its species affinities are given, along with the designation of lectotypes for the two new transfers are presented.

Key words

Aquatic flora, Commelinales, Hydrothrix, mudplantains, pickler-weed, Scholleropsis

Introduction

Pontederiaceae was one of the first families of flowering plants to be the focus of studies dealing with its phylogenetic history, based on morphological and molecular data (Eckenwalder & Barrett 1986; Graham & Barrett 1995; Kohn et al. 1996; Barret & Graham 1997; Graham et al. 1998; Ness et al. 2011). Regardless of the dataset, those studies invariably recovered most genera in the family as paraphyletic, including large genera as *Pontederia* and Heteranthera (either s.s. or sensu Horn 1985). The latter genus has always been recovered as paraphyletic by the inclusion of the monospecific Eurystemon Alexander, Hydrothrix Hook.f., Scholleropsis H.Perrier and Zosterella Small, in those phylogenies. Since Zosterella had already been treated as part of Heteranthera (MacMillan 1892), while the sole species of Eurystemon was originally described in Heteranthera (Watson 1883), new combinations are unnecessary for both. Phylogenies using morphologic datasets have recovered Hydrothrix and Scholleropsis nested within Heteranthera (Eckenwalder & Barrett 1986); while molecular and combined datasets have recovered Hydrothrix either nested within Heteranthera (Graham & Barrett 1995; Graham et al. 1998; Ness et al. 2011), in a polytomy with *Heteranthera* (Barret & Graham 1997; Graham et al. 1998; Ness et al. 2011), or as its sister-group (Kohn et al. 1996; Barret & Graham 1997; Graham et al. 1998; Ness et al. 2011). Despite the intimate phylogenetic relation between these genera being evident, based on different phylogenetic analysis and datasets, the species of *Hydrothrix* and *Scholleropsis* have never been formally transferred to *Heteranthera*. Thus, the present work provides the two needed combinations, together with the lectotypification of both names.

Methods

Specimens from the following herbaria were also analyzed: ALCB, B, BHCB, BRIT, CEPEC, CESJ, CRVD, ESA, FCAB, FLOR, FURB, GUA, HAS, HB, HUEFS, HURB,

HUSC, IAC, ICN, K, L, MBM, MBML, NY, P, R, RB, RFA, RFFP, SP, SPF, UEC, UPCB, US and VIES (herbaria acronyms according to Thiers, cont. updated). The inflorescence terminology and morphology follows Weberling (1965, 1989) and Panigo et al. (2011), with some modifications; and general terminology follows Horn (1985). Species distribution is based on herbaria specimens and field work data.

Taxonomy

1. Heteranthera gardneri (Hook.f.) M.Pell., comb. nov.

Basionym: *Hydrothrix gardneri* Hook.f. (1887, p. 90).

Lectotype (**designated here**): BRAZIL. Ceará. Lavras da Mangabeira. In the sandy bed of the rio Salgado at the Lavras de Mangabeira, between Icó and Crato, Aug. 1838, fl., fr., *G. Gardner 1863* (K barcode K 000644015!; isolectotypes: K barcode K 000644016!, B barcode B 10 0242079!, NY barcode NY 00247529!, NY barcode NY 00872433!). (Fig. 1) Based on the same type: *Hookerina gardneri* (Hook.f.) Kuntze (1891, p. 718).

Other designations: Hydrothrix verticillaris Hook.f. (1887, tab. vii.), nom. nud.

Endemic to Brazil, more specifically to the states of Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe and Minas Gerais. It can be found growing in slow water ponds and rivers in the Caatinga biome.

Hydrothrix was described as a monospecific genus, being possibly related to Schollera graminea (Michx.) Raf. [= Heteranthera dubia (Jacq.) MacMillan] (Hooker 1887). However, it was still regarded by the author as a deviant taxon, due to its apparently verticillate leaves, inflorescences reduced to two mirrored-flowers, and androecium reduced to a sole stamen. Nevertheless, 2-flowered inflorescences and flowers with a sole stamen are known in other species of Heteranthera (Verdcourt 1968, Horn 1985), and only the verticillate leaves would differentiate Hydrothrix and Heteranthera. The plate presented by Hooker (1887, tab. vii,2)

shows alternate leaves with an extremely expanded leaf-sheath, and with several acicular projections fused in a ring. In the same plate, it can be noted that the true leaves (euphylls) are inserted just below the acicular projections. Furthermore, the euphyll blades possess a discrete midvein, whereas the acicular projections possess no apparent vascularization. This pattern is also corroborated by the studies of Goebel (1913) and Rutishauser (1999). The latter focused on the anatomy and ontogeny of *Hydrothrix*, in which the author observed that the euphyll primordium is the first to be formed, and that the remaining leaf-like projections emerge from the closed and cup-like leaf-sheath (called ochrea by the author). Furthermore, the basal most nodes only produce euphylls, or sometimes only producing one to three projections in the leaf-sheath. Aside from the clearly different morphological arrangement between these two laminar projections, only one leaf trace and one meristematic bud are found per node. The bud and the leaf trace are always produced in the same direction as the euphyll. Thus, the "verticillate leaves", once thought to be exclusive to Hydrothrix, actually represent spirallyalternate leaves bearing leaf-sheaths with acicular to linear projections (Goebel 1913; Rutishauser 1999; Pellegrini pers. obs.), equivalent to the ones found in *Heteranthera*. This leaf arrangement has long been reported for Heteranthera (Horn 1895) and adds yet another morphological character that supports the present classification.

A second species of *Hydrothrix* (i.e. *H. barrosoana* Machado) was described by Machado (1947), as possessing an elongate inflorescence, one fertile stamen and two staminodes. Nevertheless, since this species is currently treated as a synonym of *Heteranthera seubertiana* Solms. (Horn 1895; BFG 2015), a new combination is not necessary.

Heteranthera gardneri is morphologically very similar to H. dubia, regarding growth form, leaf morphology and floral morphology (Fig. 3A–B). Nevertheless, they can be differentiated by the presence of various acicular projections on the leaf-sheath margin (vs. two linear projections on the leaf-sheath margin in H. dubia), acicular sessile leaves (linear

sessile leaves), inflorescence two-flowered (vs. one-flowered), perianth zygomorphic (vs. actinomorphic) and one stamen (vs. three stamens) (Fig. 1).

Kuntze (1891) erroneously believed that the name *Hydrothrix* is occupied and cannot be used for this plant, and he published a new generic name that is illegitimate.

In the protologue of the name *H. gardneri*, Hooker (1887) cited a single gathering (*Gardner 1863*) which is a syntype collection because it is represented by more than one specimen. Hooker never mentioned in which herbaria the specimens where deposited and which is to be treated as the type (holotype). Since Hooker worked at the Royal Botanical Gardens, Kew (Stafleu & Cowan 1976), and the material from K is accompanied with handwritten notes and illustrations by Hooker himself, it seems to be the logical choice for a lectotype. Hooker also mentioned that specimens of his new taxon were analyzed by more than one botanist, with the "contributions from the American botanist Dr. Asa Gray being noteworthy". The specimens analyzed by Gray are deposited at NY herbarium, with an extra specimen being known to be deposited at B herbarium. These specimens are isolectotypes.

2. Heteranthera lutea (H.Perrier) M.Pell., comb. nov. (Fig. 2)

Basionym: Scholleropsis lutea H.Perrier (1936, p. 158).

Lectotype (designated here): MADAGASCAR. Mahajanga, Melaky ("dans le Boina"), bassin moyen du Bemarivo, October 1907, fl., fr., *H. Perrier* 7178 (P barcode P 02189314!; isolectotypes: P barcode P 02189317!).

Restricted to Cameroon, Chad & Madagascar. It can be found growing in slow water ponds and rivers. *Scholleropsis lutea* H.Perrier was described as distinct from *Heteranthera s.s.* based solely on its (3–)4-merous perianth (Perrier de la Bâthie 1936). Nevertheless, this character seems to be connected with the submerged habit of this taxon and the influence of the variation in water levels. A great deal of plasticity in reproductive characters can be

observed in different species of *Heteranthera*. *Heteranthera* callifolia Kunth (from Africa) is known to produce cleistogamous and chasmogamous flowers, depending on the water level. Added to that, the submerged cleistogamous flowers can either possess three fertile stamens, one fertile stamen and two staminodes, or a sole fertile stamen (Verdcourt 1968, Horn 1983, 1985, 1988). Thus, it is the authors opinion that the number of perianth lobes could be under the same epigenetic pressure, and should not be considered enough to maintain *Scholleropsis* as an independent genus.

Heteranthera lutea is morphologically very similar to H. limosa and H. rotundifolia due to its sessile leaves persistent in mature plants, petiolate leaf-blades ovate to oblong to rhombic, and one-flowered inflorescences. Nevertheless, they can be differentiated due to the perianth color, number of lobes in the perianth, and the lobes' orientation (Fig. 2, 4C–D).

When describing *Scholleropsis lutea*, Perrier (1936) cites eight gatherings analyzed by him (syntypes), only indicating collectors and collection numbers. While studying the specimens at P herbarium, I noticed that the collection "*H. Perrier 7178*" had the word type written in the same handwriting as the identification. This handwriting most likely belongs to Perrier himself, indicating that the author probably intended for this specimen to be the holotype. Thus, making this material the logical choice for a lectotype.

Discussion

All the morphological characters used for differentiating these genera seem to be connected to the submerged habit of these taxa. Submerged habit is known to lead to miniaturization and loss of floral structures in many plant groups (e.g. Cabombaceae, Ceratophyllaceae, Haloragaceae, Lentibulariaceae, Potamogetonaceae, etc.) (Sculthorpe 1967; Cook 1978; Horn 1983, 1985, 1988). Thus, the loss of petiolate leaves (i.e. *Heteranthera dubia*, *H. zosterifolia* and *Hydrothrix*), the reduction in the number of flowers per

inflorescence (i.e. *Heteranthera dubia*, *H. zosterifolia*, *Hydrothrix* and *Scholleropsis*) and the loss of perianth parts (i.e. *Scholleropsis*) are not unexpected.

Conclusion

Pontederiaceae is now composed by four genera (i.e. Eichhornia, Heteranthera, Monochoria and Pontederia). However, since Eichhornia is hopelessly paraphyletic (Eckenwalder & Barrett 1986; Graham & Barrett 1995; Kohn et al. 1996; Barret & Graham 1997; Graham et al. 1998; Ness et al. 2011), accepting Pontederia s.l. (including Eichhornia, Monochoria and Pontederia s.s.) seems to be the best taxonomic option, instead of pulverizing Eichhornia into several monospecific genera. With the recognition of Pontederia s.l., the family would be composed by only two monophyletic genera. Both genera are also morphologically coherent and of easy recognition, both in field and with herbaria material. They could be easily differentiated by thyrsi with more than one cincinni, six stamens, and by the presence of septal nectaries in Pontederia (vs. thyrsi reduced to a solitary cincinnus, sometimes even reduced to one or two flowers, one to three stamens, and absent septal nectaries in Heteranthera s.l.). Nevertheless, further studies sampling all the morphologic diversity and nomenclatural types of these three genera seem necessary before a consistent taxonomic decision can be taken.

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the pictures of *H. rotundifolia*, Ramon Teobaldo for the pictures of *H. seubertiana*, and Glauco Oliveira and Samuel S. de Oliveira for the pictures of *H. zosterifolia*.

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FIGURE 1. *Heteranthera gardneri*. **A,** habit, showing a flowered population during dryseason; **B,** detail of the stem. **C,** detail of the flower-like inflorescence, showing how the upper perianth-lobes mimic androecium parts. A–B by A.P. Fontana, C by C.P. Bove.



FIGURE 2. *Heteranthera lutea*. **A,** habit, showing an individual with petiolate and sessile leaves; **B,** habit, showing a submerged individual with only sessile leaves; **C,** detail of the one-flowered inflorescence, showing the tetramerous flower. Plate modified from the Flore de Madagascar et des Comores, Pontédériacées (1946), vol. 38: pp. 5; acquired through the Biodiversity Heritage Library (BHL).

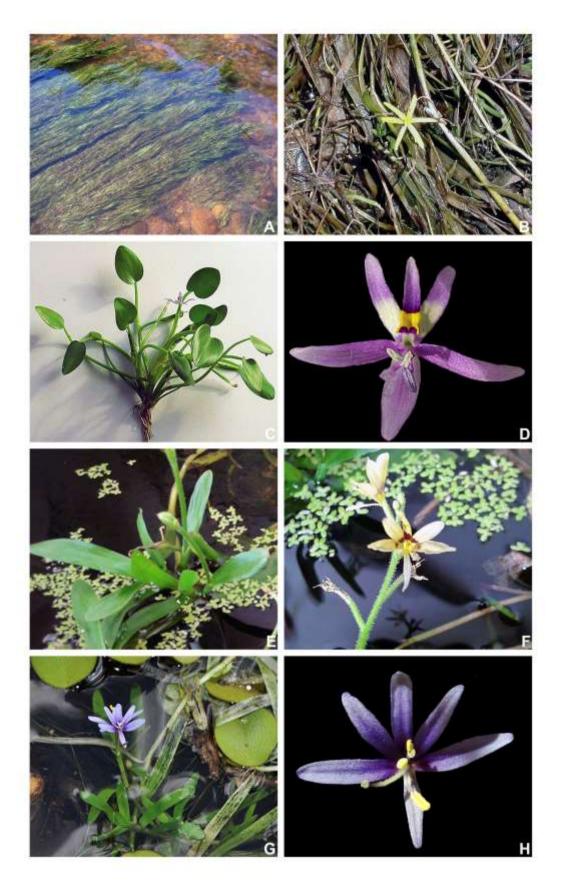


FIGURE 3. Related *Heteranthera* species. **A–B,** *Heteranthera dubia*, from the United States: **A,** habit showing submerged individual with sessile and linear leaves; **B,** detail of the

one-flowered inflorescence. **C–D,** *Heteranthera rotundifolia*, from Northeastern Brazil: **C,** habit, showing; **D,** detail of the flower; **E–F,** *Heteranthera seubertiana*, from Northeastern Brazil: **E,** detail of the sessile leave rosette; **F,** detail of the inflorescence, showing the open yellow flowers. **G–H,** *Heteranthera zosterifolia*, from Southeastern Brazil: **G,** habit, showing the emerged stem with sessile linear leaves; **H,** detail of the flower. A–B by C.N. Horn, C–D by A. Popovkin, E–F by R. Teobaldo, G by G. Oliveira and H by S.S. de Oliveira.

SECTION 4— PONTEDERIACEAE KUNTH

Chapter 4.2. Two peculiar new species of *Heteranthera* Ruiz & Pavón (Pontederiaceae) from Brazil, with notes on inflorescence architecture in the family

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Abstract

Two new and peculiar species of *Heteranthera* are herein described. *Heteranthera* catharinensis is unique in the genus due to its glomerulate, many-flowered inflorescences, in which the flowers are restricted to the base and apex of the cincinni. It also possesses the biggest flowers in the *H. reniformis* Ruiz & Pavón species complex, with glabrous perianth lobes, medial filament, and style. On the other hand, *Heteranthera pumila* is described as the smallest known species of Pontederiaceae, with its dwarf stature, petiolate leaves with especially diminute blades, inflorescences 1–2–(3)-flowered, peduncle densely covered with glandular hairs, basal bract with glandular hairs at base, and smooth seeds, rarely possessing 7–9 inconspicuous longitudinal wings. We present detailed descriptions, illustrations, comments, a distribution map, and conservation assessments for the new species, and an identification key to the Brazilian species of *Heteranthera s.l.* Finally, we discuss inflorescence morphology and terminology in Pontederiaceae, characterizing it as thyrsoid.

Key words

Atlantic Forest, aquatic flora, Commelinales, mudplantains, Neotropical flora, pickerelweed

Introduction

Heteranthera Ruiz & Pavón, nom. cons. is currently the largest genus of Pontederiaceae, comprising 12 neotropical species, and two paleotropical species restricted to continental Africa and Madagascar [i.e. H. callifolia Rchb. ex Kunth, and H. lutea (H.Perrier) M.Pell.] (Horn 1985; Pellegrini 2017). In Brazil, Heteranthera is currently represented by nine species (i.e. 75% of the diversity of the genus), widely distributed throughout permanent and temporary freshwater bodies in the country (BFG 2015). The genus is especially diverse in the Atlantic Forest domain, where seven species are known to occur (BFG 2015).

Heteranthera was described based on Peruvian collections of H. reniformis Ruiz & Pavón, being originally characterized by its three dimorphic stamens, six-lobed perianth, and polyspermic capsules (Ruiz López and Pavón 1794). Since then, several different genera have been segregated or described to accommodate species which were considered aberrant from Heteranthera s.s. (i.e. Eurystemon Alexander, Hydrothrix Hook.f., Schollera Schreb., nom. illeg., Scholleropsis H.Perrier, and Zosterella Small). These genera were described mainly based on autapomorphic characters, such as vegetative differences (e.g. number of projections in the ligule, misinterpreted as verticillate leaves) and minor reproductive characters (e.g. number of flowers per inflorescence, number of fertile stamens, filament inflation, and anther curvature at post-anthesis; Pellegrini 2017). Several phylogenetic studies evidenced the paraphyly of *Heteranthera* (Eckenwalder and Barrett 1986; Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998; Ness et al. 2011), and pointed towards a broader sense of the genus, which was subsequently accepted in taxonomic and floristic treatments worldwide (Horn 1987a, 1987b, 2002; Horn and Haynes 2001; BFG 2015; Pellegrini 2017). The genus is currently easily recognized by its non-pulvinate petiolate leaves, inflorescence reduced to a solitary cincinnus, stamens (1–)3, staminodes sometimes present, the lack of septal nectaries, and its unevenly trilobate stigma (Pellegrini 2017; Pellegrini and Horn, unpublished data).

Despite *Heteranthera* being currently monophyletic and well circumscribed (Pellegrini 2017), some widely distributed taxa are still problematic. The main neotropical species complex is represented by *H. reniformis s.l.*, which also includes the *H. multiflora s.l.* subcomplex. *Heteranthera reniformis s.l.* is the most widespread and morphologically variable taxon in the genus (Horn 1985). It is also known to be an aggressive weed, especially in rice fields around

the world (Ferrero 1996; Vescovi et al. 1996; SWSS 1998; Karov et al. 2005; Domingos et al. 2005; Arakaki 2013; Csurhes 2016). Nonetheless, species identification is extremally difficult due to the poorly understood specific limits in this group. As part of our ongoing systematic studies in Pontederiaceae, based on extensive field and herbaria studies, we describe two peculiar new species segregated from *H. reniformis*, and clarify the complex's composition and morphological characterization.

Methods

The description and phenology of the species is based on herbaria, spirit, and fresh material, and is complemented by literature information. Specimens from the following herbaria were also analyzed: AAU, ALCB, B, BA, BAF, BHCB, BHZB, BM, BOL, BOTU, BR, C, CAS, CEPEC, CESJ, COL, CORD, CTES, CVRD, E, ESA, F, FCAB, FLOR, FUEL, FURB, G, GH, GUA, HAMAB, HAS, HB, HBR, HERBAM, HRB, HRCB, HSTM, HUEFS, HUFSJ, HURB, IAC, ICN, INPA, IPA, K, KANU, LIL, LP, MA, MBM, MBML, MG, MO, MVM, MY, NBYC, NY, PMSP, PRC, R, RB, RFA, RFFP, S, SJRP, SP, SPF, UEC, UNA, UPCB, and US (herbaria acronyms according to Thiers, continuously updated). The distribution of the species is based on herbaria materials, field data, and literature. The classification of the vegetation patterns follows IBGE (2012). The indumenta and shapes terminology follows Radford et al. (1974); the inflorescence terminology and morphology follows Weberling (1965, 1989) and Panigo et al. (2011); the fruit terminology follows Spjut (1994); and general terminology follows Horn (1985). The conservation status is proposed following the recommendations of IUCN Red List Categories and Criteria, Version 3.1 (IUCN 2001). GeoCAT (Bachman et al. 2011) was used for calculating the Extent of Occurrence (EOO) and the Area of Occurrence (AOO).

Results

We update the number of species of *Heteranthera* in Brazil from nine to 11, including the number of species endemic to the country from one to three, and the total number of species in the genus from 14 to 16. Both new species belong to the *H. reniformis* species complex, being differentiated from *H. reniformis s.s.* based on several reproductive features (Table 1). We provide detailed morphological descriptions, comments, illustrations, and a distribution map for the new species, along with an identification key for the species of *Heteranthera* in Brazil. A morphological characterization and general comments are also provided for the *H. reniformis* species complex, with special attention to *H. multiflora* (Griseb.) C.N.Horn.

Taxonomy

1. Heteranthera catharinensis C.N.Horn & M.Pell., sp. nov.

Figs 1-3

Diagnosis. Similar to *Heteranthera reniformis* Ruiz & Pavón due to is petiolate leaves with reniform to broadly cordate blades, glandular-pubescent cincinnus axis, perianth lobes with a 5+1 arrangement, and straight filaments. It is unique due to its 3.2–5.5 cm long, glabrous peduncles, basal bract with spatulate-mucronate apex, 6–17-flowered, glomerulate cincinnus; externally glabrous perianth lobes, central superior perianth lobe 6.6–9.2 mm long, central stamen with glabrous filament, lateral anthers 1–1.8 mm long, central anther 1.7–2.4 mm long, and glabrous style.

Type. BRAZIL. Santa Catarina: Ipumirim, 4–7 km south of the Rio Irani, 26° 59' S, 52° 11' W, alt. 500–600 m, 9 Dec 1964, L.B. Smith & R.M. Klein 13919 (holotype: US barcode US01936706!; isotypes: FLOR barcode FLOR3365!, LP!, MO!, NY!, R!).

Description. Herbs annual or short-lived perennials. Roots thin, delicate, unbranched, white. Stems repent on the substrate or floating in shallow water, delicate, spongy, rooting at the nodes; internodes 1.6-4.3 cm long, glabrous. Sessile leaves not seen. Petiolate leaves distichously-alternate, distributed along the stem, floating to emergent; sheaths 2.6-5.5 cm long, glabrous, covered with mucilage, longitudinally split and green when mature, ligule 2parted, barely surpassing the sheath, 0.1–0.3 mm long, membranous, light green, glabrous, apex triangular; petiole 3.3–21 cm long, not inflated, glabrous; blades $1.3-3.3 \times (1.4-)3-4.6$ cm, reniform to broadly cordate, membranous, glabrous, base cordate, margins glabrous, apex obtuse to slightly acute. *Inflorescences* axillary or apparently terminal, reduced to a solitary pedunculate cincinnus; peduncle 3.2-5.5 cm long, glabrous; basal bract (spathe) $1.6-3.3 \times 0.3-$ 0.5 cm, spathaceous, elliptic, conduplicate, glabrous, green, margins hyaline, apex spatulatemucronate; cincinnus bract absent; cincinnus 6–17-flowered, flowers congested at the base and apex of the cincinnus, 1–2 flowers included in the basal bract, axis 3–6.5 cm long, slightly to glandular-pubescent. **Flowers** bisexual, tubular, chasmogamous, enantiostylous; floral buds narrowly ellipsoid, light green, glabrous; perianth tube 5-7.5 mm long, light green, glandular-pubescent, lobes 5 superior and 1 inferior, white, lateral superior lobes 6.6–8.3 × 1.2–2.5 mm, elliptic, base cuneate, apex acute to acuminate, central superior lobe 6.6–9.2 × 1.6–2.5 mm, ovate to broadly ovate, base obtuse, slightly involute, apex acute, with a nectar guide at base, pale to medium yellowish green with an upper mauve to vinaceous spot, inferior lobe $6.5-9.5 \times 0.4-1$ mm, linear elliptic, base cuneate, apex acuminate; stamens 3, lateral stamens with filaments straight, 1.5–2 mm long, not inflated, apically barbate with eglandular, multi-celled hairs, anthers 1–1.8 × 0.3–0.4 mm, oblongoid to ellipsoid, yellow, central stamen with filament straight, 3–3.6 mm long, not inflated, glabrous, anthers 1.7–2.4 × 0.4-0.6 mm, ovate to slightly sagittate, white; ovary $3.2-3.8 \times 1.1-1.3$ mm, linear ovoid to linear oblongoid, glabrous, 1-locular, placentation intrusive-parietal, style gently sigmoid, 5.1– 9.3 mm long, glabrous, stigma unevenly trilobate, densely glandular-pubescent. Capsules not seen; persistent perianth base (anthocarp) smooth, medium brown. Seeds not seen.

Specimens seen (paratypes). BRAZIL. Santa Catarina: Caçador, slough, 33 km W of Caçador, fl., 23 Dec 1956, L.B. Smith & R. Reitz 9103 (HBR!, NY!, P barcode P02188433!, US barcode US01936705!)

Etymology. The epithet makes reference to the type locality, the state of Santa Catarina, Brazil.

Distribution, habitat and ecology. *Heteranthera catharinensis* is currently endemic to the state of Santa Catarina, in the Atlantic Forest domain (Fig. 3). Is was found growing on open marshy areas and slow water environments within the Uruguay River watershed.

Phenology. *Heteranthera catharinensis* can be found in bloom in December. Unfortunately, neither of the two currently known collections present mature fruits, thus fruiting time remains unknown.

Conservation status. Following the IUCN recommendations (IUCN 2001), *H. catharinensis* should be considered as Data Deficient (DD), since it is known from only two collections, which are more than 50 years old.

Morphological notes. The inflorescence of *H. catharinensis* is extremely peculiar, meriting explanation. The glomerulate appearance of the inflorescence (i.e. flowers congested at the base and apex of the inflorescence) seems to be due to changes in the length of the cincinnus internodes. The first one to three internodes are contracted, similarly to most species in the genus, thus making the basalmost flowers to be partially enclosed by the basal bract. Nonetheless, the following internode is considerably and consistently elongated, being commonly three to five times longer than the previous internodes. The subsequent internodes are also contracted, giving the impression that the flowers are also congested at the apex of the inflorescence. This alternation between contracted and elongated internodes, produces a unique inflorescence architecture in the genus (Fig. 2B).

Affinities. Heteranthera catharinensis is morphologically similar to H. reniformis s.s. due to its petiolate leaves with reniform to broadly cordate blades, pedunculate inflorescences, cincinnus axis glandular-pubescent, glandular-pubescent perianth tube, perianth lobes with a 5+1 arrangement and acute to acuminate at apex, lateral stamens apically barbate, and intrusiveparietal placentation (Horn 1985). It is also superficially similar to H. multiflora s.l. due to its bigger stature, many-flowered inflorescence with few flowers included in the basal bract, and gross floral morphology (Horn 1985). Nonetheless, H. catharinensis can be easily differentiated from all remaining species of Heteranthera by its unique inflorescence architecture (where flowers are congested at the base and the apex of the cincinnus), larger flowers size, numerous flowers on an elongate axis, main axis many times longer that the basal bract, and basal bract with spatulate-mucronate apex. Aside from that, specimens of H. catharinensis have been erroneously identified as H. peduncularis Benth, due to their robust habit and long inflorescences. However, both species can be easily differentiated based on inflorescence architecture, and pubescence of the tepals and filaments. Furthermore, H. catharinensis has larger floral features, when compared to the remaining species of the *H. reniformis* complex, including longer perianth lobes and larger anthers. It is also the only species in the complex with externally glabrous perianth lobes, and glabrous central filament and style (Table 1).

2. *Heteranthera pumila* **M.Pell. & C.N.Horn, sp. nov.** Figs 3–5

Diagnosis. Similar to *H. reniformis* Ruiz & Pavón due to its petiolate leaves with blades two or more times wider than long, reniform to broadly cordate, cincinnus enclosed by the basal bract, glandular-pubescent cincinnus axis, perianth lobes with a 5+1 arrangement and acute to acuminate at apex, filaments straight, and intrusive-parietal placentation. It differs due to its diminute petiolate leaves $[3.5-11.8-(13.2)\times3.2-12.1 \text{ mm}]$, inflorescences 1-2-(3)-flowered, peduncle densely glandular-pubescent, basal bract glandular-pubescent at base, apex aristate, flowers pale lilac to lilac or light pink, seeds smooth or with 7-9 inconspicuous longitudinal wings.

Type. BRAZIL. São Paulo: Piraju, várzea do rio Paranapanema, na divisa com o município de Manduri, 23° 07' 50" S 49° 19' 32" W, fl., fr., 10 Oct 2016, M.O.O. Pellegrini & R.F. Almeida 495 (holotype: RB!; isotypes: NBYC!, SPF!, US!).

Description. Herbs annual or short-lived perennials. Roots thin, delicate, unbranched, white. Stems repent on the substrate or floating in shallow water, delicate, spongy, rooting at the nodes; internodes 1.7-64.1 mm long, glabrous. Sessile leaves not seen. Petiolate leaves distichously-alternate, distributed along the stem, floating to emergent; sheaths 2.8-7.5 mm long, glabrous, covered with mucilage, longitudinally split and light green when mature, ligule 2-parted, surpassing the sheath, 0.2-0.8 mm long, membranous, light green, glabrous, apex triangular; petiole 8.5–82.9 mm long, not inflated, glabrous; blades 3.5–11.8–(13.2) × 3.2–12.1 mm, cordate to broadly cordate to reniform, rarely narrowly cordate, membranous, glabrous, base cordate, margins glabrous, apex acute to obtuse. Inflorescences axillary or apparently terminal, reduced to a solitary pedunculate cincinnus; peduncle 0.5–3.4 cm long, deflexed and submerged in fruit, densely glandular-pubescent; basal bract (spathe) 0.9–1.9 × 0.4–0.8 cm, spathaceous, broadly elliptic, conduplicate, green, glandular-pubescent at base, margins hyaline, apex aristate; cincinnus bract absent; cincinnus 1–2–(3)-flowered, all flowers included in the basal bract, when present the third flower always exerted, axis 0.2–1.8 mm long, densely glandular-pubescent. Flowers bisexual, tubular, chasmogamous, sessile, enantiostylous; floral buds narrowly ovoid, light green to lilac or pink, densely glandular-pubescent; perianth tube 4.9–7.3 mm long, light green, densely covered with glandular hairs, lobes 5 superior and 1 inferior, pale lilac to lilac or light pink, lateral superior lobes $3.6-5 \times 0.8-1.4$ mm, elliptic, base cuneate, apex acute to acuminate, central superior lobe 3.6–4 × 1.7–2.1 mm, ovate to broadly ovate, base obtuse to rounded, slightly involute, apex acute, with a nectar guide at base, yellowish green to green with an upper vinaceous to brown spot, inferior lobe $4.2-4.9 \times 0.5-$ 0.8 mm, narrowly elliptic to linear elliptic, base cuneate, apex acuminate; stamens 3, lateral stamens with filaments straight, 1.6–1.8 mm long, pale lilac to light pink, not inflated, apically barbate with eglandular, multi-celled, lilac to pink hairs, anthers $0.4-0.6 \times 0.3-0.5$ mm, broadly oblongoid to quadrangular, yellow, central stamen with filament straight, 2–2.3 mm long, lilac to pink, not inflated, medially sparsely villose with eglandular, white hairs, anthers $1.2-1.6 \times$ 0.3-0.5 mm, ellipsoid, greyish blue to greyish mauve; ovary $3.1-3.5 \times 1-1.2$ mm, linear ovoid, glabrous, 1-locular, placentation intrusive-parietal, style gently sigmoid, 4.2–5.1 mm long, lilac to pink, terete, densely villose in the distal portion with eglandular, white hairs, stigma unevenly trilobate, purple to pink, densely glandular-pubescent. Capsule 5.3–7.2 × 1.1–1.9 mm, linear ovoid, glabrous, smooth, light green when immature, light to medium brown when mature; persistent perianth base (anthocarp) smooth, medium to dark brown. Seeds 0.5–0.7 × 0.2–0.3 mm, oblongoid, light brown to yellowish brown, testa smooth, sometimes with 7-9 inconspicuous longitudinal wings; hilum punctate; embryotega dorsal, inconspicuous, without a prominent apicule.

Specimens seen (paratypes). BRAZIL. Minas Gerais: São Sebastião do Paraíso, Fazenda Fortaleza, fl., 20 Apr 1945, A.C. Brade & A. Barbosa 17846 (RB, SP, UNA). Paraná: Guaratuba, Boa Vista, fl., 28 Jan 1964, G. Hatschbach 11078 (MBM); Rio da Divisa, fl., fr., 16 Dec 1971, G. Hatschbach 28523 (MBM, UPCB). Rio Grande do Sul: Bom Jesus, Rio Socorro, fl., 19 Feb 2008, Grupo de Estudos Reófitas UHBG 2116 (MBM). Vacaria, vale do Rio Ibitíria, ca. 30 km NE de Vacaria, fl., s.dat., J.C. Lindeman et al. s.n. (ICN9466). Santa Catarina: Lages, Santo Antônio, near Passo de Socorro, estrada de rodagem Federal km 67–71, south of Lages, fl., 14 Jan 1957, L.B. Smith & R. Reitz 9959 (HBR, RFA, US). São Paulo: Americana, Praia Azul, fl., 2 Mar 1993, Faria 96/16 (UEC). Bálsamo, estrada sentido Bálsamo-Mirassolândia, fl., 30 Jan 1997, A.D. Faria et al. 97/350 (UEC). Dracena, margem do Rio do Peixe, fl., fr., 7 Sep 1995, L.C. Bernacci et al. 2124 (IAC, SP, SPF, UEC). Estrela D'Oeste, SP-320, lago localizado na Fazenda Santo Antônio, lado direito da pista no sentido Estrela D'Oeste-Jales, fl., fr., 30 Jan 1997, L.Y.S. Aona et al. 97/167 (UEC). Igarapava, lagoa localizada na Fazenda Flor das Frutas, lado direito da pista no sentido Igarapava-Rifaina, na altura do km 16, fl., 15 Jan 1997, A.D. Faria et al. 97/102 (UEC). Ouro Verde, SP-563, km 113, Ponte Nova, Rio do Peixe, fl., 10 Jul 1996, A.D. Faria et al. 96/122 (UEC); loc. cit., fl., fr., 10 Jul 1996, A.D. Faria et al. 96/130 (BOTU, IAC, SP, SPF, UEC). Paulo de Faria, fl., Oct 1994, V.C. Souza et al. 12294 (ESA, IAC, UEC). Pedregulho, rodovia Antônio Giolo, acesso à Estreito, solo encharcado próximo à uma cachoeira, fl., fr., 14 Jan 1997, A.D. Faria et al. 97/64 (UEC). Piraju, várzea do Ribeirão São Bartolomeu, fl., fr., 15 May 1996, E.L.M. Catharino et al. 2090 (PMSP). Riolândia, brejo localizado em estrada de terra no sentido Riolândia-Paulo de Faria, fl., 29 Jan 1997, L.Y.S. Aona et al. 97/152 (UEC). Santa Rita do Passa Quatro, rodovia Anhanguera, km 239, Sítio Aubiri, fl., 13 Jan 1997, A.D. Faria et al. 97/20 (UEC). São José do Rio Preto, represa, fl., 25 Nov 1965, G. Marinis & E.M.P. Martins 20 (FUEL, SJRP, SP); Estação Experimental de Zootecnia de São José do Rio Preto, fl., 28 Dec 1977, M.A. Coleman 220 (SP). São Pedro do Turvo, 8 km da estrada em direção à Marília, desvio em estrada de terra ca. 3.5 km, 49° 70' W 22° 48' S, est., 9 Dec 1994, M.C.E. Amaral & V. Bittrich 94/48 (UEC). Sud Mennucci, distrito de Bandeirantes D'Oeste, fl., 4 Aug 1995, M.R. Pereira-Noronha et al. 1552 (SP). Teodoro Sampaio, margem do lago ao lado da estrada Teodoro Sampaio-Planalto, ca. Km 11.5, fl., Oct 1997, L.Y.S. Aona et al. 97/241 (UEC).

Etymology. The epithet means "small", making allusion to the small stature of the new species, especially its diminute leaf blades.

Distribution, habitat and ecology. *Heteranthera pumila* is endemic to the Paraná, Uruguay, and Southeastern Atlantic watersheds, in the Atlantic Forest domain. It is restricted to Brazil, in the states of Minas Gerais, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul (Fig. 2), growing on open marshy areas and slow water environments along the Paraná, Paranapanema and Rio Grande rivers (and their respective tributaries), from 700 to 1,800 meters above the sea level. It is very likely that *H. pumila* also reaches the state of Mato Grosso do Sul. Nonetheless, we have been unable, so far, to find any vouchers from this state in the visited herbaria.

Phenology. Heteranthera pumila blooms throughout the year, with flowering peaks during the wet season, and was found in fruit from September to October and from January to March.

Conservation status. Heteranthera pumila is widely distributed across the upper Paraná. Uruguay, and Southeastern Atlantic watersheds, with a wide EOO (ca. 318,815.754 km²) which would render this species as Least Concern. On the other hand, its AOO is considerably smaller (ca. 88.000 km²), which would render H. pumila as Endangered. The Paraná, Uruguay, and Southeastern Atlantic watersheds cover eight Brazilian states (Distrito Federal, Goiás, Mato Grosso do Sul, Minas Gerais, Rio Grande do Sul, Santa Catarina, São Paulo, and Paraná), embedded in the Atlantic Forest and Cerrado domains. Its main tributaries are the Iguaçu, Paranaíba, Paranapanema, Rio Grande and Tietê rivers. It possesses the greatest energy generation potential in Brazil, with 176 active hydropower plants, the largest being Itaipu, Furnas, Porto Primavera and Marimbondo. Nonetheless, all the major rivers are currently saturated with hydropower plants, and new projects aim to occupy the smaller tributaries, in order to fulfil the growing energy demand in the region (ANA 2002). Almost all the known subpopulations of *H. pumila* coincide with areas currently flooded, and might already have gone extinct, due to the construction of the aforementioned water dams. The few extant subpopulations vary from medium to large, with many clones and mature individuals. Nonetheless, they are currently strongly threatened due to pollution, deforestation, and by ongoing and future constructions of new hydropower plants. Thus, following the IUCN recommendations (IUCN 2001), H. pumila should be considered as Critically Endangered [CR, A2acd+B1b(ii, iii, iv)+B2ab(ii, iii, iv)+C1+E].

Morphological notes. Extensive morpho-ecological studies (Horn 1983, 1988) have shown that *Heteranthera* species are highly polymorphic vegetatively, as an adaptation to submersion and variations in water level. The same can be observed in the new species herein described, that despite the diminute general stature, may sometimes possess extremely long petioles and peduncles. *Heteranthera pumila* has been kept in cultivation by the senior author, and even under different environmental conditions, little change was observed in the species' vegetative morphology. Nevertheless, when cultivated in aquariums with different water depths, the change in the length of petioles and peduncles could be observed in less than a week. The already existing structures elongated in order to keep the leaf blades floating and flowers emerged, and the subsequently produced petiolate leaves and inflorescences were considerably longer than the previous ones of the same individual.

Affinities. Heteranthera pumila is morphologically similar to H. reniformis due to its petiolate leaves with blades two or more times wider than long, cordate to reniform, rarely narrowly cordate, cincinnus enclosed by the basal bract, glandular-pubescent cincinnus axis, perianth lobes with a 5+1 arrangement with acute to acuminate apex, filaments straight, lateral stamens apically barbate, central stamen basally sparsely villose, and intrusive-parietal placentation (Horn 1985). It is also similar to *H. multiflora* due to its petiolate leaves with blades two or more times wider than long, cordate to broadly cordate to reniform, rarely narrowly cordate, perianth lobes with a 5+1 arrangement and acute to acuminate apex, and straight filaments (Horn 1985). Nonetheless, it can be easily differentiated from all remaining species of *Heteranthera* by its petiolate leaves with diminute blades [i.e. $3.5-11.8-(13.2) \times 3.2-12.1$ mm], inflorescences 1–2–(3)-flowered, peduncle densely glandular-pubescent, basal bract basally glandular-pubescent with aristate apex, and seeds smooth or with 7-9 inconspicuous longitudinal wings (Fig. 5). The only other species in Heteranthera that possesses seeds not conspicuously winged is H. gardneri, in which the wings are very short, giving the seeds a striate appearance. Nevertheless, in H. pumila, the testa is almost smooth, with the stripes representing only pigmentation. All the remaining species of *Heteranthera* possess seeds with 8–19 conspicuous longitudinal wings (Horn 1985; Table 1).

Key to the species of Heteranthera in Brazil

- 1. Ligule with several filiform (leaf-like) projections, sessile leaves appearing verticillate, blades filiform to acicular; flowers non-enantiostylic, stamen 1, staminodes commonly absent, if present consisting of a filiform projection... *H. gardneri* (Hook.f.) M.Pell.
- Ligule 2-parted, sessile leaves clearly distichously or spirally-alternate, blades linear oblong to narrowly obovate; flowers enantiostylic, stamens 3, staminodes generally absent, if present not filiform... 2
- 2. Sessile leaves persistent in mature plants, petiolate leaves rarely produced, floating, blades linear oblong to narrowly obovate... 3
- Sessile leaves marcescent in mature plants, rarely persistent, petiolate leaves always produced, floating or emersed, blades narrowly cordate to broadly cordate to reniform or broadly ovate to broadly elliptic... 4
- 3. Inflorescences 5–12-flowered, glandular-pubescent when emersed, basal bract (spathe) with aristate apex; perianth yellow, rarely lilac or white... *H. seubertiana* Solms
- Inflorescences (1–)2-flowered, always glabrous, basal bract (spathe) with mucronate to retuse apex, perianth lilac to purple... *H. zosterifolia* Mart.
- 4. Petiolate leaves typically with blades longer than wide, base rounded to auriculate; perianth lobes with a 3+3 arrangement, nectar guide yellow to bright yellow, filaments sigmoid, glandular-pubescent, placentation axial... 5
- Petiolate leaves typically with blades wider than long, base conspicuously cordate; perianth lobes with a 5+1 arrangement, nectar guide yellowish green to green, filaments straight, barbate or villose with eglandular hairs, sometimes glabrous, placentation intrusive-parietal... 7
- 5. Sessile leaves abaxially green; inflorescence (1–)2-flowered, spathe flattened, slightly to distinctly falcate, narrowly ovate to ovate, apex obtuse; perianth lobes obovate to broadly elliptic, three superior lobes without a white band at base... *H. oblongifolia* Mart. *ex* Schult. & Schult.f.
- Sessile leaves abaxially white; inflorescence 1-flowered, spathe cylindrical, straight, linear to narrowly obovate, apex acute to acuminate; perianth lobes oblong to linear elliptic, three superior lobes with a white band at base... 6
- 6. Leaf blades rounded to oblong, cordate to truncate at base; floral tube glandular-pubescent, perianth lobes slightly to distinctively falcate, upper central perianth lobe auriculate near base; pollen dispersed in monads... *H. rotundifolia* (Kunth) Griseb.
- Leaf blades oblong to ovate, truncate to cuneate at base; floral tube glabrous, perianth lobes flat, upper central perianth lobe not auriculate; pollen dispersed in tetrads... *H. limosa* (Sw.) Willd.
- 7. Petiolate leaves with smaller blades, 3.5–11.8–(13.2) × 3.2–12.1 mm; inflorescences 1–2–(3)-flowered, basal bract (spathe) with aristate apex; seeds smooth or with 7–9 inconspicuous longitudinal wings... *H. pumila* M.Pell. & C.N.Horn
- Petiolate leaves with larger blades, $12-75\times10-81$ mm; inflorescences 3–30-flowered, basal bract (spathe) with acute to mucronate, rarely spatulate-mucronate apex; seeds with 8–19 conspicuous wings... 8

- 8. Petiolate leaves glandular-pubescent when emersed; inflorescence sessile, 10–30-flowered, flowers opening over several days, peduncle densely glandular-pubescent; central superior perianth lobe without a nectar guide, apex obtuse... *H. spicata* C.Presl
- Petiolate leaves always glabrous; inflorescence pedunculate, 3–8–(9–17)-flowered, flowers opening in one or two days, peduncle glabrous; central superior perianth lobe with a nectar guide, apex acute to acuminate...
- 9. Inflorescences with flowers condensed at the base and apex of the cincinnus, 6–17-flowered, basal bract with spatulate-mucronate apex; perianth lobes externally glabrous, central superior perianth lobe 6.6–9.2 mm long; central stamen with filament glabrous, style glabrous... *H. catharinensis* C.N.Horn & M.Pell.
- Inflorescences with flowers evenly distributed on cincinnus, 3–13-flowered, basal bract with acute to mucronate apex; perianth lobes externally glandular-pubescent, central superior perianth lobe 2.3–5 mm long; central stamen with filament villose or barbate, style villose...
 10
- 10. Leaf blade cordate (length/width ~ 1); peduncle < 1 cm long, cincinnus main axis glabrous; all filaments barbate with long, purple hairs... *H. multiflora* (Griseb.) C.N.Horn
- Leaf blade commonly reniform (length/width mostly < 1); peduncle > 1 cm long, cincinnus main axis glandular-pubescent; lateral stamens barbate with long hairs, central stamen sparsely villose, hairs white... H. reniformis Ruiz & Pavón

Discussion

Inflorescence morphology and terminology in Pontederiaceae

The inflorescence in Pontederiaceae, has traditionally been regarded as consisting of panicles and spikes, or more rarely, reduced to one-flowered racemose inflorescence (Lowden 1973; Dahlgren et al. 1985; Horn 1985; Rosatti 1987; Cook 1998). Nonetheless, some studies have described the inflorescence in the family as being thyrsoid, with an indeterminate main axis and cymose branches (Cook 1989; Richards and Barrett 1984; Pellegrini 2017). More specifically, Richards and Barrett (1984), based on developmental studies in E. paniculata (Spreng.) Solms, described the cymose secondary branches as representing cincinni with greatly reduced bracteoles. This is consistent with the commonly zig-zag or scorpioid pattern observed in many Pontederiaceae inflorescences (Pellegrini & Horn, pers. obs.), the occurrence of mirror-image flowers in H. gardneri (Hook.f.) M.Pell. (which is comparable to the 2-flowered cincinni with mirror-image flowers of Marantaceae; Kirchoff 1985), and the predominant occurrence of cincinni and other cymose inflorescences in Commelinid Monocots (Fahn 1953; Uhl 1969; Kirchoff 1985; Panigo et al. 2011; Kellogg et al. 2013; Remizowa et al. 2013; Stützel and Trovó 2013). Thus, the inflorescence in the family is to be regarded as thyrsoid, being composed of a many-branched thyrse, with spirally arranged cincinni in Pontederia s.l., and reduced to a solitary cincinnus in Heteranthera s.l. Cincinni bracts and bracteoles are greatly reduced in most species, being not observable to the naked eye, but consisting of ephemeral rudimentary ridges under the scanning electron microscope (Richards and Barrett 1984). Bracteoles are only macroscopically visible in E. meyeri A.G.Schulz, a species closely related to E. paniculata, being a key character in differentiating both taxa (Horn 1998).

Inflorescence architecture, has a great unexplored taxonomic potential in the Pontederiaceae, also supporting the family's bigeneric circumscription, proposed by Pellegrini (2017). Aside from that, different inflorescence patterns seem to support different lineages within the family's two major clades. In *Heteranthera s.l.*, the reduction to 1–2-flowered inflorescence seems to be, at least, partially correlated with a reversal from intrusive-parietal

placentation to axial placentation, and sigmoid filaments in the *H. limosa* (Sw.) Willd. species group [i.e. *H. limosa*, *H. lutea*, *H. oblongifolia* Mart. *ex* Schult. & Schult.f., and *H. rotundifolia* (Kunth) Griseb.]. Furthermore, in the permanently submersed species of *Heteranthera* [i.e. *H. dubia* (Jacq.) MacMill., *H. gardneri*, and *H. zosterifolia* Mart.], reduction to 1–2-flowered inflorescence seems to be correlated with the partial or complete loss of petiolate leaves, with the reversion from zygomorphic to actinomorphic flowers, and the loss of enantiostyly. In *Pontederia s.l.*, *E. meyeri* and *E. paniculata* can be readily differentiated from the remaining species on the clade by their elongated cincinni, and inflorescence erect at post-anthesis. In *Monochoria* C.Presl, the cincinni can range from obviously spirally arranged to fascicle-like, and from one to several-flowered, being very useful in species delimitation. Furthermore, great reduction is observed in the inflorescences of *E. diversifolia* (Vahl) Urb. and *E. natans* (P.Beauv.) Solms, with thyrsi always producing 1-flowered cincinni, and the number of cincinni being useful in differentiating both species. Finally, in *Pontederia s.s.*, the inflorescence is a spike-like thyrse, due to the increase in the number of cincinni, contraction of the cincinni peduncle and internodes, and finally, due to the shortening of the main florescence internodes.

Heteranthera reniformis species complex and H. multiflora subcomplex

As aforementioned, *H. reniformis s.l.* is an economically important, but poorly understood weed. This species complex can be easily characterized by its petiolate leaves typically with blades wider than long, base conspicuously cordate; flowers opening in one or two days; perianth lobes with a 5+1 arrangement and acute to acuminate apex, nectar guide yellowish green to green; straight filaments, barbate or villose with eglandular hairs, sometimes glabrous; and intrusive-parietal placentation (Fig. 1 & 2, 4–6). The group is currently composed of five neotropical species: *H. catharinensis* (Fig. 1 & 2), *H. multiflora s.l.* (Fig. 6A & B), *H. peduncularis* (Fig. 6C & D), *H. pumila* (Fig. 4 & 5), and *H. reniformis s.s.* (Fig. 6E & F). Characters such as inflorescence architecture, pubescence, and flower morphology are key in species delimitation (Pellegrini & Horn, pers. obs.).

Despite our present contribution to the *H. reniformis* species complex, further studies are still necessary to better understand some polymorphic species. Heteranthera multiflora s.l. is widely but disjunctively distributed, occurring in the United States, Venezuela, and widespread across Brazil, Argentina, and Paraguay (Horn 1985). It is currently circumscribed as comprising plants with many-flowered inflorescences with most flowers exerted from the basal bract, glabrous cincinnus axis, and stamens bearded with long, uniseriate, purple hairs (Horn 1985; Horn 2002; Horn & Pellegrini, pers. obs.). However, throughout this species' range, it is possible to recognize five different morphotypes: (1) specimens with petiolate leaf blades longer than wide, smaller sessile inflorescences, with most flowers included in the basal bract, flowers white to pale lilac, and distributed along the Atlantic Coast of the United States; (2) specimens with round petiolate leaf blades, longer sessile inflorescences, with few flowers included in the basal bract, flowers lilac to blue with darker perianth lobes base, and distributed in the Great Plains of the United States; (3) a sole peculiar collection from northern Venezuela; (4) specimens with petiolate leaf blades longer than wide, sessile inflorescences, lilac flowers, and distributed in Northeastern Brazil (i.e. states of Alagoas, Bahia, Paraíba, Pernambuco and Sergipe); and (5) specimens with petiolate leaf blades as wide as long, pedunculate inflorescences, white flowers, and distributed from Northern, Northeastern and Central-Eastern Brazil (i.e. states of Alagoas, Bahia, Maranhão, Mato Grosso do Sul, Pará, Rondônia, and Tocantins) to Southeastern Brazil (i.e. states of Espírito Santo, Minas Gerais, and Rio de Janeiro), Argentina, and Paraguay (Horn 1985; Horn & Pellegrini, pers. obs.). A new circumscription for *H. multiflora s.l.*, based on macromorphology and morphometric analyses, is currently in the works (Horn & Pellegrini, in prep.), and will shed new light in this poorly understood taxon.

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Table 1. Morphological characters differentiating the South American species of *Heteranthera reniformis* species complex. States in bold represent unique or distinguishing characteristics for that species. *Populations of *H. multiflora* in Argentina and Paraguay have a much more elongate cincinnus with only a few flowers within the basal bract (spathe). **In North America, *H. multiflora* has smaller perianth tube lengths.

Characters	H. catharinensis	H. multiflora	H. pumila	H. reniformis
Leaf blade width	(14–)30–46 mm	29–65 mm	3.2–12.1 mm	13–40 mm
Peduncle	3.2–5.5 cm long , glabrous	0.1–1.2 cm long, glabrous	0.5–3.4 cm long, glandular- pubescent	0.5–2.2(–3) cm long, glabrous
Basal bract (spathe)	Spatulate- mucronate	Mucronate	Aristate	Mucronate
Flower arrangement	Glomerulate (condensed at the base and apex of the cincinnus)	Evenly distributed along the cincinnus	Evenly distributed along the cincinnus	Evenly distributed along the cincinnus
Cincinnus	6–17-flowered, main axis glandular- pubescent	3–13 flowered, main axis glabrous	1–2(–3)- flowered, main axis glandular- pubescent	3–8-flowered, main axis glandular- pubescent
Flowers exerted from the basal bract (spathe)	5–15	0–3(–10)*	0(-1)	0–3
Perianth tube length	5–7.5 mm	(3–)6–10 mm	4.9–7.3 mm	2.5–5 mm
Perianth lobes pubescence	Glabrous	Glandular- pubescent	Glandular- pubescent	Glandular- pubescent
Central superior perianth lobe length	6.6–9.2 mm	3–7.5 mm	3.6–4 mm	2.3–5 mm

Lateral stamens	Filaments barbate with hairs of unknown color, anthers 1.0–1.8 mm long	Filaments barbate with purple hairs, anthers 0.5–1.1 mm long	Filaments barbate with lilac to pink hairs, anthers 0.4–0.6 mm long	Filaments barbate with white hairs, anthers 0.2–0.6 mm long
Central stamen	Filament glabrous, anther 1.7–2.4 mm long	Filament barbate with purple hairs, anther 1–1.9 mm long	Filament villose with white hairs, anther 1.2–1.6 mm long	Filament villose with white hairs, anther 0.6–1.4 mm long
Seeds	Unknown	Testa with 9– 12 conspicuous longitudinal wings	Testa smooth or with 7–9 inconspicuous longitudinal wings	Testa with 8– 14 conspicuous longitudinal wings



Figure 1. Holotype of *Heteranthera catharinensis* C.N.Horn & M.Pell. Image courtesy of the Smithsonian Institution, NMNH, US herbarium.

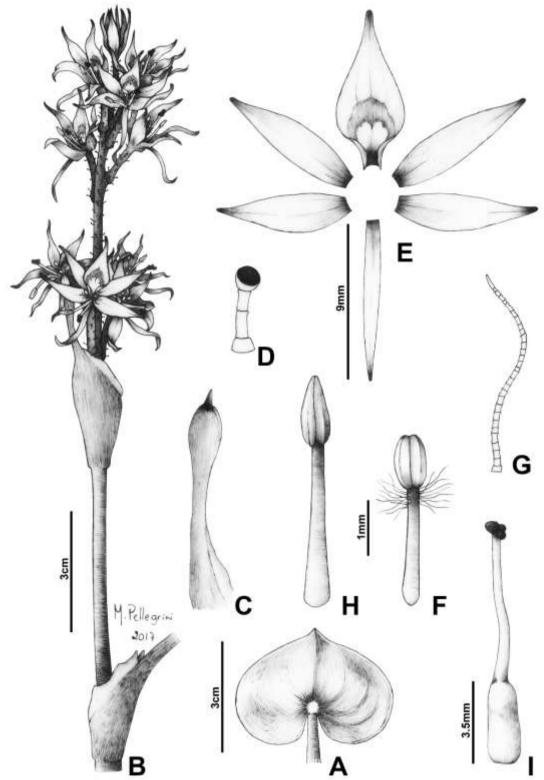


Figure 2. Line drawing of *Heteranthera catharinensis* C.N.Horn & M.Pell. **A,** Detail of the leaf blade. **B,** Detail of the apex of the stem, showing the ligule and an inflorescence at anthesis. **C,** Detail of the basal bract, showing the spatulate-mucronate apex. **D,** Glandular hair from the cincinnus axis and floral tube. **E,** Dissected perianth lobes, showing the 5+1 arrangement. **F,** Lateral stamen. **G,** Uniseriate hair from the lateral stamen. **H,** Central stamen. **I,** Gynoecium, showing the glabrous style and unevenly trilobate stigma. Illustration by M.O.O. Pellegrini, based on the paratype (Smith & Reitz 9103, US).

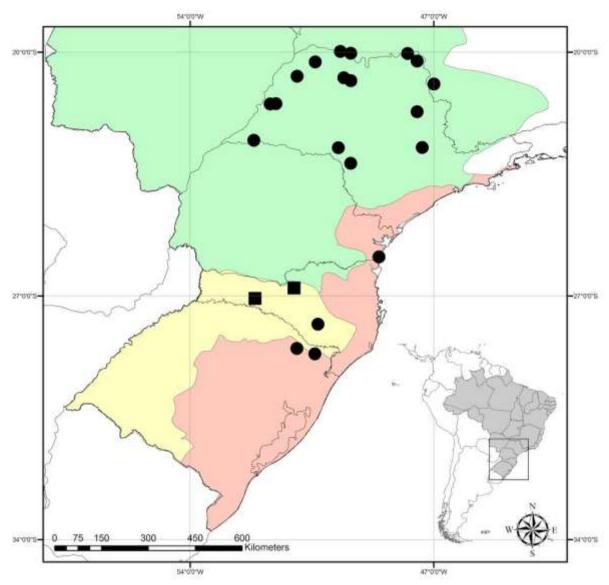


Figure 3. Distribution map. ■ *Heteranthera catharinensis* C.N.Horn & M.Pell.; • *H. pumila* M.Pell. & C.N.Horn. Green Paraná watershed; Yellow Uruguay watershed; Red-Southeastern Atlantic watershed; following ANA – Agência Nacional de Águas (2002).

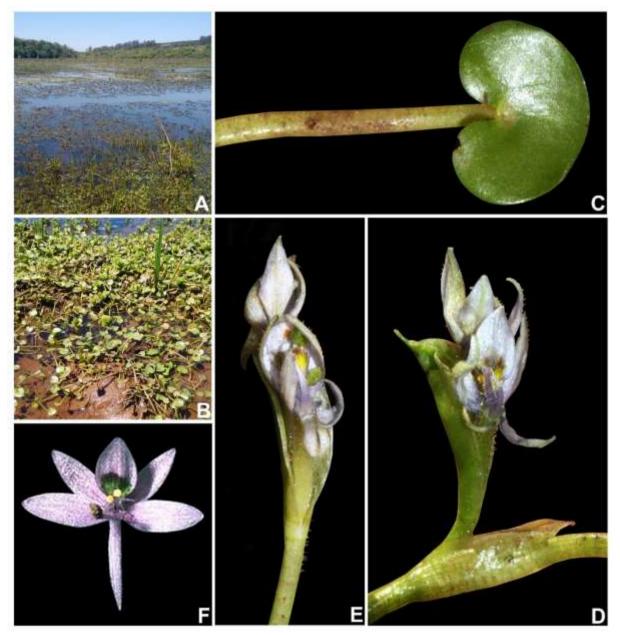


Figure 4. Field photos of *Heteranthera pumila* M.Pell. & C.N.Horn. **A,** Bog at the Paranapanema river, Piraju, São Paulo, Brazil. **B,** Habit, showing the dense subpopulation at the muddy shore of the bog. **C,** Leaf. **D,** Detail of the apex of the stem, showing the ligule and the inflorescence. **E,** Detail of the inflorescence, showing the glandular hairs at the peduncle, base of the basal bract and cincinnus. **F,** Front view of the flower, the shape of the perianth lobes and the color of the nectar guide. Photographs A–E by M.O.O. Pellegrini, F by V. Bittrich.

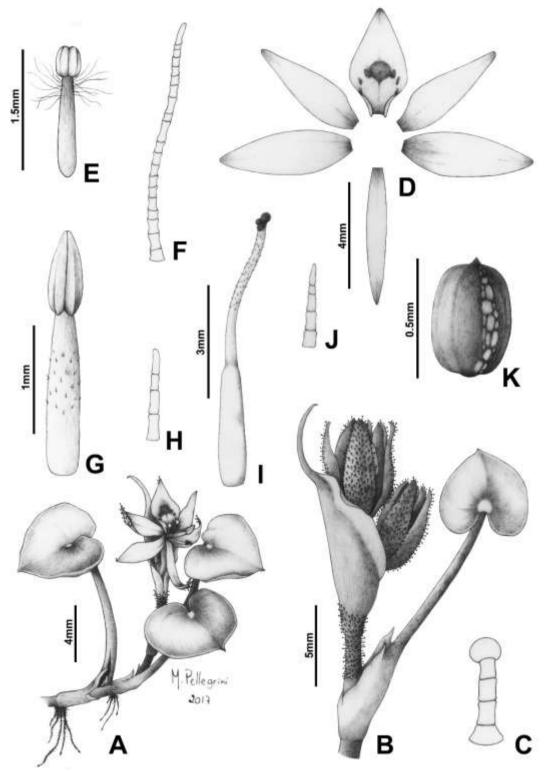


Figure 5. Line drawing of *Heteranthera pumila* M.Pell. & C.N.Horn. **A,** Habit. **B,** Detail of the apex of the stem, showing a petiolate leaf, the ligule and a pre-anthesis 2-flowered inflorescence. **C,** Glandular hair from the inflorescence, perianth tube and lobes. **D,** Dissected perianth lobes, showing the 5+1 arrangement. **E,** Lateral stamen. **F,** Uniseriate hair from the lateral stamen. **G,** Central stamen. **H,** Eglandular hair from the central stamen. **I,** Gynoecium, showing the stigma. **J,** Eglandular hair from the style. **K,** Detail of the inconspicuously winged seed, showing the persistent funiculus with raphid crystals. Illustration by M.O.O. Pellegrini, based on the holotype.

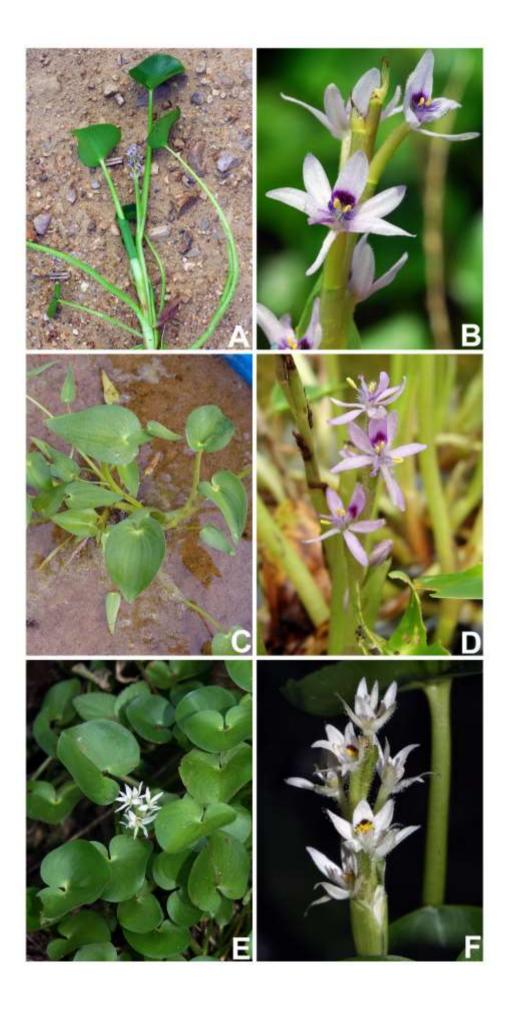


Figure 6. *Heteranthera reniformis* Ruiz & Pavón complex. **A–B,** *H. multiflora* (Griseb.) C.N.Horn *s.l.*, from Missouri, USA: **A,** Habit; **B,** Inflorescence. **C–D,** *H. peduncularis* Benth., from Michoacán, Mexico: **C,** Habit; **D,** Inflorescence. **E–F,** *H. reniformis* Ruiz & Pavón *s.s.*, from Bahia state, Brazil: **E,** Habit; **F,** Inflorescence. Photos A–B by Steve R. Turner, C–D by C.N. Horn, and E–F by M.O.O. Pellegrini.

SECTION 4—PONTEDERIACEAE KUNTH

Chapter 4.3. Total evidence phylogeny of Pontederiaceae (Commelinales) sheds light on the necessity of its recircumscription and synopsis of *Pontederia* L.

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Abstract

A total evidence phylogeny for Pontederiaceae is herein presented based on new morphological and previously published molecular data. Our results led us to re-circumscribe *Pontederia* to include *Monochoria*, *Pontederia* s.s., and the polyphyletic *Eichhornia*. We provide the needed 10 new combinations and 16 typifications, arrange a total of 25 accepted species (six representing reestablished names) in 5 new subgenera. Furthermore, we provide an identification key for the two genera accepted by us in Pontederiaceae, an identification key to the subgenera, identification keys to the species of each subgenus, and commentaries on *Pontederia* s.l., as well as for each subgenus, and for each species.

Key words

Aquatic flora, Eichhornia, Monochoria, pickerelweed, Reussia, water-hyacinth

Introduction

Pontederiaceae is a small aquatic monocot family, placed in Commelinales as sister to Haemodoraceae, with both families being sister to Philydraceae (Saarela et al. 2008). This clade can be morphologically characterized by its: distichously-alternate and unifacial leaves, with xylem and phloem alternate (or rarely phloem circular with central xylem); the presence of styloid crystals; perianth whorls partially to completely connate forming a hypanthium, perianth petaloid, flowers bisexual, zygomorphic, and enantiostylous; pollen shed with raphides; the presence of placental sclereid idioblasts; and seeds longer than wide with longitudinal wings or striations (Simpson 1990; Prychid et al. 2003; Simpson and Burton 2006; Pellegrini, unpublished data). Furthermore, the relationship between Pontederiaceae and Haemodoraceae is morphologically supported by their endothecium with a basal thickening, non-columellatetectate exine, and the presence of septal nectaries (Simpson 1987, 1990). Pontederiaceae can be easily distinguished from the remaining families of Commelinales by its roots not sand-binding; dimorphic, late bifacial, and ligulate leaves, ptyxis involute enclosing the petiole of the preceding leaf; xylem and phloem alternate near the center of the blades, plus xylem abaxial and phloem adaxial near the margins; bisulcate pollen grains; and the presence of an anthocarp (Arber 1925; Simpson 1987, 1990; this study). The family is currently arranged in four genera (i.e., Eichhornia Kunth, Heteranthera Ruiz & Pavón, Monochoria C.Presl, and Pontederia L.) and possesses ca. 45 species (Lowden 1973; Horn 1985; Cook 1989; Pellegrini 2017a; Pellegrini and Horn 2017). Pontederiaceae has a pantropical distribution, with the Neotropical region as its diversity center, where ca. 70% of its species can be found (Barrett 2004; Pellegrini and Horn 2017). Furthermore, Brazil retains most of the diversity for the group, with 24 species know to occur in all kinds of aquatic and damp environments (BFG 2015; Pellegrini and Horn 2017). Despite being unquestionably monophyletic (Eckenwalder and Barrett 1986; Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011), generic boundaries in Pontederiaceae are still in great need of revision (Ness et al. 2011; Pellegrini 2017a). A total of 30 genera have been described and assigned to Pontederiaceae throughout the years (eMonocot 2010; Govaerts 2017; Tropicos.org 2017), and some authors have accepted up to nine genera in the family (e.g., Cook 1998). All phylogenetic studies invariably recover most genera as non-monophyletic, with *Eichhornia* and *Heteranthera* being the most problematic groups (Eckenwalder and Barrett 1986; Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011). Based on these published phylogenies, it is clear that these genera have been circumscribed based either on autapomorphic or homoplastic characters. Thus, traditionally proposed generic boundaries need to be urgently revisited.

Recently, *Heteranthera* was recircumscribed to include *Hydrothrix* Hook.f. and *Scholleropsis* H.Perrier, thus being finally rendered monophyletic (Pellegrini 2017a). Nonetheless, the *Pontederia* clade (i.e., *Eichhornia s.l.*, *Monochoria*, and *Pontederia*) remains neglected (Pellegrini 2017a), with the hopelessly polyphyletic *Eichhornia* being recovered as three distinct lineages within it (Eckenwalder and Barrett 1986; Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011). The first *Eichhornia* lineage is composed by the erect-emergent, non-clonal species, with perianth spirally-coiled at post-anthesis. The second lineage is composed exclusively by *E. crassipes* (Mart.) Solms, which is characterized by its free-floating and stoloniferous rosette, flabellate ligules, and its peculiarly inflated petioles. The last *Eichhornia* lineage is composed by procumbent-emergent species, with distichously-alternate leaves evenly distributed along the stems, infundibuliform perianth, and glabrous styles (Pellegrini and Horn, pers. observ.).

According to Pellegrini (2017a), there are two approaches for solving the generic limits in the *Pontederia* clade: (1) sink *Eichhornia* and *Monochoria* into a broader, but morphologically cohesive *Pontederia*; or (2) split *Eichhornia* into three ill-defined genera, in order to maintain *Pontederia* and *Monochoria* as independent genera. The first option is considerably more taxonomically stable, and would greatly facilitate the identification of Pontederiaceae specimens, especially for the non-specialists, ecologists, plant growers, farmers, etc.

Here, we present a total evidence phylogeny for Pontederiaceae, based on plastid and morphological data, in order to recircumscribe *Pontederia* to include *Eichhornia* and *Monochoria*, and provide an identification key to the genera in Pontederiaceae. We also present a synopsis for *Pontederia s.l.*, with an updated description for the genus, propose five new subgenera, provide an identification key to the accepted subgenera of *Pontederia*, and identification keys to the species of each subgenus. Finally, we propose the needed 10 new combinations, present six new synonyms, and accept a total of 25 species, five of these representing reestablished names. The present study concludes the bi-generic classification of Pontederiaceae initiated by Pellegrini (2017a) and is a result of the first author ongoing systematic studies on Commelinales.

Methods

Taxonomy

Specimens from the following herbaria were analyzed: AAU, ALCB, B, BA, BAF, BHCB, BHZB, BLH, BM, BOL, BOTU, BR, BRIT, C, CAS, CEPEC, CESJ, COL, CORD, CTES, CVRD, DS, E, EA, ESA, F, FCAB, FLOR, FURB, G, GH, GMUF, GOET, GUA, HAL, HAMAB, HAS, HB, HBR, HERBAM, HNMN, HRB, HRCB, HSTM, HUEFS, HUFSJ, HURB, IAC, IBE, ICN, INPA, IPA, K, KANU, L, LE, LG, LIL, LL, LP, M, MA, MBM, MBML, MG, MO, MVM, MY, NBYC, NY, OS, P, PH, PMSP, PR, PRC, PRE, R, RB, RFA, RFFP, S, SMU, SP, SPF, SRGH, TEX, UEC, UMO, UNA, UPCB, US, USF, VDB, VIC, W and WAG (herbaria acronyms according to Thiers, cont. updated). Fresh specimens, field notes, photographs and specimens for cultivation were gathered by the authors during several field trips across North, Central and South America, between 1980–2017. The indumentum and shape terminology follows Radford et al. (1974); the inflorescence terminology and morphology follow Weberling (1965, 1989) and Panigo et al. (2011), as implemented by Pellegrini and Horn (2017); fruit terminology follows Spjut (1994); and seed terminology follows Faden (1991). Species distribution is based on literature, herbarium specimens, and field work data.

Morphological character selection, coding, mapping, and morphological analysis

Characters were scored mainly from living specimens in the field and specimens in cultivation, and later complemented by spirit and herbarium samples from the aforementioned herbaria. When no living or herborized specimens were available for examination, information was taken from published literature. We have studied at least five specimens for each taxon, with the most representative specimen chosen as the voucher for the morphological matrix (Table 1). Some characters were chosen based on previous studies (i.e., Eckenwalder and Barrett 1986; Simpson 1987; Barrett and Graham 1997; Simpson and Burton 2006), with most characters being scored for the present study. Character coding followed the recommendations of Sereno (2007) for morphological phylogenies. Primary homology hypotheses (De Pinna 1991) were proposed for root, stem, leaf, inflorescence architecture, floral, fruit, seed, palynological, and anatomical characters. A total of 96 discrete micro and macromorphological characters were scored, being treated as unordered and equally weighted (Appendix 1).

Data was entered into a matrix of characters per taxa using the software Mesquite 3.20 (Maddison and Maddison 2017; Appendix 2). All characters were treated as unweighted and unordered. Maximum Parsimony (MP) analysis was performed using PAUP* 4 (Swofford 2003), with a heuristic search with 1000 random taxon additions and tree bisection-reconnection (TBR) branch swapping. Consistency index (CI) and retention index (RI) were used to assess the degree of homoplasy in the dataset and using character optimization of ACCTRAN (accelerated transformation optimization; Swofford and Maddison 1987). Statistical support for each branch of the cladogram was evaluated with Bootstrap Support (BS) analyses with 1000 random addition replication. The search parameters used to estimate the bootstrap values were the same as the initial heuristic search. The Bremer Index (BI) was also used to evaluate clade reliability based on the presence of secondary homologies (Bremer 1994). The Bremer Index was calculated by increasing the number of the optimal tree steps until all clades collapsed. Mesquite 3.20 was used to reconstruct the ancestral character states, while WinClada ver. 1.0000 (Nixon 2002) was used to trace the synapomorphic characters on the strict consensus tree.

Taxon sampling, alignment and phylogenetic analysis

Sequences of the genes *ndhF* and *rbcL* were retrieved from GenBank for 26 taxa representing all currently accepted genera in Pontederiaceae, including outgroups *Anigozanthos* Labill. and *Xiphidium* Aubl. (Haemodoraceae) and the tree was rooted with Philydraceae. All sequences were aligned using Muscle (Edgar 2004) implemented on Geneious software (Kearse *et al.* 2012), with subsequent adjustments in the preliminary matrices made by eye.

Combined analyses of the plastid regions and plastid+morphology datasets were performed. Prior to combining our data, we performed the incongruence length-difference (ILD) test (Farris *et al.* 1994) to investigate incongruence between DNA data sets. Analyses using maximum parsimony (MP) on both matrices were conducted with PAUP 4.0b10a (Swofford 2002). A heuristic search was performed using TBR swapping (tree-bisection reconnection) and 1,000 random taxon-addition sequence replicates with TBR swapping limited to 15 trees per replicate in order to prevent extensive searches (swapping) in suboptimal islands, followed by TBR in the resulting trees with a limit of 1,000 trees. In all analyses, the characters were equally weighted and unordered (Fitch 1971). Relative support for individual nodes was assessed using non-parametric bootstrapping (Felsenstein 1985), with 1,000 bootstrap pseudoreplicates, TBR swapping, simple taxon addition and a limit of 15 trees per replicate.

For the DNA partitions of the model-based approach, we selected the model using hierarchical likelihood ratio tests (HLRT) on J Modeltest 2 (Darriba *et al.* 2012, results presented in Table 2). For the morphological partition, the standard discrete Markov model (Mkv) was used following Lewis (2001) with rates set to equal. A Bayesian analysis (BA) was

conducted with a mixed models and unlinked parameters, using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). The Markov Chain Monte Carlo (MCMC) was performed using two simultaneous independent runs with four chains each (one cold and three heated), saving one tree every 1,000 generations, for a total of ten million of generations. We excluded as 'burn in' trees from the first two million generations, and tree distributions were checked for a stationary phase of likelihood. The posterior probabilities (PP) of clades were based on the majority-rule consensus, using the remaining trees, calculated with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003).

Results

Morphological analysis

The cladistic analysis retrieved 228 equally parsimonious trees with 209 steps, Consistency Index (CI) of 0.5913, Homoplasy Index (HI) of 0.4087, Retention Index (RI) of 0.8618, and Rescaled Consistency Index (RC) of 0.5096. All 96 coded characters were parsimony-informative. The strict consensus (Fig 1) and the majority-rule trees (Fig 2) are presented and discussed below.

The Haemodoraceae+Pontederiaceae clade is supported by seven characters: the presence of septal nectaries (Character 44), perianth 6-lobed (Character 58, plesiomorphic), perianth with 3+3 arrangement (Character 59, plesiomorphic), epipetalous stamens (Character 66, homoplastic), stamens dimorphic (Character 69), endothecium with a basal thickening (Character 72), and non-tectate-columellate exine (Character 76). Pontederiaceae is recovered as monophyletic with high statistical support (BS= 100; BI= 7; Fig 2), being supported by: dimorphic leaves (Character 12), leaf-blades late bifacial (Character 13), involute ptyxis where the blade of the new leaf encloses the petiole of the preceding leaf (Character 14), leaf-blades with xylem and phloem alternate in the central portion of the blade and xylem abaxial and phloem adaxial at the margins (Character 15), the presence of a ligule (Character 16), nonequitant leaves (Character 18, reversion), sessile leaves early-deciduous (Character 18), inflorescence deflexed at post-anthesis and in fruit (Character 37), sessile flowers (Character 39), absence of fibrillar tannin cells in the perianth (Character 47), presence of aerenchymatous tissue in the receptacle (Character 48) and in the perianth (Character 49), perianth connate producing a conspicuous tube (Character 56, homoplastic), perianth ranging from lilac to purple or blue (Character 57, homoplastic), posterior lobe(s) with a nectar guide (Character 63, homoplastic), pollen grains bisulcate (Character 75), presence of aerenchymatous tissue in the ovary walls (Character 79), and the presence of an anthocarp (Character 91).

Heteranthera sensu Pellegrini (2017a), is recovered as monophyletic with high statistical support (BS= 99; BI= 3; Fig 2). It is supported by: plants mostly to completely submersed (Character 3, homoplastic), indefinite base (Character 4), water-binding/mucilaginous roots (Character 6), rhizome absent (Character 7), stems freely branching and elongated (Character 9 and 10, homoplastic), ligules 2–several parted (Character 17), spirally-alternate sessile leaves (Character 18), sessile leaves evenly distributed along the stem (Character 20, homoplastic), basal bract conduplicate (Character 30), main florescence reduced to a solitary cincinnus (Character 32), sparse aerenchymatous tissue in the perianth (Character 49), perianth tubular (Character 50), filaments obliquely inserted (Character 65), and unevenly trilobate stigma (Character 87). Within Heteranthera s.l. we recover two main clades in the majority rule (Fig 2), with only one of these being also recovered in the strict consensus (Fig 1). The H. limosa group is composed by H. limosa (Sw.) Willd., H. oblongifolia Mart. ex Schult. & Schult.f., and H. rotundifolia (Kunth) Griseb., being characterized by: the absence of clonal reproduction (Character 2, homoplastic), sessile leaves late-deciduous (Character 19, homoplastic), petiolate leaves with elliptic to ovate blades (Character 27, homoplastic), the posterior perianth lobe with

flanged base (Character 62) and a nectar guide consisting of a sole spot or dark band (Character 63. homoplastic), sigmoid filaments (Character 67), ovary hemiseptalous (Character 80, homoplastic), axile-parietal placentation (Character 83), and placentation 2-flanged (Character 84, homoplastic). The second clade is named by us the *H. dubia* group is composed by *H. dubia* (Jacq.) MacMill., *H. gardneri* (Hook.f.) M.Pell., *H. seubertiana* Solms, and *H. zosterifolia* Mart. This group is characterized by: the presence of cleistogamous flowers (Character 43), inflated filaments (Character 68), gynoecium 1-locular (Character 77, homoplastic), ovary aposeptalous (Character 80, homoplastic), intrusive-parietal placentation (Character 83, homoplastic), and placentation slightly 2-flanged (Character 84).

Pontederia s.l. is also recovered as monophyletic with high statistical support (BS= 93; BI= 6; Fig 2), being supported by: distichously-alternate sessile leaves (Character 18), petiolate leaves pulvinate (Character 25), tristylous flowers (Character 42), dense aerenchymatous tissue in the perianth (Character 49), perianth campanulate or infundibuliform or hypocrateriform (Character 50, homoplastic), perianth coiled and tightly enclosing the fruit at post-anthesis (Characters 53 and 55), perianth lobes equal in shape in the same whorl (Character 60) and with obtuse apex (Character 61, homoplastic), stamens 6 (Character 64, reversion), filaments Jshaped or recurved-decurved (Character 67), anthers dorsifixed (Character 71), style J-shaped (Character 85), stigmas evenly trilobate to trifid or capitate (Characters 87), stigma wet (Characters 88), anthocarp tightly enveloping the fruit (Character 92), and anthocarp hardened and ornamented (Characters 93 and 94). Pontederia s.l. is recovered by us arranged in five clades in the strict consensus (Fig 1) and in the majority rule (Fig 2). The E. paniculata group is highly supported (BS= 95; BI= 1; Fig 2), being composed by E. paniculata (Spreng.) Solms and E. paradoxa (Mart. ex Schult. & Schult.f.) Solms. It is characterized by: its annual life cycle (Character 1, homoplastic), the lack of clonal reproduction (Character 2, homoplastic), inflated sheath of the leaf subtending the inflorescence (Character 29, homoplastic), flat basal bract (Character 30, homoplastic) with a caudate apex (Character 31, homoplastic), main florescence with a fistulose main axis (Character 34, homoplastic), inflorescence erect at post-anthesis and in fruit (Character 37, reversion), floral organs lacking tannin cells of the homogeneous type (Character 45), perianth with a moderate amount of granular tannin cells (Characters 51 and 52), perianth spirally-coiled at post-anthesis (Character 54, homoplastic), ovary walls lacking tannin cells (Character 78, homoplastic), ovary hemiseptalous (Character 80, homoplastic), and septae lacking tannin cells (Character 82, homoplastic). Based on morphology, E. meyeri A.G.Schulz should also be placed in the *E. paniculata* group. *Monochoria* is recovered as monophyletic with high statistical support (BS= 96; BI= 2; Fig 2), being characterized by eight non-homoplastic synapomorphies: pedicellate flowers (Character 39, reversion), perianth only basally connate (Character 56, reversion), absence of a nectar guide (Character 63, reversion), presence of a petalo-staminal tube (Character 66), stamens unequal (Character 69), presence of a filament appendage (Character 70), enantiostylous flowers (Character 71, reversion), and poricidal anthers (Character 72). Eichhornia crassipes is recovered as a sole species with high statistical support (BS= 94; BI= 1; Fig 2), being characterized by: its free-floating habit (Character 5), the production of new rosette through stolons (Character 8), flabellate ligules (Character 17), spirally-alternate petiolate leaves (Character 22, homoplastic), perianth loosely enveloping the fruit (Character 55, homoplastic), and nectar guide consisting of a sole spot (Character 63, homoplastic). Eichhornia s.s. was recovered with low statistical support (BS= 56; BI= 2; Fig 2), being composed by E. azurea (Sw.) Kunth, E. diversifolia (Vahl) Urb., and E. heterosperma Alexander. It is characterized by: growing as mostly submerged plants (Character 3, homoplastic), stems freely branching and elongated (Character 9 and 10, homoplastic), sessile leaves late-deciduous (Character 19, homoplastic), petiolate leaves evenly distributed along the stem (Character 23, homoplastic), flowers self-compatible (Character 38, homoplastic), floral tissues lacking granular tannin cells (Character 46, homoplastic) and

presenting fibrillar tannin cells (Character 47, reversion), nectar guide consisting of a sole spot or dark band (Character 63, homoplastic), and ovary walls lacking aerenchymatous tissue (Character 79, reversion). Finally, *Pontederia sensu* Lowden (1973) was recovered by us as monophyletic with high statistical support (BS= 97; BI= 3; Fig 2). It is characterized by: flowers self-compatible (Character 38, homoplastic), nectar guide consisting of two spots (Character 63, homoplastic), pseudomonomerous ovary (Character 77), the presence of epithelial cells in the septae (Character 81, homoplastic), pendulous and unflanged placentation (Characters 83 and 84), fruit an achene (Character 89), seeds one per locule (Character 90), and smooth testa (Character 95). Nonetheless, the subgenera proposed by Lowden (1973) cannot be maintained, due to *P. rotundifolia* L.f. (i.e., *P.* subg. *Reussia*), being nested within *P.* subg. *Pontederia* (sensu Lowden 1973).

Plastid and combined analyses

The ndhF characters represented 503 characters of the plastid dataset, with GTR+G as the nucleotide model selected. The rbcL characters represented 1355 characters of the plastid dataset, with HKY+G+I as the nucleotide model selected. The plastid dataset represented 1858 characters, of which 241 characters were variable, and 119 characters were parsimonyinformative. The plastid Bayesian analysis recovered a mostly resolved tree with 23 wellsupported clades (>PP95%) (Fig. 2). The congruence between the plastid and morphological datasets is illustrated in Figure 2. In both analyses *Pontederia s.l.* and *Heteranthera sensu* Pellegrini (2017a) are strongly supported, but the relationship between the species is greatly different. In *Heteranthera* the morphologically based topology is better resolved and recovers two clades, while the plastid dataset recovers two clades plus *H. gardneri* in a polytomy (Fig. 2). In *Pontederia s.l.* both datasets recover the genus arranged in five clades, but the relationship between them is different. In the morphological dataset Eichhornia s.s. is the first lineage to diverge, followed by E. crassipes, Pontederia s.s., and Monochoria sister to the E. paniculata group. Alternatively, in the plastid dataset the *E. paniculata* group is undoubtfully recovered as the first lineage, followed by E. crassipes, Monochoria, and Pontederia s.s. sister to Eichhornia s.s.

Topologies produced by MP and BI analyses, based on the combined plastid + morphology datasets, were highly congruent and provided higher support for more clades than the results based on independent datasets (Fig. 3). Thus, based on the combined plastid + morphological datasets (1,858 analyzed characters, of which 353 were variable and 140 parsimony-informative), the maximum parsimony analysis found 24 trees (CI = 0.6471, RI = 0.7858) whose MRC presented 23 highly supported clades (BSP75%). The combined Bayesian analysis recovered a fully resolved tree with 25 mostly well-supported clades (>PP95%) (Fig. 3). The topology recovered for the Bayesian combined analysis (Fig. 3) is almost identical to the one recovered for the plastic dataset (Fig. 2), differing in only very small details. On the other hand, the Parsimony combined analysis recovers *E. crassipes*, *Pontederia s.s.*, and *Eichhornia s.s.* in as well-supported clade, with this clade being recovered in a polytomy together with the *E. paniculata* group and *Monochoria*.

Discussion

Phylogenetics of Pontederiaceae

The topologies recovered from the combined plastid and the total evidence datasets strongly corroborate the bi-generic circumscription of Pontederiaceae suggested by Pellegrini (2017a). They are also congruent with previous phylogenetic studies using molecular and/or combined datasets (Graham and Barrett 1995; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011), and partially congruent with the morphologically based phylogenetic tree of

Eckenwalder and Barrett (1986). The phylogenetic tree recovered by Kohn et al. (1996) differs greatly from our results and from all previous studies due to part of the polyphyletic *Eichhornia* being recovered as sister to *Heteranthera s.l.* Most molecular studies in the family (Graham and Barrett 1995; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011) recover a well-supported Pontederiaceae, divided in two main lineages, corresponding to a well-supported *Heteranthera s.l.* (*sensu* Pellegrini 2017a) and poorly-supported *Pontederia s.l.*; using *ndhF*, *rbcL*, plus a restriction-site in the chloroplast genome in Graham et al. (1998, 2002), and five nuclear gene families recovered employing a expressed sequence tag (EST) study by Ness et al. (2011). As in previous studies (Graham and Barrett 1995; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011), we recover *Pontederia s.l.* arranged in five main lineages, each representing a well-supported morphological group (i.e., *Eichhornia paniculata* group, *Monochoria*, *E. crassipes* group, *Eichhornia s.s.*, and *Pontederia s.s.*). The monophyly of *Heteranthera sensu* Pellegrini (2017a) is indisputable, and the inclusion of *Hydrothrix* and *Scholleropsis* in *Heteranthera* was strongly corroborated.

Morphology and Systematics of Pontederiaceae

The monophyly of Pontederiaceae was rarely, if ever, questioned by previous authors. Perhaps for this reason, little attention was ever given to the family's putative morphological synapomorphies. Among the 18 morphological synapomorphies recovered for Pontederiaceae, one was previously suggested by Arber (1925; i.e., with xylem and phloem alternate near the center of the blades, plus xylem abaxial and phloem adaxial near the margins), three were suggested by Simpson (1987, 1990; i.e., late bifacial and ligulate leaves, and bisulcate pollen grains), and four were suggested by Simpson and Burton (2006; absence of fibrillar tannin cells in the perianth, and presence of aerenchymatous tissue in the receptacle, perianth, and ovary walls). Nonetheless, the peculiar involute ptyxis where the blade of the new leaf encloses the petiole of the preceding leaf, non-equitant leaves, sessile leaves early-deciduous, inflorescence deflexed at post-anthesis and in fruit, sessile flowers, perianth connate producing a conspicuous tube, and the presence of an anthocarp, are suggested here for the first time as synapomorphies for Pontederiaceae.

Almost, if not all, leaf synapomorphies recovered for Pontederiaceae seem to be directly correlated. These characters seem to be related to the adaptive shift to a completely aquatic lifestyle in the family, and an adaptation to changes in water level. The leaves of Pontederiaceae are characteristically dimorphic, being morphologically divided into sessile and petiolate leaves (Horn 1988). Leaf dimorphism is widely distributed across the Embryopsida, being generally related to changes in function (e.g., reproductive leaves in ferns), growth form (e.g., juvenile and mature leaves of Monstera spp.), or environmental changes (Allsopp 1965). The dimorphic leaves of Pontederiaceae seem to fit the latter situation, since the petiolate leaves are always floating or aerial, while the ribbon-like or acicular sessile leaves are the first type produced by the germinating plantlet and seen to be an adaptation to the aquatic environment. Furthermore, the presence of a petiole greatly helps to keep the leaves at or above the water level, through cell elongation in the petiolar region. This strategy can be easily observed in several distantly related aquatic plant families (e.g., Alismataceae, Asteraceae, Cabombaceae, Haloragaceae, Nymphaeaceae, Onagraceae, Ranunculaceae, etc.; Allsopp 1965; Sculthorpe 1967; Cook 1996). The peculiar vascular bundle arrangement observed in Pontederiaceae is exclusive to the family and few other monocots (Arber 1925). This feature seems to be a result of the reversion from abaxialized unifacial leaves to bifacial leaves, which according to Simpson (1990) might be related to the adaptive shift and radiation to an aquatic lifestyle in the family. The remaining closely related families (i.e., Haemodoraceae and Philydraceae) possess consistently abaxialized unifacial leaves, with blades ranging from cylindrical, terete, laterally compressed, and more rarely plicate (Simpson 1990, 1998; Hamann 1998). Nonetheless, the evolutionary

relevance of bifacial leaves is significantly harder to infer, since unifacial leaves are noticeably common in several aquatic plants. The reversal from equitant to alternate leaves seems to be a byproduct from the reversion from unifacial to bifacial leaves. As aforementioned, the involute ptyxis in Pontederiaceae is extremely unusual, since the blade of the new leaf encloses the petiole of the preceding leaf. This feature is also unique in the Angiosperms and is easily observed in most species in the family but is especially obvious in *E. crassipes* (Fig 7C). This feature might also be related to the adaptive shift and radiation to a completely aquatic lifestyle in Pontederiaceae, being most likely a result of the reversion to bifacial leaves. Developmental studies focusing on the ontogeny of the leaves in Pontederiaceae, in comparison to some members of Haemodoraceae and Philydraceae, might help us better understand the mechanics of the reversal from unifacial to bifacial leaves in the family, and how this shift might have affected general leaf morphology and the appearance of novel structures such as the ligule.

As aforementioned, the leaves of Pontederiaceae are dimorphic, with both sessile and petiolate leaves being produced in different moments of the plants' life. Sessile leaves represent the plesiomorphic state and are the first ones produced after seed germination. They vary in number from 5-many per plant and allow plants to become established in a submersed habitat (Horn 1988). The sessile leaves can range from early-deciduous to persistent in mature plants, while in some species of *Heteranthera s.l.*, petiolate leaves are never or very rarely produced (Horn 1985, 1988; Eckenwalder and Barrett 1986). The petiolate leaves are produced at posteriori and are considered the mature leaf type in the family. The initial petiolate leaves are morphologically plastic, allowing for a transition from a submersed to emersed environment. This plasticity, coupled with the elongation of the stem, allows Pontederiaceae plants to successfully develop to and at the water surface (Horn 1988). In Heteranthera s.l., the sessile leaves suffer a reversion from distichously to spirally arranged, producing the characteristic basal rosettes in the juvenile phase of many Heteranthera species (Horn 1988). Thus, earlydeciduous sessile leaves and early production of petiolate leaves give a clear adaptive advantage to the Pontederiaceae, enabling them to tolerate a wide variation in water depth during their development, also allowing juvenile plants to successfully reach mature emergent or floating growth-forms (Horn 1988). This might have ultimately allowed the diversification of Pontederiaceae and their complete invasion of the aquatic environment.

The presence of a leaf sheath projection is striking in Pontederiaceae, with its morphology being relevant to the systematic of the family. Ligules and ligule-like structures are recorded for several members of Embryopsida, being especially common in some lycophytes (i.e., Selaginellales and Isoëtales) and several monocots (i.e., Alismatales, Arecales, Asparagales, Commelinales, Dioscoriales, Poales, and Zingiberales) (Kubitzki 1998; Rudall and Buzgo 2002; Kellogg 2015). Despite possessing the same name, there is no evidence supporting the homology of these structures between lycophytes and monocots, and not even between different groups within the monocots (Rudall & Buzgo 2002). The definition and characterization of ligules in monocots has varied greatly depending on the author, having Poaceae as their main focus. These authors have proposed three distinct definitions for ligules: (1) a subtype of stipule (Bischoff 1834; Regel 1843; Lubbock 1891, 1895; Arber 1925); (2) a structure of mixed origin between stipules and petioles (Glück 1901; Majumbdar 1956); and (3) an avascular projection of the leaf-sheath, situated between the leaf-sheath and the blade (Colomb 1887; Philipson 1935; Dahlgren et al. 1985; Chaffey 1994; Rudall & Buzgo 2002). In Commelinid monocots, ligules and ligule-like structures are recorded for Arecales (i.e., the hastulae present is some Arecaceae leaves), several families of Poales (e.g., Cyperaceae, Joinvilleaceae, Juncaceae, Poaceae, Restionaceae), Commelinales (exclusively in Pontederiaceae), and Zingiberaceae (i.e., Costaceae and Zingiberaceae) (Kubitzki 1998; Rudall & Buzgo 2002; Kellogg 2015). As aforementioned, ligules and ligule-like structures in Commelinales seem to be restricted to Pontederiaceae, being unknown to any of the other four families of the order (Kubitzki 1998; Rudall & Buzgo 2002; Pellegrini pers. obs.). These structures might also be a result of the reversion from unifacial leaves to bifacial leaves, or even an independent adaptation to the in the family. In the unifacial-leaved clade. Philydraceae(Haemodoraceae+Pontederiaceae), Pontederiaceae is the only exclusively aquatic family, and also the only one to possess ligule-like structures (Figs 4F, 6C, 7C & 9E), dimorphic leaves, petiolate leaves, and bifacial leaves. Nonetheless, ontogenetic studies are necessary to understand the origin of these structures in the family. In Pontederiaceae, these ligule-like structures have been treated under different names according to the authors, having been named stipules (Schwartz 1926), ligules (Castellanos 1958; Pellegrini & Horn 2017), ochreas (Rutishauser 1999), or simply as leaf-sheath projections (Pellegrini 2017a). Different names have also been applied by the same author, depending on the development and shape of these structures (i.e., Cook 1998). Regardless of the name adopted for these ligule-like structures in Pontederiaceae, their systematic and taxonomic relevance is undeniable. As aforementioned, this structure is recovered as synapomorphic for the family. Alternatively, within Pontederiaceae the morphology of this structure can be easily used to define the two clades recovered in phylogenetic studies. Pontederia s.l. can be easily characterized by it mainly truncate ligules, being rarely flabellate (i.e., E. crassipes); while Heteranthera s.l. can be characterized by its 2-several-parted ligules.

Out of the reproductive synapomorphies recovered by us for Pontederiaceae, some of them seem to be related to pollination, while the others seem to be related to fruit dispersal. Sessile flowers are recovered by us as a synapomorphy of Pontederiaceae, with the sole reversion occurring in Monochoria. This character seems to be directly related to another reproductive synapomorphy for the family (i.e., perianth connate to part of the receptacle and the filaments producing a conspicuous tube). Pedicel and floral tube length seem to be inversely correlated, with tube elongation helping with floral display by elevating the perianth lobes. Added to that, the contraction of the pedicel might also provide extra stability for heavier floral visitors that require landing platforms in order to properly visit flowers (e.g., butterflies). Alternatively, the reversion from sessile to pedicellate flowers in Monochoria might have played a key role, by giving flowers the needed mobility in order to avoid floral damage during buzz pollination (Wang et al. 1995). Bisulcate pollen grains are rather rare in the monocots, being recorded for only a handful of families, such as: Araceae (Grayum 1992), Arecaceae (Harley and Baker 2001), Dioscoreaceae (Caddick et al. 1998), Iridaceae (Rudall and Wheeler 1988), and Velloziaceae (Halbritter and Hesse 1993). Of the aforementioned families, only Arecaceae (Arecales) is a member of the Commelinid monocots, and it is but distantly related to Pontederiaceae (Saarela et al. 2008; Hertweck et al. 2015; APG IV 2016). In Haemodoraceae, Simpson (1983) recorded the occurrence of biporate pollen grains in some genera from subfamily Conostylidoideae. Nonetheless, Simpson (1987, 1990) considers the biporate pollen grains in Haemodoraceae not homologous to the bisulcate pollen grains in Pontederiaceae. This view is also shared by us in the present study.

The first synapomorphy related to diaspore dispersal is the deflexed position of the inflorescence at post-anthesis and in fruit. This shift in the inflorescence position during fruit development will almost certainly allow the mature fruits to reach the water after their maturity. The deflexed inflorescences also elongate in length, which ultimately place the maturing fruits at or under the water surface. This seems to be the first step in diaspore dispersion in most species of Pontederiaceae. The following adaptations are related to increasing the floatation period of the diaspores. The first and most obvious seems to be the presence of an anthocarp. According to Spjut (1994), an anthocarp is a type of fruit which possess attached and developed floral parts, that aid in its dispersal. It is more commonly recorded for plants with inferior ovaries, but it is not exclusive to them (Spjut 1994). In Commelinales, all fruits have persistent perianth parts, but only in Pontederiaceae an enlarged perianth actively aids in the dispersal of

the diaspores (Pellegrini, pers. observ.); with *Tradescantia zanonia* (L.) Sw. (Commelinaceae) being an exception (Pellegrini 2017b; Pellegrini and Faden 2017). In Pontederiaceae, the anthocarp seems to be related to hydrochoric dispersion, which is also supported by the remaining synapomorphies for the family (i.e., presence of aerenchymatous tissue in the receptacle, perianth, and ovary walls). The anthocarp is especially developed with thick aerenchymatous tissue in *Monochoria*, *Pontederia s.s.*, and in the *E. paniculata* group (Lowden 1973: Cook 1989, 1998: Simpson and Burton 2006: Pellegrini, pers. obsery.: Figs 5F, 6K & 9K), that provides long flotation periods for the diaspores (i.e., around 15 days; Barrett 1988). In the remaining lineages of Pontederiaceae (i.e., Heteranthera s.l., E. crassipes group, and Eichhornia s.s.), the anthocarp is thin, probably resulting in a much shorter flotation period (i.e., probably around 24h), with seeds being secondarily dispersed by other biotic and/or abiotic means (Barrett 1978; Pellegrini and Horn, pers. observ.). In the closely-related Haemodoraceae and Philydraceae, the perianth is also connate, producing a characteristic hypanthium, and partially to completely persistent in fruit (Hamann 1998; Simpson 1998). Nonetheless, they do not aid in the dispersal of diaspores, since in all species the persistent perianth is only marcescent, and does not develop during fruit development, being ultimately torn open by the mature fruit (Pellegrini, pers. observ.). These observations are also supported by the complete lack of aerenchymatous tissues in floral organs of both families, with aerenchyma being recorded only in the septae of the hydrochoric Philydraceae (Simpson and Burton 2006). In Commelinaceae and Hanguanaceae, the persistent perianth also does not develop during fruit maturation; with the exception of Buforrestia C.B.Clarke (Commelinaceae), where the persistent sepals are as long or longer than the mature capsule (Bayer et al. 1998; Faden 1998). Nonetheless, the perianth of *Buforrestia* does not seem aid in the dispersion of the diaspores, since the perianth only loosely involves the capsules, which remain attached to the pedicel and dehisce at maturity (Pellegrini, pers. observ.). In Hanguanaceae the fruits consist of variously colored berries, that detach from the persistent sepaloid perianth and are most probably zoochoric (Bayer et al. 1998). On the other hand, in Commelinaceae the fruits are primarily dehiscent capsules (rarely indehiscent capsules or berries), that do not rely on the persistent sepals for dispersion, with fruits or seeds being autochoric or more rarely zoochoric (Pellegrini and Faden 2017).

Systematics and characterization of *Pontederia s.l.*

All 18 synapomorphies recovered by us for *Pontederia s.l.* are suggested here for the first time. Sand-binding roots were recovered by Smith et al. (2011) as plesiomorphic for Haemodoraceae and probably for all Commelinales, despite the authors not sampling Hanguanaceae in their analysis. These sand-binding roots produce specialized hairs that bind soil, especially larger sand crystals, creating a protective layer that envelops the roots (Smith et al. 2011). These authors also state that all studied specimens of Philydraceae and Pontederiaceae had non-sandbinding roots, in contrast to Haemodoraceae. On the other hand, sand-binding roots are commonly observed in several lineages of Commelinaceae, but especially in species growing in dry environments (Smith et al. 2011; Pellegrini, pers. observ.). After several field studies and cultivation of several species of Pontederiaceae, we have observed that all species of Heteranthera s.l. possess water-binding (i.e., mucilaginous) roots, while the absence of an external mucilage layer on the roots was characteristic to Pontederia s.l. The water-binding roots of Heteranthera s.l. are most probably not homologous to the sand-binding roots in the order, since they don't seem to have specialized hairs, like those described for Haemodoraceae (Smith et al. 2011). The mucilage layer seems to be produced by the secretion of chemical compounds near the root apex, that polymerize in contact with water (Pellegrini, pers. observ.). Nonetheless, further anatomical and histochemical studies are needed to better understand this feature.

The presence of leaves with pulvinate petioles in *Pontederia s.l.* is easily observed in the field, since most pulvini are lighter or darker than the rest of the petiole. On the other hand, in dried specimens this difference in coloration is only sometimes maintained, making this character not always obvious to untrained eyes. Added to that, the pulvini in *Pontederia s.l.* are seldom swollen, as it would be expected in most eudicot plants with articulated leaves. Nonetheless, this feature seems to be key for the emergent and floating species, especially the perennial ones, since they are subjected to the greatest amount of environmental variation. Floating species like *E. crassipes* are easily dragged by water currents, forcing all leaf-blades to change their position in order to better absorb sunlight. Perianth-coiling at post-anthesis seems to be poorly-documented in the literature for most Angiosperm families, and more so in the monocots. It is known to occur in the monocots only in the distantly related Bromeliaceae (Poales), being characteristic to some genera of subfamilies Pitcairnioideae and Puyoideae (Smith et al. 1998; Hornung-Leoni and Sosa 2008). In Commelinales, the persistent perianth is marcescent in Philydraceae, Haemodoraceae, and Hanguanaceae, while in Commelinaceae the sepals are marcescent and the petals are deliquescent (Pellegrini, pers. observ.). In Pontederiaceae, the perianth in Heteranthera s.l. is also marcescent at post-anthesis, only loosely enclosing the developing capsule. In *Pontederia s.l.*, the perianth is either spirally-coiled or revolute at post-anthesis, tightly enclosing the developing fruit, with two independent shifts to deliquescent perianths loosely enclosing the developing fruit (i.e., E. crassipes and Eichhornia s.s.). This might be related with increasing long-distance diaspore dispersal in the rooted species, with the anthocarp ridges possessing aerenchymatous tissue in most species. This character seems to greatly increase the dispersion range of most *Pontederia s.l.* lineages, that unlike E. crassipes and Eichhornia s.s., are not easily vegetatively dispersed by the fragmentation of floating stems. In E. crassipes, the plants are free-floating and can easily disperse in waterbodies with moving waters, while in Eichhornia s.s. the plants have elongated stems, which possibly help diaspores to disperse further away from the mother plant's base, and thus decreasing parental/offspring competition.

Tristyly is an extremely rare type of heterostyly, recorded for handful of families, only two being monocots (i.e., Amaryllidaceae and Pontederiaceae; Barrett 1993). According to Kohn et al. (1996), tristyly evolved only once in Pontederiaceae. As aforementioned, in Kohn et al. (1996), they recover part of the polyphyletic Eichhornia as sister to Heteranthera s.l., and tristyly as a synapomorphy for Pontederiaceae as a whole, with four reversions to homostyly. however, we recover tristyly as a synapomorphy of *Pontederia s.l.* alone, with only two reversions to homostyly. In E. diversifolia (Vahl) Urb. and E. natans (P.Beauv.) Solms, the flowers seem to be consistently pseudo-homostylous, which could be related to miniaturization connected with these species' floating growth-form (Barrett 1988). In Monochoria there is a shift from tristyly to enantiostyly (i.e., two different types of heterostyly; Barrett 1993), that could be easily explained by the shift in the group's pollination syndrome. *Monochoria* species are enantiostylous, lack septal nectaries and exclusively offer pollen as a floral reward (Wang et al. 1995), and this most likely is connected with the buzz pollination syndrome of their flowers. Added to that, poricidal, basifixed, polymorphic anthers are typical to buzz-pollinated flowers (Cook 1989; Wang et al. 1995). This shift from nectar-flowers to pollen-flowers seems to be the main cause of the peculiar floral morphology and loss of tristyly in *Monochoria*.

In Pontederiaceae three different patterns in perianth-lobe shape can be observed: (1) perianth lobes all equal, thus producing an actinomorphic perianth (e.g., *H. dubia*); (2) equal to subequal in the same whorl, producing either actinomorphic or zygomorphic perianths, depending on the presence of a nectar guide [e.g. actinomorphic in *M. hastata* (L.) Solms, and zygomorphic in *E. crassipes*]; and (3) unequal perianth lobes, with more than one morph in the same whorl, producing strongly zygomorphic perianths (e.g. *H. gardneri*). In Commelinales, the perianth lobes pattern seems to be extremely variable, being equal in the same whorl in

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Hanguanaceae, unequal in Philydraceae (due to the fusion of three posterior lobes), and variable in Commelinaceae and Haemodoraceae (Pellegrini, pers. observ.). In Commelinaceae, sepals are almost invariably different from the petals, except in *Palisota* Rchb. ex Endl. in which the sepals are characteristically petaloid (Faden 1998). Furthermore, both sepals and petals can range from equal to unequal, producing strongly zygomorphic flowers (e.g., Aneilema R.Br., Commelina L., Polyspatha Benth.: Faden 1998). In Haemodoraceae, there is much variation in the shape of the perianth lobes (Simpson 1990, 1998). Nonetheless, equal perianth lobes seem to be plesiomorphic in the monocots (Sauguet et al. 2017; Stevens 2001–onwards) and dominant in the family, being recorded for 11 out of 14 genera (Pellegrini, pers. observ.). Thus, equal to subequal lobes in one perianth whorl (the apices are obtuse to round) is recovered by us as a homoplastic synapomorphy for *Pontederia s.l.* (Fig. 1). The perianth in *Pontederia s.l.* ranges from campanulate to infundibuliform to hypocrateriform, while in *Heteranthera s.l.* it is almost exclusively tubular, a distinctive synapomorphy for the latter genus. The only exception is H. gardneri, who possesses an infundibuliform perianth, which might be explained by miniaturization. In Philydraceae the perianth is consistently infundibuliform, while the perianth in Haemodoraceae shows great plasticity, depending on the genus, ranging from flat to hypocrateriform to tubular to the peculiar split and falcate perianth of *Anigozanthos* (Simpson 1990, 1998).

Systematics and characterization of the five main lineages of Pontederia s.l.

Out of the four synapomorphies recovered for the *E. paniculata* group, two had been previously proposed by Eckenwalder and Barrett (1986; annual life cycle) and Barrett and Graham (1997; annual life cycle, and the absence of clonal reproduction). All currently accepted species in this group are known to inhabit seasonal, and generally short-lived waterbodies. Thus, the annual life cycle and the absence of clonal reproduction are more than expected. However, all previous studies in the family failed to notice the peculiarly inflated sheath of the leaf subtending the inflorescence and the flat basal bract (Fig 5B). These characters are easily observed in *E. paniculata* and *E. meyeri*, due to their elongated inflorescences, while in *E. paradoxa* the inflorescence has its internodes greatly contracted, thus making the flat basal bract extremely hard to observe, especially in dried specimens.

Monochoria comprises species with extremely autapomorphic morphology, being traditionally grouped based on their: pedicellate, actinomorphic and enantiostylous flowers, basally connate perianth, and its basifixed and poricidal anthers (Cook 1989, 1998). Due to its enantiostylous flowers and basifixed anthers, Monochoria has traditionally been considered closely related to Heteranthera (Eckenwalder and Barrett 1986; Cook 1998). Nonetheless, molecular data provides strong support that *Monochoria* is instead sister to the clade composed by E. crassipes, Eichhornia s.s., and Pontederia s.s. (Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011; this study). Aside from the six aforementioned synapomorphies, Monochoria is also supported in our present analysis by other six characters. Out of these characters, only the basal bract with a caudate apex was previously described as characteristic of *Monochoria* by Cook (1989). The presence of an inflated sheath in the leaf subtending the inflorescence, flat basal bract, and fistulose main axis are shared between the E. paniculata group and Monochoria, and are most likely plesiomorphic for *Pontederia s.l.* The caudate apex in the basal bract is observed in all species of Monochoria. Nonetheless, M. korsakowii can also present a leaf-like basal bract (Cook 1989). The actinomorphic perianth is a result of the loss of the nectar guide in this lineage, which as aforementioned, is directly related to the shift of pollination syndrome in the group. Additionally, other four floral modifications in *Monochoria* seem to be associated to this shift in the group's pollination syndrome: (1) pedicellate, actinomorphic and enantiostylous flowers; (2) basally connate perianth (which helps to expose the stamens and allows the bees to properly

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visit the flowers); (3) unequal, basifixed and poricidal anthers; and (4) the loss of septal nectaries. The presence of a petalo-staminal tube is also unique in the family, and most probably is a result of the reduction of the length of the hypanthium. Finally, the thickened and ridged anthocarps are also observed in the *E. paniculata* group and *Pontederia s.s.*, being directly related to the fruits primary hydrochoric dispersal syndrome (see comment above).

Despite being well-known, E. crassipes possesses the most peculiar vegetative morphology in the polyphyletic *Eichhornia*, and one of the most peculiar in the family as a whole. It is so peculiar that specimens are easily identified, even when lacking any reproductive structures (Pellegrini and Horn, pers. observ.). It is the only species in the family to possess a free-floating growth form, the only to produce stolons, and the only to possess inflated petioles. Nonetheless, one of the most peculiar characters in E. crassipes has been greatly disregarded by most specialists in the family. Castellanos (1958) was one of the first to properly describe and illustrate the flabellate ligules of E. crassipes. All synapomorphies recovered for E. crassipes seem to be directly related to its peculiar free-floating growth form, which also enabled it to become the most troublesome weed of the world (Gopal and Sharma 1981). The morphology of Eichhornia s.s. is clearly a result of it floating growth form and the tendency of these plants to grow in deeper water bodies. The late-deciduous sessile leaves (sometimes persistent for most of the plant's adult life) are characteristic to this group, but especially striking in E. diversifolia, hence its name. This protraction of the submerged phase seems to give the species in this clade a clear developmental advantage by helping them to reach the water surface and produce enough petiolate leaves to allow them to properly float. Furthermore, the even arrangement of the petiolate leaves along the mature stem might help provide the needed stability to the elongated floating stem.

From all the recovered clades in Pontederia s.l., Pontederia s.s. goes hand-in-hand with Monochoria in the number of reproductive synapomorphies. Out of the eight recovered synapomorphies for this clade, six are reproductive, with only the presence of epithelial cells in the septae, which is shared with Monochoria, being homoplastic. All the remaining five reproductive synapomorphies are directly correlated, but their evolutionary chronology is much harder to infer. The most parsimonious view is probably that all characters were triggered concomitantly by the appearance of the pseudomonomerous ovary, which caused the change in placentation morphology and ovule number. The abortion of most of the gynoecium, might have caused a key shift in the reproductive strategy in this lineage from investing in a great number of small seeds with little chances of reaching maturity, to investing into a single big seed with a good amount of provision and guaranteeing that it has bigger changes of reaching maturity. The smooth testa seems to be a simple byproduct of negative selection of ornamentation, since the seeds stopped being individually dispersed with the change of reproductive strategy. Finally, the achene gives this lineage a great evolutionary advantage since it is easily dispersed by water, with a long floatation period due to its thick parenchymatous walls. Furthermore, many species also possess complexly ornate achenes, with teeth and spikes that efficiently stick to fur, feathers, fabric, etc., mostly likely having animals as their primary dispersers (Pellegrini, pers. observ.).

Taxonomy

With the present recircumscription of *Pontederia*, Pontederiaceae now is organized in two monophyletic genera (i.e., *Heteranthera* and *Pontederia*). As stated by Pellegrini (2017a) and corroborated by nine phylogenetic studies (Eckenwalder and Barrett 1986; Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011; this study), the recognition of two genera seems to be the best and most taxonomically conservative option available, since it avoids the description of new genera, and the

reestablishment of names that were rarely, if ever, used in any relevant taxonomic or florist study. Finally, this option makes the differentiation of the two accepted genera easy using either fresh, liquid or herbarium samples. Thus, the genera of Pontederiaceae can be differentiated using the key below:

Key to the genera of Pontederiaceae

- 1. Sessile leaves spirally-alternate, petiolate leaves sometimes present in mature specimens, when present non-pulvinate, blade membranous; inflorescence reduced to a solitary cincinnus; stamens (1–)3, staminodes sometimes present, septal nectaries absent, stigma unevenly trilobate... *Heteranthera* Ruiz & Pavón (Fig 4)
- Sessile leaves distichously-alternate, petiolate leaves always present in mature specimens, pulvinate, blade chartaceous to coriaceous; inflorescence a 2-many branched thyrsi (rarely reduced to a solitary flower); stamens 6, staminodes absent, septal nectaries present (if absent than flowers pedicellate and anthers poricidal), stigma capitate or trilobate, rarely trifid... *Pontederia* L. (Figs 5-9)

Pontederia L., Sp. Pl. 1: 288. 1753. Figs 5–9

Type species (designated by Lowden 1973). Pontederia cordata L.

Description. Herbs perennial or annual, aquatic to amphibious, erect-emergent, procumbent-emergent or free-floating. Roots thin, fibrous or spongy. Rhizome short and generally inconspicuous. Stems trailing to erect, delicate to spongy, branching at the base, rarely branching at the upper half, rooting at the basal nodes or along the whole stem; internodes reduced to elongate, producing stolons or not. Sessile leaves distichously-alternate, congested at the apex of the stem, submerged, deciduous or persistent in mature plants, blades linear to linear-obovate, membranous, rarely chartaceous. Petiolate leaves distichously or spirallyalternate, congested at the apex of the stem or evenly distributed along the stem, floating or emergent, ligule truncate or with a flabellate projection; petioles conspicuous, rarely indistinct, inflated or not; blades elliptic to lanceolate or ovate to cordate to reniform or obovate to rounded, chartaceous to coriaceous. Synflorescence composed by a solitary main florescence subtended by a vegetative, petiolate leaf. Main florescences (inflorescences) axillary or apparently terminal, consisting of a pedunculate, many-branched thyrse, rarely a reduced thyrse; inflorescence leaf with or without an inflated leaf-sheath; basal bract flat or tubular; cincinnus' bract absent; cincinni (1-3-)4-many per thyrse, alternate or fascicle-like, 1-many-flowered, sessile or pedunculate, internodes contracted, rarely elongate; bracteoles absent, rarely present. Flowers bisexual, sessile or pedicellate, chasmogamous, pseudo-homostylous or tristylous, enantiostylous, zygomorphic, perianth connate usually forming a tube (hypanthium), rarely only basally fused, campanulate or infundibuliform or hypocrateriform, white to light pink to pink to mauve to pale lilac to lilac to bluish lilac to purple, lobes 6 (3 outer and 3 inner), elliptic to oblong to obovate, 3 superior and 3 inferior, rarely 5 superior and 1 inferior, the central superior lobe generally with a nectar guide, consisting of 1–2 yellow to green spots, generally surrounded by a dark purple to bluish purple, rarely white blur, spirally-coiling or revolute at post-anthesis, deliquescent or not; stamens 6, epipetalous, dimorphic (the superior 3 shorter than the inferior 3) or unequal (1 inferior longer with a differently colored anther), filaments Jshaped or recurved-decurved, terete, glabrous to glandular-pubescent, anthers dorsifixed, sometimes basifixed, rimose or poricidal, oblong to elliptic or sagittate; ovary ellipsoid to oblongoid, glabrous, locules 3, (1–)3 fertile, (1–)multi-ovulate, placentation axial or pendulous, septal nectaries generally present, rarely absent, style J-shaped, glabrous to glandularpubescent, stigma capitate to trilobate, rarely trifid. *Fruit* a capsule with loculicidal or irregular dehiscence, rarely an achene, ellipsoid to oblongoid to subglobose or ovoid, rarely pyriform, light to medium brown, apiculate due to persistent style base; anthocarp thin or hardened, smooth or ridged, ridges ornamented or not. *Seeds* oblongoid or ellipsoid or subglobose to broadly oblongoid or ovoid or curved narrowly ovoid, brown to light-brown, testa longitudinally conspicuously to inconspicuously winged, rarely smooth, when present wings membranous and testa also transversally striated between each wing; funiculi generally persistent, hilum punctate; embryotega dorsal, not prominently apiculate, darker than the rest of the seed.

Distribution and habitat. *Pontederia* currently comprises 26 mainly Neotropical species. Almost all Paleotropical species belong to *P.* subg. *Monochoria* (C.Presl) M.Pell. & C.N.Horn *comb. et stat. nov.*; except for *P. natans* P.Beauv., which is restricted to Africa and is a member of *P.* subg. *Eichhornia* (Kunth) M.Pell. & C.N.Horn *comb. et stat. nov.* Species in *Pontederia* can range from paludal to free-floating plants, thus occurring in a wide range of water bodies, from perennial to temporary, but most commonly in slow or stagnated water.

Generic circumscription and infrageneric classification. The circumscription adopted by us is almost equivalent to the original one proposed by Linnaeus (1753). It differs only by the exclusion of *P. ovata* L., which is currently placed in Marantaceae as a synonym for *Phrynium pubinerve* Blume (Horn and Haynes 1987; eMonocot 2010). Thus, no amendments are necessary for the herein adopted circumscription. We propose the subdivision of *Pontederia* in five monophyletic subgenera, based on the previously published molecular and morphological phylogenies (Eckenwalder and Barrett 1986; Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011), added to the new morphological and molecular analyses presented by us, and data gathered by us while working on the family. Despite being monophyletic, these subgenera are not easily morphologically differentiated, since many of the characters supporting each clade are not always ease to observe, especially in dried specimens. Thus, it is our opinion that a broader sense of *Pontederia* should be accepted, instead of elevating each *Eichhornia* lineage (i.e., the herein proposed subgenera) to the generic rank.

Key to the subgenera of Pontederia

- 1. Basal bract commonly with a caudate apex, rarely leaf-like; flowers pedicellate, enantiostylous, perianth only basally connate, campanulate; stamens with filaments connate forming a petalo-staminal tube, anthers basifixed, poricidal; septal nectaries absent... *Pontederia* subg. *Monochoria* (C.Presl.) M.Pell. & C.N.Horn (Fig 6)
- Basal bract with an acute to acuminate to aristate apex, rarely caudate; flowers sessile, non-enantiostylous, perianth connate forming a conspicuous tube, infundibuliform or hypocrateriform; stamens with free filaments, anthers dorsifixed, rimose; septal nectaries present... 2
- 2. Ovary 1-locular by abortion, fertile locule 1-ovulate, placentation pendulous; fruit an achene, anthocarp hardened, ridges sinuate, thoothed or echinate; seeds smooth... *Pontederia* L. subg. *Pontederia* (Fig 9)
- Ovary 3-locular, locules many-ovulate, placentation axial; fruit a capsule, anthocarp thin to thickened, if thickened ridges smooth; seeds longitudinally winged... 3
- 3. Herbs procumbent-emergent, stems elongate; sessile leaves late deciduous, rarely persistent in mature plants, petiolate leaves distichously-alternate, evenly distributed along the stem;

perianth infundibuliform, style glabrous... *Pontederia* subg. *Eichhornia* (Kunth) M.Pell. & C.N.Horn (Fig 8)

- Herbs erect emergent or free-floating, stems inconspicuous; sessile leaves early deciduous, petiolate leaves spirally-alternate, congested at the apex of the stem; perianth hypocrateriform, style glandular-pubescent... 4
- 4. Herbs stoloniferous; ligule flabellate, petioles generally inflated; inflorescences deflexed post-anthesis and in fruit, emerging from a non-inflated leaf-sheath, basal bract tubular; flowers ca. 4–6 cm diam., perianth loosely enclosing the developing fruit; seeds oblongoid... *Pontederia* subg. *Oshunae* M.Pell. & C.N.Horn (Fig 7)
- Herbs never producing stolons; ligule truncate, petioles never inflated; inflorescences erect at post-anthesis, emerging from an inflated leaf-sheath, basal bract flat; flowers ca. 2–3 cm diam., perianth tightly enclosing the developing fruit; seeds subglobose to broadly oblongoid... *Pontederia* subg. *Cabanisia* (Klotzsch *ex* Schltdl.) M.Pell. & C.N.Horn (Fig 5)

1. Pontederia subg. Cabanisia (Klotzsch ex Schltdl.) M.Pell. & C.N.Horn, comb. et stat. nov.

Fig 5

Cabanisia Klotzsch *ex* Schltdl., Abh. Naturf. Ges. Halle 6: 176. 1862. Type species (designated here). *Cabanisia caracasana* Klotzsch *ex* Schltdl., nom. illeg. (≡ *P. paniculata* Spreng.).

Description. Herbs perennial or annual, aquatic to amphibious, erect-emergent. Rhizome short and generally inconspicuous. Stems erect, spongy, branching at the base. Sessile leaves early deciduous. Petiolate leaves spirally-alternate, congested at the apex of the stem, emergent, ligule truncate, petioles not-inflated, blades cordate to broadly cordate, rarely elliptic to lanceolate or narrowly ovate. Main florescences (inflorescences) terminal, sessile or pedunculate; inflorescence leaf with an inflated leaf-sheath; basal bract flat; cincinni alternate or fascicle-like, 1–3-flowered, pedunculate, rarely sessile, internodes elongate, rarely contracted. Flowers sessile, chasmogamous, tristylous, zygomorphic, non-enantiostylous, perianth conate forming a tube, hypocrateriform, spirally-coiled at post-anthesis, nondeliquescent and tightly enclosing the developing fruit, lobes 3 superior and 3 inferior, rarely 5 superior and 1 inferior, the central superior lobe with a nectar guide, consisting of 2 yellowish green to green spots, generally surrounded by a dark purple to bluish purple, rarely white blur; stamens dimorphic, filaments free from each other, J-shaped, glandular-pubescent, anthers dorsifixed, rimose; ovary with 3 fertile locules, multi-ovulate, septal nectaries present, style glandular-pubescent, stigma capitate to trilobate. Capsules loculicidal, ellipsoid to oblongoid; anthocarp thickened, ridged. Seeds subglobose to broadly oblongoid, testa longitudinally winged.

Circumscription. *Pontederia* subg. *Cabanisia* is composed by *P. meyeri* (A.G.Schulz) M.Pell. & C.N.Horn *comb. nov.*, *P. paniculata* Spreng., and *P. paradoxa* Mart. All three species occur in moist environments or shallow waters, being in habit similar to well-known species of *P.* subg. *Pontederia*, such as *P. cordata* L. Nonetheless, both subgenera can be differentiated based on gynoecium, fruit and seed morphology.

Distribution. Mainly Central-West and Northeastern Brazil (reaching Argentina and Paraguay), growing in temporary water bodies in the Caatinga, Cerrado and Chaco domains. However, two species have very peculiar disjunctions in their distributions, also occurring in northwestern South America (Colombia, Ecuador, Guyana and Venezuela), Central America (Costa Rica, Guatemala and Nicaragua), Antilles (Jamaica), and North America (Mexico).

Key to the species of Pontederia subg. Cabanisia

- 1. Petiolate blades without posterior divisions, elliptic to lanceolate or narrowly ovate in outline; inflorescences 2–5-flowered, sessile, cincinni sessile, fascicle-like; perianth arranged in a 5+1 pattern, tube 2–2.5 cm long... *P. paradoxa* Mart.
- Petiolate blades with posterior divisions, cordate to broadly ovate in outline; inflorescences 10-many-flowered, pedunculate, cincinni pedunculate, alternate; perianth arranged in a 3+3 pattern, tube 0.8-1.6 cm long... 2
- 2. Main axis with a mixture of glandular and eglandular hairs, basal bract with cordate base and caudate apex, basal cincinni 1–2(–3)-flowered, bracteoles present; central superior perianth lobe with one green spot, surrounded by purple striations, all stamens exserted from the floral tube, anthers yellow... *P. meyeri* (A.G.Schulz) M.Pell. & C.N.Horn
- Main axis glandular-pubescent, basal bract with round base and acute to acuminate apex, basal cincinni 4–9-flowered, bracteoles absent; central superior perianth lobe with two green spots, surrounded by a white blur, 3 stamens included and 3 stamens exserted from the floral tube, anthers bluish lilac to lilac... *P. paniculata* Spreng.

1.1. Pontederia meyeri (A.G.Schulz) M.Pell. & C.N.Horn, comb. nov.

Eichhornia meyeri A.G.Schulz, Darwiniana 6: 56. 1942. Lectotype (designated here). ARGENTINA. Chaco, Cote Lai, 25 June 1939, fl., fr., *T. Meyer 2640* (SI barcode SI000621!; isolectotypes: GH barcode GH00057534!, LIL barcode LIL000196!).

Distribution. Restricted to Argentina, Paraguay and Brazil (states of Ceará, Mato Grosso, and Mato Grosso do Sul).

Nomenclatural notes. Schulz (1942), when describing his new *E. meyeri* cites two specimens from the same collection, one housed at SI and another at GH. Furthermore, a third specimen, housed at LIL was found by us. After carefully analyzing the syntypes, we noticed that the specimen at SI matches perfectly the original illustration. Added to that, it is widely known that Schulz worked at the Instituto de Botánica Darwinion, thus, making the specimen at SI the obvious choice of a lectotype.

Taxonomical notes. Current databases (eMonocot 2010; The Plant List 2013; Govaerts 2017; Tropicos.org 2017) have treated E. meyeri ($\equiv P$. meyeri) as a synonym of E. paniculata ($\equiv P$. paniculata). Nonetheless, as indicated in our identification key and by Horn (1998) both species are distinct, being easily differentiated in the field and herbaria. Thus, E. meyeri is here reestablished and transferred to $Pontederia\ s.l.$

1.2. *Pontederia paniculata* **Spreng.**, Neue Entdeck. Pflanzenk. 3: 18. 1822.

Piaropus paniculatus (Spreng.) Small, Fl. S.E. U.S. (ed. 2): 1328. 1913.

Eichhornia paniculata (Spreng.) Solms, Monogr. Phan. 4: 530. 1883.

Cabanisia caracasana Klotzsch *ex* Schltdl., Abh. Naturf. Ges. Halle 6: 176. 1862, nom. superfluous. Neotype (designated here). BRAZIL. S.loc., fl., Mar 1817, M. Wied s.n. (BR barcode BR0000005188734!).

Distribution. *Pontederia paniculata* possesses a peculiarly disjunctive distribution between Northeastern Brazil (states of Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Rio Grande do Norte, and Sergipe), northwestern South America (Colombia, Ecuador, Guyana and Venezuela), Central America (Nicaragua), Antilles (Cuba and Jamaica), and North America (Mexico).

Nomenclatural notes. When describing *P. paniculata*, Sprengel (1822) makes no mention of any specimen, just mentioning that his newly described species is native to Brazil. According to Stafleu and Cowan (1985), Sprengel's herbarium was acquired by B, but later entirely lost during the WWII. The specimen *Wied s.n.* (BR0000005188734) is an excellent match to the diagnosis provided by Sprengel, was collected prior to the publication of *P. paniculata*, and was originally part of the Martius Herbarium. Despite having no proof that this specimen might have been examined by Sprengel, this specimen was surely available at the time of the publication, being originally identified as *P. paniculata*, and later examined by Seubert (1847) and identified as *Eichhornia tricolor* Seub. Thus, making it a good choice for a neotype for *P. paniculata*, and being here designated as so.

Taxonomical notes. The very evident disjunctions in the distribution of *P. paniculata* might indicate a species complex, instead of a sole species. Nonetheless, we believe that without proper studies, it would be precocious to reestablish any names or recognize any new taxa at this time.

1.3. *Pontederia paradoxa* Mart., Syst. Veg. (ed. 15 bis) 7(2): 1144. 1830.

Eichhornia paradoxa (Mart.) Solms, Monogr. Phan. 4: 531 1883.

Eichhornia schultesiana Seub., Fl. Bras. 3(1): 94. 1847, nom. superfluous. Lectotype (designated here). BRAZIL. Maranhão: Alcântara oppidium at ad Porto de Carvalho, fl., fr., 1817, C.F.P. Martius 2575 (M barcode M0242209!).

Distribution. *Pontederia paradoxa* has a disjunctive distribution between Northern and Northeastern Brazil (states of Pará, Bahia, Ceará, and Rio Grande do Norte), northwestern South America (Venezuela), and Central America (Costa Rica and Guatemala).

Nomenclatural notes. In the original description of *P. paradoxa* (Roemer and Schultes 1830), it is mentioned that the description was based on a Martius collection, from the state of Maranhão, Brazil. After consulting M, we came across the specimen *Martius* 2575 (M0242209) that matches in great detail the protologue. Thus, it is the obvious choice for a lectotype. Later, Seubert (1847) noticed that *P. paradoxa* did not fit in the circumscription of *Pontederia* at the time. When describing *E. schultesiana*, Seubert clearly mentions *P. paradoxa*, even citing the *Martius* 2575 specimen. According to the Code (McNeill et al. 2012, Art. 52.1.), Seubert provided a superfluous replacement name, thus rendering *E. schultesiana* illegitimate.

Taxonomical notes. In a similar way as *P. paniculata*, *P. paradoxa* possesses a very mind-boggling distribution, which makes us believe that it might actually represent a species complex. Two names are available for the putative disjunctive taxa, but since *P. paradoxa* in its current circumscription is known for only a handful of specimens, we discourage any taxonomic changes before the species is properly studied.

2. *Pontederia* subg. *Monochoria* (C.Presl) M.Pell. & C.N.Horn, comb. et stat. nov. Fig 6

- *Monochoria* C.Presl, Reliq. Haenk. 1(2): 127. 1827. Type species. *Monochoria hastifolia* C.Presl., nom. illeg. (≡ *P. hastata* L.).
- Calcarunia Raf., Med. Fl. 2: 106. 1830. Type species. Calcarunia hastata (L.) Raf., nom. inval. (≡ P. hastata L.).
- Carigola Raf., Fl. Tellur. 2: 10. 1837. Type species. Carigola hastata (L.) Raf. (≡ P. hastata L.).
- Gomphima Raf., Fl. Tellur. 2: 10. 1837. Type species. Gomphima vaginalis (Burm.f.) Raf. (≡ *P. vaginalis* Burm.f.).
- Kadakia Raf. Fl. Tellur. 2: 9. 1837. Type species. Kadakia dilatata (Buch.-Ham.) Raf. (= P. hastata L.). Syn. nov.
- *Limnostachys* F.Muell., Fragm. 1: 24. 1858. Type species. *Limnostachys cyanea* F.Muell. [≡ *P. cyanea* (F.Muell.) M.Pell. & C.N.Horn].

Description. Herbs perennial or annual, aquatic to amphibious, erect-emergent or procumbent-emergent. Rhizome short to elongated. Stems erect, spongy, branching at the base. Sessile leaves early deciduous. Petiolate leaves distichously to spirally-alternate, congested at the apex of the stem, sometimes evenly distributed along the stem, floating to emergent, ligule truncate, petioles not-inflated, blades cordate to broadly cordate, rarely elliptic to narrowly ovate. Main florescences (inflorescences) terminal, sessile or pedunculate; inflorescence leaf with an inflated leaf-sheath; basal bract tubular, apex caudate, sometimes acute to acuminate, rarely leaf-like; cincinni alternate or fascicle-like, 1–3-flowered, sessile or pedunculate, internodes elongate, rarely contracted. Flowers pedicellate, chasmogamous, monostylous, actinomorphic or zygomorphic, enantiostylous, perianth conate only at base, campanulate, spirally-coiled at post-anthesis, non-deliquescent and tightly enclosing the developing fruit, lobes 3 superior and 3 inferior, the central superior lobe lacking a nectar guide; stamens unequal, filaments conate forming a petalo-staminal tube, J-shaped or recurved-decurved, glabrous, anthers basifixed, poricidal, dehiscent through two apical pores; ovary with 3 fertile locules, multi-ovulate, septal nectaries absent, style glabrous, stigma capitulate to capitate or trilobate to trifid. Capsules loculicidal, ellipsoid to oblongoid to subglobose; anthocarp thickened, ridged. Seeds cylindrical or ellipsoid to narrowly oblongoid to broadly oblongoid to subglobose or ovoid, testa longitudinally winged.

Circumscription. *Pontederia* subg. *Monochoria* is composed by ten exclusively Paleotropical species. All species occur in permanently moist environments or shallow waters, growing either as erect or procumbent-emergent, resembling in habit smaller members of *P.* subg. *Pontederia* and even some species of *Heteranthera*. The members of this subgenus are quite unique within *Pontederia s.l.* due to their pedicellate flowers, perianth only basally conate, unequal stamens, basifixed and poricidal anthers, and due to the secondary loss of the septal nectaries.

Distribution. Exclusively Paleotropical (Cook 1989), with two species native to Africa (Verdcourt 1961), four to Australia (two endemic, Aston 1985), and six to Asia (Wang et al. 2004).

Key to the species of *Pontederia* subg. *Monochoria*

- 1. Filaments without a tooth-like appendage, anthers yellow; stigma trilobate to trifid, with glandular hairs... 2
- Central inferior filament with 1(-2) tooth-like appendage, anthers greyish blue to purple, remaining stamens with unappendaged filaments and yellow anthers; stigma capitulate to capitate, with eglandular hairs... 3
- 2. Petiole of the leaves bearing inflorescences shorter than or ca. equal to the length of its leaf-sheath; anthers equal or longer than the filaments... *P. australasica* (Ridl.) M.Pell. & C.N.Horn
- Petiole of the leaves bearing inflorescences 2/5 to 5 times longer than its leaf-sheath; anthers smaller than the filaments... *P. cyanea* (F.Muell.) M.Pell. & C.N.Horn
- 3. Basal bract leaf-like, rarely reduced to a bladeless sheath, lower cincinni 3–several-flowered; capsules ovoid; seeds cylindrical... *P. korsakowii* (Regel & Maack) M.Pell. & C.N.Horn
- Basal bract always reduced to a bladeless sheath, lower cincinni 1(-2)-flowered; capsules ellipsoid to broadly ellipsoid; seeds oblongoid to ellipsoid or ovoid or subglobose... 4
- 4. Rhizome robust; petiolate leaves with posterior divisions with acuminate apex; flowers opening from apex to base of the inflorescence; perianth strongly spirally-coiled at post-anthesis... 5
- Rhizome delicate to inconspicuous; petiolate leaves with posterior divisions generally absent,
 if present posterior divisions with round apex; flowers opening from base to apex of the
 inflorescence; perianth strongly patent to slightly spirally-coiled at post-anthesis... 7
- 5. Petioles longitudinally sulcate, leaves narrowly hastate or narrowly sagittate to linear sagittate, narrower than 3 cm wide; inflorescences surpassing the leaves; inner tepals obovate... *P. elata* (Ridl.) M.Pell. & C.N.Horn
- Petioles smooth, leaves hastate to broadly hastate or sagittate to broadly sagittate, equal or broader than 8 cm wide; inflorescences shorter than the leaves; inner tepals elliptic to oblong... 6
- 6. Petiolate leaf-blades patent, posterior division 2–5 cm long; inflorescences sessile to subsessile, cincinni fascicle-like... *P. hastata* L.
- Petiolate leaf-blades upright, posterior division 7–11 cm long; inflorescences pedunculate, cincinni alternate... P. valida (G.X.Wang & Nagam.) M.Pell. & C.N.Horn

- 7. Leaf blades patent; thyrsi lax, raceme- or fascicle-like, deflexed post-anthesis and in fruit; pedicels ca. as long as the floral buds... 8
- Leaf blades pendulous; thyrsi dense, spike-like, erect post-anthesis and in fruit; pedicels equal to shorter than ½ the length of the floral buds... 9
- 8. Petiolate leaf-blades without posterior divisions, base round to obtuse, sometimes auriculate; inflorescence 2–7-flowered; seeds oblongoid, longitudinally conspicuously winged... *P. plantaginea* Roxb.
- Petiolate leaf-blades with conspicuous posterior divisions, base characteristically cordate; inflorescence 9–25-flowered; seeds ovoid, longitudinally inconspicuously winged... *P. vaginalis* Burm.f.
- 9. Petiolate leaves cordate to ovate, leaves bearing inflorescences with petioles (5–)10–12(–16) cm long; seeds ellipsoid to narrowly oblongoid, with 8–10 longitudinal wings... *P. africana* (Solms) M.Pell. & C.N.Horn
- Petiolate leaves narrowly ovate to elliptic to linear, leaves bearing inflorescences with petioles (0.7–)1–2(–4) cm long; seeds subglobose to broadly oblongoid, with 12–14 longitudinal wings... *P. brevipetiolata* (Verdc.) M.Pell. & C.N.Horn

2.1. Pontederia africana (Solms) M.Pell. & C.N.Horn, comb. nov.

Monochoria africana (Solms) N.E.Br., Fl. Trop. Afr. 8: 5. 1901.

Monochoria vaginalis var. africana Solms, Monogr. Phan. 4: 525. 1883. Holotype. B†; Lectotype (designated here). CENTRAL AFRICAN REPUBLIC: Djur Region, Seriba Ghattas, fl., 27 Aug 1869, G.A. Schweinfurth 2296 (PRE barcode PRE0792113-0!; isolectotypes: K barcodes K000321232!, K000321233!).

Distribution. Angola, Kenya, Malawi, Mozambique, South Africa, and Sudan.

Nomenclatural notes. Solms-Laubach (1883), clearly designates the specimen at B as the holotype for his new taxon *Monochoria vaginalis* var. *africana*. However, since the holotype was destroyed during WWII (Cook 1989), a lectotype is needed. The specimen at PRE is in great condition and possesses a complete preserved individual, thus being selected by us as the lectotype.

2.2. Pontederia australasica (Ridl.) M.Pell. & C.N.Horn, comb. nov.

Monochoria australasica Ridl., J. Straits Branch Roy. Asiat. Soc. 79: 100. 1918. Lectotype (designated by Aston 1985). AUSTRALIA. Northern Territory near Darwin, fl., fr., 4 Feb 1914, C.E.F. Allen 81 (K barcode K000873495!; isolectotype: NSW barcode NSW686319!).

Distribution. Restricted to northern Australia.

2.3. Pontederia brevipetiolata (Verdc.) M.Pell. & C.N.Horn, comb. nov.

Monochoria brevipetiolata Verdc., Kirkia 1: 81 1961. Type. GUINEA-BISSAU. Gabú, depressões alagadas de savana entre Pitche e Canquelifá, fl., fr., 18 Sep 1950, J.V.G. Espírito Santo 2777 (holotype: K barcode K000321231!).

Distribution. Gabón, Gambia, Guinea-Bissau, Ivory Coast, Mali, Níger, Senegal, and Sierra Leone.

2.4. Pontederia cyanea (F.Muell.) M.Pell. & C.N.Horn, comb. nov.

Monochoria cyanea (F.Muell.) F.Muell., Fragm. 8: 44. 1872.

Limnostachys cyanea F.Muell., Fragm. 1: 24. 1858. Lectotype (designated by Aston 1985). AUSTRALIA. Northern Territory, Depot Creek, upper Victoria River, fl., fr., 1 Apr 1856, F.W.L. Leichhardt s.n. (K barcode K000873493!: isolectotypes: G barcode G00164431!, K barcode K000873494!. MEL barcodes MEL665251! MEL665252!).

Distribution. Restricted to northern and western Australia.

2.5. Pontederia elata (Ridl.) M.Pell. & C.N.Horn, comb. nov.

Monochoria hastata var. elata (Ridl.) Backer, Fl. Males. 4: 258. 1951.

Monochoria elata Ridl., J. Straits Branch Roy. Asiat. Soc. 79: 99. 1918. Lectotype (designated by Cook 1989). MALAYSIA. Kedah: Jenun, fl., fr., 19 Nov 1915, M. Haniff 1208 (K barcode K000291970!; isolectotypes: BM barcode BM000958428!, K barcode K000291971!).

Distribution. From Myanmar to Malaysia, Thailand, and China.

Taxonomical notes. *Monochoria elata* ($\equiv P.$ *elata*) was treated by Cook (1989) as well as Guofang and Horn (2000) as an accepted name, but subsequent floras (e.g., Wang et al. 2004) and online databases (eMonocot 2010; The Plant List 2013; Govaerts 2017; Tropicos.org 2017) have either considered M. *elata* a synonym of M. *hastata* ($\equiv P.$ *hastata*), or as a variety of the later. Nonetheless, both species can be easily differentiated based on the petiolate ornamentation, width of the petiolate leaf-blades, length of their inflorescences, and number of flowers per inflorescences. Thus, M. *elata* is here reestablished and transferred to *Pontederia s.l.*

2.6. *Pontederia hastata* L., Sp. Pl. 1: 288. 1753.

Monochoria hastata (L.) Solms, Monogr. Phan. 4: 523. 1883.

Carigola hastata (L.) Raf., Fl. Tellur. 2: 10. 1837.

Calcarunia hastata (L.) Raf., Med. Fl. 2: 106. 1830. Lectotype (designated by Horn and Haynes 1987). SRI LANKA. Herb. P. Hermann 2: 52, No. 129 (BM barcode BM000621681!).

Distribution. Bangladesh, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, New Guinea, Philippines, Sri Lanka, Thailand, and Vietnam.

2.7. Pontederia korsakowii (Regel & Maack) M.Pell. & C.N.Horn, comb. nov.

Monochoria vaginalis var. korsakowii (Regel & Maack) Solms, Monogr. Phan. 4: 525. 1883.
Monochoria korsakowii Regel & Maack, Mém. Acad. Imp. Sci. Saint Pétersbourg, Sér. 7, 4(4): 155. 1861. Lectotype (designated here). RUSSIA. Ussuri, Keugxa Laa, fl., fr., 1859, R.K. Maack s.n. (LE barcode LE01007092!; isolectotypes: K barcode K000873544!; LE barcodes LE01007090!, LE01007091!, LE01007093!, P barcode P00730337!).

Distribution. China, India, Indonesia, Japan, Korea, Malaysia, Pakistan, Russia, Sri Lanka, and Vietnam.

Nomenclatural notes. Cook (1989) in his revision for *Monochoria*, cites one of the specimens at LE as a holotype. Nonetheless, Regel and Maack (1861) make no direct mention of which herbaria the type specimens were deposited, and which specimen was to be considered the type. Thus, we designate the specimen LE01007092 as the lectotype, since it possesses well-preserved flower, and seems to have been to model for the original illustration.

2.8. *Pontederia plantaginea* **Roxb.**, Fl. Ind. (ed. 1832) 2: 123. 1832.

Monochoria vaginalis var. plantaginea (Roxb.) Solms, Monogr. Phan. 4: 524. 1883.

Monochoria plantaginea (Roxb.) Kunth, Enum. Pl. 4: 135. 1843. Lectotype (designated here). NEPAL: Nathpur, fl., Aug. 1821, N. Wallich 5096 (K barcode K001104737!; isolectotypes: K barcodes K001104733!, K001104734!, K001104735!, K001104736!, K001104738!, K001104739!, K001104740!).

Monochoria vaginalis var. angustifolia G.X.Wang, Acta Phytotax. Sin. 41: 569. 2003. Type. THAILAND. Koksung: in a marshy place, fl., 18 Sep 1984, N. Fukuoka T-36166 (holotype: KYO!; isotypes: A n.v., BKF n.v., L n.v.). Syn. nov.

Boottia mairei H.Lév., Cat. Pl. Yun-Nan 131. 1916. Type. CHINA. Yunnan: Dongchuan [Tangdan], fl., Aug 1912, E.E. Maire s.n. (holotype: E barcode E00386692!). **Syn. nov.**

Monochoria junghuhniana Hassk., Flora 35: 115. 1852. Lectotype (designated here). INDONESIA. Java, Yogyakarta, Djokjakarta, prope Samas ad affim Opar, fl., s.dat., Junghuhn s.n. (L barcode L0041652!). **Syn. nov.**

Monochoria linearis (Hassk.) Miq., Fl. Ned. Ind. 3: 549. 1859.

Pontederia linearis Hassk., Flora 25(2, Beibl.): 4. 1842. Type (not found). INDONESIA. Java (L?). **Syn. nov.**

Monochoria ovata Kunth, Enum. Pl. 4: 665. 1843.

Pontederia ovata Hook. & Arn., Bot. Beechey Voy. 218 1837, nom. illeg. non *P. ovata* L. Lectotype (designated here). SRI LANKA. Canton, fl., s.dat., Millet s.n. (G barcode G00164757!; isolectotype: E n.v.).

Pontederia cernua L. ex B.D.Jacks., Index Linn. Herb.: 129. 1912, nom. nud.

Pontederia alba Buch.-Ham. ex Wall., Numer. List: 5095 D. 1831, nom. nud.

Pontederia racemosa Buch.-Ham. ex Wall., Numer. List: 5095C. 1831, nom. nud.

Pontederia lanceolata Wall. ex Kunth, Enum. Pl. 4: 135. 1843, pro. syn.

Distribution. Australia, Bangladesh, Cambodia, China, India, Indonesia, Myanmar, Nepal, Sri Lanka, Thailand, and Vietnam.

Nomenclatural notes. Cook (1989), cites that no suitable specimens, collected by Roxburgh were found. Nonetheless, according to Stafleu and Cowan (1983) and Forman

(1997), many of Roxburgh's new species described after 1831 were based on specimens at the Wallich Herbarium (currently housed at K). After visiting Kew, we came across a series of specimens at Wallich Herbarium (*Wallich 5096*) collected in the Bengal region (Bangladesh, Myanmar, Nepal and India), that matched perfectly the protologue of *P. plantaginea*. One of the herbarium sheets contained several complete flowering specimens in perfect condition. Thus, we designate the gathering under the barcode K001104737, as the lectotype for *P. plantaginea*.

Hasskarl (1852), when describing *M. junghuhniana*, makes no reference to any specimens. However, the author does mention that his new species is native to Sumatra, near Samas and Opar. After analyzing the collection at L, we came across a specimen from the same exact locality as indicated in the protologue, and most likely collected by Junghuhn. Thus, it is designated by us as the lectotype for *M. junghuhniana*.

Taxonomical notes. *Monochoria vaginalis* in its current circumscription (Cook 1989) is widely morphologically variable and distributed. However, recent studies (Wang et al. 2003; Tungmunnithum et al. 2016) have highlighted the need to revisit the species boundaries in this taxon. Recently, Tungmunnithum et al. (2016) published a thorough morphometric study on *M. vaginalis s.l.* from Thailand and showed that two taxa are easily recognizable. The authors informally recognized *M. vaginalis* Burm.f. var. *vaginalis* and *M. vaginalis* var. *angustifolia* G.X.Wang, as representing each of the recovered morphotypes. Nonetheless, after studying all the names treaded as synonyms of *M. vaginalis s.l.* by Cook (1989), we concluded that *M. vaginalis* var. *angustifolia* and *M. junghuhniana* are conspecific to *P. plantaginea* Roxb. Thus, *P. plantaginea* is here reestablished and *M. vaginalis* var. *angustifolia* and *M. junghuhniana* are treated as synonyms of the later.

2.9. *Pontederia vaginalis* **Burm.f.**, Fl. Indica: 80. 1768.

Monochoria vaginalis (Burm.f.) C.Presl ex Kunth, Enum. Pl. 4: 134. 1843.

Gomphima vaginalis (Burm.f.) Raf., Fl. Tellur. 2: 10. 1837.

Monochoria hastifolia C.Presl., Reliq. Haenk. 1(2): 127. 1827, nom. illeg. Lectotype (designated by Cook 1989). INDIA. Ind. Orien., fl., s.dat., W. Roxburgh s.n. (G barcode G00164756!).

Distribution. Widespread throughout Asia (Afghanistan, Bangladesh, Bhutan, Cambodia, China, India, Indonesia, Iran, Japan, Korea, Laos, Malaysia, Myanmar, Nepal, Pakistan, Philippines, Russia, Sri Lanka, Thailand, and Vietnam) and Oceania (Australia, Fiji, Papua New Guinea, and Pacific Islands).

2.10. Pontederia valida (G.X.Wang & Nagam.) M.Pell. & C.N.Horn, comb. nov.

Monochoria valida G.X.Wang & Nagam., Acta Phytotax. Geobot. 45(1): 41. 1994. Type. CHINA. Hainan: Sanya, Yanglan, fl., 21 Sep 1990, G.X. Wong 901001 (holotype: WH; isotype: KYO!).

Distribution. Southern China and Thailand.

Taxonomical notes. *Monochoria valida* ($\equiv P.$ *valida*) was described by Wang and Nagamasu (1994), being compared to M. *elata* ($\equiv P.$ *elata*) and M. *hastata* ($\equiv P.$ *hastata*). These species are morphologically similar, due to their robust rhizomes, petiolate blades hastate to sagittate, and posterior division with acuminate apex. However, they can be easily differentiated

by inflorescence morphology (inflorescence sessile, many-flowered, not surpassing the leaves, and cincinni fascicle-like in *P. hastata*; inflorescence pedunculate, many-flowered, surpassing the leaves, and alternate cincinni in *P. valida*; inflorescence pedunculate, few-flowered, surpassing the leaves, and alternate cincinni in *P. elata*). Aside from that, leaf morphology is also helpful in species delimitation in this group. Thus, *M. valida* is here reestablished and transferred to *Pontederia s.l.*

3. *Pontederia* subg. *Oshunae* M.Pell. & C.N.Horn, subg. nov. Fig 7

Type species. *Pontederia crassipes* Mart. $[\equiv Eichhornia crassipes (Mart.) Solms].$

Piaropus Raf., Fl. Tellur. 2: 81. 1837, nom. rej. Type species. Piaropus mesomelas Raf., nom. illeg. (≡ Pontederia crassipes Mart.). Syn. nov.

Description. Herbs perennial, aquatic, free-floating. Rhizome short and inconspicuous. Stems inconspicuous, unbranched, producing stolons. Sessile leaves early deciduous. Petiolate leaves spirally-alternate, congested at the apex of the stem, emergent, ligule flabellate, petioles inflated, blades broadly ovate to cordate to reniform. Main florescences (inflorescences) terminal; inflorescence leaf without an inflated leaf-sheath; basal bract tubular; cincinni alternate, 1(-2)-flowered, sessile, internodes contracted. Flowers sessile, tristylous, zygomorphic, non-enantiostylous, perianth conate forming a tube, hypocrateriform, spirally-coiled at post-anthesis, deliquescent and loosely enclosing the developing fruit, 3 superior and 3 inferior, the central superior lobe with a nectar guide, consisting of 1 yellow spot, surrounded by a dark purple to bluish purple blur; stamens dimorphic, filaments free from each other, J-shaped, glandular-pubescent, anthers dorsifixed, rimose; ovary with 3 fertile locules, multi-ovulate, septal nectaries present, style glandular-pubescent, stigma capitate to trilobate. Capsules loculicidal, oblongoid; anthocarp thin, smooth. Seeds oblongoid, testa longitudinally winged.

Circumscription. *Pontederia* subg. *Oshunae* is monospecific, being composed solely by *P. crassipes*.

Distribution. Widespread throughout South America.

Etymology. The name of this new subgenus derives from the Yoruba words "Oxum", "Oshun" and "Osun". These are the names given in the Candomblé religion to the orisha (i.e., a deity that reflects one of the manifestations of God) mother and guardian of fresh-water bodies. Oshun is known for her beauty and vanity, being also known as the deity of luxury, pleasure, sexuality, fertility, beauty, and love. The sole species accepted in *Pontederia* subg. Oshunae is commonly named "mãe d'água" (i.e., mother of the fresh-waters) in Brazil, also one of the popular names for Oshun. This popular name in Brazil, makes reference to the waterhyacinth's ability to dominate fresh water environments, but also producing beautiful flowers.

3.1. Pontederia crassipes Mart., Nov. Gen. Sp. Pl. 1: 9. 1823.

Eichhornia crassipes (Mart.) Solms, Monogr. Phan. 4: 527. 1883.

Piaropus mesomelas Raf., Fl. Tellur. 2: 81. 1837, nom. illeg. Lectotype (designated by Horn 1994). BRAZIL. Bahia. Provinciae Minas Gerais, in stagnis ad fl. St. Francisci prope Malhada, s.dat., C.F.P. Martius 60 (M barcode M0242217!).

Distribution. Widespread throughout South America and naturalized worldwide.

4. Pontederia subg. Eichhornia (Kunth) M.Pell. & C.N.Horn, comb. et stat. nov. Fig 8

Eichhornia Kunth, Enum. Pl. 4: 129. 1843. Type species. *Eichhornia azurea* (Sw.) Kunth. (≡ *P. azurea* Sw.).

Leptosomus Schltdl., Abh. Naturf. Ges. Halle 6: 174. 1862. Type species. *Leptosomus natans* (P.Beauv.) Schltdl. (≡ *P. natans* P.Beauv.).

Description. Herbs perennial, aquatic, procumbent-emergent. Rhizome short and generally inconspicuous. Stems trailing, spongy, branched to unbranched. Sessile leaves late deciduous, sometimes persistent in mature plants. Petiolate leaves distichously-alternate, evenly distributed along stem, emergent, ligule truncate, petioles not-inflated, blades cordate to ovate or obovate to broadly obovate to rounded. Main florescences (inflorescences) axillary or terminal, pedunculate; inflorescence leaf without an inflated leaf-sheath; basal bract tubular; cincinni alternate, 1–3-flowered, sessile to subsessile, internodes contracted. Flowers sessile, chasmogamous, tristylous or pseudo-homostylous, zygomorphic, non-enantiostylous, perianth conate forming a tube, infundibuliform, revolute at post-anthesis, deliquescent and loosely enclosing the developing fruit, lobes 3 superior and 3 inferior, rarely 5 superior and 1 inferior, the central superior lobe with a nectar guide, consisting of 2 yellowish green to green spots, generally surrounded by a dark purple to bluish purple, rarely white blur, coiling or postanthesis; stamens dimorphic, filaments free from each other, J-shaped, glandular-pubescent, anthers dorsifixed, rimose; ovary with 3 fertile locules, multi-ovulate, septal nectaries present, style glabrous, stigma capitate to trilobate. Capsules loculicidal or with irregular dehiscence, ellipsoid to oblongoid; anthocarp thin, smooth. Seeds subglobose to broadly oblongoid, testa longitudinally winged.

Circumscription. *Pontederia* subg. *Eichhornia* is composed of four species. All species occur in permanently or seasonal water bodies, growing as procumbent-emergent and resembling in habit some members of *P.* subg. *Monochoria* and *P.* subg. *Pontederia*. The members of this subgenus are peculiar within *Pontederia s.l.* due to their late deciduous sessile leaves (sometimes persistent throughout the plants entire life spam), perianth infundibuliform, revolute at post-anthesis, deliquescent and loosely enclosing the developing fruit, glandular-pubescent filaments, glabrous styles, and anthocarp thin and smooth.

Distribution. Mainly Neotropical, except for *P. natans*, which is restricted to contineltal Africa and Madagascar.

Key to the species of *Pontederia* subg. *Eichhornia*

- 1. Petiolate leaves floating, blades cordate to ovate, base auriculate to cordate; inflorescences 1–4-flowered; flowers pseudo-homostylous; margins if the internal lobes of the perianth entire... 2
- Petiolate leaves emergent, blades obovate to broadly obovate to rounded, base cuneate; inflorescences 5-many-flowered; flowers heterostylous; margins of the internal lobes of the perianth erose to fimbriate, rarely entire... 3

- 2. Inflorescences (1–)2–4-flowered; flowers 2–3.2 cm diam., perianth lilac to bluish lilac, central superior lobe with a yellow spot, surrounded by a purple to bluish purple blur, filaments glandular-pubescent; capsules 3-valved... *P. diversifolia* (Vahl) M.Pell. & C.N.Horn
- Inflorescences 1(-2)-flowered; flowers 0.7-1 cm diam., perianth purple to mauve, central superior lobe concolorous with the remaining lobes or with a dark purple blur, filaments glabrous; capsules with irregular dehiscence... *P. natans* **P.Beauv.**
- 3. Inflorescences axillary, much exceeding the basal bract, main axis glandular-pubescent; perianth with central superior lobe with a yellow spot, filaments glandular-pubescent; seeds monomorphic... *P. azurea* Sw.
- Inflorescences terminal, enclosed or approximately the same size as the basal bract, main axis glabrous; perianth with central superior lobe with a dark purple to bluish purple blur, filaments glabrous; seeds dimorphic... *P. heterosperma* (Alexander) M.Pell. & C.N.Horn

4.1. Pontederia azurea Sw., Prodr. 57. 1788.

Eichhornia azurea (Sw.) Kunth, Enum. Pl. 4: 129. 1843.

Piaropus azureus (Sw.) Raf., Fl. Tellur. 2: 81. 1837. Type. JAMAICA. s.loc., s.dat., *Brown s.n.* (holotype: S No. S-R-5196!).

Distribution. Widespread in the American continent from Mexico to Uruguay.

4.2. Pontederia diversifolia (Vahl) M.Pell. & C.N.Horn, comb. nov.

Eichhornia diversifolia (Vahl) Urb., Symb. Antill. 4: 147. 1903.

Heteranthera diversifolia Vahl, Enum. Pl. 2: 44. 1805. Lectotype (designated here). GUIANA. s.loc., fl., s.dat., L.C. Richard s.n. (C barcode C10017422!).

Distribution. Antilles (Cuba, Dominican Republic, and Puerto Rico), Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama), and South America (Bolivia, Colombia, Ecuador, French Guiana, Guyana, Suriname, Venezuela, and Brazil – states of Acre, Amazonas, Amapá, Pará, Rondônia, Roraima, Tocantins, Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe, Goiás, Mato Grosso do Sul, Mato Grosso, Minas Gerais, and Rio de Janeiro –).

Nomenclatural notes. When describing *Heteranthera diversifolia*, Vahl (1805) makes no direct mention to any analyzed specimens in which he might have based the description of his new species. The author only mentions that his new species is native to Guiana and was sent to him by "Richard". After analyzing the collection at C, we came across a specimen part of Herb. Vahlian., collected by *Richard s.n.*, and identified in Vahl's handwriting as *H. diversifolia*. Thus, it is chosen by us as the lectotype.

4.3. Pontederia heterosperma (Alexander) M.Pell. & C.N.Horn, comb. nov.

Eichhornia heterosperma Alexander, Lloydia 2: 170. 1939. Lectotype (designated here). GUIANA. Basin of Rupununi River, Wichabai, fl., fr., 25–26 Oct 1937, A.C. Smith 2290 (NY barcode NY00247522!; isolectotypes: F barcode F0047046F!, G barcode G00168031!, GH barcode GH00255059!, K barcode K000644009!, MO barcode MO-1936311!, NY barcode NY00247521!, P barcode P00730322!, S No. S05-5985!, U barcode U0005719!, US barcode US00091644!).

Distribution. Antilles (Cuba), Central America (Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, and Panama), and South America (Bolivia, Colombia, Ecuador, French Guiana, Guyana and Suriname, Venezuela, and Brazil – states of Acre, Amazonas, Amapá, Pará, Rondônia, Tocantins, Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, Sergipe, Goiás, Mato Grosso do Sul, Mato Grosso, and Minas Gerais).

4.4. Pontederia natans P.Beauv., Fl. Oware 2: 18. 1807.

Eichhornia natans (P.Beauv.) Solms, Abh. Naturwiss. Vereins Bremen 7: 254. 1882. Leptosomus natans (P.Beauv.) Schltdl., Abh. Naturf. Ges. Halle 6: 174. 1862. Lectotype (designated here). NIGERIA. Benin, fleuve Formosa, fl., fr., s.dat., A.M.F. Palisot de Beauvois s.n. (G on 3ex barcode G00418251!; isolectotype: G-DC on 4ex GDC048496!).

Distribution. Angola, Benin, Botswana, Burkina Faso, Cameroon, Central African Republic, Chad, Congo, Egypt, Ethiopia, Gabon, Gambia, Ghana, Guinea, Guinea-Bissau, Ivory Coast, Liberia, Madagascar, Mali, Mozambique, Niger, Nigeria, Rwanda, Senegal, Sierra Leone, South Sudan, Sudan, Tanzania, Togo, Uganda, Zaire, Zambia, and Zimbabwe.

Nomenclatural notes. When describing *P. natans*, Palisot de Beauvois (1807) comments that his new species is common at the margins of Formosa River (currently called Benin River). After analyzing specimens from G and G-DC herbarium, we came across two specimens, mounted in seven sheets. The specimen GDC048496 is mounted in four sheets, composed of several flowering and fruiting specimens, and an extremely detailed annotation in the handwriting of Palisot de Beauvois. Nonetheless, the specimen G00418251 is mounted in three sheets; with the second sheet possessing a detached petiolate leaf and a copy of the original illustration, and the third possessing the specimen in which the illustration was based on. Thus, the G00418251 specimen is the obvious choice for a lectotype.

Taxonomical notes. The African E. natans ($\equiv P$. natans) is currently treated as a synonym of the Neotropical Eichhornia diversifolia ($\equiv P$. diversifolia) by all online databases (i.e., eMonocot 2010; The Plant List 2013; Govaerts 2017; Tropicos.org 2017). Nonetheless, as indicated in our identification key (see above), both species can be easily differentiated based on the number of flowers per inflorescence, floral diameter, presence or absence of a nectar guide, pubescence of the filaments, and capsule dehiscence. Thus, P. natans is here reestablished.

5. Pontederia L. subg. Pontederia

Fig 9

Michelia Adans., Fam. Pl. 2: 201. 1763, nom. illeg. Type species (designated here). Pontederia cordata L.

Narukila Adans., Fam. Pl. 2: 54. 1763, nom. illeg. Type species (designated here). Narukila cordata (L.) Nieuwl. (≡ P. cordata L.).

Pontederaea Kuntze, Revis. Gen. Pl. 2: 718. 1891, orth. var.

Pontederas Hoffmanns., Verz. Pfl.: 137. 1824, orth. var.

Reussia Endl., Gen. Pl.: 139. 1836. Type species (designated by Lowden 1973). Reussia triflora Endl. ex Seub. [≡ P. triflora (Endl. ex Seub.) G.Agostini et al.].

Unisema Raf. Med. Repos. 5: 352. 1808, nom. illeg. Type species. *Unisema obtusifolia* (Raf.) Raf. (≡ *P. cordata* L.).

Umsema Raf. Med. Repos. 5: 352 1808, orth. var.

Unisemma D.A.Godron, in Orbigny CVD, Dict. Univ. Hist. Nat.: 761. 1848, orth. var.

Description. Herbs perennial or annual, aquatic to amphibious, erect-emergent or procumbent-emergent. Rhizome short and generally inconspicuous. Stems erect or trailing, spongy, unbranched to branching only at the base to branched. Sessile leaves early deciduous. Petiolate leaves distichously-alternate, evenly distributed along the stem or congested at the apex of the stem, emergent, ligule truncate, petioles not-inflated, blades cordate to broadly cordate, rarely elliptic to lanceolate or narrowly ovate. Main florescences (inflorescences) terminal, sessile or pedunculate; inflorescence leaf without an inflated leaf-sheath; basal bract flat; cincinni alternate, 1–3-flowered, sessile to shortly-pedunculate, internodes contracted. Flowers sessile, tristylous, zygomorphic, non-enantiostylous, perianth conate forming a tube, infundibuliform, revolute at post-anthesis, non-deliquescent and loosely enclosing the developing fruit, lobes 3 superior and 3 inferior, rarely 5 superior and 1 inferior, the central superior lobe with a nectar guide, consisting of 2 yellowish green to green spots, generally surrounded by a dark purple to bluish purple, rarely white blur, coiling or post-anthesis; stamens dimorphic, filaments free from each other, J-shaped, glandular-pubescent, anthers dorsifixed, rimose; ovary with 1 fertile locule, 1-ovulate, septal nectaries present, style glandular-pubescent or glabrous, stigma truncate or capitate or trilobate. Achene ovoid or pyriform; anthocarp hardened, ridged, ridges sinuate, toothed or echinate. Seeds curved narrowly ovoid or ovoid, testa smooth.

Circumscription. *Pontederia* subg. *Pontederia* is circumscribed by us to comprise eight species. Our concept of *P.* subg. *Pontederia* is equivalent to the concept of *Pontederia* adopted by Lowden (1973). Nonetheless, we accept *P. triflora* as distinct from *P. subovata*, and increase the number of species in the *P. cordata* complex by the reestablishment of *P. ovalis*. The members of this subgenus are peculiar within *Pontederia s.l.* due to their spike-like main florescences, ovaries 1-locular by abortion, fertile locule 1-ovulate, pendulous placentation, fruit an achene, hardened and ornate anthocarps, and smooth seeds.

Distribution. Exclusively Neotropical.

Key to the species of *Pontederia* subg. *Pontederia*

- 1. Rhizomes absent; stems elongated, trailing; leaves evenly distributed along the stem; anthocarp echinate; seeds straight, ovoid... 2
- Rhizomes present, short; stems short, erect; leaves congested at the apex of the stem;
 anthocarp toothed or with sinuate ridges; seeds curved, narrowly ovoid... 4
- 2. Petiolate leaf-blades with cordate to sagittate base; inflorescences 30–80-flowered, cincinni 2–3-flowered; flowers lilac or light to medium pink, rarely white, perianth lobes with a 3+3 arrangement... *P. rotundifolia* L.f.
- Petiolate leaf-blades with obtuse to cuneate base; inflorescences 2–15-flowered, cincinni 1-flowered; flowers light to medium blue, rarely white, perianth lobes with a 5+1 arrangement... 3
- 3. Petiolate leaf-blades emergent, elliptic to narrowly ovate to ovate to rhomboid; inflorescences (6–)8–20-flowered... *P. subovata* (Seub.) Lowden
- Petiolate leaf-blades floating, linear lanceolate to linear elliptic to linear rhomboid; inflorescences 2–4(–5)-flowered... *P. triflora* (Endl. *ex* Seub.) G.Agostini et al.
- 4. Petioles green, blades with a thickened midvein; inflorescences and flowers covered with light yellow hairs, flowers homostylous, central superior lobe with 1 spot, anthers dark brown to black, style equal in length with the inferior stamens... *P. parviflora* Alexander
- Petioles red to vinaceous to purple, rarely green, blades lacking a thickened midvein; inflorescences and flower covered with hyaline hairs, flowers tristylous, central superior lobe with 2 spots, anthers yellow or greyish blue to purple, style either shorter or longer than the inferior stamens... 5
- 5. Basal bract deflexed, main axis glabrous; central superior lobe with 2 green spots, style glandular-pubescent, stigma trilobate; anthocarp with toothed ridges... *P. cordata* L.
- Basal bract upright, main axis velutine or sparsely to densely villose; central superior lobe with 2 yellow spots, style glabrous, stigma truncate; anthocarp with sinuate ridges... 6
- 6. Petiolate leaf-blades elliptic to narrowly ovate to ovate to broadly ovate; cincinni 2–3-flowered... *P. ovalis* Mart.
- Petiolate leaf-blades sagittate to broadly sagittate or hastate to broadly hastate; cincinni 4–6-flowered... *P. sagittata* C.Presl

5.1. *Pontederia cordata* L., Sp. Pl. 1: 288. 1753.

Unisema cordata (L.) Farw., Pap. Michigan Acad. Sci. 3: 91. 1924.

Narukila cordata (L.) Nieuwl., Amer. Midl. Naturalist 3: 101. 1913. Lectotype (designated by Reveal et al. 1987). UNITED STATES. Virginia and Maryland, fl., fr., s.dat., P. Kalm s.n. (LINN barcode LINN-HL407-4).

Pontederia lancifolia Muhl., Cat. Pl. Amer. Sept.: 34. 1813.

Unisema cordata fo. lancifolia (Muhl.) Farw., Pap. Michigan Acad. Sci. 3: 92. 1924.

Narukila cordata var. lancifolia (Muhl.) Nieuwl., Repert. Spec. Nov. Regni Veg. 12: 101. 1913. Pontederia cordata var. lancifolia (Muhl.) Torr., Fl. N. Middle United States: 343. 1824.

Lectotype (designated by Lowden 1973). UNITED STATES. Carolina, fl., fr., s.dat., G.H.E. Muhlenberg 242 (PH barcode PH00033652!).

Distribution. Widely distributed in North, Central and South America, and the West Indies, from Canada to Uruguay.

Taxonomical notes. *Pontederia cordata* has always been the origin of much debate and taxonomical confusion in the genus. Most of the species currently accepted by us in *Pontederia s.l.* have either been confused or compared with *P. cordata*, at some point. This can be demonstrated by how many of them have been treated either as synonyms or infraspecific taxa by different authors (Fernald 1950; Lowden 1973; Godfrey & Wooten 1979; Novelo & Lot 1994). *Pontederia cordata* is morphologically and phylogenetically related to *P. lancifolia*, with only weak differences related to leaf morphology, thus should not be recognized taxonomically. Otherwise, we believe that based on the current phylogenetic and morphological data, *P. cordata*, *P. ovalis*, *P. parviflora*, and *P. sagittata* should be treated at the species level, until further studies can properly deal with the problem.

5.2. *Pontederia ovalis* Mart. *ex* Schult. & Schult.f., Syst. Veg. (ed. 15 bis) 7(2): 1140. 1830.

Pontederia lanceolata f. ovalis (Mart. ex Schult. & Schult.f.) A.Cast., Arch. Jard. Bot. Rio de Janeiro 15: 62. 1957.

Pontederia cordata var. ovalis (Mart. ex Schult. & Schult.f.) Solms, Monogr. Phan. 4: 533. 1883. Lectotype (designated here). BRAZIL. s.loc., fl., s.dat., C.F.P. Martius 14 (M barcode M0242238!).

Distribution. Costa Rica, Guatemala, Honduras, Bolivia, Brazil (states of Bahia, Maranhão, Paraíba, Distrito Federal, Goiás, Mato Grosso, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul), Colombia, Paraguay, and Uruguay.

Nomenclatural notes. When describing *P. ovalis*, Schultes and Schultes (1830) mention that their new species is based in Martius specimens from Brazil. However, the author makes no mention in which herbarium the specimens are housed, or their collectors' numbers. While consulting the specimens at M, we came across two Martius' specimens (i.e., *Martius 14* M0242238; *Martius 16* M0242244) that matched the protologue of *P. ovalis*. Both specimens were annotated in Martius handwriting and were probably analyzed by Schultes. Since the specimen *Martius 14* (M0242238) is a more complete collection, when compared with *Martius 16* (M0242244) which is composed of two detached leaves and two inflorescences, it is selected by us as the lectotype for *P. ovalis*.

Taxonomical notes. *Pontederia ovalis* has been considered by most authors and online databases as either a variety (Dubs 1998, Tropicos 2018) or a synonym (Schulz 1942, Tropicos 2018) of *P. cordata*. Nonetheless, both morphologically and phylogenetically, *P. ovalis* is much more similar to *P. sagittata*, due to their pubescent inflorescence main axis, and fruits with sinuate ridges. Thus, *P. ovalis* is here reestablished, being also part of the *P. cordata* species complex.

5.3. *Pontederia parviflora* **Alexander**, N. Amer. Fl. 19: 59. 1937.

Pontederia cordata var. *parviflora* (Alexander) Schery, Ann. Missouri Bot. Gard. 31: 156. 1944. Lectotype (designated here). PANAMA. Camino del Boticario, near Chapo, fl., Oct

1911, H. Pittier 4556 (NY barcode NY00260019!: isolectotypes: NY barcode NY00260020!, US barcode US00091647!).

Distribution. Panama, Venezuela, Colombia, and Brazil (states of Tocantins, Alagoas, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso, Minas Gerais, and São Paulo).

5.4. *Pontederia rotundifolia* L.f., Suppl. Pl. 192 1782.

Reussia rotundifolia (L.f.) A.Cast., Lilloa 25: 593. 1952. Lectotype (designated by Lowden 1973). SURINAM. s.loc., fl., s.dat., C.G. Dahlberg 137 (LINN barcode LINN-HL407-2!; isolectotype: S No. S09-33701!).

Distribution. Mexico, Belize, Costa Rica, El Salvador, Guatemala, Honduras, Nicaragua, Panama, French Guiana, Guyana, Suriname, Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina, Paraguay, Uruguay, and Brazil (states of Amazonas, Pará, Rondônia, Roraima, Tocantins, Alagoas, Bahia, Maranhão, Paraíba, Pernambuco, Distrito Federal, Goiás, Mato Grosso do Sul, Mato Grosso, Minas Gerais, Rio de Janeiro, Paraná, Rio Grande do Sul, and Santa Catarina).

5.5. *Pontederia sagittata* **C.Presl**, Reliq. Haenk. 1(2): 116. 1827.

Pontederia cordata f. sagittata (C.Presl) Solms, Monogr. Phan. 4: 533. 1883.

Pontederia cordata var. sagittata (C.Presl) Schery, Ann. Missouri Bot. Gard. 31: 157. 1944.

Holotype. MEXICO. s.loc., fl., fr., s.dat., T.P.X. Haenke s.n. (PRC barcode PRC450416!).

Distribution. Mexico, Costa Rica, Guatemala, Honduras, Panama, and Brazil (states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Rio Grande do Sul, and Santa Catarina).

Taxonomical notes. *Pontederia sagittata* is a poorly circumscribed taxon that is morphologically similar to *P. cordata*, due to the shape of the blade of their petiolate leaves. However, it is molecular more closely related to *P. ovalis*, having in common the anthocarp with sinuate ridges. The disjunctive distribution of *P. sagittata* is probably related to misidentified specimens and/or the presence of cryptic species in what we currently accept as *P. sagittata s.l.* Great variation in petiolate leaf shape can be observed throughout its distribution, especially in Brazil. We believe that *P. sagittata* should be properly studied, using different approaches than traditional taxonomy, in order to solve this issue.

5.6. *Pontederia subovata* (Seub.) Lowden, Rhodora 75: 478. 1973.

Reussia subovata (Seub.) Solms, Monogr. Phan. 4: 534. 1883.

Eichhornia subovata Seub., Fl. Bras. 3(1): 91. 1847. Lectotype (designated by Lowden 1973). BRAZIL. Goiás: Provincia de Goyaz, fl., 1836–1841, G. Gardner 4022 (NY barcode NY00247524!; isolectotypes: BM, G barcodes G00168015!, G00168018!, G00168019!, K barcode K000644012!, P barcodes P00730329!, P00730589!, US barcode US00091645!).

Distribution. Venezuela, Guyana, Bolivia, Argentina, Paraguay, and Brazil (states of Acre, Amazonas, Amapá, Pará, Tocantins, Bahia, Piauí, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, São Paulo, Paraná, Rio Grande do Sul, and Santa Catarina).

5.7. *Pontederia triflora* (Endl. ex Seub.) G.Agostini et al., Ernstia 27: 9. 1984.

Reussia triflora Endl. ex Seub., Fl. Bras. 3(1): 96. 1847. Type (not found). BRAZIL. Pohl; Sellow (B?).

Distribution. Colombia, Venezuela, Guyana, Bolivia, Argentina, and Brazil (states of Roraima, Mato Grosso, Mato Grosso do Sul, and Minas Gerais).

Nomenclatural notes. Due to the impossibility to find the type specimen(s?) of *Reussia triflora* in any of the visited herbaria, we do not designate any types for this name at this point.

Taxonomical notes. *Pontederia triflora* has been greatly confused with *P. subovata*, since its original description as *R. triflora* by Seubert (1847). Both species share similar habit, leaf and floral morphology. Nonetheless, in *P. triflora* the petiolate leaf-blades are linear lanceolate to linear elliptic or linear rhomboid (*vs.* emergent and elliptic to narrowly ovate to ovate or subrhomboid in *P. subovata*), and the inflorescences are 2–4(–5)-flowered [vs. (6–)8–20-flowered]. Thus, we reaffirm *P. triflora* as an accepted name, distinct from *P. subovata*.

Conclusions

Pontederiaceae was one of the first families of flowering plants to be the focus of studies dealing with its phylogenetic history, based on morphological, molecular, and combined data (Eckenwalder and Barrett 1986; Graham and Barrett 1995; Kohn et al. 1996; Barrett and Graham 1997; Graham et al. 1998, 2002; Ness et al. 2011). Nonetheless, until very recently (Pellegrini 2017a), the taxonomy of the family remained dogmatic and outdated, with the recognition of several non-monophyletic taxa. The arguments used as basis to maintain such assembles are based especially on misunderstandings of the principles of phylogenetic systematics (Schmidt-Lebuhn 2012). According to Simpson (2006), one of the main paradigms of modern phylogenetic systematics is the proposal of classification systems that accurately reflect the evolutionary history of the studied group, being simultaneously easy to use. In order to achieve that, novel classification systems should be based on molecular phylogenetic studies, together with morphological and, whenever possible, also including less commonly characters (e.g., anatomy, ecology, geography, palynology, micromorphology, phytochemistry, etc.; Pellegrini 2017b). Furthermore, without the inclusion of morphological characters in a phylogenetic analysis, there is no way to obtain morphological synapomorphies to support the recovered relationships and any proposed new classification (Lipscomb et al. 2003; Wiens 2004; Assis and Rieppel 2011). The implementation of these ideals on the systematics of Pontederiaceae has generated not only monophyletic genera but has considerably facilitated the taxonomy of the group. With the classification implemented here, species of Pontederiaceae are easily and unambiguously placed under two genera supported by morphological and molecular data. An infrafamiliar classification for Pontederiaceae has always been of little taxonomic and systematic relevance, due to the families' reduced size. With Pontederiaceae consisting now of only two genera, the recognition of subfamilies and tribes seems rather pointless, since each genus would be placed in its own subfamily/tribe. Thus, we do not accept any taxonomic ranks between family and genus, in Pontederiaceae.

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Table 1. Voucher specimens used in the morphological and combined phylogenetic analyses, and Genbank accession numbers for all DNA regions sampled in this study. *Type species of the genus.

Family	Species	Collector	Herbarium	ndhF	rbcL
		& no.	acronym		
Philydraceae	*Helmholtzia acorifolia F.Muell.	Mueller 1876	K	EF422989.1	AF206774.1
Philydraceae	*Philydrum lanuginosum Banks & Sol. ex Gaertn.	Banks & Solander s.n.	BM barcode BM000990702	U41622.2	U41596.2
Haemodoraceae	Anigozanthos flavidus DC.	Brown s.n.	K barcode K000846259	EF422987.1	EF422992.1
Haemodoraceae	*Xiphidium caeruleum Aubl.	Perdiz 2376	RB	AF547013.1	AY149359.1
Pontederiaceae	Monochoria cyanea (F.Muell.) F.Muell.	Leichhardt s.n.	K barcode K000873493	U41613.1	U41588.1
Pontederiaceae	Monochoria korsakovii Regel & Maack	Maack s.n.	K barcode K000873544	U41615.2	U41590.1
Pontederiaceae	*Monochoria hastata (L.) Solms	Hermann s.n.	BM barcode BM000621681	U41614.1	U41589.1
Pontederiaceae	Monochoria vaginalis Burm.f.	Boeea 8471	US	U41616.1	KX527476.1
Pontederiaceae	Eichhornia crassipes (Mart.) Solms	Martius 60	M	FJ861142.1/ U41599.2	FJ861142.1/ EF422991.1
Pontederiaceae	Eichhornia diversifolia (Vahl) Urb.	Harley 10248	RB	U41600.1	U41575.1
Pontederiaceae	*Eichhornia azurea (Sw.) Kunth	Martinelli 18669	RB	U41598.1	U41573.1
Pontederiaceae	Eichhornia heterosperma Alexander	Smith 2290	NY	U41601.1	U41576.1
Pontederiaceae	Eichhornia paniculata (Spreng.) Solms	Machado 574	RB	U41603.1	U41578.1

Pontederiaceae	Eichhornia paradoxa (Mart.) Solms	Harley 21401	K	U41607.1	U41579.1
Pontederiaceae	*Pontederia cordata L.	Barton s.n.	PH barcode PH00038346	U41617.1	U41592.1
Pontederiaceae	Pontederia lancifolia Muhl.	Muhlenberg 242	РН	U41618.1	U41593.1
Pontederiaceae	Pontederia rotundifolia L.f.	Alvarenga 952	RB	U41620.1	U41595.1
Pontederiaceae	Pontederia ovalis Mart.	Pellegrini 474	RB	U41619.1	U41594.1
Pontederiaceae	Pontederia sagittata C.Presl	Catharino 342	RB	U41621.1	U41597.1
Pontederiaceae	Heteranthera gardneri (Hook.f.)	Gardner 1863	K	U41606.2	U41582.1
Pontederiaceae	M.Pell. Heteranthera rotundifolia (Kunth) Griseb.	Walter 6644	RB	U41610.1	U41585.1
Pontederiaceae	Heteranthera limosa (Sw.) Willd.	Assunção 721	RB	U41608.2	U41583.1
Pontederiaceae	Heteranthera zosterifolia Mart.	Fontana 8316	RB	U41612.1	U41587.1
Pontederiaceae	Heteranthera seubertiana Solms	Gardner 1864	ВМ	U41611.1	U41586.1
Pontederiaceae	Heteranthera oblongifolia Mart. ex Schult. & Schult.f.	Araújo 38	RB	U41609.1	U41584.1

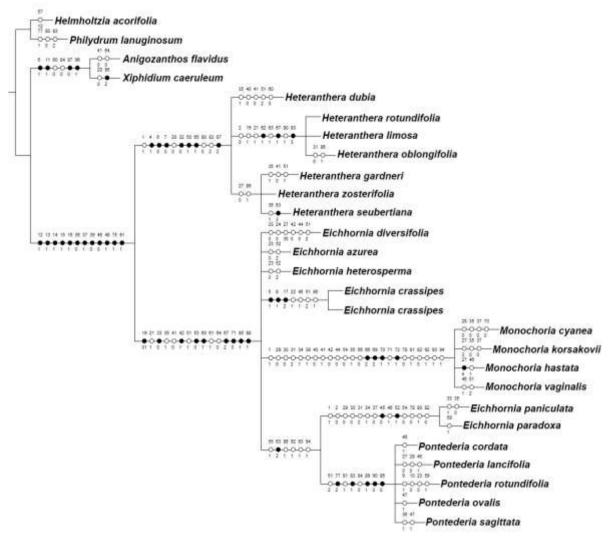


Figure 1. Strict consensus tree (length= 209 steps; CI= 0.5913; RI= 0.8618) recovered by the morphological dataset, showing the character state optimizations at each node of the cladogram, represented by circles. In each circle, the numbers above and below represent the character and character state numbers, respectively (as presented in Appendix 1).

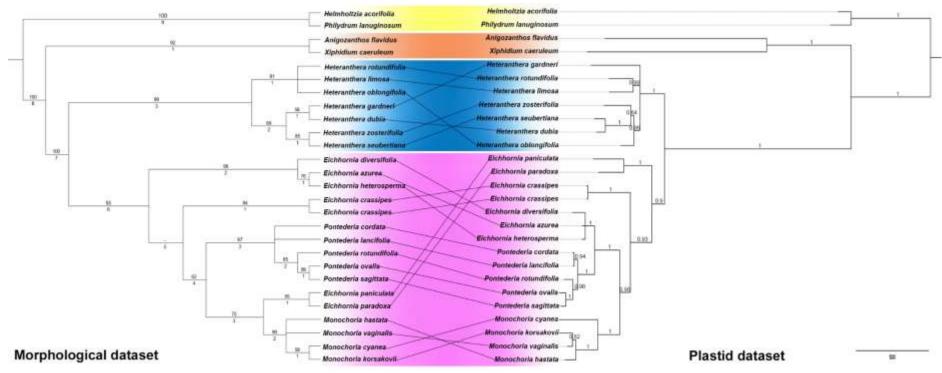


Figure 2. Majority-rule tree recovered for the morphological and plastid datasets. Morphology: bootstrap support values are depicted over the branches, while Bremer Index support values are depicted under the branches. Plastid: posterior probability values are depicted over the branches. Yellow: Philydraceae. Orange: Haemodoraceae. Blue: *Heteranthera s.l.* Pink: *Pontederia s.l.*

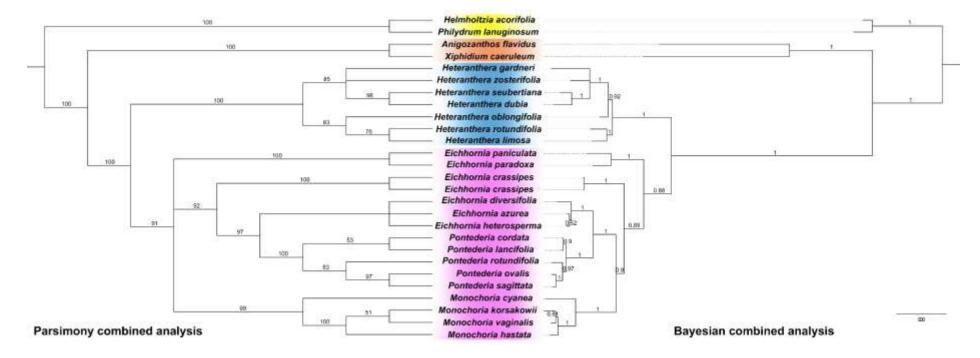


Figure 3. Majority-rule tree recovered for the parsimony and Bayesian analysis of the combined morphological + plastid dataset. Yellow: Philydraceae. Orange: Haemodoraceae. Blue: *Heteranthera s.l.* Pink: *Pontederia s.l.*

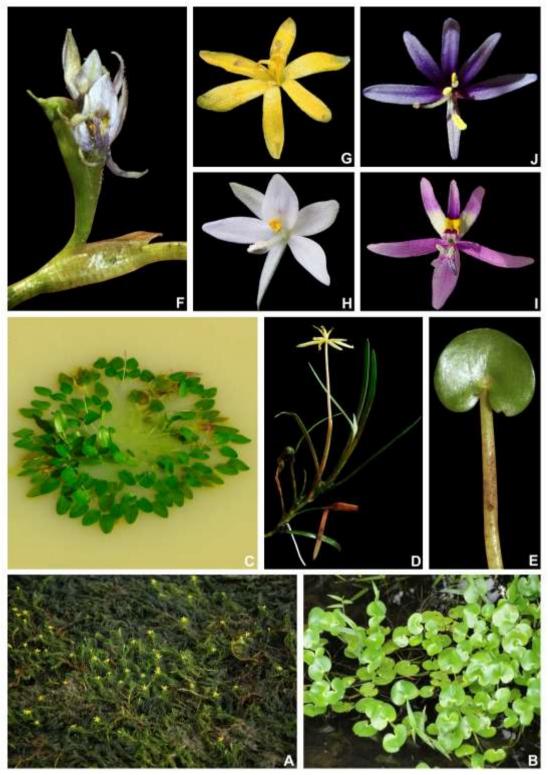


Figure 4. *Heteranthera* Ruiz & Pav. **A–D**, habit: **A**, emerged and flowering population of *H. gardneri* (Hook.f.) M.Pell. during the dry season; **B**, floating specimen of *H. reniformis* Ruiz & Pav.; **C**, emergent habit with floating and emerged leaves of *H. rotundifolia* (Kunth) Griseb.; **D**, habit of *H. dubia* (Jacq.) MacMill., showing the persistent sessile leaves. **E**, petiolate leaf of *H. pumila* M.Pell. & C.N.Horn, showing the lack of a pulvinus. **F**, Ligule and inflorescence of *H. pumila*. **G–J**, flowers: **G**, pseudanthium of *H. gardneri*; **H**, *H. reniformis*; **I**, *H. rotundifolia*; **J**, *H. zosterifolia* Mart. A by A.P. Fontana, B & H by C.N. Horn, C & I by A. Popovkin, D by S.R. Turner, E & F by M.O.O. Pellegrini, G by C.P. Bove, and J by S.S. Oliveira.



Figure 5. *Pontederia* subg. *Cabanisia* (Klotzsch *ex* Schltdl.) M.Pell. & C.N.Horn. **A,** habit. **B**–**C,** inflorescence: **B,** young inflorescence, showing the inflated leaf-sheath and flat basal bract wit caudate apex; **C,** mature inflorescence showing the pedunculate cincinni with elongate internodes. **D,** detail of a cincinni, showing (from left to right) an immature floral bud, a preanthesis floral bud, and a post-anthesis flower. **E,** front view of a flower. **F,** detail of an immature capsule, showing the ridged anthocarp. All photos of *P. paniculata* Spreng.; A by C. Willig & L. Nusbaumer, remaining photos by M.O.O. Pellegrini.

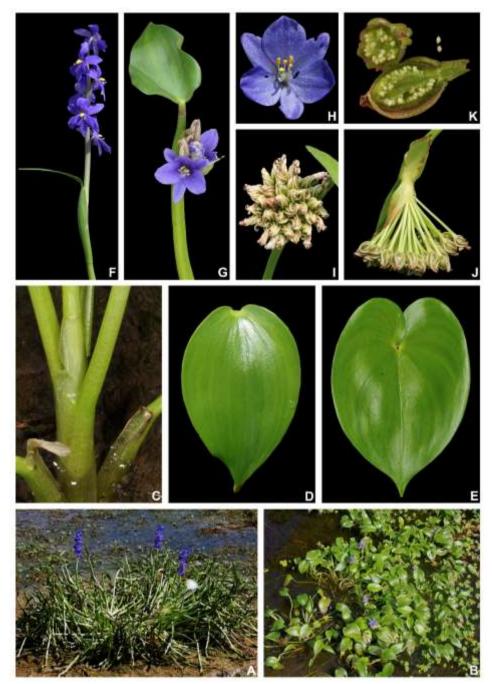


Figure 6. *Pontederia* subg. *Monochoria* (C.Presl) M.Pell. & C.N.Horn. **A–B**, habit: **A**, paludal habit of *P. australasica* (Ridl.) M.Pell. & C.N.Horn; **B**, paludal habit of *P. cyanea* (F.Muell.) M.Pell. & C.N.Horn. **C**, ligule of *P. vaginalis* Burm.f., showing the truncate apex. **D–E**, petiolate leaf-blades: **D**, blade of *P. cyanea*, showing the lack of a posterior division; **E**, blade of *P. vaginalis*, showing the presence of a posterior division. **F–G**, inflorescences: **F**, inflorescence of *P. australasica*, showing the developed main axis; **G**, inflorescence of *P. plantaginea* Roxb., showing the contracted main axis. **H**, front view of a flower of *P. korsakowii* (Regel & Maack) M.Pell. & C.N.Horn. **I–J**, inflorescences at post-anthesis: **I**, erect inflorescence of *P. hastata* L. bearing flowers at post anthesis; **J**, infrutescence of *P. hastata*, showing the deflexed posture and the elongated pedicels. **K**, sections of immature capsules of *P. vaginalis*, showing developing seeds. A & F by M. Barritt, B by R. Cumming, C, E & K by P.B. Pelser & J.F. Barcelona, D by A. & S. Pearson, G by D. Valke. H by Ashitaka-f Studio, and I & J by Cerlin Ng.



Figure 7. *Pontederia* subg. *Oshunae* M.Pell. & C.N.Horn. **A–B**, habit: **A**, dense population of the pink-flowered form; **B**, detail of a population, showing the free-floating rosettes, stolons, and inflated petioles. **C–D**, petiolate leaves: **C**, blade; D, detail of a young leaf showing its blade enclosing the inflated petiole of the presiding leaf. **E–G**, inflorescence: **E**, young inflorescence of a lilac-flowered form; **F**, inflorescence of a lilac-flowered form at anthesis; **G**, inflorescence of a pink-flowered form at anthesis. **H–J**, flowers: **H**, oblique view of a lilac flower; **I**, detail of the nectar guide; **J**, detail of the androecium and gynoecium showing the glandular hairs. All photos of *P. crassipes* Mart.; A by C. Willig & L. Nusbaumer, B by O. Gaubert, C by K. Pritchard & S.A. Harris, D–F & H–I by R. Aguilar, and G by M.O.O. Pellegrini.



Figure 8. *Pontederia* subg. *Eichhornia* (Kunth) M.Pell. & C.N.Horn. **A–B**, habit: **A**, habit of *P. heterosperma* (Alexander) M.Pell. & C.N.Horn, showing the emerged petiolate leaves; **B**, habit of *P. diversifolia* (Vahl) M.Pell. & C.N.Horn, showing the floating petiolate leaves. **C–F**, inflorescence: **C**, 2–3-flowered inflorescences of *P. diversifolia*, showing the flowers with a yellow nectar guide in the posterior perianth lobes; **D**, 1-flowered inflorescence of *P. natans* P.Beauv., showing the lack of a nectar guide; **E**, inflorescence of *P. heterosperma*, showing the lack of nectar guides in the posterior perianth lobes; **F**, morphological variation of inflorescences and perianth color of *P. azurea* Sw. **G**, front view of a flower of *P. azurea*. **H**, front view of a flower of *P. natans*. A & B by O. Gaubert, C by A.S. Castro, D by P. Birnbaum, E by H. Medeiros, F by L.O.A. Teixeira, G by M.O.O. Pellegrini, and I by T.C. Buruwate.

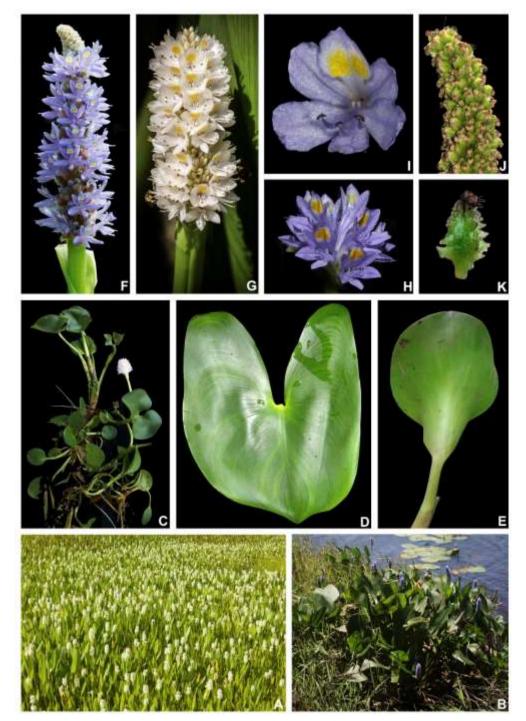


Figure 9. Pontederia L. subg. Pontederia. **A–C**, habit: **A**, dense population of *P. parviflora* Alexander; **B**, population of *P. ovalis* Mart. ex Schult. & Schult.f.; **C**, habit of *P. rotundifolia* L.f. **D–E**, petiolate leaves: **D**, blade of *P. rotundifolia*; **E**, blade of *P. parviflora*. **F–H**, inflorescences: **F**, inflorescence of *P. cordata* L., showing flowers with two yellow nectar guides in the posterior perianth lobes; **G**, inflorescence of *P. parviflora*, showing flowers with a sole yellow nectar guides in the posterior perianth lobes; **H**, inflorescence of *P. rotudifolia*, showing a lilac-flowered form. **I**, oblique view of a flower of *P. ovalis*. **J–K**, fruits: **J**, detail of the apex of the infrutescence of *P. ovalis*, showing the anthocarp with sinuate ridges; **K**, detail of an achene of *P. cordata*, showing the toothed ridges. A by C. Willig & L. Nusbaumer, B, I & J by M.O.O. Pellegrini, C by L.O.A. Teixeira, D & H by R. Aguilar, E by M.R. Engels, F by Ashitaka-f Studio, G by M.V. Lameiras, and K by A. Haines.

Appendix 1. List of morphological characters and coding.

- 1. Life cycle, duration: perennial (0); annual (1)
- 2. Clonal reproduction, presence: absent (0); present (1)
- 3. Habitat, emergence: paludal or emergent (0); mostly to completely submersed (1); terrestrial (2)
- 4. Habit, base: definite (0); indefinite (1)
- 5. Habit, attachment to the substrate: rooted (0); free-floating (1)
- 6. Roots, surface: water-binding/mucilaginous (0); sand-biding (1); non-binding (2)
- 7. Stem, rhizome: absent (0); present (1)
- 8. Stem, stolon: absent (0); present (1)
- 9. Stem, branching: unbranched to branched just at base (0); freely branching (1)
- 10. Stem, elongation: elongated (0); contracted (1)
- 11. Stem, fibrous layer: absent (0); present (1)
- 12. Leaves, dimorphic: absent (0); present (1)
- 13. Leaves, blade: unifacial (0); late bifacial (1)
- 14. Leaves, ptyxis: equitant (0); conduplicate-involute, enclosing the petiole of the preceding leaf (1)
- 15. Leaves, vascular bundles, organization: xylem and phloem alternate or circular phloem with central xylem (0); xylem abaxial, phloem adaxial + xylem and phloem alternate (1)
- 16. Leaves, sheath, projection (ligule): absent (0); present (1)
- 17. Leaves, sheath, projection (ligule), shape: truncate (0); 2-several-parted (1); flabellate (2)
- 18. Leaves, sessile, phyllotaxy: distichous (0); spiral (1); equitant (2)
- 19. Leaves, sessile, duration: early deciduous (0); late deciduous (1); persistent (2)
- 20. Leaves, sessile, distribution: distributed along the stem (0); congested (1)
- 21. Leaves, petiolate, production: never or rarely produced (0); always produced (1)
- 22. Leaves, petiolate, phyllotaxy: distichous (0); spiral (1)
- 23. Leaves, petiolate, distribution: distributed along the stem (0); congested (1)
- 24. Leaves, petiolate, posture: floating (0); emersed (1)
- 25. Leaves, petiolate, pulvinus: absent (0); present (1)
- 26. Leaves, petiolate, blade, consistency: membranous (0); chartaceous to coriaceous (1)

- 27. Leaves, petiolate, blade, overall shape: linear to tapered (0); elliptic to ovate (1); obovate (2); cordate (3); sagittate (4); rotund (5)
- 28. Leaves, petiolate, blade, base, posterior divisions: absent (0); present (1)
- 29. Synflorescence, leaf, sheath: inflated (0); not inflated (1)
- 30. Inflorescence, basal bract, posture: flat (0); conduplicate (1); tubular (2)
- 31. Inflorescence, basal bract, apex, shape: obtuse to truncate (0); acute to acuminate to aristate (1); caudate (2)
- 32. Inflorescence, cincinni, number per thyrse: one (0); two to many (1)
- 33. Inflorescence, cincinni, peduncle, presence: absent (0); present (1)
- 34. Inflorescence, cincinni, peduncle, internal consistency: solid (0); fistulose (1)
- 35. Inflorescence, cincinni, main axis, condensation: elongate (0); contracted (1)
- 36. Inflorescence, cincinni, flower per cincinni, number: one or two (0); three to many (1)
- 37. Inflorescence, in fruit, posture: erect (0); deflexed (1)
- 38. Flower, self-incompatibility: self-incompatible (0); self-compatible (1)
- 39. Flower, pedicel, length: sessile (0); pedicellate (1)
- 40. Flower, symmetry: actinomorphic (0); zygomorphic (1)
- 41. Flower, enantiostyly: absent (0); present (1)
- 42. Flower, morphs: monostylous or pseudomonostylous (0); tristylous (1)
- 43. Flower, cleistogamy: absent (0); present (1)
- 44. Flower, septal nectaries: absent (0); present (1)
- 45. Flower, tannin cells, homogeneous: absent (0); present (1)
- 46. Flower, tannin cells, granular: absent (0); present (1)
- 47. Flower, tannin cells, fibrillar: absent (0); present (1)
- 48. Receptacle, aerenchyma: absent (0); present (1)
- 49. Perianth, aerenchyma: absent (0); sparse (1); dense (2)
- 50. Perianth, shape: campanulate or infundibuliform or hypocrateriform (0); tubular (1); falcate (2); flat (3)
- 51. Perianth, tannin cells, distribution: absent to sparse (0); moderate (1); abundant (2)
- 52. Perianth, tannin cells, type: homogeneous (0); granular (1); fibrillar (2)
- 53. Perianth, at post-anthesis: coiled (0); marcescent (1)
- 54. Perianth, at post-anthesis, coiling, type: spirally-coiled (0); revolute (1)
- 55. Perianth, at post-anthesis, coiled, enclosing the fruit: loosely (0); tightly (1)

- 56. Perianth, conation: basally conate (0); forming a conspicuous tube (1)
- 57. Perianth, color: yellow to orange to red (0); white (1); pink (2); blue to lilac to purple (3)
- 58. Perianth, lobes, number: 4 (0); 6 (1)
- 59. Perianth, lobes, arrangement: 3+3 (0); 5+1 (1)
- 60. Perianth, lobes, shape, between one another: all equal (0); equal in the same series (1); different in the same series (2)
- 61. Perianth, lobes, shape, apex: acute to acuminate (0); obtuse (1)
- 62. Perianth, lobes, anterior lobe, base: flat (0); folded or flanged (1)
- 63. Perianth, lobes, anterior lobe, nectar guide: absent (0); one spot or band (1); two spots (2); dark-colored band or blur (3)
- 64. Androecium, stamens, fertile, number: six (0); three or one (1)
- 65. Androecium, filaments, insertion: straight (0); oblique (1)
- 66. Androecium, filaments, conation: free (0); epipetalous (1); forming a petalo-staminal tube (2)
- 67. Androecium, filaments, posture: straight (0); sigmoid (1); J-shaped to recurved-decurved (2)
- 68. Androecium, filaments, inflation: not inflated (0); inflated (1)
- 69. Androecium, stamens, diversity: monomorphic (0); dimorphic (1); unequal (2)
- 70. Androecium, stamens, filament, appendage: absent (0); present (1)
- 71. Androecium, stamens, anther, insertion: dorsifixed (0); basifixed (1)
- 72. Androecium, stamens, anther, dehiscence: rimose (0); poricidal (1)
- 73. Androecium, endothecium, basal thickening: absent (0); present (1)
- 74. Androecium, tapetum, type: glandular (0); amoeboid (1)
- 75. Androecium, pollen, aperture, number: monosulcate (0); bisulcate (1)
- 76. Androecium, pollen, exine, ornamentation: tectate-columellate (0); non-tectate-columellate (1)
- 77. Gynoecium, ovary, locule fertile, number: three (0); one (1); pseudomonomerous (2)
- 78. Gynoecium, ovary, wall, tannin cells: absent (0); present (1)
- 79. Gynoecium, ovary, wall, aerenchyma: absent (0); present (1)
- 80. Gynoecium, ovary, septae, conation: aposeptalous (0); hemiseptalous (1); synseptalous (2)
- 81. Gynoecium, ovary, septae, epithelial cells: absent (0); present (1)

- 82. Gynoecium, ovary, septae, tannin cells: absent (0); present (1)
- 83. Gynoecium, ovary, placentation, type: axial (0); pendulous (1); intrusive-parietal (2); axile-parietal (3)
- 84. Gynoecium, ovary, placentation, flanges: unflanged (0); slightly 2-flanged (1); 2-flanged (2)
- 85. Gynoecium, style, posture: straight to recurved-decurved (0); J-shaped (1);
- 86. Gynoecium, style, pubescence: glabrous (0); pubescent or glandular-pubescent (1)
- 87. Gynoecium, stigma, shape: truncate (0); evenly trilobate to trifid or capitate (1); unevenly trilobate (2)
- 88. Gynoecium, stigma, moisture: dry (0); wet (1)
- 89. Fruit, type: capsule (0); achene (1)
- 90. Fruit, seeds per locule: one (0); several (1)
- 91. Fruit, anthocarp, presence: absent (0); present (1)
- 92. Fruit, anthocarp, envelopment of the fruit: loose (0); tight (1)
- 93. Fruit, anthocarp, development: thin (0); hardened (1)
- 94. Fruit, anthocarp, ornamentation: smooth (0); ridged (1)
- 95. Seed, testa, ornamentation: smooth (0); longitudinally winged or striated (1); tuberculate (2)
- 96. Chemistry, phenalenones: absent (0); present (1)

Appendix 2. Matrix with the 27 terminals and the first 29 characters. The characters that were not coded due to lack of data of the analyzed specimens and/or from literatures sources are coded as "?"; characters that did not apply were coded as "-"; and the polymorphic characters were coded with a "/" between each state it presented.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Helmholtzia acorifolia	0	1	0	0	0	2	1	0	0	1	0	0	0	0	0	0	-	2	2	1	0	-	-	-	-	-	-	-	1
Philydrum lanuginosum	0	1	0	0	0	2	1	0	0	1	0	0	0	0	0	0	-	2	2	1	0	-	-	-	-	-	-	-	1
Anigozanthos flavidus	0	1	2	0	0	1	1	0	0	1	1	0	0	0	0	0	-	2	2	1	0	-	-	-	-	-	-	-	1
Xiphidium caeruleum	0	1	2	0	0	1	1	0	0	1	1	0	0	0	0	0	-	2	2	0	0	-	-	-	-	-	-	-	1
Monochoria cyanea	1	1	0/1	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	0/1	1	1	1	0	0
Monochoria korsakovii	1	1	0	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	3	1	0
Monochoria hastata	1	1	0	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	4	1	0
Monochoria vaginalis	1	1	0/1	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	0/1	1	1	1/3	1	0
Eichhornia crassipes	0	1	0	0	1	2	1	1	0	1	0	1	1	1	1	1	2	0	0	1	1	1	1	1	1	1	1/3	0/1	1
Eichhornia crassipes2	0	1	0	0	1	2	1	1	0	1	0	1	1	1	1	1	2	0	0	1	1	1	1	1	1	1	1/3	0/1	1
Eichhornia diversifolia	0	1	1	0	0	2	1	0	1	0	0	1	1	1	1	1	0	0	1	1	1	0	0	0	1	1	3/5	1	1
Eichhornia azurea	0	1	1	0	0	2	1	0	1	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1	1/2/5	0	1
Eichhornia heterosperma	0	1	1	0	0	2	1	0	1	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1	1/2/5	0	1
Eichhornia paniculata	1	0	0	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	3/4	1	0
Eichhornia paradoxa	1	0	0	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	1	0	0
Pontederia cordata	0	1	0	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	1/3	1	1
Pontederia lancifolia	0	1	0	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	0	0	1
Pontederia rotundifolia	0	1	0/1	0	0	2	1	0	1	0	0	1	1	1	1	1	0	0	0	1	1	0	0	1	1	1	3/4	1	1
Pontederia ovalis	0	1	0	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	1/3	0/1	1
Pontederia sagittata	0	1	0	0	0	2	1	0	0	1	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	3	1	1
Heteranthera gardneri	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	2	0	0	-	-	-	-	-	-	-	1
Heteranthera rotundifolia	1	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	0/1	0	0	1/5	0	1
Heteranthera limosa	1	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	0/1	0	0	0/1	0	1
Heteranthera zosterifolia	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	2	0	0	1	1	0	0	0	0	0	1

Heteranthera seubertiana	1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	2	0	0	1	1	0/1	0	0	0	0	1
Heteranthera oblongifolia	1	0	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	0	1	1	1	0/1	0	0	0/1	0	1
Heteranthera dubia	0/1	1	1	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	2	0	0	-	-	-	-	-	-	-	1

Continuation. Matrix with the 60 terminals and characters 30 to 58.

Taxon	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
Helmholtzia acorifolia	1	1	1	0	0	1	0	1	1	1	1	0	0	1	1	1	1	0	0	0	2	0/1/2	1	-	-	0	1/2	0	1
Philydrum lanuginosum	1	1	1	0	0	0/1	0	1	1	1	1	0	0	0	1	1	1	0	0	0	2	0/1/2	1	-	-	0	0	0	1
Anigozanthos flavidus	1	1	1	0	0	1	0	0	1	1	0	0	0	1	1	1	1	0	0	2	0	0/1/2	1	-	-	1	0	1	1
Xiphidium caeruleum	1	1	1	0	0	1	0	0	1	1	1	0	0	1	1	1	1	0	0	3	0	-	1	-	-	0	0/1	1	1
Monochoria cyanea	2	1	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	1	2	0	1	0/1	0	0	1	0	3	1	2
Monochoria korsakovii	2	1	0	1	0	0/1	0	0	1	0	1	0	0	0	1	0	0	1	2	0	1	0	0	0	1	0	3	1	2
Monochoria hastata	2	1	0	1	1	0	1	0	1	0	1	0	0	0	1	1	0	1	2	0	1	0/1	0	0	1	0	3	1	2
Monochoria vaginalis	2	1	0	1	1	0	1	0	1	0	1	0	0	0	1	1	0	1	2	0	2	0/1	0	0	1	0	3	1	2
Eichhornia crassipes	1	1	0	0	1	0/1	1	0	0	1	0	1	0	1	1	1	0	1	2	0	2	0/1	0	1	0	1	1/2/3	1	1
Eichhornia crassipes2	1	1	0	0	1	0/1	1	0	0	1	0	1	0	1	1	1	0	1	2	0	2	0/1	0	1	0	1	1/2/3	1	1
Eichhornia diversifolia	1	1	0	0	1	0	1	1	0	1	0	0	0	0	1	0	1	1	2	0	2	0/2	0	1	0	1	2/3	1	1
Eichhornia azurea	1	1	0	0	1	0/1	1	1	0	1	0	1	0	1	1	0	1	1	2	0	1	2	0	1	0	1	1/3	1	1
Eichhornia heterosperma	1	1	0	0	1	0/1	1	1	0	1	0	1	0	1	1	0	1	1	2	0	1	2	0	1	0	1	1/3	1	1
Eichhornia paniculata	2	1	1	1	0	0/1	0	0	0	1	0	1	0	1	0	1	0	1	2	0	1	1	0	0	1	1	2/3	1	2
Eichhornia paradoxa	2	1	0	1	1	0	0	0	0	1	0	1	0	1	0	1	0	1	2	0	1	1	0	0	1	1	1/3	1	2
Pontederia cordata	1	1	0	0	1	0/1	1	1	0	1	0	1	0	1	1	1	0	1	2	0	2	0/1	0	1	1	1	1/2/3	1	1
Pontederia lancifolia	1	1	0	0	1	0/1	1	1	0	1	0	1	0	1	1	1	0	1	2	0	2	0/1	0	1	1	1	1/2/3	1	1
Pontederia rotundifolia	1	1	0	0	1	0	1	1	0	1	0	1	0	1	1	0	0	1	2	0	2	0	0	1	1	1	1/2	1	1
Pontederia ovalis	1	1	0	0	1	0/1	1	1	0	1	0	1	0	1	1	0	1	1	2	0	2	0/1/2	0	1	1	1	1/3	1	1
Pontederia sagittata	1	1	0	0	1	1	1	1	0	1	0	1	0	1	1	0	1	1	2	0	2	0/1/2	0	1	1	1	1/3	1	1
Heteranthera gardneri	0	0	1	0	1	0	1	0	0	1	0	0	1	0	1	0	0	1	1	1	1	0/1	1	-	-	1	0	1	0

Heteranthera rotundifolia	1	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	1	0	-	1	-	-	1	1/3	1	1
Heteranthera limosa	1	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	1	0	-	1	-	-	1	1/3	1	1
Heteranthera zosterifolia	0	0	1	0	0	0	1	0	0	1	1	0	1	0	1	0	0	1	1	1	0	0	1	-	-	1	3	1	0
Heteranthera seubertiana	1	0	1	0	0	1	1	0	0	1	1	0	1	0	1	0	0	1	1	1	0	0	1	-	-	1	0/1/3	1	1
Heteranthera oblongifolia	0	0	1	0	0	0	1	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	1	-	-	1	1/3	1	0
Heteranthera dubia	1	0	1	0	1	0	1	0	0	0	0	0	1	0	1	0	0	1	1	1	2	0/1	1	-	-	1	0	1	1

Continuation. Matrix with the 60 terminals and characters 59 to 87.

Taxon	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87
Helmholtzia acorifolia	1	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	2	0	1	0	2	0	0	1
Philydrum lanuginosum	1	2	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	1	2	2	0	0	1
Anigozanthos flavidus	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	1	0	2	0	1	0	0	0	0	0
Xiphidium caeruleum	0	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	0	1	0	1	0	2	0	1	0	0	0	0	0
Monochoria cyanea	0	1	1	0	0	0	0	2	2	0	2	0	1	1	1	1	1	1	0	0	1	2	1	0	0	2	1	0	1
Monochoria korsakovii	0	1	1	0	0	0	0	2	2	0	2	1	1	1	1	1	1	1	0	0	1	2	1	0	0	2	1	0	1
Monochoria hastata	0	1	1	0	0	0	0	2	2	0	2	1	1	1	1	1	1	1	0	0	1	2	1	0	0	2	1	0	1
Monochoria vaginalis	0	1	1	0	0	0	0	2	2	0	2	1	1	1	1	1	1	1	0	0	1	2	1	0	0	2	1	0	1
Eichhornia crassipes	0	1	1	0	1	0	0	1	2	0	1	0	0	0	1	1	1	1	0	1	1	2	0	1	0	2	1	1	1
Eichhornia crassipes2	0	1	1	0	1	0	0	1	2	0	1	0	0	0	1	1	1	1	0	1	1	2	0	1	0	2	1	1	1
Eichhornia diversifolia	0	1	1	0	1	0	0	1	2	0	1	0	0	0	1	1	1	1	0	1	0	2	0	1	0	2	1	0	1
Eichhornia azurea	0	1	1	0	1	0	0	1	2	0	1	0	0	0	1	1	1	1	0	1	0	2	0	1	0	2	1	0	1
Eichhornia heterosperma	0	1	1	0	0/3	0	0	1	2	0	1	0	0	0	1	1	1	1	0	1	0	2	0	1	0	2	1	0	1
Eichhornia paniculata	0	1	1	0	2	0	0	1	2	0	1	0	0	0	1	1	1	1	0	0	1	1	0	0	0	2	1	1	1
Eichhornia paradoxa	1	1	1	0	2	0	0	1	2	0	1	0	0	0	1	1	1	1	0	0	1	1	0	0	0	2	1	1	1
Pontederia cordata	0	1	1	0	2	0	0	1	2	0	1	0	0	0	1	1	1	1	2	1	1	2	1	1	1	0	1	1	1
Pontederia lancifolia	0	1	1	0	2	0	0	1	2	0	1	0	0	0	1	1	1	1	2	1	1	2	1	1	1	0	1	1	1
Pontederia rotundifolia	1	1	1	0	2	0	0	1	2	0	1	0	0	0	1	1	1	1	2	1	1	2	1	1	1	0	1	1	1

Pontederia ovalis	0	1	1	0	2	0	0	1	2	0	1	0	0	0	1	1	1	1	2	1	1	2	1	1	1	0	1	1	1
Pontederia sagittata	0	1	1	0	2	0	0	1	2	0	1	0	0	0	1	1	1	1	2	1	1	2	1	1	1	0	1	1	1
Heteranthera gardneri	0	2	0	0	0	1	1	1	0	0/1	1	0	1	0	1	1	1	1	1	0	1	0	0	0	2	1	0	1	2
Heteranthera rotundifolia	0	2	0	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1	0	0	1	1	0	0	3	2	0	0	2
Heteranthera limosa	0	2	0	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1	0	0	1	1	0	0	3	2	0	0	2
Heteranthera zosterifolia	1	2	1	0	0/3	1	1	1	0	1	1	0	1	0	1	1	1	1	1	0	1	0	0	0	2	1	0	1	2
Heteranthera seubertiana	1	2	1	0	3	1	1	1	0	1	1	0	1	0	1	1	1	1	1	0	1	0	0	0	2	1	0	1	2
Heteranthera oblongifolia	0	2	0	1	1	1	1	1	1	0	1	0	1	0	1	1	1	1	0	0	1	1	0	0	3	2	0	1	2
Heteranthera dubia	0	0	0	0	0	1	1	1	0	1	1	0	1	0	1	1	1	1	1	1	1	0	0	1	2	1	0	0	2

Continuation. Matrix with the 60 terminals and characters 88 to 96.

Taxon	88	89	90	91	92	93	94	95	96
Helmholtzia acorifolia	0	0	1	0	-	-	-	1	0
Philydrum lanuginosum	0	0	1	0	-	-	-	1	0
Anigozanthos flavidus	0	0	1	0	-	-	-	1	1
Xiphidium caeruleum	0	0	1	0	-	-	-	2	1
Monochoria cyanea	1	0	1	1	1	1	1	1	0
Monochoria korsakovii	1	0	1	1	1	1	1	1	0
Monochoria hastata	1	0	1	1	1	1	1	1	0
Monochoria vaginalis	1	0	1	1	1	1	1	1	0
Eichhornia crassipes	1	0	1	1	0	0	0	1	0
Eichhornia crassipes2	1	0	1	1	0	0	0	1	0
Eichhornia diversifolia	1	0	1	1	0	0	0	1	0
Eichhornia azurea	1	0	1	1	0	0	0	1	0
Eichhornia heterosperma	1	0	1	1	0	0	0	1	0
Eichhornia paniculata	1	0	1	1	1	1	1	1	0
Eichhornia paradoxa	1	0	1	1	1	1	1	1	0

Pontederia cordata	1	1	0	1	1	1	1	0	0
Pontederia lancifolia	1	1	0	1	1	1	1	0	0
Pontederia rotundifolia	1	1	0	1	1	1	1	0	0
Pontederia ovalis	1	1	0	1	1	1	1	0	0
Pontederia sagittata	1	1	0	1	1	1	1	0	0
Heteranthera gardneri	0	0	1	1	0	0	0	1	0
Heteranthera rotundifolia	0	0	1	1	0	0	0	1	0
Heteranthera limosa	0	0	1	1	0	0	0	1	0
Heteranthera zosterifolia	0	0	1	1	0	0	0	1	0
Heteranthera seubertiana	0	0	1	1	0	0	0	1	0
Heteranthera oblongifolia	0	0	1	1	0	0	0	1	0
Heteranthera dubia	0	0	1	1	0	0	0	1	0

CONSIDERAÇÕES FINAIS

O presente trabalho apresentou a mais bem sustentada e amostrada hipótese filogenética para Commelinales. Essa foi a primeira vez que uma hipótese baseada exclusivamente em dados morfológicos foi proposta, além de ser a primeira vez que uma hipótese com base na combinação de dados morfológicos e moleculares também foi proposta. Entretanto, a presente hipótese filogenética não é de maneira alguma final e maiores estudos e esforços filogenômicos e morfológicos serão necessários para esclarecer pontos ainda não completamente solucionados. Os dados moleculares disponíveis no GenBank para as cinco famílias de Commelinales, mais as novas sequências produzidas ainda se mostram insuficientes devido à grande quantidade de dados faltantes nos vários marcadores que foram investigados para apenas uma ou poucas famílias da ordem. Assim, ainda é necessário homogeneizar a amostragem de marcadores entre as cinco famílias para uma hipótese molecular ainda mias robusta e bem sustentada, principalmente em relação ao backbone de Commelinales, possa ser apresentada. Em relação aos dados morfológicos, a presente matriz contém 570 caracteres, que abrangeram dados macro- e micromorfológicos, citogenéticos e fitoquímicos. Apesar da enorme congruência entre o presente conjunto de dados morfológicos e os dados moleculares, incongruências ou baixa resolução interna foram observadas dentro de grupos específicos, tais como: Callisia Loefl., Gibasis Raf. e Tripogandra Raf. (Commelinaceae), Hanguanaceae, Anigozanthos Labill., Conostylis R.Br., Haemodorum Sm. e Tribonanthes Endl. (Haemodoraceae), e Philydraceae. Assim, a inclusão de novos caracteres é essencial para tentar solucionar esses problemas. Estudos anatômicos (tanto de órgãos vegetativos quando de reprodutivos), palinológicos, citogenéticos, fitoquímicos e de morfologia de frutos, sementes e plântulas se mostraram essenciais para aumentar a congruência entre os dados morfológicos e moleculares, além de auxiliar a refinar as hipóteses filogenéticas dentro doss grupos. Caracteres essenciais a serem estudados em Commelinales são: (1) arquitetura vascular caulinar; (2) ontogenia foliar, especialmente em Haemodoraceae, Philydraceae e Pontederiaceae para entender a reversão de folhas unifaciais para bifaciais na última família; (3) anatomia floral, focando na morfologia de células de tanino; (4) ontogenia floral para entendimento do surgimento da enantiostilia, com foco especial em Hanguanaceae; (5) anatomia de anteras, focando especialmente na morfologia do tapete; (6) anatomia do gineceu, focando na morfologia da placenta e (7) morfologia e distribuição de cristais de oxalato de cálcio em órgãos vegetativos e reprodutivos. Acredita-se que com esse refinamento será possível propor uma hipótese filogenética ainda mais robusta, que assim poderá ser datada e calibrada. Com base nessa filogenia datada e calibrada será possível investigar a história biogeográfica da ordem, além de permitir o desenvolvimento de um estudo de otimização de caracteres morfológicos e ecológicos chave.

Em reação às famílias de Commelinales, com as contribuições da presente tese, Pontederiaceae passa a se tornar a família mais bem compreendida da ordem. Pontederiaceae apresenta o maior número de hipóteses filogenéticas, com diferentes conjunto de dados mostrando grande congruência entre eles. Além disso, *Pontederia* L. já foi parcialmente revisado, com tratamentos taxonômicos disponíveis para *P.* subg. *Monochoria* e *P.* subg. *Pontederia*, bem como uma sinopse para todo o gênero. Já para *Heteranthera* Ruiz & Pav. s.str. há uma revisão taxonômica não-publicada, que está em processo de atualização para abranger a circunscrição atual do gênero e incluir outras novidades taxonômicas. Entretanto, estudos anatômicos, citogenéticos e fitoquímicos ainda são necessários para preencher as lacunas na matriz morfológica para a ordem. Finalmente, a família carece de uma filogenia datada e calibrada e, consequentemente, uma hipótese biogeográfica.

A segunda família mais bem estudada da ordem é Commelinaceae, com enorme número de trabalhos taxonômicos, anatômicos e citológicos publicados. Entretanto, devido ao seu tamanho, boa parte de seus gêneros ainda carece de revisão taxonômica, especialmente os maiores gêneros da família, tais como: *Aneilema* R.Br., *Commelina* L., *Cyanotis* D.Don, *Dichorisandra* J.C.Mikan, *Murdannia* Royle e *Tradescantia* L. emend M.Pell., além de gêneros com posicionamento filogenético crítico (e.g., *Cartonema* R.Br., *Dictyospermum* Wight, *Floscopa* Lour., *Palisota* Rchb. *ex* Endl., *Pollia* Thunb. e *Tinantia* Scheidw.). Também devido ao seu tamanho, trabalhos focando na anatomia vegetativa e reprodutiva, palinologia, citogenética, fitoquímica e morfologia de plântulas e sementes são necessários para amostrar gêneros e espécies não estudados e preencher as lacunas na matriz morfológica da ordem. Nessa tese foi apresentada a primeira filogenia datada e calibrada para Commelinaceae, juntamente com a primeira hipótese biogeográfica para a família.

Entretanto, uma amostragem mais completa, de grupos com grande diversidade de espécies e ampla distribuição, é necessária para refinar nossa hipótese biogeográfica. Além disso, também é preciso incluir no conjunto de dados moleculares os gêneros *Gibasoides* D.R.Hunt, *Matudanthus* D.R.Hunt e, especialmente, *Triceratella* Brenan para obtenção de uma hipótese consistente, uma vez que os dados deste último gênero serão decisivo para as análises biogeográficas.

Haemodoraceae recebeu bastante atenção nos últimos 40 anos. Entretanto, boa parte de seus gêneros carecem de revisões taxonômicas, uma vez que os dados disponíveis aparecem apenas em tratamentos florísticos. Por melhores que sejam essas floras, grupos grandes e complicados como Anigozanthos, Conostylis e Haemodorum necessitam de uma revisão taxonômica completa e detalhada. Além disso, gêneros pequenos, tais como: Dilatris P.J.Bergius, Paradilatris (Hopper ex J.C.Manning) Hopper et al., Phlebocarya R.Br., Wachendorfia Burm. e Xiphidium Aubl. necessitam de revisões taxonômicas para que saibamos ao certo quantas espécies os compõem. A família como um todo é bem entendida do ponto de vista filogenético, anatômico, citológico e palinológico. Entretanto, vários caracteres anatômicos incluídos na matriz morfológica apresentada no presente estudo da ordem foram investigados para poucos grupos (e.g., morfologia de estigmas e suas papilas) ou apenas superficialmente investigados (e.g., morfologia de tricomas). Uma nova hipótese filogenética para Haemodoraceae está em fase final de elaboração e este trabalho apresentará uma filogenia datada e calibrada, além de uma primeira hipótese biogeográfica para a família, bem como amostrará todos os gêneros aceitos.

Philydraceae é a menor família da ordem, com quatro gêneros e oito espécies. Durante a elaboração desta tese foi necessário reestabelecer o gênero *Orthothylax* (Hook.f.) Skottsb., além de reconhecer uma segunda espécie de *Philydrum* Banks & Sol. ex Gaertn., bom como uma terceira espécie de *Philydrella* Caruel. A família apresenta um número relativamente grande de trabalhos investigando diferentes aspectos de sua biologia, como taxonomia, anatomia, palinologia, morfologia de plântulas e sementes, e citogenética. Entretanto, o grupo carece de um tratamento taxonômico moderno, que foi iniciado durante o desenvolvimento dessa tese e que será concluído e publicado posteriormente, além de estudos fitoquímicos e de alguns aspectos anatômicos. Esses caracteres são necessários para resolver as incongruências entre a morfologia e os dados moleculares disponíveis atualmente. Além disso, é

necessário amostrar molecularmente todas as espécies de Philydraceae, para que se possa propor uma hipótese filogenética robusta e conclusiva.

Hanguanaceae é, ainda, a família menos estudada e compreendida de Commelinales, apesar das inúmeras contribuições para a taxonomia do grupo nos últimos anos. Inúmeras espécies ainda precisam ser descritas, permitindo com isso o avanço dos estudos taxonômicos na família, além de estudos em outras áreas. Estudos fitoquímicos são esparsos em Hanguanaceae e pouco conclusivos devido aos problemas taxonômicos no grupo. Estudos anatômicos, palinológicos, citogenéticos e filogenéticos são pontuais ou inexistentes, geralmente amostrando apenas uma única espécie que muitas vezes não está nem identificada ao nível de espécie. Hanguanaceae é bastante peculiar morfologicamente e necessita de estudo detalhados sobre sua macromorfologia, anatomia vegetativa e reprodutiva, palinologia, citogenética, morfologia de plântulas e sementes, ontogenia floral, e biologia reprodutiva. Esses estudos são essenciais para a taxonomia do grupo em si, mas também para viabilizar o melhor entendimento da ordem Commelinales e de sua relação com Commelinaceae.

Finalmente, a presente tese representou uma contribuição significativa para os estudos em Commelinales, mas está longe de ser final. Os resultados aqui apresentados responderam algumas perguntas sobre o grupo, mas levantaram um número ainda maior de questionamentos. Assim, esta tese foi um pontapé inicial em uma longa série de estudos colaborativos e interdisciplinares em desenvolvimento sobre a ordem Commelinales.

ANEXO

The identity and application of *Coletia madida* and notes on the typification of Mayacaceae

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The identity and application of *Coletia madida* and notes on the typification of Mayacaceae

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Abstract A great deal of doubt surrounds the name *Coletia madida* concerning its identity, application and relation to *Mayaca sellowiana*. In order to better understand this issue we analyzed Vellozo's original description and plate, as well as the original description for *M. sellowiana*. We conclude that *C. madida* is a synonym of *M. fluviatilis* and that *M. sellowiana* is the older name for the species with one-flowered inflorescences and anthers that are dehiscent through an apical tube. Also, we designate a lectotype and an epitype for *C. madida* and comment on the typification of *M. fluviatilis* (the type of the family).

Keywords aquatic plants; bog-moss; Commelinaceae; Flora Fluminensis; Neotropical flora; Poales

■ INTRODUCTION

Mayacaceae is a small monogeneric family of Monocots, composed of five species; four of which are restricted to the Neotropics and a single species endemic to Africa (Lourteig, 1952; Carvalho & al., 2009; Carvalho & Machado, 2015). All four Neotropical species can be found throughout Brazil in damp or aquatic environments (Monteiro & Carvalho, 2014). The family was described by Kunth (1842), based on Mayaca fluviatilis Aubl. Before the description of Mayacaceae, and even for nearly a century afterwards, Mayaca Aubl. and its synonyms (i.e., Biaslia Vand., Coletia Vell. and Syena Schreb.), were commonly treated within the families Commelinaceae (e.g., Vandelli, 1788; Schreber, 1789; Roemer, 1796; Vellozo, 1831; Schott & Endlicher, 1832; Hutchinson, 1934) or Xyridaceae (e.g., Endlicher, 1840; Grisebach, 1866; Van Tieghem, 1898). Nonetheless modern authors unambiguously have treated Mayacaceae as a distinct family within Poales (Pichon, 1946; Lourteig, 1952; APG, 2009; Carvalho & al., 2009; Carvalho & Machado, 2015). However, its exact position in the order still remains unresolved, being recovered either as sister to the remaining families of the Cyperid clade (Stevens, 2001–; APG, 2009; Chase & al., 2000, 2006; Christin, & al., 2008), or as a member of the Xyrid clade (Stevenson & Loconte, 1995; Bremer, 2002; APG, 2003; Givnish & al., 2004, 2010; Linder & Rudall, 2005; Soltis & al., 2005; Bouchenak-Khelladi & al., 2014).

In the last revision of Mayacaceae, Lourteig (1952) pointed out the importance of inflorescence and androecium morphology in the delimitation of species within the family.

That author gave important information on most names and solved some of the existing taxonomic confusion. Nevertheless, an account of *Coletia madida* Vell. was only given 15 years later by Stellfeld (1967), with the proposal of a new combination: *Mayaca madida* (Vell.) Stellfeld. Subsequently Lourteig (1968) proposed the conservation of *M. sellowiana* Kunth over *M. madida*, which was rejected by the Committee of Spermatophyta. Nevertheless, since no formal report of this decision was published, it is not possible to clearly understand the reasons which led the committee to reject Lourteig's proposal. After the rejection of this proposal, no other account on the issue was made. Recent publications and modern indexes of plant names have accepted one name or the other depending on the author's interpretation (Carvalho & Machado, 2015).

The monumental *Flora Fluminensis* (Vellozo, 1829) was the first compilation of names for Brazilian plants, written and edited by a Brazilian researcher. It is composed of descriptions and illustrations of 1640 plants, arranged in one volume of descriptions and 11 volumes of plates (Borgmeier, 1961; Carauta, 1973; Cervi & Rodrigues, 2010). Each species listed by Vellozo (1829) possesses a generally brief diagnosis, accompanied by a reference to the original illustration, held in the Biblioteca Nacional do Rio de Janeiro. As was mentioned above, Vellozo described a new genus and species of Commelinaceae, which is now known to be a member of Mayacaceae. During the revision of the names of Commelinaceae published in *Flora Fluminensis* (Pellegrini & al., 2015; Pellegrini & Forzza, in press), new data regarding the identity and application of *Coletia madida* arose and led to the present contribution.

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Typification of Vellozo's names. — Despite many attempts by different botanists over many years, material has neither been found nor is there information known about the current whereabouts of any of Vellozo's specimens (e.g., Lima, 1995; Pastore, 2013). Due to the lack of vouchers, the original illustrations are usually the best option that botanists have for reviewing the taxa described by Vellozo (Carauta, 1969; Mello Filho, 1975; Cervi & Rodrigues, 2010; Buzatto & al., 2013; Pastore, 2013; Knapp & al., 2015; Pellegrini, 2015; Pellegrini & al., 2015). These illustrations are sometimes incomplete or inaccurate for many different plant groups (Lima, 1995; Buzatto & al., 2013; Pastore, 2013; Knapp & al., 2015). Nevertheless, the illustrations of Commelinales species presented by Vellozo (1831) are in general accurate, with few being considered inaccurate (Pellegrini, 2015; Pellegrini & al., 2015; Pellegrini & Forzza, in prep.). Since none of Vellozo's original specimens have been located, and in accordance with the requirements of the Code (McNeill & al., 2012: Art. 9.3), the original illustrations, although only published later in 1831, are considered part of that author's original material.

■ NOMENCLATURE AND TAXONOMY

Mayaca fluviatilis Aubl., Hist. Pl. Guiane 1: 42. 1775 – Lectotype (designated by Lanjouw & Uittien in Recueil Trav. Bot. Néerl. 37: 153. 1940): FRENCH GUIANA. Cayenne, ad ripam & in aquâ rivuli defluentis ad fluvium Sinémari, s.d. [Nov 1762], fl., fr., J.B.C.F. Aublet s.n. (P-JJR 1: 51!; isolectotypes: BM barcode BM001191236!, LINN-SM-XVIII.13 n.v.).

= Coletia madida Vell., Fl. Flumin.: 32. 1829 ≡ Mayaca madida (Vell.) Stellfeld in Tribuna Farm. (Curitiba) 35: 2. 1967, syn. nov. – Lectotype (designated here): [illustration] Original parchment plate of Flora Fluminensis in the Manuscript Section of the Biblioteca Nacional do Rio de Janeiro [mss1095062_083] and later published in Vellozo, Fl. Flumin. Icon. 1: t. 79. 1831 (published plate designated as lectotype by Kunth, Enum. Pl. 4: 32. 1843) – Epitype (designated here): BRAZIL. Rio de Janeiro. Duas Barras, Monnerat, Fazenda da Cachoeira, fl., fr., 21 Feb 1925, M.C. Vaughan Bandeira s.n. (RB No. 18993!). — For images of the lectotype, see Fig. 1A & B; for a field photo, see Fig. 1C; for a photo of herbarium material, see Fig. 1D.

■ TYPIFICATION OF COLETIA MADIDA Vell.

The relationship between *Coletia madida* and *Mayaca sellowiana* began with the description of the latter, in which Kunth (1843) mentioned *C. madida* as a possible synonym of his newly described species by writing "*Coletia madida* Vell. *Flora Flumin*. 1 t. 79?". According to the principle of priority (McNeill & al., 2012: Art. 11.1), *C. madida* should have priority over the widely used *M. sellowiana*, and is treated as the accepted name by many modern indexes of plant names (e.g., eMonocot, 2010; The Plant List, 2015; Tropicos, 2015). For the

same reason, Stellfeld (1967) proposed the new combination *M. madida* in order to accommodate this name in the correct genus. Nevertheless, Lourteig (1968) argued that the poor description provided by Vellozo (1829) for *C. madida* made it impossible for this name to be properly linked to any species of *Mayaca*. This was largely based on the lack of details of androecium morphology in the description, which neither stated the dehiscence type nor the presence or absence of an apical tube. That author also argued that the staminal proportion described by Vellozo linked *C. madida* to two species listed for Brazil, but made no mention of which species those were. As a result of these arguments Lourteig (1968) proposed the rejection of *C. madida* and the conservation of *M. sellowiana*.

While Lourteig (1968) concluded that Coletia madida could not be assigned to a single species of Mayaca, our examination of the protologue and comparison to other species led us to conclude otherwise. The plant illustrated by Vellozo clearly has one-flowered inflorescences, which makes it impossible for it to represent M. longipes Seub., which together with M. baumii Gürke, are the only two species in the family with flowers arranged into many-flowered inflorescences (Lourteig, 1952). The remaining three species have one-flowered inflorescences, and can be differentiated from each other exclusively by androecium morphology. Mayaca fluviatilis and M. kunthii Seub., in particular, are morphologically very similar and can be only differentiated by their sporangia disposition, anther shape and ornamentation of the anther pores (Lourteig, 1952; Carvalho & al., 2009). These morphological differences would hardly have been noticed by Vellozo's illustrator in the early decades of the 19th century. Importantly, Vellozo's work is known to have been based on plants growing in the state of Rio de Janeiro (Lima, 1995) and only two species of Mayaca are known to occur in that region: M. fluviatilis and M. sellowiana (BFG, 2015). Since M. kunthii does not occur in Rio de Janeiro, it is very unlikely to be conspecific with Coletia madida.

After thoroughly analyzing the plate and description from the protologue of Coletia madida, we noticed that the stamens illustrated by Vellozo match closely in shape those of M. fluviatilis and not M. sellowiana. The difference in anther shape is mainly due to the difference in sporangia position in both species, where M. fluviatilis possesses late bi-sporangiate anthers due to fusion of the vertically arranged microsporangia; while M. sellowiana is clearly tetra-sporangiate with microsporangia arranged in pairs (Carvalho & al., 2009). Furthermore, the anthers depicted by Vellozo (1831: t. 79) (Fig. 1A, B) do not possess an apical tube, which is characteristic of M. sellowiana and is perceptible to the naked eye without a hand lens (Fig. 1E, F). The apical tube in M. sellowiana is generally $\frac{1}{3}$ to ½ the length of the anther sacs and lighter than the anther sacs, with a mild constriction at its base—and is easily seen in herbarium material, where the tube becomes light yellow and the anther sacs become dark yellow to ochre when dried (Fig. 1E, F). Since Vellozo's plates were mostly prepared based on pressed-dry specimens (H.C. de Lima, pers. comm.), the apical tubes would have been evident and would hardly have been missed by Vellozo's illustration artist. Furthermore, the proportion between the ovary and the anthers is congruent

with that of *M. fluviatilis*. Indeed, in that species the anthers are smaller to approximately the same size as the ovary (Fig. 1B, C), whereas in *M. sellowiana* the anthers are much larger than the ovary (Fig. E, F).

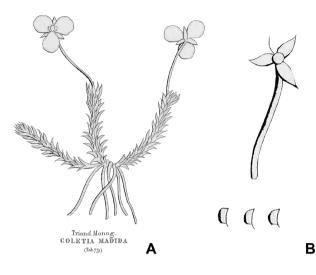
Given the single-flowered inflorescences, details of the anthers, and the congruence in geographic distribution, we assert that *Coletia madida* (\equiv *Mayaca madida*) is conspecific with *M. fluviatilis*. Thus we treat *C. madida* as a junior synonym of *M. fluviatilis* here. The result of this treatment is that *M. sellowiana* is the older and accepted name for the species with one-flowered inflorescences and anthers that are dehiscent through an apical tube. Furthermore, since Vellozo's plate has been the subject of considerable misinterpretation (Lourteig, 1952, 1968; Stellfeld, 1967; Carvalho & Machado, 2015), and in accordance to the *Code* (McNeill & al., 2012: Art. 9.8), we herein designate an epitype in order to avoid future confusions and to fix the application of this name.

■ TYPIFICATION OF MAYACA FLUVIATILIS Aubl.

When describing the monospecific Mayaca, Aublet (1775a) presented a diagnosis for his new species M. fluviatilis, together with some ecological comments, details of the locality in which this species was collected, and an illustration (1775b: pl. 15). The author made no direct reference to any specimen. Nevertheless, Aublet (1775a: 44) stated: "I found this plant on the banks of a stream that flows into the river Sinémari; it was in flower and fruit in the month of November" [trans. by the authors]. Thus, making clear that the original specimens were collections made by Aublet himself, and not by Martin, as previously asserted by Lourteig (1952: 239). In fact, the lectotypes for many of Aublet's names have been already correctly designated (i.e., Lanjouw & Uittien, 1940), as is the case of M. fluviatilis. Nevertheless, since this publication is of difficult access and thus, poorly known, many unnecessary and incorrect typifications have been made by later authors unaware of the earlier typifications introduced in 1940 (Delprete, 2015). Thus, the specimens at BM and LINN-SM are here treated as isolectotypes, since their labels match the one of the lectotype and they are also very similar to the original illustration presented by Aublet (1775b: pl. 15).

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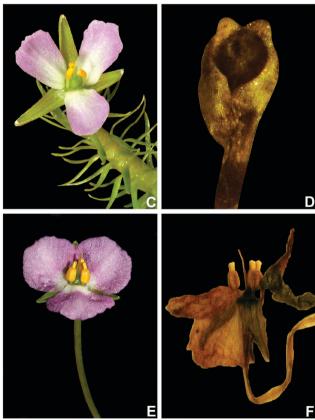


Fig. 1. Mayacaceae *fluminensis.* **A–B,** Original plate of Vellozo's *Coletia madida*: **A,** line drawings of habit; **B,** line drawings of androecium and gynoecium; **C–D,** *Mayaca fluviatilis*: **C,** detail of the flower, showing the stamens without apical tubes; **D,** detail of an anther from a herbarium specimen, showing the ornamentation of the pore; **E–F,** *Mayaca sellowiana*: **E,** detail of the flower, showing the stamens with an evident apical tube; **F,** detail of the flower from a herbarium specimen, showing the lighter apical tubes and darker anther sacs. — Photo of the *Coletia madida* plate modified from the Biodiversity Heritage Library; C by M. Blanco; D–F by M.O.O. Pellegrini.

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