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BULBOSTYLIS (CYPERACEAE): FILOGENIA, ESPÉCIES NOVAS E CHAVE DE IDENTIFICAÇÃO ILUSTRADA PARA OS TÁXONS SUL-BRASILEIROS

Rodrigo Endres Ardissone

Tese apresentada ao Programa de Pós-Graduação em Botânica da Universidade Federal do Rio Grande do Sul, como parte dos requisitos para obtenção do título de Doutor em Ciências, ênfase Botânica.

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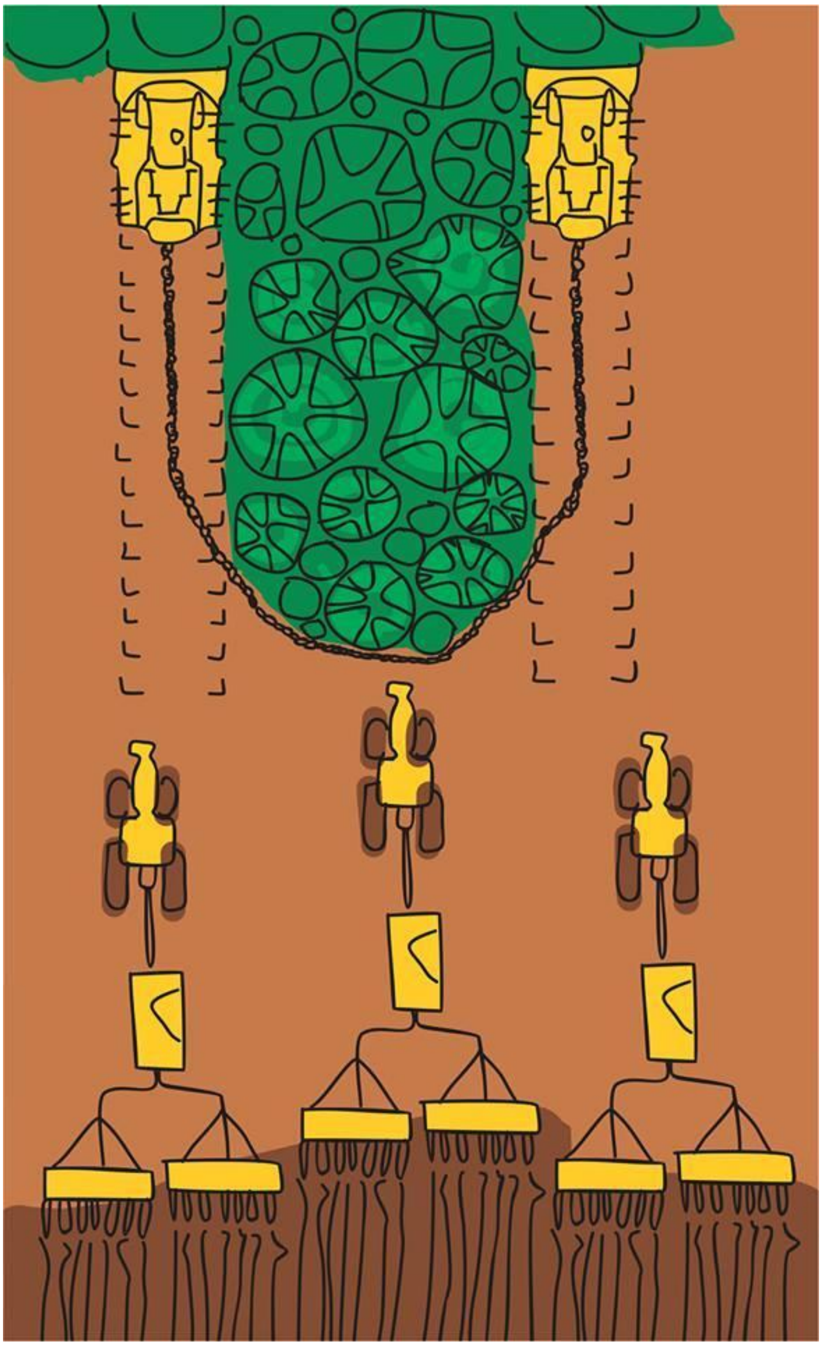

O avanço do retrocesso...

Máquinas de morte e plantadeiras de veneno.

Ilustração digital, 2018

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SUMÁRIO

RESUMO

Bulbostylis é um gênero parafilético de plantas heliófilas de pequeno porte, aspecto graminóide e hábito normalmente cespitoso, com a maioria de suas espécies adaptadas a ambientes secos. O gênero tem riqueza aproximada de 220 espécies, com distribuição pantropical e com centros de diversidade na África e no Brasil. A acentuada semelhança morfológica entre grande parte das espécies de *Bulbostylis* está associada a variações morfológicas ao longo de uma distribuição geográfica ampla, o que torna identificação de amostras do gênero dependente de chaves dicotômicas e imagens com alto detalhamento. A redução ou ausência de partes florais, característica da família, tem como implicação uma taxonomia apoiada na análise minuciosa da morfologia dos aquênios. Distinguimos *Bulbostylis* dos demais gêneros da tribo Abildgaardieae por suas espécies possuirem lâminas foliares com até 0.5 mm de largura, ápice das bainhas foliares com tricomas, células da superfície do aquênio alongadas longitudinalmente em relação ao corpo do aquênio e estilopódio persistente no ápice. Aqui trazemos a primeira filogenia molecular com foco em *Bulbostylis*; a descrição de duas espécies novas, *Bulbostylis divaricata* e *Bulbostylis scabriculmis*; a ampliação da distribuição de *Bulbostylis rugosa* e *Bulbostylis contracta*; e uma chave de identificação para as espécies sul-brasileiras com imagens em microscopia eletrônica de varredura dos aquênios. Os resultados estão apresentados em três capítulos, sendo cada um adequado às normas para publicação em revistas científicas pertinentes.

Palavras-chave—Taxonomia, América do Sul, monocotiledôneas, Abildgaardieae, MEV – microscopia eletrônica de varredura, biologia molecular, filogenia.

ABSTRACT

Bulbostylis is a paraphyletic genus of small heliophitic plants, with graminoid appearance and a usually cespitose habit. Most of its species are adapted to dry environments. The genus comprises 220 species with a pantropical distribution and centers of diversity in Africa and Brazil. The morphological similarity between most of the species currently classified as *Bulbostylis* isassociated with variations in the morphology of species along a large geographic distribution, makes the identification dependent of identification keys and images with high detail. The reduction or absence of floral pieces, characteristic in the family, has as implication a taxonomy based on the detailed analysis of achene morphology. Bulbostylis is different from other genera of the tribe Abildgaardieae because their species have leaf blades up to 0.5 mm wide, apex of foliar sheaths with trichomes, cells of the achene surface longitudinally elongated in relation to achene body and stylopodium persistent on the achene apex. Here we present the first molecular phylogeny focused in *Bulbostylis*; the description of two new species, *Bulbostylis divaricata* and *Bulbostylis scabriculmis*; the enlargement of distribution of two other species, *Bulbostylis rugosa* and *Bulbostylis contracta*; and an identification key illustrated with images generated with scanning electron microscopy of achenes for the species of Southern Brazil. The results are presented in three chapters, each adapted to the standards for publication of articles in relevant scientific journals.

Keywords—Taxonomy, South America, monocotyledons, Abildgaardieae, SEM - scanning electron microscopy, molecular biology.

INTRODUÇÃO

AS CIPERÁCEAS

Frequentemente associada a ambientes úmidos e com distribuição cosmopolita, a família Cyperaceae Juss. *nom. cons.* figura como a terceira mais rica entre as monocotiledôneas e a décima entre as angiospermas, com aproximadamente 5680 espécies alocadas em 98 gêneros (Govaerts et al. 2016). *Carex* L. é o maior gênero em riqueza, com aproximadamente 2000 espécies, seguido por *Cyperus* L., onde o número de espécies varia bastante conforme a circunscrição (Muasya et al. 2002; Larridon et al. 2011a, b; Hinchcliff & Roalson 2013) e seguramente é maior do que 500. A classificação supragenérica dentro da família diverge nos trabalhos mais recentes, com 14 tribos e quatro subfamílias (Goetghebeur 1998) ou duas subfamílias (Muasya et al. 2009). Cyperaceae compõe um clado dentro da ordem Poales juntamente com a Juncaceae Juss. *nom. cons.*, considerado seu grupo irmão. Dados moleculares e morfológicos suportam Cyperaceae como monofilética e dividida em duas subfamílias: Cyperoideae Beilschmied, cosmopolita e expressivamente mais rica que Mapanioideae C. B. Clarke, restrita aos trópicos. Dentre os gêneros da família, 1/3 são monotípicos, ¼ possuem de 2 a 5 espécies, outros 7 (cerca de 6%) têm mais de 200 espécies cada e o restante com o número de espécies entre 6 e 200 (Muasya et al. 2009, APWeb 2017). *Bulbostylis* está classificado na tribo Abildgaardieae, que como boa parte da família passa por um momento de instabilidade taxonômica, evidenciada em trabalhos recentes, como o de Ghamkhar et al. (2007), a filogenia apresentada no primeiro capítulo desta tese e o levantamento de Govaerts et al. (2007), esse último abrangente a toda família.

As ciperáceas se distinguem macromorfologicamente das demais famílias botânicas pela estrutura floral diminuta e pobre, o perianto ausente, reduzido ou modificado em cerdas ou escamas, o pequeno número de estames (1-3), e o óvulo único por ovário. Características importantes no nível microscópico incluem pólen do tipo pseudomônade, mais frequente, ou tipo “mapania” (Simpson et al. 2003), os cromossomos holocinéticos, e os corpos silicosos distribuídos nos diferentes órgãos das plantas. Estes caracteres também conferem singularidade à família e têm grande valor taxonômico. As espécies da família apresentam polinização anemófila, entomófila ou ambofila e dispersão anemocórica, hidrocórica ou atelocórica (Lye 2000, Costa et al. 2012).

Em relação à importância histórica, formas rudimentares de papel (papiro), no Egito antigo, eram confeccionadas a partir de fibras de *Cyperus papyrus* L (Figura1). Outros usos que se destacam são o alimentício, como matéria prima para artesanato (Figura 2) (MacÍa & Balslev 2000, Hurtado et al. 2011), na ornamentação de lagos e jardins, na perfumaria, como medicinal e na recuperação de áreas degradadas. Ao mesmo tempo, as ciperáceas são alvo de toda uma literatura voltada à sua erradicação, e são tratadas como pragas a serem combatidas com agroquímicos específicos às custas do envenenamento do solo, da água e do alimento.

Figura 1 a., b. Ciperáceas ornamentais. a. *Cyperus papyrus* L. de uso milenar na confecção de papiro, hoje com importância econômica devido á difusão como ornamental. b. Sombrinha-chinesa (*Cyperus alternifolius* L.) Fotos: a. disponível em https://horomidis.gr/product/cyperus-papyrus-%CF%80%CE%B1%CF%80%CF%85%CF%81%CE%BF%CF%83/?lang=en

e b. em http://www.plantmaster.com/share/eplant.php?plantnum=206

Figura 2 a-c. Uso tradicional de ciperáceas na alimentação e no artesanato. a. ‘Chufas’ e ‘horchata de chufas’. As ‘chufas’ são produzidas a partir dos bulbos desidratados de *Cyperus esculentus* L e ‘horchata de chufas’ é uma bebida preparada com esse ingrediente, tradicional na Espanha. b. ‘Horchateria de Santa Catalina’, comércio especializado em sevir horchatas há mais de dois séculos em Valencia, Espanha. c. Artesanato equatoriano a partir de colmos de totora, que no Brasil é conhecida como junco [(*Schoenoplectus californicus* (C.A.Mey.) Soják] de grande importância cultural e econômica para povos originários e tradicionais da América Latina. Fotos: a - b disponíveis em https://www.easyvoyage.co.uk/spain/l-horchata-de-chufa-6336; c em https://lampa.evisos.cl/aresania-en-totora-esteras-id-573110

O GÊNERO BULBOSTYLIS, DOS POPULARES CABELOS-DE-PORCO

Bulbostylis possui distribuição majoritariamente pantropical, e algumas espécies ocorrem em regiões temperadas quentes. Sua diversidade se concentra na África tropical e na América do Sul, onde as espécies vegetam em ambientes abertos e ensolarados, geralmente com solo seco e bem drenado ou ainda sobre rochas. Deste modo contribui na diversidade desde campos densamente cobertos pela vegetação a areais e dunas costeiras, onde o solo está bastante exposto. As espécies de *Bulbostylis* também podem se estabelecer em ambientes recentemente perturbados pela ação antrópica na remoção da vegetação original, aí cumprem importante papel na revegetação desses ambientes e na sucessão ecológica.

O histórico de trabalhos com sistemática molecular em que são amostradas espécies de *Bulbostylis* é apresentado no artigo que consta no primeiro capítulo desse manuscrito, ‘Phylogenetic relationships in *Bulbostylis* (Abildgaardieae: Cyperaceae) inferred from nuclear and plastid DNA sequence data’ aceito para publicação na revista Systematic an Biodiversity, Natural History Museum of London, UK.

MORFOLOGIA DE *BULBOSTYLIS*

A caracterização morfológica aqui proposta segue na linha de trabalhos anteriores para o gênero e para a família, e trabalhos clássicos com ênfase em terminologia e morfologia vegetal. Para se identificar uma espécie são comparadas as diversas estruturas, muitas vezes com o auxílio de estereomicroscópios devido ao tamanho reduzido do fruto (tipo aquênio). Esta seção se destina a mostrar a diversidade morfológica que compõe o gênero, da maneira mais abrangente possível.

Bulbostylis é um gênero composto por espécies herbáceas, em sua maioria perenes, de hábito cespitoso, aspecto graminoide, rizoma curto e sistema radicular fasciculado bem desenvolvido. Os espécimes possuem de 5 a 80 cm de altura e em geral não se destacam na paisagem, por estarem em ambientes com diversas outras espécies com características macromorfológicas semelhantes e por não possuirem cores chamativas, com folhas e colmos variando do paleáceo aos diversos tons de verde, raro glaucos, e inflorescências em tons de castanho claro, estramíneo, até castanho escuro quase preto.

Em *Bulbostylis sellowiana* (Kunth) Palla e *Bulbostylis emmerichiae* T.Koyama (Figura 3a-e) a base das plantas apresenta restos de bainhas velhas, desfiadas, que conferem aspecto lanoso à esta região, como resposta adaptativa à exposição ao fogo. *Bulbostylis paradoxa* (Spreng.) Lindm., espécie também associada à ambiente com incidência de queimadas, tem como proteção uma base caudiciforme (Figura 4a, b). Já *Bulbostylis leucostachya* C.B. Clarke apresenta um cáudice ramificado e de aspecto bastante peculiar quando comparado à morfologia vegetativa da maioria das espécies do gênero.

Figura 3. Parátipo de *Bulbostylis emmerichiae*. a. Hábito; b. Aquênios com estilopódio decíduo; c. Base da planta; d. Inflorescência fasciculada; e. Etiquetas de herbários. [Harley & Souza 10146 (K000632283)].

Figura 4. Cáudex em *Bulbostylis*. a. *Bulbostylis leucostachya* C.B. Clarke [Gaillard 105 P00234919]; b. *Bulbostylis paradoxa* (Spreng.) Lindm [Glaziou 22326 (P00238355)].

O **colmo** em *Bulbostylis* é escaposo, rígido e ereto, não ramificado. Geralmente cilíndrico ou achatado lateralmente, costelado ou liso, glabro, piloso-híspido ou escabroso. Porta no ápice brácteas involucrais, folhosas na maioria das espécies, com pilosidade ou escabrosidade desde escassa a abundante nos bordos, e inflorescências complexas. Os diferentes padrões das sinflorescências serão discriminados mais adiante em seções próprias. Espiguetas prolíferas foram verificadas em *Bulbostylis subaphylla* C.B. Clarke (Figura 3c).

A **folha** típica é sempre basal, com bainha fechada tubular, ausência de lígula, com dois tufos de tricomas no ápice, referidos também na literatura como 'tricomas na boca da bainha'. *Bulbostylis* sp. nov. (cap. 2, Figure 6 e, f, capítulo 2, p.72) e *Bulbostylis juncoides* (Vahl) Kük. ex Herter possuem lígula pilosa pouco desenvolvida em alguns espécimes e, quando presente, varia na orientação, de oblíqua a transversal em relação à folha. A maioria das espécies possui folhas com lâminas desenvolvidas, escabrosas (Figure 6 c, d, capítulo 2, p. 72), piloso-híspidas (Figura 6 c) ou glabras com 1/3 a 2/3 do comprimento dos colmos. Lâminas foliares com menos de ¼ do comprimento dos colmos foram encontradas em *B. brevifolia* Palla, *B. subaphylla* (Figura 5 a, b) e *Bulbostylis* sp. nov. (Figure 1 e Figure 2, capítulo 2, p. 66).

Figura 5. *Bulbostylis subaphylla* C.B. Clarke. a. hábito; b. detalhe da base, com lâminas foliares pouco desenvolvidas; c. espigueta prolífera (Harris 12890 / K000632305).

Brácteas involucrais foliáceas, raro glumiformes, curtas, exceto a basal que pode ser maior que o diâmetro da inflorescência, as demais cada vez menores no sentido da base para o ápice da inflorescência (Figura 9 a, b, e).

Inflorescência com uma, poucas ou centenas de espiguetas. Em *Bulbostylis*, como no restante da família Cyperaceae, as espiguetas são uma importante unidade a ser analisada na delimitação das espécies. A quantidade e disposição espacial das espiguetas na inflorescência são aspectos a serem levados em conta nessa análise. A ráquila é o eixo onde estão fixadas as glumas e as flores, geralmente em arranjo espiralado,. A quantidade de flores e a configuração da inflorescência podem variar muito em algumas espécies, como *B. juncoides* e *Bulbostylis communis* M.G. López & D.A. Simpson, esse último fielmente ilustrado em López & Simpson (2012).

Nas espécies do gênero *Bulbostylis*, reconhecemos os seguintes tipos de inflorescências:

Uniespicado, com apenas uma espigueta no ápice do colmo. Pouco frequente, e em algumas espécies pode ser resposta morfológica de alguns indivíduos a especificidades ambientais (Figura 7 a, b; Figura 8 a, d).

ISOTYPE OF: *Isolepis vestita* Kunth
Enum. Pl. 2: 210. 1837.
= ***Bulbostylis vestita*** (Kunth) C.B. Clarke

determined by M.T. Strong, 2006
for the treatment of Cyperaceae, Flora of the Guianas
UNITED STATES NATIONAL HERBARIUM

Figura 6 a-d. Isótipo de *Bulbostylis vestita* (Kunth) C.B.Clarke. a. Hábito; b. Inflorescência antelódio de fascículos; c. Folhas e colmos híspido-tricomatosos; d. Etiqueta com informações sobre a tipificação [Weigelt s.n. K!]

Figura 7. a–e. Isótipo de *Bulbostylis splendens* M.T.Strong. a. Hábito; b. inflorescência com ráquila exposta (seta); c. Aquênio do tipo tuberculado com filete ainda ligado à base; d. comparativo entre gluma e aquênio; e. bainhas foliares vináceas com tricomas alvos no ápice [G. T. Prance et al. 6016 (K000632279)].

Figura 8. a–f. Isótipo de *Scirpus tenuispicatus* Boeck. [sinônimo de Bulbostylis funckii (Steud.) C. B. Clarke] a. Hábito; b. Gluma e aquênios de espiguetas apicais; c. Gluma e aquênios de espiguetas basais, d. Espigueta apical; e. Base da planta com aquênios, f. Etiquetas de herbarios. [Schaffner s.n. (P00234911)].

Capítulo (Figura 9 a, b) ou **fascículo** (Figura 10 a, c), de formato globoso ou turbinado, com espiguetas sésseis fixas espiraladamente a uma ráquila. A diferenciação entre os dois tipos se dá a partir do número de espiguetas, com o fascículo formado por até 5 espiguetas e o capítulo com mais de 5 dessas unidades. O formato hemisférico foi verificado em *Bulbostylis amambayensis* Barros (Figura 11 a,c) e *Bulbostylis guaglianoneae* M. G. López. Turbinado pseudo-lateral (Figura 9 b) em *Bulbostylis scabriculmis* sp. nov., descrito e ilustrado no Capítulo 2.

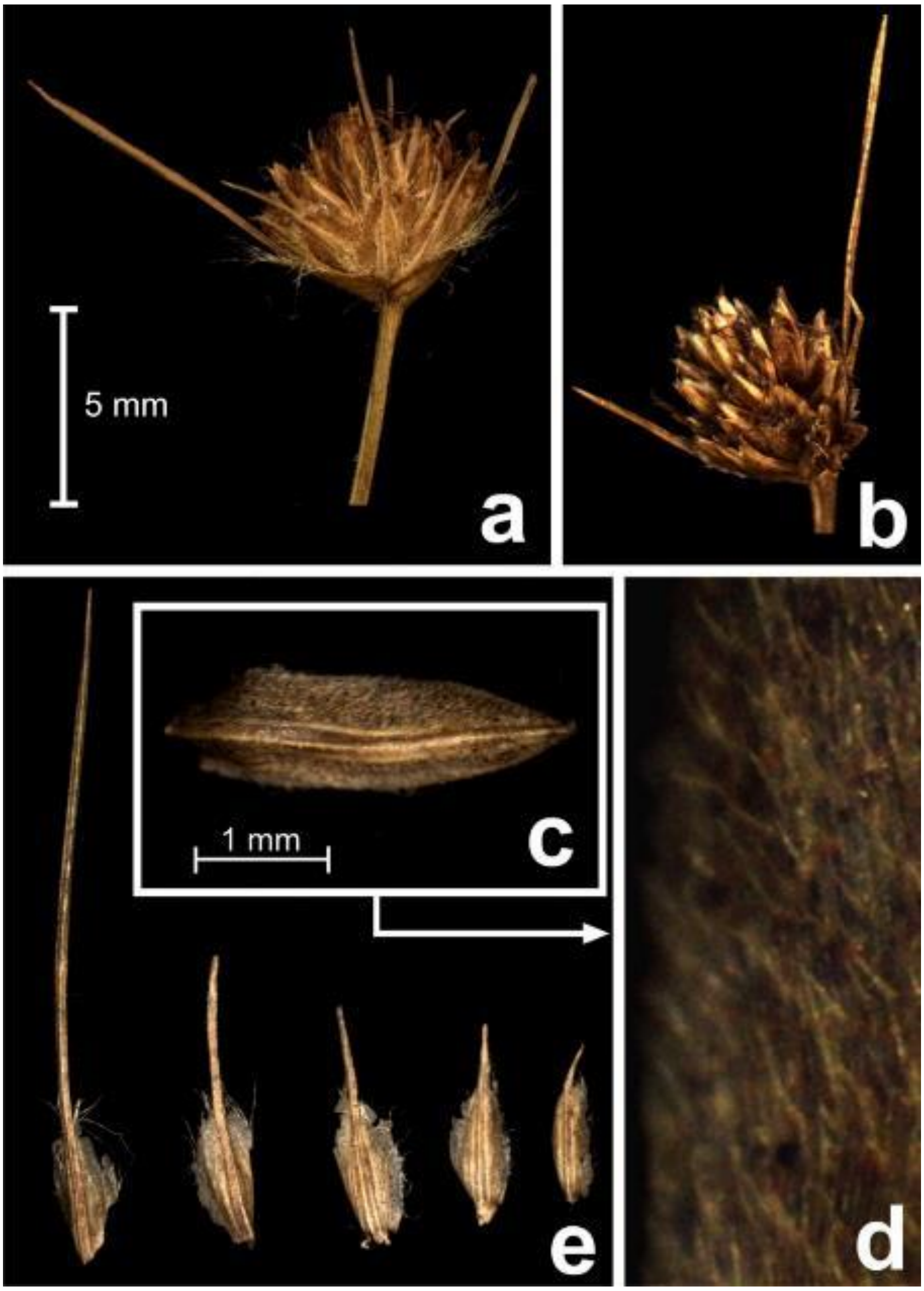
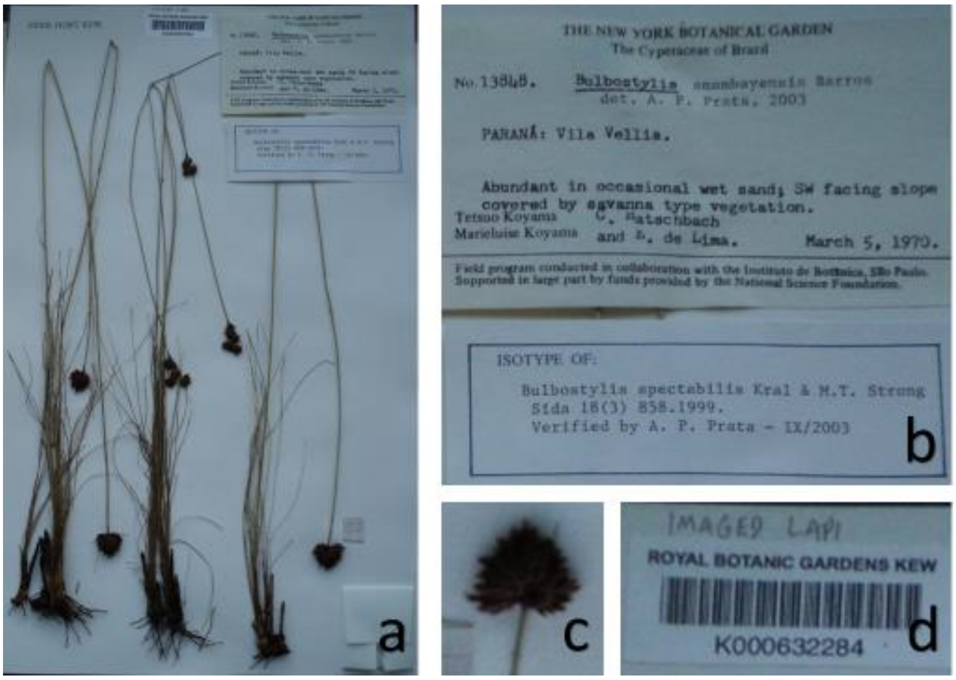


Figura 9. a–e. Inflorescência e brácteas de *Bulbostylis sp*. a. Inflorescência com tricomas evidentes nas margens da base das brácteas involucrais. b. Inflorescência pseudolateral. c. Gluma em vista dorsal. d. Detalhe dos tricomas na superfície dorsal da gluma. e. Sequência de brácteas involucrais de uma mesma inflorescência.em vista dorsal: quanto maior mais basal. [a. L.B. Smith 14499 (FLOR); b.–e. R. Ardissone & A. Vanzela 430 (ICN)].

Figura 10 a-c. Isótipo de *Bulbostylis distichoides* Lye. a. Hábito; b. Etiquetas de herbário; c. Espiguetas com glumas dísticas. [Harley 19356 (K000188999)].



THE NEW YORK BOTANICAL GARDEN
The Cyperaceae of Brazil

No. 13848. Bulbostylis amambayensis Barros
det. A. P. Prata, 2003

PARANÁ: Vila Vellia.

Abundant in occasional wet sand; SW facing slope covered by savanna type vegetation.

Tetsuo Koyama
Marieluise Koyama
G. Hatschbach and L. de Lima. March 5, 1970.

Field program conducted in collaboration with the Instituto de Botânica, São Paulo. Supported in large part by funds provided by the National Science Foundation.

ISOTYPE OF:

Bulbostylis spectabilis Kral & M.T. Strong
Sida 18(3) 858.1999.
Verified by A. P. Prata - IX/2003

IMAGED LAPI
ROYAL BOTANIC GARDENS KEW
K000632284

Figura 11. a-d. Isótipo de Bulbostylis spectabilis Kral & M.T. Strong (sinônimo de *Bulbostylis amambayensis* Barros). a. Hábito; b. Etiquetas de herbários; c. Inflorescência; d. Etiqueta Eletrônica. [Koyama 13848].

Antelódio simples (Figura 12 a) ou **composto** (Figura 13 a, b; Figura 14 a, b), com espiguetas isoladas, binadas, em fascículos ou capítulos nas extremidades dos pedúnculos, onde o comprimento dos pedúnculos no antelódio o torna laxo ou congesto, com as espiguetas terminais mais distantes ou próximas da central séssil, respectivamente. Uma característica importante a observar nos antelódios é a orientação dos pedicelos, se ascendentes, e este é o tipo mais frequente (Figura 14 a, b; Figura 15 a) ou divergentes (Figura 12 a; Figura 13 a). Deve-se tomar em conta inflorescências plenamente desenvolvidas para estabelecer de que tipo são. Antelódios jovens sempre têm eixos ascendentes, porém algumas espécies mudam de orientação em inflorescências plenamente desenvolvidas. *Bulbostylis wanderleyana* A. Prata & M.G. López, *Bulbostylis jacobinae* (Steud.) Lindm. (Figura 12) e *Bulbostylis loefgrenii* (Boeckeler) A. Prata & M.G. López, por exemplo, passam a ter eixos divergentes quando maduras.

Figura 12. a-c. Bulbostylis sp. a. Inflorescência antelódio simples de eixos divergentes; b. Inscrições de C.B. Clarke; c. Etiqueta eletrônica [Koyama 13848].

Figura 13 a-d. Isótipo de *Bulbostylis jacobinae* (Steud.) Lindm. a. Hábito; b. inflorescência antelódio composto de espiguetas isoladas nas extremidades; c. Aquênio; d. Etiquetas de herbário [Blanchet 3744 (K000189922)].

Figura 14 a-d. Isótipo de *Bulbostylis stenocarpa* Kük. a. Hábito; b. Inflorescência tipo antelódio composto de eixos ascendentes; c. Etiqueta eletrônica; d. Etiqueta com informações sobre a tipificação [Ule 8069 K000307833].

A **espigueta** em *Bulbostylis* apresenta glumas densamente arranjadas em espiral (Figura 8 d; Figura 12 a), raro dísticas (Figura 10 c), decíduas, onde cada gluma subtende uma flor bissexual. As **glumas** são naviculares (Figura 9 c), 1,5 - 3 × 1 – 2.5 mm, carenadas; face abaxial (externa) convexa, pilosa, esverdeada e ou estramínea na carena e nos bordos, com manchas castanhas nas laterais; face adaxial (interna) côncava, lisa, lustrosa, glabra, bordo curtamente ciliado (visível apenas à lupa ou ao microscópio). O ápice das glumas pode ser agudo, obtuso ou emarginado, mútico, mucronado ou mucronulado.

Figura 15 a-c. Isótipo de *Bulbostylis schomburgkiana* (Steud.) M.T.Strong. a. Hábito; b. Aquênios; c. Etiqueta de herbário [Schomburgk 1023 K000632280].

As **flores** são bissexuais e têm um a três **estames** de **filetes** alongados, achatados dorso-ventralmente e protegidos pela gluma, **anteras** oblongas, basifixas, com conetivo prolongado, cerdas perigíneas ausentes, estilete achatado dorso-ventralmente, liso, alongado, estigma trífido, raro bífido, exserto, papiloso, estilopódio distinto, espessado, bulboso, persistente no ápice do aquênio, raro decíduo ou indistinto.

Fruto tipo **aquênio** (Figura 3 b; Figura 7 c; Figura 8 b, c; Figura 13 c; Figura 15 b), 0,6 – 1,5 mm de comprimento, esbranquiçado, castanho ou quase negro, trígono arredondado, raro biconvexo. Obovoide ou obcônico, raro cordado, oblongo ou piriforme; superfície tuberculada, reticulada, transversalmente rugosa, suavemente ondulada ou lisa. Células da superfície alongadas longitudinalmente em relação ao fruto, com ou sem corpos silicosos. Anficarpia rara, verificada em *Bulbostylis funckii* (Steud.) C. B. Clarke (Figura 13 d).

Objetivos

O presente estudo tem como objetivos aprofundar o conhecimento acerca das relações filogenéticas dentro do gênero *Bulbostylis* e desse com os demais que compõem a tribo Abildgaardieae, e fornecer meios para a identificação das espécies de *Bulbostylis* que ocorrem na Região Sul do Brasil.

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CAPÍTULO I

Phylogenetic relationships in *Bulbostylis* (Abildgaardieae: Cyperaceae) inferred from nuclear and plastid DNA sequence data

Rodrigo Endres Ardissone (rodrigoardissone@hotmail.com)[2,*], Andrea Guadalupe Reutemann[1,6,*], María Gabriela López (mglopez@agr.unne.edu.ar)[3], Sebastián Elias Muchut (sebamuchut@yahoo.com.ar)[1], Ilsi Boldrini (ilsi.boldrini@ufrgs.br)[4], Abelardo Carlos Vegetti (avegetti@fca.unl.edu.ar)[1] and Liliana Mónica Giussani (lgiussani@darwin.edu.ar)[5]

Running title: Phylogenetic relationships in *Bulbostylis*

[1] Facultad de Ciencias Agrarias, Universidad Nacional del Litoral, Consejo Nacional de Investigaciones Científicas y Técnicas, Kreder 2805. Esperanza CP 3080, Santa Fe, Argentina. Tel +5434 9642 6400.

[2] Programa de Pós-graduação em Botânica, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Av. Paulo Gama 110. Porto Alegre, Brazil. Tel +5551 3308 6000.

[3] Facultad de Ciencias Agrarias, Universidad Nacional del Nordeste, Instituto de Botánica del Nordeste, Consejo Nacional de Investigaciones Científicas y Técnicas,

Sargento Cabral 2131. Corrientes CP 3400, Corrientes, Argentina. Tel +5437 9442 6218.

[4] Departamento de Botânica, Instituto de Biociências, Universidade Federal do Rio Grande do Sul, Conselho Nacional Científico e Tecnológico, Av. Paulo Gama 110. Porto Alegre, Brazil. Tel +5551 3308 6000.

[5] Instituto de Botánica Darwinion, Consejo Nacional de Investigaciones Científicas y Técnicas, Labardén 200 C. C. 22. San Isidro B1642HYD, Buenos Aires, Argentina. Tel +5411 4743 4800.

[6] Corresponding author (e-mail: areutemann@fca.unl.edu.ar)

*Joint first authors.

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Abstract

Previous molecular phylogenetic analyses of the family Cyperaceae based on *rbc*L sequences showed *Bulbostylis* as paraphyletic, with *B. atrosanguinea* and *B. hispidula* forming a clade with *Nemum spadiceum*. On the contrary, phylogenetic analyses of the tribe Abildgaardieae based on nuclear (ITS ribosomal region) and plastid sequences (*trn*L-F region) showed *Bulbostylis* as monophyletic, although they only incorporated four species of *Bulbostylis* and none of *Nemum*. In this work, we present, for the first time, a phylogenetic hypothesis of *Bulbostylis* based on a comprehensive sampling including species from different continents. New sequences of *Abildgaardia*, *Crosslandia, Fimbristylis* and *Nemum* were included to test the monophyly of *Bulbostylis*. In total, eighty-four sequences of both ITS and *trn*L regions were generated. Analyses were performed using Bayesian inference, maximum likelihood, and parsimony. Ancestral state reconstruction was performed using ML, MCMC and parsimony methods. In all analyses, *Bulbostylis* was paraphyletic as *Nemum atracuminatum* is nested within it. Most American species of *Bulbostylis* grouped together, but relationships among them appear poorly resolved. Ancestral state reconstructions of native distribution suggest an African ancestor of the *Bulbostylis*-*Nemum* complex, with at least three independent introduction events of the genus into the Americas. Morphological diagnostic characters such as “style base permanence” or “detachment from the ripe achene”, and the “micromorphological patterns of the achene surface” are homoplastic in this phylogenetic context and, therefore, unsuitable for proposing infrageneric groupings within *Bulbostylis*.

Keywords: Bayesian inference - ITS - maximum likelihood - molecular phylogenetic analysis - parsimony - *trn*L intron

Introduction

The genus *Bulbostylis* Kunth nom. cons. is included in tribe Abildgaardieae (sensu Goetghebeur, 1998), together with *Abildgaardia* Vahl, *Crosslandia* W. Fitzg., *Fimbristylis* Vahl, *Nelmesia* Van der Veken, and *Nemum* Desv. ex Ham. *Bulbostylis* has *c.* 200 species (Govaerts et al., 2016) with a pantropical distribution, mainly concentrated in South America and tropical Africa (Goetghebeur, 1998). In previous studies, *Bulbostylis* has been characterized by long hairs at the mouth of the leaf sheath, spikelets with deciduous glumes, 3(2)-fid styles with their base thickened and persistent (rarely deciduous) on the ripe fruit, trigonous (rarely biconvex) achene with the pericarp cells vertically elongated and commonly with silica bodies (=silicophytoliths), and *Bulbostylis*-type embryo (Barros, 1947; Goetghebeur, 1998; Goetghebeur & Coudijzer, 1984, 1985; Gonzalez & López, 2010; Guaglianone, 1970; Kral, 1971; Kral & Strong, 1999; Lye, 1971; Pedersen, 1969; Svenson, 1957; Van der Veken, 1965).

Based on morphological characters some authors have attempted to establish infrageneric categories for this complex genus of Cyperaceae. Clarke (1908), for a reduced number of species, proposed infrageneric groupings for *Bulbostylis* according to inflorescence configuration and the number of stigmatic branches. These groupings are not currently accepted, since most species of *Bulbostylis* have a trifid style and inflorescences are highly variable (e.g. *B.*

juncoides (Vahl) Kük. ex Herter and *B. communis* M.G. López & D.A. Simpson), even among individuals of the same population. López (2012) and López & Gonzalez (2017) in their taxonomic study of *Bulbostylis* for the southern part of South America, observed that the most stable characters for distinguishing *Bulbostylis* species are related to micromorphology of fruit surface, particularly the presence or absence of silicophytoliths in the exocarp cells. Based on these characters, López (2012) and López & Gonzalez (2017) suggest informal groupings for *Bulbostylis* (Table 1).

Up to now, no molecular phylogenetic studies have attempted to clarify relationships in *Bulbostylis*. Phylogenetic analyses of the Cyperaceae family based on *rbc*L sequence data (Muasya, Simpson, Chase, & Culham, 1998; Muasya et al., 2009; Simpson et al., 2007) have included a limited sampling of this genus. Based only in two species of *Bulbostylis* [*B. hispidula* (Vahl) R.W. Haines and *B. atrosanguinea* (Boeckeler) C.B. Clarke], these studies showed *Bulbostylis* as paraphyletic, with *B. atrosanguinea* and *B. hispidula* forming a clade with *Nemum spadiceum* (Lam.) Desv. ex Ham. On the other hand, phylogenetic analyses of the tribe Abildgaardieae based on nuclear (ITS ribosomal region) and plastid sequences (*trn*L-F region) (Ghamkhar, Marchant, Wilson, & Bruhl, 2007) showed *Bulbostylis* as monophyletic; however this phylogenetic hypothesis included only four species of *Bulbostylis* and none of *Nemum*.

In this work, to clarify the evolutionary history of the *Bulbostylis* and to test the validity of the infrageneric groups proposed by López (2012) and López & Gonzalez (2017), we increased the sampling of *Bulbostylis* including other Abildgaardieae species and used molecular data based on the nuclear internal transcribed spacer (ITS) region and the plastid *trn*L region. Additionally, we discussed morphological features and biogeographical distribution in the current phylogenetic context.

Material and methods

Taxon sampling

Our sampling consists of 39 species of *Bulbostylis*, and 18 species representing six other genera of tribe Abildgaardieae, and of the closely related tribe Arthrostylideae. Sequences to represent genera of both tribes were selected from Ghamkhar et al. (2007), Muasya et al. (1998, 2009), and Simpson et al. (2007). *Actinoschoenus composita* is here included following results by Ghamkhar et al. (2007) where this species is clearly apart from *Fimbristylis*; however, the valid name would be *Fimbristylis composita* until a new combination is accepted. Additionally, we included seven putative new species of *Bulbostylis*, whose names are being published independently of this phylogeny (Ardissone ined.). A complete list of taxa, voucher information, their locations, and GenBank accession numbers for DNA sequences are shown in Table 1. A total of 84 out of 117 sequences were generated in this work; 33 were downloaded from GenBank. Plant material was collected in the field and dried in silica gel (voucher specimens stored at SF, CTES, ICN or FLOR) or amplified from herbarium specimens (Table 1).

DNA extraction, amplification, and sequencing

Total DNA was extracted from silica-dried culms and leaves using a modified CTAB protocol by Doyle & Doyle (1987), or from herbarium material using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. The internal transcribed spacer region comprising the ITS1-5.8S-ITS2 nuclear ribosomal DNA (ITS) was amplified by the polymerase chain reaction (PCR), using primers 17SE and 26SE designed by Sun, Skinner, Liang, & Hulbert, (1994). The cpDNA *trn*L UAA intron was amplified using primers C and D by Taberlet, Gielly, Pautou, & Bouvet (1991). Reactions were performed on a TGradient Thermocycler (Biometra, Göttingen, Germany) in 25 µL volume containing template DNA, 0.25 µM of each primer, 25 µM dNTP, 5 mM MgCl2, 1× buffer and 1.5 units of Taq polymerase. PCR amplifications for ITS were carried out under the following conditions: initial denaturation (94°C for 3 min) followed by 38 cycles of denaturation (94°C for 30 sec), annealing (53°C for 1 min) and elongation (72°C for 90 sec) and a final elongation at 72°C for 10 min. Thermal cycling parameters for *trn*L were: an initial denaturation step (3 min, 94°C) followed by 38 cycles of denaturation (30 sec, 94°C), annealing (1 min, 50°C) and elongation (90 sec, 72°C) and a termination step of 10 min at 72°C. In species for which these parameters were unsuccessful, variation in the annealing temperature were used (48 - 55 ºC). Additionally, PCR additives and enhancing agents [bovine serum albumin, dimethyl sulfoxide, Q of the Taq PCR Core Kit (Qiagen)] were used to increase the yield, specificity and consistency of PCR reactions. To confirm the presence of a simple product of the amplified DNA, PCR products were electrophoresed using a 1% agarose gel in a 1× Tris-acetate-EDTA (TAE) buffer, stained with GelRed^{TM} Nucleic Acid Gel Stain (BIOTIUM) and visualized under UV light. PCR products were cleaned and sequenced by Macrogen, Inc. (Seoul, Korea) using the ABI PRISM BigDye Terminator Cycle Sequencing Kits with AmpliTaq DNA polymerase (Applied Biosystems, Seoul, Korea). Both forward and reverse strands were sequenced; single-pass sequencing was performed on each template using the same primers used for PCR reactions. Editing and assembling of sequences was conducted using the ChromasPro v.1.7.5 program (Technelysium Pty, Ltd), which was also used for checking the quality of sequences. Sequence alignments were performed using Muscle v.3.8 (Edgar, 2004), and inspected by eye using BioEdit v.7.2.0 (Hall, 1999). Aligned matrices were submitted to TreeBase (accession no. xxxxx).

Phylogenetic analyses

Phylogenetic analyses were conducted for individual (ITS or *trn*L intron) and combined ITS+*trn*L intron data sets under parsimony (P), Maximum Likelihood (ML) and Bayesian Inference (BI). The P analyses were performed using TNT v.1.1 program (Goloboff, Farris, & Nixon, 2003, 2008) under heuristic searches with 1,000 random addition sequences and Tree Bisection and Reconnection branch swapping (TBR), retaining a maximum of 2 trees in each replicate. The optimal trees obtained were then submitted to a new round of TBR branch swapping to completion. All characters were equally weighted, treated as unordered, and gaps were scored as missing data. Prior to heuristic searches, all uninformative characters were deactivated. To evaluate the relative support for individual clades, bootstrap analysis (Felsenstein, 1985) was performed using a total of 10,000 replicates. The

ML analyses were carried out using RAxML v.8.2.4 (Stamatakis, 2014), conducted on the CIPRES Science Gateway Web server (https://www.phylo.org). We selected the GTRGAMMA model and the rapid bootstrapping algorithm and ran 1,000 bootstrap replicates. Bootstrap values (BS) over 50% are reported for both P and ML analyses. For BI, we used the Bayesian Markov Chain Monte Carlo (MCMC) method, implemented in MrBayes v.3.2 (Ronquist et al., 2012) on the CIPRES Science Gateway. Models of nucleotide substitution were determined by the Akaike Information Criterion (AIC) using jModelTest v.2.1.6 (Darriba, Taboada, Doallo, & Posada, 2012); the model selected was different for each partition analyzed; ITS1: TIM2ef+G, 5.8S: K80, ITS2: SYM+G, and *trn*L: TIM3+G. Two simultaneous runs of 10 million generations, with random starting trees, were performed and sampled every 1,000 generations. The first 2,500 trees of each run (25%) were discarded as burn-in. The remaining trees (15,002) were combined to obtain the 50% majority rule consensus tree. Posterior probability (PP) values > 0.65 were recorded on the tree.

Ancestral state reconstruction

The native distribution was coded as a three-state character (0, America; 1, Africa; 2, Asia+Oceania). The character state assignment was based on Govaerts et al. (2007), herbarium specimens, and the information available in the portals Tropicos (http//www.tropicos.org) and e-Monocot (http://families.e-monocot.org).

Ancestral state reconstruction was performed using ML, MCMC and parsimony methods. Parsimony reconstruction was carried out in Mesquite 3.04 software (Maddison & Maddison, 2015) using the ‘trace character history’ option (character states were treated as unordered). The reconstruction with ML and MCMC methods was performed using the ‘mulstistate’ module in BayesTraits software (Pagel, Meade, & Barker, 2004). In order to choose a model for MCMC runs, an initial ML run was carried out with 15,002 trees to set the range of hyperprior (0-779) and seed an exponential distribution. Many exploratory chains had to be run to establish a correct rate deviation parameter (ratedev = 60) for the characters in order to achieve an approximate 20-40% acceptance rate. Once all the MCMC parameters were set, ancestral states were estimated using the Most Recent Common Ancestor (MRCA) command, which finds the proportion of the likelihood associated with each of the possible states at the nodes. The analysis was run for 10 million generations, discarding the first million as burn-in and sampling every 1,000th generation to ensure independence. Convergence and ESS were checked with Tracer v1.5.0 (Rambaut & Drummond, 2007). The ‘fossil’ command was performed to test whether a particular state was significantly more likely at each node. The results of these MCMC runs were tested by estimating Bayes factor (BF), an approach based on smoothed estimates of marginal likelihood analyzed with Tracer v1.5.0 (Rambaut & Drummond, 2007), which applies the method used by Newton & Raftery (1994) with modifications by Suchard, Weiss & Sinsheimer (2001).

Results

The data matrix of the entire ITS region consisted of 59 sequences and 589 aligned characters, of which 219 were parsimony-informative; the length of the ITS sequences within the ingroup varied from 507 base pairs (bp) (*B. sphaerocephala*) to 545 bp (*B. paradoxa*). Parsimony analysis yielded 864 shortest trees of 807 steps (CI=0.445; RI=0.788). The *trn*L intron alignment included 58 sequences and 664 characters, of which 89 were informative in the P analysis; the length of the *trn*L intron sequences within the ingroup varied from 485 bp (*N. atracuminatum*) to 573 bp (*B. mucronata*). The *trn*L intron data set resulted in 6,972 most parsimonious trees with a length of 171 steps (CI=0.667; RI=0.922). The strict consensus trees from individual ITS and *trn*L intron analyses are found in the supplement (Fig. S1, S2). For each of both markers, BI, ML, and P recovered similar topologies, showing similar clades with high confidence values. Hence, we present the best ML trees from ITS (Fig. 1) and *trn*L intron (Fig. 2) data.

The concatenated data set (ITS+*trn*L intron) included 61 sequences and consisted of 1,253 characters, of which 308 are parsimony-informative. Parsimony analysis resulted in 198 optimum trees of 1,019 steps (CI=0.464; RI=0.808); the strict consensus tree is shown in Fig. S3. The best ML tree from the combined analysis is illustrated in Fig. 3. Similar to results of both ITS and *trn*L intron individual partitions, the topologies obtained for the combined ITS+ *trn*L intron data set by P, IB and ML analyses were highly congruent.

In all analyses conducted for individual (ITS or *trn*L intron) and combined (ITS+*trn*L intron) data sets, the genus *Bulbostylis* is paraphyletic as *Nemum atracuminatum* is embedded within it. The '*Bulbostylis*-*Nemum* clade' is sister to a clade including all other Abildgaardieae species: the '*Abildgaardia*-*Crosslandia*-*Fimbristylis* clade' (Figs. 1-3 and S1-3).

In all three ML hypotheses, the *Bulbostylis*-*Nemum* clade is well-supported and includes a derived clade that comprises most American species of *Bulbostylis* (hereinafter referred to as 'American clade'; Figs. 1-3). However, the three hypotheses show differences in the order of divergence of basal species, as well as in the composition and support of subclades. Other minor groups are recognized: a well-supported subclade is formed by *Bulbostylis conifera* and *B. paradoxa*, in the ITS and combined analyses, where both species are included (Figs. 2 and 3); a subclade is composed by *B. funckii*, *B. hispidula* and *B. pseudoperennis* (in the ITS and combined analyses, Figs. 1 and 3), or only by *B. hispidula* and *B. pseudoperennis* (in the *trn*L intron analysis, where *B. funckii* is not included, Fig. 2), forming highly-supported clades, respectively.

Incongruences among the trees from the individual and combined data sets are related to the location of: 1) *B. macra*, *B. pusilla* and *B. scleropus*, which form a polytomy within the American clade (*trn*L intron tree; Fig. 2), or group together in one highly-supported clade but not related to the American clade (ITS and combined trees; Fig. 1 and 3); and 2) *B. junciformis*, *B. scabricaulis*, *B. sphaerocephala* and *B. stenocarpa*, which form a moderately to highly-supported clade outside the American clade (*trn*L intron tree; Fig. 2), or alternatively form a polytomy (ITS tree; Fig. 1), or a moderately to highly-supported clade (combined tree; Fig. 3), within the American clade.

The American clade in the ITS and combined ITS+*trn*L intron trees consists of all American species: *Bulbostylis aspera*, *B. capillaris*, *B. communis*, *B. consanguinea*, *B. contracta*, *B. hirtella*, *B. junciformis*, *B. juncoides*, *B. loefgrenii*, *B.*

rugosa, *B. scabra*, *B. sphaerocephala*, *B. sphaerolepis*, *B. stenocarpa*, *B. subtilis*, *B. wanderleyana*, all unpublished species of *Bulbostylis* (*sp1*-*sp8*) and two species not found in America: *B. densa* and *B. scabricaulis* (Figs. 1 and 3). Additionally, the American clade in the *trn*L intron tree is similar to that observed in the ITS and ITS+*trn*L intron trees, although not including *B. junciformis*, *B. scabricaulis*, *B. sphaerocephala* nor *B. stenocarpa*, (*B. contracta* is not represented by a *trn*L intron sequence), and contains three additional African species: *B. pusilla*, *B. scleropus* and *B. macra* (Fig. 2).

Within the American clade, relationships among species are barely resolved. For such clade, both the ITS and combined ITS+*trn*L intron trees show weakly to moderately-supported monophyletic groups (*B. sp6*+*B. loefgrenii*, *B. sp1*+*B. sp2*, *B. rugosa*+*B. sp7*, *B. scabra*+*B. sphaerolepis*, *B. wanderleyana*+*B. sp3*, *B. sp5*+*B.subtilis*; Figs. 1 and 3), which do not match the weakly to moderately-supported groups retrieved for the American clade in the *trn*L intron ML tree (*B. subtilis*+*B. sp3*, *B. sp5*+*B. communis*, *B. sp1*+*B.consanguinea*, *B. wanderleyana*+*B. sp7*+*B. sp6*; Fig. 2).

The ancestral state reconstruction of the native distribution (Fig. 4) suggests an African ancestor of the *Bulbostylis*-*Nemum* complex based both on P and BI (lnBF = 2.83). Additionally, the introduction of species of *Bulbostylis* to America is reconstructed here in three independent events; with the American clade being the most diversified after colonization. If *B. densa* and *B. scabricaulis* are included in the American clade, both species represent posterior reintroduction to Africa probably by long dispersal events. The introduction of species to Asia and Oceania is reconstructed as several independent events.

Discussion

This work is the most comprehensive phylogenetic study of *Bulbostylis* to date, including species from different continents. A previous work (Ghamkhar et al. 2007) that examined *Bulbostylis*, only incorporated four species, three of them Australian, and one native to Africa. Our phylogenetic results show a paraphyletic *Bulbostylis*, with *Nemum atracuminatum* nested within the genus. These findings, along with those results obtained by Muasya et al. (1998, 2009) and Simpson et al. (2007), who observed a close relationship between *B. atrosanguinea*, *B. hispidula* and *N. spadiceum*, are strong signals to consider *Bulbostylis* and *Nemum* as part of a natural group.

The presence in both genera of woolly hairs at the mouth of leaf sheaths (Goetghebeur, 1998; Goetghebeur & Coudijzer, 1984; Larridon et al., 2008) and of a wide turbinate embryo with the embryonic axis totally recurved and the radicle and plumule in basal position (=*Bulbostylis*-type embryo; Van der Veken, 1965), represent probable synapomorphies of the *Bulbostylis*-*Nemum* clade. Unlike *Bulbostylis* and *Nemum*, in *Abildgaardia*, *Crosslandia* and *Fimbristylis* the leaf sheaths orifice is glabrous (Goetghebeur, 1998; Goetghebeur & Coudijzer, 1984), and the embryo is about turbinate with the radicle in lateral position and the plumule in basal position (=*Fimbristylis*-type embryo; Van der Veken, 1965), or it is similar to those of *Bulbostylis*-type but with a great development of the second leaf and with a third additional leaf (=*Abildgaardia*-type embryo; Van der Veken, 1965).

Within *Bulbostylis*, none of the infrageneric groups suggested by López (2012) and by López & Gonzalez (2017) based on micromorphology of achene surfaces were retrieved as monophyletic in our molecular phylogenetic study (Fig.4;

Table 1). López (2012) and López & Gonzalez (2017) proposed three large groups of species: a) fruit exocarp without silicophytoliths (group 1; Figs. 5.1, 5.2); b) fruit exocarp with silicophytoliths of undefined shape, which occupy most of the cell (group 2; Figs. 5.3, 5.4); and c) fruit exocarp with silicophytoliths of defined shape, located at the center of the cell or excentrically (group 3; Figs. 5.5, 5.6). Our results show the limited value of the fruit micromorphology to establish infrageneric groups in *Bulbostylis*.

Otherwise, the current phylogenetic context reveals the homoplasic condition of the diagnostic character “style-base permanence on the ripe fruit”. The style base duration has been commonly used to differentiate *Bulbostylis* from *Abildgaardia* and *Fimbristylis*. The style base is a persistent structure in most species of *Bulbostylis* and a deciduous one in *Abildgaardia* and *Fimbristylis*. However, this character is not decisive, since there are species of *Bulbostylis* without persistent style base (e.g. *B. communis*, *B. hispidula*, *B. sellowiana*). Moreover, the species of *Bulbostylis* with a deciduous style base included in the analyses, *B. communis* and *B. hispidula*, do not form a clade in any of the analyses. Although *Nemum atracuminatum* also present a deciduous style base, this species is apart from *B. communis* or *B. hispidula*.

The deciduous style base of *B. communis* and *B. hispidula* belong to different morphological types according to Reutemann, Vegetti, & Pozner (2012). These authors describe two types of style base: 1) *Bulbostylis* type, which has two joints: one at the ovary apex and another one at the distal end of the style base (Figs. 5.7, 5.8); and 2) *Abildgaardia-Fimbristylis* type, with a single joint with the ovary apex (Figs. 5.9, 5.10). *B. communis* has a *Bulbostylis*-type style base (which is typical of *Bulbostylis* species), whereas *B. hispidula* shows an *Abildgaardia-Fimbristylis*-type (which is typical of *Abildgaardia* and *Fimbristylis* species). In *B. hispidula*, the presence of an *Abildgaardia-Fimbristylis*-type style base has led other authors to consider this taxon as *Fimbristylis*; however, the presence of a *Bulbostylis* embryo type and woolly hairs at the apex of the leaf sheath emphasize its association to *Bulbostylis*. Our phylogenetic analyses support the inclusion of *B. hispidula* within *Bulbostylis*, as well as the concept of independent acquisition of an *Abildgaardia-Fimbristylis*-type style base (Fig. 4).

All three ML trees obtained in this work (Figs. 1-3) show very short branch lengths for most of the species of the American clade, compared to the rest of the species. Based on this fact, and considering the high morphological similarity of species in the American clade, we might assume a rapid diversification of this clade, which might result from the acquisition of some key structural innovation possibly accountable for a burst of speciation. A thorough morphological study covering broadly distributed species of *Bulbostylis* might identify synapomorphies for the American clade, and thus supporting or refuting this assumption. Incorporation of additional markers might also contribute towards resolving this polytomy; moreover, new technologies based on next-generation sequencing might better deal with difficulties posed by polyploidy, hybridization, and recent radiations (Harrison & Kidner, 2011); Larridon et al. (2013) mention this issue regarding the polytomy obtained for the majority of C_4 *Cyperus* spp.

Bulbostyllis conifera and *B. paradoxa* appear as a moderately to highly-supported monophyletic group in all analyses. Both species, along with *B. funckii*, are the only species native to America that fall outside the American clade in all analyses. These three species show a contrasting morphology not shared with the other American species, such as the presence of a caudex in *B. paradoxa*, and unispicate inflorescences in *B. conifera* and *B. funckii*.

Based on the reconstruction pattern of the native distribution presented in this work, the ancestor of *Bulbostylis*-*Nemum* complex is likely to be African. It is necessary to obtain sequences of the monotypic genus *Nelmesia* to test its likely closeness to the *Bulbostylis*-*Nemum* complex, so far assumed on the basis both of its African distribution (Goetghebeur, 1998) and its *Bulbostylis*-type embryo (Van der Veken, 1965).

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Table 1. List of the samples used in the molecular analysis with species names, voucher information (collector, number, and where the specimen is housed), country of collection, and GenBank accession for DNA sequences of ITS and *trn*L regions (**bold** indicates new accession); a dash (–) indicates missing data; *trated as in Ghamkhar et al. (2007), but combination is not yet published; ***Bulbostylis* species included in López (2012), and their informal infrageneric grouping; n.a.=not applicable data; *sp1*-*sp7* are unpublished species included in this study; *sp8* is an unpublished specie included in Ghamkhar et al. (2007).

Taxon	Voucher (Herbarium Code)	Provenance	ITS	*trn*L intron	Group**
OUTGROUP					
Abildgaardia ovata (Burm. f.) Kral	V. Klaphake 1410 (NSW)	Australia	AY506758	AY506708	n.a.
Abildgaardia ovata (Burm. f.) Kral	A. Reutemann 173 (SF)	Argentina	**xxxxxxxx**	**xxxxxxxx**	n.a.
Abildgaardia schoenoides R.Br.	K. L. Clarke 70 (NE)	Australia	AY506761	AY506706	n.a.
*‘Actinoschoenus composita’** (*Fimbristylis composita* Latz)	K. L. Clarke 213 (NE)	Australia	AY506755	AY506702	n.a.
Arthrostylis aphylla R.Br.	K. L. Clarke 183 (NE)	Australia	AY506757	AY506700	n.a.
Crosslandia setifolia W.Fitzg.	K. L. Clarke 246 (NE)	Australia	AY506768	AY506718	n.a.
Crosslandia setifolia W.Fitzg.	Cowie 13158 (DNA)	Australia	**xxxxxxxx**	**xxxxxxxx**	n.a.
Fimbristylis arnhemensis Latz	K. L. Clarke 177 (NE)	Australia	AY506776	AY506722	n.a.
Fimbristylis autumnalis (L.) Roem. & Schult.	L. Lucero 28 (SF)	Argentina	**xxxxxxxx**	**xxxxxxxx**	n.a.
Fimbristylis bisumbellata (Forssk.) Bubani	K. L. Clarke 107 (NE)	Australia	AY506778	AY506724	n.a.
Fimbristylis cinnamometorum (Vahl) Kunth	J. J. Bruhl 2058 (NE)	Australia	AY506772	AY506721	n.a.
Fimbristylis complanata (Retz.) Link	A. Reutemann 37 (SF)	Argentina	**xxxxxxxx**	**xxxxxxxx**	n.a.
Fimbristylis cymosa R.Br.	K. L. Wilson 10041 (NSW)	Australia	AY506798	AY506750	n.a.
Fimbristylis dichotoma (L.) Vahl	M. G. López 376 (CTES)	Argentina	**xxxxxxxx**	-	n.a.
Fimbristylis dichotoma (L.) Vahl	R. Ardissone 415 (ICN)	Brazil	-	**xxxxxxxx**	n.a.
Fimbristylis dichotoma (L.) Vahl	A. Reutemann 103 (SF)	Argentina	-	**xxxxxxxx**	n.a.
Fimbristylis laxiglumis Latz	K. L. Clarke 106 (NE)	Australia	AY506785	AY506736	n.a.
Fimbristylis pterigosperma R.Br.	K. L. Clarke 118 (NE)	Australia	AY506794	AY506729	n.a.
Fimbristylis spadicea (L.) Vahl	A. Reutemann 76 (SF)	Argentina	**xxxxxxxx**	**xxxxxxxx**	n.a.
Fimbristylis squarrosa Vahl	A. Reutemann 63 (SF)	Argentina	**xxxxxxxx**	**xxxxxxxx**	n.a.
Fimbristylis tetragona R.Br.	K. L. Clarke 173 (NE)	Australia	AY506799	AY506746	n.a.
Nemum atracuminatum Larridon, Reynders & Goetgh.	S. Lisowski 5003 (PRE)	Zaire	**xxxxxxxx**	**xxxxxxxx**	n.a.
INGROUP					
Bulbostylis aspera M.G.López	R. Ardissone 117 (FLOR)	Brazil	**xxxxxxxx**	**xxxxxxxx**	1
Bulbostylis barbata (Rottb.) C.B.Clarke	K. L. Clarke 113 (NE)	Australia	AY506764	AY506709	n.a.
Bulbostylis capillaris (L.) C.B.Clarke	R. Ardissone 384 (ICN)	Brazil	**xxxxxxxx**	**xxxxxxxx**	n.a.
Bulbostylis communis M.G.López & D.A.Simpson	A. Reutemann 23 (SF)	Argentina	-	**xxxxxxxx**	1
Bulbostylis communis M.G.López & D.A.Simpson	A. Reutemann 181 (SF)	Argentina	**xxxxxxxx**	-	1

Bulbostylis conifera (Kunth) C.B.Clarke	Dias-Melo 116 (NY)	Brazil	-	xxxxxxxx	n.a.
Bulbostylis consanguinea (Kunth) C.B.Clarke	R. Ardissone 197 (FLOR)	Brazil	xxxxxxxx	xxxxxxxx	3
Bulbostylis contracta (Kük.ex Osten) M.G.López & D.A.Simpson	R. Ardissone 269 (FLOR)	Brazil	xxxxxxxx	-	1
Bulbostylis cruciformis (Lye) R.W.Haines	Faden 74/776 (PRE)	Kenya	xxxxxxxx	xxxxxxxx	n.a.
Bulbostylis densa (Wall.) Hand.-Mazz.	R.P. Glen 720 (PRE)	South Africa	xxxxxxxx	-	n.a.
Bulbostylis densa (Wall.) Hand.-Mazz.	V. Klaphake 1411 (NSW)	Australia	AY506763	AY506710	n.a.
Bulbostylis funckii (Steud.) C.B.Clarke	E. H. Roalson 1384 (RSA)	Mexico	AF190616	-	1
Bulbostylis hirtella (Schrad. Ex Schult.) Nees ex Urb.	R. Ardissone 200 (FLOR)	Brazil	xxxxxxxx	xxxxxxxx	3
Bulbostylis hispidula (Vahl) R.W.Haines	L. Smook 9956 B (PRE)	Namibia	xxxxxxxx	xxxxxxxx	n.a.
Bulbostylis junciformis (H.B.K.) C.B.Clarke ex S.Moore	R. Ardissone 189 (FLOR)	Brazil	xxxxxxxx	xxxxxxxx	2
Bulbostylis juncoides (Vahl) Kük. Ex Herter	A. Reutemann 153 (SF)	Argentina	xxxxxxxx	xxxxxxxx	3
Bulbostylis loefgrenii (Boeck.) Prata & López	R. Ardissone 186 (FLOR)	Brazil	xxxxxxxx	-	3
Bulbostylis loefgrenii (Boeck.) Prata & López	A. Reutemann 158 (SF)	Argentina	-	xxxxxxxx	3
Bulbostylis macra (Ridl.) C.B.Clarke	C.J. Kayombo 1725 (PRE)	Tanzania	xxxxxxxx	xxxxxxxx	n.a.
Bulbostylis mucronata C.B.Clarke	D.S. Hardy 6511 A (PRE)	Namibia	xxxxxxxx	xxxxxxxx	n.a.
Bulbostylis paradoxa (Spreng.) Lindm.	R. Ardissone 372 (ICN)	Brazil	xxxxxxxx	xxxxxxxx	1
Bulbostylis pseudoperennis Goetgh.	Malaisse 317 (PRE)	Zaire	xxxxxxxx	xxxxxxxx	n.a.
Bulbostylis pusilla (Hochst. ex A.Rich.) C.B.Clarke	Retief 1545 (PRE)	Namibia	xxxxxxxx	xxxxxxxx	n.a.
Bulbostylis rugosa M.G.López	A. Reutemann 85 (SF)	Argentina	xxxxxxxx	xxxxxxxx	1
Bulbostylis scabra (J.Presl & C.Presl) C.B.Clarke	A. Reutemann 100 (SF)	Argentina	xxxxxxxx	xxxxxxxx	1
Bulbostylis scabricaulis Cherm.	C. Reid 1728 (PRE)	South Africa	xxxxxxxx	xxxxxxxx	n.a.
Bulbostylis scleropus C.B.Clarke	A. de Castro 478 (PRE)	South Africa	xxxxxxxx	xxxxxxxx	n.a.
Bulbostylis sphaerocephala (Boeck.) Lindm.	A. Reutemann 161 (SF)	Argentina	xxxxxxxx	xxxxxxxx	2
Bulbostylis sphaerolepis (Boeck.) Beetle	A. Reutemann 169 (SF)	Argentina	xxxxxxxx	xxxxxxxx	3
Bulbostylis stenocarpa Kük.	R. Ardissone 162 (FLOR)	Brazil	xxxxxxxx	xxxxxxxx	3
Bulbostylis striatella C.B.Clarke	J. J. Bruhl 2084 (NE)	Australia	AY506765	AY506711	
Bulbostylis subtilis M.G.López	A. Reutemann 156 (SF)	Argentina	xxxxxxxx	xxxxxxxx	3

Bulbostylis trabeculata C.B.Clarke	C. J. Ward 11981 (PRE)	Namibia	**xxxxxxxx**	**xxxxxxxx**	n.a.
Bulbostylis wanderleyana Prata & M.G.López	A. Reutemann 159 (SF)	Argentina	**xxxxxxxx**	**xxxxxxxx**	3
Bulbostylis sp1	R. Ardissone 370 (ICN)	Brazil	**xxxxxxxx**	**xxxxxxxx**	n.a.
Bulbostylis sp2	R. Ardissone 196 (FLOR)	Brazil	**xxxxxxxx**	**xxxxxxxx**	n.a.
Bulbostylis sp3	R. Ardissone 135 (FLOR)	Brazil	**xxxxxxxx**	**xxxxxxxx**	n.a.
Bulbostylis sp4	R. Ardissone 382 (ICN)	Brazil	**xxxxxxxx**	**xxxxxxxx**	n.a.
Bulbostylis sp5	R. Ardissone 27 (FLOR)	Brazil	**xxxxxxxx**	**xxxxxxxx**	n.a.
Bulbostylis sp6	R. Ardissone 352 (FLOR)	Brazil	**xxxxxxxx**	**xxxxxxxx**	n.a.
Bulbostylis sp7	R. Ardissone 418 (ICN)	Brazil	**xxxxxxxx**	**xxxxxxxx**	n.a.
Bulbostylis sp8	K. L. Clarke 184 (NE)	Australia	AY506766	AY506713	n.a.

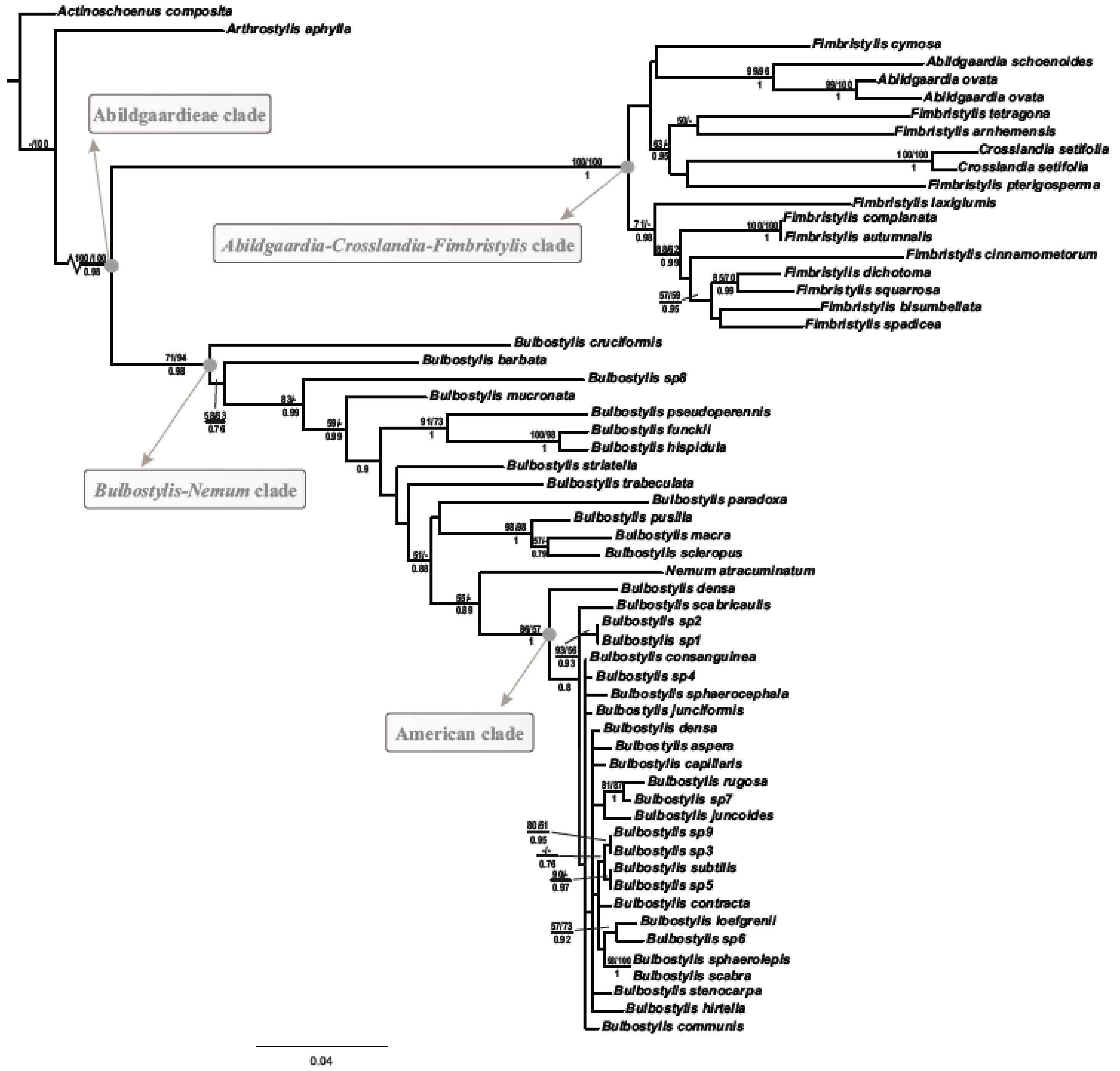

Fig. 1. Maximum likelihood tree inferred from analysis of nuclear ITS sequences. Numbers above branches represent bootstrap values from maximum likelihood/parsimony respectively; numbers below branches are Bayesian posterior probabilities.

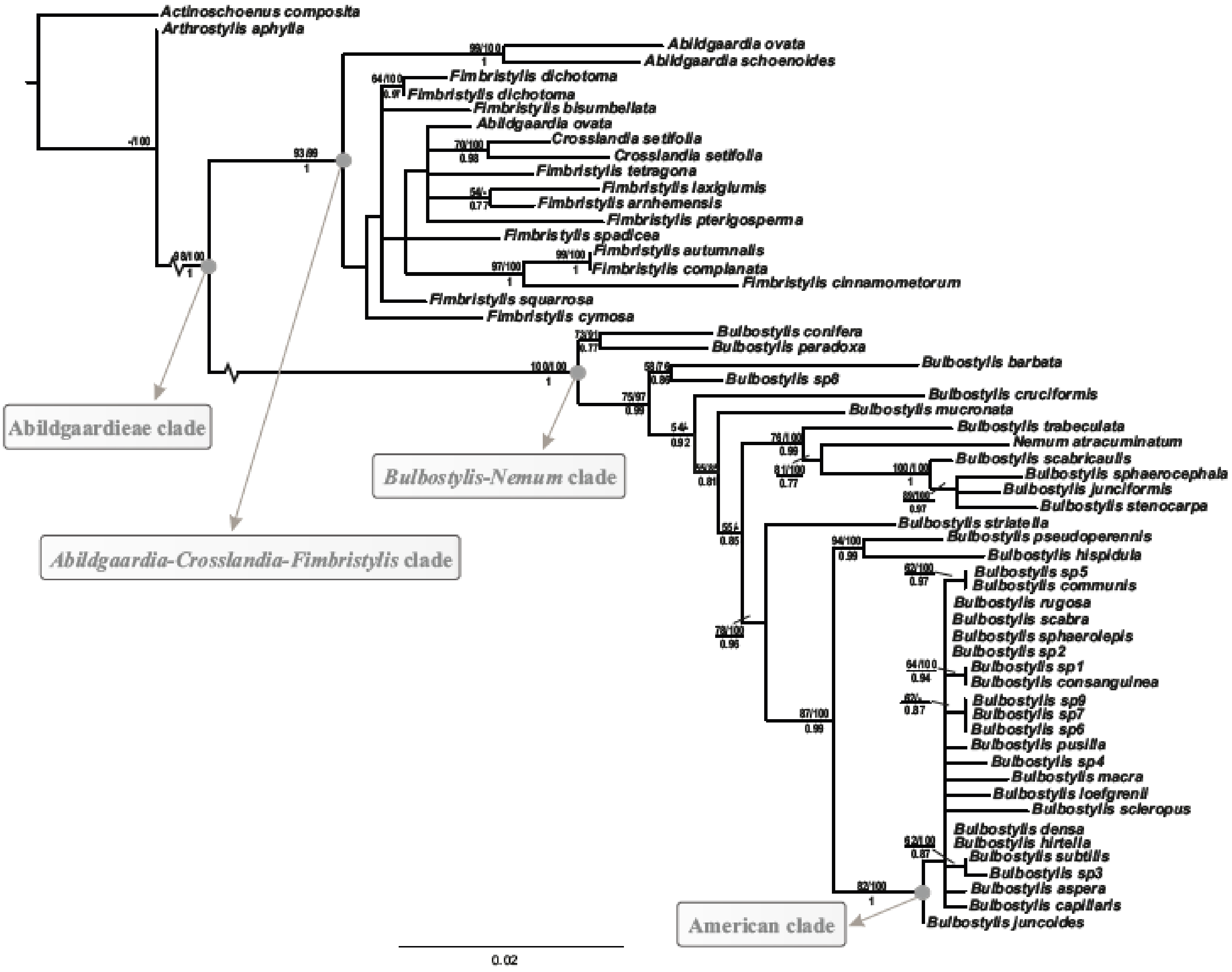

Fig. 2. Maximum likelihood tree inferred from analysis of plastid *trn*L intron sequences. Numbers above branches represent bootstrap values from maximum likelihood/parsimony respectively; numbers below branches are Bayesian posterior probabilities.

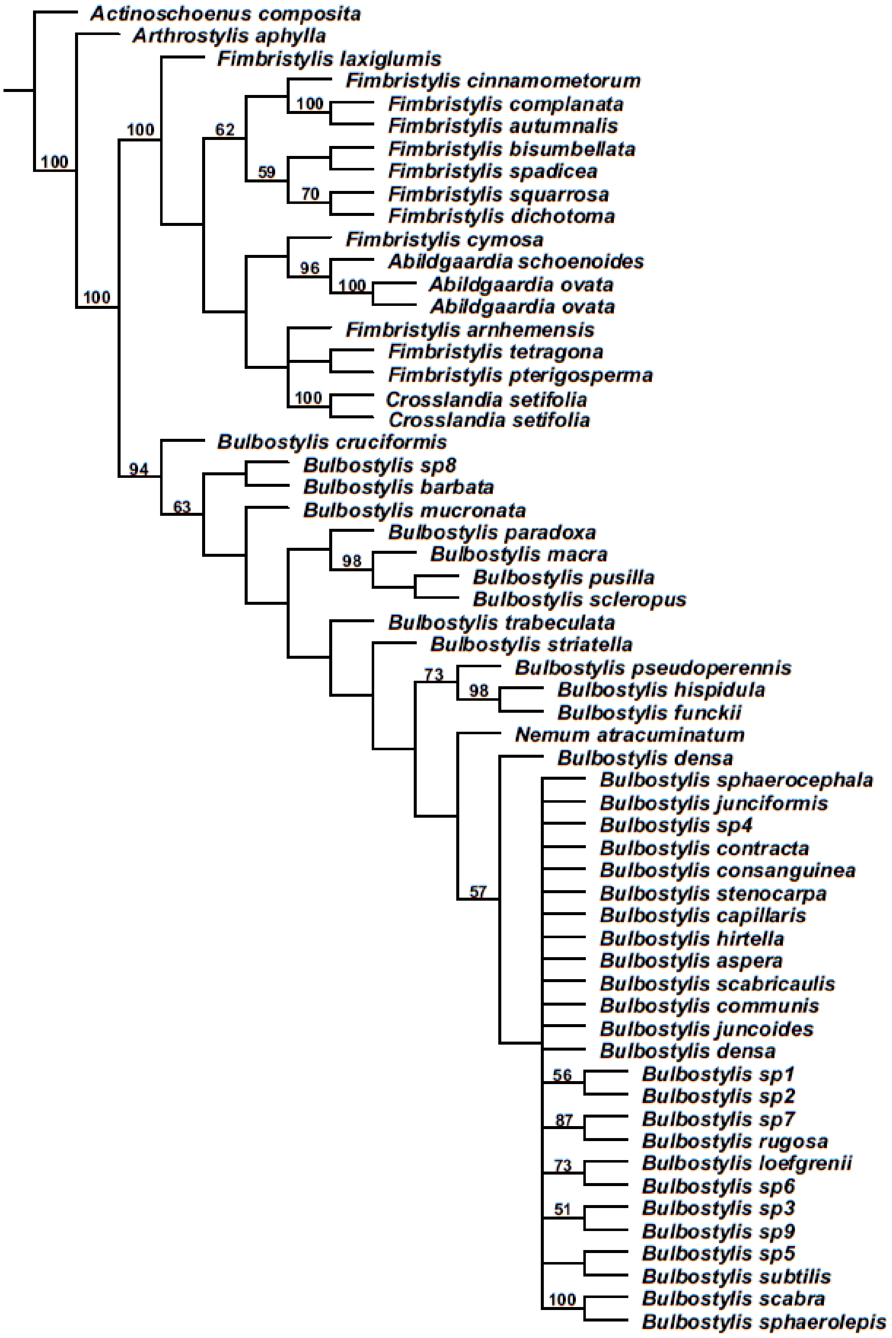

Fig. 3. Maximum likelihood tree inferred from analysis of combined *trn*L intron and ITS sequences. Numbers above branches are bootstrap values from maximum likelihood/parsimony respectively; numbers below branches are Bayesian posterior probabilities.

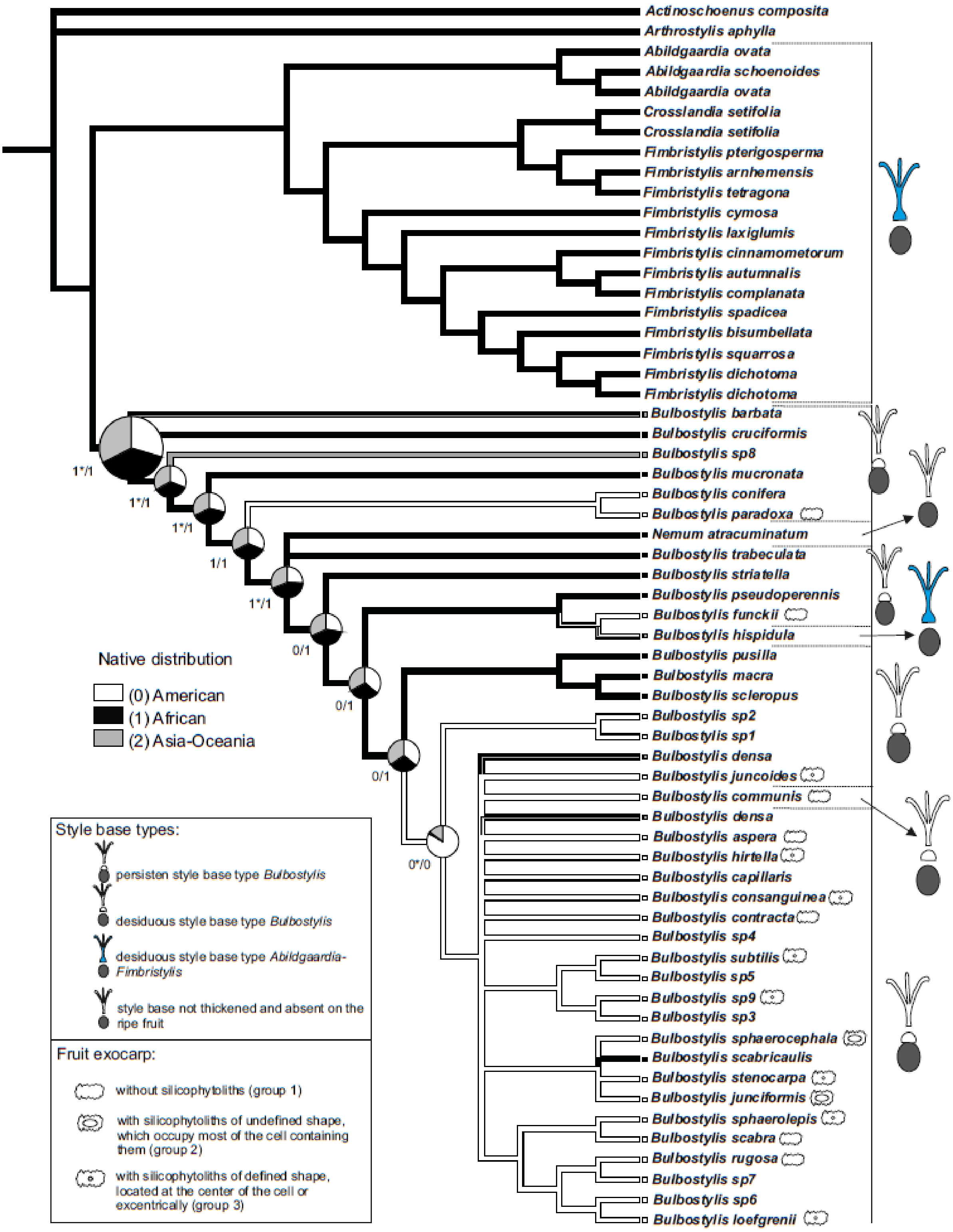
Actinoschoenus composita
Arthrostylis aphylla
Abildgaardia ovata
Abildgaardia schoenoides
Abildgaardia ovata
Crosslandia setifolia
Crosslandia setifolia
Fimbristylis pterigosperma
Fimbristylis arnhemensis
Fimbristylis tetragona
Fimbristylis cymosa
Fimbristylis laxiglumis
Fimbristylis cinnamometorum
Fimbristylis autumnalis
Fimbristylis complanata
Fimbristylis spadicea
Fimbristylis bisumbellata
Fimbristylis squarrosa
Fimbristylis dichotoma
Fimbristylis dichotoma
Bulbostylis barbata
Bulbostylis cruciformis
Bulbostylis sp8
Bulbostylis mucronata
Bulbostylis conifera
Bulbostylis paradoxa
Nemum atracuminatum
Bulbostylis trabeculata
Bulbostylis striatella
Bulbostylis pseudoperennis
Bulbostylis funckii
Bulbostylis hispidula
Bulbostylis pusilla
Bulbostylis macra
Bulbostylis scleropus
Bulbostylis sp2
Bulbostylis sp1
Bulbostylis densa
Bulbostylis juncoides
Bulbostylis communis
Bulbostylis densa
Bulbostylis aspera
Bulbostylis hirtella
Bulbostylis capillaris
Bulbostylis consanguinea
Bulbostylis contracta
Bulbostylis sp4
Bulbostylis subtilis
Bulbostylis sp5
Bulbostylis sp9
Bulbostylis sp3
Bulbostylis sphaerocephala
Bulbostylis scabricaulis
Bulbostylis stenocarpa
Bulbostylis junciformis
Bulbostylis sphaerolepis
Bulbostylis scabra
Bulbostylis rugosa
Bulbostylis sp7
Bulbostylis sp6
Bulbostylis loefgrenii
1*/1
1*/1
1*/1
1/1
1*/1
0/1
0/1
0/1
0*/0
Native distribution
☐ (0) American
■ (1) African
▨ (2) Asia-Oceania
Style base types:
persisten style base type Bulbostylis
desiduous style base type Bulbostylis
desiduous style base type Abildgaardia-Fimbristylis
style base not thickened and absent on the ripe fruit
Fruit exocarp:
without silicophytoliths (group 1)
with silicophytoliths of undefined shape, which occupy most of the cell containing them (group 2)
with silicophytoliths of defined shape, located at the center of the cell or excentrically (group 3)

Fig. 4. Reconstructed ancestral character states of native distribution on the Bayesian MCMC majority rule consensus tree (15002 trees), and mapped of some morphological characters discussed in the text. Branch shading indicates parsimony reconstruction. Pie charts indicate Bayesian ancestral characters posterior probabilities at selected nodes. First number below charts indicates the state with the highest likelihood based on the Bayes factor (the asterisks imply Bayes factor > 2). The second numbers specify the state indicated by the parsimony reconstruction.

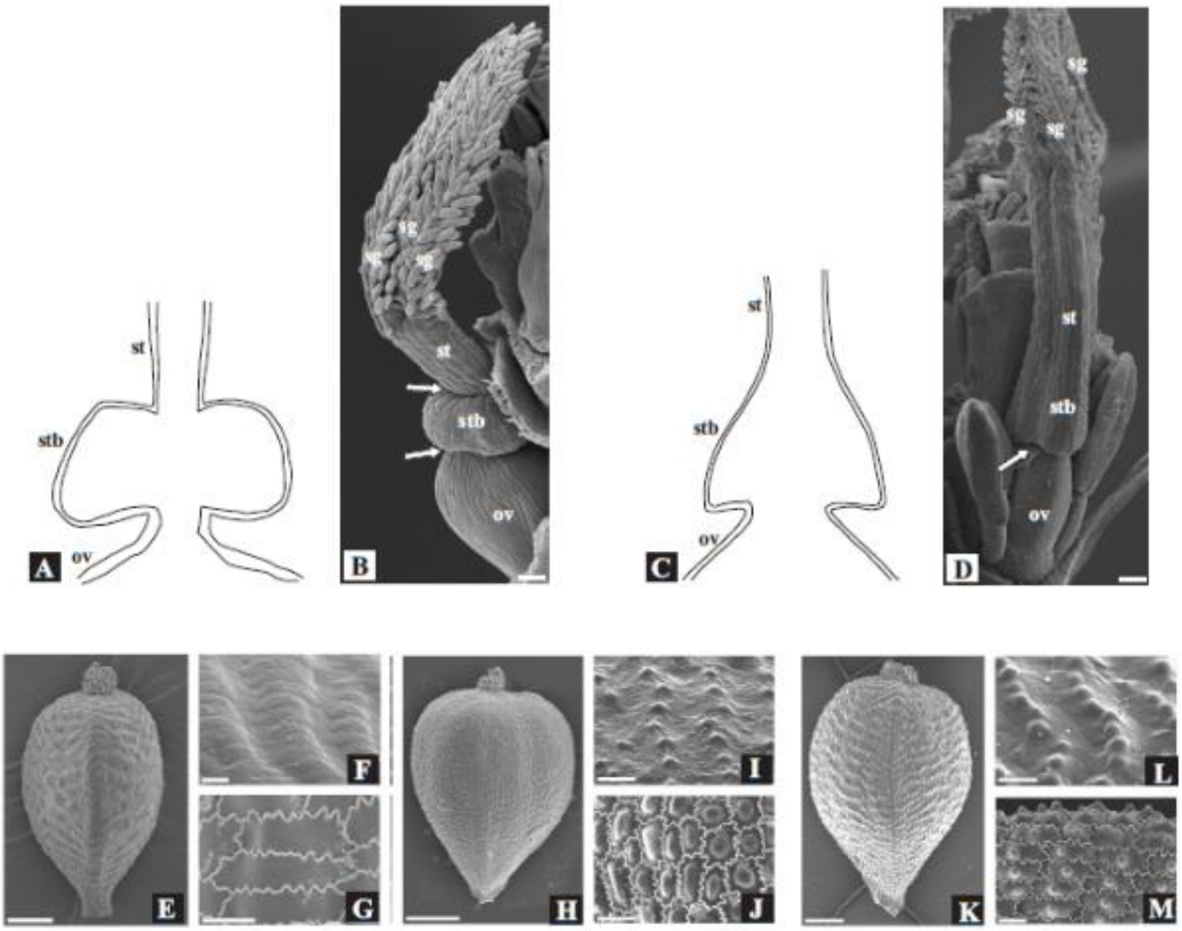

Fig. 5.1-5.10. Character states of fruit micromorphology in South American species of *Bulbostylis* according to López (2012) and López & Gonzalez (2017), and style base structure in *Abildgaardia*, *Bulbostylis* and *Fimbristylis* according to Reutemann et al. (2012): **2.1-2.2**- *Bulbostylis aspera*, fruit exocarp without silicophytoliths (group 1), **2.3-2.4**- *Bulbostylis sphaerocephala*, fruit exocarp with silicophytoliths of undefined shape, which occupy most of the cell containing them (group 2), **2.5-2.6**- *Bulbostylis juncoides*, fruit exocarp with silicophytoliths of defined shape, located at the center of the cell or eccentrically (group 3), **2.7-2.8**- *Bulbostylis juncoides*, style base type *Bulbostylis*, **2.9-2.10**- *Fimbristylis complanata*, style base type *Abildgaardia-Fimbristylis,*. References: ov, ovary wall; sg, stigma; st, style; stb, style base. Scale bars = 50 µm.

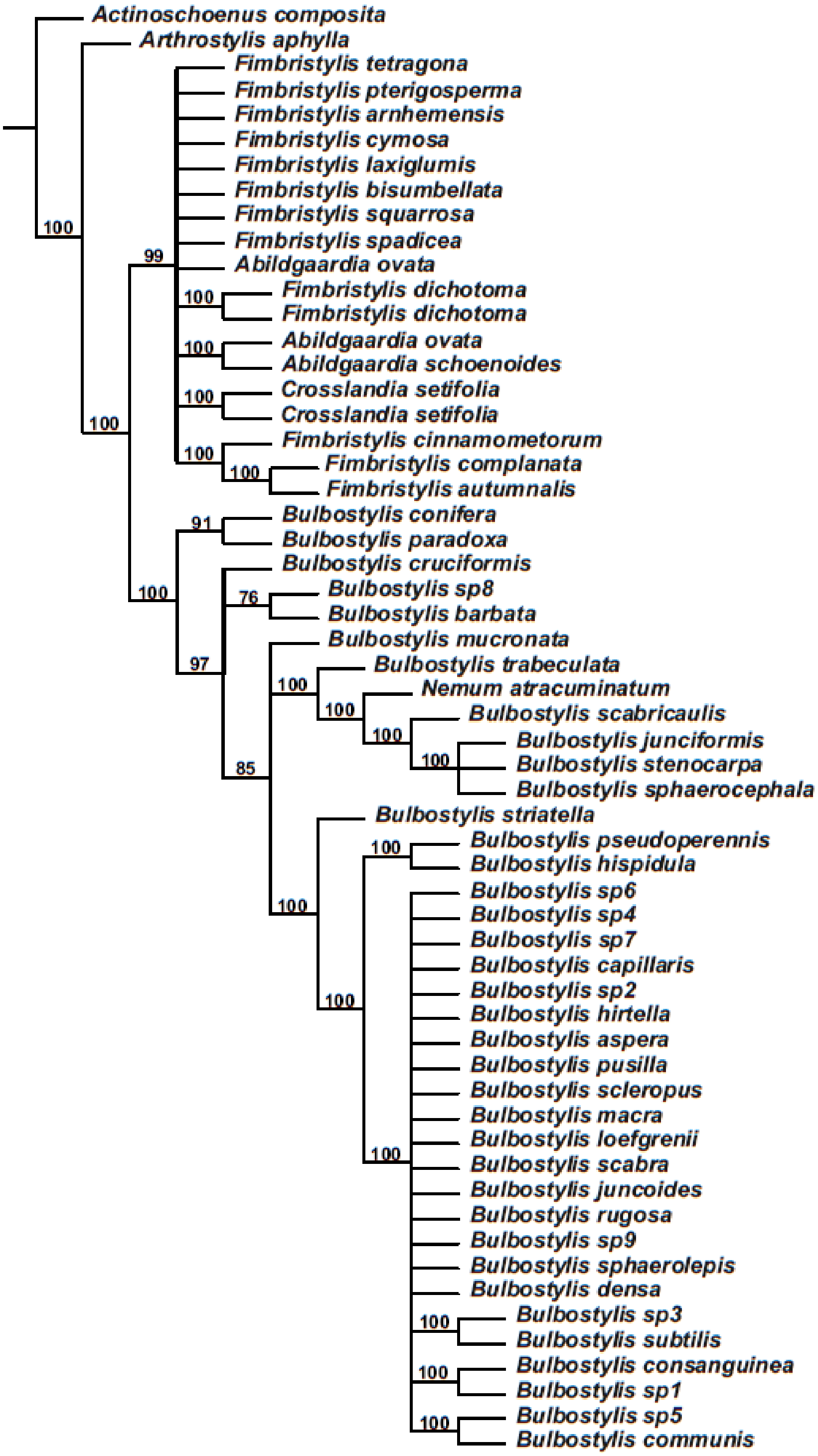

Fig. S1. Parsimony strict consensus tree of the ITS data set, produced from 864 most parsimonious trees with a length of 807 steps. Values above branches represent bootstrap supports (>50%).

Fig. S2. Parsimony strict consensus tree of the *trn*L intron data set, produced from 6972 most parsimonious trees with a length of 171 steps. Values above branches represent bootstrap supports (>50%).

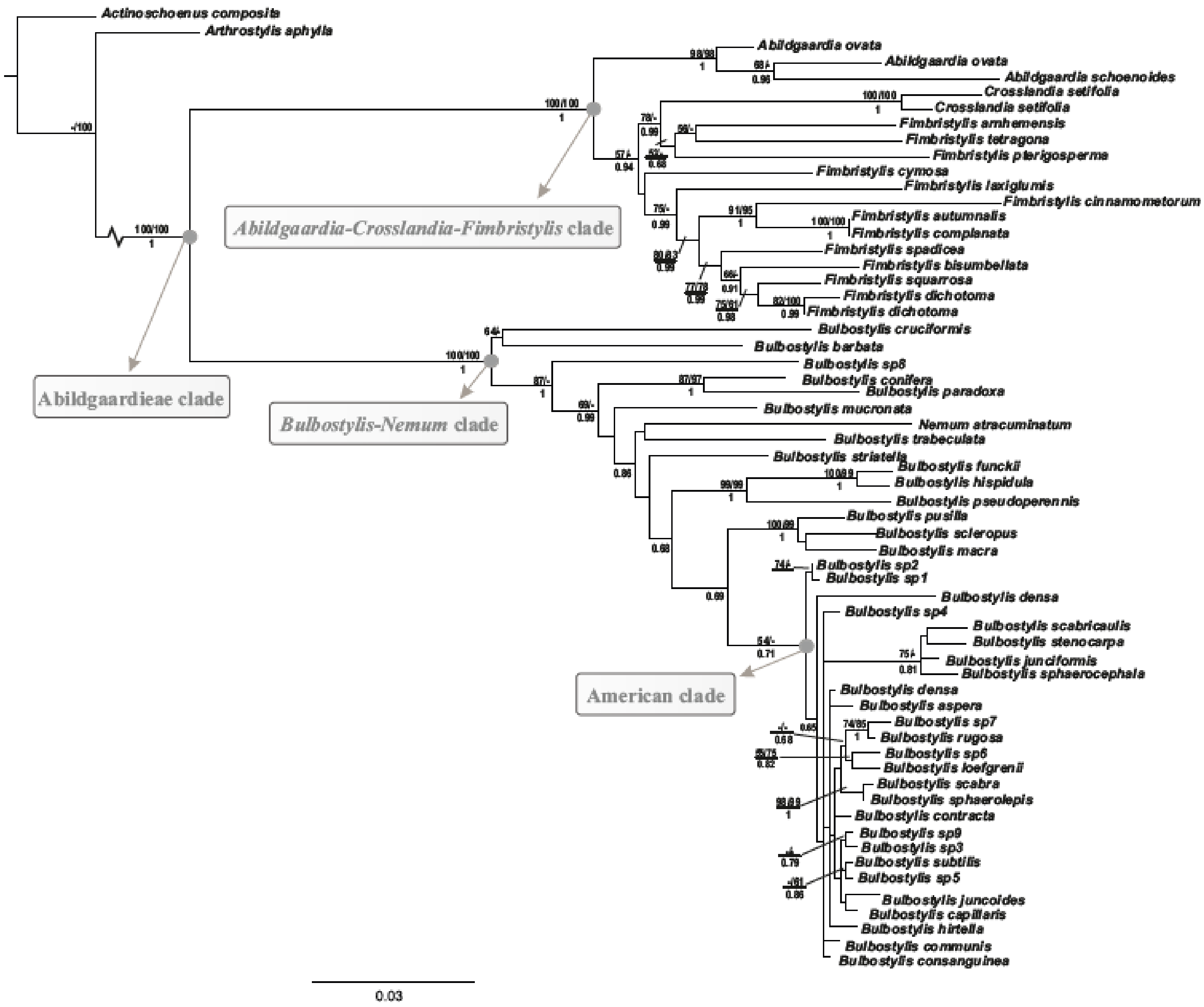

Fig. S3. Parsimony strict consensus tree of the combined ITS+*trn*L intron data set, based on 198 optimum trees with a length of 1019 steps. Values above branches represent bootstrap supports (>50%).

CAPÍTULO II

Bulbostylis (Cyperaceae, Abildgaardieae) in Brazil: New Species and Geographic Distribution Update

Rodrigo Ardissone,[1] Ilsi Boldrini,[1] André Vanzela,[2] and Rafael Trevisan[3]

[1]Programa de Pós-graduação em Botânica, Instituto de Biociências,
Universidade Federal do Rio Grande do Sul, 91509-900, Porto Alegre, RS, Brazil.

[2]Programa de Pos-graduação em Genética e Biologia Molecular, Departamento
de Biologia Geral, Universidade Estadual de Londrina, 86057-970, Londrina, PR,
Brazil.

[3]Departamento de Botânica, Centro de Ciências Biológicas, Universidade
Federal de Santa Catarina, 88040-900, Florianópolis, SC, Brazil.

Abstract—*Bulbostylis* comprises ca. 220 species distributed in the tropical and subtropical regions of both hemispheres, most of them concentrated in Africa and Brazil. The species of genus have graminoid appearance, strogly heliophilia and can be found in both newly disturbed or in conserved environments. Here we describe two new species, ***Bulbostylis scabriculmis*** and ***Bulbostylis divaricata***, whose taxonomic treatment includes morphological descriptions, ecological information, geographic distribution and conservation status. We also provided new geographic distribution data for *Bulbostylis contracta* and *Bulbostylis rugosa*, previously without records from Brazil.

Keywords—Taxonomy, Poales, Campos Sulinos, Cyperoideae, SEM - scanning electron microscopy, Pampa, South America

Resumo—*Bulbostylis* compreende aproximadamente 220 espécies distribuídas em regiões tropicais e subtropicais de ambos hemisférios, a maioria delas concentradas na África e no Brasil. As espécies do gênero possuem aspecto graminóide, forte heliofilia e podem ser encontradas tanto em ambientes recém perturbados como nos mais conservados. Nesse artigo descrevemos duas espécies novas para a ciência, ***Bulbostylis scabriculmis*** e ***Bulbostylis divaricata***, incluindo nos tratamentos taxonômicos descrições morfológicas, informações ecológicas, distribuição geográfica e estado de conservação. Nós ainda fornecemos novos dados de distribuição geográfica para *Bulbostylis contracta* e *Bulbostylis rugosa*, até então sem registros no Brasil.

Bulbostylis Kunth (1837) *nom. cons*. differ morphologically from other genus of Cyperaceae both by the sheaths that have firm and white trichomes at the apex and by the achenes obtusely trigonous with stylopodium persistent. The plants is small and cespitose, perennial or annual. Among perennial species, rarely form an elongated rhizome or caudex. The inflorescences is anthelate, capitate or formed by a single spikelet. The spikelets is composed by deciduous glumes, spirally arranged, rarely distichous, each subtending a flower bisexual. Bristles absent, stamens 1-3, Style 3 (-2) –fid, stylopodium thickened, persistent rarely deciduous. Achene obovate to obpyruform, rounded trigonous, variously ornamented, rarely smooth (Goetghebeur 1998; Kral and Davidse 1987).

The species are heliophiles, grow abundantly in open areas, on acid and well-drained soils, but humid in some season. We found populations of *Bulbostylis* in dry grasslands, coastal dunes, rocky or sandy outcrops. The plants are frequently pioneers in the colonization of disturbed areas with soil exposed or removed. It has C4 metabolism, and Kranz anatomy of the eleocharoid or fimbristyloid types (Prata et al. 2017; Govaerts et al*. 2016;* Prata et al. 2007; Soros and Bruhl 2000). Usually the species of *Bulbostylis* flourish and fruit in the summer. It is common to find samples with young flowers and mature achenes in the same inflorescence, depending to the position in spikelets.

For Brazil is mentioned 59 species (20 endemic), one subspecies, and two varieties of *Bulbostylis* (Cyperaceae in Flora do Brasil 2020 under construction. Jardim Botânico do Rio de Janeiro. Available at: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB7153>. Accessed on: 3 May 2017) (Alves *et al*. 2009) four others recently described (Prata *et al*. 2017), and the presented here, totaling 67 species for the country.

The gap in knowledge of Cyperaceae Juss. (1789) *nom*. *cons*. is accentuated when we refer to South America, and therefore, that region requires a greater collection effort and review of herbarium material for us to know all this biodiversity. In the XXI century, many taxonomic studies in Cyperaceae focused on describing new species and genera, and updating taxonomic status of taxa previously described (Prata et al. 2017; Ronchi et al. 2016; Ferreira et al. 2015; Trevisan et al. 2014, 2012; Gilmour et al. 2013; Thomas et al. 2013; Zika 2012; López & Simpson 2012; Muasya et al. 2012; Larridon et al. 2011; Sorrie et al. 2011; Hinchliff et al. 2010; Huygh et al. 2010; Trevisan and Boldrini 2010; López 2007; Prata et al. 2001;).

The species treated here occurring in the subtropical grasslands of South America regionally called 'Campos Sulinos'. These grasslands comprise two extensive ecosystems in the Southern Brazil, each with distinct floristic elements and climactic characteristics of different geomorphological systems, the grasslands of biomes Pampa and Atlantic Rain Forest. Actually these ecosystems are under heavy threat due to their conversion into monocultures of, among others, soybean and pine.

The Pampa biome is a major grassland with forest adjacent to the river channels located in the southern half of Rio Grande do Sul, the southernmost Brazilian State. These grasslands are the north part of a larger formation with total area of 760.000 km² which extends from the lowlands of Brazilian coast through Argentina and Uruguay. The Pampa soils are shallow and easy to disaggregate, characteristics that favor the formation of grasslands instead of forest. The climate is subtropical humid with precipitation around 1300 mm annually and temperatures that in the summer surpass 40° C.

The grasslands of Atlantic Rain Forest biome is located in the highlands [700 - 1.300 (1.800) m.a.s.l.] of Rio Grande do Sul, Santa Catarina and Paraná states. The climate is also subtropical humid, but, compared to the Pampa, with milder temperatures in summer and more extreme in winter. On the other hand, precipitation is higher, reaching 2.000 mm annually on the eastern edge of the plateau (Overbeck et al. 2015). Grasslands of Pampa and Atlantic Rain Forest share 45% of the plant species, while the levels of endemism can distinguish the two formations. These relicual grasslands occupy much larger areas and have fragmented during the climate changes of Holocene, especially in the last 1000 years ago when the forests previously confined in the river channels advanced on the grasslands (Behling et al. 2009). Mosaics between grasslands and forest, without a definitive explanation, are verified at higher altitudes in the two biomes. The grasslands of these mosaics also have more floristic similarities in relation to the lowland grasslands, constituting an zone of ecological tension characterized by the presence of more than one vegetative formation on a small area (IBGE 1986).

The grasslands of Atlantic Forest are restricted to plateaus, with the presence of snow and temperatures below 0° C in the winter. The Brazilian southern plateau is discontinuous and has several canyons and escarpments, this reflects directly in the grasslands of the Atlantic Forest, also discontinuous. These grasslands are present in Rio Grande do Sul, Santa Catarina and Paraná states, Brazil. Portions in northern Paraná already have floristic, physiognomic and climatic characteristics that resemble those of the Cerrado biome, constituting an important transitional region and a limit of distribution for several species.

Here we describe two new species, *Bulbostylis scabriculmis* and *Bulbostylis divaricata*, and we add collection data that expands the distribution of *Bulbostylis rugosa* M. G. López (1996) and *Bulbostylis contracta* (Kük. ex Osten) M. G. López & D.A. Simpson (2012) previously unknown in Brazil.

MATERIALS AND METHODS

We conducted expeditions in southern Brazil between 2011 and 2016, when looking for natural grasslands, mostly still used for livestock. The collections of *Bulbostylis* at FLOR, HAS, HBR, HCF, HUCS, ICN, MBM, MPUC, PACA, PEL, and UPCB and the type collections of the herbaria P, K, L, W, WU, C, B and M were studied using a stereomicroscope. We also consulted images of collections available on “INCT Herbário Virtual da Flora e dos Fungos” (http://inct.florabrasil.net) and JSTOR (https://www.jstor.org/). The assessment of conservation status followed the IUCN (2012, 2014) criteria in http://geocat.kew.org/ website, based on a distribution cell width of 10 km. For SEM, we extracted a few mature achenes from samples. The achenes, without pre-treatment, were fixed on aluminum stubs with double-sided carbon tape and sputter coated with gold in a LEICA MET metalalizer model SCD 500. Images were captured and observations were made using a SEM JEOL model JSM-brand 6390LV at the Central Laboratory of Electron Microscopy at the Federal University of Santa Catarina, in Florianópolis, Santa Catarina, Brazil and at the Electron Microscopy and Microanalysis Laboratory, State University of Londrina, in Londrina, Paraná, Brazil. The morphological descriptions and the images presented in the plates were taken with a Leica S6D stereoscopic microscope, equipped with a EC3 camera and LAS EZ software (Leica, Wetzlar, Germany), and edited with Adobe Photoshop CS3 (Adobe Systems Inc., San Jose, California). Plates were prepared in Corel from fresh and pressed samples. The length measurements of the achenes do not include stylopodium. The terminology used to describe morphology characteristics followed Stearn (1983) and Bruhl (1995). The maps were made using the software DIVA-GIS 7.5, LizardTech, Inc., University of California.

TAXONOMIC TREATMENT

NEW SPECIES

Bulbostylis divaricata R. Ardiss. & M. G. López sp. nov. TYPE: BRAZIL. Paraná: Piraí do Sul, próximo ao Canion Guartelá, 16 de março de 2016, R. Ardissone, P. Burchardt & A. Vanzela 426 (holotype: ICN).

Annual, cespitose, 15−35 cm tall, the base pale castaneous and not thickened. Roots capillary-fibrous; rhizome absent. Leaves few per culm, 1/5 the length of the culm or less; sheaths 1−5 cm long, membranaceous, pale castaneous, the apex oblique, ciliate with few trichomes, the trichomes white; ligule absent; blade 20−100 (150) × 0.2 mm, capillary, erect, flat to slightly concave, the abaxial surface 3-costate, the adaxial surface flat to canaliculate, margin and nerves smooth, 2-nerved, the nerves smooth. Culm 0.4 mm diam., terete, longitudinally 6−8 costate, slightly salient, smooth to the touch. Involucral bracts glume-like, the basal bract 0.5−0.8 cm, much shorter than the diameter of inflorescence, slightly antrorsely scabrous, the margin short-ciliate. Inflorescence terminal 1−1.5 × 1−2 mm, anthelate, simple or compound, the primary branches 0.6 − 1 cm with axes divergent or patent, the secondary branches 0.2 − 0.3 cm with 2−4 (6) spikelets, the central one sessile and others pedicellate; spikelet ovoid 2.5−7 × 1.5−2 mm, 5−12-flowered; rachilla contracted, winged, persistent; glume 1.2−2 × 0.6−1 mm, oval, deciduous, navicular, keeled, the abaxial surface pilose, the adaxial surface glabrous, the keel 3-nerved, the apex acute or obtuse, muticous or mucronate, stramineous or green along the keel and at the base, brown on the sides and distally, the margin ciliate.

Stamens 3, the filament band-shaped, the anthers 0,7 mm. Style trifid, the margin not fimbriate except for the stigmatic branches, the base thickened, stylopodium persistent on the achene body. Achene obovoid 0.8−0.9 × 0.7−0.8 mm, trigonous, the base often slightly attenuate, brown when mature, the surface transversely wrinkled, the epidermal cells longitudinally elongate, the apex slightly depressed without constriction in the insertion of stylopodium; stylopodium 0,1 mm, discoid to plane-convex, brown, the surface wrinkled. Figs 1, 2, 3, 4 and 9.

Phenology—Flowering and fruiting in the summer, between the months of December and March.

Distribution—High altitude grasslands of Atlantic Forest biome in Santa Catarina and Paraná states.

Habitat—Rocky outcrops, directly on the rock, in full sun.

Conservation Status—Endranged (EN), both for Area of Occupancy (AOO - 400.000 km²) and Extent of Occurrence (EOO - 1,388,000 km²). Although only few collections of this species are known, their wide distribution including southern Brazil.

Etymology—The epithet refers to the well-developed inflorescences with branches arranged at obtuse angles, a diagnostic feature of this species**.**

Paratypes—BRAZIL. Paraná: Balsa Nova, estrada para Ponte dos Arcos, 956 m.s.m., 31 March 2012, *R. Ardissone & P. Weber 131*; Lapa, Pedra da Gruta do Monge, 6 November 2005, *R. Wasum et al. 3135* (MBM); Ponta Grossa, 25°10'15" S, 50°10'42" W, near Tibagi River, road BR 376, 2 km to Vila Velha, 01/25/1997, H. M. Longhi-Wagner 3766 (ICN).

Observations—*Bulbostylis divaricata* resembles *Bulbostylis brevifolia* Palla (1908) in the antheloid inflorescence and the undeveloped leaf blade, without exceeding 1/5 the length of the stems. However, these two species differs in achenes features, with well-marked wrinkles on the surface vs. smooth surface characteristic of *B. brevifolia*. *Bulbostylis divaricata* resembles *Bulbostylis loefgrenii* (Boeck.) A. Prata & M. G. López (2001) in its anthela with divergent axes, but differs in leaf length and the morphology of achenes. *Bulbostylis loefgrenii* has leaves that surpass 1/3 the length of culms, achenes 1.3-1.5 × 0,8-1 mm and a smooth surface vs. leaves with up to 1/5 of stem length, achenes 0.8-0.9 × 0.7-0.8 mm and transversely wrinkled surface in *B. divaricata*.

Fig. 1. Overview of *Bulbostylis divaricata* habit. L.B. Smith & R. Reitz 14361 (FLOR).

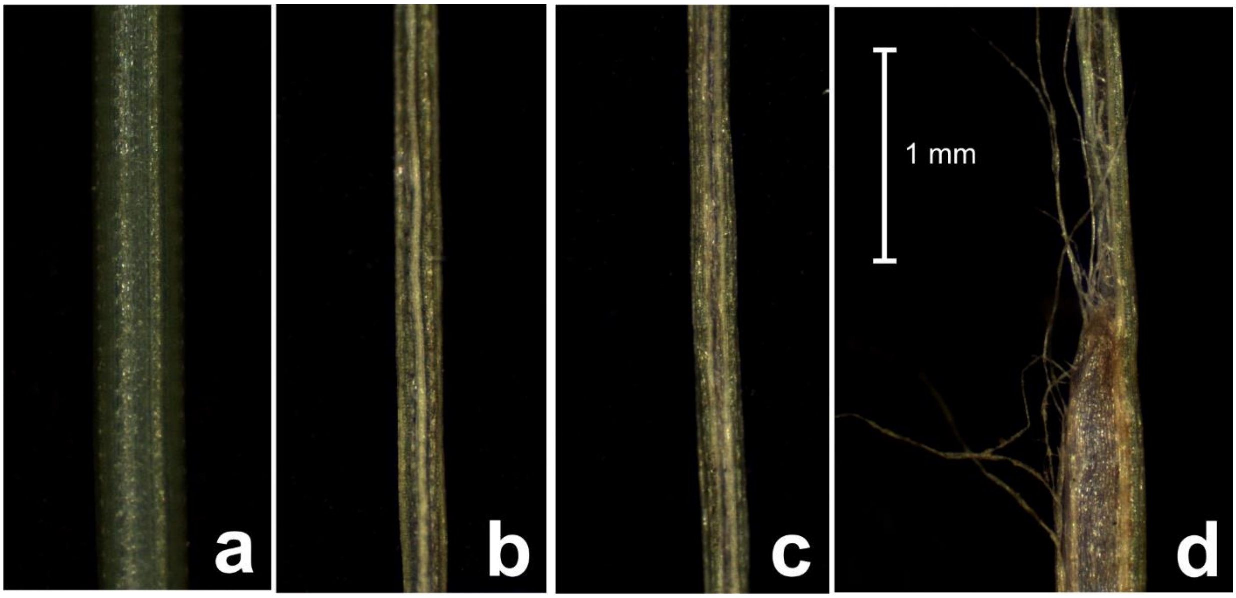

Fig. 2. a–d. Vegetative parts and general appearance of *Bulbostylis divaricata*. a. Culm. b. Leaf in abaxial view. c. Leaf in adaxial view. d. Sheath apex with trichomes in lateral view. The bar of 1 mm in “d” represents also the sections in “a, b, and c”. [a–d Photos of R. Ardissone et al. 426 (ICN);].

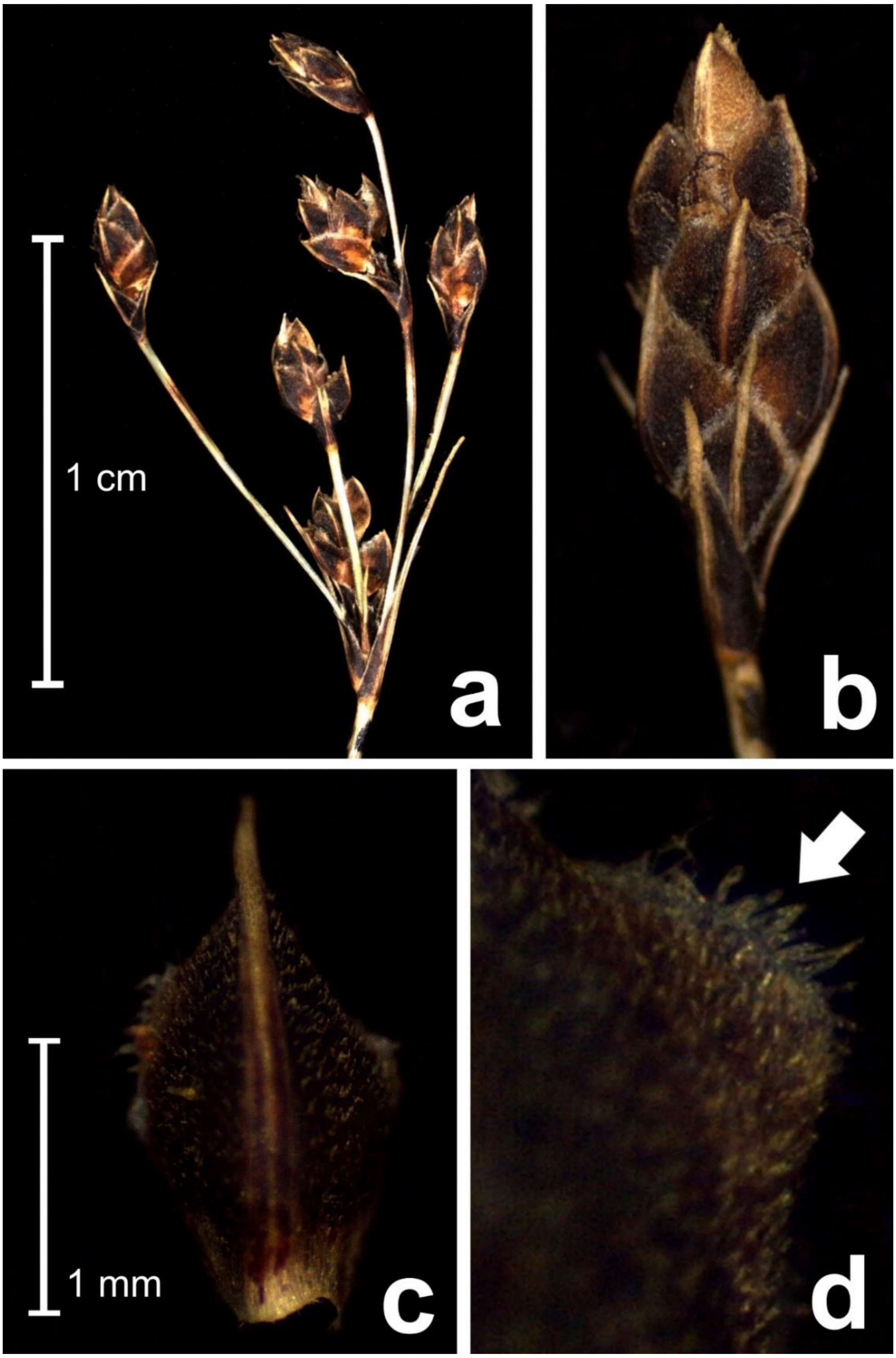

Fig. 3. a–d. Reprodutive parts of *Bulbostylis divaricata*. a. Young inflorescence. b. Terminal spikelet with about 3.5 mm, containing involucral bracts and terminal portion of pedicel. c. Mucronate glume in dorsal view. d. Margin of glume in dorsal view which was enlarged seven times; Arrow point out detail of trichomes. [a–d Photos of R. Ardissone et al. 426 (ICN)].

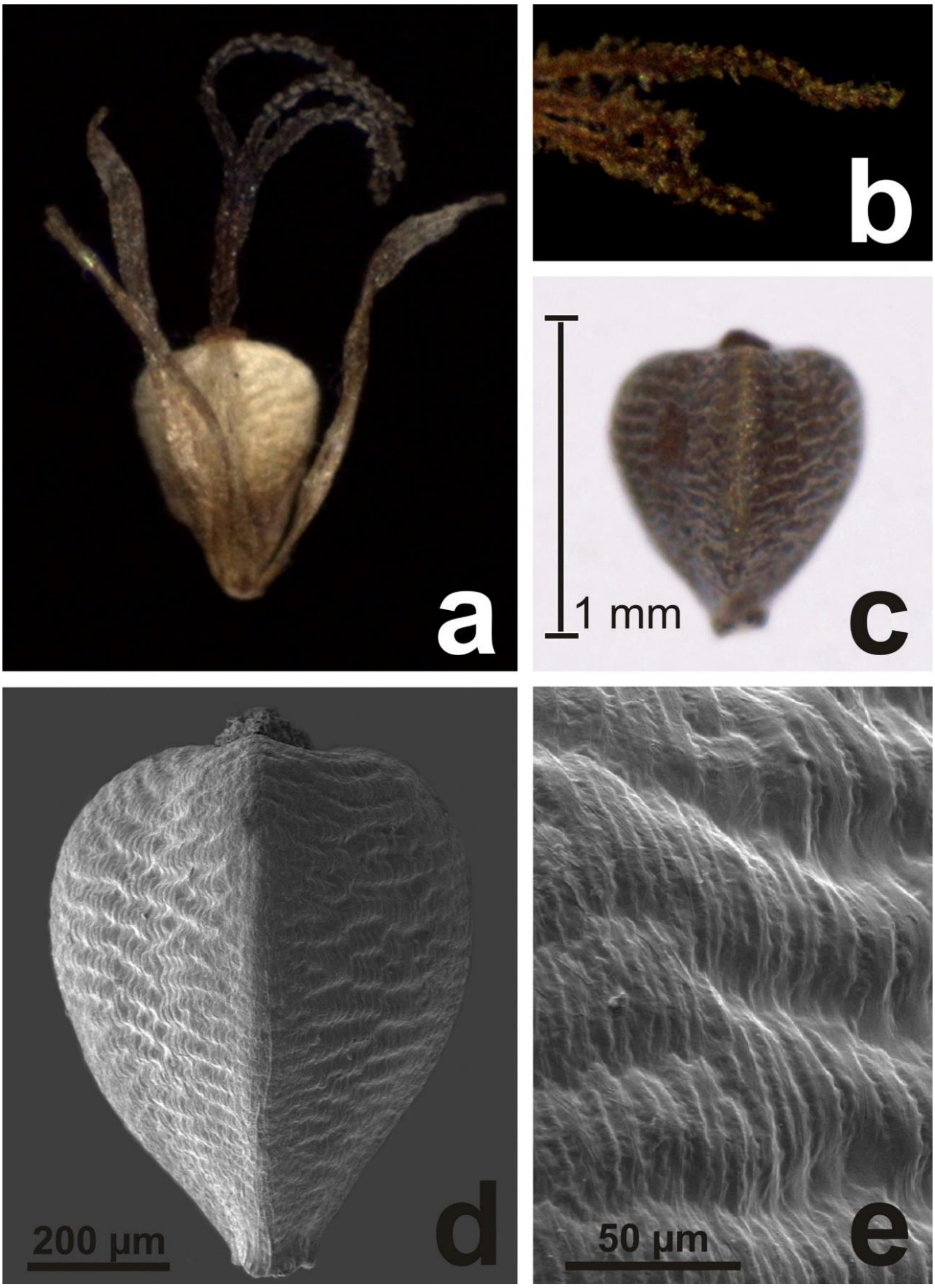

Fig. 4. a–e. Fruits and reprodutive details of *Bulbostylis divaricata*. a. Young achene (~1 mm length without stylus), with style and filaments in a dorsal view. b. Detail of stigmatic branches (image enlarged two times). c. Mature achene in dorsal view. d. Mature achene in dorsal view. e. Detail of right side of dorsal surface of mature achene [a–c Photos of R. Ardissone et al. 426 (ICN); d–e SEM images of R. Ardissone & P. Weber 131 (FLOR)].

Bulbostylis scabriculmis R. Ardiss. & R. Trevis. sp. nov.—TYPE: BRAZIL. Paraná: Jaguariaíva: Trilha do Parque do Cerrado, 15 de março de 2016, *R. Ardissone & A. Vanzela 430* (Holotype: ICN).

Perennial, densely cespitose, 15−35 cm tall, the base pale castaneous and not thickened. Roots capillary-fibrous; rhizome short, lignified. Leaves few per culm, 1/3–2/3 the length of the culm; sheath 2−9 cm long, papery, pale castaneous, the apex oblique, ciliate with many trichomes, the trichomes white; ligule pilose, transversal or oblique; blade 50−250 × 0,3−0,4 mm, capillary, erect, flat to slightly concave, the abaxial surface 3-costate, the adaxial surface grooved 2-nerved, the margin and the nerves antrorsely scabrous. Culm 0,6 mm diam., terete, longitudinally 9- costate, the nerves antrorsely scabrous. Involucral bracts leaf-like, the basal bract 1.5−4 times longer than inflorescence, scabrous, margin with long and abundant white trichomes. Inflorescence terminal or pseudo-lateral, reduced to a single head or fascicle, turbinate to hemispherical, 0.6−1 × 0.5−0.9 mm, with 5−30 spikelets; spikelet ovoid, 4−7 × 2−4 mm, 5−10 flowered, sessile, grouped in a fascicle or in fascicles clustered in a head; rachilla contracted, winged, persistent; glume 3.5 × 1.5−2 mm, oval, deciduous, navicular, keeled, the abaxial surface pilose, the adaxial surface glabrous, the keel 3-nerved, the apex muticous or mucronate, stramineous along the keel, brown on the sides, the margin ciliate. Stamens 3, filament band-shaped; anthers 1.5 mm; style trifid, the margin not fimbriate, the base thickened, stylopodium persistent on the achene body. Achene ellipsoid to obovoid, 0.8−1.1 × 0.8−1 mm, trigonous, brown to blackish brown when mature, the surface transversely wrinkled, the epidermal cells longitudinally elongated, the apex obtuse to truncated and constricted at stylopodium insertion;

stylopodium 0,2 mm, conical-pyramidal, chestnut-brown, the surface wrinkled. Figures 4, 5, 6 and 9.

Phenology—Flowering and fruiting in the summer, between the months of December and March.

Distribution— High altitude grasslands in Santa Catarina and Paraná states.

Habitat—Rocky outcrop directly on the rock in full sun.

Conservation Status—Vulnerable (VU) based on the Area of Occupancy (AOO - 600.000 km²) and Near Threatened (NT) to Extent of Occurrence (EOO 20,500.000 km²). The distribution is restricted to high altitude grasslands of Atlantic Forest biome, in the Paraná, Rio Grande do Sul and Santa Catarina states, Brazil.

Etymology—The epithet refers to the strongly scabrous culm, an evident and diagnostic characteristic of this species.

Paratypes—BRAZIL. **Paraná**: Castro: Carambeí near Rio São João, 24°30’ S 50°02’ W, 15 January 1965, *L. B. Smith, R. M. Klein & G. Hatschbach 14499* (FLOR, HBR, MBM); Carambeí near Rio São João, 17 December 1965, *Pe. R. Reitz & R. M. Klein 17857* (FLOR, B); Piraí do Sul, Cânion Guartelá, 15 March 2016, *R. Ardissone & A. Vanzela 427* (ICN); Rio Grande do Sul: Bom Jesus, 29 October 1983, *Daniel Falkenberg 1198*; **Santa Catarina**: São Joaquim: Varginha, 15 January 1956, *Mattos 2803* (HAS); 18 km SW of São Joaquim, 6 January 1965, *L. B. Smith & R. Reitz* 14361 (HBR, FLOR).

Observations— Before the present study, collections of *B. scabriculmis* were identified as *Bulbostylis juncoides* (Vahl) Kük. ex Herter (1931: 40) or as *Bulbostylis* sp. The significant morphological characteristics used to distinguish *B.*

scabriculmis from the other species of the genus are the leaves and culms markedly scabrous, the involucral bracts with abundant white trichomes on the margins and the very small ligule present. The individuals form a mat over the rock, associated with mosses, ferns and high-altitude flora. *B. juncoides* resembles *B*. *scabriculmis* in achene morphology and synflorescence configuration, however the scabrous culms of *B*. *scabriculmis* and its mat-forming habit differ from *B*. *juncoides*, that presents smooth culms and form tufts without covering a surface like a rug. *Bulbostylis sellowiana* (Kunth) Palla (1908) resembles *B*. *scabriculmis* in the inflorescence in fascicle or head, but differs from it by the woolly base that result from shredded remains of old persistent sheaths, culm smooth and form tufts without covering a surface like a rug, involucral bracts without a laminar projection developed, and stylopodium deciduous. *Bulbostylis fimbriata* (Nees) C.B. Clarke (1900) resembles *B. scabriculmis* in the involucral bracts with trichomes, but differs on the culms, glabrous in *B. fimbriata* vs. scabrous in *B. scabriculmis*.

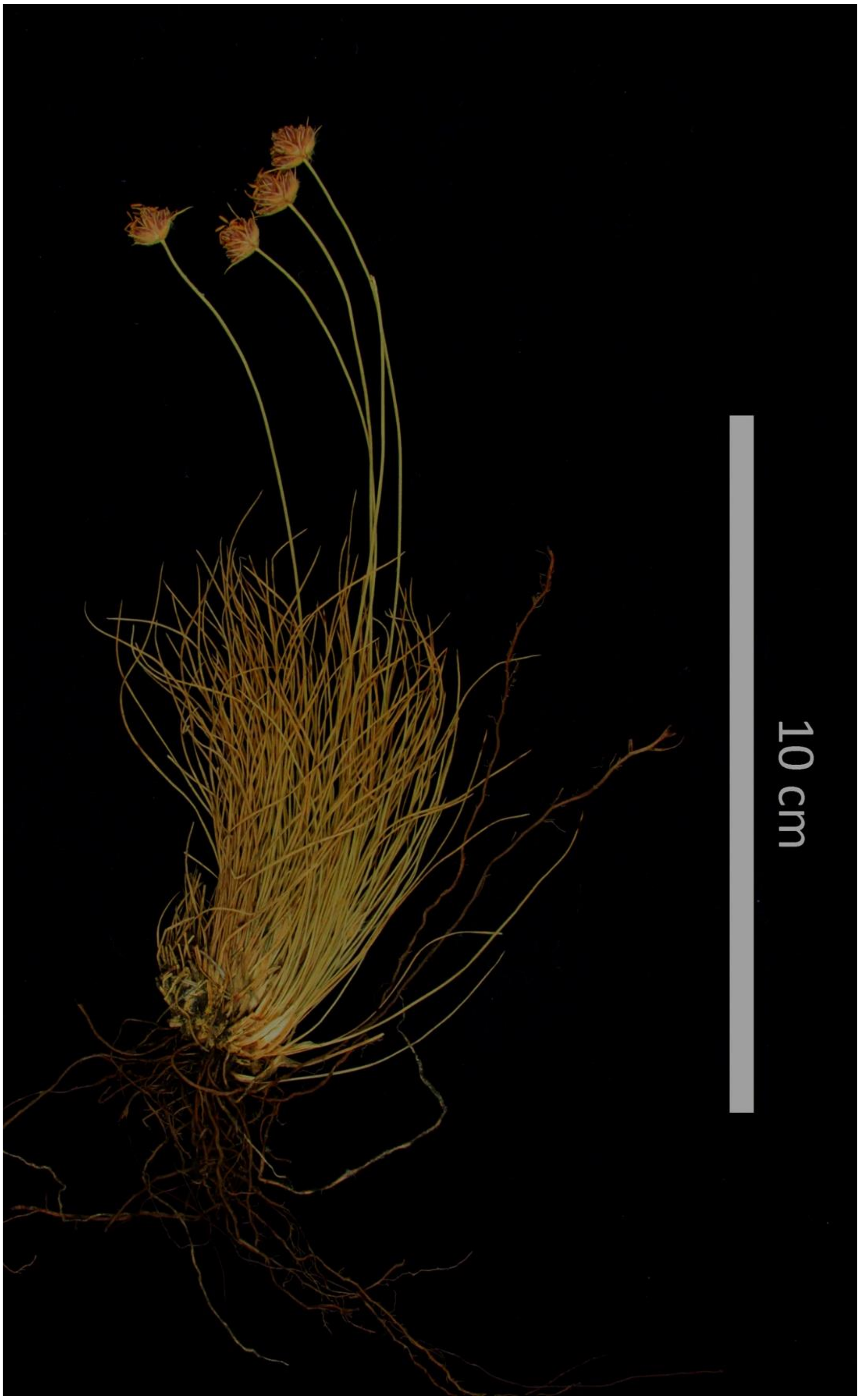

Fig. 5. Overview of *Bulbostylis scabriculmis* habit. R. Ardissone & A. Vanzela 430 (ICN).

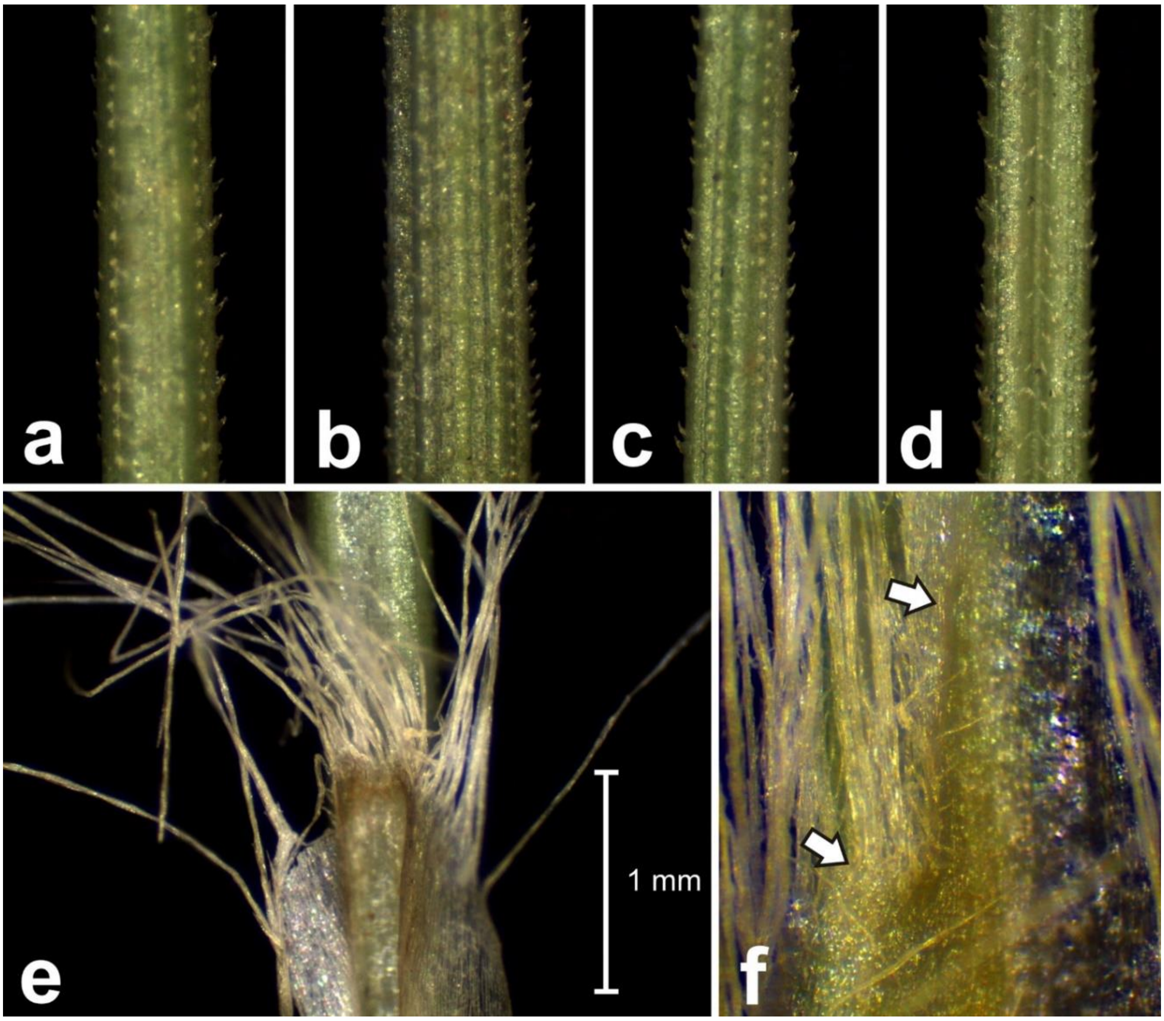

Fig. 6. a–f. Vegetative parts of Bulbostylis scabriculmis. a. Terminal portion of culm. b. Basal portion of culm. c. Leaf in abaxial view . d. Leaf in adaxial view. e. Sheth apex in adaxial view. The bar of 1 mm in “e” represents also the sections in “a, b, c and d”. f. Detail of oblique ligule (enlarged three times) in adaxial view, arrows inferior in proximal and superior in distal limits. [a–f Photos of R. Ardissone & A. Vanzela 430 (ICN)].

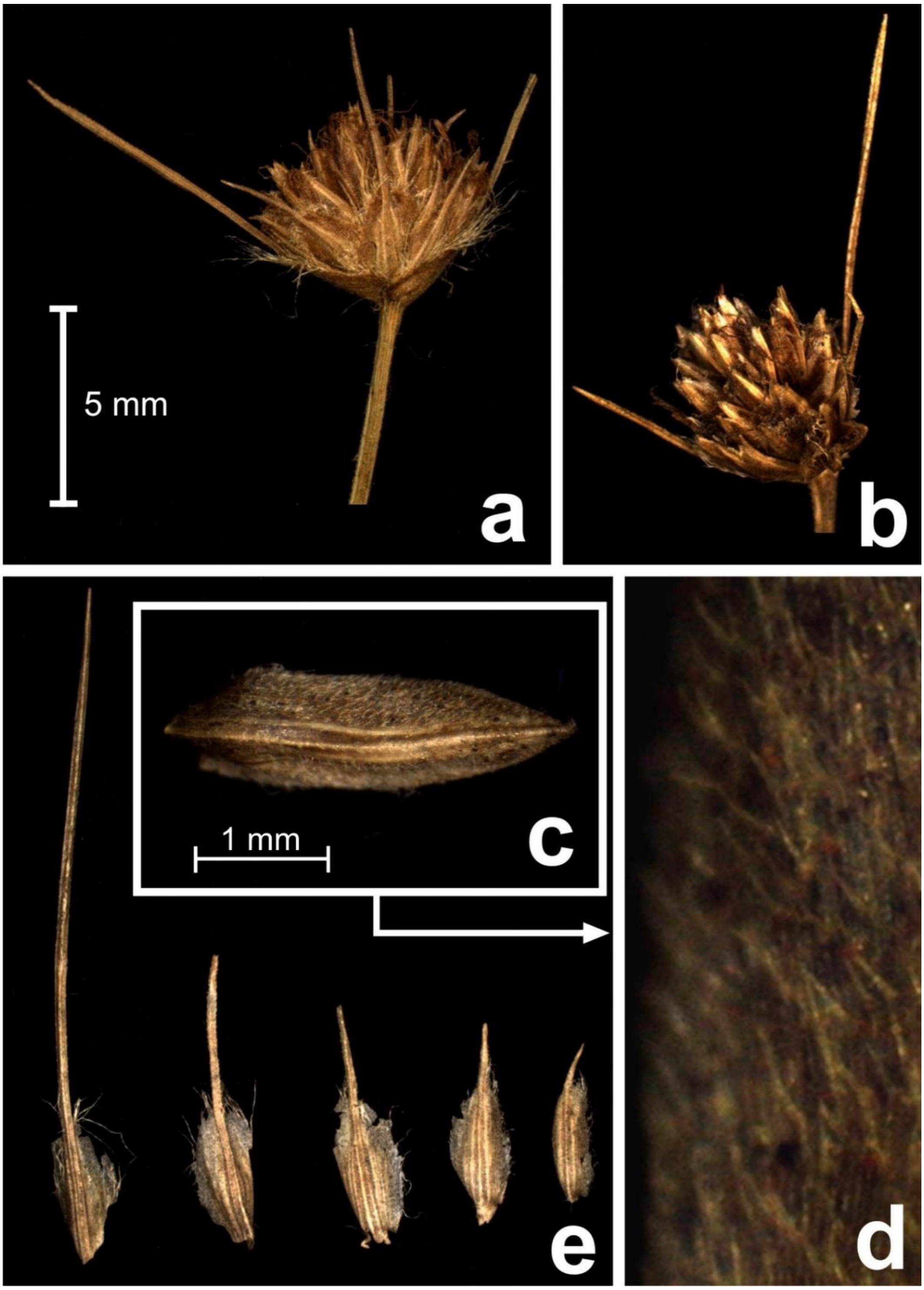

Fig. 7. a–e. Inflorescence and bracts of Bulbostylis scabriculmis. a. Inflorescence with evident trichomes on the margin of involucral bracts. b. Pseudolateral inflorescence. The bar of 5 mm in “a” represents also “b”. c. Glume in dorsal view. d. Detail of trichomes on the dorsal surface of glume (image enlarged four times). e. Involucral bracts of a same inflorescence in dorsal view. Each bract exhibits about 3 mm without mucron: the most inferior at the left and the other internal. [a Photo of L.B. Smith 14499 (FLOR); b–e Photos of R. Ardissone & A. Vanzela 430 (ICN)].

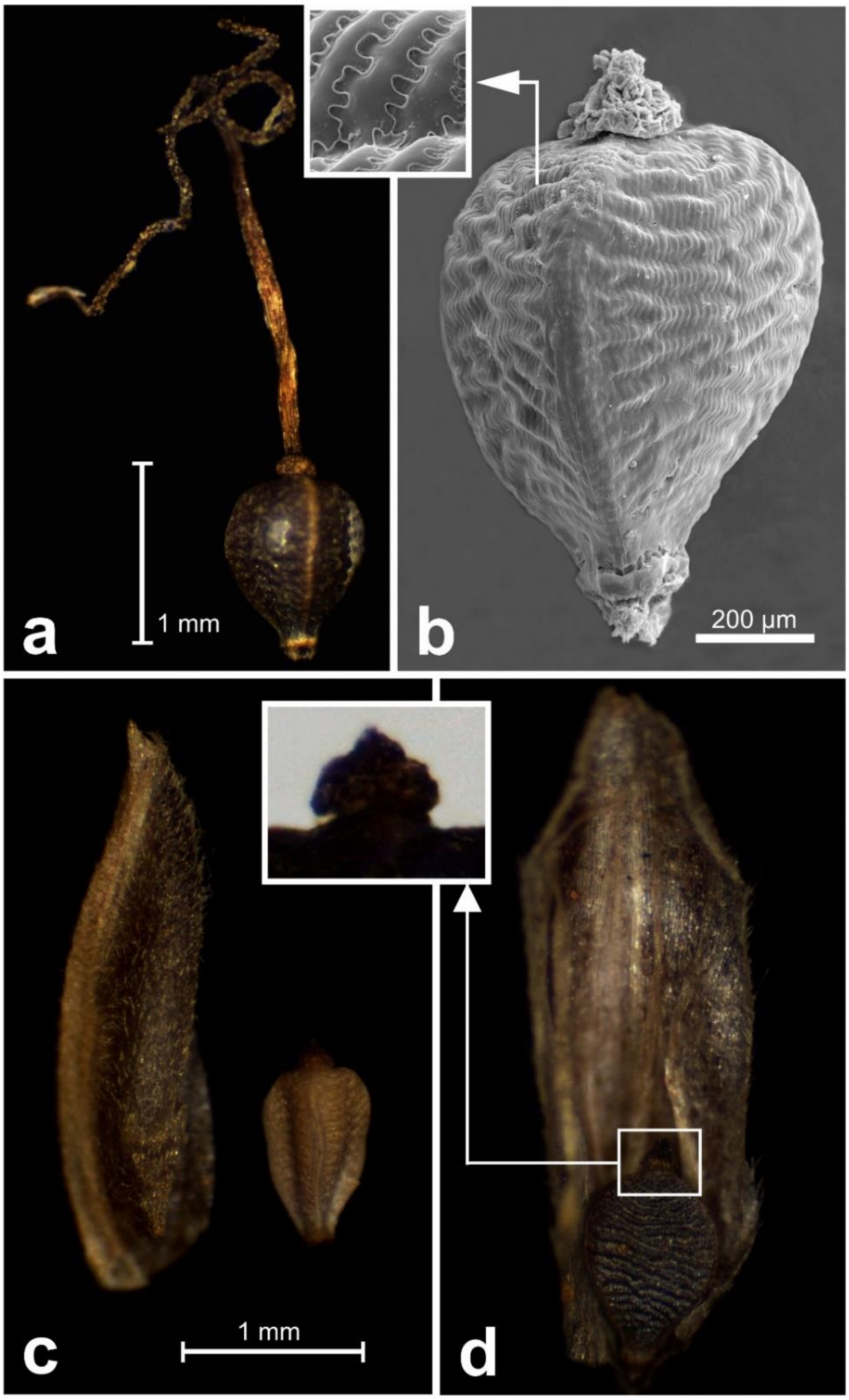

Fig. 8. a–d. Achenes and glumes of Bulbostylis scabriculmis. a. Achene with style. b. Achene in dorsal view, box detail of achene surface cells. c. Imature achene in dorsal view and glume in lateral view. d. Glume with achene in ventral view, box detail of achene apex with style base. The bars of 1 mm in “a and c” represent also “d”. [a and d Photos of R. Ardissone & A. Vanzela 430 (ICN); b SEM images of R. Ardissone & A. Vanzela 430 (ICN); c Photo of L.B. Smith 14499 (FLOR)].

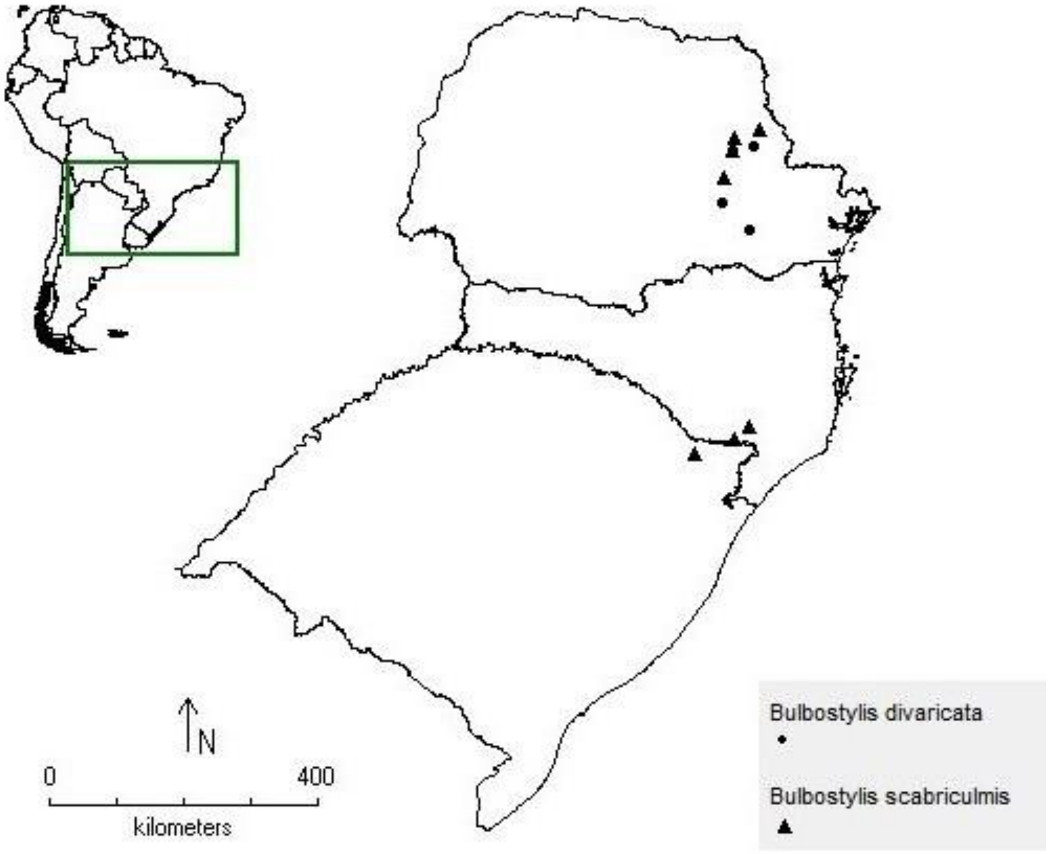

Fig. 9. Distribution map of *Bulbostylis divaricata* and *Bulbostylis scabriculmis*.

EXPANDING DISTRIBUTION: NOVELTIES TO BRAZIL

Bulbostylis contracta was previously known only from Central and Western Argentina and southern Uruguay (López & Simpson 2012). We collect samples from southern Brazil, in Paraná, Santa Catarina and Rio Grande do Sul states. In addition to these collections, several others were found in herbaria, previously identified as *Bulbostylis capillaris* (L.) C. B. Clarke (1893), *Bulbostylis capillaris* (Elliott) Fernald f. *stenantha* Kük. ex Barros (1941), *Bulbostylis capillaris* (Elliott) Fernald var. *elatior* Osten (1931), *B. juncoides*, *Bulbostylis scabra* (J. Presl & C. Presl) C. B. Clarke (1898), *Bulbostylis glaziovii* (Boeckeler) C.B. Clarke (1908). SELECTED SPECIMENS: **Paraná.** Palmas, 26°33'15"S 51°39'54"W, 31 March 2012, *R. Ardissone et P. Weber 358*, (FLOR); **Rio Grande Do Sul.** Alegrete, 29°37'45" S 55°31'58" W, 16 January 2014, *P. J. Silva Filho et R. Borges 1952* (ICN); Alegrete, Cêrro do Tigre 29°39'58" S 55°23'40" W, 15 January 2014, *P. J. Silva Filho et R. Borges 1930* (ICN); Bagé 31°15'23,76"S 54°11'44,84"W, 19 December 2011, *R. Ardissone, P. J. Silva Filho et R. Trevisan 277* (FLOR); Canela, near the city, 9 December 1990, *L. Garcés* (ICN); Dom Pedrito, Serrinha, 3 December 1983, *M. Sobral 1526* (ICN); Pelotas, Horto Botânico Universidade Federal de Pelotas, 01 December 1987, *M. Sobral et J.A. Jarenkow 5448* (ICN); Porto Alegre, Estrada da Ponta Grossa, 16 September 1939, *Ir. Augusto* (ICN); Porto Alegre, Morro Santana, 311 m, 8 March 2005, *G. H. Silveira et Longhi-Wagner 314* (ICN); Tapes, Saco de Tapes 30°41'0.88" S 51°23'27.36" W, 18 January 2005, *G. H. Silveira et S. M. Hefler 76* (ICN); Quaraí, Cerro do Jarau, 30°12'02,06" S 56°30'38,13" W, 17 December 2011, *R. Ardissone, P. J. Silva Filho et R. Trevisan 246* (FLOR); Santana do Livramento, Cerro Palomas, 30°49'27,23" S 55°20'58,94" W, 18 December 2011, *R. Ardissone, P. J. Silva Filho et R. Trevisan 269* (FLOR); São Gabriel, Cêrro do Ouro 30°34'58,20'' S 54°01'14,7'' W, 15 November 2013, *P. J. Silva Filho et R. B. Macedo 2032* (ICN); São Gabriel, BR 290 próximo à ponte sobre o Arroio das Pedras 2, 12 January 1997, *A. C. Araujo 546* (ICN); São Gabriel, Cêrro do Ouro 30°34'58,20'' S 54°01'14,7'' W, 15 November 2013, *P. J. Silva Filho et R. B. Macedo 2014* (ICN); São Lourenço do Sul, Av. S. Lourenço esquina com Rua São Paulo 31°22'33.1" S 51°57'52.0" W 10 m, 16 November 2003, *S. M. Hefler et al. 154* (ICN); São Lourenço, Estrada Pedra Mole 31°21'01,1'' S 51°57'41,4'' W, 19 January 2005, *G. H. Silveira et S. M. Hefler 140* (ICN); São Lourenço do Sul, Fazenda Pedra Mole, 12 December 2011, *C. Bonilha 466* (ICN); Torres, 20 June 1970, *L. Baptista et M.L. Lorcheiter* (ICN); Tramandaí, Rio Tramandaí, 6 April 1983, *B. Irgang and D. B. Falkemberg* (ICN); Viamão, Parque Estadual de Itapuã, Praia de Fora, 23 October 2006, *R. Trevisan et al. 669* (ICN); Viamão, Parque Estadual do Itapuã, Morro do Araçá, 30°21'37,1'' S 51°02'27,3'' W, 22 December 2005, *R. Trevisan 571* (ICN); Viamão, Parque Estadual do Itapuã, Morro do Araçá, 22 December 2005, *R. Trevisan 566* (ICN); Viamão, Parque Estadual de Itapuã, near Lagoa Negra 30°22'44,8'' S 51°00'1,7'' W, 10 November 2005, *R. Trevisan 465* (ICN); **Santa Catarina.** Bom Jardim da Serra, beira de estrada, 28°19'41'' S 49°40'28'' W, 20 April 2012, *R. Ardissone, P. Weber, S. Campestrini, G. Hassemer et R. Trevisan 109* (FLOR); Laguna 28°23'23'' S 48°44'36'' W, 13 March 2012, *R. Ardissone et Ivo Ghizoni Jr. 26* (FLOR); Fig. 10.

Bulbostylis rugosa M. G. Lopez was previously known only from eastern Argentina and Paraguay (López 1996). We collect samples from southern Brazil, in Parana state. Voucher: *R. Ardissone & P. Weber 134* (FLOR 1003). **Paraná.** Balsa

Nova, caminho para Ponte dos Arcos, 49°40'46"W , 25°34'05"S, 31 March 2012. **Fig. 10.**

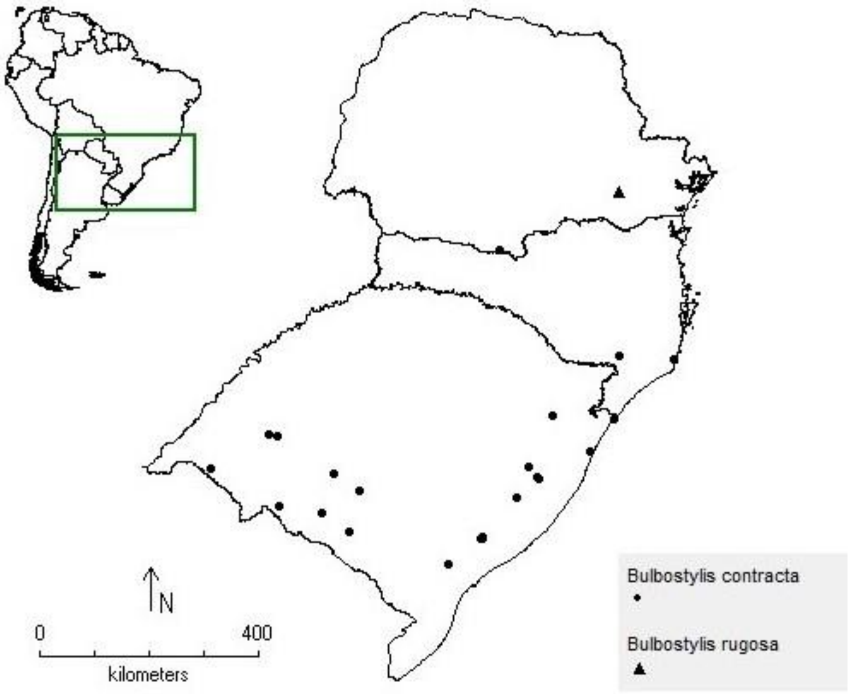

Fig. 10. Distribution map of *Bulbostylis contracta* and *Bulbostylis rugosa* in Southern Brazil.

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CAPÍTULO III

Identification key to *Bulbostylis* (Cyperaceae, Abildgaardieae) of Southern Brazil

Rodrigo Ardissone[1], Ilsi Boldrini[1] and Rafael Trevisan[2]

[1]Programa de Pós-graduação em Botânica, Instituto de Biociências,
Universidade Federal do Rio Grande do Sul, 91509-900, Porto Alegre, RS, Brazil.

[2]Departamento de Botânica, Centro de Ciências Biológicas, Universidade
Federal de Santa Catarina, 88040-900, Florianópolis, SC, Brazil.

Abstract—*Bulbostylis* (Cyperaceae) is a genus of heliophilic plants, with cespitose habit and graminoid appearance. It has a pantropical distribution and comprises around 220 species, mostly concentrated in Africa and Brazil. Most species of southern Brazil (the states of Paraná, Rio Grande do Sul and Santa Catarina) have strong morphological similarities, requiring accurate observation of achene morphology for the identification of samples to the specific level. Here we present a identification key to the 25 species and two varieties of *Bulbostylis* that occur in southern Brazil, Scanning Electron Microscopy images of 15 of these species are provided as are literature citations for other SEM images of other species in this key.

Keywords— Abildgaardieae, taxonomy, South America, biodiversity, Poales

Resumo— *Bulbostylis* é um gênero de plantas heliófilas, com hábito cespitoso e aspecto graminóide. Possui distribuição pantropical e riqueza aproximada de 220 espécies, concentradas em sua maior parte na África e no Brasil. A maioria das espécies Sul-Brasileiras apresenta acentuada semelhança morfológica, o que resulta na necessidade de minuciosa observação da morfologia dos aquênios para a determinação de amostras no nível de espécie ou até gênero. Aqui apresentamos uma chave de identificação para as 25 espécies que ocorrem na Região Sul do Brasil, imagens de Microscopia Eletrônica de Varredura dos aquênios de 15 dessas espécies e bibliografia onde são fornecidas imagens obtidas com a mesma técnica para as demais espécies presentes neste tratamento.

INTRODUCTION

Bulbostylis Kunth is generally found growing on dry soils most of the year, but moist in some seasons, in contrast to the majority of the family that has strong relation with humid environments. Rocky grasslands, coastal dunes, or strong and recently disturbed areas without original vegetation are examples of where we can find *Bulbostylis*. Fruiting occurs in summer, and it is common to find samples with young flowers and mature achenes in the same inflorescence, according to their position in spikelets. To delimit morphologically the species of *Bulbostylis*, SEM is an excellent tool due high-resolution images that can be generated of achenes surfaces (see Prata et al. 2008; Hefler & Longhi-Wagner 2008; López & Simpson 2012; Ronchi et al. 2016; López & Gonzalez 2017; and Prata et al. 2017). The taxonomic treatments published for American *Bulbostylis* are restricted to limited geographical areas far from southern Brazil [Prata (2009), Prata & López (2003), Adams (1994), Kral (1971)] or need updates, [Barros (1960 and 1945) and Nees (1842)], making it difficult to identify samples from this area until now.

With the aim of enabling the identification of samples of *Bulbostylis* from southern Brazil, we present here a identification key to the 25 species and two subspecies of *Bulbostylis*. Scanning Electron Microscopy (SEM) of 15 of these species (Figures 1, 2 and 3) were made. In addition, we gathered together references of publications that contains SEM images of achenes of the species we did not photograph, along with information about species distributions in southern Brazil and vouchers preserved in indexed herbaria (Table 1).

MATERIALS AND METHODS

We used optical microscope and SEM to analyze the samples that were collected during the expeditions and the material reviewed in herbaria. The entire *Bulbostylis* collections at FLOR, HAS, HBR, HCF, HUCS, ICN, MBM, MPUC, PACA, PEL, and UPCB were observed at stereomicroscope, and observed photographs of collections available on “INCT Herbário Virtual da Flora e dos Fungos” (http://inct.florabrasil.net). We also conducted fieldwork in Southern Brazil between 2011 and 2016. For SEM, we extracted a few dehydrated achenes from samples, and then the achenes were attached with double-sided carbon tape on aluminum stubs and coated with gold in a metallizer LEICA EM model SCD 500. Images were captured and observations were made using a SEM JEOL model JSM-brand

6390LV at the Central Laboratory of Electron Microscopy at the Federal University of Santa Catarina, in Florianópolis, Brazil and at the Electron Microscopy and Microanalyses Laboratory, State University of Londrina, State of Paraná, Brazil.

To differentiate angles formed by branches of developed anthelodium, we consider “ascending” to be those that maintain an acute angle (less than 90°) between peduncles, and “divergent” to be ones that form an obtuse angle (greater than 90°). The terminology used to describe morphological characters adapted of Stearn (1983), Bruhl (1995), and taxonomic treatments already mentioned.

KEY TO THE SPECIES OF *BULBOSTYLIS* IN SOUTHERN BRAZIL

1. Inflorescence with a solitary spikelet at culm apex

2. Plant base with a well-developed caudex, involucral bracts with long and abundant trichomes at the margins, achene cordiform, apex depressed, 1.2-1.8 × 1-1.4 mm, surface transversely wrinkled……*Bulbostylis paradoxa* (Spreng.) Lindm.

2'. Plant base without a caudex, involucral bracts glabrous or with short trichomes, achene obovoid, apex not depressed, 1 × 0.8 mm or less, surface with tuberculate without forming wrinkles……………..*Bulbostylis subtilis* M. G. López, Figure 2, K-L

1'. Inflorescence with two or more spikelets grouped in heads, fascicles, or anthelodia

3. Plant base with a caudex well-developed; involucral bracts with long and abundant trichomes at the margins; achene cordiform, apex depressed, 1.2-1.8 × 1-1.4 mm, surface transversely wrinkled .... *Bulbostylis paradoxa* (Spreng.) Lindm.

3'. Plant base without a caudex; involucral bracts glabrous or with few and short trichomes; achene with different configurations

4. Spikelets grouped in a head or a fascicle

5. Spikelets in a single fascicle with up to 5 spikelets at the culm apex

6. Base woolly due to shredded remains of old persistent sheaths; involucral bracts glumaceous without a developed blade; achene obconic, thickened angles, stylopodium deciduous ..……………................... *Bulbostylis sellowiana* (Kunth) Palla

6’. Base not woolly; involucral bracts foliaceous with extended blade; achene obovoid, angles not thickened, stylopodium persistent in achene body………………………………………….. *Bulbostylis juncoides* (Vahl) Kük. ex Herter, Figure 2, E-F

5’. Spikelets in a single head at the culm apex with more than 10 spikelets

7. Culms, leaves and involucral bracts scabrous; involucral bracts filiform, foliaceous, the base with a papery enlargement, ribs scabrous and surface covered with trichomes; spikelets in single fascicle or fascicles clustered in turbinate or hemispheric single head; achenes surface transversely wrinkled…………………………………………….... *Bulbostylis scabriculmis* R. Ardiss. & R. Trevis., Figure 3, A-B

7’ Culms glabrous; margin leaves scabrous, pilose or glabrous, stiff, or slightly antrorsely scabrous; base of involucral bracts without enlargement, if enlargement present, membranous hyaline or papery, glabrous; spikelets arranged in spherical single head; achenes surface transversely wrinkled, smooth, wavy or tuberculate

8. Inflorescence a single head of 20-50 spikelets; achenes surface smooth

9. Blades of senescent leafs erect or slightly flexuous, not recurved, glabrous; culms glabrous; involucral bracts erect, the base papillose; glumes leathery, 3.5-4.5 × 1.3-1.5 mm; achenes 1-1.2 × 0.6-0.7 mm ……………*Bulbostylis amambayensis* Barros

9’. Blades of senescent leafs recurved, scabrous on margin or covered with stiff trichomes; culms glabrous or with stiff trichomes; involucral bracts flexuous; the base not papillose; glumes membranous, 1.5-3 × 0.8-1.4 mm; achenes 0.7-0.9 (-1) × 0.6-0.8 mm

10. Leaf blades glabrous or scabrous along margins; sheath stramineous........*Bulbostylis sphaerocephala* (Boeck.) Lindm. var. *sphaerocephala*

10'. Leaf blades with stiff trichomes; sheath brown ……………………………............... …………….*Bulbostylis sphaerocephala* var. *brunneovaginata* (Boeck.) C. B. Clarke

8’. Inflorescence a single head with up to 15 spikelets; achenes surface transversely wrinkled or slightly tuberculate

11. Achene attenuated from the middle third toward the base; surface smooth to lightly tuberculate ……... *Bulbostylis junciformis* (Kunth) C. B. Clarke, Figure 2, A-B

11’. Achene attenuated from the lower third toward the base; surface transversely wrinkled or wavy

12. Spikelet ovoid to oblong; glume apex muticous; achene surface transversely wrinkled, epidermis with silica bodies forming continuous wrinkles………………….*Bulbostylis juncoides* (Vahl) Kük. ex Herter, Figure 8, E-F

12’. Spikelet lanceolate; glume apex mucronate; achene surface wavy or smooth, epidermis without silica bodies protruding neither forming continuous wrinkles……….*Bulbostylis contracta* (Kük. ex Osten) M. G. López & D. A. Simpson, Figure 2, C-D

4’. Spikelets grouped in a simple or a compound anthelodia, sometimes with tiny branches (contracted anthelodium) but never in a head; terminal spikelets isolated or grouped in fascicles or spherical heads

13. Inflorescence anthelodium of heads or anthelodium of fascicles

14. Inflorescence lax anthelodium with spikelets grouped in heads; achene obconical attenuated from the middle third toward the base, surface softly tuberculate ....……………………*Bulbostylis junciformis* (Kunth) C. B. Clarke, Figure 2, A-B

14’. Inflorescence anthelodium of fascicles, lax or contracted; achene oblong or obconical attenuated only on the inferior third or not attenuated, surface tuberculate, smooth, wavy or transversely wrinkled

15. Achene surface tuberculate

16. Inflorescence anthelodium simple or compound; glumes papery; achene oblong 1.1-1,3 x 5-0.8 mm ……….................................. *Bulbostylis stenocarpa* Kük., Figure 2, I-J

16' Inflorescence simple anthelodium; glumes leathery; achene obconical 1.2-1.6 × 0.8 mm ……........................... *Bulbostylis consanguinea* (Kunth) C. B. Clarke, Figure 1, I-J

15’. Achene surface smooth, wavy or transversely wrinkled

17. Achene surface transversely wrinkled with protuberances on epidermis…………..………….............. *Bulbostylis juncoides* (Vahl) Kük. ex Herter, Figure 2, E-F

17’. Achene surface smooth or wavy without protuberances on epidermis

18. Base of involucral bracts with pilosity developed, trichomes larger than 2 mm; achene surface smooth ………... *Bulbostylis conostachya* (Boeckeler) Beetle, Figure 1, K-L

18’. Base of involucral bracts glabrous or with pilosity discreet, achene surface wavy ……….…………………………………………….. *Bulbostylis* sp. Figure 3, G-H

13’. Inflorescence anthelodium of spikelets isolated or in pairs

19. Leaves and culms covered with stiff trichomes

20. Achene 1-1.3 mm of length, surface transversely wrinkled……………………. .... *Bulbostylis aspera* M. G. López, Figure 1, A-B

20’. Achene 0.7-0.9 mm of length, surface tuberculate ……………………………. ……….......................... *Bulbostylis hirtella* (Schrad. ex Schult.) Nees ex Urb.

19’. Leaves and culms glabrous

21. Inflorescence anthelodium with up to 5 (8) spikelets in divergent branches

22. Involucral bracts densely ciliate ………………………………………………. ……………………. *Bulbostylis wanderleyana* Prata & M.G. López, Figure 3, E-F

22’. Involucral bracts glabrous or poorly ciliate

23. Achene 1.3-1.5×0.8-1 mm, surface smooth …………………………………… ....…………… *Bulbostylis loefgrenii* (Boeck.) Prata & López, Figure 2, G-H

23’. Achene up to 1.1 mm long, surface tuberculate or transversely wrinkled

24. Plants up to 15 (-18) cm tall; achene 1−1.25 × 0.7−0.8 mm, the surface tuberculate with tubercles transversely aligned, stylopodium persistent……………………………. *Bulbostylis subtilis* M. G. López; Figure 2, K-L

24'. Plants up to 35 (-50) cm tall; achene 0.8−0.9 × 0.5−0.6 mm, the surface smooth, and whitish, covered with waxy layer that comes off in tiny plates, or light brown shiny, andslightly wavy, stylopodium deciduous or persistent

25. Stylopodium subulate, deciduous or persistent, 1/8 of achene length ………….. ………..……..*Bulbostylis communis* var*. communis* M.G. López & D.A. Simpson, Figure 1, E-F

25'. Stylopodium discoid, flat to hemispheric, persistent, rare deciduous, less to 1/10 of achene length...*Bulbostylis communis* var*. scabrida* M.G. López & D.A. Simpson, Figure 1, G-H

21’. Inflorescence anthelodium with more to 5 (8) spikelets in ascending branches

26. Blade leaves poorly developed, less than 10 cm long or up to 1/5 of culm length

27. Achene surface smooth …....................................... *Bulbostylis brevifolia* Palla

27'. Achene surface transversely wrinkled

28. Achene apex truncated …………………………………………………………...
………………........... *Bulbostylis divaricata* R. Ardiss. & R. Trevis., Figure 3, C-D

28'. Achene apex obtuse *………........……………………. Bulbostylis rugosa* López

26'. Blade leaves well developed, more than 10 cm long or 1/3 or more of culm length

29. Anthelodium contracted, the primary branches 0−3 (5) mm, the secondary up to 2 mm

30. Glume with apex emarginate, not mucronate; achene obovoid slightly attenuate towards the base …………… *Bulbostylis capillaris* (L.) C. B. Clarke, Figure 1, C-D

30’. Glume with apex acute, mucronate or mucronulate; achene cordiform not attenuate towards the base or pear-shaped strongly attenuate towards the base

31. Achene cordiform not attenuate towards the base …………………….............
…..……………………………………………………… *Bulbostylis* sp. Figure 3, G-H

31’. Achene pear-shaped or obconical, strongly attenuate towards the base

32. Achene surface distinctly transversely undulate; stylopodium wart-like, persistent…….. *Bulbostylis contracta* (Kük. ex Osten) M. G. López & D. A. Simpson, Figure 2, C-D

32’. Achene surface indistinctly transversely undulate or lightly wavy; stylopodium conical, generally deciduous

33. Culms and leaves scabrous………………………………………………… …………........ *Bulbostylis communis* var. *scabrida* M.G. López & D. A. Simpson, Figure 1, G-H

33’. Culms and leaves glabrous ……………………..……………………………………

………………… *Bulbostylis communis* var. *communis* M.G. López & D. A. Simpson, Figure 1, E-F

29’. Anthelodium lax, the primary and secondary branches greater than 3 mm

34. Involucral bracts glume-like; achene surface with uniformly distributed punctations and some small plates ….......... *Bulbostylis jacobinae* (Steud.) Lindm.

34'. Involucral bracts leaf-like; achene surface transversely wrinkled or smooth, without plates

34. Achene (1) 1.2−1.5 × 1−1.2 mm, the surface transversely wrinkled, the wrinkles with hemispheric protuberance………….... *Bulbostylis sphaerolepis* (Boeck.) Beetle

34'. Achene 0.6−0.8 × 0.5−0.7 mm, the surface smooth or transversely wrinkled, and if transversely wrinkled, the wrinkles without hemispheric protuberances

35. Achene cordate, surface softly wavy ..…………… *Bulbostylis* sp. Figure 3, G-H

35’. Achene obconic, surface transversely wrinkled or smooth

36. Glume apex emarginate; achene surface transversely wrinkled ……………..
……………………............... *Bulbostylis capillaris* (L.) C. B. Clarke, Figure 1, C-D

36' Glume apex acute; achene surface smooth …………………………………….
……………………………………………*Bulbostylis tenuifolia* (Rudge) J.F. Macbr.

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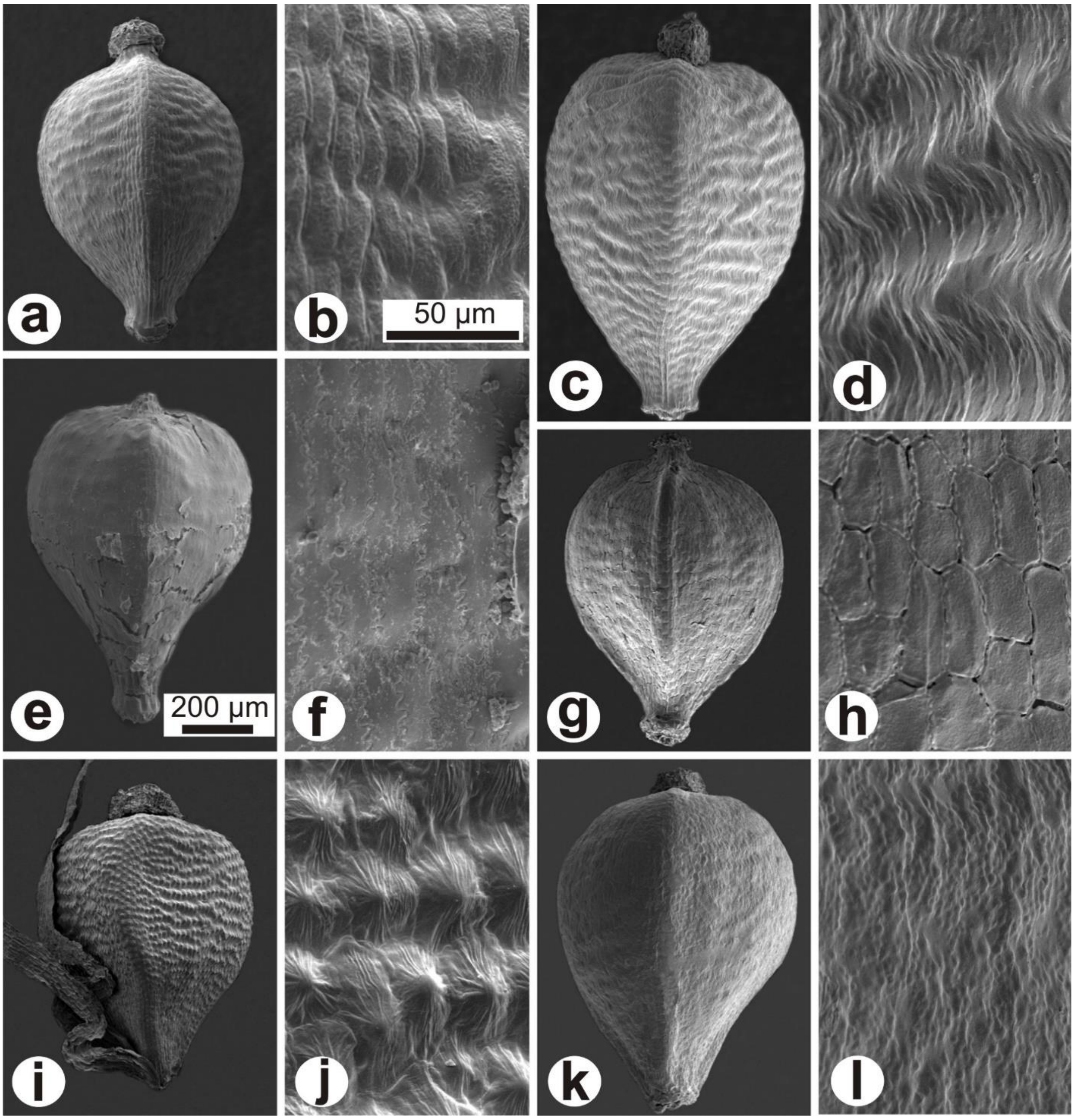

Fig. 1. a–l. SEM of entire achenes and detail of surfaces. a-b. *Bulbostylis aspera* (M.H.Nervo 109 - PACA) c-d. *Bulbostylis capillaris* (L.) C. B. Clarke; e-f. *Bulbostylis communis* var. *communis* (R. Ardissone 257 - FLOR); g-h. *Bulbostylis communis* var. *scabrida* (R. Ardissone 286 - FLOR); i-j. *Bulbostylis consanguinea* (R. Ardissone 197 - FLOR); k-l. *Bulbostylis conostachya* (R. Ardissone 370 - FLOR).

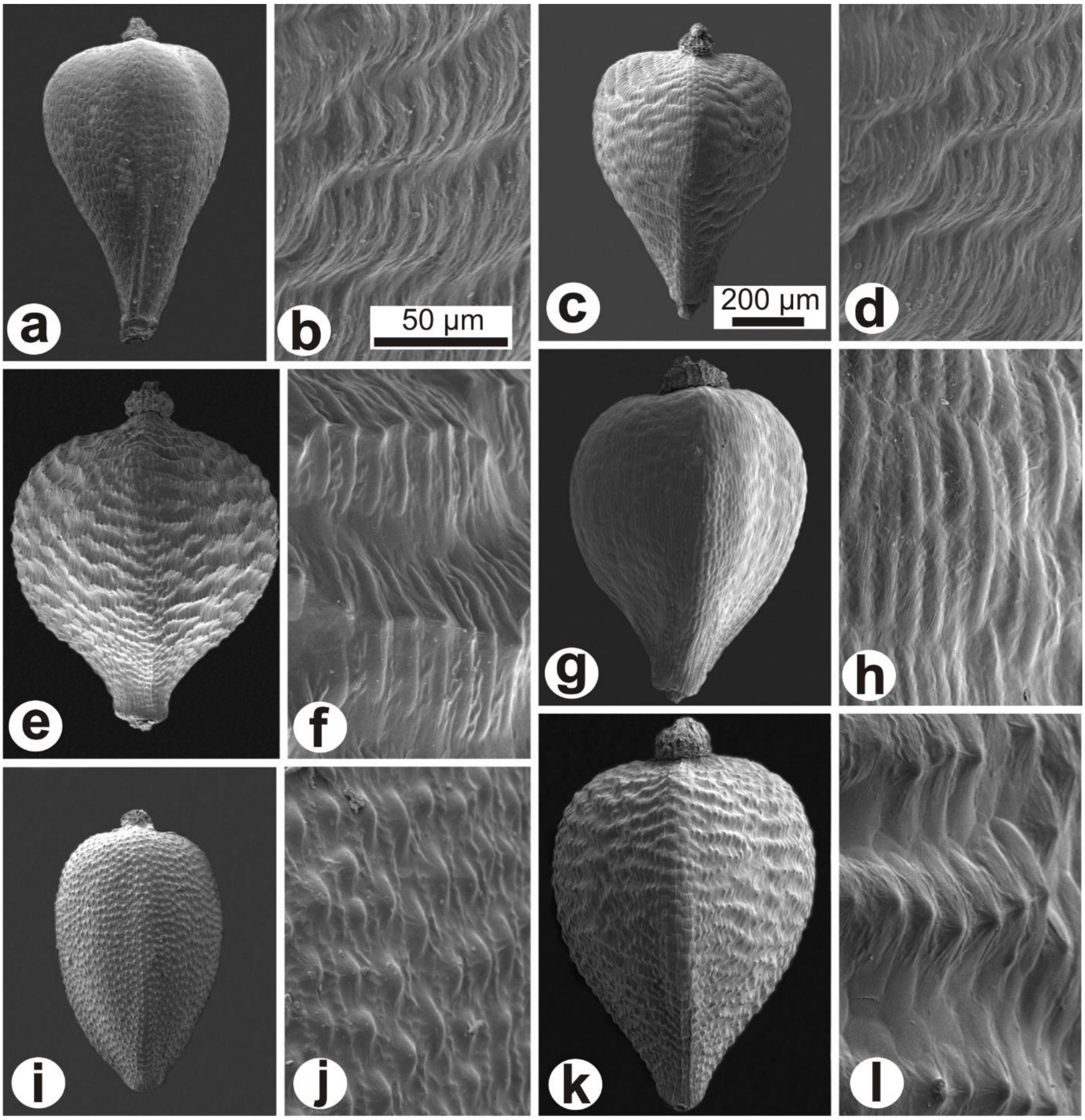

Fig. 2. a–l. SEM of entire achenes and detail of surfaces. a-b. *Bulbostylis junciformis* R. Ardissone 189 (FLOR); c-d. *Bulbostylis contracta* J. A. Jarenkow 672 (MBM); e-f. *Bulbostylis juncoides* R. Ardissone 96 (FLOR); g-h. *Bulbostylis loefgrenii* R. Ardissone 183 (FLOR); i-j. *Bulbostylis stenocarpa* R. Ardissone 193 (FLOR); k-l. *Bulbostylis subtilis* R. Ardissone 155 (FLOR).

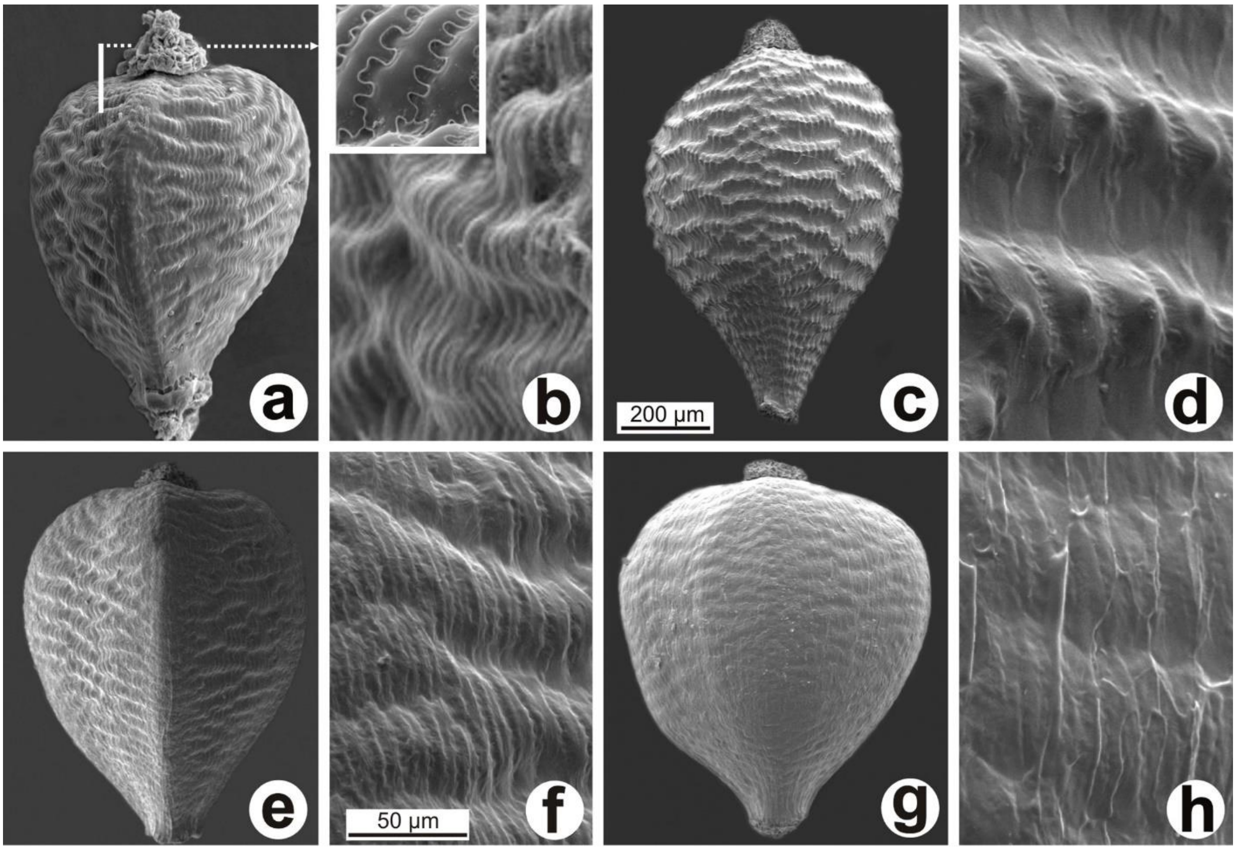

Fig. 3. a–h. SEM of entire achenes and detail of surfaces. a-b. *Bulbostylis scabriculmis* R. Ardissone 430 (ICN); c-d. *Bulbostylis divaricata* R. Ardissone 131 (FLOR); e-f. *Bulbostylis wanderleyana* R. Ardissone 135 (FLOR); g-h. *Bulbostylis sp.* R. Ardissone 230 (FLOR).

Table 1. Species of *Bulbostylis* occurring in the Southern Brazil. Vouchers, publications with scanning electron microscopy images of the achenes (iconography) and their distribution in the Southern Brazil.

Species	**Selected Voucher**	**Iconography**	**Occurrence in Southern Brazil**
1. Bulbostylis amambayensis Barros	C.F.S. Muniz 412 (SP)	Prata et al. 2008: Fig. 17, p. 594.	Guaíra, **PR**
2. Bulbostylis aspera M. G. López	R. Ardissone 80; R. Ardissone et al. 117, 263	Here presented, figure 1, a-b.	Quaraí, **RS**; Bom Jardim da Serra, São Joaquim, **SC**, **PR**
3. Bulbostylis brevifolia Palla	R. Ardissone et al. 166, 256, 261	López & Gonzalez 2017: Fig 2, g-l, p. 73	Uruguaiana, Barra do Quaraí, **RS;** Balsa Nova, **PR**
4. Bulbostylis capillaris (L.) C. B. Clarke	R. Ardissone & P. Weber 160	Here presented, figure 1, c-d.	Balsa Nova, **PR**
5. Bulbostylis communis var. *communis* M.G. López & D.A. Simpson	R. Ardissone & A. Tavares 32; R. Ardissone et al. 226, 227, 239, 244, 248, 250, 252, 254, 257, 258, 259, 260, 261, 264, 266, 268, 271, 274, 279, 282	Here presented, figure 1, e-f.	Alegrete, Barra do Quaraí, Lavras do Sul, Quaraí, Santana do Livramento, Uruguaiana, **RS** Florianópolis, **SC**
5.1 Bulbostylis communis var. *scabrida* M.G. López & D.A. Simpson	R. Ardissone 371; R. Ardissone & I. Guizoni Jr. 27; R. Ardissone et al. 233, 251B, 280, 286	Here presented, figure 1, g-h.	Alegrete, Dom Feliciano, Lavras do Sul, Porto Alegre, Quaraí, **RS**, Laguna, **SC**
6. Bulbostylis conostachya (Boeckeler) Beetle	R. Ardissone & P. Weber 370	Here presented, figure 1, k-l.	Jaguariaíva, **PR**
7. Bulbostylis consanguinea (Kunth) C. B. Clarke	R. Ardissone & P. Weber 197	Here presented, figure 1, i-j.	Jaguariaíva, **PR**
8. Bulbostylis contracta (Kük. ex Osten) M. G. López & D. A. Simpson	R. Ardissone 246; R. Ardissone & I. Guizoni Jr. 26; R. Ardissone & P. Weber 358; R. Ardissone et al. 109, 238, 245, 269, 277	Here presented, figure 2, c-d.	Palmas, **PR;** Bagé, Quaraí, Santana do Livramento, **RS**; Bom Jardim da Serra, Laguna, **SC**
9. Bulbostylis divaricata R. Ardiss. & R Trevis. sp nov.	R. Ardissone & P. Weber 131, 288, R. Ardissone et al. 126, 135, 283, 426	Here presented, figure 3, e-f.	Balsa Nova, Lapa, Piraí do Sul, **PR**; Pantano Grande, **RS**; Urupema **SC**

10. Bulbostylis hirtella (Schrad. ex Schult.) Nees ex Urb.	R. Ardissone & P. Weber 352, 369	López & Gonzalez 2017: Fig. 4, p-r, p. 76.	Palmas, Jaguariaíva, **PR**; **SC**
11. Bulbostylis jacobinae (Steud.) Lindm.	L. TH. Dombrowski 6694 (CTES - López); M.R.B. do Carmo s.n. ICN 151104	Prata et al. 2008: Fig. 21, p. 594.	Tibagi, **PR**
12. Bulbostylis junciformis (Kunth) C. B. Clarke	R. Ardissone 189, 194; R. Ardissone & P. Weber 170; R. Kummrow 183 (CTES - López); G. Hatschbach et al. 12158 (CTES - López).	Here presented, figure 2, a-b.	Curitiba, Jaguariaíva, Piraí do Sul, **PR**
13. Bulbostylis juncoides (Vahl) Kük. ex Herter	R. Ardissone et al. 86, 92, 93, 96, 100, 237, 255, 262, 265, 267, 293, 294, 357	Here presented, figure 2, e-f.	Palmas, **PR**; Alegrete, Quaraí, Uruguaiana, **RS**; Bom Jardim da Serra, **SC**
14. Bulbostylis loefgrenii (Boeck.) Prata & López	R. Ardissone 186; S.M. Hefler et al. 246 (ICN).	Here presented, figure 2, g-h.	Guarapuava, **PR**; Santa Bárbara, **RS**
15. Bulbostylis paradoxa (Spreng.) Lindm.	C. Kozera & R. Kersten, 2209 (ICN)	López & Gonzalez 2017: Fig 2, s-u, p. 73	Balsa Nova, **PR**
16. Bulbostylis rugosa López	R. Ardissone & P. Weber 134	López 1996: Fig. 2 A (a-b), p. 31.	Balsa Nova, **PR**
17. Bulbostylis scabriculmis R. Ardiss. & R Trevis.	R. Ardissone & A. Vanzela 430; J. Mattos 2803; L.B. Smith & R. Reitz 14361; L.B. Smith, R.M. Klein & G. Hatschbach 14499	Here presented, figure 3, a-b.	Castro, Jaguariaíva, Piraí do Sul, **PR**; São Joaquim, **SC**
18. Bulbostylis sellowiana (Kunth) Palla	C. Kozera 3296; C. Kozera & J.W. Morais 3271 (MBM); G. Hatschbach 14639 (MBM)	Prata et al. 2008 Fig. 26, p. 594	Balsa Nova, Ponta Grossa, **PR**
19. Bulbostylis sphaerocephala (Boeck.) Lindm. var. *sphaerocephala*	R. Ardissone & I. Guizoni Jr. 28, R. Ardissone & P. Weber 185,	López & Gonzalez 2017: Fig 3, j-l, p.74	Guarapuava, **PR**; Laguna, **SC**; **RS**
19.1 Bulbostylis sphaerocephala (Boeck.) C. B. Clarke var. *brunneovaginata* (Boeck.) C. B. Clarke	R. Ardissone & P. Weber 188, 325, 326, 356; R. Ardissone et al. 85, 91, 94, 103, 108, 119, 110, 116, 124	López & Gonzalez 2017: Fig 3, j-l, p.74	Balsa Nova, Guarapuava, Palmas, **PR**; Bom Jardim da Serra, São Joaquim, Urupema, **SC**

20. Bulbostylis sphaerolepis (Boeck.) Beetle	R. Ardissone et al. 272; A. A. Filho (SMDB 1233)	López & Gonzalez 2017: Fig. 4, g-i, p. 76.	**PR**, **SC** e **RS**. Eldorado do Sul, Santana do Livramento
21. Bulbostylis stenocarpa Kük.	R. Ardissone & P. Weber 162, 193	Here presented, figure 2, i-j.	Balsa Nova, Jaguariaíva, **PR**
22. Bulbostylis subtilis M. G. López	R. Ardissone & P. Weber 142, 155, 156, 353, 354	Here presented, figure 2, k-l.	Balsa Nova, Palmas, **PR** e **RS**
23. Bulbostylis tenuifolia (Rudge) J.F. Macbr.	R. Ardissone & P. Weber 195, 198, 205, 216	Prata et al. 2008 Fig. 18, p. 594.	Jaguariaíva, **PR**.
24. Bulbostylis wanderleyana Prata & M.G.López	R. Ardissone & P. Weber 135, Hatschbach 5108	Here presented, figure 3, c-d.	Balsa Nova, Sengés, **PR**
25. Bulbostylis sp.	R. Ardissone 29, 225, 230; Pe. R. Reitz 6727	Here presented, figure 3, g-h.	Quaraí, **RS**

CONSIDERAÇÕES FINAIS

Bulbostylis é um gênero que proporciona diversos desafios, do ponto de vista taxonômico. A semelhança morfológica entre muitas das espécies sul-americanas coincide com a baixa resolução encontrada na separação entre elas quando analisamos a informação genética. A identificação de amostras vegetais é dependente da presença de frutos maduros que, em geral, têm menos de 1 mm de comprimento, e de imagens com boa resolução para comparação. Ainda assim não é uma tarefa simples, exceto nos raros casos em que alguma parte vegetativa peculiar proporcione maior segurança no parecer do taxonomista.

Em relação à citogenética, é importante mencionar o tamanho diminuto dos cromossomos e seu grande número, muitas vezes maior que 100 em um único núcleo. Isso torna a contagem e caracterização um processo mais complicado do que em outros gêneros na família. Soma-se o fato de as espécies de *Bulbostylis* sul-brasileiras serem mais exigentes que as demais ciperáceas quanto às condições de cultivo na casa de vegetação, fator limitante em protocolos que exigem material fresco.

Embora as peculiaridades do gênero se mostrem como um desafio a mais, com o conhecimento acumulado nas duas décadas mais recentes e a rede de pesquisa consolidada entre pesquisadoras e pesquisadores da América do Sul, é crível um futuro onde as lacunas no conhecimento acerca da história natural de *Bulbostylis* sejam preenchidas. Após sete anos dedicados ao estudo desse gênero instigante, percebo diversas possibilidades de pesquisa biológica, como as implicações morfológicas da dinâmica cromossómica e como isso interage adaptativamente com o ambiente, por exemplo. O fluxo gênico entre espécies simpátricas, como boa parte das que ocorrem na América do Sul austral, também é desconhecido. Ainda, informações genéticas podem embasar uma reformulação do conceito de espécie para a família, nos taxa onde a morfologia não é suficiente. Uma filogenia com maior amostragem, principalmente com mais representantes do gênero *Nemum* e espécies hoje classificadas como *Bulbostylis* com comportamento reprodutivo e morfologia peculiares poderia dar maior solidez a uma nova circunscrição para esses dois gêneros. O sequenciamento do genoma de alguma espécie de *Bulbostylis* seguramente traria também novas possibilidades de pesquisa.

Do ponto de vista aplicado, podemos citar relatos de propriedades medicinais das espécies de *Bulbostylis*, usos em biorremediação, e como frequentes em pastagens naturais, onde servem de alimento para o gado. Essa pecuária que respeita e se vale da biodiversidade local tem extrema importância na manutenção da fisionomia da paisagem e na cultura a ela associada. Com os avanços da silvicultura e das monoculturas de soja e outros grãos esses ecossistemas naturais se tornam cada vez mais raros e desconectados, mesmo onde já foram a fisionomia dominante como no Sul da América do Sul, por exemplo.

De qualquer forma, com a atual precarização dos recursos vinculados à produção de ciência no Brasil, em especial à ciência de base ou não aplicada, temos o maior dos desafios no campo político. Um país rico que não investe em educação, ciência e tecnologia está fadado à subserviência. Nossa atual situação tem sido exaustivamente noticiada na imprensa internacional e em revistas científicas de alto impacto, sem eco na sociedade como um todo, na grande mídia ou nos mandatários do poder. O acúmulo de capital e privilégios para poucos tem se acentuado e o povo é ridicularizado em programas de televisão pelos ocupantes, hoje por estratagemas judicializados, dos mais altos cargos públicos. Com as universidades e institutos de pesquisa sucateados; a demissão massiva de professores nas universidades privadas para uma nova contratação em outros termos; as áreas naturais convertidas em sistemas produtivos sem comprometimento com a sustentabilidade ambiental e social, nem com a soberania alimentar; o genocídio dos povos originários e do povo negro, a miserabilidade evidente na volta do desemprego e da massiva população em situação de rua; e o entreguismo de nossos recursos naturais como um todo, o futuro se mostra cada vez mais nebuloso. Nos resta resistir à locomotiva neoliberal, que nos traz o assombro da fome e da escravidão institucionalizada através da perda dos direitos da classe trabalhadora e leva embora nossas riquezas em ritmo de ‘queima de estoque’.