

RODRIGO SAMPAIO RODRIGUES

Estudos sistemáticos em *Isachne* R. Br. (Poaceae,  
Micrairoideae, Isachneae) na região Neotropical

Tese apresentada ao Instituto de Botânica da  
Secretaria de Infraestrutura e Meio Ambiente como  
parte dos requisitos para a obtenção do título de  
DOUTOR em BIODIVERSIDADE VEGETAL E  
MEIO AMBIENTE, na Área de Concentração de  
Plantas Vasculares em Análises Ambientais.

SÃO PAULO

2019

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ORIENTADOR: PROF. DR. TARCISO DE SOUSA FILGUEIRAS

Ficha Catalográfica elaborada pelo **NÚCLEO DE BIBLIOTECA E MEMÓRIA**

Rodrigues, Rodrigo Sampaio  
R696e Estudos sistemáticos em *Isachne* R. Br. (Poaceae, Micrairoideae, Isachneae) na região Neotropical / Rodrigo Sampaio Rodrigues -- São Paulo, 2019.  
265p.; il.

Tese (Doutorado) -- Instituto de Botânica da Secretaria de Infraestrutura e Meio Ambiente, 2019.  
Bibliografia.

1. Gramíneas americanas. 2. Micromorfologia. 3. Revisão taxonômica.  
I. Título.

CDU: 582.542.1

*Evaluation committee / Comissão avaliadora*

Prof. Dr. Tarciso S. Filgueiras  
(Advisor/Orientador)

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Prof. Dr. Ana Rita Giraldes Simões  
(External member/Titular externo)

Prof. Dr. Lúcia Rossi  
(External member/Titular externo)

Thesis defended on February 27, 2019 and approved unanimously by the evaluation committee.

Tese defendida em 27 de fevereiro de 2019 e aprovada por unanimidade pela comissão avaliadora.

*Ao meu orientador (in memoriam) pela força e confiança e  
à minha família pelo amor e suporte,  
Dedico.*

## Agradecimentos/Acknowledgments

O conteúdo dessa tese não corresponde a um esforço apenas meu, mas também de muitas pessoas que fizeram parte da minha trajetória nos últimos dez anos, trabalhando para minha formação e aperfeiçoamento profissional, e colaborando direta ou indiretamente com a produção dos conteúdos aqui apresentados.

Faço aqui um esforço mental especial para lembrar e honrar, por suas contribuições, cada um dos que estiveram ao meu lado nessa jornada, tendo também a consciência de que estarei sendo injusto com tantos outros em decorrência da minha memória já um tanto debilitada.

Essa tese jamais teria sido idealizada e produzida sem a efetiva participação e envolvimento do meu mais que querido professor, orientador e amigo, doutor *Tarciso de Sousa Filgueiras*, a quem, a semelhança da minha dissertação de mestrado, dedico mais essa obra. Ao meu orientador são e serão sempre devidos todos os créditos por cada uma das obras botânicas sob meus ombros, pela minha filosofia e pelo meu rigor de trabalho, pela minha visão sobre a botânica, minha paixão pelas gramíneas e flora brasileira como um todo. Tarciso me proporcionou muito mais que orientação – proporcionou-me cultura, novos hábitos (inclusive alimentares), nova forma de lidar com pessoas e conflitos, apoio emocional durante as crises pessoais, quando nada parecia dar certo, além de apoio financeiro em meio ao caos e incertezas econômicas que certamente teriam inviabilizado a realização de praticamente tudo o que propusemos inicialmente, etc.

À minha família agradeço por todo suporte. Embora apoiando nos bastidores, eu nada seria sem o esforço e colaboração de meus pais, humildes e maravilhosos, que sacrificaram tudo para que seus filhos tivessem condições de acessar e aproveitar as oportunidades que a eles foram negadas. *Luzia Sampaio Rodrigues* e *Antônio Rodrigues*, a vocês eu devo mais que a vida! Tenho muito orgulho e me sinto privilegiado em poder ter vindo a este mundo como seu filho!

Às minhas irmãs, *Regiane Sampaio Rodrigues dos Santos* e *Rosângela Sampaio Rodrigues* pelo incentivo e por acreditarem que eu seria capaz de chegar até aqui. Mesmo mais distantes fisicamente, nossos laços são eternos! Obrigado por compreenderem a minha ausência necessária. Eis aqui parte do resultado!

Às princesinhas do titio coruja, *Ana Luiza Rodrigues dos Santos* e *Líarah Rodrigues*, devo a dívida de estar vivo, firme e de dispor hoje da força necessária para encarar a vida. Vocês são tão pequenas, frágeis e inocentes, mas já me salvaram mais vezes do que eu posso recordar. Com lágrimas nos olhos, eu agradeço por vocês simplesmente existirem no momento certo e me darem uma razão para ir um pouco mais além! O titio as ama mais que tudo nessa vida!

Agradeço e ao mesmo tempo me desculpo com os demais membros da minha família, aqueles que estiveram mais próximos durante essa fase, tendo que lidar com minha ausência dos

eventos, meus compromissos e mensagens esquecidas, minhas desculpas repetitivas para declinar de seus pedidos, etc. Encerro aqui um ciclo produtivo e conturbado da minha vida, esperando que o próximo possa ser mais ameno e gentil com todos nós. Agradeço imensamente aos meus tios: *Paulo César, Ivone Barros, Teodora Rodrigues (Guil), Nice Barros e Crispina (in memoriam)*; meus primos: *Rodger Antunes, Lilian Rodrigues, Lidia Rodrigues, Jéssica Rodrigues, Lucas Rodrigues (in memoriam), Alexandre Muniz, Angela Rodrigues, Raiane Barbosa, Rian Barbosa*; e meu cunhado *Eduardo Ferreira dos Santos*. O incentivo de vocês em diferentes momentos foi fundamental para que esse trabalho pudesse ser concretizado.

Não posso deixar de agradecer a *Beatriz Sofia Rozenfeld e Fabio Rozenfeld* pelo cuidado com minha família, pela amizade, por todo o apoio durante a minha infância, me acolhendo como a um filho, sempre investindo e incentivando meus estudos. Minha família e eu somos gratos por tê-los em nossa trajetória!

Agradeço ao *João Marcelio Santos* por compartilhar comigo os últimos sete anos das nossas vidas. Infelizmente, a vida coloca diante de nós caminhos e situações que nunca pensamos trilhar (...) e, de repente, nos vemos frente à necessidade de escolher por onde seguir (...). Fizemos escolhas muito diferentes, mas, de qualquer forma, guardarei sempre comigo as melhores experiências, o apoio e o tempo a mim dedicados. Muito obrigado!

Ao querido *Marcelo Oliveira Basso* pelos dias e noites de ideias profissionais discutidas, por mesmo a distância me ajudar a manter a sanidade mental, pela parceria e por me ajudar nos momentos mais tensos que já passei (...). Falei uma vez e repito: você é o meu anjo-da-guarda e um grande exemplo para mim!

Ao *Guilherme Pastrello Salmazio* pelo incentivo na fase final do trabalho quando, pela exaustão, nem mesmo eu encontrava forças em mim. A sua entrada em minha vida foi um presente! Obrigado por acreditar em mim e no meu sonho!

À *Deuza Melo* pela parceria e incentivo durante todos esses anos! Obrigado por me acolher como a um filho!

Oficialmente, a realização de um doutoramento leva cerca de quatro anos, porém o processo de formação se inicia muito antes e perdura por muitos anos após o encerramento desse ciclo. Dessa forma, muitos são os profissionais responsáveis pela formação e capacitação de um indivíduo. Cabe-me agora expressar a imensa e eterna gratidão que tenho por todos aqueles que tiveram participação em meu processo de formação profissional, e em especial:

Agradeço à professora *Emiko* (Biologia Geral) por despertar e alimentar em mim a paixão pela Biologia, pelo funcionamento do mundo e dos seres vivos; à professora *Adriana Sampaio Ratão* (Língua Portuguesa), que viu em mim potencial, investindo em um curso pré-vestibular quando as condições de minha família não me permitiriam essa oportunidade; à professora *Flavia*

*de Campos Martins* (Ecologia), meu primeiro contato durante a universidade, por me incentivar, me acalmar e acreditar que eu era suficientemente competente para seguir a diante durante todo o curso; ao exigente professor *Fabio Mesquita do Nascimento* (Genética e Evolução), por ter se tornado um amigo e requisitado de mim sempre o melhor (agradeço também as dicas sobre os Tephritidae); à professora *Fernanda Torello de Mello* (Paleontologia), minha estimada orientadora durante a graduação, por aceitar o desafio de me orientar em um estudo com Dípteros, confiar no meu trabalho e no meu potencial para aprender tudo a partir do zero, bem como em meu julgamento e decisões diante dos vários problemas que surgiram durante essa fase – embora não publicado, ainda guardo comigo uma cópia desse trabalho como registro do meu amadurecimento profissional dos últimos dez anos; à Professora *Renata Sebastiani* (Botânica), agora estimada amiga e colega de profissão, por me levar um passo adiante no mundo da Botânica e me fazer enxergar com outros olhos essa disciplina maravilhosa!

Agradeço ainda a todos os professores/colegas que tive o prazer de ter ao meu lado durante esses dez anos como estagiário, mestrando, colaborador e doutorando dentro do Núcleo de Pesquisa e Curadoria do Herbário do Instituto de Botânica, em especial aos doutores *Cintia Kameyama, Gerleni Lopes Esteves, Inês Cordeiro, Jefferson Prado, Lúcia Rossi, Maria das Graças Lapa Wanderley, Rosângela Simão-Bianchini, Sérgio Romaniuc-Neto, Mizué Kirizawa e Sonia Aragaki*. Agradecimento especial é devido à doutora *Maria Margarida da Rocha Fiuza de Melo* pelos anos de suporte emocional, por enxergar em mim um potencial ímpar, pelo estímulo para produzir, seguir à diante, envolver-me em outras atividades e me ver como um profissional já completo e preparado, ao invés de apenas um mero aluno/estagiário. Sou muito grato pela confiança e pela porta que me abriu em poder ter a oportunidade de atuar como editor técnico da *Hoehnea*, revista pela qual tenho especial carinho!

Aos meus mestres, espero ter correspondido às expectativas de todos vocês, que me deram o preparo necessário para ingressar na graduação e na pós-graduação, dando passos importantes adiante nessa minha jornada de aperfeiçoamento profissional. Em especial, agradeço aos mestres agrostólogos que muito me ensinam e abrem caminho para que nós da nova geração possamos galgar também grandes realizações: doutores *José Francisco Montenegro Valls, Hilda Maria Longhi-Wagner, Regina Célia de Oliveira, Ana Paula Santos-Gonçalves, Reyjane Patrícia de Oliveira, Pedro Lage Viana, Ana Zanin e Lynn G. Clark*. Muito obrigado por compartilharem seu conhecimento e expertise comigo e com tantos outrosestudantes.

Aos colegas das gramíneas e amigos queridos, *Christian Silva, Ronaldo Vinícius-Silva, Mayco Werllen Santos Souza, Evandro Pianissola, Cassiano Welker, Clapton Olímpio, Kazue Kawakita, Regina Shirasuna, André Rodolfo, Kaio Vidal*. Galera, obrigado mesmo por todo o apoio logístico, profissional e/ou emocional (...). Definitivamente, vocês são sensacionais!



Agradeço à doutora *Ana Rita Simões* pela disposição em me ajudar com os estudos moleculares e sempre estar disponível quando precisei de apoio. Espero que a parceria que não pôde ser concretizada durante meu doutorado torne-se possível em um futuro próximo!

À doutora *Luciana Benatti* e ao *André Aguilera* pelos vários dias e dezenas de horas analisando e obtendo milhares de imagens a partir de dezenas de espécimes em microscópio eletrônico de varredura. Muito obrigado pela enorme paciência e colaboração!

Aos meus amigos mais que queridos, colegas e ex-colegas de Instituto, registro aqui a importância de todos na minha jornada: *Adenilsa Aparecida Rodrigues, Ana Angélica Sousa, André Luíz Gaglioti, Fernanda Satori Petrongari, Mayara Pastore, Barbara Púglia, Gisele Oliveira, Allan Carlos Pcheidt, Cátia Takeuchi, Gisela Pelissari, Ulisses Gonçalves Fernandes, Valéria Leobina, Fernanda Urbath, André Moreira, Rafaela Freitas, Zedenil Mendes Rodrigues, Amanda Noronha, Carolina Brandão, Marcos Enoque, Suzana E. Martins, Juliana Guedes, Anderson Santos, Lucas Cardinelli, Higor Domingues, Viviana Motato, Karina Margareth e Simone Silva*. Ainda, aos colegas que estiveram comigo por pouco tempo, mas se tornaram igualmente especiais: *Alexander Rockinger, “Book” e Sebastião Maciel*, Muito obrigado a todos pelos anos e momentos compartilhados!

Devo menção especial à *Marcela Inácio da Silva*, minha parceira desde o começo do doutorado, a quem devo muitos dos avanços possíveis com o projeto, quer me estimulando a ir trabalhar “de madrugada”, quer sentada por horas abrindo caixas de empréstimos, conferindo guias e amostras, me avisando “em off” que os empréstimos conseguidos à duras penas do Herbário de Nova Iorque estavam retidos nos Correios pela falta de pagamento de taxas (indevidas), ou até mesmo ouvindo minhas muitas lamúrias diárias. Aprecio a sua paciência (às vezes a falta dela) e tenho muito orgulho de vê-la executando, também com muito esforço e maestria, o seu projeto de mestrado. Aqueles que nos veem sorrindo, irreverentes, tentando permanecer são numa realidade tão ingrata, voraz e incerta, ignoram que, muitas vezes, só temos uns aos outros; ignoram ainda todo o esforço que é feito na calada da noite, aos finais de semana enquanto todos curtem as manhãs de sol, ou até mesmo o que acontece nos corredores após as 17:00 hs. Por isso, mantenhamo-nos sorrindo sempre, pois um único sorriso já é capaz de adoçar um pouco a vida! Muito obrigado por sorrir comigo!

Agradeço a *Ana Célia Calado*, minha mãe dentro do Instituto de Botânica, a quem devo os melhores conselhos sobre a vida que alguém já pôde me dar, os inúmeros abraços com um suspiro profundo e sem uma única palavra dita, por meio dos quais todas as emoções contidas no meu coração se tornavam mais leves. Não poder tê-la todos os dias durante essa etapa da minha vida, como fora durante o mestrado, foi muito difícil e doloroso! Perdoe-me também pela minha demasiada ausência.

À minha amada amiga/irmã, doutora *Cintia Vieira da Silva*, a quem sempre agradecerei pelo apoio e parceria, pelas viagens de campo, pelas risadas e lágrimas, pelos ouvidos emprestados, pelos conselhos e broncas, pelos desabafos, pelos curativos na cabeça (...), pelas lições de vida e exemplos de superação. Você é sem a menor sombra de dúvidas um dos seres humanos mais completos que existem! Obrigado por extrair de mim sempre o melhor!

Ao meu amigo, doutor *Victor Martins González*, pela convivência desde a graduação, iniciação científica, mestrado e grande parte do doutorado, pelas longas discussões de trabalho depois do expediente, pelos passeios nos finais-de-semana, pelas experiências novas que compartilhamos juntos, pelos estranhamentos e reconciliações.

Agradeço à *Claudinéia Inácio* e *Suellen Inácio da Silva* pela irreverência e convivência diária; à doutora *Maria Cândida Henrique Mamede*, curadora do herbário SP, pelas facilidades.

Aos colegas do Núcleo de Pesquisa em Briologia, doutor *Denilson Peralta*, *Dimas Marchi do Carmo*, *Jessica de Lima*, *Bianca Canestraro*, *Marina Koga* e *Lauro*. Obrigado pelos cafés da tarde e pela amizade.

Agradeço aos curadores de todos os herbários que consultei fisicamente ou por meio da análise de imagens. Disponibilizar um pouco do seu tempo para me receber em suas instituições ou para obter imagens dos mais variados espécimes resultou em avanços substanciais na execução do projeto dessa tese. Registro aqui meu mais sincero obrigado a cada um.

Devo também especial agradecimento ao doutor *Otávio L. Marques* pelo suporte na obtenção de imagens detalhadas e pela análise de espécimes-chave no Herbário de Paris.

*I am really in debt with the doctors Åsa Dalsätt (Swedish Museum of Natural History) and Marc Pignal (Muséum National D'Histoire Naturelle, Paris) for providing high-quality images from some essential type specimens.*

*I would like also to express my gratitude to the doctors Thomas R. Soreng, Garrit Davidse and Paul M. Peterson for the facilities regarding the loan of specimens from the American Herbaria. Without their help this Ph.D. dissertation would never be finished.*

Agradeço ao *Programa de Pós-graduação em Biodiversidade Vegetal e Meio Ambiente*, em especial à Comissão do Programa, por entender as dificuldades pelas quais passei no decorrer do projeto (...), pela liberação de auxílio para minha expedição ao estado do Espírito Santo, pela extensão do período de vigência da bolsa de doutorado e pela compreensão das dificuldades relacionadas ao prazo para defesa.

Por fim, espero ter correspondido às expectativas e feito jus à confiança que todos aqueles mencionados direta ou indiretamente nesses agradecimentos depositaram em mim.

A todos sou enormemente grato.

*Rodrigo Sampaio Rodrigues*

**ABSTRACT**

*Isachne* R. Br. includes ca. 103 species distributed throughout the tropical and temperate regions of the world, with the center of diversity in Asia. Species of this genus occur, preferably, in humid places, associated to the herbaceous or shrubby vegetation, sometimes also to the arboreal component in forest edges and gallery forests, at altitudes ranging from the sea level to ca. 3000 m. It encompasses annual or perennial species with spikelets disarticulating above the glumes; anthoecia similar or dissimilar in shape, consistency, texture and/or pilosity, being the lower staminate, pistillate or bisexual, and the upper bisexual or pistillate. The genus used to be classified in the subfamily Panicoideae, on the basis of the morphological similarity of its flowering characters with those found in members of the tribe Paniceae *s.l.* However, molecular evidence revealed that the genus is closely related to the subfamily Micrairoideae, being currently classified in the tribe Isachneae, along with *Coelachne* R. Br., *Heteranthoecia* Stapf, *Sphaerocaryum* Nees ex Hook f., and *Hubbardia* Bor. Molecular evidence including only a few species suggests that *Isachne* is monophyletic; although, as it is the largest genus within Micrairoideae, a more robust sampling is still necessary to properly assess its monophyly. Regarding the infrageneric classification of *Isachne*, it is based on the consistency, pilosity, and similarity of the anthoecia and also lacks molecular support. Considering that *Isachne* has never been fully revised for the Neotropical region, several species of the genus are in a state of great taxonomic confusion. In this thesis, we aimed to review the American species and evaluate their taxonomic boundaries by means of macro- and micromorphological evidence of the leaf blade epidermis and anthoecia. Micromorphology was applied for circumscribing close related species in *Isachne* for the first time. The analysis of the leaf blade epidermis revealed a broader variation of the epidermal features in the genus, mostly regarding the shape of intercostal long cells, type of silica bodies, and presence and distribution of papillae. It was concluded that a qualitative analysis considering the distribution pattern and arrangement of the micromorphological characters associated with the macromorphological ones may aid substantially in the delimitation of related species. On the other hand, the analysis of the anthoecia revealed a peculiar vestiture in the genus, which is characterized by the abundant presence of silica bodies of various types, panicoid bicellular microhairs and the occurrence of twisted macrohairs of two different types: sharp-pointed and narrow-tipped. Five ornament patterns were observed and described, and the rachilla was taxonomically informative in the separation of some taxa. A numerical analysis revealed a weak congruence between the ornament of the anthoecia and the current infrageneric classification of the genus, although the species with homomorphic anthoecia and without macrohairs throughout the lemmas form a cohesive group. Finally, based on data from the original descriptions, micromorphological studies, analysis of herbarium specimens, and field expeditions, the Neotropical species of *Isachne* were revised. As a result, 15 species were recognized (two new to science: *I. burchellii* and *I. soderstromii*), one new subspecies (*I. angustifolia* subsp. *dominicensis*) and one new South American variety (*I. glaucescens* var. *trichomatosa*). *Isachne glaucescens* is reestablished; the identity of *I. arundinacea* is reviewed and *I. disperma* is included in its synonymy. Descriptions, identification keys, illustrations, comments on the morphology, taxonomy, distribution, and phenology are presented.

**Keywords:** American grasses, micromorphology, New World grasses, taxonomic revision.

## RESUMO

*Isachne* R. Br. inclui ca. 103 espécies distribuídas pelas regiões tropicais e temperadas do mundo, com centro de diversidade na Ásia. Espécies deste gênero ocorrem, preferencialmente, em locais úmidos, associados à vegetação herbácea ou arbustiva, às vezes também ao componente arbóreo em bordas de florestas e matas de galeria, em altitudes que variam do nível do mar até ca. 3000 m. Abrange espécies anuais ou perenes com espiguetas desarticulando acima das glumas, antécios similares ou dissimilares em forma, consistência, textura e/ou pilosidade, sendo o inferior estaminado, pistilado ou bissexual, e o superior bissexual ou pistilado. O gênero era classificado na subfamília Panicoideae com base na similaridade morfológica de seus caracteres florais e aqueles encontrados em membros da tribo Paniceae *s.l.* Entretanto, evidências moleculares revelaram que o gênero está intimamente relacionado à subfamília Micrairoideae, sendo atualmente classificado na tribo Isachneae, juntamente com *Coelachne* R. Br., *Heteranthoecia* Stapf, *Sphaerocaryum* Nees ex Hook f. e *Hubbardia* Bor. Evidências moleculares incluindo apenas algumas espécies também sugerem que *Isachne* é monofilético, entretanto, por ser o maior gênero em Micrairoideae, uma amostragem mais robusta ainda é necessária para avaliar adequadamente seu monofiletismo. Em relação à classificação infragenérica de *Isachne*, esta se baseia na consistência, na pilosidade e na similaridade dos antécios e também carece de suporte molecular. Considerando que *Isachne* nunca foi totalmente revisado para a região Neotropical, várias espécies do gênero estão em um grande estado de confusão taxonômica. Nesta tese, objetivamos revisar as espécies americanas e avaliar seus limites taxonômicos por meio de evidências macro e micromorfológicas da epiderme da lâmina foliar e dos antécios. A micromorfologia foi aqui aplicada para circunscrever espécies proximamente relacionadas em *Isachne* pela primeira vez. A análise da epiderme da lâmina foliar revelou uma variação mais ampla das características epidérmicas do gênero, principalmente em relação à forma de células longas intercostais, tipo de corpos silicosos, além da presença e distribuição das papilas. Concluiu-se que uma análise qualitativa considerando o padrão de distribuição e arranjo dos caracteres micromorfológicos associados aos caracteres macromorfológicos pode auxiliar substancialmente na delimitação de espécies relacionadas. Por outro lado, a análise dos antécios revelou um revestimento peculiar no gênero, caracterizado pela presença abundante de corpos silicosos de vários tipos, microtricomas bicelulares do tipo panicoide e a ocorrência de macrotricomas retorcidos de dois tipos diferentes: pontiagudos e com o ápice estreitado. Cinco padrões de ornamento foram observados e descritos, e a ráquila mostrou-se taxonomicamente informativa para separação de alguns táxons. Uma análise numérica revelou uma fraca congruência entre o ornamento dos antécios e a atual classificação infragenérica do gênero, embora as espécies com antécios homomorfos e sem macrotricomas ao longo dos lemas formem um grupo coeso. Finalmente, com base em dados das descrições originais, estudos micromorfológicos, análise de espécimes de herbário e expedições de campo, as espécies neotropicais de *Isachne* foram revisadas. Como resultado, 15 espécies são reconhecidas (duas novas para a ciência: *I. burchellii* e *I. soderstromii*), uma nova subespécie (*I. angustifolia* subsp. *dominicensis*) e uma nova variedade Sul-Americana (*I. glaucescens* var. *trichomatosa*). *Isachne glaucescens* é restabelecida; a identidade de *I. arundinacea* é revisada e *I. disperma* é incluída em sua sinonímia. Descrições, chaves de identificação, ilustrações, comentários sobre a morfologia, taxonomia, distribuição e fenologia são apresentados.

**Palavras-chave:** Gramíneas americanas, micromorfologia, gramíneas do Novo Mundo, revisão taxonômica.

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TAXONOMIC HISTORY OF THE GENUS *ISACHNE* R. BR.

Figure 1. Three based on *ndhF* and *rpl16* intron sequence data and structural data. Arrows indicate the PACCMAD and Micrairoideae clades. Black bars indicate 100% bootstrap support and > 10 decay values, those with lower values are below the branches separated by a slash (values for Bs below 69 and Br below 5 are not shown). Branches with no support collapse in the strict consensus. Numbers above branches indicate number of changes. Numbers in circles indicate unambiguous synapomorphies; numbers in squares indicate homoplastic characters. Ari = Aristidoideae, Aru = Arundinoideae, Chl = Chloridoideae, Dan = Danthoioideae, CP = Centothecoideae + Panicoideae, OG = Outgroup.  
 Extracted from Sánchez-Ken *et al.* (2007)..... 39

## CHAPTER 1

Figure 1. Photograph of the lectotype [right] of *Panicum salzmannii* (K-000643013) and an isolectotype [left] (K-000004793), collected by Philipp Salzmann in Bahia, Brazil. (©The Board of Trustees of the Royal Botanic Gardens, Kew. Reproduced with the consent of the Royal Botanic Gardens, Kew)..... 52

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## I. GENERAL INTRODUCTION

The Poaceae (Gramineae), including grasses and bamboos, is a large botanical family of ca. 768 genera and approximately 11506 species (Soreng *et al.* 2017). It is a monophyletic family (GPWG 2001) included in the Poales, in the clade of Commelinids, and presents as synapomorphies the bracteate inflorescences (i.e., glumes, lemmas, and paleas), absence or reduction of the perianth, presence of bicellular microhairs, ligulate leaves, uniovulate ovary (central, amphitropous, or hemianatropous), short funicle, fruit a caryopsis, embryo placed laterally, and intraexin channels in the pollen grains (APG 2009, GPWG 2001). Currently, Poaceae is divided into 12 subfamilies and 52 tribes (Soreng *et al.* 2017) and is distributed throughout the tropical and temperate regions, with representatives also in the polar region (Gould & Shaw 1983). This family also presents notably ecological and economic importance.

The subfamily Micrairoideae has been subject of profound modifications since it was established by Pilger (1954), mainly in relation to the placement of its genera considering the morphology (e.g., Clifford 1964, Clayton & Renvoize 1986), anatomy (e.g., Potztl 1952), physiology and phylogeny (GPWG 2001, Sánchez-ken *et al.* 2007). The subfamily is characterized by including plants with leaves alternate or in whorls; bisexual spikelets articulated above the glumes and usually with the anthoecia pistillate; lemma and paleas cartilaginous or coriaceous or less often chartaceous; developed paleas; linear hilum, and endosperm with simple starch grains. The photosynthetic pathway is C<sub>3</sub>, except for *Eriachne* which is C<sub>4</sub>, and the basic chromosome number is 10 (Sánchez-Ken *et al.* 2007).

Currently, Micrairoideae encompasses three tribes Micraireae, Eriachneae, and Isachneae (incl. Hubbardieae) (Soreng *et al.* 2017). Micraireae is endemic from Australia and includes only the genus *Micraira* F. Muell. Eriachneae is native from Asia and Australia and includes *Eriachne* R. Br. and *Pheidochloa* S.T. Blake. Isachneae is Pantropical and Subtropical, and includes *Coelachne* R. Br., *Heteranthoecia* Stapf, *Hubbardia* Bor., *Isachne* R. Br., *Limnopoa* C.E. Hubb., and *Sphaerocaryum* Nees ex Hook f.

In the Neotropical region, Micrairoideae is represented only by Isachneae and the genus *Isachne*. Isachneae includes ca. 113 species, most of them [ca. 103 spp. (Kellogg 2015)] belonging to *Isachne*.

*Isachne* is characterized by including annual or perennial grasses with spikelets articulated above the developed and subequal glumes, anthoecia similar or dissimilar in relation to the consistency, shape, and pilosity, being the lower staminate, pistillate or bisexual, and the upper bisexual or pistillate (Hitchcock 1920, Clayton & Renvoize 1986). Based on chloroplast (trnL-F, atpβ-rbcL) and ribosomal (ITS1-ITS2) molecular data, Teerawatanon *et al.* (2011)

portrayed *Isachne* as monophyletic with high support; however, their analyses included a limited number of taxa (three Asiatic species in their consensus phylogram) in view of the greatness and diversity found in the genus.

The traditional infrageneric approach divides the genus into two sections, according to the spikelets' characteristics (cf., Honda 1930, Prakash & Jain 1987). Plants with homomorphic (similar) anthoecia are included in *Isachne* sect. *Albentes* V. Prakash & S.K. Jain, and plants with dissimilar (heteromorphic) anthoecia are included in *Isachne* sect. *Isachne* (Iskandar & Veldkamp 2004, Rodrigues & Filgueiras 2016, Veldkamp 2016). This proposal of infrageneric classification is still in need of molecular support.

Iskandar & Veldkamp (2004) pointed out the deficiency in the use of the indumentum as a characteristic for the infrageneric classification of the genus, but they did not rule out that future studies combined with other molecular and morphological characters may bring further contributions on this issue. In the same work, they commented about the curious types of trichomes in the anthoecia which may aid in specific and infrageneric delimitations; however, no data on this subject has ever been published.

*Isachne* is the only representative of Micraiorideae in the Neotropical region, where 15 species have been reported (Zuloaga & Morrone 2003, Longhi-Wagner & Welker 2014, Rodrigues & Filgueiras 2018, 2019). The most robust taxonomic treatment for *Isachne* in the Neotropical region was provided by Hitchcock (1920), in which only the North and Mesoamerican species were included. The other studies including the American species of the genus are composed of regional floras, lists in databanks, and descriptions of new taxa. According to Longhi-Wagner (2012), *Isachne* is in need of urgent revision in Brazil. Soreng *et al.* (2017) highlighted that the genus needs to become subject of a worldwide revision.

The absence of a complete revision of all the Neotropical species, along with the occurrence of inconsistencies in their circumscription, identification, and distribution led us to propose and carry out this thesis. In addition, based on the statements of Iskandar & Veldkamp (2004) regarding the indumentum of the anthoecia and considering the existence of ill-circumscribed species among the Neotropical *Isachne*, we proposed to investigate if the micromorphological characters of leaf blade epidermis and the anthoecia are taxonomically informative within the genus to characterize related species and/or groups.

Further research is still needed to understand this interesting genus regarding aspects of its ecology, anatomical adaptations, biogeography, and phylogenetic relationships at higher and lower levels as well as a broader micromorphological analysis including other Asiatic and Australian taxa. Extensive fieldwork is mandatory as a basis for all the above mentioned research topics.

## II. TAXONOMIC HISTORY OF THE GENUS *ISACHNE* R. BR.

The genus *Isachne* was established in 1810 by Robert Brown in his ‘*Prodromus Florae Novae Hollandiae*’ based on a single species, *Isachne australis* R. Br. While describing the genus, Brown cited Paul Hermann’s *Meneritana* (1717) as related to *Isachne*, although without a clear indication that *Meneritana* was under the recently established genus<sup>1</sup>. Later, the name ‘*Isachne meneritana*’ was attributed to Brown but apparently, it has never been validly published, resulting in a *nomen nudum* used for the subsequent three years.

Sixty-seven years after *Meneritana* was established, Thunberg (1784) described *Milium globosum* from Japan, which was transferred to *Isachne* [*Isachne globosa* (Thunb.) Kuntze] in 1891.

Swartz (1788) described *Panicum rigens* [p. 23] and *Panicum arundinaceum* [p. 24] from Jamaica, which are the first Neotropical species currently accepted in *Isachne*. Later, Lamarck (1791) described *Panicum dispernum* [p. 73] from ‘*South America*’, and in 1798 he described *Panicum polygonoides* [p. 792] from French Guiana.

Poiret (1810) described *Agrostis rigidifolia* from the Dominican Republic. Three years later, he (Poiret 1813) formally published *Isachne meneritana*<sup>2</sup> which was subsequently transferred to *Neurachne* R. Br. by Roemer & Schultes (1817), then to *Panicum* L. by Sprengel (1825), and finally included in the synonymy of *Isachne globosa* along with Brown’s *Isachne australis*. Roemer & Schultes (1817) also added three species from Roth’s manuscript to *Isachne*<sup>3</sup> and combined *Agrostis rigidifolia* to *Milium rigidifolium*.

Brown (1810) was the first author to comment about the morphological affinity between *Isachne* and *Panicum*<sup>1</sup>. As expected, several species previously described by various authors in *Panicum* were transferred to *Isachne*<sup>4</sup>, although even after the establishment of *Isachne* by Brown (1810), some species were still described in *Panicum*<sup>5</sup>.

Raspail (1825), while transferring *Isachne australis* to *Panicum*, apparently was the first to refute the concept of *Isachne* as a distinct genus. However, the name ‘*Panicum australe*’

<sup>1</sup> Brown (1810, page 196). “*Affinitate proxima Panico et facie fere Panici colorati. Hujus generis est Meneritana Herm. zeyl. 24. fide specim. in illius Herb.*”

<sup>2</sup> Poiret (1813, page 185). “*Isachne paniculâ, compositâ, ramis pedicellisque capillaribus, floribus minimis, foliis ore vagina hirsutis*”

<sup>3</sup> *Isachne miliacea* Roth [= *Isachne globosa* (Thunb.) Kuntze], *Isachne pulchella* Roth and *Isachne tricarinata* Roth [= *Panicum brevifolium* L.].

<sup>4</sup> E.g., *Panicum arundinaceum* Sw. [= *Isachne arundinacea* (Sw.) Griseb.] published by Swartz in 1788 and transferred by Grisebach in 1864; *Panicum dispernum* Lam. [= *Isachne disperma* (Lam.) Döll] published by Lamarck in 1791 and transferred by Döll in 1877; *Panicum polygonoides* Lam. [= *Isachne polygonoides* (Lam.) Döll] published by Lamarck in 1798 and transferred by Döll in 1877; *Panicum atrovirens* Trin. [= *Isachne atrovirens* (Trin.) Trin., syn. of *I. globosa* (Thunb.) Kuntze] published in 1821 and transferred by Trinius in 1826, etc.

<sup>5</sup> E.g., *Panicum atrovirens* Trin. (1821).



was unavailable because Sprengel published it in 1824-1825. Therefore, Sprengel (1825) described *Panicum antipodum* [p. 314] [*nom. nov.* for *Isachne australis*], and transferred *Isachne meneritana* [p. 321] and *Isachne pulchella* Roth [p. 322] to *Panicum*. In addition, he accepted *Panicum ventricosum* Lam. [= *Isachne ventricosa* (Lam.) Döll] [p. 316], *Panicum atrovirens* Trin. [= *Isachne atrovirens* (Trin.) Trin.] [p. 318], *Panicum arundinaceum* [= *Isachne arundinacea*] [p. 321] and *Panicum dispernum* [= *Isachne disperma*] [p. 321] in *Panicum* instead of *Isachne*.

Trinius (1826) recognized *Isachne* as a distinct genus, describing *Isachne panicea* [= *Isachne arundinacea*] and transferring *Panicum atrovirens* and *Panicum rigens* Sw. to *Isachne*. Later, Trinius (1827) described *Isachne albens* Trin. and *Isachne dispar* Trin. [= *Isachne pulchella*].

Nees (1829) treated *Isachne* as a synonym of *Panicum*<sup>6</sup>, describing the Neotropical *Panicum trachyspermum* for Brazil, which he combined in 1857 to *Isachne trachysperma* (Nees) Nees. Later, *Isachne trachysperma* was found to be a synonym of *Isachne polygonoides*.

Kunth (1829) accepted *Isachne* as a distinct genus by listing seven species<sup>7</sup> and retaining a few others in *Panicum*<sup>8</sup>. In 1833, he listed ten species of *Isachne* by adding four names<sup>9</sup> to his previous list with six accepted names.

Trinius (1834) reduced *Isachne* to a section of *Panicum* [*Panicum* sect. *Isachne* (R. Br.) Trin.<sup>10</sup>], based on the fertility and texture of the anthoecia (mostly the lower one)<sup>11</sup>. Within *Panicum* sect. *Isachne*, he included eight species<sup>12</sup> and recognized three informal subgroups based on the pubescence of the spikelets<sup>13</sup>.

Steudel (1840) listed 14 names of *Isachne* and also placed them under *Panicum*.

Nees (1850) accepted *Isachne* in a generic rank and described *Isachne myosotis* Nees based on a specimen from Lindley Herbarium.

<sup>6</sup> Nees (1829). "*Panicum et Isachne*, Rob. Brown."

<sup>7</sup> *Isachne australis*, *Isachne dubia* Kunth [nom. superfl. = *Isachne disperma*], *Isachne lamarckii* Kunth [= *Panicum brevifolium*], *Isachne meneritana* Poiret, *Isachne miliacea* [= *Isachne globosa*], *Isachne pulchella* and *Isachne tricarinata* [= *Panicum brevifolium*].

<sup>8</sup> E.g., *Panicum arundinaceum* [= *Isachne arundinacea*], *Panicum rigens* [= *Isachne rigens*], *Panicum polygonoides* [= *Isachne polygonoides*], *Panicum ventricosum* [= *Isachne ventricosa*], etc.

<sup>9</sup> *Isachne albens*, *Isachne dispar* [= *Isachne pulchella*], *Isachne mauritiana* Kunth and *Isachne minutula* Kunth.

<sup>10</sup> Trinius (1834). The indication of the rank of Section is given in page 193, along with commentaries about the Section Cabrera: "*Ob glumulam inferiorem frequentius manifestam quam nullam et ob inflorescentiam Panicum (Digitariae) propiorem quam Paspalo, illi nec huic associanda sectio*" – The section is formally described in the item 12, page 195.

<sup>11</sup> Trinius (1834, page 195). "*flosculus inferior ejusdem cum hermaphrodito formae ac substantiae, saltem glumis firmior*"

<sup>12</sup> *Panicum albens*, *Panicum antipodum*, *Panicum arundinaceum*, *Panicum dispar*, *Panicum meneritana*, *Panicum minutulum* Gaudich, *Panicum rigens* and *Panicum trachyspermum*.

<sup>13</sup> Trinius (1834). "*a) Flosculo utroque glabro*" (page 328); "*b) Flosculo superiore pubescente*" (page 330); "*c) Flosculo utroque pubescente*" (page 331).

Steudel (1854), following Trinius (1834), presented *Isachne* as a section of *Panicum*<sup>14</sup> and recognized the same three subgroups. Based on Trinius' Manuscript, he described *Panicum salzmannii* Trin. ex Steud. from Brazil and included other three American species in his treatment.

Grisebach (1862) described *Isachne leersioides* from Cuba without further comments. In 1864, he transferred *Panicum arundinaceum* to *Isachne* and described *Isachne pygmaea* from Jamaica; therefore, including three American species in his '*Flora of the British West Indian Islands*', and highlighting that the difference between *Isachne* and *Panicum* is in the consistency of the spikelets.

Döll (1877) accepted *Isachne* and included five American species<sup>15</sup> in the '*Flora Brasiliensis*', although some of them with controversial circumscription, such as *Isachne disperma* and *Isachne ventricosa*<sup>16</sup>.

Bentham (1878) placed *Isachne* in the subtribe Milieae together with *Coelachne* R. Br., *Eriachne* R. Br., *Micraira* F. Muell., and *Sporobolus* R. Br. [p. 457]. In the case of *Isachne* [and some other genera], it is clear that its placement in the tribe Milieae instead of Paniceae [as usually done at the time] was based on the articulation of the spikelets<sup>17</sup>. According to Bentham (1878), this feature '*settles also the position of a few genera such as Polypogon, Milium, Isachne, etc. (...), and appears close to connect the two great series [i.e., the series Paniceae and Poaceae]*'. Three years later, Bentham (1881) recognized Isachneae as a distinct tribe<sup>18,19</sup>, making a series of comments about this subject [p. 92 and 93].

Bentham & Hooker (1883) placed *Isachne* again in the tribe Paniceae, Series Paniceae, remarking that the genus is an exception by the occurrence of a bisexual lower anthoecium and by the articulation of the glumes<sup>20,21</sup>.

<sup>14</sup> Steudel (1854). The acceptance of the sections is presented in page 38, and the species are divided into three different groups from page 94 to 97.

<sup>15</sup> Döll (1877). *Isachne disperma*, *Isachne leersioides* Griseb., *Isachne polygonoides*, *Isachne rigens* and *Isachne ventricosa*.

<sup>16</sup> Döll (1877) transferred *Panicum dispermum* to *Isachne disperma* and included *Panicum arundinaceum* [= *Isachne arundinacea*] in the synonymy by mixing different specimens of these species. For a detailed discussion regarding *Isachne ventricosa* sensu Döll, see Rodrigues *et al.* (2016).

<sup>17</sup> Bentham (1878, page 620). "*The genera here collected, together with Milium and a few others not Australian, appear to me to form a fairly limited and not unnatural group. They have been generally dispersed in Paniceae, Agrostideae, and Festucaceae, but they have neither the articulate pedicel of the first, nor the twisted awn and reduced palea of the second, nor the terminal bristle or empty glume so general in Festucaceae.*"

<sup>18</sup> Bentham (1881, page 30). "*Tribus ix. Isachneae. Spiculae aequaliter biflorae. Glumae saepius muticae. Rhachilla ultra flores non producta.*"

<sup>19</sup> Including the genera *Eriachne*, *Isachne*, *Micraira*, *Prionachne* Nees ex Lindl. and *Zenkeria* Trin.

<sup>20</sup> Bentham & Hooker (1883, page 1077). "*Excepta: Flos inferior hermaphoditus perfectus in Isachne (...). Glumae infimae vacuae infra articulationem persistentes in Isachne.*"

<sup>21</sup> Bentham & Hooker (1883, page 1100). "*Genus caractere artificiali, spicularum rhachilla supranec infra glumas inferiores vacuas articulata, ad seriem Poacearum nec Panicearum pertinet (...).*"

Fournier (1886)<sup>22</sup> included *I. disperma* and *I. ventricosa* in his ‘*Mexicanas Plantas*’ and considered *P. arundinaceum* as a distinct species. However, his concept of *I. ventricosa* was also confusing because the material he consulted is, in fact, *P. arundinaceum*, a robust species that is related neither with *I. ventricosa sensu* Döll (1877) [= *Isachne salzmannii*] nor with *I. ventricosa sensu* Lamarck (1791) [cf. footnote 16].

Hackel (1887) also placed *Isachne* in Paniceae, remarking that the anthoecia fall before the glumes<sup>23</sup>. In the subsequent years, he described a few other species and varieties of *Isachne*<sup>24</sup>.

Despite the great variation in the persistence of the glumes on the pedicels, Hooker (1897) stated that the articulation of the anthoecia on the rachilla [above the subequal glumes] was important to separate *Isachne* from *Panicum*. Based on Randle’s personal communication, he also commented about the possibility of occurrence of a vestigial ‘*fifth glume*’ or a prolongation of the rachilla at the base of the palea of the second anthoecium<sup>25</sup> in *Isachne* [in which he included five new species<sup>26</sup>]. According to Hooker (1897), this feature ‘*favours the claim of the genus to be referred to [the Series] Poaceae*’ instead of Paniceae.

Lindman (1900) described *Isachne hackelii* and compared it with *I. leersioides*. Currently, Lindman’s species is accepted as a synonym of *Chascolytrum poomorphum* (J. Presl) L. Essi, Longhi-Wagner & Souza-Chies.

Post & Kuntze (1903) included *Sphaerocaryum* Nees ex Hook. f. in *Isachne* and recognized two sections within the latter based on the number of flowers in the spikelets<sup>27</sup>.

Nash (1903) described *Isachne angustifolia*<sup>28</sup> from Porto Rico. In the same year, Urban (1903) included three species of *Isachne* in his “*Symbolae Antillanae*” and transferred *P. rigidifolium* to *Isachne rigidifolia*.

<sup>22</sup> The combination of *Isachne disperma* to ‘*Ichnanthus dispermus*’ is attributed to Fournier (1886) by he apparently never proposed it, although the name is accepted in the synonymy in Tropicos and in Soreng *et al.* (2003, CNWG).

<sup>23</sup> Hackel (1887, page 35). “(...) in Rispen, 2 blütig, die Fruchtsp. [Fruchtspelzen] aus den stehenbleibenden Hüllsp. [Hüllspelzen] ausfallend.”

<sup>24</sup> *Isachne myosotis* var. *nudiglumis* Hack., from Japan (1889); *Isachne buttneri* Hack., from Gabon (1890); *Isachne beneckeii* Hack., *Isachne miliacea* var. *dispar* (Trin.) Hack., and *Isachne schmidtii* Hack., from Java, India and Thailand (1901), respectively.

<sup>25</sup> The development of this unusual character was considered as “*an error of enthusiasm*” by Iskandar & Veldkamp (2004), since this feature may also occur in some Panicoideae. The “vestigial prolongation” at the base of the palea of the lower anthecium in some specimens may be quite visible under Scan Electron Microscopy (SEM) but rarely ends up in a perfect third anthecium. Effectively, in Panicoideae (e.g., *Panicum*, *Parodiophyllochloa* Zuloaga & Morrone, *Trichantheicum* Zuloaga & Morrone, etc.) the occurrence of a third anthecium also appears to be rarer than the development of the lower one, giving an *Isachne*-like aspect to the spikelets.

<sup>26</sup> Hooker (1897, pages 21 to 26). *Isachne elatior* Kook. f. [= *Isachne kunthiana* (Wight & Arn. ex Steud.) Nees ex Miq.]; *Isachne lisboae* Hook. f.; *Isachne scabrosa* Hook. f.; *Isachne himalaica* Hook. f.; *Isachne clarkei* Hook. f.

<sup>27</sup> Post & Kuntze (1903, page 301). “*Isachna* R. Br. 1810, Graminaceae Sp. – 20. Reg. calid. § 1 Typisachna OK. spiculis semper bifloris § 2 Graya OK. (Nees 1833 in Wight Cat. Nr. 2033; *Sphaerocaryum* Nees 1841) spiculis saepissime unifloris”

Chase (1911) provided further comments about the dehiscence of the glumes and anthoecia and a brief taxonomic history of *Isachne*.

Stapf (1911) described *Heteranthoecia* and provided a relevant taxonomic discussion on the placement and the morphological affinities among *Heteranthoecia*, *Isachne*, and *Coelachne* R. Br. According to him, positioning *Isachne* in the tribe Isachneae, as did Bentham (1881), is ‘a conception very much in accord with the structure of the whole facies of the grass’. However, despite this statement, Stapf (1917) treated *Isachne* under Paniceae and established the subtribe Isachninae [nom. alt. Isachnastrae] to accommodate *Isachne* and *Heteranthoecia*.

Hitchcock (1920) presented the first revision of *Isachne* for North America [which actually included also Central American species], with eight species<sup>29</sup>. Following Chase (1911) and previous authors, he commented about the “anomalous” position of the genus in Paniceae based on the structure of spikelets and fertility of the anthoecia. In the ‘*Manual of the Grasses of the West Indies*’, Hitchcock (1936) presented essentially the same information of 1920.

Camus & Camus (1922) treated *Isachne* under Paniceae. In the subsequent years, the second author described several other species in *Isachne*<sup>30</sup>.

Honda (1930) proposed two sections within *Isachne* based on the morphology of the spikelets and anthoecia<sup>31</sup>. He probably borrowed the concept of Trinius’ informal subgroups based on the anthoecia pubescence and added elements of similarity and consistency of the anthoecia to separate the sections. However, neither the first nor the second names proposed by him were valid according to art. 22 of the ICN (Turland *et al.* 2018).

Stapf & Hubbard (1934) in their treatment for the African species divided the genus into two sections, following Honda’s (1920) proposal.

Hubbard (1943) proposed the reestablishment of Bentham’s Isachneae as a distinct tribe from Paniceae to accommodate *Coelachne*, *Heteranthoecia*, *Isachne*, *Limnopoia* C.E. Hubb. and *Sphaerocaryum*.

Swallen (1943) recorded *Isachne arundinacea* and *Isachne polygonoides* for Panama.

<sup>28</sup> As *Isachne angustifolium* Nash.

<sup>29</sup> Despite of mentioning seven species in the introduction, Hitchcock (1920) included eight species in his revision: *Isachne angustifolia* Nash, *Isachne arundinacea*, *Isachne disperma*, *Isachne leersioides*, *Isachne polygonoides*, *Isachne pygmaea* Griseb., *Isachne rigens* and *Isachne rigidifolia* (Poir.) Urb.

<sup>30</sup> From Madagascar: *Isachne perrieri* A. Camus (in 1925), *Isachne ciliaris* Boinvin ex A. Camus, *Isachne hirtissima* A. Camus, *Isachne laevis* Boinvin ex A. Camus (in 1926), *Isachne musicola* A. Camus (in 1947), *Isachne humicola* A. Camus (in 1949), and *Isachne hubertiana* A. Camus (in 1952); from Vietnam: *Isachne petelotii* A. Camus (in 1928); from Senegal: *Isachne trichainii* A. Camus (in 1933); from Thailand: *Isachne smitinandiana* A. Camus (in 1952).

<sup>31</sup> Honda (1930). “Sect. 1. *Euisachne*, Honda sect. nov. [–] 2 flosculi consimiles; uterque hirsuti v. uterque glabri, ad haec uterque coriacei.” (page 278), “Sect. 2. *Paraisachne*, Honda sect. nov. [–] 2 flosculi dissimiles; inferior glaber, membranaceus, superior hirsutus, coriaceus.” (page 282).

Bor (1949a, 1949b, 1949c) described four new species<sup>32</sup> from India.

Swallen (1950) described *Isachne pubescens* from Guatemala. Two years later, Swallen & García-Barriga (1953) described *Isachne ligulata* from Colombia.

Potztal (1952) conducted an anatomical analysis of the leaves of the Isachneae as circumscribed by Hubbard (1943), and suggested the inclusion of *Sphaerocaryum* in Sporobolae (Chloridoideae), based on the occurrence of spikelets with one floret, lemma 1-nerved and the typical ‘*Sporobolae bicellular hairs*’. Tateoka (1957), however, based on anatomical analysis of the transversal leaf section, provided evidence in favor of placing *Sphaerocaryum* in Isachneae.

Jansen (1953) studied the ‘Malesian’ species and described three new taxa and 11 varieties<sup>33</sup>. He apparently applied the same criteria as Honda (1930) to differentiate two sections within *Isachne*. Nevertheless, his circumscription of *Isachne* sect. *Eu-Isachne* was equivalent to Honda’s concept of *Isachne* sect. *Paraisachne* [i.e., *Isachne dispar* plus *Isachne globosa*]. In *Isachne* sect. *Pseudoisachne* Ohwi ex Jansen were included those species that agree with Honda’s concept of *Isachne* sect. *Euisachne*. Once again, the two names proposed by Jansen (1953) are invalid because: (1) an autonym should have been taken for *Isachne* sect. *Eu-isachne*, according to art. 22 of the ICN (Turland *et al.* 2018); (2) a Latin description and a type-specimen were not provided for *Isachne* sect. *Pseudoisachne*, according to arts. 39 and 9 of the ICN, respectively (Turland *et al.* 2018).

Swallen (1955) recorded four species<sup>34</sup> in his treatment of the ‘*Flora of Guatemala*’.

Bor (1960) transferred *Panicum oreades* Domin to *Isachne* and placed Isachneae in Pooideae. Later, Bor (1965) described *Isachne puberula* Bor, from Thailand.

Metcalf (1960) in ‘*Anatomy of Monocotyledons*’ stated that the leaf structure of *Isachne* is panicoid “*but of a rather special type*”, pointing out that the occurrence of somewhat cubical and acutely angular silica bodies, microhairs, angular vascular bundles, mesophyll radiate with long and loosely arranged assimilatory cells, and almost cubical long-cells was very characteristic of *Isachne* and related genera in Isachneae<sup>35</sup>.

Keng (1965) published a revision of *Isachne* from China. As far as it was possible to gather from the English summary at the end of his Chinese treatment, he accepted Isachninae

<sup>32</sup> *Isachne deccanensis* Bor; *Isachne dimyloides* Bor; *Isachne fischeri* Bor; *Isachne sikkimensis* Bor.

<sup>33</sup> Jansen (1953). *Isachne algens* var. *elatiuscula* (Ohwi) Jansen; *Isachne albens* var. *magna* (Merr.) Jansen; *Isachne albens* var. *sylvestris* (Ridl.) Jansen; *Isachne albomarginata* Jansen; *Isachne albomarginata* var. *hirsuta* Jansen; *Isachne clementis* var. *vulcanica* (Merr.) Jansen; *Isachne globosa* var. *duviumbuensis* Jansen; *Isachne langkawiensis* Jansen; *Isachne miliacea* var. *madurensis* Jansen; *Isachne miliacea* var. *ovatifolia* Jansen; *Isachne myosotis* var. *micrantha* (Merr.) Jansen; *Isachne pangerangensis* var. *marginata* (Buse) Jansen; *Isachne pauciflora* var. *depauperata* (Hack. ex Merr.) Jansen; *Isachne surgens* Jansen.

<sup>34</sup> Swallen (1955). *Isachne arundinacea*, *Isachne polygonoides*, *Isachne pubescens* and *Isachne rigens*.

<sup>35</sup> Metcalfe (1960). cf., *Coelachne* (pages 106, 107, 109), *Cyrtococcum* (pages 129, 131), *Heteranthoecia* (page 235) and *Sphaerocaryum* (pages 459, 460).

as a subtribe included in Paniceae (cf. Stapf 1917), and complementarily accepted two sections within *Isachne*, following Honda's (1930) proposal.

Pohl & Davidse (1971) accepted *Isachne* under Paniceae and provided chromosome numbers for two American species of the genus<sup>36</sup>.

Brown (1977) placed Isachneae apart from the Paniceae, along with other non-Kranz tribes<sup>37</sup> of Panicoideae, and associated them with some non-Kranz genera of Paniceae and non-Kranz subgenera of *Panicum*. He assumed that Isachneae includes modern descendants of the two-fertile florets [regarded as the '*pre-panicoid condition*'], non-Kranz and pre-Paniceae, which retained the plesiomorphic structure of the spikelets.

Pohl (1980) included two species of *Isachne* in his treatment of '*Flora Costaricensis*', however without citing any vouchers.

Prakash & Jain (1984) described *Isachne* sect. *Albentes* to accommodate the species with homomorphic anthoecia [formerly included in the invalid sections '*Euisachne*' of Honda (1930) and '*Pseudoisachne*' of Ohwi ex Jansen (1953)], and finally they grouped the species with heteromorphic anthoecia in *Isachne* sect. *Isachne* [formerly sections '*Paraisachne*' of Honda (1930) and '*Eu-Isachne*' sensu Jansen (1953)].

Renvoize (1984a) transferred *P. salzmannii* to *I. salzmannii*, pointing out the similarity between these '*two genera not closely related*'. Renvoize (1984b) included *I. salzmannii* in his treatment of '*The Grasses of Bahia*' and cited also for Brazil the occurrence of *I. polygonoides* and '*Isachne glaziouii* Hack.'<sup>38</sup>, a *nomen nudum* written on sheets of specimens currently accepted as *Isachne goiasensis*. Later, Renvoize (1987) formally described *I. goiasensis*<sup>39</sup> to accommodate Hackel's unpublished names '*I. glaziouii*' and '*I. goyazensis*' and provided a key for the New World species.

Clayton & Renvoize (1986), following Bentham (1881) and Stapf (1911), recognized Isachneae under Panicoideae, pointing out that, although questionable, it is more appropriate to treat Isachneae at a tribal level than accept it as an anomalous group in Paniceae. According to them, the plesiomorphic character of both bisexual florets in Isachneae is more likely a derived status resulting from reversion to bisexuality of the lower floret. In their treatment, *Isachne* was divided into two sections, according to Honda's (1930) proposal.

Judziewicz (1990) recorded *I. ligulata* and *I. polygonoides* for the Guianas, indicating that the '*yellow viscid bands*' on the pedicels of *I. polygonoides* are similar to that found in *Panicum hirtum* Lam., and that the significance of this character is still unknown.

<sup>36</sup> *Isachne arundinacea* 2n=40 and *Isachne polygonoides* 2n=20.

<sup>37</sup> Brown (1977). i.e., Cyphochlaeneae Bosser, Lecomtelleae Pilg. ex Potz. tal.

<sup>38</sup> Sometimes the alternative spellings '*Isachne glaziouii*' and '*Isachne glaziouvii*' may be found in the literature or written on exsiccatae labels.

<sup>39</sup> The labels of some specimens may bring the alternative spelling '*Isachne goyazensis*'.

Pohl & Davidse (1994) included four species in their treatment of *Isachne* of the 'Flora Mesoamericana' and commented about the similarity between *I. arundinacea* and *I. pubescens*. According to the authors, the second should be treated as a variety of the first.

Renvoize (1998) recorded *I. arundinacea* and *I. polygonoides* for the grass flora of Bolivia.

GPWG (2001) included Isachneae in Panicoideae. Following this proposal, Soreng *et al.* (2003) placed Isachninae under Isachneae in Panicoideae. Additionally, Zuloaga & Morrone (2003) provided a list of 12 Neotropical species of *Isachne* and a taxonomic compilation for each taxon, including acceptance and status of names, synonymy, and distribution.

Iskandar & Veldkamp (2004) revised the Malesian species of *Isachne* sect. *Isachne* and provided the first historical review with relevant taxonomic and nomenclatural data regarding the genus.

In a phylogenetic study by Duvall *et al.* (2007) and Sánchez-Ken *et al.* (2007), *Isachne* surprisingly was resolved in a well-supported clade with the *incertae sedis* genera *Eriachne* and *Micraira*<sup>40</sup>. This clade emerged as sister to Arundinoideae (Figure 1). As a result, the subfamily Micrairoideae Pilg.<sup>41</sup> was reestablished and amended to accommodate eight genera grouped in three tribes: Micraireae (including only *Micraira*), Eriachneae (including *Eriachne* and *Pheidochloa* S.T. Blake) and Isachneae (including *Coelachne*, *Heteranthoecia*, *Isachne*, *Limnopoa*, and *Sphaerocaryum*). This proposal has been strongly supported and was followed in subsequent classifications (e.g., Sánchez-Ken & Clark 2010, GPWG II 2012, Kellogg 2015, Soreng *et al.* 2015).

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<sup>40</sup> The relationship between *Eriachne*, *Isachne* and *Micraira* was suggested by Bentham (1881) who placed them in the tribe Isachneae, along with some small genera currently grouped elsewhere.

<sup>41</sup> The subfamily Micrairoideae was primarily established in German by Pilger (1954) and two years later (1956) he validated the name presenting a Latin description.

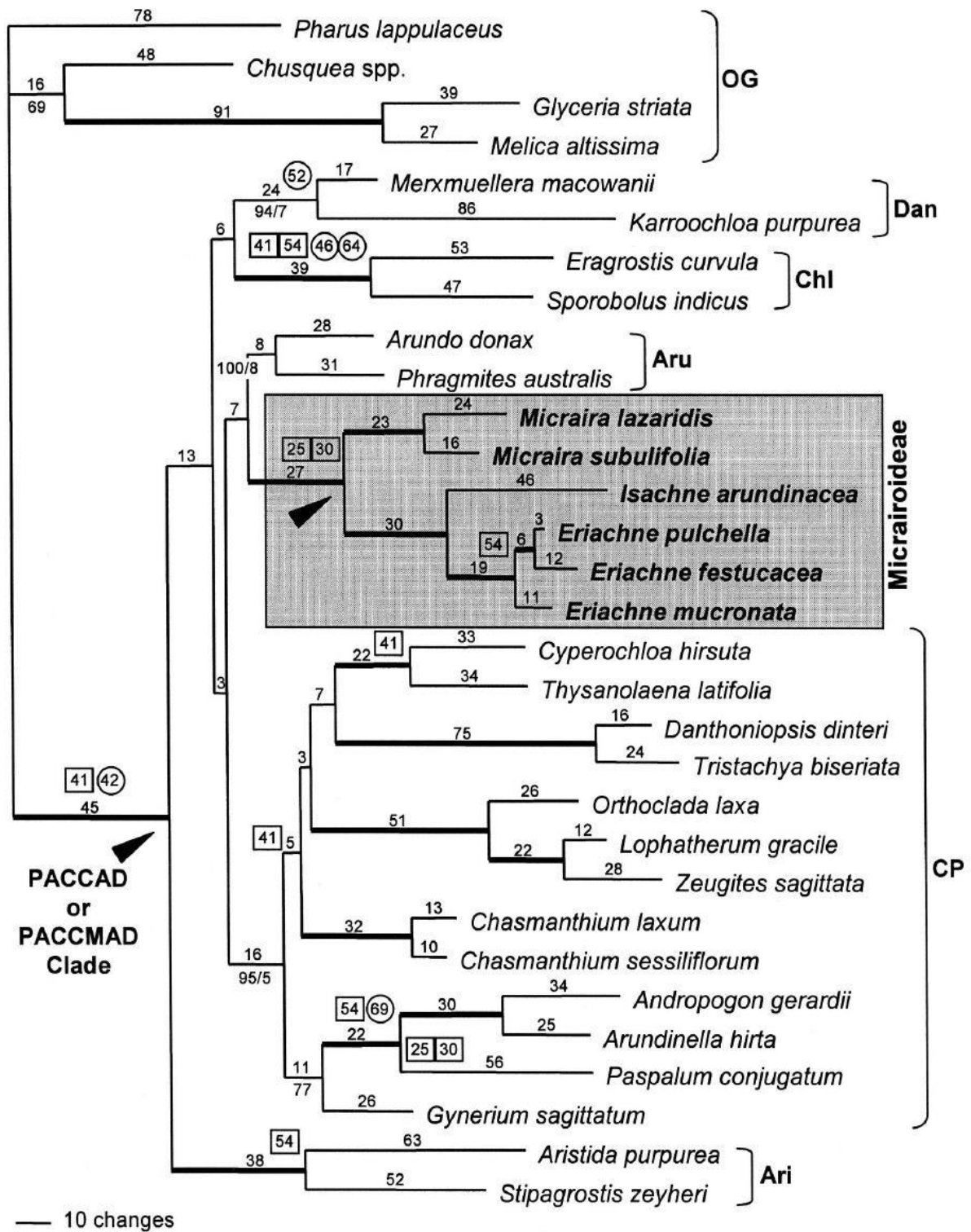


Figure 1. Three based on *ndhF* and *rpl16* intron sequence data and structural data. Arrows indicate the PACCMAD and Micrairoideae clades. Black bars indicate 100% bootstrap support and > 10 decay values, those with lower values are below the branches separated by a slash (values for Bs below 69 and Br below 5 are not shown). Branches with no support collapse in the strict consensus. Numbers above branches indicate number of changes. Numbers in circles indicate unambiguous synapomorphies; numbers in squares indicate homoplastic characters. Ari = Aristidoideae, Aru = Arundinoideae, Chl = Chloridoideae, Dan = Danthonioideae, CP = Centothechoideae + Panicoideae, OG = Outgroup. Extracted from Sánchez-Ken *et al.* (2007).



Longhi-Wagner & Welker (2014) described *Isachne hirtiglumis* from Brazil and presented a synopsis for the four known Brazilian species of the genus<sup>42</sup>.

Filgueiras & Rodrigues (2015) published an account of *Isachne* for the ‘*Brazilian Flora List*’ and included the same four species.

Veldkamp (2016) presented an account and nomenclatural changes for two East-African species, plus a nomenclatural survey for the African species.

Rodrigues *et al.* (2016) presented a detailed discussion about the taxonomy of the Brazilian endemic and poorly known *I. salzmannii* and indicated a lectotype for the name *P. salzmannii*.

Rodrigues & Filgueiras (2016) expanded to Brazil the range of occurrence of *I. ligulata*. Later, Rodrigues (2017) included five species in his treatment for the ‘*Flora do Brasil 2020*’. Rodrigues & Filgueiras (2018) described *I. soderstromii* from Dominica, and provided a key for the species in Central America and the Antilles. In the next year, Rodrigues & Filgueiras (2019) segregated *I. burchellii* from *I. goiasensis* and increased to six the number of Brazilian species of the genus.

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<sup>42</sup> *Isachne goiasensis*, *Isachne hirtiglumis*, *Isachne salzmannii* and *Isachne polygonoides*.

### III. OBJECTIVES

1. Carry out the taxonomic revision of the Neotropical species of *Isachne*;
2. Perform macromorphological (external morphology) and micromorphological (SEM) studies with a taxonomic objective to circumscribe and differentiate closely related species;
3. Analyze and reevaluate the known geographic distribution of the species.

#### IV. STRUCTURE OF THE THESIS

This thesis is divided into seven chapters which were prepared in the form of Journal Articles. The first four chapters have been previously published in separate Journals, as indicated below. The other chapters are not being considered for publication and have been formatted in outline according to the standards of Hoehnea.

Chapters are organized in a sequence of publication date (for the published chapters), followed by an expected publication sequence (for the unpublished chapters). Therefore, the taxonomic novelties included in chapter 7 are not necessarily adopted in the previous chapters.

Chapter 1. Lectotypification of *Panicum salzmannii*, basionym of *Isachne salzmannii* (Poaceae, Micrairoideae). Phytotaxa 246(2): 155-158 (2016).

Chapter 2. First record of *Isachne ligulata* (Poaceae: Micrairoideae) in Brazil and a key for the Brazilian species of the genus. Acta Botanica Brasilica 30(4): 700-704 (2016).

Chapter 3. *Isachne soderstromii* sp. nov. (Poaceae, Micrairoideae, Isachneae) from Dominica, Lesser Antilles. Nordic Journal of Botany 36(1-2): njb-01847 (2018).

Chapter 4. *Isachne burchellii* (Poaceae, Micrairoideae) from Rio de Janeiro, Brazil - an endemic new species segregated from *Isachne goiasensis*. Brittonia <https://doi.org/10.1007/s12228-019-09576-x> (2019).

Chapter 5. Micromorphology of the leaf blade epidermis in the Neotropical species of *Isachne* (Poaceae, Micrairoideae).

Chapter 6. Anthoecia and rachilla micromorphology in the Neotropical species of *Isachne* (Poaceae, Micrairoideae): a contribution to the taxonomy and species delimitation.

Chapter 7. Revision of the Neotropical species of *Isachne* R. Br. (Poaceae, Micrairoideae).

Besides the chapters above mentioned, in the course of production of this thesis, the taxonomic treatment of *Isachne* for the project Flora do Brasil 2020 (under construction) was elaborated. This treatment includes identification keys, morphological descriptions, comments, and photographs. The results are accessible at: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB20394>

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# Chapter 1

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## **Abstract**

Analyses of herbarium collections and of the original description of *Panicum salzmannii* (basionym of *Isachne salzmannii*) revealed inconsistencies in the typification of this name. The existence of two specimens of the original material stored in the same herbarium, without a clear previous designation of which one carries the status of lectotype, requires a second-step lectotypification. Thus, we propose herein a second-step lectotype to effectively typify the name *P. salzmannii*.

## **Resumo**

Análises de coleções de herbário e da descrição original de *Panicum salzmannii* (basiônimo de *Isachne salzmannii*) revelaram inconsistências na tipificação desse nome. A existência de dois espécimes da coleção original, depositados no mesmo herbário, sem uma clara designação prévia de qual deles carrega o status de lectótipo, requer um segundo passo de lectotipificação. Portanto, propomos aqui uma segunda lectotipificação para efetivamente tipificar o nome *P. salzmannii*.

Keywords: Brazilian grasses, endemic species, Neotropical grasses, nomenclature, typification

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**The following chapter was submitted (2015) and published in Phytotaxa (2016). Text format, citations, and references are presented according to the standards of the Journal.**

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Full reference: Rodrigues, R.S., Dórea, M.C., Filgueiras, T.S. & Oliveira, R.P. 2016. Lectotypification of *Panicum salzmannii*, basionym of *Isachne salzmannii* (Poaceae, Micrairoideae). *Phytotaxa* 246(2): 155-158. D.O.I.: 10.11646/phytotaxa.246.2.8

**Lectotypification of *Panicum salzmannii*, basionym of *Isachne salzmannii*  
(Poaceae, Micrairoideae)**

**RODRIGO S. RODRIGUES<sup>1\*</sup>, MARCOS DA COSTA DÓREA<sup>2</sup>, TARCISO S. FILGUEIRAS<sup>1</sup> &  
REYJANE PATRICIA DE OLIVEIRA<sup>2\*</sup>**

<sup>1</sup>*Programa de Pós-graduação em Biodiversidade Vegetal e Meio Ambiente, Núcleo de Pesquisa Curadoria do Herbário, Instituto de Botânica, Caixa Postal 68041, São Paulo, SP, Brazil.*

<sup>2</sup>*Programa de Pós-graduação em Botânica, Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Av. Transnordestina s.n., Novo Horizonte, 44036-900, Feira de Santana, Bahia, Brazil.*

\*Corresponding authors: [rosaro\\_3588@yahoo.com.br](mailto:rosaro_3588@yahoo.com.br); [rpatricia@uefs.br](mailto:rpatricia@uefs.br)

In Poaceae, many species names now accepted in distinct genera were originally described in *Panicum* Linnaeus (1753: 55), such as *P. salzmannii* Trinius ex Steudel (1854: 95), which is now recognized as a species of *Isachne* Brown (1810: 196) [i.e., *P. salzmannii* is the basionym of *I. salzmannii* (Trin. ex Steud.) Renvoize (1984a: 184)].

*Isachne* belongs to subfamily Micrairoideae (GPWG II 2012, Soreng *et al.* 2015) and includes ca. 95 species (Iskandar & Veldkamp 2004), about thirteen of them occurring in the Neotropics (Zuloaga & Morrone 2003a, Longhi-Wagner & Welker 2014). Members of this genus have a bisexual, pistillate or staminate lower floret, and a bisexual or pistillate upper floret; both florets are usually similar in texture, mostly coriaceous to subcoriaceous (Hitchcock 1920, Clayton & Renvoize 1986), and disarticulate together above the glumes. Most of the species have a glandular band on the pedicels (Iskandar & Veldkamp 2004, Longhi-Wagner & Welker 2014).

*Isachne* is the only genus of Micrairoideae with representatives in Brazil, where four species have been reported: *I. goiasensis* Renvoize (1987: 928), *I. hirtiglumis* Longhi-Wagner & Welker (2014: 846), *I. polygonoides* (Lamarck 1798: 742) Döll (1877: 273), and *I. salzmannii* (Longhi-Wagner & Welker 2014, Filgueiras & Rodrigues 2015). Three of them are endemic to Brazil, and one (*I. polygonoides*) occurs throughout tropical America (Zuloaga & Morrone 2003a).

*Isachne salzmannii* is a rare and poorly known grass, considered endemic to swampy areas from Bahian coast (Renvoize 1984a, Longhi-Wagner & Welker 2014, Filgueiras & Rodrigues 2015). There are few sheets of this species in herbaria, including

the type collection made by Philipp Salzmann in the 19th century, plus a few other gatherings made by Agnes Chase in the 20th century.

In the protologue of *Panicum salzmannii*, Steudel (1854) only cited the gathering “*Salzm. Hrbr. Bahia*”. When Renvoize (1984a) transferred *P. salzmannii* to *Isachne* (*I. salzmannii*), he indicated one “isotype” housed at K (herbaria acronyms according to Thiers 2016). In the Catalogue of New World Grasses, Zuloaga & Morrone (2003b) indicated that the “holotype” of *Panicum salzmannii* is housed at P with isotypes at K, LE, MO and US, probably unaware that in P there are five syntypes. This indication does not represent a valid typification statement because it is not in conformity with Art. 7.10 and 9.19 ICN (McNeill *et al.* 2012). In the nomenclatural survey of *Isachne* presented by Iskandar & Veldkamp (2004) no type material was cited for *I. salzmannii*. Longhi-Wagner & Welker (2014) followed Zuloaga & Morrone (2003b) and they additionally indicated isotypes from P, without mention of what specimen was the “holotype”.

During our revision of Brazilian grasses in European herbaria, we found at K two specimens that correspond to the original material cited by Steudel (1854) mounted on a single sheet, with two different labels and two different barcodes (Fig.1). Additionally, we found several specimens housed at MPU and P, also corresponding to Salzmann’s original material, which were not previously reported in the literature, including one Cibachrome housed at HUEFS obtained from K (K-000643013 and K-000004793).

According to Art. 9.5 ICN, all the representatives of the type collection are syntypes, because a single specimen was not designated as the type in the protologue (Steudel 1854). Renvoize (1984a) thus made an “inadvertent lectotypification” by using the term “isotype” and by indicating one specimen from a single herbarium [see Prado *et al.* (2015)], which is acceptable according to Art. 7.10, 9.22 and 9.23 ICN for works published before 1 January 2001. Following Art. 9.9 ICN, the erroneous application of the term “isotype” is treated as an error to be corrected to lectotype. Because there is more than one specimen of the original material at K, we propose a second-step lectotype to typify the name *Panicum salzmannii* (Art. 9.17 ICN).



**FIGURE 1.** Photograph of the lectotype [right] of *Panicum salzmannii* (K-000643013) and an isotype [left] (K-000004793), collected by Philipp Salzman in Bahia, Brazil. (©The Board of Trustees of the Royal Botanic Gardens, Kew. Reproduced with the consent of the Royal Botanic Gardens, Kew). Available from: <http://specimens.kew.org/herbarium/K000643013>.

## Typification

*Isachne salzmannii* (Trinius ex Steudel) Renvoize (1984a: 184). (Fig. 1)

Basionym: *Panicum salzmannii* Trinius ex Steudel (1854: 95).

First-step lectotype:—BRAZIL. Bahia: without locality, without date, *Salzmann s.n.* (K), designated by Renvoize (1984a: 184), corrected from “isotype”. Second-step lectotype: K-000643013!, here designated. Isolectotypes: K-000004793!, LE-TRIN-0556.01 (fragment and illustration), MO-2099177!, MPU-024600!, MPU-024601!, MPU-024602!, MPU-024603!, MPU-024604!, P-00740915!, P-00740916!, P-00740917!, P-01936067!, P-02382030!, US-975976! (fragment ex P). An image of the K specimens is housed at HUEFS [HUEFS-41943! (image ex K)].

**Notes:**—Döll (1877) in *Flora Brasiliensis* erroneously included *Panicum salzmannii* in the synonymy of *Isachne ventricosa* (Lamarck 1791: 173) Döll (1877: 274), an Asiatic species probably related to the widespread *I. globosa* (Thunberg in Murray 1784: 109) Kuntze (1891: 778). As stated by Renvoize (1984b), Döll mixed several collections of different Brazilian *Isachne* (e.g., *I. goiasensis*, *I. polygonoides* and *I. salzmannii*), and misapplied them to Salzmann’s and Lamarck’s collections. Chase in 1935 [her notes can be found on labels of the specimens she collected housed at P (P-00740917) and RB (RB-78518), and in one specimen collected by Salzmann at MPU (MPU-024601)] and Renvoize (1984b) considered *P. salzmannii* (*I. salzmannii*) and *I. ventricosa* as distinct taxa. Despite their determinations, Zuloaga & Morrone (2003a) and Iskandar & Veldkamp (2004) treated *I. salzmannii* and *I. ventricosa* as the same species. The synonymy is currently accepted in *Tropicos* (2016).

The isolectotype P-00740915 is the only sheet with Steudel’s handwriting on it (strongly stricken through) and was used to illustrate the species *Isachne ventricosa* in *Flora Brasiliensis* (tab. 35). The illustration is in fact *Panicum salzmannii* (*I. salzmannii*), as currently recognized.

## Acknowledgements

We thank the curators of the herbaria consulted for the support during our visits, mainly to the Re flora team in K and P (Catia Canteiro and Claudia Gonçalves, respectively), and to Jeffery M. Saarela and Jefferson Prado for their assistance with typification issues; to CNPq/Brazil for the financial support (grants numbers 562349/2010-3, 563558/2010-5). The authors also thank CAPES/Brazil for the fellowships received as part of the Re flora Programme. RSR and MCD also thank CAPES, respectively, for a Doctoral and PNPd fellowships, and RPO thanks CNPq for a Productivity grant (PQ1D).

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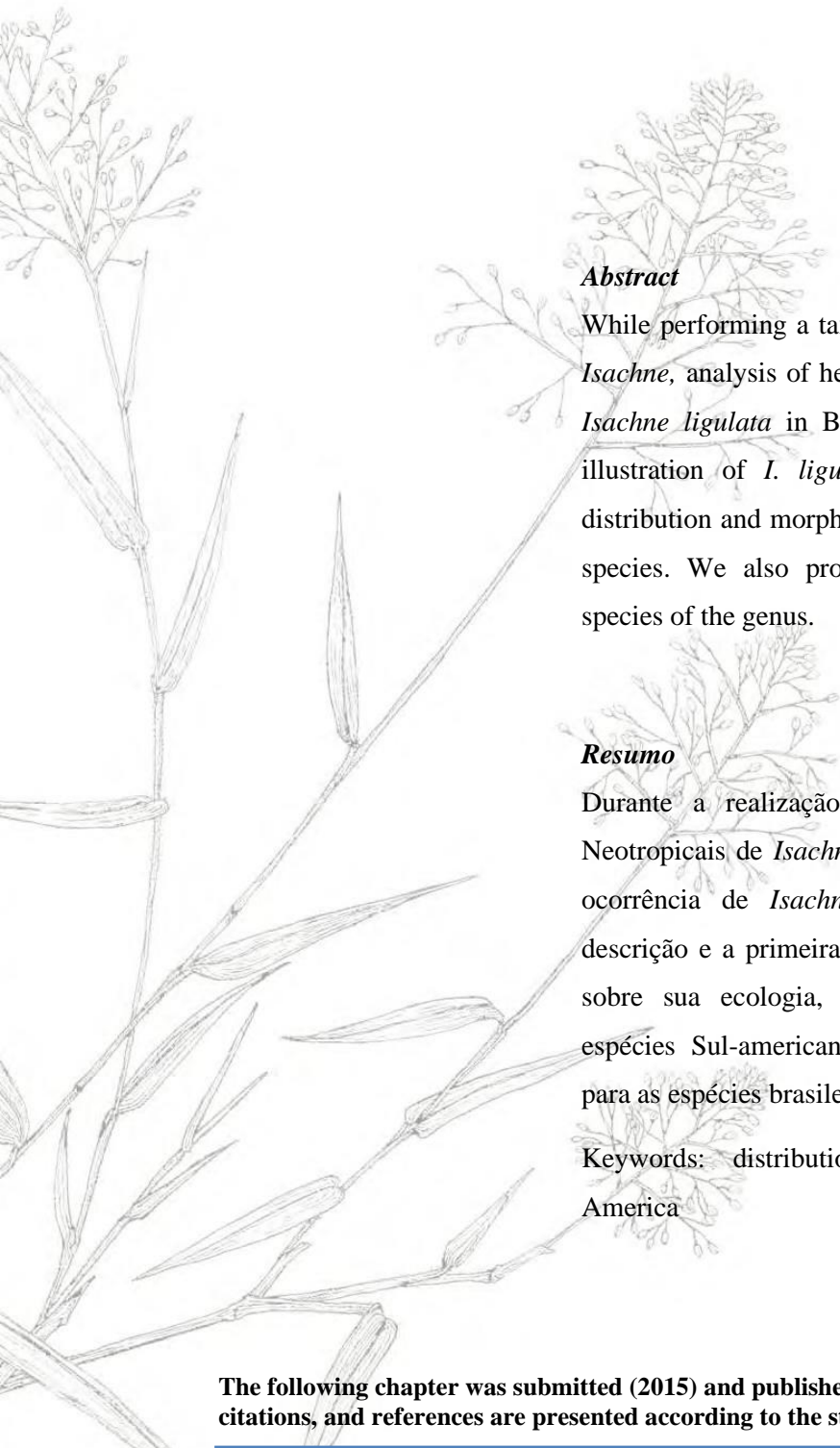
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# Chapter 2

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## **Abstract**

While performing a taxonomic revision of the Neotropical species of *Isachne*, analysis of herbarium collections revealed the occurrence of *Isachne ligulata* in Brazil. We provide a description and the first illustration of *I. ligulata*, along with comments on its ecology, distribution and morphological affinities with related South American species. We also provide an identification key for the Brazilian species of the genus.

## **Resumo**

Durante a realização de uma revisão taxonômica das espécies Neotropicais de *Isachne*, a análise de coleções de herbário revelou a ocorrência de *Isachne ligulata* no Brasil. São fornecidas uma descrição e a primeira ilustração de *I. ligulata*, além de comentários sobre sua ecologia, distribuição e afinidades morfológicas com espécies Sul-americanas relacionadas. Uma chave de identificação para as espécies brasileiras do gênero também é fornecida.

**Keywords:** distribution, grasses, Isachneae, Neotropics, South America

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**The following chapter was submitted (2015) and published in Acta Botanica Brasilica (2016). Text format, citations, and references are presented according to the standards of the Journal.**

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Full reference: Rodrigues, R.S. & Filgueiras, T.S. 2016. First record of *Isachne ligulata* (Poaceae: Micrairoideae) in Brazil and a key for the Brazilian species of the genus. Acta Botanica Brasilica 30(4): 700-704. D.O.I.: 10.1590/0102-33062016abb0269

## First record of *Isachne ligulata* (Poaceae: Micrairoideae) in Brazil and a key for the Brazilian species of the genus

Rodrigo S. Rodrigues<sup>1\*</sup> and Tarciso S. Filgueiras<sup>1</sup>

*Isachne* R. Br. includes ca. 100 species (Veldkamp 2016), and is the largest and the most widespread genus of the subfamily Micrairoideae. The genus has its greatest diversity in tropical and temperate Asia (Judziewicz 1990), but also occurs in Africa, the Americas, Pacific Islands and Australia (Clayton *et al.* 2006). Thirteen species are recorded for the Neotropics (Rodrigues *et al.* 2016), and are distributed from southern Mexico to Bolivia and southeastern Brazil (Renvoize 1987). Despite the extensive area of occurrence of the genus *Isachne* in the Neotropics, most of the species are restricted to Mesoamerica, the Antilles and northern South America.

Historically, *Isachne* was placed in the subfamily Panicoideae, and considered as a distinct genus or as a section of *Panicum* L., mainly because of the apparent similarity of the spikelets in the members of these two genera. Surprisingly, recent phylogenetic studies resolved *Isachne* (tribe Isachneae Benth.) as belonging to a clade that also included the tribes Micraireae Pilg. and Eriachneae Eck-Boorsb., within the resurrected and emended subfamily Micrairoideae (Duvall *et al.* 2007; Sánchez-Ken *et al.* 2007). Currently, *Isachne* is included in tribe Isachneae and is artificially divided into two sections according to the degree of similarity of the anthercia. *Isachne* sect. *Isachne* includes the species with heteromorphic anthercia (i.e., anthercia very dissimilar or completely different in texture and pilosity), whereas *Isachne* sect. *Albentes* V. Prakash & S.K. Jain includes the species with homomorphic anthercia (i.e., anthercia similar or almost similar in texture and pilosity) (Iskandar & Veldkamp 2004; Veldkamp 2016).

*Isachne* comprises annual or perennial plants, usually with trailing or scandent culms, which may vary from being short and delicate to long, robust, rigid, thick and very branched (Renvoize 1987). The genus can be recognized by the spikelets disarticulating above the subequal glumes; the anthercia frequently homomorphic (less often heteromorphic); mostly coriaceous to subcoriaceous; the lower staminate, pistillate or bisexual; the upper bisexual or pistillate (Hitchcock 1920; Clayton & Renvoize 1986).

Species of *Isachne* predominantly inhabit localities with damp or muddy soils, such as swamps, along streams, brooks, headwaters, rivers, edges of lakes, waterfalls, etc., usually associated with flooded grasslands or riparian vegetation (Longhi-Wagner 2012; Longhi-Wagner & Welker 2014).

<sup>1</sup> Programa de Pós-graduação em Biodiversidade Vegetal e Meio Ambiente, Núcleo de Pesquisa Curadoria do Herbário SP, Instituto de Botânica, P.O. Box 68041, São Paulo, SP, Brazil.

\* Corresponding author: rosaro\_3588@yahoo.com.br

Longhi-Wagner (2012) drew attention for the urgent need of a revision for the Brazilian species of *Isachne*. Two years later, Longhi-Wagner & Welker (2014) provided a compilation of the genus in Brazil and described a new species. Currently, four species are recorded for Brazil: *Isachne goiasensis* Renvoize, *I. hirtiglumis* Longhi-Wagner & Welker, *I. polygonoides* (Lam.) Döll and *I. salzmännii* (Trin. ex Steud.) Renvoize (Filgueiras & Rodrigues 2015).

We conducted studies at BHCB, HUEFS, IAC, IBGE, INPA, OUPR, R, RB, SP, SPF, UB, UEC and VIC (herbaria acronyms according to Thiers 2016), and consulted the Re flora Virtual Herbarium (available at <http://reflora.jbrj.gov.br/reflora/herbarioVirtual/>) and the virtual collections from K, MO, NY, P and US. As a result, the first record of *I. ligulata* Swallen in Brazil is confirmed. Additionally, the first illustration of the species and further comments on its ecology, conservation, distribution and morphological affinities with related species occurring in South America are provided. A key for the Brazilian species of *Isachne* is also presented.

*Isachne ligulata* Swallen, *Caldasia* 2(8): 305. 1943.

Type: COLOMBIA. Department of Cauca: [Cauca Valley], Cuatro Esquinas, 5/VI/1922, FW Pennell & EP Killip 6343 (holotype US-1140437; image!).

Fig. 1.

Perennials, climbing or leaning plants, 1.5-3.5(-4) m long; culms robust, branched, re-branching at the top, glabrous; nodes glabrous. Sheaths pubescent to densely pilose towards the apex, trichomes tuberculate, dehiscent in old sheaths, margins densely ciliate; ligule 2-3 mm long, ciliate; leaf blades linear-lanceolate, 3-15 × 0.3-1.5 cm, apex acute, base obtuse to rounded, not amplexicaul, scabrous-pubescent to scabrous-pilose, margins scabrous. Panicles 5-15 cm long, primary branches usually spreading, secondary branches divergent, axillary glands conspicuous; pedicels inconspicuously scabrous, glandular bands absent. Spikelets solitary, elliptic-globose to oblong, 1.8-2.3 mm long, anthercia homomorphic; glumes subequal, 0.1-0.3 mm shorter than the lower anthercium, lower glume 7-9-nerved, upper glume 9-11-nerved, both pubescent at the apex; lower anthercium bisexual, pistillate or staminate, oblong-elliptic to elliptic, 1.8-2.3 mm long, subequal or ca. 0.5 mm longer than the upper anthercium, apex rounded to subacute, coriaceous, stramineous, lemma and palea with minutely appressed and sparse bicellular trichomes; upper anthercium bisexual, oblong-elliptic, 1.3-1.5 mm long, coriaceous, callus pilose, lemma and palea with minutely appressed-sparse bicellular trichomes, nearly glabrous. Caryopsis oblong, blackish, 0.2 × 0.1 mm.

Flowering in January, March, April, June, and from August to November. In the Guyana highlands, according to Judziewicz (1990), the species flowers from September through February.

Material examined: BRAZIL. Amazonas: Santa Isabel do Rio Negro, Parque Nacional do Pico da Neblina, 0°47'14"N, 66°01'26"W, 22/IX/2012, RC Forzza *et al.* 7275 (RB, SP).

Additional material examined: COLOMBIA. Cundinamarca: Salto de Tequendama, 1-3/X/1938, J Cuatrecasas 165 [paratype] (P; image). PERU. Pasco: Prov. Oxapampa, 5/III/1986, H van der Werff *et al.* 8405 (US; image). VENEZUELA. Bolívar: Sarvén-tepuí, slopes and talus forest, 13/I/1953, JJ Wurdack 34138 (RB).

Distribution and ecology: *Isachne ligulata* is an endemic South American species reported from mountainous areas of the Amazon Basin and the Guiana Shield, at altitudes ranging 1700-2500 m. It was originally described from Colombia but later its distribution was found to extend to Guyana, Peru and Venezuela (Swallen & García-Barriga 1943; Renvoize 1987; Zuloaga & Morrone 2003). Individuals are found along forest edges, especially along streams (Judziewicz 1990), and are sometimes associated with shrubby vegetation.

This is the first record of *I. ligulata* for Brazil, 73 years after its original description (Swallen & García-Barriga 1943). In Brazil this species is known only from the region of Santa Isabel do Rio Negro, in the state of Amazonas, in Pico da Neblina National Park, near the border with Venezuela. The long span of time between the original description and the discovery of the species in the Brazilian Amazon is probably due to the difficulty of accessing the area where it is found and there having been few studies undertaken there, most of them focused on woody rather than herbaceous species, and are conducted in relatively limited and isolated locations (BFG 2015).

Conservation: In Brazil, *I. ligulata* has only been recorded from a conservation unit, the Pico da Neblina National Park. The lack of information about the species' distribution and population size are barriers to assessing the conservation status of this species in Brazil, and so according to IUCN criteria, it should be considered as data deficient (IUCN 2015).

Morphological affinities: As commonly occurs with other species of *Isachne*, the culms in *I. ligulata* rebranch at the tips and produce one inflorescence branch per node (Fig. 1). Specimens currently accepted under the circumscription of *I. ligulata* used to be primarily identified as *I. arundinacea* Griseb., a species recorded for Mexico, Mesoamerica, and northern and northwestern South America (Zuloaga & Morrone 2003; Clayton *et al.* 2006).

*Isachne arundinacea* has been traditionally circumscribed as having longer leaf blades, glabrous sheaths, ascending panicles, often with secondary branches and pedicels appressed to the spreading primary branches; the pedicels are extremely short, and the spikelets are 1.4-1.8

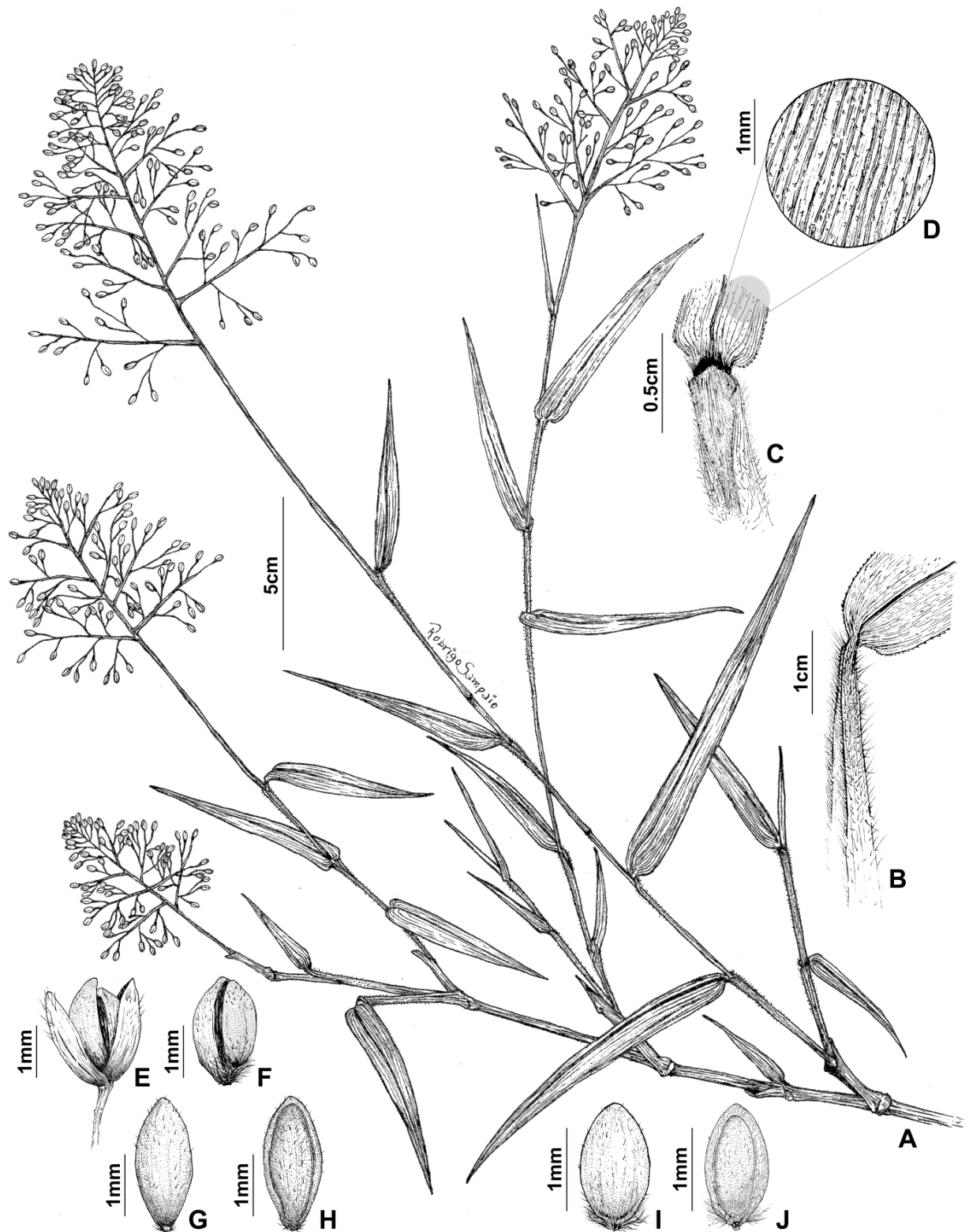
mm long, globose, and clustered at the branch tips. Micromorphological characters of the leaf blade and spikelets also support *I. ligulata* and *I. arundinacea* as distinct species (RS Rodrigues & TS Filgueiras unpubl. res.).

The morphology of the spikelets of *I. ligulata* closely resembles that of *I. rigens* Trin., another Meso- and South American species not yet recorded for Brazil, but which has a similar habit and distribution (Zuloaga & Morrone 2003; Clayton *et al.* 2006). *Isachne rigens*, however, can be distinguished by the more delicate culms, panicle size, spikelets regularly or loosely distributed along the branches, and pedicels usually inserted directly on the primary branches.

The morphological distinctions between *I. ligulata* and other species that occur in Brazil are highlighted in the following dichotomous key.

#### Key to the Brazilian species of *Isachne*

1. Culms 100-400 cm long, somewhat lignified, robust ..... 2
2. Leaf-sheaths glabrous; panicles 18-27(-30) cm long, flexible; pedicelar bands present; upper anthercium conspicuously appressed-pilose, hemispheric to sub-hemispheric ..... *I. goiasensis*
- 2'. Leaf-sheaths pubescent to densely pilose towards the apex; panicles 5-15 cm long, rigid; pedicelar bands absent; upper anthercium inconspicuously appressed-pubescent to nearly glabrous, oblong-ellipsoid ..... *I. ligulata*
- 1'. Culms 10-90 cm long, herbaceous, slender ..... 3
3. Glumes entirely hirsute; anthercia homomorphic, similar in texture and pilosity ..... *I. hirtiglumis*
- 3'. Glumes glabrous or the upper 1/4 glabrescent to sparsely pubescent; anthercia heteromorphic, dissimilar in texture and pilosity ..... 4
4. Leaf-sheaths glabrous; leaf blades linear-lanceolate, base slightly attenuate, not amplexicaul; lemma of the lower anthercium conspicuously sulcate on the back towards the base ..... *I. salzmannii*
- 4'. Leaf-sheaths pubescent to hirsute; leaf blades lanceolate, base cordate to subcordate, amplexicaul; lemma of the lower anthercium not sulcate ..... *I. polygonoides*



**Figure 1.** *Isachne ligulata*. A: apex of the culm with flowering branches; B: apex of the leaf-sheath and base of leaf blade; C: apex of the leaf-sheath, ligular region and base of leaf blade; D: detail of the adaxial surface of leaf blade; E: spikelet, lateral view; F: anthercia (note the pilosity at the rachilla between the upper and the lower anthercia); G: lower anthercium, lemma view; H: lower anthercium, palea view; I: upper anthercium, lemma view; J: upper anthercium, palea view. [Based on: A - JJ Wurdack 34138 (RB); B-J - RC Forzza *et al.* 7275 (SP)]. Illustration by Rodrigo S. Rodrigues.

Additional remarks: Zuloaga & Morrone (2003) cited “Caldas” as the department of Colombia where the type was collected. However, the label of the holotype at the US herbarium bears the printed information: “Department of El Cauca, Cauca Valley”, therefore “Caldas” and “Cauca” are two distinct Departments in Colombia. The same wrong information is recorded in the databank of Tropicos (2016).

### Acknowledgements

We are grateful to Dr. Pedro L. Viana and to Dr. Rafaela C. Forzza for their collaboration. We also thank the curators of the visited herbaria, and the anonymous reviewers for their contributions to the text. We thank the Instituto de Botânica in São Paulo and its Post-Graduation Program for the continuous support of our research. RSR thanks CAPES for a doctoral fellowship.

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# Chapter 3

A detailed botanical line drawing of the grass *Isachne soderstromii*. The illustration shows a central culm with several long, narrow, lanceolate leaves arranged in distichous rows. At the top of the culm is a panicle with multiple branches, each bearing numerous small, spikelet-like flowers. The drawing is rendered in a fine-line style, showing the venation of the leaves and the structure of the inflorescence.

## **Abstract**

*Isachne soderstromii*, a new species from Dominica in the Lesser Antilles, is described and illustrated. The new species can be recognized by the combination of the following features: distichous leaves, blades with conspicuous midrib, panicle branches and pedicels with glandular bands, and glabrous rachilla between the lower and the upper similar anthoecia. The new taxon is compared with morphologically related Central American and Caribbean species of the genus. Additionally, a key to the species of *Isachne* occurring in Central America and the Antilles is provided.

## **Resumo**

*Isachne soderstromii*, uma nova espécie de Dominica, nas Pequenas Antilhas, é descrita e ilustrada. A nova espécie pode ser reconhecida por meio da combinação dos seguintes caracteres: folhas dísticas, lâminas com uma nervura central conspícua, ramos da panícula e dos pedicelos com faixas glandulares e ráquila glabra entre os antécios inferior e superior. O novo táxon é comparado com outras espécies morfológicamente relacionadas da América Central e Caribe. Adicionalmente, uma chave para as espécies de *Isachne* ocorrentes na América central e Antilhas é fornecida.

Keywords: Central America, Neotropical grasses, Caribbean.

**The following chapter was submitted (2017) and published in the Nordic Journal of Botany (2018). Text format, citations, and references are presented according to the standards of the Journal.**

Full reference: Rodrigues, R.S. & Filgueiras, T.S. 2018. *Isachne soderstromii* sp. nov. (Poaceae, Micrairoideae, Isachneae) from Dominica, Lesser Antilles. Nordic Journal of Botany 36(1-2): e01847.  
D.O.I.: 10.1111/njb.01847

## ***Isachne soderstromii* sp. nov. (Poaceae, Micrairoideae, Isachneae) from Dominica, Lesser Antilles**

**Rodrigo S. Rodrigues and Tarciso S. Filgueiras**

R.S. Rodrigues (<http://orcid.org/0000-0001-9519-4677>) (rosaro\_3588@yahoo.com.br) and T.S. Filgueiras, Programa de Pós-graduação em Biodiversidade Vegetal e Meio Ambiente, Núcleo de Pesquisa Curadoria do Herbário SP, Instituto de Botânica, São Paulo, SP, Brazil.

### **Introduction**

*Isachne* R. Br. includes 103 species worldwide (Kellogg 2015). The highest number of species occurs in tropical and temperate Asia, but there are some species also in Africa, the Americas, Pacific Islands and Australia (Renvoize 1987, Judziewicz 1990, Clayton et al. 2006).

Based on recent phylogenetic studies, *Isachne* has been transferred to the subfamily Micrairoideae, within the pantropical tribe Isachneae Benth., which includes 113 species in six genera (Duvall et al. 2007, 2017, Sánchez-Ken et al. 2007, Soreng et al. 2017). The infrageneric classification of *Isachne* is still unresolved and arguable. Traditionally, the genus is divided into two sections according to the similarity of the anthoecia. Species with similar anthoecia (homomorphic) are grouped in *Isachne* sect. *Albentes* V. Prakash & S.K. Jain, whereas species with dissimilar anthoecia (heteromorphic) are grouped in *Isachne* sect. *Isachne* (Iskandar and Veldkamp 2004, Rodrigues and Filgueiras 2016, Veldkamp 2016).

*Isachne* is the only representative of Micrairoideae in the neotropical region. It comprises annual or perennial grasses, usually with slender to stout, trailing, erect or clambering culms (Renvoize 1987). The spikelets often disarticulate above the subequal glumes, and the anthoecia can be similar or dissimilar in shape, consistency, texture and/or pilosity; the lower is staminate, pistillate or bisexual, and the upper is bisexual or pistillate (Hitchcock 1920, Clayton and Renvoize 1986). In addition, several species have conspicuous glandular bands on the pedicels (glandular ‘rings’ or ‘patches’) and/or axillary glands (Chen and Phillips 2006, Longhi-Wagner and Welker 2014, Rodrigues et al. 2016), or even a ringed-stripe below the nodes.

Thirteen species of *Isachne* have been recorded from the neotropics (Zuloaga and Morrone 2003, Longhi-Wagner and Welker 2014), most of them restricted to Central America, the Antilles and the north of South America (Rodrigues and Filgueiras 2016). Nine of these species occur in Central America and the Antilles and several are endemic to these regions. The species often inhabit sites with humid soils, associated with flooded grasslands or riparian vegetation (Rodrigues and Filgueiras 2016), as well as dry or wet montane vegetation, cracks in rocky outcrops, banks over mosses, sandy banks, disturbed places or cultivated lands, in altitudes ranging 0–2400 m a.s.l.

While studying the Central American and Caribbean species of *Isachne* for a taxonomic revision of the genus in the Neotropics, a new species was discovered. This new taxon is here described and illustrated, and its affinities with morphologically related species are discussed.

***Isachne soderstromii* R.S. Rodrigues & Filg. sp. nov. (Fig. 1–2)**

*Herba perennis, delicata; culmi ramosi decumbentes vel suberecti; nodi glabri. Folia disticha; vaginae glabrae striatae; laminae tenues, nervis centralibus manifestis; ligula ciliata. Panicula glabra, rami annulato-glandulosi. Spiculae lanceolatae; pedicelli erecti. Anthoecia homomorpha, subcoriacea; glumae subequalae, glabrae; anthoecium inferum masculum; anthoecium superum hermaphroditum. Rhachilla glabra. Species nova Isachni rigenti (Sw.) Trin. similis sed panicula glabra, ramosa, ramisque glandulosis, laminis nervis centralibus manifestis et rhachilla glabra differt. Insuper Isachni rigidifoliae (Poir.) Urb. inflorescentia glandulosa similis sed paniculis ramis flexilibus et laminis tenuibus differt.*

**Type:** Dominica. Upper northwest slope of Morne Trois Pitons, ca 750–1050 m a.s.l., montane woodland. Exposed opening or outcrop on very steep slope that otherwise was clothed with relatively low densely interwoven vegetation, 4 May 1964, W. R. Ernst 1227 (holotype: US-2880046, barcode 01016988).

***Etymology***

The new species is named in honour of the late Dr Thomas Robert Soderstrom (1936–1987), an outstanding American agrostologist who dedicated his career to the study of grasses worldwide, especially the bamboos.

The specimen used here to describe the new species was first analysed by Dr Soderstrom. Along with the specimen we received on loan from the US herbarium, there was one typed page with the following heading: “Key to the species of *Isachne* in the West Indies: TRS, 12 February 1965”, which includes in couplet 8: “I. sp. nov. (Ernst 1227)”. This key is adapted from Hitchcock (1920). In the specimen label the inscription “Holotype” and the annotation “det. T.R. Soderstrom” can be seen. This is a clear indication that Soderstrom intended to use this specimen as the holotype of a new species. Unfortunately, he never published it. We here describe it to honour his memory.

### ***Description***

Perennial, suberect to decumbent or trailing, 15–40(–90) cm long. Culms rooting at the lower nodes, branched at the upper portion, sterile and flowering branches erect; nodes glabrous, brownish to blackish. Sheaths longer than the internodes, glabrous, strongly nerved, one margin ciliate, the other glabrous, cilia 0.5–1.0 mm long, those towards the ligular region ca 1.5 mm long, colourless; ligule ciliate, ca 0.5 mm long; leaf blades distichous, mostly concentrated over the secondary flowering and/or sterile branches, linear-lanceolate, (1.5–)4.5–8.5 × (0.3–)0.5–1.0 cm, flexible (not rigid), midrib conspicuous, base rounded, slightly constricted near the ligular region, apex acute, glabrous on both surfaces, margins entire, glabrous or with a few trichomes near the ligular region. Panicle terminal and secondary, open, loose, flexible, 6–8 × 4–5 cm, glabrous, provided with second-order branches, glandular bands, and axillary glands; pedicels 1–5 mm, cylindrical, glabrous, glandular bands present. Spikelets unequally pedicelled, erect on the pedicels, elliptic, 1.2–1.8(–2.0) mm long; glumes subequal, elliptic-lanceolate, subacute, glabrous, greenish, both equalling the spikelet or slightly shorter; lower glume 1.3–1.9(–2.0) mm long, 6–7-nerved, margins pale or purplish; upper glume 1.2–1.8 mm long, 7–8-nerved, margins pale or purplish; anthoecia 2 (rarely 3 in unusual spikelets, then the third similar to the second in shape and texture, and always bisexual), similar, subcoriaceous, whitish, sometimes purplish in the upper 1/3; lower anthoecium staminate, 1.2–1.9 mm long, lemma glabrous or with inconspicuous appressed trichomes near the margins, palea glabrous, 1.2–1.5 mm long; rachilla conspicuous between the anthoecia, 1–2 mm long, glabrous; upper anthoecium bisexual, 1.0–1.4 mm long, lemma glabrous or with inconspicuous appressed whitish trichomes near the margins, palea glabrous, 1.0–1.2 mm long. Lodicules ca 0.1 mm long. Stamens 3, filaments ca 0.5 mm, yellowish; anthers 0.8–0.9 mm long, purplish when young, yellowish in maturity. Stigmas 2, plumose, purplish. Caryopsis not seen.

### ***Distribution and habitat***

*Isachne soderstromii* is described based on a single collection from Morne Trois Pitons, Dominica. The collection site is located in the south-central part of the island (Fig. 3). The Morne Trois Pitons National Park was established in 1975 and included in the World's Heritage List in 1997 by UNESCO because of its diverse flora with endemic species of vascular plants, its volcanoes, rivers and waterfalls, which illustrate the ongoing geomorphological processes with high scenic value (criteria VIII and X) (UNESCO 2017).

A large number of collections from Mesoamerica, the Antilles and South America were examined and no other specimen corresponding to *I. soderstromii* was found, which suggests that this species is probably endemic to Dominica.

According to the information provided by the collector, *I. soderstromii* grows in exposed openings or outcrops of slopes that formerly were covered by low and densely interwoven vegetation. Collected in flower in May.

### ***Conservation status***

*Isachne soderstromii* is so far known by a single collection taken before the establishment of The Morne Trois Pitons National Park (1975). No additional data about its population size and geographic range are available. Therefore, it is here considered as 'Data Deficient' (DD). Additional information and studies are necessary to effectively assess the conservation status of this species (IUCN 2017).

### ***Comments and similar species***

The combination of the following morphological characters allows the prompt recognition of *I. soderstromii* amongst all known American species of *Isachne*: sheaths, leaf blades, panicles and spikelets glabrous; thin blades, not rigid but with a conspicuous midrib; glandular bands on the pedicels and panicle branches; and glabrous rachilla between the similar lower and upper anthoecia (Fig. 1–2).

*Isachne soderstromii* is morphologically similar to *I. rigens* (Sw.) Trin. in its general gestalt and by its habit, plant size, inflorescence and spikelets size and shape. However, *I. soderstromii* is distinct by having glabrous sheaths, leaves and panicle branches, leaves conspicuously distichous and mostly concentrated towards the apex of the secondary branches, and by the leaf blades with distinct midribs (Fig. 1B–2D). *Isachne rigens* usually presents pilose sheaths, leaves and panicle branches; the leaves are frequently more regularly distributed along the secondary branches, without distinct midribs. The inflorescence in *I. soderstromii* is flexible, composed of first and second order branches with conspicuous glandular bands on the branches and pedicels (Fig. 1C–D, 2A–B) whereas in *I. rigens* the inflorescence is rigid, usually with only first order branches and without glandular bands. The spikelets in both species are similar, differing in the pilosity of the rachilla between the lower and the upper anthoecia, which is glabrous in *I. soderstromii* (Fig. 1D, 2C) and typically hirsute in *I. rigens*.

The distichous arrangement of the leaves along the branches and the presence of a conspicuous midrib in the leaf blades also occur in *I. rigidifolia* (Poir.) Urb., however, this

species has rigid and pungent leaves with well-marked thick midribs and rigid panicles with few-flowered first order branches.

The slender *I. leersioides* Griseb., *I. polygonoides* (Lam.) Döll and *I. pygmaea* Griseb. are also distinct from *I. soderstromii*. *Isachne leersioides* is endemic to Cuba and presents linear leaf blades, few-flowered glandular panicle branches and similar pubescent upper and lower anthoecia. *Isachne polygonoides* occurs in Central and South America and presents hirsute sheaths, amplexicaul leaf blades and dissimilar lower and upper anthoecia. *Isachne pygmaea* occurs in Jamaica and is morphologically distinguished by its small size (5–15 cm tall) and contracted spike-like non-glandular panicles. All the other species of *Isachne* recorded for Central America and the Antilles are robust, with culms several meters long.

Among the neotropical species of *Isachne*, only the widespread *I. polygonoides*, the Caribbean *I. leersioides* and *I. rigidifolia*, and the Brazilian endemic *I. goiasensis* Renvoize, *I. hirtiglumis* Longhi-Wagner & Welker and *I. salzmännii* (Trin. ex Steud.) Renvoize present glandular bands in the panicle branches and pedicels (Rodrigues 2017).

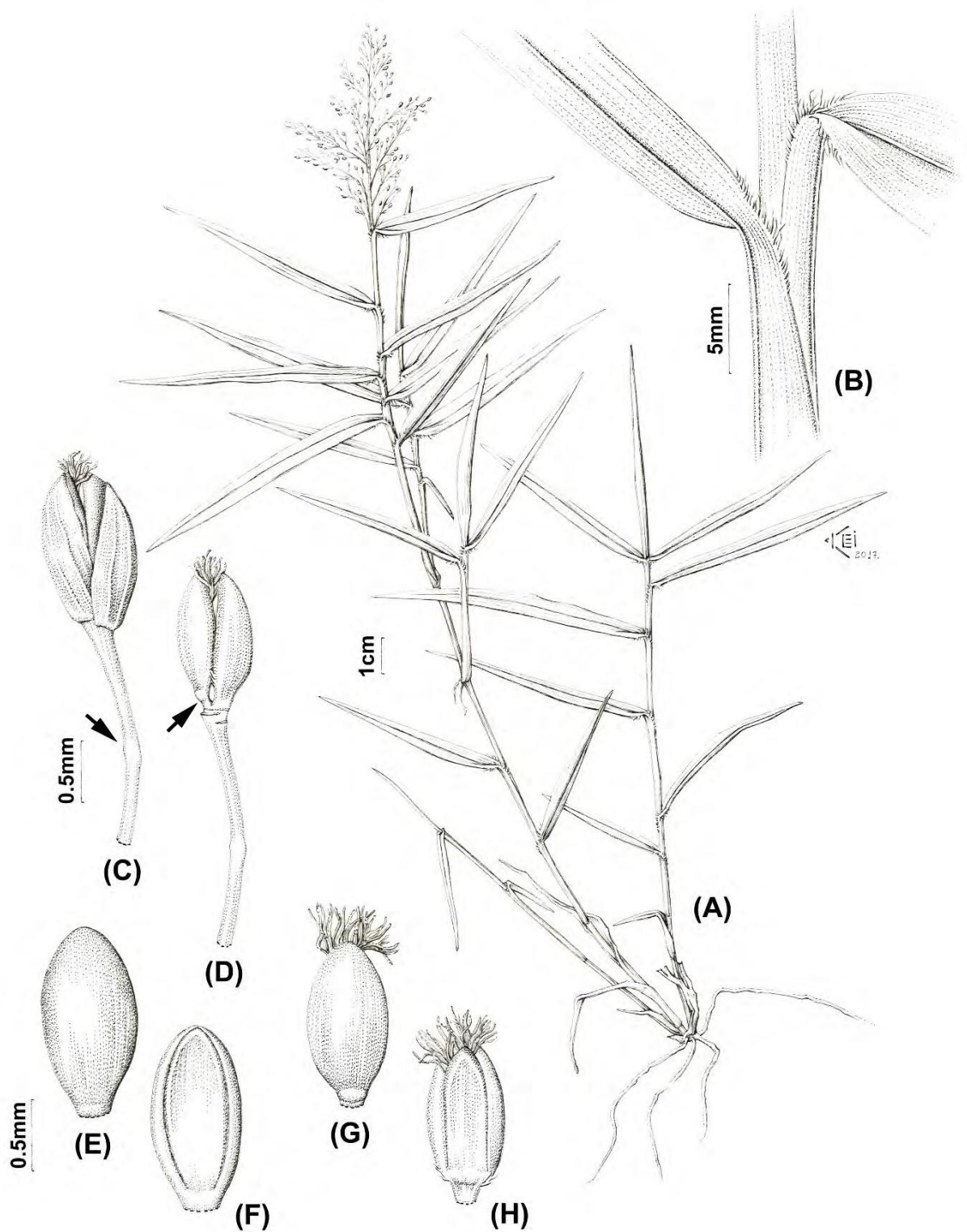


Figure 1. *Isachne soderstromii* sp. nov. (A) habit, (B) fragment of a culm showing upper portion of sheaths and lower portion of leaf blades (note evident midrib and marginal hairs at the ligular region), (C) pedicel and spikelet [note the glandular band (arrow) on the pedicel], (D) pedicel and anthoecia (glumes removed) [note the glabrous rachilla internode between the anthoecia (arrow)], (E) lower anthoecium, lemma view, (F) lower anthoecium, palea view, (G) upper anthoecium lemma view, (H) upper anthoecium, palea view. Based on W. R. Ernst 1227 (US). Drawing by Klei R. Sousa.

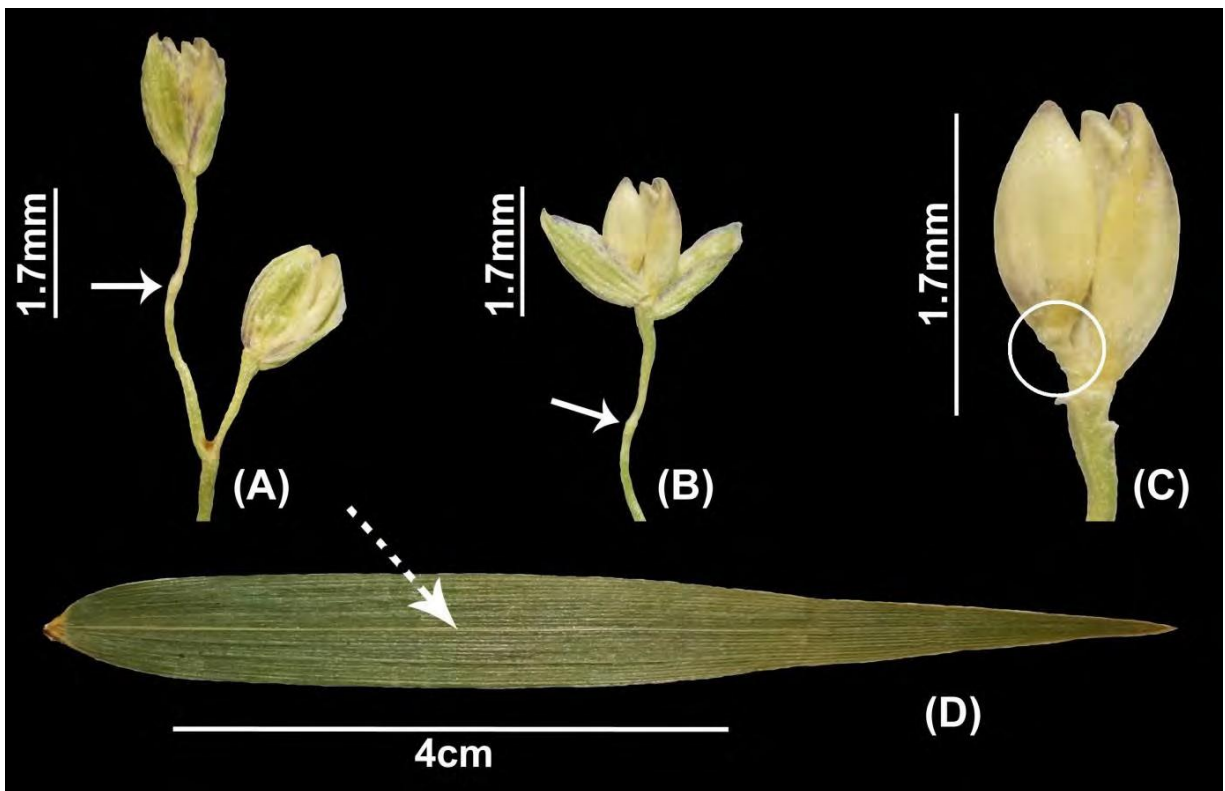


Figure 2. *Isachne soderstromii* sp. nov. (A) apex of the inflorescence branch with pedicels and spikelets in lateral view (top) and dorsal view of the upper glume (bottom) (full arrow = glandular band), (B) pedicel and spikelet, lower and upper glumes partially opened and exposing part of the lower and the upper anthoecia (full arrow = glandular band), (C) pedicel, lower and upper anthoecia, glumes removed (circle = glabrous rachilla between the anthoecia), (D) adaxial surface of the leaf blade with conspicuous midrib (dash arrow). Based on W. R. Ernst 1227 (US). Photographs by Rodrigo S. Rodrigues.

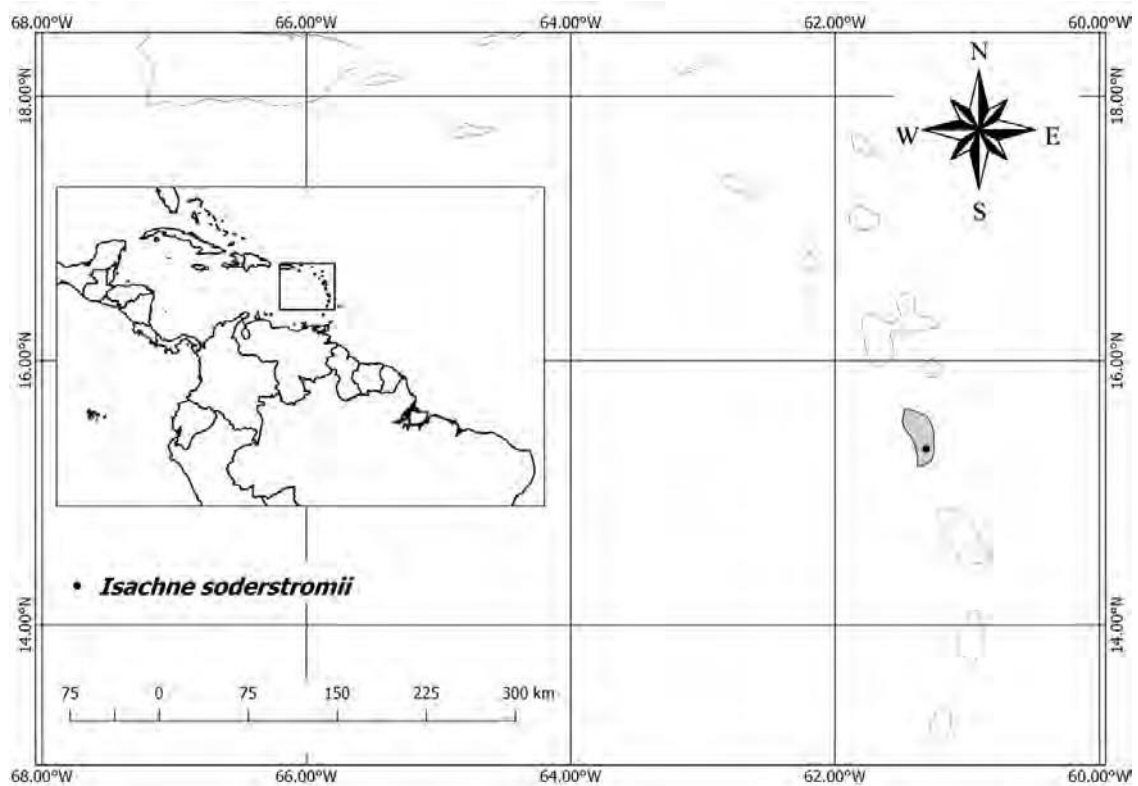


Figure 3. Known distribution of *Isachne soderstromii* sp. nov. in Morne Trois Pitons, south-central Dominica, Lesser Antilles. Dominica island shown in grey. Map elaborated by Rodrigo S. Rodrigues.



We present a key to the Central American and Caribbean species of *Isachne* below. This key will not necessarily work for specimens collected in South America.

The occurrence of a third well-developed anthoecium was observed in one spikelet of the type specimen of *I. soderstromii*. This feature in *Isachne* was considered “an error of enthusiasm” by Iskandar and Veldkamp (2004), although it is not uncommon to find specimens of several species with three anthoecia or with a rachilla tip at the base of the second anthoecia in one, two or most of the spikelets in a given inflorescence. Such anomalous spikelets have also been recorded in *I. arundinacea* Griseb., *I. hirtiglumis* and *I. goiasensis* (Rodrigues and Filgueiras unpubl.).

### Key to the species of *Isachne* occurring in Central America and the Antilles

1. Upper anthoecium appressed-pubescent .....2
  - Upper anthoecium glabrous or with occasional minute trichomes.....3
2. Leaf blades lanceolate, base amplexicaul; anthoecia dissimilar (heteromorphic), the lower cartilaginous, glabrous..... *Isachne polygonoides*
  - Leaf blades linear, base not amplexicaul; anthoecia similar (homomorphic), both indurate, pilose..... *Isachne leersioides*
3. Plants clambering; culms robust, somewhat lignified, 100–400 cm long; leaf blades 10–30 cm long .....4
  - Plants trailing to sub-erect; culms slender, herbaceous, 5–90 cm long; leaf blades 1.5–8.5(–9.0) cm long..... 7
4. Blades firm, not more than 1 cm wide; spikelets paired or aggregated in distinctive small fascicles with 2–4 spikelets at the tips of the inflorescence branches ..... *Isachne angustifolia*
  - Blades flexible, usually more than 1 cm wide; spikelets solitary, not aggregated in fascicles or, if aggregated, all the spikelets crowded toward the end of the inflorescence branches (but not in distinct fascicles with 2–4 spikelets)..... 5
5. Panicle open to lax, loosely flowered, more than 15 × 13 cm; glumes slightly cuspidate to slightly crested at the apex.....*Isachne disperma*
  - Panicle subcontracted to open, densely flowered, less than 13 × 12 cm; glumes not cuspidate or crested at the apex .....6
6. Leaf blades glabrous; inflorescence branches glabrous or densely hispid
  - ..... *Isachne arundinacea*
  - Leaf blades pilose; inflorescence branches pilose, with soft trichomes .... *Isachne pubescens*
7. Panicle contracted, spike-like ..... *Isachne pygmaea*

- Panicle open, not spike-like..... 8
- 8. Midrib of the leaf blades indistinct; pedicels without conspicuous glandular bands; rachilla between the lower and the upper anthoecia hirsute .....*Isachne rigens*
- Midrib of the leaf blades distinct; pedicels with conspicuous glandular bands (rarely absent in some specimens of *I. rigidifolia*, then with pungent leaves); rachilla between the lower and the upper anthoecia glabrous ..... 9
- 9. Leaf blades thick, rigid, pungent; panicle rigid with first-order branches only ..... *Isachne rigidifolia*
- Leaf blades thin, flexible, not pungent; panicle loose, flexible, with second-order branches.....*Isachne soderstromii*

*Acknowledgements* – The authors are grateful to Dr Robert J. Soreng and Dr Paul M. Peterson for facilitating the loan of herbarium specimens, MSc Zedenil M. Rodrigues for testing the key, Mr Klei R. Sousa for the illustration of plate 1, the Subject Editor and the anonymous reviewers for several constructive suggestions.

*Funding* – RSR also thanks CAPES for a doctoral fellowship.

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# Chapter 4

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**Abstract**

*Isachne burchellii*, an endemic new species from the Brazilian Atlantic Forest, is here recognized as distinct from *Isachne goiasensis* based on macro and micromorphological characters, geographic distribution and ecological evidence. This new species is illustrated and its taxonomic and morphological affinities with *I. goiasensis* are discussed.

**Resumo**

*Isachne burchellii*, uma nova espécie endêmica da Mata Atlântica do Brasil, é aqui reconhecida como distinta de *Isachne goiasensis* com base em características macro e micromorfológicas, distribuição geográfica e evidências ecológicas. Esta nova espécie é ilustrada e suas afinidades taxonômicas e morfológicas com *I. goiasensis* são discutidas.

Keywords: endemism, Gramineae, Isachneae, micromorphology, South American grasses

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**The following chapter was submitted (2018) and published in Brittonia (2019). Text format, citations, and references are presented according to the standards of the journal.**

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Full reference: Rodrigues, R.S. & Filgueiras, T.S. 2019. *Isachne burchellii* (Poaceae, Micrairoideae) from Rio de Janeiro, Brazil – an endemic new species segregated from *Isachne goiasensis*. Brittonia D.O.I.:10.1007/s12228-019-09576-x.

***Isachne burchellii* (Poaceae, Micrairoideae) from Rio de Janeiro, Brazil - an endemic new species segregated from *Isachne goiasensis***

**RODRIGO S. RODRIGUES<sup>1,2</sup> AND TARCISO S. FILGUEIRAS<sup>1</sup>**

<sup>1</sup>Programa de Pós-graduação em Biodiversidade Vegetal e Meio Ambiente, Núcleo de Pesquisa Curadoria do Herbário SP, Instituto de Botânica, Avenida Miguel Stefano, 3687, CEP: 04301-902, Água Funda, São Paulo, SP, Brazil

<sup>2</sup>Author for correspondence; e-mail: rosaro\_3588@yahoo.com.br

*Isachne* R. Br. includes 103 species worldwide (Kellogg, 2015). Fourteen species are recorded in the Neotropical region (Zuloaga & Morrone, 2003; Longhi-Wagner & Welker, 2014; Rodrigues & Filgueiras, 2018). In Brazil, five species have been reported:

*I. goiasensis* Renvoize, *I. hirtiglumis* Longhi-Wagner & Welker, *I. ligulata* Swallen, *I. polygonoides* (Lam.) Döll and *I. salzmännii* (Trin. ex Steud.) Renvoize (Rodrigues, 2017). The principal taxonomic studies of *Isachne* in Brazil are those of Döll (1877), Renvoize (1984, 1987), Longhi-Wagner and Welker (2014), Rodrigues et al. (2016), Rodrigues and Filgueiras (2016) and Rodrigues (2017).

When Renvoize (1987) described the Brazilian endemic *I. goiasensis*, the specimen *Glaziou 22,533* (K) from the state of Goiás was designated the holotype. Additionally, the collection *Glaziou 17,400* from the state of Rio de Janeiro was included in the list of paratypes. He also commented that the duplicate at Kew of the latter collection has the annotation “*I. glaziouii* Hack.”. Thus, according to his concept, the plants named “*I. goiasensis*” and “*I. glaziovii*” represent the same species. As a result, *I. goiasensis* presents an intriguing distribution, occurring in humid Cerrado areas of Central Brazil and in the highlands of the Atlantic Forest of Rio de Janeiro (Renvoize, 1987; Longhi-Wagner & Welker, 2014; Rodrigues, 2017). Despite the peculiar distribution of *I. goiasensis*, Renvoize’s concept of the species has not been contested.

More than three decades before the publication of Renvoize’s species, Potztl (1952) cited *Glaziou 22,533* under the name “*Isachne goyazensis* Hack. msr”. Potztl’s citation was followed by the annotation “*Typus*” but her work lacked a validating description or diagnosis. She cited “*Glaziou 74,400*” [apparently a mistyping of *Glaziou 17,400*, cf. Longhi-Wagner & Welker (2014)] under the name “*Isachne glaziovii* Hack. msr”, also with the annotation “*Typus*” and without a validating description or diagnosis.

Therefore, according to Art. 38.1 of the ICN (Turland et al., 2018), both “*I. goyazensis* Hack. ex Potztal” and “*I. glaziovii* Hack. ex Potztal” are nomina nuda.

Although Renvoize (1987) effectively published *I. goiasensis*, the name “*I. glaziovii*” and its orthographic variations were still propagated in the literature. Felfili et al. (1998) accepted *I. goiasensis* (spelled as “*I. goyasensis*”) with the annotation “(=*I. glaziouvii*)”, suggesting agreement with Renvoize’s circumscription. Filgueiras (1991) included “*I. glaziovii* Hack.”, “*I. arundinacea* (Sw.) Griseb.” and “*I. sp. (Heringer 14,579)*” (which is *I. goiasensis*) in his analysis of the grasses from Distrito Federal. Later, Filgueiras (2010) included “*I. glaziovii* Hack.” in an early version of the Brazilian List of Plants and cited *Burchell 2294* at K from the state of Rio de Janeiro as the representative specimen. On the other hand, *I. goiasensis* was omitted from this list.

*Burchell 2294* was first referred to by Döll (1877) as *I. ventricosa* (Lam.) Döll, and later regarded as a paratype of *I. goiasensis* by Renvoize (1987). *Isachne ventricosa* is based on *Panicum ventricosum* Lam., which was originally described from India.

While studying the Brazilian *Isachne* to prepare a taxonomic revision of the Neotropical species of the genus, a series of morphological characters along with geographic and ecological evidence led us to contest the identity of *I. goiasensis*. In addition, micromorphological studies of spikelets and the analysis of the original material from Goiás and Rio de Janeiro suggested that the name *I. goiasensis* has been applied inadvertently to more than one taxon. In this study, we propose to split *I. goiasensis* by segregating the specimens from Rio de Janeiro [initially named *I. glaziovii*, nom. nud. (Potztal, 1952)], which are here described as a new species.

### Material and methods

This study is based on the analysis of macro- and micromorphological characters, as well as on geographic and ecological evidence. The original material of *I. goiasensis* (including a series of paratypes and additional collections) from American (MO and NY), European [B, K, P and W (examined only in the form of online images)], and Brazilian herbaria (CEN, IBGE, HEPH, HUEFS, MG, SP, UB, and UEC) was carefully examined. The herbaria in Rio de Janeiro (R and RB) were also consulted. Additionally, field trips were carried out in Brazil’s Distrito Federal and Goiás, with the aim of finding the species in the wild.

For the Scanning Electron Microscopy (SEM), anthoecia were obtained from herbarium specimens collected in Distrito Federal, Goiás, and Rio de Janeiro. These

samples were mounted onto aluminum stubs using adhesive tape without previous treatment and coated with gold in a sputter coater at the Centro de Microscopia Eletrônica of the Universidade Federal de São Paulo (CEME-UNIFESP). SEM images were obtained using the following microscopes: Philips® XL 20, operating at 10kV, at the Laboratory of Electronic Microscopy of the Instituto de Botânica, São Paulo; and FEI Quanta FEG® 250, operating at 30kV, at CEME-UNIFESP. SEM terminology follows Metcalfe (1960) and Ellis (1979). The distribution map was made using the software QGIS® 2.14.1.

## Results and discussion

Robust *Isachne* plants from the Brazilian states of Goiás, Distrito Federal and Rio de Janeiro have traditionally been grouped under the name “*I. goiasensis*”, mainly on the basis of its general gestalt and synflorescence characters. However, as usually circumscribed, *I. goiasensis* includes two distinct species: *I. goiasensis* sensu stricto from Goiás and Distrito Federal, and an overlooked new species from Rio de Janeiro, which is described below and referred hereafter as *I. burchellii*. The two species differ in morphological, ecological and geographical particularities, providing evidence in favor of their segregation.

Macromorphologically, *I. burchellii* typically presents dark-purple to blackish internodes, absence of glandular bands on the pedicels and homomorphic (similar) anthoecia (Fig. 1A–B). On the other hand, *I. goiasensis* s.s. presents greenish, brownish or less often purple-stained internodes, conspicuous glandular bands on the pedicels and heteromorphic (dissimilar) anthoecia (Fig. 1C–D). With respect to the infrageneric classification of *Isachne* proposed by Prakash and Jain (1984) and based on the similarity, consistency, and indumentum of the anthoecia, *I. burchellii* is assigned to *I. sect. Albentes* Prakash & Jain (Figs. 1A, 2A–B), and *I. goiasensis* s.s. to *I. sect. Isachne* (Figs. 1C, 3A–B).

Micromorphological features of the spikelets and anthoecia also reinforce the distinction of *I. burchellii* from *I. goiasensis* s.s. Although both species share a similar ellipsoid lower anthoecium, with the lemmas and paleas bearing abundant cross-shaped silica bodies (these often coalescent towards the apices and at the bases of the lemmas and paleas) arranged in longitudinal rows and covered with occasional panicoid bicellular microhairs (Figs. 2C–E, 3C–E), the upper anthoecium is notably very distinct between these taxa. In *I. burchellii* the upper anthoecium is ellipsoid, similar to the

lower one in texture and indumentum (i.e., bearing bicellular microhairs and abundant cross-shaped silica bodies, these occasionally saddle-shaped on the middle portion of the palea), and lacking macrohairs (or rarely with a few at the base of the palea) (Fig. 2F–H). In *I. goiasensis* s.s. the upper anthoecium is ovoid, ellipsoid-ovoid or orbicular, conspicuously dissimilar to the lower one, bearing rounded to dumbbell-shaped (sometimes coalescent) silica bodies, and densely covered with bicellular microhairs and twisted narrow-tipped macrohairs (Fig. 3F–H).

*Isachne burchellii* and *I. goiasensis* s.s. are known also from different biomes.

The first inhabits mountainous areas of the Atlantic Rainforest, while the second inhabits humid localities and campos of the Cerrado biome (Fig. 4). Table 1 summarizes the ecological and morphological differences between *I. burchellii* and *I. goiasensis* s.s. The taxonomic treatment of *Isachne* for Brazil (Rodrigues, 2017) must be updated to include the new species described here.

**TABLE 1.** Ecological and morphological comparison between *Isachne burchellii* and *Isachne goiasensis* s.s.

	<i>Isachne burchellii</i>	<i>Isachne goiasensis</i> s.s.
Biome	Atlantic Rainforest	Cerrado
Phytophysiognomy	low-montane or montane rainforest vegetation, on margins or interior of gallery forests or in transitional areas with adjacent humid campos	margins of “Cerradão” with campos, margins of gallery forests, swamps or in cerrado slopes, usually associated with humid soils
Culm-internodes	dark-purple to blackish	greenish, brownish or purple-stained towards the nodes
Glandular bands on pedicels	absent	present
Anthoecia	homomorphic (similar)	heteromorphic (dissimilar)
Upper anthoecium shape	ellipsoid	ovoid, ellipsoid-ovoid or orbicular
Upper anthoecium silica bodies	cross-shaped (saddle-shaped on the middle portion of the palea)	rounded to dumbbell-shaped
Upper anthoecium indumentum	glabrous to inconspicuously puberulous (macrohairs absent)	conspicuously pilose to appressed pilose (macrohairs present, <u>twisted, narrow-tipped</u> )



### Taxonomic treatment

***Isachne burchellii*** R.S. Rodrigues & Filg., **sp. nov.** Type: Brazil. Rio de Janeiro: [Teresópolis], [30 Jan 1888] (from the isotypes at K-001055180 and P)], *A. F. M. Glaziou 17,400* (holotype: NY-00381251; isotypes: B-100460905, K-001055179, K-001055180, P-01923969, P-01923971, P-01923973, W-1987-0002167, W-1916-0021686). (Figs. 1A–B, 2, 5)

Perennials, suberect to decumbent or trailing, (0.5–)1.5–2(–4) m long. Culms rooting at the lower nodes, branched in the upper portion, sterile and flowering branches erect; nodes glabrous; internodes inconspicuously hollow, glabrous, dark-purple to blackish, sometimes slightly sulcate towards the nodal region. Sheaths shorter than the internodes, persistent, glabrous, strongly nerved, one margin ciliate, the other glabrous, cilia 0.5–1.5 mm long, those towards the ligular region 1–3.5 mm long, colorless; ligule ciliate, 4–5 mm long, collar glabrous; leaf blades lanceolate to linear-lanceolate, 8.5–14 × 0.8–1.5 cm, flexible (not rigid nor pungent), midrib conspicuous, base rounded, apex acute, glabrous on both surfaces, margins entire to minutely serrate. Panicles terminal, open to lax, densely flowered, the younger ones subcontracted and partially included in the leaf sheaths, (7–)12–20 × (3–)5–10 cm, glabrous to minutely scabrous, glandular bands on the synflorescence branchlets absent, axillary glands inconspicuous, yellowish; pedicels 2–8 mm long, cylindrical, glabrous or minutely scabrous, glandular bands absent. Spikelets solitary, unequally pedicelled, erect on the pedicels, ellipsoid, 1.5–2 mm long; glumes subequal, ellipsoid-lanceolate, subacute, glabrous or minutely scaberulous towards the apex, greenish to stramineous, slightly shorter to longer than the lower anthoecium; lower glume 1.5–2 mm long, 5-nerved, margins pale, involute in maturity; upper glume 1.4–2 mm long, 5-nerved, margins pale; anthoecia 2, homomorphic (similar), subcoriaceous, pale green to stramineous; lower anthoecium ellipsoid, staminate, lemma 1.3–1.7(–2) mm long, subacute, glabrous or inconspicuously puberulous (bicellular microhairs), palea 1.3–1.5(–1.8) mm long, subacute, glabrous or inconspicuously puberulous; rachilla inconspicuous between the anthoecia, 0.3–0.5 mm long, glabrous; upper anthoecium ellipsoid, bisexual, lemma 1.3–1.5 mm long, subacute, glabrous or inconspicuously puberulous, palea 1.3–1.4 mm long, subacute, glabrous or inconspicuously puberulous. Lodicules ca. 0.1 mm. Stamens 3, filaments 0.1–0.2 mm long, anthers 0.2–0.3 mm long, brownish in maturity. Stigmas 2, plumose, purplish. Caryopsis not seen.

*Distribution and habitat.*—*Isachne burchellii* is here described based on Burchell’s and Glaziou’s historical collections. According to the labels of the isotypes and paratypes, both collectors sampled this new species in the municipality of Teresópolis, in the mountainous region of the state of Rio de Janeiro in southeastern Brazil (Fig. 4). Based on Burchell’s itinerary and label data on the specimens collected by Glaziou (P-01923969, P-01923971 and P-01923973), we conclude that the collections of *I. burchellii* were gathered from sites in what was the farm of Mr. George March and now contained within the modern districts of Quebra Frascos and Bairro do Alto (Prefeitura Municipal de Teresópolis, 2017).

The municipality of Teresópolis lies within the Atlantic Rainforest domain. Its phytophysiology, determined largely by differences in elevation, is predominated by low-montane or montane rainforest (below 1600 m), high-montane rainforest (at ca. 1300–1800 m), and grassy fields and rocky outcrops (above 1800 m) (ICMBio, 2008).

The evidence presently available suggests that *I. burchellii* inhabits low-montane and montane rainforests, growing on the margins or interior of gallery forests or in areas that are transitional to humid campos.

*Phenology.*—Collected in flower in January and February.

*Etymology.*—*Isachne burchellii* is named after John William Burchell, a celebrated British botanical naturalist and collector of the oldest known sample of this newly recognized species. Burchell worked in Brazil from 1825 to 1830 as a member of the English mission for the recognition of the Brazilian independence and was responsible for a great number of botanical collections from what are now the states of Goiás, Minas Gerais, Pará, São Paulo and Rio de Janeiro (Pirani, 2010).

*Conservation status.*—*Isachne burchellii* is known only from the environs of Teresópolis. The most recent collection of the species was made by Glaziou about 130 years ago. Since then, the Teresópolis region has experienced profound urban growth, and the area is now famous for tourism (Prefeitura Municipal de Teresópolis, 2017). Natural habitats at the locations where *I. burchellii* was collected have been lost to urbanization, and the species has not been found in the nearby Serra dos Órgãos National Park. According to the current information available, *I. burchellii* presents small EOO and AOO (<100 km<sup>2</sup> and <10 km<sup>2</sup>, respectively) and meets the criteria B1, B2, a, b (i, ii, iii), being classified as critically endangered “CR” (IUCN, 2012; IUCN Standards and Petitions Subcommittee, 2017). Future data may change the conservation status of the species.

**Additional specimens examined. BRAZIL. [Rio de Janeiro]:** [Teresópolis], [15 Feb 1826?], *J. W. Burchell* 2294 (K-001055181, P-01936049).

*Note.*—*Isachne burchellii* includes those plants originally named *I. glaziovii* Hack. ex Potztal, nom. nud. [cf. Potztal (1952) and Turland et al. (2018)]. In order to avoid taxonomic and nomenclatural confusion due to the extensive use of the name *I. glaziovii* in the literature, we opted for describing the species using a new epithet.

**Isachne goiasensis** Renvoize, Kew Bulletin 42(4): 928. 1987. Type: Brazil. Chiefly province of Goyaz: [Formoza, au Brejinho, 9 Dec 1894 (from the isotypes at P and W)], A. F. M. Glaziou 22533 (holotype: K-000643014; isotypes: B-100460904, P-01923972, P-01923976, W-1916-0021683, W-1916-0021684). (Figs. 1C–D, 3, 6)

*Description.*—Descriptions of *I. goiasensis* s.s. are available from Renvoize (1987), Clayton et al. (2006) and Rodrigues (2017).

*Distribution and habitat.*—The present circumscription of *I. goiasensis* s.s. encompasses only the specimens from the state of Goiás and the Distrito Federal (Fig. 4). *Isachne goiasensis* s.s. occurs most frequently on humid soils, in the margins or interior of gallery forests, margins of “Cerradão” with humid and adjacent campos, or in cerrados slopes (Longhi-Wagner & Welker, 2014).

*Phenology.*—Collected in flower from December to May, and in September and October.

*Etymology.*—The epithet refers to the Brazilian state of Goiás, from where the type specimen originated.

*Conservation status.*—*Isachne goiasensis* s.s. is known from several locations in Goiás and Distrito Federal, and includes large populations with a great number of individuals in some Conservation Units, such as the reserves of the Jardim Botânico de Brasília and IBGE. Therefore, *I. goiasensis* s.s. should be considered as Least Concern “LC” (IUCN, 2017).

**Additional specimens examined: BRAZIL. Distrito Federal:** Brasília, Bacia do Rio São Bartolomeu, 16 Apr 1980, E. P. Heringer et al. 4435 (CEN, RB, SP); *ibid.*, 30 Mar 1981, E. P. Heringer et al. 6654 (IBGE, SP, UEC); Parque do Guarará, 16 Apr 1975, E. P. Heringer 14,579 (NY, SP, UB, UEC); Chapada da Contagem, ca. 15 km E of Brasília, 30 Jan 1966, H. S. Irwin et al. 12,143 (MO, NY, UB) [paratypes]; Parque Olhos d’Água, 22 Oct 2002, J. G. A. Paiva & S. F. Carvalho 56 (UB); Estação Ecológica do Jardim Botânico de Brasília, 15 Feb 2008, R. G. Chacon & I. N. C. Azevedo 354 (HEPH); *ibid.*, 28 Mar 2009, R. C. Martins et al. 820, 831 (HEPH); Jardim Botânico de Brasília, área de reserva, Mata do Taquara, região do “Cristo Redentor” ao longo da fronteira entre as reservas do JB, IBGE e FAL/UNB, 15°55’52.28”S, 47°54’7.32”W, 20 Jan 2017, R. S. Rodrigues et al. 479 (HUEFS, SP); *ibid.*, 20 Jan 2017, R. S. Rodrigues et al. 480

(MG, SP); *ibid.*, 20 Jan 2017, *R. S. Rodrigues et al. 481* (MBM, SP); Parque Nacional de Brasília, 15 Feb 2009, *R. C. Martins 1094* (UB); *ibid.*, 28 Sep 2012, *P. Reis & R. R. A. Dias 70* (CEN); Riacho Fundo, 4 Dec 1991, *P. E. A. M. Oliveira 1694* (HEPH). **Goiás:** Cocalzinho de Goiás, 20 km NW of Corumbá de Goiás, near Pico dos Pirineus, Serra dos Pirineus, 27 Jan 1968, *H. S. Irwin et al. 19,315* (MO, NY, UB) [paratypes]; Serra dos Pirineus, 20 km E of Pirenópolis, 16 Jan 1972, *H. S. Irwin et al. 34,309* (MO, NY, UB) [paratypes]; Brejo entre Guará e Setor da Indústria, 21 Feb 1981, *F. Chagas-Silva 387* (K, MO, UEC) [paratypes]; Alto Paraíso de Goiás, Fazenda Água Fria, 2 May 1998, *R. C. Oliveira et al. 1073* (HEPH).

*Note.*— The description provided by Renvoize (1987) perfectly agrees with the type (*Glaziou 22533*) and all the other specimens collected in Goiás and Distrito Federal. The following statement in the original description leaves no doubt regarding the identity of the species: “*Anthoecium inferum glabrum. Anthoecium superum pubescens, brevius quam anthoecium inferum*” (cf. Renvoize, 1987) (Fig. 1C, 3A–B,6).

### Acknowledgments

The authors thank the curators and staff of the herbaria we physically consulted in Brazil, and those from which we requested loans or high-resolution images. Special thanks are due to Dr. Otávio L. Marques da Silva, Dr. Sérgio Romaniuc Neto and Dr. Marc Pignal for their help in obtaining high-resolution images of reproductive structures from type collections at P, and Dr. Matthew Pace for allowing us to sample from the holotype of *I. burchellii* at NY. We would also like to thank Dr. Regina Célia de Oliveira, Dr. André Rodolfo de Oliveira, and MSc. Mayco Werllen for their support during the stay of the first author at the Universidade de Brasília; Dr. José Francisco Montenegro Valls for sharing his knowledge and valuable taxonomic commentaries; Dr. Priscila Rosa for facilitating the collection of *I. goiasensis* in the Jardim Botânico de Brasília; Dr. Luciana Benatti and Mr. André Aguilera for the SEM images; Mr. Klei Rodrigo Souza for the line drawings; Dr. Rosangela Simão-Bianchini, Dr. Maria da Graças Wanderley, and two anonymous reviewers for their valuable contributions. RSR thanks CAPES for a doctoral fellowship and the Instituto de Botânica for the continuous support of our research on the Brazilian grasses. Finally, we would also like to dedicate this work to the memory of the late Mr. Diacis Alvarenga, an esteemed friend who worked for years in the Reserva Ecológica do IBGE with the second author, and who helped us during our recent expeditions in Goiás and Distrito Federal.

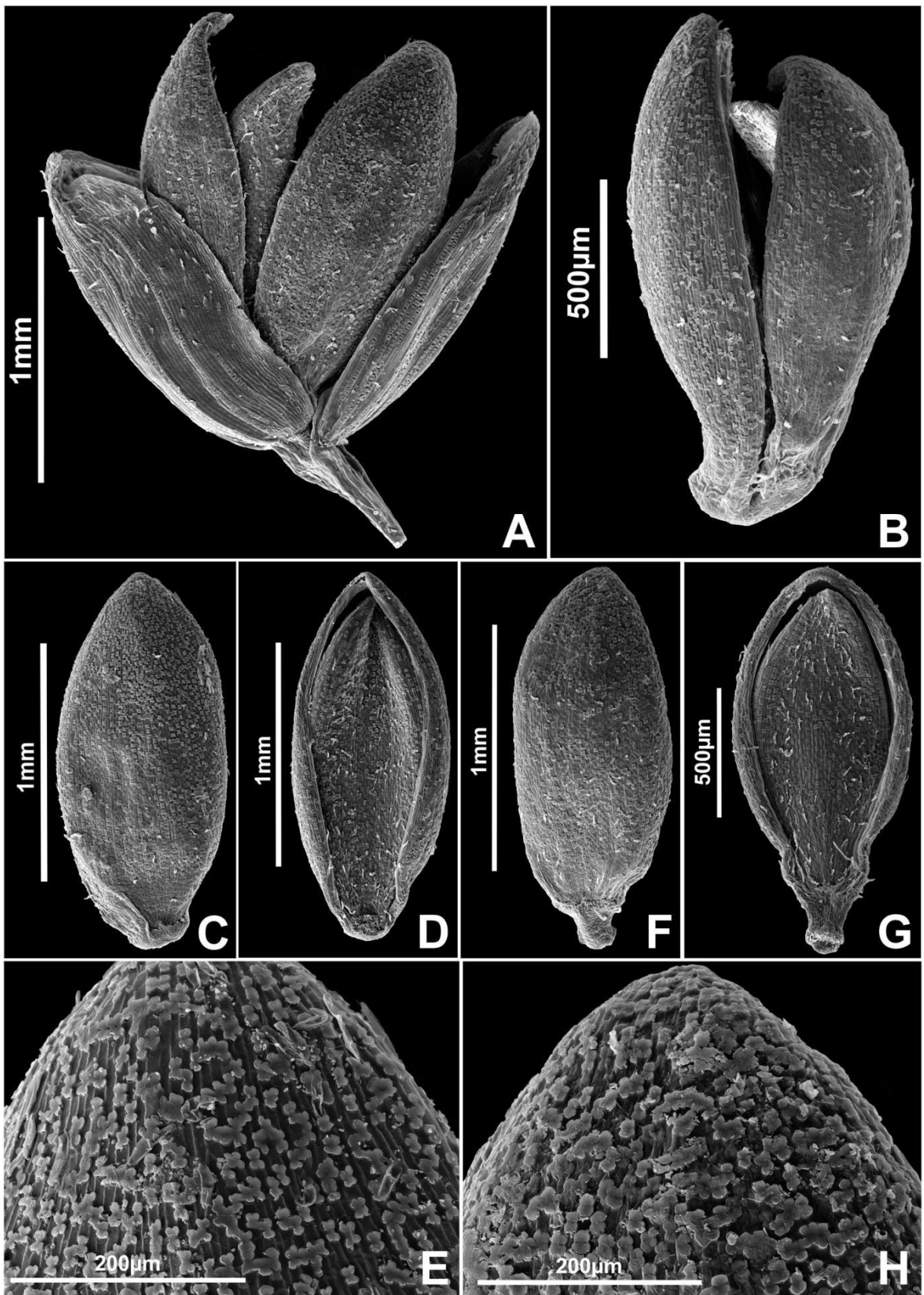
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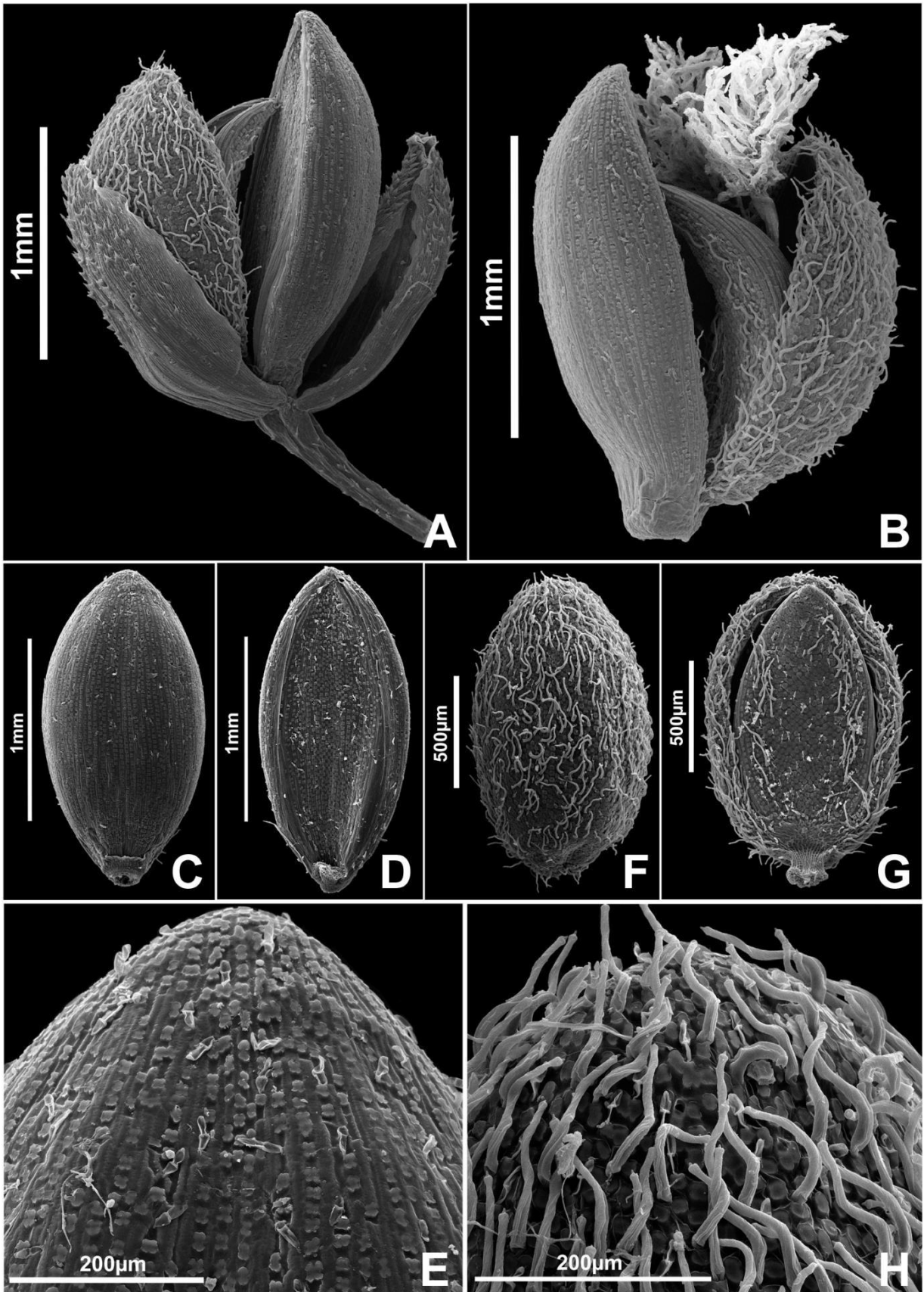


**FIG. 1.** Macromorphological differentiation between *Isachne burchellii* and *Isachne goiasensis* s.s. **A–B.** *Isachne burchellii*. **A.** Spikelet in lateral view, showing part of the pedicel, the lower and the upper glumes, and the lower and the upper anthoecia. **B.** Fragment of the culm, showing a branched lower node and the internodal region. **C–D.** *Isachne goiasensis* s.s. **C.** Spikelet in lateral view, showing part of the pedicel and the glandular band (arrow), the lower and the upper glumes, and the lower and the upper anthoecia. **D.** Fragment of the culm, showing a branched lower node and the internodal region. (A–B, from A. F. M. Glaziou 17400, NY; C–D, from R. S. Rodrigues et al. 481, SP).



**FIG. 2.** Scanning electron micrographs of the spikelets and anthoecia of *Isachne burchellii*. **A.** Spikelet in lateral view. **B.** Anthoecia in lateral view (glumes removed). **C.** Lower anthoecium, lemma view. **D.** Lower anthoecium, palea view. **E.** Detail of the apex of the lower anthoecium. **F.** Upper anthoecium, lemma view. **G.** Upper anthoecium, palea view. **H.** Detail of the apex of the upper anthoecium. (From A. F. M. Glaziou 17,400, NY)





**FIG. 3.** Scanning electron micrographs of the spikelets and anthoecia of *Isachne goiasensis* s.s. **A.** Spikelet in lateral view. **B.** Anthoecia in lateral view (glumes removed). **C.** Lower anthoecium, lemma view. **D.** Lower anthoecium, palea view. **E.** Detail of the apex of the lower anthoecium. **F.** Upper anthoecium, lemma view. **G.** Upper anthoecium, palea view. **H.** Detail of the apex of the upper anthoecium (From *R. S. Rodrigues et al.* 479, SP)

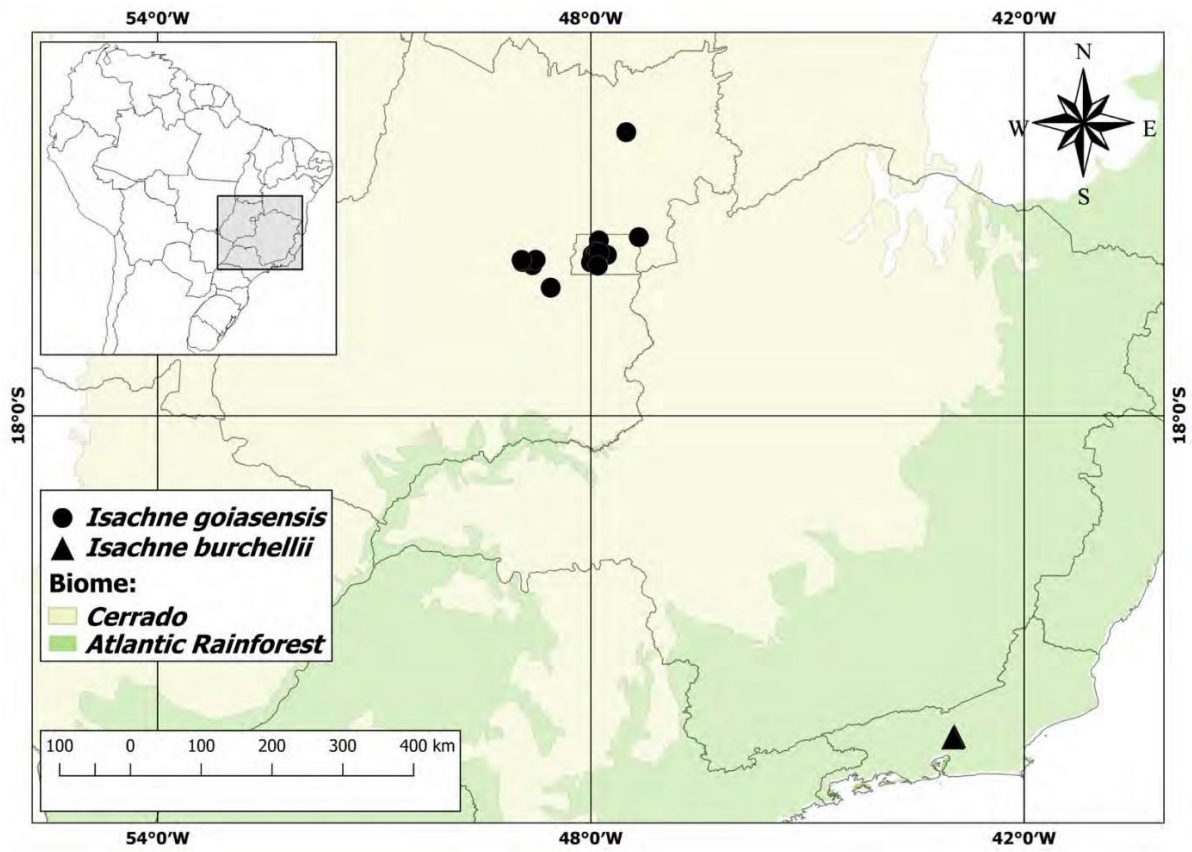
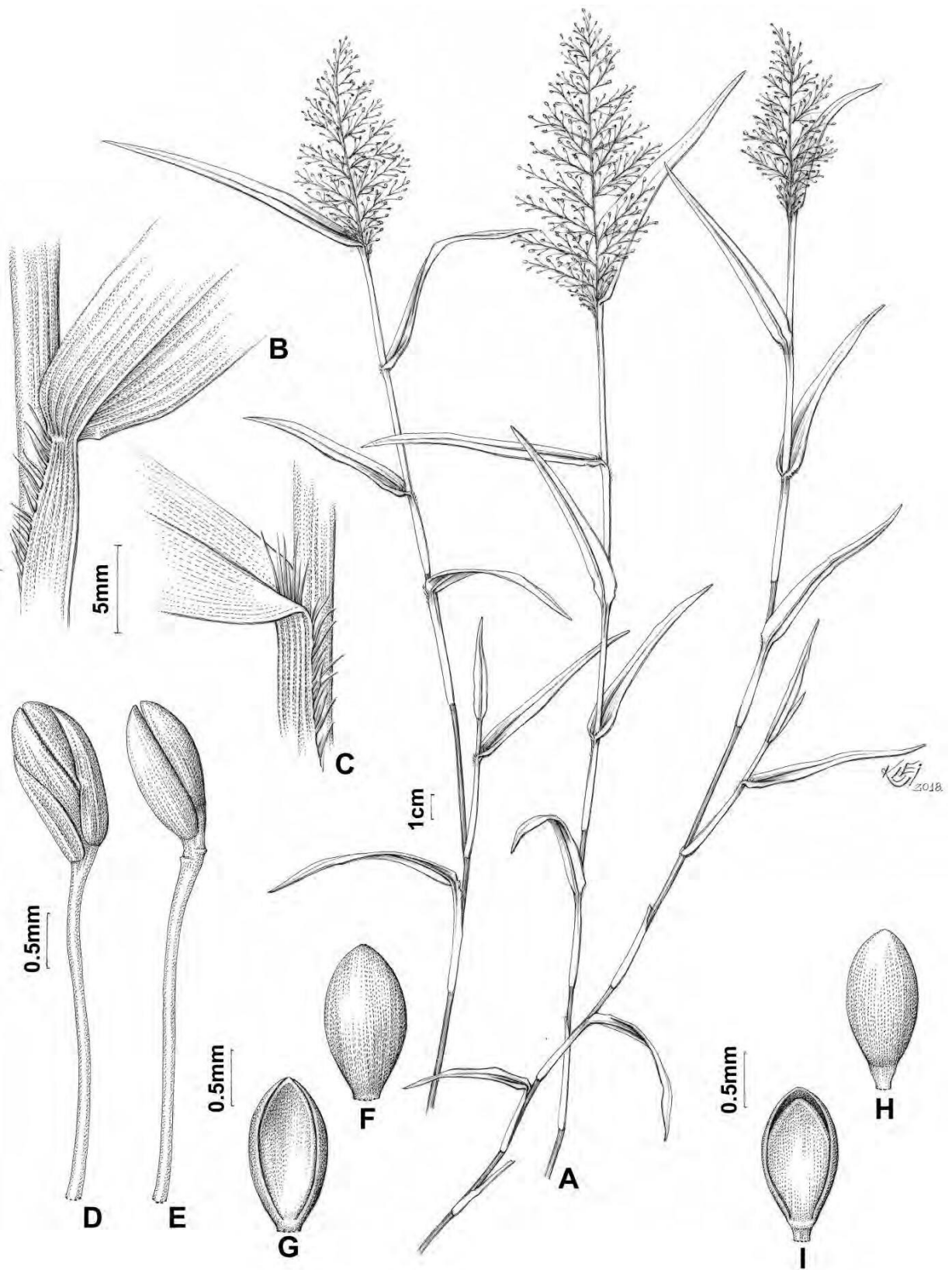
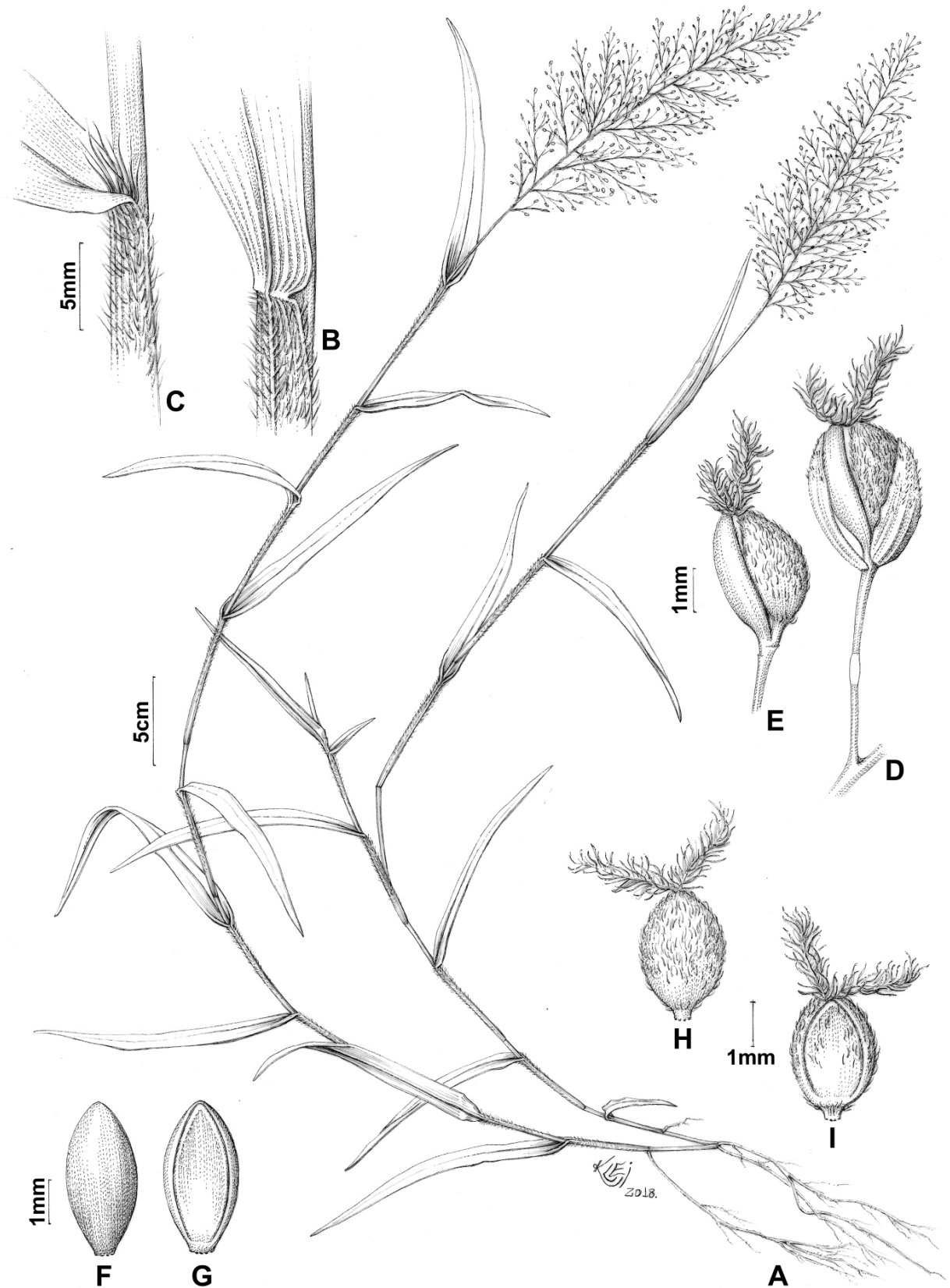


FIG. 4. Known distribution of *Isachne burchellii* and *Isachne goiasensis* s.s.



**FIG. 5.** *Isachne burchellii*. **A.** Apex of the culms with flowering branches and synflorescences. **B.** Apex of the leaf sheath with ciliate margin, collar region, and base of the leaf blade. **C.** Apex of the leaf sheath with ciliate margins, base of the leaf blade and part of the ciliate ligule. **D.** Spikelet in lateral view and pedicel without a glandular band. **E.** Homomorphic (similar) anthoecia (glumes removed) and pedicel without a glandular band. **F.** Lower anthoecium, lemma view. **G.** Lower anthoecium, palea view. **H.** Upper anthoecium, lemma view. **I.** Upper anthoecium, palea view. (From A. F. M. Glaziou 17,400, NY; drawing by Klei R. Sousa)



**FIG. 6.** *Isachne goiasensis* s.s. **A.** Habit with flowering branches and synflorescences. **B.** Apex of the leaf sheath, collar region, and base of the leaf blade. **C.** Apex of the leaf sheath, base of the leaf blade and part of the ciliate ligule. **D.** Spikelet in lateral view and pedicel with a glandular band. **E.** Heteromorphic (dissimilar) anthoecia (glumes removed) and part of the pedicel. **F.** Lower anthoecium, lemma view. **G.** Lower anthoecium, palea view. **H.** Upper anthoecium, lemma view. **I.** Upper anthoecium, palea view. (From R. S. Rodrigues et al. 479, SP; drawing by Klei R. Sousa)

# Chapter 5

## Abstract

A micromorphological study of the foliar epidermis of the 15 Neotropical species of *Isachne* plus a South American morphospecies is presented. As a total, 31 American specimens were examined under a scanning electron microscope (SEM). For comparative purposes, we also analyzed one species from Africa (*I. pangerangensis*), three species from Asia (*I. globosa*, *I. myosotis* and *I. sylvestris*), as well as *Eriachne semiciliata* and *Micraira dentata* from Australia. A Cluster Analysis was conducted to evaluate the taxonomic value of micromorphological epidermal characters in *Isachne*, and a Principal Component Analysis (PCA) was also carried out to assess the correlation among foliar micro-characters and the species. Micromorphological features of the leaf blade epidermis were not informative above the species level; however, a broader variation in the epidermal features of *Isachne* was found, mostly regarding the type of silica bodies, shape of intercostal long cells, and presence and distribution of papillae. Our results also indicate that both leaf blade surfaces can be useful for circumscription and characterization of a species. The phenetic analyses revealed that considering solely the presence/absence of micromorphological characters, the species of *Isachne* included in this study form a morphological gradient without an evident taxonomic, ecological or geographical correlation. Five main groups were obtained, but none possessing a unique character that defines it. Therefore, a qualitative analysis of the micromorphological features, considering also their distribution pattern and arrangement, associated with macromorphological characters, may aid substantially for delimiting Neotropical closely related species. Descriptions and comments on the foliar epidermal micromorphology and images are included for all Neotropical species.

## Resumo

Apresenta-se um estudo micromorfológico da epiderme foliar das 15 espécies Neotropicais de *Isachne*, além de uma morfoespécie Sul-americana. Ao todo, 31 espécimes da América foram examinados em microscópio eletrônico de varredura (MEV). Para comparação, analisou-se também uma espécie da África (*I. pangerangensis*), três espécies da Ásia (*I. globosa*, *I. myosotis* e *I. sylvestris*), além de *Eriachne semiciliata* e *Micraira dentata*, ambas da Austrália. Uma Análise de Grupamento foi realizada para avaliar o valor taxonômico dos caracteres micromorfológicos da epiderme em *Isachne*, bem como uma Análise de Componentes Principais (PCA) para avaliar a correlação entre os microcaracteres foliares e as espécies. As características micromorfológicas da epiderme da lâmina foliar não foram informativas acima do nível específico; todavia, uma variação mais ampla dos microcaracteres epidérmicos foi observada, a maioria relacionada ao tipo de corpo silicoso, forma das células longas intercostais e presença e distribuição de papilas. Os resultados indicam que ambas as superfícies da lâmina foliar são úteis para circunscrição e caracterização de uma espécie. A análise fenética indicou que, considerando somente a presença/ausência de microcaracteres, as espécies de *Isachne* incluídas nesse estudo formam um gradiente morfológico sem correlação com grupos taxonômicos, ecológicos ou geográficos. Cinco grupos principais foram obtidos, mas nenhum sustentado por um caráter exclusivo. Portanto, uma avaliação qualitativa das características micromorfológicas, considerando também o padrão de distribuição e arranjo dos elementos, associados aos caracteres macromorfológicos, pode auxiliar substancialmente na delimitação de espécies Neotropicais relacionadas. Descrições e comentários sobre as características micromorfológicas da epiderme e imagens são fornecidos para todas as espécies Neotropicais.

Keywords: Grasses, Isachneae, Leaf morphology, Neotropical grasses, SEM.

The following chapter was prepared according to the standards of Hoehnea.

## Micromorphology of the leaf blade epidermis in the Neotropical species of *Isachne* (Poaceae, Micrairoideae)

Rodrigo S. Rodrigues<sup>1,2</sup> and Tarciso S. Filgueiras<sup>1</sup>

### Introduction

The subfamily Micrairoideae Pilg. includes three tribes of grasses predominantly from Eurasia and Australasia (Soreng *et al.* 2017). Isachneae Benth. is the largest tribe within Micrairoideae, with six genera and 113 species (Duvall *et al.* 2007, Sánchez-Ken *et al.* 2007, Soreng *et al.* 2017), mostly belonging to *Isachne* R. Br.

*Isachne* comprises 103 species worldwide (Kellogg 2015), most of them from tropical and temperate Asia (Judziewicz 1990), and some other species occurring in Africa, America, the Pacific Islands and Australia (Clayton *et al.* 2006). For the Neotropical region, are recorded 15 species, distributed mainly through Mesoamerica and the north of South America (Rodrigues & Filgueiras 2019).

*Isachne* is characterized by including annual or perennial plants, usually with trailing culms, spikelets disarticulating above the equal or subequal glumes, and anthoecia similar (homomorphic) or dissimilar (heteromorphic), the lower with variable fertility and the upper bisexual or pistillate (Hitchcock 1920, Clayton & Renvoize 1986). With some exceptions, species in this genus predominantly inhabit localities with damp or muddy soils, usually associated with flooded grasslands or riparian vegetation (Longhi-Wagner 2012, Longhi-Wagner & Welker 2014), in altitudes of 0-3,000 m a.s.l.

Micromorphological features have been fairly used as a tool to solve taxonomic issues, delimiting taxa and assessing phylogenetic relationships (e.g., Peterson *et al.* 1989, Dávila & Clark 1990, Piperno & Pearsall 1998, Gomes & Neves 2009, Zhang 2014, Leandro *et al.* 2016, Leandro *et al.* 2017). Although the relevance of anatomical and micromorphological studies applied to the taxonomy has been increasing in last decades, the information about morphologically related to grasses in the vegetative stage is still scarce (Leandro *et al.* 2015). This is particularly relevant when considering large taxonomic groups with broader or very restricted distribution. In this case, sampling is a

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<sup>1</sup> Programa de Pós-graduação em Biodiversidade Vegetal e Meio Ambiente, Núcleo de Pesquisa Curadoria do Herbário SP, Instituto de Botânica, Avenida Miguel Stefano, 3687, CEP: 04301-902, Água Funda, São Paulo, SP, Brazil.

<sup>2</sup> Corresponding author: rosaro\_3588@yahoo.com.br

rather difficult task and, therefore, requires the selection of representative taxa of major groups (Dávila & Clark 1990). This is the case of *Isachne*, which has both a high number of species and a wide geographic distribution, with many species locally restrict and/or rare.

Only a few micromorphological studies including *Isachne* or other members of Isachneae and Micrairoideae are available, and they treat only with some representative species. Potztal (1952) presented a series of anatomical and epidermal characters common to the tribe Isachneae, such as the absence or occurrence of bicellular microhairs, or thread-like hairs, or rarely multicellular hairs and the silica bodies variable in shape, but all of a panicoid type.

Metcalf (1960) pointed out that the leaf structure in *Isachne* is overall panicoid of a special type, and the presence of acutely angled silica bodies, long narrow assimilatory cells in the mesophyll and the almost cubical long cells are very characteristic of the genera within Isachneae.

Palmer & Gerbeth-Jones (1986) presented a survey of the East-African grasses, including micromorphological descriptions and images of the leaf epidermis of three species within Isachneae.

Sánchez-Ken *et al.* (2007) characterized the foliar micromorphology of Micrairoideae by the occurrence of stomata with dome-shaped subsidiary cells, panicoid bicellular microhairs and papillae sometimes present, usually one per cell or over the stomata. However, none of these characters, together or separately, is exclusive or can be assigned as synapomorphy to the subfamily.

Rodrigues & Filgueiras (2019) provided the first study including micromorphological characters of the spikelets of *Isachne*. In this study, the circumscription of *Isachne goiasensis* Renvoize was reevaluated, from which *Isachne burchellii* R.S. Rodrigues & Filg. was recognized as a new species.

Thus, considering that at higher taxonomic levels the use of foliar micromorphological features appears to have limited value, we investigated the significance of the leaf epidermal micromorphology in *Isachne*, with emphasis on the Neotropical species, as a tool to study the taxonomy of the genus and to test their contribution for circumscribing closely related species.

## Material and methods

This work is based on micromorphological studies of the foliar epidermis of 15 species of *Isachne* currently accepted for the Neotropical region (Rodrigues & Filgueiras 2019), plus a South American morphospecies related to *I. arundinacea* Griseb. (herein included as *Isachne* sp. 1). A total of 31 Neotropical specimens were examined under a scanning electron microscope (SEM). For comparative purposes, we also analyzed one specimen of *I. globosa* (Thunb.) Kuntze, *I. myositis* Nees, and *I. sylvestris* Ridley, from Asia; *I. pangerangensis* Zoll. & Moritzzi, from Africa; *Eriachne semiciliata* Lazarides and *Micraira dentata* Lazarides, from Australia (Table 1).

The samples were obtained from herbarium specimens and mounted onto aluminum stubs using double-sided adhesive tape without previous treatment, and coated with gold in a sputtering at Centro de Microscopia Eletrônica, Universidade Federal de São Paulo (CEME-UNIFESP). After prepared, the samples were examined under SEM: Philips® XL 20, operating at 10 kV, at the Laboratory of Electronic Microscopy of the Instituto de Botânica, São Paulo State, Brazil; and FEI Quanta FEG® 250, operating at 30 kV at CEME-UNIFESP.

For the SEM analysis, it was taken the second leaf fully developed from the apex of the culm branches and prepared small cutouts across the medium portion (Ellis 1979). When necessary, these cutouts were trimmed again to fit the stubs and show both the adaxial and abaxial surfaces.

Based on the images and the data obtained, micromorphological descriptions and additional comments were made for each Neotropical species. The terminology used in the morphological descriptions follows Metcalfe (1960) and Ellis (1979).

A cluster analysis was carried out to evaluate the taxonomic value of the micromorphological characters of the leaf blade epidermis for *Isachne*. The micromorphological data were compiled into a matrix of 19 binary characters (1-8 for the adaxial and 9-19 for the abaxial characters) (Tables 2, 3). Uninformative or doubtful characters were disregarded. The similarity matrix was constructed based on Jaccard's coefficient and the unweighted pair group method using arithmetic averages (UPGMA) was applied to the plotted dendrogram. A Principal Component Analysis (PCA) was conducted based on the correlation matrix. Statistical analyses were made using Past® 3.15 (Hammer 2001). *Isachne pangerangensis* and *M. dentata* were not included in the phenetic analysis due to their foliar characteristics, which made it impossible to observe and codify most of their micromorphological characters.



Table 1. List of species and specimens included in the SEM analysis.

Species	Section ( <i>sensu</i> Prakash & Jain 1984)	Origin (collection site)	Voucher	Herbarium acronym
<i>Isachne angustifolia</i> Nash	<i>Albentes</i>	Porto Rico	<i>F.W. Gould et al.</i> 15855	SP
<i>Isachne arundinacea</i> Griseb.	<i>Albentes</i>	Panama	<i>A.S. Hitchcock</i> 8277	IAC
<i>Isachne burchellii</i> R.S. Rodrigues & Filg.	<i>Albentes</i>	Brazil	<i>A.F.M. Glaziou</i> 17400	NY
<i>Isachne disperma</i> Lam.	<i>Albentes</i>	Guadeloupe Dominica	<i>G.R. Proctor</i> 20351 <i>R.L. Wilbur et al.</i> 8245	US US, NY
<i>Isachne goiasensis</i> Renvoize	<i>Isachne</i>	Brazil Brazil Brazil Brazil	<i>E.P. Heringer et al.</i> 4435 <i>E.P. Heringer et al.</i> 6654 <i>F. Chagas-Silva</i> 387 <i>R.S. Rodrigues et al.</i> 479	RB, SP, CEN SP, UEC UEC SP, HUEFS
<i>Isachne hirtiglumis</i> Longhi- Wagner & Welker	<i>Isachne</i>	Brazil Brazil	<i>L. Damazio s.n.</i> <i>R.S. Rodrigues et al.</i> 465	SP SP
<i>Isachne leersioides</i> Griseb.	<i>Albentes</i>	Cuba Cuba	<i>N.L. Britton &amp; J.F.</i> <i>Cowell</i> 12786 <i>A.S. Hitchcock</i> 23413	NY US
<i>Isachne ligulata</i> Swallen	<i>Albentes</i>	Venezuela Brazil	<i>J.J. Wurdack</i> 34183 <i>R.C. Forzza et al.</i> 7275	RB SP
<i>Isachne polygonoides</i> (Lam.) Döll	<i>Isachne</i>	Brazil Brazil Brazil Brazil	<i>Moraes &amp; Souza</i> 1039 <i>D. Sucre</i> 10326 <i>A. Chase</i> 8124 <i>L. Rossi</i> 2539	UEC RB, SP RB SP
<i>Isachne pubescens</i> Swallen	<i>Albentes</i>	Mexico Guatemala	<i>D.E. Breedlove &amp;</i> <i>G. Davidse</i> 55225 <i>W.D. Stevens &amp; E.S.</i> <i>Martinez</i> 25256	MO MO
<i>Isachne pygmaea</i> Griseb.	<i>Albentes</i>	Jamaica Jamaica	<i>W. Herris</i> 12490 <i>N.L. Britton</i> 220	US NY
<i>Isachne rigens</i> (Sw.) Trin.	<i>Albentes</i>	Jamaica Colombia	<i>A.S. Hitchcock</i> 9362 <i>R.W. Pohl &amp; J.C.</i> <i>Betancur</i> 15465	RB RB
<i>Isachne rigidifolia</i> (Poir.) Urb.	<i>Albentes</i>	Dominican Republic Dominican Republic	<i>G.J. Gastony et al.</i> 487 <i>P. Acevedo-</i> <i>Rodriguez et al.</i> 12671	NY NY
<i>Isachne salzmannii</i> (Trin. ex Steud.) Renvoize	<i>Isachne</i>	Brazil Brazil	<i>A. Chase</i> 7894 <i>M. Elisabeth</i> 40896	RB HRB
<i>Isachne soderstromii</i> R.S. Rodrigues & Filg.	<i>Albentes</i>	Dominica	<i>W.R. Ernst</i> 1227	US
<i>Isachne</i> sp. 1 (South America)	<i>Albentes</i>	Ecuador	<i>V. Zak &amp; J.</i> <i>Jaramillo</i> 3204	MO
<i>Isachne globosa</i> (Thunb.) Kuntze	<i>Isachne</i>	Japan	<i>H. Ohashi et al.</i> 11449	SP
<i>Isachne myosotis</i> Nees	<i>Albentes</i>	China	<i>X. Bai-Zhong</i> 4859	MBM
<i>Isachne pangerangensis</i> Zoll. & Moritzi	<i>Albentes</i>	Singapura	<i>Shah &amp; Ahmad</i> 3603	RB
<i>Isachne sylvestris</i> Ridley	<i>Albentes</i>	China	<i>X. Bai-Zhong</i> 4812	MBM
<i>Eriachne semiciliata</i> Lazarides	-	Australia	<i>B.K. Simon et al.</i> 3657	SP
<i>Micraira dentata</i> Lazarides	-	Australia	<i>L.A. Craven &amp; G.M.</i> <i>Wightman</i> 8333	MBM

Table 2. Micromorphological characters and character states of the foliar epidermis of the Neotropical *Isachne* and additional taxa used in the UPGMA and PCA analyses.

Character	State
1. Adaxial long cells papillae	(0) absent; (1) present
2. Adaxial costal macrohairs	(0) absent; (1) present
3. Adaxial epicuticular wax	(0) absent; (1) present
4. Adaxial costal long cells	(0) absent; (1) present
5. Adaxial costal prickles	(0) absent; (1) present
6. Adaxial costal hooks	(0) absent; (1) present
7. Adaxial costal bicellular microhairs	(0) absent; (1) present
8. Adaxial intercostal bicellular microhairs	(0) absent; (1) present
9. Abaxial long cells papillae	(0) absent; (1) present
10. Abaxial epicuticular wax	(0) absent; (1) present
11. Abaxial costal long cells	(0) absent; (1) present
12. Abaxial costal prickles	(0) absent; (1) present
13. Abaxial intercostal prickles	(0) absent; (1) present
14. Abaxial costal hooks	(0) absent; (1) present
15. Abaxial intercostal hooks	(0) absent; (1) present
16. Abaxial costal bicellular microhairs	(0) absent; (1) present
17. Abaxial intercostal bicellular microhairs	(0) absent; (1) present
18. Abaxial costal macrohairs	(0) absent; (1) present
19. Abaxial intercostal macrohairs	(0) absent; (1) present

Table 3. Matrix of binary descriptors used in the cluster analysis of the Neotropical *Isachne* and additional taxa. Character states according to Table 2.

Species	Character states																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>I. angustifolia</i>	0	0	0	1	1	0	0	0	0	0	0	1	0	0	0	1	1	0	0
<i>I. arundinacea</i>	0	1	0	1	1	0	0	0	0	1	1	1	0	0	0	0	1	0	1
<i>I. burchellii</i>	0	1	1	1	1	0	1	0	0	1	1	1	0	0	0	1	1	0	0
<i>I. disperma</i>	0	1	1	1	1	0	0	0	0	1	0	1	0	0	0	1	1	0	0
<i>I. goiasensis</i>	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	0	0
<i>I. hirtiglumis</i>	1	1	1	1	1	0	1	0	1	1	0	1	0	0	0	1	1	0	0
<i>I. leersioides</i>	1	1	1	1	1	0	1	0	0	1	1	1	0	0	0	1	1	0	0
<i>I. ligulata</i>	1	1	1	1	1	0	1	0	1	1	1	1	0	0	0	0	0	1	1
<i>I. polygonoides</i>	1	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	1
<i>I. pubescens</i>	0	1	1	1	0	0	1	0	0	1	0	1	0	0	0	1	1	1	0
<i>I. pygmaea</i>	0	1	0	1	1	1	1	1	0	1	1	1	0	0	1	1	1	0	0
<i>I. rigens</i>	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	1	1	0
<i>I. rigidifolia</i>	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0
<i>I. salzmannii</i>	1	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	1	0	0
<i>I. soderstromii</i>	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0
<i>Isachne</i> sp. 1 (South America)	1	1	0	1	0	1	1	1	1	0	1	1	0	1	0	1	1	0	1
<i>I. globosa</i>	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0
<i>I. myosotis</i>	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	0	1	0	1
<i>I. sylvestris</i>	1	1	0	1	1	0	1	0	0	1	0	0	1	0	0	0	1	0	0
<i>E. semiciliata</i>	0	0	1	1	0	1	0	0	1	0	1	1	0	0	0	1	0	1	0

## Results and discussion

According to Metcalfe (1960), the leaf structure in *Isachne* is panicoid of a special type, differing by the rectangular, often acute-angular silica bodies, variable subsidiary cells, and cubical intercostal long cells; the mesophyll consists of narrow, elongate cells with developed intercellular spaces, tending to be spongy especially near the veins.

As we did not investigate the leaf blade in the cross section, our findings will contribute only towards a broader understanding of the epidermal structure as seen in surface view. According to our results, the foliar micromorphology in *Isachne* is, in general terms, characterized by the frequent presence of papillate long cells in the intercostal and/or costal zones of one or both leaf blade surfaces; simple papillae, centric to sub-centric, usually dome-shaped, roundish or oblique, sometimes elongated; silica bodies notably variable from roundish, saddle-shaped, cross-shaped, dumbbell-shaped, intermediate between cross-shaped and dumbbell-shaped or Oryzoid; panicoid bicellular microhairs; unicellular macrohairs, straight, usually sunken with cushion cells at base, less often superficial; stomata with subsidiary cells variable in shape, usually dome-shaped, low dome-shaped, triangular or rectangular in outline, usually intercostal, but sometimes present across the costal zones. Figures 1-9 depict most of the general and specific micromorphological structures of the Neotropical *Isachne* and some related taxa.

Metcalfe (1960) provided descriptions only for the abaxial epidermis and the transverse section of leaves. As it is known from other groups of grasses, the analysis of the adaxial and abaxial epidermises may reveal important characters to distinguish closely related species. Similarly, our results revealed significant differences between both foliar epidermal surfaces in *Isachne* (e.g., occurrence, type, and arrangement of long cells, short cells and papillae, presence and pattern of deposition of epicuticular wax, presence and distribution of microhairs, macrohairs and prickle hairs).

Micromorphological features are generally invariant within one species and allow confident circumscription among macromorphologically similar species. Intraspecific variations were found only in *I. leersioides* (related to the presence of adaxial papillate long cells, deposition of epicuticular wax and variation in the abaxial costal long cell's anticlinal walls) and *I. ligulata* (related to the presence of adaxial papillate long cells only). Interspecific variations are more evident, although a series of characters are common to all Neotropical species analyzed. In this scenario, the use of combined macro and micromorphological features may be useful systematically to characterize a species and its related taxa (Silva *et al.* 2015).

*General features of the leaf blade epidermis:*

Costal and intercostal long cells: Long cells can be quite variable among species, between the adaxial and the abaxial epidermises, and sometimes across the intercostal epidermis of the same foliar surface. Long cells shape is determined by the position (i.e., center or margins of leaves and along the intercostal/costal zones), size and shape of adjacent cells, or can reflect the maturation and/or environmental conditions (Ellis 1979).

The use of long cells is taxonomically arguable. According to Ellis (1979), long cells show an extreme degree of phenotypic variation and their taxonomic use must be carefully considered.

With some exceptions, the American species of *Isachne* generally present papillate shortened intercostal long cells, which sometimes become slightly elongated near the costal zones (e.g., *I. disperma*, *I. leersioides*, *I. polygonoides*, *I. pubescens*, *I. soderstromii*, *Isachne* sp. 1, etc.) (figures 1d; 2e; 4b, g; 7c, f). The cells are frequently quadrangular (figure 4b), rectangular or hexagonal (figure 7c), and followed by variations such as polygonal, rounded or cuboid (figure 2e). When present, costal long cells are generally elongated, non-papillate (with some exceptions), and with straight or sinuous anticlinal walls (figures 1d; 2e; 3d; 4c; 5c; 7d).

Papillae - The occurrence of papillate long cells in *Isachneae* is fairly documented (cf. Potztal 1952, Metcalfe 1960, Palmer & Gerbeth-Jones 1986, Sánchez-Ken *et al.* 2007). All the American species presented papillate long cells on the abaxial surface of their leaves, except for *I. angustifolia* (probably because of problems during sample preparation) (figure 1a-b). In fact, the papillae frequently become deflated in preparations (figures 1f; 2c, g; 3f; 4h; 5h; 9b). On the adaxial surface, a broader variation regarding the presence/absence and distribution of papillae was observed. Costal papillate long cells are not common among species. Variation in the distribution of the papillae may also occur across long cells of a same intercostal zone and appears to be an interesting feature to be considered for species characterization [e.g., *I. ligulata* (figure 5a-b), *Isachne pubescens* (figure 4e) and *Isachne* sp. 1 (figure 4g)].

Epicuticular wax - The secretion of epicuticular wax has never been mentioned for *Isachne*. Actually, Potztal (1952) reported the presence of a thin cuticle layer in *Sphaerocaryum malaccense* (Trin.) Pilg. Although the production of epicuticular wax is common in plants, its composition, role, and ecological implications may be potentially unique to a species, group of species, genera or subpopulations (Jenks & Ashworth 1999).

The epicuticular wax was observed on the leaves of all species analyzed, except *I. angustifolia*, *I. soderstromii* and *Isachne* sp. 1 (figures 1a-h; 4f-h). Variation in the presence and deposition of epicuticular wax may also occur within specimens of the same species (e.g., *I. hirtiglumis*). In the Neotropical species, as well as in *I. globosa*, the epicuticular wax forms small

rod-shaped crystals coating the long cells of the intercostal zones (and less often the costal zones) (figures 2c; 3h; 7b). Sometimes these crystals aggregate in platelets over the papillae (e.g., *I. arundinacea*, *I. disperma*, *I. ligulata*, and *I. pubescens*) (figure 3f).

In *I. pangerangensis* the secretion of epicuticular wax is intense, forming dense platelets all over the cells and making it difficult to visualize and describe the remaining epidermal structures, except for the large dome-shaped papillae, macrohairs and the protruding bicellular microhairs (figure 9g-h).

Although incipient, the occurrence and deposition pattern of more varied types of waxes suggest a potential application in the taxonomy and opens space for investigations related to ecology and biochemistry.

**Short cells** - Short cells are restricted to the costal zones and leaf margins in all species analyzed (Metcalf 1960, Palmer & Gerbeth-Jones 1986). They are solitary or in pairs of cork-silica cells in variable arrangements across the costal zones, sometimes alternating with rows and/or files of long cells and associated cells (prickle hairs, microhairs, and macrohairs). Costal papillate short cells are uncommon (Figures 6h; 9b).

**Prickle hairs** - Prickle hairs are systematically divided into prickles and hooks on the basis of size and shape of their bases (Metcalf 1960). They can be absent or present throughout the foliar epidermis, either on the costal and intercostal zones. Prickles occur frequently in the costal zones, regularly or irregularly arranged, and interspersed along rows of long cells, short cells or silica cells (figures 1a-b, g; 2f-h; 3b-d; 5a-c; 6g-h; 7a-d; 8e; 9a-d). Hooks occasionally occur in the costal or intercostal zones [e.g., *I. goiasensis* (figure 5h), *I. pygmaea* (figure 8d) and *Isachne* sp. 1].

Sometimes, the distinction between prickles, hooks, and macrohairs is not clear (Metcalf 1960, Ellis 1979). Young leaves tend to present longer elements that would be named more appropriately as macrohairs; however, as the leaves get older, these elements become shorter, typically as prickle hairs. This variation was observed in *I. goiasensis* (figure 5f-g) and *I. ligulata* (figure 5a-b). In this case, the nature of hairs' bases seems to be crucial to determine the identity of these elements when analyzing immature samples.

Interlocking costal prickles may also occur. According to Ellis (1969), interlocking prickles serve to protect the underlying stomatal groove and is frequently found in leaves with narrow and deep furrows of xeromorphic plants, especially on the abaxial surface. Amongst the Neotropical *Isachne*, only *I. angustifolia* featured interlocking prickle hairs (figure 1b).

**Silica bodies** - Metcalf (1960) observed acutely-angular silica bodies in *I. kunthiana* Wight & Arn., *I. walkeri* (Arn. ex Steud.) Wight & Arn. ex Hook. f., and *I. mauritiana* Kunth, and gave special emphasis to this character when circumscribed *Isachne* and its related genera.

The American species and specimens analyzed presented great variation in the shape of their silica bodies (figures 2h; 3d, f; 4c; 5c; 6b, h; 7a; 8b, e; 9b). These differences in the same preparation appear to be related to the position (i.e., near the margins or in the central portion of the leaves, in the edges of veins, etc.), the maturation degree of the silica cells, and sometimes coalescence (which commonly occurs in the spikelet's phytoliths). No idioblast is present on the intercostal zones of the abaxial or adaxial epidermises.

Bicellular microhairs - According to Tateoka *et al.* (1959) and Graciano-Ribeiro (2002), the shape of the microhairs is believed to be more constant in the species and can be systematically useful. However, Johnston & Watson (1977) highlighted that, although constant for species, the presence/absence, and shape of microhairs are more consistent at generic or major group levels. In fact, the morphology of microhairs is quite uniform among the species included in this study; therefore, its applicability to distinguish species in *Isachne* seems to be highly questionable. In this scenario, the amount and distribution pattern rather than the morphology appear to be more promising characters to be used taxonomically at the species level; nevertheless, it should be adopted with parsimony.

Microhairs are common on both or one of the foliar epidermises, tending to be more frequent on the abaxial epidermis (Graciano-Ribeiro 2002). They are often restricted to the intercostal zones or associated with the margins of the costal zones (figures 1f; 2c, f-h; 3d-f; 4e-h; 8d). The length of the basal and distal cells can be approximately equal (figure 8d), the basal longer or slightly longer than the distal (figure 2c, h), or the distal cell slightly longer than the basal one (as seen in *Isachne* sp. 1).

Macrohairs - Macrohairs may also occur throughout the foliar epidermis (figure 7g-h) or only on the costal or intercostal zones (figures 2a-b; 3e; 4a, d-f; 5a, d, g; 6e-f; 7e-f). The frequency of macrohairs varies according to leaf maturity and environmental conditions (Ellis 1979). For Metcalfe (1960), macrohairs have no more than a specific diagnostic value in taxonomy. However, for Mensah & Gill (1997), differences in the pattern of distribution of hairs are taxonomically relevant. In fact, the absence of macrohairs on the leaves of various species analyzed (e.g., *I. angustifolia*, *I. burchellii*, *I. disperma*, *I. globosa*, *I. goiasensis*, *I. leersioides*, *I. pygmaea*, *I. rigidifolia*, *I. salzmännii*, and *I. soderstromii*) appears to be a reliable character to circumscribe these taxa.

In *Isachne* there occur two types of macrohairs: straight and acute cushion hairs on the leaf blades and twisted hairs with narrow tips on the anthoecia (Rodrigues & Filgueiras, unpubl. data). The typical cushion base of the foliar macrohairs is visible even when the hair is lost due to glabrescence or friction during sample preparation (see macrohairs bases in figure 6f) (Ellis 1979).

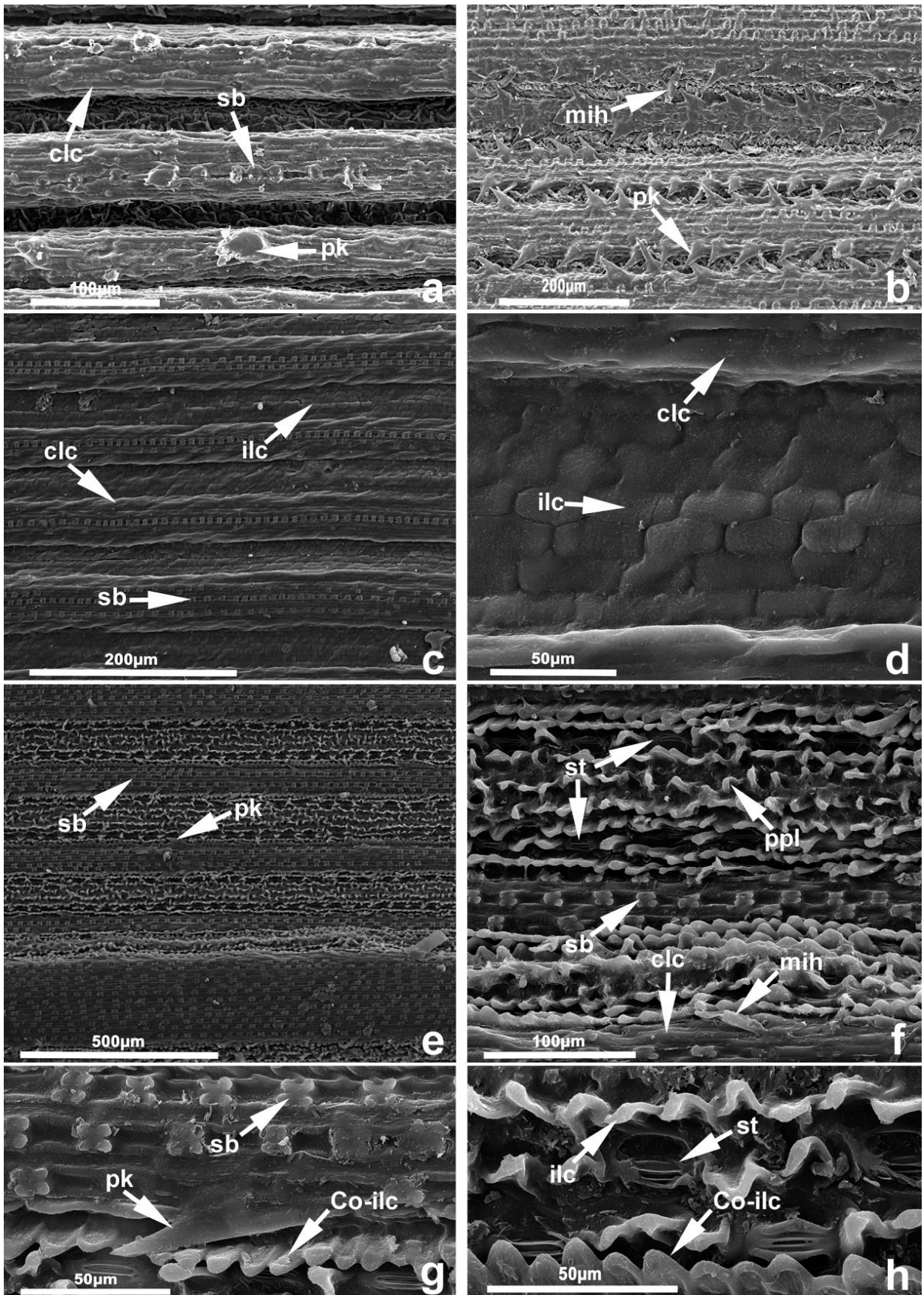


Figure 1. a-b. *Isachne angustifolia*. a. General overview of the adaxial epidermis. b. General overview of the abaxial epidermis. c-h. *Isachne soderstromii*. c. General overview of the adaxial epidermis. d. Adaxial epidermis, detail of the intercostal zone. e. General overview of the abaxial epidermis. f. Abaxial epidermis, detail of the costal and intercostal zones. g. Abaxial epidermis, costal zone. h. Abaxial epidermis, intercostal zone. clc: costal long cell; Co-ilc: coalescent intercostal long cells; ilc: intercostal long cell; mih: bicellular microhair; pk: prickle; ppl: papillae; sb: silica body; st: stomata. Based on: a-b. F.W. Gould et al. 15855 (SP); c-h. A.F.M. Glaziou 17400 (NY).

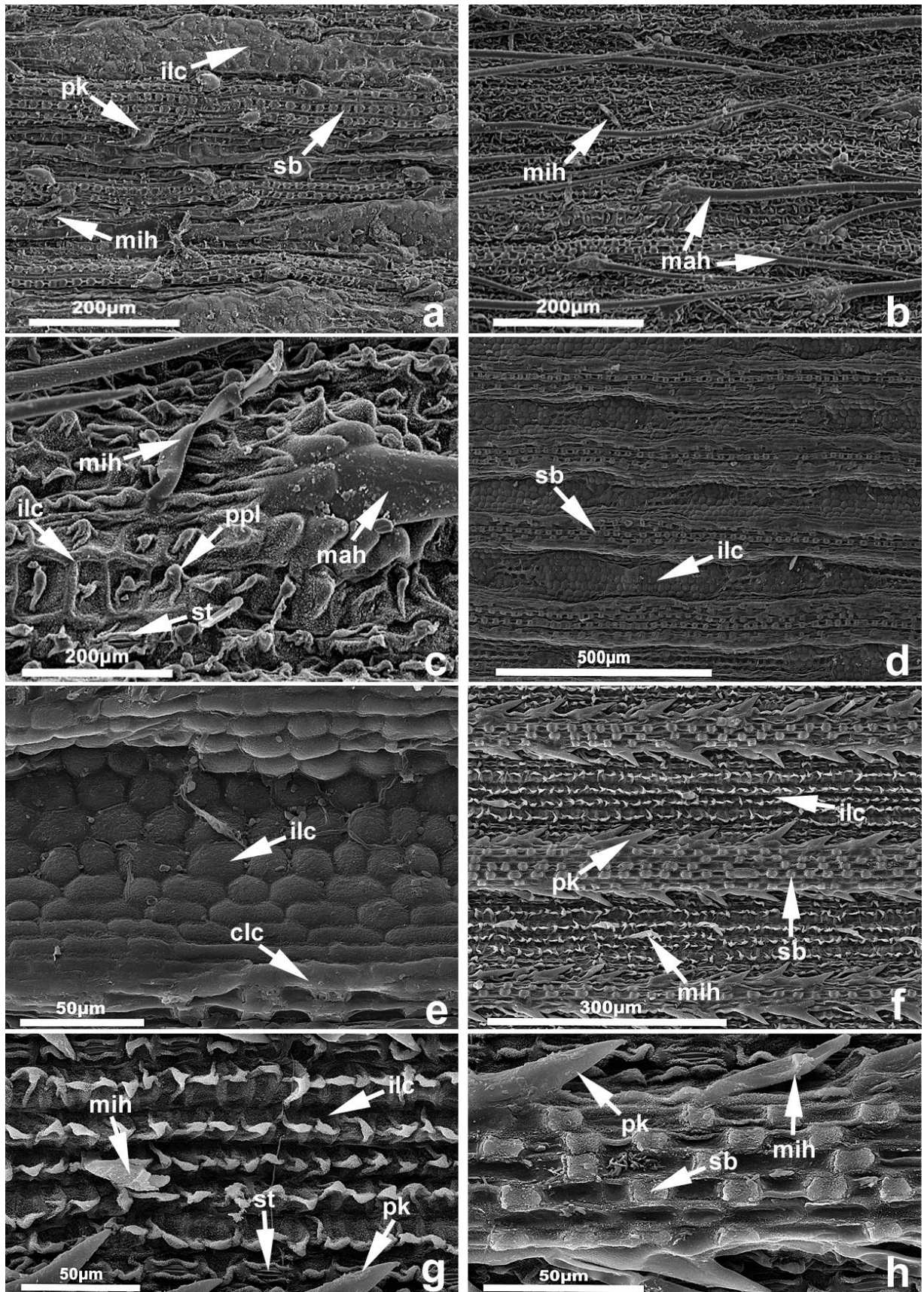


Figure 2. a-c. *Isachne rigens*. a. General overview of the adaxial epidermis. b. General overview of the abaxial epidermis. c. Abaxial epidermis, detail of the costal zone and base of cushion macrohair. d-h. *Isachne disperma*. d. General overview of the adaxial epidermis. e. Adaxial epidermis, detail of the intercostal zone. f. General overview of the abaxial epidermis. g. Abaxial epidermis, detail of the intercostal zone. h. Abaxial epidermis, detail of the costal zone. clc: costal long cell; ilc: intercostal long cell; mah: macrohair; mih: bicellular microhair; pk: prickle; ppl: papillae; sb: silica body; st: stomata. Based on: a-c. R.W. Pohl & J.C. Betancur 15465 (RB); d-h. R.L. Wilbur et al. 8245 (US).



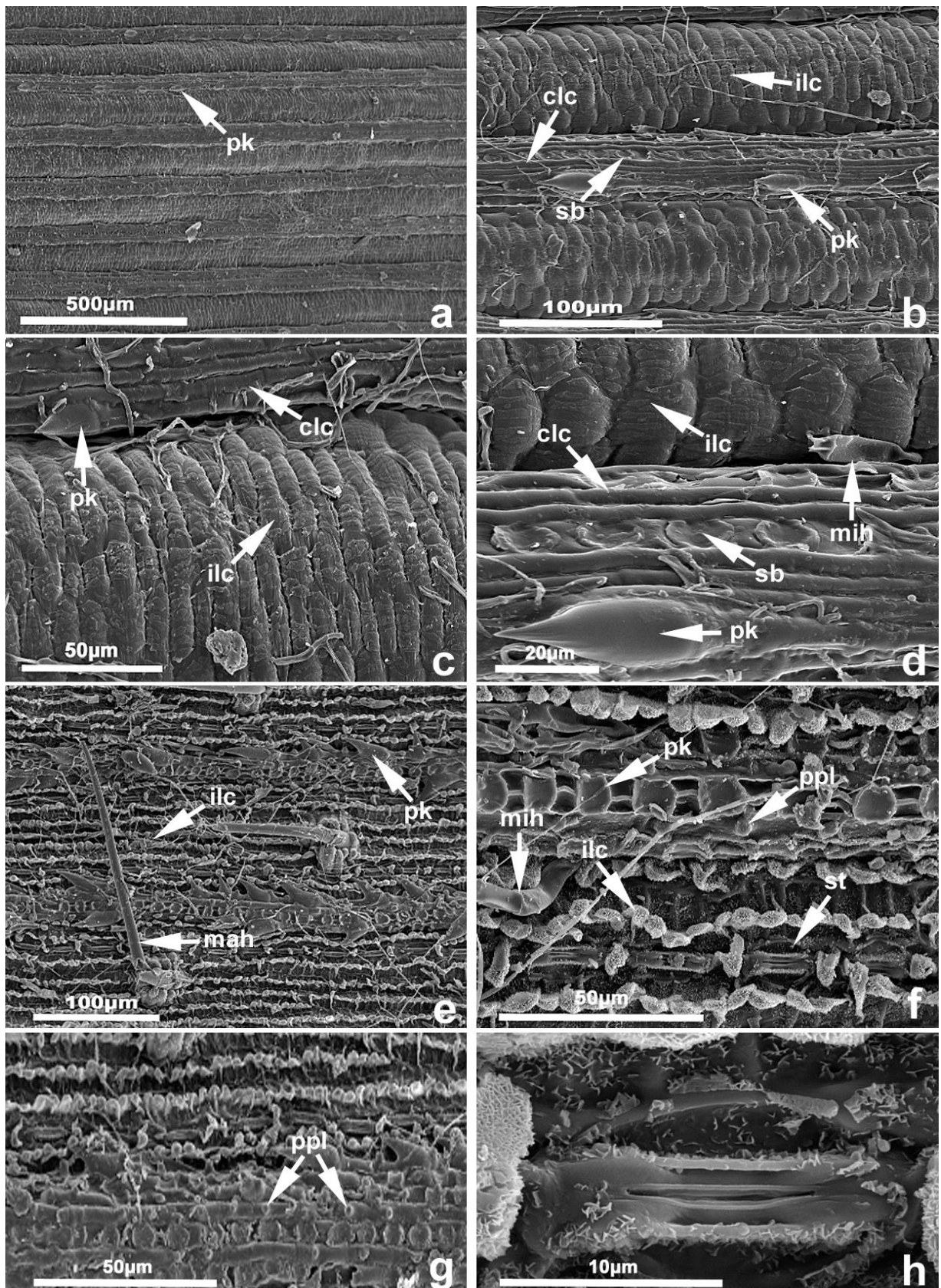


Figure 3. a-h *Isachne arundinacea*. a. General overview of the adaxial epidermis. b. Adaxial epidermis, detail of the costal and intercostal zones. c. Adaxial epidermis, detail of the costal and intercostal zones (note the striated intercostal long cells). d. Adaxial epidermis, detail of the costal and part of the intercostal zone. e. General overview of the abaxial epidermis. f. Abaxial epidermis, detail of the costal and intercostal zones. g. Abaxial epidermis, detail of the costal and part of the intercostal zone (note the papillate costal long cells). h. Abaxial epidermis, detail of the stomata (note the rod-shaped epicuticular wax). clc: costal long cell; ilc: intercostal long cell; mah: macrohair; mih: bicellular microhair; pk: prickles; ppl: papillae; sb: silica body; st: stomata. Based on a-h. A.S. Hitchcock 8277 (IAC).

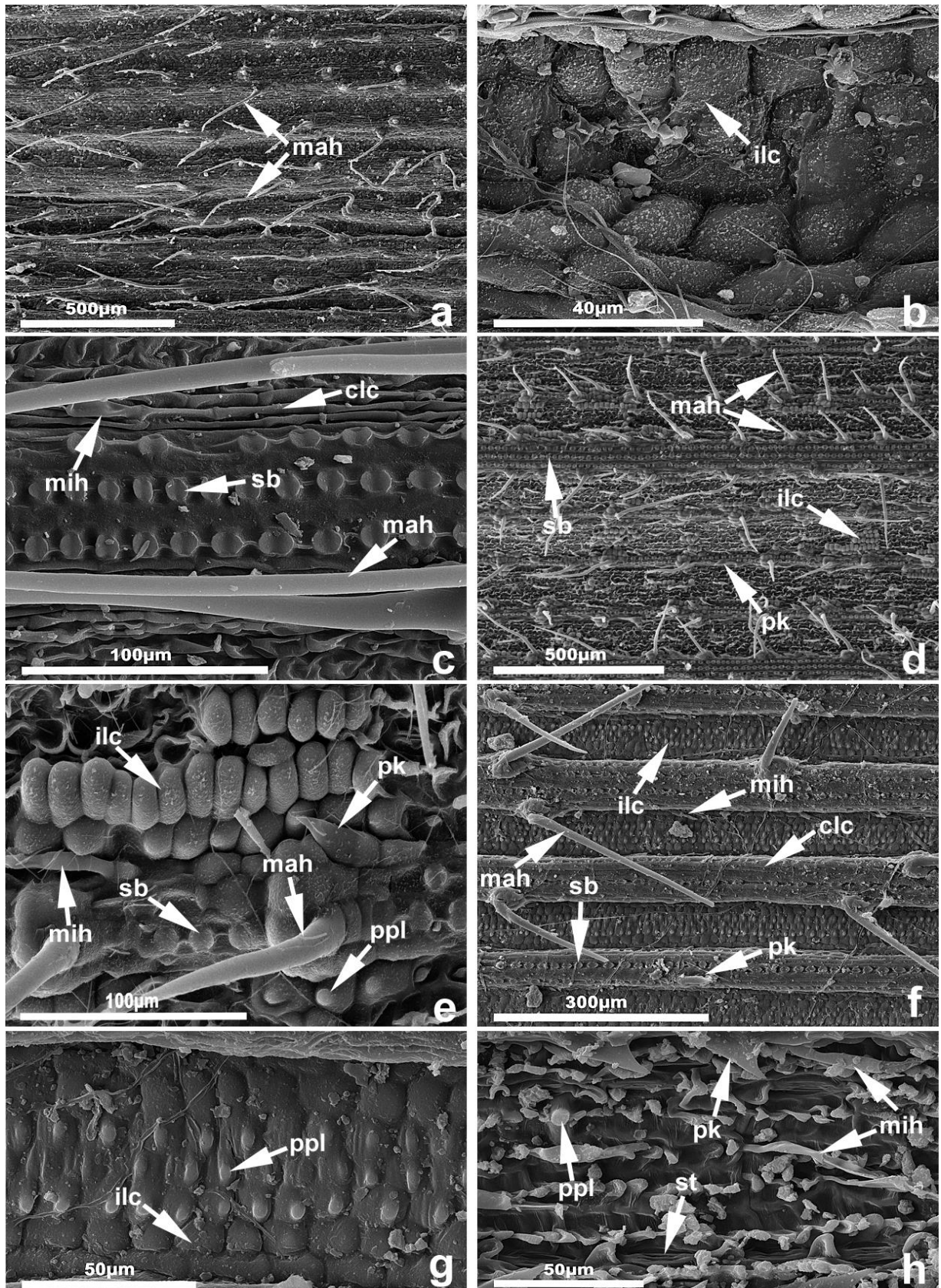


Figure 4. a-e. *Isachne pubescens*. a. General overview of the adaxial epidermis. b. Adaxial epidermis, detail of the intercostal zone. c. Adaxial epidermis, detail of the costal zone. d. General overview of the abaxial epidermis. e. Abaxial epidermis, detail of the costal and the intercostal zones (note the papillae on the intercostal long cells adjoined the costal zones). f-h. *Isachne* sp. 1. f. General overview of the adaxial epidermis. g. Adaxial epidermis, intercostal zone (note the papillae restricted to the 3-4 central rows of long cells). h. Abaxial epidermis, detail of the intercostal zone. clc: costal long cell; ilc: intercostal long cell; mah: macrohair; mih: bicellular microhair; pk: prickle; ppl: papillae; sb: silica body; st: stomata. Based on: a-b, d-e. *W.D. Stevens & E.S. Martinez 25256 (MO)*; c. *D.E. Breedlove & G. Davidse 55225 (MO)*; f-h. *V. Zak & J. Jaramillo 3204 (MO)*.

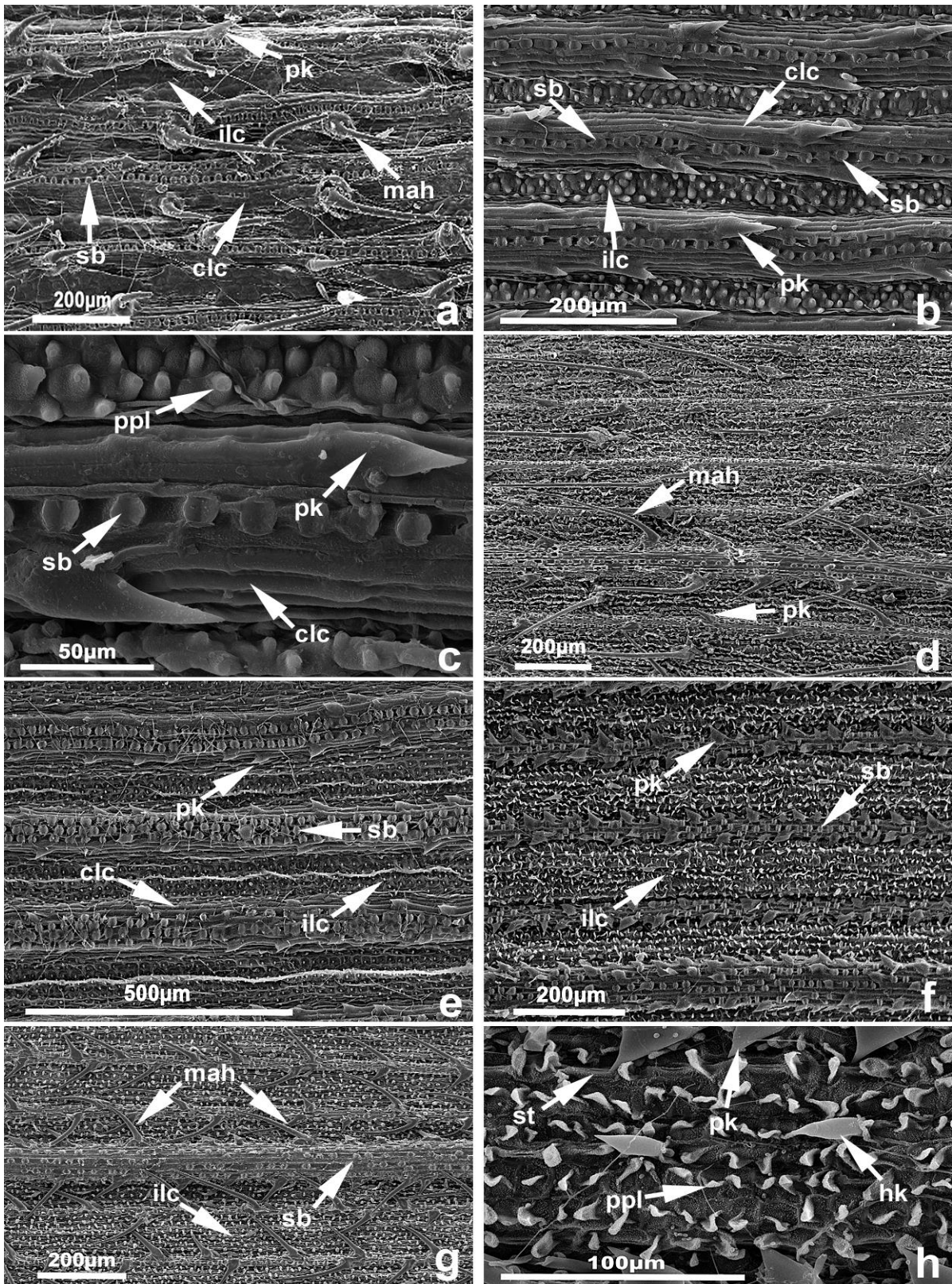


Figure 5. a-d. *Isachne ligulata*. a. General overview of the adaxial epidermis (note the presence of costal and intercostal macrohairs and non-papillate intercostal long cells). b. General overview of the adaxial epidermis (note the presence of costal prickles and papillate intercostal long cells). c. Adaxial epidermis, detail of the costal zone and part of the intercostal zone with papillate long cells. d. General overview of the abaxial epidermis. e-h. *Isachne goiasensis*. e. General overview of the adaxial epidermis. f. General overview of the abaxial epidermis (note the presence of costal prickles). g. General overview of the abaxial epidermis of young leaf blade (note the presence of costal macrohairs). h. Abaxial epidermis, detail of the intercostal zone. clc: costal long cell; hk: hook; ilc: intercostal long cell; mah: macrohair; pk: prickle; ppl: papillae; sb: silica body; st: stomata. Based on: a, d. J.J. Wurdack 34138 (RB); b-c. R.C. Forzza et al. 7275 (SP); e-f, h. R.S. Rodrigues et al. 479 (SP); g. F. Chagas-Silva 387 (UEC).

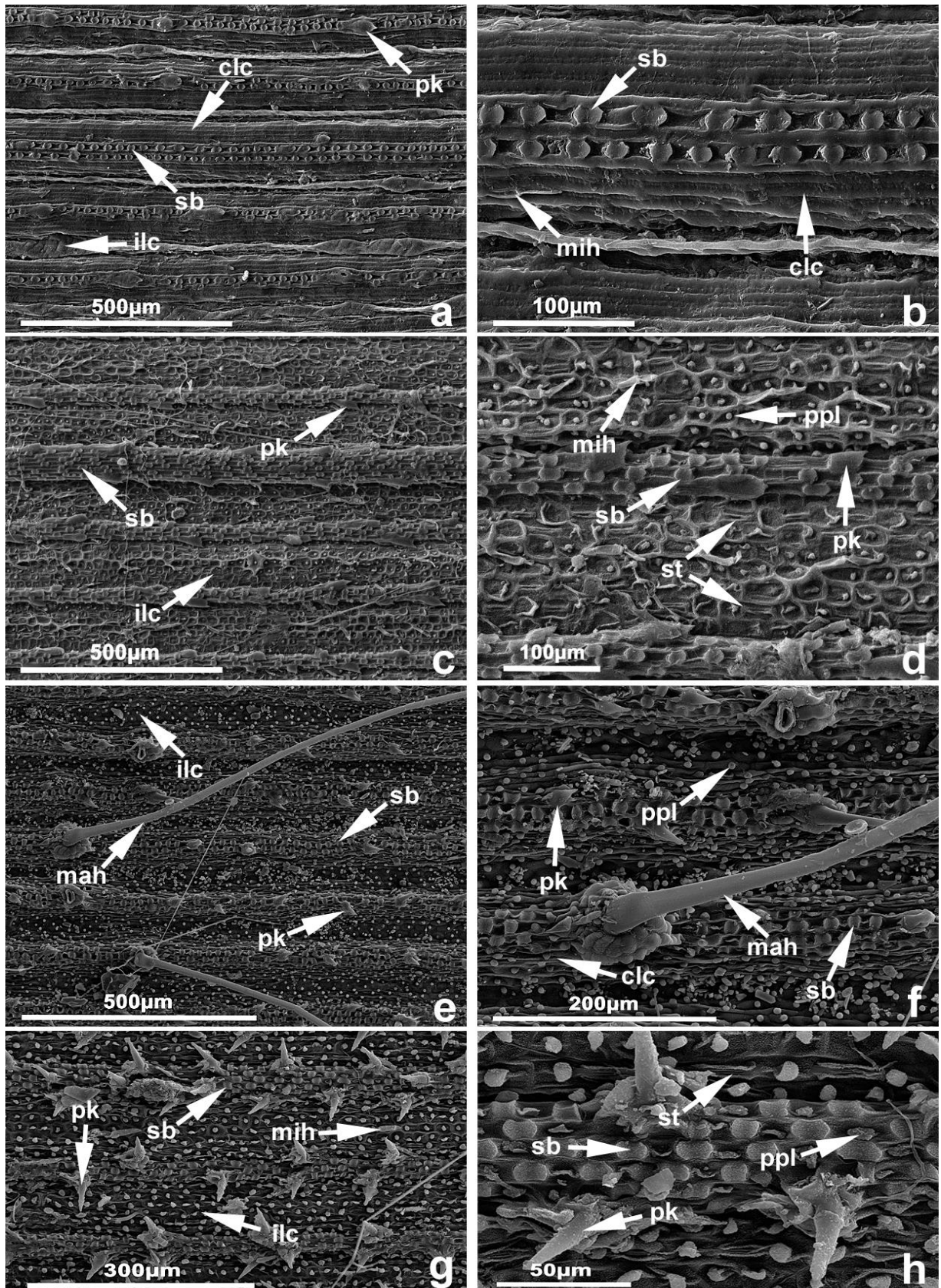


Figure 6. a-d. *Isachne burchellii*. a. General overview of the adaxial epidermis. b. Adaxial epidermis, detail of the costal zone and part of the intercostal zone. c. General overview of the abaxial epidermis. d. Abaxial epidermis, detail of the intercostal and costal zones. e-h. *Isachne hirtiglumis*. e. General overview of the adaxial epidermis. f. Adaxial epidermis, detail of the costal and intercostal zones (note the papillate costal and intercostal long cells). g. General overview of the abaxial epidermis. h. Abaxial epidermis, detail of the costal zone and part of the intercostal zone. clc: costal long cell; ilc: intercostal long cell; mah: macrohair; mih: bicellular microhair; pk: prickle; ppl: papillae; sb: silica body; st: stomata. Based on: a-d: A.F.M. Glaziou 17400 (NY); e-h: R.S. Rodrigues et al. 465 (SP).

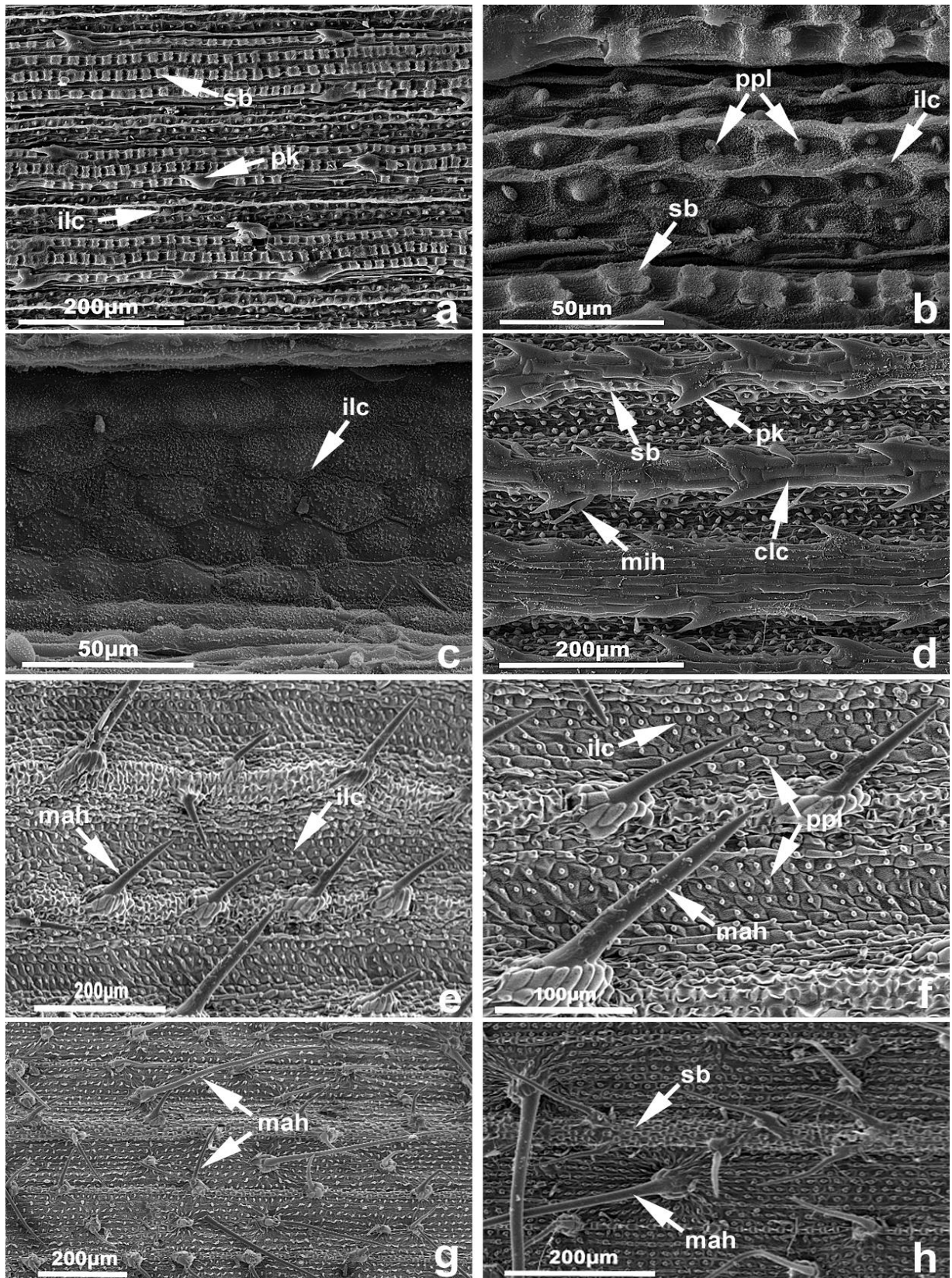


Figure 7. a-d. *Isachne leersioides*. a. General overview of the adaxial epidermis. b. Adaxial epidermis, detail of the intercostal zone (note the papillate intercostal long cells) and the cross-shaped silica bodies on the costal zones. c. Adaxial epidermis, detail of the intercostal zone (note the non-papillate intercostal long cells). d. Abaxial epidermis, detail of the costal and intercostal zones. e-h. *Isachne polygonoides*. e. General overview of the abaxial epidermis. f. Abaxial epidermis, detail of the costal and intercostal zones. g. General overview of the abaxial epidermis. h. Abaxial epidermis, detail of the costal and intercostal zones (note the macrohairs on both the costal and intercostal zones). clc: costal long cell; ilc: intercostal long cell; mah: macrohair; mih: bicellular microhair; pk: prickle; ppl: papillae; sb: silica body. Based on: a-b, d. *N.L. Britton & J.F. Cowell 12786 (NY)*; c. *A.S. Hitchcock 23413 (US)*; e-f. *L. Rossi 2539 (SP)*; g-h. *Moraes & Sousa 1039 (UEC)*.

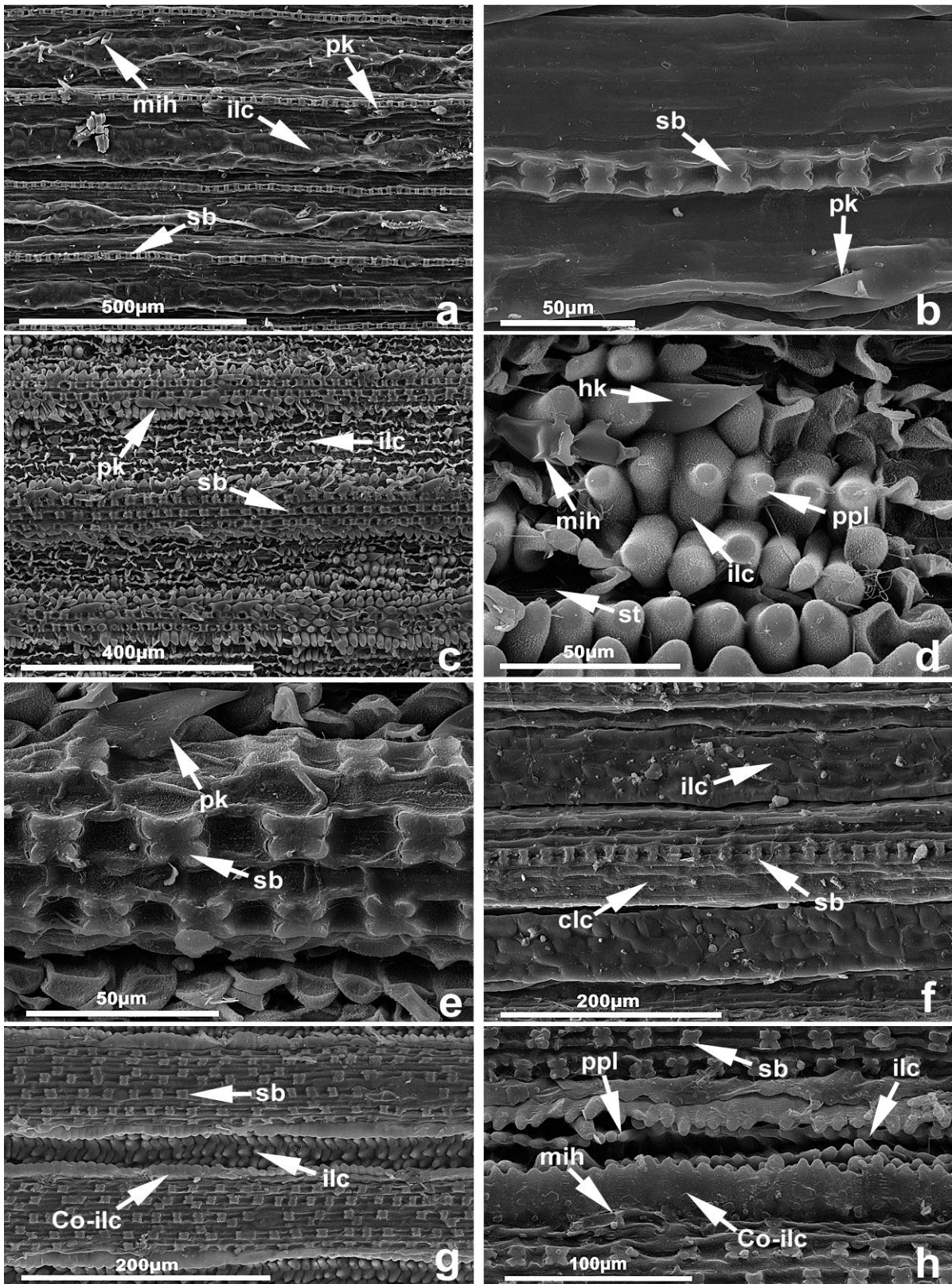


Figure 8. a-e. *Isachne pygmaea*. a. General overview of the adaxial epidermis. b. Adaxial epidermis, detail of the costal zone. c. General overview of the abaxial epidermis. d. Abaxial epidermis, detail of the intercostal zone. e. Abaxial epidermis, detail of the costal zone. f-h. *Isachne rigidifolia*. f. Adaxial epidermis, detail of the costal and intercostal zones. g. Abaxial epidermis, detail of the costal and intercostal zones (note the intercostal zones inserted in grooves between successive costal zones). h. Abaxial epidermis, detail of the intercostal zones and part of the costal zones (note the marginal coalescent intercostal long cells partially covering the central papillate cells of the intercostal zones). clc: costal long cell; Co-ilc: coalescent intercostal long cells; hk: hook; ilc: intercostal long cell; mih: bicellular microhair; pk: prickle; ppl: papillae; sb: silica body; st: stomata. Based on: a-d. W. *Herris* 12490 (US); e. N.L. *Britton* 220 (NY); f, h. P. *Acevedo-Rodriguez et al.* 12671 (NY); g. G.J. *Gastony et al.* 487 (NY).

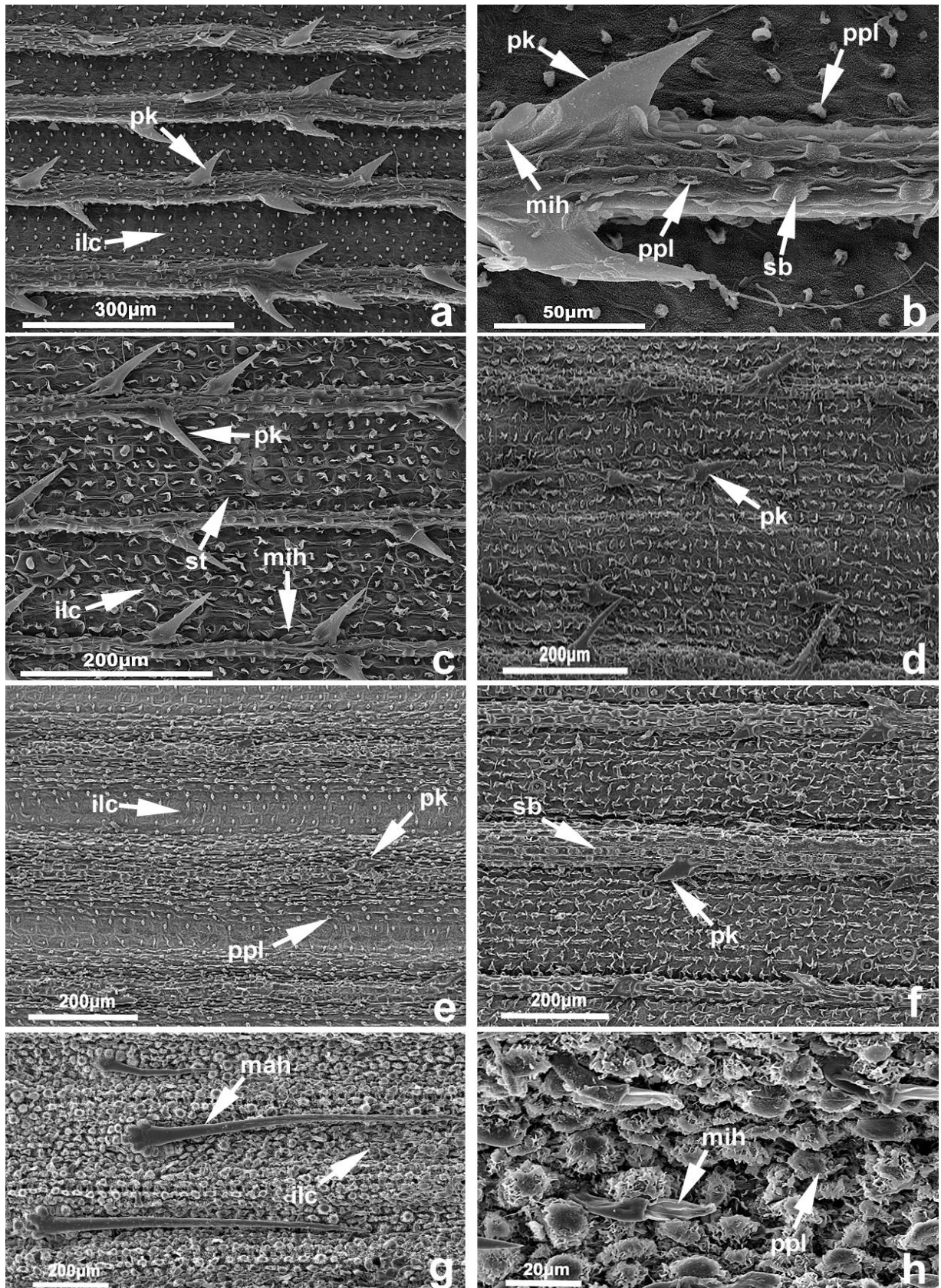


Figure 9. a-d. *Isachne salzmannii*. a. General overview of the adaxial epidermis. b. Adaxial epidermis, detail of the costal zone and part of the intercostal zone. c. General overview of the abaxial epidermis. d. General overview of the abaxial epidermis showing the occurrence of intercostal prickles. e-f. *Isachne globosa*. e. General overview of the adaxial epidermis. f. General overview of the abaxial epidermis. g-h. *Isachne pangerangensis*. g. General overview of the abaxial epidermis. h. Abaxial epidermis, detail of the intercostal zone (note the dense platelet epicuticular wax). ilc: intercostal long cell; mah: macrohair; mih: bicellular microhair; pk: prickle; ppl: papillae; sb: silica body; st: stomata. Based on: a-c. M. Elisabeth 40896 (HRB); d. A. Chase 7894 (RB); e-f. H. Ohashi et al. 11449 (MBM); g-h. Shah & Ahmad 3603 (RB).

*Phenetic analysis:*

Figure 10 presents the relationship among the analyzed species considering the micromorphological characters of the abaxial and adaxial leaf blade epidermises, according to Jaccard's similarity coefficient. A correlation of 0.7706 was found between the cophenetic and the similarity matrices.

The UPGMA dendrogram shows that there is a morphological gradient regarding the foliar epidermal characters of most of the Neotropical *Isachne* and additional taxa. Considering that the infrageneric classification of *Isachne* (as so is in most of the Poaceae) is based on reproductive features (cf. Prakash & Jain 1987), it was not surprising that no correspondence was found between the dendrogram and taxonomic entities. However, neither strong ecological nor geographical correlations were found among or within groups of species.

Five major groups can be highlighted (Figure 10). Group 1 (*I. ligulata* and *I. polygonoides*) shares most micromorphological characters, except the occurrence of adaxial costal microhairs, adaxial and abaxial costal long cells and prickles, and abaxial intercostal microhairs. Group 2 (*I. rigidifolia* and *I. arundinacea*) shares all the adaxial characters but diverges abaxially in relation to the costal prickles, costal and intercostal microhairs, and intercostal macrohairs. Group 3 (*I. goiasensis*, *I. pygmaea*, and *Isachne* sp. 1) shares almost half of their foliar characters, except the occurrence of adaxial costal prickles, adaxial and abaxial papillate long cells and epicuticular wax, abaxial costal and intercostal hooks, and intercostal macrohairs. *Isachne* sp. 1 is distant from the other species of its group because of the absence of adaxial costal prickles, abaxial epicuticular wax and intercostal hooks, and the presence of abaxial papillate long cells and intercostal macrohairs. The large group 4 (*I. disperma*, *I. burchellii*, *I. globosa*, *I. hirtiglumis*, *I. leersioides*, *I. pubescens*, *I. salzmannii* and *I. sylvestris*) share less than half of the characteristics and is concisely formed by species that lack adaxial costal hooks and intercostal microhairs, abaxial costal and intercostal hooks, and intercostal macrohairs, but present adaxial costal macrohairs and abaxial epicuticular wax and intercostal microhairs. Within this group, *I. salzmannii* and *I. sylvestris* form a subgroup distinct by the presence of abaxial intercostal prickles and costal microhairs. Group 5 (*I. angustifolia* and *I. soderstromii*) also shares most characters except the occurrence of adaxial costal macrohairs and prickles.

However, none of these groups has a unique character that defines them. *Isachne rigens* and the remaining extra-neotropical species did not group significantly with other species.

In the PCA analysis, the five main components were responsible for ca. 70% of the variance [20,927% (axis 1); 15,392% (axis 2); 14,55% (axis 3); 11,165% (axis 4); and 7,7953 (axis 5)]. Figure 11 represents the relationship among the three main components that explain ca. 51% of the variance.



The variables that most contributed to grouping species were the occurrence of adaxial costal long cells, hooks, and intercostal microhairs; abaxial costal long cells and hooks, and costal and intercostal hooks and costal microhairs (supporting group 3); presence of adaxial costal prickles, abaxial epicuticular wax and intercostal prickles (supporting group 4). The occurrence of adaxial and/or abaxial papillate long cells, adaxial epicuticular wax, and abaxial costal microhairs and macrohairs contributed with groups 1, 2 and 5. The complete relationship among the five main components of the PCA is included in Appendix 1.

Although no foliar micromorphological feature is attributable as exclusive to a group, qualitative analysis may aid substantially in the circumscription of morphologically closely related species, notably, considering not only the presence/absence but also the distribution pattern and arrangement of the epidermal elements.

*Micromorphological characters of the leaf blade epidermis for delimiting Neotropical close related species of Isachne:*

The diversity of species of *Isachne* in the Neotropical region is insipient when compared to the Australasian region. Nevertheless, amongst the 15 accepted American species, there are taxa whose distinction strictly based on macromorphological characters has been traditionally confusing. The most notable cases are those of *I. angustifolia*, *I. arundinacea*, *I. burchellii*, *I. disperma*, *I. goiasensis*, *I. ligulata*, *I. pubescens*, *I. rigens* and *I. soderstromii*.

*Isachne angustifolia* is morphologically related to *I. soderstromii* regarding its habit, indumentum and distichous arrangement of leaves. As shown in this study, these taxa also share a series of similarities related to their foliar micromorphology (table 3; figure 10). However, *I. angustifolia* is a non-glandular species, micromorphologically distinct from *I. soderstromii* by presenting adaxial costal long cells in simple rows vertically alternated with rows of short cells, and sparse small prickle hairs along the central portion of the costal zones (figure 1a). Abaxially, there occur costal interlocking prickle hairs (figure 1b). The presence of papillae was not confirmed for *I. angustifolia*. On the other hand, *I. soderstromii* is a glandular species (Rodrigues & Filgueiras 2018) whose leaf blades present adaxial costal long cells arranged in 3-4 rows at the margins of the costal zones and no prickle hair (figure 1c-d). Abaxially, there occur intercostal papillate long cells and some occasional costal prickle hairs (figure 1e-g).

Rodrigues & Filgueiras (2018) also compared *I. rigens* with *I. soderstromii* due to their habit and similarities in the spikelets. Regarding the foliar micromorphology, *I. rigens* differs adaxially by the absence of costal long cells and by the presence of costal prickles and some scarce microhairs (figure 2a). Sometimes abundant costal macrohairs or intercostal prickles occur along the abaxial epidermis of *I. rigens* (figure 2b-c), but they are absent in *I. soderstromii* (figure 1e-f, h).

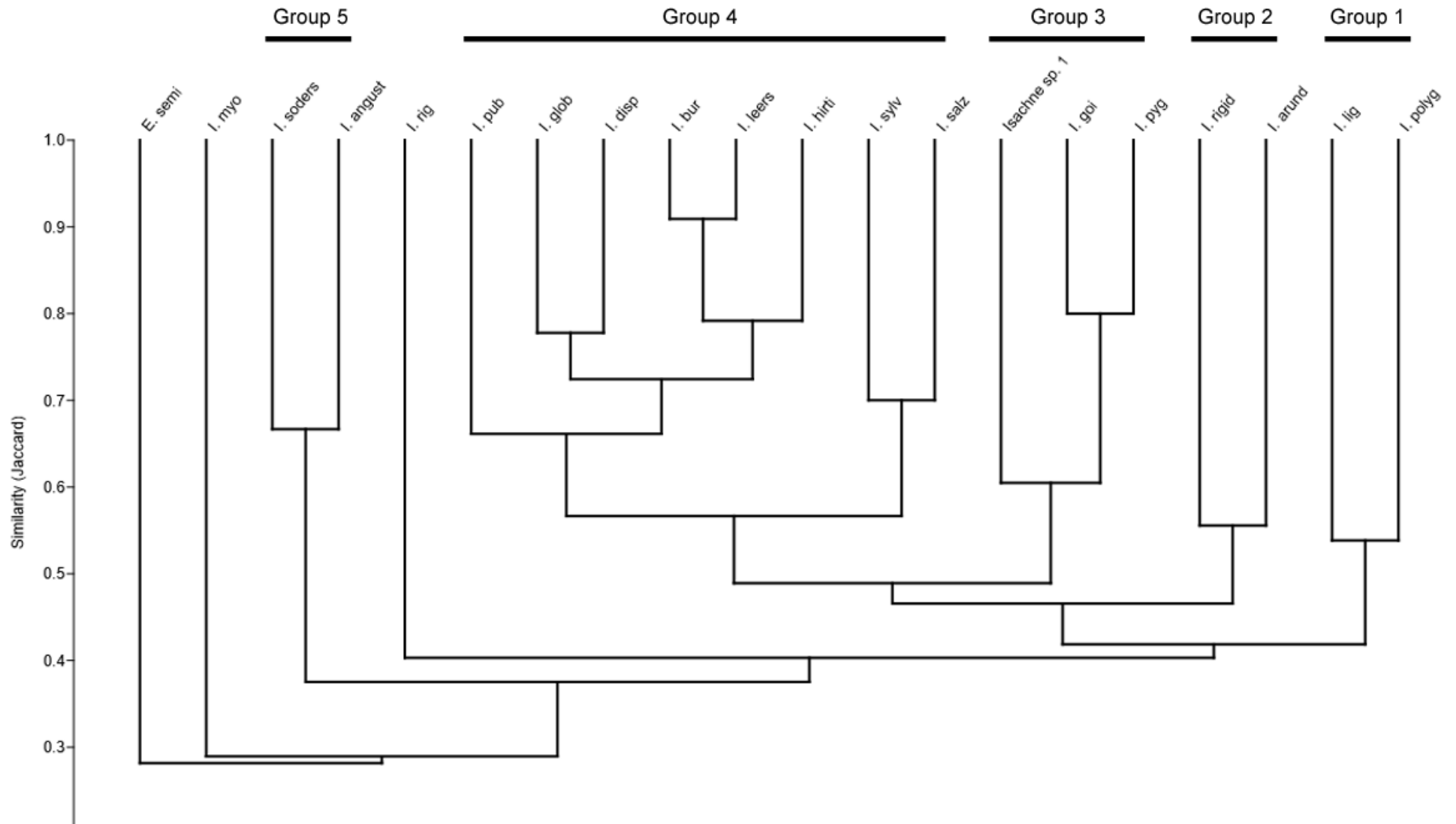


Figure 10. UPGMA Dendrogram based on Jaccard's similarity using micromorphological characters of the leaf blade epidermis of species of *Isachne* and *E. semiciliata*. Cophenetic correlation: 0.7706.

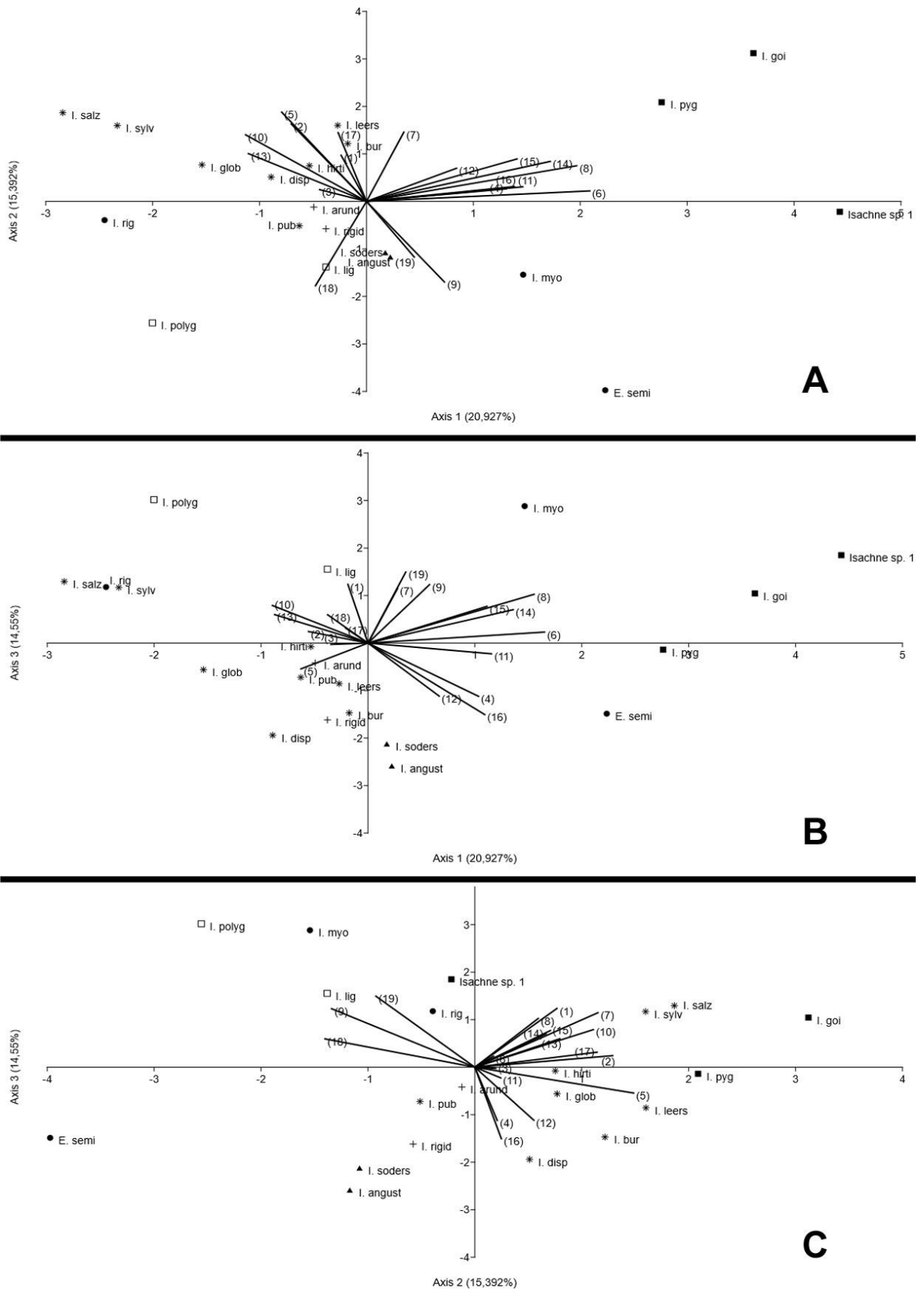


Figure 11. PCA using micromorphological characters of the leaf blade epidermis of *Isachne* and *E. semiciliata*. Graphic representation of the relationship among the three main components (explaining ca. 51% of the variation). A. axis 1 × axis 2; B. axis 1 × axis 3; C. axis 2 × axis 3. Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.

A series of additional comments about the distinction of *I. soderstromii* from other Central American and Caribbean species of *Isachne* can be found in Rodrigues & Filgueiras (2018).

*Isachne disperma* has been traditionally associated with *I. arundinacea* by its robust habit, leaf blade size and general characters of the synflorescence and spikelets. Notably, the greatest confusion rests on those specimens of *I. arundinacea* that present panicles larger than the usual and less congest spikelets at the apex of the secondary branches. The leaf micromorphology revealed a set of characters that allow a better delimitation of these taxa. *Isachne disperma* is distinct from *I. arundinacea* by presenting adaxial non-striated intercostal long cells (figure 2d-e) and abaxial papillate intercostal long cells overarching the stomata, absence of abaxial costal long cells and macrohairs (figure 2f-h). *Isachne arundinacea* is typically characterized by the adaxial conspicuously striated intercostal long cells (figure 3a-d) and by the abaxial papillate intercostal and costal long cells not overarching the stomata, the absence of costal microhairs, and presence of intercostal macrohairs (figure 3e-g).

Pohl & Davidse (1994) discussed the morphological affinities between *I. arundinacea* and *I. pubescens* and suggested that the second should be better classified as a variety of the first. In fact, the two species are very closely related morphologically and overlap in their geographic distribution. In addition to the traditional distinctive characters that separate the two species (i.e., pilosity of sheaths, leaves and panicle branches), the foliar micromorphology support *I. arundinacea* and *I. pubescens* as distinct taxa. Besides the typical striated intercostal long cells on the adaxial surface and the presence of papillate costal long cells abaxially (figure 3c), *I. arundinacea* also has adaxial costal prickles and lack costal microhairs and macrohairs (figure 3d). Alternatively, *I. pubescens* has non-striate adaxial intercostal long cells (figure 4b), and the abaxial costal long cells are absent (figure 4e). Moreover, the costal zones of both leaf blade surfaces in *I. pubescens* are ornamented by microhairs and macrohairs (figure 4c, e).

*Isachne arundinacea* has been accepted as a highly polymorphic species widely distributed across the Americas. It is evident that the taxonomic boundaries of this ill-defined taxon are still unclear, including some dissonant entities from the typical form throughout its area of occurrence.

During the analysis of the South American species of *I. arundinacea*, a set of peculiar and morphologically well-characterized specimens was identified (included in this study as *Isachne* sp. 1). These specimens are known from the northwest of South America, in Colombia, Ecuador, and Peru, and present extremely dense, rustic and pilose to somewhat hirsute panicles, tiny globose spikelets (ca. 1mm long) with the anthoecia mostly similar in length. Surprisingly, the foliar micromorphological characters of these specimens are also very distinct from the typical form of *I. arundinacea*. *Isachne* sp. 1 has non-striated intercostal long cells on the adaxial leaf blade surface, being the innermost cells papillate (ca. 3-4 rows) and the outermost cells non-papillate (ca. 2 rows) (figure 4g). Also, there occur adaxial costal and intercostal microhairs and costal macrohairs (figure 4f), and abaxial costal microhairs (figure 4h).

This set of macro and micromorphological evidence, along with a more restricted geographic distribution, suggest that specimens of *Isachne* sp. 1 may integrate a distinct population from the typical *I. arundinacea*. Furthermore, since no intermediary between the two forms was detected, it is plausible to consider that such specimens might deserve the status of a new variety or even a new species.

*Isachne ligulata* is another South American species that used to be primarily identified as *I. arundinacea*. Rodrigues & Filgueiras (2016) briefly commented on the macromorphological similarities between these two species. The distinctive foliar micromorphological characters they referred for *I. ligulata* are the non-striate and variably papillate intercostal long cells (especially absent in younger materials) on the adaxial surface (figure 5a-c), and the occurrence of abundant costal macrohairs and non-papillate costal long cells on the abaxial surface (figure 5d).

The identity of the Brazilian endemic *I. goiasensis* was assessed by Rodrigues & Filgueiras (2019) based on a series of ecological, geographical, macro and micromorphological evidence. Through the analysis of the micromorphological characters of the anthoecia, *I. burchellii* was segregated from *I. goiasensis*, putting an end to a very problematic taxonomic history (c.f., Rodrigues & Filgueiras 2019). Although no micromorphological characteristic of the leaf has been cited, it is worth mentioning that there are also expressive differences in the foliar morphology between the two species. *Isachne goiasensis* has papillate long cells and scarce microhairs in the intercostal zones of the adaxial surface (figure 5e). On the abaxial surface, some occasional hooks or prickles and, sometimes, stomata arranged in rows and separated by ca. 1-2 interstomatal cells throughout the intercostal zones may occur (figure 5f-h). *Isachne burchellii* has non-papillate long cells and apparently no microhair in the intercostal zones of the adaxial leaf epidermis (figure 6a-b). On the abaxial surface, intercostal hooks are absent and the stomata are always arranged in 1-2 rows near the costal zones (figure 6c-d); costal microhairs are present.

Other Neotropical species also have foliar micromorphological characters that we consider useful for their circumscription.

*Isachne hirtiglumis* has adaxial costal and intercostal papillate long cells (which also occurs in the abaxial epidermis of *I. arundinacea*) and abundant long costal macrohairs and small prickly hairs (figure 6e-f). On the abaxial surface, there are papillate short cells, abundant silica bodies and prickly hairs regularly distributed along successive rows throughout the costal zones; macrohairs are absent (figure 6g-h).

*Isachne leersioides* has adaxial intercostal papillate or non-papillate long cells, abundant silica bodies arranged in successive rows and prickly hairs throughout the costal zones (figure 7a-c). On the abaxial surface, the midrib is composed predominantly by non-papillate long cells, marginal prickly hairs and microhairs, and less frequently short cells and cross-shaped or Oryzoid silica bodies (figure 7d).

*Isachne polygonoides* is characterized by having both leaf epidermises with papillate intercostal long cells, abundant macrohairs and rarely some microhairs. The adaxial macrohairs are restricted to the costal zones (figure 7e-f), and those of the abaxial surface occur on the costal and intercostal zones (figure 7g-h). Silica bodies are also abundant and regularly distributed throughout the costal zones (figure 7h).

*Isachne pygmaea* presents intercostal non-papillate long cells and a single row of silica bodies along the central portion of the costal zones on the adaxial epidermis (figure 8a-b). On the abaxial surface, there occur intercostal papillate long cells interspersed with microhairs and some scarce hooks. Costal prickle hairs are frequent, but macrohairs are totally absent (figure 8c-e).

*Isachne rigidifolia* is a well-defined species whose most striking features are the pungent leaves with a conspicuous large midrib. Similarly to *I. pygmaea*, the adaxial leaf epidermis of *I. rigidifolia* is characterized by the occurrence of intercostal non-papillate long cells and 1(-2) rows of silica bodies along the central portion of the costal zones (figure 8f). On the abaxial epidermis, the intercostal zones are inserted in grooves caused by the thickened girth of the veins (on the adaxial epidermis only the midrib is conspicuously enlarged) (figure 8g). The combination of a great number of intercostal cells with an elongated papilla inserted in grooves may suggest a potential adaptation to water storage. The long cells along the edges of the costal zones are often coalesced and can act as a 'roof', partially covering the intercostal zones and thus reducing the exposure to air (figure 8g-h). A similar structure was observed in *I. sodestromii* (figure 1g-h).

Finally, *I. salzmannii* is a poorly known Brazilian endemic species easily recognized from all the other American species of the genus by a conspicuous longitudinal groove on the back of the lemma in the lower anthoecium (Rodrigues 2017). This morphological particularity close connects *I. salzmannii* and some forms of *I. globosa*, notably those occurring in India and in Southeast Asia (Shouliang & Phillips 2006).

The adaxial leaf epidermis of *I. salzmannii* is characterized by the occurrence of papillate intercostal long cells, an abundance of costal prickles of different sizes, scarce costal microhairs, and absence of macrohairs (figure 9a-b). The abaxial epidermis is similar to the adaxial one, except by the occurrence of prickle hairs in the intercostal zones and by the scarce microhairs closely associated with the edges of the costal zones (figure 9c-d).

Unfortunately, we could only include one specimen of *I. globosa* from Japan in our micromorphological analysis. In fact, considering the Japanese specimen, tenuous differences are evident in relation to the foliar micromorphology of *I. salzmannii* and *I. globosa* (figure 9e-f). Further studies including specimens from India may reveal new evidence and clarify the relationship between these taxa.

*Micromorphological description of the leaf blade epidermis of the Neotropical species of Isachne:*

1. *Isachne angustifolia* Nash, Bull. Torrey Bot. Club 30(7): 377. 1903.

Figure 1a-b

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, mostly hexagonal to very compressed, sometimes those near the costal zones with variable shapes, shortened, not striate; epicuticular wax absent; papillae absent; stomata not visible; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells present, rectangular, grouped in single rows and alternated with rows of short cells; stomata absent; short cells arranged in horizontal rows and in files with pairs of cork-silica cells, usually restricted to the central portion of the costal zones; silica bodies dumbbell to cross-shaped; prickles present, arranged at the central portion of the costal zones, sometimes irregularly interspersed with rows of cork-silica cells; hooks absent; bicellular microhairs not seen; macrohairs absent. ABAXIAL SURFACE: *Intercostal zone* – long cells cubical to somewhat hexagonal, shortened, not striate; epicuticular wax absent; papillae absent; associated cells present as bicellular microhairs; stomata not visible; prickles absent; hooks absent; bicellular microhairs present, panicoid, occasional, adjoined the costal zones; macrohairs absent. *Costal zone* – long cells absent; stomata absent; short cells and silica cells arranged in 1-3-more rows, usually restricted to the central portion of the costal zones; silica bodies dumbbell to cross-shaped; prickles present, arranged at the margins of the costal zones, interlocking; hooks absent; bicellular microhairs present, panicoid, adjoined the margins of the costal zones, occasional; macrohairs absent.

2. *Isachne arundinacea* Griseb., Fl. Brit. W. I. 553. 1864.

Figure 3a-h

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, mostly polygonal, bowed, inflated, shortened, usually length less than width but those near the costal zones shorter or wider, square to rectangular, conspicuously striated; epicuticular wax absent; papillae absent; stomata not seen; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells present, arranged in 3-4 successive rows and alternating vertically with rows of short and silica cells; stomata absent; short cells arranged in individual horizontal rows, associated with silica cells, vertically alternating with (1-)2-3(-4) rows of long cells with irregular sinuous walls, silica cells closely associated with tall and narrow cork cells (silico-suberose couples); silica bodies mostly rounded; prickles present, regularly interspersed along rows of both short or long cells; hooks absent; bicellular microhairs

not seen; macrohairs absent. **ABAXIAL SURFACE:** *Intercostal zone* – long cells rectangular or quadrangular, shortened; epicuticular wax present as rod-shaped crystals, sometimes forming platelets on the papillae; papillae present, dome-shaped, centric or sub-centric; stomata in 2 rows near the costal zones, separated by ca. 4 rows of long cells, subsidiary cells dome-shaped to rounded in outline, interstomatal cells 1; short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, abundant; macrohairs present, unicellular, soft, frequent, with a cushion base. *Costal zone* – long cells rectangular, mostly with a conspicuous rounded papilla, walls slightly sinuous; stomata absent; short cells and silica cells vertically alternating with (1-)2-3(-4) rows of long cells with slightly sinuous walls; silica bodies mostly rounded; prickles present, mostly arranged at the margins, abundant; hooks absent; bicellular microhairs not seen; macrohairs absent.

3. *Isachne burchellii* **R.S. Rodrigues & Filg.**, Brittonia D.O.I.:10.1007/s12228-019-09576-x.

Figure 6a-d

**ADAXIAL SURFACE:** *Intercostal zone* – long cells variable in shape, mostly hexagonal or bowed, inflated, shortened, not striate; epicuticular wax present as rod-shaped crystals, providing a rugulose texture to the cells; papillae absent; stomata not seen; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells present, arranged in 3-7 successive marginal rows, rectangular, walls  $\Omega$ -shaped; stomata restricted to the margins, subsidiary cells dome-shaped, interstomatal cells 2-more (long cells), adjoined one another; short cells and silica cells restricted to the central portion of the costal zones, regularly arranged in (1-)2 rows; silica bodies mostly rounded; prickles present, associated with rows of both short and silica cells; hooks absent; bicellular microhairs present, regularly arranged and associated with rows of long cells; macrohairs absent. **ABAXIAL SURFACE:** *Intercostal zone* – long cells variable in shape and size, polygonal, pentagonal or sometimes square, shortened, not striate; epicuticular wax present as rod-shaped crystals; papillae present, dome-shaped, centric to sub-centric; stomata in 1-2 rows near the costal zones, subsidiary cells rectangular in outline, interstomatal cells 1-3, adjoined one another; short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, frequent; macrohairs absent. *Costal zone* – long cells absent or sometimes a few long cells interspersed along rows of short cells, rectangular, walls straight; stomata absent; short cells regularly interspersed with silica cells along rows, all rows similar in composition; silica bodies somewhat oblong to dumbbell-shaped, elongated, with wide central portion; prickles present, more or less regularly arranged at the margins; hooks absent; bicellular microhairs present, irregularly arranged at the margins; macrohairs absent.



4. *Isachne disperma* (Lam.) Döll, Fl. Bras. 2(2): 274. 1877.

Figure d-h

ADAXIAL SURFACE: *intercostal zone* – long cells variable in shape and size, hexagonal and/or pentagonal centrally and rectangular laterally, sometimes roundish, inflated, shortened, not striate; epicuticular wax present as conspicuous platelets or rod-shaped crystals; papillae absent; stomata not seen; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells present, arranged in 3-4 successive marginal rows, rectangular, walls straight; stomata not seen; short cells and silica cells restricted to the central portion of the costal zones, regularly arranged in 1-7 rows, covered by a thin cuticle layer and rod-shaped epicuticular wax; silica bodies rounded to square; prickles present, associated with rows of both short and silica cells; hooks absent; bicellular microhairs not seen; macrohairs absent. ABAXIAL SURFACE: *Intercostal zone* – long cells quadrangular, shortened, not striate; epicuticular wax present as rod-shaped crystals; papillae present, oblique, centric to sub-centric, overarching the stomata; stomata arranged in 1(-2) rows near the costal zones, subsidiary cells rectangular in outline, interstomatal cells 1(-2); short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, occasional; macrohairs absent. *Costal zone* – long cells absent; stomata absent; short cells in rows, predominantly interspersed with cork and silica cells, but sometimes different alternating conditions may occur, rows usually similar in composition, covered by a thin cuticle layer and rod-shaped epicuticular wax; silica bodies square or slightly rectangular, regularly arranged throughout the costal zone; prickles present, abundant, regularly arranged along the margins (midrib) or more or less central on the secondary veins; hooks absent; bicellular microhairs present, panicoid, regularly arranged along the margins; macrohairs absent.

5. *Isachne goiasensis* Renvoize, Kew Bull. 42(4): 928. 1987.

Figure 5e-h

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, mostly hexagonal to somewhat quadrangular, shortened, not striate; epicuticular wax present as minutely epicuticular rod-shaped crystals; papillae present, roundish to oblique, centric to sub-centric; stomata present, in 1-2 rows near the costal zones, subsidiary cells not visible, interstomatal cells 1-2(-3); short cells absent; prickles absent; hooks absent; bicellular microhairs present, scarce (occasionally some deciduous near the margins of young leaves); macrohairs absent. *Costal zone* – long cells present, arranged in 3-4 rows at the margins, rectangular, walls slightly sinuous; stomata absent; short cells and silica cells arranged in 1-3

central rows; silica bodies variable from rounded to dumbbell-shaped with a wide central portion; prickles present, arranged along the margins; hooks present, usually arranged at the margins or in both the margins and the central portion; bicellular microhairs present, panicoid, scarce; macrohairs absent. **ABAXIAL SURFACE:** *Intercostal zone* – long cells quadrangular to polygonal, shortened, not striate; epicuticular wax present as dense rod-shaped crystals; papillae present, oblique, centric to sub-centric; stomata arranged throughout the intercostal zone but more frequently in (1-)2 rows near the costal zones and vertically separated by 1(-2) rows of long cells, subsidiary cells variable in shape, mostly triangular or flat-topped in outline, interstomatal cells 1-2; short cells absent; prickles absent; hooks present, occasional; bicellular microhairs present, occasional; macrohairs absent. *Costal zone* – long cells few, irregularly distributed, interspersed with rows of short and silica cells; stomata absent; short cells rectangular, interspersed with silica cells and some long cells; silica bodies variable from rounded to dumbbell-shaped with a wide central portion; prickles present, regularly distributed, arranged mostly at the margins, sometimes interlocking, longer in younger leaves and shorter in mature leaves; hooks present, regularly distributed, mostly at the margins; bicellular microhairs present, panicoid, frequent; macrohairs absent.

6. *Isachne hirtiglumis* Longhi-Wagner & Welker, Syst. Bot. 39(3): 846. 2014.

Figure 6e-h

**ADAXIAL SURFACE:** *Intercostal zone* – long cells variable in shape and size, hexagonal to sometimes cubical centrally and rectangular laterally, shortened, not striate; epicuticular wax present as minute rod-shaped crystals; papillae present, roundish to dome-shaped, centric to sub-centric; stomata present, arranged in 1-2 rows near the costal zones, subsidiary cells dome-shaped, interstomatal cells 2-3; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells present, in 1-2 marginal rows, rectangular, papillate, walls  $\Omega$ -shaped; stomata absent; short cells and silica cells regularly arranged in 2-5 central rows; silica bodies variable from rounded to dumbbell-shaped with a wide central portion; prickles present, regularly distributed; hooks absent; bicellular microhairs present, panicoid, scarcely arranged at the margins; macrohairs present (visible even with the naked eyes), frequent, unicellular, soft, with a cushion base. **ABAXIAL SURFACE:** *Intercostal zone* – long cells variable, quadrangular, rectangular or hexagonal, shortened, not striate; epicuticular wax absent or present as dense rod-shaped crystals; papillae present, rounded to dome-shaped, centric to sub-centric; stomata regularly arranged in single rows or often in 1-2 rows adjoined the costal zones, subsidiary cells rectangular in outline, interstomatal cells 1-2-more; short cells absent; prickles absent; hooks absent;

bicellular microhairs present, panicoid, occasional; macrohairs absent. *Costal zone* – long cells absent; stomata absent; short cells rectangular, papillate, interspersed with silica cells; silica bodies saddle-shaped to dumbbell-shaped, sometimes squarish in outline, concave; prickles present, regularly distributed; hooks absent; bicellular microhairs present, sparsely distributed along the margins, panicoid, occasional; macrohairs absent.

7. *Isachne leersioides* Griseb., Pl. Wright. 2: 533. 1862.

Figure 7a-d

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape across the intercostal zones, mostly hexagonal to slightly bowed in outline, but also rectangular in 1-2 rows adjoined the costal zones, shortened, not striate; epicuticular wax present as conspicuous rod-shaped crystals; papillae absent or present, rounded, centric; stomata not seen; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells present, arranged in 1-2 rows and vertically alternated with 1(-2-3) rows of short and silica cells, rectangular, walls straight; stomata absent; short cells and silica cells in 1(-2-3) rows, sometimes with a long cell interspersed; silica bodies cross-shaped or Oryzoid; prickles present, mostly marginal, less often central; hooks absent; bicellular microhairs present, associated with the margins, occasional; macrohairs absent. ABAXIAL SURFACE: *Intercostal zone* – long cells hexagonal to somewhat quadrangular or bowed, shortened, not striate; epicuticular wax present as rod-shaped crystals or forming granules; papillae present, rounded to somewhat oblique, centric to sub-centric; stomata arranged in 1-2 rows near the costal zones, subsidiary cells rectangular in outline, interstomatal cells 2(-3); short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, scarce; macrohairs absent. *Costal zone* – long cells present, abundant, mostly adjoined one another but sometimes with some silica cells irregularly interspersed, cell walls straight to  $\Omega$ -shaped; stomata absent; short cells and silica cells irregularly arranged (most common), solitary or in rows; silica bodies cross-shaped or Oryzoid, irregularly distributed; prickles present, marginal (midrib) or throughout the costal zones; hooks absent; bicellular microhairs present, panicoid, frequent; macrohairs absent.

8. *Isachne ligulata* Swallen, Caldasia 2(8): 305. 1943.

Figure 5a-d

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape, size and structure across the intercostal zone, laterally rectangular or quadrangular and centrally hexagonal to somewhat rounded or bowed in outline, shortened, not striate; epicuticular wax present as

minute rod-shaped crystals, sometimes forming platelets on the papillae (when papillae are present); papillae absent or present, rounded to sub-oblique, centric; stomata not seen; short cells absent; prickles absent, hooks absent, bicellular microhairs not seen; macrohairs absent or present (in young leaves, then reducing to prickles in maturity), with a cushion base. *Costal zone* – long cells present, arranged in 3-5(-7) rows and separated vertically by 1-2 rows of silica and short cells, rectangular; cell walls U-shaped; short cells quadrangular to somewhat rectangular, regularly arranged in 1-2 central rows and interspersed with some silica cells; silica bodies usually rounded, but some more or less square or Oryzoid may occur; prickles present (commonly abundant in the mature leaves), irregularly arranged along the margins; hooks absent; bicellular microhairs absent or less often scarce, panicoid; macrohairs present (commonly abundant in the young leaves), variable in length, stiff, with a cushion base.

ABAXIAL SURFACE: *Intercostal zone* – long cells mostly quadrangular but some polygonal in outline, shortened, not striate; epicuticular wax present as minute epicuticular rod-shaped crystals; papillae present, dome-shaped, centric to sub-centric; stomata present, in 2-4 rows near the costal zones and vertically separated by 1-2 rows of long cells, subsidiary cells not seen, interstomatal cells not seen; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs present, abundant, stiff, with a cushion base. *Costal zone* – long cells present, arranged in (1-)2-3 rows and vertically separated by 1-2 rows of silica and short cells, rectangular; stomata absent; short cells rectangular, interspersed with silica cells along rows; silica bodies rounded, but some more or less cubical or Oryzoid; prickles present, variable in size, those of the mibrid regularly arranged at the margins; hooks absent; bicellular microhairs not seen; macrohairs present, abundant, stiff, with a cushion base.

9. *Isachne polygonoides* (Lam.) Döll, Fl. Bras. 2(2): 273. 1877.

Figure 7e-h

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, centrally hexagonal, quadrangular or bowed but tending to become rectangular near the margins and veins, shortened, not striate; epicuticular wax present as minute rod-shaped crystals; papillae present, dome-shaped, centric to sub-centric; stomata present, in 1-2 rows near the costal zones, subsidiary cells rectangular in outline, interstomatal cells 1-2; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells absent; stomata absent; short cells rectangular to quadrangular, regularly interspersed with silica cells along single rows; silica bodies variable from dumbbell to irregular dumbbell-shaped, sometimes rounded, slightly concave; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs present, stiff, base swollen, with a cushion

base. ABAXIAL SURFACE: *Intercostal zone* – long cells variable, centrally quadrangular, hexagonal or bowed, and rectangular near the margins, shortened, not striate; epicuticular wax present as minute rod-shaped crystals; papillae present, dome-shaped, centric to sub-centric; stomata in 4-6 rows vertically separated by 1-more rows of long cells, subsidiary cells flat-topped; interstomatal cells 1-2; short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, scarce; macrohairs present, stiff, base swollen, with a cushion base, usually with different lengths across the leaf epidermis. *Costal zone* – long cells absent; stomata absent; short cells and silica cells regularly interspersed in single rows; silica bodies variable from dumbbell to irregular dumbbell-shaped, sometimes rounded, slightly concave; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs present, stiff, base swollen, with a cushion base, usually with different lengths across the leaf epidermis.

10. *Isachne pubescens* Swallen, Contr. U.S. Natl. Herb. 29(9): 426. 1950.

Figure 4a-e

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, centrally quadrangular and/or pentagonal, and laterally rectangular, sometimes roundish or inflated, shortened, not striate; epicuticular wax present as conspicuous platelets or rod-shaped crystals; papillae absent; stomata in 1-2 rows near the costal zones, subsidiary cells rectangular in outline, interstomatal cells 1-3; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells present, arranged in 3-4 marginal rows, rectangular, walls straight; stomata absent; short cells and silica cells regularly arranged in 1-7 central rows; silica bodies rounded to cuboid; prickles absent; hooks absent; bicellular microhairs present, panicoid, scarce; macrohairs present, abundant, stiff, superficial or with a cushion base. ABAXIAL SURFACE: *Intercostal zone* – long cells quadrangular or inflated, shortened, not striate; epicuticular wax present as rod-shaped crystals; papillae present, roundish, centric to sub-centric, restricted to a single row of cells adjoined the costal zones; stomata in 1(-2) rows near the costal zones, subsidiary cells rectangular in outline, interstomatal cells 1(-2); short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, occasional; macrohairs absent. *Costal zone* – long cells absent; stomata absent; short cells predominantly interspersed with cork and silica cells, but sometimes an intermediate alternating condition may occur, rows usually similar in composition; silica bodies square, round or slightly rectangular, regularly distributed; prickles present, abundant, marginal (midrib) or more or less central on the lateral veins; hooks absent; bicellular microhairs present, panicoid, marginal; macrohairs present, abundant, stiff, with a cushion base.

11. *Isachne pygmaea* Griseb., Fl. Brit. W. I. 553. 1864.

Figure 8a-e

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, mostly rectangular or quadrangular, sometimes roundish or polygonal centrally, shortened, not striate; epicuticular wax absent; papillae absent; stomata not visible; short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, scarce; macrohairs absent. *Costal zone* – long cells present, arranged in single central rows and vertically alternate with a single rows of cork-silica cells, rectangular, walls slightly sinuous; stomata absent; short cells in single central rows and interspersed with cork-silica cells; silica bodies cross-shaped to dumbbell-shaped; prickles present, irregularly distributed, occasional; hooks present, irregularly distributed, scarce; bicellular microhairs present, panicoid, irregularly distributed, scarce; macrohairs absent. ABAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, mostly pentagonal to polygonal, inflated, shortened, not striate; epicuticular wax present as minute rod-shaped crystals; papillae present, rounded, dome-shaped, usually deflated, centric; stomata in 1-2 rows near the costal zones, subsidiary cells dome-shaped to low dome-shaped in outline, interstomatal cells 1-2; short cells absent; prickles absent; hooks present, scarce; bicellular microhairs present, panicoid, irregularly distributed, occasional; macrohairs absent. *Costal zone* – long cells present, rectangular in outline, arranged in single central rows and vertically alternate with rows of short and silica cells; stomata absent; short cells quadrangular in outline, in 2-3 rows and regularly alternating with silica cells; silica bodies mostly cross-shaped, acute-angled or dumbbell-shaped; prickles present, irregularly distributed, mostly marginal; hooks absent; bicellular microhairs present, panicoid, frequent at the margins; macrohairs absent.

12. *Isachne rigens* Trin., Gram. Panic. 252. 1826.

Figure 2a-c

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, mostly rectangular, hexagonal or sometimes somewhat rounded, inflated, shortened, not striate; epicuticular wax absent; papillae absent; stomata not seen; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells absent; stomata absent; short cells quadrangular to rectangular, regularly arranged in rows and interspersed with silica cells; silica bodies mostly rounded to saddle-shaped; prickles present, mostly marginal; hooks absent; bicellular microhairs present, panicoid, scarce; macrohairs absent. ABAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, mostly quadrangular, shortened, not striate; epicuticular wax present as dense rod-shaped crystals;

papillae present, dome-shaped, centric; stomata in 4-6 rows, subsidiary cells dome-shaped or rectangular in outline, interstomatal cells 1-2; short cells absent; prickles absent; hooks present or absent; bicellular microhairs present, panicoid, frequent; macrohairs present or absent, stiff, with a cushion base. *Costal zone* – long cells absent; stomata absent; short cells quadrangular to rectangular, regularly arranged in rows and interspersed with silica cells; silica bodies rounded to saddle-shaped; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs present, abundant, stiff, with a cushion base.

13. *Isachne rigidifolia* (Poir.) Urb., Symb. Antill. 4: 85. 1903.

Figure 8f-h

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, rectangular to hexagonal and sometimes quadrangular, shortened, not striate; epicuticular wax absent; papillae absent; stomata absent; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells present, rectangular, regularly distributed, cell walls straight; stomata absent; short cells and silica cells interspersing, restricted to 1-2 central rows; silica bodies variable from Oryzoid to cross-shaped; prickles present, irregularly interspersed with short and silica cells; hooks absent; bicellular microhairs not seen; macrohairs absent. ABAXIAL SURFACE: *Intercostal zone* – long cells pentagonal to polygonal, inflated, shortened, not striate, those near the margins coalescent; epicuticular wax present as rod-shaped crystals; papillae present, rounded, dome-shaped, sometimes deflated, centric; stomata not visible; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells occasional, rectangular, irregularly interspersed along rows of short and silica cells; stomata absent; short cells rectangular to quadrangular, interspersed with silica cells and less often with long cells; silica bodies variable from Oryzoid to cross-shaped; prickles absent; hooks absent; bicellular microhairs present, panicoid, marginal, occasional; macrohairs absent.

14. *Isachne salzmannii* (Trin. ex Steud.) Renvoize, Kew Bull. 39(1): 184. 1984.

Figure 9a-d

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape and size, hexagonal to somewhat quadrangular, pentagonal or bowed, shortened, not striate; epicuticular wax present as minute rod-shaped crystals; papillae present, rounded to sub-oblique, centric; stomata in 1-2 rows adjoined the costal zone, subsidiary cells rectangular in outline, interstomatal cells 1(-2-3); short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells absent; stomata absent; short

cells rectangular, papillate, regularly arranged in rows across and interspersed with silica cells; silica bodies variable from rounded to dumbbell or cross-shaped with a relatively wide central portion; prickles present, variable in size and length, abundant; hooks absent; bicellular microhairs present, panicoid, scarce; macrohairs absent. ABAXIAL SURFACE: *Intercostal zone* – long cells quadrangular to somewhat hexagonal, shortened, not striate; epicuticular wax present as minute rod-shaped crystals; papillae present, dome-shaped, centric to sub-centric; stomata in 2-4 rows, subsidiary cells flat-topped to low dome-shaped in outline, interstomatal cells 1(-2); short cells absent; prickles absent or present, abundant, central; hooks absent; bicellular microhairs present, panicoid, scarce, closely associated with the margins of the costal zones; macrohairs absent. *Costal zone* – long cells absent; stomata absent; short cells rectangular, papillate, regularly arranged in rows and interspersed with silica cells; silica bodies variable from rounded to dumbbell or cross-shaped with a relatively wide central portion; prickles present, mostly marginal, abundant; hooks absent; bicellular microhairs not seen; macrohairs absent.

15. *Isachne soderstromii* R.S. Rodrigues & Filg., Nordic J. Bot. 36(1-2): e01847. 2018.

Figure 1c-h

ADAXIAL SURFACE: *Intercostal zone* – long cells variable, the central mostly hexagonal and those near the costal zones rectangular, shortened, not striate; epicuticular wax absent; papillae absent; stomata not visible; short cells absent; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. *Costal zone* – long cells present, arranged in 3-4 marginal rows, rectangular, cell walls slightly sinuous; stomata absent; short cells quadrangular to slightly rectangular, mostly regularly arranged and interspersed with silica cells along successive and/or in individual rows of long cells; silica bodies cross-shaped to dumbbell-shaped with roundish ends; prickles absent; hooks absent; bicellular microhairs not seen; macrohairs absent. ABAXIAL SURFACE: *Intercostal zone* – long cells, quadrangular, shortened, not striate, sometimes the cells near the costal zones with papillae overarching the neighboring intercostal cells; epicuticular wax absent; papillae present, oblique, centric; stomata in 2-4 rows near the costal zones; subsidiary cells dome-shaped to low dome-shaped in outline; interstomatal cells 1-2(-3); short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, irregularly present near the costal zones, occasional; macrohairs absent. *Costal zone* – long cells absent; stomata absent; short cells rectangular, regularly arranged in rows and interspersed with some silica cells; silica bodies cross-shaped to dumbbell-shaped with roundish ends; prickles present, marginal; hooks absent; bicellular microhairs present, panicoid, occasional at the margins; macrohairs absent.



## 16. *Isachne* sp. 1.

Figure 4f-h

ADAXIAL SURFACE: *Intercostal zone* – long cells variable in shape, size and structure across the intercostal zone, hexagonal to somewhat quadrangular or bowed centrally and rectangular laterally (1 row near the costal zones), shortened, not striate; epicuticular wax absent; papillae present, rounded to sub-oblique, centric, occurring only in the 3(-4) innermost rows of long cells; stomata not seen; short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, scarce; macrohairs absent. *Costal zone* – long cells present, arranged in 3-4 successive rows and separated by rows of silica and short cells, rectangular, cell walls straight; short cells and silica cells regularly arranged in single rows; silica bodies rounded to oblong; prickles absent; hooks present, associated with the margins of the costal zones; bicellular microhairs present, panicoid, scarce, associated with the margins; macrohairs present, unicellular, stiff, abundant, with a cushion base. ABAXIAL SURFACE: *Intercostal zone* – long cells somewhat quadrangular to hexagonal, tall and narrow, shortened, not striate; epicuticular wax absent; papillae present, rounded, dome-shaped; stomata arranged in 1-2 rows near the costal zones, subsidiary cells rectangular in outline, interstomatal cells 1(-2); short cells absent; prickles absent; hooks absent; bicellular microhairs present, panicoid, abundant; macrohairs present, unicellular, stiff, abundant, with a cushion base. *Costal zone* – long cells present, arranged in 2-3 rows, vertically separated by rows of silica and short cells, rectangular, walls straight; stomata absent; short cells and silica cells in single rows, regularly arranged and vertically alternated with 2-3 rows of long cells; silica bodies oblong to rounded; prickles present, abundant, regularly distributed along the margins; hooks present, abundant; bicellular microhairs present, panicoid, associated with the margins; macrohairs absent.

### Acknowledgments

We are grateful to Dr. Eduardo P.C. Gomes and Dr. Sonia Aragaki for their contribution and critic discussion on the phenetic analysis; Dr. Luciana Benatti and Mr. André Aguilera, respectively, for the SEM analyses in the Laboratory of Electron Microscopy of the Institute of Botany and CEME-UNIFESP. We also thank the curators and staff of the Missouri Botanical Garden (MO), the New York Botanical Garden (NY) and the United States National Herbarium (US) for the loans and facilities to study their incredible collections of Neotropical *Isachne*; the curators of the Brazilian herbaria for the donation of samples, loans and/or permission to accessing the national collections. Finally, RSR thanks CAPES for a Doctoral fellowship and the Post-graduation Program of the Institute of Botany for the continuous support of our research.

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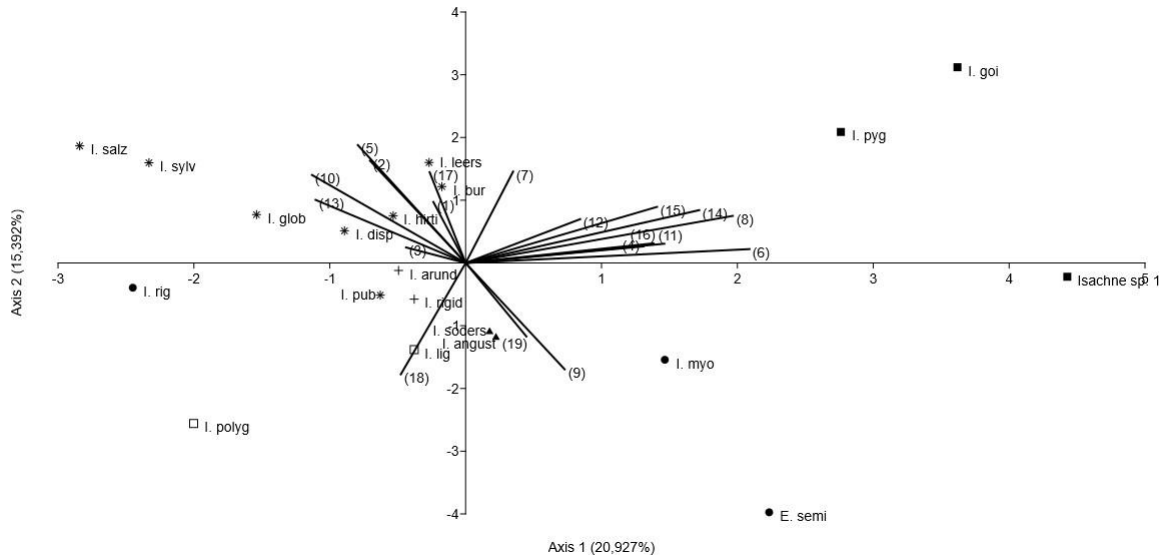
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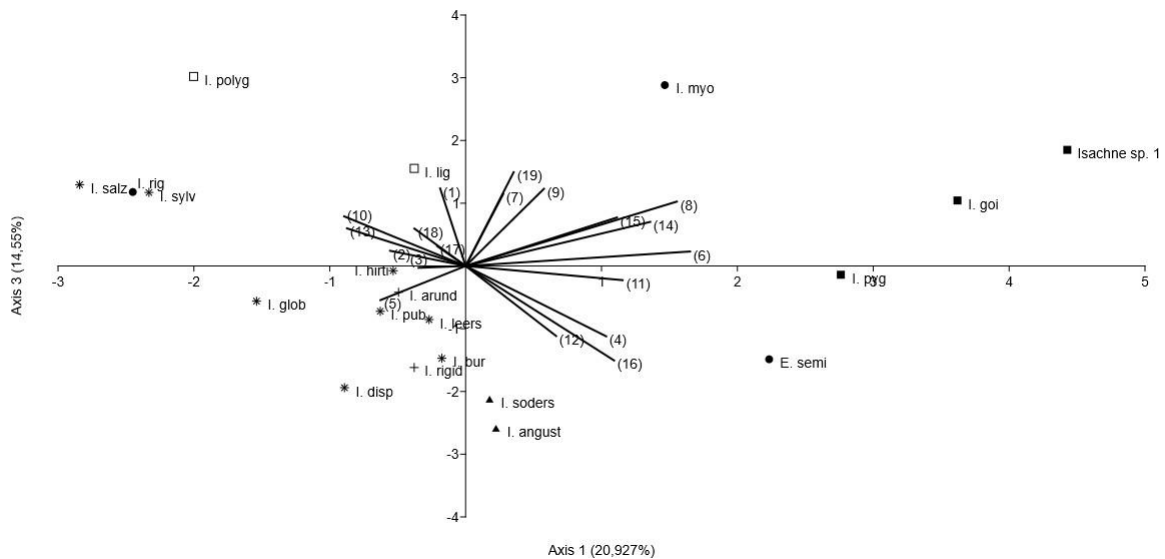
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Appendix

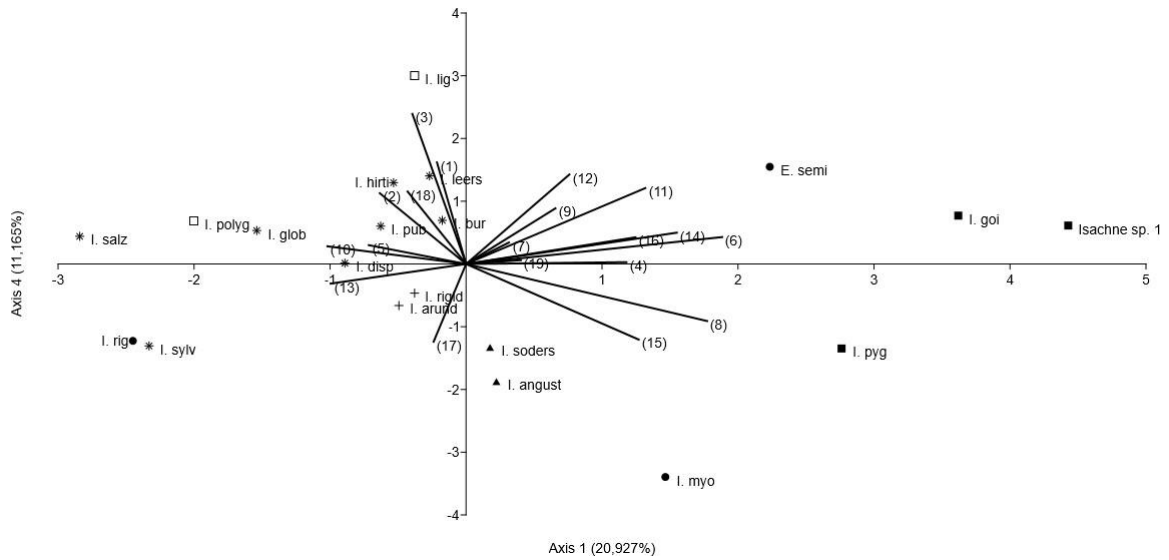
Graphic representation of the relationship among all the Components of the PCA for the leaf blade epidermis of *Isachne* and *E. semiciliata*.



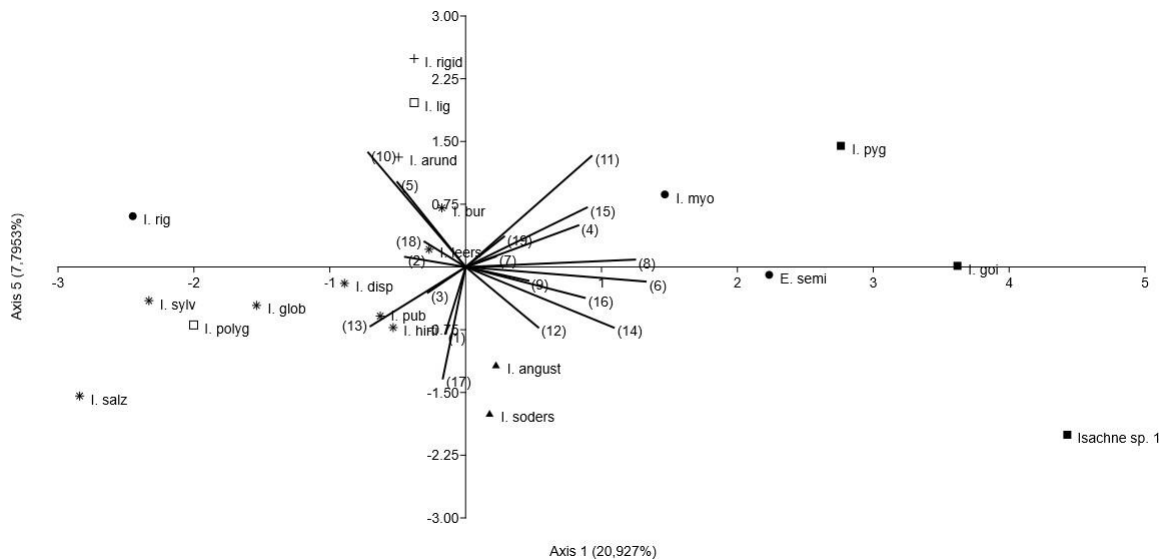
Appendix 1. Graphic representation of the relationship between the Principal Components 1 and 2 (explaining ca. 36% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.



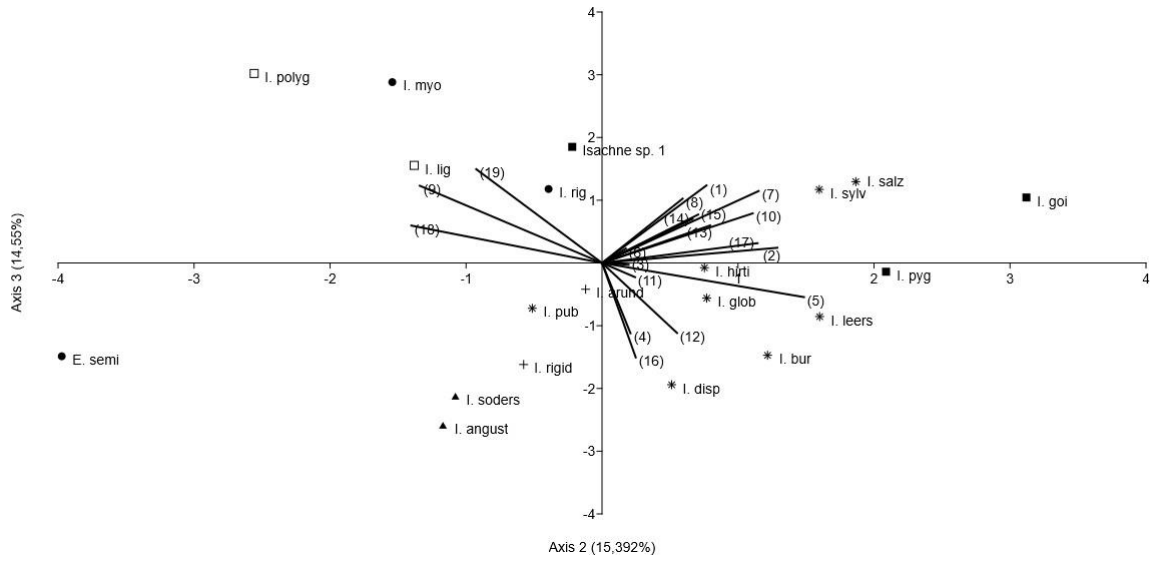
Appendix 2. Graphic representation of the relationship between the Principal Components 1 and 3 (explaining ca. 35.5% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.



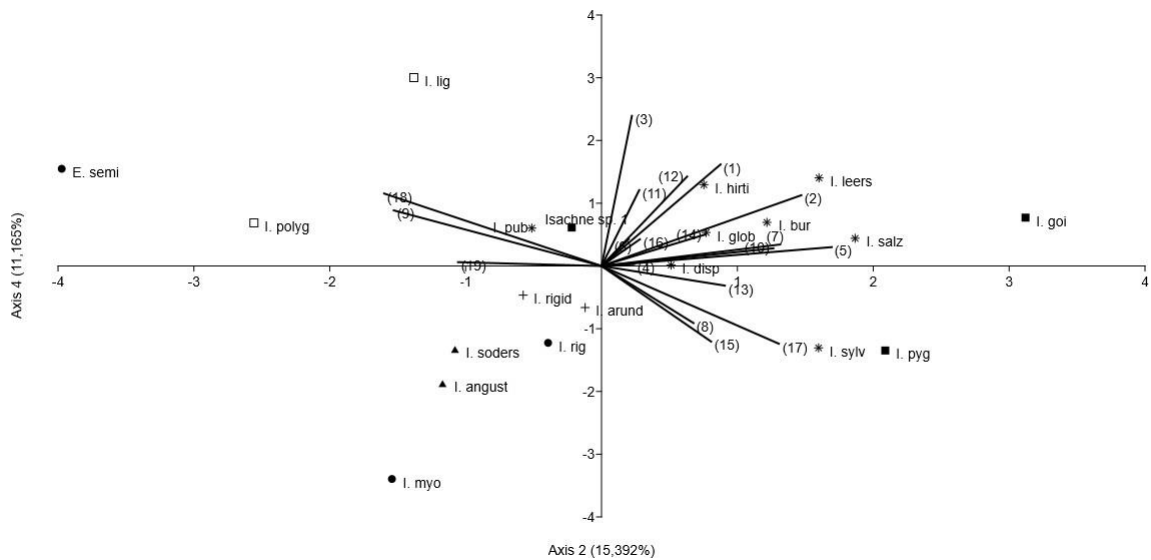
Appendix 3. Graphic representation of the relationship between the Principal Components 1 and 4 (explaining ca. 32% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.



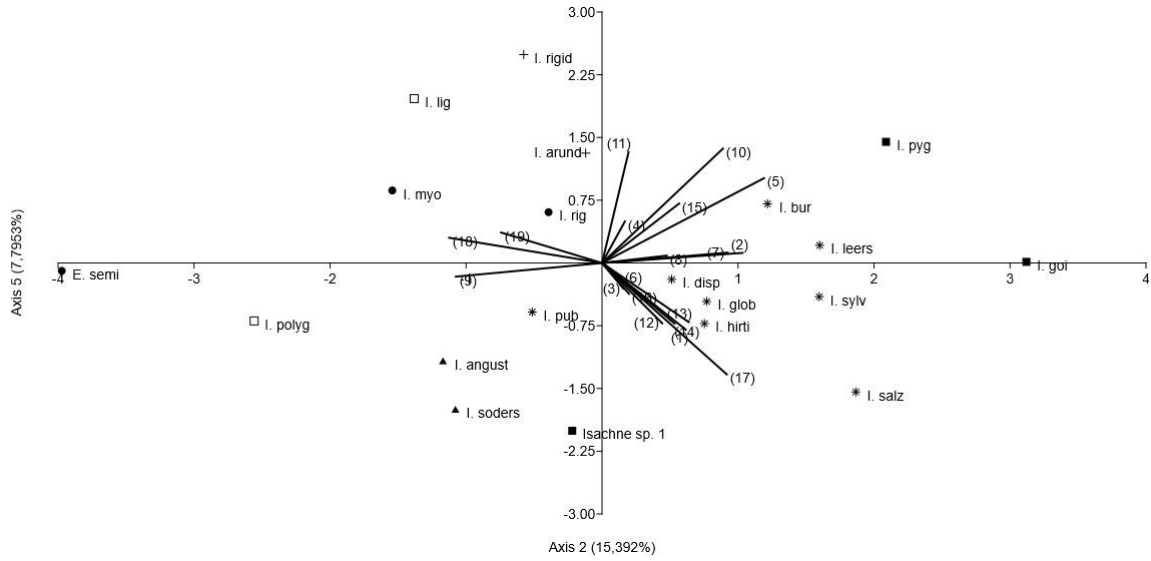
Appendix 4. Graphic representation of the relationship between the Principal Components 1 and 5 (explaining ca. 29% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.



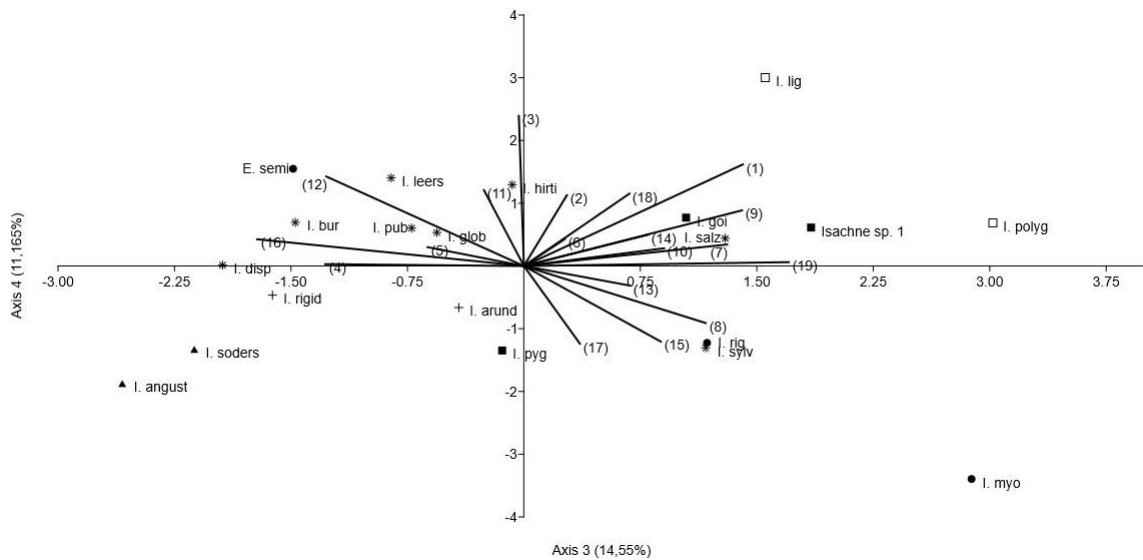
Appendix 5. Graphic representation of the relationship between the Principal Components 2 and 3 (explaining ca. 30% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.



Appendix 6. Graphic representation of the relationship between the Principal Components 2 and 4 (explaining ca. 26.5% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.

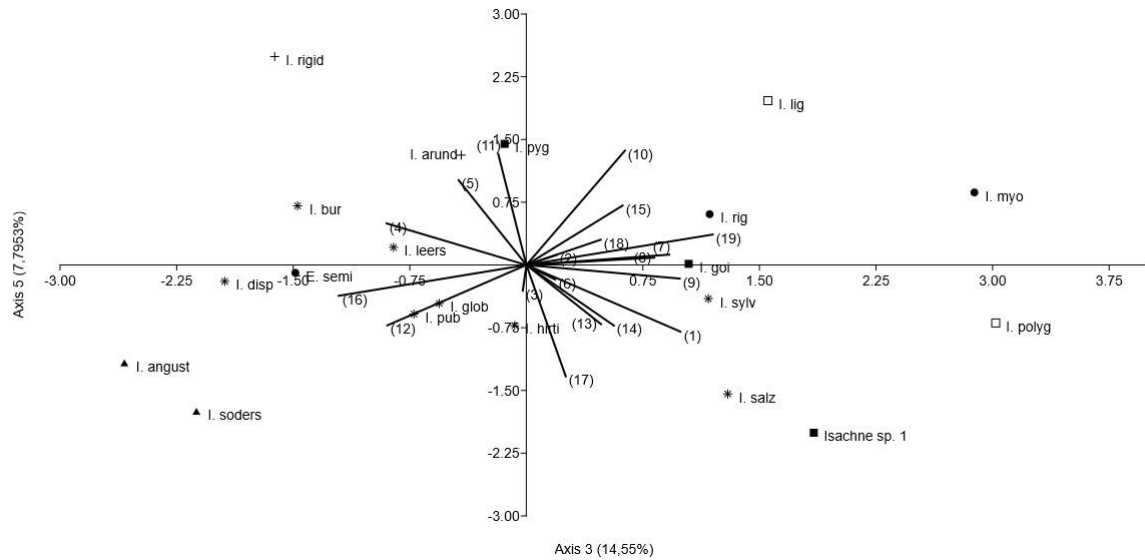


Appendix 7. Graphic representation of the relationship between the Principal Components 2 and 5 (explaining ca. 23% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.

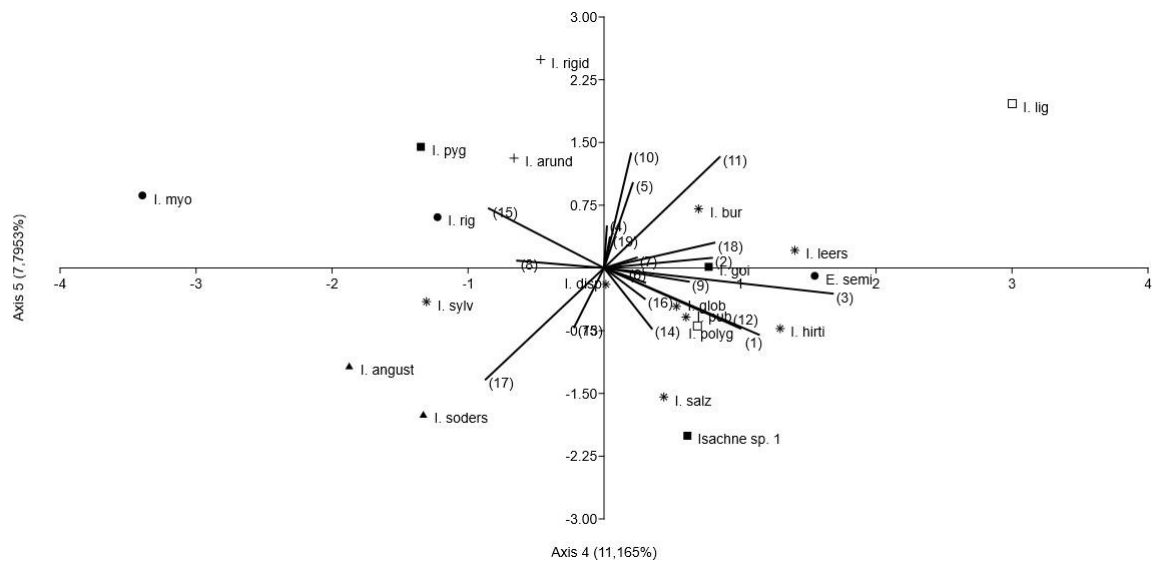


Appendix 8. Graphic representation of the relationship between the Principal Components 3 and 4 (explaining ca. 25.5% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.





Appendix 9. Graphic representation of the relationship between the Principal Components 3 and 5 (explaining ca. 22.5% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.



Appendix 10. Graphic representation of the relationship between the Principal Components 4 and 5 (explaining ca. 19% of the variation). Groups found (according to the cluster analysis): group 1 = □; group 2 = +; group 3 = ■; group 4 = \*; group 5 = ▲; ungrouped taxa = ●. Vectors according to table 2.

# Chapter 6

## *Abstract*

The first micromorphological study including the anthoecia and rachilla in the genus *Isachne* is presented. Fifteen Neotropical species and one morphospecies were studied in relation to both the lower and the upper anthoecia. A phenetic analysis was conducted to assess the taxonomic value of the micromorphological characters of the anthoecia and rachilla in the genus and the correlation among these characters and the species. As a result, the vestiture in *Isachne* is characterized by the abundant presence of several types of silica bodies, panicoid bicellular microhairs, and twisted sharp-pointed or narrow-tipped macrohairs. The studied species were classified into five distinct ornament patterns, evidencing a great variability in the genus. Our results also indicate that the lower and the upper anthoecia are taxonomically informative and variable, as so is the rachilla in relation to its length, presence and absence of micro and macrohairs, and distribution of hairs. The phenetic analysis resulted in clusters weakly congruent to the current infrageneric classification of *Isachne*, although it is clearly evident the micromorphological uniformity between most of the species with similar and coriaceous lower and upper anthoecia.

## *Resumo*

É apresentado o primeiro estudo micromorfológico incluindo antécios e ráquila para o gênero *Isachne*. Quinze espécies e uma morfoespécie foram estudadas em relação aos seus antécios inferiores e superiores. Uma análise fenética foi conduzida para se avaliar o valor taxonômico dos caracteres micromorfológicos dos antécios e da ráquila no gênero, bem como a correlação entre esses caracteres e as espécies. Como resultado, a ornamentação em *Isachne* se caracteriza pela presença abundante de vários tipos de corpos silicosos, microtricomas bicelulares e macrotricomas retorcidos pontiagudos ou de ponta estreitada do ápice. As espécies estudadas foram classificadas em de acordo com cinco padrões de ornamentação, evidenciando a grande variabilidade dentro de gênero. Os resultados indicam ainda que tanto o antécio inferior quanto o superior são taxonomicamente informativos e variáveis, bem como a ráquila em relação ao seu comprimento, presença ou ausência e distribuição de micro e macrotricomas. A análise fenética resultou em grupamentos fracamente congruentes com a classificação infragenérica atual de *Isachne*, embora seja claramente evidente a uniformidade existente entre a maioria das espécies com antécios coriáceos e similares em relação aos seus caracteres micromorfológicos.

Keywords: Grasses, Isachneae, Anthoecium morphology, Neotropical grasses, SEM.

The following chapter was prepared according to the standards of Hoehnea.

# **Anthoecia and rachilla micromorphology in the Neotropical species of *Isachne* (Poaceae, Micrairoideae): a contribution to the taxonomy and species delimitation**

Rodrigo S. Rodrigues<sup>1,2</sup> & Tarciso S. Filgueiras<sup>1</sup>

## **Introduction**

*Isachne* R.Br. is a pantropical genus of ca. 103 species worldwide (Kellogg 2015) with the center of diversity in tropical and temperate Asia (Judziewicz 1990). It includes annual or perennial species with spikelets articulated above the developed subequal glumes, and two anthoecia, being the lower bisexual, staminate or pistillate, and the upper bisexual or pistillate (Hitchcock 1920, Clayton & Renvoize 1986).

The genus was established by Brown (1810) but its acceptance was historically controversial and subject of discussion for centuries. Trinius (1834) reduced *Isachne* to a section of *Panicum* L. on the basis of the unusual bisexuality of the lower anthoecium and development of both the glumes. He also accepted three informal subgroups within *Panicum* sect. *Isachne* Trin. according to the pilosity of the anthoecia. Honda (1930) proposed an invalid infrageneric classification for *Isachne* and established two sections (sects. “*Euisachne*” and “*Paraisachne*”) based on the consistency and pilosity of the anthoecia. Later, Jansen (1953) used the same criteria to propose also two invalid sections for the genus (sects. “*Eu-Isachne*” and “*Paraisachne*”). Prakash & Jain (1984) validly established *Isachne* sect. *Isachne* to include species with heteromorphic (dissimilar) anthoecia, and *Isachne* sect. *Albentes* to include species with homomorphic (similar) anthoecia. The classification of *Isachne* into sections was adopted in subsequent treatments (e.g., Stapf & Hubbard 1934, Keng 1965, Clayton & Renvoize 1986, and Iskandar & Veldkamp 2004). However, such classification still requires further investigations using molecular data.

There are 15 species of *Isachne* in the Neotropical region (Rodrigues & Filgueiras, unpubl. res., Chapter 7), most of them endemic or geographically restricted. Hitchcock (1920) provided the largest taxonomic revision for the genus in the Americas, with the exception of the South American taxa which were not included in his work. The absence of a

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<sup>1</sup> Programa de Pós-graduação em Biodiversidade Vegetal e Meio Ambiente, Núcleo de Pesquisa Curadoria do Herbário SP, Instituto de Botânica, Avenida Miguel Stefano, 3687, CEP: 04301-902, Água Funda, São Paulo, SP, Brazil.

<sup>2</sup> Corresponding author: rosaro\_3588@yahoo.com.br

comprehensive taxonomic treatment for the Neotropical species of the genus has been a barrier to assess the morphological boundaries of several species.

Micromorphology and ornamentation of the anthoecia have been fairly applied in grass systematics (e.g., Clark & Gould 1975, Rost & Simper 1975, Thompson & Estes 1986, Peterson 1989, Giraldo-Cañas 2002, 2004, Salariato *et al.* 2008), and proved to be useful in circumscribing closely related species of *Isachne* (cf., Rodrigues & Filgueiras, 2019).

Considering that the texture, consistency, and ornamentation of the anthoecia have been used as the main characters for the specific and infrageneric delimitation of *Isachne*, and that the genus has never been adequately surveyed in relation to its floral micromorphological structures, the purpose of this study was to provide the first data on the micromorphology of the anthoecia and rachilla in *Isachne* and identify specific characters to aid in the circumscription of the Neotropical species.

### Material and methods

This study is based on micromorphological features of the flowering elements of the 15 Neotropical species of *Isachne* (Rodrigues & Filgueiras, unpubl. res., Chapter 7) and one South American morphospecies (*Isachne* sp. 1) related to *I. arundinacea* Griseb. [as currently circumscribed] (Table 1).

Lemmas, paleas, and rachillas of 31 specimens were examined under a stereomicroscope (OM) and scanning electron microscope (SEM). The samples were obtained from herbarium specimens and mounted onto aluminum stubs using double-sided sticky tape without previous treatments. After prepared, the samples were carried to a sputtering at the Centro de Microscopia Eletrônica, in the Universidade Federal de São Paulo (CEME-UNIFESP) to be coated with gold. The SEM images were obtained using a Philips® XL 20 and a FEI Quanta FEG® 250 microscopes, operating at 10 kV at the Laboratory of Electronic Microscopy of the Instituto de Botânica, and at 30 kV at CEME-UNIFESP, respectively.

Terminology for micromorphological epidermal features follows Metcalfe (1960) and Ellis (1979).

A phenetic analysis was carried using Past® 3.15 (Hammer 2001). The cluster analysis was performed based on micromorphological data of the anthoecia and rachilla compiled into a matrix of 13 binary characters (Tables 2, 3). The similarity matrix was constructed based on Jaccard's coefficient and the unweighted pair group method using arithmetic averages (UPGMA) was applied to the dendrogram. A PCA analysis was made based on the correlation matrix.

Table 1. List of species and specimens included in the SEM analysis.

Species	Section ( <i>sensu</i> Prakash & Jain 1984)	Origin (collection site)	Voucher	Herbarium acronym
<i>Isachne angustifolia</i> Nash	<i>Albentes</i>	Porto Rico	<i>F.W. Gould et al.</i> 15855	SP
<i>Isachne arundinacea</i> Griseb.	<i>Albentes</i>	Panama	<i>A.S. Hitchcock</i> 8277	IAC
<i>Isachne burchellii</i> R.S. Rodrigues & Filg.	<i>Albentes</i>	Brazil	<i>A.F.M. Glaziou</i> 17400	NY
<i>Isachne disperma</i> Lam.	<i>Albentes</i>	Guadeloupe	<i>G.R. Proctor</i> 20351	US
		Dominica	<i>R.L. Wilbur et al.</i> 8245	US, NY
<i>Isachne goiasensis</i> Renvoize	<i>Isachne</i>	Brazil	<i>E.P. Heringer et al.</i> 4435	RB, SP, CEN
		Brazil	<i>E.P. Heringer et al.</i> 6654	SP, UEC
		Brazil	<i>F. Chagas-Silva</i> 387	UEC
		Brazil	<i>R.S. Rodrigues et al.</i> 479	SP, HUEFS
<i>Isachne hirtiglumis</i> Longhi-Wagner & Welker	<i>Isachne</i>	Brazil	<i>L. Damazio s.n.</i>	SP
		Brazil	<i>R.S. Rodrigues et al.</i> 465	SP
<i>Isachne leersioides</i> Griseb.	<i>Albentes</i>	Cuba	<i>N.L. Britton &amp; J.F. Cowell</i> 12786	NY
		Cuba	<i>A.S. Hitchcock</i> 23413	US
<i>Isachne ligulata</i> Swallen	<i>Albentes</i>	Venezuela	<i>J.J. Wurdack</i> 34183	RB
		Brazil	<i>R.C. Forzza et al.</i> 7275	SP
<i>Isachne polygonoides</i> (Lam.) Döll	<i>Isachne</i>	Brazil	<i>Moraes &amp; Souza</i> 1039	UEC
		Brazil	<i>D. Sucre</i> 10326	RB, SP
		Brazil	<i>A. Chase</i> 8124	RB
		Brazil	<i>L. Rossi</i> 2539	SP
<i>Isachne pubescens</i> Swallen	<i>Albentes</i>	Mexico	<i>D.E. Breedlove &amp; G. Davidse</i> 55225	MO
		Guatemala	<i>W.D. Stevens &amp; E.S. Martinez</i> 25256	MO
<i>Isachne pygmaea</i> Griseb.	<i>Albentes</i>	Jamaica	<i>W. Herris</i> 12490	US
		Jamaica	<i>N.L. Britton</i> 220	NY
<i>Isachne rigens</i> (Sw.) Trin.	<i>Albentes</i>	Jamaica	<i>A.S. Hitchcock</i> 9362	RB
		Colombia	<i>R.W. Pohl &amp; J.C. Betancur</i> 15465	RB
<i>Isachne rigidifolia</i> (Poir.) Urb.	<i>Albentes</i>	Dominican Republic	<i>G.J. Gastony et al.</i> 487	NY
		Dominican Republic	<i>P. Acevedo-Rodriguez et al.</i> 12671	NY
<i>Isachne salzmännii</i> (Trin. ex Steud.) Renvoize	<i>Isachne</i>	Brazil	<i>A. Chase</i> 7894	RB
		Brazil	<i>M. Elisabeth</i> 40896	HRB
<i>Isachne soderstromii</i> R.S. Rodrigues & Filg.	<i>Albentes</i>	Dominica	<i>W.R. Ernst</i> 1227	US
<i>Isachne</i> sp. 1 (South America)	<i>Albentes</i>	Ecuador	<i>V. Zak &amp; J. Jaramillo</i> 3204	MO

Table 2. Micromorphological characters and character states for the lower and the upper anthoecia, and the rachilla of *Isachne* used in UPGMA and PCA analyses. L.A. = Lower anthoecium; U.A. = Upper anthoecium.

Character	State
1. L.A. consistency	coriaceous (0); cartilaginous (1)
2. L.A. lemma silica bodies	absent (0); present(1)
3. L.A. lemma bicellular microhairs	absent (0); present (1)
4. L.A. lemma macrohairs (in the middle portion, excluding margins and base)	absent (0); present (1)
5. L.A. lemma papillae	absent (0); present (1)
6. L.A. lemma prickles/hooks	absent (0); present (1)
7. L.A. palea silica bodies	absent (0); present (1)
8. L.A. palea bicellular microhairs	absent (0); present (1)
9. L.A. palea papillae	absent (0); present (1)
10. U.A. lemma macrohairs (in the middle portion, excluding margins and base)	absent (0); present (1)
11. U.A. palea macrohairs (in the middle portion, excluding margins and base)	absent (0); present (1)
12. Rachilla dilation	not dilated (0); dilated (1)
13. Rachilla pilosity	macrohairs absent (0); macrohairs present (1)

Table 3. Matrix of binary descriptors used in the cluster analysis of the Neotropical *Isachne*. Character states according to Table 2.

Species	Character states												
	1	2	3	4	5	6	7	8	9	10	10	12	13
<i>I. angustifolia</i>	0	1	1	0	0	0	1	1	0	0	0	1	0
<i>I. arundinacea</i>	0	1	1	0	0	0	1	1	0	0	1	0	0
<i>I. burchellii</i>	0	1	1	0	0	0	1	1	0	0	0	0	0
<i>I. disperma</i>	0	1	1	0	0	0	1	1	0	0	0	0	0
<i>I. goiasensis</i>	1	1	1	0	0	0	1	1	0	1	1	0	0
<i>I. hirtiglumis</i>	1	1	1	0	0	0	1	1	0	1	1	0	0
<i>I. leersioides</i>	0	1	1	1	0	0	1	1	0	1	1	0	0
<i>I. ligulata</i>	0	1	1	0	0	0	1	1	0	0	0	0	1
<i>I. polygonoides</i>	1	0	0	0	0	0	0	0	0	1	1	0	0
<i>I. pubescens</i>	0	1	1	0	0	0	1	1	0	0	0	0	0
<i>I. pygmaea</i>	0	1	1	0	0	0	1	1	0	0	0	0	0
<i>I. rigens</i>	0	1	1	1	0	0	1	1	0	0	0	0	1
<i>I. rigidifolia</i>	0	1	1	0	0	0	1	1	0	0	0	1	1
<i>I. salzmännii</i>	1	1	1	1	1	1	0	0	1	1	1	0	0
<i>I. soderstromii</i>	0	1	1	0	0	0	1	1	0	0	0	1	0
<i>Isachne</i> sp. 1 (South America)	0	1	1	0	0	0	1	1	0	0	0	0	0

## Results and discussion

### *General features of the anthoecia micromorphology:*

The two anthoecia in *Isachne* are taxonomically informative. Differently from the Paniceae, in which usually only the upper anthoecium is surveyed, *Isachne* cumulates also a series of characters on the lower anthoecium epidermis that can be used in the taxonomy at different levels. Consequently, the efforts to prepare and analyze each specimen are substantially increased.

In general, the anthoecia in *Isachne* can be micromorphologically characterized by the abundant occurrence of silica bodies of several types and panicoid bicellular microhairs; twisted flexile macrohairs are frequent in the upper anthoecium and at the base (callus) of the lower and the upper anthoecia. The micromorphological elements of the anthoecia in *Isachne* can be summarized and described as follows:

**Silica bodies** - Abundant and variable, mostly cross-shaped, dumb-bell-shaped, saddle-shaped or roundish, and less frequently squarish. Not infrequently, more than one type of silica-body is present in the same specimen. Coalescence of adjacent silica bodies is also common, mainly towards the apex, at the base and/or margins of lemmas and paleas. The coalescence of cross-shaped silica bodies observed in *I. burchellii* resulted in a multangular, often irregular compound pattern termed here as “*compound cross-shaped*” (Figure 1a).

Although the occurrence of silica bodies is frequent in *Isachne*, it is remarkable the lower density and more sparse distribution of these elements in the species with cartilaginous lower anthoecium, rather than in the species with coriaceous lower anthoecium. On the other hand, the occurrence of silica bodies appears to be mandatory on the lemmas and paleas of the upper anthoecium within the genus.

**Bicellular microhairs** - Panicoid, uniform in shape, abundant and regularly distributed on both the lower and upper anthoecia. The ratio of the length of the proximal and the distal cell varies from approximately equal (1:1) to the basal cell slightly shorter than the distal cell (Figure 1b). Although the occurrence of microhairs is constant in the genus, considering reproductive traits, the taxonomic significance of these elements at lower levels is null.

**Macrohairs** - Unicellular, characterized in being flexible, twisted, sharp-pointed or narrow-tipped. A longitudinal groove can be also present along its extension (Figure 1c-d). They are frequent on the lemmas of the upper anthoecium, either on the back, at margins or at the base, at the callus of the lower and/or upper anthoecia, and ornamenting the rachilla. It should be also highlighted that the microhairs observed on the vegetative structures and in the glumes are distinct from those found in the anthoecia; they differ in being straight, brittle and acute, often with cushion cells at the base (Rodrigues & Filgueiras, unpubl. res., Chapter 5).

Prickle hairs and hooks - Uncommon epidermal elements of the anthoecia in *Isachne*, but they appear to be common in the vestiture of glumes, with relative taxonomic value. They vary in size, length, and quantity on a single specimen. If present, tend to occur more frequently in the upper third of glumes; rarely towards the apex of the lower lemma (Figure 1e).

Papillae - One type of papillus was observed. If present, it is small (less than half of the width of the epidermal cell), single and simple (Figure 1f). It is considered here an uncommon epidermal element in the vestiture of the anthoecia in *Isachne*. Future studies can reveal the occurrence of papillae in other species of the genus, besides a greater variability of this character. The occurrence of papillae is a common feature in the foliar micromorphology of the genus (Potzta 1952, Metcalfe 1960, Palmer & Gerbeth-Jones 1986, Sánchez-Ken *et al.* 2007, Rodrigues & Filgueiras, unpubl. res., Chapter 5).

*Lower and upper anthoecia vestiture in the Neotropical species:*

Tables 4 and 5 summarize the main micromorphological characters found in the Neotropical species in relation to the lower and the upper anthoecia, respectively.

Four types of vestiture were found in the lower anthoecium: bicellular microhairs, macrohairs, prickle hairs, and papillae. Bicellular microhairs occurred in all taxa investigated, except in *I. polygonoides*; they are frequent and generally regularly distributed all over the lemma and palea epidermises. Macrohairs are uncommon but, when present, tend to be restricted to the margins and base of lemmas and bases of paleas; they were found on the lemmas of *I. leersioides*, which has similar appressed-pilose anthoecia, and occasionally on the lemmas of *I. rigens* and *I. salzmannii*. Prickle hairs and simple papillae were exclusively observed in *I. salzmannii*, in which the lower lemma is longitudinally grooved. Prickle hairs are occasional on the upper third of the lemma.

The consistency of the lower anthoecium in the examined taxa was cartilaginous in *I. goiasensis*, *I. hirtiglumis*, *I. polygonoides*, and *I. salzmannii* (Figure 2 a-d); and coriaceous in *I. angustifolia*, *I. arundinacea*, *I. burchellii*, *I. disperma*, *I. leersioides*, *I. ligulata*, *I. pubescens*, *I. pygmaea*, *I. rigens*, *I. rigidifolia*, *I. soderstromii*, and *Isachne sp. 1* (Figure 2e-I, 3a-g).

Two types of vestiture were found in the upper anthoecium: bicellular microhairs and macrohairs. Both bicellular microhairs and macrohairs are similar to those found in the lower anthoecium. Microhairs were observed abundantly in all species examined, whereas macrohairs were found only to occur in *I. goiasensis*, *I. hirtiglumis*, *I. leersioides*, *I. polygonoides*, *I. salzmannii*, and occasionally on the paleas of *I. arundinacea* (Figure 4a-f).

All the examined taxa presented a coriaceous consistency of the upper anthoecium.



Table 4. Micromorphological characters of the lower anthoecium in the Neotropical species of *Isachne*. (+) = present; (-) = absent.

Species	Lower anthoecium consistency	Lower lemma					Lower palea			
		Silica body	Bicellular microhairs	Macrohairs*	Papillae	Prickles/Hooks	Silica body	Bicellular microhairs	Macrohairs*	Papillae
<i>I. angustifolia</i>	Coriaceous	Cross-shaped	+	-	-	-	Cross-shaped (restricted to the apex)	+	-	-
<i>I. arundinacea</i>	Coriaceous	Dumb-bell shaped	+	-	-	-	Dumb-bell shaped	+	-	-
<i>I. burchellii</i>	Coriaceous	Compound cross-shaped	+	-	-	-	Cross-shaped (often coalescent, compound cross-shaped or irregular shaped)	+	-	-
<i>I. disperma</i>	Coriaceous	Saddle-shaped or squarish	+	-	-	-	Squarish	+	-	-
<i>I. goiasensis</i>	Cartilaginous	Cross-shaped or compound cross-shaped	+	-	-	-	Cross-shaped	+	-	-
<i>I. hirtiglumis</i>	Cartilaginous	Cross-shaped (saddle-shaped towards the apex)	+	-	-	-	Saddle-shaped (less often cross-shaped)	+	-	-
<i>I. leersioides</i>	Coriaceous	Dumb-bell shaped elongated	+	+	-	-	Saddle-shaped elongated or squarish	+	-	-
<i>I. ligulata</i>	Coriaceous	Cross-shaped to saddle-shaped	+	-	-	-	Cross-shaped to dumb-bell shaped	+	-	-
<i>I. polygonoides</i>	Cartilaginous	Absent*	-	-	-	-	Absent*	-	-	-
<i>I. pubescens</i>	Coriaceous	Dumb-bell shaped to saddle-shaped	+	-	-	-	Dumb-bell shaped	+	-	-
<i>I. pygmaea</i>	Coriaceous	Cross-shaped	+	-	-	-	Cross-shaped	+	-	-
<i>I. rigens</i>	Coriaceous	Dumb-bell shaped to cross-shaped	+	+	-	-	Saddle-shaped to cross-shaped	+	-	-
<i>I. rigidifolia</i>	Coriaceous	Cross-shaped	+	-	-	-	Cross-shaped	+	-	-
<i>I. salzmännii</i>	Cartilaginous	Cross-shaped to roundish	+	+	+	+	-	-	-	+
<i>I. soderstromii</i>	Coriaceous	Cross-shaped	+	-	-	-	Cross-shaped	+	-	-
<i>Isachne sp. 1</i>	Coriaceous	Dumb-bell shaped, less often roundish to squarish	+	-	-	-	Dumb-bell shaped	+	-	-

\* Considering the occurrence only on the back of lemmas and paleas (excluding margins and base).

Table 5. Micromorphological characters of the upper anthoecium, rachilla, and callus in the Neotropical species of *Isachne*. (+) = present; (-) = absent.

Species	Upper anthoecium consistency	Upper lemma				Upper palea				Rachilla		
		Silica body	Bicellular microhairs	Macrohairs*	Papillae	Silica body	Bicellular microhairs	Macrohairs*	Papillae	Dilation	Pilosity	Callus
<i>I. angustifolia</i>	Coriaceous	Cross-shaped	+	-	-	Cross-shaped to dumb-bell shaped	+	-	-	Dilated at the apex	Glabrous	Occasional, twisted narrow- tipped macrohairs
<i>I. arundinacea</i>	Coriaceous	Dumb-bell shaped	+	-	-	Dumb-bell shaped (often coalescent)	+	+	-	Not dilated	Microhairs	Frequent, twisted narrow- tipped macrohairs
<i>I. burchellii</i>	Coriaceous	Cross-shaped (compound cross- shaped)	+	-	-	Cross-shaped to eventually saddle- shaped	+	-	-	Not dilated	Glabrous	Occasional, twisted narrow- tipped macrohairs
<i>I. disperma</i>	Coriaceous	Squarish	+	-	-	Squarish or saddle- shaped	+	-	-	Not dilated	Microhairs	Occasional, twisted macrohairs
<i>I. goiasensis</i>	Coriaceous	Roundish	+	+	-	Roundish	+	+	-	Not dilated	Glabrous	Occasional, twisted narrow- tipped macrohairs
<i>I. hirtiglumis</i>	Coriaceous	Roundish	+	+	-	Roundish	+	+	-	Not dilated	Glabrous	Occasional, twisted narrow- tipped macrohairs
<i>I. leersioides</i>	Coriaceous	Saddle- shaped to saddle- shaped elongated	+	+	-	Dumb-bell shaped	+	+	-	Not dilated	Glabrous	Glabrous
<i>I. ligulata</i>	Coriaceous	Cross-shaped to dumb-bell shaped	+	-	-	Squarish to dumb-bell shaped	+	-	-	Not dilated	Macrohairs at the apex	Frequent, twisted narrow- tipped macrohairs

<i>I. polygonoides</i>	Coriaceous	Roundish	+	+	-	Roundish	+	+	-	Not dilated	Glabrous	Occasional, twisted narrow-tipped macrohairs
<i>I. pubescens</i>	Coriaceous	Dumb-bell shaped	+	-	-	Dumb-bell shaped	+	-	-	Not dilated	Microhairs	Glabrous or occasionally twisted macrohairs
<i>I. pygmaea</i>	Coriaceous	Cross-shaped	+	-	-	Cross-shaped	+	-	-	Not dilated	Microhairs	Occasional, twisted narrow-tipped macrohairs
<i>I. rigens</i>	Coriaceous	Saddle-shaped	+	-	-	Roundish	+	-	-	Not dilated	Macrohairs all over	Frequent, twisted narrow-tipped macrohairs
<i>I. rigidifolia</i>	Coriaceous	Cross-shaped	+	-	-	Cross-shaped	+	-	-	Dilated at the apex	Microhairs and macrohairs	Occasional, twisted macrohairs
<i>I. salzmannii</i>	Coriaceous	Roundish	+	+	-	Roundish to cross-shaped	+	+	-	Not dilated	Glabrous	Glabrous
<i>I. soderstromii</i>	Coriaceous	Cross-shaped	+	-	-	Cross-shaped	+	-	-	Dilated at the apex	Glabrous	Occasional, twisted macrohairs
<i>Isachne sp. 1</i>	Coriaceous	Roundish to dumb-bell shaped	+	-	-	Dumb-bell shaped	+	-	-	Not dilated	Microhairs	Occasional, twisted narrow-tipped macrohairs

\* Considering the occurrence only on the back of lemmas and paleas (excluding margins and base).

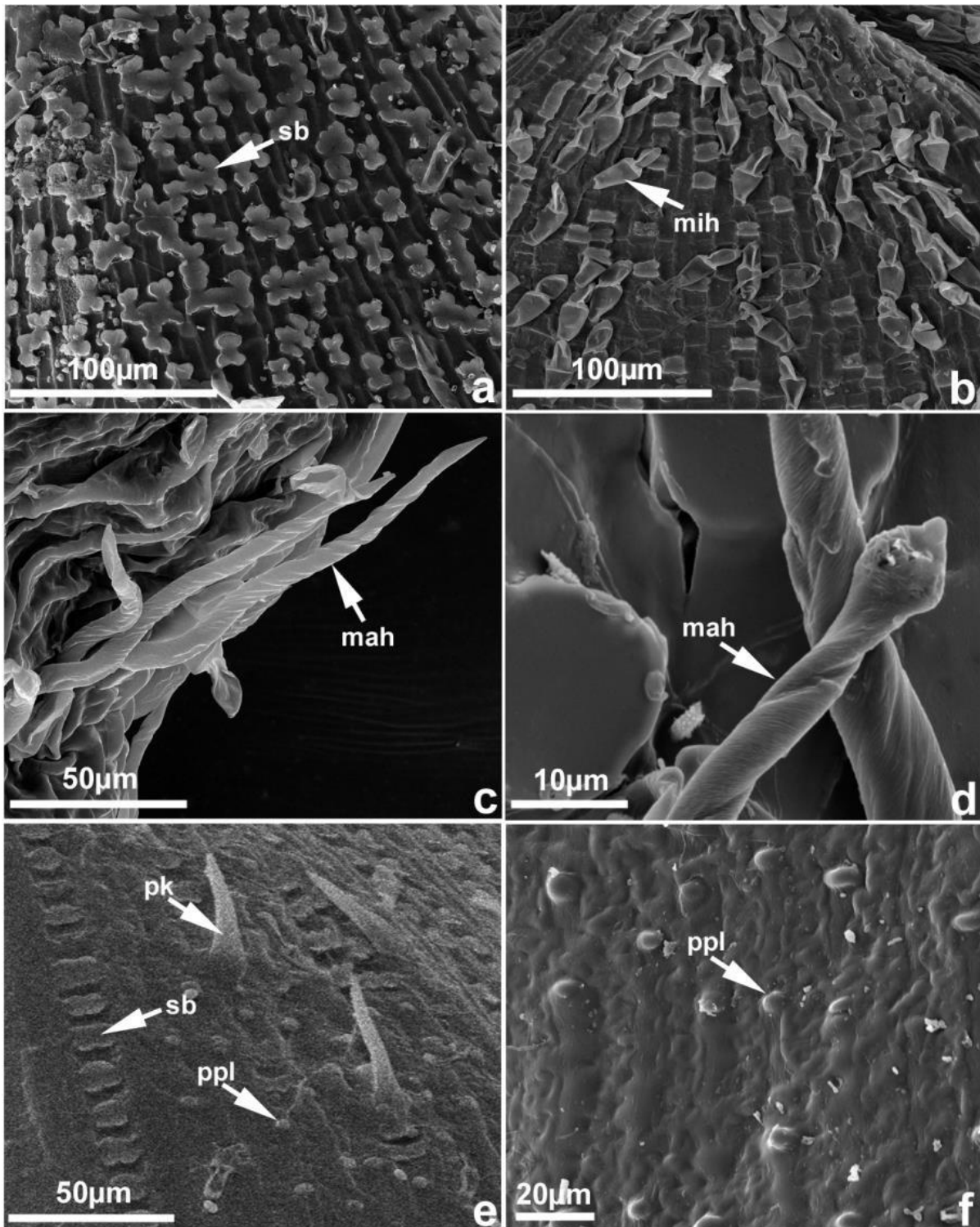


Figure 1. General characters of the anthoecia in *Isachne*. a. Detail of the lower lemma surface of *I. burchellii* showing the coalescent cross-shaped silica bodies (compound cross-shaped). b. Apex of the lower palea surface in *I. disperma* showing several panicoid bicellular microhairs. c. Callus of the upper anthoecium of *I. rigidifolia* showing a twisted sharp-pointed macrohair. d. detail of the apical portion of a twisted narrow-tipped macrohair in *I. hirtiglumis*. e. Detail of prickles on the lower lemma in *I. salzmannii*. f. Detail of the papillae on the lower palea of *I. salzmannii*. mah: macrohair; mih: microhair; pk: prickle hair; ppl: papillae; sb: silica-body. Based on: a. A.F.M. Glaziou 17400 (NY); b. G.R. Proctor 20351 (US); c. G.J. Gastony et al. 487 (NY); d. L. Damazio s.n. (SP); e. M. Elisabeth 40896 (HRB); f. A. Chase 7894 (RB).

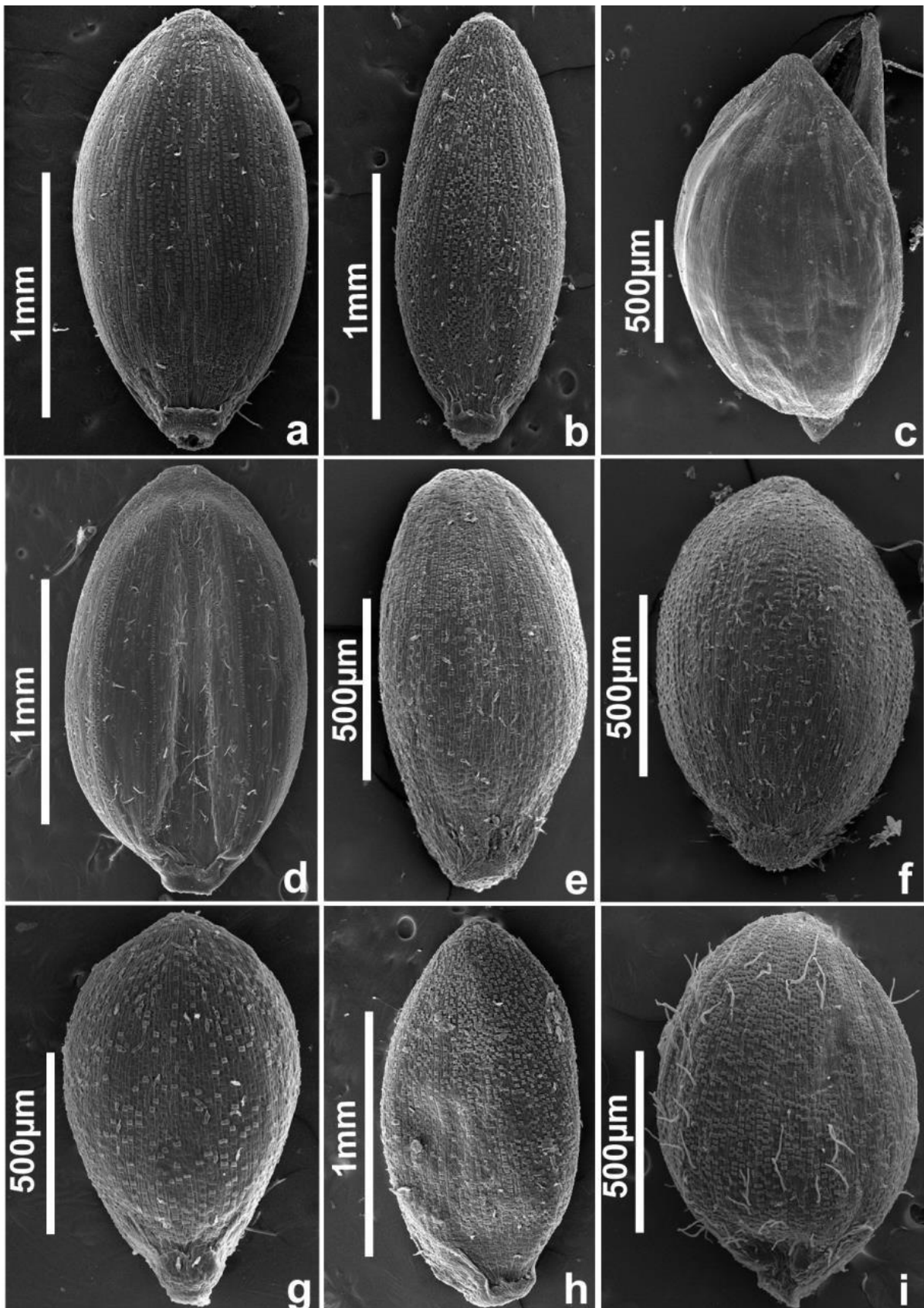


Figure 2. Vestiture of the lower anthoecium of the Neotropical species of *Isachne*. a-d. Species with cartilaginous lower anthoecia (lemma view): a. *I. goiasensis*. b. *I. hirtiglumis*. c. *I. polygonoides*. d. *I. salzmännii* (note lemma longitudinally groove). e-i. Species with coriaceous lower anthoecia (lemma view): e. *I. angustifolia*. f. *I. arundinacea*. g. *I. disperma*. h. *I. burchellii*. i. *I. leersioides*. Based on: a. R.S. Rodrigues et al. 479 (SP); b. R.S. Rodrigues et al. 465 (SP); c. A. Chase 8124 (RB); d. M. Elisabeth 40896 (HRB); e. F.W. Gould et al. 15855 (SP); f. A.S. Hitchcock 8277 (IAC); g. R.L. Wilbur et al. 8245 (US); h. A.F.M. Glaziou 17400 (NY); i. A.S. Hitchcock 23413 (US).

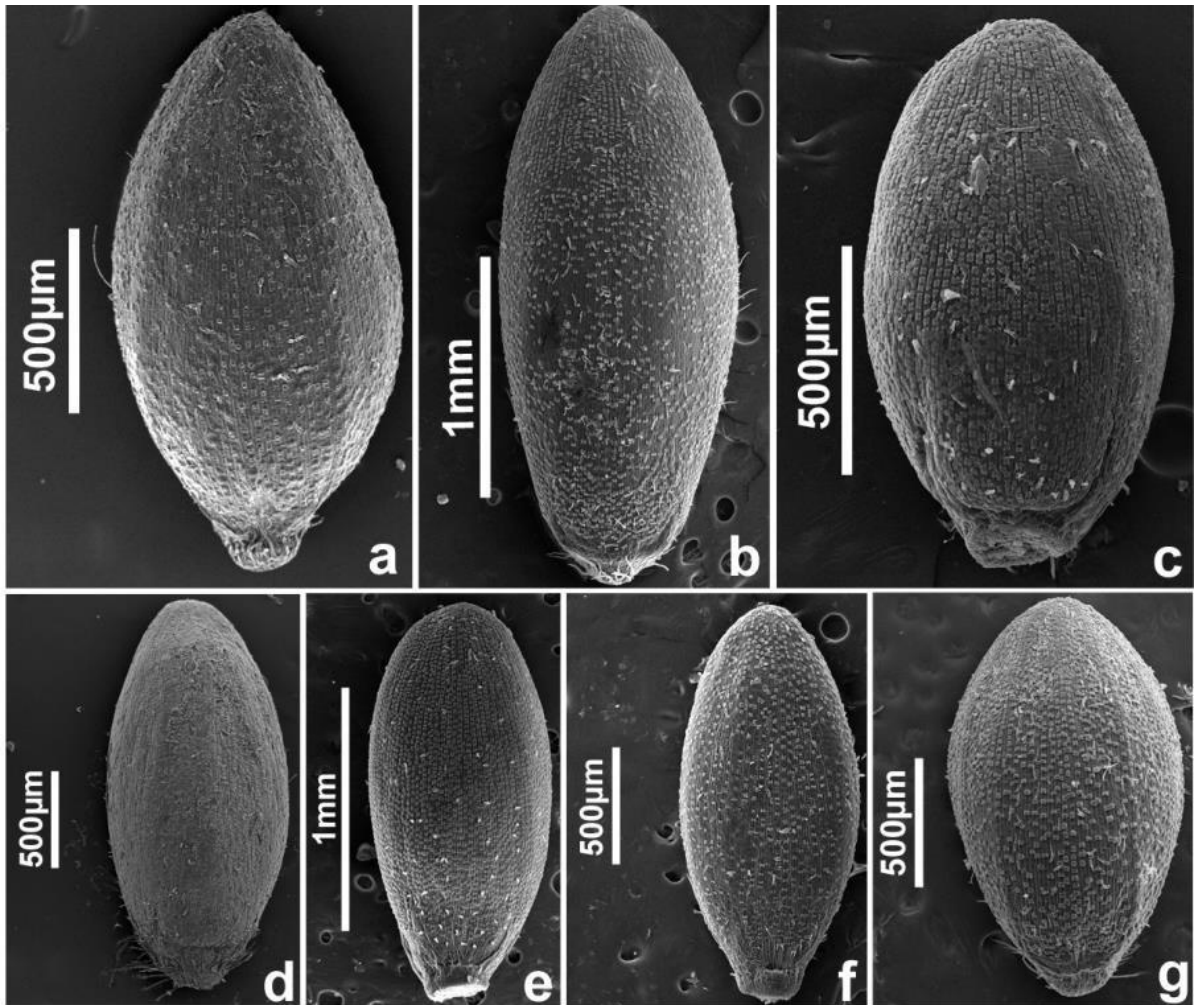


Figure 3. Lemma view of the lower anthoecium of the Neotropical species of *Isachne*. a-g. Coriaceous lower anthoecia: a. *I. ligulata*. b. *I. pubescens*. c. *I. pygmaea*. d. *I. rigens*. e. *I. rigidifolia*. f. *I. soderstromii*. g. *Isachne* sp. 1. Based on: a. J.J. Wurdack 34183 (RB); b. D.E. Breedlove & G. Davidse 55225 (MO); c. W. Herris 12490 (US); d. R.W. Pohl & J.C. Betancur 15465 (RB); e. P. Acevedo-Rodriguez et al. 12671 (NY); f. W.R. Ernst 1227 (US); g. V. Zak & J. Jaramillo 3204 (MO).

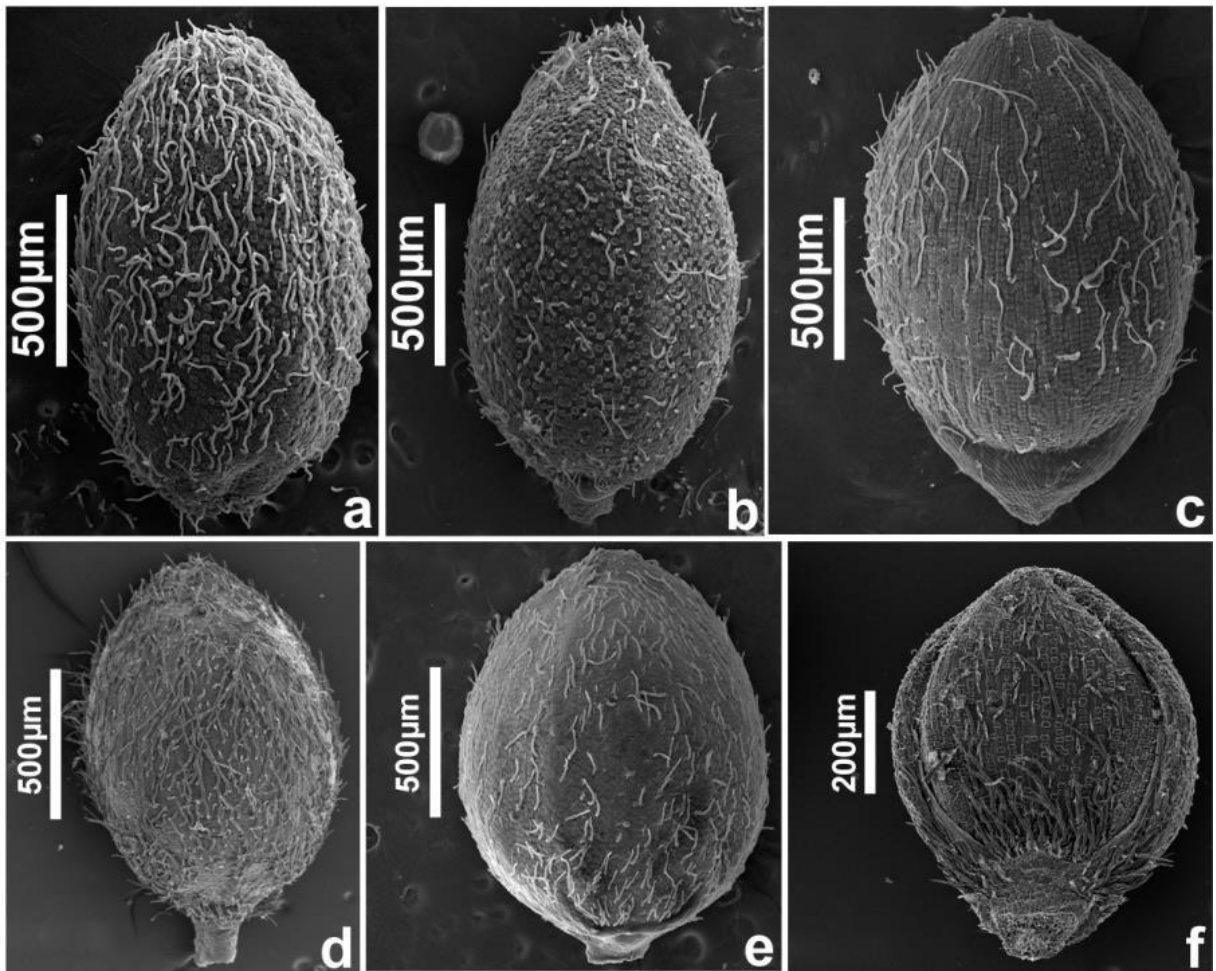


Figure 4. Vestiture of the upper anthoecium of the Neotropical species of *Isachne*. a-e. Species with macrohairs on the upper lemma: a. *I. goiasensis*. b. *I. hirtiglumis*. c. *I. leersioides*. d. *I. polygonoides*. e. *I. salzmannii*. f. Species with macrohairs on the upper palea (*I. arundinacea*). Based on: a. R.S. Rodrigues *et al.* 479 (SP); b. R.S. Rodrigues *et al.* 465 (SP); c. A.S. Hitchcock 23413 (US); d. Moraes & Souza 1039 (UEC); e. M. Elisabeth 40896 (HRB); f. A.S. Hitchcock 8277 (IAC).

#### *Ornament patterns in the Neotropical species:*

Five distinct ornament patterns were observed in the Neotropical species of *Isachne*. One or two different patterns can be found between the anthoecia. A single or more than one pattern can be found in a species. Therefore, the lower and the upper anthoecia can be both classified into one or two of the following patterns:

Hirsute silicose type (Leersioid-type) (Figure 5a-b) - This pattern includes anthoecia in which the epidermal long cells have indistinctive (or nearly so) anticlinal walls (often long cells also indistinctive); therefore, the surface is densely covered by roundish or roundish/cross-shaped (less often saddle-shaped or dumb-bell shaped) silica bodies, abundant bicellular microhairs and twisted narrow-tipped macrohairs. Papillae and other elements are absent. It gives the anthoecium a coriaceous texture and an appressed-pubescent to appressed-pilose indumentum when examined under optical microscopy. In this pattern are included the upper and lower anthoecium of *I.*

*leersioides*, and the upper anthoecium of *I. goiasensis*, *I. hirtiglumis*, *I. polygonoides*, and *I. salzmannii* (Figure 4a-e).

Bicellular silicose type (Arundinacea-type) (Figure 5c) - This pattern includes lemmas and paleas in which epidermal long cells have distinct irregular anticlinal cell walls; therefore, the surface is abundantly covered by variable types of silica bodies and bicellular microhairs. Papillae and macrohairs (except eventually at margins and/or at the base) are absent. It gives the anthoecium a coriaceous or less often a cartilaginous texture, and a glabrous indumentum under optical microscopy. In this pattern is included the lower and the upper anthoecia of *I. arundinacea*, *I. burchellii*, *I. disperma*, *I. ligulata*, *I. pubescens*, *I. pygmaea*, *I. rigens*, and *Isachne* sp. 1 (Figures 2f-h; 3a-d, g); the lower anthoecium of *I. hirtiglumis* (Figure 2b); and the upper anthoecium of *I. rigidifolia*.

Silicose type (Angustifolia-type) (Figure 5d) - This pattern is similar to the “Bicellular silicose type” differing by the protrusion of the periclinal and anticlinal omega-shaped long cell walls. It gives the anthoecium a coriaceous or cartilaginous texture and a glabrous indumentum under optical microscopy. In this pattern are included the lower and the upper anthoecia of *I. angustifolia* and *I. soderstromii*; and the lower anthoecium of *I. goiasensis* and *I. rigidifolia* (Figures 2a; 3e).

Papillose type (Salzmannii-type) (Figures 1e-f; 5e) - This pattern includes anthoecia with epidermal periclinal and anticlinal omega-shaped long cell walls; the surface is irregularly covered by silica bodies which are more abundantly concentrated along the nerves and towards the apex of the lemmas. Bicellular microhairs and macrohairs present. Papillae are irregularly present, single, simple, distally situated on the cells. This pattern gives the anthoecium a cartilaginous texture and a glabrous indumentum under optical microscopy. In this pattern is included only the lower anthoecium of *I. salzmannii* (Figure 2d).

Naked type (Polygonoid-type) (Figure 5f) - This pattern is similar to the “Papillose type” differing by the absence of bicellular microhairs and papillae. Silica bodies are present, but never entirely along the nerves. It gives the anthoecium a cartilaginous texture and a glabrous indumentum under optical microscopy. In this pattern is included only the lower anthoecium of *I. polygonoides* (Figure 2c).



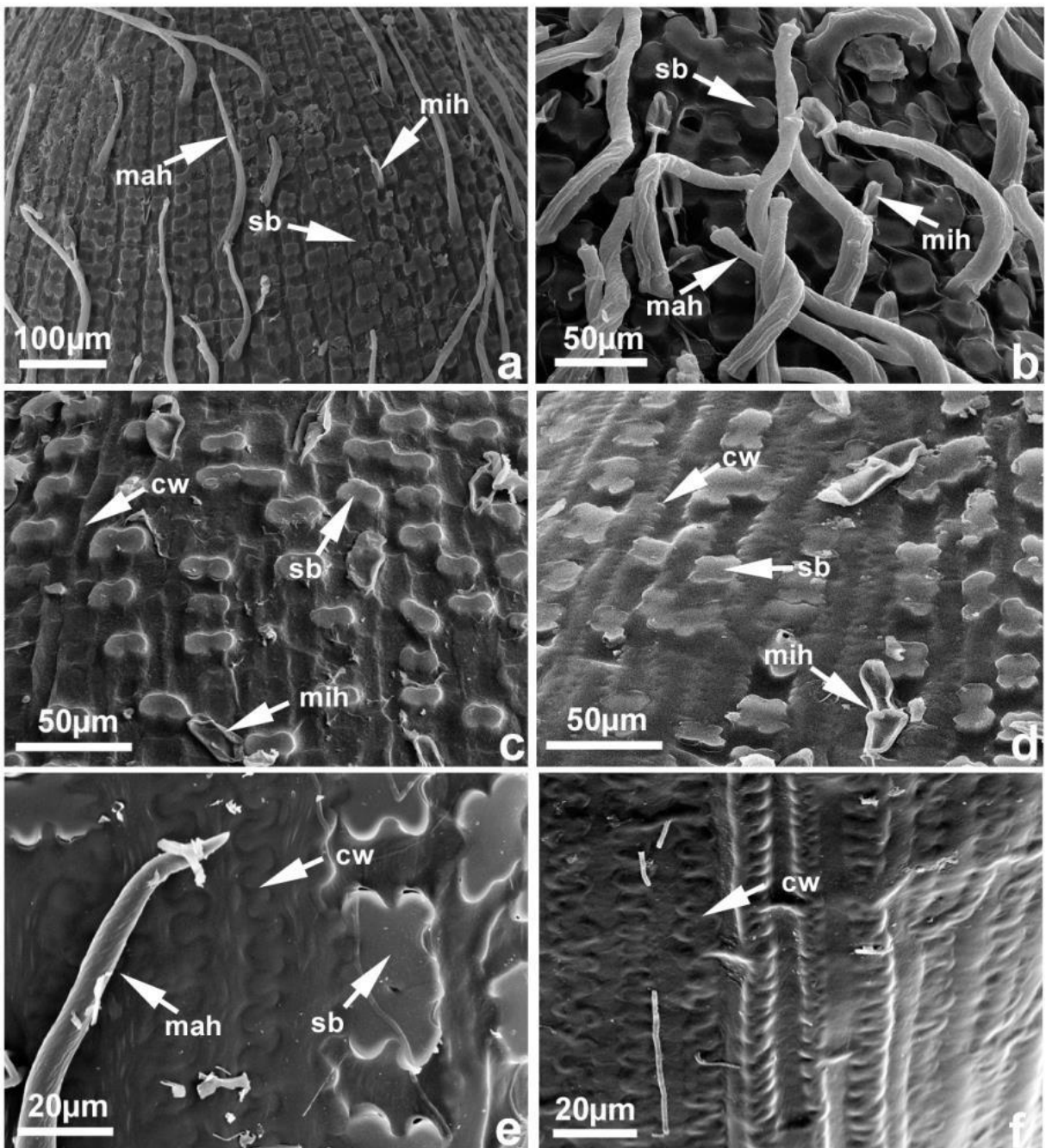


Figure 5. Ornament patterns found in the Neotropical species of *Isachne*. a. Hirsute silicose pattern: upper lemma of *I. leersioides*. b. Hirsute silicose pattern: upper lemma of *I. goiasensis*. c. Bicellular silicose pattern: upper lemma of *I. pubescens*. d. Silicose pattern: lower lemma of *I. goiasensis* (note the omega-shaped anticlinal cell walls). e. Papillose type: lower lemma of *I. salzmannii* (note the omega-shaped anticlinal cell walls). f. Naked pattern: lower lemma of *I. polygonoides* (note the omega-shaped anticlinal cell walls). cw: anticlinal cell wall; mah: macrohair; mih: microhair; sb: silica-body. Based on: a. *N.L. Britton & J.F. Cowell 12786 (NY)*; b. *R.S. Rodrigues et al. 479 (SP)*; c. *D.E. Breedlove & G. Davidse 55225 (MO)*; d. *R.S. Rodrigues et al. 479 (SP)*; e. *A. Chase 7894 (RB)*; f. *A. Chase 8124 (RB)*.

*Rachilla ornament and its systematic value in the Neotropical species:*

Figures 6 and 7 illustrate the characteristics of the rachilla in the Neotropical species of *Isachne*. The rachilla has been used macromorphologically as an important character to distinguish and characterize several species of *Isachne* (e.g., Hitchcock 1920, Iskandar & Veldkamp 2004, Rodrigues & Filgueiras 2016, 2018, Rodrigues & Filgueiras, unpubl. res., Chapter 7). It can be conspicuous (more or less elongated) (Figure 6a, c-d, f-j; 7a, c) or inconspicuous (very short) (Figure 6b, e, k; 7b, d) between the anthoecia. Although taxonomically informative, the micromorphology of the rachilla has never been investigated.

Rachilla vestiture is composed by bicellular microhairs and/or macrohairs, or not infrequently none of these elements. Microhairs and macrohairs are both of the types previously described for the reproductive structures in the genus. The epidermal long cells are shortened and elongated, not papillate, with irregular to sinuous anticlinal walls; they also vary in shape towards the distal portion of the rachilla and frequently form a reticulate pattern dorsally towards the apex (callus) and ventrally (Figure 6e).

In relation to its significance for the Neotropical species of *Isachne*, rachillas densely ornamented with macrohairs were observed in *I. rigens* along all its extension (Figure 6l). *Isachne ligulata*, which is frequently designated as presenting a pilose rachilla, is characterized by the macrohairs sparingly associated to the rachilla margins and to the callus of upper anthoecium (Figure 6h). In *I. rigidifolia*, the rachilla is scarcely ornamented with macrohairs and bicellular microhairs (Figure 7a).

Rachillas without macrohairs (macrohairs associated to the callus of the lower anthoecium) and with scarce bicellular microhairs were found in *I. arundinacea*, *I. disperma*, *I. pubescens*, *I. pygmaea*, and *Isachne* sp. 1 (Figures 6b, d, j, k; 7d).

Glabrous rachillas were observed in *I. angustifolia*, *I. burchellii*, *I. goiasensis*, *I. hirtiglumis*, *I. leersioides*, *I. polygonoides*, *I. salzmannii*, and *I. soderstromii* (Figures 6a, c, e-f, g, i; 7b-c).

The Caribbean *Isachne angustifolia*, *I. rigidifolia*, and *I. soderstromii* present a conspicuous dilation of the distal portion of the rachilla towards the articulation with the callus (Figures 6a; 7a, c).

It is recommended that the analysis of species with inconspicuous rachillas under stereomicroscope be conducted carefully. Misinterpretations regarding the position of macrohairs, whether on the rachilla or at the callus of both the lower and the upper anthoecia may contribute to imprecise identifications of closely related species.

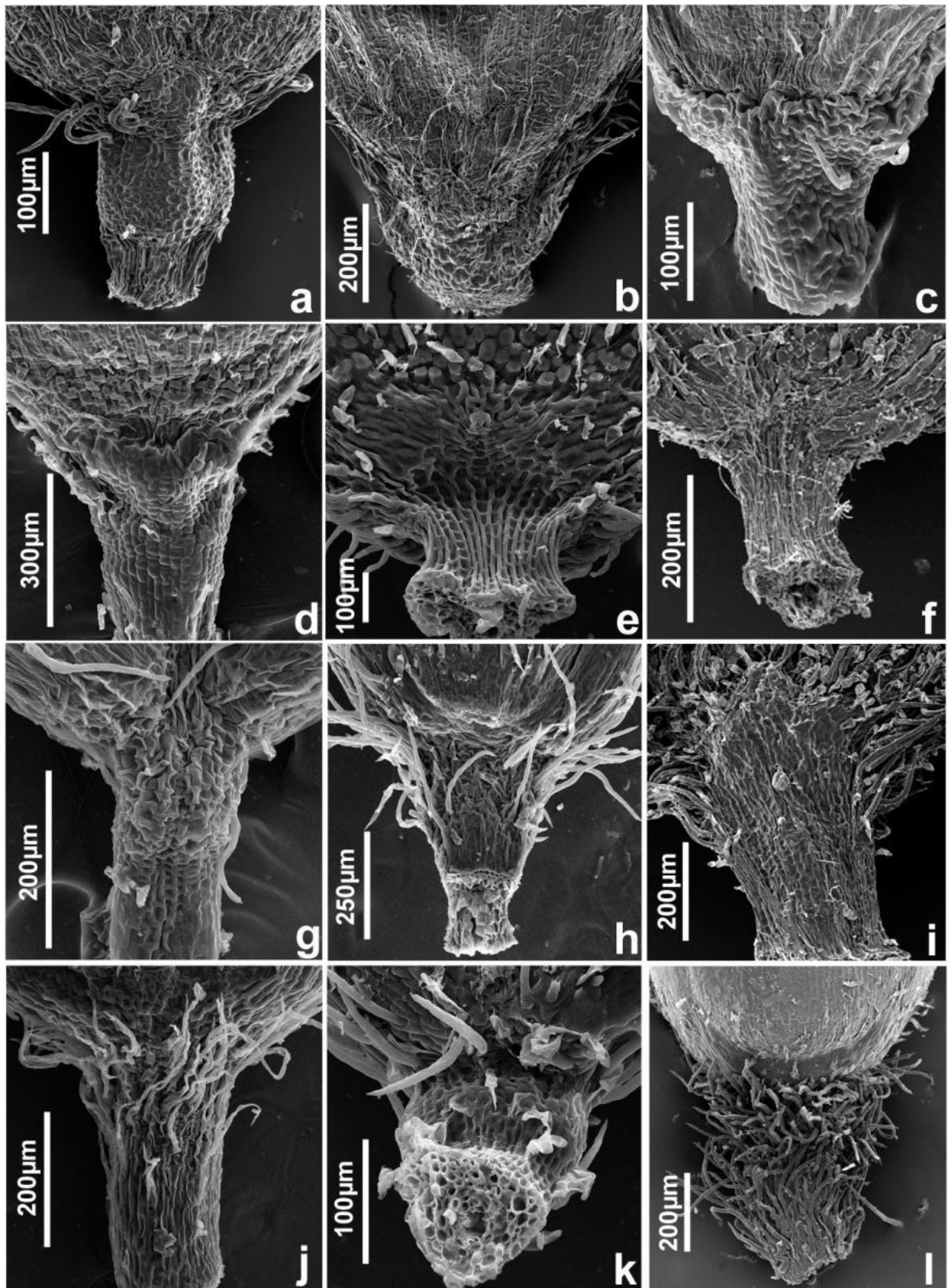


Figure 6. Rachilla morphology and ornament in the Neotropical species of *Isachne*. a. *I. angustifolia*. b. *I. arundinacea*. c. *I. burchellii*. d. *I. disperma*. e. *I. goiasensis*. f. *I. hirtiglumis*. g. *I. leersioides*. h. *I. ligulata*. i. *I. polygonoides*. j. *I. pubescens*. k. *I. pygmaea*. l. *I. rigens*. Based on: a. F.W. Gould et al. 15855 (SP); b. A.S. Hitchcock 8277 (SP); c. A.F.M. Glaziou 17400 (NY); d. R.L. Wilbur et al. 8245 (US); e. R.S. Rodrigues et al. 479 (SP); f. L. Damazio s.n. (SP); g. A.S. Hitchcock 23413 (US); h. R.C. Forzza et al. 7275 (SP); i. A. Chase 8124 (RB); j. D.E. Breedlove & G. Davidse 55225 (MO); k. W. Herris 12490 (US); l. R.W. Pohl & J.C. Betancur 15465 (RB).

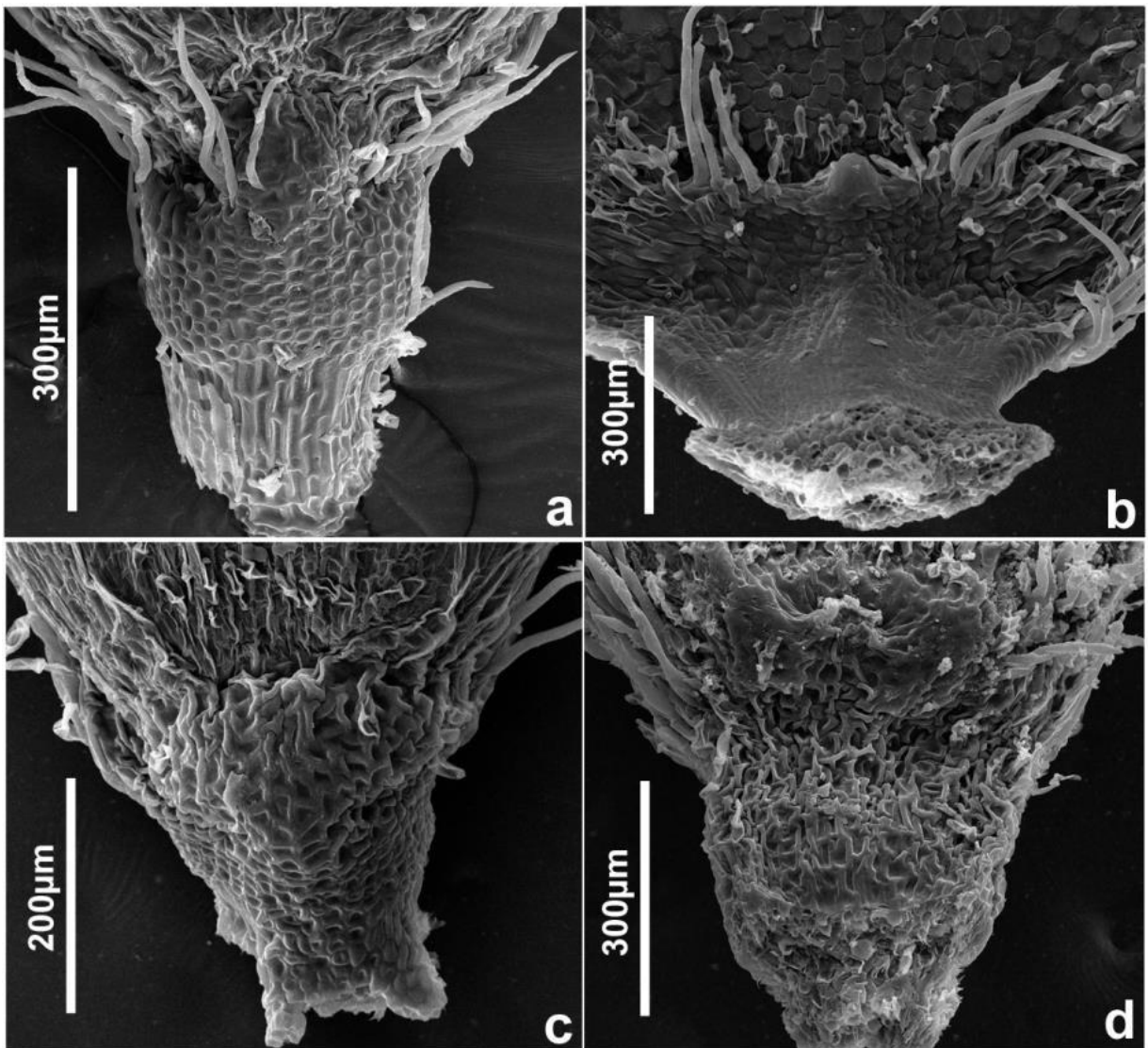


Figure 7. Rachilla morphology and ornament in the Neotropical species of *Isachne*. a. *I. rigidifolia*. b. *I. salzmannii*. c. *I. soderstromii*. d. *Isachne* sp.1. Based on: a. G.J. Gastony *et al.* 487 (NY); b. M. Elisabeth 40896 (HRB); c. W.R. Ernst 1227 (US); d. V. Zak & J. Jaramillo 3204 (MO).

#### *Phenetic analysis:*

The relationship among the Neotropical species of *Isachne* regarding the micromorphological characters of the lower and upper anthoecia and the rachilla is presented in figure 8. The UPGMA dendrogram was elaborated according to Jaccard's similarity coefficient and the correlation between the cophenetic and the similarity matrices was 0.9392.

Two main clusters were obtained. Cluster A includes *I. polygonoides* and *I. salzmannii*. Although these two species are macromorphologically related and share both a cartilaginous lower anthoecium and an appressed-pilose upper anthoecium, they differ enormously in the vestiture of the lower lemma. Cluster B includes the remaining species and differs from the species in Cluster A by the occurrence of silica bodies on the palea of the lower anthoecium.

Within cluster B, two sub-clusters were obtained: sub-cluster B1, including *I. goiasensis*, *I. hirtiglumis*, and *I. leersioides*, which is characterized by the presence of macrohairs on the back lemma of the upper anthoecium; and sub-cluster B2, encompassing the species without macrohairs on the back of the lemma of the upper anthoecium. Sub-cluster B2 can also be divided into three minor groups: b1, including *I. ligulata* and *I. rigens*, and characterized by the presence of pilose rachillas; b2, including *I. angustifolia*, *I. soderstromii*, and *I. rigidifolia*, and characterized by the rachilla dilated at the apex; b3, including *I. arundinacea*, *I. burchellii*, *I. disperma*, *I. pubescens*, and *I. pygmaea*, and characterized by the absence of macrohairs on the back of the lower and upper lemmas, and the glabrous and not dilated rachillas.

A weak congruence with taxonomic clades was observed. Although cluster A includes only species with cartilaginous lower anthoecium, *I. goiasensis* and *I. hirtiglumis*, which also present this characteristic, did not group with it. However, in sub-cluster B2 all species assigned to *Isachne* sect. *Albentes* were grouped with the exception of *I. leersioides*, in which the anthoecia vestiture is similar to that of the species with cartilaginous lower anthoecium.

In the PCA analyses, the three main components explained ca. 80% of the variance [47,012% (component 1); 21,802% (component 2); and 11,783 (component 3)]. Figure 9 presents the relationship between the two main components that explain ca. 70% of the variance. Different variables supported the clusters, sub-clusters, and groups above mentioned. The most contributing variables were the consistency, occurrence of papillae and bicellular microhairs, and the presence and distribution of silica bodies on the lower anthoecium, in addition to the occurrence of macrohairs on the back of the upper lemmas and paleas.

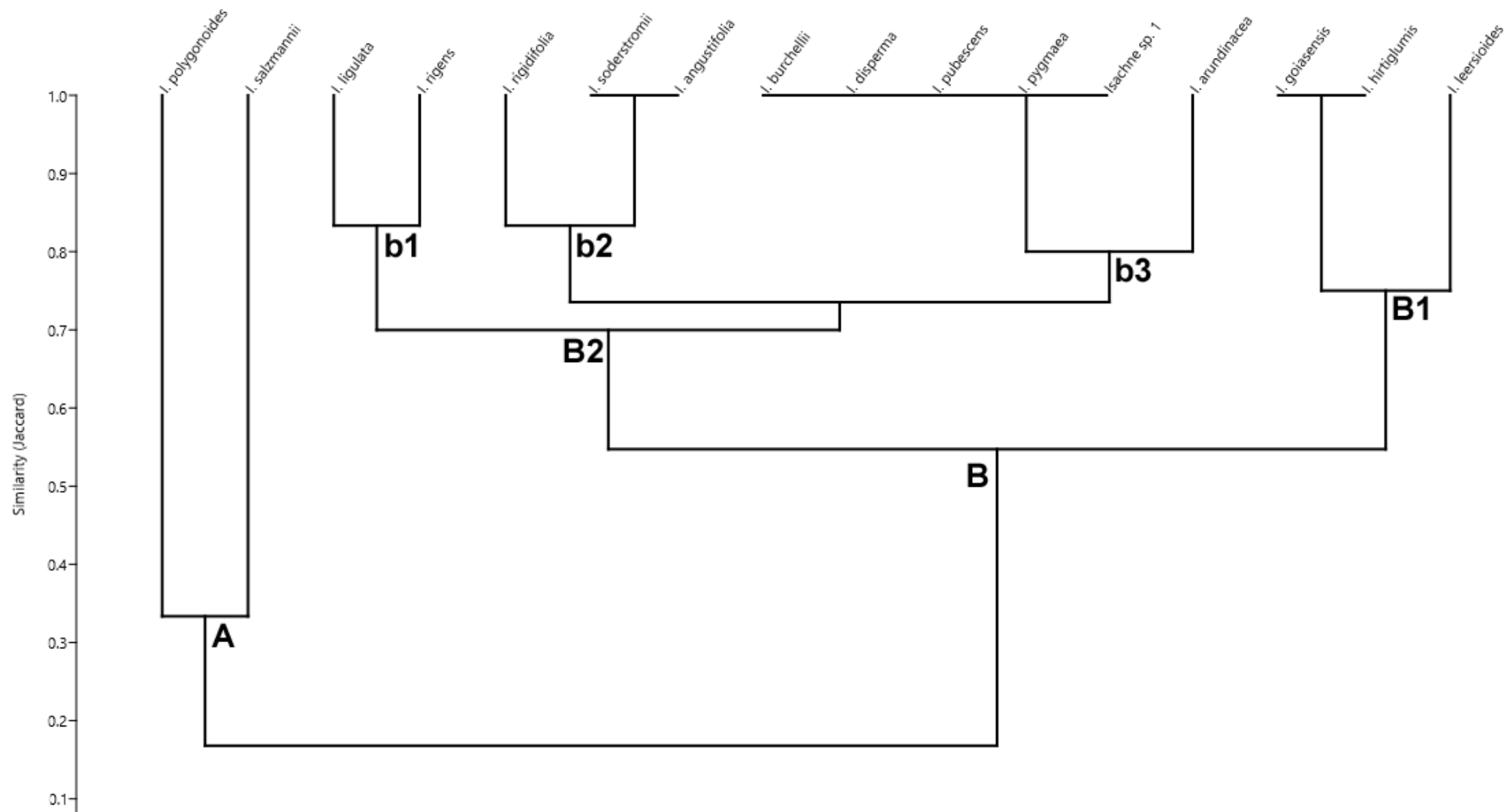


Figure 8. UPGMA Dendrogram based on Jaccard's similarity using micromorphological characters of the anthoecia and the rachilla of *Isachne*. Cophenetic correlation: 0.9392.

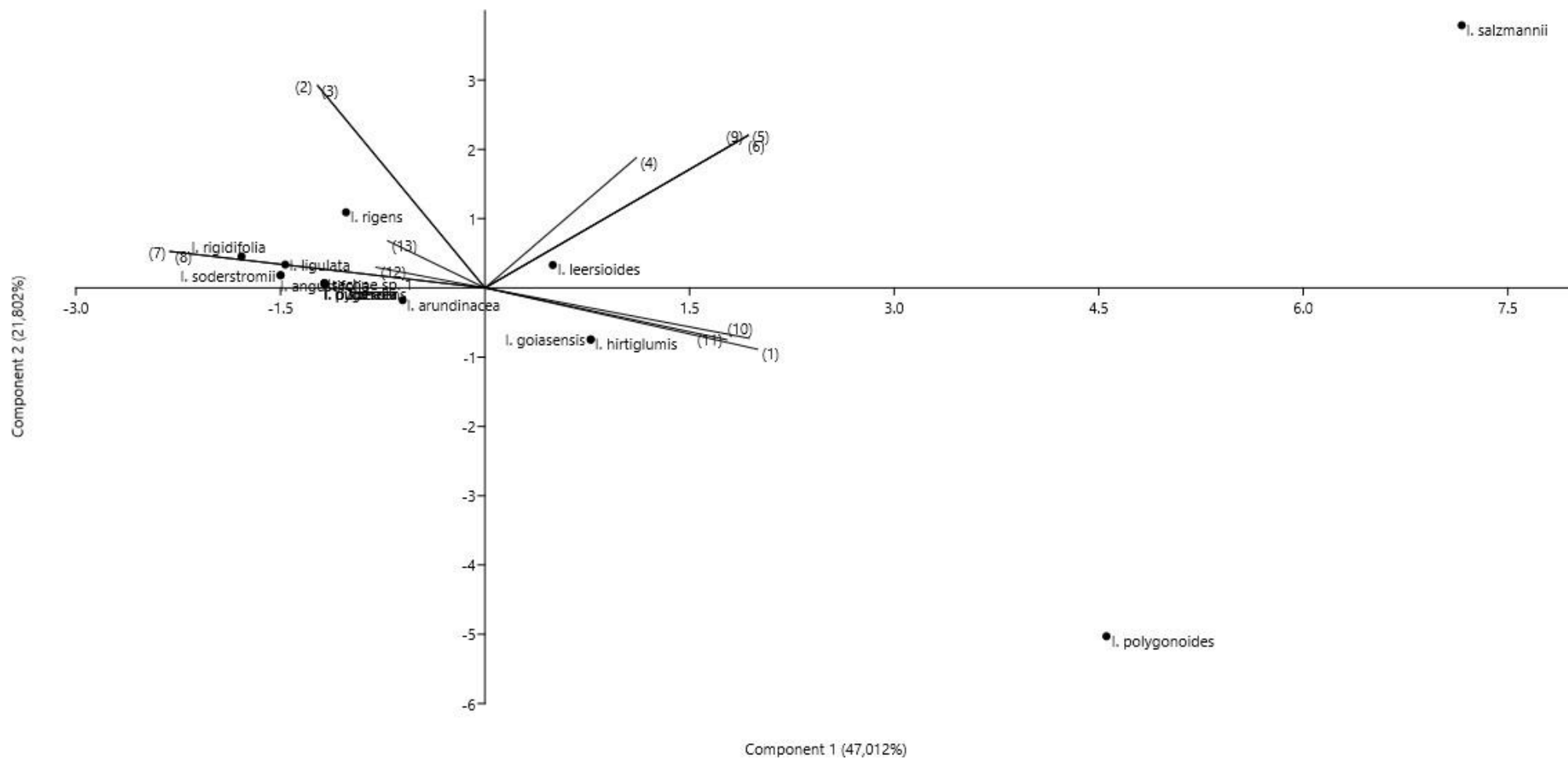


Figure 9. PCA using micromorphological characters of the lower and upper anthoecia and the rachilla of *Isachne*. Graphic representation of the relationship between the two main components (explaining ca. 70% of the variation). Vectors according to table 2.

### Acknowledgments

We are grateful to Dr. Luciana Benatti and Mr. André Aguilera, for the SEM analyses in the Laboratory of Electron Microscopy of the Institute of Botany and CEME-UNIFESP, respectively. We also thank the curators and staff of the Missouri Botanical Garden (MO), the New York Botanical Garden (NY) and the United States National Herbarium (US) for the loans and facilities; the curators of the Brazilian herbaria for the donation of samples, loans and/or permission to accessing the national collections; and Luzia S. Rodrigues for the assistance during the preparation of the manuscript. This study was conducted with private financial resources, with additional support by CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) and the Post-graduation Program in Plant Biodiversity and environment of the Institute of Botany, Brazil.

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# Chapter 7

## Abstract

A comprehensive revision of the Neotropical species of *Isachne* (Poaceae) is presented. Based on the study of herbarium specimens and fieldwork expeditions, 15 species, one new subspecies, and one new variety are accepted. This revision includes comments about macro and micromorphology, taxonomic issues and affinities, distribution data, ecology, and phenology. Illustrations are provided for all the species, nine of which are published here for the first time. Additionally, distribution maps and identification keys for the Neotropical taxa are also provided. The main novelties included in this treatment are: the reevaluation of the identity and circumscription of *I. arundinacea* and the reestablishment of *I. glaucescens* as an accepted name; acceptance of *I. disperma* as a synonym of *I. arundinacea*; description of a new subspecies for *I. angustifolia*; description of a new South American variety for *I. glaucescens* based on macro and micromorphological characters and geographical evidence; lectotypification of *I. arundinacea* and *I. rigens*; reevaluation of the identity and neotypification of *Panicum confertum* Desv. (synonym of *I. glaucescens*); designation of new synonyms; expansion of the distribution extent of *I. pygmaea* and *I. pubescens*; the discovery of a series of specimens dispersed in many herbaria throughout the world which we formally designate here as original material. Finally, the identity of *I. salzmännii* in the context of *I. ventricosa* is discussed.

## Resumo

Apresenta-se uma revisão abrangente das espécies Neotropicais de *Isachne* (Poaceae). Com base em análise de materiais de herbário e expedições de campo, 15 espécies, uma nova subespécie e uma nova variedade são aceitas. Esta revisão inclui comentários relacionados à macro e micromorfologia, questões e afinidades taxonômicas, dados sobre distribuição, ecologia e fenologia. Ilustrações são fornecidas para todas as espécies, nove das quais inéditas. Adicionalmente, mapas de distribuição e uma chave de identificação para as espécies Neotropicais do gênero são também fornecidas. As principais novidades apresentadas nesse tratamento são: a reavaliação da identidade e circunscrição de *I. arundinacea* e o restabelecimento de *I. glaucescens* como nome aceito; aceitação de *I. disperma* como um sinônimo de *I. arundinacea*; descrição de uma nova subespécie para *I. angustifolia*; descrição de uma nova variedade sul-americana para *I. glaucescens* com base em características macro e micromorfológicas e evidências geográficas; lectotipificação de *I. arundinacea* e *I. rigens*; reavaliação da identidade e neotipificação de *Panicum confertum* (sinônimo de *I. glaucescens*); designação de novos sinônimos; expansão da área de distribuição de *I. pygmaea* e *I. pubescens*; descoberta de uma série de espécimes em vários herbários pelo mundo que estão sendo aqui formalmente designados como material original. Por fim, a identidade de *I. salzmännii* no contexto de *I. ventricosa* é discutida.

Keywords: blood grass, Gramineae, grasses, *Isachneae*, the Americas.

**The following chapter was prepared according to the standards of Hoehnea.**

According to Article 30.8 of the International Code of Nomenclature for algae, fungi, and plants (Turland *et al.* 2018), the taxonomic novelties included in this Chapter do not represent an effective publication.

## Revision of the Neotropical species of *Isachne* R. Br. (Poaceae, Micrairoideae)

Rodrigo S. Rodrigues<sup>1,2</sup> and Tarciso S. Filgueiras<sup>1</sup>

### Introduction

*Isachne* R.Br. is the largest genus of the tribe Isachneae, subfamily Micrairoideae (Soreng *et al.* 2017). The genus includes ca. 103 species worldwide (Kellogg 2015) and is distributed throughout the tropical and subtropical regions, with greatest diversity in Asia (Judziewicz 1990). *Isachne* encompasses annual or perennial species with spikelets disarticulating above the subequal glumes, anthoecia similar or dissimilar in shape, consistency, texture and/or pilosity, being the lower staminate, pistillate or bisexual, and the upper bisexual or pistillate (Hitchcock 1920, Clayton & Renvoize 1986).

Recent account for the Neotropics revealed the occurrence of 15 species (Rodrigues & Filgueiras 2019); some of them have been a matter of much confusion. The only revision available for the American species is that presented by Hitchcock (1920) for the North American species of the genus. The South American taxa have never been revised, and the identity of some Mesoamerican species is still taxonomically obscure.

Therefore, the aim of the present paper is to review and elucidate the taxonomy of the Neotropical species of *Isachne* in order to collaborate with future studies and contribute with the knowledge on the diversity, circumscription, and distribution of the American taxa.

### *Taxonomic history:*

Brown (1810) established *Isachne* based on a single species, *Isachne australis* R. Br., and cited that *Meneritana* (1717) was related to the newly described genus. Later, the name '*Isachne meneritana*' was erroneously attributed to Brown. Poiret (1813) formally published *I. meneritana*, which was found to be, along with *I. australis*, a synonym of *I. globosa* (Thunb.) Kuntze.

The acceptance of *Isachne* in a generic level was historically controversial. Raspail (1825) apparently was the first to refute the concept of *Isachne* as a distinct genus and attempted to transfer *I. australis* to *Panicum* L. This proposal was initially followed by Sprengel (1825), who transferred also a few other species to *Panicum* and accepted the classification of various species previously treated under *Isachne*, and Nees (1829), who treated *Isachne* as a synonym of *Panicum*.

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<sup>1</sup> Programa de Pós-graduação em Biodiversidade Vegetal e Meio Ambiente, Núcleo de Pesquisa Curadoria do Herbário SP, Instituto de Botânica, Avenida Miguel Stefano, 3687, CEP: 04301-902, Água Funda, São Paulo, SP, Brazil.

<sup>2</sup> Corresponding author: rosaro\_3588@yahoo.com.br

Trinius (1826, 1827) recognized *Isachne* at the generic level and described three new species. Kunth (1829) accepted *Isachne* but retained a few other species in *Panicum*.

Some years later, Trinius (1834) reduced *Isachne* to a section of *Panicum* [*Panicum* sect. *Isachne* (R. Br.) Trin.] and included eight species in it. In addition, he recognized three informal subgroups based on the pubescence of the spikelets. This approach was followed by Steudel (1840, 1854).

Nees (1850) treated *Isachne* in a generic rank. Grisebach (1862, 1864) accepted *Isachne* highlighting that the difference between *Isachne* and *Panicum* is in the consistency of the spikelets.

Döll (1877) included five American species of *Isachne* in the '*Flora Brasiliensis*', some of them with controversial circumscription.

Bentham (1878) placed *Isachne* in the subtribe Milieae together with *Coelachne* R. Br., *Eriachne* R. Br., *Micraira* F. Muell., and *Sporobolus* R. Br. (cf., p. 457). In the case of *Isachne*, it is clear that the placement in the tribe Milieae instead of Paniceae was based on the articulation of the spikelets. According to him, this feature '*settles also the position of a few genera such as Polypogon, Milium, Isachne, etc. (...), and appears close to connect the two great series (i.e., the series Panicaceae and Poaceae)*'. Three years later, Bentham (1881) recognized Isachneae as a distinct tribe.

Bentham & Hooker (1883) placed *Isachne* again in the tribe Paniceae, remarking that the genus is an exception by the occurrence of a bisexual lower anthoecium and by the articulation of the glumes. The same approach was followed by Hackel (1887).

Hooker (1897) stated that the articulation of the anthoecia is important to separate *Isachne* from *Panicum*.

Post & Kuntze (1903) included *Sphaerocaryum* Nees ex Hook f. in *Isachne* and recognized two sections (i.e., *Typisachna* and *Graya*) within the latter based on the number of flowers in the spikelets.

Chase (1911) commented about the dehiscence of the glumes and anthoecia and provided a brief taxonomic history for *Isachne*.

Stapf (1911) discussed the placement and the morphological affinities among *Heteranthoecia*, *Isachne*, and *Coelachne* R. Br. According to him, positioning *Isachne* in the tribe Isachneae, as did Bentham (1881), is '*a conception very much in accord with the structure of the whole facies of the grass*'. However, despite his own statements, Stapf (1917) treated *Isachne* under Paniceae and established the subtribe Isachninae (with the nom. alt. Isachnastrae) to accommodate *Isachne* and *Heteranthoecia*.

Hitchcock (1920) presented the first revision of *Isachne* for North America with eight species (which actually included also Central American and Caribbean species). Following Chase (1911) and previous authors, he commented about the “*anomalous*” position of the genus in Paniceae because of the structure of spikelets and fertility of the anthoecia.

Honda (1930) divided *Isachne* into two sections (i.e., *Euisachne* and *Paraisachne*) on the basis of the spikelets and anthoecia morphology. This approach is similar to that originally proposed by Trinius (1834). However, none of the infrageneric names proposed by Honda were validly published because they are not in conformity with Art. 22 ICN (Turland *et al.* 2018). This approach was later followed by Stapf & Hubbard (1934), Jansen (1953), Keng (1965) and Clayton & Renvoize (1986).

Hubbard (1943) proposed the reestablishment of Isachneae as a distinct tribe from Paniceae to accommodate *Coelachne*, *Heteranthoecia*, *Isachne*, *Limnopoa* C.E. Hubb., and *Sphaerocaryum*. Later, Potztl (1952) conducted anatomical analyses of leaves in Isachneae (sensu Hubbard 1943) and suggested that *Sphaerocaryum* should be placed in Sporobolae (Chloridoideae). Tateoka (1957), based on anatomical analysis of the transversal leaf section, provided evidence in favor of keeping *Sphaerocaryum* in Isachneae.

Metcalf (1960) studied the leaf anatomy of *Isachne*, indicating that its structure is panicoid “*but of a rather special type*” and pointing out that the occurrence of cubical and acutely angular silica bodies, microhairs, angular vascular bundles, a radiate mesophyll with long and loosely arranged assimilatory cells, and almost cubical long-cells was very characteristic of *Isachne* and related genera in Isachneae.

Pohl & Davidse (1971) accepted *Isachne* under Paniceae and provided chromosome counts for two American species of the genus.

Brown (1977) placed Isachneae apart from the Paniceae, along with other non-Kranz tribes of Panicoideae, but related them to some non-Kranz genera of Paniceae and non-Kranz subgenera of *Panicum*. According to him, Isachneae represents modern descendants of the two-fertile florets (regarded as the ‘*pre-panicoid condition*’), non-Kranz and pre-Paniceae, which retained the plesiomorphic structure of the spikelets.

Prakash & Jain (1984) described *Isachne* sect. *Albentes* to accommodate the species with homomorphic anthoecia [formerly included in the invalid sections ‘*Euisachne*’ of Honda (1930) and ‘*Pseudoisachne*’ of Ohwi ex Jansen (1953)], and grouped the species with heteromorphic anthoecia in *Isachne* sect. *Isachne* [formerly sections ‘*Paraisachne*’ of Honda (1930) and ‘*Eu-Isachne*’ sensu Jansen (1953)].

Clayton & Renvoize (1986), following Bentham (1881) and Stapf (1911), recognized Isachneae under Panicoideae, pointing out that, although questionable, it is more

appropriate to treat Isachneae in a tribal level than accept it as an anomalous group in Paniceae. According to them, the plesiomorphic character of both bisexual florets in Isachneae is more likely a derived status resulting of reversion to bisexuality of the lower floret.

GPWG (2001) included Isachneae in Panicoideae. Following this proposal, Soreng *et al.* (2003) placed Isachninae under Isachneae in Panicoideae. Additionally, Zuloaga & Morrone (2003) provided a list of 12 Neotropical species of *Isachne* and a taxonomic compilation for each taxon, including acceptance and status of names, synonymy, and distribution.

Iskandar & Veldkamp (2004) revised the Malesian species of *Isachne* sect. *Isachne* and provided the first historical background with relevant taxonomic and nomenclatural data regarding the genus.

In a phylogenetic study by Duvall *et al.* (2007) and Sánchez-Ken *et al.* (2007), *Isachne* surprisingly was resolved in a well-supported clade with the *incertae sedis* genera *Eriachne* and *Micraira*. This clade emerged as sister to Arundinoideae. The subfamily Micrairoideae Pilg. was reestablished and amended to accommodate eight genera grouped in three tribes: Micraireae (including only *Micraira*), Eriachneae (including *Eriachne* and *Pheidochloa* S.T. Blake) and Isachneae (including *Coelachne*, *Heteranthoecia*, *Isachne*, *Limnopoa*, and *Sphaerocaryum*). This proposal has been strongly supported and was followed in subsequent classifications (e.g., Sánchez-Ken & Clark 2010, GPWG II 2012, Kellogg 2015, Soreng *et al.* 2015).

Recently, Soreng *et al.* (2017) presented an updated classification of the Poaceae, in which Isachneae is expanded to include *Isachne*, *Coelachne*, *Heteranthoecia*, *Sphaerocaryum*, and *Hubbardia* Bor.

### Material and methods

Field trips were conducted in Brazil during 2015-2018 in the following states: Espírito Santo, Bahia, Minas Gerais, Goiás, and Distrito Federal.

Morphological descriptions, distribution, and phenology were based on herbarium specimens. Herbarium collections were physically consulted (ALCB, BHCB, CEN, CESJ, CVRD, ESA, FLOR, HEPH, HRB, HUEFS, IAC, IAN, IBGE, MBM, MBML, MO, NY, OUPR, PMSP, R, RB, SP, SPF, UEC, UB, US, VIC, and VIES), and virtual collections were also examined (ARIZ, ASU, B, BAA, BM, BR, CAS, CONN, F, FLAS, FSU, GENT, GH, GOET, IND, K, MICH, MPU, NO, NY, P, PH, S, SBT, TUB, UPS, US, USF, UTC, UVMVT, VSC, and W). Additionally, online records of duplicates were associated to the

examined material (BRU, CM, FI, ILLS, K, LE, M, MG, MO, NMC, NY, S, and VEN) (acronyms according to Thiers 2019, continuously updated).

Specimens were examined using a stereomicroscope and measurements were taken with aid of a ruler. Synflorescence structures, spikelets, and trichomes were measured using a ruler coupled to an Olympus® SZ51 stereomicroscope ocular lens. Spikelets without previous treatments were also examined with a Philips® XL 20 or a FEI Quanta FEG® 250 scanning electron microscope operating at 10 kV and 30 kV, respectively. The terminology used in the SEM analyses follows Metcalfe (1960) and Ellis (1979).

Maps were elaborated using QGIS 2.14.1-Essen software. Coordinates were obtained directly from the label of herbarium specimens or during field expeditions. When necessary, approximate coordinates were obtained on the basis of the information provided by the collector. When a large number of samples was available, representative specimens were selected and incorporated into the maps to illustrate the distribution of the taxa.

### Results and discussion

The genus *Isachne* is represented in the Neotropical region by 15 species, one subspecies, and one variety. Some of the American species of the genus were subject of great taxonomic confusion because of a problematic circumscription allied to the great morphological affinity and sympatry with other congeners. This is particularly evident by the great number of specimens misidentified in the herbaria (pers. obs.) or formerly considered synonyms.

Morphologically, the species classified within *Isachne* are quite uniform in relation to the vegetative and reproductive features but differ enormously in size. The tendency of separating the genus into two distinct sections on the basis of the similarity, consistency and pilosity of the anthoecia is artificial and sometimes unfeasible. This approach is still in need of tests with molecular data.

As currently circumscribed, we accept the following taxa of *Isachne* for the Neotropics: *I. angustifolia* subsp. *angustifolia*, *I. angustifolia* subsp. *dominicensis* R.S. Rodrigues & Filg. (subsp. nov.), *I. arundinacea* Griseb., *I. burchellii* R.S. Rodrigues & Filg., *I. glaucescens* var. *glaucescens* (var. nov., autonym), *I. glaucescens* var. *trichomatosa* R.S. Rodrigues & Filg. (var. nov.), *I. goiasensis* Renvoize, *I. hirtiglumis* Longhi-Wagner & Welker, *I. leersioides* Griseb., *I. ligulata* Swallen, *I. polygonoides* (Lam.) Döll, *I. pubescens* Swallen, *I. pygmaea* Griseb., *I. rigens* (Trin.) Griseb., *I. rigidifolia* (Poir.) Urb., *I. salzmännii* (Trin. ex Steud.) Renvoize, and *I. soderstromii* R.S. Rodrigues & Filg.

*Morphology:*

*Habit:* Species of *Isachne* are annuals or perennials. Annual species are usually delicate; perennials are robust or delicate, often with short rhizomes but some long rhizomatous species may also occur. The habit is variable and includes cespitose, decumbent, stoloniferous, trailing, scandent or leaning plants. Decumbent, trailing, scandent and stoloniferous species frequently have a spreading growth and may form dense tangles on the ground. Decumbent plants often root in the proximal nodes, becoming geniculate-ascending in the distal ones, especially in the flowering branches.

*Culms:* Culms are slender to robust, thin to thick, straight to geniculate in the lower, intermediary and/or upper nodes, frequently branching, and sometimes each branch develops into a flowering branch (Rodrigues & Filgueiras 2016). Nodes are glabrous to pilose. In the slender species nodes appear as a dark-brown to blackish bottleneck, and in the robust species as a bottleneck (from which leaf sheaths develop) or as a swollen region at the lower nodes of the main culms. In some species, conspicuous nodal crateriform scars protected by old sheaths are present in a whorl, from which aerial roots may opportunely develop. A conspicuous or inconspicuous ringed-stripe is also present below the nodes of some species. Internodes are full or hollow (which is particularly evident in robust species) and may vary in color.

*Leaves (morphology and micromorphology):* The pilosity of the sheaths can be largely variable, from glabrous to pilose, with soft or hispid-tuberculate trichomes. Ligules in most species are pilose, but some membranous, membranous-ciliate or eligulate species are also recorded. Blades are flat to somewhat involute, ranging from filiform to linear-lanceolate, lanceolate, large-lanceolate to oblong or ovate, glabrous to pilose; bases are attenuate to cordate or amplexicaul, without pseudopetiole; the apex can be obtuse to acute or strongly acuminate. Nerves are conspicuous or inconspicuous, with a prominent or non-prominent midrib. Leaves of decumbent, trailing, scandent or leaning plants are deciduous along the basal portion of the culms, but notably abundant in the upper portions and along the branches.

Significant micromorphological differences between the abaxial and adaxial leaf blade epidermises may occur. The foliar epidermal micromorphology in *Isachne* is characterized by the occurrence of frequent single-papillate long cells in the intercostal and/or costal zones; papillae are centric to sub-centric, dome-shaped, roundish, oblique or less often elongated; short cells are absent or rare in the intercostal zones; silica bodies are notably variable in shape (roundish, saddle-shaped, cross-shaped, dumbbell-shaped, intermediate between cross-shaped and dumbbell-shaped or *Oryza*-type) and restricted to the costal zones and margins; bicellular microhairs are panicoid; macrohairs are straight, usually with cushion bases; stomata mostly intercostal, with subsidiary cells variable in shape, mostly dome-shaped, low dome-shaped, triangular or rectangular in outline (Rodrigues & Filgueiras unpubl. res., Chapter 5).



*Synflorescences:* Synflorescences are uniformly exerted or partially exerted panicles, terminal and/or axillary, loosely or densely flowered. They are very branched or composed of first-order branches only (e.g., *I. rigens*, *I. rigidifolia*), ranging from lax to open or contracted (sometimes showing a spike-like appearance as seen in *I. pygmaea*), with variable sizes and pilosity. Pedicels are long or short, usually straight, glandular in many species or eglandular, bearing solitary and less often paired spikelets.

*Glandules:* Glandular plants are common in *Isachne*. Pulviniform glands can be found abundantly in the synflorescence axils of some species (e.g., *I. ligulata* and *I. leersioides*). Many other species in the genus carry one or more glandular bands on the pedicels (also called as glandular ‘rings’ or ‘patches’) (Chen & Phillips 2006; Longhi-Wagner & Welker 2014; Rodrigues & Filgueiras 2018). The occurrence of ringed-stripes below the nodes of some species was also associated with glands by Veldkamp (2016) [‘annular glands’]. Bicellular microhairs are largely present in the leaves and in the anthoecia, and its role as secretory elements is subject of further investigations.

*Spikelets (morphology and micromorphology):* In general, the spikelets in *Isachne* have a morphological convergence to those of the tribe Paniceae *s.l.* (Subfamily Panicoideae). This is the reason many agrostologists included this genus under that tribe or in its own tribe within Panicoideae. However, differently from the Paniceae *s.l.*, in *Isachne* the spikelets disarticulate above the glumes that are both equally developed, shorter, subequal or longer than the anthoecia, glabrous to densely hirsute, 3-11-nerved and muticous. The two anthoecia are always composed by one perfect lemma and palea (i.e., without reduction or loss) and can be similar (homomorphic) or dissimilar (heteromorphic) in shape, size, texture, consistency, and pilosity, being the lower staminate, pistillate or bisexual, and the upper bisexual or pistillate (Hitchcock 1920; Clayton & Renvoize 1986). The lower anthoecium can be membranous, cartilaginous, indurate to coriaceous, whereas the upper one is indurate, coriaceous or less often chartaceous; both are glabrous to densely pilose.

As expected, the lower anthoecium is micromorphologically distinct from the upper one in the species with heteromorphic anthoecia. The most remarkable differences are in relation to the absence and/or distribution of silica bodies, bicellular microhairs and macrohairs, and the presence of simple papillae. No difference is noteworthy in the species with homomorphic anthoecia (Rodrigues & Filgueiras unpubl. res., Chapter 6).

Five different ornamentation patterns of the upper anthoecium were observed in *Isachne*; i.e., hirsute silicose (leersioid-type), bicellular silicose (arundinacea-type), silicose (angustifolia-type), papillose (salzmannii-type), and naked (polygonoid-type) (Rodrigues & Filgueiras unpubl. res., Chapter 6). Both the lemma and palea of the upper anthoecium have panicoid

bicellular microhairs and are covered by abundant silica bodies that are variable in shape among species

Twisted narrow-tipped or sharp-pointed macrohairs are found exclusively in the spikelets of *Isachne* (Figure 1a). They occur at the calluses of the anthoecia, on lemmas and paleas, or covering the rachilla (Figure 1b-c). This type of macrohair is distinct from the usual straight and sharp macrohairs found in the leaves and glumes (Rodrigues & Filgueiras unpubl. res., Chapter 6).

The rachilla can be taxonomically informative. It can be distinct (long) or indistinct (short) and varies in relation to dilation and/or pilosity.

*Unusual features of the spikelets:* The occurrence of a rachilla tip at the base of the upper anthoecium and of a well-developed third anthoecium in *Isachne* was pointed out by Rodrigues & Filgueiras (2018). The rachilla tip is probably the same intriguing morphological structure referred by Hooker (1897). These unusual features (i.e., the rachilla tip and the third anthoecium) are atypical conditions in the genus. Iskandar & Veldkamp (2004) regarded the occurrence of a third anthoecium as an ‘error of enthusiasm’, once it may also occur in some Paniceae, such as *Panicum* L. and *Trichantheicum* Zuloaga & Morrone.

The rachilla tip is usually inconspicuous (when not ending up in an unusual developed third anthoecium) and better detectable under Scanning Electron Microscope (SEM) (Figure 1c-d); although in some cases a stereomicroscope is enough to visualize it. However, it is not clear to us whether this vestigial structure is responsible to develop the atypical third anthoecium in *Isachne* because no intermediary condition (i.e., a rudimentary third anthoecium) was found.

When present, the third anthoecium is perfect and similar to the second one in texture, pilosity, fertility (Figure 1e-g) and sometimes develops a caryopsis (Figure 1h). A third anthoecium was occasionally observed in *I. hirtiglumis* [L. Damasio s.n. (SP-490353)], *I. goiasensis* [Irwin et al. 19315 (NY)], *Isachne soderstromii* [W.R. Ernst 1227 (US)], and *I. glaucescens*.

*Fruit and embryo:* The fruit in *Isachne* is a typical caryopsis slightly compressed dorsiventrally and with a thin pericarp adhered to the seed. The hilum is linear and the embryo is large, up to 1/2 the length of the caryopsis.

#### *Anatomy:*

*Isachne* is entirely C<sub>3</sub> and presents the typical non-Kranz leaf anatomy as seen in Isachneae as a whole (Brown 1977, Sánchez-Ken et al. 2007), characterized by a radiate mesophyll with narrow and long chlorenchymatous cells with well-developed intercellular

spaces, tending to be spongy near the veins. In general, vascular bundles are small and usually with single bundle-sheaths, but larger vascular bundles and sometimes inconspicuous inner bundle-sheaths may occur (Metcalf 1960).

*Chromosome numbers:*

According to the traditional information available, *Isachne* has a chromosome number of  $x=10$  (GPWG 2001, Sánchez-Ken *et al.* 2007). Kaur *et al.* (2014) investigated sixteen species and suggested a new base chromosome count of  $x=5$  for the genus.

The following accounts for the Neotropical species of *Isachne* are recorded in the literature:

*Isachne glaucescens* (as *I. arundinacea*):  $2n=40$  (Tateoka 1962, Pohl & Davidse 1971);  $2n=20$  (Morrone *et al.* 2006).

*Isachne polygonoides*:  $2n=20$  (Pohl & Davidse 1971);  $n=10$  (Davidse & Pohl 1978).

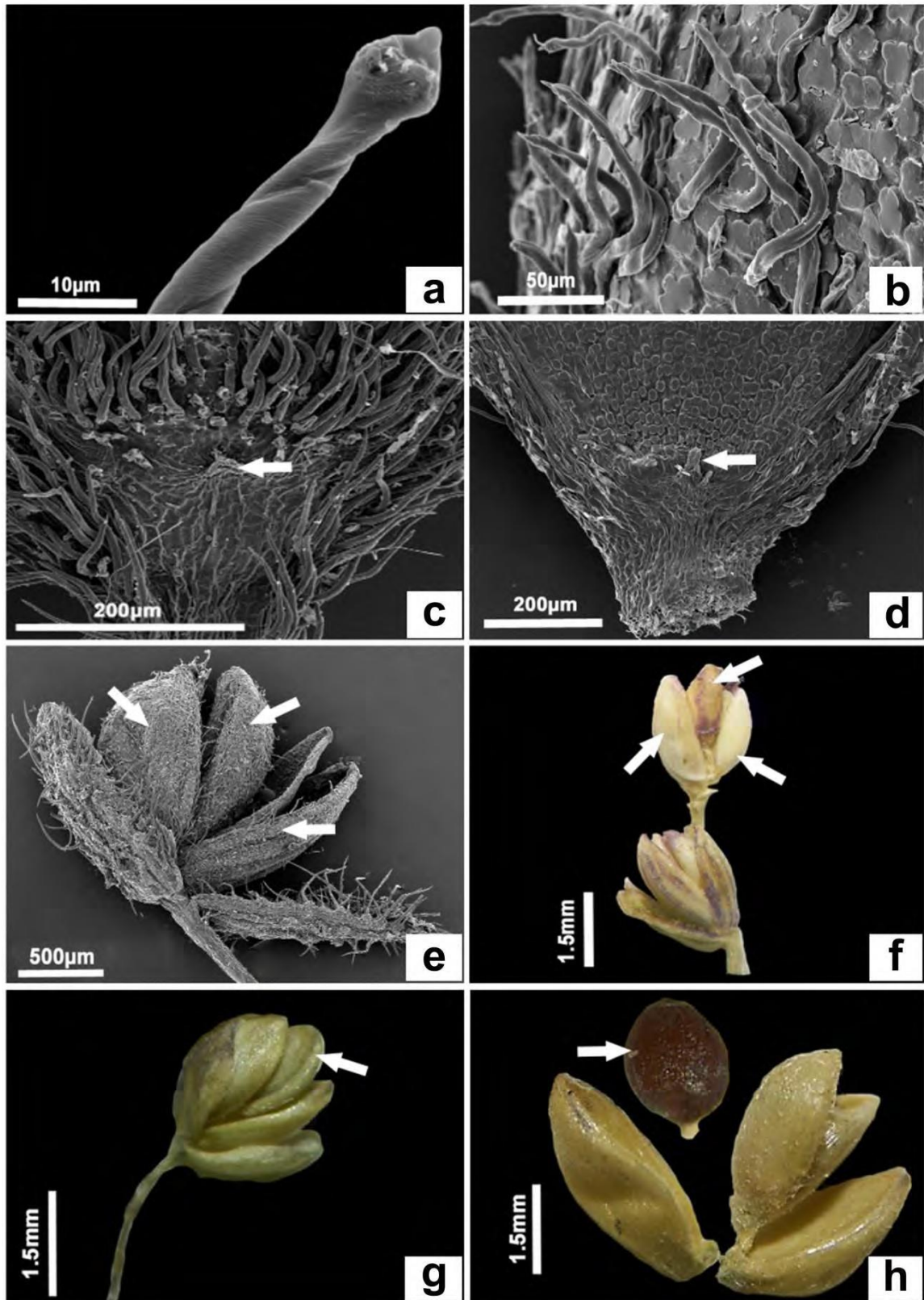


Figure 1. a. Scanning electron micrograph (SEM) of a twisted narrowed-tipped macrohair of *I. hirtiglumis*. b. Lemma of the upper anthoecium of *I. salzmannii* under SEM showing the silicose surface and several twisted narrow-tipped macrohairs. c. Base of the upper anthoecium of *I. polygonoides* under SEM showing a rachilla extension (arrow). d. Base of the upper anthoecium of *I. globosa* under SEM showing a rachilla extension (arrow). e. Spikelet of *I. hirtiglumis* under SEM showing the three developed anthoecia (arrows). f. Spikelets of *I. soderstromii* under stereomicroscope showing one lower spikelet with two anthoecia, and one upper spikelet (glumes removed) with three anthoecia (arrows). g. Spikelet of *I. goiasensis* under stereomicroscope showing the three developed anthoecia (third anthoecium indicated by the arrow). h. Spikelet of *I. goiasensis* under stereomicroscope showing the three anthoecia and a perfect caryopsis removed from the third anthoecium (arrow). Based on: a, e. *L. Damasio s.n. (SP-490353)*; b. *A. Chase 7894 (RB)*; c. *A. Chase 8124 (RB)*; d. *H. Ohashi et al. 11449 (SP)*; f. *W.R. Ernst 1227 (US)*; g-h. *H.S. Irwin et al. 19315 (NY)*.

### Taxonomic treatment

- Isachne* R. Br.**, Prodr. 196. 1810. ≡ *Isachne* R. Br. sect. *Isachne* [autonym]. ≡ *Isachne* sect. *Euisachne* Honda, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 3(1): 278. 1930. [nom. inval.]. ≡ *Isachne* [publ. as “*Isachna*”] sect. *Typisachna* Post ex Kuntze, Lex. Gen. Phan., pars. 1, 301. 1903. [nom. inval.]. ≡ *Panicum* sect. *Isachne* (R. Br.) Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3, 1(2-3): 195, 328. 1834. [the rank of section is given in p. 193]. Type: *Isachne australis* R. Br. [= *Isachne globosa* (Thunb.) Kuntze].
- = *Isachne* sect. *Paraisachne* Honda, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 3(1): 278, 282. 1930. Type: *Isachne dispar* Trin. [= *Isachne pulchella* Roth].
- = *Isachne* sect. *Pseudoisachne* [publ. as “*Pseudo-Isachne*”] Ohwi ex Jansen, Reinwardtia 2: 290. 1953. [nom. nud.].
- = *Isachne* sect. *Albentes* V. Prakash & S.K. Jain, Fasc. Fl. India 14: 8. 1984. Type: *Isachne albens* Trin.

Annuals or perennials, rhizomatous or not, cespitose, suberect, erect, decumbent, stoloniferous, scandent (clambering) or leaning. Culms slender to strongly robust, branched or unbranched; nodes glabrous to pilose; internodes full or hollow. Leaves concentrated at the base or regularly distributed along the culms; sheaths fibrous or not, glabrous to pilose; leaf blades linear to lanceolate or ovate-lanceolate, flat, less frequently convolute or conduplicate, acute, acuminate or obtuse; ligule ciliate, rarely absent. Synflorescence a panicle, lax, open, subcontracted, or rarely apparently spike-like (*I. pygmaea*) or racemose, axillary glands present or absent; rachis narrow, usually cylindrical or angular, glabrous, scabrous or pilose; pedicels long and/or short, glandular bands absent or present. Spikelets solitary, rarely in pairs, 1-2-flowered, articulated above the glumes, globose, orbicular, obovate, elliptic or elliptic-lanceolate, glabrous to pilose; glumes 2, developed, equal to subequal, less frequently one or both slightly longer than the anthoecia, persistent or dehiscent, membranous to chartaceous, obtuse to acute, muticous, glabrous to densely pilose, the lower (3-)5-9(-11)-nerved, the upper (3-)5-7(-11)-nerved; anthoecia 2, similar or dissimilar in shape, consistency and pilosity; lower anthoecium staminate, pistillate or bisexual, usually flat-convex, lemma and palea chartaceous, cartilaginous or coriaceous, muticous, glabrous to pilose; rachilla conspicuous or inconspicuous between the anthoecia, glabrous to densely pilose; upper anthoecium bisexual or pistillate, usually flat-convex, lemma and palea coriaceous, less usually subcoriaceous or chartaceous, muticous, glabrous to pilose. Fruit a caryopsis, ellipsoid to orbicular or obovoid, laterally or ventrally compressed, or flat-convex.

*Etymology:* From the Greek: “*isos*”, equal; “*achne*”, scale (Clifford & Bostock 2007).

The generic name refers to the equal/subequal developed glumes.

*Distribution:* *Isachne* is distributed mainly through the tropical and subtropical regions. Most of the species occur in tropical and temperate Asia, but there are some species also in Africa, the Americas, Pacific Islands and Australia (Renvoize 1987, Judziewicz 1990, Clayton *et al.* 2006). In the Neotropical region, *Isachne* is distributed from the South of Mexico to the Midwest and Southeast Brazil. The species occupy preferably sites with humid soils, associated with flooded grasslands or riparian vegetation (Rodrigues & Filgueiras 2016), as well as dry or wet montane vegetation, cracks in rocky outcrops, banks over mosses, sandy banks, disturbed places or cultivated lands, in altitudes ranging 0–2400 m (Rodrigues & Filgueiras 2018).

#### Key to the Neotropical species of *Isachne*

1. Anthoecia evidently dissimilar in pilosity, being the lower glabrous to glabrescent, and the upper with appressed pubescent to appressed pilose trichomes
  2. Lower lemma longitudinally sulcate on the back [Brazil] ..... *I. salzmannii*
  2. Lower lemma not sulcate on the back
    3. Culms robust, somewhat lignified; leaf blades 10-30 cm long; panicles 15-30 × (6-) 9-15 cm [Brazil] ..... *I. goiasensis*
    3. Culms herbaceous, slender; leaf blades up to 6.5 cm long; panicles (1-)2.5-10 × 1-6 cm
      4. Leaf blades base rounded to slightly attenuate, not amplexicaul; glumes entirely hirsute [Brazil] ..... *I. hirtiglumis*
      4. Leaf blades base cordate to subcordate, amplexicaul; glumes glabrous, scaberulous or hispidulous towards the apex [Mexico to Brazil and Bolivia] ..... *I. polygonoides*
1. Anthoecia evidently similar in pilosity, both glabrous to glabrescent or with appressed pubescent trichomes
  5. Culms herbaceous, slender
    6. Panicle contracted, spike-like [Jamaica and Haiti] ..... *I. pygmaea*
    6. Panicle open to subcontracted
      7. Leaf blades linear; both anthoecia with appressed-pilose trichomes [Cuba] ..... *I. leersioides*
      7. Leaf blades linear-lanceolate to lanceolate; both anthoecia glabrous to glabrescent

8. Leaf blades rigid, pungent [Antilles] ..... 13. *I. rigidifolia*
8. Leaf blades flexible, not pungent
9. Midrib of the leaf blades inconspicuous; panicle mostly with first-order branches; pedicels without a conspicuous glandular band; rachilla between the anthoecia hirsute [Antilles and North and Northwest of South America]..... 12. *I. rigens*
9. Midrib of the leaf blades conspicuous; panicle with first and second-order branches; pedicels with a conspicuous glandular band; rachilla between the anthoecia glabrous [Dominica].....*I. soderstromii*
5. Culms robust, somewhat lignified
10. Culm-internodes blackish to dark-purple [Brazil] .....*I. burchellii*
10. Culm-internodes greenish, stramineous or dark-brown (sometimes purple-stained towards the nodes)
11. Glumes hispidulous at the apex [Puerto Rico and Dominica]..... 1. *I. angustifolia*
11. Glumes glabrous, pubescent, puberulous or pilose towards the apex, trichomes present as a tuft
12. Rachilla conspicuously pilose at the apex near the callus of the upper anthoecium [North and Northwest of South America]..... 8. *I. ligulata*
12. Rachilla glabrous between the lower and the upper anthoecia
13. Panicle open to lax, loose, flexible; glumes distinctly acuminate to cuspidate, glabrous or rarely with tiny scarce trichomes at the apex [Antilles] .....2. *I. arundinacea*
13. Panicle subcontracted to open; glumes not distinctly acuminate or cuspidate, often with a tuft of trichomes at the apex
14. Main axis of the synflorescence, branches, and branchlets pubescent, trichomes sparse, silky, soft, non-tuberculate; spikelets regularly distributed in the synflorescence branches [Mexico, Guatemala, Belize, and Nicaragua] .....10. *I. pubescens*
14. Main axis of the synflorescence, branches, and branchlets glabrous, minutely scaberulous or densely hirsute, trichomes often tuberculate; spikelets often aggregated towards the tips of the synflorescence branches [Mexico to the north and west of South America] ..... 4. *I. glaucescens*

1. *Isachne angustifolia* Nash, Bull. Torrey Bot. Club 30(7): 377. 1903 [publ. as “*Isachne angustifolium*”]. Type: PORTO RICO: Luquillo Mountains, on the summit of El Yunque, [July 1902], P. Wilson 160 (holotype NY-00071108 image!; isotype US-0102598!).

Perennial, suberect, trailing or clambering, 75-150(-250) cm long. Culms rooting at the lower nodes, branched in the distal portion, robust, somewhat lignified, sterile and flowering branches erect to suberect; nodes glabrous, blackish, dark-brown or stramineous, without a glandular stripe below; internodes inconspicuously hollow, glabrous, greenish to stramineous. Sheaths longer or shorter than the internodes, glabrous or pilose, trichomes tuberculate, deciduous, one margin ciliate, the other glabrous, cilia ca. 2-3 mm long, those toward the ligular region ca. 2-4 mm long, colorless; ligule ciliate, ca. 0.1-0.5 mm long; leaf blades distichous, most abundant in the ascending flowering and/or flowering branches, linear-lanceolate to lanceolate, 5-15 × 0.5-1.3 cm, flexible (not rigid), midrib absent or present, base rounded, slightly constricted near the ligular region, apex acute, glabrous on both surfaces, margins entire, often involute, glabrous or with a few sparse trichomes near the ligular region. Panicle terminal, open to subcontracted, semi-rigid, 7-23 × 3-13 cm, densely scabrous or glabrous, provided with second-order branches, branches ascending, sometimes purplish, glandular bands absent, axillary glands present; pedicels 0.2-5.5(-7) mm long, cylindrical, glabrous to pubescent, glandular bands absent. Spikelets unequally pedicelled, erect on the pedicels, elliptic, (0.7-)1.3-1.7 mm long, grouped in numbers of 2-4 at the branchlets tips forming small fascicles, or ungrouped and not forming small fascicles; glumes subequal, elliptic-obovate to obovate or elliptic, obtuse, hispidulous at the apex, greenish to purple-stained or almost completely purple, both ca. 0.1-0.3 mm shorter than the anthoecia; lower glume 0.9-1.4 mm long, 5-6-nerved, margins pale-green or purple; upper glume 1-1.4 mm long, 5-6-nerved, margins pale-green or purple; anthoecia 2, similar, coriaceous, greenish or usually purple-stained at the tips; lower anthoecium bisexual or staminate, 1-1.5 mm long, lemma glabrous or with minute scarce trichomes, mostly at the base and margins, not sulcate, palea glabrous or with scarce trichomes, mostly at the base and margins, 1-1.4 mm long; rachilla conspicuous between the anthoecia, 0.2-0.3 mm long, somewhat enlarged towards the apex, glabrous or with some occasional trichomes; upper anthoecium bisexual, 0.7-1.3 mm long, lemma glabrous or with scarce trichomes, palea glabrous or with scarce trichomes, mostly at the base and margins, 0.7-1.2 mm long. Lodicules ca. 0.1 mm long. Stamens 3, filaments up to 1 mm long, yellowish; anthers 0.7-1 mm long, purple, yellowish to orange in maturity. Stigmas 2, plumose, purple. Caryopsis 0.7 × 0.5 mm, suborbicular, flat-convex, dark-brown.



*Etymology:* From the Latin: “*angustus*”: narrow; “*folium*”: leaf (Clifford & Bostock 2007). The epithet refers to the narrow, somewhat rigid and ascending leaf blades.

*Distribution:* Puerto Rico and Dominica, in the Antilles. There are also unconfirmed records from Guadeloupe, Saint Kitts and Nevis, and Martinique. The occurrence of *I. angustifolia* in the Windward Islands is presently confirmed only to Dominica.

*Comments:* Hitchcock (1920, 1936) previously cited the collections “*Duss 2705 (NY)*” from Guadeloupe and “*Box 146 (US)*” from Saint Kitts (Leeward Islands) as *I. angustifolia*; however, these are sterile individuals with culms and leaves only. Acevedo-Rodríguez & Strong (2012) reported the occurrence of *I. angustifolia* also in Martinique, without citing vouchers. Consequently, the identity of the specimens could not be checked and the occurrence of the species in those localities could not be confidently confirmed.

After analyzing a large set of samples, we concluded that all plants of *I. angustifolia* collected in Puerto Rico agree morphologically with the type specimen [i.e., *P. Wilson 160 (NY, US)*]. There are also a few collections of *I. angustifolia* from Dominica. It is noteworthy that the plants found in Dominica differ from the typical plants found in Puerto Rico, notably in relation to the synflorescence architecture. The most evident differences are the occurrence of glabrous synflorescences branches and branchlets, longer pedicels, and ungrouped spikelets that do not form small fascicles at the synflorescence tips.

Such morphological differences added to the geographical isolation of the populations in these two islands suggest a probable speciation process in *I. angustifolia*. Therefore, it appears to be plausible to give the specimens from Dominica an infraspecific status, considering that both the geographical and the morphological evidence to support this decision.

#### Key to the subspecies of *Isachne angustifolia*

1. Synflorescence branches and branchlets densely scabrous; pedicels 0.2-1.5 mm long; spikelets grouped in numbers of 2-4 at the branchlets tips, clearly forming small fascicles; plants from Puerto Rico .....*Isachne angustifolia* subsp. *angustifolia*
- I.* Synflorescence branches and branchlets glabrous; pedicels (0.7-)2-5.5(-7) mm long; spikelets regularly distributed, not grouped at the branchlets tips nor clearly forming small fascicles; plants from Dominica ..... *Isachne angustifolia* subsp. *dominicensis*

1.1. *Isachne angustifolia* Nash subsp. *angustifolia* [autonym]. Type: PORTO RICO: Luquillo Mountains, on the summit of El Yunque, [July 1902], *P. Wilson 160* (holotype NY-00071108 image!; isotype US-0102598!).

Figure 2

*Diagnosis:* Perennial. Culms branched, rooting at the lower nodes. Sheaths glabrous or pilose, trichomes tuberculate, deciduous; leaf blade midrib absent or inconspicuous. Panicle branches and branchlets densely scabrous; pedicels 0.2-1.5 mm long, glabrous to pubescent. Spikelets grouped in numbers of 2-4 at the branchlets tips, clearly forming small fascicles; lower and upper anthoecia glabrous or with scarce trichomes at the base.

*Distribution:* This subspecies is known only from Puerto Rico, in the Greater Antilles (Figure 3). As previously discussed, although probable and recorded by Acevedo-Rodríguez & Strong (2012), the occurrence of this taxon in Guadeloupe, Saint Kitts and Nevis and Martinique could not be confidently confirmed. It inhabits preferably montane rainforest, associated with wet and moist places, streams, gallery forest, slopes, rocky hills, open places, disturbed areas and roadsides; ca. 450-1340 m alt.

*Phenology:* Collected in flower from December to October.

*Comments:* *Isachne angustifolia* subsp. *angustifolia* is characterized by presenting 2-4 short-pedicelled spikelets (pedicels 0.2-1.5 mm long) grouped at the synflorescence branchlets tips, forming small fascicles.

Aggregate spikelets also occur in various specimens of *I. glaucescens*. In this species, however, all the spikelets tend to be crowded towards the ends of the branches and branchlets, in a clearly indistinct pattern of small fascicles. In addition, *I. glaucescens* has a much broader distribution, occurring from Mexico to the north of South America, while *I. angustifolia* subsp. *angustifolia* is presently known from Puerto Rico, with probable occurrence in some of the Leeward Islands.

Exceptional variation in the fertility of the lower anthoecium was observed in the specimens “*Stevens et al. 256 (NY)*”, “*I. Vélez 1893 (MO)*” and “*F. Hahn s.n. (MO-5391851)*”. Although the lower anthoecium is commonly staminate, these specimens have a bisexual lower anthoecium.

Material examined: PUERTO RICO. ADJUNTAS: Monte Capáez, 29 March 1886, *P. Sintenis 4045* (MO, NY image, P image); Monte Gilarte summit, 25 May 1940, *J.I. Otero 739* (NY). BARRANQUITAS: Monte Torrecillas, mountain summit, alt. 900-1100 m, 19-20 March 1915, *N.L. Britton et al. 5595* (NY image). CEIBA: Pico del Oeste, Sierra de Luquillo, alt. 1020 m, 18 March 1966, *L. Evans 49* (NY). JAYUYA: Cerro de Punta, alt. 1300 m, 11 July 1962, *Bro. Alain 9475* (NY image); Saliente, alt. 1000-1200 m, 27 September 1987, *P.M. McKenzie 744* (NY image); Cordillera Central, Hwy 143 at and along road to top of Cerro Punta, alt. 3775-4000 ft., 07 July

2008, *R.D. Worthington* 35258 (ASU image). LUQUILLO: Sierra de Luquillo, 1852-1853, *Blauner* 240? (NY-01051427 image); Sierra de Luquillo, in monte Yunque, 14 July 1885, *P. Sintenis* 1355 (NY image, P-01936060 image, P-01936061 image); El Yunque, 28 August 1913, *F.L. Stevens & W.E. Hess* 2783 (NY image); El Yunque, Mount Britton, 15 June 1939, *J.I. Otero* 651 (NMC, NY image); El Yunque, Britton Towers, edge of woods, 04 October 1941, *H.L. Blomquist* 11964 (IND image, MO); El Yunque, Mount Britton, high elevation, May 1943, *I. Vélez* 1893 (MO); El Yunque, 31 December 1953, *C. Rossy-Valderrama* s.n. (FSU-19416 image); El Yunque, March 1959, *M. Medina* 573 (NY image); El Yunque National Forest hanging on vertical earth bank near summit of Mt. El Yunque, alt. 3490 ft., 08 August 1965, *W.R. Stimson* 1857 (MO, NY image); Luquillo Forest, disturbed area of Pico del Toro, 24 May 1970, *S.R. Hill* 53 (UVMVT image); Luquillo National Forest, zone above Sierra Palms, path to summit of El Yunque, 24 March 1973, *D. Burch et al.* 6625 (MO, NY image, USF image); Along the Navy road to Pico del Este, alt. ca. 3000 ft., 09 March 1989, *C.M. Taylor* 8562 (P image); Caribbean National Forest, El Yunque area, 21 January 1994, *P. Acevedo-Rodriguez & A. Siaca* 6219 (MO); On the top of the Sierra de Luquillo, along the Pico del Este road, about 2-3 km west of the end of the road, 18°20'N, 65°40'W, alt. 1000 m, 06 June 1994, *C.M. Taylor & L. Walker* 11852 (MO); El Yunque, Caribbean National Forest, along El Toro Pk. trail., 18°16.2'N, 65°49.3'W, alt. 850-1075 m, 04 January 1995, *P. Acevedo-Rodriguez* 7110 (NY image, US). MARICAO: Maricao to Mt. Alegrillo, alt. 750 m, 03 April 1913, *N.L. Britton et al.* 2566 (NY image); La Chiquita, near Maricao, alt. 650-700 m, 15 February 1915, *N.L. Britton & J.F. Cowell* 4271 (MO, NY image); Without locality, dry bank, mountain forest, 19 May 1935, *F. Hahn* s.n. (MO-5391851). NAGUABO: Sierra de Naguabo, Rio Icaco and adjacent hills, alt. 465-720 m, 30 July-05 August 1914, *J.A. Shafer* 3477 (NY image); Bo. Río Blanco, Caribbean National Forest, along 1.5 km stretch up Río Sabana S of closed portion of Rt 191, alt. 480-600 m, February 1991, *F. Axelrod & P. Chavez* 4128 (NY). PATILLAS: Carite Forest Reserve, alt. 835 m, 20 October 1990, *F. Axelrod & C. Lumer* 1485 (P image); PONCE: Summit of Cerro de la Punta, alt. 1320 m, 18 March 1926, *H.A. Gleason & M.T. Cook* P-36 (NY image); Cerro de la Punta, moist hillside, 25 March 1937, *I. Vélez* 1092 (NY image); Toro Negro, 04 April 1964, *J.A. Duke* 7376 (MO, NY image); Toro Negro, alt. 1000-1100 m, 30 January 1979, *A.H.L.P. Liogier & L.F. Martorell* 28276 (NY); Cerro de la Punta, alt. 1338 m, 26 March 1980, *F.W. Gould et al.* 15855 (MO); Toro Negro Forest Reserve, Rt 143, km 19.1, ridge road in mountain forest, alt. ca. 1200 m, 05 January 1992, *F. Axelrod et al.* 3575 (NY); Cordillera Central, Hwy 143, about km 19, just E of junction Hwy 143 and Hwy 139, ca. 18°9.507'N, 66°33.832'W, alt. ca. 1200 m, 11 February 2003, *H.I. Stevens et al.* 256 (MO, NY). RIO GRANDE: Caribbean National Forest, along Mt. Britton trail, wet mountain forest, alt. 825-900 m, 26 May 1993, *F. Axelrod* 6208 (MO). UTUADO: without precise locality, March 1887, *P. Sintenis* 6421 (NY-01051407 image, NY-01051416 image[fragm.]).

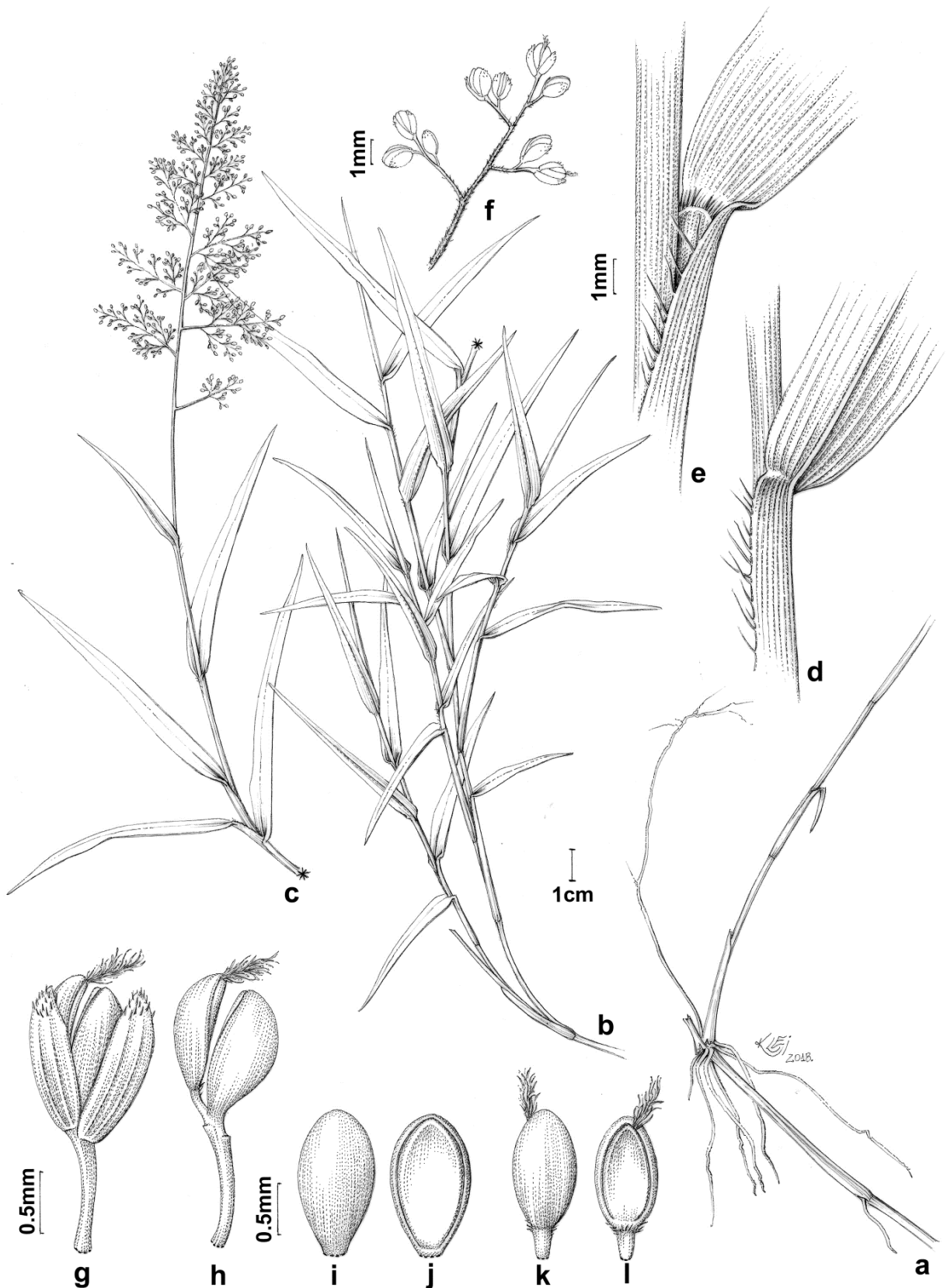


Figure 2. *Isachne angustifolia* subsp. *angustifolia*. a. Basal portion of the culm. b. Branched middle portion of the culm. c. Apex of a flowering branch with a synflorescence (note the spikelets grouped in small fascicles at the top of the panicle branchlets). d. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath. e. Fragment of the culm showing the base of the leaf blade, the ciliate ligule, and the apex of the leaf sheath. f. Detail of a synflorescence branchlet with spikelets in fascicles. g. Spikelet in lateral view and pedicel without a glandular band. h. Anthoecia (glumes removed) and pedicel without a glandular band. i. Lower anthoecium, lemma view. j. Lower anthoecium, palea view. k. Upper anthoecium, lemma view. l. Upper anthoecium, palea view. Based on: a-l. *L. Evans 49 (NY)*. Illustration by Klei R. Sousa.

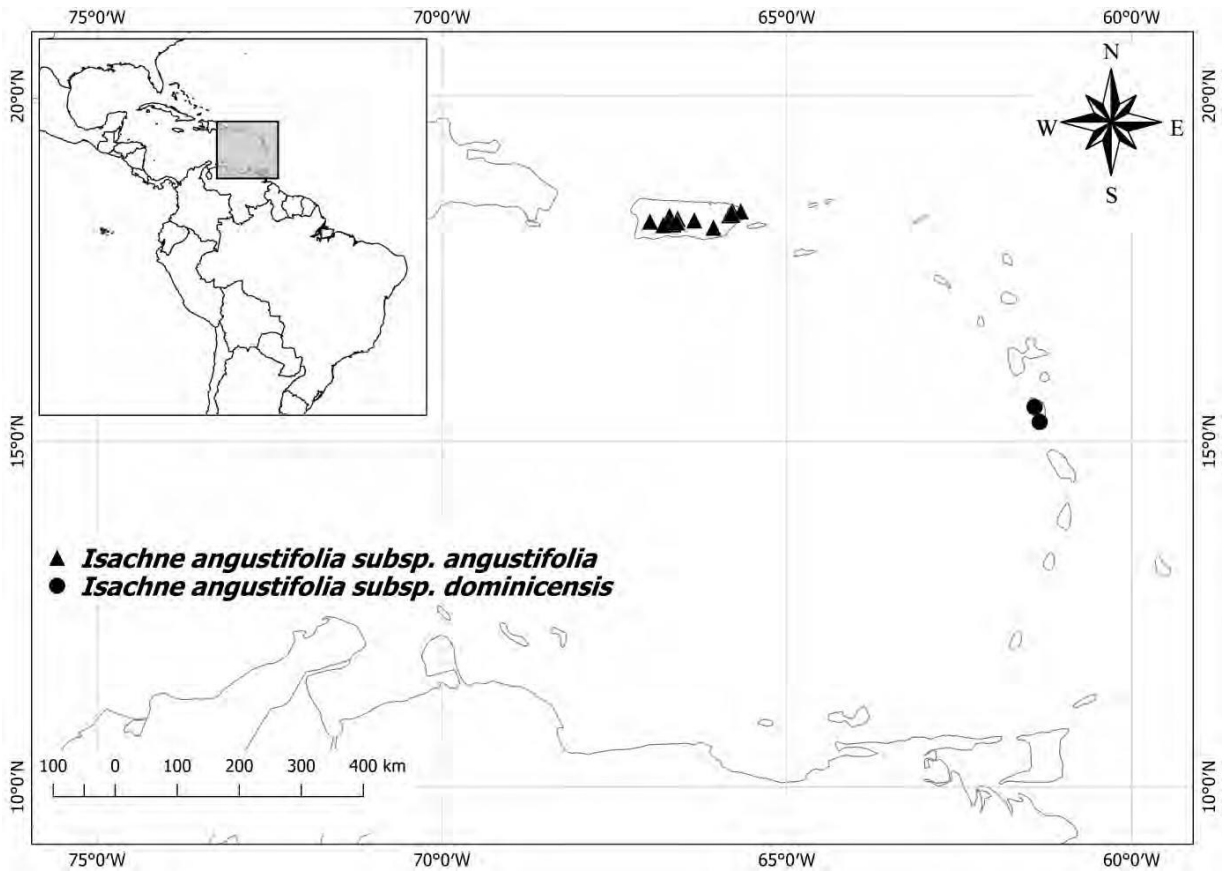


Figure 3. Known distribution of *Isachne angustifolia* subsp. *angustifolia* (excluding the unconfirmed records from Guadeloupe and Saint Kitts and Nevis), and *I. angustifolia* subsp. *dominicensis*.

1.2. *Isachne angustifolia* Nash subsp. *dominicensis* R.S. Rodrigues & Filg., *subsp. nov.* Type: DOMINICA. Saint George Parish: trail to summit of Morne Anglais from Giraudel, old volcanic peak, forested, 15°17'N, 61°20'W, 02 June 1996, S.R. Hill 28081 (holotype MO!; isotypes ILLS image!, NY!).

Figure 4

Diagnosis: Perennial. Culms branched, rooting at the lower nodes. Sheaths glabrous; leaf blade midrib present. Panicle branches and branchlets glabrous; pedicels (0.7-)2-5.5(-7) mm long, glabrous. Spikelets ungrouped, regularly distributed, not forming small fascicles at the branchlets tips; lower and upper anthoecia with scarce trichomes irregularly distributed, mostly at the margins of lemmas and base of paleas.

*Etymology:* From the Latin: “-ensis”: denoting origin (Clifford & Bostock 2007). The epithet refers to the locality of origin of this subspecies, Dominica, in the Lesser Antilles.

*Distribution:* This subspecies is known only from Dominica, in the Lesser Antilles (Figure 3). It inhabits preferably montane nebular forests and volcanic peaks, trailing or scrambling in the understory vegetation, forest edges, and trails; at ca. 1060-1220 m.

*Phenology:* Collected in flower in June.

*Comments:* *Isachne angustifolia* subsp. *dominicensis* is similar to *I. angustifolia* subsp. *angustifolia* in relation to the vegetative morphology, but greatly differ in the synflorescence architecture and pedicels length, as previously discussed.

This subspecies is also morphologically related to *I. soderstromii*. Despite their similarities, *I. soderstromii* is promptly distinct by the smaller synflorescences and by the occurrence of glandular bands on the pedicels.

The architecture of the synflorescence of *I. angustifolia* subsp. *dominicensis* is similar to that found in several Neotropical species of the genus, such as in some specimens of *I. arundinacea*, *I. burchellii*, *I. goiasensis*, and *I. pubescens*; however, a series of other morphological particularities in the vegetative and reproductive characters allow the distinction among these species.

Although it is recognized and described here as a new subspecies, *I. angustifolia* var. *dominicensis* cumulates geographical and morphological characters that may be interpreted in the future as deserving a specific status. Future studies are required to clarify the relationship among this taxon and their close congeners.

Material examined: DOMINICA. SAINT PETER: Morne Diablotin, NW ridge, mossy cloud forest, alt. 3500-4000 ft., 11 June 1965, G.L. Webster 13336 (US) [paratype].

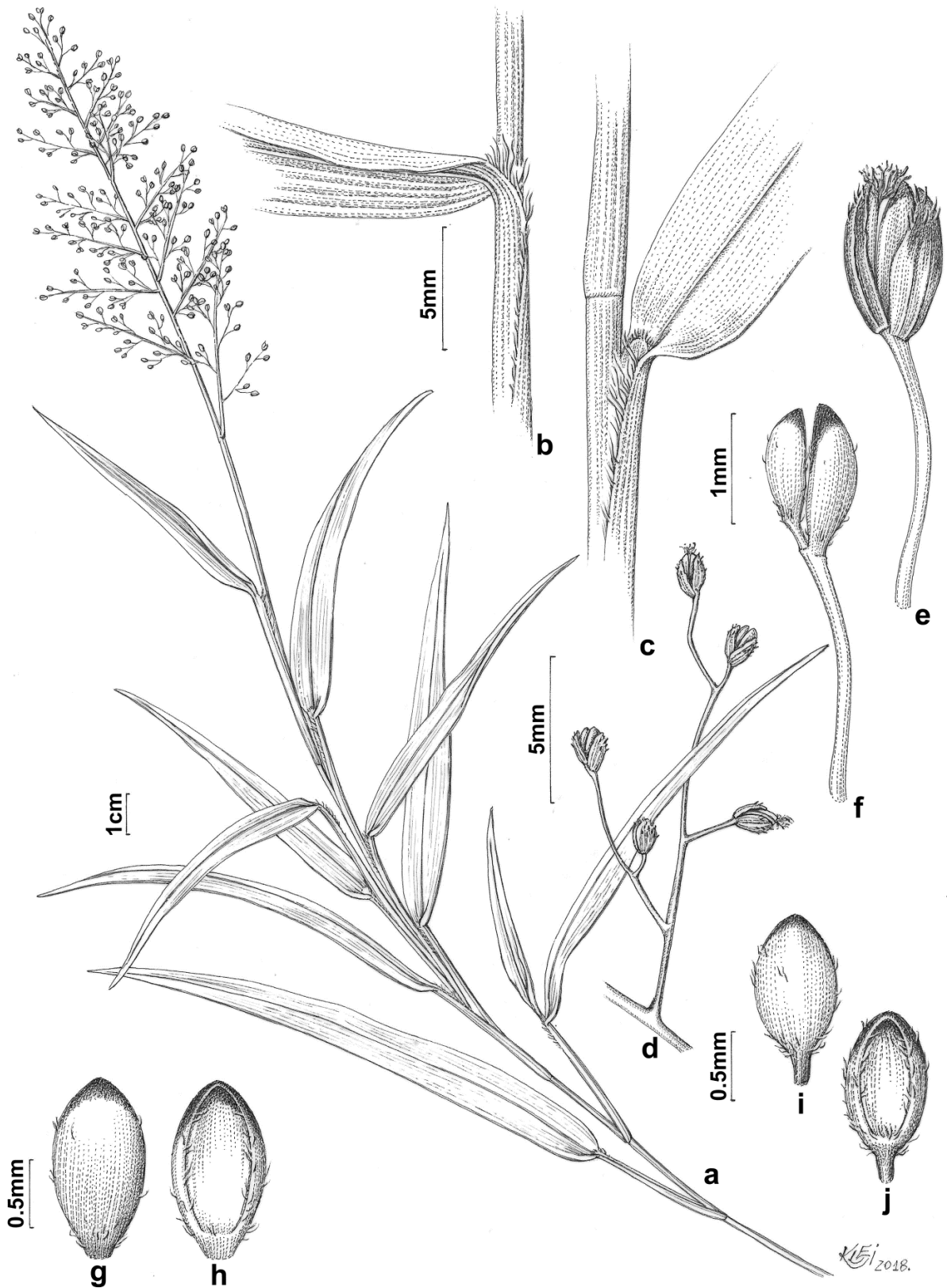


Figure 4. *Isachne angustifolia* subsp. *dominicensis* R.S. Rodrigues & Filg. a. Middle portion of the culm and apex of a flowering branch with a synflorescence (note the spikelets not grouped in small fascicles at the top of the panicle branchlets). b. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath. c. Fragment of the culm showing the base of the leaf blade, the ciliate ligule, and the apex of the leaf sheath. d. Detail of a synflorescence branchlet with spikelets not grouped in fascicles. e. Spikelet in lateral view and pedicel without a glandular band. f. Anthoecia (glumes removed) and pedicel without a glandular band. g. Lower anthoecium, lemma view. h. Lower anthoecium, palea view. i. Upper anthoecium, lemma view. j. Upper anthoecium, palea view. Based on: a-i. *S.R. Hill 28081 (MO, US)*. Illustration by Klei R. Sousa.

2. *Isachne arundinacea* (Sw.) Griseb., Fl. Brit. W. I. 533. 1864.  $\equiv$  *Panicum arundinaceum* Sw., Prodr. 24. 1788. Type: JAMAICA. s.l., s.a., O.P. Swartz s.n. [lectotype (here designated) S-R-3937, pro parte (incl. spec. dexter, excl. spec. sinister)].
- = *Isachne disperma* (Lam.) Döll, Fl. Bras. 2(2): 274. 1877.  $\equiv$  *Panicum dispernum* Lam., Tabl. Encycl. 1: 173. 1791. Type: SOUTH AMERICA. Ex Amer. merid. Com. D. Richard., s.a., L.C.M. Richard s.n. [holotype P-00563958 image!; isotype US- 2830913 (fragment ex P) image!].
- = *Panicum multinerve* Desv. ex Poir., Encycl., Suppl. 4: 279. 1816. Type: PUERTO RICO. Cette plante croît aux Antilles, s.a., ex *Herb. Desvaux* s.n. [holotype P-00740912 image!; isotype US-2830914 (fragment ex P) image!].
- = *Isachne dubia* Kunth, Révis. Gramin. 1: 42. 1829 [nom. illeg. superfl.].

#### Figure 5

Perennial, suberect to scandent, (100-)150-650 cm long. Culms rooting at the lower nodes and branched at the middle and upper portion/nodes, robust, lignified, sterile and flowering branches usually ascending-scandent; nodes glabrous, dark-brown to blackish, sometimes purplish in the young culms; internodes hollow, glabrous, greenish to stramineous in the older culms. Sheaths usually longer than the internodes in the sterile and flowering branches, shorter and usually deciduous in the basal and the middle portion of the culms, glabrous, strongly nerved, one margin ciliate, the other glabrous, cilia 0.7-1 mm long, those near the ligular region ca. 2 mm long, colorless; ligule ciliate, 2 -3.5 mm long; leaf blades distichous, regularly distributed along the culms, but more abundant in the flowering or sterile branches, lanceolate, 10-30  $\times$  0.9-3.5 cm, flexible (not rigid), midrib conspicuous, base rounded, slightly constricted near the ligular region, not amplexicaul, apex acute to acuminate, glabrous on both surfaces and inconspicuously scaberulous on the abaxial surface of the young leaves, margins inconspicuously scabrous. Panicle terminal, open to lax, loose, flexible, 11-30  $\times$  10-25 cm, glabrous, provided with second-order branches, glandular bands absent, axillary glands present; pedicels 0.2 -1.6 mm long, cylindrical, glabrous, glandular bands absent. Spikelets unequally pedicelled, erect on the pedicels, elliptic to obovate, 1.3-1.7 mm long; glumes subequal, elliptic to obovate, typically acuminate to cuspidate (nerves converging at the apex), glabrous, rarely with tiny trichomes scarce at the apex, greenish or purple-stained, becoming stramineous or dark-brown in maturity, both usually longer than or less frequently almost subequal the anthoecia; lower glume 1.1-1.6 mm long, 5-7-nerved, margins pale-green to hyaline; upper glume 1.1-1.6 mm long, 7-9-nerved, margins pale-green to hyaline; anthoecia 2, similar, subcoriaceous to coriaceous, elliptic or elliptic-obovate, greenish, purple-stained to stramineous in maturity; lower anthoecium bisexual, 1.1-1.2 mm, lemma glabrous or



with some lateral trichomes at the base, not sulcate, palea glabrous, ca. 1.1 mm long; rachilla inconspicuous between the anthoecia, 0.1-0.2 mm long, glabrous; upper anthoecium bisexual, 0.9-1.1 mm, lemma glabrous or with some lateral trichomes at the base, palea glabrous or with an inconspicuous fringe of trichomes at base, 1 mm long. Lodicules ca. 0.2-0.3 mm long. Stamens 3, filaments ca. 0.5 mm long, yellowish; anthers 0.5-0.6 mm long, dark-brown. Stigmas 2, plumose, orange to dark-brown in maturity. Caryopsis  $0.7 \times 0.5$  mm, sub-orbicular, flat-convex, dark-brown.

*Etymology:* From the Latin: “*arundo*”: reed, cane; “*-acea*”: like (Clifford & Bostock 2007). The epithet refers to the tall culms, thereby resembling a reed, or even to the robust habit and synflorescences like those of *Arundo* L.

*Distribution:* Antilles, with confirmed records for Jamaica, Puerto Rico, Saint Kitts and Nevis, Guadeloupe, Dominica, Martinique, Saint Lucia, Saint Vincent and Grenada (Figure 6). Acevedo-Rodríguez & Strong (2012) recorded this species (as *I. disperma*) also for Montserrat, Saint Martin and Tobago, but we have examined no material from these localities that corresponds to *I. arundinacea*, as circumscribed in this revision. It inhabits montane nebular forests, forest slopes, and peaks; at ca. 500 -1600 m.

*Phenology:* Collected in flower throughout the year, except in May.

*Comments:* *Isachne arundinacea* is morphologically similar to *I. glaucescens* mostly in relation to its habit and vegetative characters. Some individuals of *I. glaucescens* with broader panicles can be also misidentified as *I. arundinacea*. Nevertheless, *I. arundinacea* can be promptly distinguished by the larger and not congest panicles, or by the spikelets regularly distributed (non-aggregated) in the synflorescences and the typical acuminate/cuspidate glumes.

The specimen “*R.A. Howard 19578 (NY)*” is unusual in having the upper anthoecium appressed-pilose, mostly along the margins and at the base, and its leaf blades are conspicuously scaberulous on the abaxial surface. This specimen corresponds to a small and poorly developed individual collected in an area covered by volcanic ash. Because the diagnostic characters leave no doubt regarding the identity of this specimen, these morphological peculiarities are considered a reflection of the environmental conditions.

*Nomenclatural notes:* *Isachne arundinacea* was described from a mixed collection. The type specimen at Stockholm (S) is mounted with two fragments of distinct collections: one fragment with a “small unexpanded and congest panicle” on the left, and another with a “large expanded and not congest panicle” on the right. There are several morphological peculiarities between these two fragments that have been contributing to a problematic circumscription of the species. Hitchcock (1920) listed a series of differences

between these fragments but regarded them to distinct stages of maturity. Curiously, such differences related to the maturity proved not to be consistent in any of the specimens of *I. arundinacea* we have examined.

The plant on the left has been traditionally accepted and scattered in the literature as the typical “*I. arundinacea*”. In fact, this fragment is much more in accord to the majority of specimens collected from Mexico to South America by presenting relative medium to small panicles, spikelets evidently aggregated towards the synflorescence tips, glumes not acuminate/cuspidate and pubescent at the summit, and anthoecia dissimilar in length (although some minor variation in the anthoecia length can be found across other American specimens).

On the other hand, the plant on the right is atypical for the traditional circumscription of “*I. arundinacea*”, in which the larger and spread panicle, the apically glabrous and acuminate/cuspidate glumes, and the anthoecia similar in length close connect this specimen with the so-called “*I. disperma*”.

A duplicate of Swartz’s collection at The Museum of Evolution Herbarium (UPS) is composed only by one plant fragment with a small and congest panicle, which is not in conformity with the protologue of *I. arundinacea*.

Essentially, the original description of *I. arundinacea* provided by Swartz (1788) does not differ from that of *I. disperma* (c.f., Lamarck 1791). Both authors are succinct and refer to robust plants with large open panicles (‘*panicula composita patente*’) and long leaf blades (‘*foliis lato-lanceolatis acuminatis rigidis*’) (Swartz 1788), versus (‘*foliis arundinaceis glaberrimis*’) (Lamarck 1791). Therefore, taking into account that the type material of *I. arundinacea* proved to be mixed and considering that its original description corresponds most nearly with the plant on the right side of the sheet, which has a large and open panicle and acuminate/cuspidate glabrous glumes, we designate this specimen as the lectotype in conformity to Art. 9.11 and 9.14 ICN (Turland *et al.*, 2018). Additionally, the name *Panicum arundinaceum* (basionym of *I. arundinacea*) has priority over *Panicum dispernum* (basionym of *I. disperma*) (Art. 11 and 12 ICN). The latter must be treated as a synonym of the first, as did some previous authors.

Hitchcock (1920) also reported that *Panicum multinerve* and *Panicum confertum* are probably the same species and included both in the synonymy of *I. disperma*. In fact, the holotypes of *P. multinerve* and *I. disperma* in Paris (P) represent the same species, which is *I. arundinacea* as circumscribed in this revision. *Panicum confertum* is a distinct taxon

and must be excluded from the synonymy of *I. arundinacea*. For a detailed discussion about nomenclatural issues related to *P. confertum*, see subsequent comments under *I. glaucescens*.

The specimen *O.P. Swartz s.n.* (S06-633), which is assigned as “type specimen of *P. arundinaceum*” at the Swedish Museum of Natural History, is, in fact, the holotype of *Panicum compactum* Sw. ex Wikstr. [= *Lasiacis compacta* (Sw. ex Wikstr.) Hitchc.].

Finally, the combination of *I. disperma* to ‘*Ichnanthus dispermus*’ is attributed to Fournier (1886). Apparently, he never published this name in his “*Mexicanas Plantas*”, although the name is accepted in the synonymy of *I. disperma* in Tropicos and in Soreng *et al.* (2003). In fact, this is an error to be corrected in the data banks.

*Material examined:* — DOMINICA. SAINT GEORGE: Laudat, 16 March 1882, *H.F.A. von Eggers 1056* (US); Laudat, woodlands below Laudat, alt. 500 m, 13 March 1940, *W.H. Hodge 2071* (NY); Morne Micotrin, south slope of Morne Macaque (Micotrin) on road to Fresh Water Lake, montane woodland, alt. ca. 2500-2700 ft., 26 June 1964, *W.R. Ernst 1720* (MO); Morne Micotrin, forested slopes of Micotrin along trail from a point about ½ mile beyond Laudat to one about ½ mile beyond Fresh Water Lake (L’etang), alt. 2300-2700 ft., 14 July 1964, *R.L. Wilbur et al. 7412* (MO, US); Fresh Water Lake, higher montane forest, alt. 900 m, 30 September 1983, *C. Whiterfoord 3822* (US). SAINT PATRICK: Morne Anglais, forested slopes near the summit and thickets at the summit, alt. 3683 ft., 25 July 1964, *R.L. Wilbur et al. 8245* (MO, NY, US). GRENADA. SAINT ANDREW: Grand Etang, mountain wood, November 1904, *W.E. Broadway 76* (NY image, US); Grand Etang, August 1910, *C.T. Brues s.n.* (NY-1603115). WITHOUT LOCALITY: Azimar?, road sides in mountain districts, alt. 1800 ft., 16 September 1904, *W.E. Broadway s.n.* (MO-2095552, NY-1603119); Fedon’s Camp, Ellin Woodland, 08 October 1945, *P. Beard 1281* (MO, US). GUADELOUPE. BASSE-TERRE: Chemin de Lac Flammarion, traces en forêt humide, alt. 1100 m, August 1936, *H. Stehlé 1167* (US); between Plateau de Papaye and Ravine Chaude, above Matouba, alt. 925-975 m, 10 December 1959, *G.R. Proctor 20351* (US); Morne à Louis (Massif des Mamelles), alt. 743 m, 29 June 1975, *A. Raynal-Roques 15953* (US). SAINT-CLAUDE: without precise locality, October 1927, *L.H. Beiley & E.Z. Beiley 64* (NY, US); Dessus des Bains Jaunes, alt. 1000 m, 30 September 1935, *H. Stehlé & M. Stehlé 361* (P image). WITHOUT LOCALITY: without precise locality, 1852, *M. Beaupertuis 1349* (P image); without precise locality, 1858, *T. Husnot 97* (P image, P image, P image, P image, P image, P image, P image, P image); without precise locality, January 1892, *P. Duss 3189* (MO, NY image, US); without precise locality, September 1893, *P. Duss 679* (P image, P image); without precise

locality, 1896-1899, *T. Husnot s.n.* (P-01936016 image); without precise locality, without date, *L.C.M. Richard s.n.* (P-01923982); without precise locality, without date, *M. Beaupertuis s.n.* (P-01923987); without precise locality, without date, without collector (P-01928008 image). JAMAICA. WITHOUT LOCALITY: Parkhurst [?], 1884, *F.L. Scribner 1* (US). MARTINIQUE. SAINT LUCE: Morne Caraïbe, in summit vertice montis, without date, *L.C.M. Richard s.n.* (P-01923989 Image). SAINT PIERRE: Case-Pilote, September 1869, *M. Hahn 1159* (P image, P image); Case-Pilote, alt. 500-1000 m, 1882, *P. Duss 1311* (NY image, US); Pitons du Carbet, Mont Pelée, alt. 1100 m, 13 August 1936, *M. Privault 182* (P image, P image); Pitons du Carbet, 25 August 1936, *M. Privault 276* (P image); Pitons du Carbet, alt. 950 m, 12 April 1940, *H. Stehlé & M. Stehlé s.n.* (US-2180475). WITHOUT LOCALITY: without precise locality, 1857, *M. Belanger 171* (P image); without precise locality, without date, without collector (P-01923990 image). SAINT KITTS AND NEVIS. [Saint Kitts island]: Belmont, in forest ravine, 08 September-05 October 1901, *N.L. Britton & J.F. Cowell 395* (NY image, US); [Nevis island]: Near “The Source”, ca. 2000 ft., 31 January 1932, *H.E. Box 169* (NY Image, US). SAINT LUCIA. QUILESSE: without precise locality, 12 July 1945, *P. Beard 1151* (MO, US). SAINT VINCENT. LA SOUFRIÈRE: On the road path to Soufrière, 23 October 1949, *I. Vélez 3394* (US); Soufrière Crater, along E. (wind-ward) side trail to Soufrière Crater, alt. ca. 1000 m, 24 March 1977, *F.W. Gould 15154* (MO); Near summit of La Soufrière, 10 February 1980, *R.A. Howard 19578* (NY). SAINT ANDREW: Mont Saint Andrew, alt. 1600 m, December 1889, without collector (P-01923977 Image). WITHOUT LOCALITY. Without date, without collector (NY-1603122).

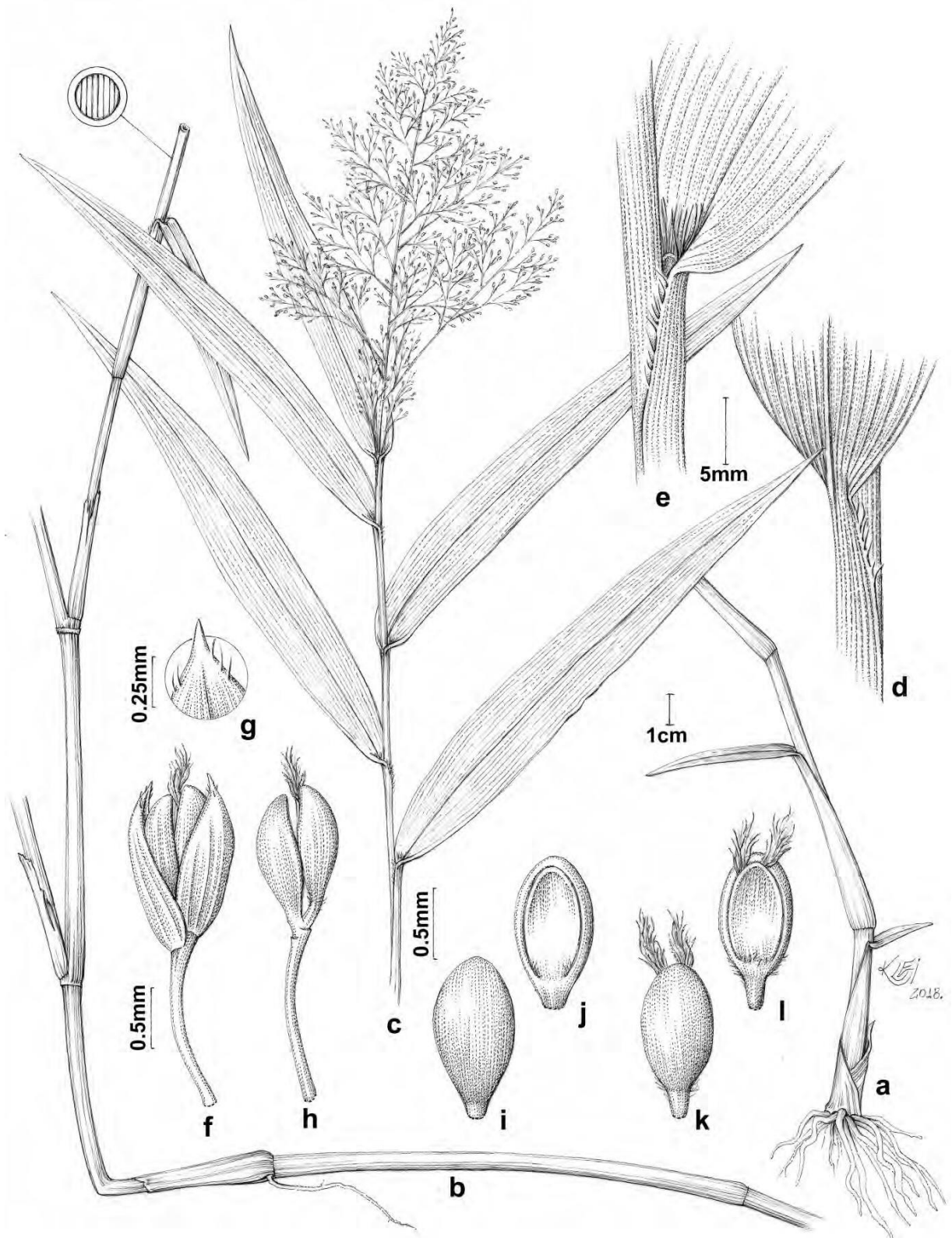


Figure 5: *Isachne arundinacea* (Sw.) Griseb. a. Basal portion of the culm. b. Middle portion of the culm (note branching at the nodes) and detail of the hollow internode. c. Apex of the flowering branch with a large and lax synflorescence and much-nerved leaf blades. d. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath. e. Fragment of the culm showing the base of the leaf blade, part of the ciliate ligule, and the apex of the leaf sheath. f. Spikelet in lateral view (note the acuminate/cuspidate apex of the glumes) and pedicel without a glandular band. g. Detail of the acuminate/cuspidate apex of the upper and the lower glumes. h. Anthoecia (glumes removed) and pedicel without a glandular band. i. Lower anthoecium, lemma view. j. Lower anthoecium, palea view. k. Upper anthoecium, lemma view. l. Upper anthoecium, palea view. Based on: a. G.R. Proctor 20531 (US); b. A. Düss 3189 (US); c. P. Beard 1151 (US); d-l. Without collector (NY-1603122). Illustration by Klei R. Sousa.

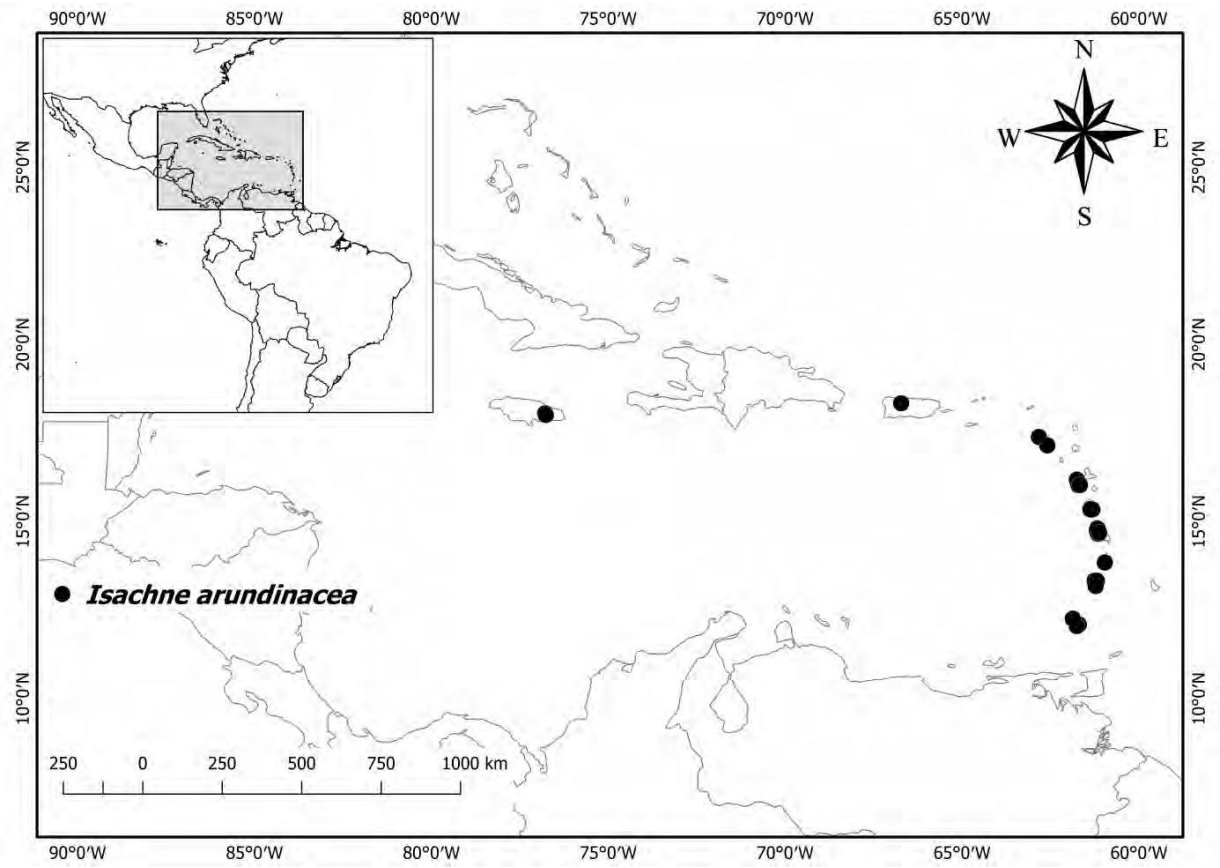


Figure 6. Known distribution of *Isachne arundinacea*.

3. *Isachne burchellii* **R.S. Rodrigues & Filg.**, Brittonia D.O.I.:10.1007/s12228-019-09576-x. Type: RIO DE JANEIRO: [Teresópolis], [30 January 1888], *A.F.M. Glaziou 17400* (holotype NY-00381251!; isotypes B-100460905 image!, K-001055179 image!, K-001055180 image!, P-01923969 image!, P-01923971 image!, P-01923973 image!, W-1987-0002167 image!, W-1916-0021686 image!).

Figure 7

Perennials, suberect to decumbent or trailing, (50-)150-200(-400) cm long. Culms rooting at the lower nodes, branched at the upper portion, robust, somewhat lignified, sterile and flowering branches erect; nodes glabrous, stramineous to blackish, without a glandular stripe below; internodes inconspicuously hollow, glabrous, dark-purple to blackish, sometimes slightly sulcate towards the nodes. Sheaths shorter than the internodes, glabrous, strongly nerved, one margin ciliate, the other glabrous, cilia 0.5 -1.5 mm long, those towards the ligular region 1-3.5 mm long, colorless; ligule ciliate, 4-5 mm long, collar glabrous; leaf blades distichous, regularly distributed over the culms and secondary flowering and/or sterile branches, lanceolate to linear-lanceolate, 8.5-14 × 0.8-1.5 cm, flexible (not rigid nor pungent), midrib conspicuous, base rounded, not amplexicaul, apex acute, glabrous on both surfaces, margins entire to minutely serrate. Panicle terminal, open to lax, the younger ones subcontracted and partially included in the leaf sheaths, flexible, much flowered, (7-)12-20 × (3-)5-10 cm, glabrous to minutely scabrous, provided with second-order branches, glandular bands absent, axillary glands present, inconspicuous; pedicels 2-8 mm long, cylindrical, glabrous or minutely scabrous, glandular bands absent. Spikelets unequally pedicelled, erect on the pedicels, elliptic, 1.5-2 mm long; glumes subequal, elliptic-lanceolate, subacute, glabrous or minutely scaberulous towards the apex, greenish to stramineous, both equaling, slightly short or longer than the anthoecia; lower glume 1.5-2 mm long, 5-nerved, margins pale, involute in maturity; upper glume 1.4-2 mm long, 5-nerved, margins pale; anthoecia 2, similar, subcoriaceous, elliptic, pale green to stramineous; lower anthoecium staminate, 1.3 -1.7(-2) mm long, lemma glabrous or inconspicuously puberulous (bicellular microhairs), not sulcate, palea glabrous or inconspicuously puberulous, 1.3-1.5(-1.8) mm long; rachilla inconspicuous between the anthoecia, 0.3-0.5 mm long, glabrous; upper anthoecium bisexual, 1.3-1.5 mm long, lemma glabrous or inconspicuously puberulous, palea glabrous or inconspicuously puberulous, 1.3-1.4 mm long. Lodicules ca. 0.1 mm long. Stamens 3, filaments 0.1-0.2 mm long, pale-green; anthers 0.2-0.3 mm long, dark-brown in maturity. Stigmas 2, plumose, purplish. Caryopsis not seen.

*Etymology:* The epithet honors John William Burchell (1781-1863), English traveler and plant collector (Clifford & Bostock 2007). Burchell was responsible for collecting the oldest known specimen of *I. burchellii* in Rio de Janeiro, Brazil (Rodrigues & Filgueiras 2019).

*Distribution:* Endemic from Brazil, known only from the mountainous region of the municipality of Teresópolis, environs of the Serra dos Órgãos National Park, Rio de Janeiro State (Figure 8). It inhabits preferably low-montane and montane rainforests, growing on margins or interior of gallery forests or in transition areas with adjacent and humid campos; below ca. 1600 m.

*Phenology:* Collected in flower in January and February.

*Comments:* *Isachne burchellii* is morphologically related to *I. goiasensis*. Both species are very similar in relation to most of their vegetative characters but differ enormously in the synflorescence and spikelet features. *Isachne burchellii* can be distinguished by presenting dark-purple to blackish culm-internodes, the absence of glandular bands on the pedicels and homomorphic anthoecia, which are similar in texture and indumentum.

A detailed discussion about macro and micromorphology, taxonomy and ecology of *I. burchellii* in the context of *I. goiasensis* is addressed in Rodrigues & Filgueiras (2019).

*Nomenclatural notes:* Plants currently named *I. burchellii* were initially treated under “*I. glaziovii*”, which is a *nomem nudum* established by Potztal (1952). Later, Renvoize (1987) validly described *I. goiasensis* and included in the concept of the new species those specimens formerly accepted by Potztal (1952) as “*I. glaziovii*”. Recently, based on macro and micromorphology added to geographical and ecological evidence, Rodrigues & Filgueiras (2019) proposed to split *I. goiasensis*. This proposal is in accordance with Potztal’s initial approach, but the species was described as *I. burchellii* in order to avoid further taxonomic confusion.

Material examined: BRAZIL. [RIO DE JANEIRO]: [Teresópolis], [15 February 1826?], J.W. Burchell 2294 (K-001055181 image, P-01936049 image) [paratypes].



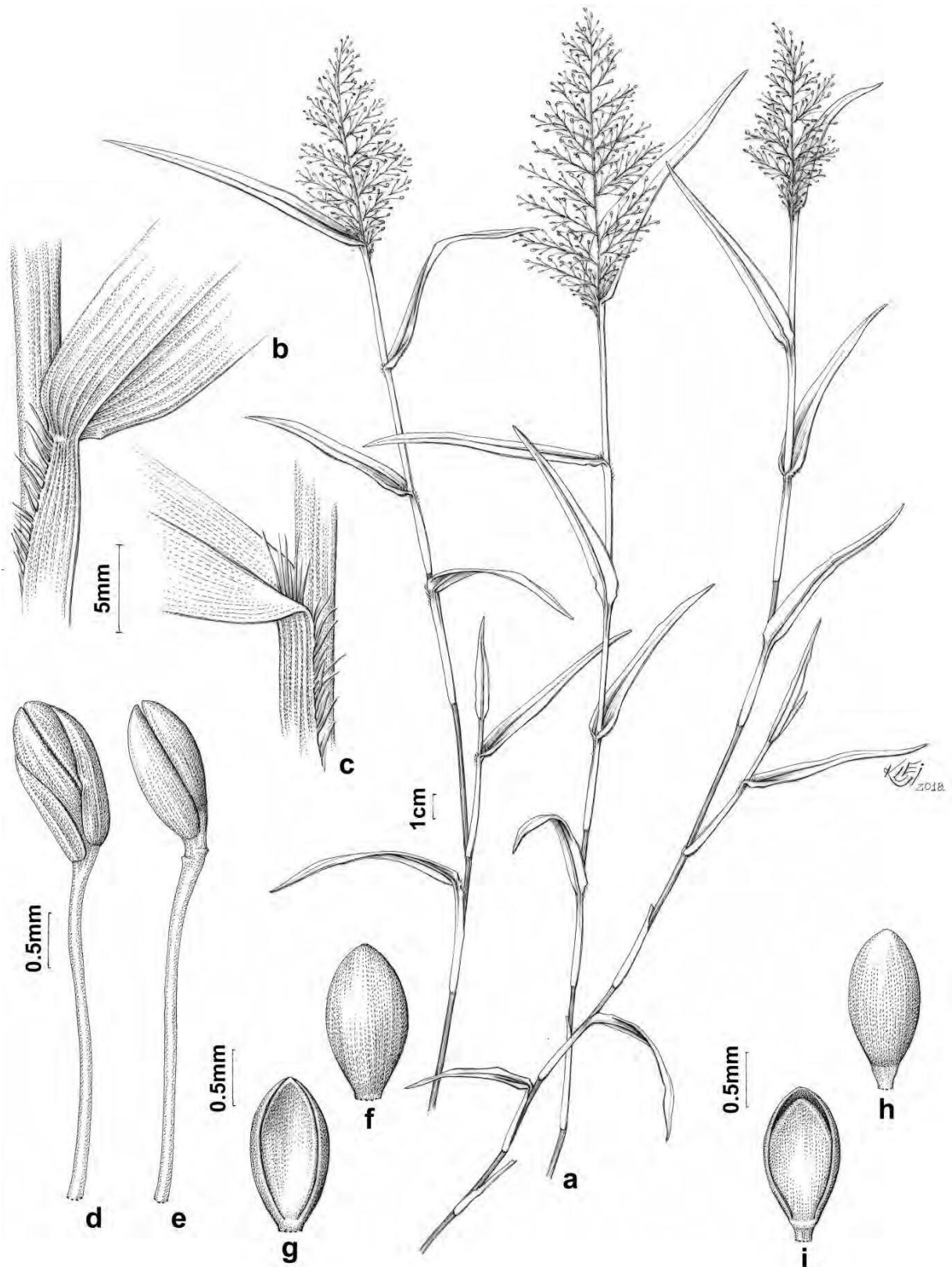


Figure 7: *Isachne burchellii* R.S. Rodrigues & Filg. a. Apex of the culms with flowering branches and synflorescences. b. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath. c. Fragment of the culm showing the base of the leaf blade, part of the ciliate ligule, and the apex of the leaf sheath. d. Spikelet in lateral view and pedicel without a glandular band. e. Anthoecia (glumes removed) and pedicel without a glandular band. f. Lower anthoecium, lemma view. g. Lower anthoecium, palea view. h. Upper anthoecium, lemma view. i. Upper anthoecium, palea view. Based on: a-i. *A.F.M. Glaziou 17400 (NY)*. Illustration by Klei R. Sousa, extracted from Rodrigues & Filgueiras (2019).

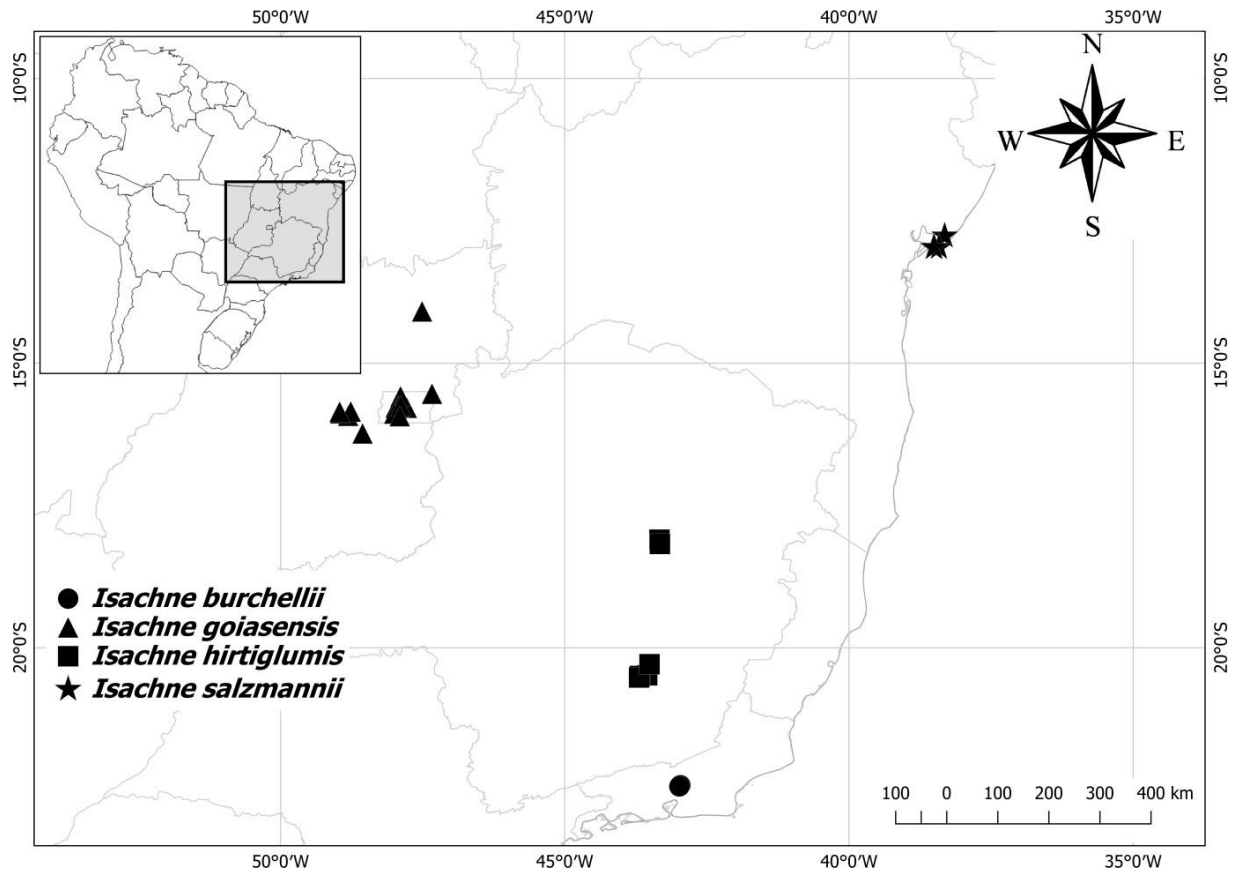


Figure 8. Known distribution of *Isachne burchellii*, *Isachne goiasensis*, *Isachne hirtiglumis*, and *Isachne salzmannii*.

4. *Isachne glaucescens* (Kunth) Pittier, Bol. Técn. Minist. Agric. 1: 49. 1937.  $\equiv$  *Panicum glaucescens* Kunth, Nov. Gen. Sp. (quarto ed.). 1: 104. [January] 1816, non *Panicum glaucescens* P. Beauv., Ess. Agrostogr. 169. 1812 [nom. inval., =*Bambusa multiplex* (Lour.) Raeusch. ex Schult. & Schult. f.], nec *Panicum glaucescens* Nees, Fl. Bras. Enum. Pl. 2(1): 100-101. 1829 [nom. illeg. hom., =*Digitaria bicornis* (Lam.) Roem. & Schult.], nec *Panicum glaucescens* Salzm. ex Döll, Fl. Bras. 2(2): 157. 1877 [nom. inval., =*Setaria parviflora* (Poir.) Kerguélen]. Type: COLOMBIA. Crescit locis planis, propatulis Novae Andalusiae juxta Bordones et in excelsis, opacatis Andium prope Pasto, inter 30 et 1500 hexap. Floret Septembri et Decembri, s.a., *Humboldt & Bonpland s.n.* [holotype P-00128881 image!; isotype US-80676 (fragment ex P) image!].
- = *Panicum confertum* Desv. ex Poir., Encycl., Suppl. 4: 279. [June] 1816. Type: COSTA RICA. Prov. Cartago: along CIA, S. of Cartago; scrambling in brush; elev. 1700 m, 4 June 1973, *R.W. Pohl 12840* [neotype (here designated) MO-2641474!] *syn. nov.*
- = *Isachne panicea* Trin., Gram. Panic. 253. 1826. [nom. illeg. superfl.] *syn. nov.*
- = *Panicum glaucescens* Willd. ex Döll, Fl. Bras. 2(2): 275. 1877 [nom. illeg. hom.], non *Panicum glaucescens* P. Beauv., Ess. Agrostogr. 169. 1812 [nom. inval., =*Bambusa multiplex* (Lour.) Raeusch. ex Schult. & Schult. f.], nec *Panicum glaucescens* Nees, Fl. Bras. Enum. Pl. 2(1): 100-101. 1829 [nom. illeg. hom., =*Digitaria bicornis* (Lam.) Roem. & Schult.], nec *Panicum glaucescens* Salzm. ex Döll, Fl. Bras. 2(2): 157. 1877 [nom. inval., =*Setaria parviflora* (Poir.) Kerguélen]. Type: SOUTH AMERICA [America Meridionali]: s.l., s.a., Willd. herb. n. 18761, *C.L. Willdenow 18761* (holotype: B-W-18761-010 image!). *syn. nov.*

Perennial, scandent to leaning, 100-600 cm long. Culms rooting from the lower nodes, branching at the intermediary and upper nodes, robust, lignified, sterile and flowering branches ascending or often leaning to scandent; nodes glabrous to pilose in the young culms, greenish, stramineous or blackish, without a glandular stripe below; internodes hollow, glabrous to puberulous or pilose, trichomes tuberculate, dehiscent, greenish to stramineous, sometimes dark-brown or purplish towards the nodes. Sheaths usually shorter than the internodes, less often equaling or slightly longer in the flowering branches, often glabrous, less often pilose, especially towards the apex, trichomes tuberculate, dehiscent, strongly nerved, one margin ciliate, the other glabrous, cilia (0.8-)1.5-2 mm long, those near the ligular region 2-2.5 mm long, colorless; ligule ciliate, 3.5-4.5 mm long; leaf blades distichous, regularly distributed along the culms, lanceolate to linear-lanceolate, (7-)11-25  $\times$  0.5-2.5 cm, flexible (not rigid), midrib conspicuous, apex acute, base rounded, slightly constricted near the ligular region, not amplexicaul, glabrous on both surfaces, less frequently pubescent on the adaxial and/or abaxial surface of the young leaves or pilose abaxially, margins entire, glabrous to minutely scaberulous. Panicle terminal, contracted, subcontracted or open, less usually lax, flexible, (4-)5-13(-18)  $\times$  (2-)3-9(-13) cm, usually glabrous to minutely scaberulous or densely tuberculate-hirsute, provided with ascending second-order branches,

strongly branching from the middle portion and/or at the tips of the primary branches, glandular bands absent, axillary glands present, sometimes inconspicuous; pedicels 0.4-1.2-2.5 mm long, cylindrical, glabrous, less usually minutely scaberulous or hirsute, glandular bands absent. Spikelets unequally pedicelled, erect on the pedicels, often aggregated towards the tips of the synflorescence branches, elliptic to subglobose or globose, (1.2-)1.4-1.8(-2) mm long; glumes subequal, elliptic to oblong or roundish, obtuse to subacute, not acuminate or cuspidate, pubescent or pilose at the apex, less usually glabrous, greenish to stramineous, both shorter than or equaling the anthoecia, sometimes equaling only the upper anthoecium; lower glume (0.9-)1.1-1.4(-1.7) mm long, 5-7-nerved, margins greenish, whitish or hyaline, sometimes stramineous; upper glume (0.9-)1.1-1.3(-1.6) mm long, 5-7-nerved, margins greenish, whitish or hyaline, sometimes stramineous; anthoecia 2, similar texture and indumentum, coriaceous, the upper sometimes suborbicular, both subequal in length or the lower longer than the upper, greenish to stramineous, sometimes dark-brown or purple-stained in maturity; lower anthoecium bisexual, 1.3-1.8(-2) mm long, lemma glabrous, not sulcate, palea glabrous, 1.2-1.7(-1.9) mm long; rachilla conspicuous or inconspicuous between the anthoecia, 0.1-0.2 mm long, glabrous; upper anthoecium bisexual, (0.8-)1-1.3(-1.5) mm long, lemma glabrous or with some inconspicuous trichomes laterally at base, palea glabrous, (0.8-)0.9-1.2(-1.3) mm long. Lodicules 0.1-0.2 mm long. Stamens 3, filaments ca. 0.5-0.6 mm long, yellowish; anthers ca. 1 mm long, yellowish to orange, becoming dark-brown in maturity. Stigmas 2, yellow, dark-brown in maturity. Caryopsis 0.6-0.7 × 0.5-0.6 mm, suborbicular, flat-convex, blackish.

*Etymology:* From the Latin: “*glaucresco*”: become glaucous, bluish-green (Clifford & Bostock 2007). The epithet refers to the abaxial surface of the leaf-blades that sometimes become glaucous.

*Distribution:* North America, Central America, Antilles, and South America, from Mexico and Guatemala to the north and west of South America.

*Phenology:* Collected in flower throughout the year.

*Comments:* *Isachne glaucescens* is presently considered an ill-defined species because of its great morphological variability across all its distributional range, either in relation to the vegetative and reproductive characters (Rodrigues & Filgueiras unpubl. res., Chapter 5). This morphological variation together with a problematic circumscription has led to confusing taxonomic approaches and imprecise identifications. Depleted individuals can also be misidentified.

The most remarkable variation found in *I. glaucescens* is related to the synflorescence size, which can vary from small to large, with spikelets aggregate or nearly aggregate at the synflorescence tips.

*Isachne glaucescens* has been traditionally associated with *I. arundinacea* (= *I. disperma*) and, not rarely, both were considered synonyms. The morphological distinction between these species was discussed under the treatment of *I. arundinacea*.

Pohl & Davidse (1994) commented about the morphological affinities between *I. pubescens* and *I. glaucescens* (treated as *I. arundinacea*), suggesting that the first should be better classified as a variety of the second. This approach is not supported by macro and micromorphological evidence (Rodrigues & Filgueiras unpubl. res., Chapter 5). *Isachne glaucescens* can be easily differentiated by the glabrous to tuberculate-hirsute synflorescences with spikelets aggregated at the branchlets tips, whereas *I. pubescens* has whitish, silky and non-tuberculate trichomes on the synflorescences, and spikelets not aggregated at the branchlets tips. Additionally, *I. glaucescens* has a much broader distribution, while *I. pubescens* is geographically more restricted, occurring in Mexico, Belize, Guatemala, and Nicaragua.

Rodrigues & Filgueiras (unpubl. res., Chapter 5) studied the leaf blade epidermis of the Neotropical *Isachne* and demonstrated that some South American specimens related to *I. glaucescens* have a series of macro and micromorphological differences in relation to the North and Central American specimens. Considering their results and the geographical evidence, a new variety for *I. glaucescens* for South America is here described.

New methodologies should be used to evaluate the morphological boundaries of *I. glaucescens* across all its distributional range, including phylogenetic, anatomic, biogeographic and morphological approaches. Morphometric studies are also desirable for a better understanding of the morphological plasticity of this taxon.

*Nomenclatural notes:* As it was previously discussed, the type specimen of *I. arundinacea* at Stockholm (S) is composed by two fragments of distinct collections, and the original description provided by Swartz (1788) is not in conformity with the current usage of the name. Because *I. arundinacea* was found to be the correct name for *I. disperma*, *I. glaucescens* was taken here as the legitimate name to accommodate the plants previously called *I. arundinacea*.

*Panicum confertum* was described in June 1816 from the Antilles and has been traditionally accepted as a synonym of *P. multinerve* (cf., Hitchcock 1920, Zuloaga *et al.* 2003). However, *P. confertum* was established to encompass plants with small panicles (*'panicule droite, d'un grandeur mediocre'*) with branches divided at the apex, bearing a great number of spikelets (*'ses ramifications (...) divisées vers leur sommet en un grand nombre de petits rameaux flexueux, (...) chargés de beaucoup de fleurs pesq'anguleuses'*). This description close connects *P. confertum* and *I. glaucescens*. Because no original material of *P. confertum* is extant at P, a neotype is here designated, according to Art. 9.7 ICN, Turland *et al.* (2018).

Key to the varieties of *Isachne glaucescens*

1. Synflorescence main axis, branches, branchlets, and pedicels glabrous to minutely scaberulous  
 ..... *Isachne glaucescens* var. *glaucescens*
1. Synflorescence main axis, branches, branchlets, and pedicels densely pilose to tuberculate-  
 hirsute ..... *Isachne glaucescens* var. *trichomatosa*

4.1. *Isachne glaucescens* (Kunth) Pittier var. *glaucescens* [autonym]. Type: COLOMBIA.

Crescit locis planis, propatulis Novae Andalusiae juxta Bordones et in excelsis, opacatis Andium prope Pasto, inter 30 et 1500 hexap. Floret Septembri et Decembri, s.a., *Humboldt & Bonpland s.n.* [holotype P-00128881 image!; isotype US-80676 (fragment ex P) image!].

## Figure 9

*Diagnosis:* Perennial. Culms branched at the intermediary and upper nodes, rooting at the lower nodes; internodes glabrous. Sheaths glabrous to tuberculate-pilose towards the apex; leaf blades glabrous on both surfaces, rarely pubescent on the adaxial and/or abaxial surface of the young leaves. Synflorescence main axis, branches, branchlets, and pedicels glabrous to minutely scaberulous. Spikelets elliptic to subglobose; glumes pubescent or pilose at the apex, less usually glabrous; anthoecia similar, subequal in length or the lower longer than the upper.

*Distribution:* North America to Central America, Antilles, and South America. Mexico, Guatemala, Honduras, Nicaragua, Panama, Honduras, Tobago, Jamaica, Costa Rica, Bolivia, Colombia, Ecuador and Venezuela (Figure 10). It inhabits preferably montane rainforest, associated with wet and moist places, streams, gallery forest, slopes, rocky hills, open places, disturbed areas, and roadsides; at ca. 255-2100 m.

*Phenology:* Collected in flower throughout the year.

*Comments:* *Isachne glaucescens* var. *glaucescens* can be easily recognized by its glabrous to scaberulous synflorescence main axis, branches, and branchlets. This variety is characterized by including plants that are glabrous or nearly glabrous, either in the vegetative or reproductive traits (with the exception of glumes). On the other hand, there may be a remarkable variability in the shape and size of spikelets and anthoecia of this taxon.

Rodrigues & Filgueiras (unpubl. res., Chapter 5) characterized the leaf blade epidermis of *I. glaucescens* var. *glaucescens* as composed of adaxial striated intercostal long cells, abaxial papillate costal and intercostal long cells not overarching the stomata, the absence of costal microhairs, and presence of intercostal macrohairs.

Material examined: BOLIVIA. LA PAZ: Prov. Nor Yungas, 16°14'S, 67°47'W, alt. 2100 m, 21 October 1982, *J.C. Solomon 8634* (MO). COLOMBIA. CAQUETA: 10 Km SW of San Jose del Fragua (SW of Florencia), alt. 320-340 m, 11 January 1974, *G. Davidse 5743* (MO); MAGDALENA: Alto Río Buritaca Finca El Paraíso, 73°48'W, 11°05'N, alt. 1100-1400 m, 21 July 1989, *S. Madriñán et al. 449* (MO). COSTA RICA. ALAJUELA: San Carlos, 10°27'10"N, 84°39'30"W, alt. 255-400 m, 27 March 2004, *A. Rodríguez 8644* (MO). ECUADOR. Junction of the provinces of Guayas, Cañar, Chimborazo e Bolivar, foothills of the western cordillera near the village of Bulcay, alt. 1000-1250 ft., 8-15 June 1945, *W.H. Camp 3718* (RB). GUATEMALA. BAJA VERAPAZ: Biotopo del Quetzal, alt. 1630 m, 22 July 1988, *E.M. Martínez et al. 23030* (MO). HONDURAS. LEMPIRA: Montaña de Celaque, SE portion of massif, represa trail between Gracias and top of Cerro Celaque, 14°33'N, 88°39'W, alt. 1750 m, 23 May 1991, *G. Davidse et al. 34597* (MO). JAMAICA. PORTLAND: Whitfield Hall, Blue Mountains, alt. 3500ft, 11 January 1913, *W.M. Harris 11583* (US). MEXICO. CHIAPAS: La Concordia, 15°41'48"N, 92°58'20"W, alt. 1400 m, 15 April 1999, *M.E.L. Molina 318* (MO); OAXACA: Puerto Antonio, 5.3 Km al N de Vista Hermosa, 17°38'N, 96°22'W, alt. 1230 m, 9 March 1986, *P.L. Tenorio et al. 11042* (MO); PUEBLA: Coatepec, 20 May 1950, *J.T. Baldwin Jr. 14271* (US). NICARAGUA. JINOTEGA: Reserva Natural Cerro Kilambé, 13°34'N, 85°41'W, alt. 900-1700 m, 22 April 2000, *R. Rueda et al. 13349* (MO); RIVAS: Isla Ometepe, Volcán Concepción, 11°32'N, 85°36'W, alt. 700-900 m, 30 October 1984, *W. Robleto 1489* (MO). PANAMA. CHIRIQUÍ: Vizinhança de El Boquete, borda da mata ao longo do rio, alt. 1000 m, 28 September 1911, *A.S. Hitchcock 8227* (IAC); COCLE: Vicinity of La Mesa, N of El Valle de Antón, 8°38'N, 80°09'W, alt. 800-900 m, 11 July 1987, *T.B. Croat 67143* (MO). TOBAGO. Center of island, 20 December 1912, *A.S. Hitchcock 10219* (US). VENEZUELA. ARAGUA: Along road from Maracay to Choroní, near Km 23, 9°21'N, 67°24'W, alt. 1420-1520 m, 3 August 1982, *T.B. Croat 54503* (MO); LARA JIMÉNEZ: Parque Nacional Yacambú, 9°41'N, 69°30'W, alt. 700 m, 28 October 1982, *G. Davidse et al. 21335* (MO).

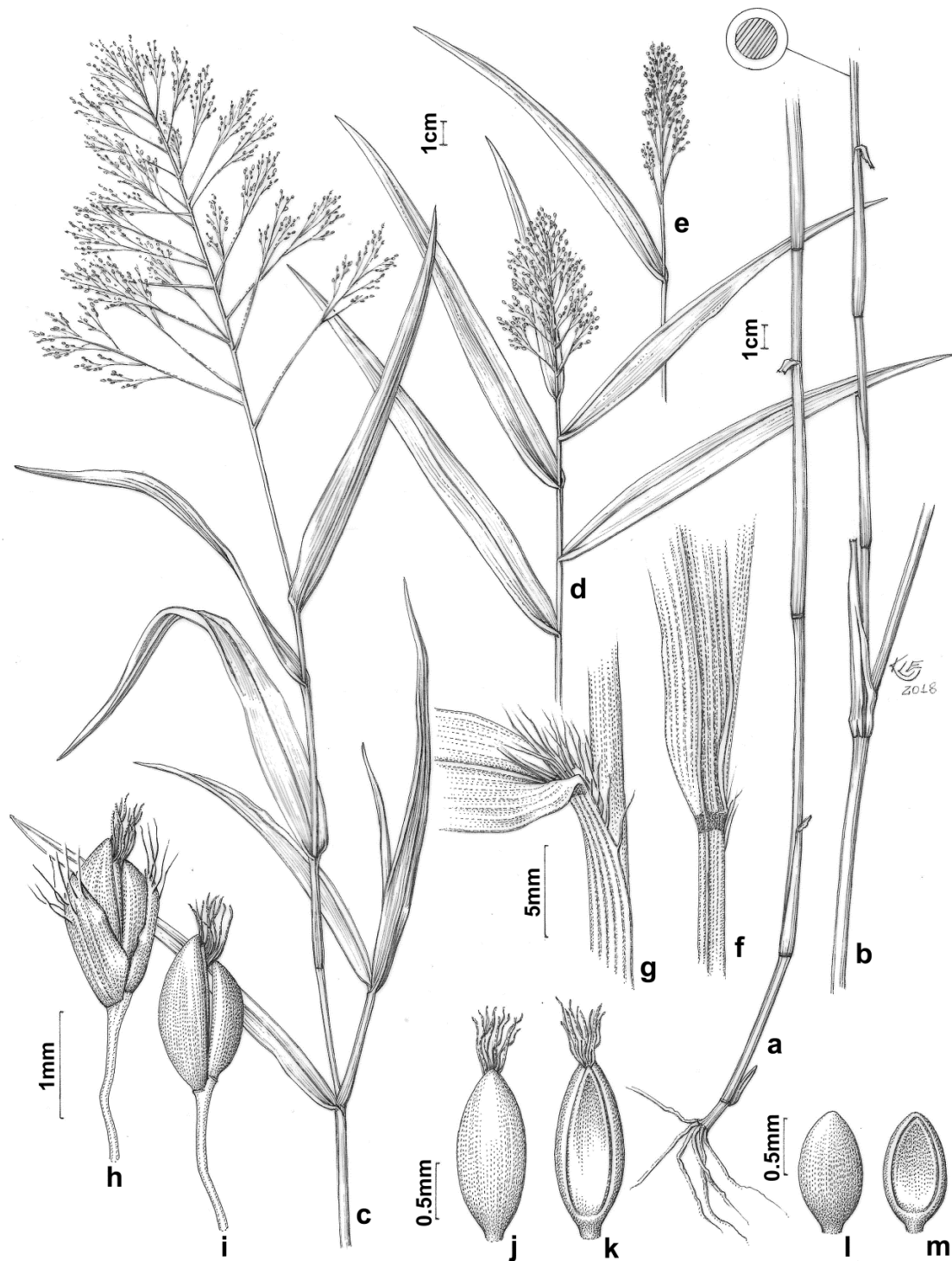


Figure 9: *Isachne glaucescens* var. *glaucescens*. a. Basal portion of the culm. b. Middle portion of the culm (note branching at the nodes and detail of the hollow internode). c. Apex of the flowering branch with a large and open to lax synflorescence (note the secondary branches, branchlets, and spikelets crowded mostly at the synflorescence tips). d. Apex of a flowering branch with a typical subcontracted and congested synflorescence (note the spikelets crowded mostly at the synflorescence tips). e. Apex of a flowering branch with a small and contracted synflorescence (note that in this type of synflorescence the spikelets are also crowded at the tips, but sometimes this feature is not promptly detectable). f. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath. g. Fragment of the culm showing the base of the leaf blade, part of the ciliate ligule, and the apex of the leaf sheath. h. Spikelet in lateral view (note the non-acuminate/cuspidate apex of the glumes and the frequent presence of apical trichomes) and pedicel without a glandular band. i. Anthoecium (glumes removed) and pedicel without a glandular band. j. Lower anthoecium, lemma view. k. Lower anthoecium, palea view. l. Upper anthoecium, lemma view. m. Upper anthoecium, palea view. Based on: a-b, f-g. A.S. Hitchcock 4728a (US); c. W.A. Haber & E. Bello 1759 (MO); d. H.H. Smith 210 (MO); e, h-m. R. Callejas et al. 9158 (MO). Illustration by Klei R. Sousa.



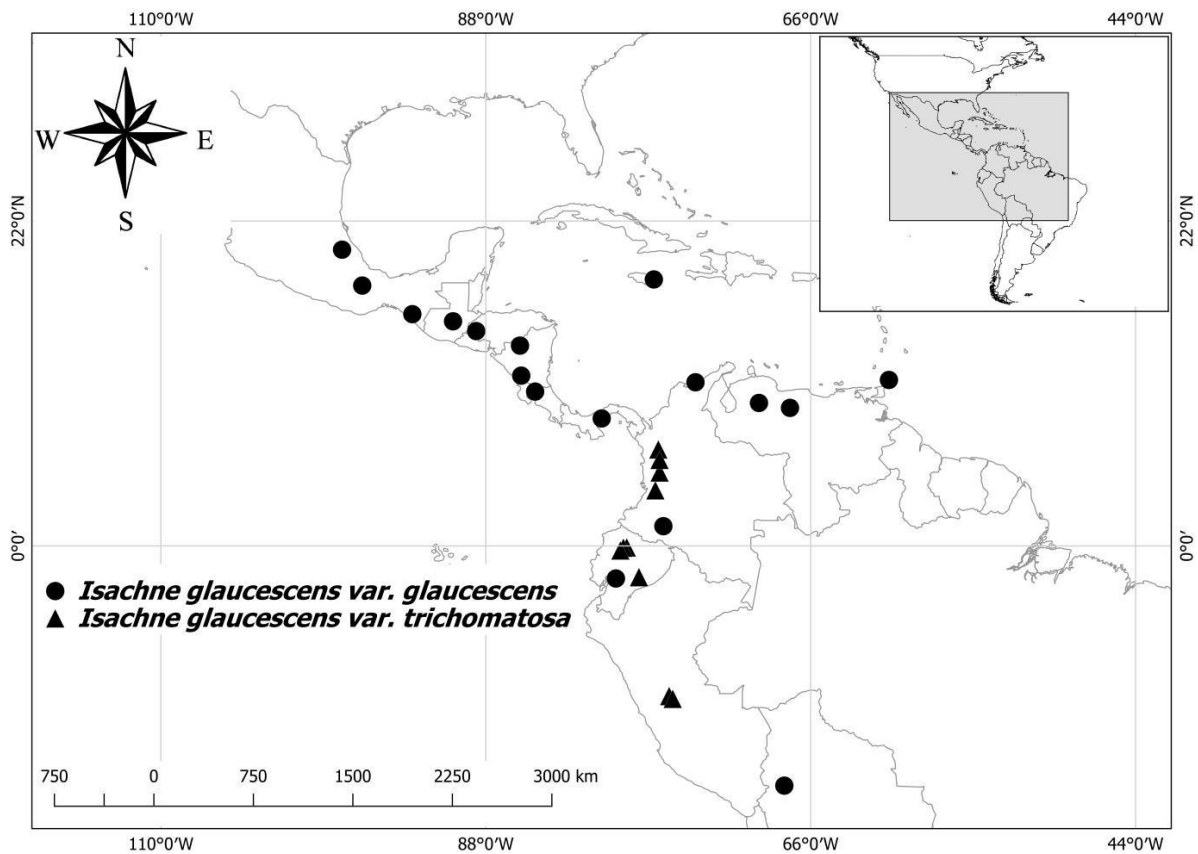


Figure 10. Known distribution of *Isachne glaucescens* var. *glaucescens* and *I. glaucescens* var. *trichomatosa*.

4.2. *Isachne glaucescens* var. *trichomatosa* R.S. Rodrigues & Filg., var. nov. Type: ECUADOR. Provincia de Pinchincha: carretera Quito-Chiriboga-Empalme, km 92, desvío a Mulaulte, en borde del carretero y en quebrada de Mulaulte, 00°15'S, 78°50'W, alt. 1200-1300 m, 13 December 1987, V. Zak & J. Jaramillo 3204 (holotype MO-3597897!; isotype US-3287133!).

Figure 11

*Diagnosis:* Perennial. Culms branched at the intermediary and upper nodes, rooting at the lower nodes; internodes puberulous in the secondary branches, notably towards the nodes, sometimes glabrescent to nearly glabrous due to the dehiscence of the trichomes. Sheaths tuberculate-pilose towards the apex or glabrous, trichomes dehiscent; leaf blades pubescent to pilose on the abaxial surface, glabrous to pubescent on the adaxial surface, trichomes dehiscent. Synflorescence main axis, branches, branchlets and pedicels densely tuberculate-hirsute, trichomes sometimes dehiscent in the uppermost portion of the panicle. Spikelets globose, less often elliptic; glumes pilose at the apex; anthoecia similar, both subequal in length and pilosity, less often the lower longer than the upper.

*Etymology:* From the Greek: “*thrix*”: hair; from the Latin: “*osa*”: abundance (Clifford & Bostock 2007). The varietal epithet refers to the abundant presence of trichomes on the culm-internodes, sheaths synflorescence branches, branchlets, pedicels and at the apex of glumes.

*Distribution:* Northwest South America, in Colombia, Ecuador, and Peru (Figure 10). It inhabits preferably montane rainforest, in association with moist places, streams, gallery forest, slopes, open and disturbed places, and roadsides; at ca. 350-1550 m.

*Phenology:* Collected in flower from January to March, May, June, October and December.

*Comments:* *Isachne glaucescens* var. *trichomatosa* is morphologically recognized by its pilose to tuberculate-hirsute synflorescence main axis, branches and branchlets. This variety is characterized by including plants that are in general terms pubescent or pilose, either in the culm internodes, sheaths, leaf blades, panicle branches and at the apex of glumes. Notably, the trichomes can be dehiscent in most of the plant vegetative characters, but tend to be indehiscent in the reproductive ones (in some cases, dehiscent in the uppermost portion of the panicle, but clearly evident elsewhere). With some exceptions, the spikelets are uniformly more globose and the anthoecia are frequently subequal in length.

The presence of trichomes close connects *I. glaucescens* var. *trichomatosa* and *I. pubescens*. However, *I. pubescens* has open to lax synflorescences with branches covered by delicate whitish silky hairs, spikelets not aggregate at the branchlets tips, and anthoecia always dissimilar in length.

Rodrigues & Filgueiras (unpubl. res., Chapter 5) characterized the leaf blade epidermis of *I. glaucescens* var. *trichomatosa* as composed of non-striated intercostal long cells on the adaxial leaf blade surface, being the innermost cells papillate (ca. 3-4 rows) and the outermost cells non-papillate (ca. 2 rows), adaxial costal and intercostal microhairs and costal macrohairs, and abaxial costal microhairs.

Material examined: COLOMBIA. ANTIOQUIA: Parque Nacional Natural “Las Orquideas”, sector Calles, 6°32’N, 76°19’W, alt. 1310-1365 m, 27 March 1988, A. Cogollo et al. 2660 (MO); CHOCÓ: Municipio de San José del Palmar, Cerro al SO de la Población, alt. 1300 m, 25 February 1977, E. Forero et al. 3437 (MO); Municipio de San José del Palmar, vereda El Tambor, alt. 1450-1550 m, 17 January 1983, P. Santiago-Díaz 3674 (MO); Highway between Bolivar and Quibdo, alt. 350 m, 31 October 1983, A. Juncosa 1132 (MO). ECUADOR. CHIMBORAZO: Cañon of the río Chanchan near Huigra, alt. 4000-4500 ft., 7-14 May 1945, W.H. Camp 3207 (MO); MORONA-SANTIAGO: Parroquia Cumandá, southern side of Río Pastaz, ca. 4km W of Mera, 06 December 1974, H.S. Lugo 4752 (MO); PICHINCHA: Puente Gloria de María (West of Quito), alt. 1200 m, 27 June 1939, E. Asplund 7278 (MO, S); Domingo-Quito highway, 11.3 km N of main highway, 00°18’29”S, 78°53’01”W, 23 March 2006, T.B. Croat et al. 96248 (MO). PERU. PASCO: Oxapampa, Dist. Huancabamba-Pozuzo, canyon de Huancabamba, below Rio Tunqui, 75°35’W, 10°10’S, alt. 1000-1500 m, 30 June 1985, R.B. Foster et al. 103222 (MO); Oxapampa, Dist. Pozuzo, Parque Nacional Yanachaga chemmillén carretera cerca a la Quebrada Misho, alt. 1210 m, A. Monteagudo et al. 4988 (MO).

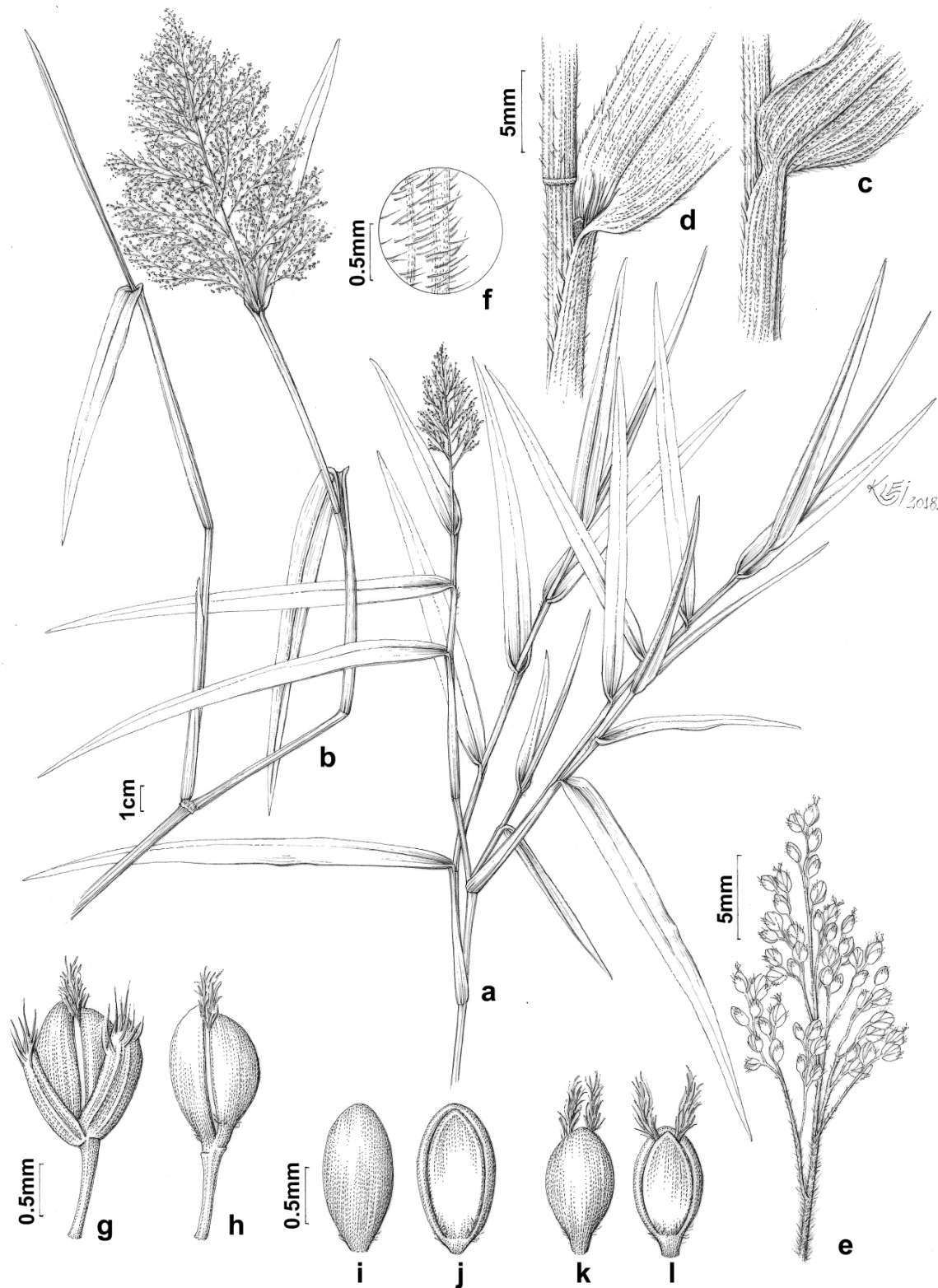


Figure 11: *Isachne glaucescens* var. *trichomatosa* R.S. Rodrigues & Filg. a. Apical portion of the culm showing one flowering branch with a small panicle and the branched nodes. b. Apical portion of the culm showing one flowering branch with a large panicle and a branched node. c. Fragment of a culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath (note the pilosity found in the culms, leaves, and sheaths). d. Fragment of a culm showing the base of the leaf blade, the ciliate ligule, and the apex of the leaf sheath (note the pilosity found in the culms, leaves, and sheaths). e. Fragment of a synflorescence branchlet (note the abundant hispid trichomes on the panicle branchlets). f. Detail of the hispid trichomes found on the main axis and branchlets of the synflorescence. g. Spikelet in lateral view (note the pilose apex of the glumes) and pedicel without a glandular band. h. Anthoecium (glumes removed) and pedicel without a glandular band. i. Lower anthoecium, lemma view. j. Lower anthoecium, palea view. k. Upper anthoecium, lemma view. l. Upper anthoecium, palea view. Based on: a. *E. Asplund* 7278 (MO); b. *R.B. Foster et al.* 10322 (MO); c-f. *V. Zak & J. Jaramillo* 3204 (MO). Illustration by Klei R. Sousa.

5. *Isachne goiasensis* Renvoize, Kew Bull. 42(4): 928. 1987 Type: BRAZIL. Goiás: [Chiefly Province of Goyas], [Formoza, au Brejinho], [09 December 1894], A.F.M. Glaziou 22533 (holotype K-000643014 image!; isotypes B-100460904 image!, P-01923972 image!, P-01923976 image!, W-1916-0021683 image!, W-1916-0021684 image!).

= *Isachne goyazensis* Hack. ex Potztl, Bot. Jahrb. Syst. 75: 555, 568. 1952 [nom. nud.].

Figure 12

Perennial, decumbent, trailing to scandent, (60-)85-360(-400) cm long. Culms rooting at the lower nodes, branched at the intermediary and upper portions, sometimes branched from the base, robust, somewhat lignified, flowering branches prostrate to ascending or erect; nodes glabrous, greenish to blackish, sometimes purplish or purple-stained, with or without a glandular stripe below; internodes hollow, glabrous, greenish, dark-brown or purple-stained towards the nodes. Sheaths shorter than the internodes, glabrous to densely hirsute, trichomes tuberculate, dehiscent in the old sheaths, strongly nerved, both margins ciliate in the young sheaths, mainly towards the ligular region, old sheaths with one margin ciliate only, cilia 0.7-1.5(-3) mm long, those towards the ligular region ca. 2-5 mm long, colorless; ligule ciliate, (1.5-)3-8 mm long; leaf blades distichous, regularly distributed on the culms, lanceolate, 10-25(-30) × (0.6-)1.4-2.5 cm, flexible (not rigid), midrib present, base slightly attenuate, not amplexicaul, apex acute, glabrous on both surfaces or minutely scabrous on the abaxial surface, margins entire, minutely scabrous. Panicle terminal, lax to open, branchlets often ascending, flexible, 15-30 × (6-)9-15 cm, glabrous, second-order branches present, glandular bands present, axillary glands absent or inconspicuous; pedicels 1.5-5.5(-10) mm long, cylindrical, glabrous to minutely scaberulous, glandular bands present. Spikelets unequally pedicelled, erect on the pedicels or often the short-pedicelled slightly oblique on the pedicels, globose to subglobose or elliptic-globose, (1.4-)1.8-2 mm long; glumes subequal, orbicular to elliptic, obtuse, less often subacute, inconspicuously scaberulous towards the apex or glabrous, greenish, pale-green or stramineous, sometimes purple-stained, both shorter than or rarely almost subequal the anthoecia; lower glume (1.2-)1.5-1.6(-2) mm long, (3-)5-7-nerved, margins greenish to pale-green or stramineous; upper glume 1.2-1.5(-1.9) mm long, (5-)7-9-nerved, margins greenish to pale-green or stramineous; anthoecia 2, dissimilar, the lower cartilaginous, elliptic-oblong to elliptic lanceolate, the upper coriaceous, orbicular to suborbicular, both greenish to stramineous, sometimes purple-stained; lower anthoecium staminate, (1.2-)1.5-1.8(-2) mm long, lemma glabrous, not sulcate, palea (1.1-)1.6-1.7(-1.9) mm long, glabrous; rachilla inconspicuous between the anthoecia, ca. 1 mm long, glabrous; upper anthoecium bisexual, (1.1-)1.3-1.5 mm long, lemma appressed pilose, palea appressed pubescent, (1-)1.2-1.4 mm long. Lodicules ca. 2 mm long. Stamens 3, filaments ca. 2 mm long, pale-green to yellowish; anthers 1-1.2 mm long, yellowish or orange, purple to dark-brown in maturity. Stigmas 2, plumose, yellowish to dark-brown in maturity. Caryopsis 1.5-1.7 × 1 mm, orbicular, flat-convex, dark-brown.

*Etymology:* From the Latin: “-ensis”: denoting origin (Clifford & Bostock 2007). The epithet refers to the locality of origin, Goiás State, in Brazil.

*Distribution:* Brazil, known only from the states of Goiás and Distrito Federal (Figure 8). It inhabits humid soils, on the margins or interior of gallery forests, margins of “Cerradão” with humid and adjacent campos or in cerrado slopes; at ca. 1000-1380 m.

*Phenology:* Collected in flower in September and October, and from December to May.

*Comments:* *Isachne goiasensis* is morphologically related to *I. burchellii*, but it differs in presenting greenish to dark-brown culm-internodes, which are sometimes purple-stained towards the nodes, presence of glandular bands on the pedicels and heteromorphic anthoecia, being the lower cartilaginous, glabrous, and the upper coriaceous and appressed pilose. Additionally, *I. goiasensis* occurs in the Cerrado biome, while *I. burchellii* occurs in montane regions in the Atlantic Rainforest domain. A detailed discussion about the identity of *I. goiasensis* can be found in Rodrigues & Filgueiras (2019).

*Isachne glaucescens* (as *I. arundinacea*) was erroneously cited for Brazil based on misidentifications of some specimens of *I. goiasensis*. Although both are robust species, *I. goiasensis* is promptly differentiated by the glandular bands on the pedicels and the anthoecia dissimilar in texture and pilosity.

The specimen *Chagas-Silva 387* (UEC) does not exhibit the typical glandular bands on the pedicels, which is here accepted as a morphological exception, although a duplicate at MO is a typical glandular specimen, as currently accepted for *I. goiasensis*.

*Nomenclatural notes:* The name *I. goiasensis* was first cited in the literature by Potztl (1952) as “*Isachne goyasensis Hack. msr*”, a nomen nudum according to Art. 38.1 ICB (Turland *et al.* 2018). Later, Renvoize (1987) validly published the species with a broader circumscription, including distinct plants from the Brazilian states of Rio de Janeiro, Goiás and Distrito Federal. Recently, Rodrigues & Filgueiras (2019) narrowed the concept of *I. goiasensis* and described *I. burchellii* to accommodate the specimens with similar anthoecia from Rio de Janeiro. Therefore, as currently circumscribed, *I. goiasensis* includes plants with dissimilar anthoecia, known only from Distrito Federal and Goiás. Detailed comments about the history and taxonomy of *I. goiasensis* can be found in Rodrigues & Filgueiras (2019).

Material examined: BRAZIL. DISTRITO FEDERAL: Brasília, Bacia do Rio São Bartolomeu, 16 April 1980, *E.P. Heringuer et al. 4435* (CEN, RB, SP); Brasília, Bacia do Rio São Bartolomeu, 30 March 1981, *E.P. Heringer et al. 6654* (IBGE, SP, UEC); Brasília, Parque do Guar, 16 April 1975, *E.P. Heringer 14579* (NY image, SP, UB, UEC). Braslia, Chapada da Contagem, ca. 15 km E. of Braslia, 30 January 1966, *H.S. Irwin et al. 12143* (CM, MO, NY image, UB) [paratypes]; Braslia, Parque Olhos d’gua, 22 October 2002, *J.G.A. Paiva & S.F. Carvalho 56* (UB); Braslia, Estcao Ecolgica do Jardim Botnico de Braslia, 15 February 2008, *R.G. Chacon & I.N.C. Azevedo 354* (HEPH); Braslia, Estcao Ecolgica do Jardim Botnico de Braslia, 28 March 2009, *R.C. Martins et al. 820* (HEPH); Braslia, Estcao Ecolgica do Jardim Botnico de Braslia, 28 March 2009, *R.C. Martins et al. 831* (HEPH); Jardim Botnico de Braslia, rea de reserva, Mata do Taquara, regio do “Cristo Redentor” ao longo da fronteira entre as reservas do JB, IBGE e FAL/UNB, 1555’52.28”S, 4754’7.32”W (-15,931188, -47,902033), 20 January 2017, *R.S. Rodrigues et al. 479* (HUEFS, SP); Jardim Botnico de Braslia, rea de reserva, Mata do Taquara, regio do “Cristo Redentor” ao longo da fronteira entre as reservas do JB, IBGE e FAL/UNB, 1555’52.28”S, 4754’7.32”W (-15,931188, -47,902033), 20 January 2017, *R.S. Rodrigues et al. 480* (MG, SP); Jardim Botnico de Braslia, rea de reserva, Mata do Taquara, regio do “Cristo Redentor” ao longo da fronteira entre as reservas do JB, IBGE e FAL/UNB, 1555’52.28”S, 4754’7.32”W (-15,931188, -47,902033), 20 January 2017, *R.S. Rodrigues et al. 481* (MBM, SP); Braslia, Parque Nacional de Braslia, 15 February 2009, *R.C. Martins 1094* (UB); Parque Nacional de Braslia, 28 September 2012, *P. Reis & R.R.A. Dias 70* (CEN); Riacho Fundo, 04 December 1991, *P.E.A.M. Oliveira 1694* (HEPH). GOIS: Cocalzinho de Gois, 20 km N.W. of Corumb de Gois, near Pico dos Pirineus, Serra dos Pirineus, 27 January 1968, *H.S. Irwin et al. 19315* (MO, NY image, UB) [paratypes]; Serra dos Pirineus, 20 km E of Pirenpolis, 16 January 1972, *H.S. Irwin et al. 34309* (MO, NY image, UB, USF image) [paratypes]; Brejo entre Guar e Setor da Indstria, 21 February 1981, *F. Chagas-Silva 387* (K image, MO, UEC) [paratypes]; Alto Paraso de Gois, Fazenda gua Fria, 02 May 1998, *R.C. Oliveira et al. 1073* (HEPH).

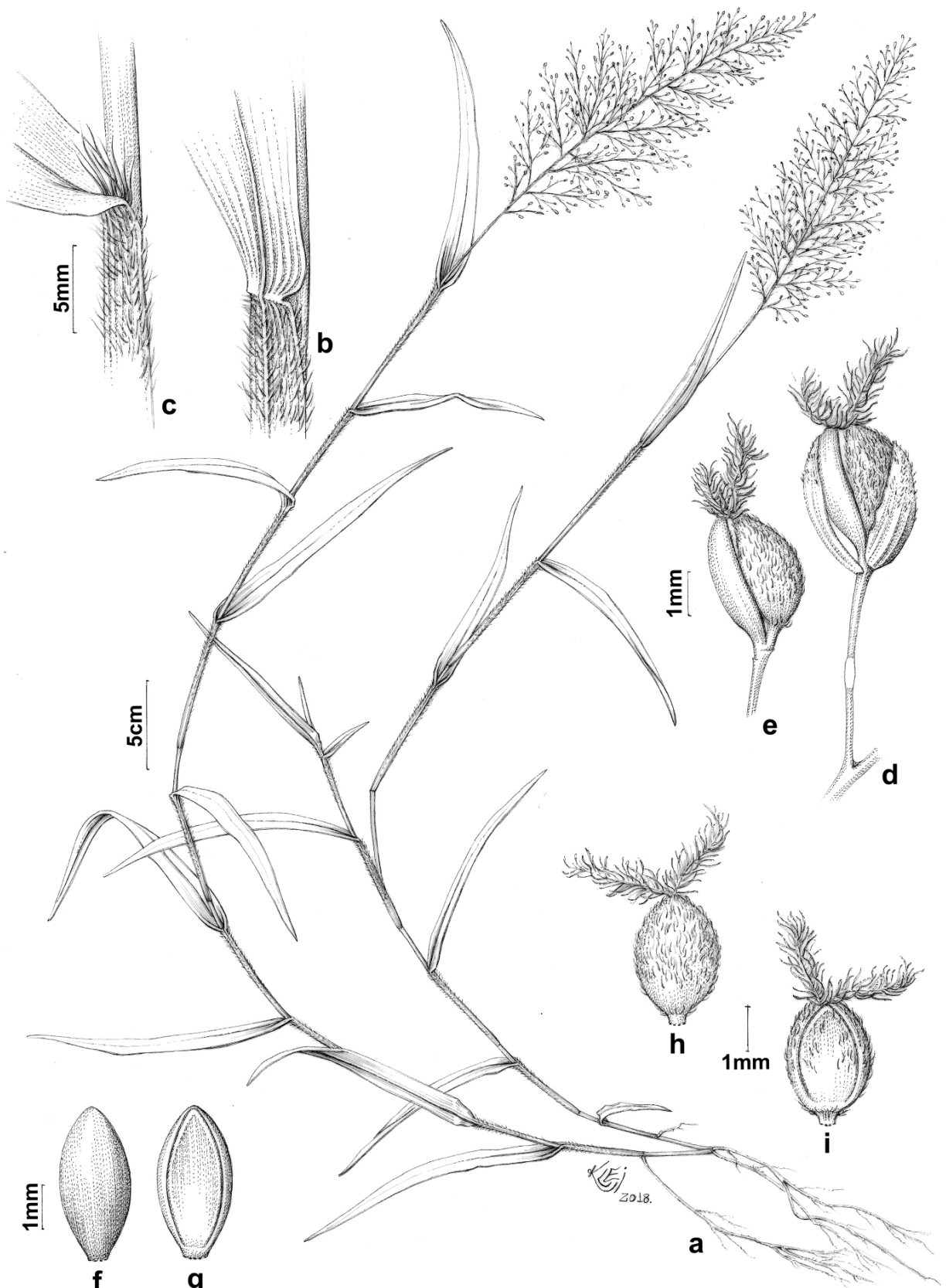


Figure 12: *Isachne goiasensis* Renvoize. a. Habit. b. Fragment of a culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath (note the hirsute pilosity towards the apex of the leaf sheath). c. Fragment of a culm showing the base of the leaf blade, part of the ciliate ligule, and the apex of the leaf sheath. d. Spikelet in lateral view and pedicel with a glandular band. e. Anthoecia (glumes removed). f. Lower anthoecium, lemma view. g. Lower anthoecium, palea view. h. Upper anthoecium, lemma view. i. Upper anthoecium, palea view. Based on: a-i. R.S. Rodrigues et al. 479 (SP). Illustration by Klei R. Sousa, extracted from Rodrigues & Filgueiras (2019).

6. *Isachne hirtiglumis* Longhi-Wagner & Welker, Syst. Bot. 39(3): 846. 2014. Type: BRAZIL. Minas Gerais: Ouro Branco, Parque Estadual da Serra do Ouro Branco, Área 2, 20°29'36.8"S, 43°40'36.1"W, 01 February 2003, C.C. Paula et al. 633 [holotype VIC! (in two parts); isotypes ICN, RB!, SP!].

Figure 13

Perennials, decumbent to scandent, mat-forming or densely tangled, 25-100(-190) cm. Culms rooting at the lower nodes, frequently branched from the base and/or at the intermediary and upper portions, herbaceous, slender, sterile and flowering branches wiry, prostrate to ascending; nodes glabrous, pubescent or pilose, trichomes tuberculate, greenish to blackish, with or without a glandular stripe below; internodes full, glabrous, greenish to stramineous. Sheaths shorter than the internodes, pilose, trichomes tuberculate, usually dehiscent, sometimes glabrous, strongly nerved, one margin ciliate, the other glabrous, cilia 0.1-0.2 mm long, those towards the ligular region 1-1.5(-2) mm long, colorless; ligule ciliate, 1-2(-4) mm long; leaf blades distichous, regularly distributed over the culms and secondary flowering and/or sterile branches, those from the base and intermediary culms often dehiscent, lanceolate to linear-lanceolate, 2.5-6.5 × 0.1-0.5 cm, flexible (not rigid), midrib inconspicuous, base rounded to slightly attenuate, not amplexicaul, apex acute, glabrous to pilose on both surfaces, notably pilose on the abaxial surface when young, pubescent to pilose on the adaxial surface, trichomes often dehiscent, margins entire, minutely scaberulous. Panicle terminal, open to subcontracted, flexible, (3-)5-10 × 1-4 cm, glabrous to minutely scaberulous, provided with second-order branches, glandular bands and axillary glands present; pedicels 0.5-4.5 mm long, cylindrical, glabrous to minutely scaberulous, glandular bands present. Spikelets unequally pedicelled, erect or often some obliquely inserted on the pedicels, elliptic to elliptic-globose, 1.2-1.7 mm long; glumes subequal, orbicular to elliptic, obtuse to subacute, densely and entirely hirsute, trichomes tuberculate, greenish to stramineous, often purple-stained, both shorter or less often subequal the anthoecia; lower glume 1.2-1.7 mm long, 7-nerved, margins involute, greenish to hyaline, usually purple-stained; upper glume 1.2-1.6 mm long, 7-9-nerved, margins greenish to hyaline, usually purple-stained; anthoecia 2, dissimilar, the lower cartilaginous to subcoriaceous, elliptic, elliptic-oblong or oblong-lanceolate, the upper coriaceous, suborbicular, both greenish to stramineous, often purple-stained; lower anthoecium staminate, 1.2-1.7 mm long, lemma glabrous or with minute sparse trichomes irregularly distributed, not sulcate, palea glabrous or with some minute sparse trichomes, 1.1-1.6 mm long; rachilla conspicuous between the anthoecia, 0.1-0.2 mm long, glabrous; upper anthoecium bisexual, (0.7-)1-1.2 mm long, lemma minutely appressed-pilose, palea glabrous to sparsely appressed-pubescent, (0.6-)1-1.1 mm long. Lodicules ca. 0.2 mm long. Stamens 3, filaments ca. 0.4 mm long, yellowish to pale-green; anthers (0.7-)1-1.1 mm long, yellow to orange, dark-brown in maturity. Stigmas 2, plumose, white in maturity, later becoming yellow to orange. Caryopsis not seen.



*Etymology:* From the Latin: “*hirtus*”: hairy; “*gluma*”: glume, husk (Clifford & Bostock 2007). The epithet refers to the occurrence of densely hirsute glumes.

*Distribution:* Brazil, known only from Minas Gerais State (Figure 8). It inhabits swamps, marshland and lake shores, gallery forests and waterfalls; at ca. 1000 -1500 m.

*Phenology:* Collected in flower from January to March and in June.

*Comments:* *Isachne hirtiglumis* is presently endemic to the Espinhaço Range and has been documented in some other localities, suggesting a relatively broader distribution. The type locality (Serra do Ouro Branco State Park) was visited in 2016 where dense populations were observed in the swamp.

The delicate and brittle decumbent culms of this species usually form tangles that are difficult to separate. The ability to form dense populations may be a suitable feature to be occasionally explored as fodder, but further studies are necessary to determine the agronomic potential of *I. hirtiglumis*.

*Isachne hirtiglumis* was originally described as an annual species (Longhi-Wagner & Welker 2014). One specimen has been cultivated since 2016 at the Instituto de Botânica, in São Paulo State, Brazil, and presented flowering events in 2018 and 2019. After flowering, the specimen produced new culms, leaves, and restarted rooting at the lower nodes. This fact is contradictory to the original description of the species; therefore, we describe *I. hirtiglumis* as a perennial grass.

Morphologically, *I. hirtiglumis* is characterized by the delicate culms, tuberculate-hirsute glumes, and dissimilar anthoecia, being the lower glabrous and the upper appressed-pilose. In some specimens, the dissimilarity of the anthoecia is not promptly evident. In this intermediary condition, a more accurate analysis may be necessary.

*Isachne hirtiglumis* is similar to *I. polygonoides* but differ in having lanceolate to linear-lanceolate leaf blades not amplexicaul at the base and tuberculate-hirsute glumes. It is also similar to *I. salzmännii*, differing by the glumes tuberculate-hirsute and spikelets shape.

The specimen “*M. Weddell s.n. (P-01882836)*” is composed of three fragments. The fragments on the left and center have spikelets with tuberculate-hirsute glumes, whereas the fragment on the right has spikelets of different sizes where the typical tuberculate-hirsute trichomes of the glumes have fallen. In spite of this, the presence of glandular

bands on the pedicels and the shape of the spikelets leave no doubt regarding the identity of this specimen.

*Nomenclatural notes:* At the time of the publication of *I. hirtiglumis*, Longhi-Wagner & Welker (2014) did not indicate the occurrence of a second sheet housed at VIC. Apparently, they did not have access to the second specimen of the same collection we found stored among other unidentified Poaceae. The second specimen had been recorded under the same herbarium number (VIC-29689) and should be cited as part of a two-sheet holotype, as stated here. Recently, isotypes were donated to RB and SP.

Material examined: BRAZIL. MINAS GERAIS: Without precise locality, 1844, *M. Weddell s.n.* (P-01882836 image); Lavras Novas, Serra de Lavras Novas, June 1896, *L. Damasio s.n.* (RB-183383, SP-490353); Ouro Preto, Parque Estadual do Itacolomi, Lagoa do Manso, 01 February 2002, *A. Oliveira & A.G. Rocha s.n.* (OUPR-17559); São Gonçalo do Rio Preto, Parque Estadual do Rio Preto, 15 February 2007, *P.L. Viana et al.* 2813 (BHCB) [paratype]; São Gonçalo do Rio Preto, Parque Estadual do Rio Preto, 18°9'90"S, 43°19'32,23"W, 21 March 2007, *P.L. Viana et al.* 2744 (BHCB) [paratype]; Ouro Branco, Parque Estadual da Serra do Ouro Branco, 20°29'36.8"S, 43°40'36.1"W, 05 January 2016, *R.S. Rodrigues et al.* 452 (HUEFS, MG, MBM, SP); Chapada, Vilarejo da Chapada, Distrito de Ouro Preto, Cachoeira do Valtinho, 20°28'56"S, 43°32'56"W, 08 January 2016, *R.S. Rodrigues et al.* 465 (ESA).

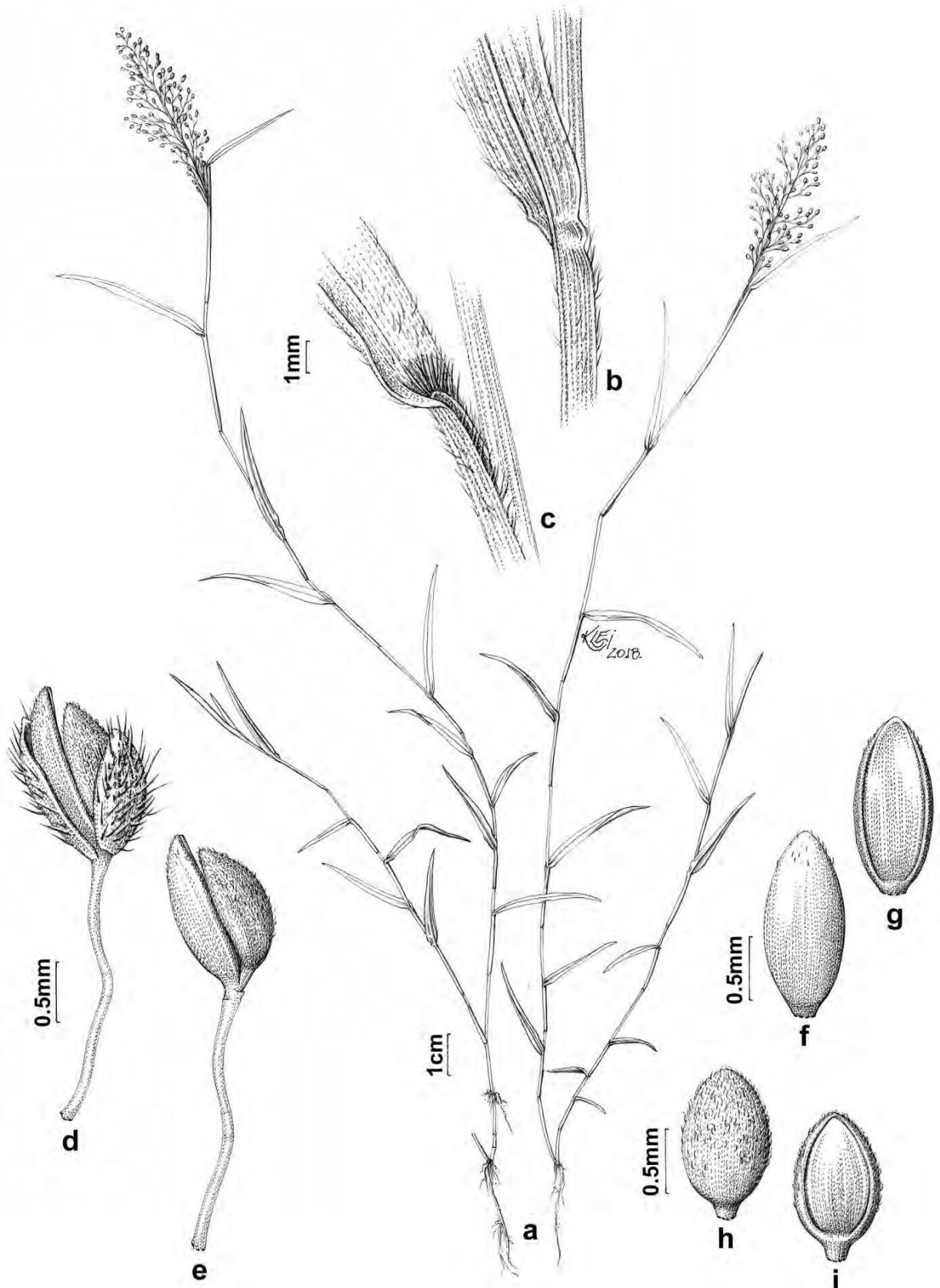


Figure 13: *Isachne hirtiglumis* Longhi-Wagner & Welker. a. Apex of a branched culm with synflorescences (note rooting in the lower nodes). b. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath. c. Fragment of the culm showing the base of the leaf blade, the ciliate ligule, and apex of the leaf sheath. d. Spikelet in lateral view and pedicel with a glandular band. e. Anthoecia (glumes removed) and pedicel with a glandular band. f. Lower anthoecium, lemma view. g. Lower anthoecium, palea view. h. Upper anthoecium, lemma view. i. Upper anthoecium, palea view. Based on: a-i. *R.S. Rodrigues et al. 452 (SP)*. Illustration by Klei R. Sousa.

7. *Isachne leersioides* Griseb., Pl. Wright. 2: 533. 1862. Type: CUBA. [Prope villam *Monte Verde* dictam, Cuba Orientali], *C. Wright* 755 (holotype GOET-006586 image!; isotypes B-10-0249140 image!, BR-686277 image!, BRU-00058482, BRU-00058483, CAS-155636 image!, GH-00023849 image!, K-000308105 image!, K-000308106 image!, MO-2095554 image!, NY-00071109 image!, NY-00071110 image!, NY-1603130!, NY-1603133 image!, P-00740911 image!, PH-00016106 image! (as *C. Wright* 756), PH-0001603132 image! (as *C. Wright* 756), S-R-3044 image!, S-06-21564 image!, S-06-21567 image!, W-1889-0123381 image!, W-1916-0020373 image!, W-1916-0020374 image!). Probable isotype: NY-1603132 image!.

Figure 14

Annual, decumbent, trailing, 30-200 cm long. Culms rooting at the lower nodes, then geniculate ascending, branched from the base and at the distal nodes, wiry, herbaceous, slender, sterile and flowering branches suberect to leaning; nodes glabrous, greenish to dark-brown. Sheaths shorter than the internodes, those of the lower nodes dehiscent, lacerate, glabrous or tuberculate-pilose, strongly nerved, one margin ciliate, the other glabrous and hyaline, cilia ca. 1 mm long, those towards the ligular region 1.5-2-5 mm long, colorless; ligule ciliate, 1-1.5 mm long; leaf blades distichous, regularly distributed, sometimes diffusely arranged along the culms, linear, 2.5-15 × 0.1-0.4 cm, flexible (not rigid), midrib conspicuous, base rounded, slightly constricted near the ligular region, not sulcate, apex acute, glabrous or minutely scaberulous on both surfaces, margins entire, thickened, glabrous. Panicle terminal, open to subcontracted, loose, flexible, 2-14 × (0.5-)1-10 cm, glabrous to minutely scaberulous, provided with second-order branches, glandular bands, and axillary glands; pedicels 1-8 mm, cylindrical, glabrous to minutely scaberulous, glandular bands present. Spikelets unequally pedicelled, erect on the pedicels, elliptic to obovate or globose, 1.2-1.9 mm long; glumes subequal, obovate to elliptic, obtuse to subacute in the young spikelets, pilose, hispidulous, greenish, both shorter or slightly shorter than the anthoecia; lower glume 1-1.5 mm long, 3-5-nerved, margins greenish to pale, involute; upper glume 1-1.6 mm long, 5-6-nerved, margins hyaline; anthoecia 2, similar, coriaceous, pale-green; lower anthoecium bisexual, 0.9-1.6 mm long, lemma appressed-pilose, not sulcate, palea glabrous, 0.9-1.5 mm long; rachilla conspicuous between the anthoecia, 0.1-0.2 mm long, glabrous; upper anthoecium bisexual, 0.9-1.4 mm long, lemma appressed-pilose, palea glabrous, 0.9-1.3 mm long. Lodicules ca. 0.1 mm long. Stamens 3, filaments ca. 0.2 mm long, yellowish; anthers 0.7-0.8 mm long, yellowish to orange, dark-brown in maturity. Stigmas 2, plumose, dark-brown in maturity. Caryopsis not seen.

*Etymology:* From the Greek: “-oides”: resembling (Clifford & Bostock 2007). The epithet refers to the habit, leaf-blades, and synflorescence resembling those of *Leersia* Sw.

*Distribution:* Greater Antilles, known only from Cuba (Figure 15). It inhabits preferably moist or dry places, among bushes and open pine woods, cliffs or stream slopes; at ca. 150-1000 m.

*Phenology:* Collected in flower from October to June and in August.

*Comments:* *Isachne leersioides* is a very peculiar and easily distinguishable species amongst all the Neotropical species of the genus. It has delicate culms with long internodes, paucity of leaves, and similar anthoecia in relation to the shape, size, consistency, and pilosity.

*Nomenclatural notes:* Charles Wright's collections from East Cuba were made during 1856-1857, part of 1859 and at the beginning of 1860. The set of specimens collected in 1856-1857, which was sent to Grisebach, was lost on its way to Göttingen and could be only partially replaced [cf., Grisebach (1862), p. 153]. The only specimen of Wright's gathering numbered 755 we found in GOET herbarium is from 1859, and is the holotype. The remaining duplicates of his gathering in the American and European herbaria have multiple dates, a range of dates or no date at all, the majority according to the interval of the collection period presented by Grisebach (1862). Since these samples have the same collection number (755), they are considered part of the same gathering and treated here as isotypes for *I. leersioides*.

The specimen NY-1603132 is also assigned as a probable isotype because this material was also collected by C. Wright in Cuba but no date and no number is present on the label. The specimen PH-0001603132 is listed as isotype because the information of the label agrees with the gathering of Wright, i.e., "*in Cuba Orientali, 1856*". In addition, the collection number "756" is interpreted as an error instead of "755" because it is not probable that a posterior collector's number should have been attributed to a previous collection.

Material examined: CUBA. [GUANTÁNAMO]: Baracoa, Sabanilla to Yumurí Arriba, 30 January 1911, *J.A. Shafer 8427* (NY); Baracoa, El Yunque, on the most easterly (=highest) of the crags, 17-18 December 1914, *E.L. Ekman 3981* (US); Baracoa, on the Via Azul between Sabanilla and Cajobabo, at 5 km from Sabanilla, dry ravine, alt. ca. 500 m, 14 January 1956, *C.V. Morton & Alain 9658* (US); La Perla, dry cliff, alt. 600-660 m, 06-18 February 1911, *J.A. Shafer 8561* (US). HOLGUÍN: Sierra Nipe, along Río Medio near Woodfred, alt. 500 m, 18 October 1941, *C.V. Morton & J. Acuna 3293* (US). [MAYABEQUE]: Guaro, hardwood forest, iron mine, alt. 2000 ft., 14 December 1926, *A.S. Hitchcock 23413* (IAN, NY, US). PINAR DEL RÍO: South. foot of Cajálbana, banks of Arroyo de las Vueltas, 06 April 1915, *F. León & Charles 4843* (US); Sierra de las Yeguas, north of S. Diego de los Baños, 28 June 1915, *F. León 5078* (US); Bahía Honda, San Diego de Tapias, at Río Maní-Maní, 22 December 1920, *E.L. Ekman 12678* (NY, US); La Palma, cerca de San Juan de Sagua, alt. 150 m, 22°47'10"N, 83°25'00"W, 18 November 2001, *W. Greuter et al. 25777* (NY). SANTA CLARA: Sierra del Caballete, 01-11 August 1916, *F. León & F. Clement 6520* (US). [SANTIAGO DE CUBA]: Mella, The Pinales, SE Paso Estancia, 01-02 May 1909, *J.A. Shafer 1723* (NY); Vicinity of El Cuero, cliffs along stream, alt. 350 m, 18-19 March 1912, *N.L. Britton & J.F. Cowell 12786* (NY); Sierra Maestra, La Gran Piedra, common in bush along the ridge, alt. ca. 1000 m, 28-29 June 1914, *E.L. Ekman 1633* (US).

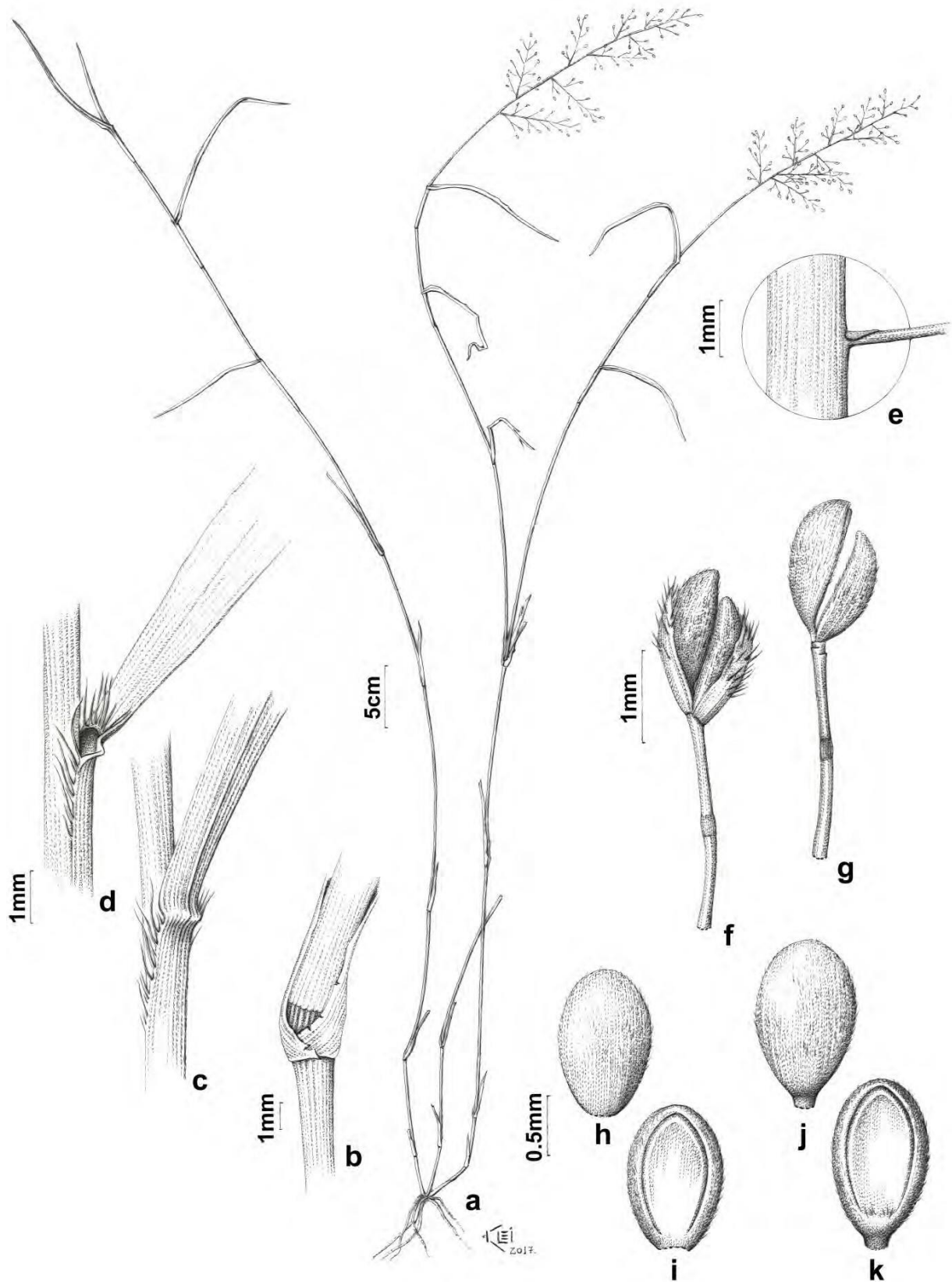


Figure 14: *Isachne leersioides* Griseb. a. Habit. b. Fragment of the culm showing a geniculate-nodal region. c. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath (note the ciliate margins of the apex of the leaf sheath). d. Fragment of the culm showing the base of the leaf blade, the ciliate ligule, and the apex of the leaf sheath. e. Detail of the synflorescence axil with an axillary gland. f. Spikelet in lateral view and pedicel with a glandular band. g. Anthoecia (glumes removed – note the similar appressed-pilose upper and lower anthoecia, being the lower slightly shorter than the upper) and pedicel with a glandular band. h. Lower anthoecium, lemma view. i. Lower anthoecium, palea view. j. Upper anthoecium, lemma view. k. Upper anthoecium, palea view. Based on: a-k. *C.V. Morton & J. Acuna 3293 (US)*. Illustration by Klei R. Sousa.

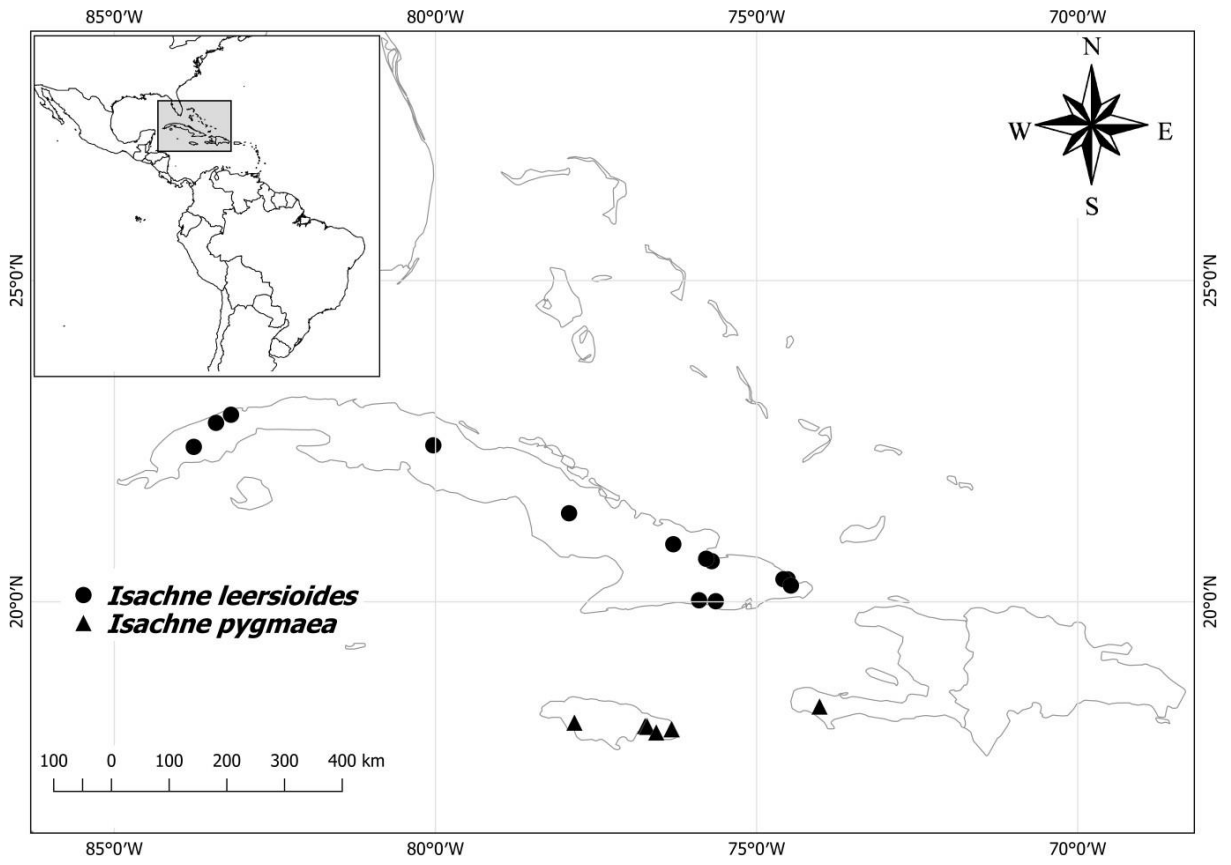


Figure 15. Known distribution of *Isachne leersioides* and *I. pygmaea*.

8. *Isachne ligulata* Swallen, *Caldasia* 2(8): 305. 1943. Type: COLOMBIA. Dept. Cauca: [Cauca Valley], Cuatro Esquinas, 05 June 1922, *F.W. Pennell & E.P. Killip 6343* (holotype US-1140437!).

Figure 16

Perennial, scandent or leaning, 150-350(-400) cm long. Culms rooting at the lower nodes, branched at the middle and upper portions, robust, somewhat lignified, sterile and flowering branches erect or ascending; nodes glabrous, blackish, brownish or dark-brown, without a glandular stripe below; internodes hollow, glabrous to minutely puberulous, greenish, stramineous or dark-brown in the older culms, sometimes purple stained towards the nodes. Sheaths shorter than the internodes in the middle portion of the culms, longer in the sterile and flowering branches, pubescent to pilose or hispid towards the apex, rarely glabrous, trichomes tuberculate, sometimes dehiscent in the old sheaths, strongly nerved, one margin ciliate, the other glabrous, cilia 0.5-0.7 mm long, those towards the ligular region 1-1.5(-2) mm long, colorless; ligule ciliate, (1.5-)2-2.5 mm long; leaf blades distichous, regularly distributed over the culms and secondary flowering and/or sterile branches, lanceolate, 3.5-15 × 0.3-1(-1.5) cm, flexible (not rigid), midrib conspicuous, base obtuse or rounded, slightly constricted near the ligular region, not sulcate, apex acute, pilose on the abaxial surface, scabrous on the adaxial surface, rarely glabrous on both surfaces, margins entire, scabrous or scaberulous. Panicle terminal, open to subcontracted, flexible to semi-rigid, (5-)7-11(-15) × (3-)4-9 cm, glabrous to scaberulous, provided with second-order branches, glandular bands absent, axillary glands present; pedicels 0.8-2.5 mm long, cylindrical, glabrous or scaberulous, glandular bands absent. Spikelets unequally pedicelled, erect on the pedicels, elliptic-globose to oblong, less usually elliptic-lanceolate, 1.8-2.3 mm long; glumes subequal, oblong to elliptic-lanceolate, obtuse to subacute, pubescent at the apex, less often glabrous, greenish to stramineous, sometimes purple-stained, both shorter or sometimes subequal the anthoecia; lower glume 1.4-2.2 mm long, 7-9-nerved, margins pale-green, greenish, stramineous or sometimes purple-stained; upper glume 1.5-2.2 mm long, 7-9(-11)-nerved, margins pale-green, greenish, stramineous or sometimes purple-stained; anthoecia 2, similar, coriaceous, usually stramineous, less often greenish and purple-stained; lower anthoecium bisexual, pistillate or staminate, 1.7-2.3 mm long, lemma glabrous or with minutely appressed-sparse trichomes, not sulcate, palea glabrous, 1.6-2.1 mm long; rachilla conspicuous or inconspicuous between the anthoecia, 0.2-0.5 mm long, pilose at the apex near the callus of the upper anthoecium; upper anthoecium bisexual, (1.2-)1.3-2 mm long, lemma glabrous or with minutely appressed-sparse trichomes, palea glabrous, 1.2-1.9 mm long. Lodicules ca. 0.3 mm long. Stamens 3, filaments ca. 0.5 mm long, yellowish; anthers ca. 0.9-1.1 mm long, purple, sometimes yellowish to purple-stained in maturity. Stigmas 2, plumose, purplish. Caryopsis 0.2 × 0.1 mm, oblong, flat-convex, blackish.



*Etymology:* From the Latin: “*ligula*”: little tongue; “-*ata*” possessing (Clifford & Bostock 2007). The epithet refers to the occurrence of conspicuous ligules.

*Distribution:* North and Northwest of South America, in Brazil, Colombia, Ecuador, Guyana, Peru, and Venezuela, in the Amazon Basin and Guyana Shields (Figure 17). It inhabits border of gallery forests, forest edges, cliffs, and slopes, usually associated with moist places and shrubby vegetation; at ca. 1400-2500 m.

*Phenology:* Collected in flower from January to November.

*Comments:* *Isachne ligulata* is morphologically related and frequently misidentified as *I. rigens*. The two species have a similar habit and geographical distribution, being in some cases treated as synonyms (e.g., Dorr 2014). Nevertheless, *I. ligulata* can be distinguished by the more robust culms, leaves usually longer with a conspicuous midrib, and synflorescences with secondary-order branches. *Isachne rigens* is distinct also by the conspicuous elongated and pilose rachilla, while in *I. ligulata* the rachilla (when conspicuous) is pilose only at the apex near the callus of the upper anthoecium.

The specimen “*R. Fonnegra et al. 6162 (MO)*” has spikelets with atypical pilose rachillas, similar to those observed in *I. rigens*; however, a more accurate analysis reviews that the lowermost part of it tends to be glabrous. All the vegetative characters in this specimen are in conformity with the circumscription of *I. ligulata*.

Material examined: BRAZIL. AMAZONAS: Santa Isabel do Rio Negro, Parque Nacional do Pico da Neblina, 22 September 2012, *R.C. Forzza et al. 7275* (CEN, MG, RB, SP). COLOMBIA. ANTIOQUIA: La Sierra, 18 Kilometers north of Medellín, alt. 2000 m, January 1931, *W.A. Archer 1344* (P image); 3Km west of Boqueron Pass, alt. 2300 m, 15 August 1955, *W.H. Hatheway 1581* (UTC-218948 image, UTC-218949 image, UTC-218950 image); Guatapé, vereda Santa Rita, alt. 1850 m, 07 August 1986, *R.W. Pohl et al. 15376* (MO); Municipio de Yarumal, 2 km antes del Alto de Ventanas, camino a Vereda Alegre, alt. 2030 m, 20 August 1986, *R. Callejas et al. 2478* (MO); Municipio de Jardín, 20 km de Jardín, alt. 2250 m, 18 September 1986, *R.W. Pohl & J. Betancur 15534* (MO); Municipio de Jardín, Cerro de Morro Amarillo, 7 km de Jardín, alt. 2100 m, 20 September 1986, *R.W. Pohl & M. Palacio 15585* (MO); Municipio de Sonsón, km 17.6 of road Sonsón-La Unión (38 km from La Unión), 05°49’N, 75°17’W, alt. 2140 m, 04 October 1987, *J.L. Zarucchi et al. 6248* (MO); Entrerrios, ca. 3 km from Entrerrios on the road to Santa Rosa de Osos, 06°32’N, 75°30’W, 04 February 1989, *J.M. McDougal & F.J. Roldán 3633* (MO); Vicinity of Salto Tequendama, road past falls leading downhill to El Colegio, 5°25’S, 74°20’W, alt. 2180-2300 m, 10 February 1989, *J.F. Smith 1289* (MO); Medellín, Parque Ecológico Piedras Blancas, 27 July 1996, *R. Fonnegra et al. 6162* (MO). CAUCA: El Tambo, Las Casitas, alt. 1800 m, 26 January 1936, *K. Sneidern 543* (MBM); El Tambo, alt. 1700 m, 06 June 1938, *K. Sneidern 1299* (MBM). CUNDINAMARCA: Salto de Tequendama [as “Tequendamama”], 01-03 October 1938, *J.*

*Cuatrecasas 165* (P-01936041, image) [paratype]; Subida ao Alto del Tigre, alt. 1700 m, 16 June 1989, *F.O. Zuloaga 4031* (MO). NARIÑO: Pasto, Corregimiento de Nariño, La Caldera, alt. 2200 m, 06 April 1990, *B.R. Ramírez 2243* (MO). ECUADOR. COTOPAXI: Pujili Canton, along road between El Corazon and Angamarca, 1°08'S, 79°03'W, alt. 1780 m, 07 April 1992, *T.B. Croat 73690* (MO). EL ORO: Near Tambillo 25 km NE of Zaruma and along mulech to Manú, 3°30'S, 79°35'W, alt. 1950-2200 m, 21 February 1988, *S. Laegaard 70287* (MO). LOJA: Parque Nacional de la Universidad Nacional de Loja, alt. 2100-2200 m, 19 August 2000, *J.E. Madsen 7134* (MO image). PICHINCHA: road Chillogallo – Santo Domingo, below Chiriboga, alt. 2000 m, 13 August 1980, *L.B Holm-Nielsen et al. 24768* (MO); Reserva Florística-Ecológica “Río Guajalito”, km 59 de la carretera Antigua Quito-Sto. Domingo, Domingo de los Colorados, a 3 ½ km al NE de la carretera, estribaciones accidentals del Volván Pichincha, 0°13'53”S, 78°48'10”W, alt. 1800-2200 m, 18 February 1986, *V. Zak 848* (MBM, MO). ZAMORA-CHINCHIPE: Loja-Zamora, 13.3 km E of pass. Roadbank, 4°00'S, 79°02'W, alt. 2100 m, 23 February 1988, *S. Laegaard 70353* (MO). GUYANA. POTARO-SIPARUNI: Mont Wokomung, easternmost pinnacle of massif, 5°5'34.4”N, 59°50'13.3”W, alt. 1524 m, 30 June 2003, *H.D. Clarke et al. 10316* (US). PERU. CAJAMARCA: San Ignacio, Santuario Nacional Tabaconas-Namballe, pampa Limón, 05°17'29”S, 079°16'32”W, alt. 1980 m, 23 November 1998, *C.S. Díaz et al. 10145* (MO). PASCO: Oxapampa, 05 March 1986, *H. van der Werff et al. 8405* (US image). VENEZUELA. AMAZONAS: Departamento de Río Negro, Serranía Tapirapecó, fila de primeira colina al norte del cerro Tamacuari, 1°14'N, 64°56'W, alt. 1500 m, 11 February 1989, *E. Gutiérrez 421* (MO). BOLÍVAR: Mount Roraima, forested southwest-facing quebrada near Rondón Camp, alt. 2040 m, 25 September 1944, *J.A. Steyermark 58656* (US); Mount Roraima, southwest-facing forested slopes between Rondón Camp and base of sandstone bluffs, alt. 2040-2255 m, 30 September 1944, *J.A. Steyermark 59009* (US); Sororopán-tepui, crest of cerro between east and west end, alt. 2255 m, 14 November 1944, *J.A. Steyermark 60107a* (US); Sarvén-tepuí, slopes and talus forest, 13 January 1953, *J.J. Wurdack 34138* (IAN, RB, NY, VEN); Cerro Venamo, cerca de los límites con la Guayana Inglesa, a lo largo del afluente Este del Río Venamo, alt. 1400-1450 m, 03 January 1964, *J.A. Steyermark et al. 92697* (US); Auyan-tepui, El Peñón, alt. 1800 m, 18 April 1956, *L. Schnee 1553* (MO); Auyan-tepui, cumber de la parte sureste del brazo noroeste (división occidental del cerro), alt. 1850 m, 11 May 1964, *J.A. Steyermark 93658* (MO, US); Auyan-tepui, cumber de la parte sur, entre “Oso Woods Camp” y “Libertador”, alt. 2050-2300 m, 15 May 1964, *J.A. Steyermark 93914* (US); Distrito Piar, cumber del Sororopán-tepui, al N de Kavanayén, 5°40'N, 61°45'W, alt. 2040 m, 28 June 1983, *O. Huber & C. Alarcon 7738* (MO). MERIDA: Distrito Andrés Bello, steep slopes between Quebrada el Trigal and Quebrada Zerpa, between Mirabel and San Benito, 10-14 km SE of La Azulita, 8°40-41'N, 71°25-26'W, alt. 1600-1900 m, 01 July 1980, *G. Davidse & A.C. González 18887* (MO). TACHIRA: Distrito Junín, Quebrada Agua Blanca, near La Rochela, along Delicias-Rubio Highway, 7°35'N, 72°26'W, alt. 1850-2000 m, 15 November 1982, *G. Davidse & A.C. González 22344* (MO).

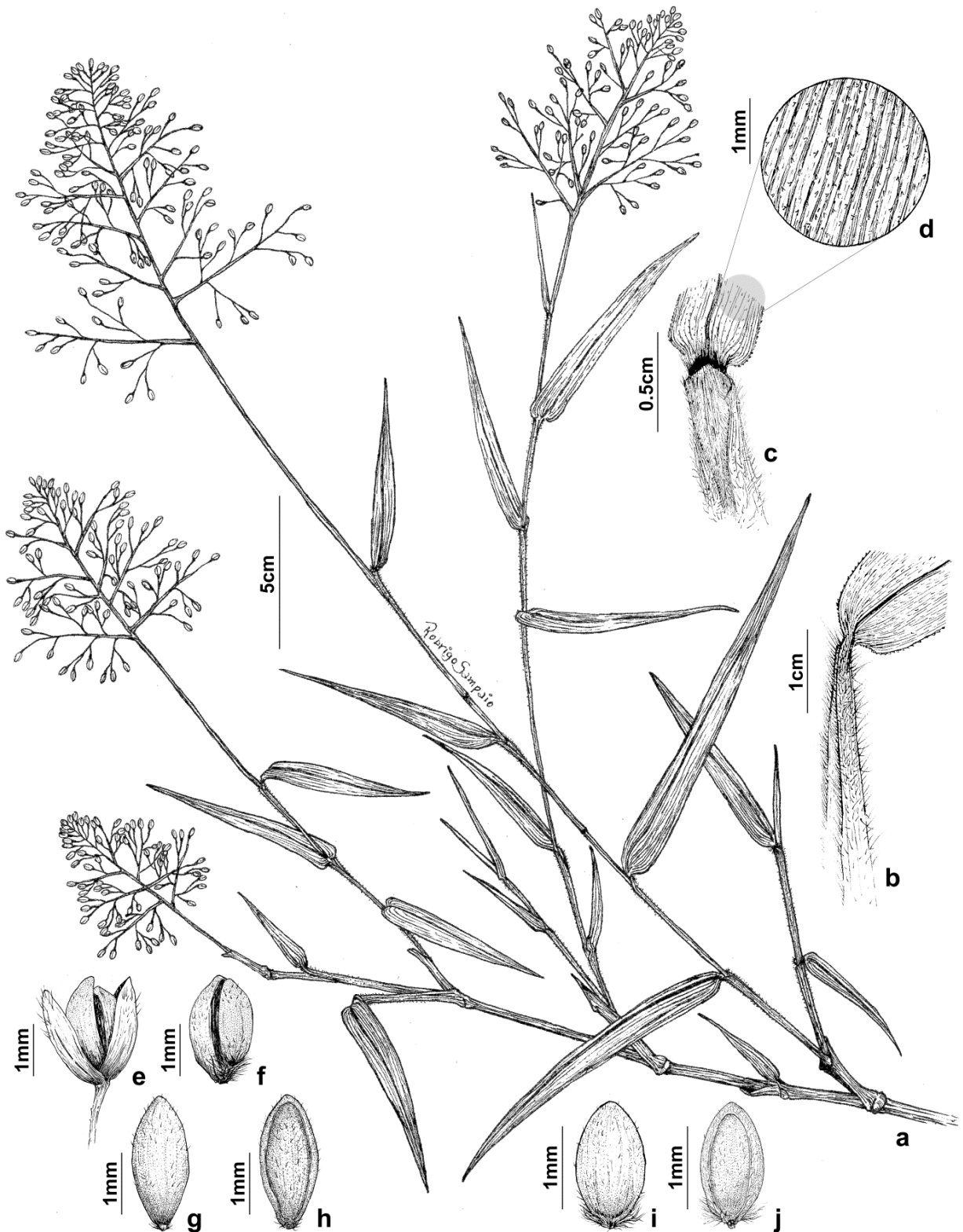


Figure 16. *Isachne ligulata* Swallen. a. Apical portion of a branched culm with flowering branches and synflorescences. b. Basal portion of the leaf blade, the collar region, and the apex of the leaf sheath (note the pilosity of the leaf sheath). c. Basal portion of the leaf blade, ciliate ligule, and apex of the leaf sheath. d. Detail of the adaxial epidermis of the leaf blade. e. Spikelet in lateral view and pedicel without a glandular band. f. Anthoecia (glumes removed – note the pilosity at the apex of the rachilla, near the callus of the upper anthoecium). g. Lower anthoecium, lemma view. h. Lower anthoecium, palea view. i. Upper anthoecium, lemma view. j. Upper anthoecium, palea view. Based on: a. J.J. Wurdack 34138 (RB); b-j. R.C. Forzza et al. 7275 (SP). Illustration by Rodrigo S. Rodrigues, extracted from Rodrigues & Filgueiras (2016).

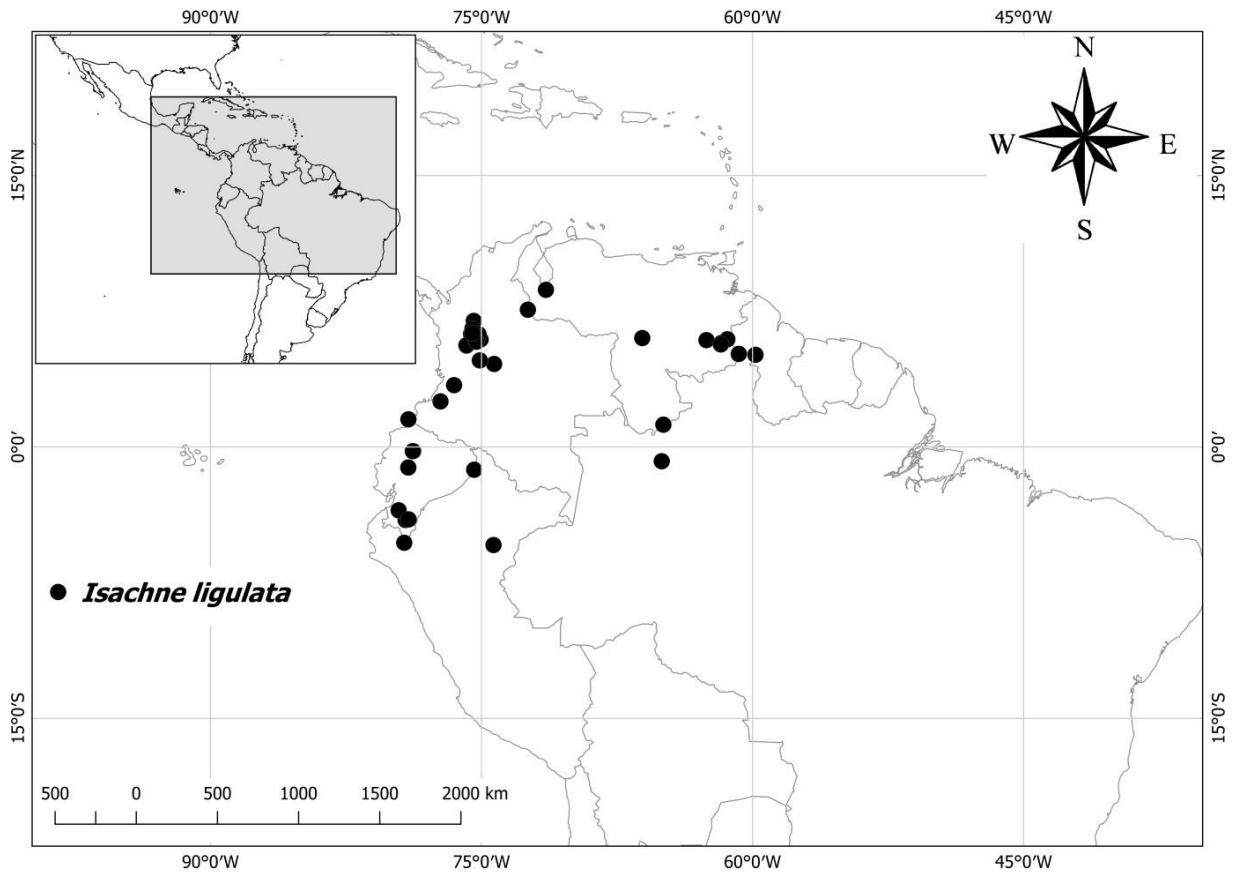


Figure 17. Known distribution of *Isachne ligulata*.

9. *Isachne polygonoides* (Lam.) Döll, Fl. Bras. 2(2): 273. 1877.  $\equiv$  *Panicum polygonoides* Lam., Encycl. 4(2): 742. 1798, non *Panicum polygonoides* Müll. Hal., Bot. Zeitung (Berlin) 19(44): 323. 1861 [nom. illeg. hom., =*Hopia obtusa* (Kunth) Zuloaga & Morrone]. Type: FRENCH GUIANA: Cette plante croît à Cayenne, & m'a été communiquée par le citoyen Leblond, s.a., *J.B. Le Blond s.n.* [holotype P-LA-00563954 image!; isotypes US-80926 (fragment and photo ex P) image!; BAA-00002392 (illustr. and fragm. ex P) image!].
- = *Isachne trachyspermum* [as "*trachysperma*"] (Nees) Balansa, J. Bot. (Morot) 4: 137. 1890 [nom. inval. isonym].  $\equiv$  *Isachne trachyspermum* [as "*trachysperma*"] (Nees) Nees, Bot. Voy. Herald 224. 1857.  $\equiv$  *Panicum trachyspermum* Nees, Fl. Bras. Enum. Pl. 2(1): 212-213. 1829. Type: BRAZIL. Pará. Habitat in graminosis prope Pará provinciae Paraensis, s.a., *K.F.P. von Martius s.n.* (holotype M; isotype: US-81145 image!).
- = *Panicum hirtum* Willd. ex Kunth, Enum. Pl. 1: 112. 1833 [hom. et nom. inval., cited as syn. of *P. trachyspermum*], non. *Panicum hirtum* Lam., Encycl. 4: 741. 1798, nec *Panicum hirtum* Roth, Nov. Pl. Sp. 46. 1821 [nom. illeg. hom., =*Panicum rothii* Spreng.]. Type: s.l., s.a., *C.L. Willdenow 18828* (holotype B-W-18828-010 image!). *syn. nov.*
- = *Panicum tetraspermum* Steud., Nomencl. Bot. (ed. 2) 2: 257. 1841 [nom. inval., err. orthogr. for "*trachyspermum*"].

#### Figure 18

Perennial, decumbent, tangled, 10-60(-90) cm long. Culms rooting at the lower nodes, branched from the base and/or at the middle and upper portions, herbaceous, slender, sterile and flowering branches ascending or decumbent; nodes glabrous or pilose, trichomes tuberculate, stramineous to dark-brown, with or without a glandular stripe below; internodes inconspicuously hollow, glabrous, greenish, stramineous, purplish or purple-stained. Sheaths shorter than the internodes, densely tuberculate-hirsute, less frequently glabrescent to glabrous, strongly nerved, one margin ciliate, the other glabrous, cilia ca. 0.5-0.9 mm long, those near the ligular region 1.5-2 mm long, colorless; ligule ciliate, 1-2.1 mm long; leaf blades distichous, regularly distributed over the culms and secondary flowering and/or sterile branches, lanceolate, 1-4.5  $\times$  0.2-1.5(-2) cm, flexible (not rigid), midrib usually inconspicuous, sometimes evident on the abaxial surface, base cordate or subcordate, amplexicaul, apex acute, glabrous, scaberulous or pubescent on both surfaces, margins entire, scaberulous, often with some long tuberculate trichomes towards the ligular region, rarely trichomes present throughout the leaf margins. Panicle terminal and axillary, open to subcontracted, flexible, (1-)2.5-10  $\times$  1-6 cm, glabrous, provided with second-order branches, glandular bands and axillary glands present; pedicels 1-9 mm long, cylindrical, glabrous, glandular bands present. Spikelets unequally pedicelled, erect on the pedicels or slightly oblique-inserted, globose, subglobose to elliptic, 1.3-2 mm long;

glumes subequal, the lower elliptic-lanceolate to ovate, the upper ovate, somewhat ventricose, both obtuse, acute or acuminate, sometimes slightly apiculate, glabrous or scaberulous or hispidulous at the apex, greenish to stramineous, sometimes purple-stained, equaling the anthoecia, sometimes slightly shorter or longer; lower glume 1.3-1.6 mm long, (5-)7(-9)-nerved, margins greenish, whitish or hyaline, sometimes involute; upper glume 1.3-1.8 mm long, 7(-9)-nerved, margins whitish or hyaline; anthoecia 2, dissimilar, the lower cartilaginous, ovate to ovate-lanceolate or lanceolate, the upper coriaceous, suborbicular to ovate, both greenish to stramineous in maturity, rarely purple-stained; lower anthoecium staminate, 1.3-1.9 mm long, lemma glabrous, not sulcate, palea glabrous, 1.2-1.8 mm long; rachilla conspicuous or inconspicuous between the anthoecia, 0.1-0.3 mm long, glabrous; upper anthoecium, bisexual, 1.1-1.5 mm long, lemma appressed-pilose, palea appressed-pilose, 1-1.4 mm long. Lodicules ca. 0.1 mm long. Stamens 3, filaments ca. 0.1-0.2 mm long, whitish to pale-green; anthers 0.3-0.4 mm long, yellowish to orange in maturity, very small in relation to the lower anthoecium. Stigmas 2, plumose, orange to dark-brown in maturity. Caryopsis 1.2 x 0.7 mm, elliptic-oblong, flat-convex, dark-brown.

*Etymology:* From the Greek: “-oides”: resembling. The epithet refers to the creeping habit like those of some *Polygonum* L. species (Clifford & Bostock 2007).

*Distribution:* North America, Central America, Antilles, and South America, from México to Bolivia and Midwest and Southeast Brazil (Figure 19). It inhabits humid places, swamps, bogs, brooks, margins of gallery forests and waterfalls, associated with hygrophilous vegetation; at ca. 0-1000 m.

*Phenology:* Collected in flower throughout the year.

*Comments:* *Isachne polygonoides* is the most widespread Neotropical species of the genus. It is an easily distinguishable species by its delicate habit, tuberculate-hirsute sheaths, amplexicaul leaf blades, and dissimilar anthoecia, being the lower cartilaginous and glabrous, and the upper coriaceous and densely appressed-pilose. The presence or absence of trichomes in the upper portion of the glumes is a variable character that appears to be related to the spikelets size and maturity.

The characteristics of the anthoecia closely resemble those of *I. goiasensis*, *I. hirtiglumis* and *I. salzmannii*. *Isachne goiasensis* is promptly distinct by the robust habit, longer leaf blades, and synflorescence dimension. *Isachne salzmannii* is distinct by its often glabrous sheaths, leaf blades not amplexicaul, ventricose glumes, and conspicuously sulcate lemma of the lower anthoecium. See comment under *I. hirtiglumis* for the distinction between *I. polygonoides* and *I. salzmannii*.

Material examined: BRAZIL. ACRE: Rio Branco, entre as fazendas Bom Intento e Capela, 31 August 1951, *G.A. Black 13238* (IAN); Rio Branco, estrada Boa Vista-Caracaraí, 12 September 1951, *G.A. Black 13486* (IAN); Boa Vista, 25 September 1951, *G.A. Black 13751* (IAN); Rio Branco, Rio Cantá, 08 October 1951, *G.A. Black 13853* (IAN); Boa Vista, 13 November 1951, *G.A. Black 14091* (IAN); Cruzeiro do Sul, ramal Pentecostes, 07°33,8'3"S, 72°49,8'W, *M.D. Moraes & M.A.V. Sousa 1039* (UEC). AMAPÁ: Município de Mazagão, região de Ariramba, 09 April 1982, *N.A. Rosa et al. 4214* (HRB); Municipality of Macapá, Parque Florestal da Fazendinha, 12 km S of Macapá, 21 July 1983, *S.A. Mori et al. 15736* (MO). AMAZONAS: Canutama, Joana D'Arce, campina ca. 20 km depois de Joana D'Arce, 8°39'27"S, 64°21'39"W, alt. 95 m, 04 May 2007, *P.L. Viana et al. 2703* (INPA, BHCB). BAHIA: Alagoinhas, alt. 25 m, 02-03 January 1925, *A. Chase 8124* (MO, RB); Vera Cruz, Ilha de Itaparica, Catu, 13°05'13,9"S, 38°47'12,8"W, 24 March 2010, *L.Y.S. Aona et al. 1253b* (HURB, HUEFS). GOIÁS: Cerrado ca. 12 km S of Guará, alt. ca. 550 m, 20 March 1968, *H.S. Irwin et al. 21552* (UB, MO). MARANHÃO: Caxias, 11 July 1954, *G.A. Black et al. 16696* (IAN). MINAS GERAIS: Serra do Cipó (110 km NE of Belo Horizonte), alt. 850 m, 28 March-01 April 1925, *A. Chase 9122* (MO). PARÁ: Óbidos, 19 July 1934, *J.R. Swallen 5123* (IAN); Altamira, Rio Xingú, October 1943, *J.R. Swallen 6905* (IAN); Santarém, 3-4 November 1943, *J.R. Swallen 6922* (MO); Ilha de Marajó, Lago Arari, opposite Jenipapo, 2-5 June 1944, *J.R. Swallen 6949* (IAN); Ilha de Marajó, Fazenda São Pedro, 04 June 1944, *J.R. Swallen 6977* (IAN); Currálinho, 22 August 1948, *J.M. Pires 1264* (IAN); Soure, Fazenda Ritlândia, fazendo limites com a fazenda Santander, 21 March 1950, *G.A. Black & J Lobato 9342* (IAN); Ilha de Marajó, Rio Camará, Fazenda Gurupatuba, 08 July 1950, *G.A. Black 9910* (IAN); Santarém, perto da Casa Santa Izabel, 28 October 1950, *G.A. Black & P. Ledoux 10372* (IAN); Cacaual Grande, Limpo dos Alemães, 01 November 1950, *G.A. Black & P. Ledoux 10501* (IAN); Ilha de Marajó, redondezas da Fazenda Tuiuiú, 28 April 1952, *G.A. Black et al. 14302* (IAN); Ilha de Marajó, Rio Ararí, Fazenda Tuiuiú, 02 May 1952, *G.A. Black et al. 14356* (IAN); Conceição do Araguaia, 02 July 1953, *R.L. Fróes 30108* (IAN); Rio Mojú, campina da Fábrica, 31 May 1954, *G.A. Black 16207* (IAN); Maicurú, Curral Velho, 16 August 1955, *G.A. Black 18712* (IAN); Muaná, Rio Anabijú, Fazenda São João, 30 June 1962, *E. Oliveira 2095* (IAN, UB); Cachoeira de Curuá, north slope of Serra do Cachimbo, alt. 300 m, 04 November 1977, *G.T. Prance et al. 24818* (MO); Conceição do Araguaia, 2 km W of town along highway PA-287, 8°15'S, 49°18'W, alt. 300 m, 24 February 1980, *T. Plowman et al. 9101* (HRB, MO); Serra Norte, 25 km NW of camp at Serra Norte, 5°54'S,

50°26'W, 10 December 1981, *D.C. Daly et al. 1995* (HUEFS, MO); Itaituba, estrada Santarém-Cuibá, BR-163, km 877, Serra do Cachimbo, Cachoeira da Luz, Rio Curuá, margem esquerda, 02 May 1983, *I.L. Amaral et al. 1095* (MO); Paraupebas, S da Bocaina, 6°18'0"S, 49°54'0"W, 15 December 2010, *N.F.O. Mota et al. 1861* (BHCB, IAN); Paraupebas, FLONA de Carajás, caminho para a Serra Sul, 6°17'04"S, 50°20'12"W, alt. 623 m, *R.C. Oliveira et al. 2599* (UB); Novo Progresso, área da Aeronáutica (Campo de Provas Brigadeiro Veloso), Serra do Cachimbo, margem do rio Braço Norte, próximo da ponte e da usina antiga, 9°21'32"S, 54°54'13"W, alt. ca. 460 m, 11 August 2015, *L. Rossi & O. Oyakawa 2539* (SP). PIAUÍ: Piracuruca, Sete Cidades, alt. 170 m, 08 October 1973, *D. Sucre 10326* (RB, SP). BOLIVIA. SANTA CRUZ: Velasco Province, Bahia Toledo, 14°42'56"S, 61°07'26"W, alt. 210 m, 10 September 1995, *N. Ritter 2414* (MO); Velasco Province, ca. 3 km to the NE of the buildings at La Toledo, 14°41'50"S, 61°09'45"W, alt. 220 m, 30 September 1995, *N. Ritter 2477* (MO); Velasco Province, Parque Nacional Noel Kempff Mercado, Lago Caiman, 13°35'42"S, 60°54'16"W, alt. 220 m, 09 April 1996, *M. Garvizu & N. Ritter 148* (MO). COLOMBIA. META: Villavicencio, alt. 450 m, 26-31 August 1917, *F.W. Pennell 1456* (MO). Carimagua, alt. 200 m, 18 September 1992, *S.A. Renvoize 5398* (MO). NARIÑO: Municipio de Barbacoas, Corregimiento de Junín, a 3 km del pueblo, alt. 1300 m, 16 June 1988, *O. Benavides 9997* (MO). COSTA RICA. CARTAGO: between Tuis and Bajo Pacuare along the road from Turrialba to Moravia de Chirripo, 9°49'N, 83°33'W, alt. 750-900 m, 15 November 1975, *W. Burger et al. 10044* (MO). GUANACASTE: La Cruz, 7.5 km E of Río Animas, November 1982, *L.D. Gómez 18983* (MO); Cantón de La Cruz along road between the Panamerican Highway and Santa Cecilia, 2 km E of Finca Los Inocentes, 11°02'N, 85°30'W, alt. 200 m, 28 December 1989, *C.M. Taylor & A.M. Chacón 9784* (MO). CUBA. ISLA DE LA JUVENTUD [ISLE OF PINES]: Nueva Gerona, at the road towards McKinley, in a brook covering the water, 17 October 1920, *E.L. Ekman 11702* (NY); between McKinley and Santa Bárbara roads, 01 February 1955, *E.P. Killip 44664* (US). DOMINICAN REPUBLIC. SANTO DOMINGO: Villa Altagracia, Cordillera Central, 19 January 1929, *E.L. Ekman 11222* (MO, US). FRENCH GUIANA. SAINT LAURENT DU MARONI: Savane Saint Maurice, 05 October 1955, without collector (IAN-95045); route de Saint Jean. 9km, 25 June 1956, *J. Hook 1033* (US). KOUROU: Campo de Passoura, 25 October 1954, *G.A. Black & Klein 17229* (IAN); fond savane Passoura, 22 June 1962, *J. Hook 984* (MO, US). SINNAMARY: piste de St-Ellie, PK 2.5, 30 June 1983, *Feuillet 957* (MO). GUYANA. UPPER TAKUTU: Essequibo, South Rupununi Savanna, Aishalton village, 02°31'N, 59°20'W, alt. 200



m, 03 August 1993, *T.W. Henkel & R. James 3974* (MO); Southern Rupununi Savanna, east side of Rupununi River, Dadanawa, 2°40'N, 59°25'W, 20 August 1995, *S.R. Hill 27297* (MO, US). HONDURAS. AHUAS: Departamento de Gracias a Dios, 84°20'N, 15°30'W, alt. ca. 0 m, 12-14 December 1972, *A.F. Clewell 3624* (MO). MORAZÁN: San Antonio road north of Zamorano, alt. 850 m, 23 July 1947, *A.R. Molina 376* (MO); region of El Jicarito, above El Zamorano, alt. 900-1000 m, 15 November 1950, *P.C. Standley 27476* (MO). OLANCHO: Municipio San Estebán, Santa Maria del Carbón, 23 mi NE of San Estebán along road to Bonito Oriental, 15°26'24"N, 85°34'57"W, alt. 480 m, 03 July 1994, *G. Davidse et al. 35554* (MO). MEXICO. CHIAPAS: Municipio of Palenque, 12 km N of Palenque along road to Catajaza, alt. 250 m, 08 November 1980, *D.E. Breedlove 47304* (MO); Municipio of Palenque, 12 km N of Palenque along road to Catajaza, alt. 250 m, 24 January 1982, *D.E. Breedlove & F. Almeda 57809* (MO). NICARAGUA. CHONTALES: 10 km NNE of Cuapa along road toward Muy Muy, 2 km past Matayagual, 12°18'57"N, 85°20'47"W, alt. 575 m, 25 January 2009, *W.D. Stevens & O.M.J. Montiel 27961* (MO). NUEVA SEGOVIA: ca. 5.2 km N of San Fernando, valley of Río San Fernando (800 m), NE de Portillo Los Coyoles (1083 m), SW up narrow Quebrada to Cerro El Peñascal (1125), 13°2-3'N, 86°19-20'W, 10-13 August 1977, *W.D. Stevens et al. 3271* (MO); Santa María de los Pinos, 5 km al NE de Dipilito, 13°45'N, 86°33'W, alt. ca. 1200 m, 21 September 1984, *P.P. Moreno et al. 24727* (MO). ZELAYA: 5.1 km W of El Empalme by road to Siuna, 13°40'N, 84°29'W, alt. 60 m, 04 July 1982, *R. Kral 69226* (MO); Municipio de Siuna, Río Matis, alt. less than 100 m, 16 September 1982, *F. Ortiz 196* (MO). PANAMÁ. BARRO COLORADO [ISLAND]: Gigante Bay, 1931, *O.E. Shattuck 433* (MO); North shoreline of Gigante Bay, 08 March 1971, *T.B. Croat 13973* (MO); in quiet cove of the Gigante Peninsula, just south of CBI, 9°09'N, 79°51'W, alt. 26-165 m, 08 March 1983, *E.J. Judziewicz 4448* (MO). PROVINCE OF PANAMÁ: Gatun Lake, Canal Zone, open grassy marsh near Mt. Hope, 15 December 1911, *A.S. Hitchcock 599* (MO); Las Sabanas, 04 December 1923, *P.C. Standley 25943* (MO); along road between Panamá and Chero, 29 November 1934, *C.W. Dodge et al. 16681* (MO); Sabanas near Chepo, alt. 30 m, 20 January 1935, *A.A. Hunter & P.H. Allen 15* (MO); between Pacora and Chepo, alt. ca. 25 m, 01 August 1938, *R.E. Woodson et al. 1655* (MO); Juan Mina, Río Aguardiente Chico, 17 July 1940, *H.H. Bartlett & T. Lasser 16500* (MO); vicinity of Rio Pescado, at southeastern part of Gatun Lake, 30 July 1940, *H.H. Bartlett & T. Lasser 16599* (MO); savannas near Chepo, 24 October 1962, *J.A. Duke 6045* (MO). PROVINCE OF SAN BLAS: along canal just north of Mandinga Airport, 27 October 1967, *J.A. Duke 14842* (MO). PROVINCE OF VERAGUAS: Hills

west of Soná, alt. ca. 500 m, 24 November 1938, *P.H. Allen 1068* (MO); roadside just S of Santa Fe, alt. ca. 450 m, 17 November 1973, *M. Nee 8076* (MO); 2 km NW of Atalaya, alt. 100 m, 19 November 1973, *M. Nee 8212* (MO). PERU. LORETO: Maynas, Departamento Iquitos, carretera de Pena Negra, 25 May 1978, *S. McDaniel et al. 21623* (MO); Maynas, Inmediaciones de la Guarnición Militar de Gueppi, sobre la margen izquierda del Río Putumayo, borde con Ecuador, 26 May 1978, *C.S. Díaz 363* (MO). MADRE DE DÍOS: Tambopata, Tambopata Nature Reserve, ca. 30 air km or 70-80 river km SSW Puerto Maldonado at effluence Río La Torre (Río D'Orbigny)/ Río Tambopata (SE bank), 12°49'S, 69°17'W, alt. ca. 260 m, 21 April 1980, *P.J. Barbour 4889* (MO); Tambopata, Explorer's Inn Tourist Camp, near Junction of Ríos La Torre and Tambopata, alt. 270 m, 26 July 1985, *A.H. Gentry et al. 51390* (MO); Tambopata, Tambopata Nature Reserve, laguna Coco Cocha, 5.2 km East of lodge, 03 June 1986, *V.A. Funk 8405* (MO); Tambopata, Parque Nacional "Bahuaia-Sonere" ex Santuario Nacional "Pampas del Heath", 04 June 1997, *C.S. Díaz & J. Pereira 8950* (MO); Manu Province, Los Amigos Biological Station, Madre de Dios River, ca. 7 km upriver from mouth of Río Los Amigos, alt. 270 m, 19 August 2002, *J.P. Janovec & A.P. Maceda 2680* (MO); Manu Province, Los Amigos Biological Station, Madre de Dios River, ca. 7 km upriver from mouth of Río Los Amigos, 24 May 2003, *A.P. Maceda 644* (MO). PUERTO RICO. UTUADO: without locality, alt. 450 m, 1943, *F.H. Sargent 3276* (MO). SURINAME. SIPALIWINI: Wilhelmina Gebergte, vic. Kayser Savanna, 45 km above confluence with Lucie River, alt. 270 m, 26 August 1963, *H.S. Irwin et al. 55247* (MO, US). TRINIDAD AND TOBAGO. TUNAPUNA-PIARCO: south of Arouca, Piarco Savanna, 28 December 1912, *A.S. Hitchcock 598* (MO). ARIMA: Aripo Savannah, Wallerfield area, 09-23 February 1950, *R.A. Howard 10499* (US). VENEZUELA. AMAZONAS: 8 km S of Pt. Ayacucho, and just S of the Río Carinagua, alt. 90 m, 31 October 1971, *G. Davidse 2758* (MO); terreno situado entre la Carretera hacia Samariapo y la pista de aterrizaje del Aeropuerto de Puerto Ayacucho, 5°37'N, 67°36'W, alt. ca. 75 m, 07 December 1977, *O. Huber 1315* (MO); Vicinity of Puerto Ayacucho, 5°39'N, 67°38'W, alt. less than 100 m, 22 November 1984, *T.B. Croat 59223* (MO, US); Vicinity of Puerto Ayacucho, 5°39'N, 67°38'W, alt. less than 100 m, 22 November 1984, *T.B. Croat 59232* (MO). ANZOÁTEGUI: Morichal El Piñal, San Diego de Cabrutica, 8°25'N, 64°50'W, 20 January 1987, *R. Montes 3525* (MO). APURE: Distrito Pedro Camejo, near the Río Meta at Fundo El Algarrobo, 25 airline km WNW of Buena Vista, Morichal de La Madera, 6°13'N, 68°49'W, alt. 70 m, 16-18 February 1978, *G. Davidse & A. González 14126* (MO); Distrito de Muñoz, Modulos F. Corrales

de la UNELLEZ, entre los caños Guaritico y Caicara, 7°30'N, 69°30'W, 13 September 1981, *B. Stergios et al.* 2879 (MO); Municipio de Mantecal, Sabana "El Rosero", Módulo "Fernando Corrales", 13 October 1983, *R. Tejos* 7 (MO); Distrito de Muñoz, Módulos "Fernando Corrales" de la UNELLEZ, 7°30'N, 69°30'W, alt. 80 m, 09 Diciembre 1986, *G. Aymard et al.* 5036 (MO).

BOLÍVAR: Cerro San Borja, alt. 100-300 m, 12 December 1955, *J.J. Wurdack & J.V. Monachino* 39832 (US); Distrito de Piar, Río Ocoine, Pie de la Roca, southeastern base of Ayuan-tepui, 5°42'N, 62°30'W, alt. 500 m, 24 November 1982, *G. Davidse & O. Huber* 22633 (MBM); 130 km SW of Caicara del Orinoco, 6°50'N, 66°40'W, alt. 80 m, 05 September 1985, *J.A. Steyermark et al.* 131363 (MO); Serranía de Pijigua, 160 km SW of Caicara de Orinoco, 6°35'N, 66°45'W, alt. 100-125 m, 12 September 1985, *J.A. Steyermark et al.* 131823 (MO); Cedeño, entre los km 12-120 de la carretera Caicara del Orinoco-Pto. Ayacucho, al sur de Caicara del Orinoco, 6°50'N, 66°30'W, alt. 100 m, 18 November 1984, *G. Aymard & B. Stergios* 3196 (MO); Cedeño, entre al margen derecho del Río Orinoco medio y el borde NW de la Serranía de Los Pijiguaos (Bajo Río Suapure), 6°18'-6°48'N, 66°30'-67°10'W, alt. ca. 80 m, 01 November 1987, *F. Guanchez & O. Huber* 4838 (MO).

GUÁRICO: Murichales Hato El Recreo, February 1961, *L. Aristeguieta & F. Tamayo* 4494 (MO); 26 km SSE of Calabozo along road Carzola, alt. 70 m, 10 November 1971, *G. Davidse* 2979 (MO); 28 km N of Santa Rita along highway 12 between Chagauramas and Cabruta, alt. 100 m, 21 November 1973, *G. Davidse* 4296 (MBM, MO); Distrito Infante, Parque Nacional Aguaró-Guariquito, Sabanas de Juan Paulino, via Los Arroyuelos, ca. 9°80'-9°84' N, 67°64'-67°68'W, alt. 60 m, December 1981, *F. Delascio et al.* 11090 (MO, NY); Distrito Infante, Parque Nacional Aguaró-Guariquito, Morichal Charcote, 9°14'-9°19'N, 67°38'-67°40'W, alt. 68 m, December 1981, *F. Delascio et al.* 11107 (MO); Distrito Infante, Parque Nacional Aguaró-Guariquito, Morichal San Ramón, 9°40'-9°44'N, 67°52'-67°56'W, alt. 100 m, December 1981, *F. Delascio et al.* 11452 (MO); Distrito Infante, Parque Nacional Aguaró-Guariquito, Morichal Indio Viejo, 9°48'-9°52'N, 67°52'-67°56'W, alt. 100 m, December 1981, *F. Delascio* 11493 (MO); Distrito Infante, Parque Nacional Aguaró-Guariquito, Morichal Lamedero, 9°52'-9°56'N, 67°52'-67°56'W, alt. 100 m, December 1981, *F. Delascio et al.* 11620 (MO).

PORTUGUESA: Distrito Guanare, terrenos de la UNELLEZ, 9°4'N, 69°49'W, 30 September 1983, *B. Stergios & G. Aymard* 6415 (MO).

TACHIRA: Distrito Libertador, 10 km S of El Piñal, 7°27'N, 71°55'W, alt. 250 m, 07 November 1982, *G. Davidse & A.C. González* 21693 (MO).

WITHOUT LOCALITY. Without date, *J. Saldanha* 203 (R-49477); without date, *J. Saldanha* 212 (R-49960).

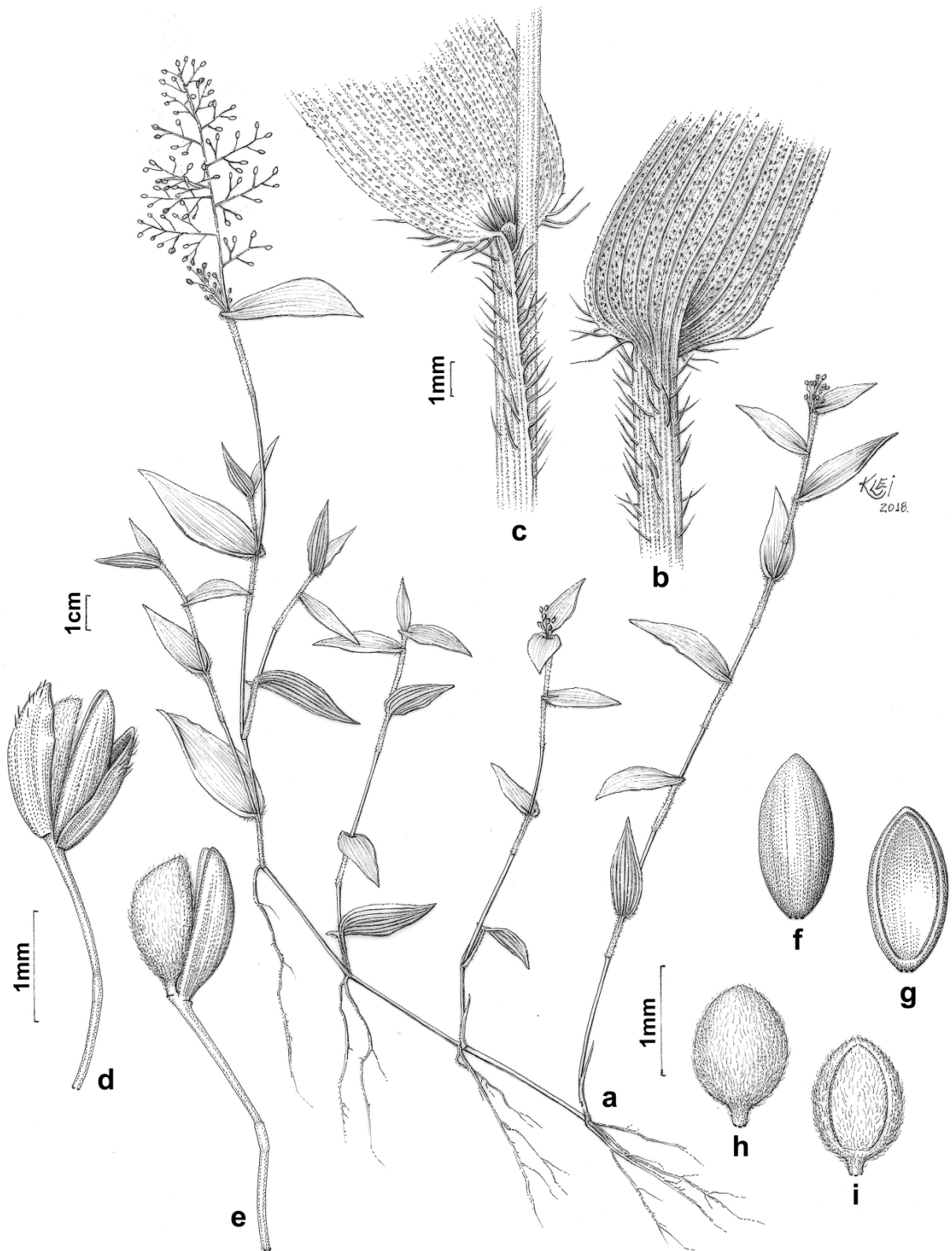


Figure 18. *Isachne polygonoides* (Lam.) Döll. a. Habit. b. Fragment of a culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath. c. Fragment of a culm showing the base of the leaf blade, part of the ciliate ligule, and the apex of the leaf sheath. d. Spikelet in lateral view and pedicel with a glandular band. e. Anthoecium (glumes removed – note the dissimilar anthoecia, being the lower cartilaginous and glabrous and the upper coriaceous and appressed-pilose) and pedicel with a glandular band. f. Lower anthoecium, lemma view. g. Lower anthoecium, palea view. h. Upper anthoecium, lemma view. i. Upper anthoecium, palea view. Based on: a-i. A.S. Hitchcock 599 (MO). Illustration by Klei R. Sousa.

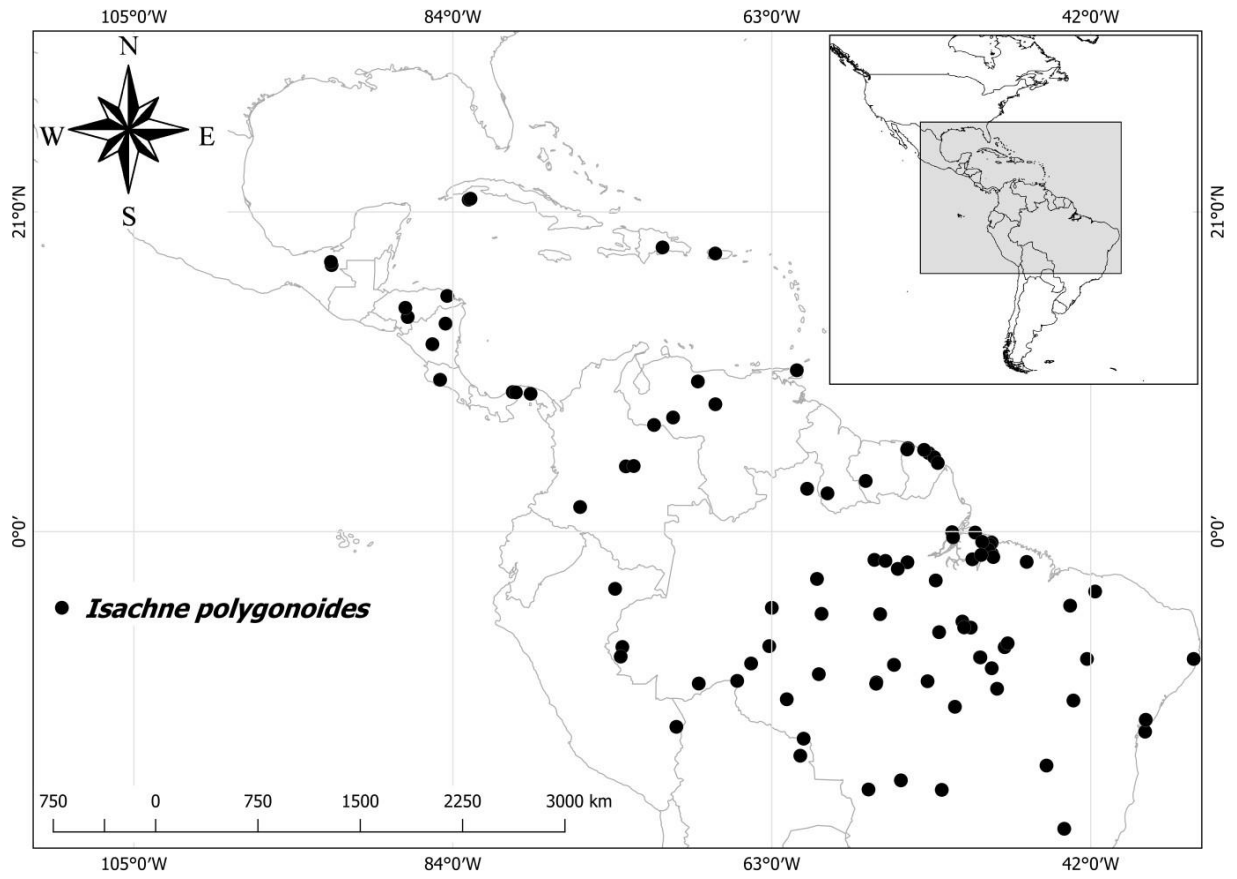


Figure 19. Known distribution of *Isachne polygonoides*.

10. *Isachne pubescens* Swallen, Contr. U.S. Natl. Herb. 29(9): 426. 1950. Type: GUATEMALA: Department of Alta Verapaz, in the vicinity of Secanquim, altitude 550 meters, 6 May 1905, H. Pittier 252 (holotype US-472909!).

Figure 20

Perennial, suberect to scandent or sprawling, 100-200(-300) cm long. Culms rooting and/or branching at the lower nodes, branched also at the middle and upper portion/nodes, robust, somewhat lignified, sterile and flowering branches ascending-scandent to erect; nodes glabrous, stramineous to blackish, sometimes slightly purplish or vinaceous, without a glandular stripe below; internodes hollow, glabrous, greenish, purplish to stramineous, sometimes dark-brown in the thicker culms or purple-stained towards the nodes. Sheaths shorter than the internodes, sometimes longer at the apex of the flowering and sterile branches, pilose to pubescent, trichomes more abundant towards the apex near the ligular region, strongly nerved, one margin ciliate, the other glabrous, cilia 0.7-0.8 mm long, those near the ligular region 1-1.5 mm long, whitish or colorless; ligule ciliate, 2-2.5 mm long; leaf blades distichous, regularly distributed along the culms, lanceolate to linear-lanceolate, (4-)7-15(-20) × 0.5-1.4 cm, flexible (not rigid), midrib conspicuous or inconspicuous, more evident on the abaxial surface, base rounded, slightly constricted near the ligular region, not amplexicaul, apex acute, pilose to pubescent on both surfaces, margins entire, inconspicuously scaberulous. Panicle terminal, subcontracted to open, sometimes imperfectly expanded when immature, flexible, 8-17 × (3.5-)5.5-14 cm, pubescent, trichomes abundant, soft, whitish, silky, provided with second-order branches, glandular bands absent, axillary glands present; pedicels 0.1-1 cm long, cylindrical, pubescent, trichomes whitish, silky, glandular bands absent. Spikelets unequally pedicelled, erect on the pedicels, regularly distributed in the synflorescence branches, elliptic to elliptic-obovate, 1.7-2.1 mm long; glumes subequal, oblong, obtuse to subacute, not acuminate or cuspidate, glabrous to pubescent towards the apex, greenish or stramineous, frequently purple-stained in maturity, both shorter than the anthoecia; lower glume 1.5-1.7 mm long, 5-7-nerved, margins greenish to stramineous or purple-stained; upper glume 1.4-1.5 mm long, 5-7-nerved margins greenish to stramineous or purple-stained; anthoecia 2, similar in texture and indumentum, but the lower longer than the upper, coriaceous, greenish to stramineous, purple-stained or completely purple in maturity; lower anthoecium bisexual or staminate, 1.5-2.1 mm long, lemma glabrous or with some inconspicuous trichomes at the margins, not sulcate, palea glabrous, 1.4-2 mm long; rachilla conspicuous between the anthoecia, 0.2-0.4 mm long, glabrous; upper anthoecium bisexual, 1-1.3 mm long, lemma glabrous or with some inconspicuous trichomes at the base, palea glabrous, 0.9-1.2 mm long. Lodicules ca. 0.2 mm long. Stamens 3, filaments ca. 0.5 mm long, yellowish; anthers 0.5-0.6 mm long, orange to dark-brown in maturity. Stigmas 2, yellow, dark-brown in maturity. Caryopsis 1.1 × 0.7 mm, oblong, flat to slightly concave-convex, dark-purple to blackish.

*Etymology:* From the Latin: “*pubesco*”: become hairy (Clifford & Bostock 2007). The epithet refers to the soft pilosity of the sheaths, leaf blades, and synflorescence branches and branchlets.

*Distribution:* North and Central America, in Belize, Guatemala, Mexico and referred here for the first time to Nicaragua (Figure 21). It preferably inhabits disturbed and humid forests, montane Rain Forest, and mixed savannas, in rocky hillsides, hills, clearings, and stream beds; at ca. 55-1495 m.

*Phenology:* Collected in flower from November to March, and from May to September,

*Comments:* Pohl & Davidse (1994) suggested that *I. pubescens* should be considered a synonym of *I. arundinacea* (treated here as *I. glaucescens*). *Isachne pubescens* is morphologically characterized by the medium to robust habit, pubescent sheaths, leaf blades and synflorescence branches, and panicles with spikelets regularly distributed, not congested at the branchlets tips. See comments under *I. glaucescens* and *I. glaucescens* var. *trichomatosa* for a distinction between *I. pubescens*.

Material examined: BELIZE. BELIZE DISTRICT: In high ridge, base of hill, Hummingbird Gap, Hummingbird Highway, 08 September 1956, *P.H. Gentle 9242* (MO). CAYO: Maya Mountain divide in the vicinity of Doyle’s Delight (DD), pineland ca. 2.3 km WNW of DD, alt. 900 m, 16°29.93’N, 89°04.09’W, 25 August 2007, *B.K. Holst et al. 9073* (MO). TOLEDO: Union Camp, alt. 750 m, 15 May 1979, *C. Whitefoord 1746* (MO); Helicopter Landing Site 500 (HLS 500) 3.5 km east of Union Camp, 16°24’02”N, 089°06’40”W, alt. 940 m, without date, *T. Hawkins 1467* (MO). GUATEMALA. ALTA VERAPAZ: 10 km south of Coban, Pine-liquidambar forest on deep humus-rich soil over red clay, 09 March 1970, *W.E. Harmon & J.D. Dwyer 4284* (MO); Along highway ca. 14,5 miles N of Coban, disturbed forest on rocky hillside, alt. 1300 m, 17 July 1977, *T.B. Croat 41366* (MO); 9 miles up road to Oxec along gravel road which turns N off Highway 7E between Tucúru and El Estor ca. 6 km NE of Panzós, alt. 800 m, 20 July 1977, *T.B. Croat 41669* (MO); a 2 km al S de Jolomylix, Telemán, Panzós, Sierra de las Minas, alt. 750 m, 20 July 1988, *E.M. Martínez et al. 22935* (MO). HUEHUETENANGO: Camino a Río Ixcán, Aldea Malpaís, Barrillas, 15°50’17”N, 91°12’57”W, alt. 1435 m, 21 September 2006, *A. Quezada 1827* (MO); Laguna Maxbal, bosque húmedo, Barrillas, 15°56’23”N, 91°18’19”W, alt. 1200-1300 m, 22 September 2006, *J. Morales 4053* (MO); Malpais, orilla del camino, Barrillas, 15°51’31”N, 91°13’40”W, alt. 902-1250 m, 22 September 2006, *DASA 4880* (MO). IZABAL: El Estor La Cumbre, al NE del Estor, camino a la Finca Moca, 15°33’N, 089°24’W, alt. 450 m, 17 July 1988, *P.L. Tenorio et al. 14502* (MO-3717628, MO-4028390); Slopes WNW of (above) El Estor, along margin of open pit nickel mine (abandoned ca. 7 years ago but scarred areas still essentially

barren), alt. 410 m, 30 August 1988, *W.D. Stevens & E.S. Martínez* 25256 (MO). PETEN: La Cumbre, km 141 of Cadenas Road, 24 September 1966, *E. Contreras* 6214 (MO); Los Arcos, on Cadenas Road, km 144/145, on hill, in clearing, 21 December 1969, *E. Contreras* 9438 (MO). MEXICO. CHIAPAS: Ocosingo, lower montane Rain Forest 70 km southeast of Palenque on road to Ocosingo along the Jol Uk'um, alt. 550 m, 31 August 1981, *D.E. Breedlove* 52526 (MO, NY); La Trinitaria, montane Rain Forest at Lago Tzisco, Lagos de Montebello National Park, alt. 1495 m, 07 November 1981, *D.E. Breedlove & G. Davidse* 55030 (MO, NY); Palenque, tropical Rain Forest adjacent to small cascading river Agua Azul, alt. 300 m, 09 November 1981, *D.E. Breedlove & G. Davidse* 55246 (MO); Ocosingo, lower montane Rain Forest, 70 km southeast of Palenque on road to Ocosingo along the Jol Uk'um, alt. 550 m, 09 November 1981, *D.E. Breedlove & G. Davidse* 55225 (MO); La Trinitaria, montane Rain Forest, 15 km east-northeast of Dos Lagos above Santa Elena, alt. 1000 m, 29 December 1981, *D.E. Breedlove* 56601 (MO, NY); La Trinitaria, montane Rain Forest, 10 km east-northeast of Dos Lagos above Santa Elena, alt. 1170 m, 09 February 1982, *D.E. Breedlove* 58458 (MO); Yajalon, alt. 1100 m, 15 July 1982, *A.M. Ton* 4429 (MO); Palenque, loc. a 23 km al norte de la desviación de Yajalón, sobre la carretera Ocosingo, 30 June 1982, *E. Cabrera & H. Cabrera* 3104 (MO-3510839, MO-3516350); 3 km al este de Tzisco, en el parque natural lagos de Montebello, 23 June 1982, *E. Cabrera et al.* 2962 (MO); a 14 km al este de las lagunas de Montebello sobre el camino a Santa Elena, 22 November 1982, *E. Cabrera & H. Cabrera* 3710 (MO); Ocosingo, Crucero Corozal, camino Palenque-Boca, Lacantum, alt. 180 m, 06 November 1985, *E.S. Martínez* 14978 (MO); Ocosingo, Crucero Corozal, camino Palenque-Boca Lacantum, alt. 180 m, 09 November 1985, *E.S. Martínez* 15467 (MO); Ocosingo, a 3 km al SE de Lacanjah Tzeltal camino Santo Domingo Nvo. Guerrero, alt. 450 m, 25 January 1986, *E.S. Martínez* 16825 (MO); Ocosingo, laguna Ocotolito a 12 km al N de Monte Líbano camino a Chancala, alt. 980 m, 02 February 1986, *E.S. Martínez* 17080 (MO); 2 km N of Naja, dry forest along stream bed, 16°59'N, 91°36'W, alt. 860 m, 24 September 1988, *W.D. Stevens & E.S. Martínez* 25837 (MO); Ocosingo, 2-3 km al SE de la Colonia Benito Juárez Miramar, sobre el camino al Potrero, 16°20'N, 91°12'W, alt. 358 m, 21 August 1993, *A. Reyes-García & M.S. Sousa* 2122 (MO). VERA CRUZ: Mirador: without precise locality, January 1843, *F.M. Liebmann* 335 (US-00487591 fragment); Zacualpan and Vicinity, August 1906, *C.A. Purpus* 2000 (MO, NY, US); Zacualpan, 1967, *C.A. Purpus* 7814 (US); CORDOVA: Without locality, without date, *Bourgeau* 1458 (US-00487586, fragment). NICARAGUA. ZELAYA: ca. 12 km NE of Mina Rosita, mixed pine savanna, ca. 13°57'N, 84°13'W, alt. ca. 55 m, 20 March 1979, *J.J. Pipoly* 4997 (MO).



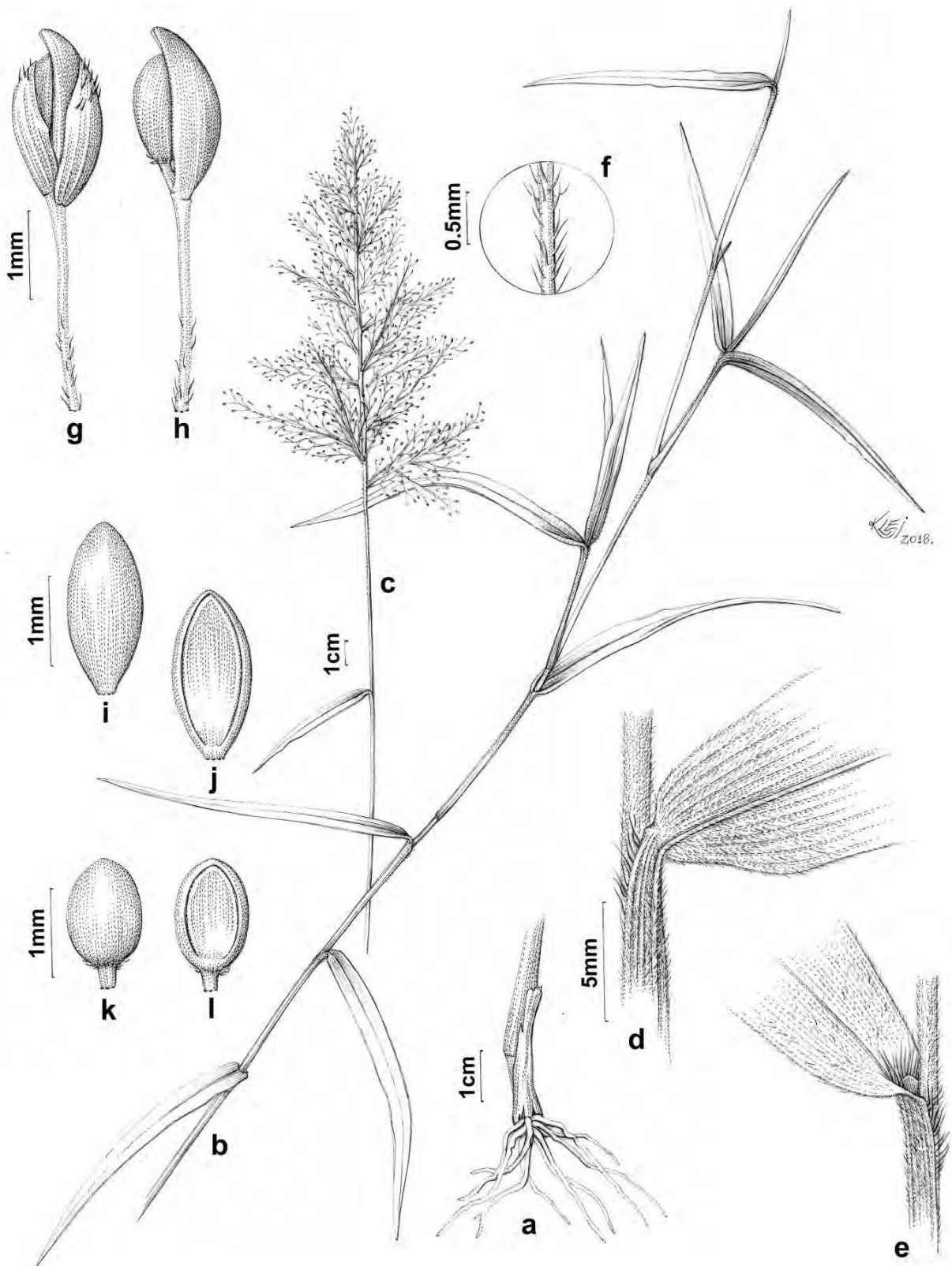


Figure 20. *Isachne pubescens* Swallen. a. Basal portion of the culm (with roots). b. Middle portion of the culm (note branching at the nodes). c. Apex of a flowering branch with an open and large synflorescence. d. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath (note the pilosity of the culm internode, leaf blades and leaf sheath). e. Fragment of the culm showing the base of the leaf blade, the ciliate ligule, and the apex of the leaf sheath. f. Detail of the soft pubescent trichomes found in the synflorescence branches and branchlets. g. Spikelet in lateral view and pedicel without a glandular band (note the pubescence of the pedicel). h. Anthoecia (glumes removed - note the lower anthoecium usually longer than the upper) and pedicel without a glandular band. i. Lower anthoecium, lemma view. j. Lower anthoecium, palea view. k. Upper anthoecium, lemma view. l. Upper anthoecium, palea view. Based on: a. D.E. Breedlove & G. Davidse 55225 (MO); b-l. D.E. Breedlove & G. Davidse 55246 (MO). Illustration by Klei R. Sousa.

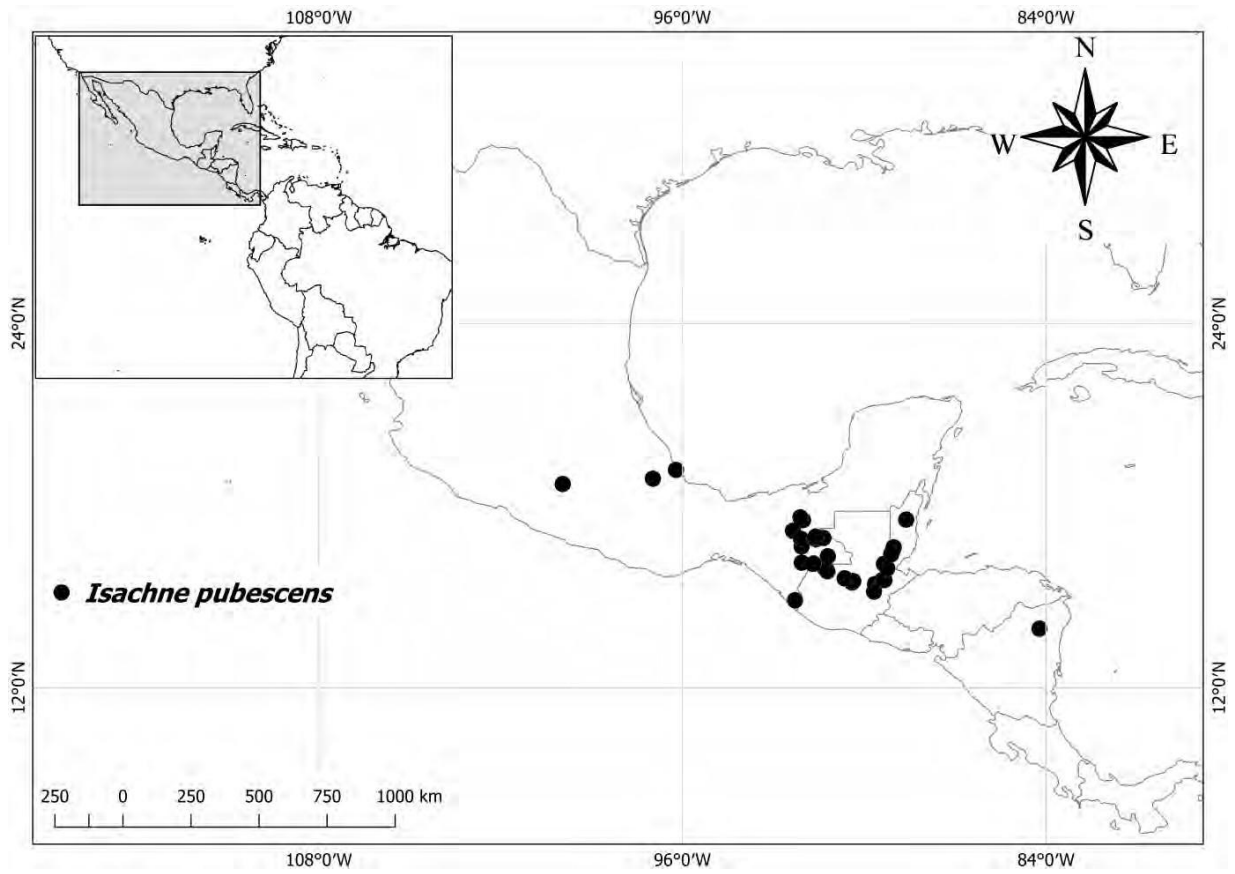


Figure 21. Known distribution of *Isachne pubescens*.

11. *Isachne pygmaea* Griseb., Fl. Brit. W. I. 553. 1864. Type: JAMAICA: Hab. Jamaica, s.a., Macfayden s.n. (holotype GOET-006587 image!; isotype B-100249139 image!).

Figure 22

Perennial, decumbent, trailing, mat-forming, 5-40 cm long. Culms rooting at the lower nodes, densely branched from the base and at the upper portion, wiry, herbaceous, slender, sterile and flowering branches erect; nodes glabrous dark-brown to blackish. Sheaths longer or shorter than the internodes, glabrous, strongly nerved, one margin ciliate towards the apex, the other glabrous, cilia 0.2-0.3 mm long, those towards the ligular region 1-1.3 mm long, colorless; ligule ciliate, ca. 0.2 mm long; leaf blades distichous, more or less regularly distributed throughout the culms but more abundant in the ascending sterile and flowering branches, lanceolate to linear-lanceolate, 0.5-4 × 0.1-0.3 cm, flexible (not rigid), midrib conspicuous, base slightly rounded, constricted near the ligular region, not amplexicaul, apex acute, glabrous on both surfaces, margins entire, thickened, glabrous. Panicle terminal, contracted, spike-like, semi-rigid, 0.2-3 cm long, glabrous to minutely scaberulous, provided with appressed first-order branches only, glandular bands absent, axillary glands absent; pedicels 0.2-1 mm long, cylindrical, glabrous to minutely scaberulous, glandular bands absent. Spikelets unequally pedicelled, erect on the pedicels, sometimes slightly oblique, elliptic, 1.1-1.4 mm long; glumes subequal, elliptic-obovate to obovate or elliptic, obtuse or truncate, apex usually lacerate, glabrous, greenish to stramineous, both 1/2 to 1/3 of the anthoecia; lower glume 0.8-0.9 mm long, 5-nerved, margins pale; upper glume 0.9-1 mm long, 5-nerved, margins pale; anthoecia 2, similar, coriaceous, greenish to stramineous, sometimes purple-stained in the upper 1/3; lower anthoecium bisexual, 1-1.2 mm long, lemma glabrous or with some inconspicuous appressed trichomes near the base, not sulcate, palea glabrous, 0.9 -1 mm long; rachilla conspicuous between the anthoecia, 0.1-0.2 mm long, glabrous or with some occasional trichomes at the apex or base; upper anthoecium bisexual, 0.7 -1 mm long, lemma glabrous or with some inconspicuous appressed trichomes near the base, palea glabrous, 0.7-0.9 mm long. Lodicules ca. 0.1 mm long. Stamens 3, filaments ca. 0.4 mm long; anthers ca. 0.7 mm long, yellowish-pale or purple-stained. Stigmas 2, plumose, dark-brown to purplish in maturity. Caryopsis not seen.

*Etymology:* From the Latin: “*pygmaeum*”: dwarf (Clifford & Bostock 2007). The epithet refers to the very small habit of this plant in relation to the other species in the genus.

*Distribution:* Greater Antilles, previously known only from Jamaica and here recorded to Haiti for the first time (Figure 15). It inhabits side of banks, slopes, and roadsides, on clay soils between mosses and lower vegetation; at ca. 750 -1380 m.

*Phenology:* Collected in flower from September to November, in January and March.

*Comments:* *Isachne pygmaea* is a very peculiar and easy distinguishable Caribbean species. It is characterized by a small habit and contracted spike-like panicles.

Material examined: HAITI. DEPARTMENT OF SUD: Massif de la Hotte, Macaya Biosphere Reserve, south slope of Morne Formon above Ville Formon, 13 November 1989, W.S. Judd *et al.* 5798 (FLAS image). JAMAICA. PORTLAND: Blue Mountains, Vinegar Hill, alt. 3480 ft., 31 March 1916, J.R. Perkins 1085 (US). SAINT ANDREW: Vicinity of Cinchona, near Vinegar Hill, 02-10 September 1906, N.L. Britton 220 (NY); Vicinity of Moody’s Gap, banks, between the parishes of Portland and St. Andrew, 10 September 1908, N.L. Britton 3375 (NY, US); Cold Spring Gap, Blue Mountains, alt. 1500 m, along the side of a bank among moss and other low vegetation, 29 October 1912, A.S. Hitchcock 419 (MO, NY, P image, US-975959, US-1062554, USF image); Cold Spring Gap, growing on roadside banks, decumbent, alt. 4523 ft., 03 November 1912, W. Harris 11314 (MO, NY, P-01882749 image, P-01882750 image, US); Cold Spring Gap, on clayey banks, 04 January 1917, W. Harris 12490 (MO, NY, P image, US); West slope of Catherine’s Peak, above Woodcutters Gap, alt. ca. 4500 ft., moist trailside bank, 16 November 1952, G.R. Proctor 7347 (US). SAINT THOMAS: Arntully, 1928, C.R. Orcutt 5756 (US). Without locality, 17 September 1886, J.H. Hart (?) 677 (NY-1603142); Without locality, from herbarium of Public Gardens and Plantations, without date, J.P. 677 (NY-1603146).

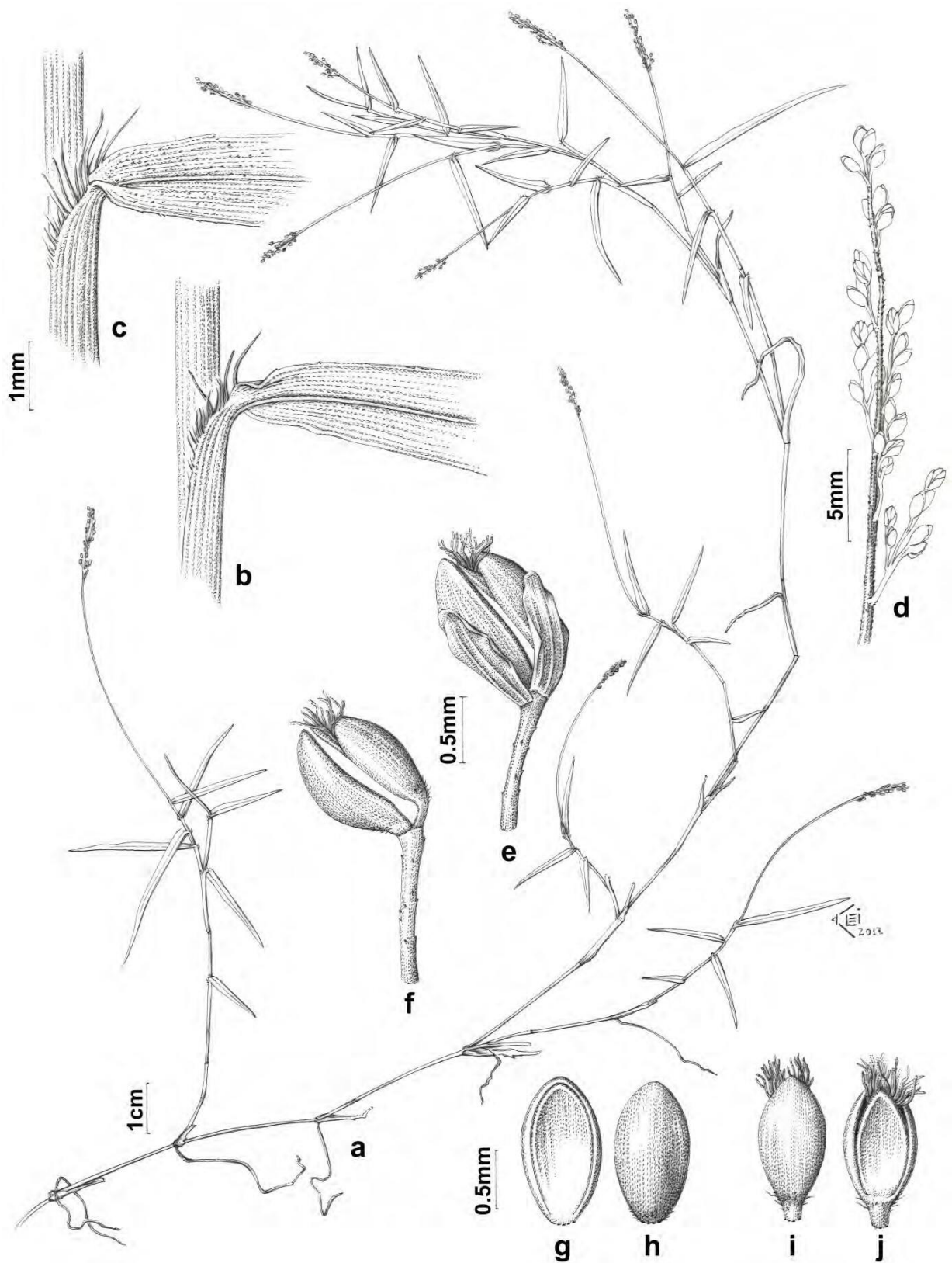


Figure 22. *Isachne pygmaea* Griseb. a. Habit. b. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath. c. Fragment of the culm showing the base of the leaf blade, part of the ciliate ligule, and the apex of the leaf sheath. d. Detail of the synflorescence showing the primary branchlets appressed to the main axis. e. Spikelet in lateral view and pedicel without a glandular band. f. Anthoecium (glumes removed) and pedicel without a glandular band. g. Lower anthoecium, lemma view. h. Lower anthoecium, palea view. i. Upper anthoecium, lemma view. j. Upper anthoecium, palea view. Based on: a. A.S. Hitchcock 419 (MO); b-j. W. Harris 11314 (US). Illustration by Klei R. Sousa.

12. *Isachne rigens* (Sw.) Trin., Gram. Panic. 252. 1826.  $\equiv$  *Panicum rigens* Sw., Prodr. 23.

1788, non *Panicum rigens* Salzm. ex Steud., Syn. Pl. Glumac. 1: 76. 1854 [nom. inval., =*Panicum rudgei* Roem. & Schult.], nec *Panicum rigens* Mez, Bot. Jahrb. Syst. 34(1): 141. 1904 [nom. illeg. hom., =*Sacciolepis rigens* (Mez) A. Chev.]. Type: JAMAICA. s.l., s.a., *O.P. Swartz s.n.* [lectotype (here designated) S-R-4004 image!; isolectotypes B-W-18748-010 image!, B-W-18748-020 image!, BM-000938804 image!, M, SBT-10757 image!, S-R-4005 image!, UPS-V-001930 image!; US-80958 (fragment ex B, M, S, photo ex S) image!].

= *Panicum arbusculum* Sieber ex Griseb., Fl. Brit. W. I. 553. 1864. [nom. inval.].

Figure 23

Perennial, trailing or sometimes suberect to erect, (45-)100-200 cm long. Culms rooting at the lower nodes, branched at the middle and upper portions, sometimes branched from the base, herbaceous, often slender, flowering branches erect or ascending; nodes glabrous to pubescent, purplish, dark-brown or blackish, without a glandular stripe below; internodes inconspicuously hollow, glabrous, greenish, stramineous or dark-brown, often purple stained towards the nodes. Sheaths shorter and often deciduous in the main culms internodes, longer in the sterile and flowering branches, glabrous, pubescent or pilose, trichomes non-tuberculate, sometimes dehiscent in the old sheaths, strongly nerved, one margin ciliate, the other glabrous, cilia 0.2-0.5 mm long, those towards the ligular region 1-1.3 mm long, colorless; ligule ciliate, 0.1-0.3 mm long; leaf blades distichous, regularly distributed but deciduous on the main culms, persistent in the secondary sterile and flowering branches, lanceolate, 1.5-6.5  $\times$  (0.1-)0.2-0.7 cm, flexible (not rigid), midrib inconspicuous, base rounded, not amplexicaul, apex acute, glabrous, puberulous, pilose or sometimes minutely scaberulous on both surfaces, margins entire, minutely scaberulous to scabrous and slightly thickened, often purple stained. Panicle terminal and axillary, open, sometimes subcontracted, flexible or semi-rigid, 2-6  $\times$  1-4 cm, minutely pubescent, scaberulous or pilose, without second-order branches or rarely some in the lowermost portion of the panicle, glandular bands absent, axillary glands present; pedicels (0.7-)1.5-3.1(-4) mm long, cylindrical, glabrous to minutely pubescent, scaberulous or pilose, glandular bands absent. Spikelets unequally pedicelled, erect on the pedicels, elliptic to elliptic-obovate, 1.5-2.3 mm long; glumes subequal, oblong to elliptic or elliptic-lanceolate, obtuse to subacute, glabrous to minutely puberulous towards the apex, greenish to stramineous, frequently purple-stained or purple,

both shorter or less often almost equaling the anthoecia; lower glume (1-)1.4-1.7 mm long, (5-)7-9-nerved, margins pale green or stramineous; upper glume (1-)1.4-1.7 mm long, 5-7-nerved, margins pale green or stramineous; anthoecia 2, similar, coriaceous, usually stramineous, often purple-stained or purple; lower anthoecium bisexual, 1.4-2.1 mm long, lemma glabrous or with minutely appressed-sparse trichomes, not sulcate, palea glabrous, 1.6-2 mm long; rachilla conspicuous between the anthoecia, 0.3-0.5 mm long, densely pilose all over; upper anthoecium bisexual, 1.1-1.4 mm long, lemma glabrous or with minutely appressed-sparse trichomes, palea glabrous, 1-1.3 mm long. Lodicules ca. 0.2 mm long. Stamens 3, filaments ca. 0.5 mm long, yellowish; anthers ca. 0.9-1 mm long, yellowish to orange in maturity. Stigmas 2, plumose, purple, dark-brown in maturity. Caryopsis 1 × 0.5 mm, elliptic to oblong, flat-convex, blackish.

*Etymology:* From the Latin: “*rigeo*”: be stiff. The epithet refers to the blades cylindrical or slightly inrolled when dry, to the culms erect or to the ascending racemes (Clifford & Bostock 2007).

*Distribution:* Antilles and North and Northwest of South America, in Jamaica, Colombia, Ecuador, and Venezuela (Figure 24). There are also unconfirmed records for Peru, Costa Rica and El Salvador. Kelloff *et al.* (2011) cited the collection “*H.D. Clarke et al. 10316 (US)*” from the Guyana but this specimen was found to be *I. ligulata*. It inhabits border of gallery forests, forest edges, cliffs and slopes, usually associated to moist places and shrubby vegetation; at ca. 1350-3000 m.

*Phenology:* Collected in flower throughout the year.

*Comments:* *Isachne rigens* can be characterized by the slender habit with culms moderately rigid, leaf blades with inconspicuous midrib, synflorescences with pedicels inserted directly in the first-order branches (rarely some second-order branches present in the lowermost branchlets of the panicles), elliptical spikelets, and rachilla densely pilose.

Some robust specimens are frequently misidentified as *I. ligulata*. See comments under *I. ligulata* for the distinction between *I. rigens*.

*Nomenclatural notes:* There are two specimens of *I. rigens* at Stockholm (S) from Swartz’s collection (S-R-4004 and S-R-4005), both in conformity with the original description of the species. Although these collections are obviously from Jamaica, only the specimen “S-R-4004” has the annotation “*Jamaica*”, as presented in the protologue. Therefore, this specimen is here designated as lectotype for *I. rigens*.

Material examined: COLOMBIA. ANTIOQUIA: Municipio de Urrao, al lado de la carretera que conduce a Caicedo, 10 km de Chuscal, alt. 2740 m, 09 September 1986, *R.W. Pohl & J. Betancur 15465* (MO, RB); Municipio de Urrao, La Nevera, Rio Las Juntas, alt. 2450 m, 09 September 1986, *R.W. Pohl & J. Betancur 15474* (MO); Municipio de Sonsón, km 12 of road Sonsón-Nariño, 5°42'N, 75°15'W, alt. 2630 m, 06 December 1986, *J.L. Zarucchi & N. Bedoya 4420* (MO); Municipio de San Pedro, km 13 of road San Pedro-Entrerriós, 06°31'N, 75°32'W, alt. 2310 m, 28 September 1987, *J.L. Zarucchi et al. 5873* (MO); Municipio de Sonsón, km 11 of road Sonsón-Nariño (25 km from Nariño), 05°42'N, 75°15'W, alt. 2700 m, 03 October 1987, *J.L. Zarucchi et al. 6213* (MO); Municipio de Entrerriós, ca. 3 km from Entrerriós on the road to Santa Rosa de Osos, 06°32'N, 75°30'W, alt. 2205-2240 m, 04 February 1989, *J.M. MacDougal & F.J. Roldán 3655* (MO). CAUCA: de Baldoa a Argelia, 11,5 km de Baldoa, alt. 2200 m, 27 June 1989, *F.O. Zuloaga & X. Landoño 4200* (MO). MEDELLÍN: Parque Ecológico Piedras Blancas, 24 August 1996, *R.G. Fonnegra & C.A. Monsalve 6185* (MO). NARIÑO: Municipio de Pasto, corregimiento de Chachagüí, alt. 2450 m, 12 May 1990, *B.R.P. Ramírez 2450* (MO); Municipio de Mallama, km 5 E de Piedrancha, alt. 2100-2200 m, 28 December 1993, *B.R.P. Ramírez & A.L.B. Jojoa 6087* (MO). PUTUMAYO: Municipio Villa Garzón, carretera a Porto Assis, 76°34'W, 1°10'N, alt. 1350 m, 03-04 May 1994, *J.L.A. Fernández et al. 11445* (MO). SANTA MARTA: without locality, 1898-1901, *H.H. Smith 207* (MO). ECUADOR. PICHINCHA: below San Juan towards Chiriboga, alt. 2250 m, 03 May 1955, *E. Asplund 16182* (P image); Road Chulloagallo – Chiriboga, between the village and km 48, alt. 1600-2000 m, 12 June 1967, *B. Sparre 16959* (R); Approximately 30 km east of Alluriquin, along old Quito road, 78°40'W, 00°17'S, alt. 2200 m, 09 February 1987, *I. Grignon 84239* (MO). BOLIVAR: Tamboloma, alt. 2050 m, 15 August 1939, *E. Asplund 8349* (P image); Km 21.6 Guaranda-Puebloviejo, 79°09'W, 01°35'S, alt. 2500 m, 06 March 1988, *S. Laegaard & S. Renvoize 70579* (MO). WITHOUT LOCALITY: without precise locality, July-August, *W. Jameson 347* (P image). JAMAICA. PORTLAND: Blue Mountains, Sir John's Peak, alt. 5500 ft., 24 January 1913, *W. Harris 11595* (MO, NY, P, US); Port Royal Mountains, along trail between Green Hills and Woodcutters Gap, alt. 4000-4500 ft., 16 November 1952, *G.R. Proctor 7353* (US). SAINT ANDREW: vicinity of Chinchona, Saint Helen's Gap, 2-10 September 1906, *N.L. Britton 77* (NY); vicinity of New Castle, Hardware Gap, 01 March 1908, *N.L. Britton & A. Hollick 1783* (NY); Chinchona, Buff Bay road, January 1912, *B.B. Brues 662a* (NY); Abbey Green, Blue Mountains, shady bank, 04-05 October 1912, *A.S. Hitchcock 9362* (RB); Chinchona, alt. 1500 m, 27 October 1912, *A.S. Hitchcock 420* (NY, P, USF); North slope of Catherine's Peak, 29 October 1912, *A.S. Hitchcock 9732* (US); Chinchona, alt. 4000 ft., 03 November 1912, *W. Harris 11316* (NY); Chinchona, alt. 5000 ft., 03 November 1912, *W. Harris 11333* (NY); Cold Spring Gap, alt. 4523 ft., 03 November 1912, *W. Harris 11336* (US); Chinchona, Monkey Hill, alt. 5600 ft., 20 November 1912, *W. Harris 11432* (MO, NY, P); Clyde River, alt. 4000 ft., 20 November 1912, *W. Harris 11445* (MO, NY, P, US); Hardware Gap, alt. 4000 ft., 03 January 1913, *W. Harris 11543* (MO, NY, P); Abbey Green, Blue Mountains, on damp banks, alt. 3900



ft., 22 January 1913, *W. Harris 11585* (NY); Chinchona, Monkey Hill, alt. 5800 ft., 28 February 1913, *W. Harris 11417* (MO, NY, P, US); Chinchona, road to Morce's Gap, alt. 4800 ft., 04 January 1917, *W. Harris 12480* (MO-821794, MO-1603148, NY, P-01882833, P-01936071); Cold Spring Gap, alt. 4500 ft., 04 January 1917, *W. Harris 12489* (MO, NY, US); Cold Spring Gap, alt. 4500 ft., 04 January 1917, *W. Harris 12491* (MO); Vicinity of St. Helens Gap, alt. 1475 m, 04 March 1920, *W.R. Maxon & E.P. Killip 614* (US, NY); Chinchona, August 1950, *G.F. Asprey 2231* (NY). WITHOUT LOCALITY: without date, *J.H. Hart 676* (NY-1603154, NY-1603166); without date, *J.H. Hart 788* (NY-1603167). VENEZUELA. ANZOÁTEGUI: Distrito Libertad, ridges and tops of Montañas Negras, along the Sucre and Azoátegui border, 20 airline km NE of Bergantín, NE of Buenos Aires, Serranía de Turimiquire, 64°11'W, 10°04'30"N, alt. 2000 m, 28 November 1981, *G. Davidse & A.C. González 19574* (MO). ARAGUA: Tovar, Colonia Tovar, 1856-1857, *A. Fendler 1637* (MO). DISTRITO FEDERAL: 1 km NW of intersection of road between El Junquito and Tovar and road to Carayaca, alt. 1800 m, 13 November 1973, *G. Davidse & G. Morillo 3998* (MO); El Junquito-Colonia Tovar, alt. 2200 m, 24 July 1993, *F.O. Zuloaga et al. 4743* (MO). LARA: Distrito de Morán, carretera desde Humocar Alto hacia Guaitó, alt. 2200 m, 14 November 1984, *H. van der Werff & R. Rivero 7924* (MO); Distrito de Morán, carretera Jabon-Paramo Los Nepes (barbacoas), alt. 2150 m, 22-25 January 1985, *F. Escalona & J. Escalona V218* (MO). MERIDA: Serra Nevada, September 1846, *N. Funk & Schlim 1074* (P-01882740, P-01882834, P-01936015). MONAGAS: Distrito Acosta, serranía del Turimiquire, 10°02'N, 63°52'W, alt. 1600 m, 12 May 1982, *O. Huber et al. 6306* (MO). SUCRE: Headwaters of Rio Colorado and ascent to 3rd southern peak, alt. 2200-2400 m, 07 May 1944, *J.A. Steyermark 62659* (MO). TACHIRA: along Quebrada Agua Azul, south of El Reposo 14 km SE of Delicias, 7°31'N, 72°24'W, alt. 2150-2300 m, 22-23 July 1979, *J.A. Steyermark & R. Liesner 118213* (MO). TRUJILLO: Boconó, along road to Guaramacal, 10 km from junction with highway to Boconó, ca. 9°14'N, 70°15'W, alt. 1950 m, 14 March 1984, *J.L. Luteyn & E. Cotton 9713* (MO); Boconó, Paramo do Guaramacal, 20 km al E de Boconó, ca. 9°14'N, 70°11'W, alt. 2800-3000 m, 26 July 1984, *G. Aymard et al. 2941* (MO); Boconó, Paramo do Guaramacal, 20 km al E de Boconó, ca. 9°14'N, 70°11'W, alt. 2800-3000 m, 26 July 1984, *G. Aymard et al. 2950* (MO); Parque Nacional Guaramacal, vertiente norte, entre casa guardaparques (P.N. 6) y campamento 1, alt. 1977-2350 m, 28 April 1998, *B. Stergios et al. 17274* (MO); Boconó, El Campamento, pele ojo, bajando hacia Quebrada Honda, alt. 1940-2120-1900 m, 09-16 July 1998, *B. Stergios 17567* (US); Boconó, Parque Nacional Guaramacal, 9°14,791'N, 70°12,3180'W, alt. 2000 m, 23 September 2000, *M. Niño et al. 1407* (US); Boconó, Parque Nacional Guaramacal, slope forests of El Pumar, SE of Boconó, Between Camp on Roberto's finca near Pozo Verde, alt. 1920-2120 m, 26 December 2000, *L.J. Dorr et al. 8585* (MO, US); Boconó, Parque Nacional Guaramacal, sector quebrada Honda-Pele Ojo, El Santuario, alt. 1950-2100 m, January 2001, *B. Stergios & R. Caracas 18982* (MO); Boconó, Parque Nacional Guaramacal, alt. 2100 m, 09 April 2003, *B. Stergios et al. 20048* (MO, US).

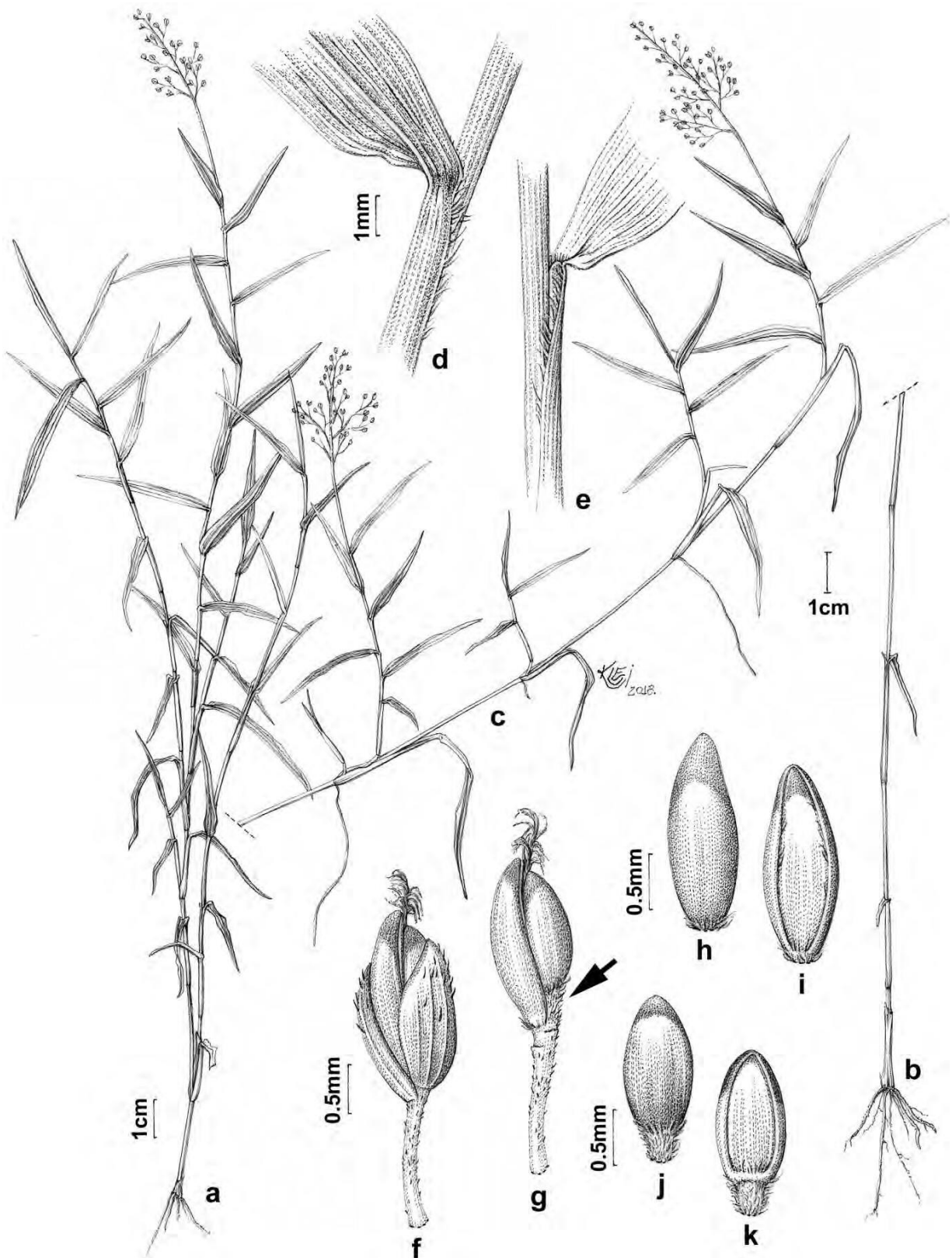


Figure 23. *Isachne rigens* (Sw.) Trin. a. Branched culm and synflorescence of a specimen with cespitose-erect habit. b. Base of the culm of a specimen with decumbent/trailing habit. c. Apex of the culm and flowering branches of a specimen with decumbent/trailing habit. d. Fragment of the culm showing the base of the leaf blade (note the indistinct midrib) the collar region, and the apex of the leaf sheath with ciliate margin. e. Fragment of the culm showing the base of the leaf blade, the ciliate ligule, and the apex of the leaf sheath with ciliate margins. f. Spikelet in lateral view and pedicel without a glandular band. g. Anthoecium [glumes removed – note the pilose rachilla between the upper and the lower anthoecium (arrow)] and pedicel without a glandular band. h. Lower anthoecium, lemma view. i. Lower anthoecium, palea view. j. Upper anthoecium, lemma view (note the pilose rachilla). k. Upper anthoecium, palea view (note the pilose rachilla). Based on: a. *W. Harris 11595 (US)*; b-k. *W. Harris 12480 (NY)*. Illustration by Klei R. Sousa.

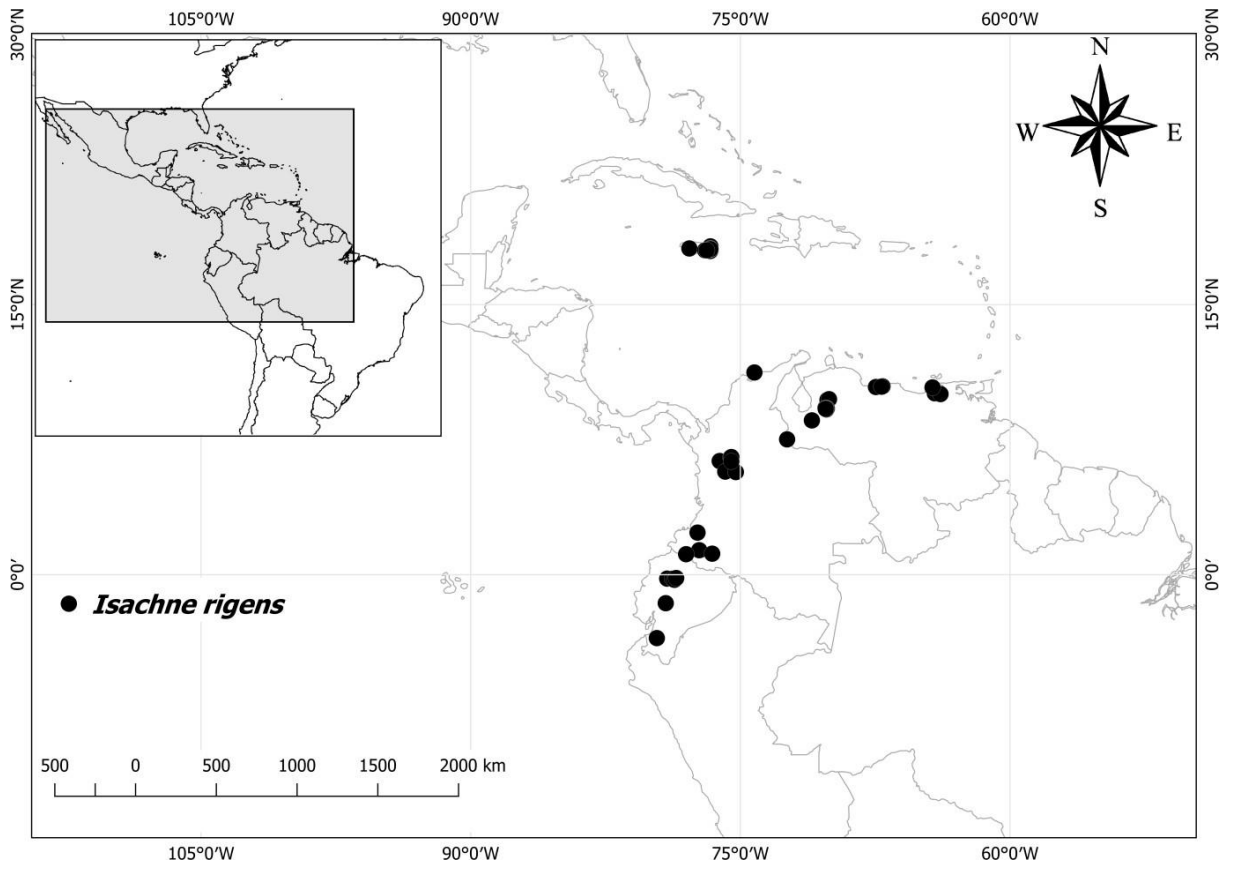


Figure 24. Known distribution of *Isachne rigens* (excluding unconfirmed records for Costa Rica, El Salvador and Peru).

13. *Isachne rigidifolia* (Poir.) Urb., Symb. Antill. 4: 85. 1903.  $\equiv$  *Panicum rigidifolium* (Poir.) Kunth, Révis. Gramin. 1: 37. 1829, non *Panicum rigidifolium* Trin., Sp. Gram. 2(18): t. 214. 1829 [nom. illeg. hom., =*Renvoizea trinii* (Kunth) Zuloaga & Morrone]. *Milium rigidifolium* (Poir.) Roem. & Schult., Syst. Veg., ed. 15 bis [Roemer & Schultes] 2: 319. 1817.  $\equiv$  *Agrostis rigidifolia* Poir., Encycl., Suppl. 1: 257. 1810. Type: DOMINICAN REPUBLIC. Santo Domingo: Cette plante croît a l'île de Saint-Domingue, s.a., *Desfontaines s.n.* [holotype FI; isotype US-80961 (fragment and photo ex FI) image!].

Figure 25

Perennial, decumbent to suberect, trailing or scandent, (7-)15-55(-200) cm long. Culms rooting at the lower and decumbent nodes, branching at the upper portion, herbaceous, slender, sterile and flowering branches ascending or erect; nodes glabrous, stramineous to brownish, sometimes dark-purplish. Leaves dimorphic, culm leaves (i.e., those of the decumbent portion of the culms) with enlarged, deciduous, fibrous and brittle sheaths, without conspicuous midribs, and with rudimentary or reduced leaf blades; branch leaves (i.e., those of the erect or ascending portion of the culms) with persistent, not fibrous nor brittle sheaths, and conspicuous midribs on the developed leaf blades and across the leaf sheaths; sheaths longer than the internodes, glabrous, one margin inconspicuously ciliate, the other glabrous, cilia ca. 0.1 mm long, those towards the ligular region ca. 0.5mm long, colorless; ligule ciliate, ca. 0.1 mm long, lateral cilia of the ligular region up to 1mm long; leaf blades distichous, mostly concentrated at the base of the flowering and/or sterile branches, less often more regularly distributed along the branching culms; culm reduced leaf blades lanceolate to filiform, 1-6  $\times$  0.5-1 mm, somewhat pungent, ascending, apex acute, glabrous on both surfaces; branches developed leaf blades lanceolate to linear-lanceolate, sometimes involute and apparently filiform, (0.7-)1-7  $\times$  0.1-0.5 cm, rigid, pungent, ascending, base rounded, slightly constricted near the ligular region, apex acute, glabrous on both surfaces, margins entire, thickened, glabrous or with a few trichomes near the ligular region. Panicle terminal, open, semi-rigid, 2-11.5  $\times$  2-6 cm, glabrous, usually provided with first-order branches only, less often occasional second-order branches present, branches ascending, frequently purple-stained, glandular bands present or absent, axillary glands present; pedicels (0.8-)1-5 mm long, cylindrical, glabrous, glandular bands present or absent. Spikelets unequally pedicelled, erect or obliquely inserted on the pedicels, elliptic, 1.4-1.7 mm long; glumes subequal, elliptic, obtuse to slightly lacerate at the apex, glabrous or inconspicuously hispidulous towards the apex, greenish to stramineous, often completely purplish or purple-stained, both equaling or ca. 0.2-0.5 mm shorter than the anthoecia; lower glume 0.6-1.3 mm long, 5-7-

nerved, margins pale-green, stramineous or whitish, sometimes purplish or purple-stained, or involute; upper glume 0.6-1.3 mm long, 5-7-nerved, margins pale-green, stramineous or whitish, sometimes purplish or purple-stained, or involute; anthoecia 2, similar, coriaceous, stramineous, dark-brown, frequently purple-stained at the tips; lower anthoecium staminate, 1.2-1.7 mm long, lemma glabrous, not sulcate, palea glabrous, 1.2-1.6 mm long; rachilla conspicuous between the anthoecia, 0.2-0.3 mm long, somewhat enlarged towards the apex, glabrous or inconspicuously pubescent towards the apex; upper anthoecium bisexual, 1.1-1.3 mm long, lemma glabrous, palea glabrous, 1.1-1.2 mm long. Lodicules ca. 0.2 mm long. Stamens 3, filaments ca. 0.4 mm long, yellowish to stramineous; anthers ca. 0.7 mm long, yellowish to purplish, dark-brown in maturity. Stigmas 2, plumose, purple, dark-brown in maturity. Caryopsis, elliptic-oblong, 0.7-0.8 × 0.3-0.4 mm, flat-convex, brownish to dark-brown.

*Etymology:* From the Latin: “*rigidus*”: stiff; “*folium*”: leaf (Clifford & Bostock 2007). The epithet refers to the rigid and pungent leaf blades due to the presence of a conspicuous thick midrib.

*Distribution:* Antilles, in Cuba, Dominica, Dominican Republic, Guadeloupe, Haiti, Martinique, Saint Kitts and Nevis (Figure 26). It inhabits preferably montane and mossy forests, savannas, in rocks, river beds, limestone, and exposed areas; at ca. 800-2300 m.

*Phenology:* Collected in flower from February to October.

*Comments:* *Isachne rigidifolia* is promptly distinguished from all the Neotropical species of the genus by the ascending rigid leaf blades with conspicuous and prominent midribs. The leaf blades are particularly intriguing in *I. rigidifolia*, being those of the lower portion of the culms reduced to rudimentary, without midrib, and those of the culm branches developed, rigid and with thickened midribs. Such dimorphism is roughly similar to that observed in woody bamboos. It can be noted also that the blades can be enlarged to almost reduced to the midribs; in this way, some specimens may present filiform or almost acicular leaf blades.

Rodrigues & Filgueiras (unpubl. res., Chapter 5) described the epidermal micromorphology of the leaf blade in *I. rigidifolia*. According to their findings, *I. rigidifolia* appears to have morphological adaptations to water storage. The long cells along the edges of the costal zones of the abaxial epidermis are often coalesced and can act as a ‘roof’, partially covering the intercostal zones and thus reducing the exposure to air.

Finally, the occurrence of glandular bands is not constant in *I. rigidifolia*, and is absent in several specimens; therefore, this character must be taxonomically adopted with parsimony.

Material examined: CUBA. HOLGUÍN: Sierra Cristal, on the very top of the mountain, alt. 1325 m, 08 March 1916, *E.L. Ekman 6839* (US). DOMINICA. SAINT PATRICK: Morne Trois Pitons, on exposed rock jutting above the crown of the pygmy forest, alt. ca 4200 ft., 21 February 1966, *K.L. Chambers 2761* (US). SAINT ANDREW: Morne Diablotin, mossy turf on exposed areas of the peak, alt. 4650 ft., 11 June 1965, *G.L. Webster 13368* (US). DOMINICAN REPUBLIC. AZUA: San José de Ocoa, Bejucal, at Río de Canal, alt. ca. 1300 m, 10 March 1929, *E.L. Ekman 11872* (NY, US). CONSTANZA: Valle Nuevo, alt. 2300 m, 10 June 1964, *B. Augusto 1683* (NY); Along road between Constanza and Valle Nuevo, 16.9S of Constanza, 18°51'13"N, 070°47'58"W, alt. 1630 m, 03 July 2006, *T.B. Croat 975887* (MO, SP); Valle Nuevo National Park, several km south of Constanza checkpoint, 22 March 2012, *B.A. Sorrie 12899* (US). INDEPENDENCIA: 5-6 km NNW of Angel Feliz, near crest of Sierra de Neiba, 18-41N, 71-47W, alt. 1750 m, 23 July 1992, *S.A. Thompson et al. 10616* (US). LA VEGA: Vicinity of Constanza, alt. 1000-1600 m, 28 October 1947, *H.A. Allard 16475* (MO); Lowland forest near La Ciénega, alt. 1100-1200 m, 25 July 1967, *G.J. Gastony et al. 401* (US); 16 km E of El Río along hwy, alt. 1220 m, 12 August 1970, *G. Davidse 2656* (MO); About 3 km E of crest of Casabito, E of El Río, 15 April 1973, *F.W. Gould & J.J. Jiménez 14133* (MO-2310746, MO-2376834); Cordillera Central, en el Valle lateral del Arroyo La Sal, sureste del poblado de La Sal, entre Loma La Sal y Loma La Golondrina, 19°03.5'N, 70°34'W, 14 April 1982, *T. Zanoni et al. 20044* (NY); Cordillera Central, al sudeste de Constanza, aprox. ½ hora caminando a pie al sur de Los Mañanguises, en el lugar que los campesinos de la zona llaman "El Alto de Sonador", 18°52'N, 70°38.5'W, alt. ca. 1580 m, 06 April 1986, *R. García & J. Pimental 1122* (US); La Nevera, 18°46'27.12"N, 70°38'24.7194"W, alt. 2237 m, 24 May 2003, *P. Acevedo-Rodriguez et al. 12493* (NY); Reserva Científica Ebano Verde, 18°46'27.12"N, 70°38'24.7194"W, alt. 2237 m, 29 May 2003, *P. Acevedo-Rodriguez et al. 12671* (NY); El Convento, 18°50'36.5994"N, 70°42'50.3994"W, alt. 1731 m, 30 May 2003, *P. Acevedo-Rodriguez et al. 12761* (US). MONTE CRISTI: District of Sabaneta, Lagunas de Cenobí, Pine forests, alt. 1100 m, 17 August 1929, *E.J. Valeur 29* (US); PEDERNALES: In Aceitillar, 30 March 1961, *J.J. Jiménez 4467* (US). PERAVIA: Loma los Palos Mojados, Norte-noroeste de El Bejucal, en la cabecera del Río El Canal, 18°37.5'N, 70°35'W, alt. 1700 m, 04 August 1982, *T. Zanoni et al. 22285* (MO). SAN JUAN: Cordillera Central, N of Río Arriba, 18 September 1946, *R.A. Howard & E.S. Howard 9098* (MO). SAN RAFAEL: limestone mountains of the Sierra de Neiba, along the Carretera Internacional near the crest of the range, along the Haitian border, vic. Line between

provinces of San Rafael and Independencia, alt. 1700-2000 m, 03 August 1967, *G.J. Gastony et al.* 487 (MO, NY-1603191, NY-1603194). SANTIAGO: at the base of La Cotorra, alt. 1110-2710 m, 26 March 1964, *E. Marcano* 4864 (US). GUADELOUPE. BASSE-TERRE: Soufrière, savane à Mulets, replat sur l'éperon de la face sud du cone, alt. 1100 m, 05 April 1979, *A. Raynal-Roques & J. Jérémie* 21091 (US); Massif de la Soufrière, savanna à Mulets, alt. 1000 m, 03 May 1974, *C. Sastre et al.* 2818 (MO); Massif de la Soufrière, partie NW, trace Victor Hugues, savane aux Ananas, alt. 1000 m, 05 May 1974, *C. Sastre* 2870 (MO); Massif de la Soufrière, sources du Carbet, alt. 1250 m, 30 April 1981, *C. Sastre* 7459 (US). WITHOUT LOCALITY: without precise locality, 1868, *T. Husnot* 98 (US); *without precise locality*, 1892, *P. Duss* 3190 (US). HAITI. DEPARTMENT OF OUEST: Vicinity of Mission, Fonds Varrettes, alt. ca. 1000 m and above, 17 April-04 May 1920, *E.C. Leonard* 3829 (NY); Vicinity of Furcy, alt. ca. 1300 m, 26 May 1920, *E.C. Leonard* 4324 (US); Massif de la Selle, at Roberjot Morne La Visite, on top of the ridge of Eocene limestone, 12 August 1924, *E.L. Ekman* 1437 (MO, US); Limestone crest of mountain ridge southward from Kenscoff (24 km south of Port-au-Prince), alt. 5600 ft., 18 May 1941, *H.H. Bartlett* 17377 (NY); Massif de la Selle, Parc National Morne la Visite, S of Park Headquarters, alt. 1880-2050 m, 09 May 1984, *W.S. Judd & J.D. Skean-Jr.* 4368 (NY). DEPARTMENT OF SUD-EST: Thiotte, Massif de la Selle, Morne des Commissaires, alt. 1600 m, 05 July 1942, *L.R. Holdridge* 1325 (US); Massif de la Selle, La Visite National Park, ca. 1 km from Inn, alt. ca. 1800 m, 13 June 1998, *F. Axelrod & R. Tremblay* 10616 (MO). MARTINIQUE. SAINT PIERRE: Pitons du Carbet, Montagne Pelée, alt. 800-1100 m, 1880, *P. Duss* 1312 (MO, NY); Near the summit of Mt. Pelée, east side, mossy forest zone, 15 July 1939, *F.E. Engler & W. Seifriz* 39-102 (NY); Culminales de la Montagne Pelée, alt. 1450 m, 14 July 1944, *H. Stehlé* 5359 (US); Slopes of Mont Pelée, alt. 3500 ft., 29 March 1945, *J. Ewan* 17087 (MO); Montagne Pelée, alt. 1100 m, 05 April 1945, *H. Stehlé* 6039 (US). WITHOUT LOCALITY: without precise locality, 1857, *M. Belanger* 171 (P image); without precise locality, May 1870, *L. Hahn* 1435 (MO). SAINT KITTS AND NEVIS. SAINT KITTS: Summit of Mont Misery [Mont Liamuiga], among rocks on exposed mountain summit, 800' above mossy forest zone, alt. 3700 ft., 19 March 1933, *H.E. Box* 313 (US).

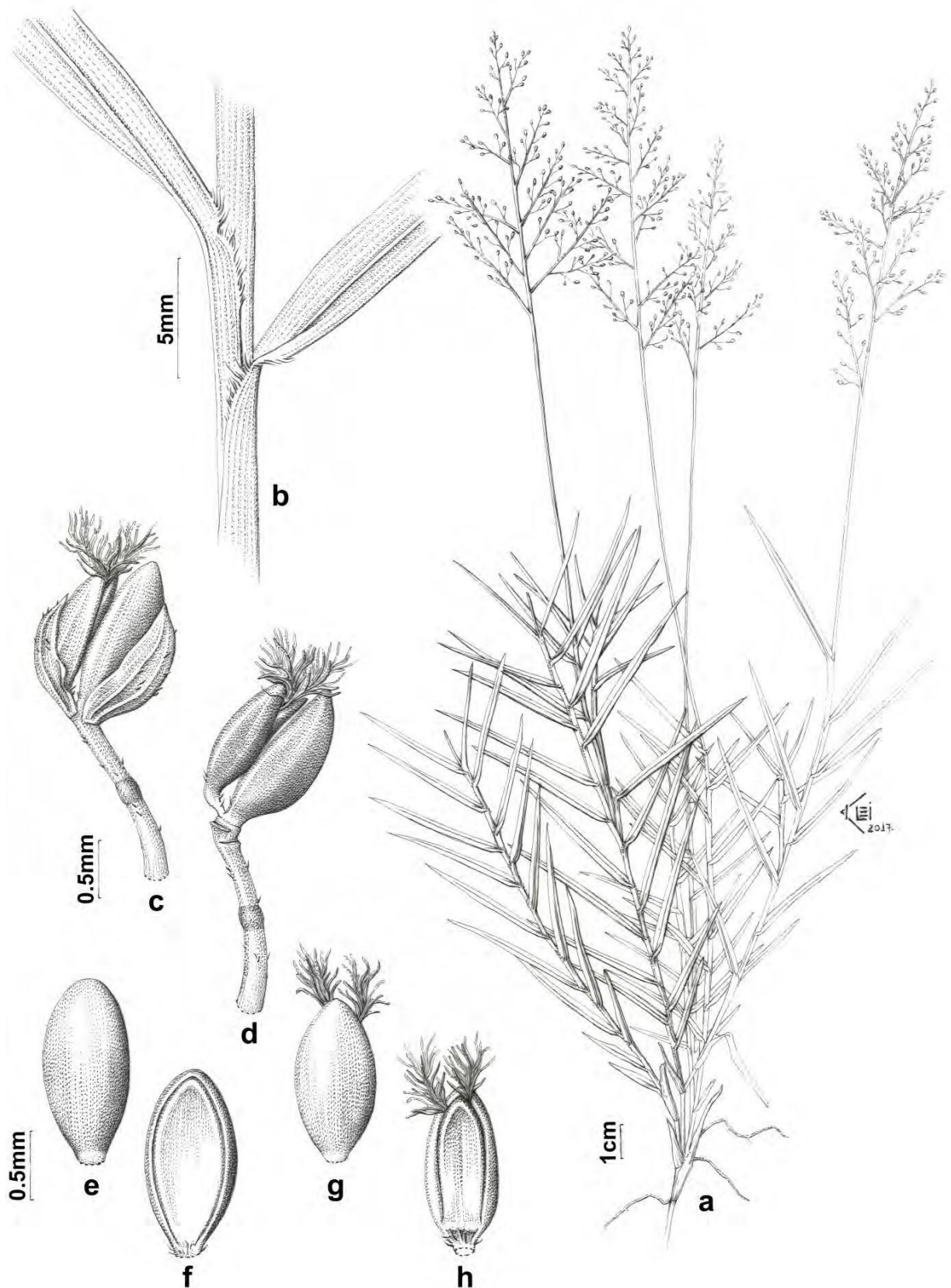


Figure 25. *Isachne rigidifolia* (Poir.) Urb. a. Habit showing a fragment of the culm with ascending branches and synflorescences. b. Fragment of the culm showing the base of the leaf blades, the collar region, and the apex of the leaf sheath (note the conspicuous thickened midrib in the leaves). c. Spikelet in lateral view and pedicel with a glandular band (occasionally the glandular band is absent). d. Anthoecia (glumes removed) and pedicel with a glandular band (occasionally the glandular band is absent). e. Lower anthoecium, lemma view. f. Lower anthoecium, palea view. g. Upper anthoecium, lemma view. h. Upper anthoecium, palea view. Based on: a. *E.J. Valeur* 29 (US); b-h. *T. Husnot* 98 (US). Illustration by Klei R. Sousa.



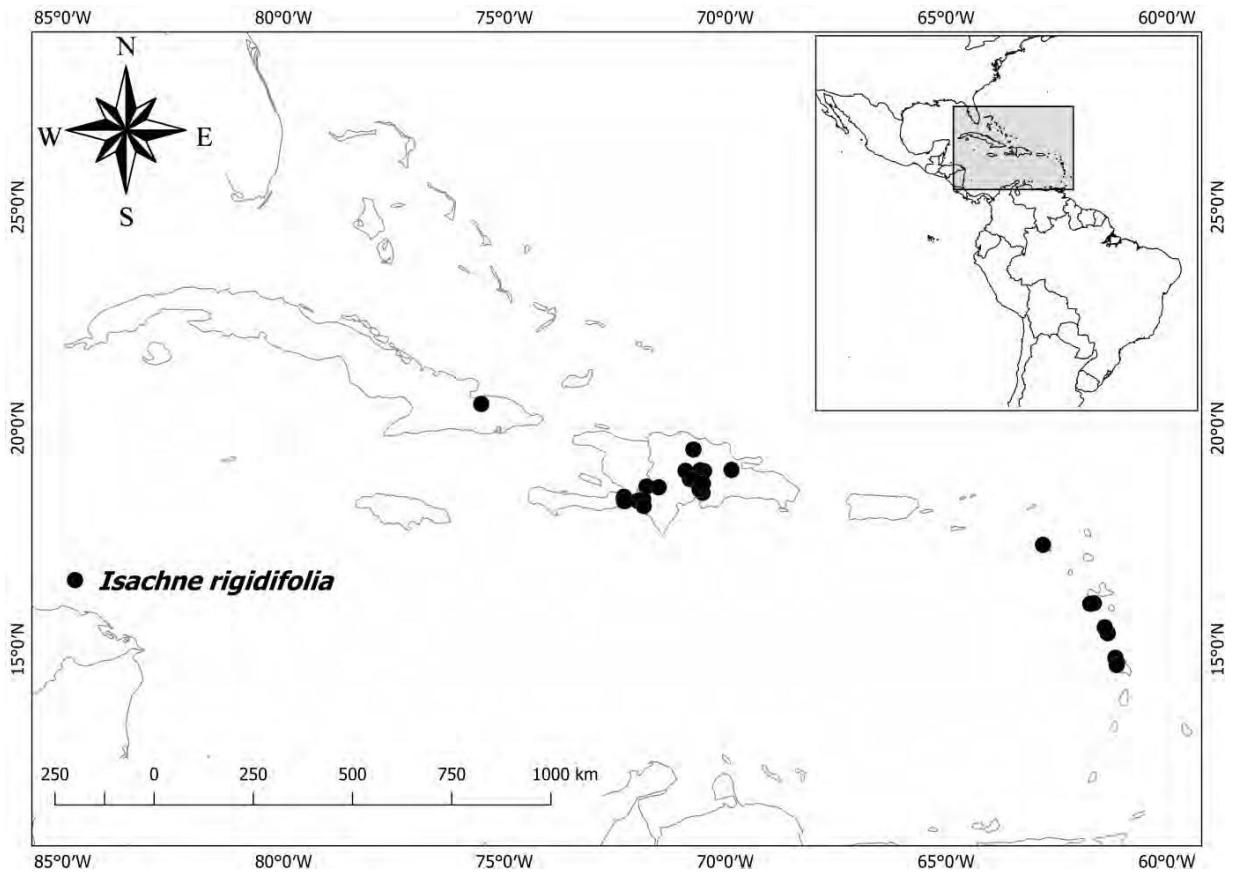


Figure 26. Known distribution of *Isachne rigidifolia*.

14. *Isachne salzmannii* (Trin. ex Steud.) Renvoize, Kew Bull. 39(1): 184. 1984. ≡ *Panicum salzmannii* Trin. ex Steud., Syn. Pl. Glumac. 1: 95. 1854. Type: BRAZIL. Bahia: s.l., s.a., *P. Salzmann s.n.* [first-step lectotype designated by Renvoize (1984) K (corrected from “isotype”); second-step lectotype designated by Rodrigues *et al.* (2016) K-000643013!; isolectotypes K-000004793!, LE-TRIN-0556.01 (fragment and illustration), MO-2099177!, MPU-024600!, MPU-024601!, MPU-024602!, MPU-024603!, MPU-024604!, P-00740915!, P-00740916!, P-00740917!, P- 01936067!, P-02356256!, P-02382030!, TUB-010075 image!; US-975976! (fragment ex P)].
- = *Panicum brizoides* Salzm. ex Döll, Fl. Bras. 2(2): 274. 1877 [nom. inval.], non *Panicum brizoides* L., Mant. Pl. 2: 184. 1771 [nom. illeg. superfl., =*Panicum punctatum* Burm. f.], nec *Panicum brizoides* Lam., Tab. Encycl. 1: 170. 1791 [nom. illeg. hom., =*Panicum paspaloides* Pers.], nec *Panicum brizoides* Jacq., Ecl. Gram. Rar. 2: 2, pl. 2. 1814 [nom. illeg. hom., =*Paspalidium flavidum* (Retz.) A. Camus].

Figure 27

Annual, decumbent, tangled or mat-forming, 15-50(-150) cm long. Culms rooting at the lower nodes, branched from the base and/or at the middle and upper portions, herbaceous, slender, sterile and flowering branches ascending; nodes glabrous to frequently pubescent or pilose in the young culms, trichomes tuberculate, stramineous, dark-brown or blackish, with a conspicuous glandular stripe below; internodes inconspicuously hollow, glabrous, greenish to stramineous, less often purplish or purple-stained towards the nodes. Sheaths usually shorter than the internodes in the basal and middle portion of the culms, longer in the secondary sterile and flowering branches, glabrous or pubescent towards the apex, trichomes sparse, tuberculate, sometimes dehiscent in the old sheaths, strongly nerved, one margin ciliate, the other glabrous, cilia 0.4-0.6 mm long, those towards the ligular region 1.2-2 mm long, colorless; ligule ciliate, 0.7-1(-1.5) mm long; leaf blades distichous, regularly distributed over the culms and secondary flowering and/or sterile branches, lanceolate to linear-lanceolate, (1.5-)3-9 × (0.2-)0.6-1 cm, flexible (not rigid), midrib conspicuous, base rounded to slightly attenuate, not amplexicaul, apex acute, minutely scaberulous on both surfaces, sometimes with some occasional trichomes irregularly distributed, margins entire, scaberulous, often with a some long trichomes towards the ligular region. Panicle terminal and axillary, lax, open or subcontracted, flexible, 5-14 × 3-7 cm, glabrous to minutely scaberulous, provided with second-order branches, glandular bands and axillary glands present; pedicels (0.1-)0.2-1(-1.5) cm long,

cylindrical, glabrous to minutely scaberulous, glandular bands present. Spikelets unequally pedicelled, erect on the pedicels or often the short-pedicelled obliquely inserted, globose to subglobose or elliptic-globose, 1.5-1.9 mm long; glumes subequal, orbicular to elliptic, ventricose, obtuse, glabrous or minutely scaberulous towards the apex, greenish or stramineous, sometimes purple-stained, both shorter or less often subequal the anthoecia; lower glume 1.4-1.7 mm long, 5-7-nerved, margins hyaline, sometimes purple-stained; upper glume 1.2-1.7 mm long, 5-7-nerved, margins hyaline, sometimes purple-stained; anthoecia 2, dissimilar, the lower cartilaginous, elliptic-oblong to elliptic-lanceolate, the upper coriaceous, orbicular to suborbicular, both greenish to stramineous, often purple-stained; lower anthoecium staminate, 1.6-1.9 mm long, lemma glabrous, longitudinally sulcate, palea glabrous, 1.5-1.8 mm long; rachilla inconspicuous between the anthoecia, ca. 0.1-0.2 mm long, glabrous; upper anthoecium bisexual, 1.3-1.8 mm long; lemma minutely appressed-pilose, palea glabrous to sparsely pubescent, 1.2-1.7 mm long. Lodicules ca. 0.2 mm long. Stamens 3, filaments ca. 0.4 mm long, yellowish to pale-green; anthers ca. 0.8-1.2 mm long, yellowish to orange when young, dark-brown to blackish in maturity. Stigmas 2, plumose, purple, dark-brown in maturity. Caryopsis not seen.

*Etymology:* The epithet honors the German naturalist Philipp Salzmann (1781-1851) (Clifford & Bostock 2007). Salzmann was the collector of the original material of *I. salzmannii* in the state of Bahia, Brazil.

*Distribution:* Endemic from Brazil, known only from the municipality of Salvador, Bahia State (Figure 8). It inhabits swampy areas, natural pools, and lakes, associated with muddy soils and sometimes floating on pond banks; at ca. 0-5 m.

*Phenology:* Collected in flower September, October, December and February.

*Comments:* *Isachne salzmannii* is known only by a few collections from Salvador, Bahia. Morphologically, *I. salzmannii* is characterized by the globose to elliptic-globose spikelets, orbicular to elliptic ventricose glumes, and dissimilar anthoecia, being the lower lemma longitudinally sulcate.

It is morphologically related to *I. hirtiglumis*, *I. goiasensis* and *I. polygonoides*, and their distinction was previously discussed under the comments of these species.

The specimen “*M. Elisabeth s.n. (HRB-40896)*” presents a vestigial but conspicuous prolongation of the rachilla above the upper anthoecium.

*Nomenclatural notes:* Döll (1877) treated *Panicum salzmannii* as a synonym of *Isachne ventricosa* (Lam.) Döll and included in the list of representative specimens plants

of distinct species, such as *I. salzmannii*, *I. polygonoides* and *I. burchellii*. Rodrigues *et al.* (2016) presented a brief discussion regarding the identity of *I. ventricosa* in the context of *I. salzmannii* and considered that both species have been erroneously synonymized. Based on the information presented in the Flora of China (Chen & Phillips 2006), the authors stated that the Asiatic *I. ventricosa* was probably related to the widespread *I. globosa*.

We have examined the type specimen of *I. ventricosa* at P and all the collections of *I. salzmannii* available but found no sharp differences between the two species. These findings apparently corroborate the taxonomic position adopted by Döll (1877). However, because other Asiatic species of *Isachne* have not yet been intensively studied by us, and considering that the current circumscription of *I. globosa* throughout its distributional range is questionable, including very distinct entities in both vegetative and reproductive traits, we opted not to make taxonomic decisions. Accepting the synonymization of *I. salzmannii* under *I. ventricosa* as did Döll (1877) would imply profound consequences for the conservation of this species in Brazil. Therefore, in the context of this work, both *I. salzmannii* and *I. ventricosa* are accepted as distinct species. Further studies are required to clarify the identity of *I. salzmannii* and *I. ventricosa*.

The current data banks consider *I. salzmannii* as the correct and valid name and *I. ventricosa* as its synonym (c.f., Tropicos.org, the Catalogue of New World Grasses III, etc.); however, if the synonymy is eventually accepted, the name *I. ventricosa* (based on *P. ventricosum* 1791) must be adopted because it has priority over *I. salzmannii* (based on *P. salzmannii* 1854).

Apparently, Salzmänn never published the name *Panicum brizoides*, which he probably attributed to a specimen stored at his herbarium. Steudel (1854) published the name *Panicum salzmannii* after Salzmänn and just cited the name “*P. brizoides* Salz.” given in the exsiccatae label. Döll included the name in the synonymy of *Isachne ventricosa* despite the former was never validly published.

Material examined: BRAZIL. BAHIA: Southern Part, 10 December 1924, A. Chase 7893 (MO, NY, SP); Southern Part of Bahia, in colonies rather than tuft in mud near pool, 10 December 1924, A. Chase 7894 (IAN, MO, NY, RB); Salvador, Museu de Ciência e Tecnologia, Mata/Boca do Rio, 02 September 1979, L.R. Noblick *s.n.* (ALCB-019473); Salvador, área de Pituauçu (UCSal), 18 February 1992, L. Paraguassú *et al.* 24 (ALCB, HRB); Salvador, Parque Metropolitano de Pituauçu, 20 October 1994, M. Elisabeth *s.n.* (ALCB-019465, HRB-40896).



Figure 27. *Isachne salzmannii* (Trin. ex Steud.) Renvoize. a. Habit and synflorescences. b. Fragment of the culm showing the base of the leaf blade, the collar region, and the apex of the leaf sheath. c. Fragment of the culm showing the base of the leaf blade, the ciliate ligule, and the apex of the leaf sheath. d. Spikelet in lateral view and pedicel with a glandular band. e. Anthoecia (glumes removed – note the conspicuous furrow on the back of the lower lemma (arrow)) and pedicel with a glandular band. f. Lower anthoecium, lemma view (note the conspicuous furrow on the back of the lemma). g. Lower anthoecium, palea view. h. Upper anthoecium, lemma view. i. Upper anthoecium, palea view. Based on: a. *P. Salzmann* s.n. (P-00740915); b-i. *M. Elisabeth* s.n. (ALCB-019465). Illustration of the habit and synflorescences by Josephus Huegel, extracted from Döll (1877, tab. 35). Illustration of details by Klei R. Sousa. Adapted by Rodrigo S. Rodrigues.

15. *Isachne soderstromii* **R.S. Rodrigues & Filg.**, Nordic Journal of Botany 36: e01847. 2018. Type: DOMINICA. Upper northwest slope of Morne Trois Pitons, ca 750-1050 m a.s.l., montane woodland. Exposed opening or outcrop on very steep slope that otherwise was clothed with relatively low densely interwoven vegetation, 04 May 1964, *W.R. Ernst 1227* (holotype US-2880046!).

Figure 28

Perennial, suberect to decumbent or trailing, 15-40(-90) cm long. Culms rooting at the lower nodes, branched at the upper portion, herbaceous, slender, sterile and flowering branches erect; nodes glabrous, dark-brown to blackish. Sheaths longer than the internodes, glabrous, strongly nerved, one margin ciliate, the other glabrous, cilia 0.5-1 mm long, those towards the ligular region ca. 1.5 mm long, colorless; ligule ciliate, ca. 0.5 mm long; leaf blades distichous, mostly concentrated over the secondary flowering and/or sterile branches, linear-lanceolate, (1.5-)4.5-8.5 × (0.3-)0.5-1 cm, flexible (not rigid), midrib conspicuous, base rounded, slightly constricted near the ligular region, not amplexicaul, apex acute, glabrous on both surfaces, margins entire, glabrous or with a few trichomes near the ligular region. Panicle terminal and lateral, open, loose, flexible, 6-8 × 4-5 cm, glabrous, provided with second-order branches, glandular bands, and axillary glands; pedicels 1-5 mm, cylindrical, glabrous, glandular bands present. Spikelets unequally pedicelled, erect on the pedicels, elliptic, 1.2-1.8(-2) mm long; glumes subequal, elliptic-lanceolate, subacute, glabrous, greenish, both equalling the spikelet or slightly shorter; lower glume 1.3-1.9(-2) mm long, 6-7-nerved, margins pale or purplish; upper glume 1.2-1.8 mm long, 7-8-nerved, margins pale or purplish; anthoecia 2, similar, subcoriaceous, whitish, sometimes purplish in the upper 1/3; lower anthoecium staminate, 1.2-1.9 mm long, lemma glabrous or with inconspicuous appressed trichomes near the margins, not sulcate, palea glabrous, 1.2-1.5 mm long; rachilla conspicuous between the anthoecia, 1-2 mm long, glabrous; upper anthoecium bisexual, 1-1.4 mm long, lemma glabrous or with inconspicuous appressed whitish trichomes near the margins, palea glabrous, 1-1.2 mm long. Lodicules ca. 0.1 mm long. Stamens 3, filaments ca. 0.5 mm, yellowish; anthers 0.8-0.9 mm long, purplish when young, yellowish in maturity. Stigmas 2, plumose, purplish. Caryopsis not seen.

*Etymology:* The epithet honors the American agrostologist Thomas Robert Soderstrom (1936-1987). Soderstrom was the first to identify the collection in the US herbarium as a new species, but never associate a name to it or published his finding (Rodrigues & Filgueiras 2018). Thirty-eight years after his death, *I. soderstromii* was published in his honor.

*Distribution:* Lesser Antilles, endemic from Dominica (Figure 29). It inhabits montane woodlands, outcrops, and slopes, associated with low vegetation; at ca. 750-1050 m.

*Phenology:* Collected in flower in May.

*Comments:* *Isachne soderstromii* is only known from the type collection. It is characterized by the glabrous sheaths, leaf blades, panicles, spikelets and rachilla, leaf midrib conspicuous and pedicels with glandular bands (Rodrigues & Filgueiras 2018).

*Isachne soderstromii* is morphologically similar to *I. rigens* but differ in having leaf blades with conspicuous midribs, pedicels with glandular bands and glabrous rachillas. See comments under *I. angustifolia* subsp. *dominicensis* for the distinction between *I. soderstromii*.

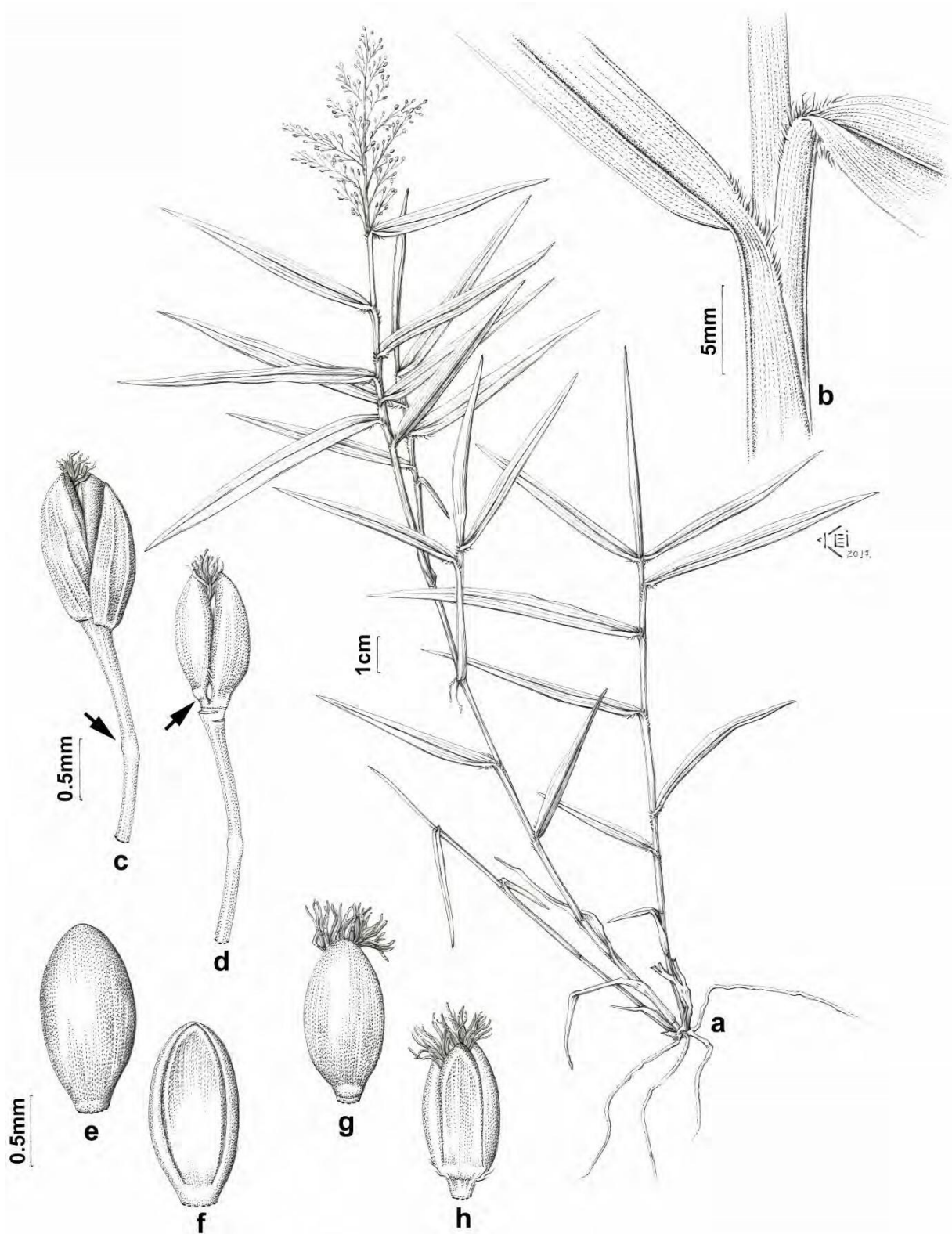


Figure 28. *Isachne soderstromii* R.S. Rodrigues & Filg. a. Habit. b. Fragment of the culm showing the base of the leaf blades, the collar region, and the apex of the leaf sheath (note the evident midrib and marginal hairs at the ligular region). c. Spikelet in lateral view and pedicel with a glandular band (arrow). d. Anthoecium (glumes removed – note the glabrous rachilla) and pedicel with a glandular band. e. Lower anthoecium, lemma view. f. Lower anthoecium, palea view. g. Upper anthoecium, lemma view. h. Upper anthoecium, palea view. Based on: a-h. W.R. Ernst 1227 (US). Illustration by Klei R. Sousa, extracted from Rodrigues & Filgueiras (2018).



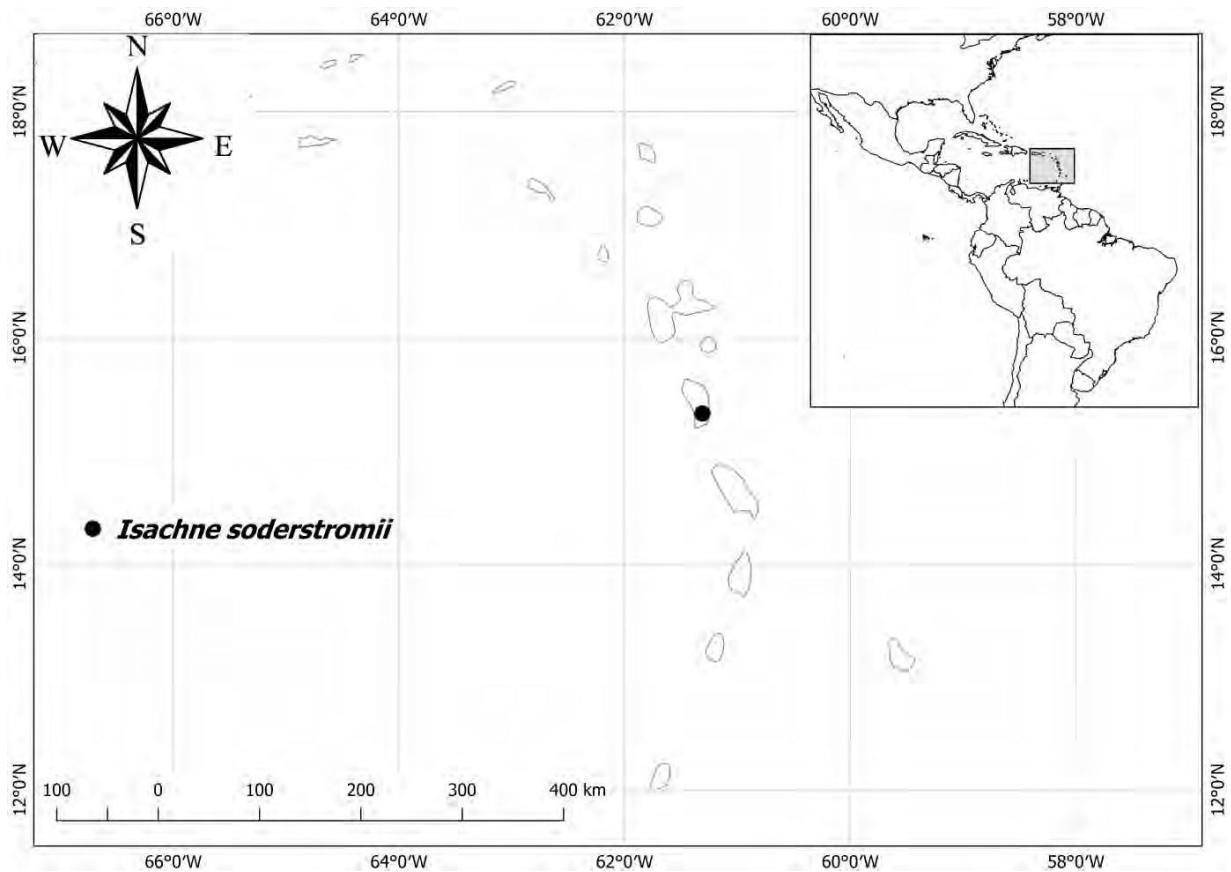


Figure 29. Known distribution of *Isachne soderstromii*.

### Acknowledgments

We thank Dr. Åsa Dalsätt from the Swedish Museum of Natural History (S) for providing high-quality images of the type specimens of *I. arundinacea*, *I. glaucescens* and *I. rigens*; Dr. Marc Pignal and Dr. Otávio L. Marques for their fundamental support and images of specimens from the Muséum National D'Histoire Naturelle (P); Dr. Sergio Romaniuc Neto for all his fundamental assistance to our research; Dr. Thomas R. Soreng, Dr. Paul M. Peterson and Dr. Garrit Davidse for loaning facilities from the US, MO, and NY, respectively; Dr. Lynn G. Clark for her precious advices in the beginning of the project; Dr. Jefferson Prado and Dr. Regina Hirai for their comments, corrections, suggestions and advices regarding the nomenclatural issues; Mr. Klei R. Sousa for the illustrations of various species published here for the first time; to Dr. Luciana Benatti and Mr. André Aguilera for the images under SEM; to Ms. Simone Silva for the support with the coordinates of some specimens; to the curators of the National and International herbaria for permitting us to access the collections physically or through digital medias. This work was sponsored by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES, Brazil and by the Post-graduation Program in Plant Biodiversity and Environment of the Institute of Botany, Brazil.

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**INDEX OF COLLECTORS AND NUMBERED COLLECTIONS EXAMINED**

Collections are listed by first collector only. Numbers in parentheses refer to the corresponding name in the text, followed by the herbarium/herbaria in which the collections are stored.

**Acevedo-Rodriguez, P.:** 6219 (1.1; MO), 7110 (1.1; NY, US), 12493 (13; NY), 12671 (13; NY), 12761 (13; US); **Alain, Bro.:** 9475 (1.1; NY); **Allard, H.A.:** 16475 (13; MO); **Allen, P.H.:** 1068 (9; MO); **Amaral, I.L.:** 1095 (9; MO); **Aona, L.Y.S.:** 1253b (9; HURB, HUEFS); **Archer, W.A.:** 1344 (8; P); **Aristeguieta, L.:** 4494 (9; MO); **Asplund, E.:** 7278 (4.2; MO, S), 8349 (12; P), 16182 (12; P); **Asprey, G.F.:** 2231 (12; NY); **Augusto, B.:** 1683 (13; NY); **Axelrod, F.:** 1485 (1.1; P), 3575 (1.1; NY), 4128 (1.1; NY), 6208 (1.1; MO), 10616 (13; MO); **Aymard, G.:** 2941 (12; MO), 2950 (12; MO), 3196 (9; MO), 5036 (9; MO); **Baldwin, J.T.:** 14271 (4.1; US); **Barbour, P.J.:** 4889 (9; MO); **Bartlett, H.H.:** 16500 (9; MO), 16599 (9; MO) 17377 (13; NY); **Beard, P.:** 1151 (2; MO, US), 1281 (2; MO, US, US); **Beaupertuis, M.:** 1349 (2; P), s.n. (2; P-01923987); **Beiley, L.H.:** 64 (2; NY, US); **Belanger, M.:** 171 (2; P); **Benavides, O.:** 9997 (9; MO); **Black, G.A.:** 9342 (9; IAN), 9910 (9; IAN), 10372 (9; IAN), 10501 (9; IAN), 13238 (9; IAN), 13486 (9; IAN), 13751 (9; IAN), 13853 (9; IAN), 14091 (9; IAN), 14302 (9; IAN), 14356 (9; IAN), 16207 (9; IAN), 16696 (9; IAN), 17299 (9; IAN), 18712 (9; IAN); **Blauner:** 240? (1.1; NY); **Blomquist, H.L.:** 11964 (1.1; IND, MO); **Bourgeau:** 1458 (10; US); **Box, H.E.:** 169 (2; NY, US), 313 (13; US); **Breedlove, D.E.:** 47304 (9; MO), 52526 (10; MO, NY), 55030 (10; MO, NY), 55225 (10; MO), 55246 (10; MO), 56601 (10; MO, NY), 57809 (9; MO) 58458 (10; MO); **Britton, N.L.:** 77 (12; NY), 220 (11; NY), 395 (2; NY, US, US), 2566 (1.1; NY), 3375 (11; NY, US), 4271 (1.1; MO, NY), 5595 (1.1; NY), 1783 (12; NY), 12786 (7; NY); **Broadway, W.E.:** 76 (2; NY-fragment, US), s.n. (2; MO-2095552, NY-1603119); **Brues, C.T.:** s.n. (2; NY-1603115); **Burch, D.:** 6625 (1.1; MO, NY, USF); **Burchell, J.W.:** 2294 (3; P, K); **Burger, W.:** 10044 (9; MO); **Cabrera, E.:** 2962 (10; MO), 3104 (10; MO, MO), 3710 (10; MO); **Callejas, R.:** 2478 (8; MO); **Camp, W.H.:** 3207 (4.2; MO), 3718 (4.1; RB); **Chacon, R.G.:** 354 (5; HEPH); **Chagas-Silva, F.:** 387 (5; K, MO, UEC); **Chambers, K.L.:** 2761 (13; US); **Chase, A.:** 7893 (14; MO, NY, SP), 7894 (14; IAN, MO, NY, RB), 8124 (9; MO, RB), 9122 (9; MO); **Clarke, H.D.:** 10316 (8; US); **Clewell, A.F.:** 3624 (9; MO); **Cogollo, A.:** 2660 (4.2; MO); **Contreras, E.:** 6214 (10; MO), 9438 (10; MO); **Croat, T.B.:** 13973 (9; MO), 41366 (10; MO), 41669 (10; MO), 54503 (4.1; MO), 59223 (9; MO, US), 59232 (9; MO), 67143 (4.1, MO), 73690 (8; MO), 96248 (4.2; MO), 975887 (13; MO, SP); **Cuatrecasas, J.:** 165 (8; P); **Daly, D.C.:** 1995 (9; HUEFS, MO); **Damazio, L.:** s.n. (6; RB-183383, SP-490353); **DASA:** 4880 (10; MO); **Davidse, G.:** 2656 (13; MO), 2758 (9; MO), 2979 (9; MO), 3998 (12; MO), 4296 (9; MBM, MO), 5743 (4.1; MO),

14126 (9; MO), 18887 (8; MO), 19574 (12; MO), 21335 (4.1; MO), 21693 (9; MO), 22344 (8; MO), 22633 (9, MBM), 34597 (4.1; MO), 35554 (9; MO); **Delascio, F.:** 11090 (9; MO, NY), 11107 (9; MO), 11452 (9; MO), 11493 (9; MO), 11620 (9; MO); **Desfontaines:** s.n. (13; FI-holotype, US); **Desvaux:** s.n. (2; P-00740912-holotype, US-2830914); **Díaz, C.S.:** 363 (9; MO), 8950 (9; MO), 10145 (8; MO); **Dodge, C.W.:** 16681 (9; MO); **Dorr, L.J.:** 8585 (12; MO, US); **Duke, J.A.:** 6045 (9; MO), 7376 (1.1; MO, NY), 14842 (9; MO); **Duss, P.:** 679 (2; P, P), 1311 (2; US), 1312 (13; MO, NY), 3189 (2; MO, NY, US), 3190 (13; US); **Eggers, H.F.A.:** 1056 (2; US); **Ekman, E.L.:** 1437 (13; MO, US), 1633 (7; US), 3981 (7; US), 6839 (13; US), 11222 (9; MO, US), 11702 (9; NY), 11872 (13; NY, US), 12678 (7; NY, US); **Elisabeth, M.:** s.n. (14; ALCB-019465, HRB-40896); **Engler, F.E.:** 39-102 (13; NY); **Ernst, W.R.:** 1227 (15; US-holotype), 1720 (2; MO, US); **Escalona, F.:** V218 (12; MO); **Evans, L.:** 49 (1.1; NY); **Ewan, J.:** 17087 (13; MO); **Fendler, A.:** 1637 (12; MO); **Fernández, J.L.A.:** 11445 (12; MO); **Feuillet:** 957 (9; MO); **Fonnegra, R.:** 6162 (8) MO), 6185 (12; MO); **Forero, E.:** 3437 (4.2; MO); **Forzza, R.C.:** 7275 (8; CEN, MG, RB, SP); **Foster, R.B.:** 103222 (4.2; MO); **Fróes, R.L.:** 30108 (9; IAN); **Funk, N.:** 1074 (12; P, P, P); **Funk, V.A.:** 8405 (9; MO); **García, R.:** 1122 (13; US); **Garzivu, M.:** 148 (9; MO); **Gastony, G.J.:** 401 (13; US), 487 (13; MO, NY, NY); **Gentle, P.H.:** 9242 (10; MO); **Gentry, A.H.:** 51390 (9; MO); **Glaziou, A.F.M.:** 17400 (3; NY-holotype, B, K, K, P, P, P, W, W), 22533 (5; K-holotype, B, W, W); **Gleason, H.A.:** P-36 (1.1; NY); **Gómez, L.D.:** 18983 (9; MO); **Gould, F.W.:** 14133 (13; MO, MO), 15154 (2; MO), 15855 (1.1; MO); **Greuter, W.:** 25777 (7; NY); **Grignon, I.:** 84239 (12; MO); **Guanchez, F.:** 4838 (9; MO); **Gutiérrez, E.:** 421 (8; MO); **Hahn, F.:** s.n. (1.1; MO-5391851); **Hahn, L.:** 1435 (13; MO); **Hahn, M.:** 1159 (2; P, P); **Harmon, W.E.:** 4284 (10; MO); **Harris, W.:** 11314 (11; MO, NY, P, P, US), 11313 (12; NY), 11333 (12; NY), 11336 (12; US), 11417 (12; MO, NY, P, US), 11432 (12; MO, NY, P), 11445 (12; MO, NY, P, US), 11543 (12; MO, NY, P), 11583 (4.1; US), 11585 (12; NY), 11595 (12; MO, NY, P, US), 12480 (12; MO, MO, NY, P, P), 12489 (12; MO, NY, US), 12490 (11; MO, NY, P, US), 12491 (12; MO); **Hart, J.H.:** 616 (12; NY, NY), 677 (11; NY), 788 (12; NY); **Hatheway, W.H.:** 1581 (8; UTC, UTC, UTC); **Hawkins, T.:** 1467 (10; MO); **Henkel, T.W.:** 3974 (MO); **Heringer, E.P.:** 4435 (5; CEN, RB, SP), 6654 (5; IBGE, SP, UEC), 14579 (5; NY, SP, UB, UEC); **Hill, S.R.:** 53 (1.1; UVMVT), 27297 (9; MO, US), 28081 (1.2; ILLS, MO-holotype, US); **Hitchcock, A.S.:** 419 (11; MO, NY, P, US, US, USF), 420 (12; NY, P, USF), 598 (9; MO), 599 (9; MO), 8227 (4.1; IAC), 9362 (12; RB), 9732 (12; US), 10219 (4.1; US), 23413 (7; IAN, NY, US); **Hodge, W.H.:** 2071 (2; NY); **Holdridge, L.R.:** 1325 (13; US); **Holm-Nielsen, L.B.:** 24768 (8; MO); **Holst, B.K.:** 9073 (10; MO); **Hook, J.:** 984 (9; MO, US), 1033 (9; US); **Howard, R.A.:** 9098 (13; MO), 10499 (9; US), 19578 (2; NY); **Huber, O.:** 1315 (9; MO), 6306 (12; MO), 7738 (8; MO); **Humboldt:** s.n. (4; P-00128881-holotype, US-



80676); **Hunter, A.A.:** 15 (9; MO); **Husnot, T.:** 97 (2; P, P, P, P, P, P), 98 (13; US), s.n. (2; P-01936016); **Irwin, H.S.:** 12143 (5; CM, MO, NY, UB), 19315 (5; MO, NY, UB), 21552 (9; UB, MO), 34309 (5; MO, NY, UB, USF), 55247 (9; MO, US); **Jameson, W.:** 347 (12; P); **Janovec, J.P.:** 2680 (9; MO); **Jiménez, J.J.:** 4467 (13; US); **Judd, W.S.:** 4368 (13; NY), 5798 (11; FLAS); **Judziewicz, E.J.:** 4448 (9; MO); **Juncosa, A.:** 1132 (4.2; MO); **J.P.:** 677 (11; NY); **Killip, E.P.:** 44664 (9; US); **Kral, R.:** 69226 (9; MO); **Laegaard, S.:** 70287 (8; MO), 70353 (8; MO), 70579 (12; MO); **Le Blond, J.B.:** s.n. (9; P-00563954-holotype, US, BAA); **Léon, F.:** 4843 (7; US), 5078 (7; US), 6520 (7; US); **Leonard, C.E.:** 3829 (13; NY), 4324 (13; US); **Liebmann, F.M.:** 335 (10; US); **Liogier, A.H.L.P.:** 28276 (1.1; NY); **Lugo, H.S.:** 4752 (4.2; MO); **Luteyn, J.L.:** 9713 (12; MO); **Maceda, A.P.:** 644 (9; MO); **Macfayden:** s.n. (11; GOET-holotype, B); **Madriñán, S.:** 449 (4.1; MO); **Madsen, J.E.:** 7134 (8; MO); **Marcano, E.:** 4864 (13; US); **Martínez, E.M.:** 22935 (10; MO), 23030 (4.1; MO); **Martínez, E.S.:** 14978 (10; MO), 15467 (10; MO), 16825 (10; MO), 17080 (10; MO); **Martins, R.C.:** 820 (5; HEPH), 831 (5; HEPH), 1094 (5; UB); **Martius, K.F.P.:** s.n. (9; M-holotype, US); **Maxon, W.R.:** 614 (12; US, NY); **McDaniel, S.:** 21623 (9; MO); **McDougal, J.M.:** 3633 (8; MO), 3655 (12; MO); **McKenzie, P.M.:** 744 (1.1; NY); **Medina, M.:** 573 (1.1; NY); **Molina, A.R.:** 376 (9; MO); **Molina, M.E.L.:** 318 (4.1; MO); **Monteagudo, A.:** 4988 (4.2; MO); **Montes, R.:** 3525 (9; MO); **Moraes, M.D.:** 1039 (9; UEC); **Morales, J.:** 4053 (10; MO); **Moreno, P.P.:** 24727 (9; MO); **Mori, S.A.:** 15736 (9; MO); **Morton, C.V.:** 3293 (7; US), 9658 (7; US); **Mota, N.F.O.:** 1861 (9; BHCB, IAN); **Nee, M.:** 8076 (9; MO), 8212 (9; MO); **Niño, M.:** 1407 (12; US); **Noblick, L.R.:** s.n. (14; ALCB-019473); **Oliveira, A.:** s.n. (6; OUPR-17559); **Oliveira, E.:** 2095 (9; IAN, UB); **Oliveira, P.E.A.M.:** 1694 (5; HEPH); **Oliveira, R.C.:** 1073 (5; HEPH), 2599 (9; UB); **Orcutt, C.R.:** 5756 (11; US); **Ortiz, F.:** 196 (9; MO); **Otero, J.I.:** 651 (1.1; NMC, NY), 739 (1.1; NY); **Paiva, J.G.A.:** 56 (5; UB); **Paula, C.C.:** 633 (6; VIC-holotype, ICN, RB, SP); **Paraguassú, L.:** 24 (14; ALCB, HRB); **Pennell, F.W.:** 1456 (9; MO), 6343 (8; US-holotype); **Perkins, J.R.:** 1085 (11; US); **Pipoly, J.J.:** 4997 (10; MO); **Pires, J.M.:** 1264 (9; IAN); **Pittier, H.:** 252 (10; US-holotype); **Plowman, T.:** 9101 (9; HRB, MO); **Pohl, R.W.:** 12848 (4; MO-neotype), 15376 (8; MO), 15465 (12; MO, RB), 15534 (8; MO), 15585 (8; MO); **Prance, G.T.:** 24818 (9; MO); **Privault, M.:** 182 (2; P, P), 276 (2; P); **Proctor, G.R.:** 7347 (11; US), 7353 (12; US), 20351 (2; US); **Purpus, C.A.:** 2000 (10; MO, NY, US), 7814 (10; US); **Quezada, A.:** 1827 (10; MO); **Ramírez, B.R.P.:** 2243 (8; MO), 2450 (12; MO), 6087 (12; MO); **Raynal-Roques, A.:** 15953 (2; US), 21091 (13; US); **Reis, P.:** 70 (5; CEN); **Renvoize, S.A.:** 5398 (9; MO); **Reyes-García, A.:** 2122 (10; MO); **Richard, L.C.M.:** s.n. (2; P-00563958-holotype, US-2830913), s.n. (2; P-01923982), s.n. (2; P-01923989); **Ritter, N.:** 2414 (9; MO), 2477 (9; MO); **Robleto, W.:** 1489 (4.1; MO); **Rodrigues, R.S.:** 452 (6; HUEFS, MG, MBM, SP), 465 (6; SP), 479 (5; HUEFS, SP),

480 (5; MG, SP), 481 (5; MBM, SP); **Rodríguez, A.:** 8644 (4.1; MO); **Rosa, N.A.:** 4214 (9; HRB); **Rossi, L.:** 2539 (9; SP); **Rossy-Valderrama, C.:** s.n. (1.1; FSU-19416); **Rueda, R.:** 13349 (4.1; MO); **Saldanha, J.:** 203 (9; R), 212 (9; R); **Salzmann, P.:** s.n. (14; K-000643013-lectotype, K, LE, MO, MPU, MPU, MPU, MPU, MPU, P, P, P, P, P, P, TUB, US); **Santiago-Díaz, P.:** 3674 (4.2; MO); **Sargent, F.H.:** 3276 (9; MO); **Sastre, C.:** 2818 (13; MO), 2870 (13; MO), 7459 (13; US); **Schnee, L.:** 1553 (8; MO); **Scribner, F.L.:** 1 (2; US); **Shafer, J.A.:** 1723 (7; NY), 3477 (1.1; NY), 8427 (7; NY), 8561 (7; US); **Shattuck, O.E.:** 433 (9; MO); **Sintenis, P.:** 1355 (1.1; NY, P, P), 4045 (1.1; MO, NY, P), 6421 (1.1; NY, NY); **Smith, H.H.:** 207 (12; MO); **Smith, J.F.:** 1289 (8; MO); **Sneidern, K.:** 543 (8; MBM), 1299 [MBM]; **Solomon, J.C.:** 8634 (4.1; MO); **Sorrie, B.A.:** 12899 (13; US); **Sparre, B.:** 16959 (12; MO); **Standley, P.C.:** 25943 (9; MO), 27476 (9; MO); **Stehlé, H.:** 361 (2; P), 1167 (2; US), 5359 (13; US), 6039 (13; US), s.n. (2; US-2180475); **Stergios, B.:** 2879 (9; MO), 6415 (9; MO), 17274 (12; MO), 17567 (12; US), 18982 (12; MO), 20048 (12; MO, US); **Stevens, F.L.:** 2783 (1.1; NY); **Stevens, H.I.:** 256 (1.1; MO, NY); **Stevens, W.D.:** 3271 (9; MO), 25256 (10; MO), 25837 (10; MO), 27961 (9; MO); **Steyermark, J.A.:** 58656 (8; US), 59009 (8; US), 60107a (8; US), 62659 (12; MO), 92697 (8; US), 93658 (8; MO, US), 93914 (8; US), 118213 (12; MO), 131363 (9; MO), 131823 (9; MO); **Stimson, W.R.:** 1857 (1.1; MO, NY); **Sucre, D.:** 10326 (9; RB, SP); **Swallen, J.R.:** 5123 (9; IAN), 6905 (9; IAN), 6922 (9; MO), 6949 (9; IAN), 6977 (9; IAN); **Swartz, O.P.:** s.n. (2; S-R-3937-holotype), s.n. (12; S-R-4004-lectotype, S-R-4005, B, B, BM, M, SBT, S, UPS, US); **Taylor, C.M.:** 8562 (1.1; P), 9784 (9; MO), 11852 (1.1; MO); **Tejos, R.:** 7 (9; MO); **Tenorio, P.L.:** 11042 (4.1; MO), 14502 (10; MO, MO); **Thompson, S.A.:** 10616 (13; US); **Ton, A.M.:** 4429 (10; MO); **Valeur, E.J.:** 29 (13; US); **van der Werff, H.:** 7924 (12; MO), 8405 (8; US); **Vélez, I.:** 1092 (1.1; NY), 1893 (1.1; MO), 3394 (2; US); **Viana, P.L.:** 2703 (9; INPA, BHCB), 2744 (6; BHCB), 2813 (6; BHCB); **Webster, G.L.:** 13336 (1.2; US), 13368 (13; US); **Weddell, M.:** s.n. (6; P-01882836); **Whitefoord, C.:** 1746 (10; MO), 3822 (2; US); **Wilbur, R.L.:** 7412 (2; MO, US), 8245 (2; MO, NY, US); **Willdenow, C.L.:** 18761 (4; B-holotype), 18828 (9; B-holotype); **Wilson, P.:** 160 (1.1; NY-holotype, US); **Woodson, R.E.:** 1655 (9; MO); **Worthinton, R.D.:** 35258 (1.1; ASU); **Wright, C.:** 755 (7; GOET-holotype, B, BR, BRU, BRU, CAS, GH, K, K, MO, NY, NY, NY, NY, P, PH, S, S, S, W, W, W); **Wurdack, J.J.:** 34138 (8; IAN, RB, NY, VEN), 39832 (9; US); **Zanoni, T.:** 20044 (13; NY), 22285 (13; MO); **Zak, V.:** 848 (8; MBM, MO), 3204 (4.1; MO); **Zarucchi, J.L.:** 4420 (12; MO), 5873 (12; MO), 6213 (12; MO), 6248 (8; MO); **Zuloaga, F.O.:** 4031 (8; MO), 4200 (12; MO), 4743 (12; MO); **Without collector:** s.n. (9; IAN-95045), s.n. (2; NY-1603122), s.n. (2; P-01928008), s.n. (2; P-01923977), s.n. (2; P-01923990).