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LOPES DE OLIVEIRA

FILOGENIA, MORFOLOGIA
E TAXONOMIA DE
DIPHYOMENE (RUHLAND) TROVÓ

SISTEMÁTICA DE PAEPALANTHOIDEAE

(ERIOCAULACEAE)

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Sistemática de Paepalanthoideae (Eriocaulaceae): Filogenia, morfologia e taxonomia de *Diphyomene* (Ruhland) Trovó

Systematics of Paepalanthoideae (Eriocaulaceae): Phylogeny, morphology, and taxonomy of *Diphyomene* (Ruhland) Trovó

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Prof. Dr. Paulo Takeo Sano
Presidente - Orientador

Ao amigo **Diogo Coutinho** (Jason),
com carinho e saudades, dedico.

"Marco Polo descreve uma ponte, pedra por pedra.

- Mas qual é a pedra que sustenta a Ponte? Pergunta Kublai Khan.

- A ponte não é sustentada por esta ou aquela pedra – responde Marco –, mas pela curva do arco que estas formam.

Kublai Khan permanece em silêncio, refletindo. Depois acrescenta:

- Por que falar das pedras? Só o arco me interessa.

Polo responde:

Sem pedras o arco não existe."

-*Italo Calvino*, As cidades invisíveis, p. 79

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RESUMO

Trovó, M.L.O. Sistemática de Paepalanthoideae (Eriocaulaceae): Filogenia, morfologia e taxonomia de *Diphyomene* (Ruhland) Trovó.

Esta tese compreende estudos sobre a filogenia de Paepalanthoideae com ênfase em *Paepalanthus*, trazendo também estudos morfológicos, nomenclaturais e taxonômicos em *Paepalanthus* sect. *Diphyomene*. O capítulo I apresenta a filogenia de Paepalanthoideae com base em dados morfológicos e moleculares (nrITS e *trn*L-*trn*F). A monofilia de *Rondonanthus*, como grupo-irmão das demais Paepalanthoideae é confirmada, assim como a monofilia de *Leiothrix* e *Actinocephalus*. *Syngonanthus* emerge parafilético e *Paepalanthus* e *Blastocaulon*, polifiléticos. No entanto, muitas categorias infragenéricas de *Paepalanthus* emergem monofiléticas. A proposição de alguns novos gêneros, assim como estudos filogenéticos complementares é indispensável para aproximar a classificação de Paepalanthoideae de um sistema natural. O capítulo II descreve as inflorescências e o eixo reprodutivo de *Paepalanthus* sect. *Diphyomene* do ponto de vista tipológico e anatômico. Dois padrões são detectados: em *P. erectifolius*, *P. giganteus* e *P. polycladus* a inflorescência é um tribótrio com dibótrio terminal, unidade básica terminal e ferofilos envolvendo os dibótrios; em *P. flaccidus* a inflorescência é um pleiobótrio com subunidade terminal e ferofilos ausentes. Estes resultados reforçam que o grupo é constituído de duas linhagens independentes, sendo que o padrão referido para as três primeiras espécies é único na família. O capítulo III traz a proposição do status genérico para as espécies de *Paepalanthus* sect. *Diphyomene* que emergem monofiléticas no capítulo I e apresentam estrutura da inflorescência única na família no capítulo II. São propostas 10 novas combinações, 18 novos sinônimos, 6 lectotipificações, 2 novos status, 1 neotipificação e 1 epitipificação. No capítulo IV é apresentada a revisão de *Diphyomene*, gênero que compreende 18 espécies distribuídas na América do Sul, principalmente no bioma Cerrado. A revisão consiste na descrição detalhada da morfologia do gênero e de uma chave de identificação, além de descrição, ilustrações, mapas de distribuição e comentários para cada espécie. Os anexos 1 e 2 trazem a descrição de oito espécies novas de *Diphyomene* ocorrentes no Brasil.

Palavras chave: Paepalanthoideae, Eriocaulaceae, Sistemática, Filogenia, Morfologia, *Diphyomene*

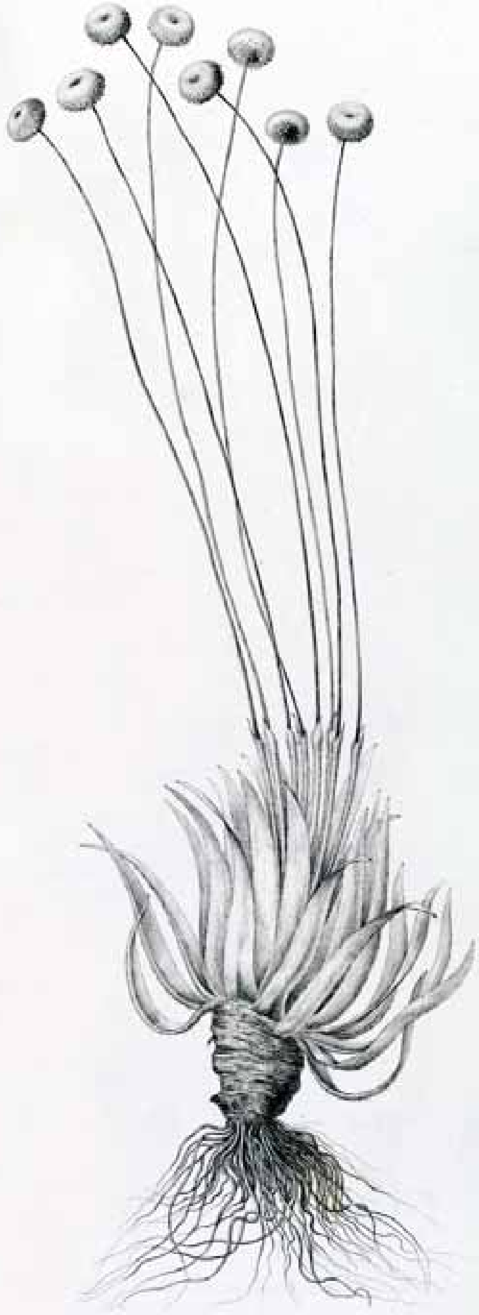
ABSTRACT

Trovó, M.L.O. Systematics of Paepalanthoideae (Eriocaulaceae): Phylogeny, morphology, and taxonomy of *Diphyomene* (Ruhland) Trovó.

This thesis consists of a phylogenetic study involving Paepalanthoideae, and a morphological, nomenclatural, and taxonomic survey of *Paepalanthus* sect. *Diphyomene*. Chapter I is a phylogenetic study of Paepalanthoideae based on morphological and molecular data (nrITS and *trn*L-*trn*L). The monophyly of *Rondonanthus*, as a sister group of the remaining Paepalanthoideae, is confirmed, as is the monophyly of *Leiothrix* and *Actinocephalus*. *Syngonanthus* emerges paraphyletic with the current acceptance of *Philodice*, whereas *Paepalanthus* and *Blastocaulon* emerge polyphyletic. However, many infra-generic categories of *Paepalanthus* emerge as monophyletic groups. The proposal of new genera, as well as complementary phylogenetic studies, is required to achieve a natural classification of Paepalanthoideae. In chapter II, we describe the inflorescence and reproductive axis of *Paepalanthus* sect. *Diphyomene*, when using typology and anatomy. Two patterns were found. In *P. erectifolius*, *P. giganteus* and *P. polycladus* the structure is a tribotryum, with a terminal dibotryum, and pherophylls bearing lateral dibotrya. In *P. flaccidus*, the inflorescence is a pleiobotryum, with a terminal subunit, and without pherophylls. These results confirm that the group consists of two independent lineages, and that the pattern described for the first three species is unique within the family. Chapter III consists of a proposal of generic status for species of *Paepalanthus* sect. *Diphyomene*, which emerge monophyletic in chapter I, and possess a unique inflorescence structure as described in chapter II. We propose 10 new combinations, 18 new synonyms, six lectotypifications, two new stati, one neotypification, and one epitypification. In chapter IV we present the taxonomic revision of *Diphyomene*, a genus with 18 species distributed throughout South America, mostly in the Brazilian Cerrado. The revision consists of a detailed description and comments on the genus, besides an identification key. Descriptions, illustrations, distribution maps and comments on each species are also given. Eight new Brazilian species of *Diphyomene* are described in appendix 1 and 2.

Key words: Paepalanthoideae, Eriocaulaceae, Systematics, Phylogeny, Morphology, *Diphyomene*

INTRODUÇÃO GERAL



PAEPALANTHUS (Eupaepalanthus) Klotzschianus.

Introdução Geral

Eriocaulaceae Martinov compreende cerca de 1200 espécies distribuídas em 12 gêneros. É distinta das demais monocotiledôneas por possuir flores diclinas reunidas em densos capítulos. Exceto por *Eriocaulon* L. e *Mesanthemum* Koern., que ocorrem respectivamente na em toda a região tropical e no sudeste africano, a diversidade da família encontra-se na região neotropical. O principal centro de diversidade é a Cadeia do Espinhaço, sobretudo no estado de Minas Gerais (Giulietti & Hensold 1990; Stützel 1998; Sano 2004; Parra & al. no prelo). Um segundo centro de diversidade é a região dos Tepuis da Venezuela, Guiana e norte do Brasil (Hensold 1991; 1999). Nestas áreas, o principal habitat ocupado por estas espécies são os campos rupestres quartzíticos, ocorrendo também em outras formações abertas do Cerrado. A maioria das espécies (ca. 95%) possui distribuição bastante restrita, muitas vezes limitada a apenas uma localidade ou mesmo a uma serra (Giulietti & al. 2005; Costa & al. 2008). Consequentemente, Eriocaulaceae é uma das famílias mais citadas nas listas vermelhas de espécies ameaçadas de extinção, sendo 94 espécies presentes na lista de Minas Gerias, e 20 espécies presentes na lista do Brasil (Biodiversitas 2008).

A família é tradicionalmente dividida em duas subfamílias: Eriocauloideae Ruhland e Paepalanthoideae Ruhland. A primeira compreende os gêneros *Eriocaulon* e *Mesanthemum*, e é caracterizada por possuir flores diplostêmones e pétalas com glândulas. Paepalanthoideae compreende 10 gêneros e cerca de 900 espécies, sendo definida por possuir flores isostêmones e pétalas sem glândulas (Koernicke 1863; Ruhland 1903). A definição dos gêneros nesta subfamília, exceto por *Actinocephalus* (Koern.) Sano, é baseada em poucas características florais, em especial da flor pistilada. A grande diversidade taxonômica e morfológica de Paepalanthoideae concentra-se em dois gêneros: *Paepalanthus* Mart., com cerca de 400 espécies e *Syngonanthus* Ruhland, com cerca de 150 espécies (Giulietti & Hensold 1990). Nesses dois gêneros estão também a maioria das espécies de importância econômica na família. Muitas dessas espécies são utilizadas na confecção de artesanatos de sempre-vivas, sendo a principal fonte de renda de comunidades artesãs (Giulietti & al. 1988; Schmidt & al. 2007; Costa & al. 2008).

Tonina Aubl., o gênero mais antigo incluído em Paepalanthoideae, foi descrito por Aublet (1775); sendo que, o primeiro grande marco na sistemática da subfamília é a obra de Bongard (1831). Nela, Bongard (1831) trabalha com 80 espécies brasileiras de *Eriocaulon*, com base em materiais coletados por Ludwig Riedel e depositados no herbário LE. Dentre essas espécies, 72 eram novas para ciência e atualmente apenas 4 ainda encontram-se incluídas *Eriocaulon*. Isso porque Koernicke (1863) realizou a segunda grande revisão das Eriocaulaceae brasileiras na *Flora brasiliensis*. Koernicke (1863) foi o primeiro a ir a fundo na divisão infra-familiar, propondo a divisão de Eriocaulaceae em duas tribos, que hoje correspondem às duas subfamílias já citadas. Koernicke (1863) também descreveu inúmeras categorias infragenéricas de *Paepalanthus*, além de dezenas de espécies novas. A última revisão mundial da família foi realizada por Ruhland (1903). Baseado na obra de Koernicke (1863), Ruhland (1903) propôs a divisão de Eriocaulaceae em duas subfamílias, descreveu novos gêneros e confeccionou chaves de identificação. Dessa forma, seu sistema de classificação é utilizado até hoje.

Durante o século XX, os trabalhos taxonômicos em Eriocaulaceae concentraram-se na descrição de novos táxons. A maioria das espécies novas foi descrita por dois autores. Álvaro Astolpho da Silveira publicou cerca de 180 espécies com base em materiais hoje depositados no herbário R, e naquela época, parte de sua coleção particular. Tais descrições estão concentradas em duas obras: Silveira (1908) e Silveira (1928). Deve-se ressaltar que nenhuma chave de identificação para as espécies foi apresentada em suas obras. O outro autor, Harold Norman Moldenke publicou mais de uma centena de táxons específicos e infra-específicos. Estas descrições encontram-se dispersas em dezenas de publicações entre as décadas de 1940 e 1970. Apesar das inúmeras descrições, a classificação no nível dos gêneros foi pouco alterada desde a obra de Ruhland (1903). Dos seis gêneros publicados, apenas três ainda são válidos: *Actinocephalus* (Koern.) Sano, *Rondonanthus* Herzog e *Comanthera* L.B. Smith. *Moldenkeanthus* Morat é sinônimo de *Paepalanthus* (Stützel, 1987), *Wurdackia* Moldenke é sinônimo de *Rondonanthus* (Hensold & Giulietti 1991) e *Carptotepala* Moldenke é sinônimo de *Comanthera* (Parra & al. no prelo).

Além dos esforços florísticos, no final do século passado iniciou-se uma série de estudos de revisão taxonômica de gêneros ou categorias infra-genéricas em Eriocaulaceae. Giulietti (1987) revisou as 51 espécies de *Leiothrix* Ruhland, distribuídas na América do Sul. Hensold (1988) revisou a taxonomia e a morfologia das 27 espécies de *Paepalanthus* subgen. *Xeractis* Koern., todas restritas à porção mineira da Cadeia do Espinhaço. Hensold & Giulietti (1991) revisaram e redefiniram as seis espécies de *Rondonanthus* que ocorrem no norte da América do Sul. Hensold (1991) revisou as espécies venezuelanas de Eriocaulaceae, descrevendo um novo subgênero de *Paepalanthus*. Tissot-Squalli (1998) revisou as 46 espécies de *Paepalanthus* subgen. *Platycaulon* Koern. distribuídas na América do Sul e na América Central. Sano (1999, 2004) e Costa (2005) redefiniram e revisaram as 47 espécies de *Actinocephalus*, todas ocorrentes no Brasil. Parra (2000) revisou as espécies de *Syngonanthus* sect. *Eulepis* (Bong. ex Koern.) Ruhland, distribuídas no Brasil e hoje pertencentes a *Comanthera* subgen. *Eulepis* (Bong.) Parra & Giul.

Paralelamente, estudos detalhados sobre a morfologia e a anatomia de Eriocaulaceae começaram a ser desenvolvidos. Stützel & Weberling (1982) e Stützel (1984) descreveram os padrões básicos de inflorescência em Eriocaulaceae. Oriani & al. (2008) descreveram os padrões de arquitetura morfológica e anatômica das espécies de *Actinocephalus*, fundamentados principalmente em características das inflorescências. Scatena & al. (2005) sumarizaram e relacionaram com a taxonomia todo o conhecimento sobre a anatomia de Eriocaulaceae. Estudos sobre a morfologia e anatomia floral na família são mais restritos. Stützel (1985) descreveu o desenvolvimento das anteras em *Blastocaulon*, apontando o seu papel incipiente na segregação deste gênero de *Paepalanthus*. Stützel & Gansser (1995) discutem o desenvolvimento das flores das Eriocaulaceae da América do Norte e suas implicações taxonômicas. Recentemente, Rosa & Scatena (2007) estudaram a anatomia floral em Paepalanthoideae, definindo parte das homologias das peças florais, em especial da flor pistilada.

Os estudos filogenéticos em Eriocaulaceae tiveram inicio no final do século XX, com a primeira filogenia morfológica da família e do gênero *Leiothrix* publicada por Giulietti & al. (1995). Giulietti & al. (2000) expandiram a filogenia anterior, utilizando-se de dados morfológicos, anatômicos e fitoquímicos, mas ainda tratando os terminais em categorias supra-específicas. Com o advento dos dados moleculares, Unwin (2004) realizou a primeira filogenia molecular da família tratando os terminais no nível específico. As principais conclusões deste trabalho (Unwin 2004) foram o monofiletismo das duas subfamílias, assim como dos gêneros *Actinocephalus*, *Lachnocaulon* Kunth e *Leiothrix*, além da indefinição sobre o parafiletismo de *Syngonanthus* Ruhland e o polifiletismo de *Paepalanthus*. Andrade (no prelo) prosseguiu com os estudos moleculares, tratando a família como um todo. Os grandes avanços deste trabalho (Andrade & al. no prelo) foram a obtenção de protocolos para marcadores mais variáveis, tais como o nrITS e trnL-trnF, o que possibilitou uma maior resolução das árvores. O aumento de resolução dos clados permitiu novas interpretações taxonômicas, como a necessidade de sinonimizar *Blastocaulon* Ruhland em *Paepalanthus* e de restabelecer *Comanthera* para abrigar parte das espécies de *Syngonanthus*. No entanto, assim como nos trabalhos anteriores *Paepalanthus* emerge polifilético, com relações ainda bastante obscuras.

Neste contexto encontra-se esta tese de doutorado. O capítulo I dá prosseguimento aos estudos filogenéticos em Eriocaulaceae, tendo como foco a subfamília *Paepalanthoideae*, em especial o gênero *Paepalanthus*. É apresentada, pela primeira vez uma, matriz morfológica em nível específico combinada aos dados moleculares. O capítulo II procura elucidar, do ponto de vista morfológico e anatômico, as inflorescências de *Paepalanthus* sect. *Diphyomene* Ruhland, bem como suas implicações na taxonomia e filogenia do grupo. O capítulo III apresenta a proposição do *status* genérico para parte das espécies de *P.* sect. *Diphyomene*, sintetizando conclusões dos capítulos I e II. Por fim, o capítulo IV é constituído da revisão taxonômica das espécies de *Diphyomene*. Nos anexos I e II encontram-se a descrição de oito novas espécies de *Diphyomene* ocorrentes no domínio do Cerrado.

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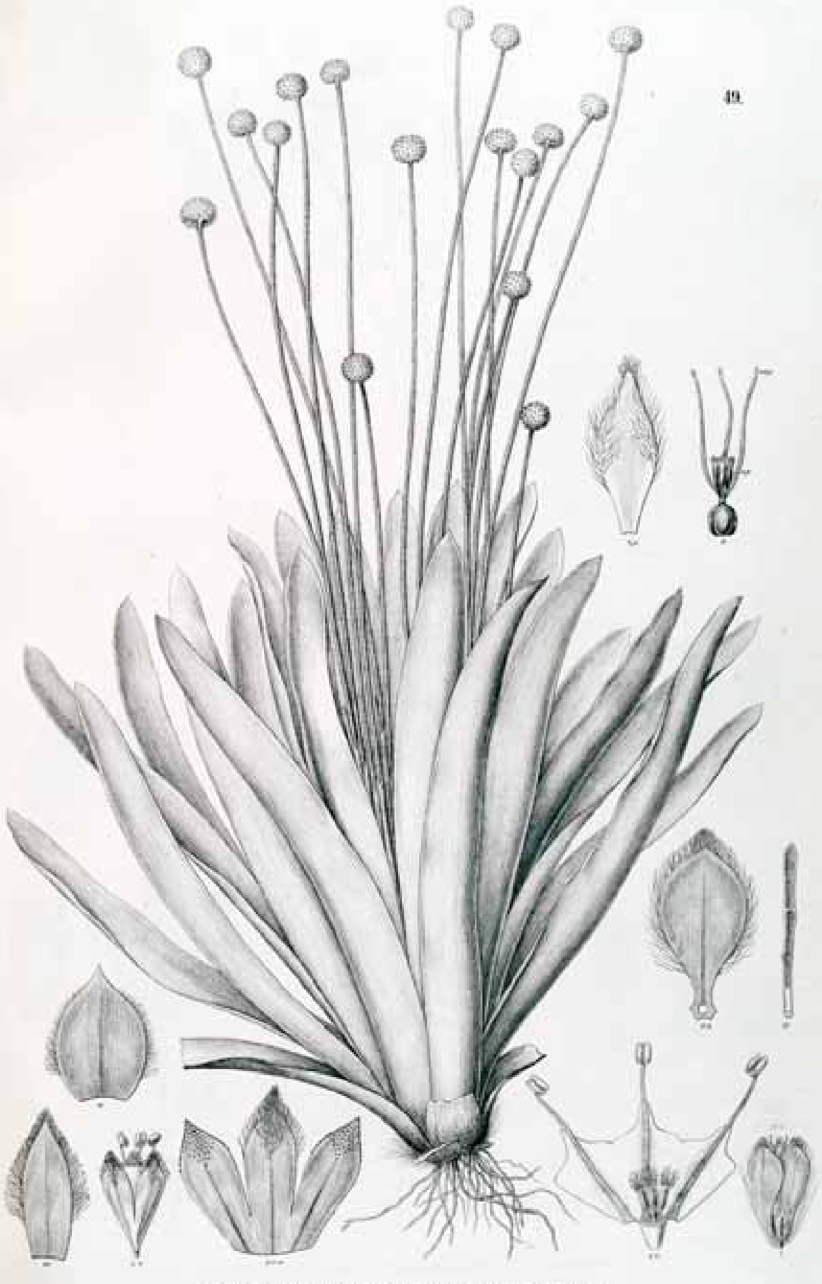
CAPÍTULO I

Filogenia molecular e morfológica de Paepalanthoideae com ênfase em *Paepalanthus* Mart. (Eriocaulaceae)



PAEPALANTHUS (Eupaepalanthus) Regelianus.

Resumo - Paepalanthoideae (Eriocaulaceae) compreende a diversidade genérica e a as espécies de importância econômica na família. É também a subfamília que possui mais problemas taxonômicos, especialmente devido a *Paepalanthus*. Este trabalho tem por objetivo inferir a filogenia de Paepalanthoideae, avaliando a consistência de caracteres morfológicos na classificação, assim servindo de base para estudos de biogeografia, conservação e taxonomia. A amostragem é composta de 94 espécies, correspondendo a todos os gêneros e grupos externos. Uma matriz morfológica e duas matrizes moleculares (nrITS e plastid *trnL-trnF*) foram analisadas por métodos de parcimônia e inferência Bayesiana. As árvores resultantes são bem resolvidas, os clados são pouco sensíveis aos diferentes regimes de custo além de bem sustentados. A monofilia de *Rondonanthus* como grupo-irmão das demais Paepalanthoideae é confirmada. *Leiothrix* e *Actinocephalus* emergem como grupos monofiléticos, *Syngonanthus* emerge parafilético em relação a *Philodice*, enquanto *Blastocaulon* emerge polifilético. Quatro subgêneros de *Paepalanthus* emergem monofiléticos, porém *P.* subgen. *Paepalocephalus* é polifilético. Caracteres morfológicos importantes na definição dos gêneros são reconhecidos como sinapomorfias; contudo muitos caracteres usados na distinção de subcategorias de *Paepalanthus* são homoplásticas e muitos clados permanecem definidos apenas por sinapomorfias moleculares. Além disso, alguns clados podem ser interpretados exclusivamente com base em distribuição geográfica, o que deve ser levado em consideração para a conservação do diversidade de Eriocaulaceae.

Palavras chave: Biogeografia; ITS; Morfologia, Poales, Sistemática; Taxonomia; *trnL-trnF*

Abstract - Paepalanthoideae (Eriocaulaceae) besides consisting of economically important species and the widest generic diversity, is taxonomically the most problematic subfamily, especially as regards *Paepalanthus*. The main goal was to infer the phylogeny of this subfamily by evaluating the important morphological characters used in the classification, as this may serve as a basis in the study of biogeography, conservation and classification. Sampling involved 94 species corresponding to all the genera, and selected outgroups. A morphological matrix and two molecular data-sets (nrITS and plastid *trnL-trnF*) were analyzed under Parsimony and Bayesian methods. The resulting trees are well-supported, with few sensitive clades. The monophyly of *Rondonanthus* as a sister to the remaining Paepalanthoideae is confirmed. *Leiothrix* and *Actinocephalus* emerge as monophyletic groups, whereas *Syngonanthus* appears paraphyletic with the current acceptance of *Philodice*, and *Blastocaulon* as polyphyletic. Four subgenera of *Paepalanthus* are monophyletic, although *P.* subgen. *Paepalocephalus* is polyphyletic. Certain morphological characters used in classifications served as synapomorphies in recognized genera. Nevertheless, many of the characters employed in defining *Paepalanthus* subcategories appear to be misleading, wherefore many clades are exclusively defined by molecular synapomorphies. Furthermore, some clades are interpreted by geographical distribution instead of taxonomic categories, perhaps important in way of conserving evolutionary processes.

Key words: Biogeography; ITS; Morphology; Poales; Systematics; Taxonomy; *trnL-trnF*.

Molecular and Morphological Phylogeny of Paepalanthoideae with emphasis in *Paepalanthus* Mart. (Eriocaulaceae).[1]

The Eriocaulaceae comprise ca. 1200 species and 11 genera distributed throughout the Tropics (Giulietti & Hensold, 1990; Stützel, 1998; Sano, 2004). The family is historically divided into two subfamilies, Paepalanthoideae and Eriocauloideae (Koernicke, 1863; Ruhland, 1903). The former is characterized by possessing isostemonous androecia and glandless corolla. All the nine genera and ca. 800 species of Paepalanthoideae are distributed mainly throughout the Neotropics (Giulietti & Hensold, 1990; Stützel, 1998). According to Giulietti & al. (2005), 95 % of these species are narrowly endemic and restricted to only a few small populations. Some species of Paepalanthoideae are of outstanding economical significance. Tons of inflorescences from *Syngonanthus* Ruhland and *Paepalanthus* Mart. are exported every year to North America and Europe as "everlasting plants", and more recently as "golden grass" (Giulietti & al., 1988; Schmidt & al., 2007; Costa & al., 2008). Species of *Paepalanthus* are also significant through presenting antioxidant and mutagenic properties (Varanda & al., 2006; Devienne & al., 2007). Nevertheless, these are not cultivated but simply harvested *in loco*, with the consequential depletion of natural populations. Hence, Paepalanthoideae species are high up on Brazilian IUCN red lists, 94 cited for Minas Gerais and 20 for Brazil as a whole (Biodiversitas, 2008). Studies in phylogenetics may be of aid in conserving both these (Faith, 1996; Ennos & al., 2005; Forest & al., 2007) and Brazilian *campos rupestres* (rocky outcrops), where Eriocaulaceae is one of the most representative families (Giulietti & al., 1987; Giulietti & Pirani, 1988; Pereira & al., 2007).

In the Paepalanthoideae, *Paepalanthus* Mart. is the largest genus with ca. 400 species. Morphological and species diversity is concentrated in Brazilian *campos rupestres* (rocky outcrops) in the Espinhaço Range and the Guyana Shield Highlands (Giulietti & Hensold, 1990; Hensold, 1991,1999). The genus is distinguished through the pistillate flowers with free petals, tetrasporangiate anthers, and stigmatic/nectariferous branches all free at the same level. Nevertheless, with the exception of these few mutual floral characters, morphological variation is great. This pronounced variation furnished the basis for proposing more than 20 infra-generic categories (Koernicke, 1863; Ruhland, 1903). Some, such as *Paepalanthus* subgen. *Platycaulon* Koern., are easily recognizable, whereas others, such as *Paepalanthus* ser. *Variabiles* Ruhland,

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[1] Manuscrito submetido ao periódico Taxon em 09 de novembro de 2009

simply represent aggregations of possibly unrelated species. Thus, the extensive morphological variation in *Paepalanthus* may well reflect complicated phylogenetic relationships and nomenclatural issues.

The first phylogenetic study involving Paepalanthoideae was restricted to morphological data (Giulietti & al., 1995). Accordingly, Paepalanthoideae emerged as monophyletic, whereas *Paepalanthus* was polyphyletic. Giulietti & al. (2000), on taking into consideration morphology, anatomy, and chemistry, concluded that Paepalanthoideae was paraphyletic, but many of its genera were monophyletic. In the same study, *Paepalanthus* appeared as polyphyletic. The outcome from recent molecular phylogenies (Unwin, 2004; Andrade, 2007; Andrade & al., in press) was fairly similar, thus furnishing added confirmation of monophyly in both subfamilies, and likewise in *Leiothrix* Ruhland and *Actinocephalus* (Koern.) Sano (sensu Costa & Sano, submitted), although there was divergence as regards *Syngonanthus*. In addition, the polyphyly of *Paepalanthus* was reinforced.

Based on the monophyly of the Paepalanthoideae (Giulietti & al., 1995; Unwin, 2004; Andrade, 2007; Andrade & al., in press), our main goal was to infer phylogenetic relationships within the subfamily, with emphasis on *Paepalanthus* species and subgroups. The inclusion of morphological characters is important for evaluating putative synapomorphies and testing the significance of characters used historically in taxonomy as applied to the group (Nixon & Carpenter, 1996; Hermsen & Hendricks, 2008; Assis, 2009). The intension was to establish relationships within Paepalanthoideae as the basis for establishing a link between phylogeny and classification.

Material and Methods

Taxa sampled—Samples of all nine genera, and all infra-generic categories of *Paepalanthus* (sensu Ruhland, 1903), with the exception of *Paepalanthus* subgen. *Psilandra* Ruhland, are represented by 94 species. The number of species by genera was: *Actinocephalus* (5), *Blastocaulon* Ruhland (3), *Lachnocaulon* Kunth (1), *Leiothrix* (6), *Paepalanthus* (70), *Philodice* Mart. (1), *Rondonanthus* Herzog (2) *Syngonanthus* (5) and *Tonina* Aubl. (1). Three species of *Eriocaulon* L. were included to define the rooting point. The complete list of taxa and voucher-specimens are in appendix 1.

Sequences, morphological data, and matrices—The nrITS region and the plastid *trnL-trnF* region based on the rate of sequence variation described by Unwin (2004), Andrade (2007); and Andrade & al. (in press) were used. Sequences for 59 species were obtained from Andrade & al. (in press) and the remaining 35 species sequenced for this study. All Genbank access numbers are listed in Appendix 1.

For DNA extraction, we used silica-gel dried leaves (5-50 mg) and a modified version of protocol 2× CTAB (Doyle & Doyle, 1987). The *trnL-trnF* spacer was amplified and sequenced by C and F universal primers (Taberlet & al., 1991). Amplification was by means of a 50 µl reaction containing PCR 1× reaction buffer 2.5 mM $MgCl_2$, 0.2 Mm dNTPs, 0.5 µM of each primer, 0.5 µg of BSA and 0.25 units of *Taq* DNA polymerase. PCR was an initial denaturing cycle at 94°C during 3 minutes, followed by 35 cycles at 94°C for 1 minute, 50-52°C for 1 minute and 72°C for 2 minutes, followed by a final extension of 72°C for 5 min. The ITS region was amplified and sequenced using primers 75 and 92 for angiosperms (Desfeaux & al., 1996). ITS amplification was with a 50 µl reaction containing PCR 1 × reaction buffer 2.5 mM $MgCl_2$, 0.2 Mm dNTPs, 0.5 µM of each primer, 1 µg of BSA, 1.0 M betaine, 2% DMSO, and 0.25 units of *Taq* DNA polymerase. PCR was an initial denaturing cycle at 94°C during 3 minutes, followed by 35 cycles of 94°C for 45 seconds, 56-58°C for 1 minute and 72°C for 2 minutes, with a final extension of 72°C for 5 minutes.

PCR products were purified by enzymatic treatment using the EXOSAP-IT kit (GE Healthcare, USB, Cleveland, Ohio, USA.). Sequencing reactions were carried out with Big Dye Terminator kit, version 3.1 (Applied Biosystems, Foster City, California, USA). Samples were sequenced in both directions by means of a SpectruMedix SCE2410 automatic sequencer, according to protocols supplied by the manufacturer. Sequences were edited using STADEN package (Staden & al., 1998), and aligned by MUSCLE software (Edgar, 2004) with posterior visual correction.

The morphological matrix was constructed through MACCLADE 4.06 (Maddison & Maddison, 2003). The 34 characters were obtained from herbarium specimens and scored through a stereoscopic microscope. Primary homology hypotheses (Pinna 1991) were based on topographical identity (Hennig 1966) and developmental studies (Stützel, 1984, 1985; Rosa & Scatena, 2007). Characters and states are listed in Appendix 2. Three data combinations were analyzed in three independent matrices, *trnL-trnF* and morphology (I) with 90 species, ITS and morphology (II) with 90 species and *trnL-trnF*, ITS and morphology (III) with 86 species. Data matrices are available at TreeBase (pin number 23241).

Phylogenetic analysis—Parsimony analysis was through PAUP 4.0b10 (Swofford, 2002). 1000 replicates with random taxon-addition were achieved with the tree-bisection-reconnection algorithm (TBR). Initially up to 25 trees were retained at each replicate. Nevertheless, if the minimum tree length was not reached at least three times in more than 50% of the search islands, the initial number was raised to do so. Multi-state characters were treated as unordered and gaps as missing data, while morphological inapplicable characters were coded as independent letters. In analysis III, the partition homogeneity test was run in PAUP. Clade sensitivity and congruence analyses were applied to five different transition/transversion parameter costs (Ts/Tv): 1/1, 1/2, 1/4, 1/6 and 1/8. ILD indexes were used to estimate the rate that maximizes congruence and minimizes conflict between data partitions (Mickevich & Farris, 1981; Aagesen, 2005). Measurements of clade support were estimated by the Bremer decay index (Bremer, 1994) and bootstrap (Felsenstein, 1985). Multiple equally parsimonious hypotheses were summarized as strict consensus trees (Sokal & Rohlf, 1981).

For Bayesian analysis, evolutionary models were chosen with hLRTs using MRMODELTEST 2.2 (Nylander, 2004). The models were run for both the ITS region split into three parts corresponding to ITS1, 5.8S and the ITS2 regions, and the *trnL-trnF* region split in two, these corresponding to the intron and spacer regions. Analysis was based on MRBAYES 3.1 (Ronquist & Huelsenbeck, 2003), initially with 5,000,000 generations in two sets of four chains, one tree being sampled every 100 generations. After the two sets of chain standard deviation having reached < 0.05, analysis was continued for an additional 2,000,000 generations. The resulting 20,000 trees constituted the final tree-set for estimating topology and bayesian posterior probabilities.

Results

Aligned matrix I consisted of 1406 characters, with the exclusion of 1-55, 550-590, 910-940, 1250-1280 and 1280-1372. 299 (25.87%) of the included characters were parsimony informative. Aligned matrix II was compiled of 1032 characters, 1-40, 507-518, 791-802 and 996-998 being excluded. Among the included characters, 457 (47.35%) were parsimony informative. 2404 characters composed aligned matrix III, with the same characters excluded as in the first two. Of the included characters, 719 (34.48%) were parsimony informative. Analysis of matrix III, making use of homogeneity partition testing, indicated no significant incongruity between molecular data sets. From congruence analysis, it was also apparent that parameter cost TS/TV: 1/2 generated less incongruence by the lowest ILD value (0.02203). The evolutionary model selected for ITS1, ITS2, the *trnL-trnF* intron and the *trnL-trnF* spacer was GTR + I + G, and for 5.8S, K80 + G. Terminals *P. bifidus*, *P. myocephalus* and *P. sessiliflorus* were excluded from all analyses. The nucleotide substitution rate in these species is distinctly higher, this implying long-branch attraction problems. A synopsis of the main results from each analysis is presented below.

trnL-F and Morphology **(I)**—A total of 8820 equally most parsimonious trees, with 918 steps were found. Strict consensus (Fig. 1) has re-scaled consistency index (RC) = 0.55 and retention index (RI) = 0.83. Paepalanthoideae monophyly (clade A) is confirmed with strong support. *Rondonanthus* is monophyletic and a sister to the remaining species of Paepalanthoideae (clade B). *Leiothrix* turned out to be monophyletic within clade B, and sister to *Syngonanthus*, which in turn, with the current acceptance of *Philodice*, is paraphyletic. Clade C comprises *Paepalanthus* core clade structured on a basal polytomy. *Paepalanthus* subgen. *Monosperma* Hensold forms a monophyletic group. The sister-genera *Tonina* and *Lachnocaulon* and *Paepalanthus* ser. *Leptocephali* Ruhland are monophyletic in a basal polytomy within clade D. The remaining clade in this polytomy is composed of three unrelated species of *Paepalanthus*, with trimerous flowers, and *Actinocephalus* (sensu Costa & Sano submitted) clustered together with a group of plants with dimerous flowers (clade E). Clade F is composed of species of *Paepalanthus* and *Blastocaulon*, although with low internal resolution.

ITS and Morphology **(II)**—A total of 24 equally most parsimonious trees with 1901 steps were found. Strict consensus (Fig. 2) has RC= 0.50 and RI = 0.87. Paepalanthoideae monophyly (clade A) is confirmed with strong support. *Rondonanthus capillaceus* emerged as sister to all the remaining species (clade B). Within clade B, *Leiothrix* is monophyletic and sister to clade C, in which *Syngonanthus* emerges paraphyletic with current acceptance of *Philodice*.

There are two distinct lineages within the *Paepalanthus* core clade. Clade D is composed of the same species as clade D of analysis I. *Tonina fluviatilis* is a sister to the remaining species. *Paepalanthus* ser. *Leptocephali*, *P.* subgen. *Thelxinöe* Ruhland and *Actinocephalus*, both strongly supported, are clustered together with a group of plants with dimerous flowers (clade E). In clade F, *P.* subgen. *Monosperma* constitutes a sister to the remaining species. Clade G is composed of the same species as in clade F of analysis I, although with higher internal resolution. Clade H is an aggregation of *Paepalanthus* species from several taxonomic categories, all occurring only in the northern portion of the Espinhaço Range and the *restingas* in the Brazilian states of Bahia and Espírito Santo. Clades I and J are formed exclusively by species occurring in the southern region of the Espinhaço and adjacent mountains. Clade I is composed of *Paepalanthus* species and *Blastocaulon scirpeum*, and are placed in several infra-generic categories. In Clade J, the monophyly of *P.* subgen. *Platycaulon*, *P.* subgen. *Xeractis* and *Paepalanthus* subsect. *Dichocladus* Ruhland, and the polyphyly of *Blastocaulon* are strongly supported.

Combined analysis **(III)**—A total of 96 equally most parsimonious trees with 4630 steps were found. Strict consensus (Fig. 3) has RC = 0.50 and RI = 0.85. The monophyly of Paepalanthoideae (clade A) is confirmed with the following morphological synapomorphies: leaves unfenestrated (homoplastic with *Mesanthemum* Koern.); corolla of the staminate flower fused; glandless petals of the pistillate flower; isostemonous androecium; central projection of the carpels originating nectariferous branches; and lateral projections of the carpels originating stigmatic branches. *Rondonanthus capillaceus* is a sister to the remaining species (clade B), and is defined by its elongate staminodes. *Leiothrix* is a sister to clade C and with nectariferous/stigmatic branches being free at different levels, and the basifixed anthers (homoplastic with *Tonina*) as its synapomorphies. Clade C contains species of *Syngonanthus*, which are now paraphyletic with current acceptance of *Philodice*, and are defined by the fused petals of the pistillate flower at the mid-region. Clade C emerges as a sister to the *Paepalanthus* core clade, based only on molecular synapomorphies.

From the standpoint polytomy, clade D is composed of *Tonina*, *Paepalanthus* ser. *Leptocephali* and clade E. The relationships among species within clade E are in accordance with those established through II analysis, with the exception of a new clade, with *Actinocephalus* as a sister-group of those *Paepalanthus* species with dimerous flowers. The presence of paraclades in *Actinocephalus*, and the absence of spathes and scapes in *Paepalanthus* subgen. *Thelxinöe*, are synapomorphies for these genera.

In accordance with analysis II, clade F is made up of *Paepalanthus* subgen. *Monosperma* as a sister to the remaining species. Synapomorphies in this subgenus are the achene fruit and unicarpellate ovaries. Clade G is formed by two lineages, namely, clade H, composed of plants exclusive to the northern region of the Espinhaço Range and the *restingas* of Bahia and Espírito Santo states, and clade I with plants restricted to the southern region of the Espinhaço Range and adjacent mountains. In clade J, *P.* subgen. *Platycaulon* is monophyletic with fused scapes, as are *P.* subsect. *Dichocladus* (molecular data) and *P.* subgen. *Xeractis* (hairs on the adaxial surfaces of both the corolla of staminate flowers and the involucral bracts). In its current circumscription and according to our trees, *Blastocaulon* is a polyphyletic group. Clades K and L are based only on molecular synapomorphies, and comprise several infra-generic categories of *Paepalanthus*.

Discussion

Through analyses trees appear highly concordant. The main clades are strongly supported and little affected by changes in parameter costs, thus indicating stable topology. Variation in the ITS region was greater than in the *trnL-trnF* (47.3 % as against 25.9 %), which is not surprising when considering Eriocaulaceae (Unwin, 2004; Andrade, 2007; Andrade & al., in press) and other families as Onagraceae, Bignoniaceae and Orchidaceae (Hoogard & al., 2004; Chen & al., 2005; van den Berg & al., 2005). Aligning ITS was a hard task due to high variation, hence the elimination of certain parts from analysis through inability to unequivocally establish primary homology. Analysis I generated a tree with low resolution and low support within the *Paepalanthus* core clade, in comparison to analysis II and analysis III. The inclusion of a morphological matrix improved tree resolution and clade support, and aided in solving inconsistencies, such as the strange position of *Rondonanthus* and the polyphyly of *Syngonanthus*, generated by purely molecular analysis. This improvement may be due to the synergistic effects of combining data sets (Nixon & Carpenter, 1996; Wahlberg & al., 2005; Hermsen & Hendricks, 2008; Assis, 2009).

Phylogenetic implications—Despite significant differences in methodology when applied to studies in morphology (Giulietti & al., 1995; Giulietti & al., 2000), some results are comparable. In relation to Giulietti & al. (1995), the existence of a clade with *Tonina* and *Lachnocaulon* and the polyphyly of *Paepalanthus* were placed in evidence. Giulietti & al. (2000) came to the conclusion that Paepalanthoideae was paraphyletic. However, re-rooting their tree (Fig. 1, p. 585) in Eriocauloideae, we came to similar conclusions. The existence of a clade with *Paepalanthus*, *Actinocephalus*, *Tonina*, *Blastocaulon* and *Lachnocaulon* could be confirmed, the only difference being the position of *Philodice* as a sister to *Tonina*. The existence of a clade including *Actinocephalus* and species of *Paepalanthus* with dimerous flowers could also be confirmed. Nevertheless, the relationship between *Leiothrix/Syngonanthus* needs to be re-evaluated, since our results indicated *Leiothrix* as being sister to a clade comprising *Syngonanthus* and other genera. *Syngonanthus* monophyly was not confirmed, through becoming paraphyletic without the inclusion of *Philodice*.

Similarities with previous molecular phylogenies (Unwin, 2004; Andrade, 2007; Andrade & al., in press) are not surprising, due to the use of the same molecular markers and shared sequences as Andrade (2007) and Andrade & al. (in press). However, the inclusion of additional terminals and a morphological matrix lead to significant differences in generic relationships, an increase in clade support and higher resolution within the *Paepalanthus* core clade. The main similarities are the monophyly of *Leiothrix*, the sister-group relationship between *Tonina* and *Lachnocaulon*, and the formation of a clade combining species from *Paepalanthus*, *Actinocephalus*, *Blastocaulon*, *Tonina* and *Lachnocaulon*. However, on contrasting previous phylogenies (Andrade, 2007; Andrade & al., in press), *Rondonanthus* appeared as sister to the remaining Paepalanthoideae, *Leiothrix* is not sister to *Syngonanthus*, and the latter is not polyphyletic but paraphyletic.

Morphological implications—Several historical characters used to separate genera in Eriocaulaceae are confirmed in this study as clade synapomorphies. In *Leiothrix*, *Rondonanthus* and *Actinocephalus*, diagnostic features are likewise (Ruhland, 1903; Hensold & Giulietti, 1991; Costa & Sano submitted). A fused petal in the mid-region of pistillate flowers, also a feature in *Mesanthemum* (Eriocauloideae), is a synapomorphy for the clade with *Syngonanthus/Philodice*. The clade *Tonina/Lachnocaulon* is defined by smaller-sized petals in pistillate flowers. In *Tonina*, this reduction is only partial, resulting in a small petal with long trichomes, whereas in *Lachnocaulon* the reduction to trichome-form is complete.

However, the type of anther (bisporangiate or tetrasporangiate) proved to be inconsistent for distinguishing between genera in Paepalanthoideae. As previously noted (Stützel,1985; Unwin, 2004; Andrade, 2007; Andrade & al., in press), distinction between *Blastocaulon* and *Paepalanthus*, and between *Philodice* and *Syngonanthus*, when based on this feature, turned out to be unsatisfactory, thereby obviating its use. Worthy of note, irrespective of the form of analysis, is that the two species originally placed in *Blastocaulon* (*B. albidum* and *B. rupestre*) are well-supported as sister-species. Polyphyly may be re-evaluated in the original context/bounds, but only if based on new characters and not only on the type of anther. Furthermore, the absence of an anther in *Philodice*, by being a striking difference in relation to *Syngonanthus*, requires more understanding.

The position of *Rondonanthus* as sister to the remaining Paepalanthoideae was expected by Hensold & Giulietti (1991). These authors stated that this genus possesses plesiomorphic characters that implied this. Although the position is exactly as expected, the arguments used have not been fully corroborated. The linear staminodes denoted synapomorphy, in contrast to a plesiomorphic interpretation. The inclusion of *Rondonanthus flabelliformis* (Mold.) Hensold & Giulietti (not sampled) is crucial to evaluating the evolution of this character, as this species possesses unique bisexual flowers, with apparently functional stamens. The inclusion of *R. flabelliformis* is also important for testing the validity of merging *Wurdackia* Mold. within *Rondonanthus.*

In *Paepalanthus*, certain characters used in separating infra-generic categories constitute clade synapomorphies. In *P.* subgen. *Xeractis*, this is illustrated by the hairs on the adaxial surface of the corolla in pistillate flowers, and on the adaxial surface in involucral bracts, in *P.* subgen. *Platycaulon*, by the fusion of scapes at various levels, and in *P.* subgen. *Monosperma*, by achene fruits and uni-carpellate ovaries. The complete reduction of spathes and scapes are the case in *P.* subgen. *Thelxinöe* (Hensold, 1988; Tissot-Squalli, 1998; Hensold, 1991; Ruhland, 1903). Nevertheless, many other important features, as floral merism, stem elongation and the spathe apex are non-correlative with phylogeny, as they are incapable of defining monophyletic groups.

Numerous groups in the *Paepalanthus* core-clade are defined exclusively by molecular synapomorphies. Searching and testing morphological synapomorphies for these clades is crucial for their recognition. Nevertheless, this search is linked to novel approaches in Eriocaulaceae morphology, which is still grounded on Ruhland (1903) concepts. Certain clades, as *P.* subsect. *Dichocladus* or *P. stannardii*/*P. distichophyllus*, possess unusual ramification patterns, which could turn out to be indicative of synapomorphy. Detailed studies on inflorescence morphology could also lead to new perspectives in the discovery of novel synapomorphies (Stützel, 1984; Oriani & al., 2008; Trovó & al., in press.). Two new synapomorphies in Paepalanthoideae (the central projection of the carpels giving rise to nectariferous branches and lateral projections of the carpels to stigmatic branches) are derived from a new developmental framework. In this context, we hereby stress the importance of seeking other unusual and less explored characters, such as embryological and developmental (Coan and Scatena, 2004; Coan & al., 2007; Rosa & Scatena, 2007).

Biogeographical implications— Two main bio-geographical patterns arose from our trees. As in Rapateaceae and Bromeliaceae (Givnish & al., 2000; Givnish & al., 2004), in Eriocaulaceae, and based on topological studies, it could be inferred that species occurring in the Venezuelan-Guyana Highlands are early-divergent in their lineages. *Rondonanthus* is sister to the remaining Paepalanthoideae and *P.* subgen. *Monosperma* sister to clade G. The explanation of such a pattern would rely on the advanced age of the region and isolation of the populations. Diversity here would be autochthonal and derived from isolated ancestries in a heterogeneous habitat (Berry & Rinna, 2005). Givinish & al. (2004) point to the possibility of mutual colonization of both these Highlands and the adjacent Lowlands, due to climate-variation. In Eriocaulaceae, species diversity is concentrated in the Highlands, although there are a few endemic ones in the Lowlands. Further inclusion of these is essential for understanding the processes of local occupation and diversification (Hensold, 1991, 1999; Trovó & Sano, 2009).

A further important pattern came to light in clade F, namely, the split between a clade formed by plants from the northern region of the Espinhaço Range and the *restingas* from Bahia and Espírito Santo States, and a clade formed by species from the southern region and adjacent mountains. This biogeographical signal was more pronounced than expected, and surpassed those of several taxonomic categories. Harley (1988) described an analogous pattern noted in Lamiaceae. He suggested that floristic composition is distinct in the two parts of the Espinhaço Range, in spite of similar physiognomies and identical geological origin. As Eriocaulaceae species are mainly narrowly distributed and have limited dispersion capacity, to elucidate this pattern we suggest an analogous vicariance explanation, as used to clarify the diversification in the Guyana and Venezuelan Guyana Highlands. Thus, the two lineages may have distinct origins with subsequently autochthonal diversification. Moreover, considering the relatively recent age of the *restingas* (Suguio, 1985), it is expected that the few species inhabiting this environment could have arisen from dispersal events with an ancestral inhabitant of the northern-part mountains (Harley, 1988; Giulietti & Hensold, 1991).

Taxonomic implications—Our topology partially corroborated the historical classification proposed for Paepalanthoideae. *Leiothrix* and *Syngonanthus*, established by Ruhland (1903) from *Paepalanthus* sect. *Glabriscula* Koern. (Koernicke, 1863), emerged out of *Paepalanthus* core clade. *Leiothrix* is monophyletic and *Syngonanthus* paraphyletic, with the exception of *Philodice*. The proposal for conserving *Syngonanthus* against *Philodice* for further synonymizing has already been presented (Giulietti & al., 2009). The results also corroborate the segregation of two sections of *Syngonanthus* in the re-established genus *Comanthera* L.B. Sm. (Parra & al., in press). The genera *Rondonanthus* and *Actinocephalus* also emerged as monophyletic in accordance with current circumscription (Hensold & Giulietti, 1991; Costa & Sano, submitted).

Thus, relationships outside the *Paepalanthus* core clade were well established, the monophyly of these lineages having been confirmed and changes in nomenclature already proposed. Nevertheless, within the *Paepalanthus* core clade, the situation appears to be more complex. In this clade, species of *Blastocaulon*, *Tonina*, *Lachnocaulon* and *Actinocephalus* are intermixed with species of *Paepalanthus*. This condition enhances the need for a series of changes in nomenclature, imperative for phylogenetic classification of Paepalanthoideae.

Various strategies could be applied to solve this deadlock. Initially, gathering all species into *Paepalanthus* appears to be plausible. Nevertheless, this is not so, for, on considering *Tonina* (monotypic genus) priority, it would require over 500 additional combinations. Furthermore, there would be a lack in morphological synapomorphies, the outcome being a large heterogeneous aggregation without practical limits. A contrary strategy would be to divide the *Paepalanthus* core clade into small, homogeneous and well-delimited genera. Probably the best solution, through raising disperse categories, such as *P.* subgen. *Xeractis*, *P.* subgen. *Platycaulon* and *P.* subsect. *Dichocladus* to the status of genera. Nevertheless, several relationships within this clade remain unstable, thereby necessitating the inclusion of additional taxa for a better understanding of the relationships and the respective morphology. This is required before visualizing changes, so as to maximize stability in nomenclature. Important clades, such as clade H (this including *Paepalanthus*), are defined only through molecular synapomorphies, this making them ineffective as regards recognition and information.

Having in mind current phylogenetic status and knowledge in morphology, we hereby consider an intermediate strategy. Whereas with clade G, comprising the larger part of *Paepalanthus* diversity, recognition of clades defined through morphology as groups is extremely difficult, species included in clade D are better known, with more stable relationships. We therefore propose maintaining *Actinocephalus*, *Tonina* and *Lachnocaulon* as they are, with current circumscription, and splitting the remaining *Paepalanthus* species into a few new, well-delimited and strongly supported genera. In clade F, *Paepalanthus* subgen. *Monosperma* would be raised to generic status, as clade-status is well-supported, with very distinctive features. The five species of *Blastocaulon* are to be merged into *Paepalanthus* (Andrade & al., in press).

Final remarks—Given the importance of biogeographical aspects, the inclusion of species from poorly sampled regions, such as Cuba and the Andean region is essential for a more complete vision of the geographical distribution of lineages, emphasizing its overwhelming importance in the conservation of biodiversity (Faith, 1996; Ennos & al., 2005; Forest & al., 2007). In the Paepalanthoideae, several lineages occur in specific regions, as in the Venezuelan Guyana Highlands or the northern and southern parts of the Espinhaço Range. Thus, in order to conserve lineage diversity, distribution patterns turn out to be extremely relevant, in contrast to a merely species-richness approach.

Although slightly different from previous phylogenies, our results are strongly supported and consistent with morphology. The changes in nomenclature proposed for solving issues involving *Syngonanthus* and *Philodice* are satisfactory. Further studies are required to solve the problems within the two lineages in the *Paepalanthus* core clade. We emphasize the need for including certain key species and encountering synapomorphies based on morphology, as a means of defining these clades. This search, within a combined morphological and molecular scenario, and together with advanced knowledge on species development, are essential for establishing the informative phylogenetic classification of Paepalanthoideae.

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Appendix 1. Voucher information and GenBank accession numbers for taxa used in this study. An asterisk indicates the number in HUEFS genetic bank. A dash indicates a molecular region not sampled. Herbarium acronyms follow Thiers & al. (continuously updated).

Actinocephalus bongardii (A. St.-Hil) Sano, *MJG Andrade 501* (HUEFS), Itacambira/MG, *1927, EU924434, EU924282; *Actinocephalus brachypus* (Bong.) Sano, *MJG Andrade 521* (HUEFS), Diamantina/MG, *1938, EU924433, EU924281; *Actinocephalus ciliatus* (Bong.) Sano, *MJG Andrade 544* (HUEFS), Diamantina/MG, *1956, EU924435, EU924283; *Actinocephalus ramosus* (Wisktr.) Sano, *BRN Araújo 78* (HUEFS), Rio de Contas/BA, *1798, EU924436, EU924284; *Actinocephalus stereophyllus* (Ruhland) Sano, *MJG Andrade 514* (HUEFS), Diamantina/MG, *1933, EU924437, EU924285; *Blastocaulon albidum* Gardner, *MJG Andrade 541* (HUEFS), Diamantina/MG, *1953, EU924439, EU924287; *Blastocaulon rupestre* (Gardner) Ruhland, *MJG Andrade 542* (HUEFS), Diamantina/MG, *1954, EU924440, EU924288; *Blastocaulon scirpeum* (Mart.) Giulietti, *JR Pirani 4162* (HUEFS), Congonhas do Norte/MG, *6876, EU924441, EU924289; *Eriocaulon ligulatum* (Vell.) L.B. Sm., *AM Giulietti 2368* (HUEFS), Mucugê/BA, *298, EU924430, EU924278; *Eriocaulon linearifolium* Koern., *AM Giulietti 2366* (HUEFS), Mucugê/BA, *297, EU924429, EU924277; *Eriocaulon modestum* Kunth, *MJG Andrade 445* (HUEFS), Rio de Contas/BA, *780, EU924431, EU924279; *Lachnocaulon anceps* Morong, *Goldman s/n* (BH), Florida/USA, *6877, EU924442, -; *Leiothrix arrecta* Ruhland, *AM Giulietti 2496* (HUEFS), Santana do Riacho/MG, *6872, EU924449, EU924296; *Leiothrix curvifolia* (Bong.) Ruhland, *MJG Andrade 553* (HUEFS), Datas/MG, *1964, EU924446, EU924293; *Leiothrix distichoclada* Herzog, *MJG Andrade 458* (HUEFS), Rio de Contas/BA, *792, EU924447, EU924294; *Leiothrix flagellaris* (Guill.) Ruhland, *MJG Andrade 485* (HUEFS), Grão-Mogol/MG, *1920, EU924450, EU924297; *Leiothrix flavescens* (Bong.) Ruhland, *MJG Andrade 440* (HUEFS), Rio de Contas/BA, *775, EU924444, EU924291; *Leiothrix vivipara* (Bong.) Ruhland, *AM Giulietti 2503* (HUEFS), Santana do Riacho/MG, *7415, EU924451, EU924298; *Paepalanthus acantholimon* Ruhland, *MLO Trovó 250* (SPF), Alto Caparaó/MG, *6924, GQ475202, GQ475232; *Paepalanthus acanthophyllus* Ruhland, *MLO Trovó 287* (SPF), Alto Paraíso de Goiás/GO, *6908, GQ475203, GQ475233; *Paepalanthus acuminatus* Ruhland, *MLO Trovó 175* (SPF), Lima Duarte/MG, *6928, GQ475204, GQ475234; *Paepalanthus aretioides* Ruhland, *MLO Trovó 357* (SPF), Diamantina/MG, *6914, GQ475205, GQ475235; *Paepalanthus argenteus* (Bong.) Koern., *MJG Andrade 539* (HUEFS), Diamantina/MG, *1952, EU924484, EU924331; *Paepalanthus augustus* Silveira, *LM Borges 178* (SPF), Santana do

Riacho/MG, *6963, -, GQ475236; *Paepalanthus bifidus* (Scharad.) Kunth, *MJG Andrade 489* (HUEFS), Grão-Mogol/MG, *1924, EU924453, EU924300; *Paepalanthus bonsai* Trovó & Sano, *PL Vianna 2776* (SPF), São Gonçalo do Rio Preto/MG, *6903, GQ475206, GQ475237; *Paepalanthus bromelioides* Silveira, *MLO Trovó 219* (SPF), Santana do Riacho/MG, *6905, GQ475207, GQ475238; *Paepalanthus bryoides* Kunth, *FN Costa 263* (HUEFS), Diamantina/MG, *6878, EU924452, EU924299; *Paepalanthus calvoides* Ruhland, *MJG Andrade 550* (HUEFS), Itacambira/MG, *6812, GQ475208, GQ475239; *Paepalanthus canescens* Koern., *MLO Trovó 351* (SPF), Diamantina/MG, *6919, GQ475209, GQ475240; *Paepalanthus caparoensis* Ruhland, *MLO Trovó 249* (SPF), Alto Caparaó/MG, *6925, GQ475210, GQ475241; *Paepalanthus chrysophorus* Silveira, *MM Lopes 951* (SPF), Grão-Mogol/MG, *6958, GQ475211, GQ475242; *Paepalanthus cinereus* Giulietti & Parra, *AM Giulietti s/n* (HUEFS), Rio de Contas/BA, *1293, EU924469, EU924316; *Paepalanthus comans* Silveira, *MJG Andrade 540* (HUEFS), Diamantina/MG, *6820, EU924482, EU924329; *Paepalanthus cordatus* Ruhland, *MLO Trovó 443* (SPF), Alto Paraíso de Goiás/GO, *6917, GQ475212, GQ475243; *Paepalanthus cylindraceus* Silveira, *MLO Trovó 383* (SPF), São Roque de Minas/MG, *9262, -, GQ475244; *Paepalanthus distichophyllus* Mart., *MLO Trovó 218* (SPF), Diamantina/MG, *6907, GQ475213, GQ475245; *Paepalanthus elongatus* (Bong.) Koern., *MJG Andrade 572* (HUEFS), Tiradentes/MG, *6884, EU924467, EU924314; *Paepalanthus erigeron* Mart. ex Koern., *AA Ribeiro-Filho 107* (HUEFS), Lençóis/BA, *6882, -, EU924306; *Paepalanthus eriophaeus* Ruhland, *MJG Andrade 504* (HUEFS), Itacambira/MG, *6811, EU924459, EU924307; *Paepalanthus exiguus* (Bong.) Koern., *E Guarçoni 710* (HUEFS), Alto Caparaó/MG, *6885, EU924481, EU924328; *Paepalanthus fraternus* N.E. Br., *P Fiaschi 3202* (SPF), Mount Roraima/Venezuela, *6912, GQ475214, GQ475246; *Paepalanthus fulgidus* Moldenke, *P Fiaschi 3196* (SPF), Mount Roraima/Venezuela, *6911, GQ475215, GQ475247; *Paepalanthus geniculatus* (Bong.) Kunth, *MLO Trovó 205* (SPF), Diamantina/MG, *6921, GQ475216, GQ475248; *Paepalanthus giganteus* Sano, *MJG Andrade 527* (HUEFS), Diamantina/MG, *1943, EU924478, EU924325; *Paepalanthus glareosus* Kunth, *MJG Andrade 548* (HUEFS), Datas/MG, *1959, EU924475, EU924322; *Paepalanthus glaziovii* Ruhland, *Sano 3851* (SPF), Diamantina/MG, *6902, GQ475217, GQ475249; *Paepalanthus henriquei* Ruhland, *MLO Trovó 179* (SPF), Lima Duarte/MG, *6927, GQ475218, -; *Paepalanthus implicatus* Silveira, *MJG Andrade 550* (HUEFS), Datas/MG, *1961, EU924472, EU924319; *Paepalanthus klotzschianus* Koern., *MLO Trovó 257* (SPF), Linhares/ES, *6959, GQ475219, GQ475250; *Paepalanthus lamarckii* Kunth, *DS Carneio-Torres 461* (HUEFS), Lagartos/SE, *6880, EU924456, EU924303; *Paepalanthus leucocephalus* Ruhland, *MJG*

Andrade 620 (HUEFS), Rio de Contas/BA, *6886, EU924487, EU924334; *Paepalanthus macrocaulon* Silveira, *MJG Andrade 431* (HUEFS), Rio de Contas/BA, *766, EU924470, EU924317; *Paepalanthus macropodus* Ruhland, *MLO Trovó 214* (SPF), Santana do Riacho/MG, *6922, GQ475220, GQ475251; *Paepalanthus microphyllus* Kunth, *MLO Trovó 225* (SPF), Santana do Riacho/MG, *6923, GQ47522, GQ475252; *Paepalanthus mollis* Kunth, *MLO Trovó 376* (SPF), Diamantina/MG, *6961, GQ475222, GQ475253; *Paepalanthus myocephalus* Mart., *MJG Andrade 613* (HUEFS), Feira de Santana/BA, *6879, EU924454, EU924301; *Paepalanthus neglectus* Koern., *BRN Araújo 85* (HUEFS), Rio de Contas/BA, *1805, EU924460, EU924308; *Paepalanthus nigrescens* Silveira, *MLO Trovó 204* (SPF), Santana do Riacho/MG, *6932, GQ475223, GQ475254; *Paepalanthus obtusifolius* Koern., *R Harley 54802* (HUEFS), Rio de Contas/BA, *1321, EU924457, EU924304; *Paepalanthus parviflorus* (Hensold) Hensold, *MLO Trovó 202* (SPF), Santana do Riacho/MG, *6962, GQ475224, -; *Paepalanthus pedunculatus* Ruhland, *MJG Andrade 547* (HUEFS), Datas/MG, *1958, GQ475225, GQ475255; *Paepalanthus planifolius* (Bong.) Koern., *MJG Andrade 526* (HUEFS), Diamantina/MG, *1942, EU924485, EU924332; *Paepalanthus polycladus* Silveira, *MLO Trovó 391* (SPF), São Roque de Minas/MG, *6909, GQ475226, GQ475256; *Paepalanthus polygonus* Koern., *MLO Trovó 413* (SPF), Diamantina/MG, *6913, GQ475227, GQ475257; *Paepalanthus pulchellus* Herzog, *AM Giulietti 2423* (HUEFS), Rio de Contas/BA, *1409, EU924461, EU924309; *Paepalanthus pulvinatus* N.E. Br., *R Harley 54634* (HUEFS), Mucugê/BA, *638, EU924465, EU924313; *Paepalanthus regalis* Mart., *R Harley 54640* (HUEFS), Mucugê/BA, *660, EU924462, EU924310; *Paepalanthus repens* Koern., *R. Abbott 21006* (FLAS), -, *7416, EU924474, EU924321; *Paepalanthus scleranthus* Ruhland, *MJG Andrade 537* (HUEFS), Diamantina/MG, *1951, EU924410, EU924335; *Paepalanthus sessiliflorus* Mart. ex Koern., *JG Jardim 2237* (HUEFS), Maraú/BA, *6881, EU924458, EU924305; *Paepalanthus silveirae* Ruhland, *MJG Andrade 568* (HUEFS), Tiradentes/MG, *1976, EU924463, EU924311; *Paepalanthus spathulatus* Koern., *R Harley 55476* (HUEFS), Itaberaba/BA, *6883, EU924464, EU924312; *Paepalanthus sphaerocephalus* Ruhland, *MJG Andrade 456* (HUEFS), Rio de Contas/BA, *790, EU924480, EU924327; *Paepalanthus stannardii* Giulietti & Parra, *MJG Andrade 438* (HUEFS), Rio de Contas/BA, *773, EU924473, EU924320; *Paepalanthus strictus* Koern., *MJG Andrade 491* (HUEFS), Grão-Mogol/MG, *1926, EU924471, EU924318; *Paepalanthus subcaulescens* N.E. Br., *P Fiaschi 3195* (SPF), Mount Roraima/Venezuela, *6957, GQ475228, GQ475258; *Paepalanthus superbus* Ruhland, *AM Giulietti 2504* (HUEFS), Santana do Riacho/MG, *6858, EU924483, EU924330; *Paepalanthus tortilis* (Bong.) Mart., *MJG Andrade 479* (HUEFS), Grão-Mogol/MG, *1914, EU924455, EU924376; *Paepalanthus trichophyllus* (Bong.) Koern., *MJG Andrade 439* (HUEFS), Rio de Contas/BA, *774, EU924479, EU924326; *Paepalanthus tuberosus* (Bong.) Kunth, *van den Berg 1364* (HUEFS), Conceição do Mato Dentro/MG, *1641, EU924486, EU924333; *Paepalanthus urbanianus* Ruhland, *MLO Trovó 435* (SPF), Alto Paraíso de Goiás/GO, *6918, -, GQ475259; *Paepalanthus vaginatus* Koern., *MLO Trovó 353* (SPF), Diamantina/MG, *6904, -, GQ475260; *Paepalanthus vellozioides* Koern., *MLO Trovó 198* (SPF), Santana do Riacho/MG, *6906, GQ475229, GQ475261; *Paepalanthus viridulus* Ruhland, *C Sarquis 12* (SPF), Lima Duarte/MG, *6915, GQ475230, GQ475262; *Philodice hoffmannseggii* Mart., *AM Giulietti 2483* (HUEFS), Nossa Senhora do Livramento/MT, *6887, EU924411, EU924336; *Rondonanthus capillaceus* (Koern.) Hensold & Giulietti, *van den Berg 1792* (HUEFS), Mount Roraima/Venezuela, *6889, GQ478282, EU924338; *Rondonanthus roraimae* (Oliver) Herzog, *P Fiaschi 3201* (SPF), Mount Roraima/Venezuela, *6916, GQ475231, -; *Syngonanthus aciphyllus* (Bong.) Ruhland, *MJG Andrade 532* (HUEFS), Diamantina/MG, *1948, EU924491, EU924339; *Syngonanthus arenarius* (Gardner) Ruhland, *MJG Andrade 493* (HUEFS), Itacambira/MG, *6802, EU924498, EU924342; *Syngonanthus caulescens* (Poir.) Ruhland, *MJG Andrade 616* (HUEFS), Rio de Contas/BA, *786, EU924500, EU924344; *Syngonanthus curralensis* Moldenke, *MJG Andrade 595* (HUEFS), Rio de Contas/BA, *6890, EU924492, EU924340; *Syngonanthus vernonioides* (Kunth) Ruhland, *AM Giulietti 2185* (HUEFS), Rio de Contas/BA, *220, EU924499, EU924343; *Tonina fluviatilis* Aubl., *MJG Andrade 616* (HUEFS), Recife/PE, *6895, EU924501, EU924345.

Appendix 2. List of morphological characters and their states.

1. **Stem**. 0: restricted to rosette; 1: elongated without secondary growth; 2: elongated with secondary growth. 2. **Elongated axis**. 0: absence; 1: presence. 3. **Paraclade**. 0: absence; 1: presence. 4. **Leaf (blade)**. 0: flat; 1: conduplicate 5. **Leaf (fenestration)**. 0: absence; 1: presence. 6. **Spathe**. 0: absence; 1: presence. 7. **Spathe (apex)**. 0: truncate; 1: opened. 8. **Scape**. 0: absence; 1: presence. 9. **Scape (fusion)**. 0: free, 1: partially fused; 2: completely fused. 10. **Floral merism**. 0: trimerous; 1: dimerous. 11. **Involucral bract**. 0: absence; 1: presence. 12. **Involucral bract (relative size)**. 0: not surpassing the capitulum; 1: surpassing o capitulum. 13. **Involucral bract (form)**. 0: same form; 1: inner most differentiated 14. **Involucral bract (trichomes in adaxial surface)**. 0: absence; 1: presence. 15. **Floral bract**. 0: absence; 1: presence. 16. **Staminate flower (sepals)**. 0: free; 1: fused at base. 17. **Staminate flower (petals)**. 0: free; 1: fused. 18. **Staminate flower (petals)**. 0: membranaceous; 1: rigid. 19. **Staminate flower (petals glands)**. 0: absence; 1: presence. 20. **Staminate flower (androecium)**. 0: isostemonous. 1: diplostemonous; 21. **Staminate flower (pistilodes)**. 0: absence; 1: presence. 22. **Staminate flower (anther)**. 0: bisporangiate; 1: tetrasporangiate. 23. **Staminate flower (anther)**. 0: dorsifixed; 1: basifixed. 24. **Staminate flower (corolla with trichomes in adaxial surface)**. 0: absence; 1: presence. 25. **Pistillate flower (petals)**. 0: absence; 1: presence; 2: reduced. 26. **Pistillate flower (petals)**. 0: free; 1: fused at base. 27. **Pistillate flower (petals)**. 0: free; 1: fused at middle. 28. **Pistillate flower (staminodes)**. 0: absence; 1: scale like; 2: presence completely reduced; 3: presence elongate. 29**. Pistillate flower (central carpels projection)**. 0: define stigmas; 1: define nectariferous branches. 30. **Pistillate flower (lateral carpel projections)**. 0: absence; 1: define stigmatic branches. 31. **Pistillate flower (stigmatic branches)**. 0: completely fused; 1: partially fused. 32. **Pistillate flower (nectariferous branch/stigmatic branch)**. 0: free at same level; 1: free at different levels. 33. **Fruit**. 0: loculicidal capsule; 1: achene. 34. **Carpels number**. 0: unicarpellate; 1: bicarpellate; 2: tricarpellate.

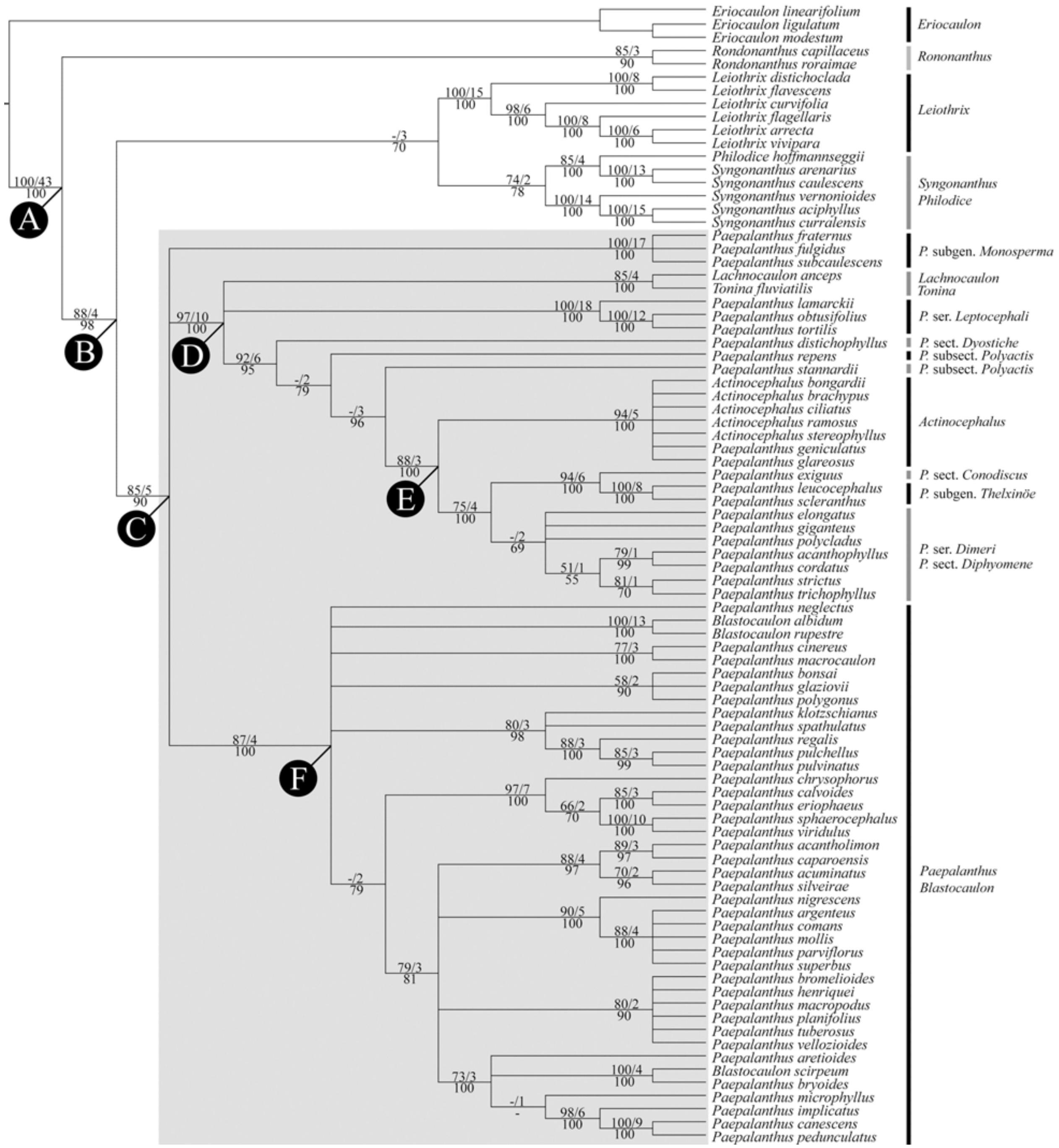

Figure 1. Strict consensus of the 8820 equally most parsimonious trees found from *trnL-trnF* and morphology datasets (RC=0.55 RI=0.83). Numbers above the branches indicate Bootstrap support and the Bremer decay index. Numbers below the branches indicate Bayesian posterior probabilities. Shaded clade comprises the *Paepalanthus* core clade. Clade names follow Ruhland's (1903) classification.

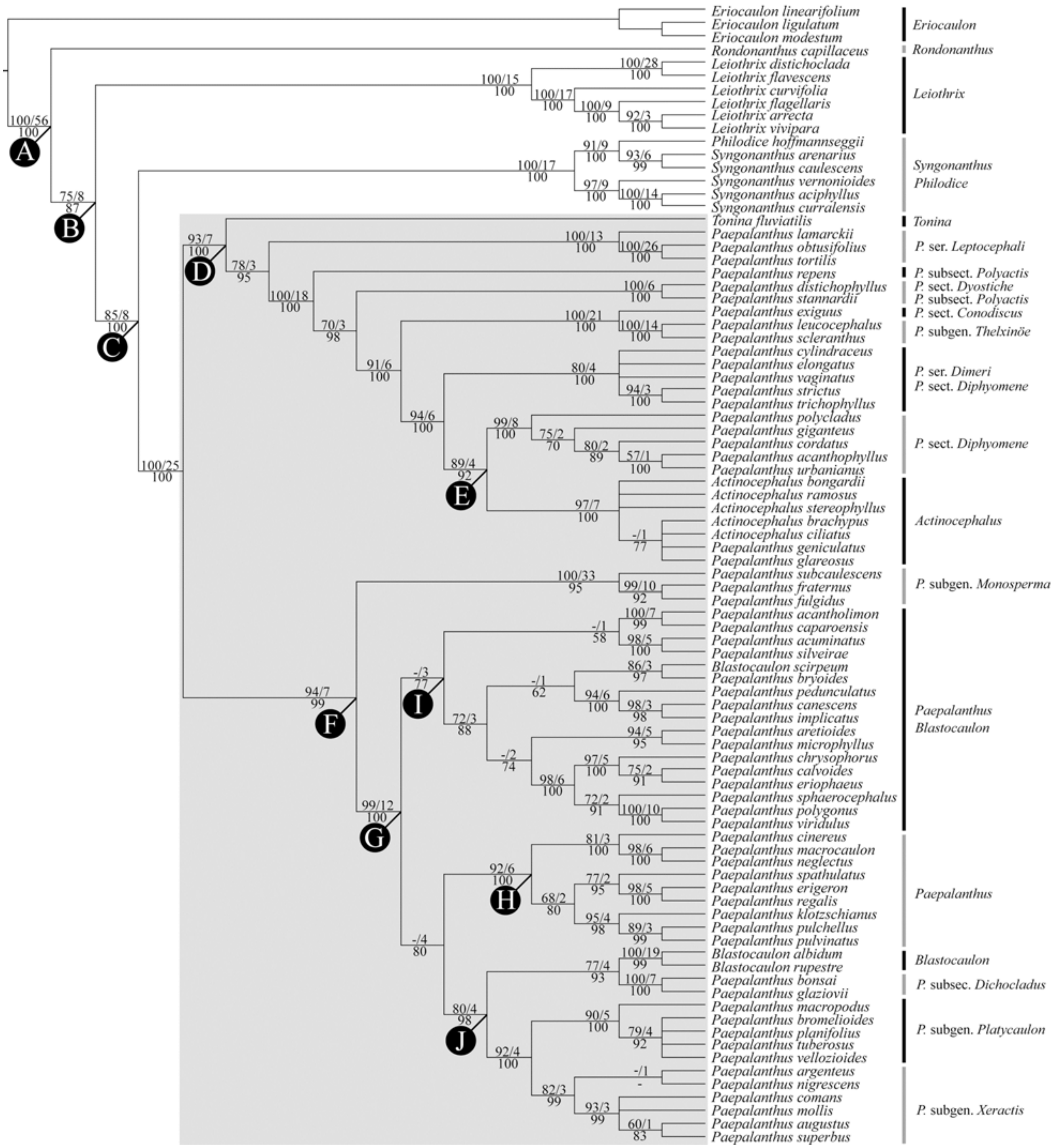

Figure 2. Strict consensus of the 24 equally most parsimonious trees found from ITS and morphology datasets (RC=0.50 RI=0.87). Numbers above the branches indicate Bootstrap support and the Bremer decay index. Numbers below the branches indicate Bayesian posterior probabilities. Shaded clade comprises the *Paepalanthus* core clade. Clade names follow Ruhland's (1903) classification.

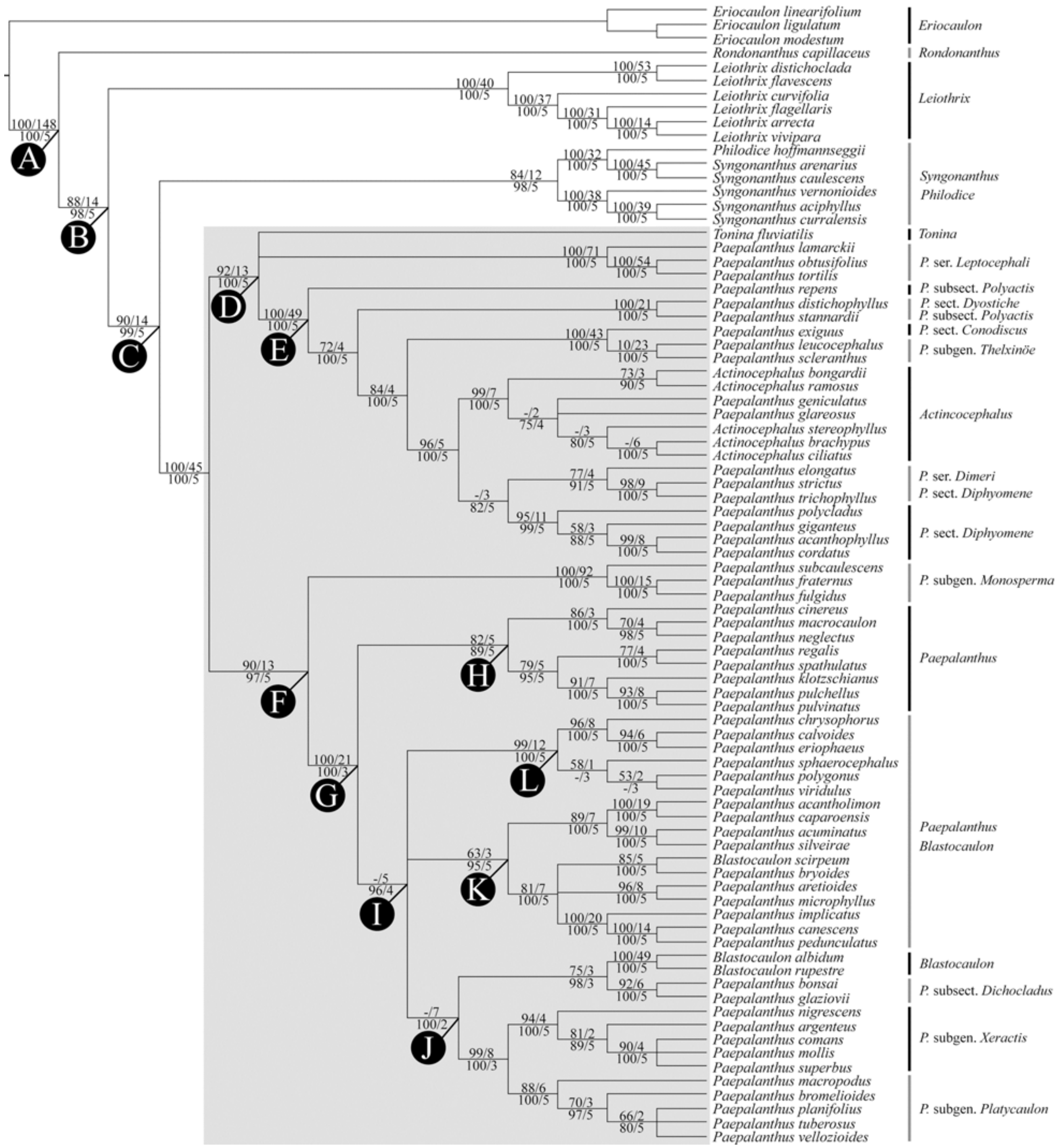

Figure 3. Strict consensus of the 96 equally most parsimonious trees found from *trnL-trnF*, ITS, and morphology datasets (RC=0.50 RI=0.85). Numbers above the branches indicate Bootstrap support and the Bremer decay index. Numbers below the branches indicates Bayesian posterior probabilities and the number of parameters costs in which the clade appears. Shaded clade comprises the *Paepalanthus* core clade. Clade names follow Ruhland's (1903) classification.

CAPÍTULO II

Morfologia e anatomia da inflorescência e do eixo de inflorescência em *Paepalanthus* sect. *Diphyomene* Ruhland (Eriocaulaceae, Poales) e suas implicações taxonômicas

PAEPALANTHUS (Dimeranthus) amoenus.

Resumo - *Paepalanthus* sect. *Diphyomene* possui inflorescências organizadas em umbelas. No entanto, tal estrutura mostra-se mais complexa, sendo composta por diversas subunidades. Neste contexto, a morfologia e a anatomia destas inflorescências podem suprir valiosas informações para a filogenia e a taxonomia do grupo. Inflorescências de *P. erectifolius*, *P. flaccidus*, *P. giganteus* e *P. polycladus* foram analisadas em relação ao padrão de ramificação e à anatomia. Em *P. erectifolius*, *P. giganteus* e *P. polycladus*, a inflorescência é um tribótrio com dibótrio terminal, unidade básica terminal e ferofilos envolvendo os dibótrios. Em *P. flaccidus*, a inflorescência é um pleiobótrio com subunidade terminal e ferofilos ausentes. Inflorescências secundárias podem ocorrer em todas as espécies, sem apresentar padrão regular. Quando as espécies habitam locais sem sazonalidade marcada, a distinção entre a zona de enriquecimento (parte da mesma inflorescência) e novas inflorescências torna-se tênue. As características anatômicas mais relevantes são: a) no eixo reprodutivo, o espessamento da parede das células epidérmicas e o tamanho do córtex; b) nas brácteas, a quantidade de células parenquimáticas; c) nos escapos, a forma e a presença de medula. Conclui-se que *P.* sect. *Diphyomene* pode ser dividida em dois grupos; o grupo A é representado por *P. erectifolius*, *P. giganteus* e *P. polycladus*; e o grupo B é representado por *P. flaccidus*. A diferenciação é baseada na estrutura e na anatomia das inflorescências. As espécies do grupo A apresentam ciclo de vida e características anatômicas similares às espécies de *Actinocephalus*. Filogenias moleculares também apontam para a estreita relação entre estas espécies, sendo que, no entanto, a estrutura da inflorescência e a sequência do desenvolvimento das flores são diferentes. As espécies do grupo B apresentam a morfologia e a anatomia da inflorescência similares a muitos outros grupos de Eriocaulaceae. As filogenias disponíveis não permitem precisar a posição deste grupo em relação as demais espécies de *Paepalanthus*.

Palavras chave: Anatomia; Filogenia; Homologia; Paepalanthoideae; Sistemática; Tipologia

Abstract - *Paepalanthus* sect. *Diphyomene* has inflorescences arranged in umbels. The underlying bauplan is however more complex and composed of several distinct subunits. Thus, the morphology and anatomy of the inflorescences may supply useful information for the understanding of the phylogeny and taxonomy of the group. Inflorescences of *P. erectifolius*, *P. flaccidus*, *P. giganteus*, and *P. polycladus* were analyzed in regard to branching pattern and anatomy. In *P. erectifolius*, *P. giganteus* and *P. polycladus* the structure is a tribotryum, with terminal dibotryum, and with pherophylls bearing lateral dibotrya. In *P. flaccidus*, the inflorescence is a pleiobotryum, with terminal subunit, and without pherophylls. Secondary inflorescences may occur in all species without regular pattern. Especially when grown in sites without a pronounced seasonality, the distinction between enrichment zone (part of the same inflorescence) and new inflorescences may be tenuous. The main anatomical features supplying diagnostic and phylogenetic information are as follows: a) in the elongated axis, the thickness of the epidermal cell walls and the cortex size; b) in the bracts, the quantity of parenchyma cells; c) in the scapes, the shape and the presence of a pith tissue. Therefore, *P.* sect. *Diphyomene* can be divided in two groups; group A is represented by *P. erectifolius*, *P. giganteus* and *P. polycladus*, and group B is represented by *P. flaccidus*. The differentiation is based in both, inflorescence structure and anatomy. Group A presents a life cycle and anatomical features similar to species of *Actinocephalus*. Molecular trees also point that these two groups are closely related. However, inflorescence morphology and blooming sequence are different. Species of group B present an inflorescence structure and anatomical features shared with many genera and species in Eriocaulaceae. The available molecular and morphology based phylogenies still do not allow a precise allocation of the group in the bulk of basal species of *Paepalanthus* collocated in *P.* sect. *Variabiles*. The characters described and used here supply however important information towards this goal.

Key words: Anatomy; Homology; Paepalanthoideae; Phylogeny; Typology; Systematics

Morphology and anatomy of inflorescence and inflorescence axis in *Paepalanthus* sect. *Diphyomene* Ruhland (Eriocaulaceae, Poales) and its taxonomic implications.[2]

Paepalanthus Mart. is the largest Neotropical genus of Eriocaulaceae, comprising about 450 species (Giulietti and Hensold, 1990; Stützel, 1998). Ruhland (1903) organized these species in 28 subcategories based on floral, inflorescence and vegetative characters. *Paepalanthus* sect. *Diphyomene* Ruhland consists of 16 species distributed in the Brazilian rocky outcrops and in the open savannas of Brazil, Bolivia and Venezuela (Ruhland, 1903; Moldenke 1971; Giulietti and Hensold, 1990). Historically, these species have belonged to several categories. First, Bongard (1831) congregated them under the name "Staminibus duobus", based exclusively on the dimerous flowers. After that, Koernicke (1863) followed Bongard (1831), and nominated the category as *Paepalanthus* subgen. *Dimeranthus* Koern. Finally, Ruhland (1903) proposed a new system for Eriocaulaceae and defined *P.* sect. *Diphyomene* by having dimerous flowers, elongated stems and capitula arranged in umbels.

Studies on inflorescence morphology are common in families such as Poaceae (Vegetti and Anton 1995, 1996, 2000), Aristolochiaceae (Gonzàlez and Rudall, 2001) and Verbenaceae (Martinez *et al.*, 1996; Múlgura de Romero *et al.*, 1998; Drewes and Martinez, 1999), but they are rare in Eriocaulaceae. The basic inflorescence unit in this family is the capitulum, generally terminating a long scape surrounded by a basal sheath. Stützel and Weberling (1982) discussed the origin and the evolution of this structure in three species, applying parts of their results for the entire family. Stützel (1984) extended these studies for 15 species describing several patterns of composed inflorescences. Recently, Oriani *et al.* (2008) established the patterns of morphological architecture for *Actinocephalus* (Koern.) Sano based on inflorescence features.

The anatomy of the reproductive parts of Eriocaulaceae revealed to be a useful tool for the taxonomy of the group. Scape and leaf anatomy of *Leiothrix crassifolia* (Bong.) Ruhland was correlated with distribution patterns of different populations (Scatena and Giulietti, 1996). Anatomical characteristics of scapes and bracts of *Actinocephalus* were evaluated by Oriani *et al.* (2005), and they confirmed the consistence of the circumscription of this genus. The anatomy of the fused scapes of *Paepalanthus* subgen. *Platycaulon* Koern. was investigated by Scatena *et al.* (1998)

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and it supports the delimitation of the group and its sections. A synthesis of the anatomy of Eriocaulaceae was presented by Scatena *et al.* (2005) in correlation with taxonomy. Rosa and Scatena (2007) analyzed the morphology and anatomy of floral structures of Paepalanthoideae Ruhland; as one result, an appropriate terminology was established.

Inflorescences in *P.* sect. *Diphyomene* are usually regarded as umbels, however its structure was never properly studied. In fact, it appears to be a more complex inflorescence presenting internal subunits. In this paper, the inflorescences of representatives of *P.* sect. *Diphyomene* are studied to establish its morphological and anatomical patterns, to evaluate the consistency of the characters proposed by Ruhland (1903), and to elucidate the phylogenetic relationships of the species within this section. The capitulum and the flowers were previously treated by Stützel & Weberling (1982) and Rosa & Scatena (2007) and are therefore not treated here.

Material and methods

Four species of *P.* sect. *Diphyomene* were analyzed: *Paepalanthus erectifolius* Silveira, *Paepalanthus flaccidus* (Bong.) Kunth, *Paepalanthus giganteus* Sano, and *Paepalanthus polycladus* Silveira (Fig. 1 A-D). These species represent the morphological variability and the geographic distribution of the group. The terminology proposed by Troll (1964) and Weberling (1989) was adopted to describe the inflorescences. Observations on branching patterns were carried out in field, since analysis of branching patterns in herbarium specimens is difficult and leads to complete destruction of the specimens. Collected material was conserved in alcohol 70%. Herbarium specimens are deposited in SPF herbarium, and voucher specimens are listed in the appendix 1.

Material for anatomical studies was fixed in FAA 50% (Johansen, 1940) and stored in alcohol 70%. The transversal sections were cut by hand in the apical region of the elongated axis, in the apical region of the inflorescence, the median region of the elongated axis bracts and inflorescence bracts, and in the median region of the scapes. The sections were double stained with fuchsine and astra blue (Roeser, 1962), and mounted in semi-permanent slides with glycerine jelly. The pictures were captured with picture capturer of the microscope Olympus PM-20. The anatomical observations were focused on inflorescence arrangement.

Results

Growth in *P.* sect *Diphyomene* starts with the formation of a small and short living (*P. flaccidus*) to rather large rosette taking a longer period until it flowers (*P. erectifolius, P. giganteus, P. polycladus*). The formation of the inflorescence is initiated by the change from rosulate to an elongated caulescent growth. In many species, the rosulate leaves get lost soon after, so that the rosette is no longer present at the flowering stage. This reproductive axis bears sterile bracts in spiral arrangement, these bracts are usually much smaller than the rosette leaves, except for *P. flaccidus* where there is no or nearly no difference. It is terminated by an inflorescence presenting two different branching patterns. In *P. erectifolius*, *P. giganteus* and *P. polycladus* it is a tribotryum with terminal dibotryum and several lateral dibotrya. Each lateral subunit is inserted in the axil of a fertile bract (pherophyll) that surrounds partially a set of basic units (Fig. 1 E, circle). Each basic unit corresponds to one scape with sheath and capitulum (botryum or raceme). A basic unit terminates the apical subunit (Fig. 1 F, arrow) as well as any of the lateral subunits. The number of subunits and the number of basic units vary among individuals of the same species and among the different species. In *P. flaccidus* the inflorescence is a pleiobotryum with terminal subunit. It is composed of an elongated axis with sterile bracts and of an inflorescence, which is formed by one subunit that may possess fertile bracts delimiting the basic units (Fig 1 G). In this species, the number of basic units varies among individuals, but one is always in terminal position.

Paepalanthus erectifolius (Fig. 1 A) has an elongated axis of up to 1.5 m. high. The inflorescence is composed of ca. 10 fertile bracts each partly surrounding a group of about 9 basic units. In *P. erectifolius*, as well as in *P. giganteus* and *P. polycladus*, secondary inflorescences lateral to the elongated axis may occur (Fig. 1 H, arrow), however with low frequency and generally associated with mechanical injuries of the elongated axis. In *P. giganteus* (Fig 1. C), the elongated axis bearing the inflorescence may be up to 2m high. The inflorescence has ca. 11 fertile bracts on the main axis, each bearing a subunit of about 10 basic units. In *P. polycladus* (Fig. 1 D), the elongated axis is about 30 to 40cm long. The inflorescence comprises ca. 4 fertile bracts, the subunits in their axils being composed only of about 4 basic units. *P. flaccidus* (Fig 1 B) is the smallest species and is usually less than 20cm high. The inflorescence comprises a single terminal subunit or additional lateral subunits, which may have or lack pherophylls. The subunits are highly variable in size and may be composed of about 15 basic units. In this species, secondary inflorescences lateral to the elongated axis frequently occur, but with irregular pattern (Fig.1 I).

They may be crowded near the distal end what makes it sometimes difficult to distinguish these renewals from the primary inflorescence at a first glance. The zone of lateral subunits is however never interrupted by sterile bracts.

The anatomical structure of the distal part of the elongated axis has a clearly distinct epidermis, cortex, and a central part composed many bifacial to subconcentric vascular bundles leaving a pith like part with fewer or even no bundles in the center. (Fig. 2 A-C). In all species, the epidermis is uniseriate and is clearly distinct from the subepidermal tissue by its much smaller cells. In the more hygromorphic *P. flaccidus*, the epidermis has thin cell walls (Fig. 2 C), while the other more xerophytic species have prominently thickened cell walls (Fig 2. A-B). In relation to the central part the cortex is much thinner. The relatively small *P. flaccidus* has a cortex only a few cell layers thick. As the axis is bearing bracts, there may appear some vascular strands in the cortex transpassing from the central part to the leaves (Fig. 2 B). In the transversal section, the cortical cells appear isodiametric round leaving triangular intercellular spaces between them. In all species, the central part is separated from the cortex by a single layer of cells with entirely sclerified walls. Sometimes, the adjacent outer layer has some cells with the anticlinal and the inner periclinal walls also thickened (Fig. 2 C). The vascular bundles are amphivasal and concentrated towards the periphery of the vascular cylinder leaving thus a pith like central part.

Longitudinal sections of the inflorescence show that the vascular supply for each subunit from the central part separates at different levels (Fig 2 D, arrow). At the base of each subunit the vascular strands arrange step by step in a way reflecting the position of the basic units (Fig. 2 E, circle). More basal from the position hit in Fig. 2 E the vasculature is more confusing and the pherophyll is also hit in the section (Fig. 2 F, arrow).

The anatomical structure of sterile (Fig. 3 A-B) and fertile bracts (Fig. 3 C-D) on the elongated axis is very similar. The epidermis is uniseriate, with thickened periclinal cell walls (Fig. 3 A-D). The stomata occur only in the abaxial surface, connected to an ample substomatal chamber. There is a continuous hypodermis of several layers in *P. erectifolius*, *P. giganteus*, and *P. polycladus* on the adaxial side, and there is a discontinuous hypodermis on the abaxial side not clearly distinguishable from the base of the buttresses with the vascular bundles. In *P. flaccidus,* the hypodermis is absent. The chlorenchyme is not clearly differentiated in spongy and palisade parenchyma. The collateral vascular bundles in the buttresses are equidistant to both epidermis (Fig. 3 A-D). Sometimes, larger and smaller bundles alternate in a regular manner. The larger vascular bundles are surrounded by double sheath and are buttressed to both sides. The smaller bundles are attached in the same way only to the adaxial epidermis (Fig. 3 C). In *P. erectifolius*, *P. giganteus* and *P. polycladus* the mesophyll is thick (Fig. 3, A, C), in *P. flaccidus* it is thin (Fig. 3 B, D).

The scapes of all the species (Fig. 3 E-F) are radially symmetric. In *P. erectifolius*, *P. giganteus* and *P. polycladus* (3 Fig. E) they are multicostate and thus cylindrical, but in *P. flaccidus* (3 Fig F) they are tricostate and thus more or less triangular. The number of ribs varies between species: 8 in *P. erectifolius*, 3 in *P. flaccidus*, 7 in *P. giganteus*, and 5 in *P. polycladus*, but is generally constant for the species. To facilitate orientation a schematic drawing is given in fig. 4. The epidermis is uniseriate. In the cortex chlorenchyme strands alternate with collechyme strands (Fig. 3 E-F). The more developed tissue forms the ribs. Dependent from species and sometimes also from the developmental stage this may be either the aerenchyme or the collenchyme. The number of vascular bundles is twice the number of chlorenchyme strands. The bundles are arranged in the way that an outer and an inner circle are separated by an undulating, usually uniseriate sclerenchymatic band. The outer bundles are adjacent to the chlorenchyme strands and separated from them by an arc of enlarged hyalinous cells. These arcs form together a second but discontinuous circular band. Size and shape of the cells of sclerenchymatic ring and hyalinous cells may be very similar. In black and white photographs it can be therefore difficult to distinguish both. They stain however usually markedly different, so that it is relatively easy to separate both in the microscope. In *P. erectifolius* (Fig. 3 E), *P. giganteus* and *P. polycladus,* the scapes have a well developed kind of pith with fine cell walls, while this tissue is strongly reduced in *P. flaccidus* (Fig 3 F).

Discussion

According to the morphological results, *P.* sect. *Diphyomene* can be divided into two homogeneous groups (Tab. 1). The inflorescence of group A is a tribotryum with terminal dibotryum. The branching pattern is shown in Fig. 5 A. Within the inflorescence (part I) all axis except the scapes of the basic units are extremely reduced. They are drawn here elongated only to allow the representation of the branching pattern. The part proximal to the inflorescence (part II), the hypotagma (“Unterbau” sensu Troll, 1964), is elongated. In this part usually no axillary ramification takes place. Each lateral subunit is born in the axil of a small bract, the pherophyl. Within the subunits pherophylls are lacking. This seems to be in conflict with the general assumption that seed plants branch exclusively from leaf axils. It is however well known that the inner flowers in the capitula of many Asteraceae as well as the inner flowers in the capitula of *Syngonanthus* Ruhland (Eriocaulaceae) lack pherophylls. The inflorescence of group B is a pleiobotryum with terminal botryum (Fig. 5 B). The pattern is very similar to the pattern in Fig. 5 A, differing only in the presence of additional dibotrya in the position of the lowermost basic unit of the lateral subunits of Fig.5 A. While the prophylls are lacking in inflorescences of this type as well, the pherophylls may obviously lack too. If pherophylls (fertile bracts) are present, one can find some bearing more than a single subunit in their axil. If the pherophylls are lacking, the higher branching degree can be detected from the blooming sequence. The pattern for a subunit with terminal basic unit is always from distal to proximal. This sequence is clearly to be seen in group A. If intermingled basic units of variable size and age obscure this blooming sequence, this indicates the presence of a higher branching order. Its detailed recognition however requires ontogenetic studies. Because of the intra-specific variability in branching and inflorescence size, such studies are highly problematic as it remains often uncertain whether documented developmental stages would have led to the same mature inflorescence.

In all species, additional axillary inflorescences inserted on the elongated axis (hypotagma) may occur without regular pattern (Fig. 1 H, arrow-Fig. 1I). In group B, this occurs more frequent. These lateral inflorescences are often weaker than those terminating the elongated axis, but their structure generally repeats the structure of the main inflorescence. The developmental stimulus for these lateral inflorescences is unknown but seems to be related to the habitat of the species. Species of group A are xerophytes, monocarpic, with ephemeral and erect reproductive axis. In these, the development of a secondary inflorescence is occasional and seems to be correlated to damages or developmental malfunctions of the apical bud or caused by mechanical injuries to the elongated axis. The species of group B are hygrophytes, perennial or, at least, longer living and several times flowering. The reproductive axis is typically erect like in group A, but frequently washed down by heavy rains and appearing then as a decumbent stem. As the habitat is irregularly flooded, the seasonal growth units (SGU) may be obscured and the ramification pattern can be affected in an unpredictable way (Stützel, unpublished data).

The anatomical structure supports the existence of two groups within *P.* sect. *Diphyomene* (Tab. 1). The main differences are as follows: a) in the elongated axis, the variation in the thickness of the epidermal cell walls and in the cortex dimension, b) in the bracts of the elongated axis and the inflorescence, the variation in the thickness of the mesophyll, and presence or not of a hypodermis, c) in the scapes, variation in format and in size of the pith-like tissue. Apart from the number of ribs per scape, there is little variation within the species of group A. Therefore, considering the anatomical variation within Eriocaulaceae (Scatena *et al.*, 2005), group A can be considered very homogeneous. At present, group B consists only of *P. flaccidus*, but there are more species showing a similar morphology and growing under similar conditions. Not all of them are confined to *P. sect. Diphyomene* but hidden in the ill defined *P.* subsect. *Eupaepalanthus* Ruhland. Further studies including more species of this type and also from this group are required and may lead to a more satisfying generic and infrageneric affiliation of these species.

The species of group A share morphological and anatomical similarities with species of *Actinocephalus*. The species of *Actinocephalus* defined in pattern 2 *sensu* Oriani *et al.* (2008), like *Actinocephalus polyanthus* (Bong.) Sano, are also monocarpic, with ephemeral elongated reproductive axis, and umbelliform inflorescences in the distal part of lateral branches (Sano, 1996). Anatomically, it is very difficult to distinguish these species from *Actinocephalus* (Oriani *et al.*, 2005). Phylogenetic studies involving these two groups point to a possible relation among them or even sister group relationship (Giulietti *et al.*, 2000; Unwin, 2004; Andrade, 2007, Andrade *et al.*, in press; Trovó *et al*, Cap. 1).

However, the morphology does not support a close relationship, as the umbel-shaped terminal inflorescences of *P.* sect. *Diphyomene* cannot be derived directly by reduction of the lateral branches from the species of *Actinocephalus* with their umbel-shaped lateral inflorescence. The inflorescence in *Actinocephalus* is open in the way that the elongated axis normally ends with the formation of sterile bracts (Oriani *et al.*, 2008). The sequence of the lateral branches is initiated and blooms from the base to the apex of the elongated axis, while the inflorescence in *P.* sect. *Diphyomene* is closed, and the subunits bloom from the apex to the base of the inflorescence. It is however striking that the blooming sequence in the terminal umbel in *P.* sect. *Diphyomene* is the same as in the lateral umbels of *Actinocephalus* with a blooming sequence from top to bottom. Therefore, it might be assumed that the entire inflorescence in *P.* sect. *Diphyomene* corresponds to one of the lateral branches of the species of *Actinocephalus* from pattern 1 *sensu* Oriani *et al.* (2008). Species like *Actinocephalus ciliatus* (Silveira) Sano have lateral branches in a proliferating rosette that also support closed composed inflorescences (Stützel, 1984; Oriani *et al.*, 2008). This hypothesis would imply a change from a lateral position to a terminal one or vice versa. It is difficult to imagine such a shift and in addition the floral morphology is not in favor of a sister group or other close relationship (Rosa and Scatena, 2007). Within well defined groups in Eriocaulaceae the stigmas are either bifid (*P.* subgen. *Platycaulon*, *P.* subgen. *Xeractis*, *Lachnocaulon*, *Tonina*) or simple

(*Actinocephalus, Syngonanthus, Leiothrix*). To clarify the relationships further studies seem to be essential, including *P.* subsect. *Eupaepalanthus* especially *P.* ser. *Variabiles*, which is inhomogeneous in any relevant aspect.

The inflorescence structure of the species of group B is relatively common in Eriocaulaceae, it can be found in other genera, *e.g.* in *Syngonanthus* sect. *Carphocephalus* Koern., and also in other subgroups of *Paepalanthus* (Stützel, 1984). The phylogenetic position of the species of group B is also not yet established, but some results points to a close relation to some species of *P.* sect. *Polyactis* Ruhland (Unwin, 2004; Andrade, 2007; Andrade *et al.*, in press; Trovó *et al*, Cap. 1). However, inflorescences in *P.* sect. *Polyactis* have not yet been studied. The intra-specific variability known now from *P. flaccidus* indicates that these studies will be even more difficult than earlier investigations in the family.

Finally, the features used by Ruhland (1903) to define *P.* sect. *Diphyomene* (umbel inflorescences and elongated steam) have diagnostic value, and work in herbarium specimens and for diagnostic purpose. They do not allow forming homogeneous groups, as the characters are probably plesiomorphic and occur in several definitely not closely related groups. They need to be reevaluated to achieve a natural classification for these species. As demonstrated by Gonzáles & Rudall (2001) and Vegetti & Anton (1995), the description of the branching pattern of inflorescences revealed to be a very important tool to attempt the phylogenetic relations in Eriocaulaceae too. The typological and anatomical approaches of inflorescences were shown to be useful for the establishment of homologies of the reproductive parts of the species of *P.* sect. *Diphyomene* and are thus a promising field in the systematics and evolution of the Eriocaulaceae.

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Weberling, F. 1989. Morphology of flowers and inflorescences. Cambridge: Cambridge University Press.

Appendix 1. Specimens observed and voucher specimens for anatomy.

***Paepalanthus erectifolius* Silveira** (voucher: *Trovó et al. 326*).

Brasil. Minas Gerais. Diamantina: 03 Mar 1980, *Giulietti 941-80* (SPF); 01 Mai 2001, *Costa & Sano 264* (SPF). Fechados: Serra do Cipó; 22 Mar 1982, *Hensold 558* (SPF); 23 Abr 1982, *Hensold 748* (SPF). Gouveia: 25 Mai 1989, *Hatschbach & Nicolack 53005* (SPF); 20 Mai 1990, *Arbo et al. 4509* (SPF); 13 Jun 1996, *Mello-Silva et al. 1119* (SPF); 14 Mar 1999, *Souza & Souza 22327* (SPF). Jaboticatubas: Parque Nacional da Serra do Cipó, 15 Jun 2000, *Costa & Fiaschi 165* (SPF); 23 Abr 2006, *Pirani et al. 5541* (SPF). Santana do Riacho: Parque Nacional da Serra do Cipó, 26 Mar 1973, *Giulietti & Menezes CFSC 4023* (SPF); 29 Mar 1973, *Semir et al. CFSC 4073* (SPF); 29 Mar 1973, *Giulietti et al. CFSC 4074* (SPF); 26 Jul 1973, *Monteiro CFSC 4298* (SPF); 27 Mai 1977, *Menezes CFSC 7309* (SPF); 12 Mar 1990, *Souza & Vitta CFSC 11784* (SPF); 15 Mar 1990, *Arbo et al. 4119* (SPF); 27 Mar 1991, *Pirani et al. CFSC 12225* (SPF); 27 Jul 1991, *Giulietti et al. CFSC 12457* (SPF); 22 Set 1999, *Costa et al. 86* (SPF); 25 Set 199, *Costa et al. 87* (SPF); 21 Mar 2000, *Costa et al. 152* (SPF); 21 Jun 2000, *Costa & Fiaschi 212* (SPF); 05 Jul 2001, *Souza et al. 25180* (SPF); 04 Fev 2006, *Trovó et al. 224* (SPF); 26 Jul 2006, *Silva et al. 16* (SPF); 15 Fev 2007, *Trovó et al. 326* (SPF); 20 Set 2007, *Trovó et al. 424* (SPF); Mar 1990, *Faria et al. 053* (SPF).

***Paepalanthus flaccidus* (Bong.) Kunth.** (voucher: *Trovó et al. 168*).

Brasil. Minas Gerais. Barão de Cocais: 4 Mai 1982, *Hensold CFCR 3941* (SPF). Botumirim: 20 Nov 2007, *Mello-Silva et al. 3064* (SPF). Datas 24 Mar 1986, *Mello-Silva et al. CFCR 9758* (SPF). Diamantina: 28 Jan 1976, *Marcio et al. 14028* (SPF); 5 Abr 1980, *Giulietti CFCR 72* (SPF); 31 Out 1981, *Hensold CFCR 3603* (SPF); 15 Out 1984, *Isejima et al. CFCR 5551* (SPF); 22 Nov 1985, *Pirani et al. CFCR 8577* (SPF); 2 Dez 1991, *Braga et al. 426* (SPF); 12 Jul 1996, *Parra et al. 50* (SPF); 14 Jul 1996, *Sano et al. 354* (SPF); 11 Fev 1998, *Sano et al. 835* (SPF); 9 Jul 2001, *Costa 305 et al.* (SPF); 22 Mai 1982, *Hensold et al. CFCR 3499* (SPF). Itacambira: 9 Jan 1986, *Cordeiro et al. CFCR 9147* (SPF); 16 Dez 1994, *Rivadavia 317* (SPF). Santana do Riacho: 28 Mai 1972, *Joly et al. CFSC 2315* (SPF); 21 Ago 1972, *Joly et al. CFSC 3095* (SPF); 29 Abr 1973, *Semir et al. CFSC 4093* (SPF); 3 Set 1973, *Giulietti et al. CFSC 4322* (SPF); 13 Out 1989, *Scatena et al. CFSC 11634* (SPF); 27 Abr 1991, *Pirani et al. CFSC 12291*(SPF); 23 Set 1999, *Costa et al. 79* (SPF); 6 Jan 2000, *Costa et al. 135* (SPF). São Tomé das Letras: 20 Jun 1962, *Mattos et al. 10346* (SPF). São Paulo. Itirapina: 7 Abr 2005, *Trovó et al. 168* (SPF).

Paepalanthus giganteus **Sano** (voucher: *Trovó et al.* 384).

Bolivia. Santa Cruz. Velasco: 19 Mai 1995, *Abbott 16850* (SPF). Brasil. Amazonas. Rodocó: 25 Out 1993, *Sanaiotti 295* (SPF). Distrito Federal. Brasília: 02 Mai 1983, *Kirkbride 5282* (SPF); 14 Jun 1988, *Mendonça & Rocha 10100* (SPF). Goiás. Alto Paraíso: 09 Mai 1987, *Menezes 1218* (SPF). Cristalina: 28 Mar 1973, *Rizzo 8927* (SPF). Sem localidade: 26 Jul 1978, *Pires & Santos 16214* (SPF). Mato Grosso. Novo Aripanã: 20 Abr 1985, *Ferreira 5155* (SPF). Sinop: 22 Set 1985. *W. Thomas et al. 3979* (SPF). Mato Grosso do Sul. Coxim: 22 Mai 1982, *Pott 2232* (SPF). Minas Gerais. Couto de Magalhães: 17 Jul 1984, *Giulietti et al. CFCR 4700* (SPF). Diamantina: 03 Abr 1980, *Giulietti 934-80* (SPF); 10 Abr 1982, *Isejima et al. CFCR 3592* (SPF); 18 Mai 1990, *Arbo et al. 4431* (SPF). São Roque de Minas: Parque Nacional da Serra da Canastra, 10 Dez 1994, *Romero & Nakajima 1581* (SPF); 22 Mar 1995, *Nakajima et al. 974* (SPF); 21 Mar 1998, *Sano et al. 968* (SPF); 14 Mai 2007, *Trovó et al. 384* (SPF). São Paulo. Itirapina: 31 Jul 1998, *Tannus & Assis 105* (SPF). Tocantins. Mateiros: 06 Ago 2006, *Trovó et al. 295* (SPF); 07 Ago 2006, *Trovó et al. 311* (SPF).

Paepalanthus polycladus **Silveira** (voucher: *Trovó & Watanabe 391*).

Brasil. Minas Gerais. São Roque de Minas: Parque Nacional da Serra da Canastra, 18 Abr 1982, *Castro 306* (SPF); 18 Abr 1982, *Castro 307* (SPF); 16 Abr 1994, *Romero et al. 844* (SPF); 18 Mar 1995, *Nakajima et al. 867* (SPF); 18 Mar 1995, *Nakajima et al. 882* (SPF); 10 Mai 1995, *Nakajima et al. 1009* (SPF); 11 Mai 1995, *Romero et al. 2219* (SPF); 15 Jul 1995, *Romero et al. 2420* (SPF); 18 Jul 1995, *Nakajima et al. 1257* (SPF); 28 Set 1995, *Romero et al. 2995* (SPF); 19 Mar 1998, *Sano et al. 942* (SPF);15 Mai 2007, *Trovó & Watanabe 391* (SPF).

Table 1. Species of *Paepalanthus* sect. *Diphyomene* Ruhland, according to characteristics of typology and anatomy of the reproductive axis.

Group	Species	Inflorescence	Anatomy
A	*P. acanthophyllus* Ruhland *P. amoenus* (Bong.) Körn. *P. chiquitensis* Herzog *P. cordatus* Ruhland *P. decussus* Körn. *P. erectifolius* Silveira *P. formosus* Moldenke *P. giganteus* Sano *P. moldenkeanus* R.E. Schult *P. polycladus* Silveira *P. urbanianus* Ruhland *P. weddellianus* Koern.	- Tribotryum with terminal subunit - Pherophylls present	Cortex of the elongated axis: - Epidermis with thickened cell walls - Parenchyma constituted of several layers Sterile and fertile Bracts: - Thick mesophyll - Presence of hypodermis Scapes: - Cylindrical - Ample pith tissue
B	*P. babyloniensis* Silveira *P. flaccidus* (Bong.) Kunth *P. strictus* Koern. *P. trichophyllus* (Bong.) Koern.	- Pleoibotryum with terminal subunit - Pherophylls absent	Cortex of the elongated axis: - Epidermis with thin cell walls - Parenchyma constituted of few layers Sterile and fertile Bracts: - Narrow mesophyll - Absence of hypodermis Scapes: - Triangular - Reduced pith tissue

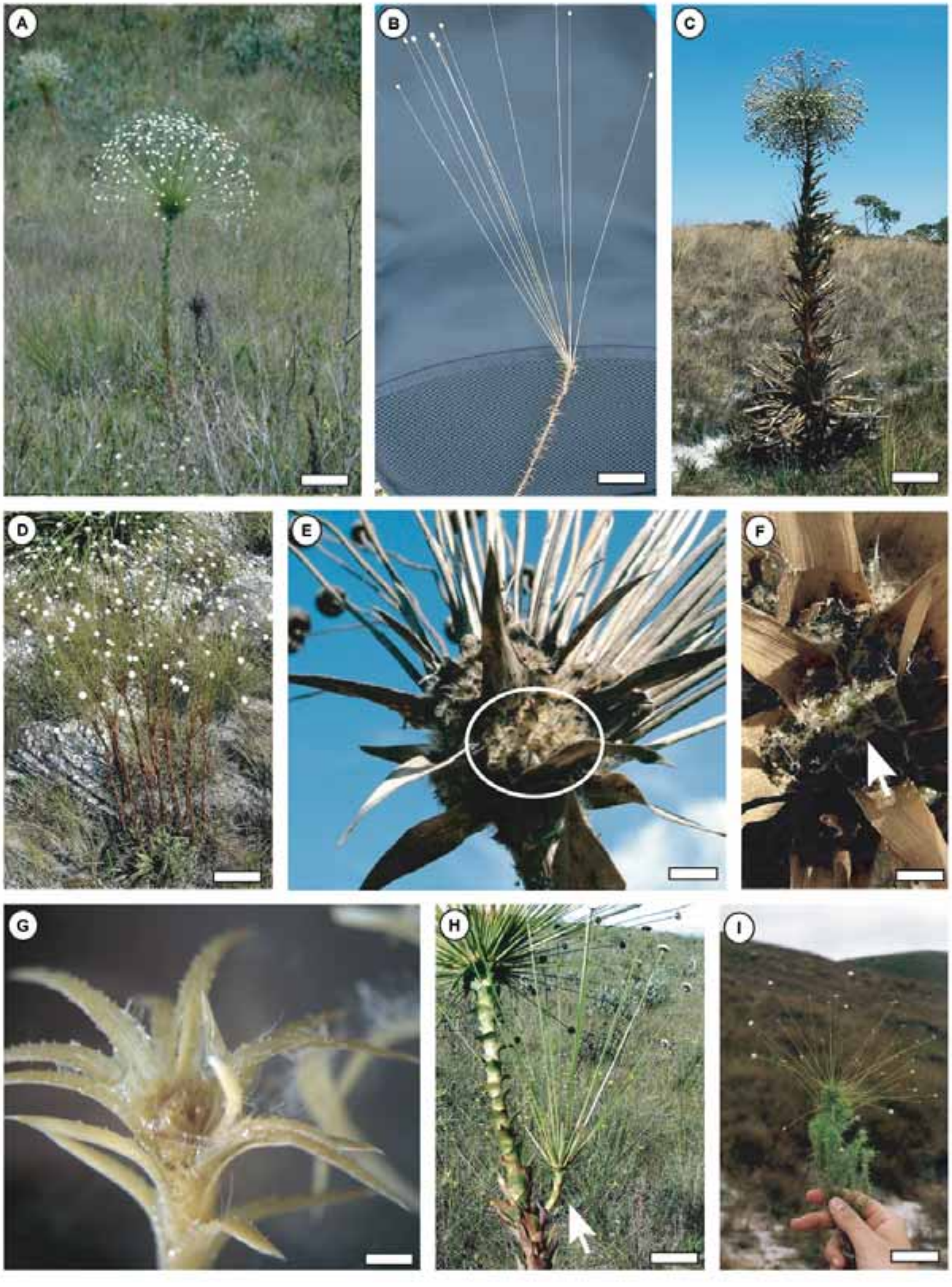


Figure 1. Habit and inflorescences of *Paepalanthus* sect. *Diphyomene*. A, E, H: *Paepalanthus erectifolius* Silveira. B, G, I: *Paepalanthus flaccidus* (Bong.) Kunth. C, F: *Paepalanthus giganteus* Sano. D: *Paepalanthus polycladus* Silveira. [A-D] habit. [E-F] inflorescences with removed scapes, circle indicates one subunit, arrow indicates the terminal basic unit of the subunit. [G-H] Lateral inflorescence, arrow indicates a lateral inflorescence in H. Scale bars = A: 15.0 cm. B: 2.5 cm. C: 20.0 cm. D: 8.0 cm. E: 0.5 cm. F: 1.5 cm. G: 0.5 cm. H: 4.0 cm. I: 4,5 cm. (*P. erectifolius, Trovó et al. 326*; *P. flaccidus, Trovó et al. 168; P. giganteus*, *Trovó et al. 384*; *P. polycladus*, *Trovó & Watanabe 391*).

Figure 2. Reproductive axis cross sections of *Paepalanthus* sect. *Diphyomene*. A, D, E, F: *Paepalanthus erectifolius* Silveira. B: *Paepalanthus giganteus* Sano. C: *Paepalanthus flaccidus* (Bong.) Kunth. [A-C] Apical region transversal sections. [D] Inflorescence longitudinal sections, arrows indicate vascular bundles ramifications. [E-F] Inflorescence transversal sections, circle indicates a basic unit, arrow indicates a pherophyll involving a subunit. Scale bars = A: 200 µm. B: 70 µm. C: 50 µm. D: 3.0 mm. E: 40 µm. F: 50 µm. (*P. erectifolius, Trovó et al. 326*; *P. flaccidus, Trovó et al. 168; P. giganteus, Trovó et al*. *384*).

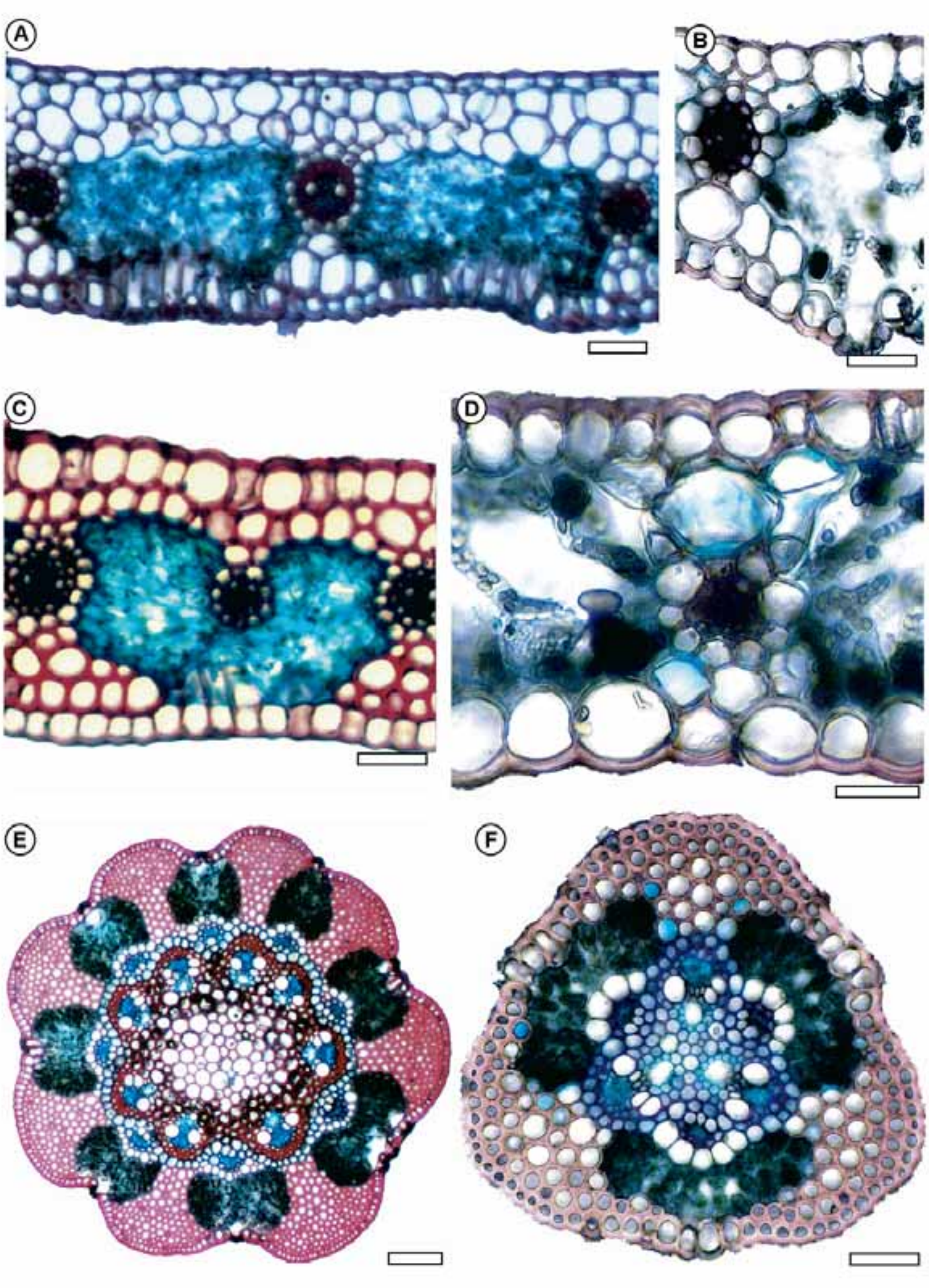


Figure 3. Bracts and scapes; cross sections of *Paepalanthus* sect. *Diphyomene*. A: *Paepalanthus giganteus* Sano. B, D, F: *Paepalanthus flaccidus* (Bong.) Kunth. C: *Paepalanthus polycladus* Silveira. E: *Paepalanthus erectifolius* Silveira. [A-B] Bracts of the elongated axis. [C-D] Inflorescence bracts. [E-F] Scapes. Scale bars = A: 50 µm. B: 30 µm. C: 50 µm. D: 40 µm. E: 80 µm. F: 50 µm. (*P. erectifolius, Trovó et al. 326*; *P. flaccidus, Trovó et al. 168; P. giganteus*, *Trovó et al*. *384*; *P. polycladus*, *Trovó & Watanabe 391*).

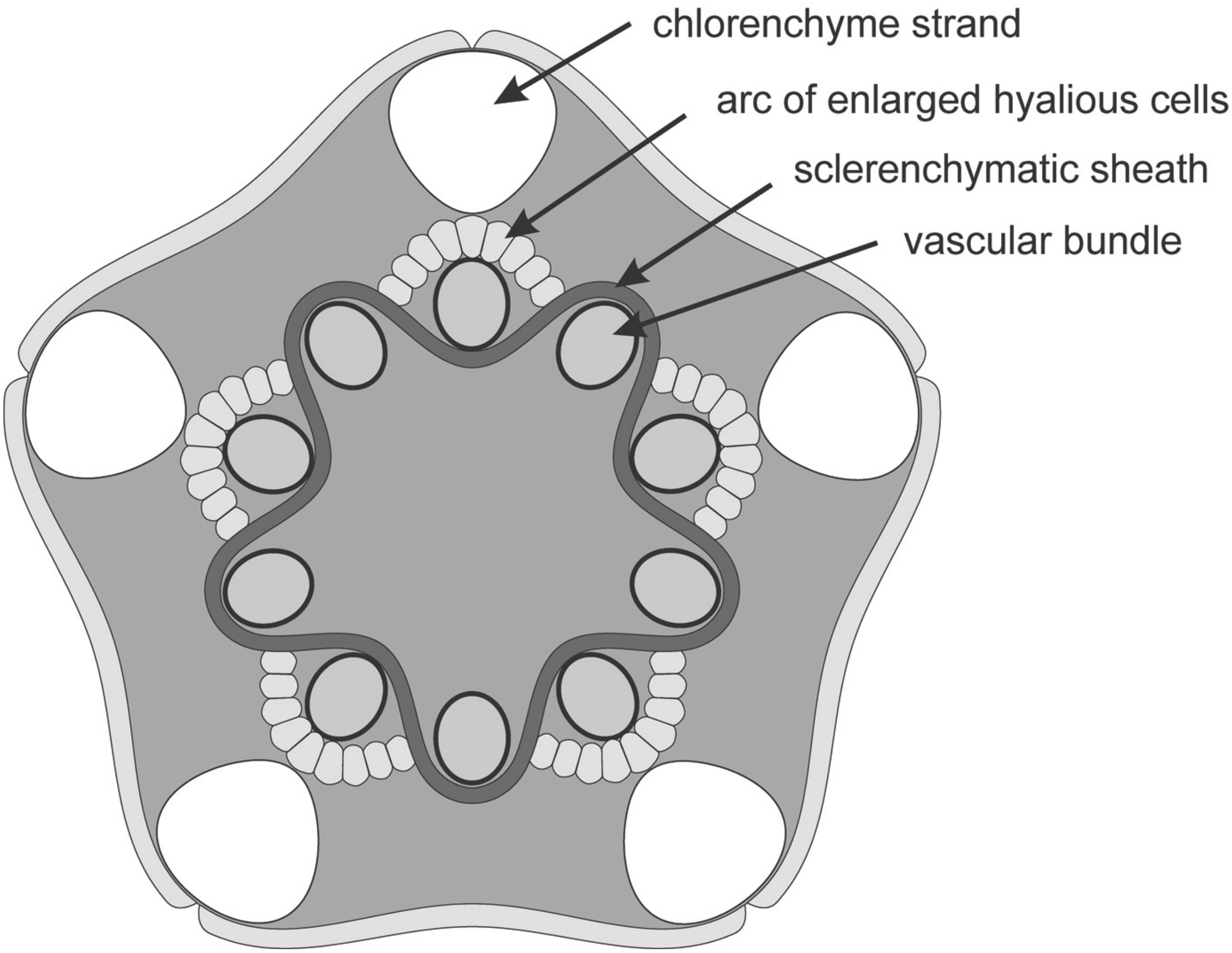


Figure 4. Transversal section of a scape in Eriocaulaceae

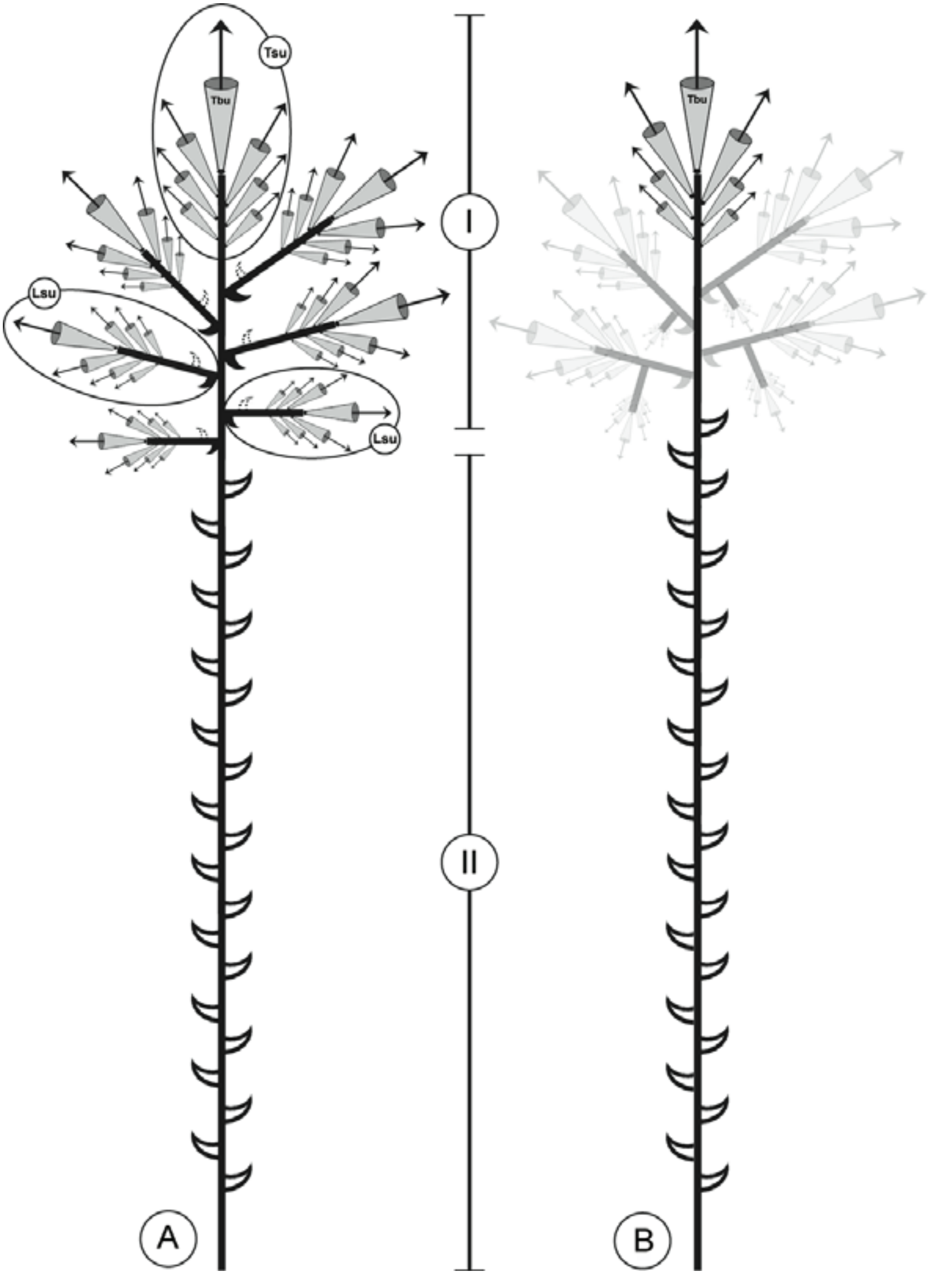
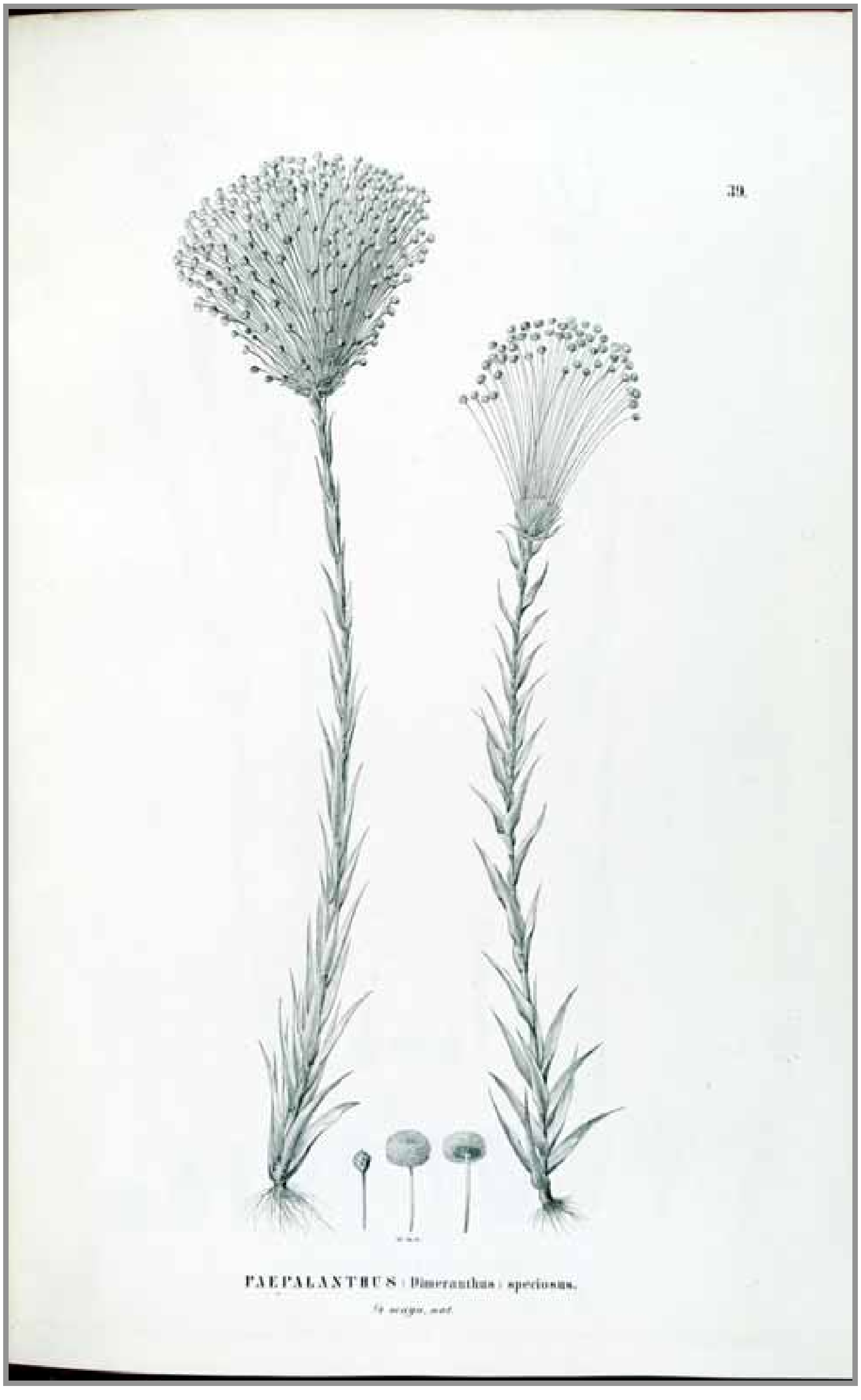


Figure 5. Ramification pattern of the inflorescences of *Paepalanthus* sect. *Diphyomene*. A: Tribotryum with terminal dibotryum B: Pleiobotryum with terminal botryum. White leaves represent sterile bracts, black leaves represent pherophylls, and doted leaves represent the expected position of the lacking prophylls. Shade structures may be present or not. Tsu = terminal subunit, Lsu = lateral subunit, Tbu = terminal basic unit. In both structures all branches but the scapes are condensed in region I in the plants.

CAPÍTULO III

O status genérico de *Paepalanthus* sect. *Diphyomene* Ruhland (Eriocaulaceae)



39.

PAEPALANTHUS (Dimeranthus) speciosus.

½ magn. nat.

Resumo - *Paepalanthus* Mart. é o maior gênero de Eriocaulaceae, compreendendo cerca de 500 espécies distribuídas majoritariamente na região neotropical. Estudos filogenéticos demonstram que o gênero é polifilético, mas que inúmeras categorias infragenéricas são monofiléticas. Com o objetivo de tornar a classificação de *Paepalanthus* congruente com as filogenias de Eriocaulaceae, tendo como base também estudos de campo e materiais de herbário, apresentamos a proposta de elevar *Paepalanthus* sect. *Diphyomene* ao status genérico. O grupo consiste de 10 espécies restritas à América do Sul. É definido por possuir inflorescências arranjadas em tribótrio com dibótrio terminal, unidade básica terminal e ferofilos presentes. Outras características marcantes do gênero são: as flores dímeras, a sépala dolabriforme na flor pistilada, os estaminódios completamente reduzidos na flor pistilada e o longo antóforo na flor estaminada. Neste trabalho propomos 10 novas combinações, 18 novos sinônimos, 6 lectotipificações, 2 novos status, 1 neotipificação e 1 epitipificação.

Palavras chave: América do Sul; *Diphyomene*; Eriocaulaceae; Nomenclatura; Taxonomia

Abstract - *Paepalanthus* Mart. is the largest genus in the Eriocaulaceae, comprising about 500 species distributed mainly throughout the Neotropics. Through phylogenetic studies it has been demonstrated that the genus is polyphyletic, although many of its infra-generic categories are monophyletic. In an attempt to place the classification of *Paepalanthus* on a par with the phylogeny of Eriocaulaceae, based on fieldwork and herbarium studies, we propose to raise *Paepalanthus* sect. *Diphyomene* to generic status. This group consists of 10 species restricted to South America, and is defined by inflorescences being arranged in the form of a tribotrium with terminal dibotrium, a terminal basic unit and pherophylls. Further important distinguishing characteristics are dimerous flowers, a pistillate flower with dolabriform sepals, bifid stigmatic branches and completely reduced staminodes, and staminate flower with an elongated antophore. We hereby propose 10 new combinations, 18 new synonyms, 6 lectotypifications, 2 new stati, 1 neotypification, and 1 epitypification.

Key words: *Diphyomene*; Eriocaulaceae; Nomenclature; South America; Taxonomy

The generic status of *Paepalanthus* sect. *Diphyomene* Ruhland (Eriocaulaceae)[3]

Paepalanthus Mart. *nom. cons*. is the largest genus in the Eriocaulaceae. Its ca. 500 species are distributed throughout the Neotropics, with one exception, this occurring disjunct on the coast of South America and Africa (Giulietti & Hensold, 1990; Stützel, 1998). Traditionally, the genus is divided into several infra-generic categories (Koernicke, 1863; Ruhland, 1903). Studies in morphological and molecular phylogeny (Giulietti & al., 2000; Unwin, 2004; Andrade, 2007; Andrade & al., in press; Trovó & al., Cap. I) indicates the genus as being polyphyletic, although many pertinent infra-generic categories are monophyletic. Sano (2004) initiated a series of taxonomic changes, necessary to establish coherence between classification and phylogeny in the family, thereby raising *Paepalanthus* sect. *Actinocephalus* (Koern.) Ruhland to generic status.

When contemplated within the context of morphological phylogeny, *Paepalanthus* sect. *Diphyomene* Ruhland is monophyletic (Giulietti & al., 2000), although paraphyletic on considering molecular phylogenies (Unwin, 2004; Andrade, 2007; Andrade & al., in press; Trovó & al., Cap. I). Detailed morphology and the anatomy of inflorescences suggest a further division into two distinct lineages (Trovó & al., Cap. II). That which corresponds to the species in group A (sensu Trovó & al., Cap. II) emerges as monophyletic and related to the species of *Actinocephalus* (Koern.) Sano. To date and in this lineage, the structure of the inflorescence is considered to be unique in the family. Extensive fieldwork and herbarium studies have lead to the conclusion that these species form a distinct group in the Eriocaulaceae. Therefore, we propose to raise the group to generic status with the exclusion of species in group B (sensu Trovó & al., Cap. II).

New Status, Synonyms, Lectotypifications and Circumscription

Diphyomene (Ruhland) Trovó, **stat. nov.** ≡ *Paepalanthus* sect. *Diphyomene* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 184. 1903.—Lectotype (here designated): *Diphyomene urbaniana* (Ruhland) Trovó

= *Paepalanthus* (*Diphyomene*) [unranked] § *Vestiti* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 184. 1903.—Lectotype (here designated): *Diphyomene acanthophylla* (Ruhland) Trovó. **syn. nov.**

= *Paepalanthus* (*Diphyomene*) [unranked] § *Foliosi* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 184. 1903.—Lectotype (here designated): *Diphyomene amoena* (Bong.) Trovó. **syn. nov.**

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[3] Manuscrito submetido ao periódico Taxon em 09 de Novembro de 2009.

Herbs perennial, 40--300 cm. Rhizome present, aerial stem 0.5--5.0 cm long. Rosette leaves persistent or deciduous, linear to lanceolate, flat, patent to contort, 1.5--35.0 x 0.1--3.0 cm, glabrous or hairy on both surfaces, entire margin ciliated or glabrous, apex round to acuminate. Elongated axis erect, 17--295 cm long, 0.2--2.0 cm diam., glabrous; elongated axis bracts linear to lanceolate, cartaceous, recurved to erect 1.5--15.0 X 0.3--2.0 cm, glabrous or hairy on both surfaces, apex round to acuminate, entire margin ciliated or glabrous, base semi-amplexicaul to amplexicaul. Spathes 2.0--8.5 cm long, glabrous, apex oblique. Scapes 10--850, arranged in spherical to obconical umbels, 18.0--32.0 cm long, glabrous. Capitula 0.5--1.5 cm diam., discoid to semi-spherical; involucral bracts in 3 to 5 series, light-brown to dark-brown, obovate to ovate, concave, ca. 0.3 cm long., glabrous, margin ciliated or glabrous, apex obtuse to acute; receptacle semi-spherical, hairy. Flowers dimerous, 50 to 350 per capitulum; floral bracts linear, light-brown to dark-brown, concave, hairy or glabrous on the abaxial surface, ciliated or glabrous toward the apex, apex acute; staminate flowers ca. 0.3 cm long; pedicel ca. 0.1 cm long, with long hairs; sepals navicular, light-brown to golden, hairy or glabrous on the abaxial surface, ciliated towards the apex, apex round to acute; antophore carnose, elongated; corolla tubular, hyaline, membranaceous; stamens free; anthers bitecous-tetrasporangiate, pistilodes 2, papillose; pistillate flowers disposed in concentric bands, ca. 0.3 cm, sessile; sepals dolabriform, light-brown to golden, hairy or glabrous on abaxial surface, ciliated towards the apex, apex obtuse; petals obovate, membranaceous to carnose, hyalines, hairy or glabrous on abaxial surface, ciliated or glabrous towards the apex, apex round to acute; gynoecium with stigmatic branches bifid; staminodes completely reduced. Fruit a loculicidal capsule. Seeds with reticulate surface, red to brown.

Bongard (1831) described the first six Brazilian species of *Eriocaulon* L. as bearing dimerous flowers, thereby the denomination “Staminibus duobus” [unranked]. Koernicke (1863) described *Paepalanthus* subgen. *Dimeranthus* Koern., as a means of accommodating these species. Koernicke (1863) also described five new species, reduced to the status of synonym those described by Kunth (1841) and Steudel (1855), and constructed the first appropriate identification key for the group. In this key, Koernicke (1863) distributed all into three groups: plants with short stems, plants with robust, elongated stems and plants with gracile, elongated stems. *Paepalanthus* subgen. *Dimeranthus* was divided by Ruhland (1903) into three new categories: *Paepalanthus* sect. *Conodiscus* Ruhland, *Paepalanthus* [unranked] *Dimeri* Ruhland, and *P.* sect *Diphyomene*, the latter being subdivided into two categories: *Paepalanthus* [unranked] *Vestiti* Ruhland, with same-sized leaves along the stem, and *Paepalanthus* [unranked] *Foliosi* Ruhland, with leaves of different sizes on both the stem and the basal rosette. Besides the supra-specific categories, Ruhland (1903) described three new species and three new varieties.

Later, most taxonomic papers bearing upon the group were descriptions of new taxa. Herzog (1924) described *Paepalanthus chiquitensis* Herzog, as a native of Bolivia, besides extending the distribution of the group. Silveira (1908, 1928) described four species and three varieties based on his own collections from Minas Gerais. Moldenke (1947, 1952, 1964, 1971, 1974, 1978, 1983, 1987) described two species, seven varieties and two forms, the majority occurring in Brazilian savannas. Shultes (1954) described *Paepalanthus moldenkeanus* R.E. Shultes collected in Colombian savannas. Hensold (1991) combined *Paepalanthus williansii* within *Syngonanthus* Ruhland. Sano (2004) proposed a final change in nomenclature by creating a new name for the homonym *Paepalanthus speciosus* (Bong.) Koern.

Trovó & al. (Cap. II) when detailing the morphology and anatomy of inflorescences in *P.* sect. *Diphyomene*, concluded that there are two inflorescence patterns in the group, implying a further division. The species of group A correspond to those described by Koernicke (1863) through having robust, elongated stems, whereas those of group B correspond to the species described by Koernicke (1863) through having gracile, elongated stems. Trovó & al. (Cap. II) also pointed out that group A species are monocarpic and with the leaves arranged in a basal rosette during the vegetative period, whereas group B species are perennial and never present leaves in rosette form. Thus, with the available morphological and phenological evidence available, the distinction proposed by Ruhland (1903) is of taxonomic value, but only reflects characters observed in herbarium reproductive collections.

Diphyomene comprises 10 species distributed throughout savannas and rocky outcrops in South America. The center of diversity is concentrated in the savannas of the state of Goiás. Most species are narrowly distributed and the limit of generic distribution is given only by the distribution of *Diphyomene chiquitensis* (Herzog) Trovó and *Diphyomene erectifolia* (Silveira) Trovó. In *Diphyomene*, inflorescences are spherical to obconical umbellate, arranged in a tribotrium with a terminal dibotrium, terminal basic unit and pherophylls (Trovó & al., Cap. II). This structure seems to be unique in the family and represents possible synapomorphy in the group. The following characteristics are also important in distinguishing *Diphyomene* from other genera in the Paepalanthoideae: dimerous flowers, a pistillate flower with dolabriform sepals, bifid stigmatic branches and completely reduced staminodes; a staminate flower with elongated antophore. The necessary typifications and taxonomic changes are presented below.

New combinations, typifications and taxonomic changes

Diphyomene acanthophylla (Ruhland) Trovó, **comb. nov.** ≡ *Paepalanthus acanthophyllus* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 186. tab. 24. 1903.—Type: Brazil. Goiás: “Entre Rio Torto et Sobradinho, dans le sable”, 25 May 1895, *Glaziou 22323* (holotype: B!; isotypes: B!, C!, G!, K!, LE! NY!, P!).

Diphyomene amoena (Bong.) Trovó, **comb. nov.** ≡ *Eriocaulon amoenum* Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Ser. 6 Sci Math. 1: 637. 1831 ≡ *Paepalanthus amoenus* (Bong.) Koern., in Martius & Eichler, Fl. bras. (3)1: 316. tab. 42. 1863 ≡ *Dupatya amoena* (Bong.) Kuntze, Revis. gen. Pl. 2: 745. 1891.—Type: Brazil. Minas Gerais: “In glareosis graminosis pr. Capanema”, Feb 1825, *Riedel s.n.* (holotype: LE! in 2 sheets).
= *Eriocaulon longipes* Mart. ex Steud., Syn. Pl. Glumac. 2: 276. 1855.—Type: Brazil. Minas Gerais: “Brasilia”, Aug—Apr 1840, *Claussen 1156* (holotype: G!).
= *Paepalanthus amoenus* f. *prolifer* Moldenke, Phytologia 21: 417. 1971.—Type: Brazil. Minas Gerais: “Bello Horizonte, Serra do Curral—Acaba Munde”, 10 Mar 1933, *Mello Barreto 2491* (holotype: NY!). **syn. nov.**
Paepalanthus amoenus var. *curralensis* Silveira. **nom. nud.**

Silveira (1928) himself refers to specimen *Silveira 348*, corresponding to *Paepalanthus amoenus* var. *curralensis*, from a list of his own collection of Eriocaulaceae. The specimen was found at R, and contains a detailed description in Silveira’s own handwriting. However, this description has never been published. According to article 32.1 and recommendation 50.1 of the ICBN (2001), the name must be treated as *nomem nudum*.

Diphyomene chiquitensis (Herzog) Trovó, **comb. nov.** ≡ *Paepalanthus chiquitensis* Herzog, Feddes Repert. 20: 86. 1924.—Type: Bolivia. Chiquitos: “Haüfig in den Kämpfen des Cerro de Santiago, 700—800 m”, May 1907, *Herzog 114* (holotype: L!—incomplete).

Epitype: Bolivia. Santa Cruz: "Velasco Province", 19 May 1995, *J. R. Abbott 16850* (epitype—here designated: SPF! in 2 sheets).

= *Paepalanthus erectifolius* var. *glabra* Silveira, Floral. Mont. 1: 192. 1928.—Type: Brazil. Minas Gerais: "In campis prope Itambé do Serro", May 1908, *Silveira 499* (holotype: R!). **syn. nov.**

= *Paepalanthus erectifolius* var. *grandifolia* Silveira, Floral. Mont. 1: 192. 1928.—Type: Brazil. Minas Gerais: "In campis in Chapada do Couto", Apr 1918, *Silveira 711* (holotype: R!). **syn. nov.**

= *Paepalanthus formosus* Moldenke, Bol. Soc. Venez. Ci. Nat. 14:11. 1952.—Type: Venezuela. Amazonas: "Cerro Guanay, alt. 2000 m", 4 Feb 1951, *B. Maguire & al. 31754* (holotype: NY!). **syn. nov.**

= *Paepalanthus moldenkeanus* R.E. Schultes, Botanical Mus. of Leaf. 16:187. 1954.—Type: Colombia. Vaupés: "Quartzite savannah near headwaters, 900—1000 feet", 4-5 Oct 1951, *R. E. Schultes & I. Cabrera 14351* (holotype: GH! in 2 sheets). **syn. nov.**

= *Paepalanthus speciosus* var. *pulverulentus* Moldenke, Phytologia 10: 489. 1964.—Type: Brazil. Goiás: "Cristaleira elev. 1250 m", 30 Mar 1963, *Edmundo Pereira 7476* (holotype: LL! in 2 sheets). **syn. nov.**

= *Paepalanthus speciosus* var. *attenuatus* Moldenke, Phytologia 28: 466. 1974.—Type: Brazil. Goiás: "Chapada dos Veadeiros", 22 Mar 1971, *H. S. Irwin & al. 32935* (holotype: LL!; isotype: LL!). **syn. nov.**

= *Paepalanthus speciosus* var. *bolivianus* Moldenke, Phytologia 28: 467. 1974.—Type: Bolivia. Santa Cruz: "Velasco, 200 m", Jul 1892, *Kuntze s.n.* (holotype: NY!). **syn. nov.**

= *Paepalanthus speciosus* f. *calvescens* Moldenke, Phytologia 28: 467. 1974.—Type: Brazil. Goiás: "Prov. de Goyaz", May-Jul 1884, *Weddell 2133* (holotype: NY!; isotypes: P!). **syn. nov.**

= *Paepalanthus speciosus* var. *goyazensis* Moldenke, Phytologia 52: 414. 1983.—Type: Brazil. Goiás: "Chapada dos Veadeiros", 16 Apr 1956, *E. Yale Dawson 14271* (holotype: LL!). **syn. nov.**

= *Paepalanthus amoenus* var. *bolivianus* Moldenke, Phytologia 61: 444. 1987.—Type: Bolivia. La Paz: "Iturralde, Sabanna Húmeda, 180 m", 2 Aug 1985, *R. Haase 685* (holotype: LL!). **syn. nov.**

= *Paepalanthus giganteus* Sano, Taxon 53: 106. 2004 ≡ *Eriocaulon speciosum* Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Ser. 6 Sci Math. 1: 636. 1831 ≡ *Paepalanthus speciosus* (Bong.) Koern., in Martius & Eichler, Fl. bras. (3)1: 315. tab. 39, 40, 41. 1863, *nom. illeg.* non Gardner (1843) ≡ *Dupatya speciosa* (Bong.) Kuntze, Revis. gen. Pl. 2: 746. 1891.—Type: Brazil. São Paulo: "In campis Batataes", Feb 1834, *Riedel 2300* (Neotype—here designated: LE! in 2 sheets; isoneotypes: B!, G!, K!, P!). **syn. nov.**

Herzog (1924) described *P. chiquitensis* on the basis of field observations. Nevertheless, he states in the protologue that just one fragment (parts of an inflorescence, *Herzog 114*) is the holotype at L. However, the original description and type specimen are insufficient to distinguish the species unambiguously without additional evidence. Thus, on the basis of article 9.7 of the ICBN (2001), we hereby designate an epitype. This is the most widespread and variable species in this genus, therefore several formerly described species are treated here as synonyms.

Sano (2004) proposed *Paepalanthus giganteus* as a new name for the later homonym *Paepalanthus speciosus* (Bong.) Koern. In the protologue, Sano (2004) stated that the collection *Riedel 2300* in LE is a holotype of the basionym. However, this material was collected 4 years after species publication. As Bongard (1831) did not clearly indicate a type specimen and no original collection belonging to the same species has been found in LE, we consider the original material lost and designate the specimen cited by Sano (2004) as a neotype for the species.

Diphyomene cordata (Ruhland) Trovó, **comb. nov.** ≡ *Paepalanthus cordatus* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 189. 1903.—Type: Brazil. Goiás: "Chapadão de Porto Seguro dans le campo sec.", 26 Dec 1894, *Glaziou 22324* (holotype: B!, isotypes: C!, G!, K!, LE!, P!)

Diphyomene decussa (Koern.) Trovó, **comb. nov.** ≡ *Paepalanthus decussus* Koern., in Martius & Eichler, Fl. bras. (3)1: 318. 1863 ≡ *Dupatya decussa* (Koern.) Kuntze, Revis. gen. Pl. 2: 745. 1891.—Type: Brazil. Minas Gerais: "Cachoeira", s.d., *Claussen s.n.* (holotype: BR!, isotype: B!).

Diphyomene erectifolia (Silveira) Trovó, **comb. nov.** ≡ *Paepalanthus erectifolius* Silveira, Fl. serr. Min. p. 51. 1908.—Type: Brazil. Minas Gerais: "In partis siccis in Serra do Cipó", Apr 1905, *Silveira 367* (holotype: R!).

= *Paepalanthus speciosus* var. *glabra* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 187. 1903.—Type: Brazil. Minas Gerais: "Serra do Cipó, dans le camp", 26 Apr 1892, *Glaziou 19977* (lectotype—here designated: B!; isolectotypes: C!, P!). **syn. nov.**

= *Paepalanthus speciosus* var. *angustifolia* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 187. 1903.—Type: Brazil. Minas Gerais: “Serra do Cipó, prov. Minarum”, Oct, *Mathieu Libon 534* (lectotype—here designated: C!). **syn. nov.**

= *Paepalanthus speciosus* var. *chlorocephala* Silveira, Fl. serr. Min. P. 50. 1908.—Type: Brazil. Minas Gerais: “In campis siccis in Serra do Cipó”, Apr 1905, *Silveira 370* (holotype: R!). **syn. nov.**

Ruhland (1903) summarily described *Paepalanthus speciosus* var. *glabra* based on eight collections. Careful fieldwork and herbarium analysis lead to the conclusion that this material corresponds to various formerly described species. The collection *Glaziou 19977* fits the description better, and thus is designated as the lectotype.

Ruhland (1903) briefly described *Paepalanthus speciosus* var. *angustifolia* based on two collections. The specimen *Mathieu Libon 534* in C fits the description more adequately, and is therefore designated as the lectotype.

Diphyomene koernickei (Ruhland) Trovó, **comb. nov. et stat. nov.** ≡ *Paepalanthus speciosus* var. *koernickei* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 187. 1903.—Type: Brazil. Goiás: “In campis Catalão—Paracatu”, Sep 1834, *Lund 566* (holotype: C! in 2 sheets).

Diphyomene polyclada (Silveira) Trovó, **comb. nov.** ≡ *Paepalanthus polycladus* Silveira, Floral. mont. 1: 189. tab. 122. 1928—Type: Brazil. Minas Gerais: “In arenosis in serra do Chapadão”, Apr 1925, *Silveira 742* (holotype: R!).

Diphyomene urbaniana (Ruhland) Trovó, **comb. nov.** ≡ *Paepalanthus urbanianus* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 188. 1903.—Type: Brazil. Goiás: “Serra dos Veadeiros, dans campo sec”, 15 Jan 1895, *Glaziou 22318* (holotype: B!; isotypes: BR!, C!, G!, K!, LE! NY!, P!).

= *Paepalanthus urbanianus* var. *angustifolius* Moldenke, Phytologia 39: 330. 1978.—Type: Brazil. Goiás: “Chapada dos Veadeiros”, 23 Mar 1969, *H. S. Irwin & al. 24936* (holotype: NY!). **syn. nov.**

Diphyomene weddelliana (Koern.) Trovó, **comb. nov.** ≡ *Paepalanthus weddellianus* Koern., in Martius & Eichler, Fl. bras. (3)1: 317. 1863 ≡ *Dupatya weddelliana* (Koern.) Kuntze, Revis.

gen. Pl. 2: 746. 1891.—Type: Brazil. Goiás: “Marais des rochers à Prov. de Goyaz”, s.d., *Weddell 2927* (holotype: BR!; isotype: P!).

Excluded taxa

According to the *Diphyomene* concept, herein proposed, and formalizing the division as suggested by both Koernicke (1863) and Trovó & al. (Cap. II), the species below must be excluded. These species correspond to group B (sensu Trovó & al., Cap. II), and are provisory placed within *Paepalanthus* sect. *Eriocaulopsis* Ruhland.

Paepalanthus babyloniensis Silveira, Floral. mont. 1: 188. tab. 121.—Type: Brazil. Minas Gerais: “In campis arenosis in serra da Babylonia”, Apr 1925, *Silveira 428* (holotype: R!).

Paepalanthus flaccidus (Bong.) Kunth, Enum. Pl. 3: 511. 1841 ≡ *Eriocaulon flaccidum* Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Ser. 6 Sci Math. 1: 643. tab. 4. 1831 ≡ *Dupatya flaccida* (Bong.) Kuntze, Revis. gen. Pl. 2: 745. 1891.—Type: Brazil. São Paulo: “Brasilia”, s.d., *Riedel 1034* (holotype: LE!).

Paepalanthus strictus Koern., in Martius & Eichler, Fl. bras. (3)1: 319. 1863 ≡ *Dupatya stricta* (Koern.) Kuntze, Revis. gen. Pl. 2: 746. 1891.—Type: Brazil. Minas Gerais: “Crescenti in prov. Minarum”, s.d., *Gardner 5258* (lectotype—here designated: B!; isolectotypes: G!, P!).

Koernicke (1963) described *Paepalanthus strictus* based on two collections. The specimen *Gardner 5258* in B is more complete and contains the author’s own handwriting, thus being designated as the lectotype.

Paepalanthus trichophyllus (Bong.) Koern., in Martius & Eichler, Fl. bras. (3)1: 318. 1863 ≡ *Eriocaulon trichophyllum* Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Ser. 6 Sci Math. 1: 636. 1831 ≡ *Dupatya trichophylla* (Bong.) Kuntze, Revis. gen. Pl. 2: 746. 1891.—Type: Brazil: “Brasilia”, s.d., *Riedel s.n.* (holotype: LE!).

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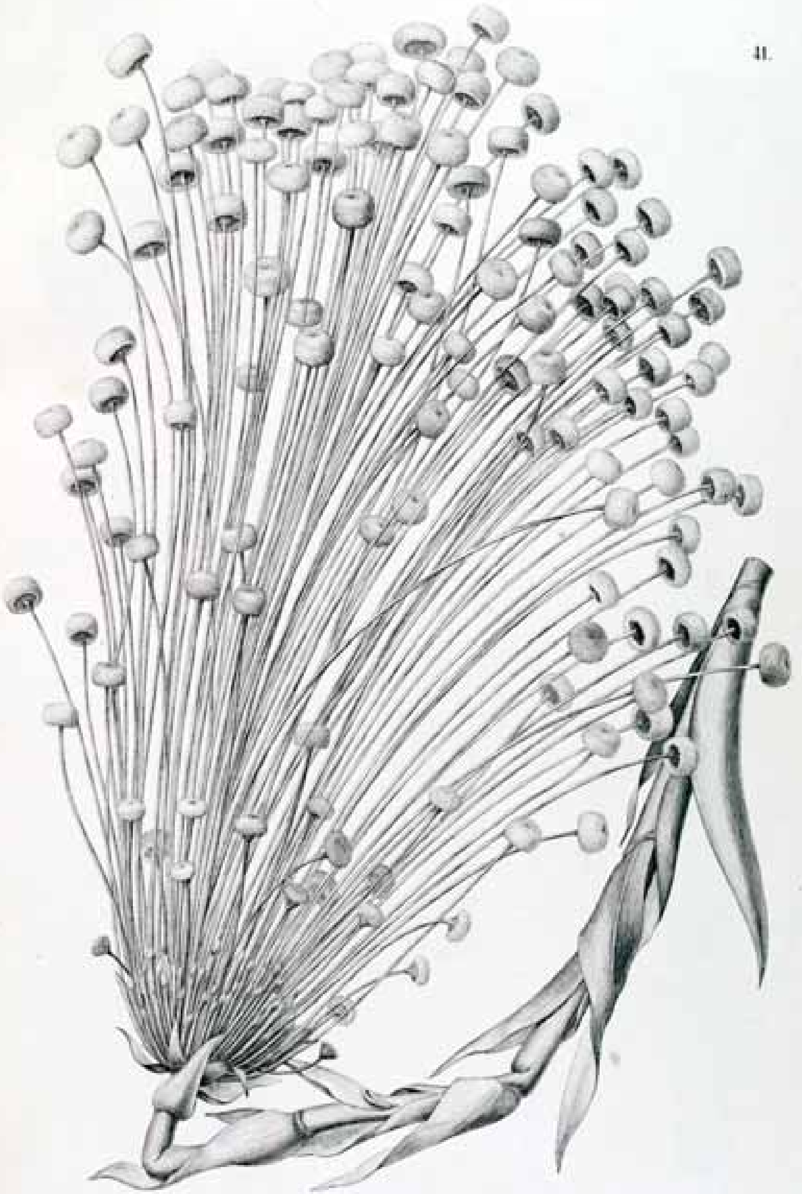
CAPÍTULO IV

Sistemática de *Diphyomene* (Ruhland) Trovó (Eriocaulaceae)



PAEPALANTHUS (Dimeranthus) speciosus.

Resumo - É apresentada a revisão taxonômica e morfológica de *Diphyomene* (Eriocaulaceae). A monografia tem como base estudos de campo e de herbário. O gênero, que consiste em 18 espécies restritas à América do Sul, é distinto pela inflorescência organizada em um tribótrio com dibótrio terminal e unidade básica terminal, sépalas dolabriformes na flor pistilada e estaminódios completamente reduzidos na flor pistilada. A maioria das espécies possui distribuição restrita, geralmente confinada a apenas uma localidade. As exceções são *D. chiquitensis* e *D. erectifolia*, amplamente distribuídas na América do Sul e na Cadeia do Espinhaço, respectivamente. As populações de *Diphyomene* ocorrem principalmente em formações savânicas do Brasil, Bolívia, Colômbia e Venezuela; no entanto algumas populações ocorrem em campinas amazônicas e campos rupestres na Cadeia do Espinhaço. A diversidade taxonômica e morfológica está concentrada na Chapada dos Veadeiros, no estado de Goiás. Com base em extensão de ocorrência, 13 espécies são consideradas criticamente ameaçadas de extinção, uma é considerada ameaçada, duas são vulneráveis e duas não sofrem risco. Além de comentários sobre o gênero, o tratamento taxonômico consiste de uma chave de identificação e a descrição completa do gênero. São fornecidas descrições detalhadas de cada espécies, comentários, mapas de distribuição, fotos e desenhos.

Palavras chave: Chapada dos Veadeiros; Paepalanthoideae; *Paepalanthus*; Savanas; Taxonomia

Abstract - A revision of the taxonomy and morphology of *Diphyomene* (Eriocaulaceae) is presented. This monograph is based on studies, both in the field and herbaria. The genus, consisting of 18 species restricted to South America, is distinguished by the tribotryum-shaped inflorescence structure with terminal dibotrya and terminal basic unit, dolabriform sepals on pistillate flowers, and completely reduced staminodes on pistillate flowers. Most species are narrowly distributed and usually restricted to a single locality, with the exception of *D. chiquitensis* and *D. erectifolia*, which are widely distributed in South America and along the Espinhaço Range, respectively. *Diphyomene* populations predominantly occur in savannas in Brazil, Bolivia, Colombia and Venezuela, although some are also distributed in the Amazonian "Campinas" and in rocky outcrops in the Espinhaço Range. Taxonomic and morphological diversity is concentrated in the Chapada dos Veadeiros in Goiás state. Based exclusively on the extent of occurrence, 13 species are considered critically endangered, one endangered, two vulnerable, and two running no risk. Besides comments on the genus, the taxonomic survey itself consists of an identification key, a generic description and detailed descriptions of each species, with commentaries, distribution maps, photos and line drawings.

Key words: Chapada dos Veadeiros; Paepalanthoideae; *Paepalanthus*; Savannas; Taxonomy

Systematics of *Diphyomene* (Ruhland) Trovó (Eriocaulaceae)[4]

Eriocaulaceae comprises ca. 1200 species and 13 genera distributed throughout the tropics. The main diagnostic feature of the family is the unisexual flowers grouped in dense capitula (Giulietti & Hensold 1990; Parra et al. in press; Sano 2004; Stützel 1998; Trovó & Sano Cap. 3). The family is divided into two sub-families, Eriocauloideae and Paepalanthoideae. The former comprises the two genera *Eriocaulon* L. and *Mesanthemum* Koern, and is characterized by diplostemonous flowers, glandular petals and stigmatic branches arising from the center of the style (Eichler 1885; Koernicke 1863; Ruhland 1903, Rosa & Scatena 2007), whereas the latter, mostly restricted to the Neotropics, with a few species of *Paepalanthus* Mart. and *Syngonanthus* Ruhland occurring in Africa, is distinguished by its isostemonous flowers, eglandular petals and nectariferous branches arising from the center of the style (Eichler 1885; Koernicke 1963; Ruhland 1903, Rosa & Scatena 2007). In the Neotropics, the centers of taxonomic and morphological diversity are located in the Espinhaço Range, especially in Minas Gerais State and the Venezuela Highlands.

The most diverse genus is *Paepalanthus*, comprising ca. 400 species. It is distinguished by its trimerous flowers, free petals on the pistillate flower, and tetrasporangiate anthers, besides the nectariferous and stigmatic branches arising on the same level. In the last full revision of Eriocaulaceae, this genus was divided into sub-categories, and now encompasses 20 infra-generic taxa above the species level (Ruhland 1903; Hensold 1988; Hensold 1991; Tissot-Squalli 1998, Sano 2004; Costa 2005, Trovó & Sano Cap. 3). Since Ruhland (1903), authors have noticed that some of these categories might represent more natural groupings than merely the genus itself, e.g. *Paepalanthus* subgen. *Xeractis* Koern. (Hensold 1988), *Paepalanthus* subgen. *Platycaulon* Koern. (Tissot-Squalli 1998), and *Paepalanthus* sect. *Actinocephalus* Koern. (=*Actinocephalus*) (Sano 2004).

The first phylogenetic studies, based on morphology, were not conclusive as to the monophyly of the subfamilies, but both pointed to the polyphyly of *Paepalanthus* (Giulietti et al. 1995; Giulietti et al. 2000). However, with recent advances in molecular and morphological studies (Unwin 2004; Andrade et al. in press; Trovó et al. Cap. 1), the monophyly of both subfamilies has now been corroborated. Nevertheless, *Paepalanthus* is confirmed as being polyphyletic, although many of its infra-generic categories are monophyletic. Four subgenera are monophyletic, but *Paepalanthus* subgen. *Paepalocephalus* Ruhland is polyphyletic.

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[4] Manuscrito a ser submetido ao periódico Systematic Botany Monographs

Paepalanthus sect. *Diphyomene* emerges as paraphyletic, although appearing as two clades consistently monophyletic (Trovó et al. Cap. 1). However, the relationships between these clades, *Actinocephalus* and other species with dimerous Ruhland flowers, remain to be clarified. One clade is composed of monocarpic species with a robust reproductive axis, whereas the other is consists of perennial species, wherein the reproductive axis is gracile. Trovó et al. (Cap. 2), on detailing the morphology and anatomy of inflorescences of *P.* sect. *Diphyomene*, concluded that the inflorescence structures in both lineages are also different. Based on phylogenetic and inflorescence studies, plus floral features, Trovó & Sano (Cap. 3) formalized the division suggested by Koernicke (1863), and Trovó et al. (Cap. 2) raised lineage A (sensu Trovó et al. Cap 2) of *Paepalanthus* sect. *Diphyomene* to generic status.

In the present monograph, the 18 species of *Diphyomene* are revised based on fieldwork and material from the following Herbaria (acronyms according to Thiers, continuously updated): ALCB, B, BHCB, BOCH, BR, C, CEN, CEPEC, CVRD, ESA, G, GFJP, HBG, HEPH, HRCB, HUEFS, IBGE, INPA, K, LE, M, MBM, OUPR, P, R, RB, S, SP, SPF, UB, UEC, UPS, W, WU. General comments on taxonomic history, morphology, phenology, reproductive biology, geographic distribution, habitat, conservation status and phylogeny, as well as a taxonomic treatment, are provided. The taxonomic survey consists of an identification keys and a generic description, as well as detailed descriptions of each species, comments, distribution maps, photos, and line drawings.

Taxonomic History

Bongard (1831) described the first Brazilian species of Eriocaulaceae with dimerous flowers. He placed six new species of *Eriocaulon* L. under the name *Staminibus duobus* [unranked]. Latter, Koernicke (1863), besides positioning these species into *Paepalanthus* subgen. *Dimeranthus* Koern., described five novelties with dimerous flowers, and reduced the species described by Kunth (1841) and Steudel (1855) to synonyms. Koernicke (1863) also provided the first identification key, thereby separating the species into three groups, namely; plants with short stems; with gracile, elongated stems; and with robust, elongated stems. Ruhland (1903) reorganized those with dimerous flowers into three new categories, *Paepalanthus* sect. *Conodiscus* Ruhland, *Paepalanthus* [unranked] *Dimeri* Ruhland (related to *P.* subgen. *Dimeranthus*) and *P.* sect *Diphyomene* Ruhland. In addition, Ruhland (1903) divided the latter into two new categories, *Paepalanthus* [unranked] *Vestiti* Ruhland, with the same-sized leaves throughout the stem and rosette, and *Paepalanthus* [unranked] *Foliosi* Ruhland, with leaves of different sizes on both the stem and rosette. Ruhland (1903) also described three new species and three new varieties of *Paepalanthus speciosus*.

Later, taxonomic papers dealing with *P.* sect. *Diphyomene* were mostly descriptions of new taxa. Herzog (1924) described *Paepalanthus chiquitensis* Herzog, at that time endemic to Bolivia. Silveira (1908, 1928) described four species and three varieties based on his own collections deposited at the R herbarium. Moldenke (1947, 1952, 1964, 1971, 1974, 1978, 1983, 1987) described two species, seven varieties and two forms. Shultes (1954) described *Paepalanthus moldenkeanus*, endemic to Colombian savannas. Hensold (1991) combined *Paepalanthus williansii* within *Syngonanthus* Ruhland. Finally, Sano (2004) detected that *Paepalanthus speciosus* (Bong.) Koern. was a latter homonym, whereby creating a new name for the species.

When studying the morphology and anatomy of inflorescences in *P.* sect. *Diphyomene*, Trovó et al. (Cap. 2) identified two inflorescence patterns, thereby implying a further division. The two patterns correspond to two groups proposed by Koernicke (1863). Trovó & al. (Cap. 2) also pointed out that, whereas group A is composed of monocarpic herbs with the leaves arranged in basal-rosette form during the vegetative period, group B consists of perennial herbs that never present leaves in this form. Thus, the distinction proposed by Ruhland (1903), although of taxonomic value, only reflects characters observed in herbarium reproductive collections. Recent phylogenetic studies (Unwin 2004; Andrade et al. in press; Trovó et al. Cap. 1) have reinforced the notion, as propounded by Koernicke (1863) and Trovó et al. (Chap. 2), of the existence of two distinct lineages within *P.* sect. *Diphyomene*. Thus, Trovó & Sano (Cap. 3) have formalized a distinction for elevating species included in group A to generic status, thereby proposing 10 new combinations, 18 new synonyms, six lectotypifications, two new stati, one neotypification, and one epitypification. Recently, Trovó and Sano (Appendix 1, 2) described eight new species for *Diphyomene.*

Morphology

Habit, roots, and stems

Diphyomene species are usually monocarpic. Vegetative individuals are composed of a single leaf-rosette covering a very short stem (Fig. 1 A, B). In certain species, such as *D. polyclada* and *D. acanthophylla*, a rhizome may link a few rosettes thereby forming clones (Fig. 1 C). In this case, these individuals may be considered monocarpic perennials. Rosette diameter may vary from a few centimeters, as in *D. flexuosa*, to more than half a meter, as in *D. chiquitensis*. During the reproductive phase, a reproductive axis emerges from the center of the rosette. This axis bears the inflorescence.

The roots in *Diphyomene* are all of the same type. As stressed by Scatena et al. (2005), the roots in this species are of a specific type, by being thin, brown and without aerenchyma. This pattern is widespread in species of Eriocaulaceae, inhabitants of non-flooded areas. This root-type is the same as that described for *Actinocephalus*, a genus occupying simillar habitats (Oriani et al. 2005).

Diphyomene species present stems of three kinds. Subterranean rhizomes, when existant, are usually associated with clonal reproduction, as described above. The clones may be released or not from individual parents. The typical vegetative stem, restricted to the rosette, is aerial, short (usually less than 4.0 cm), with reduced internodes, and, as in all the Eriocaulaceae, with hairs covering the leaf axil. The reproductive axis is an elongated stem covered by axis bracts. Detailed comments on the reproductive axis are given below.

Leaves

Leaves in *Diphyomene* are either permanent (evergreen) or, rarely, deciduous as in *D. acanthophylla* or *D. polyclada*. Most leaves are lanceolate, although linear leaves are also encountered. In some species, such as *D. erectifolia*, they may be of both shapes, but in different populations. *Diphyomene cordata* has the most distinct leaves, these being oblong-shaped. This species also possesses a unique cuspidate leaf-apex. The apex is generally acute, but can be acuminate as in *D. amoena* and *D. conferta*, mucronate as in *D. brachycaule* and *D. urbaniana*, or fairly rounded as in *D. polyclada* (Fig. 1 C). In all species, the leaves are more or less flat, except in *D. cipoensis*, where these are incurvate. The leaf-position is usually patent at the base, to sub-erect at the uppermost part. Nevertheless, in some species, as *D. brachycaule* and *D stenophylla*, even basal leaves are erect. The leaves of *D. erectifolia* populations from Bahia are frequently recurvate. There is another variation in leaf-position characterizing *D. urbaniana*, whereby the uppermost leaves are contorted.

Figure 1. Rosettes in *Diphyomene*. A. Large rosette in *D. chiquitensis*. B. Small rosette in *D. urbaniana*. C. Several rosettes linked by a rhizome in *D. polyclada*. Scale bars, A: 10 cm, B: 4 cm, C: 3 cm.

The most variable characteristics are size and pilosity. Both features vary even within a single population. Leaf-size may vary from 0.5 cm in *D. flexuosa* to 40.0 cm in *D. chiquitensis*. Leaf-pilosity is more or less constant in reproductive individuals of the same population. However, younger individuals and younger leaves tend to be hairier than those older, in both cases. Individuals growing in the shade tend to be more glabrous than those growing in open sunlight. Pilosity is also related to the drying process, as herbarium specimens are often more glabrous than free-living plants.

Reproductive Axis and Axis Bracts

The reproductive axis of *Diphyomene* species is one of the most distinctive features of the genus (Fig 2 A-D). It emerges from the center of the rosette during the reproductive stage, although there are doubts as to whether it originates from the apical or the uppermost lateral bud, a crucial point for correctly evaluating homology between this structure and the elongated axis and paraclades of *Actinocephalus*. The reproductive axis is unbranched and erect in all species except *D. flexuosa*, wherein it is tortuous. The size may vary from 4.0 cm in *D. brachycaule* to 2.75 m in *D. chiquitensis*. Diameter is not always directly related to size, since in *D. conferta* and *D. amoena* these axes are relatively long and thin. The diameter varies from 0.2 cm in *D. flexuosa* to 1.8 cm in *D. chiquitensis*. In almost all species the reproductive axis is glabrous (except at the axil of axis bracts), but not so in *D. decussa*, wherein it is sparsely hairy.

The reproductive axis is covered with bracts. Axis bracts, although variable among species, are one of the most constant characters in both species and populations of *Diphyomene*, thereby constituting one of the most important distinguishing features. They may be of the same shape throughout the axis, or may be markedly smaller from the base to the apex. The latter pattern is only found in *D. chiquitensis*, *D. longiciliata* and *D. brachycaule*. In most species these bracts are chartaceous, although in *D. hymenobracteata*, they are membranaceous and in *D. koernickei* more rigid. The shape is generally lanceolate, although linear forms are recurrent, as in *D. weddelliana*, whereas in *D. cordata*, this is cordate. In the latter, they are also recurvate, a distinctive position, as positioning usually varies from patent to erect. Another exception is the adpressed axis bract in *D. conferta*. The base may be completely amplexicaul, semi-amplexicaul, or non-amplexicaul as in *D. weddelliana*. As with leaves, the size and pilosity of axis bracts may vary slightly according to both the habit and developmental stage. However, most are either glabrous or glabrescent, although the margins are normally glabrous. In a few species they are ciliated, and in *D. longiciliata*, besides being ciliated, there are long hairs toward the margin. Bract-size may vary from 1.0 cm in *D. amoena* to 20.0 cm in *D. chiquitensis*.

Inflorescences

The arrangement of the scapes in terminal umbellate inflorescences (Fig. 3 A-B) is another of the most distinctive features of *Diphyomene*. During taxonomic history, and in every morphological treatment involving the genus, the inflorescences were always treated as simple umbels. However, Trovó et al. (Cap. 2), when analyzing inflorescences from a typological and anatomical viewpoint, came to the conclusion that these are more complex structures. The basic unit is composed of a capitulum subtended by a scape, which, in turn, is enclosed by a spathe. This basic unit constitutes a botryum of the first order. Some basic units are grouped and enclosed by a bract (pherophyll) (Fig. 3 C). In this subunit (botryum of the second order), there is always a terminal basic unit. Finally, a set of subunits is grouped at the apex of the reproductive axis, forming a tribotryum, with a terminal dibotryum. This inflorescence pattern is unique within the family (Trovó et al. Cap 2), and its codification into characters in a morphological matrix may lead to synapomorphies. For practical purposes, when dealing with inflorescences on describing the genera and species, as well as in commentaries, the term umbel is used in a merely descriptive sense.

As discussed by Trovó et al. (Chap. 2), it appears that lateral reproductive axis and inflorescences rarely emerge from the axil of axis bracts (Fig. 3 D). From field observations, it has been concluded that this is a consequence of damage to the apical bud. This pattern of lateral reproductive axes and new inflorescences is identical to that of the main structure.

Mature capitula of *Diphyomene* (Fig. 4 A-B) are discoid, semi-spherical, or spherical, except for *D. hymenobracteata*, which are obconic. Capitula width varies from 4 mm to 20 mm. The enclosing involucral bracts are sterile, light to dark-brown, mostly glabrous on both surfaces and ciliated toward the apex, with shapes varying from ovate to obovate. The number of scapes per individual varies from 3 to 460. Each scape has generally a few ribs, the number, liable to variation among species. Their arrangement varies from spherical (Fig. 4 A) to more or less obconic (Fig. 4 B), and their sizes range from 13 cm. to 50 cm. They are usually glabrous, except for *D. decussa* and *D. cipoensis*, sparsely hairy, and *D. sericoscapa*, sericeous.

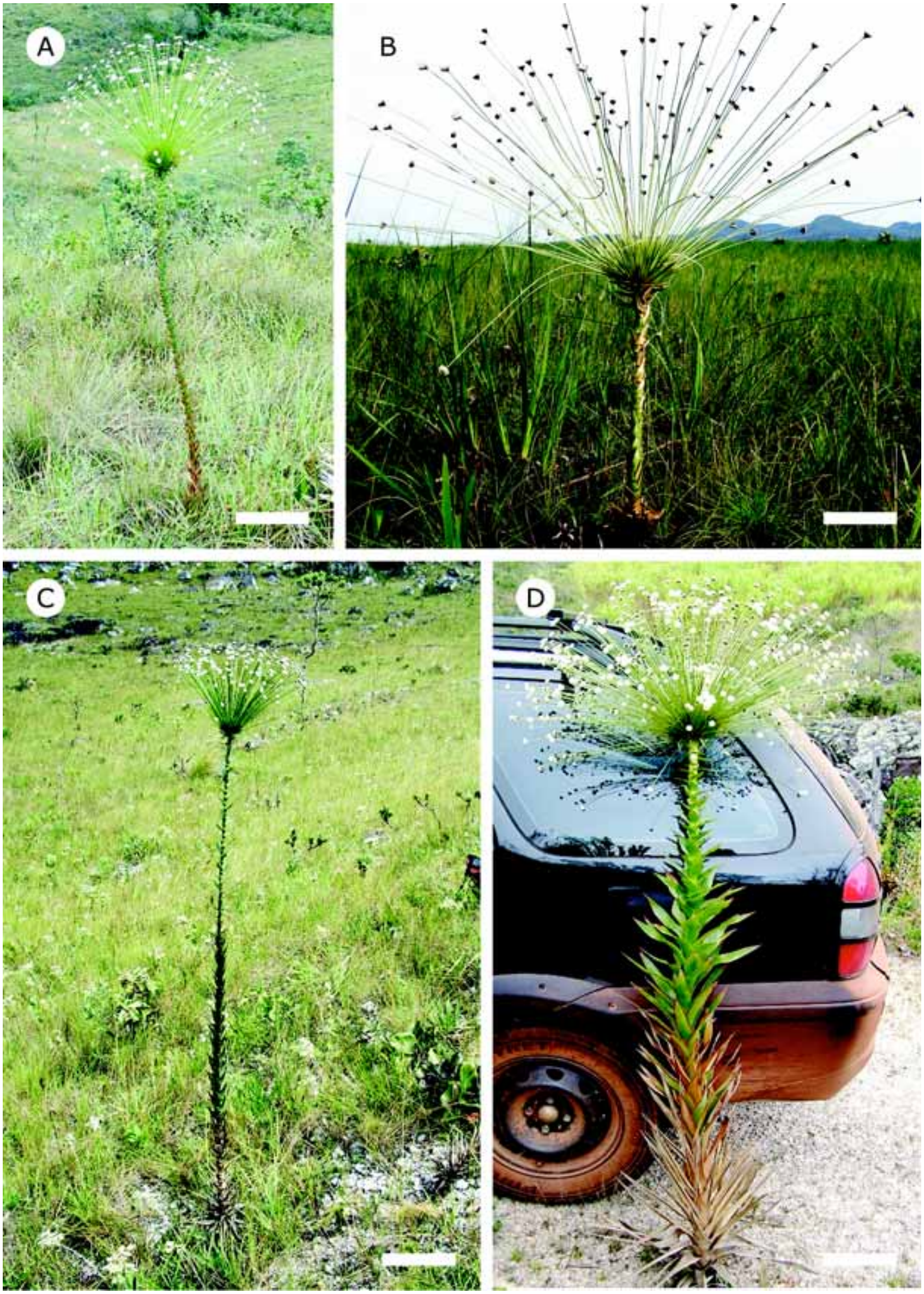

Fig. 2. Habits in *Diphyomene*, emphasizing the reproductive axis. A. Medium sized individual of *D. erectifolia*. B. Small sized individual of *D. urbaniana*. C. Large sized individual of *D. koernickei*. D. Large individual in *D. chiquitensis*. Scale bars, A: 20 cm. B: 5 cm. C: 18 cm. D: 25 cm.

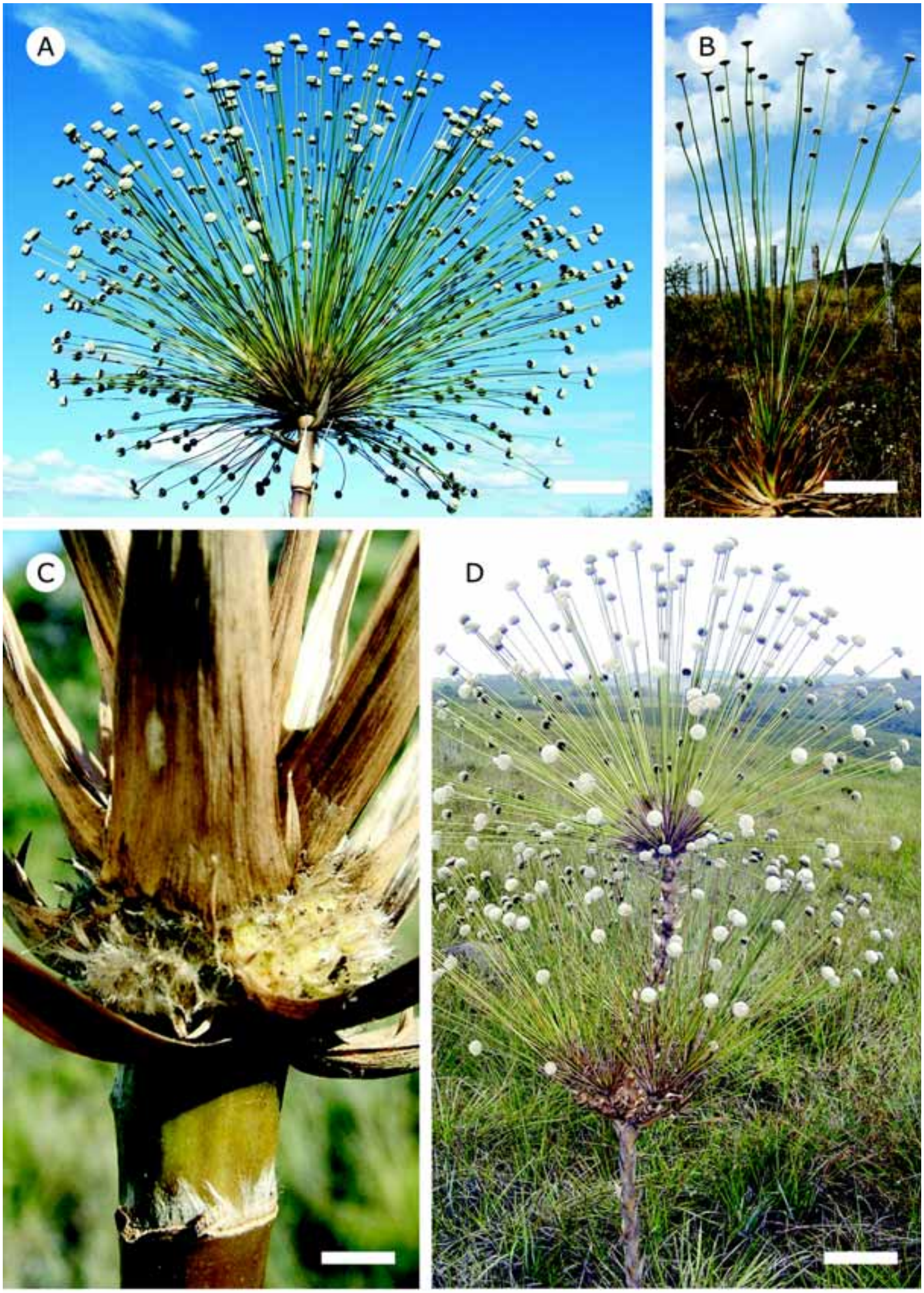

Fig. 3. Architecture of inflorescences in *Diphyomene*. A. Spherical umbel of *D. chiquitensis*. B. Obconic umbel of *D. cipoensis*. C. Lateral subunits of *D. chiquitensis*. D. Lateral inflorescences of *D. erectifolia*. Scale bars, A: 10 cm. B: 6 cm. C: 1 cm. D: 8 cm.

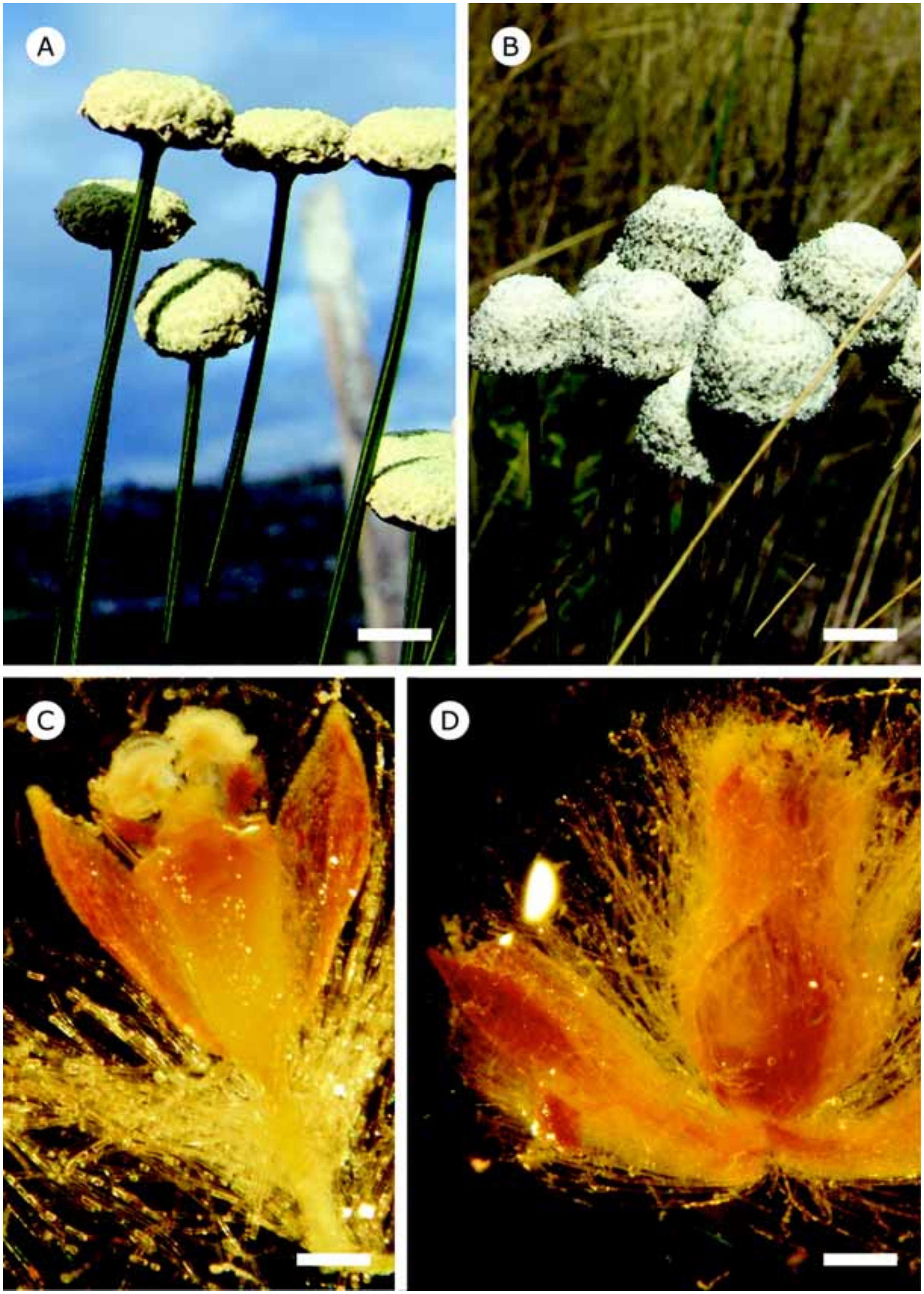

Fig. 4 Capitula and flowers in *Diphyomene*. A. Sulfurous discoid capitula of *D. erectifolia*. B. White hemispherical capitula of *D. acanthophylla*. C. Staminate flower of *D. erectifolia*. D. Pistillate flower of *D. erectifolia.* Scale bars, A: 5 mm. B: 7 mm. C: 0.3 mm. D: 0.3 mm.

Diphyomene spathes are the less variable feature. They are always glabrous, obliquely opened, with an acute apex, and varying in size from 2 cm to 8 cm.

Flowers, fruits, and seeds

The flowers in *Diphyomene* are generally diclinous and the species are monoecius, since both staminate and pistillate flowers are assembled on the same capitulum. *Diphyomene* flowers are dimerous, a less frequent condition among the Paepalanthoideae. Maturation on a capitulum is centripetal and cyclic, forming zones of both staminate and pistillate flowers. Pistillate flowers are usually arranged in concentric rings, except in *D. hymenobracteata*, in which it is punctual. In all the species, staminate flowers bloom first, thus, many specimens were collected without pistillate flowers. Furthermore, the former occur in greater numbers. A single floral bract subtends the flowers in *Diphyomene*. These, with only slight variation, are ca. 3 mm long, linear to oblanceolate, and flat with an acute apex. The only exception occurs in *D. decussa*, with two kinds, the normal linear and a novel obovate. Pilosity may vary from glabrous to hairy on the abaxial apex surface, whereas the margin is ciliated and occasionally glabrescent. The color of floral structures is quite variable throughout maturation, thereby justifying its exclusion from identification keys.

Staminate flowers in *Diphyomene* (Fig. 4 C) are not very different from those in the remaining species of Paepalanthoideae with dimerous flowers. The striking difference is the fleshy, distinctly elongated antophore. They are usually ca. 3 mm to 4 mm long, with short pedicels bearing long trichomes. The sepals are normally navicular with acute apices. Their margins are ciliated towards the apex, and possibly hairy on the abaxial surface. This pilosity may vary with maturation, becoming glabrescent throughout development. The corolla is fused and emerges from the apex of the elongated antophore. As in *Actinocephalus*, it is relatively small (ca. 1 mm) and membranaceous, but without lobes. The stamens, with dorsifixed anthers, are usually either free or fused at the base of the corolla. They may or not be exerting, and may even surpass the sepals. There are always two, probably nectariferous, papillose pistilodes attached to the apex of the antophore.

The pistillate flowers of *Diphyomene* (Fig. 4 D) have two unique features, which may constitute synapomorphies within the *Paepalanthus* core clade (sensu Trovó et al. Cap 1). The easiest to observe are the dolabriform sepals. The other is the completely reduced staminodes. Within the *Paepalanthus* core clade, most species possess scale-like staminodes, whereas in

Diphyomene these are absent. However, as the genus is in a group with reduced staminodes, they are considered as completely reduced. Pistillate flowers are in general sessile, except for *D. decussa* and *D. sericoscapa*, both presenting short pedicels. In the dolabriform sepals, the apex may be obtuse, acute or mucronate. The margins are usually ciliated towards the apex. When existent, pilosity is restricted to the apex, base or central portion of the abaxial surface. As in the staminate flowers, pilosity may become glabrescent during maturation. The petals are typically elliptic and membranaceous, although slightly dolabriform and fleshy ones are also encountered. The variation in petal hairs is the same as that in sepals. The morphological interpretation of the gynoecium, as propounded by Eichler (1885), and corroborated by Rosa & Scatena (2007), is here accepted. The ovary is composed of two carpels, each containing one ovule. The stigmatic branches are not completely fused, and thus appear to be bifid. They may be of approximately the same size as nectariferous branches, or twice as long.

As with most of the Eriocaulaceae, fruits in *Diphyomene* consist of a loculicidal capsule. The gynoecium and the reaming parts of pistillate flowers are usually retained in the fruit. The seeds of all the observed species were alike, with the length not exceeding 1 mm, reddish to brown in color and reticulate surfaces.

Phenology & Reproductive Biology

The blooming period, well-defined in most *Diphyomene* species, lasts four to six months, except for *D. cordata*, where it is shorter, and *D. chiquitensis*, where both flowers and fruits were collected all the year round. Even so, there are marked flowering peaks in the various populations from diverse localities. As individuals are monocarpic, flowering only occurs once yearly. Phenological data on many species is poorly recorded, through sparse representation in few herbarium collections.

As with certain species of *Actinocephalus*, especially the monocarpic *Actinocephalus polyanthus* (Bong.) Sano (Sano 1996), the life cycle in *Diphyomene* is clearly linked with the rainy season. In both groups, most populations begin the transition from vegetative rosette to development of the reproductive axis, together with the beginning of the rains. However, in *Diphyomene* the reproductive phase seems to last longer, as the first fully developed flowers are usually available in March, whereas seed dispersal extends from May to September, with the exception of *D. conferta* and *D. urbaniana*, wherein the development of both flowers and fruits occurs earlier.

As with all *Diphyomene* species, there are distinct phases in each capitulum during the formation of unisexual flowers. Development starts with staminate flowers and then with pistillates. This sequence, easily detected by flower arrangement, may be repeated several times. A direct consequence is that several specimens may possess either only staminate or staminate and juvenile pistillate flowers. Unfortunately, this occurred with species known only from the type collection, thus pistillate flowers were poorly described.

Recent studies have demonstrated that entomophily, instead of anemophily, is the primary pollination process in Eriocaulaceae, with self-pollination playing only a minor role (Ramos et al. 2005; Oriani et al. 2009). There is a lack of information on pollination in *Diphyomene*. Field observations probably confirm the pattern as described in other Eriocaulaceae. Many individuals of Coleoptera, Diptera, and Hemiptera were observed visiting capitula of *Diphyomene* species (Fig. 5 A-B). Moreover, the presence of papillose pistilodes in staminate flowers and that of nectariferous branches in the gynoecium reinforce this postulate.

There is also a lack of knowledge concerning seed dispersal. Based exclusively on field observations, two dispersal mechanisms are possible. In some species, as *D. erectifolia*, capitula attached to scapes may be the dispersion unit through being deciduous at the end of the life-cycle (Fig 5 C). Sano (1996) described the same situation in *Actinocephalus*. In other species, such as *D. acanthophylla*, fruits may be the dispersal unit. In these, the scapes and capitula are persistent, whereas mature fruits are easily detached (Fig 5 D). These two mechanisms are not mutually exclusive; some species, as *D. chiquitensis*, may resort to both simultaneously.

Geographic Distribution, Habit & Conservation

The 18 species of *Diphyomene* are restricted to South America (Fig. 6), 17 of which are endemic to Brazil, and one, *D. chiquitensis*, occuring in Bolivia, Brazil, Colombia and Venezuela. Species richness is higher in the state of Goiás with 10 species, followed by Minas Gerais with seven. The center of diversity is situated in the Chapada dos Veadeiros, where eight species occur. All subsist in the Cerrado domain, although *D. chiquitensis* is also present in the Amazonian and *D. erectifolia* in the Caatinga. Most occupy campos rupestres and/or open fields, with a few in typical savannas (cerrado *sensu stricto*) (Fig. 7).

Diphyomene chiquitensis is widely spread throughout South America. The distribution of this species is highly coincident with generic distribution, with the exception of the northern

Espinhaço Range (Bahia State) and extreme south of the Espinhaço Range in Minas Gerais. It is unique in the Amazonian domain, in open grass fields (200-400 m) in the south Amazonian Forest. In the Cerrado domain, its presence was observed in campos rupestres, open fields and typical savannas. In the states of Minas Gerais and Goiás, it is mostly to be found in campos rupestres and open fields of the Espinhaço Range, Serra da Canastra and Chapada dos Veadeiros. In the states of the Mato Grosso, Mato Grosso of Sul and Tocantins, the species occurs in typical savannas and open fields. Outside Brazil, the species is found in typical savannas in Bolivia and Colombia, as well as rocky fields at high altitudes (1000-2000 m) in Venezuela.

In four species, distribution is regionally restricted, with occurrence in more than one locality. Among these, *D. erectifolia*, the most widely spread, occurs disjunct in campos rupestres of the Espinhaço Range in Minas Gerais and Bahia. In Bahia, it is alone in the Caatinga, where it is restricted to the southern part of the Chapada Diamantina, in the vicinity of Rio de Contas and Abaíra. In Minas Gerais, occurrence is concentrated in the Diamantina Plateau, Serra do Cabral, and Serra do Cipó. The discontinuous distribution between the northern and southern sectors of the Espinhaço Range deserves special attention, as few plant species possesses this distribution pattern. This may be unique within the Eriocaulaceae (Giulietti & Pirani 1988; Harley 1988).

Diphyomene acanthophylla and *D. koernickei* are restricted to Goiás and the Distrito Federal. Both occur in campos rupestres and savannas in the Chapada dos Veadeiros and the vicinity of Brasília, whereas *D. acanthophylla* is also present in the savannas of Cristalina to the south. This pattern is contrary to certain expectations of floristic regions, as proposed for the Cerrado on the basis of trees and shrubs (Ratter et al. 2003). In this proposal, the Chapada dos Veadeiros would be related to areas in Tocantins and Mato Grosso do Sul, and the Distrito Federal to southeastern Goiás and northwestern Minas Gerais (Ratter et al. 2003). Nevertheless, this relationship does not apply to the species studied here. The association of areas, as suggested for *Diphyomene* species, is coincident with the relationship of provinces as designated by Simon & Proença (2000), and based on the distribution of *Mimosa* (Fabaceae). The explanation for these aspects could be related to habitat restriction, as species occurrence is mainly confined to high altitude quartizitic soils.

Diphyomene amoena, restricted to Minas Gerais, is distributed in the extreme south of the Espinhaço Range, in a region known as the "Quadrilátero Ferrífero", rich in iron ore soils. The species occurs in mountains between the towns of Belo Horizonte and Ouro Preto.

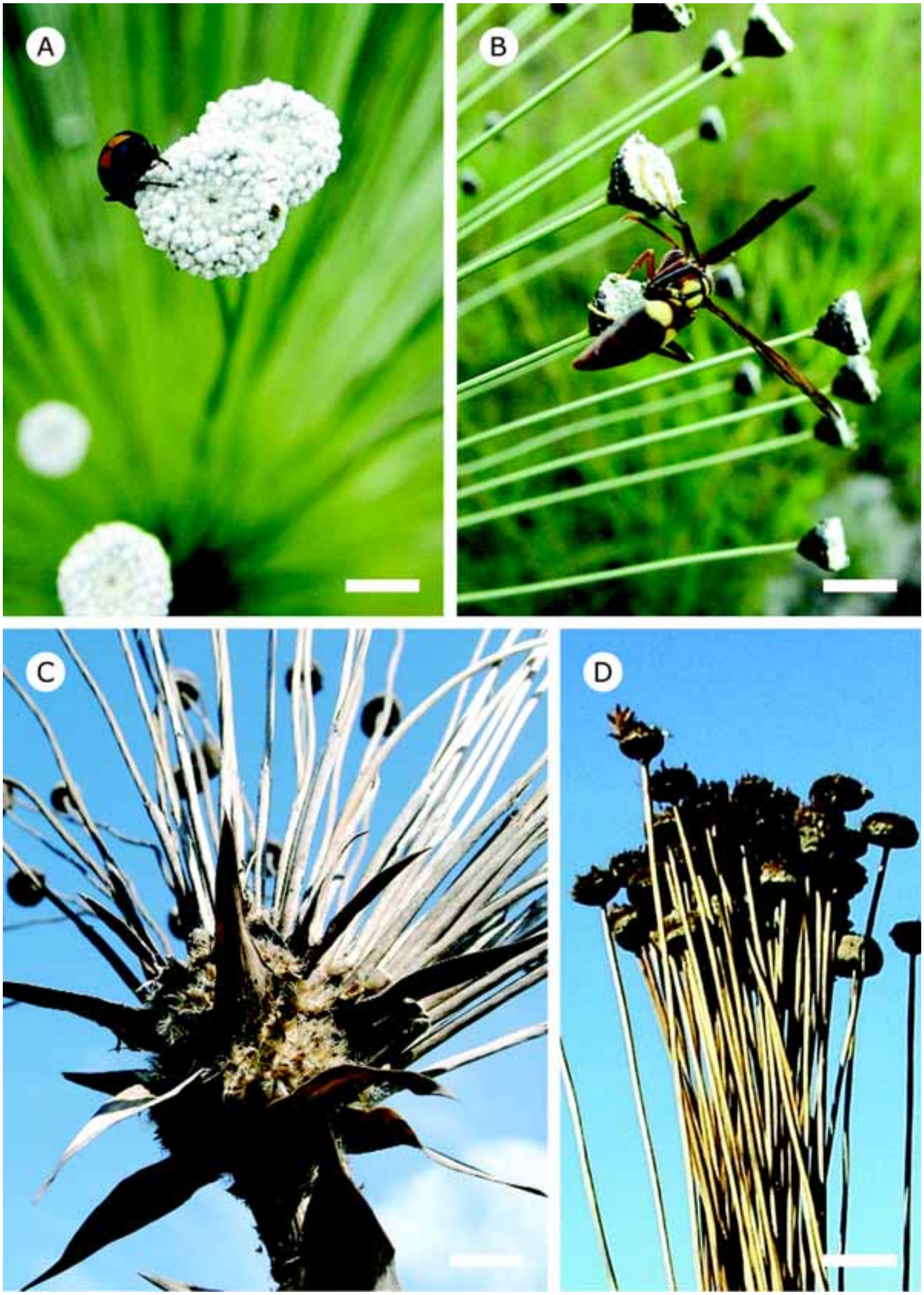

Fig. 5. Visitors and dispersal in *Diphyomene*. A. Coleoptera on a capitulum of *D. hymenobracteata*. B. Hymenoptera on a capitulum of *D. hymenobracteata*. C. Inflorescence of *D. erectifolia* with deciduous scapes. D. Inflorescence of *D. acanthophylla* with persistent scapes and deciduous fruits. Scale bars, A: 3 mm. B: 5 mm. C: 1.5 cm. D: 6 cm.

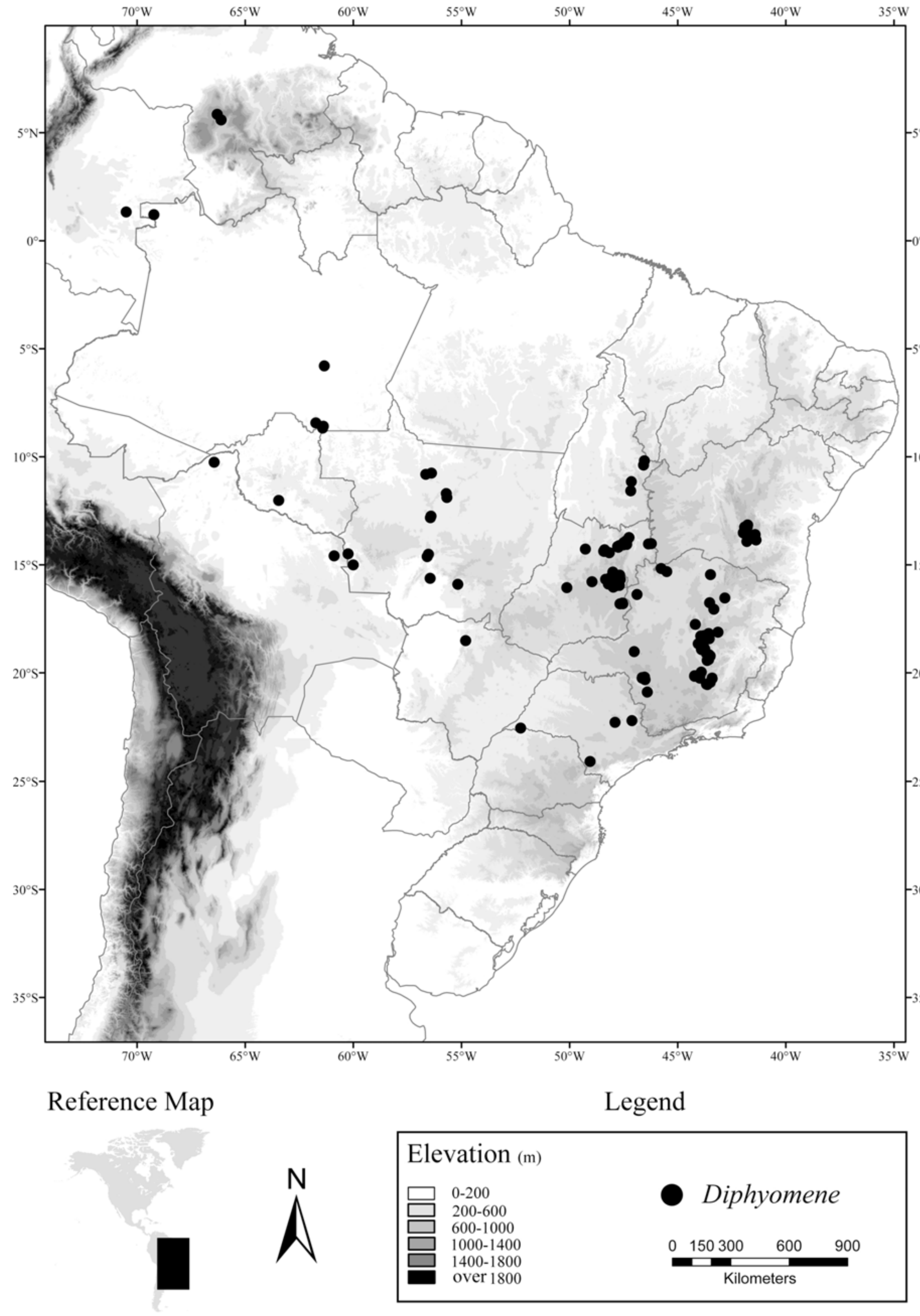

Fig. 6. Geographical distribution of *Diphyomene*.

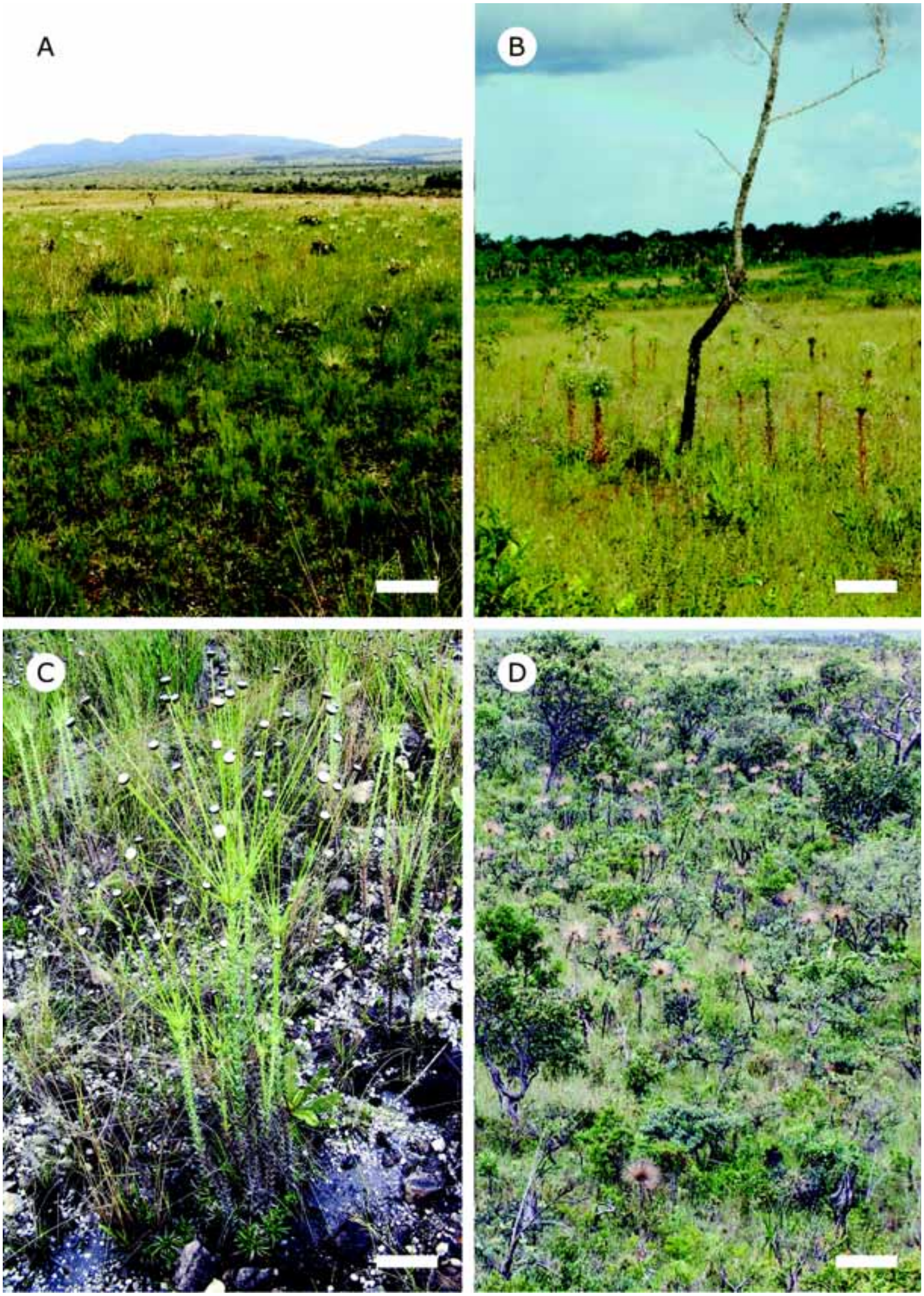

Fig. 7. Habitats and populations of *Diphyomene*. A: Open grass savannas in the Chapada dos Veadeiros. B. Campinas in the Amazon. C. Rocky outcrops in the Chapada dos Veadeiros. D. Shrubby savannas in the Chapada dos Veadeiros. Scale bars, A: 25 cm. B: 35 mm. C: 20 cm. D: 70 cm. (Photo B by L. Lima)

Due to the unusual soil composition, outstanding vegetation, and distinct geologic origin, some authors consider this region as apart from the Espinhaço Range (Renger et al. 1994; Knauer 2007).

Most *Diphyomene* species are narrowly distributed, comprising 13 species restricted to only one locality, this including those known only by the type collection. It is also the most frequent pattern in the Eriocaulaceae, in which almost 95% of the species are restricted to only one locality (Giulietti & Pirani 1988; Giulietti & Hensold 1990; Giulietti et al. 2005; Costa et al. 2008). This pattern is generally related to rocky altitudinal fields. Harley (1995) and Simon & Proença (2000) suggest that the high degree of endemism in these areas could be related to the relatively high degree of isolation. These high areas are surrounded by low lands, which may represent adverse ecological conditions, thereby restricting dispersion, and leading to "insular" conditions.

Most of the narrowly distributed species: *D. cordata*, *D. hymenobracteata*, *D. longiciliata*, *D. conferta*, and *D. urbaniana*, are concentrated in the Chapada dos Veadeiros in Goiás, Although relatively large (~70.000 ha.), this region is here considered as a single locality, since, apart from the habitats of *Diphyomene* species being interconnected, it is isolated from other elevated areas, thereby forming a single block. Here, *Diphyomene* species form large populations, generally on argillaceous open fields. The exception is *D. longiciliata*, known only from two small populations on the rocky soils of the western border.

There are three more narrowly distributed species in Goiás and Distrito Federal. *Diphyomene flexuosa* is restricted to Niquelândia, in a single mountain. Local edaphic conditions are very particular, with a typical savanna growing on rocky soils in a nickel mining complex. Endemic species of *Paspalum* L., as *Paspalum crispulum* Swallen - Poaceae (Oliveira & Valls 2002), also occur thereabouts. *Diphyomene brachycaule* is endemic to the Distrito Federal, a single population having been collected in a savanna area in the Brasilia Botanical Garden Ecological Station. *Diphyomene weddelliana* occurs in Goiás, and is known exclusively from the type collection. Unfortunately, the type locality, close to the town of Goiás and on rocky soil, is doubtful.

The high diversity in the state of Goiás is unique within Eriocaulaceae, since family diversity is concentrated in the Espinhaço Range and the Tepuis of Venezuela (Giulietti & Hensold 1990). The reasons for this pattern are still uncertain. We could again argue in favor of insularism, as the Cerrado domain is a mosaic of vegetational formations comprising different isolated plant communities (Simon & Proença 2000; Peninnington et al. 2006; Ratter et al. 2006). However, this explanation does not account for the high diversity concentrated in the Chapada dos Veadeiros, where species habitats are somewhat continuous. The insights arising from phylogenetic studies indicate that the oldest species are distributed in the mountains of Minas Gerais (Trovó et al. Cap. 1), possibly pointing to a neo-endemic situation in Goiás. Detailed phylogenetic and phylogeographyc studies are still required in order to furnish appropriate answers.

In Minas Gerais, all the narrowly distributed species are concentrated in the Serra da Canastra and the Espinhaço Range. The former, a mountain complex isolated from other elevated areas, is the habitat of *D. polyclada* and *D. sericoscapa*. *Diphyomene polyclada* form extensive populations and the latter is known only from the type collection. Numerous endemic species of Eriocaulaceae occur locally, most of them described by Silveira (1928).

The three species endemic to the Espinhaço Range in Minas Gerais are mutually allopatric. *Diphyomene decussa* is restricted to areas with quartzitic soil in the "Quadrilátero Ferrífero", and is known only from the type collection (imprecise locality) and a recent collection near the town of Mariana. As described, the unique edaphic conditions may explain the high number of endemic species in this region. *Diphyomene stenophylla* is endemic to the campos rupestres in Itacambira, and is known by two collections from the same population. *D. cipoensis* is known from a single collection in Serra do Cipó.

The inclusion of *Diphyomene* species under risk categories based on criteria defined by IUCN (2001) was an arduous task. Difficulties arose mainly through the lack of information on population size and dynamics, apart from the lack of quantitative analyses on probability of species extinction. The only applicable criterion is geographic distribution, i.e. criterion B (IUCN 2001). This is based on the extension of species occurrence and area of occupation. Thus, in the present case, conservation *status* and geographic distribution are directly related.

Only the two most widely spread species, *D. chiquitensis* and *D. erectifolia*, are considered of least concern. Both occur within national conservation units; such as the Serra do Cipó National Park, Chapada dos Veadeiros National Park, and Campos Amazônicos National Park. Both *D. acanthophylla* and *D. koernickei* are narrowly distributed in no more than 10 spots in Goiás and Distrito Federal, thus being considered vulnerable. These species occur in the Chapada dos Veadeiros National Park and the Brasilia National Park. *Diphyomene amoena* is found in no more than five places within the "Quadrilátero Ferrífero", as well as the Itacolomi State Park, thereby being classified as endangered.

All the narrowly distributed species are considered critically endangered. Two groups may be detected within this category. *Diphyomene cipoensis*, *D. brachycaule*, *D. sericoscapa*, and *D. weddelliana* are known only from type collections. The first occurs in the Serra do Cipó National Park, *D. brachycaule* in the Brasilia Botanical Garden Ecological Station, and *D. sericoscapa* in the Serra da Canastra National Park. The species *D. cordata*, *D. hymenobracteata*, *D. conferta*, *D. urbaniana*, *D. polyclada*, *D. stenophylla*, *D. longiciliata*, *D. decussa*, and *D. flexuosa*, are known from more than one collection at the type locality. The first four occur in the Chapada dos Veadeiros National Park, *D. polyclada* in the Serra da Canastra National Park, and the remainders are not protected.

Phylogeny

In the first phylogenetic study, Giulietti et al. (1995) treated *P.* sect. *Diphyomene* as part of an informal group denominated "*Paepalanthus* 1". The position of this assemblage emerged uncertain and in polytomy with other genera, such as *Syngonanthus*, *Leiothrix*, *Rondonanthus*, *Tonina*, and *Lachnocaulon*, as well as other species of *Paepalanthus* itself. Later, Giulietti et al. (2000) presented a more detailed phylogeny of Eriocaulaceae, this comprising all the genera and most of the infra-generic categories within the family. In this study, *P.* sect. *Diphyomene* emerged as sister to *Paepalanthus* ser. *Dimeri*, a surplus group possessing dimerous flowers. This clade also appeared as sister to a clade formed by species from *Actinocephalus* (sensu Costa 2005). Based on initial molecular studies (Unwin 2004), *P.* sect. *Diphyomene* emerged as polyphyletic, due to the two included species (*P. speciosus* and *P. flaccidus*) appearing in distinct clades. Andrade et al. (in press.) came to similar conclusions, although in one of the cladograms, the three included species, *P. giganteus*, *P. trichophyllus*, and *P. strictus* (misidentified as *Paepalanthus extremensis* Silveira) form a distinct clade. In both studies, *P. chiquitensis* (= *P. giganteus* and *P. speciosus*) is somehow related to species of *Actinocephalus*, whereas the remaining species of *P.* sect. *Diphyomene* appear related to species of *P.* ser. *Dimeri.* This was the insight for dividing *P.* sect. *Diphyomene* into two groups.

Once aware of the problem, Trovó et al. (Cap. 1) added further species of *P.* sect. *Diphyomene*, so as to better analyze Paepalanthoideae, with emphasis on *Paepalanthus*, and based on molecular and morphological evidence. From the results, it became clear that the group is composed of two distinct lineages. One contains monocarpic herbs and the other perennial. The distinction between the two lineages was previously suggested by Koernicke (1863), reinforced by Trovó et al. (Cap. 2) and formalized by Trovó & Sano (Cap. 3). Nevertheless, the relationships between these lineages are still unclear (Fig. 8). Both may form a monophyletic group, or they may be related to those species of *Actinocephalus* and *Paepalanthus* with dimerous flowers.

As discussed above, correlations within *Diphyomene* continue obscure, and point to the necessity for phylogenetic analysis involving the genus itself, *Actinocephalus* and the remaining species with dimerous flowers. As quite similar features define species of this genus, postulations as to the scenario of phylogenetic affinities are meaningless. However, by the pronounced biogeographical influence coming to light from the findings of Andrade et al. (in press) and Trovó et al. (Cap. 1), we can expect to encounter near relationships among species that inhabit closely related areas. This would imply close correlations among species distributed throughout the Espinhaço Range, as well as among species occurring in the Chapada dos Veadeiros.

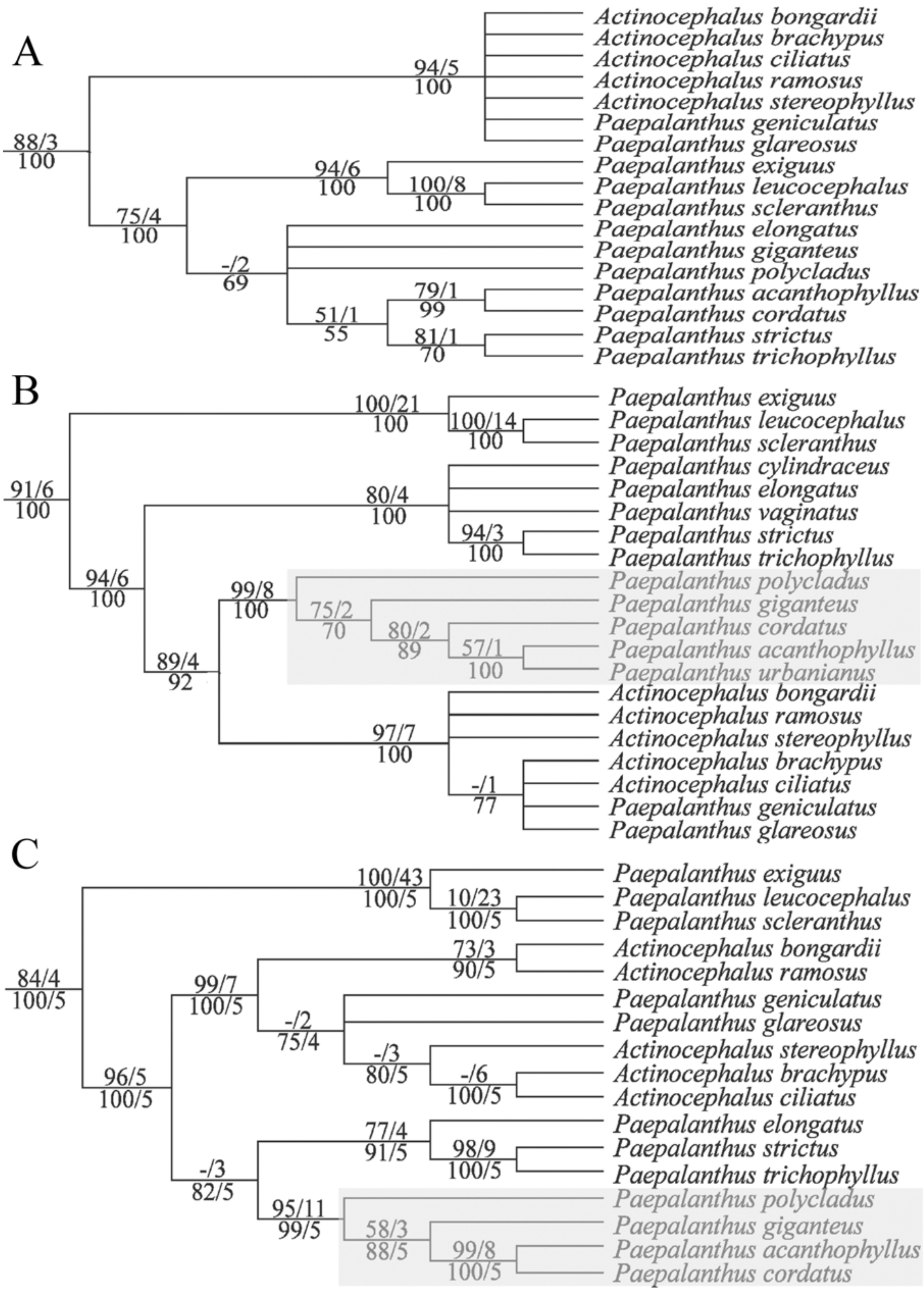

Fig. 8. Relationships within Paepalanthoideae involving *Diphyomene*. A. *trnL-trnF* and morphology datasets. B. ITS and morphology datasets. C. *trnL-trnF*, ITS, and morphology datasets. Numbers above the branches indicate Bootstrap support and the Bremer decay index. Numbers below the branches indicate Bayesian posterior probabilities. Shaded clades comprise the *Diphyomene* species.

Diphyomene (Ruhland) Trovó, Cap. 3. *Paepalanthus* sect. *Diphyomene* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 184. 1903.—LECTOTYPE, designated by Trovó and Sano (Cap. 3): *Diphyomene urbaniana* (Ruhland) Trovó & Sano.

Paepalanthus (*Diphyomene*) [serie] § *Vestiti* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 184. 1903.—LECTOTYPE, designated by Trovó and Sano (Cap. 3): *Diphyomene acanthophylla* (Ruhland) Trovó & Sano.

Paepalanthus (*Diphyomene*) [serie] § *Foliosi* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 184. 1903.—LECTOTYPE (designated by Trovó and Sano (Cap. 3): *Diphyomene urbaniana* (Ruhland) Trovó & Sano.

Monocarpic herbs, 20–300 cm tall; rhizome present or absent, aerial stem 0.5–3.5 cm long. Leaves persistent or deciduous, linear to oblong, flat to contort, patent to recurvate, 1.0–40.0 X 0.1–3.0 cm, hairy to glabrous, margin ciliated or glabrous, apex acute to cuspidate. Reproductive axis erect or tortuous, 3.5–270.0 cm long., 0.2–1.8 cm diam., hairy or glabrous; axis bracts with same shape or with different shapes along the axis, membranaceous to rigid, linear to cordate, recurvate to adpressed, 1.0–20.0 X 0.2–2.5 cm, hairy to glabrous, margin ciliated or glabrous, apex acute to rounded, amplexicaul or not. Spathes 2.0–8.0 cm long, glabrous, apex acute. Scapes 3–460, arranged in a spherical or obconic umbel, 13.0–50.0 cm long, hairy or glabrous. Capitula 4–2 mm diam., discoid to spherical, white or sulfurous; involucral bracts in 3–5 series, light-brown to black, ovate to obovate, glabrous or rarely hairy in abaxial surface, margin ciliated toward the apex, apex acute or obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 46–500 per capitulum, always more staminates than pistillates; floral bracts linear or rarely obovate, hyaline to brown, flat, ca. 3 mm long, hairy in abaxial surface apex to glabrescent, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, hyalines to brown, ca. 3 mm long, hairy in abaxial surface to glabrescent, margin ciliated toward the apex, apex acuminate to obtuse; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings or punctual disposed, ca. 3 mm, sessile or rarely with short pedicel; sepals dolabriform, white to brown, ca. 3 mm long., hairy in the abaxial surface to glabrescent, margin ciliated toward the apex, apex obtuse to mucronate; petals obovate to elliptic or rarely dolabriform, hyaline to rarely golden, ca. 2 mm long, hairy in abaxial surface to glabrescent, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, with the same size or longer than the nectariferous branches, staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Note on methods: The taxonomic species concept, as proposed by Stuessy (1990), was applied in this taxonomic treatment as a whole. Herbarium acronyms are according to Thiers (continuously updated). For comments on species conservation status, we adopted the criteria as described in IUCN (2001). All the cited type specimens were actually seen by the authors. Type specimens deposited in North American herbaria were examined by photos available on-line or sent by the curators themselves. Species measurements were taken from herbarium sheets, although the resultant morphological descriptions reflect both herbarium specimens and living plants. As the *Diphyomene* specimens were usually incompletely gathered, the identification key is intended for contemplating either complete or incomplete sheets.

Key to the species of *Diphyomene*

1. Entire specimens

2. Axis-bract shape varied along the axis, becoming smaller from the base to the apex.

3. Basal leaves erect, apex mucronate, less than 5.5 cm long; reproductive axis less than 10.0 cm long. ……………………………………………………………………………… 13. *D. brachycaule.*

3’ Basal leaves patent to semi-erect, apex not mucronate, longer than 6.0 cm; reproductive axis longer than 21.0 cm.

4. Plants less than 50 cm high; leaves less than 8.0 cm long; reproductive axis less than 35.0 cm long; axis-bract margin long-haired; less than 10 scapes. …………………..... 11. *D. longiciliata.*

4’. Plants higher than 65 cm; leaves longer than 9.0 cm; reproductive axis longer than 50.0 cm; axis-bract margins ciliated or glabrous; more than 30 scapes. ……..…….. 3. *D. chiquitensis.*

2’. All the axis bracts of the same size and same-shaped throughout the axis.

5. Species restricted to Minas Gerais and Bahia.

6. Species restricted to the Serra da Canastra.

7. Plants less than 25 cm high; rhizome absent; reproductive axis less than 10.0 cm long; scapes arranged in an obconic umbel, sericeous; pistillate flowers with short pedicel. ……………………………………………………………………………….. 15. *D. sericoscapa.*

7’. Plants more than 45 cm high; rhizome present; reproductive axis longer than 30.0 cm; scapes arranged in a spherical umbel, glabrous; pistillate flowers sessile. ……. 14. *D. polyclada.*

6’ Species restricted to the Espinhaço Range.

8. Reproductive axis hairy; pistillate flowers with short pedicel. ……………………………………………………………………………….. 6. *D. decussa.*

8’. Reproductive axis glabrous; pistillate flowers sessile.

9. Reproductive axis less than 10.0 cm long; leaves incurvate; scapes hairy. … 4. *D. cipoensis.*

9’. Reproductive axis longer than 20.0 cm; leaves flat; scapes glabrous.

10. Axis bracts erect, apex acuminate; species restricted to southern Espinhaço Range (Mountains between Belo Horizonte and Ouro Preto). ……….……………... 2. *D. amoena.*

10’. Axis bracts patent to sub-erect, apex acute; species not present in the southern Espinhaço Range (Mountains between Belo Horizonte and Ouro Preto).

11. Leaves deciduous, semi-erect; axis bracts semi-amplexicaul; species restricted to Itacambira. ………………………………………………………….. 10. *D. stenophylla.*

11'. Leaves persistent, patent or recurvate; axis bracts amplexicaul; species not present in Itacambira. ………………………………………………………….. 7. *D. erectifolia.*

5'. Species restricted to Goiás and Distrito Federal.

12. Scapes longer than the reproductive axis.

13. Reproductive axis tortuous; scapes arranged in obconic umbel form; species restricted to Niquelândia. ……………………………………………..………………. 16. *D. flexuosa.*

13'. Reproductive axis erect; scapes arranged in semi-spherical or spherical umbel form; species restricted to Chapada dos Veadeiros.

14. Leaves lanceolate, uppermost series contort, apex mucronate; axis bracts lanceolate, semi-amplexicaul. ……………………………………………..…………... 17. *D. urbaniana.*

14'. Leaves linear, patent, apex acute; axis bracts linear, non-amplexicaul. ……………………………………………………………………….. 18. *D. weddelliana.*

12'. Scapes shorter than reproductive axis.

15. Leaves oblong, apex cuspidate; axis bracts recurvate, cordate. …………..…. 5. *D. cordata.*

15'. Leaves lanceolate, apex acute; axis bracts patent to erect or adpressed, lanceolate.

16. Axis bracts adpressed; capitula sulfurous. ………………………….…….. 12. *D. conferta.*

16'. Axis bracts patent to erect; capitula white.

17. Axis bracts membranaceous, erect to sub-erect; mature capitula obconic; pistillate flowers punctually arranged. …………………………...…..………… 8. *D. hymenobracteata.*

17'. Axis bracts chartaceous, patent; mature capitula discoid to semi-spherical; pistillate flowers arranged in concentric rings.

18. Plants shorter than 120 cm; leaves deciduous, less than 8.0 cm long; reproductive axis shorter than 80.0 cm; scapes no more than 100; stigmatic branches twice as long as nectariferous branches. ……………………………………………….. 1. *D. acanthophylla.*

18'. Plants higher than 125 cm; leaves persistent, longer than 13.0 cm; reproductive axis longer than 110.0 cm; scapes more than 130; stigmatic branches of the same size as nectariferous. ………………………………………………………… 9. *D. koernickei.*

1'. Incomplete specimens[5]

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[5] Specimens comprising the inflorescence and more than 10 cm of the reproductive axis may be considered entire. Even in incomplete specimens steps, all the features are included.

19. Leaves oblong, apex cuspidate; axis bracts recurvate and cordate. ……..………. 5. *D. cordata.*

19'. Leaves linear or lanceolate, apex never cuspidate; axis bracts patent to erect or adpressed, linear or lanceolate.

20. Reproductive axis entirely hairy. …………………………………………….….. 6. *D. decussa.*

20'. Reproductive axis hairy only at leaves basis.

21. Axis bracts membranaceous; mature capitula obconic; pistillate flowers punctually arranged. ……………………………………………………………….. 8. *D. hymenobracteata.*

21'. Axis bracts chartaceous or rigid; mature capitula discoid, semi spherical or spherical; pistillate flowers arranged in concentric rings.

22. Scapes sericeous; pistillate flowers with short pedicel. …………………… 15. *D. sericoscapa.*

22'. Scapes glabrous, or sparsely hairy only at the apex; pistillate flowers sessile.

23. Apex of the axis bracts acuminate; endemic to the mountains between Belo Horizonte and Ouro Preto in the southern Espinhaço Range. …………….…………... 2. *D. amoena.*

23'. Apex of the axis bracts not acuminate; absent from the mountains between Belo Horizonte and Ouro Preto in the southern Espinhaço Range.

24. Leaves incurvate; scapes sparsely hairy. …………………..…………. 4. *D. cipoensis.*

24'. Leaves flat; scapes glabrous or hairy only at the apex.

25. Axis bracts adpressed; capitula sulfurous. …………………..……… 12. *D. conferta.*

25'. Axis bracts patent to erect; capitula white or seldom sulfurous, if sulfurous, species restricted to Minas Gerais.

26. Scapes hairy at the apex; species restricted to Itacambira. ………. 10. *D. stenophylla.*

26'. Scapes glabrous; species absent from Itacambira.

27. Leaves erect, reproductive axis no longer than 10.0 cm; axis bracts hairy. …………………………………………………………….…… 13. *D. brachycaule.*

27'. Leaves patent; reproductive axis longer than 10.0 cm; axis bracts glabrous, rarely glabrescent.

28. Leaves erect; axis-bract margin long-haired; staminate flower floral bracts differently-shaped from those of pistillate. ………………………… 11. *D. longiciliata.*

28'. Leaves not erect; axis-bract magins ciliated or glabrous; same-shaped floral bracts of both staminate and pistillate flowers.

29. Reproductive axis tortuous; species restricted to Niquelândia. .... 16. *D. flexuosa.*

29’. Reproductive axis erect; species absent from Niquelândia; if present with more than 30 scapes arranged in spherical umbel form.

30. Scapes arranged in obconic umbel form. …………………. 1. *D. acanthophylla.*

30’. Scapes arranged in spherical or semi-spherical umbel form.

31. Scapes longer than the reproductive axis.

32. Leaves lanceolate, the uppermost series contort, apex mucronate; axis bracts lanceolate, semi-amplexicaul. …………..………..…… 17. *D. urbaniana.*

32’. Leaves linear, patent, apex acute; axis bracts linear, non-amplexicaul. ……………………………………...………………….. 18. *D. weddelliana.*

31’. Scapes shorter than the reproductive axis.

33. Leaves less than 4.5 cm long; axis bracts erect. …...……… 14. *D. polyclada.*

33’. Leaves longer than 6.0 cm; axis bracts patent to sub-erect.

34. Stigmatic branches only slightly surpassing nectariferous branches. ……………………………………………………………. 3. *D. chiquitensis.*

34’. Stigmatic branches of the same size as nectariferous branches.

35. Leaves less than 13.0 cm long; axis bracts less than 4.5 cm long; pistillate flower sepal hairy on the abaxial surface central portion. ……….……………………………………………….... 7. *D. erectifolia.*

35’. Leaves longer than 13.0 cm.; axis bracts longer than 4.5 cm; pistillate flower sepal glabrous on the abaxial surface central portion. ………………………………………………………..….. 9. *D. koernickei.*

1. Diphyomene acanthophylla (Ruhland) Trovó, Cap. 3. *Paepalanthus acanthophyllus* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 186. tab. 24. 1903.—TYPE: BRAZIL. Goiás: "Entre Rio Torto et Sobradinho, dans le sable". 25 May 1895, *Glaziou 22323* (holotype: B!; isotypes: B!, C!, G!, K!, LE!, NY!, P!). Figs. 9–10.

Herbs, 43–112 cm tall; rhizome present, aerial stem 1.0–2.5 cm long. Leaves deciduous, rarely persistent, lanceolate, flat, patent, 3.5–8.0 X 0.3–0.7 cm, glabrous, margin glabrous, apex acuminate. Reproductive axis erect, 23.0–77.0 cm long., 0.3–0.8 cm diam., glabrous; axis bracts with same shape, chartaceous, obovate to lanceolate, patent, 1.0–5.5 X 0.8–1.2 cm, glabrous, margin glabrous, apex acute to acuminate, amplexicaul. Spathes 2.0–4.5 cm long, glabrous, apex acute. Scapes 12–77, arranged in an obconic umbel, 16.0–28.0 cm long, glabrous. Capitula 8–14 mm diam., discoid to obconic, white; involucral bracts in 4–5 series, dark-brown to black, ovate to elliptic, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 200 per capitulum, ca. 10 X more staminates than pistillates; floral bracts linear, brown, flat, ca. 3 mm long, hairy in abaxial surface apex to glabrescent, margin ciliated toward the apex, apex acute; staminate flowers ca. 4 mm long; pedicel ca. 0.5 mm long., with long trichomes; sepals navicular, hyalines to light-brown, ca. 4 mm long, glabrous, margin ciliated toward the apex, apex acuminate; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings, ca. 3 mm, sessile; sepals dolabriform, white, ca. 3 mm long., hairy in the abaxial surface apex and base to glabrescent, margin ciliated toward the apex, apex mucronate; petals obovate to elliptic, hyaline, ca. 2 mm long, hairy in abaxial surface apex and base, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, twice longer than the nectariferous branches, staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. *Diphyomene acanthophylla* was collected with flowers and fruits between January and September. Pistillate and staminate flowers were predominantly in full anthesis between March and July, and mature fruits are completely developed from June to September. Blooming peak coincides with the end of the rainy season.

Distribution, Habitat, and Conservation Status. *Diphyomene acanthophylla* occurs in the state of Goiás and Distrito Federal (Fig. 11). Most specimens are from the Chapada dos Veadeiros (GO), with a few from Cristalina (GO) and only one from Brazlândia (DF). Populations in Cristalina occur in typical savanna, whereas those in the Chapada dos Veadeiros are present either in typical savanna or rocky fields. According to IUCN (2001) criteria, *D. acanthophylla* is considered vulnerable (criteria B1a, B1b, B2a).

Commentaries. Ruhland (1903) described *Paepalanthus acanthophyllus* Ruhland based on *Glaziou 22323*, collected in Goiás. Two materials corresponding to this collection were found at B. As the original handwriting in one is jointly attributed to Ruhland and Glaziou, this was interpreted as the holotype. The patent, rigid axis bracts, densely arranged on the axis as highlighted in the protologue, are extremely useful in distinguishing the species. Ruhland (1903) pointed out that the axis bracts were extremely pungent, thereby using this feature on giving the species epithet. Additionally, the scapes arranged in obconic umbel form, deciduous leaves and geographic distribution, all constitute useful features for separating this species from *D. erectifolia*, the morphologically most similar species.

Morphological variation in *Diphyomene acanthophylla* is three-fold. The type specimen is related to individuals occurring in the Chapada dos Veadeiros in open grass savannas. This is the most frequent form, and thus the most representative among herbarium specimens. Those abiding in rocky soils are relatively smaller, with thin reproductive axis and few scapes. On the other hand, those from Cristalina are the most robust, with longer and wider elongated axis, longer scapes and longer axis bracts.

In some individuals from Chapada dos Veadeiros, the axis bract pattern may be somewhat variable, whereat the uppermost bracts are both sparsely arranged and relatively smaller than the basal. As in several collections of *Diphyomene*, only the uppermost part of reproductive individuals was present, many herbarium specimens were found to be misidentified as *D. erectifolia.*

Selected specimens examined: Brazil. **Distrito Federal**: Brazlândia, *Melo, E. et França, F.* 361, 15.3.2000 (SPF); **Goiás**. Alto Paraíso de Goiás, Irwin, *H.S. et al. 24649*, 19.3.1969 (RB), *Rizzo, A. 7915*, 6.4.1972 (SPF), *Romaniuc-Neto et S. Sajo, M.G. 292*, 25.7.1985 (SPF), *Menezes, N.L. 1216*, 9.5.1987 (SPF), *Cavalcanti, T. et al. 674*, 15.8.1990 (HUEFS), *Marquete, R. et al. 2347*, 17.8.1995 (SPF, RB, UEC), *Uliana, V.L.C.R. et al. 651*, 5.2002 (ESA), *Munhoz, C. et al. 1621*, 17.6.2000 (SPF), *Trovó, M.L.O. et al. 287*, 5.8.2006 (SPF), *Trovó, M.L.O. et al. 457*, 19.3.2009 (SPF), *Trovó, M.L.O. et al. 463*, 19.3.2009 (SPF), *Trovó, M.L.O. et al. 472*, 20.3.2009 (SPF); <u>Cristalina</u>, *Rizzo, A. 9052*, 25.5.1973 (SPF), *Romaniuc-Neto, S. Sajo, M.G. 405*, 31.7.1985 (SPF), *Souza, V.C. et al. 21372*, 10.9.1998 (ESA), *Souza, V.C. et al. 21374*, 10.9.1998 (ESA), *Magenta, M. Magenta, J.E. 368*, 21.1.2002 (SPF), *Fonseca, M.L. et al. 3416*, 10.6.2002 (SPF); <u>Montes Belos</u>, *Rizzo, A. 7971*, 6.4.1972 (SPF); <u>Teresina de Goiás</u>, *Forzza, R.C. et al. 1606*, 31.7.2000 (SPF), *Souza, V.C. et al. 24748*, 31.7.2000 (ESA).

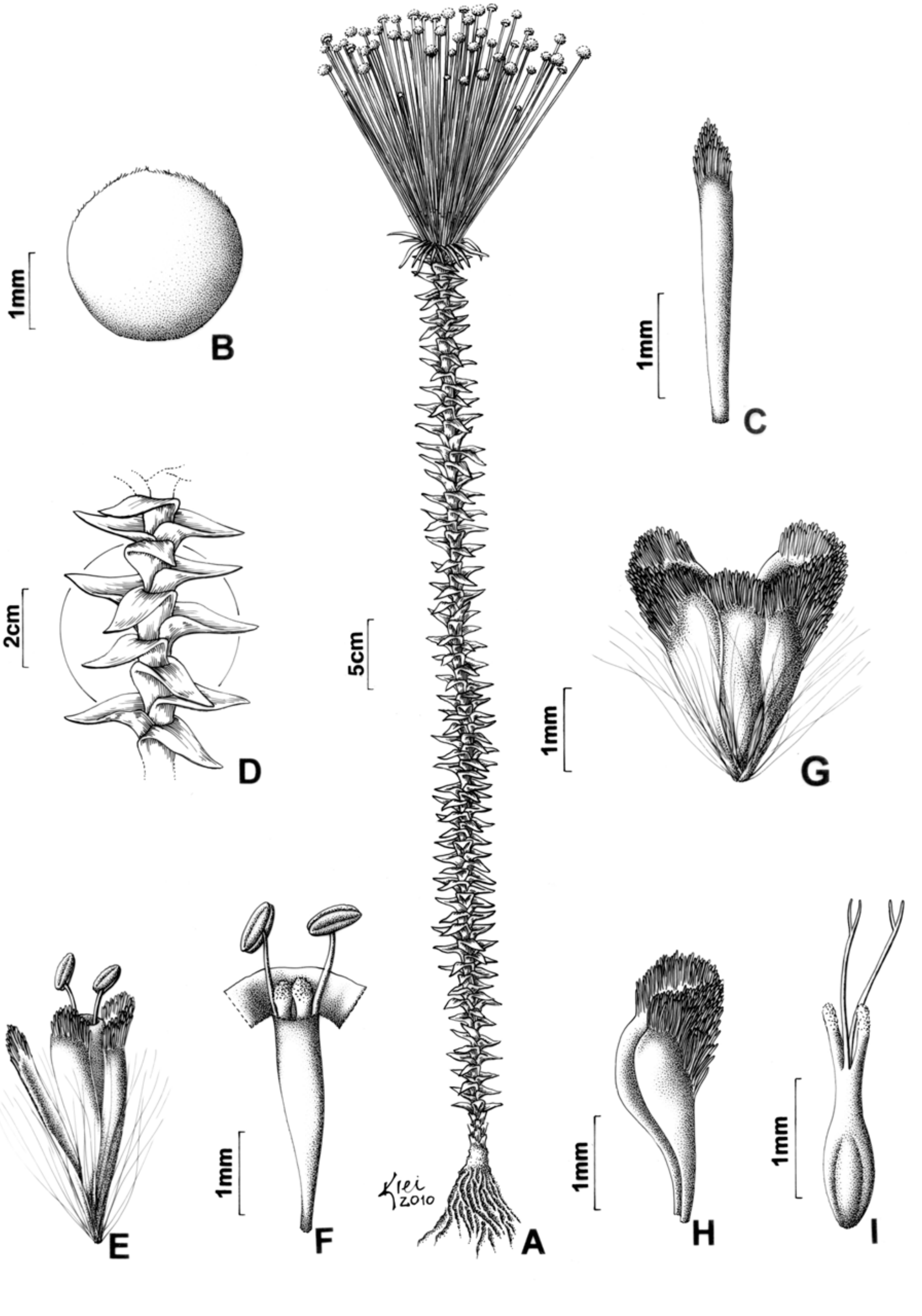

Figure 9. *Diphyomene acanthophylla* (from *Trovó* et al. *465*). A. Habit. B. Involucral bract abaxial surface. C. Floral bract abaxial surface. D. Detail of the reproductive axis. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower. H. Pistillate flower sepal. I. Gynoecium.

Figure 10. *Diphyomene acanthophylla*. A. Population from savannas of Chapada dos Veadeiros (GO). B. An individual occurring on rocky soil in the Chapada dos Veadeiros (GO). C. Population from Cristalina (GO). D. Detail of axis bracts. Scale bars, A: 30 cm. B: 10 cm. C: 12 cm. D: 2 cm.

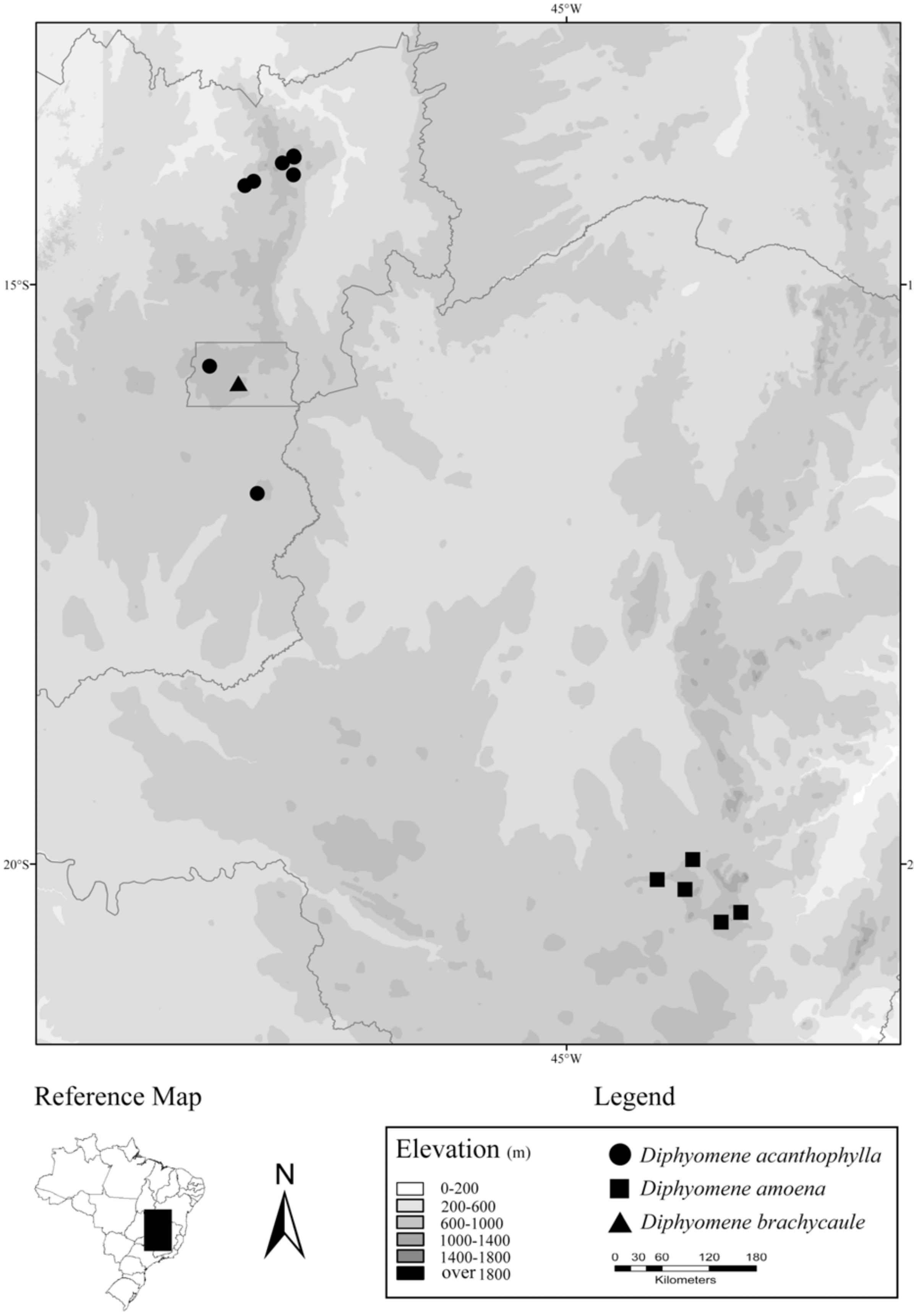

Figure 11. Geographical distribution of *D. acanthophylla*, *D. amoena* and *D. brachycaule*.

2. Diphyomene amoena (Bong.) Trovó, Cap. 3. *Eriocaulon amoenum* Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Ser. 6 Sci Math. 1: 637. 1831. *Paepalanthus amoenus* (Bong.) Koern., in Martius & Eichler, Fl. bras. (3)1: 316. tab. 42. 1863. *Dupatya amoena* (Bong.) Kuntze, Revis. gen. Pl. 2: 745. 1891.—TYPE: BRAZIL. Minas Gerais: "In glareosis graminosis pr. Capanema". Feb 1825, *Riedel s.n.* (holotype: LE! in two sheets). Figs. 12–13.

Eriocaulon longipes Mart. ex Steud., Syn. Pl. Glumac. 2: 276. 1855.—TYPE: BRAZIL. Minas Gerais: "Brasilia". Ago—Apr 1840, *Claussen 1156* (holotype: G!).

Paepalanthus amoenus fn. *prolifer* Moldenke, Phytologia 21: 417. 1971.—TYPE: BRAZIL. Minas Gerais: "Bello Horizonte, Serra do Curral—Acaba Munde". 10 Mar 1933, *Mello Barreto 2491* (holotype: NY!; isotype: SPF!).

Paepalanthus amoenus var. *curralensis* Silveira. nom. nud.

Herbs, 40–90 cm tall; rhizome present, aerial stem 0.5–1.0 cm long. Leaves persistent or deciduous, linear, flat, patent, 3.5–8.5 x 0.1–0.2 cm, glabrescent, margin ciliated to glabrescent, apex acuminated. Reproductive axis erect, 20.0–80.0 cm long, 0.2–0.4 cm diam., glabrous; axis bracts with same shape, chartaceous, lanceolate, erect, 2.5–4.0 X 0.3–0.5 cm, glabrous, apex largely acuminate, base semi-amplexicaul. Spathes 2.0–4.5 cm long, glabrous, apex acute. Scapes 10–40, arranged in a spherical umbel, 18.0–32.0 cm long, glabrous. Capitula 5–7 mm diam., semi-spherical to discoid, white; involucral bract in 3–4 series, dark-brown, oblong-elliptic, concave, ca. 4 mm long, glabrous, ciliated toward the apex, apex obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 60 per capitulum, ca. 4 X more staminates than pistillates; floral bract linear to oblanceolate, light-brown, concave, ca. 3 mm long, hairy in abaxial surface apex to glabrescent, ciliated toward the apex, apex acute to acuminate; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, golden to dark-brown, ca. 3 mm long, hairy in abaxial surface apex to glabrescent and hairy in central portion, ciliated toward the apex, apex; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 2 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings ,ca. 3 mm, sessile; sepals dolabriform, golden to dark-brown, ca. 3 mm long, hairy in abaxial surface to glabrescent and hairy in central portion, ciliated toward the apex, apex obtuse, mucronate; petal elliptic, hyaline, fleshy, ca. 2 mm long, hairy in abaxial surface to glabrescent and hairy in central portion, ciliated toward the apex, apex obtuse; gynoecium ca. 2 mm long, stigmatic branches bifid, twice longer than the nectariferous branches, staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. Individuals with flowers and fruits were collected between January and September. The blooming peak is from March to June. Mature fruits were collected from April to September.

Distribution, Habitat, and Conservation Status. *Diphyomene amoena* is one of the two species of the genus occurring in the southern region of the Espinhaço Range, between Belo Horizonte and Ouro Preto, in a mountain-complex known as the “Quadrilátero Ferrífero” (Fig. 11). It occurs in a vegetation type locally known as “Canga”, typical of soils with high iron content (Fig 13 A). This is an area of extreme economical importance, thus incurring intense human interference. According to IUCN (2001) criteria, *D. amoena* is considered endangered (criteria B1a, B1b, B2a).

Commentaries. The thin reproductive axis and erect axis bracts with an eminently acuminate apex are the most distinctive features of *Diphyomene amoena*. The species is also distinguishable by its geographical distribution, i.e., restricted to the “Quadrilátero Ferrífero”. The morphologically most similar species is *Diphyomene stenophylla*, which also bears linear leaves. Nevertheless, the latter is endemic to Itacambira in the northern part of the Espinhaço Range, with a smaller habit and different-shaped axis bracts.

Bongard (1831) briefly described *Eriocaulon amoenum* based on Ludwig Riedel’s collection at Serra do Capanema. Two sheets were encountered at LE, one in Bongard’s own handwriting and the other in that of both Bongard and Riedel. However, the second sheet was obviously a fragment of the first, whereby both were considered as part of a single collection.

In most European Herbaria, numerous sheets labeled as Mart. 878 are identified as “*Eriocaulon longipes* Mart”. However, the name was never formally published by Karl Friedrich Philipp von Martius. Steudel (1855) validated the name with another type-specimen, *Claussen 1156*, deposited at G. As Koernicke (1863) had already asserted the impossibility of separating this species from *D. amoena*, it must be treated as synonymous.

Moldenke (1971) described *Paepalanthus amoenus* fn. *prolifera* based on a single specimen (*Mello Barreto 2491*) deposited at NY, distinguishing it from *D. amoena* solely by its pseudo-viviparous capitula. This feature, often a non-stable character within populations, is a common teratogenetic occurrence among many of the Eriocaulaceae. As the isotype deposited at SPF (probably not seen by Harold Moldenke) does not present this feature, such a distinction is meaningless.

Silveira (1928) cited *Paepalanthus amoenus* var. *curralensis* within a list of his own collections (Silveira 1928, p. 401). The referred specimen was found at R, with a full description attached. However, the name has never been formally published. As with the remaining collections from Serra do Curral in Minas Gerais, this specimen fully matches the delimitations as applied to *D. amoena*.

Selected specimens examined: Brazil. **Minas Gerais**: Belo Horizonte, *Barreto, M.* 2521, 31.3.1993 (SPF), *Barreto, M. 2521a*, 31.5.1933 (SPF), *Barreto, M. 10837*, 26.4.1940 (BHCB, SPF), *Roth, B. L. 16579*, 1.5.1952 (SPF), *Duarte, A.P. 12740*, 6.4.1970 (BHCB); Brumadinho, *s.c. 212*, s.d. (SPF); Itabirito, *Teixeira, W.A. s.n.*, 5.3.1995 (SPF), *Vianna, P.L. 714*, 12.7.2002 (BHCB); Moeda, *Grandi, T.S.M. et al. s.n.*, 28.3.1990 (SPF); Nova Lima, *Barreto, M. 2520*, 16.3.1933 (SPF), *Barreto, M. 2493*, 6.4.1934 (BHCB); Ouro Branco, *Sá, R.A. et al. s.n.*, 15.5.1988 (BHCB), *Alves, R.V et Becker. J. 1507*, 18.9.1990 (SPF), *Souza, V.C. et al. 7863*, 8.3.1995 (ESA), *Souza, V.C. et al. 8027*, 9.3.1995 (SPF, ESA), Ouro Preto, *Magalhães, M. 1216*, 28.1.1942 (BHCB), *Davis, P.H. et Shepherd, G. J. 59648*, 31.7.1976 (UEC), *Davis, P.H. et Shepherd, G. J. 59605*, 31.7.1976 (UEC), *Stützel, T. et al. 65*, 26.2.1987 (SPF).

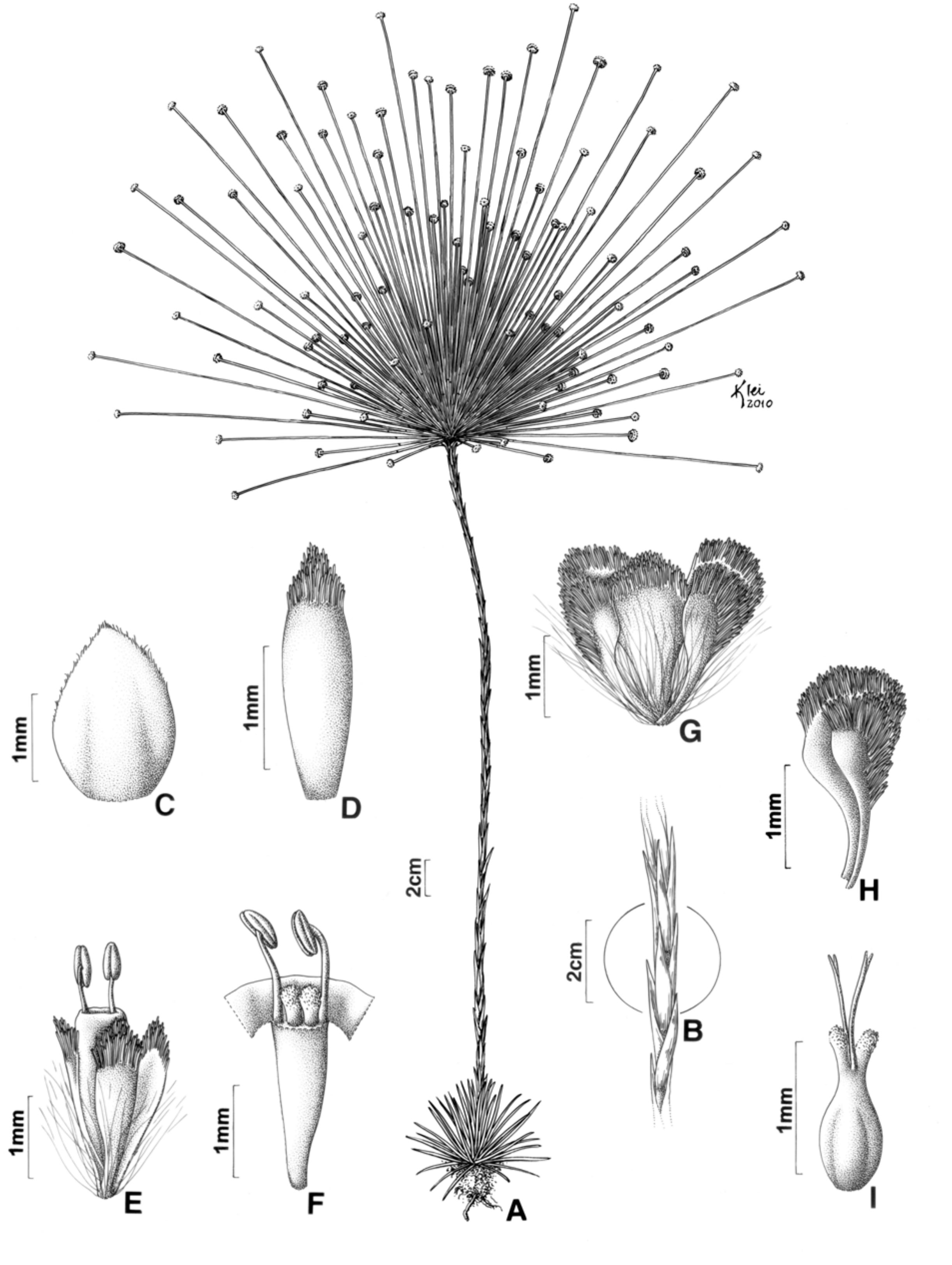

Figure 12. *Diphyomene amoena* (from *Trovó* et al. *465*). A. Habit. B. Detail of the axis bracts. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower. H. Pistilate flower sepal. I. Gynoecium.

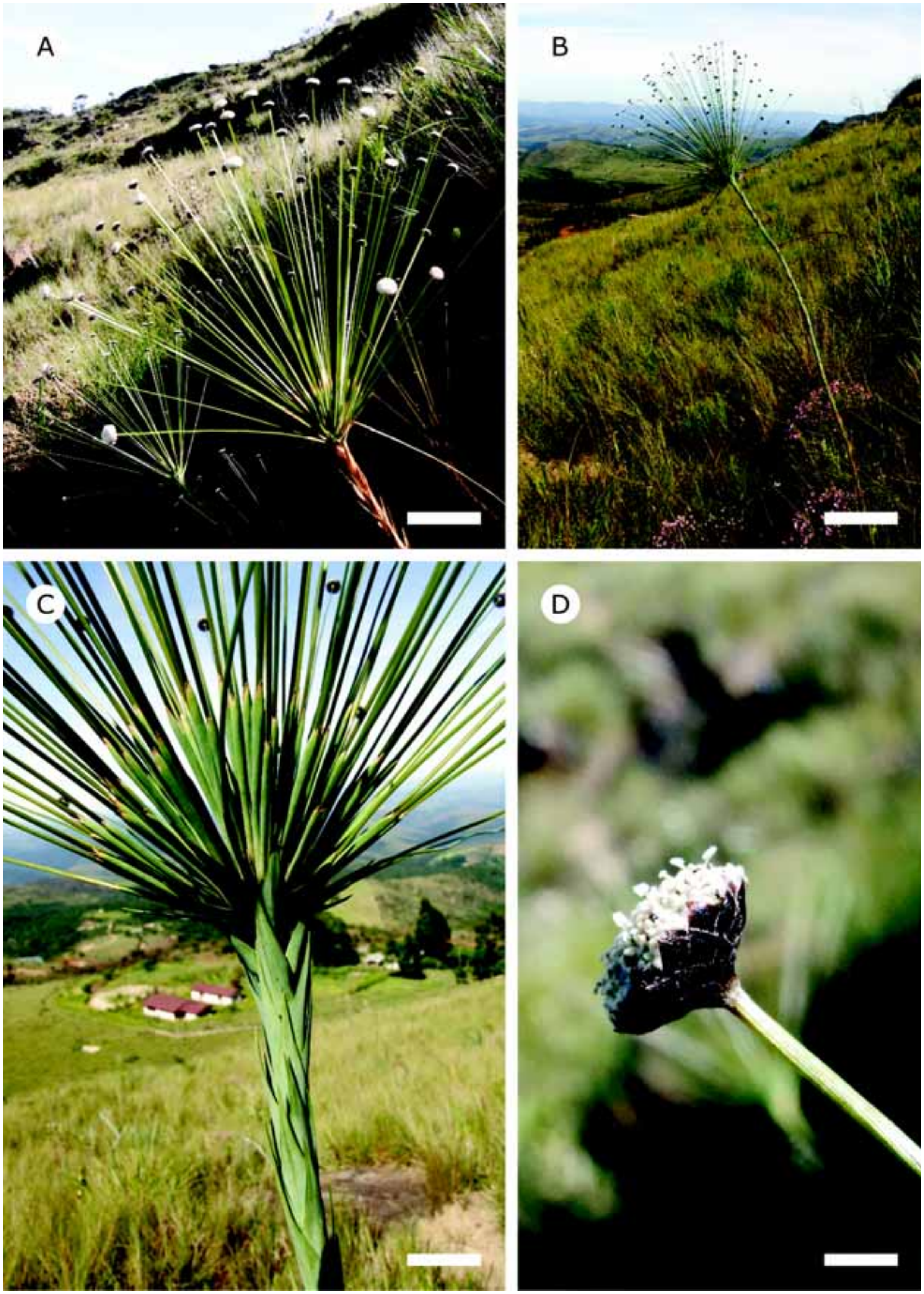

Figure 13. *Diphyomene amoena*. A. Population from Serra do Capanema (MG). B. Habit. C. Detail of axis bracts. D. Detail of capitula. Scale bars, A: 8 cm. B: 15 cm. C: 6 mm. D: 3 mm. (Photos: L. Echternacht)

3. Diphyomene brachycaule Trovó, Appendix 1.—TYPE: BRAZIL. Distrito Federal: "Brasília, EEJBB, prox. à área de lazer, lado esquerdo que dá acesso CASEB. 15° 52'0" S/ 47° 51' 0" W". 03 Jul 2000, *M. G. Nobrega & L. C. Mendes 1187* (holotype, HEPH!). Figs. 14–15.

Herbs, 24–26 cm tall.; rhizome absent, aerial stem 0.5–1.0 cm long. Leaves persistent, lanceolate, flat, erect, 4.0–5.5 X 0.3–0.5 cm, hairy, margin ciliated, apex mucronate. Reproductive axis erect, 3.5–4.0 cm long, 0.3–0.4 cm diam., glabrous; axis bracts gradually smaller from the base to the apex, chartaceous, lanceolate, erect, 1.5–4.5 X 0.3–0.5 cm, hairy, margin ciliated to glabrescent, apex mucronate, base amplexicaul. Spathes 2.5–3.5 cm long, glabrous, apex acute. Scapes 6–10, arranged in an obconic umbel, 15.0–21.0 cm long, glabrous. Capitula 8–10 mm diam., discoid, white; involucral bracts in 3–4 series, dark-brown, deltoid to ovate, concave, ca. 4 mm long, glabrous, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 150 per capitulum, ca. 8 X more staminates than pistillates; floral bracts linear, light-brown, flats, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, brown, ca. 3 mm long, glabrous, margin ciliated toward the apex to glabrescent, apex acute; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistilate flowers disposed in concentric rings, ca. 3 mm, sessile; sepals dolabriform, white, ca. 3 mm long, hairy in the abaxial surface base, margin ciliated toward the apex to glabrescent, apex mucronulate; petals elliptic, fleshy, ca. 3 mm long, hairy in abaxial surface, margin ciliated toward the apex, apex obtuse; gynoecium ca. 3 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds not seen.

Phenology. Individuals with mature staminate and pistillate flowers and juvenile fruits were collected in July.

Distribution, Habitat, and Conservation Status. *Diphyomene brachycaule* is restricted to Brasília (DF) (Fig. 11). The type specimen was gathered from a large population in an area of open grass savanna in the Brasília Botanical Garden. According to IUCN (2001) criteria, the species is considered critically endangered (criteria B1a).

Commentaries. The species is easily distinguished by the erect leaves covering the reproductive axis and the hairy mucronate leaves. It is the only species restricted to the Distrito Federal, where it is sympatric with *D. chiquitensis* and *D. koernickei*, which differ by their overall size (both are usually more than 1 meter high) and the size of their reproductive axis.

Diphyomene brachycaule and *D. decussa* are the most morphologically alike. Both are around the same size, possess short reproductive axis and ciliated leaves, and are without rhizomes. Nevertheless, the smaller *D. brachycaule* has hairy erect leaves with mucronate apex, and different-shaped reproductive axis bracts throughout the axis. It is also distinguished by possessing less glabrous scapes, wider capitula, and pistillate flowers with mucronate apex. Both species are allopatric, as *D. decussa* is restricted to the south of the Espinhaço Range in Minas Gerais State.

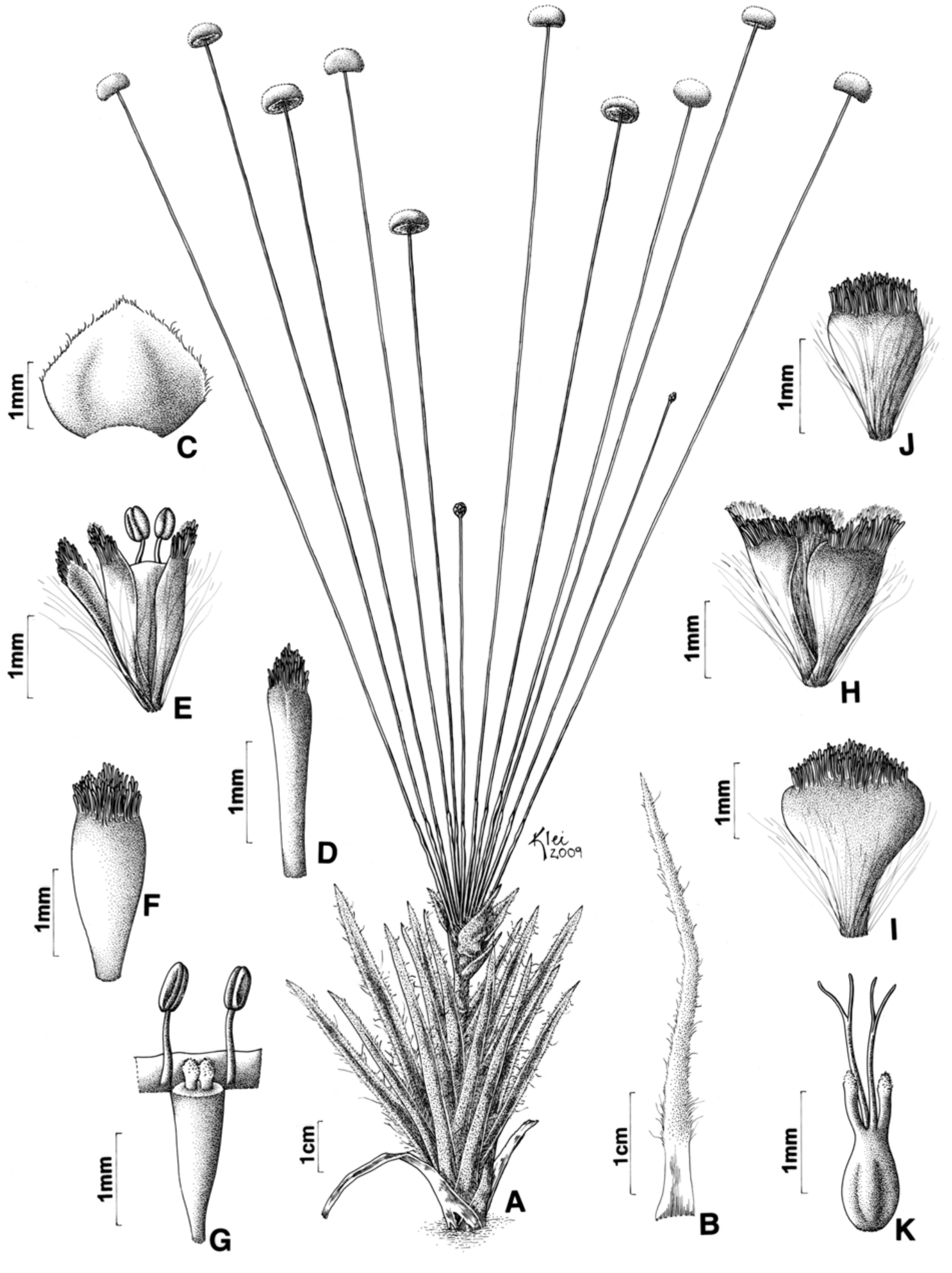

Figure 14. *Diphyomene brachycaule* (from *Nóbrega* & *Mendes 1187*). A. Habit. B. Detail of a leaf. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower sepal. G. Staminate flower with sepals removed and opened corolla. H. Pistillate flower. I. Pistillate flower sepal. J. Pistillate flower petal. K. Gynoecium.

Figure 15. *Diphyomene brachycaule*. Holotype deposited in HEPH.

4. *Diphyomene chiquitensis* (Herzog) Trovó, Cap. 3. *Paepalanthus chiquitensis* Herzog, Feddes Repert. 20: 86. 1924.—TYPE: BOLIVIA. Chiquitos: "Haüfig in den Kämpfen des Cerro de Santiago, 700—800 m". May 1907, *Herzog 114* (holotype: L!—incomplete). EPITYPE: BOLIVIA. Santa Cruz: "Velasco Province". 19 May 1995, *J. R. Abbott 16850* (EPITYPE—designated by Trovó & Sano (Cap. 3): SPF! in 2 sheets). Figs. 16–18.

Paepalanthus erectifolius var. *glabra* Silveira, Floral. Mont. 1: 192. 1928.—TYPE: BRAZIL. Minas Gerais: "In campis prope Itambé do Serro". May 1908, *Silveira 499* (holotype: R!).

Paepalanthus erectifolius var. *grandifolia* Silveira, Floral. Mont. 1: 192. 1928.—TYPE: BRAZIL. Minas Gerais: "In campis in Chapada do Couto". Apr 1918, *Silveira 711* (holotype: R!).

Paepalanthus formosus Moldenke, Bol. Soc. Venez. Ci. Nat. 14:11. 1952.—TYPE: VENEZUELA. Amazonas: "Cerro Guanay, alt. 2000 m". 4 Feb 1951, *B. Maguire & al. 31754* (holotype: NY!).

Paepalanthus moldenkeanus R.E. Schultes, Botanical Mus. of Leaf. 16:187. 1954.—TYPE: COLÔMBIA. Vaupés: "Quartzite savannah near headwaters, 900—1000 feet". 4-5 Oct 1951, *R. E. Schultes & I. Cabrera 14351* (holotype: GH! in 2 sheets).

Paepalanthus speciosus var. *pulverulentus* Moldenke, Phytologia 10: 489. 1964.—TYPE: BRAZIL. Goiás: "Cristaleira elev. 1250 m". 30 Mar 1963, *Edmundo Pereira 7476* (holotype: LL! in 2 sheets).

Paepalanthus speciosus var. *attenuatus* Moldenke, Phytologia 28: 466. 1974.—TYPE: BRAZIL. Goiás: "Chapada dos Veadeiros". 22 Mar 1971, *H. S. Irwin & al. 32935* (holotype: LL!; isotype: LL!).

Paepalanthus speciosus var. *bolivianus* Moldenke, Phytologia 28: 467. 1974.—TYPE: BOLIVIA. Santa Cruz: "Velasco, 200 m". Jul 1892, *Kuntze s.n.* (holotype: NY!).

Paepalanthus speciosus f. *calvescens* Moldenke, Phytologia 28: 467. 1974.—TYPE: BRAZIL. Goiás: "Prov. de Goyaz". May-Jul 1884, *Weddell 2133* (holotype: NY!; isotypes: P!).

Paepalanthus speciosus var. *goyazensis* Moldenke, Phytologia 52: 414. 1983.—TYPE: BRAZIL. Goiás: "Chapada dos Veadeiros", 16 Apr 1956, *E. Yale Dawson 14271* (holotype: LL!).

Paepalanthus amoenus var. *bolivianus* Moldenke, Phytologia 61: 444. 1987.—TYPE: BOLIVIA. La Paz: "Iturralde, Sabanna Húmeda, 180 m". 2 Aug 1985, *R. Haase 685* (holotype: LL!).

Paepalanthus giganteus Sano, Taxon 53: 106. 2004. *Eriocaulon speciosum* Bong., Mém. Acad. Imp. Sci. St.-Pétersbourg, Ser. 6 Sci Math. 1: 636. 1831. *Paepalanthus speciosus* (Bong.) Koern., in Martius & Eichler, Fl. bras. (3)1: 315. tab. 39, 40, 41. 1863, *nom. illeg.* non Gardner (1843).

Dupatya speciosa (Bong.) Kuntze, Revis. gen. Pl. 2: 746. 1891.—TYPE: BRAZIL. São Paulo: "In campis Batataes". Feb 1834, *Riedel 2300* (NEOTYPE—designated by Trovó & Sano (Cap. 3): LE! in 2 sheets; isoneotypes: B!, G!, K!, P!).

Herbs, 65–300 cm tall; rhizome present or absent, aerial stem 1.0–3.5 cm long. Leaves persistent or rarely deciduous, linear to lanceolate, flat, patent, 9.0–40.0 X 0.3–3.0 cm, hairy or glabrous, margin ciliated or glabrous, apex acute. Reproductive axis erect, 50.0–270.0 cm long., 0.4–1.8 cm diam., glabrous; axis bracts gradually smaller from the base to the apex, chartaceous, lanceolate, sub-erect to patent, 2.0–20.0 X 0.4–2.5 cm, glabrous rarely glabrescent, margin ciliated or glabrous, apex acute, semi-amplexicaul to amplexicaul. Spathes 2.0–6.5 cm long., glabrous, apex acute. Scapes 30–460, arranged in a spherical umbel, 15.0–40.0 cm long, glabrous. Capitula 6–20 mm diam., discoid to spherical, white; involucral bracts in 3–5 series, brown to dark-brown, obovate to elliptic, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; receptacle semi-spherical, hairy. Flowers dimerous, ca. 550 per capitulum, ca. 5 X more staminates than pistillates; floral bracts linear, light-brown, flat, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long., with long trichomes; sepals navicular, light-brown, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings, ca. 3 mm, sessile; sepals dolabriform, white to light-brown, ca. 3 mm long., hairy in the abaxial surface apex and base, margin ciliated toward the apex, apex mucronate; petals elliptic, hyaline to golden, ca. 2 mm long, hairy in abaxial surface, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, briefly surpassing the nectariferous branches, staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. The blooming period of *D. chiquitensis* is relatively continuous. Nevertheless, this may vary according to the local. In each the blooming period is related to the end of the rainy season, if seasonality is prevalent. Most of the flowering individuals were collected from February to September. Those with mature fruits were collected regularly between March and November.

Distribution, Habitat, and Conservation Status. *Diphyomene chiquitensis* is the most widely distributed species, thereby bestowing most genus distribution limits. It is the only species encountered outside Brazil, by also occurring in the savannas of Bolivia, Venezuela and Colombia. In Brazil, it prevails in typical cerrados from São Paulo to the Amazon, as well as in grass fields at several rocky heights of central and eastern Brazil (Fig. 19). According to IUCN (2001) criteria, *D. chiquitensis* is considered of least concern.

Commentaries. *Diphyomene chiquitensis* is the most variable species within the genus. It can be discriminated from the remainder by its axis-bract pattern, altering from large at the base to small at the apex, and by its usually robust habit. However, these features may vary. In some sheets from Caldas Novas, Goiás, and Pirenópolis, the axis-bract pattern may not be in evidence. Moreover, some populations at Brasília consist of small individuals.

On the premise that species morphological variation is mainly associated with geographic distribution and habitat, six morphological patterns were detected, and are discussed below. They are not completely discontinuous, whereby the incidence of mutual morphological overlapping at different localities is frequent. Thus, on considering the taxonomic species concept, they can be considered as part of a single species, unrelated to any infra-specific taxa. As biogeographical aspects are relevant to phylogenetic relationships in Eriocaulaceae, the following discrimination should be included in sampling, as part of a phylogenetic study of the genus. Studies involving population genetics are also relevant for clarifying species delimitation.

The typical *D. chiquitensis* pattern is restricted to type location, situated in the savannas of Bolivia. This pattern is composed of medium-sized individuals, more or less 1.2 m high. They are outstanding by the unusual glandulous pilosity of both leaves and axis bracts, and the wide spherical capitula. The names applied to this morphological variant are: *Paepalanthus chiquitensis*, *Paepalanthus speciosus* var. *bolivianus*, and *Paepalanthus amoenus* var. *bolivianus*.

The most common pattern is distributed throughout the savannas of South America from São Paulo (Brazil) to Vaupés (Colombia), and more rarely on rocky elevations of Goiás (Brazil) and Amazonas (Venezuela). It is characterized by medium-sized individuals around 1.2 m high, these, usually possessing sparsely hairy leaves and glabrescent axis bracts. The latter are curvate. The names applied to this morphological variant are: *Paepalanthus formosus*, *Paepalanthus moldenkeanus*, and *Paepalanthus giganteus*.

The pattern occurring in the Espinhaço Range in Minas Gerais and in the Chapada dos Veadeiros in Goiás is morphologically related to the most common pattern described above, by possessing very similar axis bracts. Nevertheless, individuals from these populations are glabrous and significantly more robust, easily reaching over 2 m in height. Sheets of medium sized individuals (ca. 1.7 m) from Chapada dos Veadeiros may be confused with those of *D. koernickei* individuals, if the basal part were lacking. However, the axis bracts in *D. koernickei* individuals are more rigid. These incomplete sheets may also be confused with specimens pertaining to a pattern occurring in Caldas Novas, Pirenópolis and Goiás, discussed below. The names applied to this morphological variant are: *Paepalanthus erectifolius* var. *glabra*, *Paepalanthus erectifolius* var. *grandifolia*, *Paepalanthus speciosus* var. *attenuatus*, *Paepalanthus speciosus* var. *goyazensis*, and *Paepalanthus speciosus* var. *pulverulentus*.

Another pattern of high individuals (over 2 meters) occurs disjunct in Goiás, mostly in the Chapada dos Veadeiros, and in Minas Gerais in the Serra da Canastra. These populations occur in rocky fields usually intermixed with shrubs. They vary from sparsely hairy to glabrescent, and possess flat axis bracts, which are, in general, remotely placed throughout the axis. This form has no formal names associated.

A few populations from Central Brazil, mostly Brasília, also possess remotely arranged and narrow axis bracts, besides narrow lanceolate leaves. They are the smallest individuals within the species, usually not reaching more than 1 m high. However, more robust individuals can be found which are morphologically continuous with those from Serra da Canastra and the vicinity of Chapada dos Veadeiros described above. There are no formal names associated to this morphological variant.

Populations from Caldas Novas, Goiás and Pirenópolis constitute the least adequately placed pattern within this species. The axis bracts, evident in the remainder, are not always so in these individuals. In such cases, it is difficult to distinguish this pattern from *D. koernickei*. Although the more rigid axis bracts of *D. koernickei* may be useful for discriminating, this feature may be too flimsy for the purpose. Nevertheless, we decided to maintain *D. koernickei* within a restricted circumscription, and immerse this morphological variation within an already variable species. This pattern also resembles the populations from the Espinhaço Range and Chapada dos Veadeiros. Distinguishment between the two relies on the relatively smaller and narrower axis bracts of the plants from Caldas Novas, Goiás and Pirenópolis. If the basal part of these individuals is missing, the distinction is based solely on geographical information. The name *Paepalanthus speciosus* fn. *calvescens* is associated with this morphological variant.

Selected specimens examined: Brazil. **Amazonas**: Apuí, *Zartman, C.E. et al. 5671*, 26.6.2006 (INPA); Bodocó, *Sanaiotti, T.M. 295*, 25.10.1995 (SPF); Manicoré, *Lima, L.C.P. et al. 640*, 8.5.2009 (HUEFS); **Distrito Federal**: Brasília, *Heringer, E. P. 7887/81*, 30.1.1961 (HEPH), *Pires, J.M. et al. 9509,* 28.4.1963 (UB), *Irwin, H.S. Soderstrom, T.R. 5313,* 19.8.1964 (UB), *Maia-Filho, P. 13,* 27.6.1965 (UB), *Irwin, H.S. et al. 13925,* 12.3.1966 (UB), *Duarte, A.P. 10164,* 17.1.1967 (SPF), *Philcox, D. et Onishi, E. 4892,* 3.5.1968 (UB), *Ratter, J.R. Fonseca, S.G. 2821,* 26.3.1976 (UEC, UB), *Davis, P.H. et Shepherd, G. J. 60095,* 10.7.1976 (UEC), *Allem, A. et Vieira, G. 1546,* 30.1.1978 (CEN), *Heringer, E.P. 16876,* 2.3.1978 (IBGE), *Heringer, E.P. et al. 474,* 8.5.1978 (UEC, IBGE), *Heringer, E.P. 17388,* 17.7.1979 (IBGE), *Kirkbride, J.H.J. et Kirkbride, M.C.G. 3127,* 24.1.1980 (SPF), *Cesar, H.L. 345,* 4.3.1980 (UB), *Heringer, E.P. et al. 4602,* 5.5.1980 (IBGE), *Kirkbride, J.H.J. 3756a,* 6.2.1981 (UEC, UB), *Carvalho, V. 14a,* 7.6.1981 (SPF), *Kirkbride, M.C.G. 1560,* 10.6.1981 (UB), *Ratter, J.R. et al. 4777,* 13.9.1982 (SPF, UB, UEC), *Alves, M.A. 103,* 25.4.1983 (HEPH, CEN), *Kirkbride, J.H.J. 5282,* 2.5.1983 (UEC, SPF, UB), *Junior, F. 1,* 19.6.1985 (UB), *Silva, M.A. et al. 354,* 28.1.1987 (IBGE), *Mendonça, R.C. 902,* 25.4.1988 (IBGE), *Mendonça, R.C. Rocha, G.I. 1010,* 14.6.1988 (SPF, IBGE, UB), *Splett, S. 08-b,* 8.3.1990 (HEPH), *Guala, G.F. et Filgueiras, T. 1333,* 8.5.1990 (IBGE), *Azevedo, M.L.M. et Brochado, A.L. 680,* 20.6.1990 (IBGE), *Ramos, P.C.M. 464,* 14.12.1990 (UB), *Ramos, P.C.M. 578,* 21.1.1991 (UB), *Ramos, P.C.M. 579,* 21.1.1991 (UB), *Vieira, R.F. et Walter, B.M. 760,* 14.5.1991 (CEN), *Azevedo, M.L.M. et Alvarenga, D. 958,* 4.6.1991 (IBGE), *Dias, T.A.B. et Vieira, R.F. 185,* 4.6.1992 (CEN), *Filgueiras, T.S. 3336,* 22.4.1996 (SPF, IBGE), *Walter, B.M.T. et al. 3733,* 28.2.1997 (CEN), *Sampaio, A.B. et al. 138,* 22.8.1997 (SPF, CEN), *Sampaio, A.B. et al. 226,* 26.8.1998 (CEN), *Faria, J.G. et al. 82,* 30.4.1999 (CEN), *Calago, K. 201,* 29.6.1999 (CEN), *Munhoz, C. et al. 834,* 15.2.2000 (IBGE, SPF), *Guarino, E.S.G. et Pereira, J.B. 283,* 4.3.2000 (CEN), *Nobrega, M.G. et al. 1134,* 7.6.2000 (HEPH, MBM), *Munhoz, C. et al. 1599,* 13.6.2000 (IBGE), *Nobrega, M.G. et Mendes, L.C. 1206,* 3.7.2000 (HEPH, IBGE), *Fonseca, M.L. et Alvarenga, D. 4812,* 25.5.2003 (SPF, HEPH), *Silva, R.R. et Milhomens, L.C. 901-c,* 16.9.2003 (HEPH), *Milhomens et al. 279-a,* 2.10.2003 (HEPH), *Silva, M.A. et Inazawa, F.K. 5862,* 27.3.2006 (SPF), *Bernardino, J. 2,* s.d. (UB); Samambaia, *Rezende, J.M. 301,* 12.1.1996 (CEN), *Rezende, J.M. 403,* 22.4.1996 (CEN), São Bartolomeu, *Sucre, D. et Heringer, E.P. 557,* 17.6.1965 (UB); **Goiás**: Alto Paraíso de Goiás, *Pirani J.R. et al.* 1858, 8.2.1987 (SPF), *Menezes, N.L. 1218*, 9.5.1987 (SPF);

Caldas Novas, *Rizzo, A. 5126*, 25.4.1970 (SPF), *Rizzo, A. 5240*, 23.5.1970 (SPF); Cristalina, *Rizzo, A. 8927*, 28.3.1973 (SPF); Formosa, *Rizzo, A. 8045*, 13.4.1972 (SPF); Goiás, *Rizzo, A. 4087*, 5.4.1969 (SPF), *Rizzo, A. 4098*, 5.4.1969 (SPF); Igarapé de Boi, *Pires, J.M. et Santos, M.R. 16214*, 26.7.1978 (SPF); Niquelândia, *Brooks, R.R. et al. BRAXPEX 147*, 21.4.1988 (SPF), *Fonseca, M.L. et al. 1447*, 25.6.1997 (SPF), *Fonseca, M.L. et Cardoso, E. 1756*, 26.3.1998 (SPF), *Filgueiras, T.S. et al. 3561*, 1.6.1999 (SPF); Pirenópolis, *Rizzo, A. 6297*, 7.4.1971 (SPF), *Rizzo, A. 6318*, 5.5.1971 (SPF), *Anderson, W. R. 10461*, 16.5.1973 (INPA); Posse, *Forzza, R.C. et al. 1557*, 29.7.2000 (SPF); **Mato Grosso**: Alto Paraguai, *Souza, V.C. et al. 16620*, 20.5.1997 (ESA, SPF); Cuiabá, *Krapovickas, A. et al. 40223*, 3.6.1985 (SPF); Novo Aripuanã, *Ferreira, C.A.C. 5655*, 20.4.1985 (SPF); Serra Ricardo Franco, *Windisch, P. 1406*, 21.7.1977 (SPF); Sinop, *Thomas, W.W. et al. 3979*, 22.9.1985 (SPF); Tabaporã, *Souza, V.C. et al. 15351*, 21.4.1997 (ESA); Tapurah, *Souza, V.C. et al. 17788*, 12.6.1997 (ESA); **Mato Grosso do Sul**: Coxim, *Pott, A. 2232*, 24.6.1986 (SPF); **Minas Gerais**: Alpinópolis, *Martins, F.R. 14*, 23.3.1975 (UEC); Conceição do Mato Dentro, *Benko-Iseppon, A.M. 216*, 19.7.1993 (SPF); Couto de Magalhães, *Giulietti, A.M. et al. CFCR 4700*, 17.7.1984 (SPF); Diamantina, *Giulietti, A.M. 934-80*, 3.4.1980 (SPF), *Isejima, E.M. et al. CFCR 3592*, 10.4.1982 (SPF), *Arbo, M.M. et al. 4431*, 18.5.1990 (SPF), *Trovó, M.L.O. et Watanabe, M.C.T. 350*, 21.4.2006 (SPF), *Trovó, M.L.O. et al. 427*, 22.9.2007 (SPF); Grão Mogol, *Lima, L.R. et al. 98*, 22.3.2000 (SPF), Guapé, *Teixeira, H. s.n.*, 12.9.1990 (ESA); Januária, *Fonseca, M.L. et al. 1905*, 21.5.1998 (SPF); Joaquim Felício, *Sano, P.T. et al. CFCR 15204*, 19.3.1994 (SPF), Passos, *Trovó, M.L.O. et al. 382*, 14.5.2007 (SPF); Patrocínio, *Farah, F.T. et al. 565*, .12.1998 (ESA); Rio Vermelho, *Mello-Silva, R. et al. CFCR 7888*, 1.8.1985 (SPF); São Roque de Minas, *Romero, R. Et Nakajima, J. 1581*, 10.12.1994 (SPF), *Nakajima, J. et al. 974*, 23.3.1995 (SPF), *Sano, P.T. et al. 968*, 21.3.1998 (SPF), *Trovó, M.L.O. et al. 384*, 14.5.2007 (SPF); **Pará**: São Félix do Xingu, *Rosário, C.S. 76*, 12.6.1978 (UEC); **Rondônia**: Costa Marques, *Nee, M. 34492*, 25.3.1987 (SPF); **São Paulo**: Itapeva, *Souza, V.C. et al. 7095*, 12.9.1994 (ESA); Itararé, *Souza, V.C. et al. 4192*, 15.8.1994 (ESA), *Miyagi, P.H. et al. 381*, 12.2.1995 (ESA, HRCB, SPF); Itatinga, *Souza, J.P. et al. 506*, 27.4.1996 (ESA); Itirapina, *Camargo, R.A. 22*, 13.1.1983 (HRCB), *Tannus, J.L.S. et Assis, M. 105*, 31.7.1998 (SPF); Mogi Guaçu, *Eiten, G. et Eiten, L.T. 2724*, s.d. (SP); São Carlos, *Barreto, K.D. et al. 2411*, 4.5.1994 (ESA); **Tocantins**: Almas, *Walter, B.M.T. et al. 5300*, 10.8.2004 (SPF); Mateiros, *Trovó, M.L.O. et al 289*, 6.8.2006 (SPF), *Trovó, M.L.O. et al 295*, 7.8.2006 (SPF), *Trovó, M.L.O. et al 311*, 9.8.2006 (SPF).

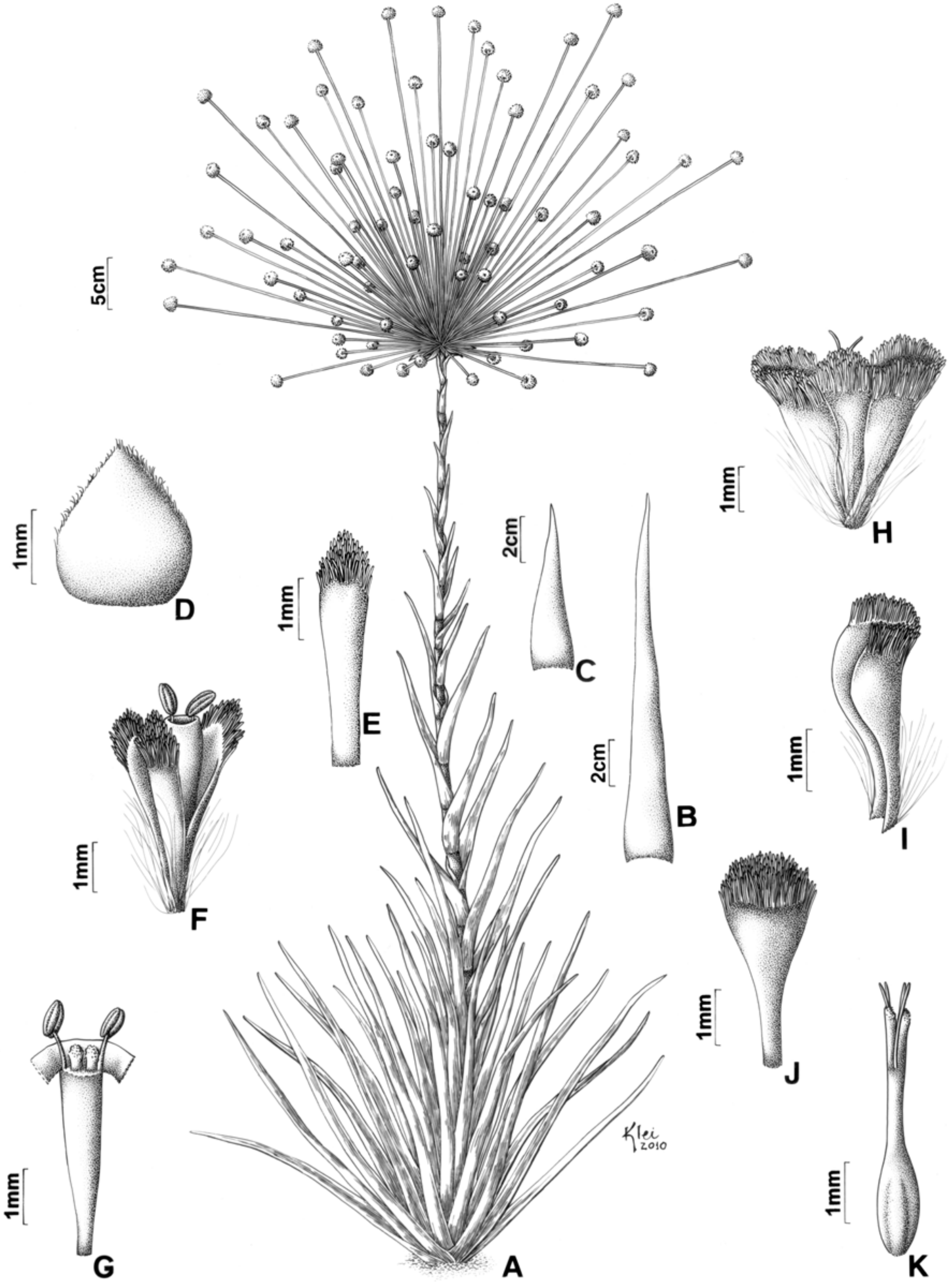

Figure 16. *Diphyomene chiquitensis* (from *Trovó* et al. *465*). A. Habit. B. Detail of the basal axis bract. C. Detail of the uppermost axis bract. D. Involucral bract abaxial surface. E. Floral bract abaxial surface. F. Staminate flower. G. Staminate flower with sepals removed and opened corolla. H. Pistillate flower. I. Pistillate flower sepal. J. Pistillate flower petal K. Gynoecium.

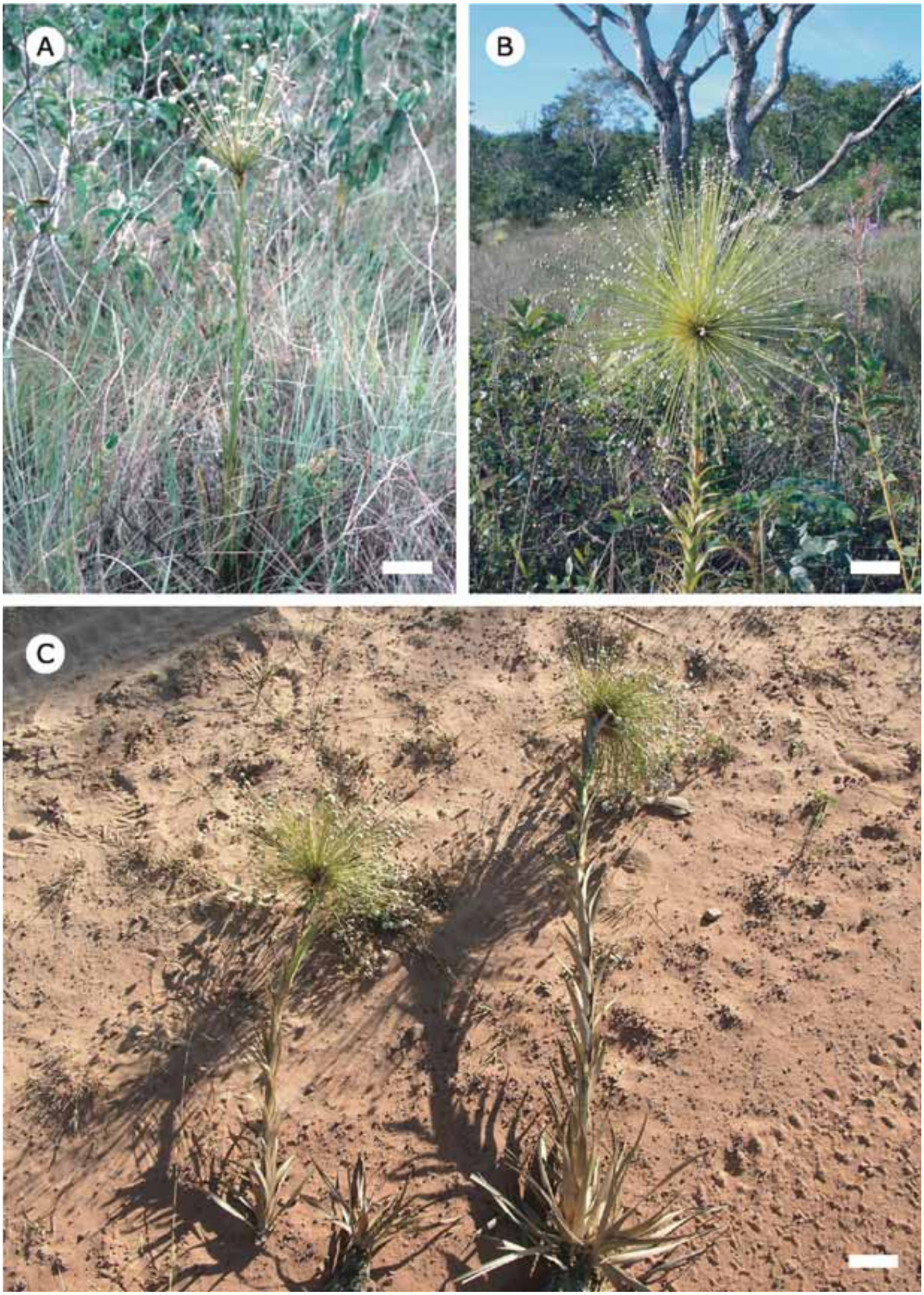

Figure 17. *Diphyomene chiquitensis*. A. Individual from the type locality in Bolivia. B. Individual from Manicoré (AM). C. Individuals from Mateiros (TO). Scale bars, A: 8 cm. B: 5 cm. C: 6 cm. (Photos by: A, J. Solomon; C, L. Lima).

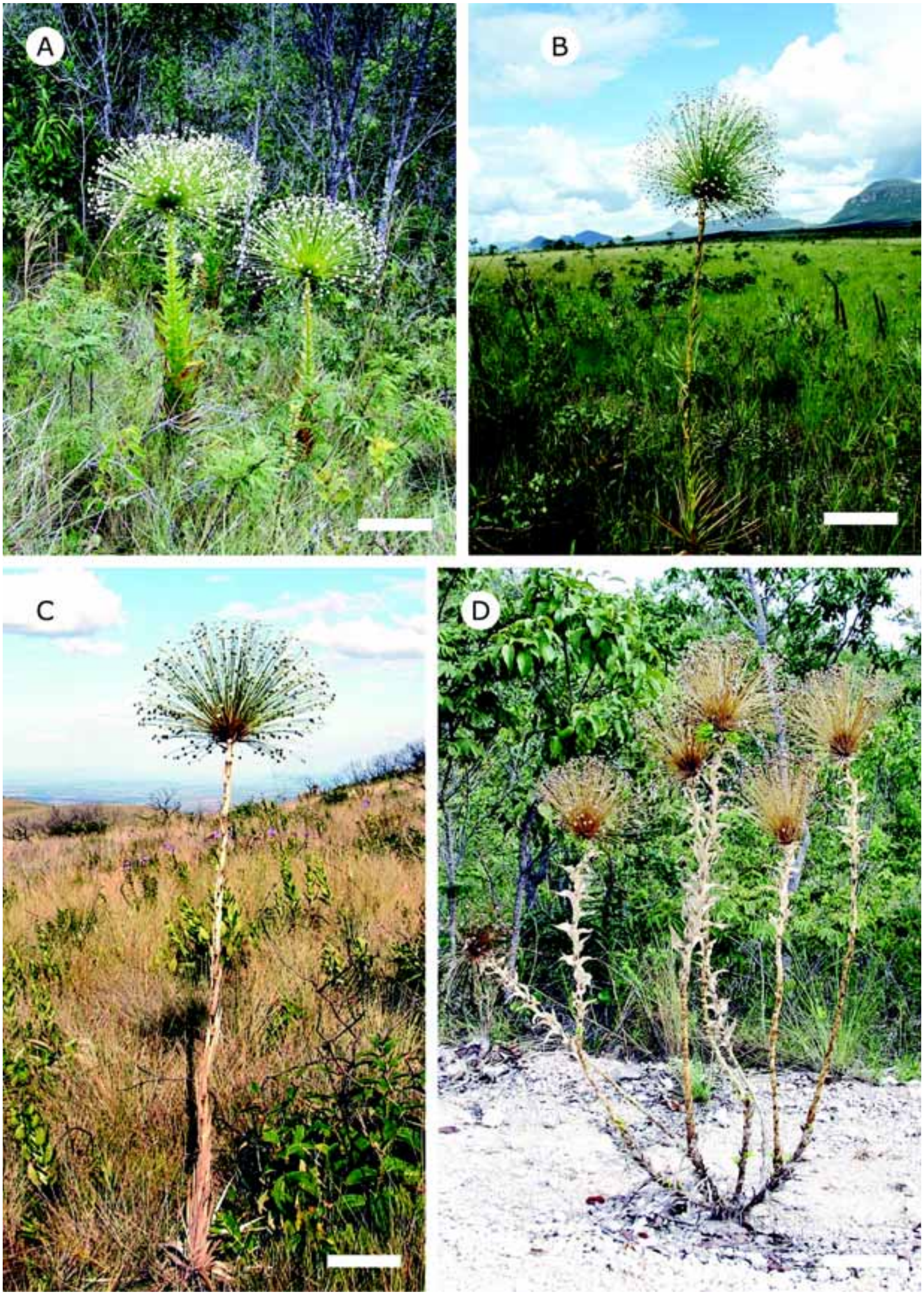

Figure 18. *Diphyomene chiquitensis*. A. Individual from Dimantina (MG). B. Individual from Chapada dos Veadeiros (GO). C. Individual from Serra da Canastra (MG). D. Individuals from Chapada dos Veadeiros (GO). Scale bars, A: 12 cm. B: 10 cm. C: 10 cm. D: 8 cm.

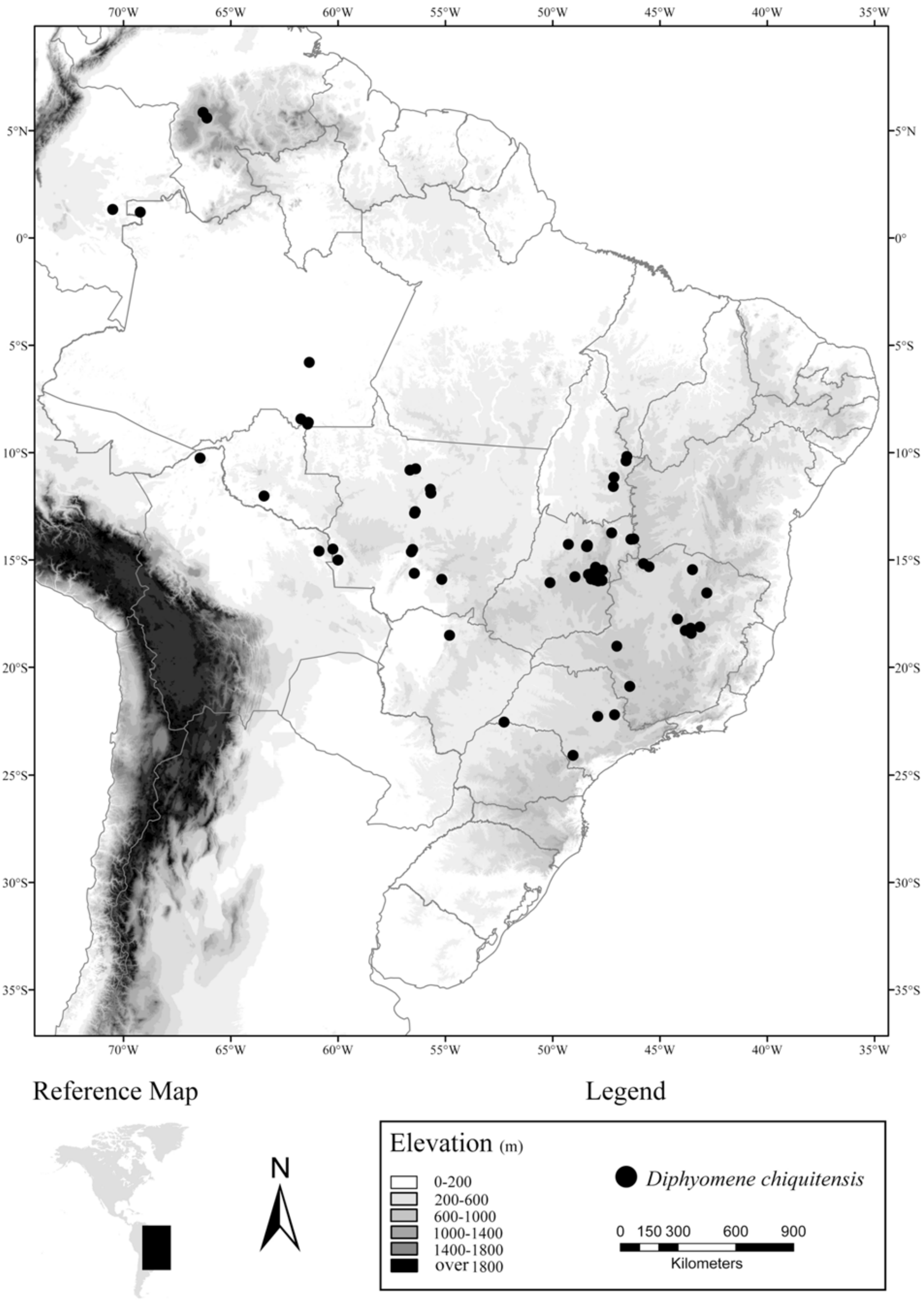

Figure 19. Geographical distribution of *D. chiquitensis.*

5. Diphyomene cipoensis Trovó, Appendix 2.—TYPE: BRAZIL. Minas Gerais: "Santana do Riacho, Parque Nacional da Serra do Cipó, MG 010, córrego duas pontinhas". 22 May 2007, *M. L. O. Trovó et al. 400* (holotype: SPF!). Figs. 20–21.

Herbs, 32 cm tall; rhizome present, aerial stem 1.5 cm long. Leaves persistent, linear to lanceolate, incurvate, patent, 5.5–7.5 X 0.3–0.4 cm, hairy to glabrescent, margin ciliated, apex acute. Reproductive axis erect, 4.5 cm long, 0.5 cm diam., glabrous; axis bracts with same shape, chartaceous, linear, erects to sub-erect, 5.0–5.5 X 0.3–0.4 cm, glabrous, margin ciliated, apex acute, semi-amplexicaul. Spathes 4.0–5.0 cm long, glabrous, apex acute. Scapes 25, arranged in an obconic umbel, 21.0–27.5 cm long, sparsely hairy. Capitula 7–8 mm diam., discoid, white; involucral bracts in 3–4 series, light-brown, ovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 46 per capitulum, ca. 45 staminates and 1 pistillate; floral bracts linear, light-brown, flats, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown to golden, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flower ca. 3 mm, sessile; sepals dolabriforms, light-brown, ca. 3 mm long., hairy in the abaxial surface base, margin ciliated toward the apex, apex mucronate; petals elliptic, light-brown, ca. 2 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruits and seeds not seen.

Phenology. Individuals of this species with fully developed staminate flowers were collected in May. The single pistillate flower was found in an early stage of maturation. Thus, fruits and seeds were not encountered.

Distribution, Habitat, and Conservation status. *Diphyomene cipoensis* is endemic to the Serra do Cipó in Minas Gerais (Fig. 22), where individuals grow among grasses in campos rupestres. A single reproductive individual was collected in an area that had already been largely exploited over the last 30 years. The specimen was collected inside the Serra do Cipó National Park following a fire event. According to IUCN (2001) criteria, *D. cipoensis* is considered critically endangered (criteria B1a).

Commentaries. *Diphyomene cipoensis* possesses one of the smallest reproductive axes within the genus. Although the species occurs sympatric to *D. erectifolia*, they are easily distinguishable, especially by the overall size, as individuals of the latter are generally more than 1 meter high. *Diphyomene cipoensis* is discernable from the remaining species by its hairy scapes and the shape of the leaves.

The species is morphologically related to *D. decussa*. They share scapes arranged in obconic umbel form and the same-shaped reproductive-axis bracts. They are also approximately the same overall size and have the same-sized hairy scapes. Nevertheless, *D. cipoensis* presents certain key differences, a shorter glabrous reproductive axis incurvate leaves, longer spathes, wider capitula and the mucronate apex of pistillate flower sepals. Moreover, the two species are allopatric, as *Diphyomene decussa* only occurs near to the town of Ouro Preto (MG).

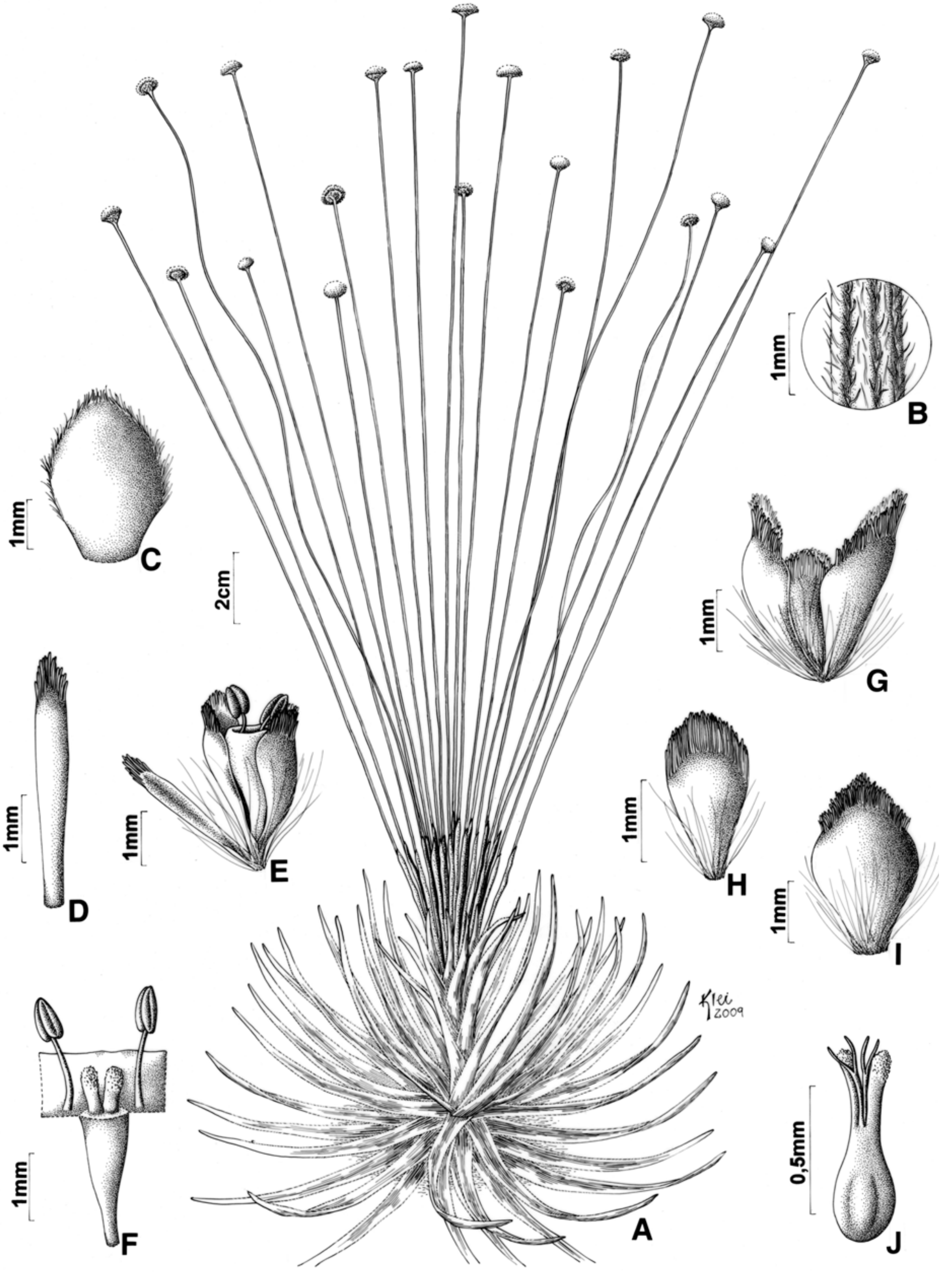

Figure 20. *Diphyomene cipoensis* (from *Trovó* et al. *400*). A. Habit. B. Detail of scape. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower. H. Pistillate flower petal. I. Pistillate flower sepal. J. Gynoecium.

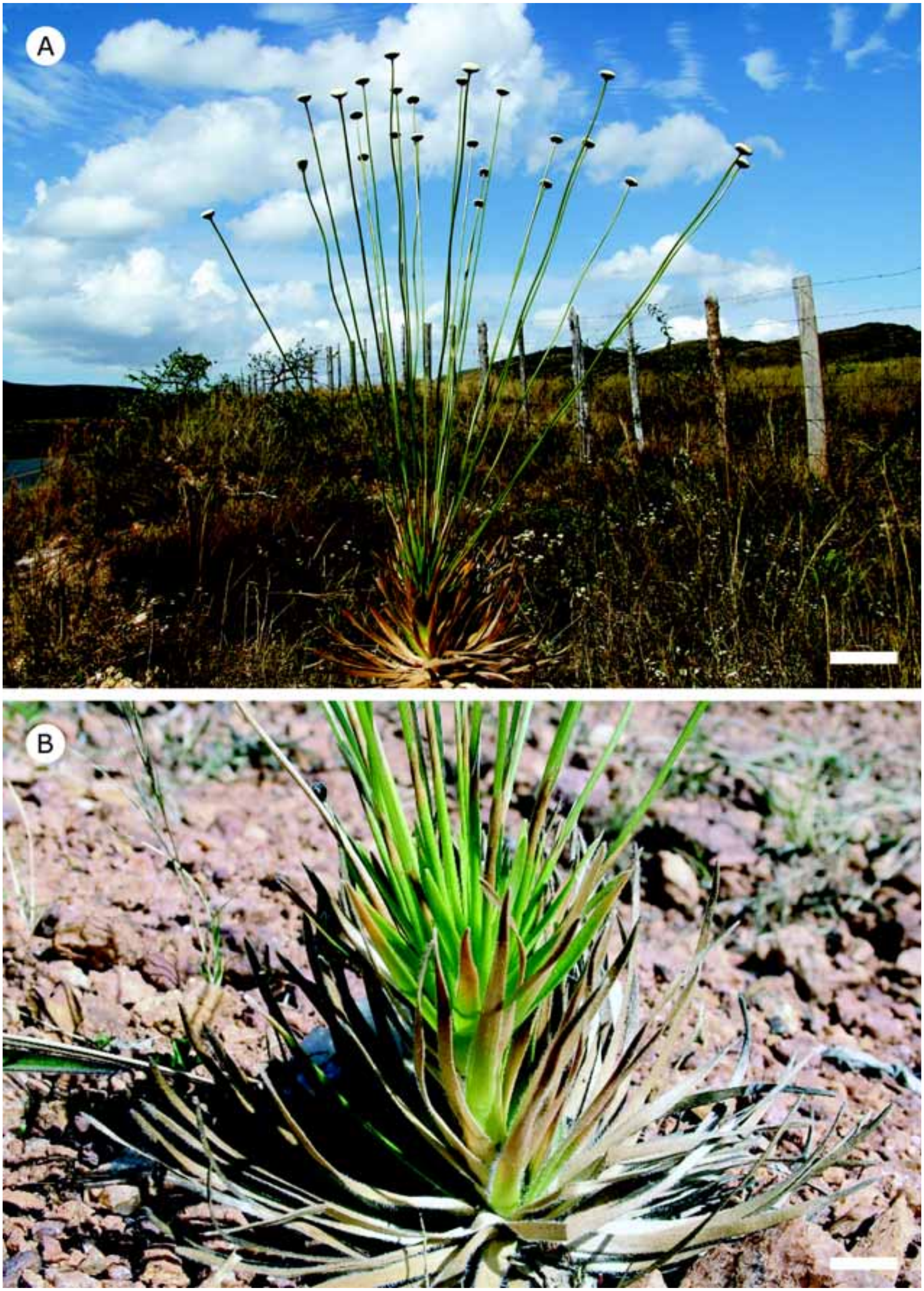

Figure 21. *Diphyomene cipoensis*. A. Habit. B. Rosette and reproductive axis. Scale bars, A: 3 cm. B: 1 cm.

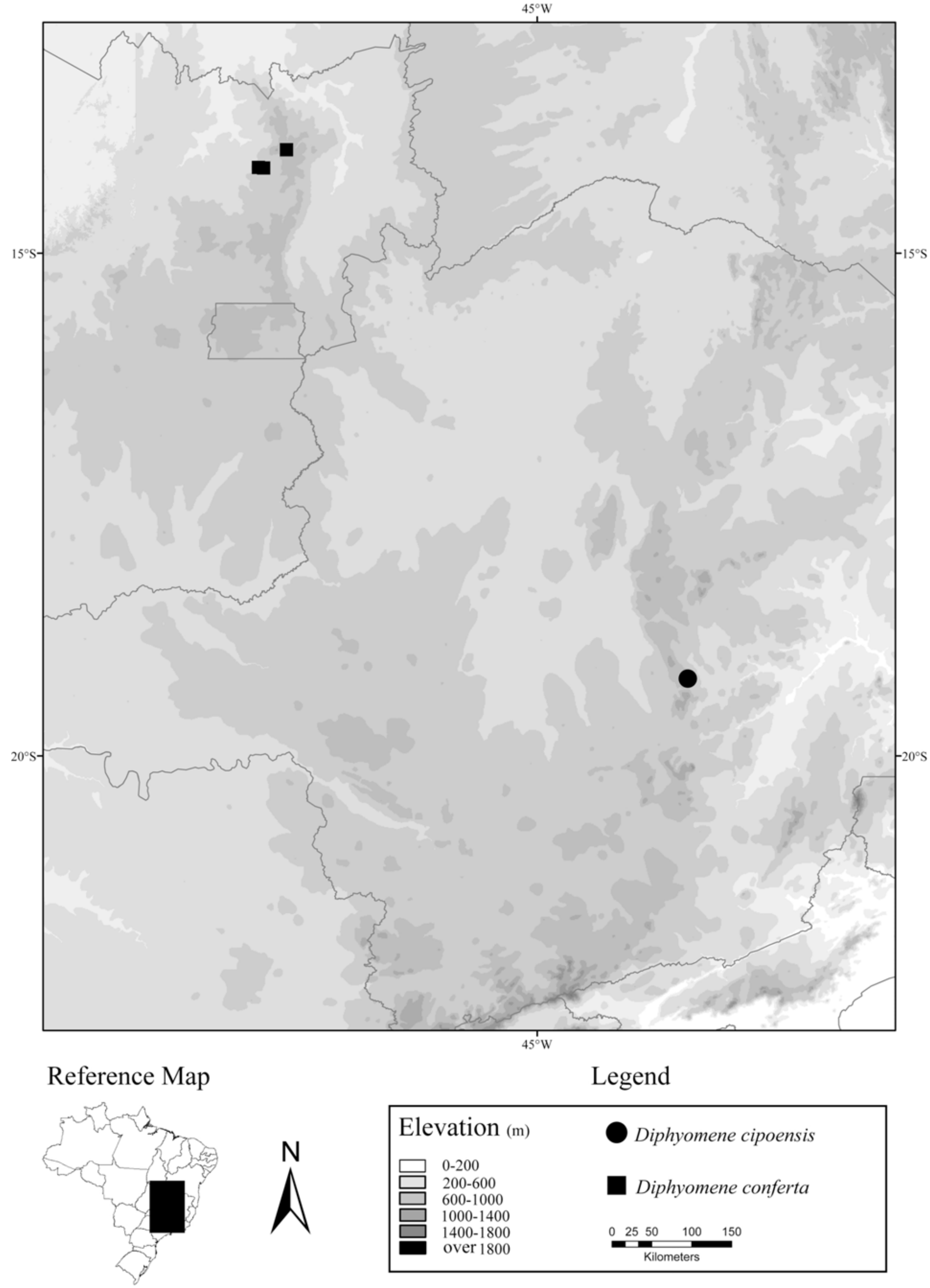

Figure 22. Geographical distribution of *D. cipoensis* and *D. conferta.*

6. Diphyomene conferta Trovó, Appendix 1.—TYPE: BRAZIL. Goiás: "Alto Paraíso de Goiás: Parque Nacional da Chapada dos Veadeiros, Estrada para a Vereda do Mulungu, 14° 06'29.7" S/ 47° 38' 34.0" W" 05 Dec 2007, *M. L. O. Trovó et al. 446* (holotype, SPF!; isotypes B!, NY! SP!). Figs. 23–24.

Herbs, 105–170 cm alt.; rhizome present, aerial stem 1.0–3.0 cm long. Rosette leaves persistent, lanceolate, flat, patent, 5.5–11.5 X 0.7–1.4 cm, hairy to glabrous, margin glabrous, apex acuminate. Reproductive axis erect, 75.0–140.0 cm long, 0.5–0.8 cm diam., glabrous; axis bracts with same shape, chartaceous, lanceolate, adpressed, 2.5–5.5 X 1.0–2.0 cm, glabrous, margin glabrous, apex acute, base amplexicaul. Spathes 4.0–7.5 cm long, glabrous, apex acute. Scapes 16–52, arranged in a spherical umbel, 27.0–45.0 cm long, glabrous. Capitula 12–20 mm diam., semi-spherical to spherical, sulfurous; involucral bracts in 4–5 series, dark-brown, ovate to oblong, concave, ca. 4 mm long, glabrous, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 330 per capitulum, ca. 3,5 X more staminates than pistillates; floral bracts linear, light-brown, flats, ca. 4 mm long, glabrous, margin ciliated toward the apex, apex acuminate; staminate flowers ca. 4 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, brown, ca. 3 mm long, hairy in abaxial surface, margin ciliated toward the apex to glabrescent, apex acute; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistilate flowers disposed in concentric rings, ca. 4 mm, sessile; sepals dolabriform, brown, ca. 4 mm long, hairy in the abaxial surface base, margin ciliated toward the apex, apex mucronulate; petals dolabriform, fleshy, ca. 3 mm long, hairy in abaxial surface base, margin ciliated toward the apex, apex obtuse; gynoecium ca. 3 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. Individuals with staminate and pistillate flowers, and mature fruits, were collected between December and March. The blooming period virtually coincides with the rainy season.

Distribution, Habitat, and Conservation Status. *Diphyomene conferta* is known only from the predominantly grassy rocky soils in the region of the Chapada dos Veadeiros National Park (Fig. 22). Populations may be remarkably large, with more than a thousand individuals occurring along three or four km of road-side. According to IUCN (2001) criteria, the species is considered critically endangered (criteria B1a, B1b, B2a).

Commentaries. Diphyomene conferta is distinguished by its unique adpressed axis bracts and sulfurous-tone capitula, the latter feature also appearing in some specimens of *D. erectifolia* (Silveira) Trovó, although without constituting a stable population characteristic. In the holotype of *D. conferta*, most of the capitula are extremely old, appearing more brown than sulfurous.

Diphyomene conferta and *D. amoena* are morphologically alike in many aspects. In both the reproductive axis are thin and the relatively few scapes arranged in spherical-umbel form. Nevertheless, individuals of the former are larger, with sulfurous-toned capitula and adpressed axis bracts. Additional distinguishing features are leaf form and width, and capitula diameter. Furthermore, both are allopatric distributed, as *D. amoena* is restricted to a few mountains in the southern Espinhaço Range.

Selected specimens examined: Brazil. **Goiás**: Alto Paraíso de Goiás, *Irwin*, *H.S, et al. 32034*, 17.3.1971 (SP), *Romaniuc-Neto*, *S. et al. 444*, 14.5.1986 (SP), *Silva*, *S.B. et Oliveira, J. 60*, 05.3.1981 (RB), *Trovó*, *M.L.O. et al. 468*, 20.3.2009 (SPF).

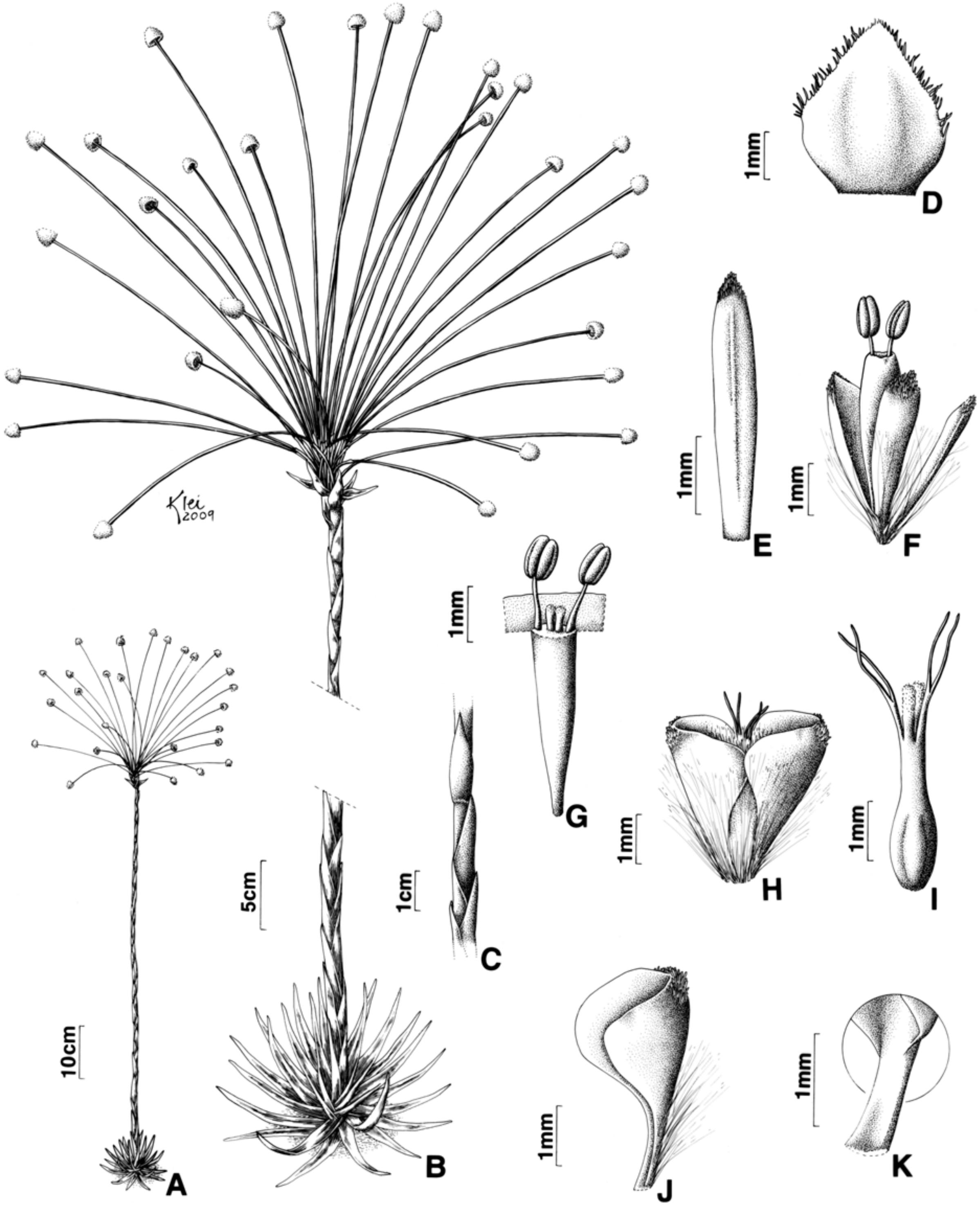

Figure 23. *Diphyomene conferta* (from *Trovó* et al. *446*). A. Habit. B. Detail of the habit. C. Detail of a reproductive axis. D. Involucral bract abaxial surface. E. Floral bract abaxial surface. F. Staminate flower. G. Staminate flower with sepals removed and opened corolla. H. Pistillate flower. I. Gynoecium. J. Pistillate flower sepal. K. Base of a pistillate flower sepal.

Figure 24. *Diphyomene conferta*. A. Habit. B. Detail of axis bracts. C. Detail of a capitulum. D. Detail of a young rosette. Scale bars, A: 15 cm. B: 1 cm. C: 0.1 cm. D: 5 cm.

7. Diphyomene cordata (Ruhland) Trovó, Cap. 3. *Paepalanthus cordatus* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 189. 1903. — TYPE: BRAZIL. Goiás. "Chapadão de Porto Seguro dans le campo sec". 26 Dec 1894, *Glaziou 22324* (holotype: B!; isotypes: C!, G!, K!, LE!, P!). Figs. 25–26.

Herbs, 100–160 cm tall; rhizome present, aerial stem 1.0–3.0 cm long. Leaves persistent, oblong, flat, patent, 5.0–9.5 x 1.0–2.0 cm, glabrous, margin ciliated, apex cuspidate. Reproductive axis erect, 97.0–157.0 cm long, 0.8–1.3 cm diam., glabrous; axis bracts with same shape, chartaceous, cordate, recurvate, 1.5–4.5 X 1.0–2.5 cm, glabrous, apex acuminate, margin glabrous, base semi-amplexicaul. Spathes 2.5–4.0 cm long, glabrous, apex acute. Scapes 210–405, arranged in spherical umbel, 20.0–28.0 cm long, glabrous. Capitula 6–10 mm diam., semi-spherical to discoid, white; involucral bract in 4–5 series, dark-brown, obovate, concave, ca. 3 mm long, glabrous, ciliated toward the apex, apex obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 100 per capitulum, ca. 9 X more staminates than pistillates; floral bract linear, light-brown to golden, concave, ca. 3 mm long, glabrous, ciliated toward the apex, apex acute; staminate flower ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown, ca. 3 mm long, glabrous, ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 2 mm long; pistilodes 2, papillose; pistilate flowers disposed in concentric rings, ca. 3 mm, sessile; sepals dolabriform, light-brown, ca. 3 mm long, hairy in abaxial surface apex and base, apex obtuse; petal navicular, hyaline, ca. 2 mm long, hairy in abaxial surface apex and central portion, ciliated toward the apex, apex obtuse; gynoecium ca. 3 mm long, stigmatic branches bifid, twice longer than the nectariferous branches, staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. In *D. cordata* the blooming period seems to be short. Staminate and pistillate flowers in full anthesis were observed between March and May, and fruits from April to July. A single individual with mature fruits was collected in December.

Distribution, Habitat, and Conservation Status. The species is endemic to the Chapada dos Veadeiros (Fig. 27), where it occurs in open savannas intermixed with grasses. Large populations of more or less 25 individuals are quite frequent within the local National Park. According to IUCN (2001) criteria, *D. cordata* is considered to be critically endangered (criteria B1a, B1b, B2a).

Commentaries. *Diphyomene cordata* is by far the easiest species to identify. The recurvate and cordate axis bracts are conspicuous features. These characters are easily noticeable, both in the field and in herbarium specimens. The oblong leaves with cuspidate apex are also discriminate. Although quite frequent in the field, it is unexpectedly poorly represented in herbaria, possibly not only due to the short reproductive period, but also to the relatively large size of the individuals, as they are high, and thus awkward to collect, dry, and store in herbaria.

Ruhland (1903) described *Paepalanthus cordatus* based on juvenile specimens (*Glaziou 22324*) deposited at B and other herbaria. These specimens were composed of a rosette, a reproductive axis, and scapes in the early developmental stage. As Ruhland (1903) had no flowers on hand to examine, he placed the species unambiguously as "imperfecte cognita" within *Paepalanthus* sect. *Diphyomene*. The flowers are hereby described for the first time, their description fully matching expectations and variations within the genus.

Selected specimens examined: Brazil. **Goiás**: Alto Paraíso de Goiás, *Trovó*, *M.L.O. et al 436*, 04.12.2007 (SPF), *Trovó*, *M.L.O. et al 471*, 20.3.2009 (SPF), *Trovó*, *M.L.O. et al 474*, 20.3.2009 (SPF), *Trovó*, *M.L.O. et al 478*, 22.3.2009 (SPF).

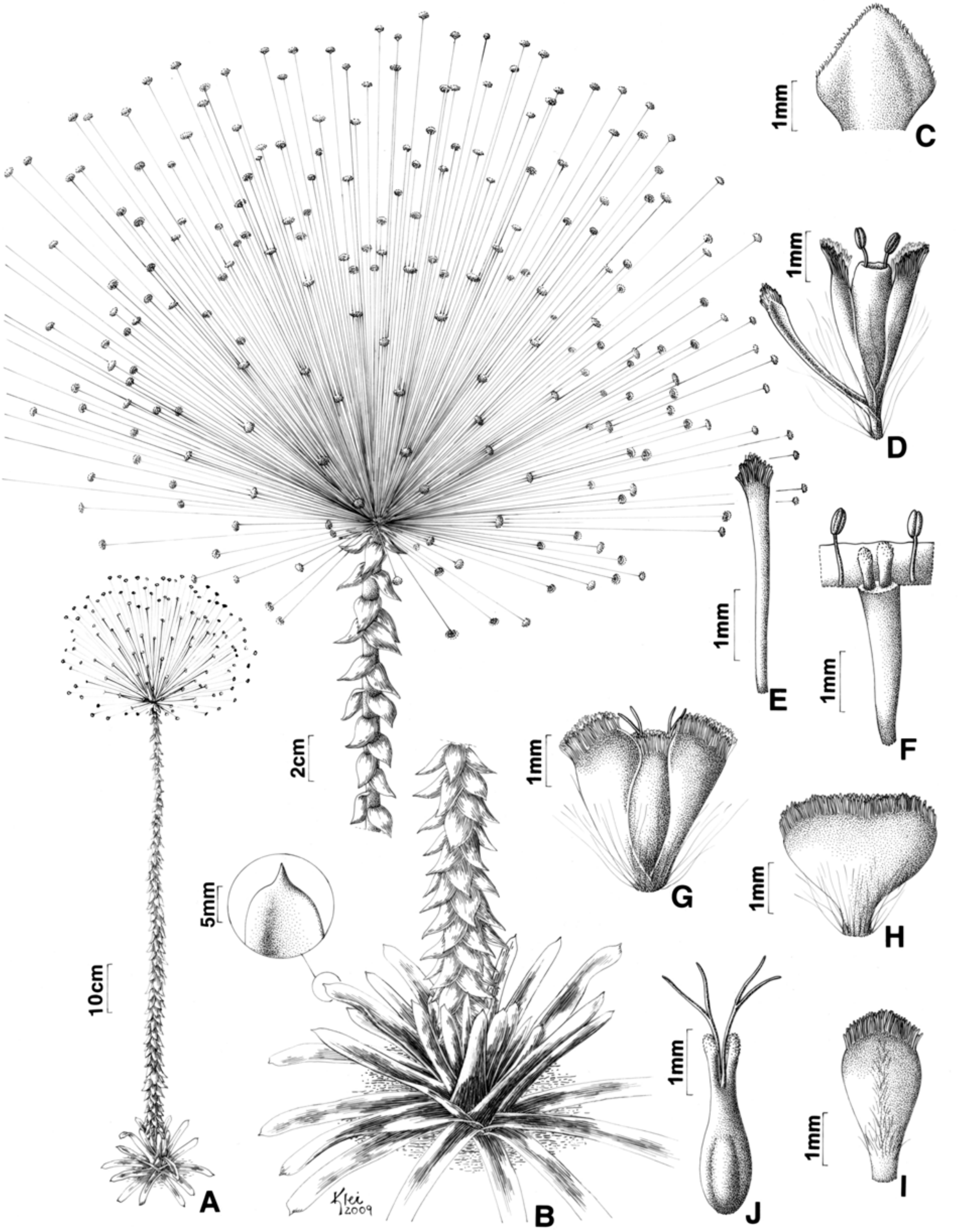

Figure 25. *Diphyomene cordata* (from *Trovó* et al. *478*). A. Habit. B. Detail of habit. C. Involucral bract abaxial surface. D. Staminate flower. E. Floral bract abaxial surface. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower. H. Pistillate flower sepal I. Pistillate flower petal. J. Gynoecium.

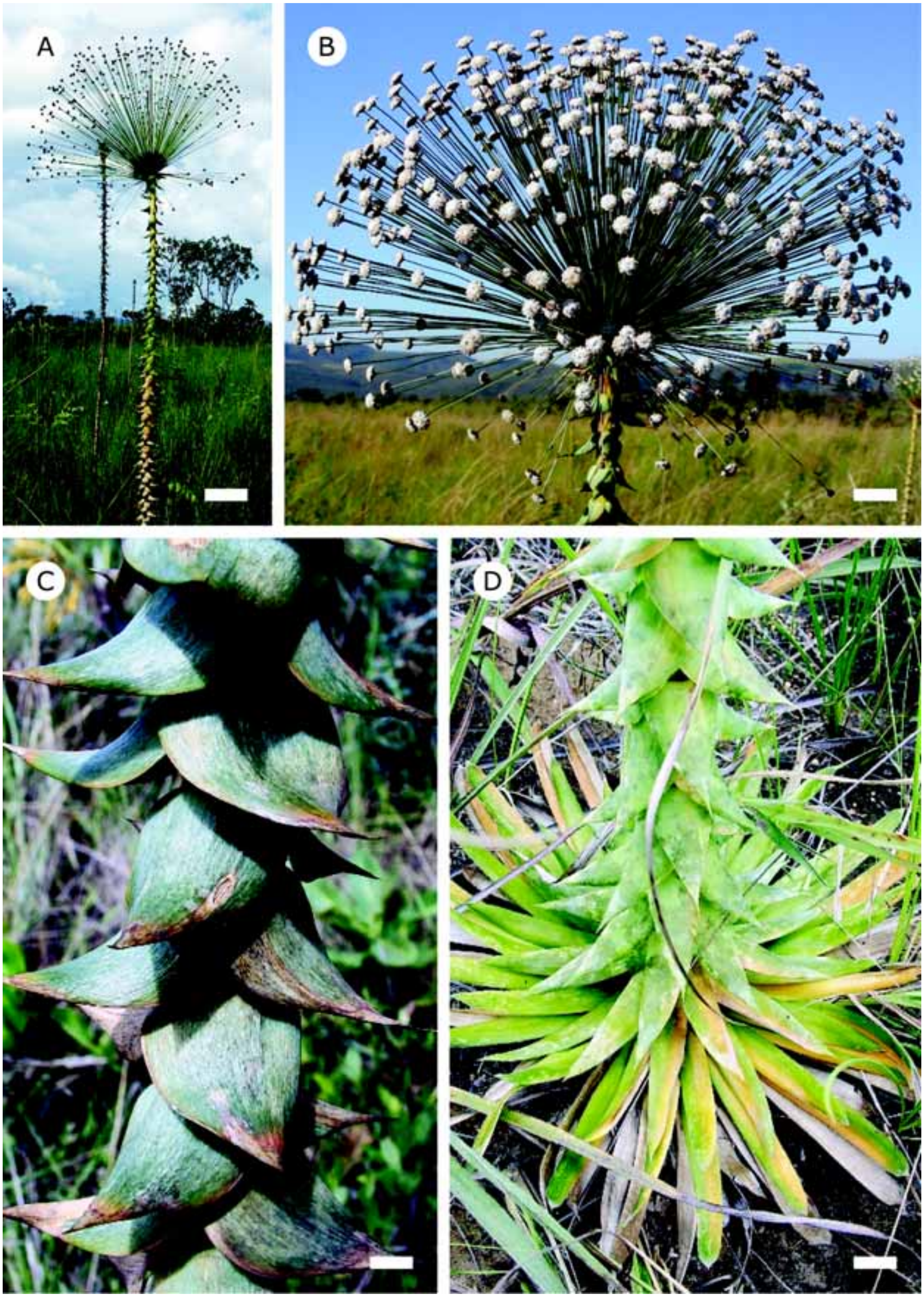

Figure 26. *Diphyomene cordata*. A. Habit. B. Detail of inflorescence. C. Detail of axis bracts. D. Detail of rosette. Scale bars, A: 10 cm. B: 3 cm. C: 0.5 cm. D: 2 cm. (Photo by: B, A. Fujikawa)

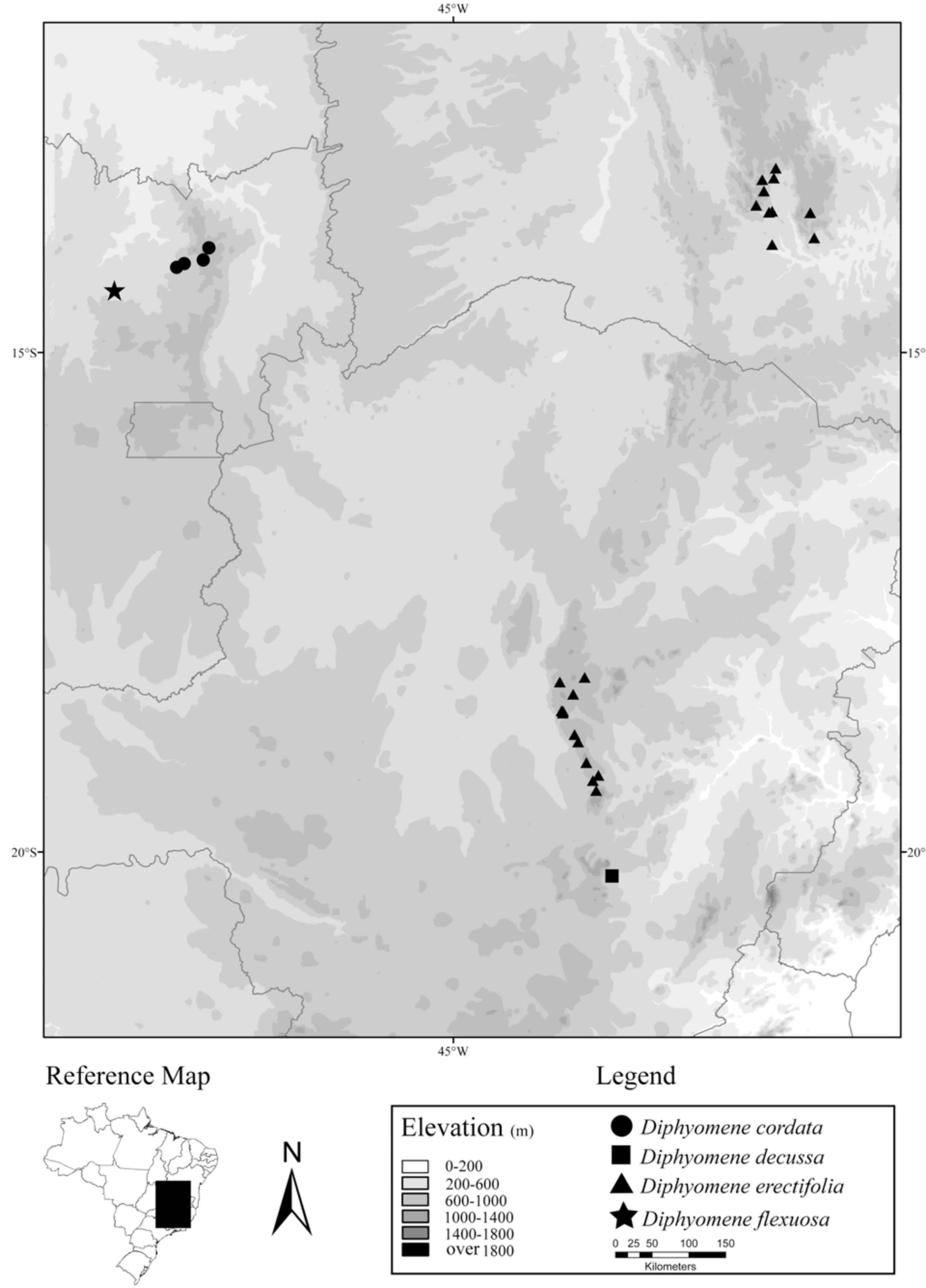

Figure 27. Geographical distribution of *D. cordata*, *D. decussa*, *D. erectifolia*, and *D. flexuosa.*

8. Diphyomene decussa (Koern.) Trovó, Cap. 3. *Paepalanthus decussus* Koern., in Martius & Eichler, Fl. bras. (3)1: 318. 1863. *Dupatya decussa* (Koern.) Kuntze, Revis. gen. Pl. 2: 745. 1891.—TYPE: BRAZIL. Minas Gerais: "Cachoeira". s.d., *Claussen s.n.* (holotype, BR!; isotype, B!). Figs. 28–29.

Herbs, 26–32 cm tall; rhizome absent, aerial stem 1.0–2.0 cm long. Leaves persistent or deciduous, linear to lanceolate, flat, patent, 6.0–9.5 X 0.4–0.6 cm, glabrescent, margin ciliated, apex acute. Reproductive axis erect, 5.5–8.0 cm long, 0.5–1.0 cm diam., hairy; axis bracts with same shape, chartaceous, lanceolate, sub-erect, 5.0–7.5 X 0.4–0.5 cm, glabrescent, margin ciliated, apex acute, base semi-amplexicaul. Spathes 3.0–4.0 cm long, glabrous, apex acute. Scapes 38–52, arranged in an obconic umbel, 18.0–23.0 cm long, with sparse hairs concentrated in the distal portion. Capitula 4–6 mm diam., semi-spherical to spherical, white; involucral bracts in 4 series, light-brown, elliptic, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; receptacle semi-spherical, hairy. Flowers dimerous, ca. 100 per capitulum, ca. 6 X more staminates than pistillates; Floral bracts linear or obovate, light-brown, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; Staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light brown, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 2 mm long; pistilodes 2, papillose; pistillate flowers (juvenile) disposed in concentric rings, ca. 2 mm, sub-sessile; sepals dolabriform, brown, ca. 2 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex obtuse; petals elliptic, hyaline, ca. 1 mm long, hairy in abaxial surface, margin ciliated toward the apex, apex rounded; gynoecium ca. 1 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruits and seeds not seen.

Phenology. Individuals with staminate flowers in full anthesis and juvenile pistillate flowers were collected in April. Mature pistillate flowers, as well as mature fruits, were not observed.

Distribution, Habitat, and Conservation Status. *Diphyomene decussa* occurs in the southern part of the Espinhaço Range (Fig. 27). It is known through only two collections, both close to the town of

Ouro Preto in (MG). Although the soils in this region are predominantly rich in iron (Quadrilátero Ferrífero), the specimen *Messias, M.C.T.B. 1963* was collected on quartizitic soils. Nevertheless, neither flowering nor sterile individuals were found during a fieldtrip to the same collection site in 2009. According to IUCN (2001) criteria, *D. decussa* is considered critically endangered (criteria B1a, B1b, B2a).

Commentaries. *Diphyomene decussa* is differentiated from the remaining species by its hairy reproductive axis and sub-sessile pistillate flowers. It may be sympatric with *D. amoena*, from which it is discernable by its gracile appearance, the obconic arrangement of the scapes, and the wider reproductive axis. It is also morphologically similar to *D. cipoensis*, although differing from the latter by its longer reproductive axis, flat leaves, shorter spathes, and narrower capitula.

Koernicke (1863) described *D. decussa* based on a single collection (*Claussen s.n.*) deposited at B and BR. Most of the species holotypes described by Friedrich Koernicke are deposited at B. Nevertheless, the material in B is composed of only leaf fragments and inflorescences. Koernicke (1863) cited this as being part of a deposited sheet containing a complete specimen, as well as the original label, at BR. The material at BR is considered as the holotype. Koernicke (1863) also described pistillate flowers from a juvenile structure, and raised doubts as to the presence of a pedicel. However, observations on the *Messias, M.C.T.B. 1963* material (also juvenile) confirm the presence of a pitillate flower with short pedicels.

Selected specimens examined: Brazil. **Minas Gerais**: Mariana, *Messias*, *M.C.T.B. 1963*, 4.4.2008 (OUPR).

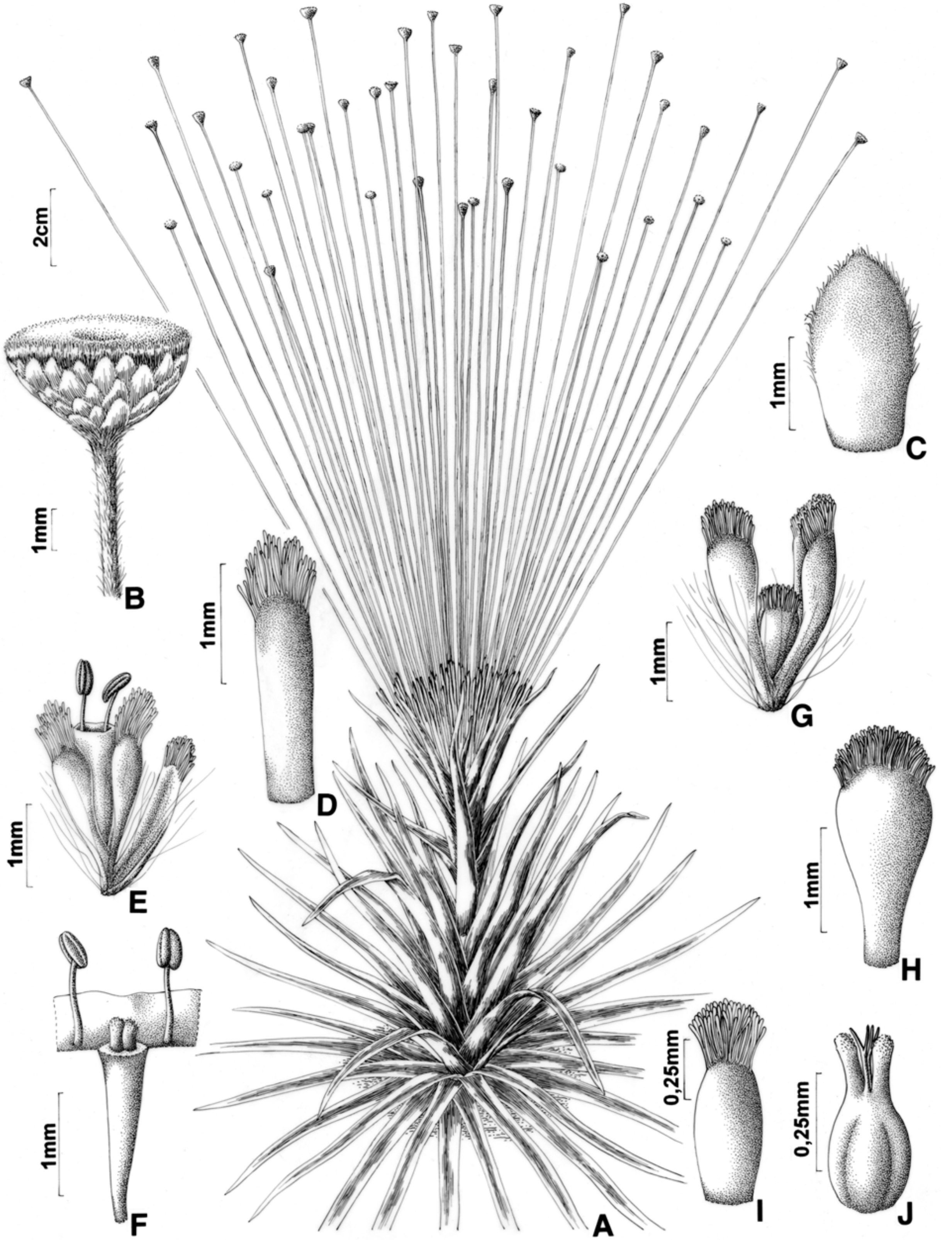

Figure 28. *Diphyomene decussa* (from *Messias 1963*). A. Habit. B. View of a capitulum. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower (juvenile). H. Pistillate flower sepal. I. Pistillate flower petal. J. Gynoecium.

Herbário Professor José Badini
1986
Nº 21428
Data 04/IV/2008
ICEB — UFOP

Universidade de São Paulo (SPF)
Paepalanthus decussus Körn.
Det: [illegible] 12.VIII.2005

HERBÁRIO "PROF. JOSÉ BADINI"- OUPR
UNIVERSIDADE FEDERAL DE OURO PRETO - DECBI
OUPR 21428

ERIOCAULACEAE

Paepalanthus pubescens Körn.
Det: M.C.T.B.Messias data: 28.IV.2008

Brasil. Minas Gerais. Mariana. Bento Rodrigues. Estrada para Santa Rita Durão.

Obs.: Erva, 40cm. Flores brancas. Em campos rupestres quartzíticos, em platôs arenosos úmidos..

Col.: M.C.T.B.Messias; J.L.Silva; A.C.Tonaco 1963 **data:** 04.IV.2008

Figure 29. *Diphyomene decussa*. Sheet deposited in OUPR.

9. Diphyomene erectifolia (Silveira) Trovó, Cap. 3. *Paepalanthus erectifolius* Silveira, Fl. serr. Min. p. 51. 1908.—TYPE: BRAZIL. Minas Gerais: "In partis siccis in Serra do Cipó". Apr 1905, *Silveira 367* (holotype: R!). Figs. 30–31.

Paepalanthus speciosus var. *glabra* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 187. 1903.—TYPE: BRAZIL. Minas Gerais: "Serra do Cipó, dans le camp". 26 Apr 1892, *Glaziou 19977* (lectotype—designated by Trovó & Sano (Cap. 3): B!; isolectotypes: C!, P!).

Paepalanthus speciosus var. *angustifolia* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 187. 1903.—TYPE: BRAZIL. Minas Gerais: "Serra do Cipó, prov. Minarum". Oct, *Mathieu Libon 534* (lectotype—designated by Trovó & Sano (Cap. 3): C!).

Paepalanthus speciosus var. *chlorocephala* Silveira, Fl. serr. min.: 50. 1908.—TYPE: BRAZIL. Minas Gerais: "In campis siccis in Serra do Cipó". Apr 1905, *Silveira 370* (holotype: R!).

Herbs, 45–175 cm tall; rhizome present, aerial stem 1.5–2.5 cm long. Leaves persistent, lanceolate to linear, flat, patent or recurvate, 6.0–13.0 X 0.3–1.0 cm, hairy to glabrescent, margin ciliated to glabrescent, apex acute. Reproductive axis erect, 22.0–140.0 cm long, 0.4–1.0 cm diam., glabrous; axis bracts with same shape, chartaceous, lanceolate, patent or rarely sub-erect, 2.5–4.5. X 0.5–1.5 cm, glabrous, margin glabrous, apex acute, amplexicaul. Spathes 3.0–4.5 cm long., glabrous, apex acute. Scapes 20–365, arranged in a spherical umbel, 18.0–35.0 cm long, glabrous. Capitula 7–10 mm diam., discoid to spherical, white rarely sulfurous; involucral bracts in 3–5 series, light-brown to brown, obovate, concave, ca. 3 mm long, glabrous rarely hairy in abaxial surface, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 500 per capitulum, ca. 4 X more staminates than pistillates; floral bracts linear, light-brown to golden, flat, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long., with long trichomes; sepals navicular, light-brown, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings, ca. 3 mm, sessile; sepals dolabriform, white, ca. 3 mm long., hairy in the abaxial surface apex and base and central portion, margin ciliated toward the apex, apex mucronate; petals elliptic to dolabriform, fleshy, ca. 2 mm long, hairy in abaxial surface, margin ciliated toward the apex, apex rounded to obtuse; gynoecium ca. 2 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. Individuals of *D. erectifolia* were collected with flowers and fruits all year long. However, mature staminate and pistillate flowers were mostly found between February and June, and fully developed fruits often collected from April to August.

Distribution, Habitat, and Conservation Status. *Diphyomene erectifolia* occurs disjunct between the Espinhaço Range in Minas Gerais and in Bahia (Fig. 27). It is the only species within the genus that occurs in the Espinhaço Range in Bahia. Individuals, growing on granitic soil, may occur isolated or forming large populations, especially in the Serra do Cipó. According to IUCN (2001) criteria, *D. erectifolia* is considered least concern.

Commentaries. *Diphyomene erectifolia* is one of the most common and widely distributed species within the genus. It is the only one in the Espinhaço Range with simultaneously patent axis bracts of the same shape throughout the axis, as well as scapes arranged in a spherical umbel. Individuals may be misidentified as *D. koernickei*, a more robust species with longer leaves, longer axis bracts, and distribution, restricted to the state of Goiás, and often confined to shaded habitats, whereas *D. erectifolia* occurs in open grass fields.

The overall size is considerably variable, ranging from 45.0 cm to 175.0 cm in height, the smallest occurring in the Serra do Cipó and the vicinities of Gouveia, whereas the largest were collected in Diamantina. Smaller individuals are occasionally misidentified as *D. amoena*, a species restricted to the south of the Espinhaço Range. Some of those growing in the first mentioned area may eventually present sulfurous capitula. The leaves of individuals from Bahia are usually recurvate, whereas in Minas Gerais they are always patent.

As with *D. chiquitensis*, specimens of *D. erectifolia* have been identified as *Paepalanthus speciosus* (Bong.) Koern., and, more recently as *Paepalanthus giganteus* Sano. However, the correct name was published by Silveira (1908), based on his own collection *Silveira 367* at the Serra do Cipó. Unfortunately, the type specimen presents atypically erect leaves and axis bracts, a feature used by Silveira (1908) to attribute the species name. Silveira (1908) also described *Paepalanthus speciosus* var. *chlorocephala* Silveira, based on his own collection *Silveira 370* at the Serra do Cipó. However, this feature, through being an unstable character within populations, invalidates such a distinction.

Ruhland (1903) briefly described *Paepalanthus speciosus* var. *glabra* and *Paepalanthus speciosus* var. *angustifolia*. These varieties were described based on numerous syntypes, which not even correspond to the same species. The lectotypes, as designated by Trovó & Sano, are clearly within the range of the *D. erectifolia* morphological variation.

Selected specimens examined: Brazil. **Bahia**: Abaíra, *Pirani, J.R. et al. H* 51506, 21.2.1992 (SPF), Stannard*, B. et al. H 51153*, 23.2.1992 (SPF), *Sano, P.T. Lassoe, T. H 52197*, 24.2.1992 (SPF), *Stannard, B. et al. H 51921*, 13.3.1992 (SPF); Barra da Estiva, *Giulietti, A.M. et al. CFCR 1282*, 19.7.1981 (SPF); Mucugê, *Borba, E.L. et al. 1856*, 4.8.2004 (HUEFS); Piatã, *Pirani, J.R. et al. CFCR 7366*, 21.12.1984 (SPF), *Harley, R.M. et al. 24256*, 15.2.1987 (SPF); Rio de Contas, *Harley, R.M. et al. 20000*, 25.3.1977 (SPF, UEC), *Pirani, J.R. et al. CFCR 2179*, 9.9.1981 (SPF), *Harley, R.M. et al. 24434*, 19.2.1987 (SPF), *Harley, R.M. et al. s.n.*, 2.1987 (SPF), *Alves, R.V. et al. 4071*, 14.5.1992 (RB), *Sano, P.T. et al. CFCR 14696*, 1.3.1994 (ESA, SPF), *Harley, R.M. et al. 4462*, 18.11.1996 (SPF), *Giulietti, A.M. et al. 2095*, 22.5.2002 (ESA); **Minas Gerais**: Diamantina, *Giulietti A.M. 941*-80, 3.4.1980 (SPF), Costa*, F. N. et Sano, P.T. 264*, 1.5.2001 (SPF); Fechados, *Hensold, N. 558*, 22.3.1982 (SPF), *Hensold, N. 748*, 23.4.1982 (SPF); Gouveia, *Semir, J. et al. 17162*, 3.6.1985 (UEC), *Hatschbach, G. et al. 53005*, 20.5.1989 (SPF, HUEFS), *Arbo, M.M. et al. 4509*, 20.5.1990 (SPF), *Mello-Silva, R. et al. 1119*, 13.6.1996 (SPF), *Souza, V.C. et Souza, J.P. 22327*, 14.3.1999 (ESA, SPF), *Trovó, M.L.O. et Watanabe, M.C.T. 334*, 30.4.2007 (SPF); Jaboticatubas, *Costa, F. N. et Fiaschi, P. 165*, 15.6.2000 (SPF), *Pirani, J.R. et al. 5541*, 23.4.2006 (SPF); Santana do Riacho, *Semir, J. et al. CFSC 4073*, 29.4.1963 (SPF), *Giulietti, A.M. et al. CFSC 4073*, 29.4.1973 (SPF), *Giulietti, A.M. et Menezes, N.L. CFSC 4023*, 26.5.1973 (SPF), *Monteiro, W.R. CFSC 4298*, 26.7.1973 (SPF), *Menezes, N.L. CFSC 7309*, 27.5.1977 (SPF), *Brantyses, M. 7054*, 14.5.1978 (UEC), *Castro, N.M. CFSC 8486*, 15.5.1982 (SPF), *Souza, V.C. et Vitta, F.A. CFSC 11784*, 12.3.1990 (SPF), *Arbo, M.M. et al. 4119*, 15.5.1990 (SPF), *Sakuragui, C.M. et Souza, V.C. 57*, 2.8.1990 (ESA), *Faria, G.M. et Mazucato, M. s.n.*, 1990 (SPF), *Pirani, J.R. et al. CFSC 12225*, 27.3.1991 (HUEFS, SPF), *Giulietti, A.M. et al. CFSC 12457*, 27.7.1991 (SPF), *Costa, F. N. et al. 86*, 25.9.1999 (SPF), *Costa, F. N. et al. 87*, 25.9.1999 (SPF), *Costa, F. N. et al. 152*, 21.3.2000 (SPF), *Costa, F. N. Fiaschi, P. 212*, 21.6.2000 (SPF), *Souza, V.C. et al. 25180*, 5.7.2001 (ESA, SPF), *Trovó, M.L.O. et al. 224*, 4.2.2006 (SPF), *Silva, C.L. et al. 18*, 26.7.2006 (SPF), *Trovó, M.L.O. et al. 326*, 15.2.2007 (SPF), *Trovó, M.L.O. et al. 399*, 22.5.2007 (SPF), *Trovó, M.L.O. et al. 424*, 20.9.2007 (SPF).

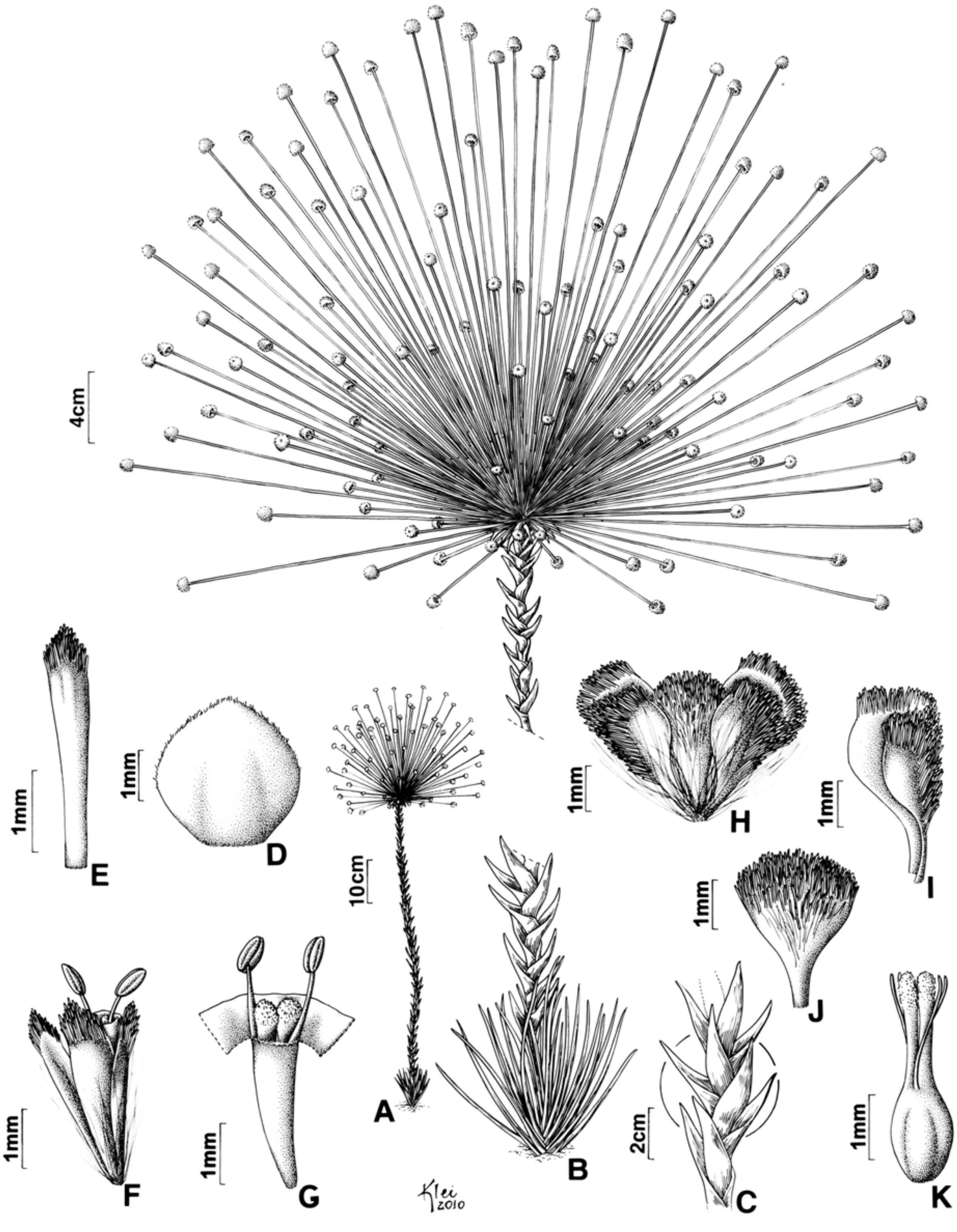

Figure 30. *Diphyomene erectifolia* (from *Trovó* et al. *465*). A. Habit. B. Habit detail. C. Detail of the axis bracts. D. Involucral bract abaxial surface. E. Floral bract abaxial surface. F. Staminate flower. G. Staminate flower with sepals removed and opened corolla. H. Pistillate flower. I. Pistillate flower sepal. J. Pistillate flower petal abaxial surface. K. Gynoecium.

Figure 31. *Diphyomene erectifolia*. A. Individual from Gouveia (MG). B. Individual from Serra do Cipó. C. Individual from Rio de Contas (MG). D. Detail of axis bracts. Scale bars, A: 7 cm. B: 10 cm. C: 7 cm. D: 1.5 cm. (Photos by: B, M. Santos; C-D, L. Echtenacht)

10. Diphyomene flexuosa Trovó, Appendix 1.—TYPE: BRAZIL. Goiás: "Niquelândia, Macedo, 15 km N of Niquelândia; 14° 18' S. 48° 23' W, facing hill slope, stable peridotite/dunite-based scree and flat area below, ca. 500-800 m east of nickel workings, ca. 1000 m alt.". 21 Apr 1988, *R. R. Brooks et al. Braspex 165* (holotype, SPF!; isotypes B!, MO!, NY!). Figs. 32–33.

Herbs, 24–35 cm long; rhizome present, aerial stem 0.3–1.0 cm long. Leaves persistent, linear, flat, patent, 0.5–2.5 x 0.1–0.2 cm, glabrescent, margin ciliated to glabrescent, apex acute. Reproductive axis tortuous, 7.0–12.5 cm long, 0.2–0.3 cm diam., glabrous; axis bracts with same shape, chartaceous, lanceolate, sub-erect, 1.0–2.0 X 0.2–0.4 cm, glabrous, margin glabrous, apex acute, base semi-amplexicaul. Spathes 2.0–3.0 cm long, glabrous, apex acute. Scapes 3–10, arranged in an obconic umbel, 13.0–20.0 cm long, glabrous. Capitula 5–9 mm diam., semi-spherical, white; involucral bracts in 3–4 series, dark-brown, ovate, concave, ca. 3 mm long, glabrous, margin completely ciliated, apex acute; receptacle semi-spherical, hairy. Flowers dimerous, ca. 100 per capitulum, ca. 4 X more staminates than pistillates; floral bracts linear, light-brown, flat, ca. 3 mm long, hairy in abaxial surface to glabrescent, margin ciliated toward the apex to glabrescent, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown to golden, ca. 3 mm long, hairy in abaxial surface, margin glabrescent toward the apex, apex mucronate; fleshy antophore elongated; corolla tubular, hyaline, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistilate flowers disposed in concentric rings ca. 3 mm, sessile; sepals dolabriform, white, ca. 3 mm long, hairy in the abaxial surface, margin glabrescent toward the apex, apex mucronulate; petals elliptic, hyaline, ca. 2 mm long, hairy in abaxial surface, margin ciliated toward the apex to glabrescent, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red do brownish.

Phenology. Individuals with staminate and pistillate flowers in full anthesis, as well as mature fruits, were collected in April and May.

Distribution, Habitat, and Conservation Status. All the three herbarium collections of *D. flexuosa* came from a mountain in Niquelândia, growing on a typical savanna (Fig. 27). The area belongs to a nickel-mining company in full operation. Sheet label information indicates that the collected individuals were encountered more than five km from the mining complex. According to IUCN (2001) criteria the species is considered critically endangered (criteria B1a, B1b, B2a).

Commentaries. Diphyomene flexuosa is clearly distinct from congeneric species. The tortuous reproductive axis, the size of the plant, and the relatively few scapes arranged into a obconic umbel are all outstanding for identification. In 2009, a fieldtrip to the type locality was undertaken during the reproduction period, although no flowering individuals or sterile rosettes were found. As no recent collections are under way, and the type locality is the center of intense human activities, we reinforce the significance of further efforts for collecting and preserving the species.

Diphyomene urbaniana is morphologically the most similar species. Both are relatively small, with scapes longer than reproductive axis. The size of the capitula and color of the involucral bracts are also features in common. *Diphyomene flexuosa* differs by the smaller habit and reproductive axis, linear leaves with acute apex, and fewer and smaller scapes arranged in a obconic umbel. *Diphyomene urbaniana* is endemic to Chapada dos Veadeiros, quite close to Niquelândia. However, and as previously pointed out, both the vegetation and soil of these regions are significantly different, thus the species can be considered allopatric.

Selected specimens examined: Brazil. **Goiás**: Niquelândia, *Reeves, R.D. et al. Braspex 226*, 29.4.1988 (MO, NY, SPF), *Silva, A. et Jesus, N. 2973*, 29.5.1996 (HUEFS).

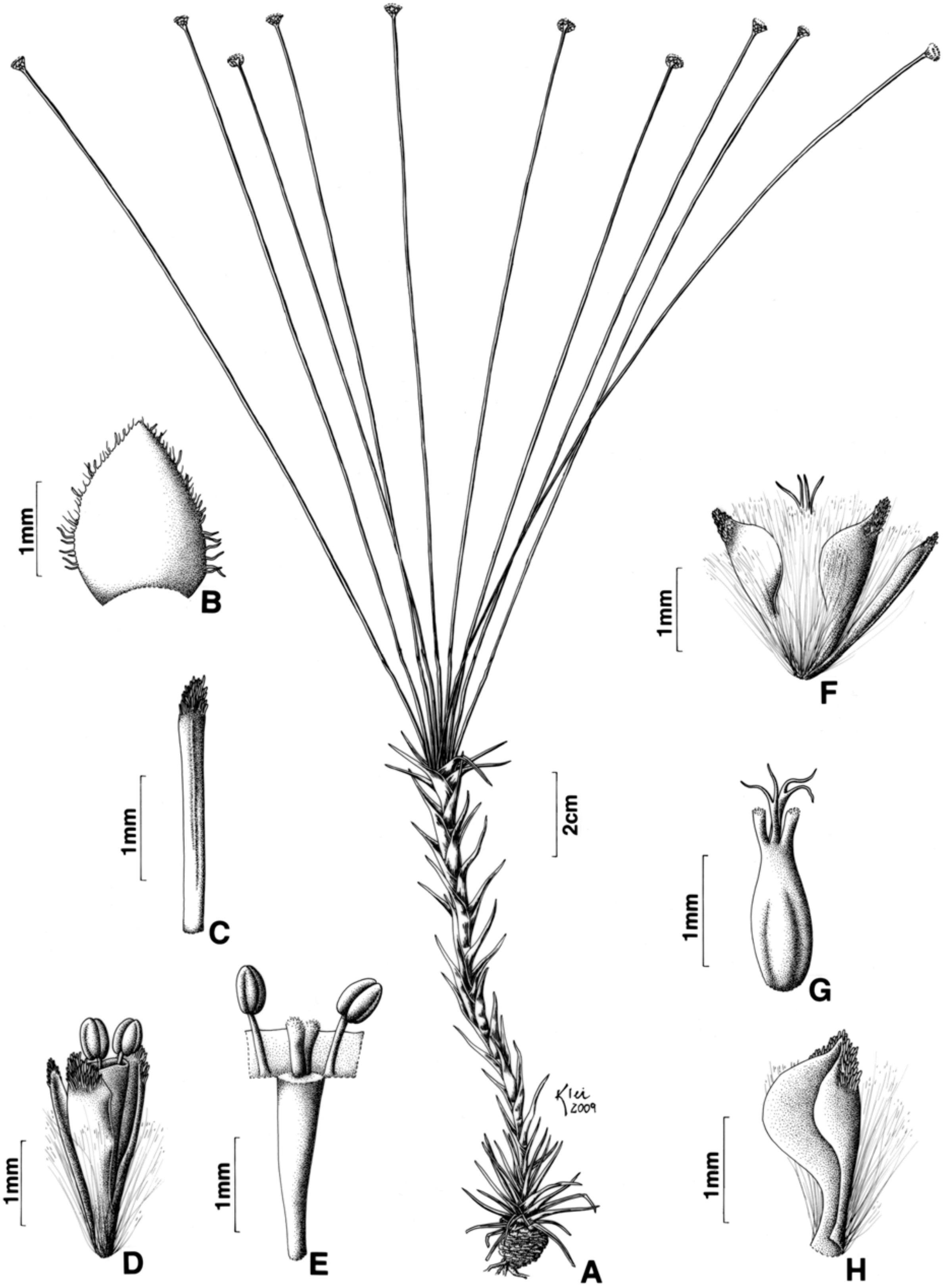

Figure 32. *Diphyomene flexuosa* (from *Brooks* et al. *165*). A. Habit. B. Involucral bract abaxial surface. C. Floral bract abaxial surface. D. Staminate flower. E. Staminate flower with sepals removed and opened corolla. F. Pistillate flower. G. Gynoecium. H. Pistillate flower sepal.

Figure 33. *Diphyomene flexuosa*. Holotype deposited in SPF.

11. Diphyomene hymenobracteata Trovó, Appendix 1.—TYPE: BRAZIL. Goiás: “Alto Paraíso de Goiás, Parque Nacional da Chapada dos Veadeiros, BR-010 entre Alto Paraíso de Goiás e Teresina de Goiás, entrada para o Morro do Cruzeiro do lado oposto da estrada”. 19 Mar 2009, *M. L. O. Trovó et al. 465* (holotype, SPF!; isotypes B!, NY!). Figs. 34–35.

Herbs, 55–85 cm tall; rhizome present, aerial stem 1.0–2.5 cm long. Leaves persistent or rarely deciduous, lanceolate, flat, patent, 8.0–13.0 X 0.5–1.0 cm, glabrous, margin glabrous, apex acute. Reproductive axis erect, 43.0–60.0 cm long., 0.5–1.0 cm diam., glabrous; axis bracts with same shape, membranaceous, lanceolate, erect to sub-erect, 6.0–11.0 X 1.5–2.5 cm, glabrous, margin glabrous, apex acute, amplexicaul. Spathes 2.0–4.5 cm long., glabrous, apex acute. Scapes 40–405, arranged in a spherical umbel, 13.0–25.0 cm long, glabrous. Capitula 4–6 mm diam., obconic, white; involucral bracts in 3–4 series, brown, obovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 55 per capitulum, ca. 10 X more staminates than pistillates; floral bracts linear, light-brown, flat, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long., with long trichomes; sepals navicular, light-brown, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers punctual disposed, ca. 3 mm, sessile; sepals dolabriform, white, ca. 3 mm long., hairy in the abaxial surface apex and base, margin ciliated toward the apex, apex obtuse; petals elliptic, hyaline, ca. 2 mm long, hairy in abaxial surface, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruits and seeds not seen.

Phenology. In March, individuals of *D. hymenobracteata* were collected with staminate flowers in full anthesis, and in April, with mature pistillate flowers. Fruits and seeds were not observed

Distribution, Habitat, and Conservation status. *Diphyomene hymenobracteata* is endemic to the open grass-dominated savannas of the Chapada dos Veadeiros, Alto Paraíso (GO) (Fig. 36), where dense populations of over 100 individuals were observed. According to IUCN (2001) criteria, the species is considered as being critically endangered (criteria B1a, B1b, B2a).

Commentaries. Diphyomene hymenobracteata is a distinctive species. Its characteristic long and membranaceous axis bracts and obconic capitula, as well as the distinct unusual punctual arrangement of the pistillate flowers within the capitulum, are unique within the genus. The pistillate flowers in both the holotype and paratype were in an early stage of development, whereby the description may be slightly different from that of mature pistillate flowers. There were certain marked differences between living plants and herbarium specimens. Reproductive axis bracts were flat and erect in the former and recurvate and sub-erect in the latter.

Diphyomene hymenobracteata is morphologically related with *D. decussa*, with shared features such as the similar position and size of axis bracts, the sizes of spathes and scapes, and the persistent or rarely deciduous rosette leaves. *Diphyomene hymenobracteata*, however, is distinguished by its robust habit and larger reproductive axis, as well as by possessing glabrous scapes arranged in a spherical umbel, membranaceous axis bracts, obconic capitula, and the unusual punctual arrangement of pistillate flowers. Furthermore, distribution of these species is allopatric.

Selected specimens examined: Brazil. **Goiás**: Alto Paraíso de Goiás, *Lopes*, *F. R. et al. 350*, 09.4.1995 (SPF); Teresina de Goiás, *Silva*, *J. M. et al. 6668*, 22.5.2008 (MBM).

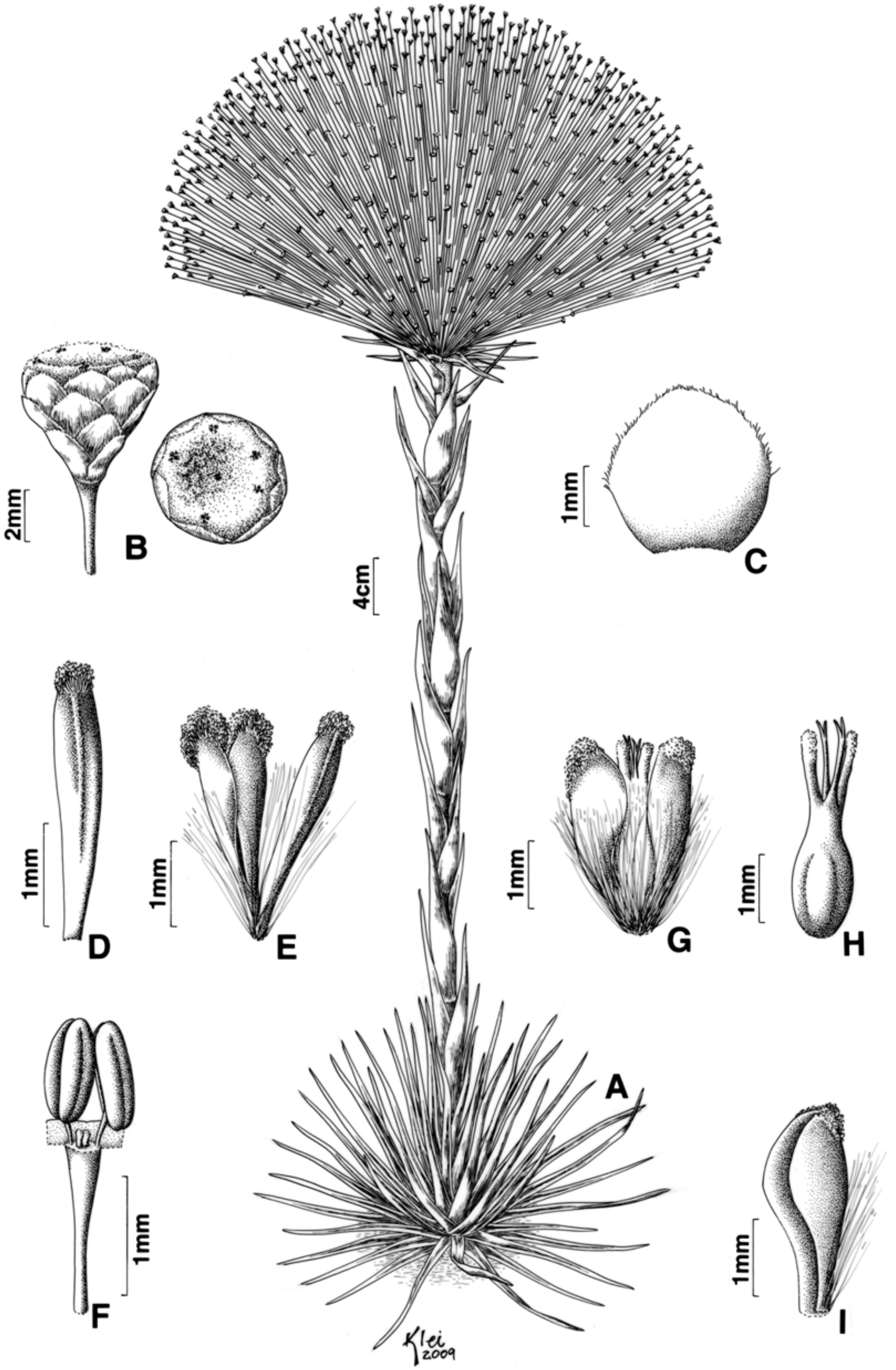

Figure 34. *Diphyomene hymenobracteata* (from *Trovó* et al. *465*). A. Habit. B. Capitulum lateral and upper view. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower (juvenile). F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower (juvenile). H. Gynoecium. I. Pistillate flower sepal.

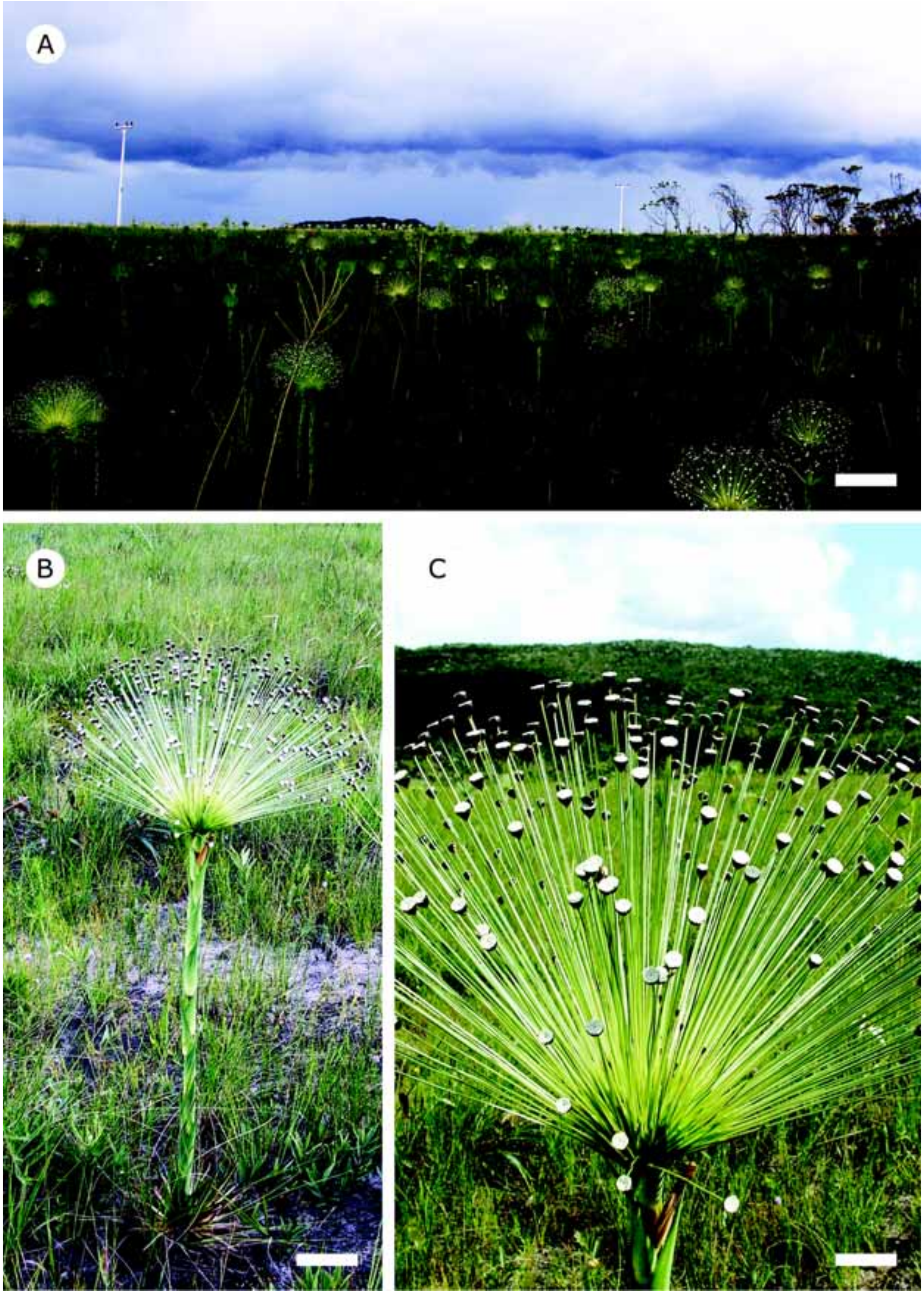

Figure 35. *Diphyomene hymenobracteata*. A. Population in the Chapada dos Veadeiros (GO). B. Habit. C. Details of an inflorescence and capitula. Scale bars, A: 20 cm. B: 8 cm. C: 4 cm.

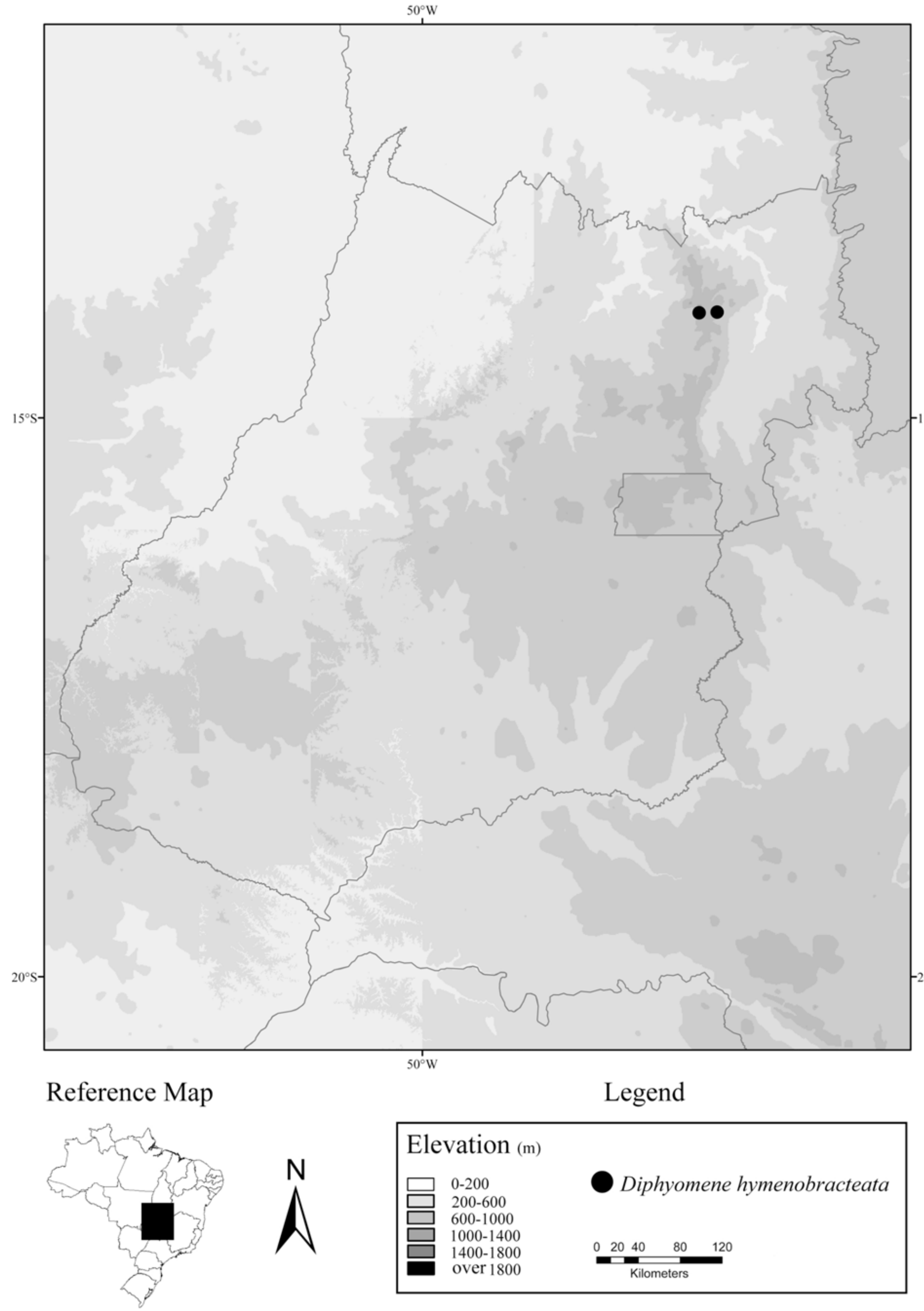

Figure 36. Geographical distribution of *D. hymenobracteata.*

12. Diphyomene koernickei (Ruhland) Trovó, Cap. 3. *Paepalanthus speciosus* var. *koernickei* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 187. 1903.—TYPE: BRAZIL. Goiás: "In campis Catalão—Paracatu". Sep 1834, *Lund 566* (holotype: C! in 2 sheets). Figs. 37–38.

Herbs, 125–200 cm tall; rhizome absent, aerial stem 1.5–2.5 cm long. Leaves persistent, lanceolate, flat, patent, 13.0–22.0 X 1.0–1.5 cm, hairy, margin ciliated, apex acute. Reproductive axis erect, 110.0–180.0 cm long., 0.6–1.2 cm diam., glabrous; axis bracts with same shape, rigid, lanceolate, patent to rarely sub-erect, 4.5–8.0 X 0.5–1.5 cm, glabrous, margin glabrous, apex acute, amplexicaul. Spathes 2.0–4.0 cm long., glabrous, apex acute. Scapes 130–365, arranged in a spherical umbel, 20.5–31.0 cm long, glabrous. Capitula 6–9 mm diam., discoid to semi-spherical, white; involucral bracts in 3–4 series, dark-brown, oblong to ovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 220 per capitulum, ca. 10 X more staminates than pistillates; floral bracts linear, brown, flat, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long., with long trichomes; sepals navicular, brown, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings, ca. 3 mm, sessile; sepals dolabriform, white, ca. 3 mm long., hairy in the abaxial surface apex and base, margin ciliated toward the apex, apex mucronate; petals dolabriform, fleshy, ca. 3 mm long, hairy in abaxial surface base, margin ciliated toward the apex to glabrescent, apex mucronate; gynoecium ca. 2 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. *Diphyomene koernickei* was collected with flowers and fruits between March and September. The blooming peak occurs between May and June. Fruits are fully developed from May to September.

Distribution, Habitat, and Conservation Status. This species is distributed throughout Central Brazil in the state of Goiás and the Distrito Federal (Fig. 39). Populations consisting of no more than 20 individuals grow in the rocky soils of typical savannas, usually in shade provided by small trees and shrubs. Collection was carried out in the Brasília and Chapada dos Veadeiros National Parks. According to IUCN (2001) criteria, *D. koernickei* is considered vulnerable (criteria B1a, B1b, B2a).

Commentaries. Ruhland (1903) considered *D. koernickei* to be a variety of *Paepalanthus speciosus*. The species has few exclusive features, but is separable from the remainder by its overall size, hairy leaves, and the dolabriform petal of the pistillate flower. Individuals can be confused with those of *D. erectifolia*, which is restricted to the Espinhaço Range. Apart from the above-mentioned aspects, the sizes of both leaves and axis bracts, as well as the pilosity of the floral pieces are unusual. Some populations of *D. chiquitensis*, especially from Caldas Novas, Goiás, Pirenópolis and Brasília, may also resemble *D. koernickei*. They can be unambiguously differentiated by the axis bract pattern, as they are all of the same shape in *D. koernickei*, although when the basal part is missing, discrimination is somewhat more complicated. The uppermost bracts in *D. koernickei* are more rigid than those of *D. chiquitensisis*, and the stigmatic branches are of the same size of the nectariferous branches, while in *D. chiquitensis* they are slightly longer.

Selected specimens examined: Brazil. **Distrito Federal**: Brasília, *Irwin, H.S. et al. 15375*, 27.5.1966 (UB), *Davis, P.H. 60116*, 12.7.1976 (UEC), *Davis, P.H. 60117*, 12.7.1976 (UEC), *Heringer, E.P. et al. 86*, 20.9.1977 (UEC, IBGE), *Heringer, E.P. et al. 483*, 8.5.1978 (IBGE, UEC), *Coradin, L. et al. 2431*, 24.9.1979 (CEN), *Roberto, M.E. 15*, 7.6.1981 (SPF), *Pererira, B.A.S. 236*, 20.4.1982 (IBGE), *Mori, S.A. et al. 16660*, 10.7.1984 (CEN), *Segre, M.G. s.n.*, 9.5.1985 (UB), *Azevedo, M.L.M. et Oliveira, F.C.A. 561*, 30.5.1990 (SPF, IBGE), *Melo, E. et França. F. 557*, 29.3.1991 (UB); **Goiás**: Alto Paraíso de Goiás, *Trovó, M.L.O. et al. 461*, 19.3.2009 (SPF), *Trovó, M.L.O. et al. 464*, 19.3.2009 (SPF); Teresina de Goiás, *Souza, V.C. et al. 24690*, 31.7.2000 (ESA).

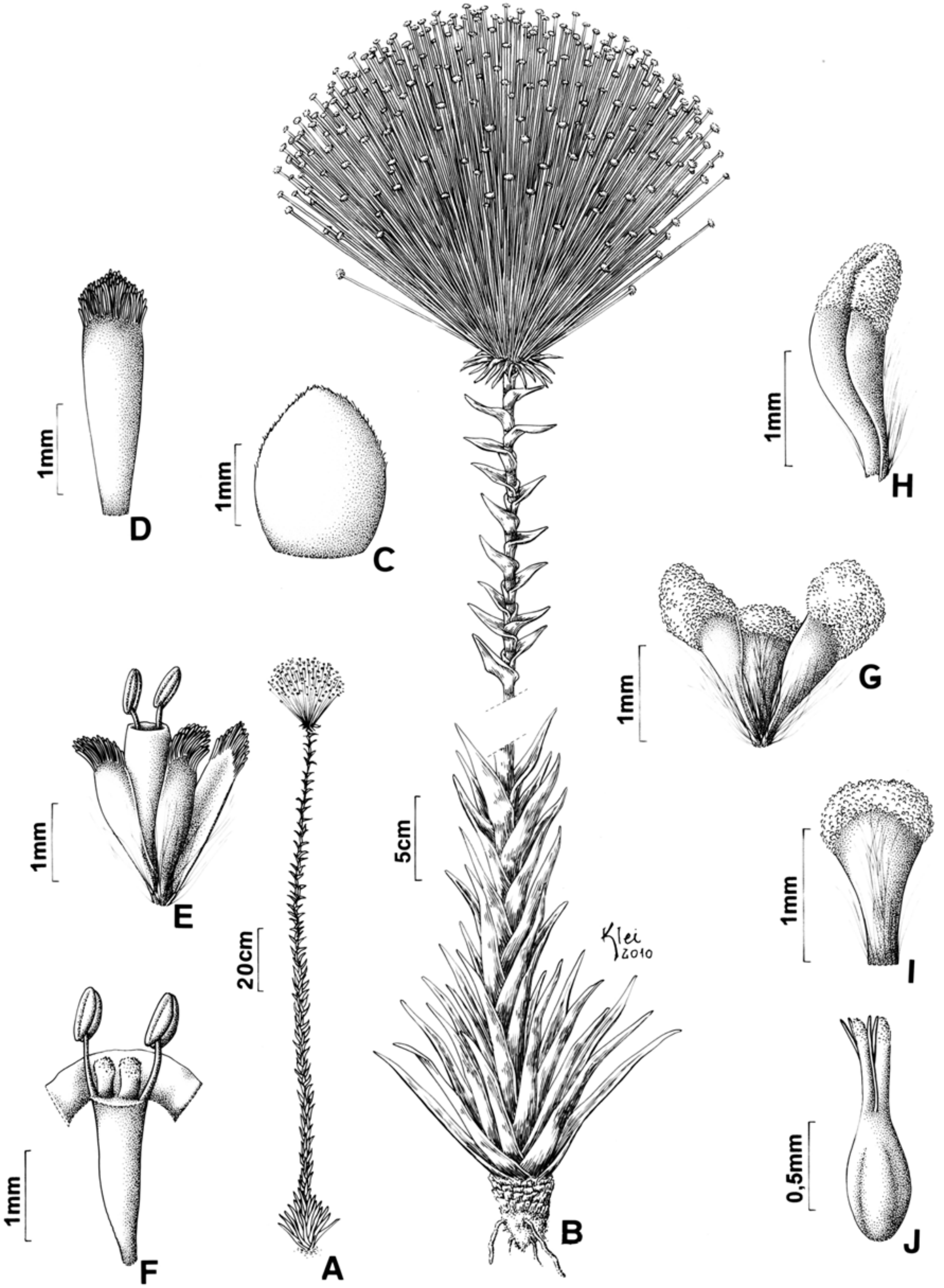

Figure 37. *Diphyomene koernickei* (from *Trovó* et al. *465*). A. Habit. B. Habit detail. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower. H. Pistillate flower sepal. I. Pistillate flower petal abaxial surface. J. Gynoecium.

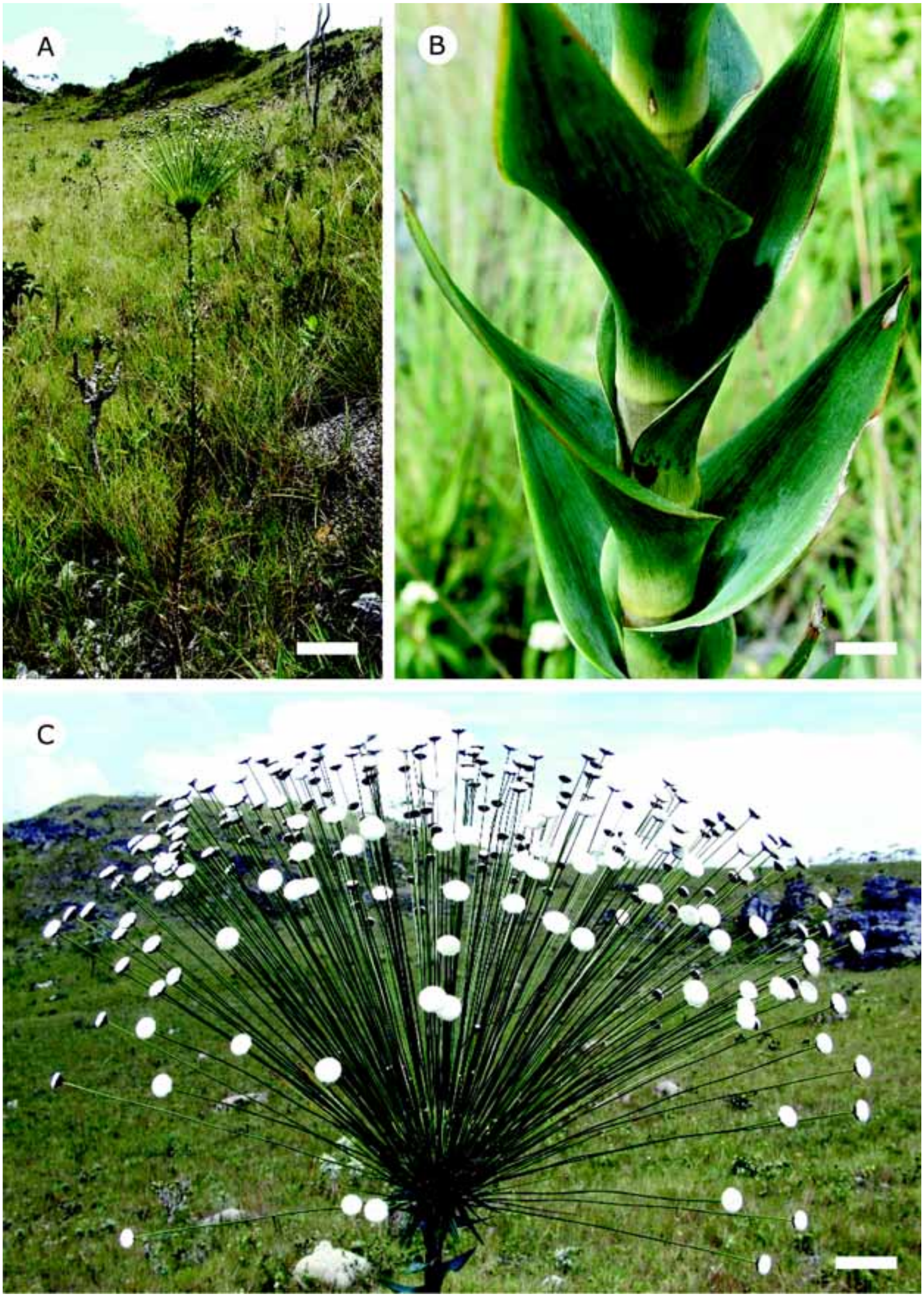

Figure 38. *Diphyomene koernickei*. A. Individual growing in full sun. B. Detail of axis bracts. C. Details of an inflorescence and capitula. Scale bars, A: 20 cm. B: 15 cm. C: 5 cm.

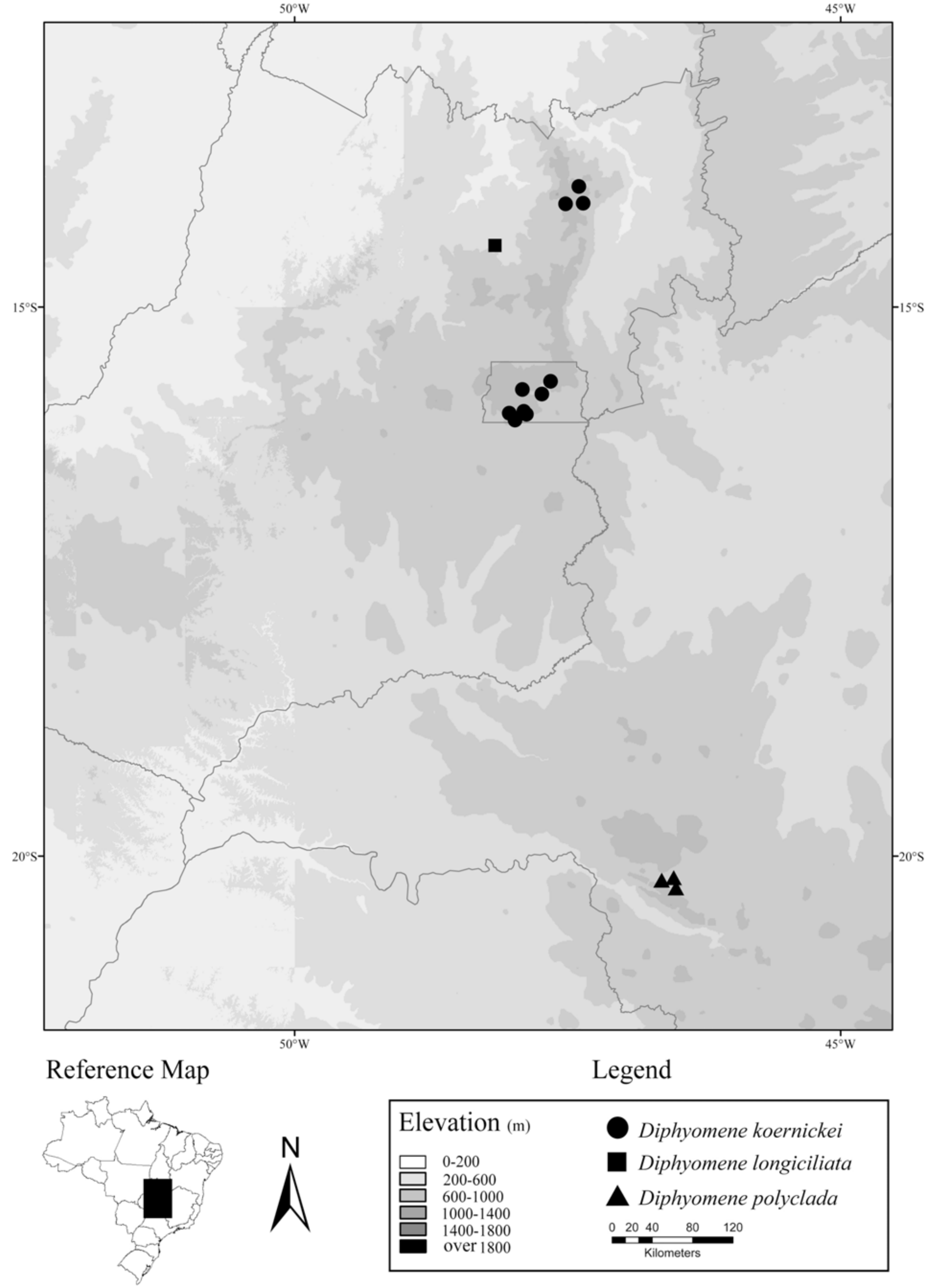

Figure 39. Geographical distribution of *D. koernickei*, *D. longiciliata*, and *D. polyclada*.

13. Diphyomene longiciliata Trovó, Appendix 1.—Type: BRAZIL. Goiás: "Niquelândia, estrada para São Jorge, 14° 26' 17" S/ 48° 09' 51" W". 21 Mar 2009, *M. L. O. Trovó et al. 475* (holotype, SPF!; isotype, B!). Figs. 40–41.

Herbs, 27–50 cm alt.; rhizome present, aerial stem 1.0–1.5 cm long. Leaves persistent or deciduous, linear, flat, semi-erect to patent, 6.0–8.0 X 0.1–0.2 cm, hairy to glabrescent, margin ciliated, apex acute. Reproductive axis erect, 21.0–35.0 cm long, 0.3–0.5 cm diam., glabrous; axis bracts gradually smaller from the base to the apex, chartaceous, lanceolate, semi-erect to patent, 2.0–5.0 X 0.2–0.5 cm, glabrous, margin with long hairs, apex acute, base amplexicaul. Spathes 3.0–4.0 cm long, glabrous, apex acute. Scapes 5–6, arranged in an obconic umbel, 18.0–29.0 cm long, glabrous. Capitula 6–7 mm diam., semi-spherical, white; involucral bracts in 3–4 series, dark-brown, obovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; receptacle semi-spherical, hairy. Flowers dimerous, ca. 100 per capitulum, ca. 4 X more staminates than pistillates; floral bracts linear, brown, concave, ca. 2 mm long, glabrous, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light brown to golden, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acuminate; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings, ca. 3 mm, sessile; sepals dolabriform, white, ca. 3 mm long, hairy in abaxial surface apex and base, margin ciliated toward the apex to glabrescent, apex mucronate; petals elliptic, fleshy, ca. 2 mm long, hairy in abaxial surface, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. Individuals of this species were collected with flowers and mature fruits between March and May.

Distribution, Habitat, and Conservation Status. Individuals were collected on the roadside from Alto Paraíso de Goiás to Niquelândia (Fig. 39). They were found growing on rocky granite soil. A small population was also observed in the vicinity of the Chapada dos Veadeiros National Park.

This area is undergoing pronounced human incursions. According to IUCN (2001) criteria, the species is considered critically endangered (criteria B1a, B1b, B2a).

Commentaries. The longhaired axis bract margins are unique within the genus. However, these hairs may be deciduous in some old bracts, thus making identification more complex. Longhaired axis bracts and a similar habit may rarely occur in teratogenetic individuals of *D. chiquitensis* (*M.L. Fonseca 2632*, SPF; *W.N. Fonseca 175*; SPF). In this case, the shorter leaves and relatively less numerous scapes arranged in a obconic umbel are useful diagnostic characteristics.

Both *D. longiciliata* and *D. weddelliana* (Koern.) Trovó are morphologically alike. Both are of the same overall size, with the same-sized capitula, linear leaves, and few scapes. As the latter is exclusively represented by the type collection in an unspecified locality in the state of Goiás, it is impossible to state whether the two are sympatric or not. However, they can be easily distinguished, for in *D. longiciliata* the reproductive axis and leaves are longer and the scapes shorter. In addition, the axis bracts of *D. weddelliana* are all of the same shape, non amplexicaul, and non-ciliated.

Selected specimens examined: Brazil. **Goiás**: Niquelândia, *Silva*, *C. et al. 464*, 22.5.1995 (HUEFS).

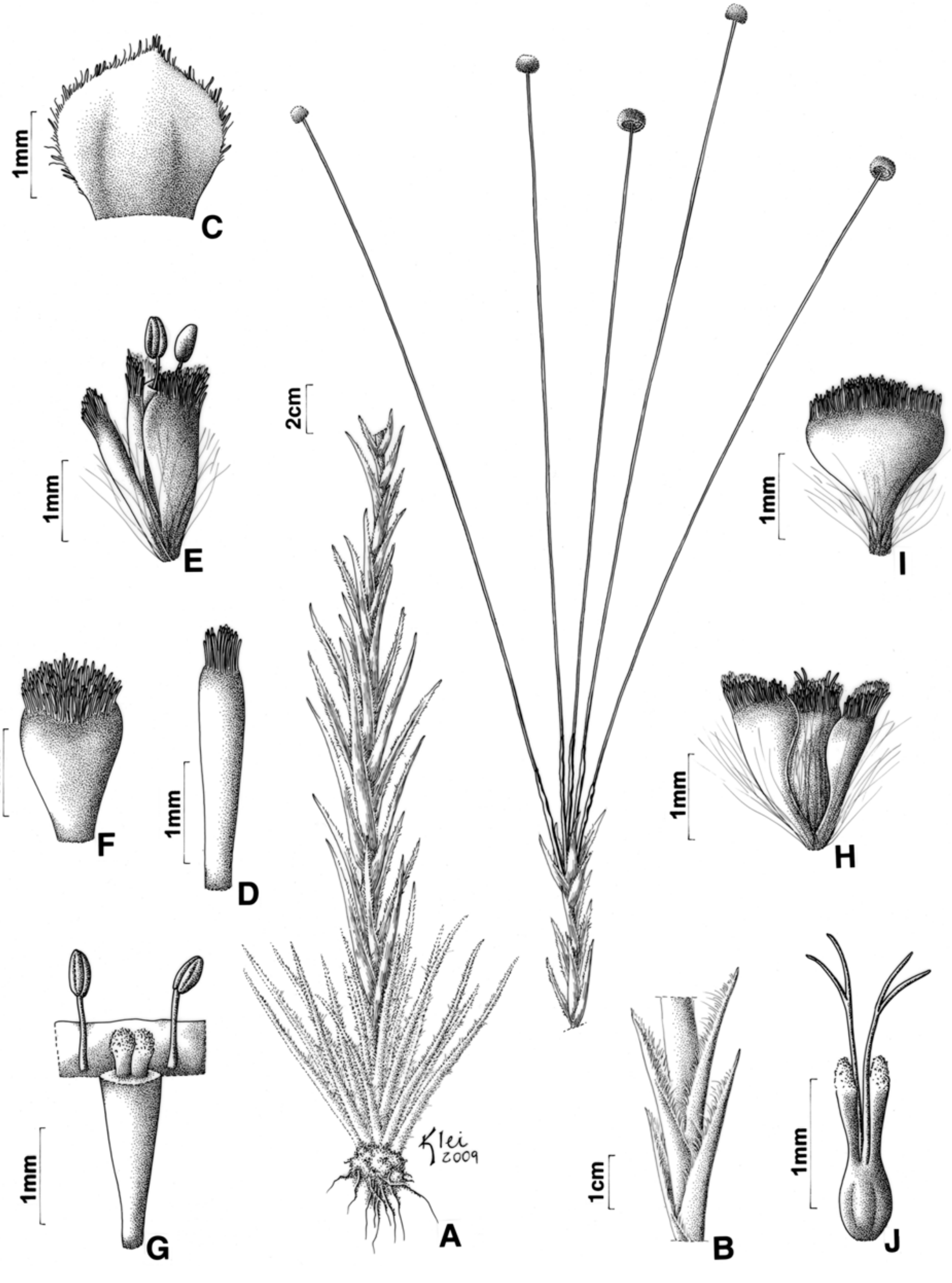

Figure 40. *Diphyomene longiciliata* (from *Silva* et al. *464*). A. Habit. B. Detail of a reproductive axis. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower sepal. G. Staminate flower with sepals removed and opened corolla. H. Pistillate flower. I. Pistillate flower sepal. J. Gynoecium.

Figure 41. *Diphyomene longiciliata*. A. Habit. B. Detail of axis bracts. C. Soil at the type locality. Scale bars, A: 5 cm. B: 2 mm. C: 5 cm.

14. Diphyomene polyclada (Silveira) Trovó, Cap. 3. *Paepalanthus polycladus* Silveira, Floral. mont. 1: 189. tab. 122.1928. —TYPE: BRAZIL. Minas Gerais: "In arenosis in serra do Chapadão". Apr 1925, *Silveira 742* (holotype: R!). Figs. 42–43.

Herbs, 45–100 cm tall; rhizome present, aerial stem 1.0–2.0 cm long, Leaves persistent or deciduous, lanceolate, flat, patent, 1.0–4.5 x 0.2–0.5 cm, glabrescent, margin ciliated, apex rounded to acute. Reproductive axis erect, 30–80 cm long, 0.3–0.5 cm diam., glabrous; axis bract with same shape, chartaceous, lanceolate, erect, 1.5–4.0 X 0.2–0.8 cm, glabrous, apex rounded to acute, margin ciliated to glabrescent, base semi-amplexicaul. Spathes 3.5–8.0 cm long, glabrous, apex acute. Scapes 7–40, arranged in a spherical umbel, 20.0–50.0 cm long, glabrous. Capitula 8–12 mm diam., semi-spherical to discoid, white; involucral bracts in 4–5 series, dark-brown, obovate, concave, ca. 4 mm long, glabrous, ciliated toward the apex, apex acute; receptacle semi-spherical, hairy. Flowers dimerous, ca. 190 per capitulum, ca. 4 X more staminates than pistillates; floral bract linear, light-brown to golden, concave, ca. 3 mm long, hairy in abaxial surface to glabrescent, ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown to golden, ca. 3 mm long, hairy in abaxial surface apex to glabrescent, ciliated toward the apex, apex acute; fleshy antophore; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings ca. 3 mm, sessile; sepals dolabriform, light brown to golden, ca. 3 mm long, hairy in abaxial surface apex to glabrescent and hairy in central portion, ciliated toward the apex, apex obtuse; petal elliptic, hyaline, ca. 2 mm long, hairy in abaxial surface apex to glabrescent and hairy in central portion, ciliated toward the apex, apex obtuse; gynoecium ca. 2 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. Individuals with staminate and pistillate flowers in full anthesis were collected between March and September. The blooming peak is from April to May. Mature fruits were found from May to September.

Distribution, Habitat, and Conservation Status. The species, endemic to the Serra da Canastra National Park (Fig. 39), occurs on rocky granitic soil, forming small, dense populations. According to IUCN (2001) criteria, the species is considered critically endangered (criteria B1a, B1b, B2a).

Commentaries. *Diphyomene polyclada* differs from the remaining species by its deciduous ciliated leaves, usually green rather than brown scape (in herbarium specimens), the acute to rounded apex of axis bracts, and geographic distribution. Clonal reproduction in populations of this species often occurs. Two species are sympatric; *D. chiquitensis*, easily distinguishable by the overall size, leaf-size and the axis bract pattern; and *D. sericoscapa*, distinct by its sericeous scapes, overall size and the size of the reproductive axis.

Silveira (1928) described *Paepalanthus polycladus* based on his own collection *Silveira 742*. This sheet comprises a teratogenetic specimen, which probably lost the apical bud and developed several lateral inflorescences, thus appearing to be a rosette with several stems, whereby the species name. This is unfortunate, since this particular feature is not the pattern within the populations.

Selected specimens examined: Brasil. **Minas Gerais**. São Roque de Minas, *Castro, N. 306*, 18.4.1982 (SPF), *Castro, N. 307*, 18.4.1982 (SPF), *Romero, R. et al. 844*, 16.4.1994 (SPF), *Nakajima, J. et al. 867*, 18.3.1995 (SPF), *Nakajima, J. et al. 882*, 18.3.1995 (SPF), *Nakajima, J. et al. 1009*, 10.5.1995 (SPF), *Romero, R. et al. 2219*, 11.5.1995 (SPF), *Romero, R. et al. 2420*, 15.7.1995 (SPF), *Nakajima, J. et al. 1257*, 18.7.1995 (SPF), *Romero, R. et al. 2995*, 28.9.1995 (SPF), *Sano, P. T. et al. 942*, 19.3.1998 (SPF), *Trovó, M.L.O. et Watanabe, M.T. 391*, 15.5.2007 (SPF).

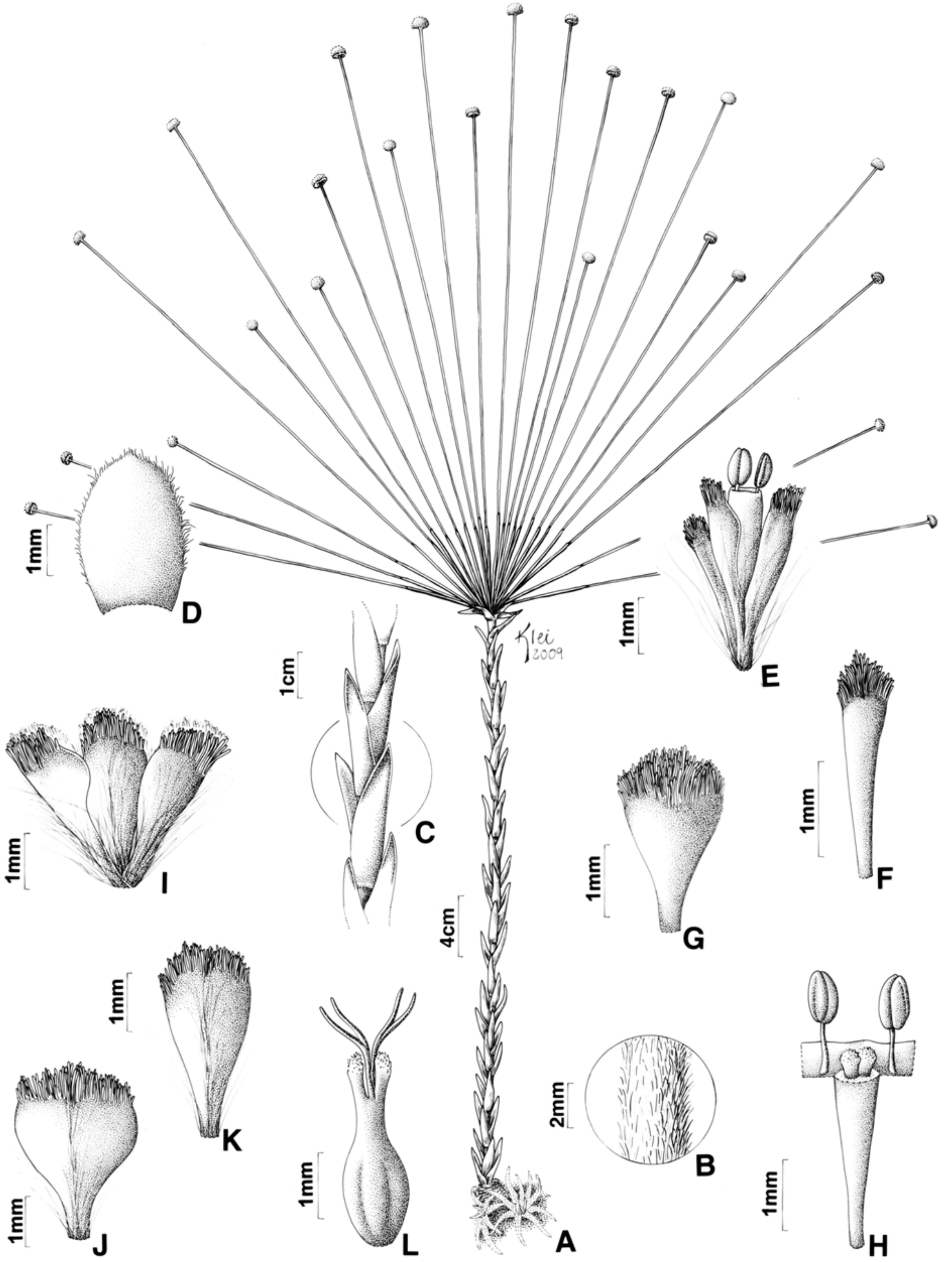

Figure 42. *Diphyomene polyclada* (from *Trovó* et al. *391*). A. Habit. B. Detail of a leaf. C. Detail of axis bracts. D. Involucral bract abaxial surface. E. Floral bract abaxial surface. F. Staminate flower. G. Staminate flower sepal. H. Staminate flower with sepals removed and corolla opened. I. Pistillate flower. J. Pistillate flower sepal. K. Pistillate flower petal. L. Gynoecium.

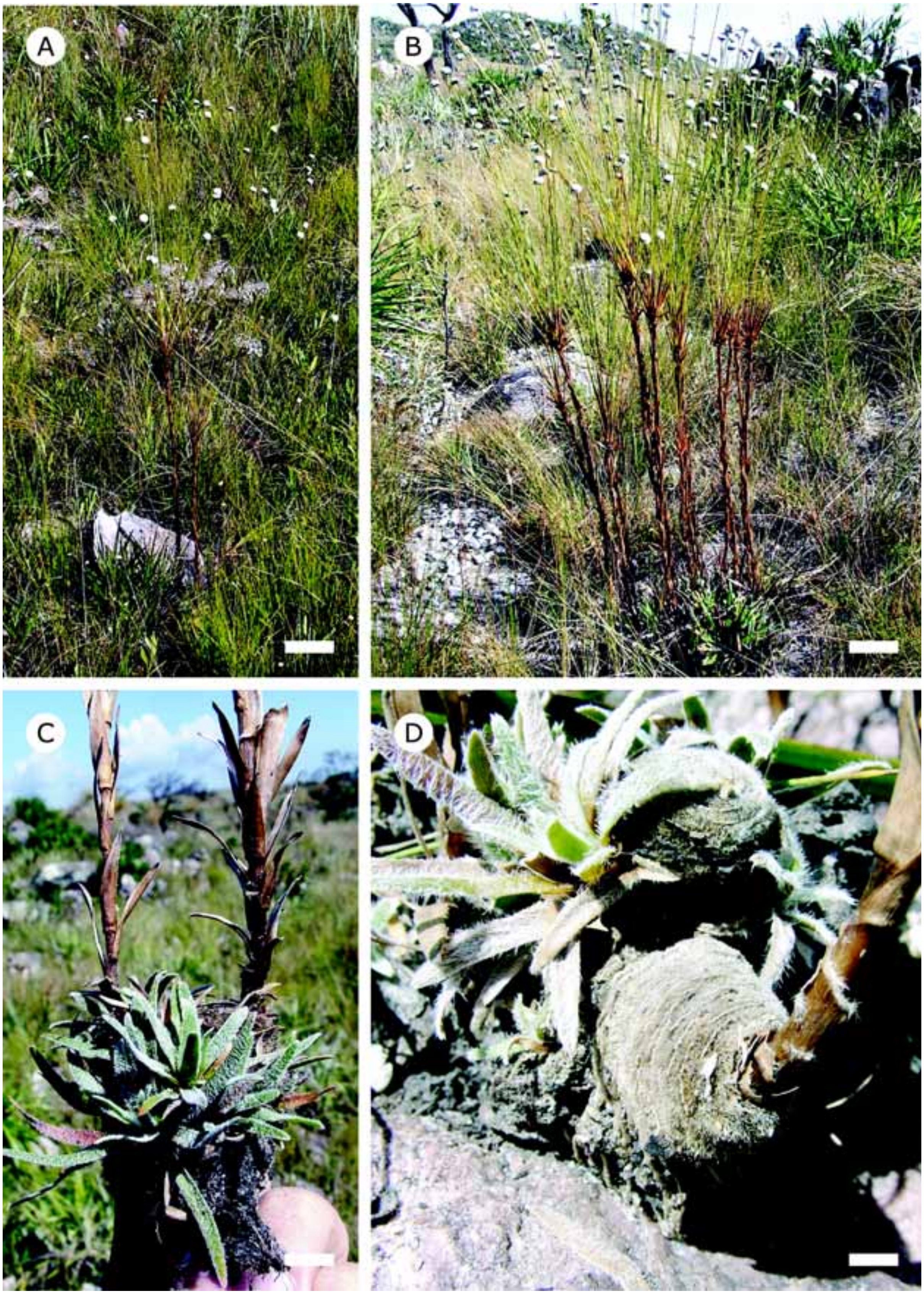

Figure 43. *Diphyomene polyclada*. A. Habit. B. Clonal individuals. C. Rosettes linked by a rhizome. D. Rosette with deciduous leaves. Scale bars, A: 8 cm. B: 10 cm. C: 2.5 cm. D: 1 cm.

15. Diphyomene sericoscapa Trovó, Appendix 2. —TYPE: BRAZIL. Minas Gerais: "São Roque de Minas, Parque Nacional da Serra da Canastra, Chapadão do Diamante". 16 Jul 1995, *Romero, R. et al. 2464* (holotype: SPF!; isotype: HUFU!). Figs. 44–45.

Herbs, 15–20 cm tall; rhizome absent, aerial stem 0.5 cm long. Leaves persistent, lanceolate, flat, patent, 1.5–2.0 X 0.4–0.6 cm, glabrous, margin glabrous, apex acute. Reproductive axis erect, 3.5–4.0 cm long, 0.5 cm diam., glabrous; axis bracts with same shape, chartaceous, lanceolate, sub-erect, 2.5–3.5 X 0.3–0.5 cm, glabrous, margin ciliated, apex acute, semi-amplexicaul. Spathes 2.5–3.0 cm long, glabrous, apex acute. Scapes 11–17, arranged in an obconic umbel, 13.5–15.0 cm long, sericeous. Capitula 7–9 mm diam., discoid, white; involucral bracts in 3–4 series, light-brown, ovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 180 per capitulum, ca. 150 staminates and 30 pistillates; floral bracts linear, brown, flats, ca. 2 mm long, glabrous, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flower (juvenile) disposed in concentric rings, ca. 3 mm, pedicel 0.3 mm; sepals dolabriforms to navicular, light-brown, ca. 3 mm long., glabrous, margin ciliated toward the apex, apex acute; petals elliptic, hyaline, ca. 1 mm long, glabrous, margin ciliated toward the apex, apex rounded; gynoecium ca. 1 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruits and seeds not seen.

Phenology. The collection of individuals with mature staminate flowers in anthesis and juvenile pistilate flowers, took place in July. Mature fruits and seeds were not observed.

Distribution, Habitat, and Conservation status. As with *D. polyclada*, *D. sericoscapa* is restricted to the Serra da Canastra National Park (Fig. 46), where it occurs in grass covered campos rupestres. According to IUCN (2001) criteria, *D. sericoscapa* is considered critically endangered (criteria B1a).

Commentaries. *Diphyomene sericoscapa* possesses distinctive sericeous scapes. Except for *D. decussa* and *D. cipoensis*, also with hairy scapes, the remaining *Diphyomene* species have glabrous scapes. The short pistillate-flower pedicels and navicular to dolabriform petals are also distinctive features. This species is sympatric with *D. polyclada* and *D. chiquitensis*, both with relatively longer elongated axes and glabrous scapes.

The most morphologically alike species is *D. cipoensis.* Mutual similarities are the relatively small size, very short reproductive axis, the similar capitula width, and the obconic scape-arrangement. Besides the hairy scapes and floral characteristics listed above, *D. sericoscapa* can also be distinguished from *D. cipoensis* by its shorter and flat leaves and reproductive axis bracts.

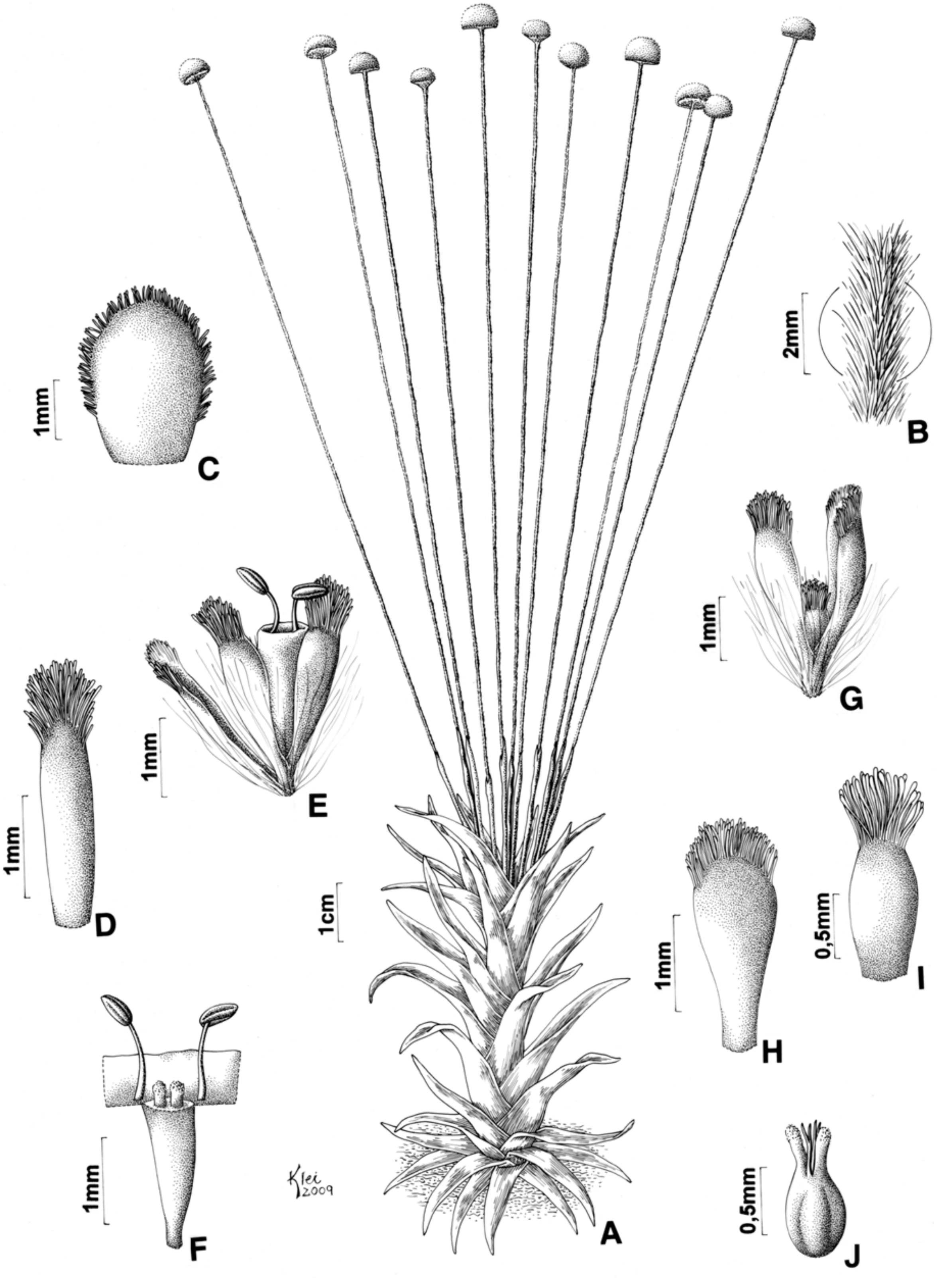

Figure 44. *Diphyomene sericoscapa* (from *Romero* et al. *2464*). A. Habit. B. Detail of the scape. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower. H. Pistillate flower sepal. I. Pistillate flower petal. J. Gynoecium.

Figure 45. *Diphyomene sericoscapa*. Holotype deposited in SPF.

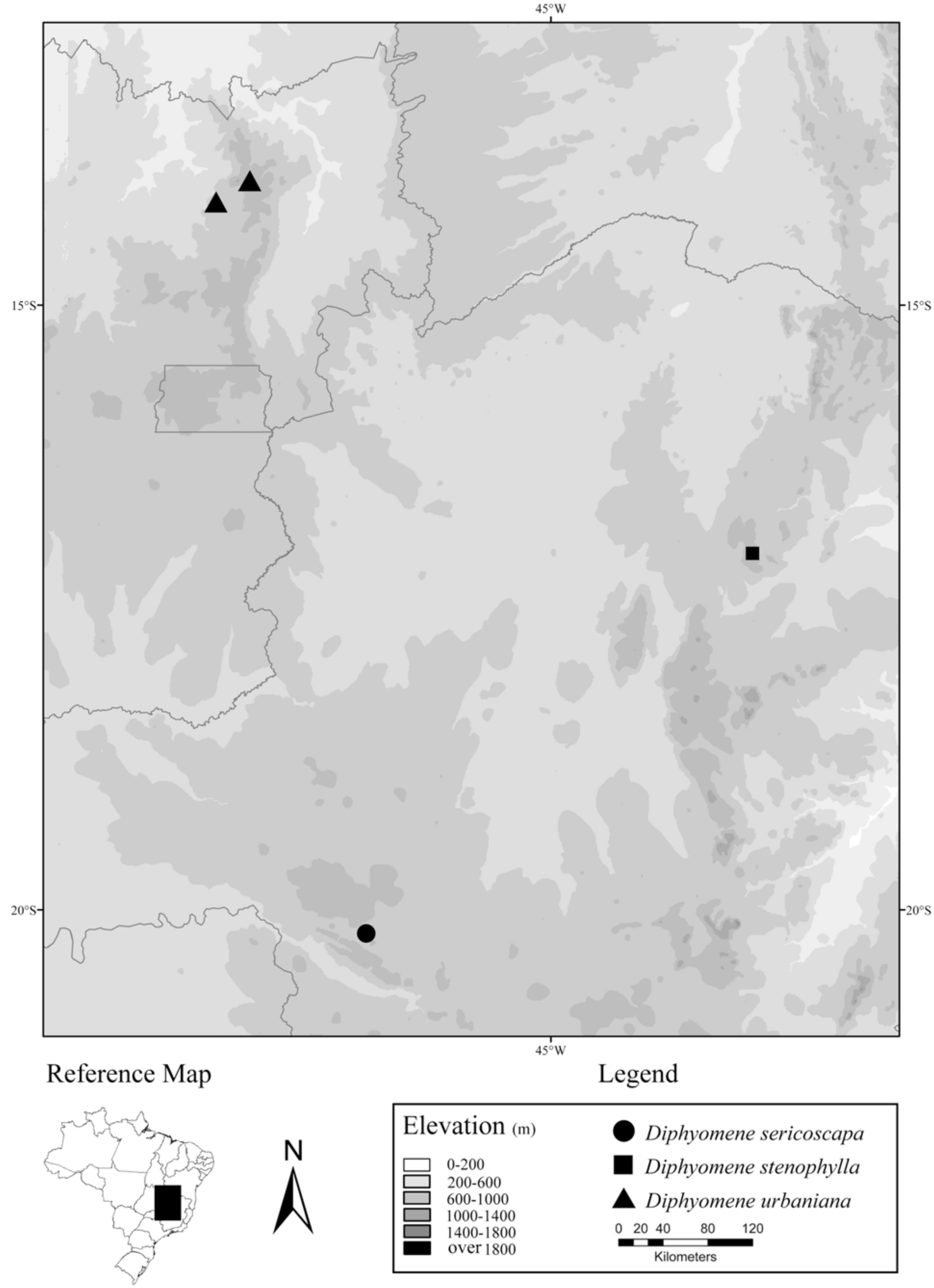

Figure 46. Geographical distribution of *D. sericoscapa*, *D. stenophylla*, and *D. urbaniana.*

16. Diphyomene stenophylla Trovó, Appendix 2.—TYPE: BRAZIL. Minas Gerais: "Itacambira, Plantar MG 15 - Fazenda Tamanduá". 10 Apr. 2005, *E. Tameirão Neto 4216* (holotype: SPF!; isotype: BHCB!). Figs. 47–48.

Herbs, 51–60 cm tall; rhizome present, aerial stem 0.5–1.5 cm long. Leaves deciduous, linear, flat, semi-erect, 3.5–13.0 X 0.1–0.2 cm, hairy to glabrescent, margin ciliated, apex acute. Reproductive axis erect, 31.0–40.0 cm long, 0.4–0.6 cm diam., glabrous; axis bracts with same shape, chartaceous, linear to lanceolate, erects to sub-erect, 2.0–4.0 X 0.2–0.4 cm, glabrous, margin glabrous, apex acute, semi-amplexicaul. Spathes 2.0–3.5 cm long, glabrous, apex acute. Scapes 25–53, arranged in a semi–spherical umbel, 21.0–25.5 cm long, hairy toward the apex. Capitula 6–8 cm diam., semi-spherical, white; involucral bracts in 4–5 series, brown, ovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; receptacle semi-spherical, hairy. Flowers dimerous, ca. 320 per capitulum, ca. 3 X more staminates than pistillates; floral bracts linear, light-brown, flats, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown to golden, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings, ca. 3 mm, sessile; sepals dolabriforms, light-brown to gold, ca. 0.3 cm long., hairy in the abaxial surface base, margin ciliated toward the apex, apex mucronate; petals elliptic, light-brown to golden, ca. 2 mm long, hairy in abaxial surface base, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. Individuals were collected, first with mature staminate and pistillate flowers in April, and then with fully developed fruits in October.

Distribution, Habitat, and Conservation status. *Diphyomene stenophylla* is restricted to Itacambira (MG), located in the mountainous area of the northern Espinhaço Range (Fig. 46). Both collections came from the same population of open, grass dominated fields. According to IUCN (2001) criteria, *D. stenophylla* is considered critically endangered (criteria B1a, B1b, B2a).

Commentaries. Diphyomene stenophylla is not sympatric with any other species within the genus. It is distinguishable by its unusual, sub-erect linear leaves. *Diphyomene amoena*, also from Minas Gerais, likewise possesses linear leaves, although these are smaller and patent. The two are allopatric, as *D. amoena* is restricted to the southern Espinhaço Range.

Diphyomene stenophylla shares morphological similarities with *D. polyclada*, with reproductive axis and scapes of approximately the same size. Nevertheless, the former differs by its erect linear leaves and the size of both spathes and capitula, besides certain pistillate floral features, such as sepals with mucronate apex, petals which are hairy at the base, and stigmatic branches with the same-sized nectariferous branches. Furthermore, as *D. polyclada* is endemic to the Serra da Canastra, the species are allopatric.

Selected specimens examined. Brazil. **Minas Gerais**: Itacambira, *Tameirão Neto*, *E. 4052*, 09.10.2005 (SPF, BHCB).

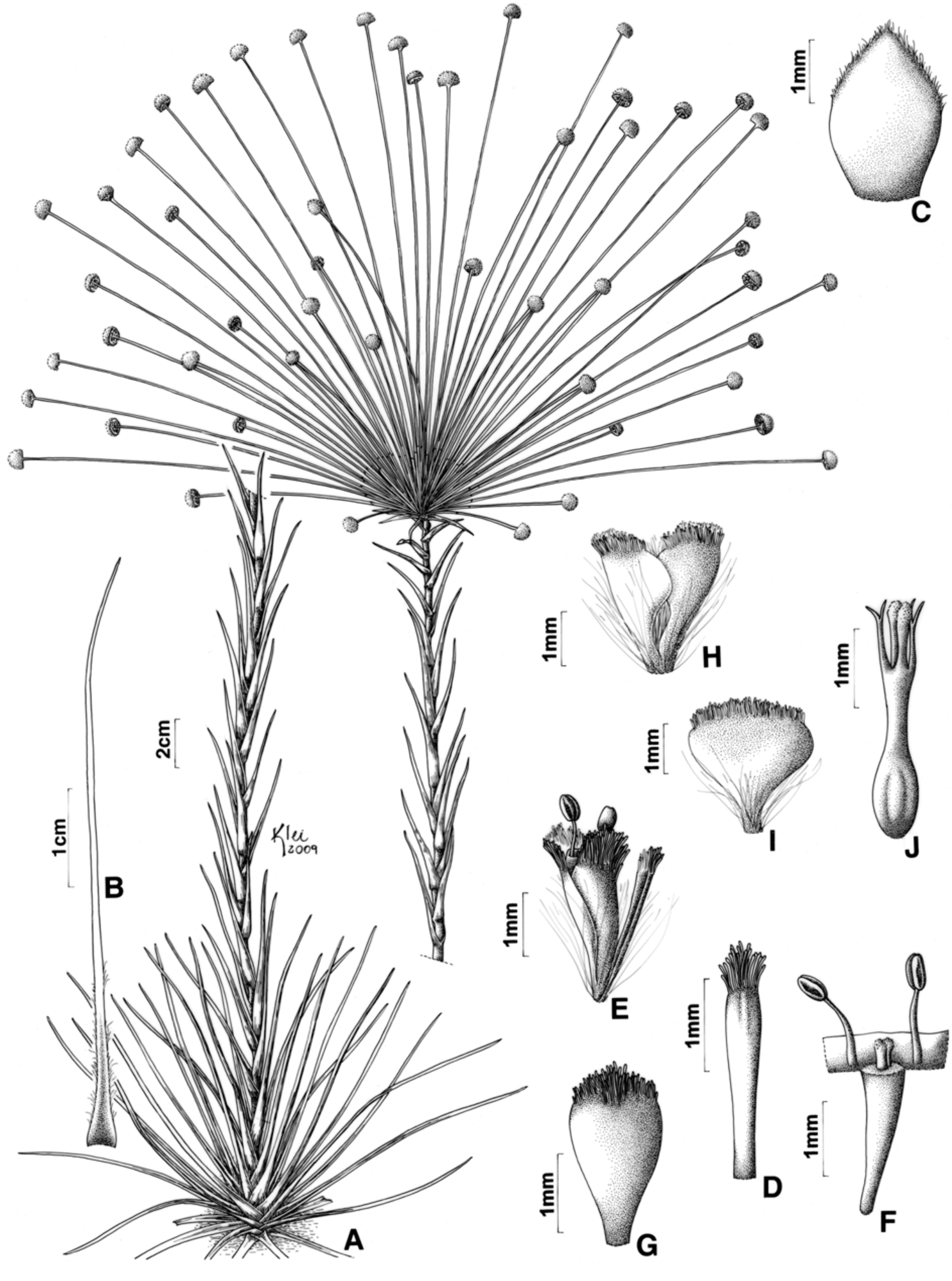

Figure 47. *Diphyomene stenophylla* (from *Tameirão Neto 4216*). A. Habit. B. Details of a leaf. C. Involucral bract abaxial surface. D. Floral bract abaxial surface E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Staminate flower sepal. H. Pistillate flower. I. Pistillate flower sepal. J. Gynoecium.

Universidade de São Paulo (SPF)
Paepalanthus amoenus (Bong.) Körn.
Det: Trovó, M.L.O. 2007

HERBÁRIO DO DEPARTAMENTO DE BOTÂNICA (BHCB) - ICB - UFMG
PLANTAS DO BRASIL
ERIOCAULACEAE

Espécie: *Paepalanthus giganteus*
Localidade: MG. Itacambira: Plantar MG 15 - Fazenda Tamanduá.
Lat.: S. Lon.: W. Alt.: m.
Data: 10/4/2005
Coletor: E. Tameirão Neto nº: 4216
Determinador:
Obs.: Cerrado, herbáceo.
BHCB 99010

UNIVERSIDADE DE SÃO PAULO
HERBÁRIO
SPF 179.266

Figure 48. *Diphyomene stenophylla*. Holotype deposited in SPF.

17. Diphyomene urbaniana (Ruhland) Trovó, Cap. 3. *Paepalanthus urbanianus* Ruhland, in Engler, Pflanzenr. 13 (IV.30): 188. 1903.—TYPE: BRAZIL. Goiás: "Serra dos Veadeiros, dans campo sec". 15 Jan 1895, *Glaziou 22318* (holotype: B!; isotypes: BR!, C!, G!, K!, LE! NY!, P!). Figs. 49–50.

Paepalanthus urbanianus var. *angustifolius* Moldenke, Phytologia 39: 330. 1978.—TYPE: BRAZIL. Goiás: "Chapada dos Veadeiros". 23 Mar 1969, *H. S. Irwin & al. 24936* (holotype: NY!).

Herbs, 45–65 cm tall; rhizome present, aerial stem 1.5–2.5 cm long. Leaves persistent, lanceolate, flat, patent to contort at the uppermost part, 1.5–5.0 x 0.5–1.0 cm, glabrous, margin glabrous, apex mucronate. Reproductive axis erect, 17.0–22.0 cm long, 0.4–0.6 cm diam., glabrous; axis bracts with same shape, chartaceous, lanceolate, erect, 1.5–4.0 X 0.5–1.0 cm, glabrous, apex acute, margin glabrous, base semi-amplexicaul. Spathes 2.5–4.0 cm long, glabrous, apex acute. Scapes 110–200, arranged in a spherical umbel, 17.0–27.0 cm long, glabrous. Capitula 5–8 mm diam., semi-spherical, white; involucral bract in 3–4 series, dark-brown, obovate to ovate, concave, ca. 3 mm long, glabrous, ciliated toward the apex, apex obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 180 per capitulum, ca. 6 X more staminates than pistillates; floral bract linear, light-brown to golden, concave, ca. 2 mm long, hairy in abaxial surface apex, ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 1.0 mm long, with long trichomes; sepal navicular, light brown to golden, ca. 2 mm long, hairy in abaxial surface apex, ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 2 mm long; pistilodes 2, papillose; pistillate flowers disposed in concentric rings, ca. 3 mm, sessile; sepals dolabriform, light-brown to golden, ca. 3 mm long, hairy in abaxial surface apex and in the central portion, ciliated toward the apex, apex obtuse; petal obovate, hyaline, ca. 2 mm long, hairy in abaxial surface base, ciliated toward the apex, apex acute; gynoecium ca. 2 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red do brownish.

Phenology. Individuals of this species were collected with flowers and fruits between November and March. Staminate and pistillate flowers were fully developed, especially from

December to February. Mature fruits were available from January to March. The blooming period coincides with the rainy season.

Distribution, Habitat, and Conservation Status. *D. urbaniana* is endemic to the Chapada dos Veadeiros National Park (Fig. 46), intermixed with grasses in open savannas, and forming large populations of over 1000 individuals. According to IUCN (2001) criteria the species is considered critically endangered (criteria B1a, B1b, B2a).

Commentaries. *D. urbaniana* is discerned by the contort leaves with mucronate apex, and scapes which are longer than the reproductive axis and arranged in a spherical umbel. While resembling the coexistent *D. flexuosa*, they are not considered sympatric, since the latter occupies different habitats in the vicinity of Niquelândia, near to the Chapada dos Veadeiros. Of the two, *D. urbaniana* presents the more robust habit, with longer reproductive axis, lanceolate leaves, and more numerous scapes, clearly distinguishing features.

Moldenke (1978) described *Paepalanthus urbanianus* var. *angustifolius* Moldenke, based on the material *H. S. Irwin et al. 24936* deposited in NY. In the protologue, Moldenke (1978) stated that this variety has oblong-lanceolate axis bracts, in contrast to the normal cordate axis bracts of the species. However, in the species itself, these are, in fact, lanceolate and not cordate. Moldenke (1978) may have arrived at this conclusion through the specified bracts not being completely amplexicaul. Thus, those features stated as different, really do fit into the range of species variation, whereby the distinction in varieties, as stated, can be considered meaningless.

Selected specimens examined: Brazil. **Goiás**: Alto Paraíso de Goiás, *Irwin, H.S.* 24936, 23.3.1969 (RB), *Shepherd, G. J. et al. 3681*, 27.11.1976 (MBM, UEC), *Silva, J.C.S. 480*, 16.11.1985 (UEC), *Cavalcanti, T. et al. 1382*, 15.3.1995 (HUEFS), *Alves, M. et al. 2271*, 17.2.2001 (SPF), *Souza, J. P. et al. 4519*, 23.1.2005 (SPF, ESA), *Trovó, M.L.O. et al. 435*, 3.12.2007 (SPF), *Trovó, M.L.O. et al. 447*, 5.12.2007 (SPF), *Trovó, M.L.O. et al. 467*, 20.3.2009 (SPF).

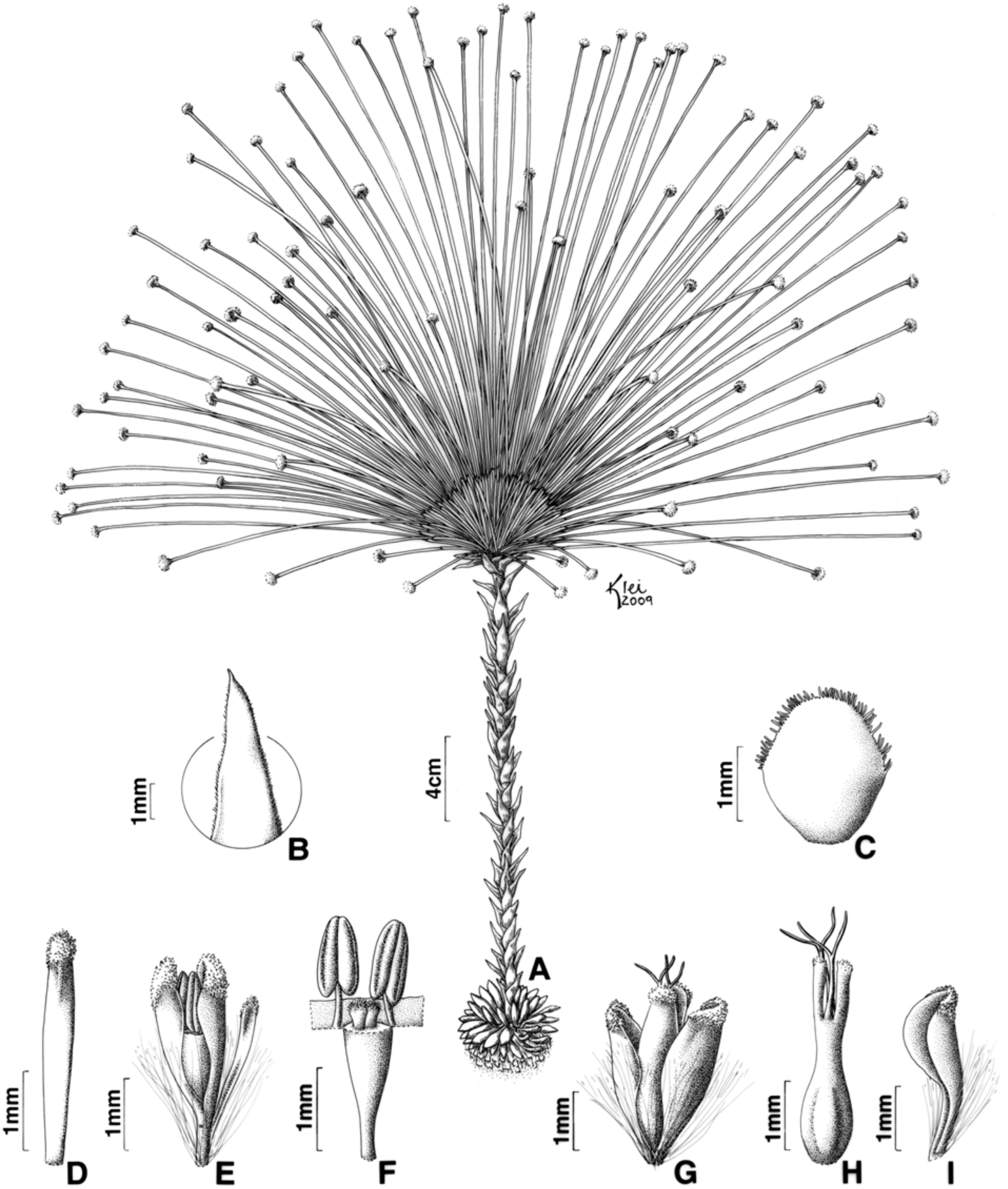

Figure 49. *Diphyomene urbaniana* (from *Trovó et al. 467*). A. Habit. B. Detail of leaf-apex. C. Involucral bract. D. Floral bract. E. Staminate flower. F. Staminate flower with sepals removed and open corolla. G. Pistillate flower. H. Gynoecium. I. Pistillate flower sepal.

Figure 50. *Diphyomene urbaniana*. A. Habit. B. Rosette with contorted leaves. Scale bars, A: 7 cm. B: 1.5 cm.

18. Diphyomene weddelliana (Koern.) Trovó, Cap. 3. *Paepalanthus weddellianus* Koern., in Martius & Eichler, Fl. bras. (3)1: 317. 1863. *Dupatya weddelliana* (Koern.) Kuntze, Revis. gen. Pl. 2: 746. 1891.—TYPE: BRAZIL. Goiás: "Marais des rochers à Prov. de Goyaz". s.d., *Weddell 2927* (holotype: BR!; isotype: P!). Figs. 51–52.

Herbs, 38–44 cm tall; rhizome present, aerial stem 1.5–2.5 cm long. Leaves persistent, linear, flat, patent, 1.0–2.5 x 0.1–0.2 cm, glabrescent, margin glabrous, apex acute. Reproductive axis erect, 6.5–10.0 cm long, 0.3–0.5 cm diam., glabrous; axis bracts with same shape, chartaceous, linear-lanceolate, patent, 1.5–2.5 X 0.1–1.2 cm, glabrous, apex acute, margin glabrous, base not amplexicaul. Spathes 4.5–6.5 cm long, glabrous, apex acute. Scapes 12–30, arranged in an spherical umbel, 30.0–36.0 cm long, glabrous. Capitula 7–10 mm diam., discoid, white; involucral bract in 4–5 series, dark-brown, obovate to elliptic, concave, ca. 3 mm long, hairy in abaxial surface apex, ciliated toward the apex, apex obtuse; receptacle semi-spherical, hairy. Flowers dimerous, 120 per capitula, ca. 3 X more staminates than pistillates; floral bract oblanceolate, dark-brown, concave, ca. 3 mm long, hairy in abaxial surface apex, ciliated toward the apex, apex acute; staminate flower ca. 4 mm long; pedicel ca. 1.0 mm long, with long trichomes; sepal navicular, dark-brown, ca. 3 mm long, hairy in abaxial surface apex and in the central portion, ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 2 mm long; pistilodes 2, papillose; pistillate flowers (juvenile) disposed in concentric rings, ca. 2 mm, sessile; sepals dolabriform, dark-brown, ca. 2 mm long, hairy in abaxial surface apex and in the central portion, ciliated toward the apex, apex obtuse; petals obovate, hyaline, ca. 2 mm long, hairy in abaxial surface apex and in the central portion, ciliated toward the apex, apex acute; gynoecium ca. 2 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruits and seeds not seen.

Phenology. The available specimens presented both mature and juvenile pistillate flowers. Hugh Weddell collected these without compiling precise information as to local and date, whereby the lack of pertinent phenological data.

Distribution, Habitat, and Conservation Status. The species is known by only four specimens from a single collection. The type locality, although imprecise, is probably in the vicinity of the town of Goiás (GO). Label information indicates that the population grows on rocky soils. According to IUCN (2001) criteria the species is considered critically endangered (criteria B1a).

Commentaries. *Diphyomene weddelliana* is known only by the type specimens. Its patent and linear-lanceolate axis bracts with a non-amplexicaul base are distinguishing features. In habit it resembles *D. longiciliata.* However, in addition to the features listed above, *D. weddelliana* differs by its shorter reproductive axis, leaves and scapes. The species is also distinct by its same-shaped and non-ciliated axis bracts.

Koernicke (1863) described the species based on *Weddell 2927*. In the protologue Koernicke (1863) states that the leaves of the type specimens had been destroyed. Although the original Hugh Weddell collection is deposited at P, the only specimen that fits this description is deposited at BR, and is therefore considered as the holotype. The specimens at P have complete leaves, and thus these structures are here properly described.

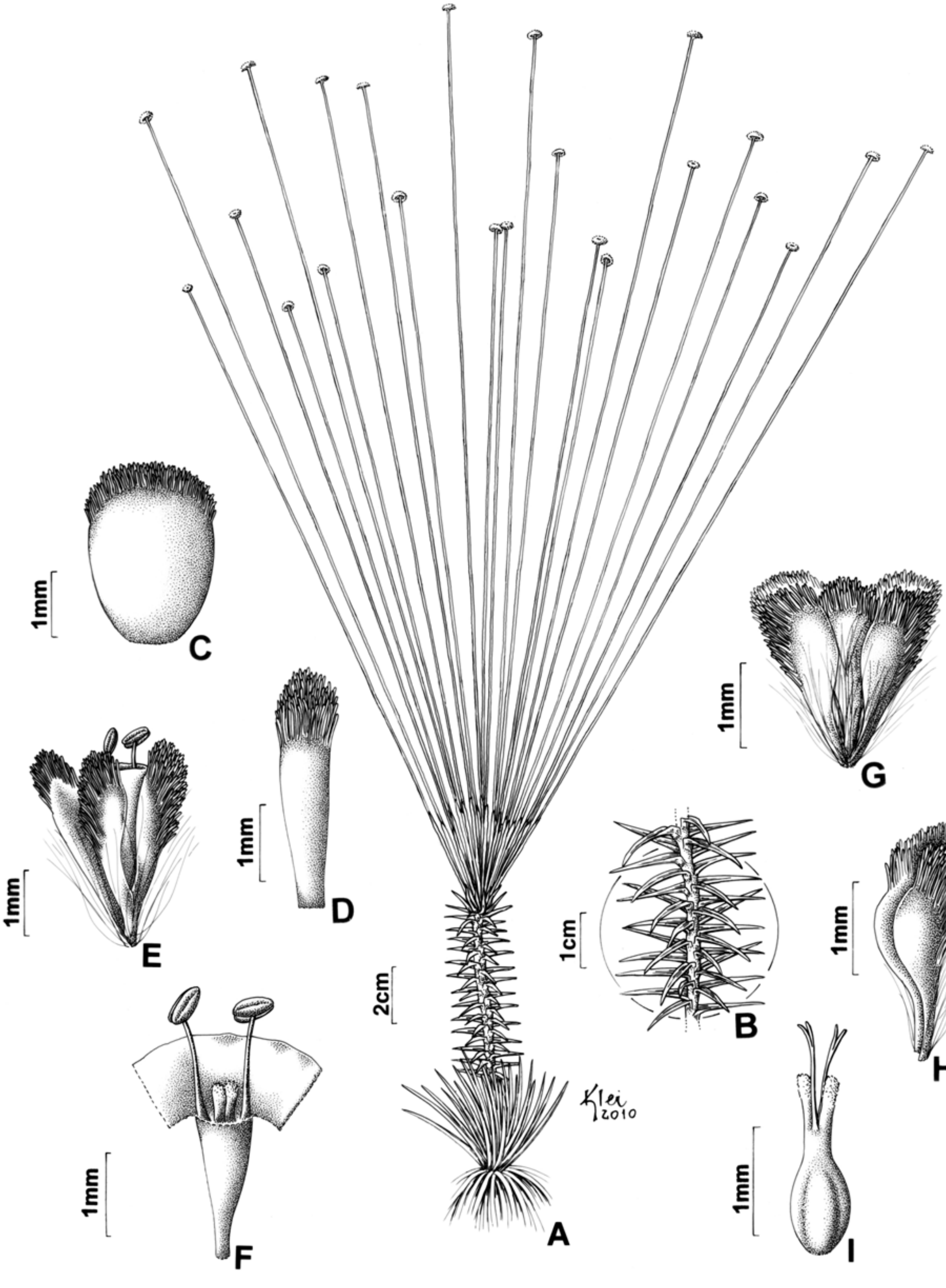

Figure 51. *Diphyomene weddelliana* (from *Weddell 2927*). A. Habit. B. Detail of the reproductive axis. C. Involucral bract. D. Floral bract. E. Staminate flower. F. Staminate flower with sepals removed and open corolla. G. Pistillate flower. H. Pistillate flower sepal. I. Gynoecium.

Figure 52. *Diphyomene weddelliana*. Isotype deposited in P.

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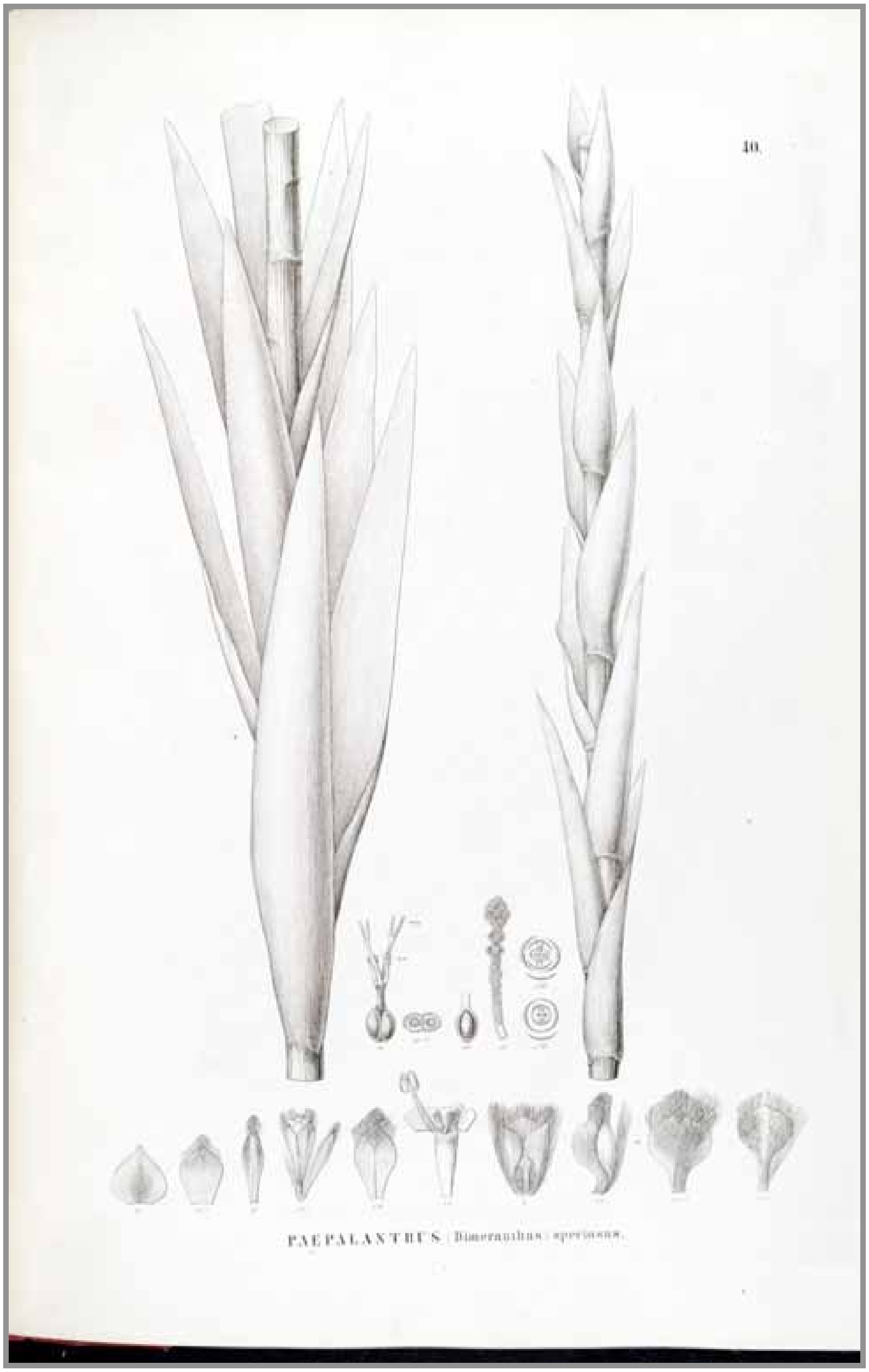
APÊNDICES I & II

Espécies novas



PAEPALANTHUS (Dimeranthus) speciosus.

Appendix I

Five new and narrowly distributed species of *Diphyomene* (Eriocaulaceae) from Central Brazil[6]

Marcelo Trovó and Paulo Takeo Sano

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Abstract - Five new Brazilian species of the genus *Diphyomene* are described and illustrated: ***D. brachycaule, D. conferta***, ***D. flexuosa***, ***D. hymenobracteata***, and ***D. longiciliata***. *Diphyomene brachycaule* is similar to *D. decussa*, from which it is easily distinguished by its shorter reproductive axis, and hairy and mucronate leaves. *Diphyomene conferta* shares similarities with *D. amoena*, differing by its sulfurous capitula and adpressed reproductive axis bracts. *Diphyomene flexuosa*, morphologically closely related to *D. urbaniana*, possesses a distinctive short and tortuous reproductive axis. *Diphyomene hymenobracteata* is affined with *D. decussa*, even though possessing unique, membranaceous reproductive-axis bracts and punctual placed pistillate flowers. *Diphyomene longiciliata*, morphologically similar to *Diphyomene weddelliana*, possesses long hairs on the margins of the reproductive axis bracts, considered as a diagnostic feature. Four of the described species are narrowly distributed in the state of Goiás, whereas *D. brachycaule* is endemic to Distrito Federal. All are considered critically endangered. Detailed comparisons of these species are presented in tables. Comments on phenology, distribution, habitat and etymology, besides an identification key, are provided.

Key words: Cerrado, Distrito Federal, Goiás, IUCN Red List, Taxonomy.

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[6] Manuscrito a ser submetido ao periódico Systematic Botany

Diphyomene (Ruhland) Trovó was recently segregated from *Paepalanthus* by Trovó and Sano (in press). It comprises 10 species occurring in South America, mainly in Brazil. Taxonomic and morphological diversity is concentrated in the Cerrado (Savanna) areas of central Brazil, especially in the state of Goiás. A secondary center is located in the Espinhaço Range in Minas Gerais (Giulietti and Hensold 1990; Trovó and Sano in press). These species are mainly to be found in open-grass savannas and rocky outcrops. Except for *Diphyomene chiquitensis* (Herzog) Trovó and *Diphyomene erectifolia* (Silveira) Trovó, all are narrowly distributed. Some are endemic to one locality or even to one single mountain (Trovó and Sano in press). Thus, detailing this distribution pattern may play a central role in conserving not only *Diphyomene* species, but the Brazilian Cerrado as a whole, especially important through constituting a biodiversity hotspot and one of the most endangered Biomes in South America (Myers et al. 2000; Silva and Bates 2002; Fiaschi and Pirani 2009).

Diphyomene species are monocarpic herbs and can be distinguished from *Paepalanthus* by the inflorescent structure, dolabriform sepals, and completely reduced staminodes in pistillate flowers, characters that may emerge as synapomorphies for the group (Trovó and Sano in press; Trovó et al. in press). Although the taxon is easily recognized, species distinction is historically difficult. To date, species descriptions were based on few herbarium specimens, without reflecting the full range of morphological variation (Koernicke 1863; Ruhland 1903; Silveira 1908; 1928). Moreover, Moldenke (1947, 1952, 1964, 1971, 1974, 1978, 1983, 1987) succinctly described two new species and nine infra-specific taxa with neither images nor identification keys as guidelines. Only recently, and then with the taxonomic and nomenclatural advances as proposed by Trovó and Sano (in press), have we been able to not only recognize previously described species, but also describe novelties

Taxonomic Treatment

Diphyomene brachycaule Trovó, sp. nov.—Type: BRAZIL. Distrito Federal , Brasília: EEJBB, prox. A área de lazer, lado esquerdo que da acesso CASEB. 15° 52’0’’ S/ 47° 51’ 0’’ W, 03 Jul 2000, *M. G. Nobrega & L. C. Mendes 1187* (Holotype, HEPH!). Fig. 1.

Haec species a *Diphyomene decussa* (Koern.) Trovó habitu humilioris (usque 26 cm vs. 32 cm), folis pilosis et erectis, caulis brevioris (usque 4.5 cm vs. 8.0 cm), bracteis caulinorum distinctis, scapis glabris non numerosis (usque 10 vs. 35), capitulis latiusculis (usque 10 mm vs. 6 mm), et sepalis florum feminorum apicis mucronatis differt.

Monocarpic herb, 24–26 cm alt.; rhizome absent, aerial stem 0.5–1.0 cm long. Rosette leaves persistent, lanceolate, flat, erect, 4.0–5.5 X 0.3–0.5 cm, hairy, margin ciliated, apex mucronate. Reproductive axis erect, 3.5–4.5 cm long, 0.3–0.4 cm diam., glabrous; axis bracts gradually smaller from the base to the apex, chartaceous, lanceolate, erect, 1.5–4.5 X 0.3–0.5 cm, hairy to glabrescent, margin ciliated to glabrescent, apex mucronate, base amplexicaul. Spathes 2.5–3.5 cm long, glabrous, apex acute. Scapes 6–10, arranged in an obconic umbel, 15.0–21.0 cm long, glabrous. Capitula 8–1 mm diam., discoid, white; involucral bracts in 3–4 series, dark-brown, deltoid to ovate, concave, ca. 4 mm long, glabrous, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 150 per capitulum, ca. 8 X more staminates than pistillates; floral bracts linear, light-brown, flats, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, brown, ca. 3 mm long, glabrous, margin ciliated toward the apex to glabrescent, apex acute; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; Pistilate flowers ca. 3 mm, sessile, disposed in concentric rings; sepals dolabriform, white, ca. 3 mm long, hairy in the abaxial surface base, margin ciliated toward the apex to glabrescent, apex mucronulate; petals elliptic, fleshy, ca. 3 mm long, hairy in abaxial surface, margin ciliated toward the apex, apex obtuse; gynoecium ca. 3 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds not seen.

Phenology. Individuals, with staminate and pistillate flowers, as well as early fruits, were collected in July.

Distribution, Habitat, and Conservation Status. Different from the other here described species, *D. brachycaule* is endemic to the Distrito Federal (Fig. 2). Individuals were collected from a large population in open-grass savanna inside the Brasília Botanical Garden. According to IUCN (2001) criteria, the species is considered critically endangered (criteria B1a).

Etymology. The epithet "brachycaule" refers to the overall size of the species reproductive species, the smallest within the genus.

Commentaries. The erect leaves covering the short reproductive axis, and the hairy, mucronate leaves are distinguishing features. Until now, *D. brachycaule* is the only species restricted to the Distrito Federal. *Diphyomene acanthophylla* (Ruhland) Trovó, *D. chiquitensis*, and *Diphyomene koernickei* (Ruhland) Trovó, although sympatric and congeneric, are distinct from *D. brachycaule* by their overall size (usually more than 1 m high) and the size of the reproductive axis.

Diphyomene brachycaule and *Diphyomene decussa* (Koern.) Trovó are morphologically similar, with approximately the same small size, short reproductive axis, no rhizome, and ciliated leaves. However, *D. brachycaule* is even smaller, possesses hairy erect leaves with mucronate apex, and variably shaped reproductive axis bracts throughout the axis. This species is also distinct by less glabrous scapes, wider capitula, and the mucronate apex of the pistillate flower. A more detailed comparison is given in Table 1. As stated, they are allopatric, with *D. decussa* restricted to the southern Espinhaço Range in Minas Gerais state, a far distant region.

Diphyomene conferta Trovó, sp. nov.—Type: BRAZIL. Goiás, Alto Paraíso de Goiás: Parque Nacional da Chapada dos Veadeiros, Estrada para a Vereda do Mulungu, 14° 06'29.7" S/ 47° 38' 34.0" W, 05 Dez 2007, *M. L. O. Trovó et al. 446* (Holotype, SPF!; isotypes B!, NY!, SP!). Fig. 3.

Haec species a *Diphyomene amoena* (Bong.) Trovó habitu robustioris (usque 170 cm vs. 90 cm), folis lanceolatis (usque 1.4 cm vs. 0.2 cm), bracteis caulinorum adpressis et capitula sulfurinis latiusculis (usque 20 mm vs. 4 mm) differt.

Monocarpic herb, 105–170 cm alt.; rhizome present, aerial stem 1.0–3.0 cm long. Rosette leaves persistent, lanceolate, flat, patent, 5.5–11.5 X 0.7–1.4 cm, hairy to glabrous, margin glabrous, apex acuminate. Reproductive axis erect, 75.0–140.0 cm long, 0.5–0.8 cm diam., glabrous; axis bracts with same shape, chartaceous, lanceolate, adpressed, 2.5–5.5 X 1.0–2.0 cm, glabrous, margin glabrous, apex acute, base amplexicaul. Spathes 4.0–7.5 cm long, glabrous, apex acute. Scapes 16–52, arranged in a spherical umbel, 27.0–45.0 cm long, glabrous. Capitula 12–20 mm diam., semi-spherical to spherical, sulfurous; involucral bracts in 4–5 series, dark-brown, ovate to oblong, concave, ca. 4 mm long, glabrous, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 330 per capitulum, ca. 3,5 X more staminates than pistillates; floral bracts linear, light-brown, flats, ca. 4 mm long, glabrous, margin ciliated toward the apex, apex acuminate; staminate flowers ca. 4 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, brown, ca. 3 mm long, hairy in abaxial surface, margin ciliated toward the apex to glabrescent, apex acute; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; Pistilate flowers ca. 4 mm, sessile, disposed in concentric rings; sepals dolabriform, brown, ca. 4 mm long, hairy in the abaxial surface base, margin ciliated toward the apex, apex mucronulate; petals dolabriform, fleshy, ca. 3 mm long, hairy in abaxial surface base, margin ciliated toward the apex, apex obtuse; gynoecium ca. 3 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Paratypes—BRAZIL. Goiás, **Alto Paraíso de Goiás**: 17 Mar 1971, *H. S. Irwin et al. 32034* (SP); 14 Mai 1986, *S. R. Neto et al. 444* (SP); 05 Mar 1981, *S. B. Silva and J. Oliveira 60* (RB); 20 Mar 2009, *M. L. O Trovó et al. 468* (SPF).

Phenology. Individuals with staminate and pistillate flowers, besides mature fruits, were collected between December and March. The floral period coincides with the rainy season.

Distribution, Habitat, and Conservation Status. This species is endemic to the region of Chapada dos Veadeiros in the state of Goiás (Fig. 2), there growing on rocky, grass covered soil. Large populations were found inside the local national park. According to IUCN (2001) criteria, the species is considered critically endangered (criteria B1a, B1b, B2a).

Etymology. The epithet "conferta" refers to the adpressed axis bracts through the reproductive axis.

Commentaries. Reproductive individuals of *D. conferta* are readily recognized by the unique adpressed axis bracts and sulfurous-tone capitula. Although some specimens of *D. erectifolia* also possess capitula of the same color, here it is not a stable character within populations. Populations of *D. conferta* may be remarkably large, with more than a thousand individuals in open formation. In the holotype most of the capitula were extremely old, thereby appearing more brownish than sulfurous.

Morphologically, *D. conferta* and *Diphyomene amoena* (Bong.) Trovó are the most alike. Both species posses a slender reproductive axis and relatively few scapes arranged in a spherical umbel. However, *D. conferta* individuals are larger, besides possessing sulfurous-tone capitula and adpressed axis bracts. They can also be differentiated by leaf form and width, and capitulum diameter. A detailed comparison of these characters is given in Table 2. *Diphyomene conferta* and *D. amoena* are allopatric, as *D. amoena* is present in mountains to the south of the Espinhaço Range.

Diphyomene flexuosa Trovó, sp. nov.—Type: BRAZIL. Goiás, Niquelândia: Macedo, 15 km N of Niquelândia; 14° 18' S. 48° 23' W, facing hill slope, stable peridotite/dunite-based scree and flat area below, ca. 500-800 m east of nickel workings, ca. 1000 m alt., 21 Apr 1988, *R. R. Brooks et al. Braspex 165* (Holotype, SPF!; isotypes B!, MO!, NY!). Fig. 4.

Haec species a *Diphyomene urbaniana* (Ruhland) Trovó habitu humilioris (usque 35 cm vs. 65 cm), caulis tortis brevioris (usque 12 cm vs. 22 cm), folis acutis linearis, scapis per minus (usque 10 vs 200), inflorescentia obconica umbellata et scapis brevioris (usque 20 cm vs. 27 cm) differt.

Monocarpic herb, 24–35 cm long; rhizome present, aerial stem 0.3–1.0 cm long. Rosette leaves persistent, linear, flat, patent, 0.5–2.5 x 0.1–0.2 cm, glabrescent, margin ciliated to glabrescent, apex acute. Reproductive axis tortuous, 7.0–12.5 cm long, 0.2–0.3 cm diam., glabrous; axis bracts with same shape, chartaceous, lanceolate, sub-erect, 1.0–2.0 X 0.2–0.4 cm, glabrous, margin glabrous, apex acute, base semi-amplexicaul. Spathes 2.0–3.0 cm long, glabrous, apex acute. Scapes 3–10, arranged in an obconic umbel, 13.0–20.0 cm long, glabrous. Capitula 5–9 mm diam., semi-spherical, white; involucral bracts in 3–4 series, dark-brown, ovate, concave, ca. 3 mm long, glabrous, margin completely ciliated, apex acute; receptacle semi-spherical, hairy. Flowers dimerous, ca. 100 per capitulum, ca. 4 X more staminates than pistillates; floral bracts linear, light-brown, flat, ca. 3 mm long, hairy in abaxial surface to glabrescent, margin ciliated toward the apex to glabrescent, apex acute; flowers staminates ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown to golden, ca. 3 mm long, hairy in abaxial surface, margin glabrescent toward the apex, apex mucronate; fleshy antophore elongated;

corolla tubular, hyaline, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; Pistilate flowers ca. 3 mm, sessile, disposed in concentric rings; sepals dolabriform, white, ca. 3 mm long, hairy in the abaxial surface, margin glabrescent toward the apex, apex mucronulate; petals elliptic, hyaline, ca. 2 mm long, Hairy in abaxial surface, margin ciliated toward the apex to glabrescent, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red do brownish.

Paratypes—BRAZIL. Goiás, **Niquelândia**: 29 Apr 1988, *R. D. Reeves et al. Braspex 226* (MO, NY, SPF); 29 May 1996, *A. Silva and N. Jesus 2973* (HUEFS).

Phenology. Individuals of this species with staminate and pistillate flowers, and mature fruits were collected in April and May.

Distribution, Habitat, and Conservation Status. The few collections of *D. flexuosa* were all undertaken at Niquelândia, in typical savanna (Fig. 2), in a mountain belonging to a nickel-mining complex. From sheet labels, there are indications that the populations were no farther than five km from the mining center, thus possibly no longer existing. According to IUCN (2001) criteria the species is considered critically endangered (criteria B1a, B1b, B2a).

Etymology. The epithet "flexuosa" refers to the consistent, tortuous shape of the reproductive axis, a unique feature within the genus.

Commentaries. *Diphyomene flexuosa* is the most distinct species within the genus. The tortuous reproductive axis, small size of the plant, and relatively few scapes arranged in an obconic umbel, are useful for identification. A fieldtrip to the type locality was undertaken in March 2009, but without success, as no flowering individuals or sterile rosettes were to be found. As no recent collections are available, and the type locality is undergoing intense human impact, we stress the importance of further field-work to collect and preserve this species.

Diphyomene flexuosa and *Diphyomene urbaniana* (Ruhland) Trovó are morphologically the most alike. Both are relatively small species, with scapes longer than the reproductive axis. The size of the capitula and color of the involucral bracts are also shared characteristics. *Diphyomene flexuosa* can, however, be distinguished by the smaller habit and reproductive axis, linear leaves with acute apex, and fewer, smaller scapes arranged in a obconic-umbel. A detailed comparison is given in Table 3. *Diphyomene urbaniana* is restricted to the Chapada dos Veadeiros region. Although this is only 60 km from Niquelândia, the vegetation and soil of the two regions are different. *Diphyomene urbaniana* is spread among open grass on granitic soil, whereas *D. flexuosa* is present on argillaceous soil in typical savanna, whereby they cannot be considered sympatric.

Diphyomene hymenobracteata Trovó, sp. nov.—Type: BRAZIL. Goiás, Alto Paraíso de Goiás: Parque Nacional da Chapada dos Veadeiros, BR-010 entre Alto Paraíso de Goiás e Teresina de Goiás, entrada para o Morro do Cruzeiro do lado oposto da estrada, 19 Mar 2009, *M. L. O. Trovó et al. 465* (Holotype, SPF!; isotypes B!, NY!). Fig. 5.

Haec species a *Diphyomene decussa* (Koern.) Trovó habitu robustioris (usque 85 cm vs. 32 cm), caulis robustioris (usque 60 cm vs. 8 cm), bracteis caulinorum membranaceis, inflorescentia globosa umbellata, scapis glabris, capitulis obconicis et floris feminei punctuatis collocatis differt.

Monocarpic herb, 55–85 cm tall; rhizome present, aerial stem 1.0–2.5 cm long. Rosette leaves persistent or rarely deciduous, lanceolate, flat, patent, 8.0–13.0 X 0.5–1.0 cm, glabrous, margin glabrous, apex acute. Reproductive axis erect, 43.0–60.0 cm long., 0.5–1.0 cm diam., glabrous; axis bracts with same shape, membranaceous, lanceolate, erect to sub erect, 6.0–11.0 X 1.5–2.5 cm, glabrous, margin glabrous, apex acute, amplexicaul. Spathes 2.0–4.5 cm long., glabrous, apex acute. Scapes 40–405, arranged in a spherical umbel, 13.0–25.0 cm long, glabrous. Capitula 4–6 mm diam., obconic, white; involucral bracts in 3–4 series, brown, obovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 55 per capitulum, ca. 10 X more staminates than pistillates; floral bracts linear, light-brown, flat, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long., with long trichomes; sepals navicular, light-brown, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; Pistillate flowers ca. 3 mm, sessile, punctual disposed; sepals dolabriform, white, ca. 3 mm long., hairy in the abaxial surface apex and base, margin ciliated toward the apex, apex obtuse; petals elliptic, hyaline, ca. 2 mm long, hairy in abaxial surface, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruits and seeds not seen.

Paratype—BRAZIL. Goiás, **Alto Paraíso de Goiás**: 09 Apr 1995, *F. R. Lopes et. al. 350* (SPF); **Teresina de Goiás**: 22 May 2008, *J. M. Silva et. al. 6668* (MBM).

Phenology. Individuals with staminate flowers in full anthesis were collected in March, and those with mature pistillate flowers in April. Completely developed fruits were unavailable.

Distribution, Habitat, and Conservation status. *Diphyomene hymenobracteata* is endemic to the Chapada dos Veadeiros in the state of Goiás (Fig. 2), where it grows in open, grass-dominated savannas. Dense populations of over 100 individuals were observed both inside and outside the local national park. According to IUCN (2001) criteria, *D. hymenobracteata* is considered critically endangered (criteria B1a, B1b, B2a).

Etymology. The epithet "hymenobracteata" alludes to the reproductive axis bracts, with their membranaceous texture.

Commentaries. *Diphyomene hymenobracteata* is a very distinctive species. It possesses long membranaceous axis bracts and obconic capitula, as yet unreported for the genus. It also possesses an unusual punctual inner-capitulum arrangement of the pistillate flowers. The regular pattern within the genus is the ring-like formation of pistillate flowers. The pistillate flowers in the holotype were in an early stage of development, thus, certain measurements, as well as pilosity, may differ on maturing. During fieldwork, differences between herbarium specimens and living plants were detected, mostly as regards the shape and position of reproductive axis bracts. These, flat and erect in living plants, are recurvate and sub-erect in herbarium sheets.

As to the remaining species of the genus, morphologically *D. hymenobracteata* is closest to *D. decussa*. This is mainly so as regards the position and size of the axis bracts, the size of the spathes and scapes, and the persistent or rarely deciduous rosette leaves. *Diphyomene hymenobracteata* is easily distinguished by its robust habit and larger reproductive axis. This species also differs from *D. decussa* by its glabrous scapes arranged in a spherical umbel, membranaceous axis bracts, obconic capitula, and the unusual pistillate-flower punctual arrangement. A detailed comparison of these species is given in Table 4. Apart from morphological differences, the two species are allopatric, as the populations of both are separated by more than 1000 km, with *D. hymenobracteata* restricted to the Cerrado of central Brazil and *D. decussa* to mountains in the southern Espinhaço Range.

Diphyomene longiciliata Trovó, sp. nov.—Type: BRAZIL. Goiás, Niquelândia: Estrada para São Jorge, 14° 26' 17'' S/ 48° 09' 51'' W, 21 Mar 2009, *M. L. O. Trovó et al. 475* (Holotype, SPF!; isotype, B!). Fig. 6.

Haec species a *Diphyomene weddelliana* (Koern.) Trovó caulis robustioris (usque 35 cm vs. 10 cm), folis longioris (8.0 cm vs. 2.5 cm), scapis brevioris (usque 29 cm vs. 36 cm), bracteis caulinorum aequalis, ciliatis et amplexicaulis differt.

Monocarpic herb, 27–50 cm alt.; rhizome present, aerial stem 1.0–1.5 cm long. Rosette leaves persistent or deciduous, linear, flat, semi-erect to patent, 6.0–8.0 X 0.1–0.2 cm, hairy to glabrescent, margin ciliated, apex acute. Reproductive axis erect, 21.0–35.0 cm long, 0.3–0.5 cm diam., glabrous; axis bracts gradually smaller from the base to the apex, chartaceous, lanceolate, semi-erect to patent, 2.0–5.0 X 0.2–0.5 cm, glabrous, margin with long hairs, apex acute, base amplexicaul. Spathes 3.0–4.0 cm long, glabrous, apex acute. Scapes 5–6, arranged in an obconic umbel, 18.0–29.0 cm long, glabrous. Capitula 6–7 mm diam., semi-spherical, white; involucral bracts in 3–4 series, dark-brown, obovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; receptacle semi-spherical, hairy. Flowers dimerous, ca. 100 per capitulum, ca. 4 X more staminates than pistillates; floral bracts obovate, brown, concave, ca. 2 mm long, glabrous, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light brown to golden, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acuminate; fleshy antophore elongated; corolla fused, hyaline, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers ca. 3 mm, sessile, disposed in concentric rings; sepals dolabriform, white, ca. 3 mm long, hairy in abaxial surface apex and base, margin ciliated toward the apex to glabrescent, apex mucronate; petals elliptic, fleshy, ca. 2 mm long, hairy in abaxial surface, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, twice longer than the nectariferous branches; staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Paratype—BRAZIL. Goiás, **Niquelândia**: 22 May 1995, *C. Silva et al. 464* (HUEFS).

Phenology. Individuals of this species were collected with flowers and mature fruits between March and May.

Distribution, Habitat, and Conservation Status. Specimens were collected along the road from Alto Paraíso de Goiás to Niquelândia (Fig. 2). Individuals normally grow on exposed granitic soil, mingled with grasses. Small populations were encountered near to the Chapada dos Veadeiros National Park, in an area undergoing intense human impact. According to IUCN (2001) criteria, the species is considered critically endangered (criteria B1a, B1b, B2a).

Etymology. The epithet "longiciliata" refers to the long hairs on the margin of reproductive axis bracts. Many species in this genus present ciliated margins, although the hairs are usually short.

Commentaries. The most distinctive and unique feature of *D. longiciliata* is the long hairs interwoven with short ones on axis bract margin. Furthermore, these bracts are differently shaped throughout the reproductive axis, generally not the case with the other species. In some old bracts these long hairs may become deciduous, thereby complicating identification. In addition, long hairs and a similar habit is the case with some teratogenetic individuals of *D. chiquitensis* (eg. *M.L. Fonseca 2632*, SPF; *W.N. Fonseca 175*; SPF), whereat, the linear leaves and the relatively small number of scapes can be considered as useful diagnostic characteristics.

Morphologically *D. longiciliata* and *Diphyomene weddelliana* (Koern.) Trovó are the most alike. Both species are approximately the same size, with the same-sized capitula, linear leaves, and relatively few scapes. Furthermore, both may be sympatric. *Diphyomene weddelliana* is exclusively represented by the type-collection in an unspecified spot in the state of Goiás, where it grows on rocky soil. However, in *D. longiciliata* the reproductive axis and leaves are longer, and the scapes shorter. The axis bracts of *D. weddelliana* are all of the same shape, non-amplexicaul and unciliated. A detailed comparison of both species is given in Table 5.

Key To The Species Of *Diphyomene* In Central Brazil

1. Axis bracts with different shapes through the axis, becoming smaller from the base to the apex …………………………………………………………………………………………………. 2
  2. Basal leaves erect, apex mucronate, shorter than 5.5 cm; reproductive axis shorter than 10.0 cm ……………………………………………………..………………………… *D. brachycaule*
  2. Basal leaves patent to semi-erect, apex not mucronate, longer than 6.0 cm; reproductive axis longer than 21.0 cm …………………………………………………………………………………. 3
    3. Plants smaller than 50 cm tall; leaves shorter than 8.0 cm; reproductive axis shorter than 35.0 cm; margin of the axis bracts with long hairs; less than 10 scapes ………………………………………………………………………………….…….. *D. longiciliata*
    3. Plants greater than 65 cm tall; leaves longer than 9.0 cm; reproductive axis longer than 50.0 cm; margin of the axis bracts ciliated or glabrous; more than 30 scapes ……………………………………..………………...……………………...... *D. chiquitensis*
1. Axis bracts with the same shape through the axis, all with same size …………..…………….. 4
  4. Scapes longer than the reproductive axis …………………………………………………….…… 5
    5. Reproductive axis tortuous; scapes arranged in an obconic umbel; species restricted to Niquelândia ………………………………………………………………….…. *D. flexuosa*
    5. Reproductive axis erect; scapes arranged in a semi-spherical or spherical umbel; species restricted to Chapada dos Veadeiros …………………………………………………….…. 6
      6. Leaves lanceolate, uppermost series contort, apex mucronate; axis bracts lanceolate, semi-amplexicaul …….………………………………………………………….. *D. urbaniana*
      6. Leaves linear, patent, apex acute; axis bracts linear, not amplexicaul ……………………………………………………………………................... *D. weddelliana*
  4. Scapes shorter than the reproductive axis ……………………………………………………... 7
    7. Leaves oblong, apex cuspidate; axis bracts recurvate, cordate …………………..... *D. cordata*
    7. Leaves lanceolate, apex acute; axis bracts patent to erect or adpressed, lanceolate ……….. 8
      8. Axis bracts adpressed; capitula sulfurous ……………………………………….. *D. conferta*
      8. Axis bracts patent to erect; capitula white ……………………………………………….…. 9

9. Axis bracts membranaceous, erect to sub-erect; mature capitula obconic; pistillate flowers punctual disposed .... *D. hymenobracteata*

9. Axis bracts chartaceous, patent; mature capitula discoid to semi-spherical; pistillate flowers disposed in concentric rings 10

10. Plants smaller than 120 cm tall; leaves deciduous, shorter than 8.0 cm; reproductive axis smaller than 80.0 cm; scapes no more than 100; stigmatic branches twice longer than the nectariferous branches. .... *D. acanthophylla*

10. Plants greater than 125 cm tall; leaves persistent, longer than 13.0 cm; reproductive axis longer than 110.0 cm; scapes more than 130; stigmatic branches with the same size of the nectariferous branches .... *D. koernickei*

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We are grateful to Lívia Echternacht for help in elaborating the map and critical analysis of the manuscript. We also thank Leandro Assis, Matheus Fortes Santos, and Leonardo Borges for critical reading of the manuscript, and Daniel Borges for fieldwork facilities. Financial support: M.T. IAPT and Capes; PTS CNPq (proc. 309376/2006-8).

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Table 1. Morphological differences between *Diphyomene brachycaule* and *D. decussa**.

	Diphyomene brachycaule	*Diphyomene decussa*
Overall size (cm)	24.0–26.0	26.0–32.0
Leaves orientation	Erect	Patent
Leaves pilosity	Hairy	Glabrescent
Reproductive axis size (cm)	3.5–4.5	5.5–8.0
Axis bracts shape	All different	All the same
Scapes number	6–10	38–52
Scapes pilosity	Absent	Present
Capitula size (cm)	0.8–1.0	0.4–0.6
Apex of pistillate flower sepal	Mucronate	Obtuse

*Measurements of *Diphyomene decussa* are taken from the specimens in appendix 1.

Table 2. Morphological differences between *Diphyomene conferta* and *D. amoena*.

	Diphyomene conferta	*Diphyomene amoena*
Overall size (cm)	105.0–170.0	40.0–90.0
Leaves form	Lanceolate	Linear
Leaves width (cm)	0.7–1.4	0.1–0.2
Axis bracts orientation	Adpressed	Erect
Capitulum diameter (cm)	1.2–2.0	0.5–0.7
Capitula colour	Sulfurous	White

*Measurements of *Diphyomene amoena* are taken from the specimens in appendix 1.

Table 3. Morphological differences between *Diphyomene flexuosa* and *D. urbaniana**.

	Diphyomene flexuosa	*Diphyomene urbaniana*
Overall size (cm)	24.0–35.0	45.0–65.0
Reproductive axis size (cm)	7.0–12.0	17.0–22.0
Leaves form	Linear	Lanceolate
Leaves apex	Acute	Mucronate
Scapes number	3–10	110–200
Scapes size (cm)	13.0–20.0	17.0–27.0
Scapes arrangement	Obconic umbel	Spherical umbel

*Measurements of *Diphyomene urbaniana* are taken from the specimens in appendix 1.

Table 4. Morphological differences between *Diphyomene hymenobracteata* and *D. decussa**.

	Diphyomene hymenobracteata	*Diphyomene decussa*
Overall size (cm)	55.0–85.0	26.0–32.0
Reproductive axis size (cm)	43.0–60.0	5.5–8.0
Axis bracts texture	Membranaceous	Cartaceous
Scapes arrangement	Spherical umbel	Obconic umbel
Trichomes in scape	Absent	Present
Capitula form	Obconic	Spherical
Pistillate flower disposition	Punctual	Forming a ring

*Measurements of *Diphyomene decussa* are taken from the specimens in appendix 1.

Table 5. Morphological differences between *Diphyomene longiciliata* and *D. weddelliana**.

	Diphyomene longiciliata	*Diphyomene weddelliana*
Reproductive axis size (cm)	21.0–35.0	6.5–10.0
Scapes size (cm)	18.0–29.0	30.0–36.0
Leaves size (cm)	6.0–8.0	1.0–2.5
Axis bracts shape	All with different shape	All same shape
Axis bracts margin	Long ciliated	Glabrous
Axis bracts base	Amplexicaul	Not amplexicaul

*Measurements of *Diphyomene weddelliana* are taken from the specimens in appendix 1.

Appendix 1. Additional specimens studied.

Diphyomene amoena (Bong.) Trovó, Brazil, Minas Gerais: Nova Lima, 16.3.1933, *Barreto, M. 2520* (SPF); Belo Horizonte, 31.3.1933, *Barreto, M 2521* (SPF); Belo Horizonte, 31.5.1933, *Barreto, M. 2521a* (SPF); Nova Lima, 6.4.1934, *Barreto, M. 2493* (BHCB); Belo Horizonte, 26.4.1940, *Barreto, M. 10837* (BHCB); Belo Horizonte, 26.4.1940, *Barreto, M. 10837* (SPF); Ouro Preto, 28.1.1942, *Magalhães, M. 1216* (BHCB); Belo Horizonte, 1.5.1952, *Roth, B.L. 16579* (SPF); Belo Horizonte, 6.4.1970, *Duarte, A.P. 12740* (BHCB); Ouro Preto, 26.2.1987, *Stützel, T. et al. 65* (SPF); Ouro Branco, 15.5.1988, *Sá, R.A. et al. s.n.* (BHCB); Moeda, 28.3.1990, *Grandi, T.S.M. et al. s.n.* (SPF); Ouro Branco, 18.9.1990, *Alves, R.V Becker. J. 1507* (SPF); Itabirito, 5.3.1995, *Teixeira, W.A. s.n.* (SPF); Ouro Branco, 9.3.1995, *Souza, V.C. et al. 8027* (SPF); Itabirito, 12.7.2002, *Vianna, P.L. 714* (BHCB); Brumadinho, s.d, *s.c. 212* (SPF). ***Diphyomene decussa*** (Koern.) Trovó, Brazil, Minas Gerais: Ouro Preto, s.d., *Claussen, P. s.n.* (BR); Mariana, 4.4.2008, *Messias, M.C.T.B. 1963* (OUPR). ***Diphyomene urbaniana*** (Ruhland) Trovó, Brazil, Goiás: Alto Paraíso de Goiás, 23.3.1969, *Irwin, H.S. 24936* (RB); Alto Paraíso de Goiás, 15.3.1995, *Cavalcanti, T. 1382* (HUEFS); Alto Paraíso de Goiás, 17.2.2001, *Alves, M. 2271* (SPF); Alto Paraíso de Goiás, 23.1.2005, *Souza, J.P. 4519* (SPF); Alto Paraíso de Goiás, 3.12.2007, *Trovó, M.L.O. 435* (SPF); Alto Paraíso de Goiás, 5.12.2007, *Trovó, M.L.O. 447* (SPF); Alto Paraíso de Goiás, 20.3.2009, *Trovó, M.L.O. 467* (SPF). ***Diphyomene weddelliana*** (Koern.) Trovó, Brazil, Goiás: Goiás, *s.d.*, *Weddell 2927* (BR, P).

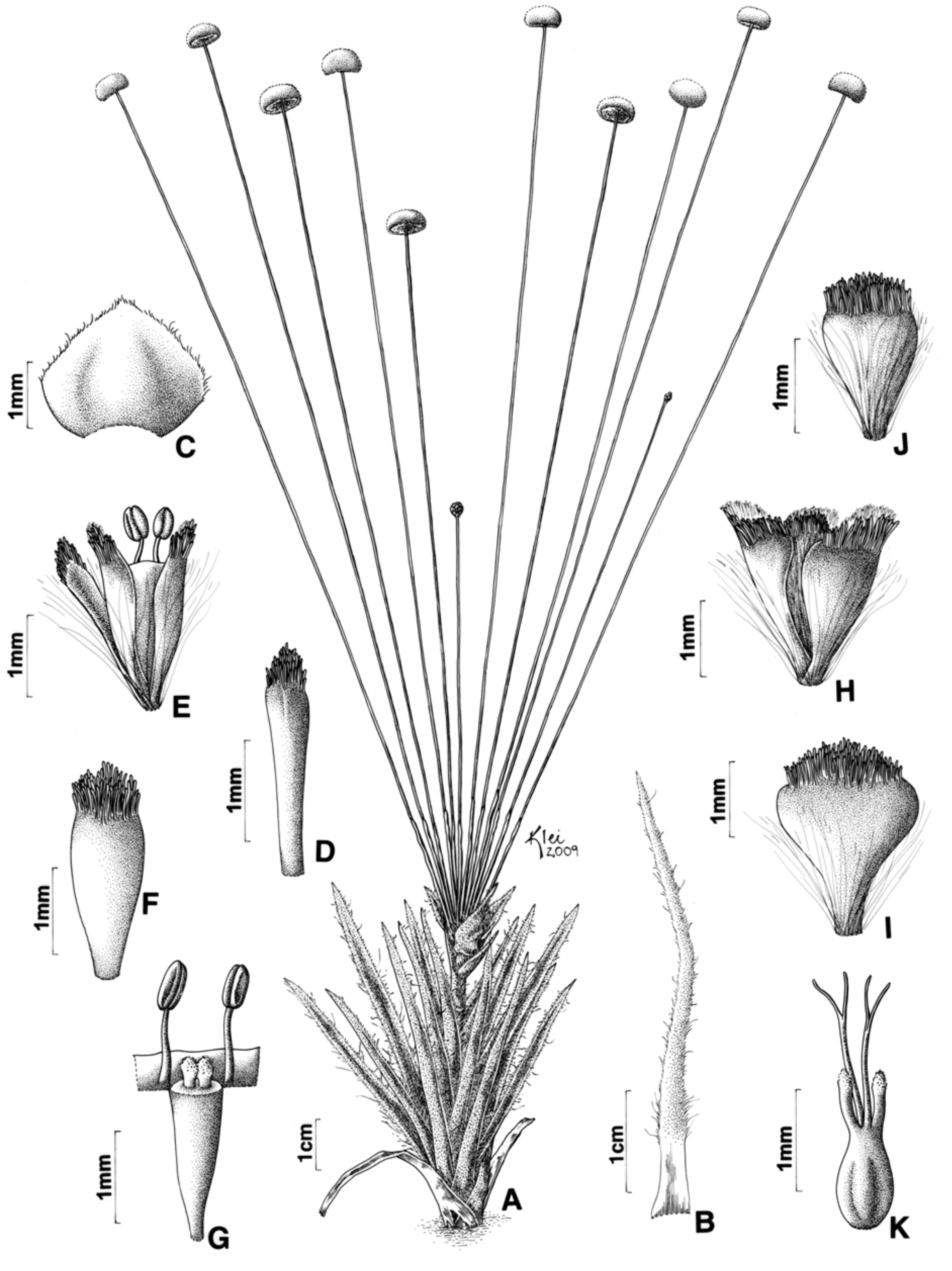

Fig. 1. *Diphyomene brachycaule* (from *Nobrega* & *Mendes 1187*). A. Habit. B. Leaf, detail. C. Involucral bract, abaxial surface. D. Floral bract, abaxial surface. E. Staminate flower. F. Sepal of the staminate flower. G. Staminate flower with sepals removed and opened corolla. H. Pistillate flower. I. Sepal of the pistillate flower. J. Petal of the pistillate flower. K. Gynoecium.

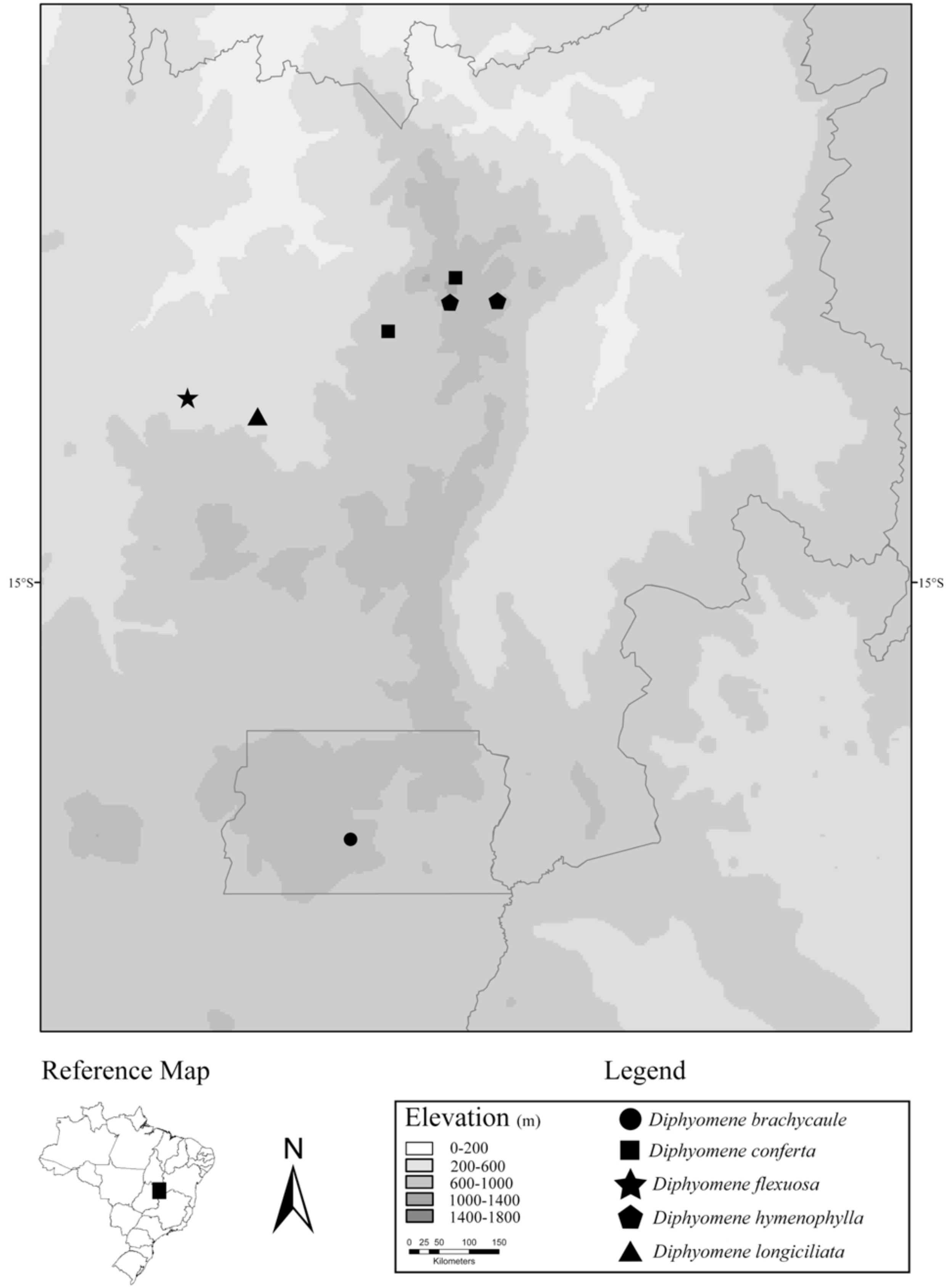

Fig. 2. Distribution map of *Diphyomene brachycaule*, *D. conferta*, *D. flexuosa*, *D. hymenobracteata*, and *D. longiciliata*.

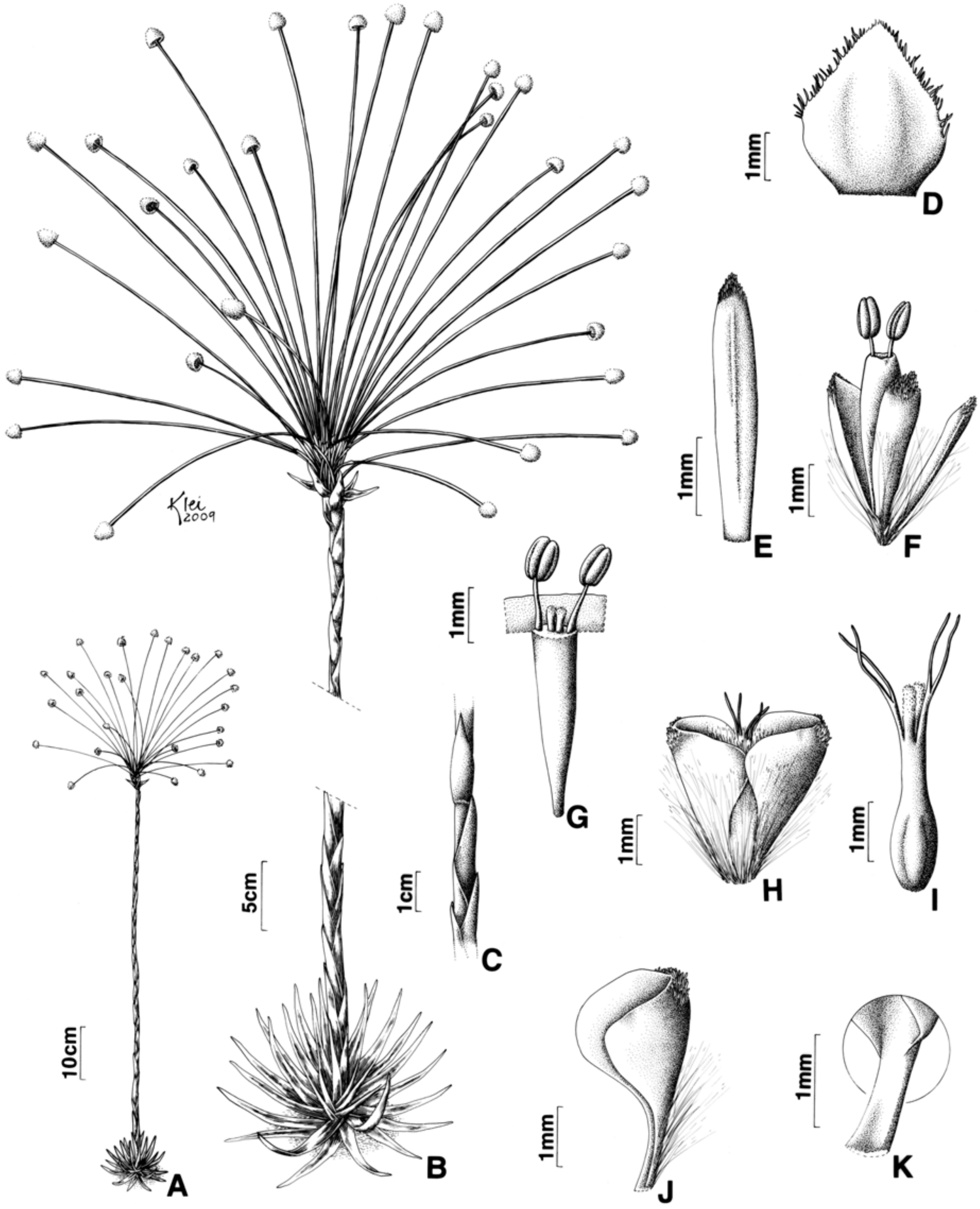

Fig. 3. *Diphyomene conferta* (from *Trovó* et al. *446*). A. Habit. B. Habit detail. C. Reproductive axis, detail. D. Involucral bract, abaxial surface. E. Floral bract, abaxial surface. F. Staminate flower. G. Staminate flower with sepals removed and opened corolla. H. Pistillate flower. I. Gynoecium. J. Sepal of the pistillate flower. K. Base of the sepal of the pistillate flower.

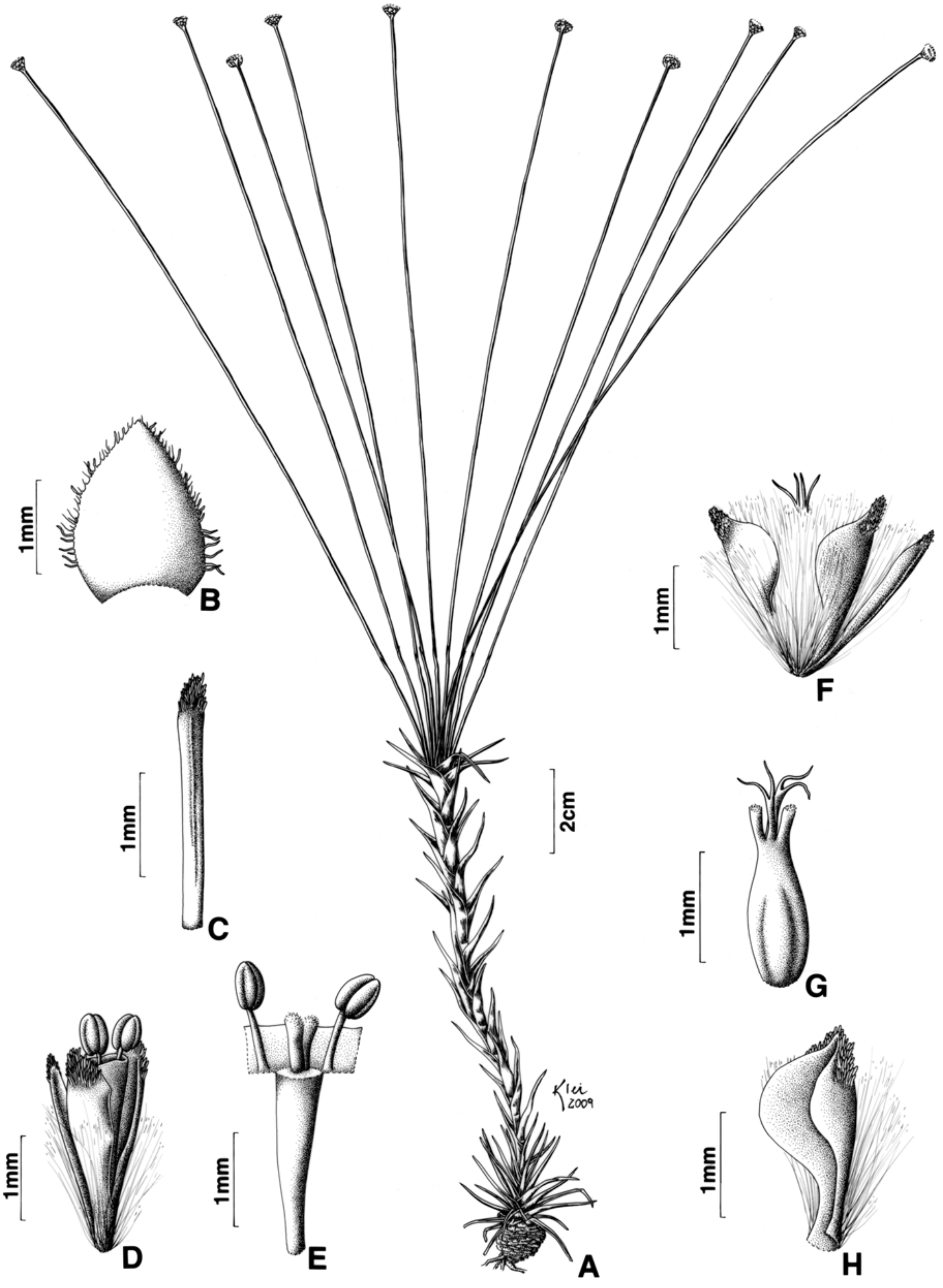

Fig. 4. *Diphyomene flexuosa* (from *Brooks* et al. *165*). A. Habit. B. Involucral bract, abaxial surface. C. Floral bract, abaxial surface. D. Staminate flower. E. Staminate flower with sepals removed and opened corolla. F. Pistillate flower. G. Gynoecium. H. Sepal of the pistillate flower.

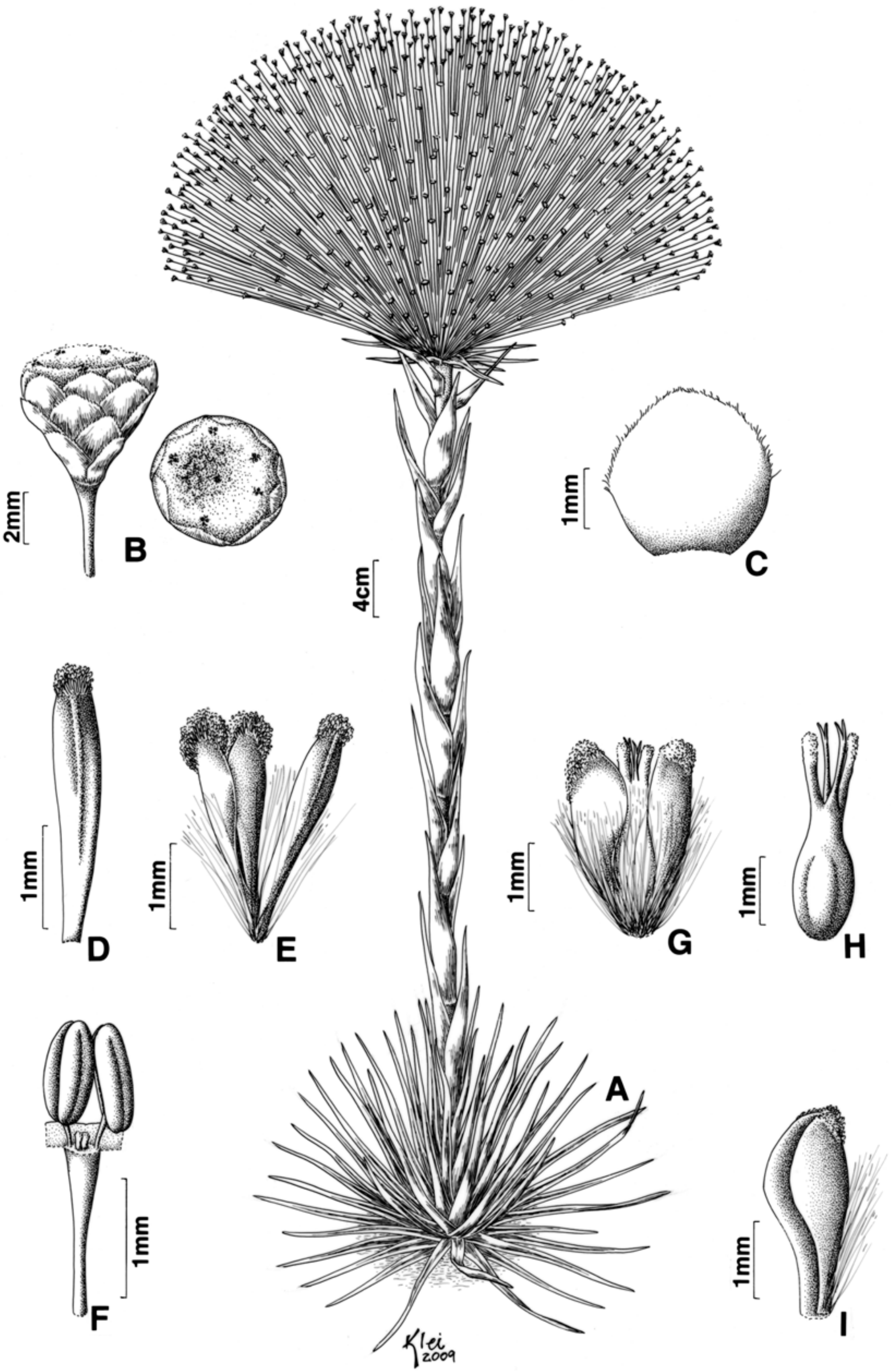

Fig. 5. *Diphyomene hymenobracteata* (from *Trovó* et al. *465*). A. Habit. B. Capitulum, lateral and upper view. C. Involucral bract, abaxial surface. D. Floral bract, abaxial surface. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower. H. Gynoecium. I. Sepal of the pistillate flower.

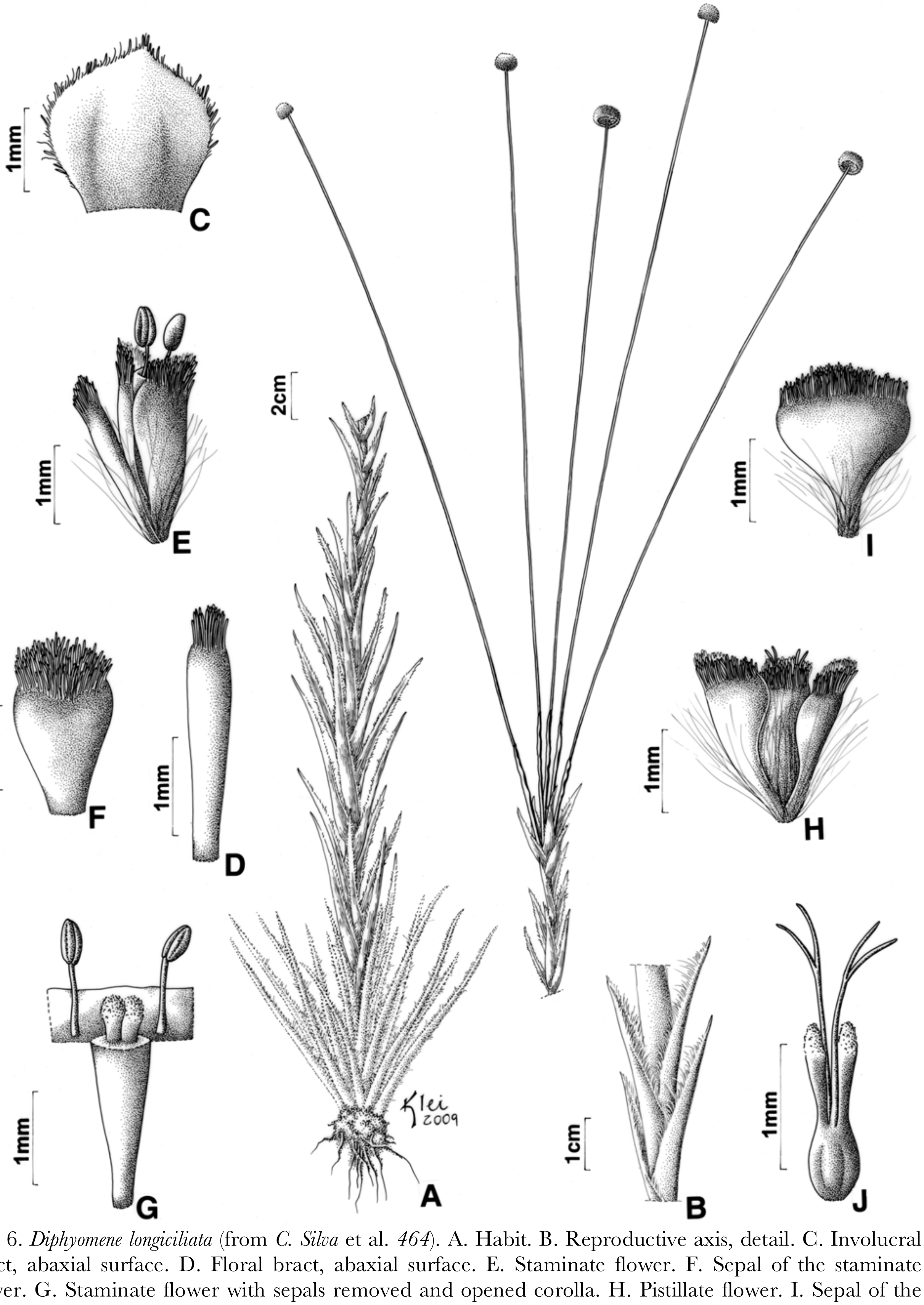

Fig. 6. *Diphyomene longiciliata* (from *C. Silva* et al. *464*). A. Habit. B. Reproductive axis, detail. C. Involucral bract, abaxial surface. D. Floral bract, abaxial surface. E. Staminate flower. F. Sepal of the staminate flower. G. Staminate flower with sepals removed and opened corolla. H. Pistillate flower. I. Sepal of the pistillate flower. J. Gynoecium.

Appendix II

Three new species of *Diphyomene* (Eriocaulaceae) from Minas Gerais, Brazil[7]

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Abstract - Three new species of *Diphyomene* (Eriocaulaceae) from Minas Gerais State (Brazil) are described and illustrated. **Diphyomene cipoensis** is restricted to the Serra do Cipó and morphologically similar to *Diphyomene decussa*. **Diphyomene sericoscapa** is restricted to the Serra da Canastra and morphologically related to *Diphyomene cipoensis*. **Diphyomene stenophylla** is endemic to Itacambira and morphologically similar to *Diphyomene polyclada*. As with other species of this genus, the distribution of the three is narrow. Morphological variation, habitat, geographic distribution, and conservation status are commented on.

Resumo - Descrevemos e ilustramos três novas espécies de *Diphyomene* (Eriocaulaceae) ocorrentes no Estado de Minas Gerais, Brasil. **Diphyomene cipoensis** é restrita a Serra do Cipó e é morfologicamente similar a *Diphyomene decussa*. **Diphyomene sericoscapa** é restrita a Serra da Canastra e é morfologicamente relacionada com *Diphyomene cipoensis*. **Diphyomene stenophylla** é endêmica de Itacambira e é morfologicamente similar a *Diphyomene polyclada*. Assim como a maioria das espécies do gênero estas, aqui descritas, são micro-endêmicas. Fazemos comentários sobre a variação morfológica, habitat, distribuição geográfica e status de conservação.

Key words: Brazil, Cerrado, IUCN Red List, Minas Gerais, Paepalanthoideae, *Paepalanthus*.

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[7] Manuscrito a ser submetido ao periódico Brittonia.

Diphyomene comprises 10 species distributed throughout South America. This genus is characterized by unique inflorescence structures and pistillate flowers with dolabriform sepals and completely reduced staminodes (Trovó & Sano, in press). Different from most of the Eriocaulaceae genera, *Diphyomene* species diversity is concentrated in the Cerrados of central Brazil, especially in the state of Goiás (Giulietti & Hensold, Stützel, 1998; 1990; Trovó & Sano, in press). In this region, the habitats occupied by these species are rocky soil grass savannas. The Espinhaço Range in Minas Gerais (Brazil) is a secondary center of diversity, where *Diphyomene* species occur in the Campos Rupestres. Within this genus and except for *Diphyomene chiquitensis* (Herzog) Trovó and *Diphyomene erectifolia* (Silveira) Trovó, the species are narrowly distributed, usually being restricted to one locality, or even one single mountain (Trovó & Sano, in press). As a result of fieldwork and revisionary studies, we describe the following three species.

Diphyomene cipoensis Trovó, **sp. nov.** TYPE: Brazil. Minas Gerais: Santana do Riacho, Parque Nacional da Serra do Cipó, MG 010, córrego duas pontinhas, 22 May 2007, *M. L. O. Trovó et al. 400* (holotype: SPF). (Fig. 1)

Ab *Diphyomene decussa* (Koern.) Trovó differt caulis glabris et brevioris 4.0 (non 5.5–8.0) cm, folis incurvatis, capitulis longioribus 0.7–8.0 (non 0.4–0.6) cm, sepalis florum feminorum apicis mucronatis.

Monocarpic herb, 32 cm tall; rhizome present, aerial stem 1.5 cm long. Leaves persistent, linear to lanceolate, incurvate, patent, 5.5–7.5 X 0.3–0.4 cm, hairy to glabrescent, margin ciliated, apex acute. Reproductive axis erect, 4.5 cm long, 0.5 cm diam., glabrous; axis bracts with same shape, chartaceous, linear, erects to sub-erect, 5.0–5.5 X 0.3–0.4 cm, glabrous, margin ciliated, apex acute, semi-amplexicaul. Spathes 4.0–5.0 cm long, glabrous, apex acute. Scapes 25, arranged in an obconic umbel, 21.0–27.5 cm long, sparsely hairy. Capitula 7–8 mm diam., discoid, white; involucral bracts in 3–4 series, light-brown, ovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 46 per capitulum, ca. 45 staminates and 1 pistillate; floral bracts linear, light-brown, flats, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown to golden, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute;

fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flower ca. 3 mm, sessile; sepals dolabriforms, light-brown, ca. 3 mm long., hairy in the abaxial surface base, margin ciliated toward the apex, apex mucronate; petals elliptic, light-brown, ca. 2 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruits and seeds not seen.

Phenology. A specimen with staminate flowers in full anthesis was collected in May. The single pistillate flower was in an early stage of development. Fruits and seeds were not observed.

Distribution, Habitat, and Conservation status. Diphyomene cipoensis, endemic to the Serra do Cipó in Minas Gerais (Fig. 2), grows in the rocky soils of campos rupestres. A single flowering individual was collected after a fire event; inside the Serra do Cipó National Park in an area widely explored by botanists. According to IUCN (2001) criteria, it is considered critically endangered (criteria B1a).

Etymology. The epithet "cipoensis" refers to the Serra do Cipó region, where the species was collected.

Commentaries. Diphyomene cipoensis turns out to be one of the smallest species within the genus. The species is only sympatric with *D. erectifolia*. The two are easily distinguished one from the other by the overall size, as the individuals of *D. erectifolia* are usually more than 1 m high. *Diphyomene cipoensis* is also distinguished from other species of the genus by its hairy scapes and incurvate leaves. The morphologically most similar species is *Diphyomene decussa* (Koern.) Trovó. The scapes in both are arranged in an obconic umbel and the reproductive axis bracts are of the same shape. The overall size and the size of the hairy scapes are the same in both. However, *D. cipoensis* presents striking differences, such as the shorter and glabrous reproductive axis, incurvate leaves, longer spathes, wider capitula, and the mucronate apex of pistillate flowers. Moreover, *D. decussa* occurs exclusively near to the town of Ouro Preto (Minas Gerais, Brazil), thus the two are allopatric. A detailed comparison of these two species is given in Table 1.

Diphyomene sericoscapa Trovó, **sp. nov.** TYPE: Brazil. Minas Gerais: São Roque de Minas, Parque Nacional da Serra da Canastra, Chapadão do Diamante, 16 Jul 1995, *Romero, R. et al. 2464* (holotype: SPF; isotype: HUFU). (Fig. 3)

Ab *Diphyomene cipoensis* Trovó & Sano differt folis planis et brevioris 1.5–2.0 (non 5.5–7.5) cm, bracteis caulinorum lanceolatis et breviores 2.5–3.5 (non 5.0–5.5) cm, scapis pilis sericis et breviores 13.5–15.0 (non 21.0–27.5) cm, floris feminei pedicelatis.

Monocarpic herbs, 15–20 cm tall; rhizome absent, aerial stem 0.5 cm long. Leaves persistent, lanceolate, flat, patent, 1.5–2.0 X 0.4–0.6 cm, glabrous, margin glabrous, apex acute. Reproductive axis erect, 3.5–4.0 cm long, 0.5 cm diam., glabrous; axis bracts with same shape, cartaceous, lanceolate, sub-erect, 2.5–3.5 X 0.3–0.5 cm, glabrous, margin ciliated, apex acute, semi-amplexicaul. Spathes 2.5–3.0 cm long, glabrous, apex acute. Scapes 11–17, arranged in an obconic umbel, 13.5–15.0 cm long, sericeous. Capitula 7–9 cm diam., discoid to obovate, white; involucral bracts in 3–4 series, light-brown, ovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute to obtuse; receptacle semi-spherical, hairy. Flowers dimerous, ca. 180 per capitulum, ca. 150 staminates and 30 pistillates; floral bracts linear, brown, flats, ca. 2 mm long, glabrous, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flower ca. 3 mm, pedicel 3 mm; sepals dolabriforms to navicular, light-brown, ca. 3 mm long., glabrous, margin ciliated toward the apex, apex acute; petals elliptic, hyaline, ca. 1mm long, glabrous, margin ciliated toward the apex, apex rounded; gynoecium ca. 1 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruits and seeds not seen.

Phenology. Individuals with staminate flowers in anthesis were collected in July. The pistillate flowers were in an early stage of development. Fruits and seeds were not encountered.

Distribution, Habitat, and Conservation status. Diphyomene sericoscapa, endemic to the Serra da Canastra National Park (Fig. 2), occurs mingled with grass in Campos Rupestres. According to IUCN (2001) criteria, *D. sericoscapa* is considered critically endangered (criteria B1a).

Etymology. The epithet "sericoscapa" refers to the distinctive densely orientated pilosity of the scapes.

Commentaries. The sericeous scapes of *Diphyomene sericoscapa* are generically unique. Actually, except for *D. decussa* and *D. cipoensis*, both with sparse scape pilosity, the remaining *Diphyomene* species possess glabrous scapes. The short pistillate-flower pedicels and the navicular to dolabriform petals of the pistillate flower itself are also remarkable. This species is sympatric with *D. polyclada* and *D. chiquitensis*, although, these are relatively larger, and have glabrous scapes.

Diphyomene sericoscapa is morphologically related to *D. cipoensis.* They are two of the smallest species within the genus, with very short reproductive axis. Capitula width and the obconic scape arrangement are also alike. Apart from the hairy scapes and the floral characteristics stated above, *D. sericoscapa* is distinguished from *D. cipoensis* by its shorter, flat leaves and reproductive axis bracts. A detailed comparison of the two is given in Table 2.

Diphyomene stenophylla Trovó, **sp. nov.** TYPE: Brazil. Minas Gerais: Itacambira, Plantar MG 15 - Fazenda Tamanduá, 10 Apr. 2005, *E. Tameirão Neto 4216* (Holotype: SPF; isotype: BHCB). (Fig. 4)

Ab *Diphyomene polyclada* (Silveira) Trovó differt folis linearis et erectis, spathis brevioris 2.0–3.5 (non 3.5–8.0) cm, capitulis brevioris 0.6–0.8 (non 0.8–1.2) cm, sepalis florum feminorum apicis mucronatis, petalis dorso apicis et ceterum pilosis, et ramis stilorum et nectariorum aequantes.

Monocarpic herbs, 51–60 cm tall; rhizome present, aerial stem 0.5–1.5 cm long. Leaves deciduous, linear, flat, semi-erect, 3.5–13.0 X 0.1–0.2 cm, hairy to glabrescent, margin ciliated, apex acute. Reproductive axis erect, 31.0–40.0 cm long, 0.4 cm diam., glabrous; axis bracts with same shape, cartaceous, linear to lanceolate, erects to sub-erect, 2.0–4.0 X 0.2–0.4 cm, glabrous, margin glabrous, apex acute, semi-amplexicaul. Spathes 2.0–3.5 cm long, glabrous, apex acute.

Scapes 25–53, arranged in a semi–spherical umbel, 21.0–25.5 cm long, hairy toward the apex. Capitula 6–8 cm diam., semi-spherical, white; involucral bracts in 4–5 series, brown, ovate, concave, ca. 3 mm long, glabrous, margin ciliated toward the apex, apex acute; receptacle semi-spherical, hairy. Flowers dimerous, ca. 320 per capitulum, ca. 240 staminates and 80 pistillates; floral bracts linear, light-brown, flats, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; staminate flowers ca. 3 mm long; pedicel ca. 0.5 mm long, with long trichomes; sepals navicular, light-brown to golden, ca. 3 mm long, hairy in abaxial surface apex, margin ciliated toward the apex, apex acute; fleshy antophore elongated; corolla fused, hyalines, membranaceous, ca. 1 mm long; stamens ca. 1 mm long; pistilodes 2, papillose; pistillate flowers ca. 3 mm, sessile, disposed in concentric rings; sepals dolabriforms, light-brown to gold, ca. 3 mm long., hairy in the abaxial surface base, margin ciliated toward the apex, apex mucronate; petals elliptic, light-brown to golden, ca. 2 mm long, hairy in abaxial surface base, margin ciliated toward the apex, apex rounded; gynoecium ca. 2 mm long, stigmatic branches bifid, with the same size of the nectariferous branches, staminodes completely reduced. Fruit a loculicidal capsule. Seeds ca. 1 mm long, reticulate surface, red to brownish.

Phenology. Individuals with staminate and pistillate flowers in full anthesis were collected in April. Fruits were collected in October.

Distribution, Habitat, and Conservation status. *Diphyomene stenophylla* is restricted to a single locality in the mountains to the north of the Espinhaço Range in Minas Gerais (Fig. 2). The two collections came from the same population, in grass dominated open savanna. According to IUCN (2001) criteria, *D. stenophylla* is considered critically endangered (criteria B1a, B1b, B2a).

Etymology. The epithet "stenophylla" refers to the linear leaves, usually deciduous in mature individuals.

Additional specimen examined. BRAZIL. Minas Gerais. Itacambira, Plantar MG 15 - Fazenda Tamanduá, 09 Oct. 2005, *E. Tameirão Neto 4052* (SPF, BHCB).

Commentaries. Diphyomene stenophylla is the only species of the genus that occurs in the northern portion of the Espinhaço Range in Minas Gerais. It can be distinguished from congeneric species by the unusually erect and linear leaves. In *Diphyomene amoena* (Bong.) Trovó, another species from Minas Gerais, the leaves are also linear, although in this case they are relatively smaller and patent. Both are allopatric, as *D. amoena* is confined to the south of the Espinhaço Range.

Diphyomene stenophylla and *Diphyomene polyclada* (Silveira) Trovó are morphologically alike. The reproductive axis and scapes of both are of approximately the same relative size, and both have deciduous leaves. On the other hand, *D. stenophylla* is distinguished by its erect and linear leaves, and the size of both spathes and capitula, besides the following features in pistillate flowers: sepals with mucronate apex, petals hairy at the base, and stigmatic branches of the same size as nectariferous. They are allopatric, as *D. polyclada* is endemic to the Serra da Canastra National Park. A detailed comparison of the two is given in Table 3.

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Table 1. Morphological differences between *Diphyomene cipoensis* and *Diphyomene decussa**.

	Diphyomene cipoensis	*Diphyomene decussa*
Reproductive axis size (cm)	4.5	5.5–8.0
Leaves transversal position	Incurvate	Flat
Spathes size (cm)	4.0–5.0	3.0–4.0
Capitula width (cm)	0.7–0.8	0.4–0.6
Apex of the pistillate flower sepal	Mucronate	Obtuse

*Measurements of *Diphyomene decussa* are taken from the specimens in appendix 1.

Table 2. Morphological differences between *Diphyomene sericoscapa* and *Diphyomene cipoensis*.

	Diphyomene sericoscapa	*Diphyomene cipoensis*
Leaves transversal position	Flat	Incurvate
Leaves size (cm)	1.5–2.0	5.5–7.5
Axis bracts form	Lanceolate	Linear
Axis bracts size (cm)	2.5–3.5	5.0–5.5
Scapes size (cm)	13.5–15	21.0–27.5
Scapes hairs	Sparse	Sericeous
Pedicel of the pistillate flower	Present	Absent

Table 3. Morphological differences between *Diphyomene stenophylla* and *Diphyomene polyclada**.

	Diphyomene stenophylla	*Diphyomene polyclada*
Leaves form	Linear	Lanceolate
Leaves orientation	Erect	Patent
Spathes size (cm)	2.0–3.5	3.5–8.0
Capitula size (cm)	0.6–0.8	0.8–1.2
Apex of the pistillate flower sepal	Mucronate	Obtuse
Hairs of pistillate flower sepal	Restricted to the base	Apex and center
Stigmatic branches/nectariferous branches	Same size	Twice longer

*Measurements of *Diphyomene polyclada* are cited from the specimens in appendix 1.

Appendix 1. Additional specimens used for morphological comparisons.

Diphyomene decussa (Koern.) Trovó, Brazil, Minas Gerais: Ouro Preto, s.d., *Claussen, P. s.n.* (BR); Mariana, 4 Apr 2008, *Messias, M.C.T.B. 1963* (OUPR). ***Diphyomene polyclada*** (Silveira) Trovó, Brazil, Minas Gerais: São Roque de Minas, 18 Abr 1982, *Castro 306* (SPF); 18 Abr 1982, *Castro 307* (SPF); 16 Abr 1994, *Romero et al. 844* (SPF); 18 Mar 1995, *Nakajïma et al. 867* (SPF); 18 Mar 1995, *Nakajïma et al. 882* (SPF); 10 Mai 1995, *Nakajïma et al. 1009* (SPF); 11 Mai 1995, *Romero et al. 2219* (SPF); 15 Jul 1995, *Romero et al. 2420* (SPF); 18 Jul 1995, *Nakajïma et al. 1257* (SPF); 28 Set 1995, *Romero et al. 2995* (SPF); 19 Mar 1998, *Sano et al. 942* (SPF);15 Mai 2007, *Trovó & Watanabe 391* (SPF).

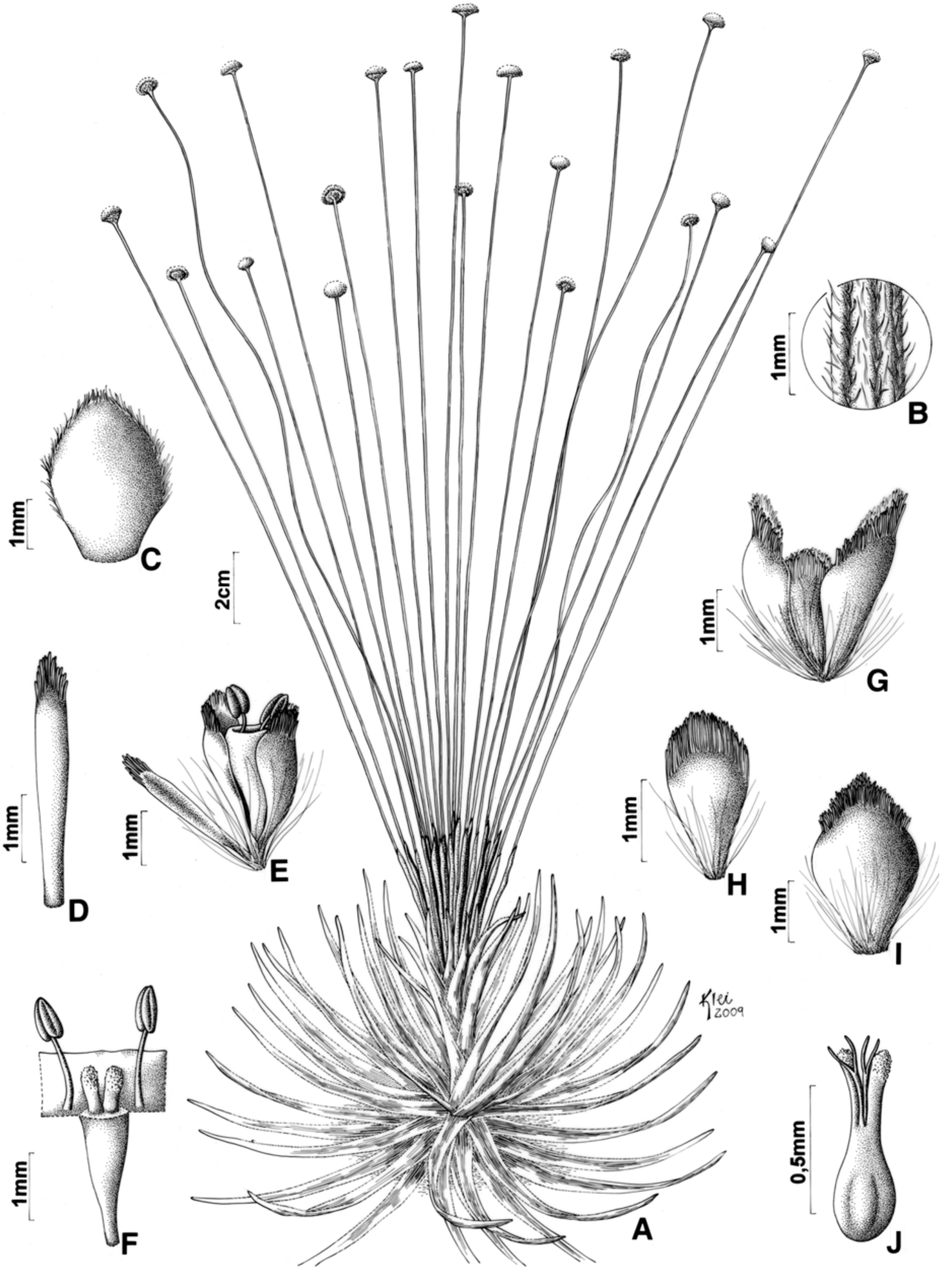

Figure 1. *Diphyomene cipoensis* (from *Trovó* et al. *400*). A. Habit. B. Scape detail. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower (juvenile). H. Petal of the pistillate flower. I. Sepal of the pistillate flower. J. Gynoecium.

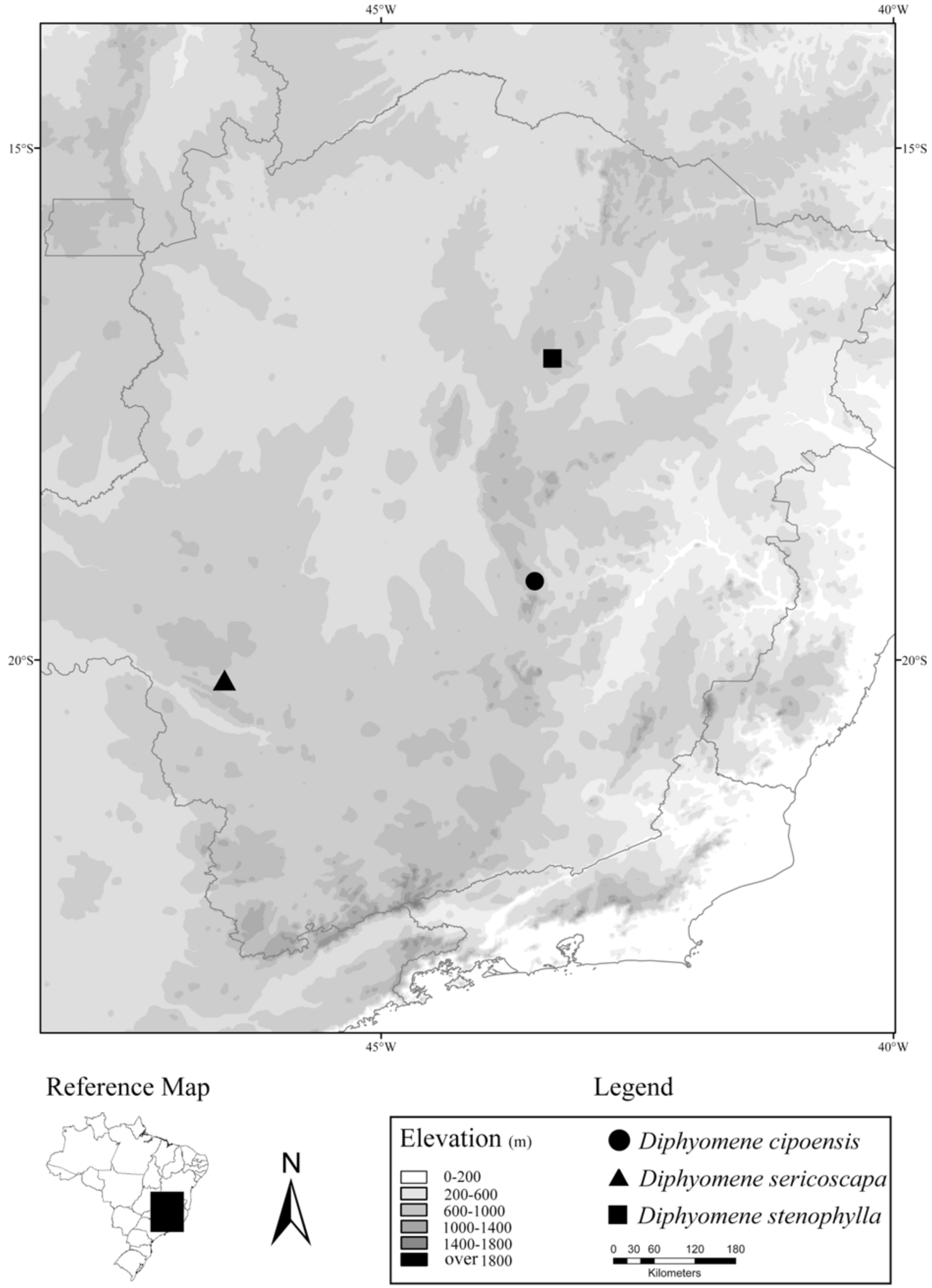

Figure 2. Distribution map of *Diphyomene cipoensis*, *Diphyomene sericoscapa*, and *Diphyomene stenophylla*.

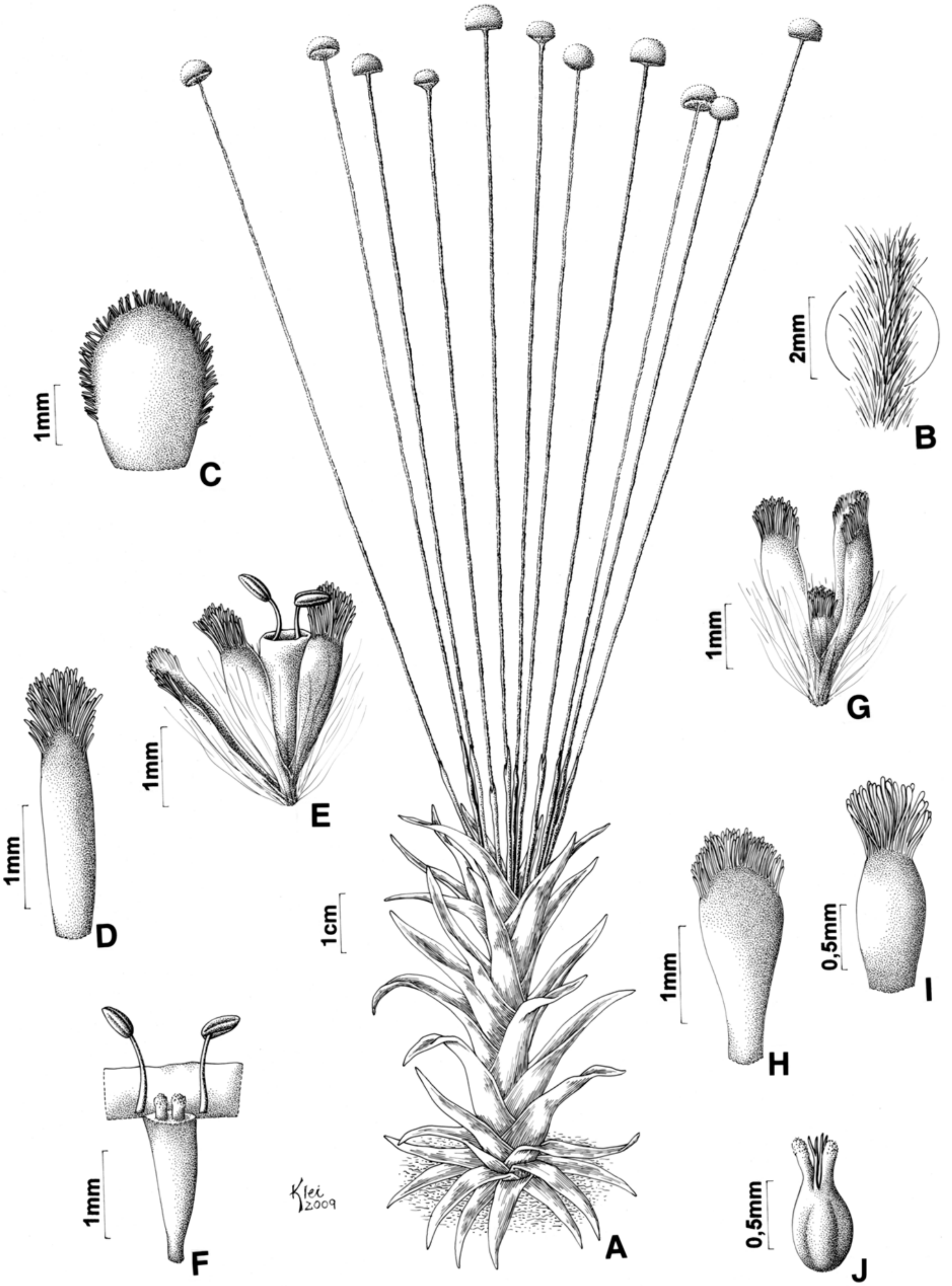

Figure 3. *Diphyomene sericoscapa* (from *Romero* et al. *2464*). A. Habit. B. Scape detail. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Pistillate flower (juvenile). H. Sepal of the pistillate flower. I. Petal of the pistillate flower. J. Gynoecium.

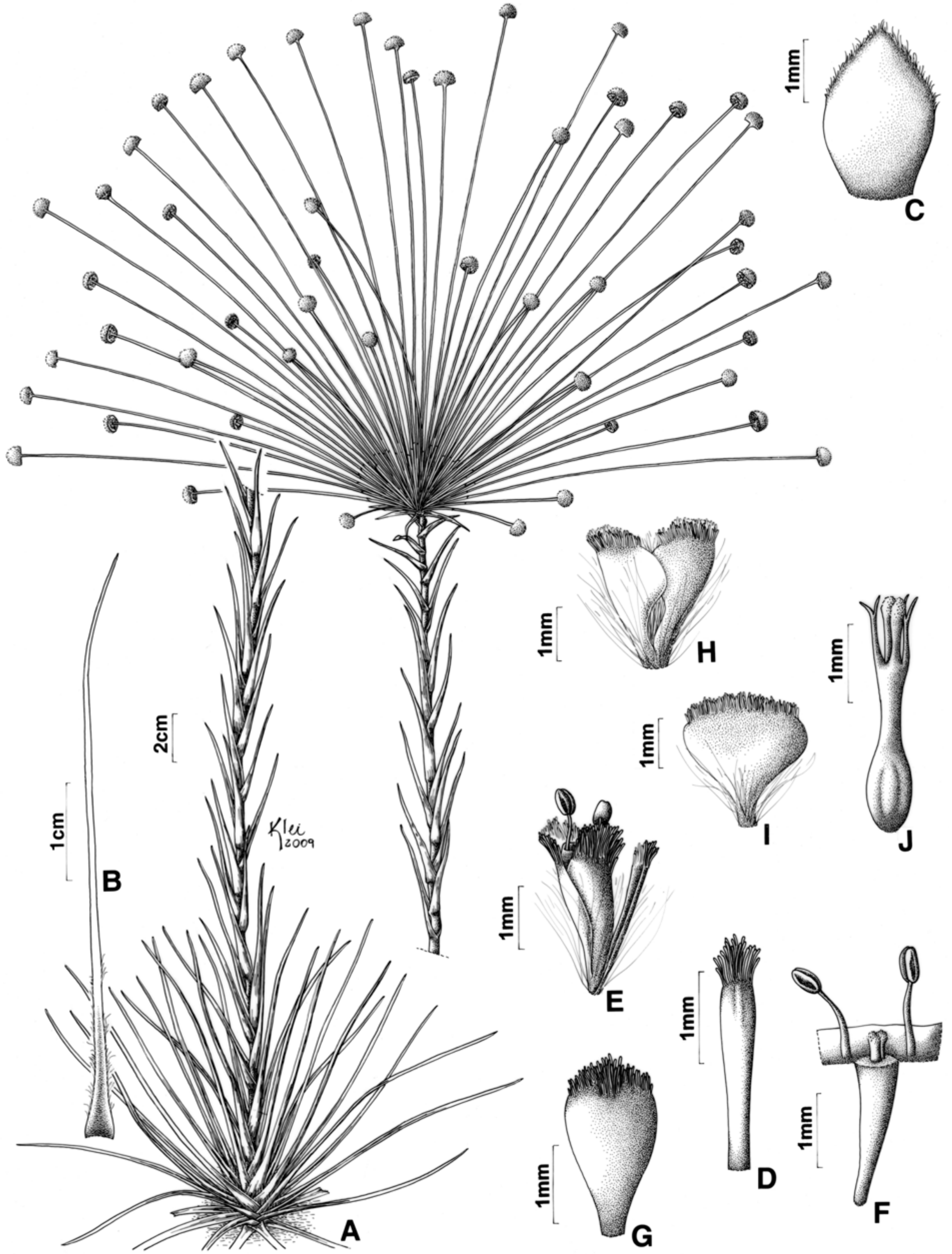

Figure 4. *Diphyomene stenophylla* (from *Tameirão Neto 4216*). A. Habit. B. Leaf detail. C. Involucral bract abaxial surface. D. Floral bract abaxial surface. E. Staminate flower. F. Staminate flower with sepals removed and opened corolla. G. Sepal of the staminate flower. H. Pistillate flower. I. Sepal of the pistillate flower. J. Gynoecium.

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