RONALDO VINÍCIUS DA SILVA

ESTUDOS TAXONÔMICOS E FILOGENÉTICOS EM *Merostachys* SPRENG. (POACEAE: BAMBUSOIDEAE: BAMBUSEAE: ARTHROSTYLIDIINAE)

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

VIÇOSA
MINAS GERAIS – BRASIL
2019

Ficha catalográfica preparada pela Biblioteca Central da Universidade Federal de Viçosa - Câmpus Viçosa

T
S586e
2019

Silva, Ronaldo Vinícius da, 1990-
Estudos taxonômicos e filogenéticos em *Merostachys* Spreng. (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae) / Ronaldo Vinícius da Silva. – Viçosa, MG, 2019.
xviii, 146 f. : il. ; 29 cm.

Orientador: Ana Paula Santos Gonçalves.
Tese (doutorado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1. Bambu - Classificação. 2. Bambu - Morfologia. 3. Gramínea. 4. Bambu - Filogenia - Aspectos moleculares. 5. DNA. I. Universidade Federal de Viçosa. Departamento de Biologia Vegetal. Programa de Pós-Graduação em Botânica. II. Título.

CDD 22. ed. 584.9

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APROVADA: 25 de março de 2019.

Pedro Lage Viana

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Ana Paula S. Gonçalves

Ana Paula Santos Gonçalves
(Orientadora)

Vá firme na direção de suas metas,

porque o pensamento cria, o desejo atrai e a fé realiza.

Lauro Trevisan

Aos meus pais, Ilton e Maria, pelo exemplo, amor, carinho, incentivo e por todos os valiosos ensinamentos que me ajudaram a me tornar quem eu sou,

Dedico!

AGRADECIMENTOS

Quando me propus a realizar o doutorado, sonhava com o título de Doutor, com uma pesquisa bem sucedida, a qual teria como ápice os artigos preparados para a submissão em periódicos renomados! A meta realmente é essa, trabalhar e colher os frutos! No entanto, no decorrer desses quatro anos pude perceber que as conquistas e o verdadeiro aprendizado está no processo, nas tentativas, nos erros e no acertos, na descoberta! Esse aprendizado não vem só, ele vem acompanhado de pessoas que, de uma forma ou de outra, somam contigo, contribuem, compartilham e, por que não, também aprendem. A todos que têm contribuído na minha formação, profissional e pessoal, durante esses quatro anos, deixo aqui um pouco da minha eterna Gratidão!

Á Deus, por me conceder força e resiliência e por abrir caminhos e não me deixar desamparado em momento algum;

À Universidade Federal de Viçosa, ao Departamento de Biologia Vegetal e ao Programa de Pós-Graduação em Botânica, pela oportunidade de realizar o doutorado e também pela infraestrutura a mim concedida para que eu pudesse conduzir esse estudo;

Às agências finaciadoras que me permitiram desenvolver essa pesquisa: a CAPES, pela concessão da minha bolsa de doutorado e bolsa de Estágio Sanduíche; CNPq, Fapemig, Ned Jaquith Foundation e BOTA pelo apoio financeiro, tão importante desde os trabalhos de campo até as atividade laboratoriais;

À minha orientadora, Ana Paula Santos Gonçalves, pelo apoio durante esses quatro anos e por acreditar em mim. Obrigado pelo incentivo, pelos ensinamentos e pela valiosa contribuição durante todo esse período;

Ao meu coorientador, Jéferson Fregonezi, pelo auxílio e incentivo. Obrigado por me encorajar em vários momentos de dificuldade e pelas conversas produtivas que tanto contribuiram na escrita desta tese;

À minha coorientadora, Lynn Clark, pelo incentivo, apoio e colaboração. Obrigado pelo empenho em relação ao meu trabalho durante meu Estágio Sanduíche na Iowa State University. Obrigado por me encorajar nos momentos de dificuldades e pelo suporte durante todo o período que eu estive nos EUA. Obrigado, também, pela paciência e compreensão. Seu exemplo de profissionalismo e como ser humano é incentivador!

Aos Professores Adriano Nesi e Wagner Araújo por me permitirem utilizar a estrutura da UCP (Unidade de Crescimento de Plantas) (Universidade Federal de Viçosa) e ao Dr. Jonathan Wendel por me permitir acesso ao Wendel’s Lab (Iowa State University). Foram nestes dois laboratórios que eu fui capaz de executar as atividades relacionadas à biologia molecular.

À Corrinne Grover, Anna Tuchin, Guanjing Hu e ao Marcelo Vaz pelo auxílio durante as atividades no laboratório de biologia molecular.

Aos queridos Christian Silva, Wallace São Mateus, Lakshmi Attigala e Cristielle Costa pelas valiosas sugestões durante a realização das análises filogenéticas.

Ao Ângelo, secretário do programa de Pós-graduação em Botânica, pela prestatividade e solicitude de sempre! Obrigado por facilitar a minha vida em meio a tantas questões burocráticas.

Aos colegas e amigos da Salinha da Pós Graduação: Clara, Túlio, Genilson, Andreza, Mayky, Samara e Wénita pelo convívio diário e pelas descontraídas conversas. Em especial, agradeço à Clara e ao Túlio pela companhia maravilhosa, pelo apoio, prestatividade, compreensão nos meus dias difíceis e por fazerem com que minha rotina ficasse mais leve e prazerosa. Chegaram de repente e de repente se tornaram imensamente importantes. Em especial também digo um muito obrigado ao Genilson, com o qual compartilhei esses quatro anos de doutorado. Não consigo, hoje, imaginar como seria sem você por aqui. Obrigado pelo apoio, pelo incentivo, por me ouvir nos momentos de dificuldades. Grato por todas as conversas sobre taxonomia e por todas as nossas gargalhadas.

Ao trio especial que eu ganhei: Nayara, Cecília e Neil. Não sou capaz de expressar nestas linhas o que vocês representam. Vocês conseguiam tirar o melhor de mim em todas as ocasiões, mesmo quando o melhor de mim não era tão bom assim. Gratidão por esse mundo de risos e sorrisos que vocês me apresentaram, pelo cuidado que sempre tiveram comigo e pelas três crianças que saltavam aos olhos quando sentávamos juntos para uma simples conversa após o almoço. Me faltam palavras para expressar tudo o que sinto quando lembro de vocês.

Aos meus queridos da Ecologia: Nayarinha, Wendelo, Alex, Fernando, Aloirta e Prímula. Obrigado meus amigos, por cada dia, cada bom dia. Os dias sempre foram belos com vocês. Cada cafezinho ou mesmo aquele abraço rápido. Gostaria que eles fossem eternos. Uma menção especial à Prímula, com a qual compartilhei vários momentos nesses anos, de modo que eu poderia escrever um livro. Obrigado pelos jantares no seu apê, pelas reflexões, por me acolher como um irmão e encher minha vida de paz e luz.

Aos amigos da anatomia: Ivan, Analu, Brenda, Luana, Paulinha, Miller e Thamires e, também, ao Evandro (Fisiologia). Obrigado pela companhia gostosa, conversas, encontros. Felicidade, a gente se vê por aqui!

À minha dupla fantástica Ivan e Ana Luísa. Juntos compomos o trio mais perigoso desse planeta. Ivan, meu amigo-irmão, que sempre foi um incentivador. Desde o ensino fundamental até a Pós-graduação. Obrigado pelo apoio e pelo ombro amigo de todos os dias. Juntos compartilhamos várias histórias incríveis que levarei sempre na minha memória. Ana, não consigo pensar em Viçosa sem lembrar de você. Obrigado pela companhia agradável, pelas palavras doces de carinho e de apoio. Vocês fazem meus dias mais leves. Grato por essa parceria e cumplicidade que só somaram na minha vida.

Ao Celso e à Fernanda, dupla ícone do Laboratório de Ecologia e Herbário. Obrigado pela convivência maravilhosa durante todos esses anos. Os cafés, as conversas, as boas gargalhadas. Obrigado, também, à Gracinha pelo apoio e pelo carinho de sempre; você é daqueles presentes que faz um bem para a alma e a gente nem sabe se merece. Enfim, o bem que vocês me fazem é imensurável.

Ao trio Sensacional: Dani Parma, Cristielle e Mônica. Dani, obrigado pelo companheirismo, pelos conselhos, por me incentivar, por sempre dizer que tudo daria certo e por me ouvir nos dias de desespero. Cris, obrigado por ser tornar uma irmã e me fazer o irmão mais feliz desse mundo. A convivência contigo foi algo maravilhoso e eu não sei expressar em palavras. Obrigado por ser meu braço direito em praticamente todos os campos e por escrever, junto comigo, as histórias mais hilárias pelos cantos do Sudeste brasileiro. Mônica, a tradução da amizade em forma de sorrisos. Obrigado por todo o cuidado comigo desde o mestrado. Obrigado por me encorajar, por acreditar em mim mesmo nos momentos que nem eu acreditava, por todas as mensagens de apoio, pelo carinho e por lutar junto comigo. Quem luta junto tem recompensa em dobro. Gratidão a vocês, meninas. É um prazer tê-las comigo!

Á Líbia e ao Michael, os colombianos mais brasileiros que eu conheci. Vocês foram uma inspiração para mim. Obrigado por cada momento que passamos juntos, cada brincadeira, cada gargalhada. Nunca esquecerei das nossas conversas em português, inglês e espanhol. Amizade é algo que rompe todas as barreira, inclusive as geográficas. Muchas gracias, my colombian friends.

Aos meus amigos botânicos Guilherme, Adriano Valentim, Van Terra, Dya, Anaïs, Júnia e Carol. Embora longe há algum tempo, vocês tiveram uma importância grandiosa nessa etapa. Tudo o que aprendi e ainda aprendo com vocês é fantástico. Obrigado por, mesmo distantes, me incentivarem e apoiarem. Obrigado por cada momento que vivemos juntos e tenham certeza que cada um deles estarão comigo onde quer que eu vá. Poderia escrever páginas e páginas sobre nossas histórias, no entanto resumo todas em uma palavra: GRATIDÃO! Foi um privilégio ter convivido com cada um de vocês. Daqui há alguns dias nos encontraremos novamente nessas voltas da vida.

Às minhas queridas da Bioquímica e também do cursinho de inglês: Gabi Alves e Luana. Gabi, minha irmã desgarrada que encontrei em Viçosa. Obrigado por me incentivar, por tranquilizar minha alma com os nossos cafezinhos e nossas caminhadas, por me “arrancar” sorrisos e também por me agraciar com os seus. Grato por todos os momentos que compartilhamos, por me encorajar nos dias de tensão e dificuldade e, também, por me permitir reviver essa criança que existe em mim. Lu, minha irmã de vida que me encontrou logo quando eu aqui cheguei. Obrigado por cuidar desse irmão desajeitado, completamente desesperado, mas que lhe ama muito. Grato por cada palavra de apoio, de coragem, e, é claro, pelos sorrisos. Aliás, como não amar suas gargalhadas. Sinceramente, não consigo imaginar como seria isso tudo aqui sem vocês! Thank you so much.

Á Bia e à Juliana, as duas surpresas mais agradáveis que eu poderia ter ganho durante o meu estágio sanduíche nos EUA. Aquela conectividade inexplicável que surge do nada e significa tudo. Vocês, talvez até mesmo sem perceber, me ajudaram grandiosamente e me forneceram um suporte gigantesco para cumprir uma etapa maravilhosa e ao mesmo tempo díficil na minha vida. Obrigado pelos momentos mais hilários e icônicos que eu poderia viver. Obrigado, também, pelos sorrisos que vocês me tiraram, todos eles muito sinceros e verdadeiros. Irei atrás de vocês e não adianta fugir!

Ás especiais Aline, Flávia, Débora, Jú Mendonça e Gabi Rolim. Os meus cafés com você, Aline, transformavam meus dias. Suas palavras de apoio, seus conselhos, seus abraços. Você com certeza foi uma das amizades mais incríveis que eu conquistei nesse período. Flávia, apesar de você quase nunca responder minhas mensagens, eu ainda lhe quero bem, viu. Amiga, companheira, irmã! Obrigado por todos os momentos agradáveis que compartilhamos. Seu sorriso me levava a outra dimensão! Débora, obrigado por me salvar diante todas as burocracias do estágio sanduíche e por se tornar, de mansinho, uma daquelas pessoas especiais e importantes que a vida, de um dia para o outro, joga em você e diz: toma, é seu presente, cuida e aguenta! Obrigado por me deixar saber que a minha loucura tinha um par (Hahahah). Jú e Gabi, me levem para o Rio e para o Nordeste, por favor? Obrigado por tudo o que vocês tem feito por mim. Cada encontro, cada palavra, cada mensagem, cada abraço! Obrigado por me acolherem, me ouvirem e por tranquilizarem minha mente, às vezes tão confusa. Gratidão resume.

Ao Gian, meu grande amigo, que sempre me apoiou em todos os momentos. Obrigado por tornar essa trajetória mais viva e com muito mais sentido.

Aos amigos que a graduação me deu: Maísa, Denise, Tiago, Val, Nara e Danuza. Sabe quando você deseja que o tempo volte alguns anos? Pois é, eu gostaria. Apenas para ter o prazer de vê-los novamente todos os dias e compartilhar, diariamente, toda aquela energia boa. Hoje, o sentimento que pulsa em mim é uma eterna gratidão. Não os vejo diarimente como antes, mas sinto a presença de cada um do mesmo jeito, com aqueles sorrisos característicos, a esperança do futuro, os planos profissionais. Apesar do tempo, as lembranças são as melhores possíveis. Galera, obrigado por me levarem junto com vocês. Segue o Baile! Continuaremos caminhando juntos.

Às amigas Juliana Mirandinha, Vivi, Tida e Nilza. Desde a graduação até os dias de hoje vocês muito tem me ajudado. Muito obrigado pelo incentivo diário, pelas palavras de apoio, por terem acreditado em mim desde o início. Serei sempre grato a cada uma pelo suporte, cuidado e carinho. Antes, um contato meramente profissional e hoje fazem parte da minha minha vida de uma maneira muito especial.

Aos meus queridos Clever, Victor, Adriano, Michel, Ediléia, Wandérica, Roberta, Lígia, Sandra, Alaíde e Raiane. Obrigado pelo apoio e suporte, por entenderem minha ausência em várias ocasiões e por sonharem junto comigo. Gratidão por todos os momentos que compartilhamos e por me incentivarem diariamente. Que venham as próximas etapas! Estarei sempre com vocês!

Ao Wagner, pelo apoio, carinho, cuidado e por todas as palavras de incentivo para comigo. Obrigado, também, por compreender minhas ausências e, muitas vezes, meus momentos de estresse. Grato por todos os maravilhosos momentos que você me proporcionou e por está ao meu lado durante essa caminhada.

À minha família, pelo apoio nesta etapa tão importante da minha vida. Agradeço, em especial, aos meus pais, Ilton e Maria, pelo suporte durante toda esta jornada, pelo exemplo e por me incentivarem diariamente. O cuidado de vocês para comigo fizeram uma enorme diferença. Eternamente grato por tudo que vocês me ensinaram (e ainda ensinam), pelos valores a mim transmitidos e a todos os sorrisos e abraços que temos aportunidade de doar uns aos outros. Me orgulho de ser filho de vocês e não há palavras o suficiente para expressar o quanto os admiro! Obrigado meus queridos pais.

A todos que de alguma forma contribuíram comigo durante esses quatro anos de esforço, dedicação, alegria, perseverança e aprendizado, meu sincero muito obrigado.

BIOGRAFIA

Ronaldo Vinícius da Silva, filho de Ilton Paulino da Silva e Maria do Carmo Silva, nasceu em Guiricema, Minas Gerais, em 14 de maio de 1990.

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Iniciou o Doutorado em Botânica, pela Universidade Federal de Viçosa, Viçosa, Minas Gerais, em março de 2015, concluindo em março de 2019.

NOTA BENE

Três novos nomes são apresentados nesta tese (*Merostachys judziewiczii* Viníc.-Silva, L.G. Clark & Santos-Gonç., *Merostachys lagevianae* Viníc.-Silva, L.G. Clark & Santos-Gonç. e *Merostachys soderstromii* Viníc.-Silva, L.G. Clark & Santo-Gonç.). Não é intenção do autor que esta tese seja considerada local de publicação de tais nomes, pois os manuscritos nos quais eles aparecerão serão submetidos, separadamente, a distintos periódicos, após a eventual aprovação desta tese pela banca examinadora. Com esta nota, o autor quer evitar a possível aplicação do conceito de nomen nudum (Turland et al. 2018) para os novos nomes aqui apresentados.

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RESUMO

Silva, Ronaldo Vinícius da, D.Sc., Universidade Federal de Viçosa, março de 2019. **Estudos morfológicos e filogenia molecular em *Merostachys* Spreng. (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae).** Orientadora: Ana Paula Santos Gonçalves. Coorientadores: Lynn Gail Clark e Jéferson Nunes Fregonezi.

Merostachys Spreng. é um gênero de bambu lenhoso Neotropical que engloba, atualmente, 54 espécies descritas, as quais apresentam um ciclo reprodutivo peculiar com um longo período de crescimento vegetativo (ca. 30-50 anos). O gênero é morfologicamente bem delimitado e facilmente reconhecido. No entanto, apesar de apresentar algumas espécies de fácil identificação com base em caracteres morfológicos, o gênero também apresenta desafios à taxonomia e estes estão relacionados, principalmente, a (1) espécimes coletados sem estruturas reprodutivas devido à dificuldade em se encontrar espécies em floração; (2) amostragem apenas de secções do ápice do colmo; (3) espécies descritas por autores clássicos com base apenas em fragmentos; (4) espécies com descrições originais pouco informativas; (5) dificuldade de recoletar as espécies descritas com base apenas em fragmento devido às condições atuais dos locais tipo; (6) mistura de materiais (a partir de diferentes táxons) na descrição de uma única espécie e (7) falta de literatura especializada com chaves de identificação. Esforços em trabalhos de campo e análises morfológicas tem sido realizados e a continuidade dos estudos é imprescindível para a resolução de questões como as expostas acima. Durante as análises morfológicas foi possível reconhecer grupos morfológicos, fato realmente relevante, uma vez que *Merostachys* não apresenta uma classificação infragenérica. Estes agrupamentos foram estabelecidos informalmente e, portanto, são necessários estudos que averiguem se há suporte desses grupos em um contexto filogenético. Estudos filogenéticos prévios a partir de dados moleculares com uma baixa amostragem em *Merostachys* sugerem o monofiletismo do gênero e também uma estreita relação ora com *Actinocladum* ora com *Athroostachys*. A pesquisa aqui proposta objetiva (1) estudar, detalhadamente o gênero em seus aspectos morfológicos; (2) realizar análises de filogenia molecular a partir de uma amostragem mais ampla a fim de testar o monofiletismo do gênero; (3) verificar as relações entre suas espécies e entre *Merostachys* e os demais gêneros de Arthrostylidiinae; e (4) averiguar a possível congruência entre dados morfológicos e moleculares. Como resultados são apresentados (1) a descrição de três novas espécies para o gênero; (2) a descrição do material reprodutivo de *Merostachys bifurcata* e *Merostachys procerrima*; (3) a redescrição e relectotipificação de *Merostachys speciosa*, espécie tipo do gênero; (4) a redelimitação específica de *Merostachys magnispicula*, *Merostachys medullosa* e *M. procerrima* e (5) a filogenia molecular de *Merostachys* baseada em sete marcadores plastidiais (um gene: *ndhF* e seis regiões não codificadoras: *rpl16*, *rps16*, *rps16-trnQ*, *trnC-rpoB*, *trnD-trnT* e *trnT-trnL*). O monofiletismo de *Merostachys* foi confirmado. Dois clados foram bem sustentados dentro do gênero, assim como também foi o posicionamento de *Merostachys* como grupo irmão de *Athroostachys*; *Actinocladum*, por sua vez, foi sustentando como grupo irmão do clado *Merostachys* + *Athroostachys*. A maioria dos grupos morfológicos não foram congruentes com os dados moleculares, exceto aquele relacionado com a surperfície do flósculo (reluzente ou opaco) que apresentou uma correlação interessante na topologia molecular. Um dos clados reconhecidos dentro do gênero apresenta uma politomia composta por várias espécies. Este cenário pode estar associado a fatores como (1) a utilização de marcadores pouco informativos para o grupo; (2) longo tempo de geração dos táxons; (3) ocorrência de hibridação e/ou (4) ocorrência de sorteio incompleto de linhagens. As duas últimas possíveis explicações estão, geralmente, relacionadas a espécies de radiação recente. A partir das nossas observações, tanto em campo quanto em herbários, acreditamos que o evento mais provável de estar influenciando na evolução de *Merostachys* é o sorteio incompleto de linhagens.

ABSTRACT

Silva, Ronaldo Vinícius da, D.Sc., Universidade Federal de Viçosa, March, 2019. **Morphological studies and molecular phylogeny in *Merostachys* Spreng. (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae).** Adviser: Ana Paula Santos Gonçalves. Co-advisers: Lynn Gail Clark and Jéferson Nunes Fregonezi.

Merostachys Spreng. is a Neotropical woody bamboo genus which currently encompasses 54 described species having a peculiar reproductive cycle with a long growth period (ca. 30-50 years). The genus is morphologically well-delimited and easily recognized. However, despite including species of easy identification through morphological characters, the genus poses challenges to taxonomy, which are mainly associated with (1) the lack of reproductive structures in collected specimens, due to the difficulty of finding flowering species; (2) sampling only of culm apical sections; (3) species having been described by classical authors based merely on plant fragments; (4) species with little informative original descriptions; (5) hampered recollection of species that were described based solely on fragments, due the current conditions of their type localities; (6) the occurrence of mixed materials (from different taxa) in the description of a single species; and (7) lack of specialized literature with identification keys. Fieldwork and morphological analyses have been carried out to address these issues, and the continuity of such research efforts is indispensable to resolve them. Morphological analyses allowed for the recognition of morphological groups, which is a truly relevant factor, as *Merostachys* has no infrageneric classification. However, these groups were established informally, and thus studies that would investigate whether they are phylogenetically supported are highly necessary. Previous low-sampling phylogenetic studies with molecular data on *Merostachys* have suggested the monophyly of the genus as well as its close relationship with either *Actinocladum* or *Athroostachys*. The present research aimed to (1) study the genus in detail, focusing on its morphological aspects; (2) perform molecular phylogenetic analyses with a broader sampling to test the monophyly of the genus; (3) verify the relationships among species in the genus and between *Merostachys* and the other genera of the Arthrostylidiinae; and (4) investigate a possible congruency between morphological and molecular data. The research brings as results (1) the description of three new species in the genus; (2) the description of reproductive material of *Merostachys bifurcata* and *Merostachys* *procerrima*; (3) the redescription and relectotypification of *Merostachys speciosa*, type species of the genus; (4) the specific redelimitation of *Merostachys magnispicula*, *Merostachys medullosa* and *M. procerrima*; and (5) the molecular phylogeny of *Merostachys* based on seven plastid markers (coding: *ndhF 3'* half and non-coding: *rpl16*, *rps16*, *rps16-trnQ*, *trnC-rpoB*, *trnD-trnT* and *trnT-trnL*). The monophyly of *Merostachys* was confirmed. Two clades within the genus were well supported, as was the placement of *Merostachys* as sister to *Athroostachys*; *Actinocladum*, on the other hand, was supported as sister to the *Merostachys* + *Athroostachys* clade. Most of the morphological groups were not congruent with molecular data, except the one related to floret surface (shiny or dull), which showed an interesting correlation in the molecular topology. One of the recognized clades within the genus has a polytomy formed by several species. This may be associated with (1) the use of low informative markers for the group; (2) long generation time of the taxa; (3) occurrence of hybridization; and/or (4) occurrence of incomplete lineage sorting. These last two possible explanations are usually associated with species of recent radiation. Based on our observations, both in the field and on herbarium specimens, we believe that the most probable event to be influencing the evolution of *Merostachys* is incomplete lineage sorting.

INTRODUÇÃO GERAL

Bambusoideae Luerss é uma das doze subfamílias pertences à família Poaceae Barnhart (Soreng et al. 2017) e atualmente inclui cerca de 1670 espécies distribuídas em 125 gêneros (Clark et al. 2015; Vorontsova et al. 2016; Soreng et al. 2017; Clark & Oliveira 2018). Os bambus são plantas rizomatosas com ausência de crescimento secundário (Soderstrom & Calderón 1980) e caracterizadas pela presença de células invaginantes ("*arm cells*") no mesofilo, as quais são altamente assimétricas (Clark et al. 2015). Além disso, essas gramíneas apresentam lâminas foliares relativamente largas e peseudopecioladas nas quais os feixes vasculares são flanqueados por células fusóides (Soreng et al. 2017). Essas espécies localizam-se entre 50ºN e 47ºS (Clark et al. 2015) e estão relacionadas principalmente a áreas florestais (Soderstrom & Calderón 1980), mas também podem se estabelecer em locais com maior exposição à luz solar e baixa umidade (Soderstrom et al. 1988) como, por exemplo, cerrado *sensu stricto* (Soderstrom 1981; Guala 2003), campos rupestres (Viana & Filgueiras 2008) e campos de altitude (Fernandez et al. 2012).

Estudos filogenéticos apontam o monofiletismo de Bambusoideae, o qual é bem sustentado, tanto por dados moleculares quanto morfológicos. Essas análises indicam a diversificação da subfamília em três tribos: Olyreae, Arundinarieae e Bambuseae (GPWG 2001; Bouchenak-Khelladi et al. 2008; Sungkaew et al. 2009; Kelchner & BPG 2013; Wysocki et al. 2015; Soreng et al. 2017). Olyreae compõe-se de espécies herbáceas ou com colmos ligeiramente lignificados as quais, geralmente, não apresentam folhas do colmo e as folhas dos ramos são desprovidas de lígula externa (Clark et al. 2015). Essas espécies apresentam floração anual ou sazonal e podem ser encontradas principalmente em sub-bosque de florestas tropicais ou, às vezes, em florestas montanas com até 1.500 m de altitude (Clark et al. 2015). Arundinarieae e Bambuseae incluem exclusivamente espécies de bambus lenhosos, os quais são caracterizados por um sistema bem desenvolvido de rizomas, colmos altamente lignificados, folhas do colmo diferenciadas das folhas dos ramos e ramificação bem desenvolvida e complexa, além da presença de lígula externa nas folhas dos ramos (Clark et al. 2015). Arundinarieae engloba os bambus lenhosos de clima temperado, típicos de áreas florestais ou vegetações campestres em altitudes elevadas. Bambuseae, por sua vez, inclui as espécies de bambus lenhosos tropicais, as quais geralmente estão associadas com florestas de terras baixas, no entanto, alguns de seus representantes são registrados para áreas florestais montanhosas ou campos abertos inseridos em uma elevada faixa altitudinal (Clark et al. 2015).

Apesar dos caracteres morfológicos que aproximam Arundinarieae e Bambuseae, estudos filogenéticos a partir de DNA plastidial têm apontado o parafiletismo dos bambus lenhosos, indicando uma relação mais próxima entre Bambuseae e Olyreae (Kelchner & BPG 2013; Wysock et al. 2015). Bambuseae engloba duas grandes linhagens: os bambus lenhosos paleotropicais, representados por oito subtribos e os bambus lenhosos neotropicais, os quais se distribuem nas subtribos Arthrostylidiinae, Guaduinae e Chusqueinae (Soreng et al. 2017). Estudos filogenéticos com os bambus lenhosos neotropicais indicam uma estreita relação entre Arthrostylidiinae e Guaduinae, sendo Chusqueinae bem sustentada como grupo irmão deste clado (Arthrostylidiinae + Guaduinae) (Kelchner & BPG 2013; Clark et al. 2015; Soreng et al. 2017).

Arthrostylidiinae inclui aproximadamente 185 espécies distribuídas em 15 gêneros (Soreng et al. 2017) e estas podem ser reconhecidas por um conjunto de caracteres morfoanatômicos na lâmina das folhas dos ramos, tais como: região discolor ("striae") na face abaxial; fibras intercostais de esclerênquima; papilas refrativas; nervura mediana reduzida e margens com diferenças estruturais acentuadas (Soderstrom & Ellis 1987). A subtribo é bem sustentada como monofilética a partir de análises com DNA plastidial (Tyrrell et al. 2012), porém algumas relações dentro de Arthrostylidiinae ainda continuam incertas. Estudos filogenéticos têm contemplado gêneros como *Atractantha* McClure (Jesus-Costa et al. 2018), *Aulonemia* Goudot e *Colanthelia* McClure & E.W. Smith (Jesus-Costa et al. em preparação). No entanto, relações interespecíficas em outros gêneros ainda necessitam ser investigadas.

Dentre os gêneros inclusos em Arthrostylidiinae, *Merostachys* Spreng. é o que apresenta maior riqueza de espécies (54) até o presente momento (BPG 2012; Santos-Gonçalves et al. 2012; Parma et al. 2016; Vinícius-Silva et al. 2016; Vorontsova et al. 2016; Clark & Oliveira 2018; Ruiz-Sanchez et al. 2018), sendo cinco destas descritas nos últimos três anos (Parma et al. 2016; Vinícius-Silva et al. 2016; Ruiz-Sanchez et al. 2018). As espécies do gênero podem ser encontradas tanto em bordas como no interior de matas (Judziewicz et al. 1999) e se distribuem desde o México até a Argentina, a partir do nível do mar até 2300 m de altitude (Judziewicz & Clark 2007). O Brasil se destaca como centro de diversidade e endemismo do gênero (McClure 1973; Judziewicz et al. 1999), onde são registradas 46 espécies (Judziewicz et al. 1999; Santos-Gonçalves et al. 2012; Parma et al. 2016; Vinícius-Silva et al. 2016; Flora do Brasil 2020). No território brasileiro, a maioria destas (43) ocorre no domínio da Mata Atlântica (Sendulsky 1992; Sendulsky 1995; Sendulsky 1997; Santos-Gonçalves et al. 2012; Parma et al. 2016; Vinícius-Silva et al. 2016); duas espécies são citadas para a Amazônia (Sendulsky 1997) e uma espécie é registrada para o domínio do Cerrado (Sendulsky 1995).

Popularmente conhecidas como taquaras, as espécies de *Merostachys* possuem uma relevante importância cultural para populações tradicionais. Nas referidas comunidades, essas plantas são utilizadas como fonte de matéria-prima para a confecção de cestos, balaios, forros e artesanatos em geral (Bystriakova et al. 2004; CEBRAC 1999; Diver 2001; Guilherme & Ressel 2001; Schwarzbach & Negrelle 2007). Considerando os aspectos ecológicos, as espécies do gênero desempenham um imprescindível papel nas áreas onde se estabelecem, pois semelhante aos demais bambus lenhosos, essas plantas desenvolvem um extenso sistema de rizomas nas camadas superiores do solo. Essa característica confere a elas a capacidade de estabilização dos solos em encostas e margens de rios, protegendo essas áreas de erosões e deslizamentos (Bystriakova et al. 2003).

Ainda sobre os aspectos ecológicos, vale ressaltar que as espécies de *Merostachys*, assim como os demais bambus lenhosos, apresentam um ciclo de vida peculiar no qual o período de crescimento vegetativo é longo (ca. 3–120 anos). Posteriormente, essas plantas atingem sua maturidade fisiológica, florescem de forma gregária, frutificam e então senescem, caracterizando assim um ciclo monocárpico (Janzen 1976; Guerreiro 2014; Clark et al. 2015). A intensa produção de sementes fornece alimento para espécies animais, principalmente roedores e aves, o que permite o crescimento de suas populações (Pereira 1941; Cestari & Bernardi 2011; Kaminski et al. 2016). Após a senescência das touceiras, clareiras são formadas nesses locais e outras espécies têm a oportunidade de ali se desenvolverem, fato que está associado com o processo de sucessão ecológica dessas áreas (Lima et al. 2012; Montti et al. 2014).

Apesar da importância ecológica e cultural que essas plantas apresentam, é importante ressaltar que, pelo fato de possuir um rápido crescimento (McClure 1966), as espécies de *Merostachys* são capazes de dominar grandes áreas no sub-bosque de florestas e diminuir a diversidade de outras espécies em uma escala local (Oliveira-Filho et al. 1994; Santos et al. 2012). Essa monodominância representa um desafio em relação à conservação (Rother et al. 2009; Lima et al. 2012; Grombone-Guaratini et al. 2013; Montti et al. 2014) e tem sido alvo de estudos para subsidiar ações que visem o controle dessas gramíneas em determinas regiões (Cupertino-Eisenlohr et al. 2017).

Sobre os aspectos taxonômicos, *Merostachys* pode ser facilmente reconhecido por um conjunto de caracteres vegetativos e reprodutivos, tais como: rizoma paquimorfo; colmos ocos, raramente medulosos a cheios; gemas únicas nos nós do mediocolmo que, posteriormente, desenvolvem-se formando uma estrutura basal de formato triangular (meristema "fan-shaped"); complemento de ramo com pouco a numerosos ramos, estes com diâmetro e comprimento semelhantes; folha do colmo com lâmina pseudopeciolada, reflexa; sinflorescências terminais, racemosas; espiguetas sésseis ou curto-pediceladas, as quais apresentam duas glumas de tamanhos diferentes e geralmente um único flósculo com uma extensão da ráquila; cariopse nucoide (McClure, 1973; Judziewicz et al. 1999); sinflorescência geralmente com espiguetas rudimentares no ápice e na base; extensão da ráquila com um rudimento apical; glumas e lema múticos, mucronados ou aristados.

Dentre as espécies do gênero, muitas podem ser facilmente identificadas e algumas, inclusive, apresentam caracteres vegetativos mais preponderantes para a taxonomia do que os reprodutivos. No entanto, existem desafios em relação à taxonomia de *Merostachys* e as principais razões são: (1) muitos espécimes são coletados sem material reprodutivo devido ao longo ciclo de crescimento vegetativo (ca. 30–50 anos). Esta situação dificulta a identificação de certas espécies que possuem nestas estruturas seus principais caracteres diagnósticos; (2) amostragem de secções apenas do ápice dos colmos. Mesmo que a espécie possua caracteres vegetativos diagnósticos, o ápice não está completamente desenvolvido como a região mediana e a análise unicamente desta porção do colmo pode culminar em identificações erradas; (3) espécies descritas há tempos (ca. 80-195 anos), com base apenas em fragmentos. Como os materiais tipo são fragmentos, é dificil se obter um conceito preciso da espécie, considerando-se a amplitude da variação morfológica. Estes fragmentos são geralmente amostras da região apical do colmo e mesmo que hajam estruturas reprodutivas, não é possivel uma análise das estruturas vegetativas completamente desenvolvidas, o que é essencial para a identificação de algumas espécies; (4) "*Opus Princeps*" constituídos por uma descrição superficial. Este fato está associado às espécies referidas no item anterior, ou seja, além de descritas com base apenas em fragmentos, elas também apresentam uma descrição original relativamente pobre, fato que dificulta ainda mais acessar a real identidade da espécie e identificar os espécimes; (5) dificuldade de recoletar as espécies descritas com base apenas em fragmentos. A maioria dos espécimes amostrados pelos coletores clássicos não apresentam informações específicas e claras do exato local da coleta. Além disso, esses locais tipo, os quais antes se referiam a áreas de mata, atualmente são beiras de estrada ou, até mesmo, áreas modificadas pelo homem (às vezes centros urbanos); (6) mistura de dados de materiais (a partir de diferentes táxons) na descrição de uma única espécie. Em algumas espécies descritas, inclusive, há relativamente pouco tempo, observa-se que alguns dos parátipos não pertencem ao mesmo táxon que o holótipo e os isótipos. Esses materais necessitam, então, de uma reavaliação para que essas espécies possam ser adequadamente redescritas; e (7) escassez de literatura especializada provida de chaves dicotômicas que possam contribuir para a identificação dos espécimes. Os poucos estudos que apresentam chaves de identificação foram desenvolvidos em regiões específicas, não contemplando todas as espécies do gênero. Além disso, em alguns desses estudos as chaves são confusas e apresentam caracteres que se sobrepõem em relação a certas espécies.

Diante dos desafios expostos acima, é necessária uma continuidade nos trabalhos de campo com o intuito de intensificar esforços na tentativa de recoletar, principalmente, espécies que apresentam questões taxônomicas a serem investigadas. Uma amostragem mais completa dos espécimes e, se possível, com material reprodutivo, possibilitaria uma análise morfológica detalhada e, consequentemente, auxiliaria a responder a esses questionamentos.

Juntamente com os dados morfológicos, a biologia molecular tem sido utilizada na tentativa de melhor compreender as relações entre as espécies dentro de gêneros em Arthrostylidiinae (Tyrrell et al. 2012; Jesus-Costa et al. 2018). Os estudos de Tyrrell et al. (2012) e Jesus-Costa et al. (2018) sugerem o monofiletismo de *Merostachys*, porém a partir de uma pequena amostragem. Tyrrell et al. (2012) realizou um estudo filogenético com a subtribo Arthrostylidiinae (porém sem a amostragem dos gêneros *Athroostachys* Benth. e *Myriocladus* Swallen), o qual indicou *Merostachys* como grupo irmão de *Actinocladum* Soderstr. Estes dois gêneros são, de fato, morfologicamente semelhantes e compartilham caracteres como, por exemplo, a presença de folhas do colmo com lâminas reflexas, complemento de ramo com inserção apsidada e cariopse nucoide (Judziewicz et al. 1999). Jesus-Costa et al. (2018) ao promover um estudo focado no gênero *Atractantha* e amostrar, pela primeira vez, o gênero *Athroostachys* em uma abordagem filogenética molecular, observaram uma relação mais próxima entre este gênero e *Merostachys*. *Actinocladum*, por sua vez, foi sustentado como grupo irmão do clado *Athroostachys* + *Merostachys*. Estes dois gêneros não são muito semelhantes morfologicamente como são *Merostachys* e *Actinocladum* e McClure (1973) menciona que as características das fímbrias e das estruturas reprodutivas são as que mais os aproximam. Há que se destacar, também, as folhas do colmo com lâminas reflexas, compartilhadas por ambos (Judziewicz et al. 1999).

Nosso grupo de pesquisa já vêm estudando o gênero *Merostachys* há alguns anos e durante esse tempo, expedições a campo e análise de espécimes (incluindo materiais tipo) depositados em herbários nos permitiram reconhecer, informalmente, grupos morfológicos com base tanto em caracteres vegetativos quanto reprodutivos. Como o gênero não possui uma classificação infragenérica, estudos de filogenia molecular a partir de uma amostragem mais ampla são extremamente importantes. Esses estudos nos permitiriam verificar, por exemplo, se os agrupamentos morfológicos, por nós detectados, possuem um suporte filogenético e nos proporcionariam avançar, mesmo que gradualmente, na tentativa de estabelecer subgêneros em *Merostachys*.

Diante do exposto, o desenvolvimento desta pesquisa teve como meta principal expandir o conhecimento sobre o gênero *Merostachys* e a partir de então, objetivou-se: (1) estudar detalhadamente o gênero em seus aspectos morfológicos, de modo a permitir-nos reconhecer suas espécies, identicar e propor soluções para problemas taxonômicos, além de descrever novos táxons; (2) realizar um estudo de filogenia molecular a partir de uma amostragem mais ampla que nos forneça condições de testar o monofiletismo do gênero; (3) verificar as relações entre suas espécies e a relação entre *Merostachys* e os demais gêneros de Arthrostylidiinae; e (4) averiguar se os grupos morfológicos, por nós reconhecidos, são congruentes com os dados moleculares.

A tese aqui apresentada encontra-se organizada em quatro capítulos, os quais foram redigidos como manuscritos científicos e são listados abaixo:

Capítulo I – Accessing the real identity of *Merostachys speciosa* (Poaceae: Bambusoideae: Bambuseae), type species of the genus, through redescription and relectotypification. Formatado de acordo com as diretrizes do periódico *Kew Bulletin*.

Capítulo II – Clarification of the circumscription of three *Merostachys* species (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae) and description of a new species from the Brazilian Atlantic Forest. Formatado de acordo com as diretrizes do periódico *Phytotaxa*.

Capítulo III – Two new species of *Merostachys* (Poaceae: Bambusoideae: Bambuseae) from the Brazilian Atlantic Forest and the complete description of *M. bifurcata*. Formatado de acordo com as diretrizes do periódico *Brittonia*.

Capítulo IV – Molecular phylogenetics of *Merostachys* (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae) based on multi-locus plastid sequences. Formatado e submetido de acordo com as diretrizes do periódico *Botanical Journal of the Linnean Society*.

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Accessing the real identity of *Merostachys speciosa* (Poaceae: Bambusoideae: Bambuseae), type species of the genus, through redescription and relectotypification

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Manuscrito de acordo com as normas do periódico *Kew Bulletin*.

Summary. *Merostachys* Spreng. is a Neotropical woody bamboo genus that encompasses 54 described species. In this study we provide a redescription and the relectotypification of *Merostachys speciosa* Spreng., type species of the genus. We also give taxonomic comments, information about geographic distribution and conservation status. Additionally, we provide a table to compare *M. speciosa* morphologically with three similar species (*M. brevigluma*, *M. kunthii* and *M. neesii*).

Keywords. Arthrostylidiinae, bamboo, grasses, morphology, taxonomy.

Introduction

Merostachys Spreng. belongs to the subtribe Arthrostylidiinae of the Bambuseae (tropical woody bamboos) and currently encompasses 54 described species (Judziewicz *et al.* 1999; Bamboo Phylogeny Group [BPG] 2012; Santos-Gonçalves *et al.* 2012; Parma *et al.* 2016; Vinícius-Silva *et al.* 2016; Vorontsova *et al.* 2016; Clark & Oliveira 2018; Ruiz-Sanchez *et al.* 2018), which have a collective distribution from Mexico to Argentina (Judziewicz & Clark 2007). These species grow in the understory or along the borders of forests, mainly in the Brazilian Atlantic Forest domain, which is the center of diversity of the genus (Judziewicz *et al.* 1999).

Species of *Merostachys*, as in other woody bamboo genera, have reproductive cycles with a prolonged period of vegetative growth. Some studies indicate the period between two flowering events in *Merostachys* species is 30-50 years (Janzen 1976; Guilherme & Ressel 2001; Liebsh & Reginato 2009; Guerreiro 2014). After a flowering event, the individuals senesce leading to the opening of gaps in the forest, which can affect the floristic composition of the area (Filgueiras 1988; Montti et al. 2011; Montti et al. 2014; Lima et al. 2012).

Merostachys speciosa Spreng., the type species of the genus, has morphological similarities with *M. brevigluma* Send., *M. kunthii* Rupr. and *M. neesii* Rupr. (Sendulsky 2001). With the exception of *M. brevigluma*, which was described in 2001, the other three species were described long ago (Sprengel 1825; Ruprecht 1839). This historic context of the description of these four species is important to provide an understanding of the close relationships among them and especially of the consequent misidentification of their specimens.

Merostachys speciosa was described in 1825 and is distinguished from the other species mainly by the characteristics of its fimbriae, which are whitish to yellow-white and basally fused. Despite this difference, specimens of two other species, *M. neesii* and *M. kunthii*, were identified as *M. speciosa* by Nees (1829) and Kunth (1830), respectively, before these taxa were described as distinct species by Ruprecht (1839). The similarities among these species are observed in their synflorescences, mainly in size and indument of the spikelets and position of the upper glume. Sendulsky (2001) described the new species *M. brevigluma* and due to the reproductive characteristics mentioned above, grouped these four species (*M. brevigluma*, *M. kunthii*, *M. neesii* and *M. speciosa*) under the informal name "Group Speciosa". Nevertheless, despite their similarities, these species can be readily separated based on a combination of vegetative and reproductive characters.

The name *Merostachys speciosa* was lectotypified by Sendulsky (2001). The material selected by her as the lectotype is stored, currently, in the LE herbarium (V.L. Komarov Botanical Institute, Saint Petersburg, Russia) but previously was part of the Trinius herbarium, which had all of its specimens incorporated into LE. The choice of this material by Sendulsky (2001) was based on two photos stored in the US herbarium (National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A) of two sheets of *Sellow s.n.* among those deposited at LE. However, these two photos from US are apparently not from the same specimen; furthermore, Sendulsky (2001) did not explicitly indicate which one is the lectotype. Therefore, the most feasible solution for this issue is the relectotypification of this name.

As *Merostachys speciosa* is the type species, detailed information about its morphology is very important to understanding the genus and its diversity. Beyond the work of Sendulsky (2001), Schmidt & Longhi-Wagner (2009) and Greco (2013) each provided a description of this species. However, with our intensive work in various herbaria studying the morphology of this genus, it was possible analyze more specimens from different localities and include more characters, which contribute to a more robust description of the type species of *Merostachys*. In this study we present a redescription of *M. speciosa* as well as an illustration of its main characters and comments about its taxonomy, conservation status, habitat and geographical distribution. Based on an analysis of all the type material, with an unambiguous selection of the most appropriate specimen, we also propose here a relectotypification of the name *M. speciosa*. Additionally, we provide a morphological comparison (Table 1) of *M. speciosa* and the three most similar species: *M. brevigluma*, *M. neesii* and *M. kunthii*.

Material and Methods

Morphological studies were based on the analysis of the type material and of specimens from the following herbaria: CRI, E, ESA, FLOR, FUEL, FURB, G, HAS, HUEFS, ICN, ISC, K, LE, MACK, MO, NY, P, PACA, RB, SP, UPCB, US and VIC (acronyms following Thiers 2018). Two materials cited in the taxonomic treatment have their herbarium acronyms designated as LE-TRIN because they had initially been deposited in the Trinius herbarium, and only later incorporated into the LE herbarium. Thus, LE-TRIN refers to materials from the LE herbarium which had the Trinius herbarium as their original source.

Morphological terminology follows McClure (1966) and Judziewicz *et al.* (1999). Measurements of the structures were taken using a ruler and caliper to obtain their minimum and maximum dimensions. The width of sheaths and blades of culm and foliage leaves was taken at their widest points. The length of the foliage leaf blades was taken excluding the pseudopetiole, which was measured separately. The map of geographical distribution was created in Arcgis 10.0 (Environmental Systems Research Institute [ESRI] 2015).

Taxonomic Treatment

Merostachys speciosa *Spreng.* (Sprengel 1825: 249). Type: Brazil, no location, no date [fl.] *Sellow s.n.* (Lectotype LE-TRIN-3189.2 Image! Isolectotypes E00745694 Image! E00745695 Image! G00099738 Image! G00099739 Image! K001212499! K001212502! K000307814! LE Image! LE-TRIN-3189.1 Image! US00134267 fragment!) (Fig. 1).

Plants with culms initially erect then clambering on vegetation. *Culms* ca. 15 m tall. *Mid-culm internodes* 35–40 cm long, 1.5–2.5 cm in diam., cylindrical, green-white, glabrous, sometimes with strigose trichomes, infranodal band of trichomes absent; walls 1–2 mm thick, ratio of wall thickness: culm diam. 0.14–0.23, very thin to thin, lumen 1.3–2.1 cm in diam., large, not filled by a pith; nodes not prominent, brown, without a fringe of trichomes at the nodal line. *Culm leaves* 30–45 cm long; sheaths 20–40 × 5–10 cm, adaxially glabrous, shiny, abaxially glabrous, sometimes with a layer of wax; margins apically fimbriate, the overlapping margin ciliate from the base toward the apex; auricles absent; fimbriae 5–35 mm long, basally fused, erect at the base and sinuous toward the apex, sometimes completely sinuous, white to yellow-white; inner ligules 1 mm long, truncate, pubescent, the apex ciliate; blades 10–15 × 0.5–2 cm, margins scabrous, adaxially glabrous, abaxially glabrous, sometimes with some strigose trichomes. *Branch complement* with 20–45 branches, the branches 20–70 cm long, 2–3.5 mm in diam., lower nodes rebranching; nodes prominent mainly in the mature branches, brown. *Foliage leaves* 5–13 per complement; sheaths 3–10 cm × 3–6 mm, glabrous, overlapping margin ciliate; auricles absent; fimbriae 8–25 mm long, basally fused, erect at the base and sinuous toward the apex, sometimes completely sinuous, white to yellow-white; outer ligules 0.3–0.5 mm long, the apex ciliate; inner ligules 0.8–1 mm long, truncate, pubescent, the apex ciliate; pseudopetioles 5–10 mm long, brown, glabrous, twisted; blades 9.5–30 × 2–4 cm, L:W = 4.5–9.2, lanceolate, adaxially with 1–3 scabrous marginal ribs along one margin, glabrous elsewhere, abaxially covered with minute strigose antrorse trichomes, the base asymmetric, the apex acuminate, margins scabrous. *Synflorescences* 7.5–17 cm long, racemose, 15–40 spikelets per raceme, rudimentary spikelets at the apex present, two rows of spikelets in one rank, rows pectinate and being less than 5 degrees apart; rachis tomentose; pedicels ca. 1 mm long, tomentose. *Spikelets* 20–25 × 2–2.5 mm, 1-flowered, solitary; glumes 2, unequal; lower glume 6–12 × 1–2 mm, ca. $^{1}/_{2}$ of the spikelet length, including the awn, awn 1–3 mm, 1–6-nerved, adaxially glabrous and sometimes dark-spotted, abaxially sericeous with white to wine-colored trichomes, margins ciliate; upper glume 11–17 × 3–6 mm, ca. $^{4}/_{5}$ of the spikelet length, including the awn, awn 2–3 mm long, 12–16-nerved, at an acute angle to the rachis, adaxially glabrous and dark-spotted, abaxially sericeous with wine-colored trichomes, margins ciliate; lemma 13–16 × 5–7 mm, mucronate, 14–20-nerved, adaxially glabrous and dark-spotted, abaxially sericeous, most of the time hispid at the apex, wine-colored trichomes dull; palea 12–16 × 4–5 mm, muticous, 8–10-nerved, abaxially glabrous, adaxially pubescent at the apex, glabrous elsewhere, 2-keeled, keels ciliate, dull; rachilla extension 10–15 mm long, with a rudiment at the apex; lodicules 3, membranous, anterior pair 2–2.3 × 1–1.3 mm, posterior 1.3–1.5 × 0.5–0.7 mm; stamens 3, anthers 5–5.5 mm, ochre; ovary elongated, style bifid, stigmas 2. *Caryopsis* not seen.

DISTRIBUTION. This species is distributed in four states in Brazil: Paraná, Rio Grande do Sul, Santa Catarina (South region) and São Paulo (Southeastern) (Map. 1). It is important to clarify that, as noted by Vinícius-Silva *et al.* (2016), two collections from Minas Gerais state (*Mosén* 4472 and *Chase 9466*) previously identified as *M. speciosa*, refer, respectively, to *M. claussenii* var. *claussenii* Munro and *M. ximenae* D.F. Parma, Viníc.-Silva & Santos-Gonç. and therefore, *M. speciosa* is not recorded for Minas Gerais state.

SPECIMENS EXAMINED. Brazil. No location, no date, *pro parte*, mounted together with *M. claussenii* var. *claussenii* and probably *M. neesii* [fl.], *Sellow s.n.* (K); No location, no date, *pro parte*, mounted together with *M. neesii* or *M. kunthii* [fl.], *Sellow s.n.* (LE); No location, no date [fl.], *Sellow 1286* (RB, US); No location, no date [fl.], *Sellow 1840* (K); Paraná, Jacarehy [Jaguariaíva], in Silva Primaeva, 23 Nov. 1915 [fl.], *Dusén 17348* (K, MO, NY, P, US); Rio Grande do Sul, Dom Pedro de Alcântara, Mata da Cova Funda, 03 Jan. 2001 [veg.], *Jurinitz 24* (ICN); idem, mato do Prof. L. Baptista, 20 Dec. 2005 [veg.], *Longhi-Wagner & Schmidt 9881* (HUEFS, ICN); Mampituba, 18 April 2008 [veg.], *Longhi-Wagner & Schmidt 10310* (ICN, K); Morrinhos do Sul, Estrada da Perdida, 16 April 2007 [veg.], *Longhi-Wagner & Schmidt 10313* (ICN, ISC, K); idem, Perdida, 08 Oct. 2011 [fl.], *Verdi & Durigon 6050* (FURB); Osório, Terra da Areia, 20 Oct. 1979 [fl.], *Waechter 1427* (HAS, ICN); Sapiranga, Alto Ferrabraz, 02 April 2007 [veg.], *Schmidt & Molz s.n.* (HUEFS, ICN, RB); idem, Alto Ferrabraz, 12 Aug. 2017 [veg.], *Schmidt & Bordignon s.n.* (VIC); Torres, Colônia São Pedro, May 1971 [veg.], *Lorscheitter & Baptista s.n.* (ICN); Três Cachoeiras, Lajeadinho 20 Oct. 1979 [fl.], *Zanette 374* (ICN); idem, 18 April 1996 [veg.], *Longhi-Wagner & Schmidt 10314* (ICN, K); Santa Catarina, Brusque, 02 Nov. 1948 [fl.], *Reitz 3717* (NY, P, PACA); idem, Mata do Hoffman, 10 Nov. 1949 [fl.], *Reitz 3200* (K, NY, PACA, UPCB, US); idem, Oct. 1959 [fl.], *Eq. Ecologia s.n.* (US); idem, Spitzkopf, 02 Nov. 1948 [fl.], *Reitz 2268* (US); Florianópolis, Morro do Ribeirão, Ilha de Santa Catarina, 20 June 1967 [veg.], *Klein 7456* (FLOR, US); idem, Morro do Ribeirão, Ilha de Santa Catarina, 20 June 1967 [veg.], *Klein 7448* (FLOR, US); idem, Morro do Saquinho, Pântano do Sul, Ilha de Santa Catarina, 26 July 1967 [veg.], *Klein & Bresolin 7498* (US); Itajaí, Morro do Baú, 29 Jan. 1948 [fl.], *Reitz s.n.* (US); Ilhota, Parque do Morro do Baú, 03 May 1979 [fl.], *Reitz 7911* (CRI); Urussanga, Linha de Transmissão Elétrica Tubarão/Urussanga, 26 Oct. 2011 [fl.], *Felitto & Petean 178* (FURB); São Paulo, Cananéia, Ilha do Cardoso, Restinga, 07 Oct. 1980 [fl.], *Forero et al. 8601A* (SP); Peruíbe, Estação Ecológica de Juréia, 07 Nov. 1985 [fl.], *Tyeno s.n.* (ESA, FLOR, FUEL, HUEFS, MACK, VIC); idem, Praia do Guaraú, trilha fechada, 10 Dec. 2011 [fl.], *Padgurschi 1853* (UEC, VIC); São Paulo, Parque Estadual Fontes do Ipiranga, IBT, 16 March 2010 [veg.], *Shirasuna 2796* (SP); idem, 16 March 2010 [veg.], *Shirasuna 2798* (SP); Santos, Morro Santa Terezinha, 15 Nov. 1913 [fl.], *Kuhlmann 1066* (SP, US).

HABITAT. *Merostachys speciosa* is found in the understory and along the borders of the Brazilian Atlantic Forest in vegetation known as Ombrophilous Forest, according to the classification of Veloso *et al.* (1991).

CONSERVATION STATUS. According to IUCN 2017.3 criteria, the taxon is considered as Least Concern (LC), because it has a large distribution in the Brazilian territory (=26 places) and some populations are in Conservation Units.

NOTES. *Merostachys speciosa* is distinguished from other species of the genus by the following set of characters: fimbriae on both culm and foliage leaves white to yellow-white, basally fused, erect at the base to sinuous toward the apex; foliage leaf blades abaxially covered by minute strigose trichomes; the upper glume at an acute angle to the rachis of the synflorescence; and lemma sericeous with wine-colored trichomes. Another species with fused fimbriae is *M. fimbriolaminata* Viníc.-Silva, Cupert.-Eisenl. & Santos-Gonç., however, its fimbriae are fused nearly to the apex and not just at the base (Vinícius-Silva *et al.* 2016). Besides that, *M. fimbriolaminata* has culms with prominent nodes, which are brown and ring-like while in *M. speciosa* this characteristic is not observed. As discussed above, *M. speciosa* was included in the "Group Speciosa" by Sendulsky (2001) together with *M. brevigluma*, *M. neesii* and *M. kunthii*. These species do exhibit some similarities, such as: branches with prominent nodes; spikelet size and proportions, and characteristics of its bracts (lower and upper glumes, lemma and palea) including indument; and the position of the upper glume at an acute angle to the synflorescence rachis. Despite these similarities, these species are easily distinguished from each other, mainly by vegetative characters. The characters used to distinguish these species include: presence/absence of fimbriae on both culm and foliage leaves; amount of fimbriae on both culm and foliage leaves; degree of fusion of the fimbriae on both culm and foliage leaves; color of the branch nodes and abaxial indument of the foliage leaf blades (Table 1).

In the process of relectotypification, we considered all specimens from *Sellow s.n.* from Brazil with no date and with no location. The *Sellow s.n.* collections do not encompass a complete sampling of all plant structures, but we selected the LE-TRIN-3189.2 specimen as the most appropriate lectotype. This specimen was mentioned by Sendulsky (2001) as the probable lectotype and, in our view, provides the best set of characters to recognize species, because it consists of a branch complement with several floriferous branches and evident fimbriae.

Two other materials from LE are cited here, yet they had not been previously deposited in Trinius herbarium and lack accession numbers. One of the materials is composed of a single floriferous branch and it is herein designated as an isolectotype. The other is composed of two floriferous branches on the right side of the sheet along with two other branches affixed on the left side of the sheet, being probably referable to *M. neesii* or *M. kunthii* given that its foliage leaves lack fimbriae. Since the sheet is composed of two different species with the same label (*Sellow s.n.*), we did not consider the *M. speciosa* specimen to be an isolectotype, as we presumed that the material may refer to a mixed collection that had probably been gathered by Sellow on a different occasion.

Lastly, a similar situation to that observed at the LE herbarium was detected in two other materials deposited at the K herbarium (Royal Botanical Garden Kew, U.K.), with different species having been found to be mixed on a single sheet. The material K000307812 consists of two branches of *M. speciosa* on the left side of the sheet and on the right side, of two other branches with accession number K000307813 (one of these branches is probably referable to *M. claussenii* var. *claussenii* Munro, and the other probably to *M. neesii*). Despite having two accession numbers and branches of three different species, this exsiccate has only one *Sellow s.n.* label. These materials are also probably from another mixed collection by Sellow, and therefore we did not consider the *M. speciosa* specimen (K000307812) to be an isolectotype either. The second specimen, K000307814, is composed of one branch of *M. speciosa* on the left side, labeled *Sellow s.n.* Two other branches are documented on the same sheet under accession number K000307815; these branches are labeled *P. Claussen 1840*, both of them probably being referable to *M. claussenii* var. *claussenii*. Despite being affixed on the same sheet, these two species are from different collections, which has thus enabled us to consider the *M. speciosa* specimen (K000307814) as an isolectotype.

Acknowledgments

We acknowledge support from the following funding agencies: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) in the International Doctoral Program in Sandwich (PDSE, nº 88881.135178/2016-01 to R. Vinícius-Silva); Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG, grant APQ-03255-16 to A.P. Santos-Gonçalves); Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grants 563545/2010-0 REFLORA to A.P. Santos-Gonçalves and 401526/2014-3-PVE to R.P. Oliveira); Bamboos of the Americas (BOTA) and the Ned Jaquith Foundation (grants to R. Vinícius-Silva to support fieldwork). We thank Rodney Schmidt for help with the fieldwork; Vladimir Dorofeyev for making the *M. speciosa* photos from LE available to us and Robert Soreng for support during a visit to the US Herbarium, Washington D.C., U.S.A. We also thank Reinaldo Pinto for the illustrations and Michael Bonilla for the preparation of the geographic distribution map.

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Table 1 – Morphological comparison of *M. speciosa*, *M. brevigluma*, *M. neesii* and *M. kunthii*

Characters	***M. speciosa***	***M. brevigluma***	***M. neesii***	***M. kunthii***
Fimbriae on both culm and foliage leaves	Present	Present	Absent	Absent
Amount of fimbriae on both culm and foliage leaves	Abundant (More than 10)	Scant (1-10)	Not applicable	Not applicable
Degree of fusion of the fimbriae	Basally fused	Free	Not applicable	Not applicable
Abaxial indument of the foliage leaf blades	Completely covered by minute strigose trichomes	Glabrous	Band of minute strigose trichomes between green stripe and rest of the surface	Band of minute strigose trichomes between green stripe and rest of the surface
Color of the branch nodes	Brown	Brown	Black	Brown
Geographical distribution	Paraná, Rio Grande do Sul, Santa Catarina and São Paulo states	Minas Gerais and São Paulo states	Paraná, Santa Catariana and São Paulo states	Bahia and Rio de Janeiro states

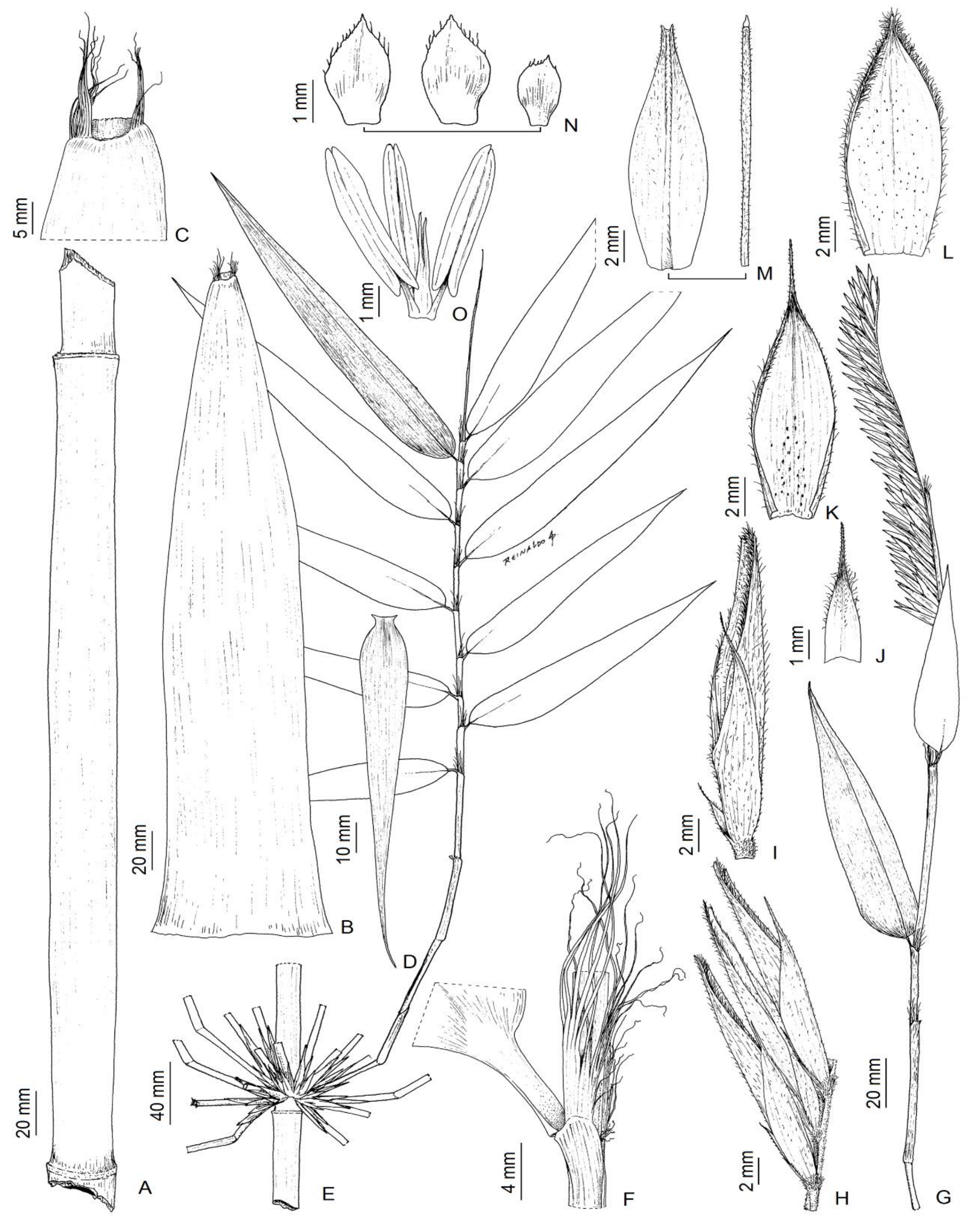
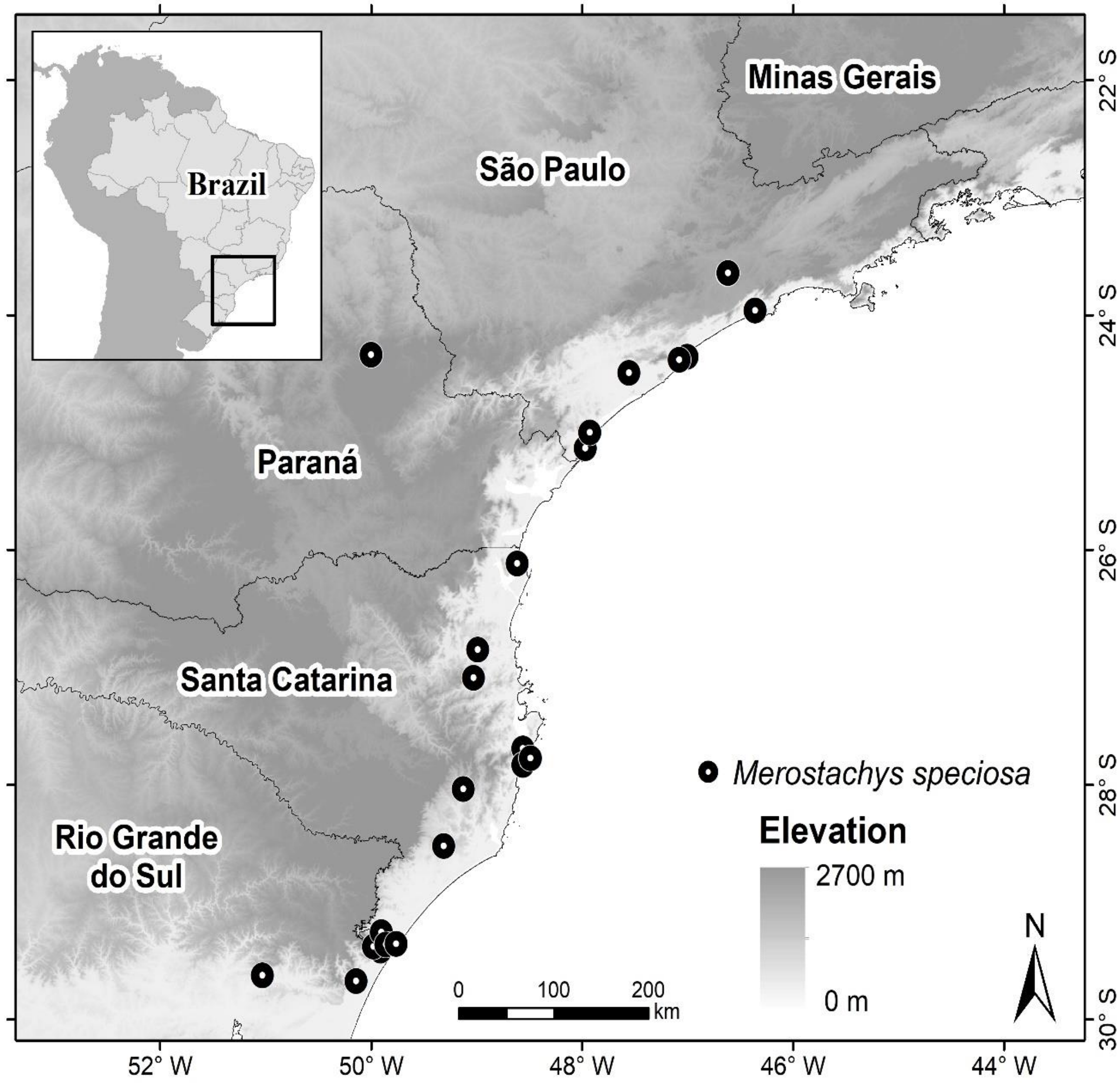


Figure 1. *Merostachys speciosa*. **A.** Internode. **B.** Culm leaf sheath. **C.** Ligular region of the culm leaf sheath with fimbriae. **D.** Culm leaf blade. **E.** Branch complement with vegetative branches. **F.** Ligular region of the foliage leaf sheath with fimbriae. **G.** Floriferous branch. **H.** Section of synflorescence. **I.** Spikelet. **J.** Lower glume (adaxial view). **K.** Upper glume (adaxial view). **L.** Lemma (adaxial view). **M.** Palea (l, abaxial view) with rachilla extension (r). **N.** Lodicules. **O.** Gynoecium and androecium. A based on *Waechter 1427*, ICN; B-C based on *H. Longhi-Wagner & R. Schmidt 10310*, ICN; D based on *H. Longhi-Wagner & R. Schmidt 10313*, ICN; E-F based on *R. Schmidt & M. Molz s.n.*, ICN; G based on *Sellow s.n.*, K001212502; H-O based on *G. Felitto & M. Petean 178*, FURB. (Illustration by Reinaldo Pinto).



Map 1. Geographic distribution of *Merostachys speciosa* in the Brazilian Atlantic Forest.

CAPITULO II

Clarification of the circumscription of three *Merostachys* species (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae) and description of a new species from the Brazilian Atlantic Forest

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Manuscrito de acordo com as normas do periódico *Phytotaxa*.

Abstract

Merostachys encompasses, at the moment, 54 described species, which collectively have a Neotropical distribution from Argentina to Mexico, with a center of diversity in Brazil. After detailed morphological analyses in several herbaria as well as fieldwork, it became clear that among the Brazilian species, *M. medullosa* and *M. procerrima* have taxonomic problems in their circumscriptions due to the mixed material in the collections cited in their protologues. One paratype of *Merostachys medullosa* refers to another taxon, which is recognized here as a new species (*M. soderstromii*). In addition, two paratypes of *Merostachys procerrima* are referable to *M. magnispicula*. Here, we corrected these errors, redescribed *M. medullosa*, *M. procerrima* and *M. magnispicula* and described *M. soderstromii*. Reproductive structures are described for the first time for *M. procerrima*, and the name is epitypified based on one of the flowering collections. Additionally, we provide illustrations and comments on the taxonomy, phenology, geographic distribution, habitat and conservation status of these four species. Comparative tables for *M. medullosa* vs. *M. soderstromii* and *M. magnispicula* vs. *M. procerrima* are included.

Keywords: Bahia, Espírito Santo, grasses, morphology, Neotropical woody bamboos

Introduction

Merostachys Sprengel (1825: 249) is a Neotropical woody bamboo genus characterized by the following combination of characters: pachymorph rhizomes; hollow culms (rarely pithy) with one bud per node, which develops into a flattened triangular structure bearing subequal branches in a fan-shaped (apsidate) array; culm leaves with the blades pseudopetiolate and reflexed; terminal racemose synflorescences bearing sessile or short-pedicellate spikelets; spikelets which present two glumes of different lengths and usually a single floret with a rachilla extension; nucoid caryopses (McClure 1973, Judziewicz *et al.* 1999); synflorescences usually with rudimentary spikelets at the apex and also at the base; glumes and lemma muticous, mucronate or awned; and rachilla extension with an apical rudiment.

Currently, the genus encompasses 54 described species (Judziewicz *et al.* 1999, Bamboo Phylogeny Group [BPG] 2012, Santos-Gonçalves *et al.* 2012, Parma *et al.* 2016, Vinícius-Silva *et al.* 2016, Vorontsova *et al.* 2016, Clark & Oliveira 2018, Ruiz-Sanchez *et al.* 2018), and is distributed from Mexico to Argentina (Judziewicz & Clark 2007). The center of diversity of *Merostachys* is the Brazilian Atlantic Forest, where 43 of these species are found (Sendulsky 1992, Sendulsky 1995, Sendulsky1997, Burman & Filgueiras 1993, Filgueiras & Santos-Gonçalves 2004, Santos-Gonçalves *et al.* 2012, Parma *et al.* 2016, Vinícius-Silva *et al.* 2016).

One of these species known to the Brazilian Atlantic Forest is *Merostachys medullosa* Sendulsky (1997: 298). This species is recorded from Bahia state and characterized mainly by the presence of internodes filled by a pith (Sendulsky 1997). Despite being easily recognized by this characteristic, we determined after detailed morphological studies of available herbarium material that the specimens used to describe this species actually consist of two distinct species.

The type collection and most of the paratypes are perfectly consistent with the description and illustration in the protologue. However, the paratype from Prado municipality, Bahia state (*Soderstrom, Russell & Hage 2149*) is another taxon, recognized here as a new species. Despite sharing the presence of a pith in the internodes, several characters support the separation of these taxa into two distinct species (Table 1).

A similar situation is observed with respect to *M. procerrima* Sendulsky (1997: 300) and *M. magnispicula* Sendulsky (1997: 296). *Merostachys procerrima* was described based on five collections, while *M. magnispicula* was described based on only one collection. After fieldwork in Bahia state and detailed morphological analyses of available herbarium material, we verified that two specimens assigned as paratypes of *M. procerrima* were wrongly identified as part of this species, but really represent *M. magnispicula*. Although these two species are very similar in several aspects, characters related to foliage leaf fimbriae and indument of the foliage leaves sheaths are useful in distinguishing them (Table 2). We also discovered specimens of *M. procerrima* with reproductive structures, which had not previously been documented for this species.

With the goal of clarifying all these taxonomic issues in these three *Merostachys* species, we provide the redescription of *M. medullosa*, *M. procerrima* and *M. magnispicula*, and describe *Merostachys soderstromii* as a new species. We also provide a description of the reproductive structures of *M. procerrima* which was known previously only by vegetative characters, and we propose an epitype for this name based on one of the flowering collections. Additionally, we illustrate and map each of the four species, and include comments about their taxonomy, phenology, geographic distribution, habitat and conservation status. Comparative tables for *M. medullosa* vs. *M. soderstromii* and *M. magnispicula* vs. *M. procerrima* are also included.

Material and Methods

The type collections and other specimens of *M. medullosa*, *M. procerrima* and *M. magnispicula* and the new species here described (*M. soderstromii*) were studied in the following herbaria: CEPEC, G, HUEFS, INPA, ISC, K, MO, NY, SP, US and VIC. The herbarium acronyms follow Thiers (2018).

Fieldwork to collect additional material of *M. medullosa*, *M. procerrima* and *M. magnispicula* was carried out in both Pau Brasil National Park and Monte Pascoal National Park, Porto Seguro municipality, Bahia state. *Merostachys soderstromii* was studied in the field and collected in Reserva Natural da Vale, Linhares municipality, Espírito Santo state.

Morphological terminology follows McClure (1966) and Judziewicz *et al.* (1999). Measurements of the structures were taken by ruler, graph paper and caliper to obtain their minimum and maximum dimensions. The width of sheaths and blades of culm and foliage leaves was taken at their widest points. The length of the foliage leaf blades was taken excluding the pseudopetiole, which was measured separately.

In addition to the descriptions, short commentaries about the conservation status of each taxon according to the standards of the International Union for Conservation of Nature (IUCN) are provided (IUCN 2017). The maps of geographic distribution were created using QGIS 3.4.1 (QGIS 2018).

Taxonomic Treatment

Merostachys soderstromii Viníc-Silva, L.G. Clark & Santos-Gonç., *sp. nov.* (Fig. 1)

This species is distinguished from all the other species of the genus by exhibiting culms 8–10 m tall, internodes scabrous, filled by a pith and with an infranodal band of velutinous trichomes in the culm; midculm internodes 1–2.5 cm in diam.; branch complement consisting of 10–66 branches, the branches 27–58 cm long, 1–2 mm in diam.; and synflorescences 4.5–6 cm long, with 19–23 spikelets per raceme.

Type:—BRAZIL. Espírito Santo: Linhares, Reserva Natural da Vale, Estrada Parajú, Aceiro Joacy, final da estrada, 22 October 1985 (fl.), *G.L. Farias 84* (holotype VIC, isotype CVRD).

Plants initially erect then arching toward the apex. Culms 8–10 m tall. Midculm internodes 30–70 cm long, 1–2.5 cm in diam., cylindrical, yellow with green spots, scabrous, infranodal band of velutinous trichomes present, bands 2–4 mm wide; walls 1–3.5 mm thick, ratio of wall thickness: culm diam. 0.3–0.6, moderately thick to thick, lumen 0.4–1.5 cm in diam., narrow to wide, filled by a pith; nodes not prominent, brown, without a fringe of trichomes at the nodal line. Culm leaf sheaths 11.5–50 × 2–7 cm, adaxially glabrous and shiny, abaxially minutely scabrous, sometimes hispid, sericeous or pubescent, overlapping margin ciliate, fimbriate apically and along approximately the upper $^1/_3$ of the overlapping margin; auricles absent; fimbriae 3–24 mm long, not fused, straight and erect at the base and sinuous toward the apex, sometimes completely sinuous, white to brown, sometimes red-white; inner ligules 0.3–1 mm long, truncate, pubescent, the apex ciliate; blades 3.5–11 × 0.2–0.7 cm, margins scabrous, adaxially and abaxially scabrous to hispid, sometimes glabrous. Branch complement consisting of 10–66 branches, the branches 27–58 cm long, 1–2 mm in diam., lower nodes not rebranching; nodes not prominent, black. Foliage leaves 5–14 per complement; sheaths 2–6.5 cm × 2–5 mm, glabrous, sometimes hirsute at the apex, overlapping margin ciliate, fimbriate apically; auricles absent; fimbriae 8–24 mm long, not fused, straight and erect at the base and sinuous toward the apex, sometimes completely sinuous, yellow-white to red-white; outer ligules 0.1–0.5 mm long, the apex ciliate; inner ligules 0.1–0.8 mm long, truncate, pubescent, the apex ciliate; pseudopetioles 1.5–5 mm long, brown to black, pubescent to hispid, twisted; blades 9.3–21.5 × 1.3–3 cm, L:W = 4.5–11.8, lanceolate, adaxially with 3–5 scabrous ribs along one margin, the opposite margin and apex with minute strigose trichomes, glabrous elsewhere, abaxially sparsely hirsute and sparsely scabrous with minute antrorse strigose trichomes concentrated in a band between the marginal stripe and the rest of the blade toward the apex, the base asymmetric, the apex acuminate, margins scabrous. Synflorescences 4.5–6 cm long, racemose, with 19–23 spikelets per raceme, rudimentary spikelets at the base and at the apex present, two rows of spikelets in one rank, rows pectinate and being less than 10 degrees apart; rachis tomentose; pedicels 1.5–2 mm long, tomentose. Spikelets 14.5–15 × 2.5–3 mm, 1-flowered, solitary; glumes 2, unequal; lower glume 2.5–3.5 × 1 mm, ca. $^1/_4$ of the spikelet length, muticous, 1-nerved, adaxially glabrous and dark-spotted, abaxially sericeous, margins ciliate; upper glume 6–7.5 × 2.5–3.5 mm, ca. $^1/_2$ of the spikelet length, including the awn, awn 1–1.5 mm long, 7–9-nerved, adaxially glabrous and dark-spotted, abaxially hispid, margins ciliate; lemma 11.5 × 5–6 mm, including the awn, awn 1 mm long, 12–16-nerved, adaxially glabrous and dark-spotted, abaxially sericeous, dull; palea 12–12.5 × 5 mm, muticous, 10-nerved, adaxially glabrous and dark-spotted, abaxially puberulous at the apex and near the keels, glabrous elsewhere, dull, 2-keleed, keels ciliate towards the apex; rachilla extension 12–12.5 mm long, with a rudiment at the apex; lodicules 3, membranous, anterior pair 2.5 × 1 mm, posterior 2 × 0.7 mm; stamens 3, anthers ca. 6 mm, ochre; ovary elongate, style bifid, stigmas 2, plumose. Caryopsis not seen.

Comments:—*Merostachys soderstromii* resembles *M. medullosa* in the presence of a pith in the internodes. However, the absence of a fringe of trichomes at the nodal line; presence of an infranodal band of trichomes in the culm; and foliage leaf sheaths glabrous and lacking auricles in *M. soderstromii* distinguish it from *M. medullosa*. A detailed comparison of these two species is provided in the Table 1.

Phenology:—This species was recorded with reproductive structures only in 1985 and this data is not enough to estimate its reproductive cycle.

Geographic Distribution and Habitat:—*Merostachys soderstromii* occurs in Bahia and Espírito Santo states (Fig. 3). Most of the material of this species was collected in the vegetation type known as Mussununga. This vegetation type is associated with Brazilian Atlantic Forest and is characterized as occurring on a sandy spodosol with low water retention, high temperature, few nutrients and high acidity (Saporetti-Junior *et al.* 2012). Additionally, in the Mussunungas it is possible to observe physiognomic forms ranging from grasslands to woodlands (Saporetti-Junior *et al.* 2012). The material *Soderstrom et al. 2149*, collected in Prado municipality, does not have any information about habitat on the label; however, Prado is located on the Brazilian coast and there is evidence of the occurrence of Mussununga within its boundaries (Rossini & Souza 2007), so it is possible this material also was collected in this type of vegetation. The elevational distribution of *M. soderstromii* ranges from 8 to 50 m.

Conservation Status:—We applied the IUCN criteria (2017.3) and propose an IUCN red list category of Endangered (EN=B2a) given the number of populations less than or equal to five.

Etymology:—The specific epithet honors Dr. Thomas Robert Soderstrom, an American agrostologist who dedicated his career to research on grasses and contributed greatly to knowledge of the Poaceae and Neotropical bamboos.

Additional specimens examined:—BRAZIL. Bahia: Prado, ca. 10 Km South of Prado, littoral forest, 12 April 1976, veg., *Soderstrom et al. 2149* (CEPEC, ISC, K, NY, SP, US). Espírito Santo: Linhares, Reserva Natural da Vale, 07 June 2007, veg., *Viana et al. 2612* (BHCB); idem, Reserva Natural da Vale, Estrada da Gávea, 07 February 2007, veg., *Viana et al. 2595* (CVRD, VIC); idem, Reserva Natural da Vale, Estrada da Gávea, entre as entradas para Jacarandá e Bomba d'água, final da trilha, 26 April 2016, veg. *Vinícius-Silva et al. 96* (VIC); idem, Reserva Natural da Vale, Estrada Parajú, 10 September 1993, veg., *Sucre 11432* (CVRD); idem, Reserva Natural da Vale, trilha da Bomba d'água, final da trilha, 26 April 2016, veg., *Vinícius-Silva et al. 97* (VIC).

Merostachys medullosa Send. (1997: 298). Type:—BRAZIL. Bahia: Porto Seguro, Forested slopes of morro on Fazenda Carvalho, ca. 26 Km West of town of Monte Pascoal at end of a road that intersects with BR 101 in Monte Pascoal, 380-460 m, 15 May 1976 (fl.), *T.R. Soderstrom, G. Russell & J. Hage 2212* (holotype US!, isotypes CEPEC! G on-line image! K! NY! SP!) (Fig. 2).

Plants initially erect then arching toward the apex or climbing. Culms 5–15 m tall. Midculm internodes 15–55 cm long, 1.5–2 cm in diam., cylindrical, yellow with green spots, scabrous and covered by sericeous and hispid trichomes, infranodal band of trichomes absent; walls 1–3 mm thick, ratio of wall thickness: culm diam. 0.17–0.50, thin to thick, lumen 0.6–1.9 cm in diam., small to large, filled by a pith; nodes not prominent, black, with a fringe of trichomes at the nodal line. Culm leaf sheaths 11.5–75 × 3–5 cm, adaxially glabrous and shiny, abaxially scabrous with sparse hispid trichomes, the overlapping margin ciliate from the base toward the apex, fimbriate apically; auricles absent; fimbriae 5–25 mm long, not fused, erect at the base and sinuous toward the apex, yellow-white to brown, sometimes red-white; inner ligules 1–2 mm long, truncate, pubescent, the apex ciliate; blades 9.5–14 × 0.3–0.4 cm, reflexed, deciduous, margins scabrous, adaxially scabrous, abaxially glabrous. Branch complement consisting of 5–22 branches, the branches 15–50 cm long, 1–2.5 mm in diam., lower nodes not rebranching; nodes not prominent, black. Foliage leaves 10–18 per complement; sheaths 3–7 cm × 4–5 mm, hispid, overlapping margin ciliate, fimbriate apically; auricles present, 1–1.5 mm wide; fimbriae 8–15 mm long, not fused, spreading in all directions, straight at the base and sinuous toward the apex, sometimes curly, yellow-white to red-white; outer ligules ca. 0.3 mm long, the apex ciliate; inner ligules ca. 1 mm long, truncate, pubescent, the apex ciliate; pseudopetioles 3–5 mm long, brown to black, hispid, twisted; blades 12–25 × 1.5–4 cm, L:W = 4.5–8.7, lanceolate, adaxially with 3–5 scabrous ribs along one margin, the opposite margin and apex with minute strigose trichomes, glabrous elsewhere, abaxially covered by minute antrorse strigose trichomes, the base asymmetric, the apex acuminate, margins scabrous. Synflorescences 5–12 cm long, racemose, with 10–25 spikelets per raceme, rudimentary spikelets at the base and at the apex present, two rows of spikelets in one rank, rows pectinate and being less than 10 degrees apart; rachis tomentose; pedicels ca. 2 mm long, tomentose to hispid. Spikelets 15–20 × 3–4 mm, 1-flowered, solitary; glumes 2, unequal; lower glume 6–6.5 × 1 mm, $^1/_3$ –$^1/_2$ of the spikelet length, muticous, 1-nerved, adaxially glabrous and dark-spotted, abaxially sericeous to hispid, margins ciliate; upper glume 13–16 × 4–5 mm, ca. $^2/_3$ of the spikelet length, including the awn, awn ca. 2 mm long, 12-nerved, adaxially glabrous and dark-spotted, abaxially sericeous to hispid, margins ciliate; lemma 16 × 6–8 mm, mucronate, 17–20-nerved, adaxially glabrous, abaxially sericeous to hispid, dull; palea 15–16 × 4 mm, muticous, 8-nerved, adaxially glabrous, abaxially pubescent, dull, 2-keleed, keels ciliate towards the apex; rachilla extension 15–16 mm long, with a rudiment at the apex; androecium and gynoecium depauperate in the material examined. Caryopsis not seen.

Comments:—*Merostachys medullosa* is recognized mainly by its scabrous internodes filled by a pith and foliage leaves with auricles and fimbriae spreading in all directions. The presence of spreading auricles and fimbriae also is found in *M. calderoniana* Send. (1997: 190). However, in contrast to *M. medullosa*, *M. calderoniana* has glabrous, hollow internodes and shiny florets. *Merostachys medullosa* also resembles

M. soderstromii (see comments under this species), and a morphological comparison of these species is provided in Table 1.

Phenology:—This species was recorded with reproductive structures only in 1976 and this data is not enough to estimate its reproductive cycle.

Geographic Distribution and Habitat:—*Merostachys medullosa* occurs only in Bahia state (Fig. 3). This species is found in the understory and along the borders of the Brazilian Atlantic Forest. Most collections have been made years ago and the labels of the specimens do not include habitat information. However, recent collections of this species were recorded in Ombrophilous Dense Forest, according to the classification of Veloso *et al.* (1991). Its elevational distribution ranges from 50 to 700 m.

Conservation Status:—We applied the IUCN criteria (2017.3) and propose an IUCN red list category of vulnerable (VU=B2a) given the number of populations less than or equal to ten.

Additional specimens examined:—BRAZIL. Bahia: Ilhéus, 3 Km North of Rodoviária, Mata da Esperança, Forest North of dam and reservoir, 11 January 1995, veg., *Thomas et al. 10748* (NY, SP, US); Idem, 22 September 1994, veg., *Thomas et al. 10601* (NY); Itapebi, Fazenda do Sr. João das Orquídeas, 13 October 2007, veg., *Ferreira et al. 1517* (CEPEC); Idem, 13 October 2007, veg., *Ferreira et al. 1520* (CEPEC); Idem, 13 October 2007, veg., *Ferreira et al. 1522* (CEPEC); Jaguaquara, 9.5 Km SE of Jaguaquara, Fazenda Mundo Novo, 13 April 1976, fl., *Calderón et al. 2379* (CEPEC, INPA, K, MO, NY, SP, US); Idem, 6–8 Km E of Jaguaquara city, Fazenda Mundo Novo, 06 May 1972, veg., *Calderón et al. 2251* (CEPEC, K, MO, NY, US); Idem, Estrada para Apuarema, 5.7 Km de Jaguaquara, 24 March 2002, veg., *Oliveira 782* (HUEFS); Porto Seguro, Parque Nacional Pau Brasil, Estrada da Jaqueira, 16 February 2017, veg., *Vinícius-Silva & Costa 112* (VIC); Ubaíra, 2 Km east Ubaíra on road to Mutuipe, forest slopes above rocky stream in Fazenda Pindoba de Dentro, 27 April 1976, veg., *Soderstrom et al. 2166* (CEPEC, ISC, K, MO, NY, SP, US); Una, 15 Km from Una on road to Santa Luzia do Salobro, 27 May 1976, fl., *Soderstrom et al. 2231* (CEPEC, ISC, K, MO, SP, US); Idem, 3.5 Km S of Una on road Una-Santa Luzia, 25 May 1976, fl., *Calderón et al. 2451* (CEPEC, K, MO, NY, SP, US).

Merostachys magnispicula Send. (1997: 296). Type:—BRAZIL. Bahia: Ilhéus, Salobrinho, 18 December 1968 (fl.), *J. Almeida & T.S. Santos 289* (holotype CEPEC!) (Fig. 4).

Plants initially erect then climbing on vegetation. Culms 3–15 m tall. Midculm internodes 15.5–40 cm long, 0.8–1.5 cm in diam., cylindrical, green to yellow-white, glabrous, sometimes covered by a layer of wax, infranodal band of trichomes absent; walls 0.8–1 mm thick, ratio of wall thickness: culm diam. 0.10–0.25, very thin to thin, lumen 0.6–1.4 cm in diam., large, hollow; nodes not prominent, brown, without a fringe of trichomes at the nodal line. Culm leaf sheaths 10.5–20 × 3–5 cm, adaxially glabrous, shiny, abaxially glabrous, sometimes covered by a layer of wax, overlapping margin ciliate, fimbriate apically; auricles absent; fimbriae 2–7 mm long, scant, sometimes deciduous, not fused, straight to sinuous, erect, brown at the base and yellow-white toward the apex; inner ligules 1–3 mm long, truncate, pubescent, the apex ciliate; blades 3.5–7.5 × 0.3–0.8 cm, margins scabrous toward the apex, adaxially scabrous, abaxially glabrous or scabrous at the base and glabrous elsewhere. Branch complement consisting of 3–13 branches, the branches 15–60 cm long, 3–4 mm in diam., lower nodes not rebranching; nodes not prominent, brown. Foliage leaves 8–24 per complement; sheaths 3.5–10 cm × 4–10 mm, scabrous in the basal leaves and glabrous in the leaves toward the apex of the branches, overlapping margin ciliate, fimbriate apically; auricles absent; fimbriae 1–15 mm long, scant, sometimes deciduous, not fused, straight to sinuous, generally straight at the base and sinuous toward the apex, erect, brown at the base and yellow-white or white toward the apex; outer ligules 0.2–0.5 mm long, the apex ciliate; inner ligules 0.8–1 mm long, truncate, pubescent, the apex ciliate; pseudopetioles 5–10 mm long, brown, glabrous, twisted; blades 15–35 × 2–5 cm, L:W = 4.8–11.1, lanceolate, adaxially with 2–3 scabrous ribs along one margin, either glabrous elsewhere or the opposite margin with minute strigose trichomes and glabrous elsewhere, abaxially covered by minute antrorse strigose trichomes, except at the marginal stripe which is glabrous, the base asymmetric, the apex acuminate, margins scabrous. Synflorescences 5–12 cm long, racemose, with 12–25 spikelets per raceme, rudimentary spikelets at the base present, two rows of spikelets in one rank, rows pectinate and being less than 10 degrees apart; rachis tomentose; pedicels 1–1.5 mm long, tomentose to hispid. Spikelets 12–15 × 2–3 mm, 1-flowered, solitary; glumes 2, unequal; lower glume 7–9 × 3 mm, $^{1}/_{2}$–$^{3}/_{5}$ of the spikelet length, muticous to mucronate, 8–10-nerved, adaxially glabrous, abaxially pubescent, margins ciliate; upper glume 10–12 × 5 mm, $^3/_4$– $^4/_5$ of the spikelet length, muticous to mucronate, 12-nerved, adaxially glabrous, abaxially hispid at the apex and pubescent elsewhere, sometimes completely pubescent, margins ciliate; lemma 10–12.5 × 5–8 mm, mucronate, 15-nerved, adaxially glabrous, abaxially glabrous, margins densely ciliate at the apex, shiny; palea 11–13 × 4–7 mm, muticous, 8–10-nerved, adaxially glabrous, abaxially glabrous, margins ciliate at the apex, shiny, 2-keeled, keels ciliate towards the apex; rachilla extension 7–12 mm long, with a rudiment at the apex; lodicules 3, membranous, anterior pair 3 × 1.3 mm, posterior 3 × 0.7 mm; stamens 3, anthers ca. 5.5 mm long, ochre; ovary elongate, style bifid, stigmas 2, plumose. Caryopsis not seen.

Comments:—*Merostachys magnispicula* was described based only on the type specimen. It resembles *M. procerrima* mainly in the diameter of the culm; indument of the internodes and thickness of the internode wall; thickness of the branches; measurements of the foliage leaf blades; and features of the spikelets such as, for example, size of the bracts and the presence of a shiny floret. However, *M. magnispicula* has scabrous foliage leaf sheaths (sometimes the sheaths of basal leaves are scabrous and the sheaths of leaves toward the apex of the branches are glabrous) and scant fimbriae on both culm and foliage leaves, and sometimes these fimbriae are deciduous. On the other hand, *M. procerrima* has glabrous foliage leaf sheaths and abundant fimbriae on both culm and foliage leaves. It is also worth highlighting the consistent absence of foliage leaf auricles in *M. magnispicula* and the presence or absence of foliage leaf auricles on the same branch complement of *M. procerrima* (for more details, see comments of this species). A morphological comparison between *M. magnispicula* and *M. procerrima* is provided in Table 2.

Another important issue about the morphology of this species is that *M. magnispicula* has spikelets with shiny florets, similar to what is observed in *M. procerrima*, *M. calderoniana*, *M. leptophylla* Send. (1997: 295) (Brazil) and *M. pauciflora* Swallen (1943: 469) (Central America). Other similar species are *M. rondoniensis* Send. (1997: 305) (Brazil) and *M. retrorsa* McClure (1964: 6) (Venezuela) in which only the palea is shiny. It is not clear whether all these species can be considered phylogenetically related based on this feature. However, this is plausible as *M. calderoniana*, *M. leptophylla*, *M. procerrima* and *M. rondoniensis* group together in a molecular phylogenetic analysis (the other taxa cited above were not sampled) (Vinícius-Silva *et al.*, in preparation).

The description of this species here presented was based on its type material (holotype); specimens previously considered wrongly as paratypes of *M. procerrima* (see comments of this species); and other materials collected in the field or stored in herbaria recognized by us as *M. magnispicula*.

Phenology:—This species was recorded with reproductive structures in 1968, 2000 and 2004, suggesting a reproductive cycle of approximately 32–36 years.

Geographic Distribution and Habitat:—*Merostachys magnispicula* is recorded, at the moment, only in Bahia state (Fig. 6). Most collections have been made some time ago and no information related to habitat is included on the label. However, the recent collections indicate this species grows along borders of Brazilian Atlantic Forest in a vegetation type known as Ombrophilous Dense Forest, according to the classification of Veloso *et al*. (1991). The elevational distribution of this species ranges from 8 to 250 m.

Conservation Status:—We applied the IUCN criteria (2017.3) and propose an IUCN red list category of Vulnerable (VU=B2av) given the number of locations/subpopulations less than or equal to ten.

Additional specimens examined:—BRAZIL. Bahia: Camamú, on road to Ubaitaba, forest on hill above stream, 22 April 1976, veg., *Soderstrom et al. 2157* (CEPEC, ISC, MO, NY, SP); Ilhéus, 2.2 Km N of Banco da Vitória, on road leading to west edge of Mata da Esperança, 22 May 1995, veg., *Thomas et al. 10976* (NY, SP); idem, Mata da Esperança, parte W, rod. Ilhéus/Itabuna, Banco da Vitória, 30 January 2000, fl., *Jardim et al. 2593* (MO, NY); Porto Seguro, Parque Nacional Monte Pascoal, 14 Km E of BR 101 at a point 13 Km N of Itamarajú, 11 May 1976, veg., *Soderstrom et al. 2198* (CEPEC, ISC, MO, NY, SP, US); idem, Parque Nacional Monte Pascoal, along Park road 1–2 Km east of path to peak and visitor center, 17 July 1997, veg., *Thomas et al. 11592* (ISC, NY, SP); idem, Parque Nacional Monte Pascoal, along road from entrance to visitor's center and road to E side of Park, 05 February 1999, veg., *Thomas et al. 11982* (CEPEC, MO, NY); idem, Parque Nacional Monte Pascoal, estrada em direção ao centro de visitantes, 18 February 2017, veg., *Vinícius-Silva & Costa* 117 (VIC); Una, Faz. São José, 3.5 Km from road Una-São José do Macuco (37 Km NW of Una), 25 April 1976, veg., *Calderón et al. 2390* (CEPEC, INPA, MO, SP, US); idem, Km 15.6 da rodovia São José/Una (10 Km por ar SE São José), 21 February 1986, veg., *Santos & Judziewicz 4112* (CEPEC); idem, Serra dos Quatis, 8.2 Km por Rodovia E de São José, Rodovia São José/Una, então 2 Km ao SW, faldas e cima da Serra 3.5 Km ar SE de São José, 21 February 1986, veg., *Santos & Judziewicz 4091* (US); Valença, RPPN Fazenda Água Branca, Distrito de Jequiriça, Estrada de Valença para Guaibim, ca. 2 Km, entrada à esquerda, 8 Km, rumo à sede da reserva, 30 October 2004, fl., *Fiaschi et al. 2621* (CEPEC, MO).

Merostachys procerrima Send. (1997: 300). Type:—BRAZIL. Bahia: Porto Seguro, Reserva Biológica do Pau Brasil (CEPLAC), primary hygrophilic forest with tall trees, 35 m, 07 May 1976 (veg.), *T.R. Soderstrom, G. Russell & J. Hage 2187* (holotype US!, isotypes CEPEC!, G on-line image!, INPA, K!, MO!, NY!, SP!).

Epitype (here designated): Brazil. Bahia: Santa Cruz Cabrália, 5 Km da estrada antiga que liga a Estação Ecológica Pau-Brasil/ Sta. Cruz de Cabrália com entrocamento no Km 17 da rodovia Porto Seguro/ Eunápolis, 11 December 1991 (fl.), *S.C. de Sant'Ana, A.M. de Carvalho, A. Amorim & A. Mayer 41* (Epitype CEPEC! Isoepitypes HUEFS!, MO!, NY! SP!, US!) (Fig. 5).

Plants initially erect then climbing on the vegetation. Culms 3–10 m tall. Midculm internodes 15–60 cm long, 0.7–1.5 cm in diam., cylindrical, green to yellow-white, glabrous, sometimes covered by a layer of wax, infranodal band of trichomes absent; walls 0.8–1.5 mm thick, ratio of wall thickness: culm diam. 0.13–0.28, very thin to thin, lumen 0.6–1.5 cm in diam., large, hollow; nodes not prominent, brown, without a fringe of trichomes at the nodal line. Culm leaf sheaths 5–19.5 × 2.5–4 cm, adaxially glabrous, shiny, abaxially glabrous, sometimes covered by a layer of wax , overlapping margin ciliate, fimbriate apically; auricles absent; fimbriae 3–20 mm long, abundant, not fused, straight at the base and sinuous toward the apex, sometimes completely sinuous, erect and sometimes entangled at the apex, brown at the base and yellow-white toward the apex; inner ligules 1–2 mm long, truncate, pubescent, the apex ciliate; blades 4–10 × 0.4–0.8 cm, margins scabrous, adaxially scabrous at the base and glabrous elsewhere, abaxially glabrous. Branch complement consisting of 3–22 branches, the branches 10–50 cm long, 3–4 mm in diam., lower nodes rebranching; nodes not prominent, brown. Foliage leaves 7–22 per complement; sheaths 2.5–6 cm × 3–8 mm, glabrous, overlapping margin ciliate, fimbriate apically; auricles sometimes present, 2–4 mm wide; fimbriae 5–15 mm long, abundant, not fused, straight at the base and sinuous toward the apex, sometimes completely sinuous, mostly erect and sometimes entangled at the apex, sometimes curly, brown at the base and yellow-white toward the apex; outer ligules 0.2–0.5 mm long, the apex ciliate; inner ligules 1–2 mm long, truncate, pubescent, the apex ciliate; pseudopetioles 5–7 mm long, brown, glabrous, twisted; blades 12–28 × 2–4 cm, L:W = 3.8–10.8, lanceolate, adaxially with 2–3 scabrous ribs along one margin, the opposite margin and apex with minute strigose trichomes, glabrous elsewhere, abaxially covered by minute antrorse strigose trichomes, except at the marginal stripe which is glabrous, sometimes these trichomes concentrated in a band between the marginal stripe and the rest of the blade toward the apex, the base asymmetric, the apex acuminate, margins scabrous. Synflorescences 5–15 cm long, racemose, with 19–23 spikelets per raceme, rudimentary spikelets present at the base, two rows of spikelets in one rank, rows pectinate and being less than 10 degrees apart; rachis tomentose; pedicels ca. 1 mm long, tomentose to hispid. Spikelets 10–15 × 2–3 mm, 1-flowered, solitary; glumes 2, unequal; lower glume 6–8 × 3–4 mm, $^{1}/_{2}$– $^{2}/_{3}$ of the spikelet length, muticous to mucronate, 3–9-nerved, adaxially glabrous and sometimes dark-spotted, abaxially hispid at the base and pubescent elsewhere, margins ciliate; upper glume 8–12 × 4–6 mm, $^{3}/_{4}$–$^{4}/_{5}$ of the spikelet length, mucronate, 13–15-nerved, adaxially glabrous, abaxially pubescent to hispid, sometimes completely pubescent, margins ciliate; lemma 8–12 × 4–5 mm, mucronate,14–16-nerved, adaxially glabrous and dark-spotted, abaxially pubescent at the apex, glabrous elsewhere, sometimes completely glabrous, margins densely ciliate at the apex, shiny; palea 8–12 × 3–4 mm, muticous, 8–10-nerved, adaxially glabrous, abaxially pubescent at the apex, glabrous elsewhere, sometimes completely glabrous, margins ciliate at the apex, shiny, 2-keleed, keels ciliate towards the apex; rachilla extension 18–12.5 mm long, with a rudiment at the apex; lodicules 3, membranous, anterior pair 3 × 1 mm, posterior 2.5 × 0.7 mm; androecium depauperate in the material examined; ovary elongate, style bifid, stigmas 2, plumose. Caryopsis not seen.

Comments:—As mentioned above, *Merostachys procerrima* is similar to *M. magnispicula* but the indument of the foliage leaf sheaths and the amount of fimbriae on both culm and foliage leaves may distinguish them (Table 2).

Sendulsky (1997) indicated in her description of *M. procerrima* that this species has auricles on its foliage leaves, similar to what is observed in *M. calderoniana* and *M. medullosa*. However, auricles are not present on all the foliage leaves of this species, but only on some of them. Thus, it is possible to observe leaves with and without auricles in the same branch complement. In contrast, the foliage leaves of *M. magnispicula* always lack auricles.

The description of *M. procerrima* was based on the type collection and four paratypes. However, our morphological analyses showed that two of these paratypes, *Soderstrom et al. 2157* (from Camamú municipality, Bahia state) and *Soderstrom et al. 2198* (from Porto Seguro municipality, Bahia state), have characteristics that place them in *M. magnispicula* and not in *M. procerrima*. Both collections were used to redescribe *M. magnispicula* and they are here cited in the additional specimens examined of this species.

It is very important to emphasize that relatively few characters distinguish these two species and that some of the differences are subtle, which caused us to consider the possibility of synonymizing them. The distributions of these two species do overlap in southern Bahia state, but populations of both species were observed and collected in the Monte Pascoal National Park, located in Porto Seguro municipality, where they develop under the same environmental conditions. The fact that the differences between the two are maintained in this area was crucial to our decision to maintain them as different species.

Phenology:—*Merostachys procerrima* was documented in flower in 1991, 1993 and 1994. These data do not allow us to infer anything about its reproductive cycle.

Geographic Distribution and Habitat:—This species was recorded for Bahia and Espírito Santo states by Sendulsky (1997). The material cited by this author from Espírito Santo (*Martinelli & Soderstrom 9710*) was collected in Conceição da Barra municipality and, according to Sendulsky (1997), deposited in the US Herbarium collection, Washington D.C., USA. However, RVS and APSG visited this herbarium in 2014 and 2018 and the *Merostachys* collection was fully examined, but the specimen was not found. Duplicates also were not found in other herbaria and we were not able collect it in the field. Therefore, we considered only specimens we examined or collected in plotting the map (Fig. 6), giving a distribution for this species restricted to southern Bahia.

Although older collections of *M. procerrima* do not give information about its habitat, this species occurs along borders of Brazilian Atlantic Forest in the vegetation types known as Ombrophilous Dense Forest, according classification of Veloso *et al.* (1991) and Tabuleiro Forest, according classification of Rizzini (1992). The elevational distribution of this species ranges from 6 to 100 m.

Conservation Status:—We applied the IUCN criteria (2017.3) and propose an IUCN red list category of Endangered (EN =B2ab) given the number of locations/subpopulations equal to five.

Additional specimens examined:—BRAZIL. Bahia: Belmonte, Barrolândia, Estação Experimental "Gregorio Bondar", CEPLAC, 48 Km east of BR 101 on road to Belmonte, 12 May 1993, fl., *Thomas et al. 9889* (CEPEC, MO, NY, SP); Porto Seguro, Parque Nacional Monte Pascoal, Região do Meio da Mata, 20 February 2017, veg., *Vinícius-Silva & Costa 123* (VIC); idem, Parque Nacional Pau Brasil, antes da porteira para a Estrada Jacuba, 17 February 2017, veg., *Vinícius-Silva & Costa 116* (VIC); idem, Reserva da Brasil Holanda de Ind. S/A. Entrada no Km 22 da Rod. Eunápolis/P. Seguro, ca. 9.5 Km da entrada, 06 April 1994, fl., *Carvalho et al. 4462* (CEPEC, HUEFS, MO, SP); Santa Cruz de Cabrália, Reserva Biológica Pau Brasil (CEPLAC), 16 Km of Porto Seguro, 31 March 1972, veg., *Calderón & Pinheiro 2194* (CEPEC, ISC, MO, NY, US).

Acknowledgments

We acknowledge support from the following funding agencies: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) in the International Doctoral Program in Sandwich (PDSE, nº 88881.135178/2016-01 to R. Vinícius-Silva), Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG, grant APQ-03255-16 to A.P. Santos-Gonçalves), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grants 563545/2010-0-REFLORA to A.P. Santos-Gonçalves and 401526/2014-3-PVE to R.P. Oliveira), Bamboos of the Americas (BOTA) and the Ned Jaquith Foundation (grants to R. Vinícius-Silva to support fieldwork). We thank Cristielle de Jesus-Costa and Tiago de Souza Costa for help with the fieldwork and Robert Soreng for support during a visit to the US Herbarium, Washington D.C., U.S.A. We also thank Reinaldo Pinto for the illustrations and Mayco S. Werllen-Sousa for the preparation of the geographic distribution maps.

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TABLE 1. A morphological comparison of *M. medullosa* and *M. soderstromii*.

Characters	***M. medullosa***	***M. soderstromii***
Culm leaf abaxial indument	Scabrous with sparse hispid trichomes	Minutely scabrous, sometimes hispid, sericeous or pubescent
Internode indument	Scabrous and covered by sericeous to hispid trichomes	Scabrous
Infranodal band of trichomes in the culm	Absent	Present
Fringe of trichomes at the nodal line	Present	Absent
Foliage leaf sheaths indument	Hispid	Glabrous, sometimes hirsute at the apex
Auricles on the foliage leaves	Present	Absent
Arrangement of the fimbriae on the foliage leaves	Spreading in all directions	Erect
Geographic distribution	Bahia state	Bahia and Espírito Santo states
Elevational distribution (m)	50–700	8–50

TABLE 2. A morphological comparison of *M. magnispicula* and *M. procerrima*.

Characters	***M. magnispicula***	***M. procerrima***
Amount of the fimbriae on both culm and foliage leaves	Scant, sometimes deciduous	Abundant
Shape of culm leaf fimbriae	Straight to sinuous	Straight at the base and sinuous toward the apex, sometimes completely sinuous, sometimes entangled at the apex
Foliage leaf sheath indument	Scabrous on basal leaves and glabrous on apical leaves	Glabrous
Shape of foliage leaf fimbriae	Straight to sinuous, generally straight at the base and sinuous toward the apex	Straight at the base and sinuous toward the apex, sometimes completely sinuous, sometimes curly, sometimes entangled at the apex
Auricles on the foliage leaves	Absent	Sometimes present
Geographic distribution	Bahia state	Bahia state
Elevational distribution (m)	8–250	6–100

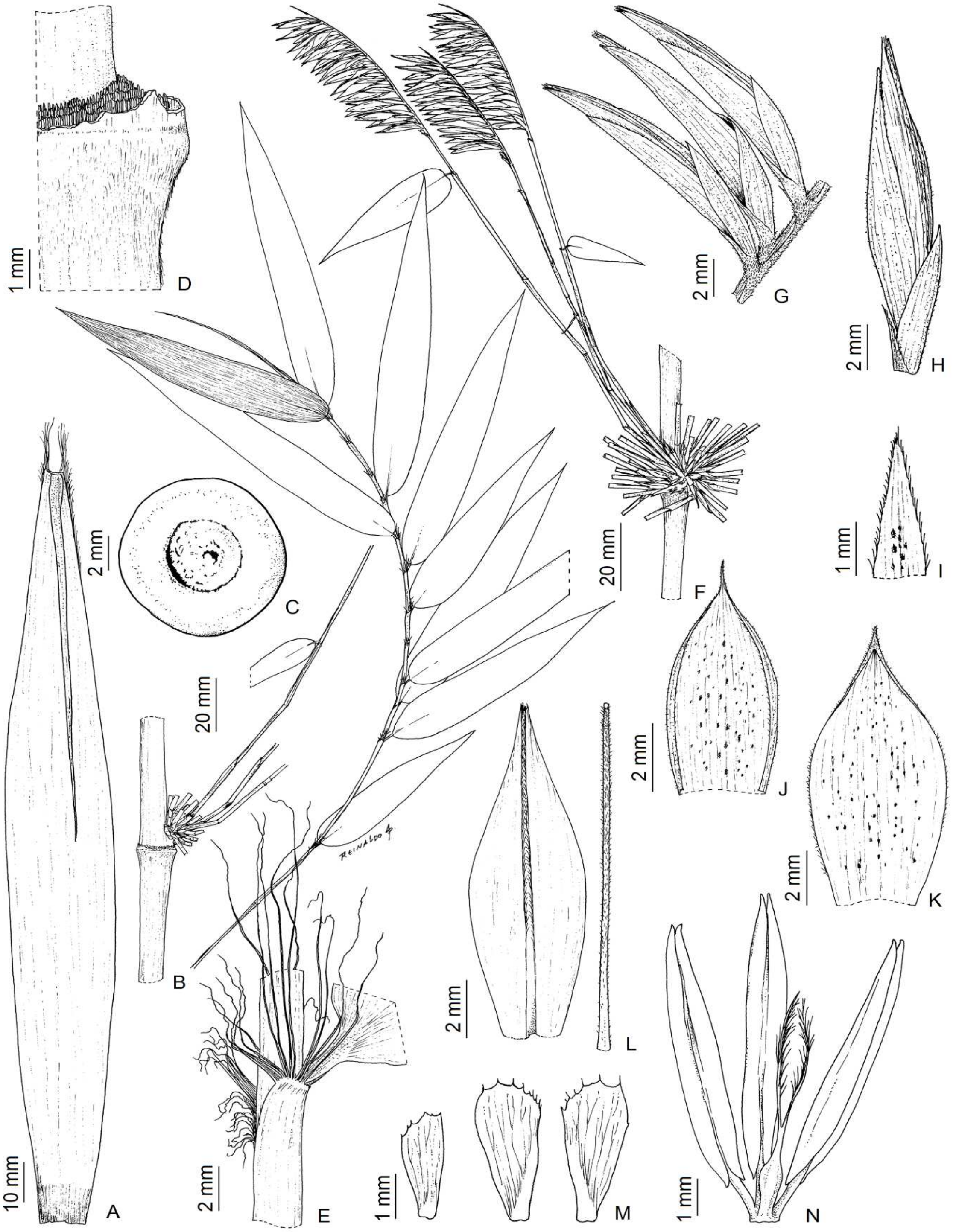

FIGURE 1. *Merostachys soderstromii*. A. Culm leaf. B. Branch complement with vegetative branches. C. Transverse section of an internode showing the pith. D. Infranodal band of velutinous trichomes in the culm. E. Ligular area of a foliage leaf with fimbriae. F. Branch complement with floriferous branches. G. Section of synflorescence. H. Spikelet. I. Lower glume (adaxial view). J. Upper glume (adaxial view). K. Lemma (adaxial view). L. Palea (l, abaxial view) and rachilla extension (r). M. Lodicules. N. Androecium and gynoecium. A-E based on *Vinícius-Silva et al. 96*; F-N based on *Farias 84*. (Illustration by Reinaldo Pinto).

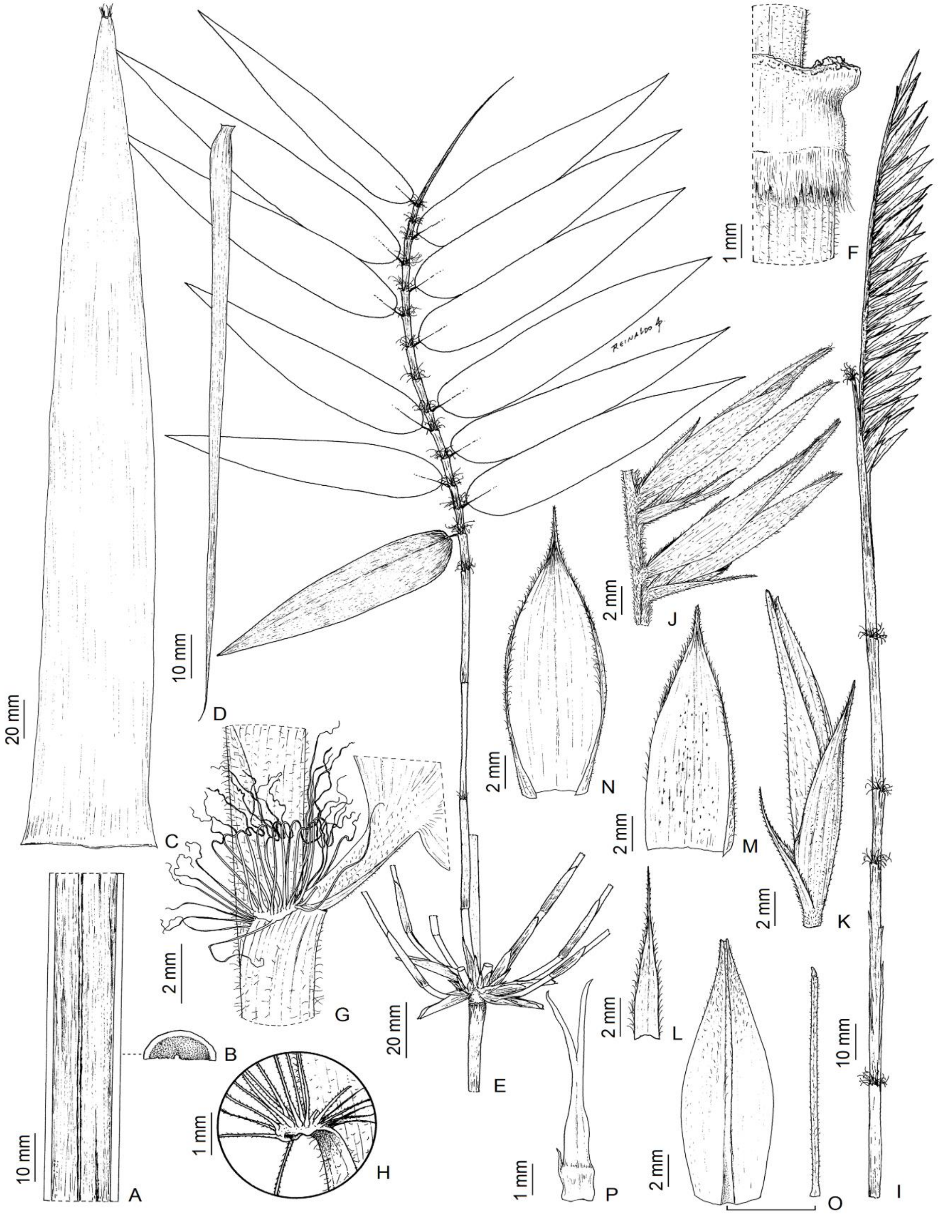

FIGURE 2. *Merostachys medullosa*. A. Longitudinal section of an internode showing the pith. B. Transverse section of an internode showing the pith. C. Culm leaf sheath. D. Culm leaf blade. E. Branch complement with vegetative branches. F. Fringe of trichomes at the nodal line. G. Ligular area of a foliage leaf with fimbriae. H. Detail of an auricle on a foliage leaf. I. Floriferous branch. J. Section of synflorescence. K. Spikelet. L. Lower glume (adaxial view). M. Upper glume (adaxial view). N. Lemma (adaxial view). O. Palea (l, abaxial view) and rachilla extension (r). P. Gynoecium. A-B and I-P based on *Calderón et al. 2379*; C and E-H based on *Vinícius-Silva & Costa 112*; D based on *Soderstrom et al. 2212*. (Illustration by Reinaldo Pinto).

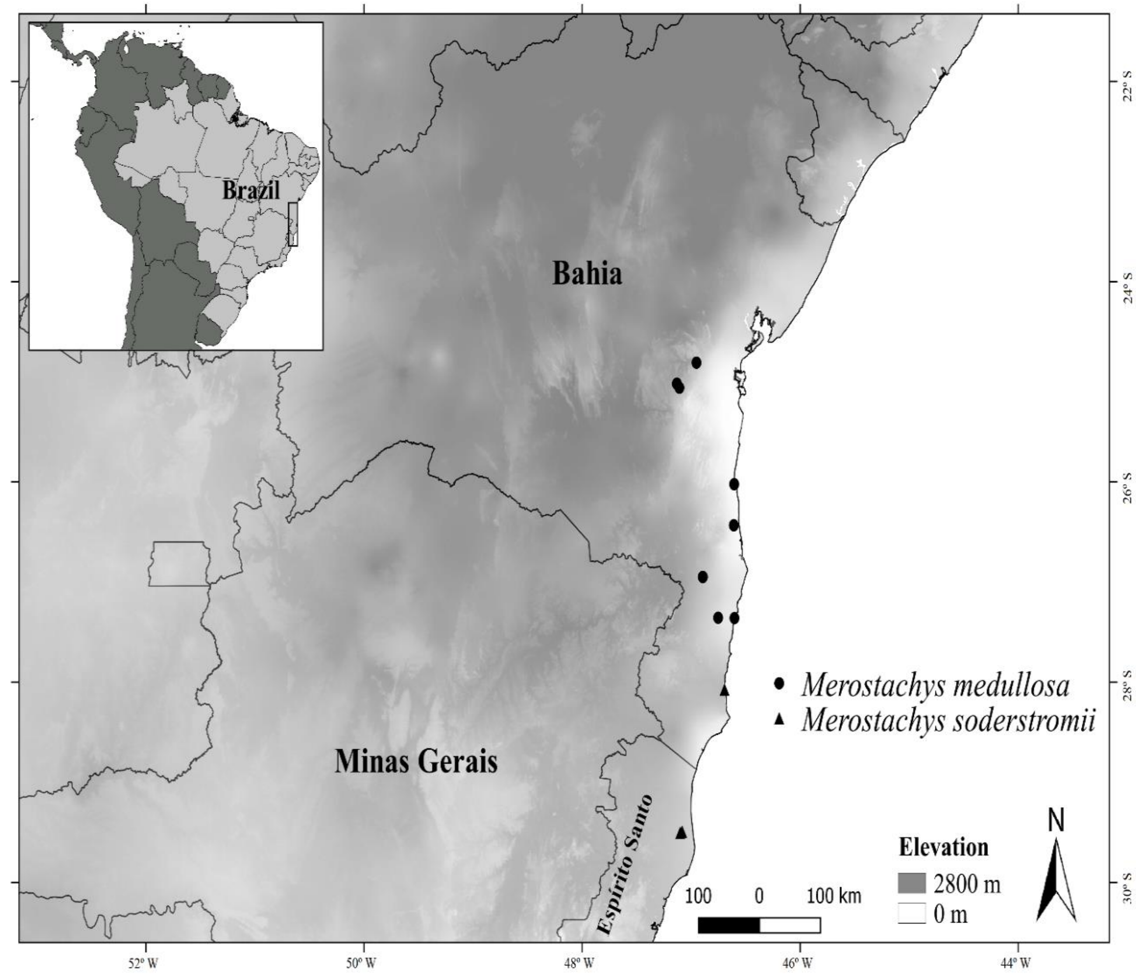

FIGURE 3. Geographic distribution of *M. medullosa* and *M. soderstromii* in the Brazilian Atlantic Forest.

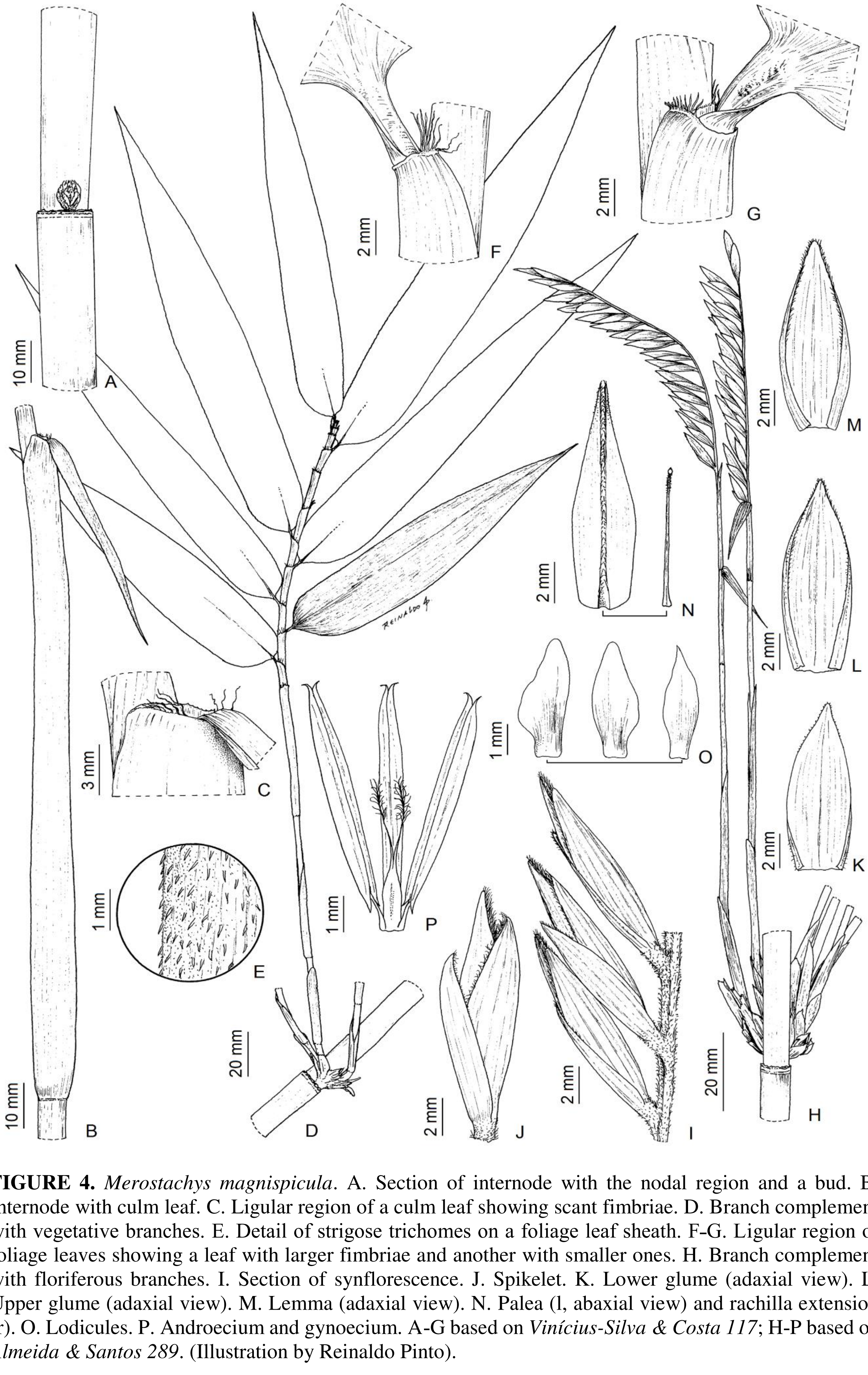

FIGURE 4. *Merostachys magnispicula*. A. Section of internode with the nodal region and a bud. B. Internode with culm leaf. C. Ligular region of a culm leaf showing scant fimbriae. D. Branch complement with vegetative branches. E. Detail of strigose trichomes on a foliage leaf sheath. F-G. Ligular region of foliage leaves showing a leaf with larger fimbriae and another with smaller ones. H. Branch complement with floriferous branches. I. Section of synflorescence. J. Spikelet. K. Lower glume (adaxial view). L. Upper glume (adaxial view). M. Lemma (adaxial view). N. Palea (l, abaxial view) and rachilla extension (r). O. Lodicules. P. Androecium and gynoecium. A-G based on *Vinícius-Silva & Costa 117*; H-P based on *Almeida & Santos 289*. (Illustration by Reinaldo Pinto).

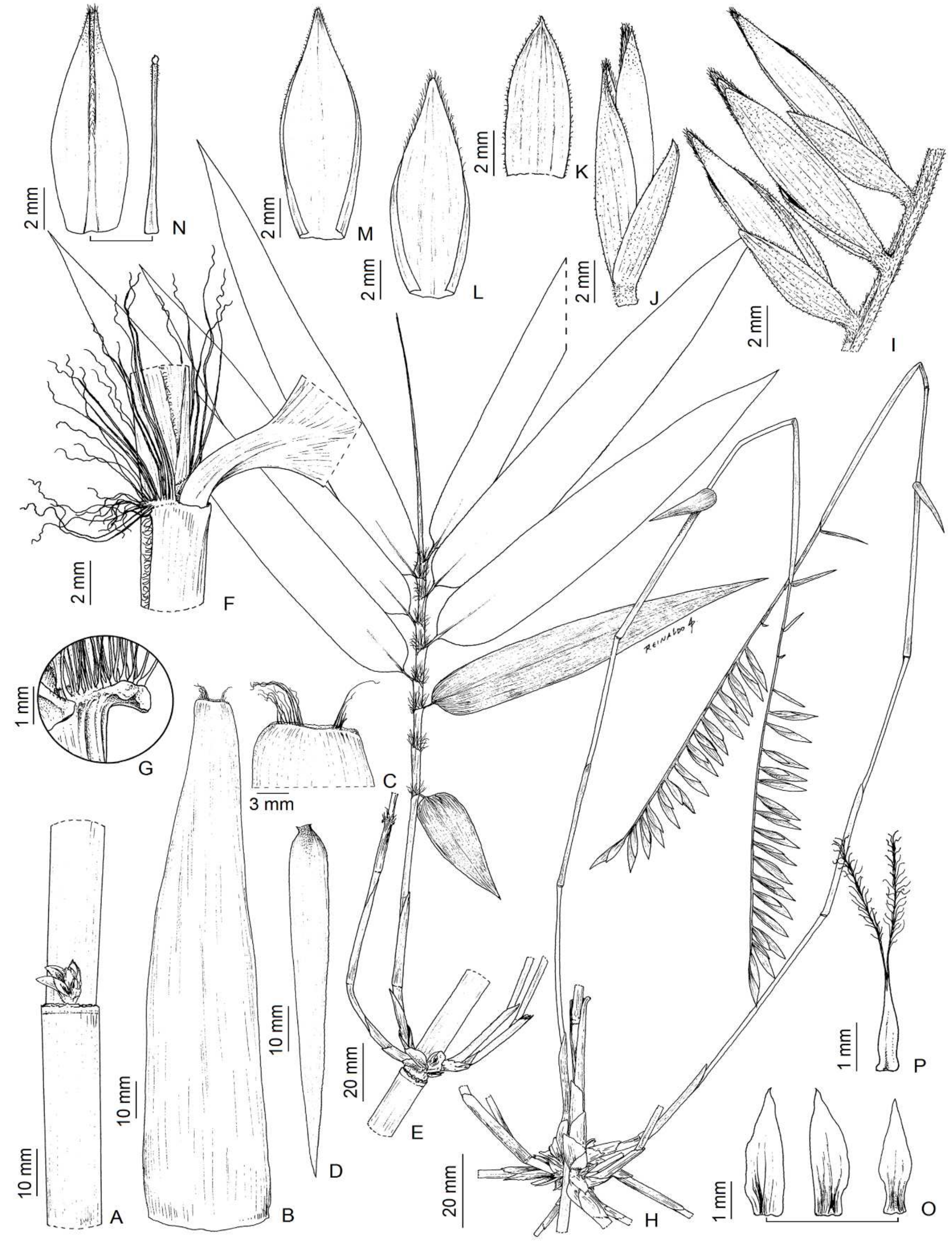

FIGURE 5. *Merostachys procerrima*. A. Section of internode with the nodal region and branch complement in initial stage of development. B. Culm leaf sheath. C. Ligular region of a culm leaf with fimbriae. D. Culm leaf blade. E. Branch complement with vegetative branches. F. Ligular region of a foliage leaf with fimbriae. G. Detail of an auricle on another foliage leaf. H. Branch complement with floriferous branches. I. Section of synflorescence. J. Spikelet. K. Lower glume (adaxial view). L. Upper glume (adaxial view). M. Lemma (adaxial view). N. Palea (l, abaxial view) and rachilla extension (r). O. Lodicules. P. Gynoecium. A-C and E-G based on *Vinícius-Silva & Costa 116*; D based on *Soderstrom et al. 2187*; H-P based on *Sant'Ana et al. 41*. (Illustration by Reinaldo Pinto).

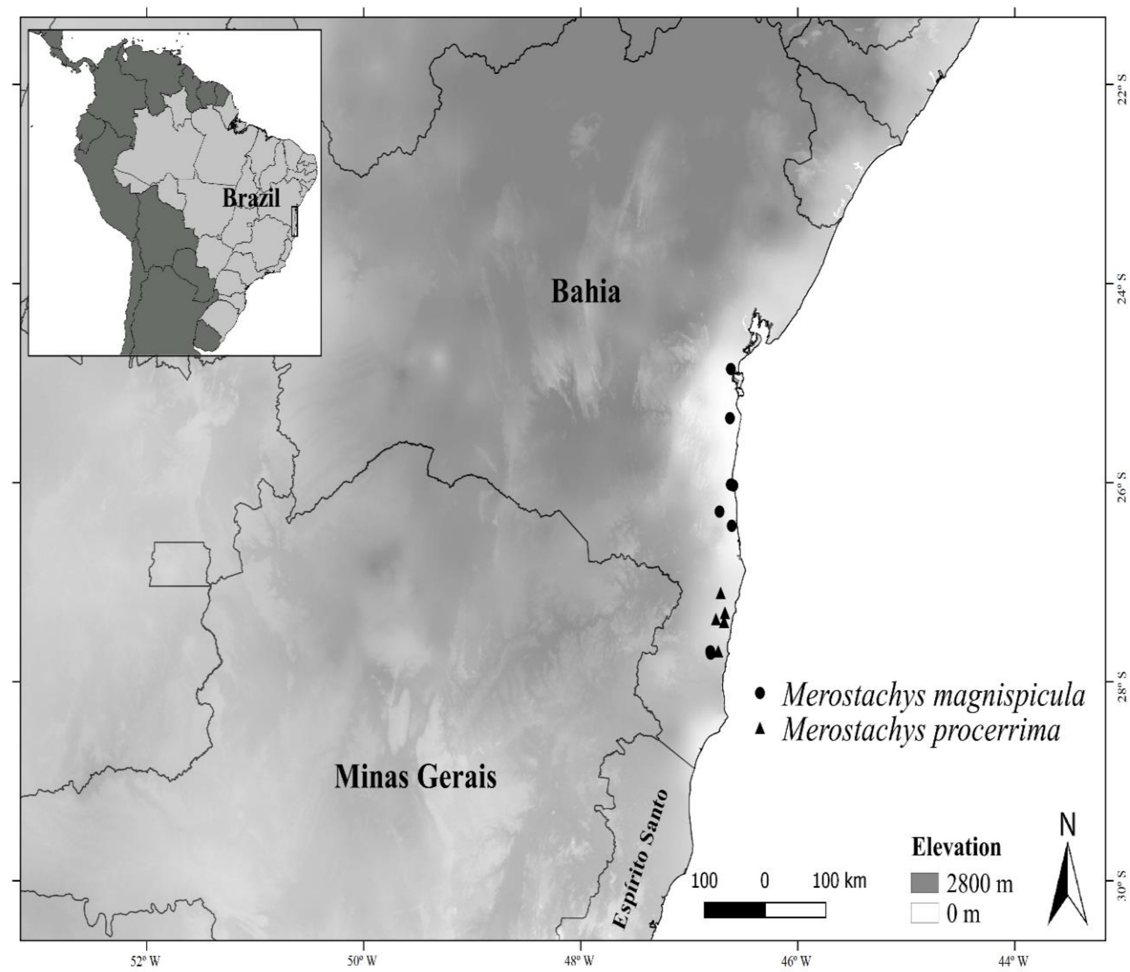

FIGURE 6. Geographic distribution of *M. magnispicula* and *M. procerrima* in the Brazilian Atlantic Forest.

CAPÍTULO III

Two new species of *Merostachys* (Poaceae: Bambusoideae: Bambuseae) from the Brazilian Atlantic Forest and the complete description of *M. bifurcata*

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[6]Co-corresponding author

Manuscrito de acordo com as normas do periódico *Brittonia*.

Abstract. *Merostachys* is one of the more species-rich genera of Neotropical woody bamboos. In total, *Merostachys* includes 54 described species; of these, 43 are found in the Brazilian Atlantic Forest, which is the center of diversity and endemism of the genus. Fieldwork done in eastern Minas Gerais and Espírito Santo states and morphological analyses in herbaria allowed us to recognize two new species, **Merostachys judziewiczii** and **M. lagevianae**, which were collected in the Brazilian Atlantic Forest domain; the first record of the reproductive structures of *M. bifurcata* is also reported. The new species are here described, and an emended description of *M. bifurcata* is provided. All three taxa are illustrated. Taxonomic comments and the conservation status for the species are provided, and a key to the species of *Merostachys* in eastern Minas Gerais and Espírito Santo states is also included.

Keywords: Arthrostylidiinae, grasses, emended description, epitype, morphology, Neotropical woody bamboos, taxonomy.

Merostachys Sprengel encompasses 54 described species and is considered one of the more species-rich genera of Arthrostylidiinae (Judziewicz et al., 1999; Bamboo Phylogeny Group [BPG], 2012; Santos-Gonçalves et al., 2012; Parma et al., 2016; Vinícius-Silva et al., 2016; Vorontsova et al., 2016; Clark & Oliveira, 2018; Ruiz-Sanchez et al., 2018). The species of the genus occur from southern Mexico to Argentina, from sea level up to 2300 m (Judziewicz & Clark, 2007) and are found in the understory and along the borders of forests (Judziewicz et al., 1999). Brazil is the center of diversity with 46 species; considering both abundance and diversity, the richest domain is the Brazilian Atlantic Forest with 43 species (Sendulsky, 1992; Sendulsky, 1995; Sendulsky, 1997; Burman & Filgueiras, 1993; Filgueiras & Santos-Gonçalves, 2004; Santos-Gonçalves et al., 2012; Parma et al., 2016; Vinícius-Silva et al., 2016). Sendulsky (1997) additionally cites two species in the Amazonian domain and one in the Cerrado domain.

Merostachys is distinguished from the other genera of Neotropical woody bamboos by the following combination of characters: pachymorph rhizomes; hollow culms (rarely pithy) with one bud per node, which develops into a triangular structure bearing subequal branches in a fan-shaped (apsidate) array; pseudopetiolate culm leaves with the blade reflexed; synflorescences terminal racemose bearing sessile or short-pedicellate spikelets, usually with rudimentary spikelets at the apex and at the base; spikelets with glumes and lemma muticous, mucronate or awned and usually with a single floret which have a rachilla extension; two glumes with different lengths; rachilla extension with an apical rudiment; and nucoid caryopses (McClure, 1973; Judziewicz et al., 1999; Vinícius-Silva et al., in preparation).

During fieldwork in eastern Minas Gerais and Espírito Santo states, and morphological analyses in herbaria, two new species of *Merostachys* were collected and the reproductive structures of *M. bifurcata* Send. were recorded. The new species are here described and a complete description of *M. bifurcata* is provided. All mentioned above species are illustrated here and the conservation status of each one is assessed. Additionally, a key to the species of *Merostachys* occurring in Espírito Santo and eastern Minas Gerais state is provided. In addition, the epitypification and an emended description of *M. bifurcata* is proposed as well.

Material and Methods

In Minas Gerais, collections were made in the Parque Estadual Alto Cariri located in the municipality of Santa Maria do Salto; additional material from the municipality of Bandeira, from a private property known as Mata do Boi Rajado, was analyzed as well. In Espírito Santo, botanical material was collected in the Reserva Ecológica Santa Lúcia, located in the municipality of Santa Teresa. Material from the herbaria BHCB, CEPEC, HRCB, HUEFS, ISC, MO, NY, SP, SPF, US and VIC was also analyzed (Thiers, 2018).

Morphological terminology follows McClure (1966) and Judziewicz et al. (1999). Measurements of the structures were taken by ruler and caliper in order to obtain their minimum and maximum dimensions. The width of sheaths and blades of culm and foliage leaves was taken at their widest points. The length of the foliage leaf blades was taken excluding the pseudopetiole, which was measured separately.

The identification key refers to species from Espírito Santo and eastern Minas Gerais states. However, as most of those species can be found in other locations, the geographical distribution of each species is also given in the key.

In addition to the descriptions, a short commentary on the conservation status of each taxon according to the standards of the International Union for Conservation of Nature (IUCN) is provided (IUCN, 2017).

Taxonomic Treatment

Merostachys bifurcata Send. Type: Brazil. Bahia: Porto Seguro, Parque Nacional Monte Pascoal, 14 Km E of BR 101 at a point 13 Km N of Itamarajú, 110 m, 12 May 1976 [veg.], *T. R. Soderstrom, G. F. Russell & J. Hage 2202* (holotype: US!; isotypes: CEPEC!, HUEFS!, ISC!, MO!, NY!, SP!).

Epitype (here designated): Brazil. Bahia: Prado, Reserva Florestal da Brasil de Holanda Industrias S.A.; the entrance at Km 18 east of Itamarajú on road to Prado, 8 Km from entrance, 17º11'S, 39º20'W, 22 Oct. 1993 [fl.], *W.W. Thomas, A. Carvalho, A. Amorim, J. Jardim & S. Sant'Ana 10134* (Epitype MO!; Isoepitypes HUEFS!, NY!, SP!) (Fig. 1).

Plants initially erect then arching toward the apex. Culms 5–10 m tall. Midculm internodes 12–78 cm long, 0.5–1.5 cm in diameter, cylindrical, yellow-white with green spots, scabrous, infranodal band of trichomes absent; walls 0.5–1.5 mm thick, ratio of wall thickness: culm diameter 0.2–0.4, thin to moderately thick, lumen 0.3–1.3 cm in diameter, large, not filled by a pith; nodes not prominent, brown to black, without a fringe of trichomes at the nodal line. Culm leaves 22–26.5 cm long; sheaths 18–25 × 2–4.5 cm, adaxially glabrous, shiny, abaxially scabrous, sometimes with layer of wax; margins apically fimbriate, the overlapping margin ciliate toward the apex; auricles absent; fimbriae 4–9 mm long, not fused, sinuous, yellow-white to brown; inner ligules 4–6 mm long, bifurcate, pubescent, the apex ciliate; blades 4–9.5 × 0.2–0.4 cm, margins scabrous, adaxially glabrous, abaxially glabrous. Branch complement with 13–28 branches, the branches 14–35 cm long, 0.8–1 mm in diameter, lower nodes not rebranching; nodes not prominent, brown to black. Foliage leaves 8–17 per complement; sheaths 1.5–2.3 cm × 2–3 mm, pubescent to hispid, overlapping margin ciliate; auricles absent; fimbriae 3–8 mm long, not fused, erect at the base and sinuous toward the apex, yellow-white to brown, generally yellow-white at the base and brown toward the apex; outer ligules 0.1–0.2 mm long, the apex ciliate; inner ligules 0.3–0.4 mm long, truncate, pubescent, the apex ciliate; pseudopetioles 1.5–2 mm long, brown to black, hispid, twisted; blades 6–13 × 0.5–1.5 cm, L:W = 4–19.5, lanceolate, adaxially with 2–4 scabrous ribs along one margin, glabrous elsewhere, abaxially with a band of minute strigose antrorse trichomes in the marginal stripe, glabrous elsewhere, without a tuft of hispid trichomes at the base, the base asymmetric, the apex acuminate, margins scabrous. Synflorescences 2–3 cm long, racemose, with 8–13 spikelets per raceme, rudimentary spikelets at the apex present, two rows of spikelets in one rank, rows pectinate and being less than 5 degrees apart; rachis tomentose to hispid; pedicels ca. 1 mm long, tomentose to hispid. Spikelets 10–12 × 1.5–2 mm, 1-flowered, solitary; glumes 2, unequal; lower glume 3–5.5 × 0.8–1 mm, ca. $^1/_4$ to $^1/_2$ of the spikelet length, including the awn, awn ca. 0.8–2 mm long, 1-nerved, adaxially glabrous, abaxially sericeous to hispid, margins ciliate; upper glume 10–11 × 3–4 mm, generally with length equal to or greater than spikelet, including the awn, awn ca. 2 mm long, 11-nerved, adaxially glabrous and dark-spotted, abaxially pubescent to hispid, margins ciliate; lemma 9–10 × 4–5 mm, including the awn, awn 0.5–1 mm, sometimes mucronate, 12–15-nerved, adaxially glabrous and dark-spotted, abaxially sericeous to hispid, dull; palea 4–10 × 2–3 mm, muticous, 6–8-nerved, abaxially glabrous, abaxially glabrous to pubescent, sometimes sericeous, dull, margins ciliate, 2-keeled, keels ciliate towards the apex; rachilla extension 6–8 mm long, with a rudiment at the apex; lodicules 3, membranous, anterior pair ca. 0.8 × 0.5 mm, posterior ca. 0.3 × 0.25 mm; stamens 3, anthers ca. 3 mm, ochre; ovary elongated, style bifid, stigmas 2. Caryopsis not seen.

Distribution and habitat.—Merostachys bifurcata is recorded for Bahia and Espírito Santo states (Sendulsky, 1997; Flora do Brasil, 2020) in an elevational range between 30 and 693 m. This species occurs in the understory and along the margins of Brazilian Atlantic Forest in vegetation known as Ombrophilous Forest, according to the classification of Veloso et al. (1991) and Tabuleiro Forest, according to the classification of Rizzini (1992).

Conservation.— We applied the IUCN (2017.3) criteria and propose an IUCN red list category of vulnerable (VU = B2a) given the low number of locations (less than ten).

Additional Specimens Examined. BRAZIL. Bahia: Belmonte: Reserva Gregorio Bondar of CEPLAC's Estação Experimental, 10 Apr. 1976 [veg.], *T. R. Soderstrom, G. F. Russell & J. Hage 2138* (CEPEC, ISC, MO, SP, US). Ibirataia: 23 Km N of Ibirataia, on side road connecting with BR 101, Fazenda Macedonia, 04 Apr. 1976 [veg.], *C. E. Calderón, T. S. Santos & L. B. Oliveira 2359* (CEPEC, MO, NY, SP, US). Ituberá: Estrada Guandú-Ituberá, 16 Km de Ituberá, 2006, [veg.], *A. P. Santos-Gonçalves 594* (VIC). Santa Luzia: Ramal do Barreiro, ca. 4.9 Km da Estrada Canavieiras/Santa Luzia, Fazenda Lagos, próximo à plantação de mamão, 03 June 2009 [veg.], *F. M. Ferreira 2118* (HUEFS). Porto Seguro: Parque Nacional Monte Pascoal, Entre Boca da Mata e Represa da Mata, 20 Feb. 2017 [veg.], *R. Vinícius-Silva, C. J. Costa & J. S. Souza 119* (VIC); Parque Nacional Pau Brasil, Estrada Pau Brasil, 16 Feb. 2017 [veg.], *R. Vinícius-Silva & C. J. Costa 115* (VIC). **Espírito Santo:** Conceição da Barra: Reserva Biológica do Córrego Grande (IBAMA), a 31 Km de Pedro Canário (na Avenida Aracruz) e 6 Km da base do IBAMA, 19 Feb. 1994 [fl.], *J. R. Pirani, J. A. Kallunki, I. Cordeiro & P. L. R. Moraes 3034* (SPF, VIC).

Merostachys bifurcata can be recognized among all the other species of the genus by its bifurcate inner ligule of the culm leaf. Besides that, this species is also distinguished by its small synflorescences 2–3 cm long which have few spikelets (8–12 spikelets per raceme).

Merostachys judziewiczii Vinic.-Silva, L.G. Clark & Santos-Gonç., **sp. nov.—**Type: Brazil. Minas Gerais: Santa Maria do Salto, Parque Estadual do Alto Cariri, Refúgio de Vida Silvestre Mata dos Muriquis, Região da Areia Branca, 16º26'09.5"S, 40º04'57.5"W, 808 m, 13 May 2014 [fl.], *R. V. Silva, J. I. Silva, J. V. Nunes & R. B. Sansão 23* (holotype: VIC; isotypes: HUEFS, ISC, MO) (Fig. 2).

Diagnosis: This species is distinguished from all the other species of *Merostachys* by the occurrence of internodes scabrous; branch complement with 30–171 branches; synflorescence racemose with two rows of spikelets in two ranks; rows pectinate and being 180 degrees apart, rachis tomentose, sinuous; and spikelets in groups of 2–4, sometimes solitary.

Plants initially erect then arching toward the apex. Culms 5–20 m tall. Midculm internodes 18–90 cm long, 0.6–3 cm in diameter, cylindrical, green, scabrous, infranodal band of trichomes absent; walls 2.3–3.8 mm thick, ratio of wall thickness: culm diameter 0.2–0.4, thin to moderately thick, lumen 0.5–1.9 cm in diameter, large, not filled by a pith; nodes not prominent, brown, with a fringe of trichomes at the nodal line. Culm leaves 28.5–41 cm long; sheaths 22.5–35 × 7.2–12.5 cm, adaxially glabrous, shiny, abaxially sericeous, sometimes sparsely hirsute; margins apically fimbriate, the overlapping margin ciliate from the base toward the apex; auricles absent; fimbriae 1.3–

5 mm long, not fused, erect at the base and sinuous toward the apex, yellow-white to red-white; inner ligules 0.7–4 mm long, truncate, pubescent, the apex ciliate; blades ca. 6 × 1.9 cm, margins scabrous, adaxially scabrous, abaxially scabrous, hirsute toward at the apex. Branch complement with 30–171 branches, the branches 20–83.5 cm long, 1.2–2 mm in diameter, lower nodes rebranching; nodes not prominent, brown. Foliage leaves 6–20 per complement; sheaths 1.3–9 cm × 1.6–7 mm, pubescent, overlapping margin ciliate; auricles absent; fimbriae 0.4–4.2 mm long, not fused, erect to sinuous, scant, often deciduous, yellow-white to red-white, generally yellow-white at the base and red-white toward the apex; outer ligules 0.1–0.5 mm long, the apex ciliate; inner ligules 0.3–1.4 mm long, truncate, pubescent, the apex ciliate; pseudopetioles 2.6–8.2 mm long, brown, glabrous to pubescent, twisted; blades 10.2–19 × 2–3.6 cm, L:W = 3.9–7.7, lanceolate, adaxially with 2–3 scabrous marginal ribs along one margin, the opposite margin and apex with minute strigose antrorse trichomes, glabrous elsewhere, sometimes sparsely hirsute, abaxially with a band of minute strigose antrorse trichomes between the marginal stripe and the rest of the blade along the upper $^{2}/_{3}$ of the marginal stripe, glabrous elsewhere, without a tuft of hispid trichomes at the base, the base asymmetric, the apex acuminate, margins scabrous. Synflorescences 3.4–13.4 cm long, racemose, with 28–90 spikelets per raceme, rudimentary spikelets at the apex present, two rows of spikelets in two ranks, rows pectinate and being 180 degrees apart; rachis tomentose and sinuous; pedicels 0.5–1 mm long, pubescent. Spikelets 8.5–9 × 1–1.5 mm, 1-flowered, in groups of 2–4, sometimes solitary; glumes 2, unequal; lower glume 0.8–2 × 0.3–1.5 mm, ca. $^{1}/_{5}$ of the spikelet length, muticous, 1-nerved, adaxially glabrous and dark-spotted, abaxially pubescent, margins ciliate; upper glume 4–6 × 1.7–2.5 mm, $^{2}/_{5}$ to $^{3}/_{5}$ of the spikelet length, including the awn, awn ca. 0.5 mm long, 7–10-nerved, adaxially glabrous and dark-

spotted, abaxially puberulous, margins ciliate; lemma 6.5–8 × 3–3.8 mm, muticous, 9–12-nerved, adaxially glabrous and dark-spotted, abaxially setose, dull; palea 6.5–8.5 × 3 mm, 6–8-nerved, adaxially glabrous and dark-spotted, abaxially puberulous, dull, muticous, 2-keleed, keels ciliate towards the apex; rachilla extension 5.5–7.5 mm long, with a rudiment at the apex; androecium and gynoecium depauperate in the material examined. Caryopsis not seen.

Distribution and habitat.—Merostachys judziewiczii is known only from the state of Minas Gerais, Brazil, where two populations have been documented, one restricted the Parque Estadual Alto Cariri, Santa Maria do Salto municipality, and another in Mata do Boi Rajado, in Bandeira municipality. The species is found at 350–808 m elevation, along the borders of Brazilian Atlantic Forest in vegetation known as Semideciduous Montane Forest, according to the classification of Veloso et al. (1991).

Conservation.— We applied the IUCN criteria (2017.3) and propose an IUCN red list category of vulnerable (VU=D2) given the low number of locations (equal to two).

Etymology.—The specific epithet honors Dr. Emmet J. Judziewicz, an American researcher who has dedicated his career to research on grasses, mainly woody bamboos, and who has contributed greatly to knowledge of this plant group.

Additional Specimens Examined. BRAZIL. Minas Gerais: Bandeira: Mata do Boi Rajado, ca. 14 Km da sede de Bandeira, na divisa com a Bahia, 04 Oct. 2003 [fl.], *A. Salino, R. C. Mota, N. F. O. Mota, & P. H. A. Melo 8994* (BHCB, HRCB). Santa Maria do Salto: Parque Estadual do Alto Cariri, Refúgio de Vida Silvestre Mata dos Muriquis, Região da Areia Branca, 16°25’54”S, 40°05’04.3”W, 13 May 2014 [fl.], *R. V. Silva, J. I. Silva, J. V. Nunes, R. B. Sansão & W. O. Marques 22* (VIC).

Merostachys judziewiczii resembles *M. burmanii* Send. in having spikelets with similar dimensions. Besides that, the spikelets of the both species are grouped. On the other hand, *M. judziewiczii* is distinguished by the indument of the internodes; presence of a fringe of trichomes at the nodal line; absence of the infranodal band of trichomes in the culm; and indument of the lemma (Table 1).

Merostachys lagevianae Vinic.-Silva, L.G. Clark & Santos-Gonç. **sp. nov.**—Type: Brazil. Espírito Santo: Santa Teresa, Estação Biológica Santa Lúcia, Trilha principal para o túmulo de Augusto Rushi, ao longo do rio Timbuí, 19º58’12.6”S, 40º31’53.9”W, 666 m, 23 Apr. 2016 [veg.], *R. Vinícius-Silva, C. J. Costa & T. S. Costa 91* (holotype: VIC; isotypes: ISC, MG, NY) (Fig. 3).

Diagnosis: This species is distinguished from all the other species of *Merostachys* by its culm internodes scabrous with an infranodal band of velutinous trichomes; culm and foliage leaf sheaths abaxially hispid; branch complement with 11–22 branches; branches 3.5–4.5 mm in diameter; and pseudopetioles gray-white to black, hispid at the base, glabrous elsewhere.

Plants with culms initially erect then clambering on vegetation. Culms 20–22 m tall. Midculm internodes 90–134 cm long, 1–3 cm in diameter, cylindrical, yellow-green, scabrous, infranodal band of velutinous trichomes present, bands 9–18 mm wide; walls 2.1–4.1 mm thick, ratio of wall thickness: culm diameter 0.1–0.6, very thin to thick, lumen 0.2–1.8 cm in diameter, narrow to large, not filled by a pith; nodes not prominent, brown, without a fringe of trichomes at the nodal line. Culm leaves 45.5–57 cm long; sheaths 29–52 × 6–13.5 cm, adaxially glabrous, shiny, abaxially hispid, margins apically fimbriate, the overlapping margin ciliate from the base toward the apex; auricles absent; fimbriae 3–26 mm long, not fused, sinuous, brown at the base and yellow-white toward the apex; inner ligules 1.5–3.9 mm long, truncate, sericeous, the apex ciliate; blades 11–16.5 × 1.2–1.4 cm, margins scabrous, adaxially sparsely scabrous, abaxially glabrous to sparsely scabrous. Branch complement with 11–22 branches, the branches 25–91 cm long, 3.5–4.5 mm in diameter, lower nodes rebranching; nodes not prominent, brown. Foliage leaves 9–17 per complement; sheaths 7.4–14.5 cm × 6.6–11.8 mm, glabrous to hispid, hispid trichomes generally found on the apex and near the margins, overlapping margin ciliate; auricles absent; fimbriae 2–21 mm long, not fused, sinuous, brown at the base and yellow-white toward the apex; outer ligules 0.2–0.6 mm long, the apex ciliate; inner ligules 1–1.7 mm long, truncate, pubescent, the apex ciliate; pseudopetioles 6.8–10.8 mm long, gray-white to black, hispid at the base, glabrous elsewhere, twisted; blades 19.5–37.5 × 3.8–8.8 cm, L:W = 3.3–7.4, lanceolate, adaxially with 1–3 scabrous marginal ribs along one margin, the opposite margin and apex with minute antrorse strigose trichomes, glabrous elsewhere, abaxially sparsely scabrous with a band of minute antrorse strigose trichomes between the marginal stripe and the rest of the blade along the marginal stripe, the base asymmetric, the apex acuminate, margins scabrous. Synflorescences not seen.

Distribution and habitat.— *Merostachys lagevianae* is known , at the moment, only from the state of Espírito Santo, Brazil, where has been documented at the Estação Biológica Santa Lúcia in Santa Teresa municipality. The species is found at ca. 670 m elevation, along the borders of Brazilian Atlantic Forest in vegetation known as Semideciduous Submontane Forest, according to the classification of Veloso et al. (1991).

Conservation.— We applied the IUCN criteria (2017.3) and propose an IUCN red list category of critically endangered (CE=B2a) given the very low number of locations (equal to one).

Etymology.— The specific epithet honors Dr. Pedro Lage Viana, a Brazilian researcher, who has contributed greatly to knowledge of the Neotropical woody bamboos, especially the Arthrostylidiinae.

Additional specimens examined. BRAZIL. Espírito Santo: Santa Teresa: Estação Biológica Santa Lúcia, trilha paralela à trilha principal, atravessar ponte José Molino e seguir à direita, ao longo do rio Timbuí, 23 Apr. 2016, [veg], *R. Vinícius-Silva, C. J. Costa & T. S. Costa 92* (VIC).

Merostachys lagevianae is similar to *M. ternata* Nees in its foliage leaf blade dimensions (19.5–37.5 × 3.8–8.8 cm, L:W = 3.3–7.4 in *M. lagevianae* and 20–42 × 3–10.7 cm, L:W= 4–6.3 in *M. ternata*). These species, however, are distinguished mainly by culm height, indument of the culm and foliage leaf sheaths and number of branches in the branch complement (Table 2).

Key to the species of *Merostachys* in Espírito Santo and eastern Minas Gerais states

1. Infranodal band of trichomes in the culm present.
    2. Fimbriae of both culm and foliage leaves fused at the base, forming a cuneiform structure of laminar appearance…………….……*M. fimbriolaminata* (Minas Gerais).
    2. Fimbriae of both culm and foliage leaves not fused.
        3. Branches 0.7–2 mm in diameter.

4. Culm internodes covered by lanose trichomes, sometimes glabrous; spikelets grouped in pairs, sometimes in groups of 4 or solitary….*M. burmanii* (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo).

4. Culm internodes glabrous or scabrous, not covered by lanose trichomes; spikelets always solitary.

5. Foliage leaf blades abaxially with minute strigose, antrorse trichomes ....*M. fischeriana* (Bahia e Minas Gerais).

5. Foliage leaf blades abaxially without minute strigose, antrorse trichomes.

6. Foliage leaf blades abaxially with a tuft of hispid trichomes at the base……………………………………………………………… ....*M. claussenii* var. *claussenii* (Minas Gerais e Rio Grande do Sul).

6. Foliage leaf blades abaxially without a tuft of hispid trichomes at the base.

7. Branches 1.8 mm in diameter; synflorescence with a sterile bract at the base; spikelets 10–14 × 2.5–4 mm………………………….. ....*M. claussenii* var. *mollior* (Minas Gerais).

7. Branches 0.7–1.2 mm in diameter; synflorescence without a sterile bract at the base; spikelets 6–8 × 1–1.5 mm……………….. ………………………………………*M. exserta* (Minas Gerais).

3. Branches 2.8–7 mm in diameter.

8. Culm leaf sheath abaxially hispid………..*M. lagevianae* (Espírito Santo).

8. Culm leaf sheath abaxially glabrous to sparsely hirsute or scabrous and covered by lanose trichomes.

9. Culm leaf sheaths abaxially scabrous and covered by lanose trichomes; branch complement with 3–7 branches; synflorescences with spikelets grouped, in pairs or triads……………………*M. ternata* (Bahia, Espírito Santo, Minas Gerais, Paraná, Rio Grande do Sul and Santa Catarina).

9. Culm leaf sheaths abaxially sparsely hirsute; branch complement with 10–46 branches; synflorescences with spikelets solitary……………..……
……………….........*M. riedeliana* (Bahia, Minas Gerais and São Paulo).

1. Infranodal band of trichomes in the culm absent.

10. Culm leaves with a bifurcate inner ligule……………………………………….. ....*M. bifurcata* (Bahia and Espírito Santo).

10. Culm leaves with a truncate inner ligule.

11. Midculm internodes hispid, covered by irritating trichomes………………….. ……………………………………………………*M. tatianae* (Minas Gerais).

11. Midculm internodes glabrous, scabrous, sericeous or tomentose, without irritating trichomes.

12. Lumen sometimes filled by a pith in the midculm; foliage leaf sheath hispid……………………………………………*M. espessa* (Minas Gerais).

12. Lumen never filled by a pith in the midculm; foliage leaf sheath glabrous, scabrous or glabrous to pubescent.

13. Fringe of trichomes at the nodal line present.

14. Branches 2.3–5 mm in diameter; spikelets always solitary and 17–20 mm long; lemma pubescent to sericeous…………..……………….
……………………………*M. fistulosa* (Minas Gerais and São Paulo).

14. Branches 1.2–2 mm in diameter; spikelets in groups of 2–4, sometimes solitary, and 8.5–9 mm long; lemma setose………………..
……………………………………*M. judziewiczii* (Minas Gerais).

13. Fringe of trichomes at the nodal line absent.

15. Culm internodes glabrous to scabrous, not covered by a white waxy layer; spikelets with dull florets, the upper glume forming an acute angle with the rachis; lemma sparsely sericeous………………
......................................*M. brevigluma* (Minas Gerais and São Paulo).

15. Culm internodes glabrous, covered by a white waxy layer; spikelets with shiny florets, the upper glume forming an obtuse angle with the rachis; lemma glabrous.

16. Branches 3–4.5 in mm diameter..
.....................................*M. procerrima* (Bahia and Espírito Santo).

16. Branches 0.5–2 mm in diameter.

17. Foliage leaves bearing auricles and curly fimbriae; foliage leaf blades abaxially with a band of minute antrorse strigose trichomes between the marginal stripe and the rest of the blade………………………………………………………
…..*M. calderoniana* (Bahia, Espírito Santo and Minas Gerais).

17. Foliage leaves without auricles, bearing straight fimbriae; foliage leaf blades abaxially without a band of minute antrorse strigose trichomes……………………………………………
..........*M. leptophylla* (Bahia, Espírito Santo and Minas Gerais).

Acknowledgments

We acknowledge support from the following funding agencies: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) in the International Doctoral Program in Sandwich (PDSE, nº 88881.135178/2016-01 to R. Vinícius-Silva), Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG, grant APQ-03255-16 to A.P. Santos-Gonçalves), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grants 563545/2010-0-REFLORA to A.P. Santos-Gonçalves and 401526/2014-3-PVE to R.P. Oliveira), Bamboos of the Americas (BOTA) and the Ned Jaquith Foundation (grants to R. Vinícius-Silva to support fieldwork). We thank Antônio Souza, Cristielle de Jesus-Costa, José Ilton da Silva and Tiago de Souza Costa for help with the fieldwork. We also thank Reinaldo Pinto for the illustrations.

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TABLE 1. A morphological comparison of *M. judziewiczii* and *M. burmanii*

Characters	***M. judziewiczii***	***M. burmanii***
Internode indument	Scabrous	Glabrous to scabrous
Fringe of trichomes at the nodal line	Present	Absent
Infranodal band of trichomes in the culm	Absent	Present
Indument of the foliage leaf sheaths	Pubescent	Glabrous
Synflorescence organization	Two rows of spikelets in two ranks, rows pectinate and being 180 degrees apart	Two rows of spikelets in one rank, rows pectinate and being less than 10 degrees apart
Spikelet grouping	2–4, sometimes solitary	Usually 2, sometimes 4 or solitary
Length of spikelets (mm)	8.5–9	8–11
Lemma indument	Setose	Pubescent
Elevation (m)	350–808	400–1600
Distribution	Minas Gerais state	Bahia, Espírito Santo, Minas Gerais, São Paulo and Rio de Janeiro states

TABLE 2. A morphological comparison of *M. lagevianae* and *M. ternata*

Characters	***M. lagevianae***	***M. ternata***
Culm height (m)	20–22	8–10
Culm leaf sheath indument	Hispid	Scabrous, covered by lanose trichomes
Number of branches per branch complement	11–22	3–7
Lower nodes rebranching	Yes	No
Foliage leaf sheaths indument	Glabrous to hispid	Glabrous to lanose, sometimes sparsely hirsute
Pseudopetiole color	Gray-white to black	Brown
Pseudopetiole indument	Hispid at the base, glabrous elsewhere	Glabrous to pubescent
Elevation (m)	ca. 670	5–500
Distribution	Espírito Santo state	Bahia, Espírito Santo, Minas Gerais, Rio Grande do Sul, Santa Catarina, São Paulo and Paraná states

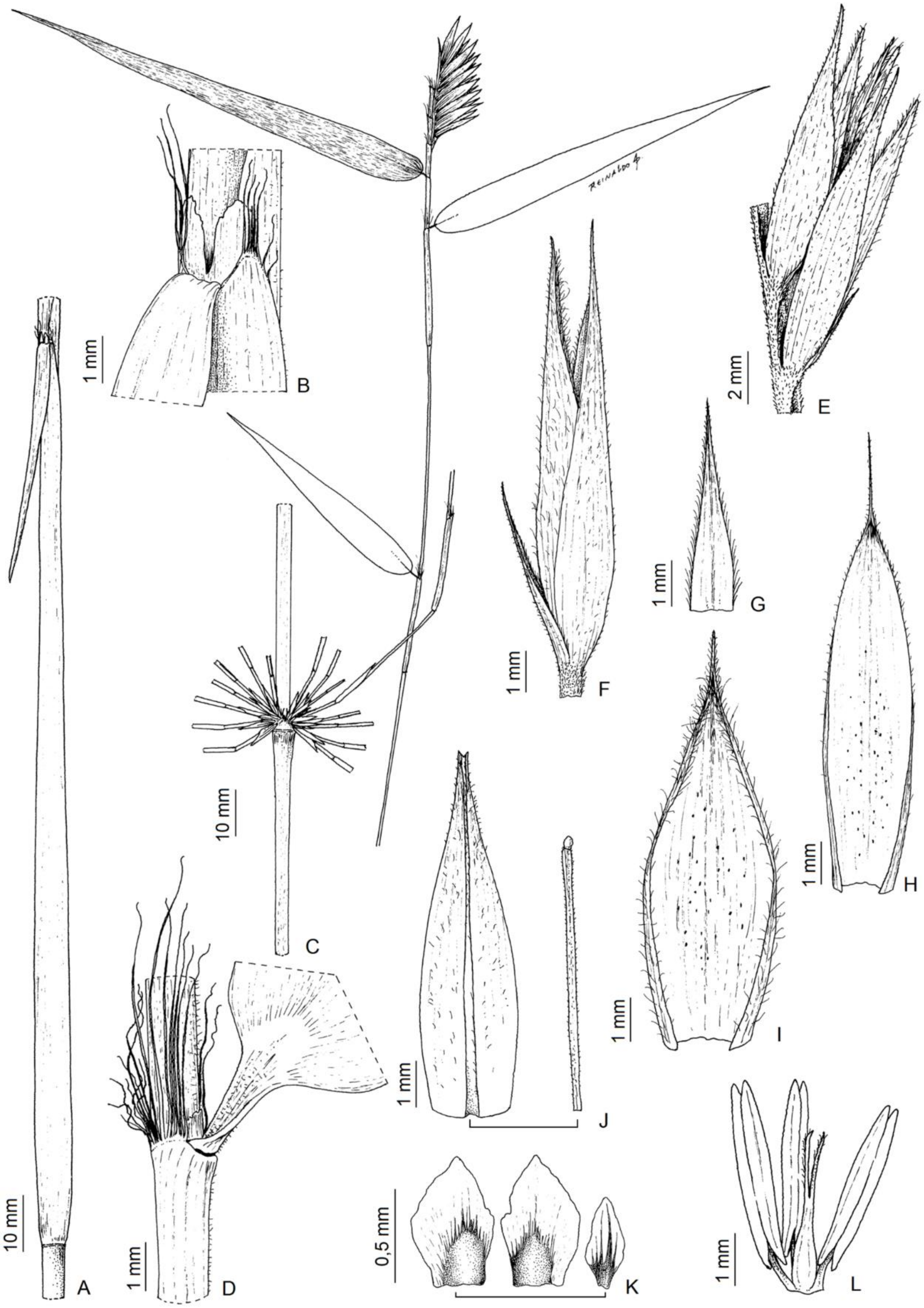

Fig. 1. *Merostachys bifurcata*. **A.** Internode and culm leaf. **B.** Ligular area of a culm leaf with fimbriae highlighting the bifurcate inner ligule. **C.** Branch complement with floriferous branch. **D.** Ligular area of a foliage leaf with fimbriae. **E.** Section of the synflorescence. **F.** Spikelet. **G.** Lower glume (adaxial view). **H.** Upper glume (adaxial view). **I.** Lemma (adaxial view). **J.** Palea (l, abaxial view) and rachilla extension (r). **K.** Lodicules. **L.** Androecium and gynoecium. A and B based on *A. P. Santos-Gonçalves 594*; C–L based on *W. W. Thomas et al. 10134*. (Illustration by Reinaldo Pinto).

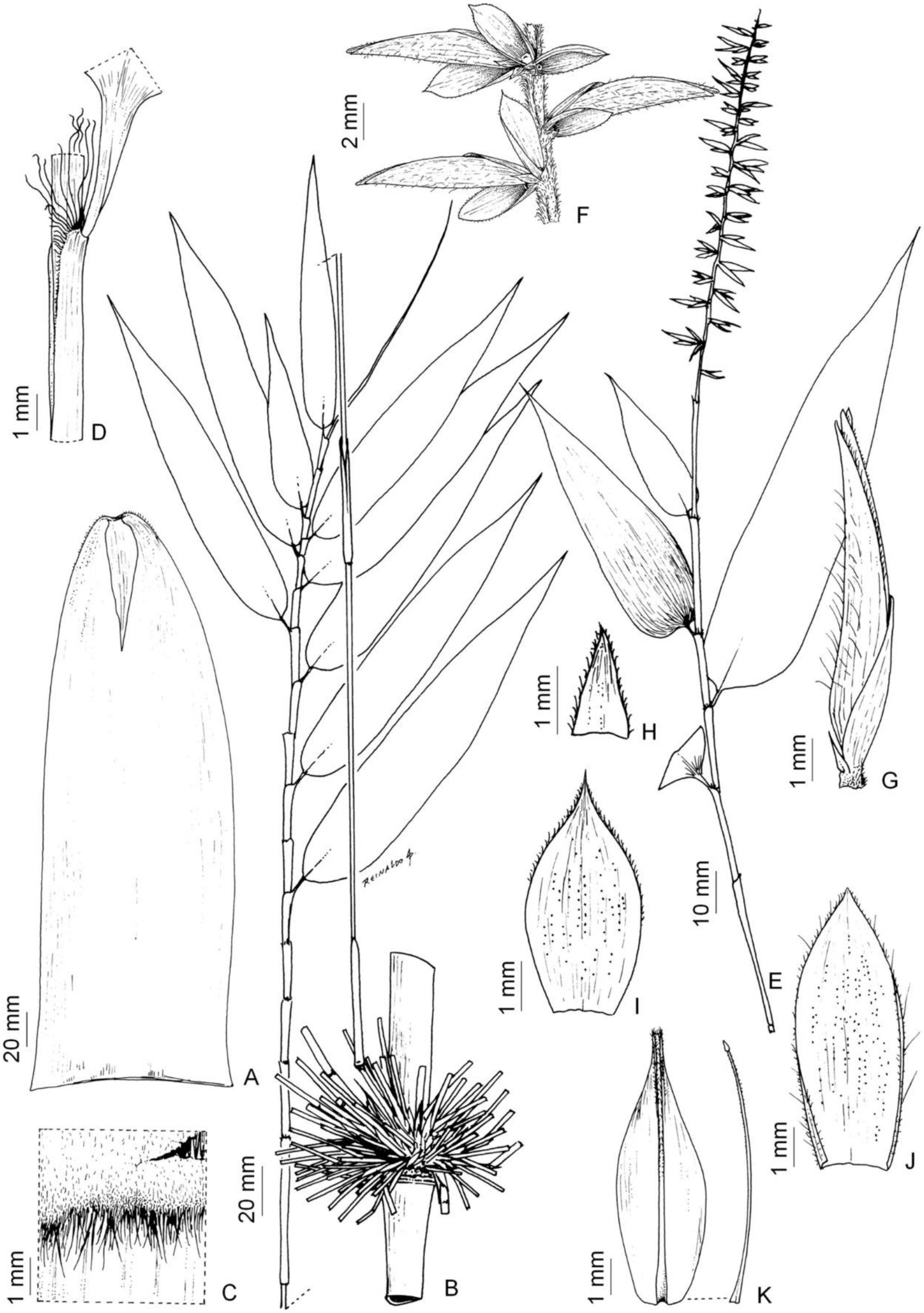

Fig. 2. *Merostachys judziewiczii*. **A.** Culm leaf. **B.** Branch complement with vegetative branches and leaves. **C.** Fringe of trichomes at the nodal line. **D.** Ligular area of a foliage leaf with fimbriae. **E.** Floriferous branch. **F.** Section of the synflorescence. **G.** Spikelet. **H.** Lower glume (adaxial view). **I.** Upper glume (adaxial view). **J.** Lemma (adaxial view). **K.** Palea (l, abaxial view) and rachilla extension (r). Based on *R. V. Silva et al. 23* - holotype. (Illustration by Reinaldo Pinto).

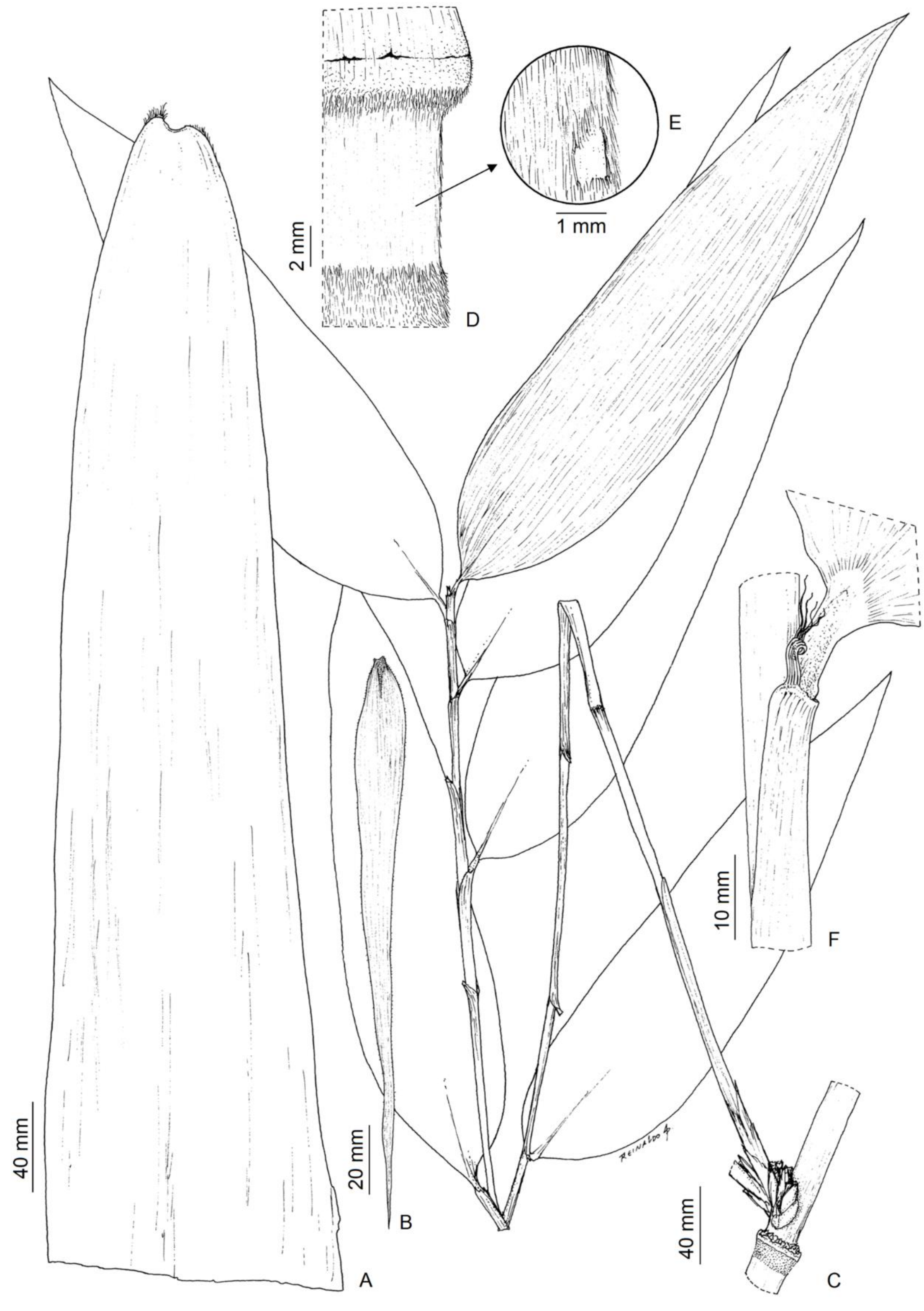

Fig. 3. *Merostachys lagevianae.* **A.** Culm leaf sheath. **B.** Culm leaf blade. **C.** Branch complement with vegetative branch and leaves. **D.** Infranodal band of velutinous trichomes in the culm. **E.** Detail of velutinous trichomes. **F.** Ligular area of a foliage leaf with fimbriae. A and C–F based on *R. Vinícius-Silva et al. 91* - holotype; B based on *R. Vinícius-Silva et al. 92*. (Illustration by Reinaldo Pinto).

CAPÍTULO IV

VINÍCIUS-SILVA *ET AL.*: MOLECULAR PHYLOGENETICS OF *MEROSTACHYS*

Molecular phylogenetics of *Merostachys* (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae) based on multi-locus plastid sequences

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Manuscrito submetido ao Periódico *Botanical Journal of the Linnean Society*

ABSTRACT

Merostachys is a Neotropical woody bamboo genus that occurs in the understory and along forest borders. Taxonomic studies of its species have been carried out by our research team and morphological analyses allowed us to recognize morphological groups within the genus. Previous sparsely sampled molecular analyses supported *Merostachys* as monophyletic and sister to *Actinocladum* or *Athroostachys*. We provide a plastid phylogenetic estimation for *Merostachys* based on a broader taxon sampling and seven markers (one coding: *ndhF 3'* half; four intergenic spacers: *rps16-trnQ*, *trnC-rpoB*, *trnD-trnT* and *trnT-trnL*; and two introns: *rpl16* and *rps16*). We aimed to test the monophyly of the genus, to verify its relationship with other genera of Arthrostylidiinae, and to test whether the previously identified morphological groups are congruent with molecular data. The monophyly of the genus was confirmed and two well supported clades inside *Merostachys* were recovered, one of which encompasses a polytomy. These clades did not exhibit consistent morphological synapomorphies and were mostly not congruent with the morphological groups; however, the floret surface (shiny vs. dull) was correlated with the two clades. The lack of resolution in *Merostachys*, as exemplified by the polytomy, can be attributed mainly to incomplete lineage sorting, which suggests a recent radiation of this group.

ADDITIONAL KEYWORDS: Evolution - molecular phylogenetics analysis - morphological characters - Plastid DNA - tropical grass.

INTRODUCTION

Merostachys Spreng., with 54 described species, is one of the most species-rich genera of the Arthrostylidiinae (Judziewicz *et al.*, 1999; Bamboo Phylogeny Group [BPG], 2012; Santos-Gonçalves, Carvalho-Okano & Filgueiras, 2012; Parma *et al.*, 2016; Vinícius-Silva *et al.*, 2016; Vorontsova *et al.*, 2016; Ruiz-Sanchez *et al.*, 2018). The genus is easily recognized in the field by the following set of features: (1) pachymorph rhizomes; (2) hollow (rarely pithy) culms with one bud per node, which develops into a triangular structure bearing branches in a fan-shaped (apsidate) array; (3) branches subequal; (4) culm leaves with pseudopetiolate, reflexed blades; (5) terminal racemose synflorescences bearing sessile or short-pedicellate spikelets; (6) synflorescences usually with rudimentary spikelets at the apex and also at the base; (7) spikelets with two unequal glumes, usually with one floret and a rachilla extension; (8) glumes and lemma muticous, mucronate or awned; (9) rachilla extension with an apical rudiment; and (10) a nucoid caryopsis (McClure, 1973; Judziewicz *et al.*, 1999; Vinícius-Silva *et al.*, in preparation).

The genus is distributed from southern Mexico to Argentina, from sea level up to 2300 m (Judziewicz & Clark, 2007) and its species are found in the understory and along the borders of forests (Judziewicz *et al.*, 1999). Most of the described species (46) are found in Brazil and 43 of them are recorded for the Brazilian Atlantic Forest domain, which is considered the center of diversity and endemism for the genus (Sendulsky, 1992; Burman & Filgueiras, 1993; Sendulsky, 1995; Sendulsky, 1997; Filgueiras & Santos-Gonçalves, 2004; Santos-Gonçalves *et al.*, 2012; Parma *et al.*, 2016; Vinícius-Silva *et al.*, 2016). Regarding the other three Brazilian species, one occurs in the Cerrado domain (Sendulsky, 1995) and two in the Amazonian domain (Sendulsky, 1997).

Despite being easily recognized in the field at the generic level, *Merostachys* encompasses species characterized by a long period of vegetative growth (about 30–50 years) between flowering events (Janzen, 1976; Guilherme & Ressel, 2001; Liebsh & Reginato, 2009; Guerreiro, 2014), which limits access to the reproductive structures and makes the identification of some species difficult. General collectors also often ignore vegetative populations of woody bamboos, even though vegetative characters may be helpful in distinguishing species (Soderstrom & Young 1983). In addition, the genus includes some species known only from the type material, which sometimes consists of only leaf or synflorescence fragments from old collections, precluding a complete morphological understanding. Furthermore, some type locations have been deforested or otherwise impacted, such that the plants no longer can be found there. These factors have all contributed to gaps in the taxonomic knowledge of the genus.

Within the Arthrostylidiinae, *Merostachys* is morphologically similar to *Actinocladum* Soderstr., *Athroostachys* Bentham, *Didymogonyx* (L.G.Clark & Londoño) C.D.Tyrrell, L.G.Clark & Londoño and *Rhipidocladum* McClure (McClure, 1973; Judziewicz *et al.*, 1999; Tyrrell *et al.*, 2012). *Merostachys* resembles *Rhipidocladum*, *Didymogonyx* and *Actinocladum* in the presence of fan-shaped branch complements, and it also shares the presence of a nucoid caryopsis and reflexed and deciduous culm leaf blades with *Actinocladum* (Soderstrom, 1981; Judziewicz *et al.*, 1999). *Athroostachys*, in turn, is considered close to *Merostachys* due to the similarity of their spikelets and their usually prominent foliage leaf fimbriae (McClure, 1973).

In a phylogenetic context, molecular studies based on plastid DNA sequence data have strongly supported *Merostachys* as monophyletic, despite the sparse sampling within the genus, and also supported its close relationship with *Actinocladum* (Tyrrell *et* *al.*, 2012; Jesus-Costa, Clark & Santos-Gonçalves, 2018) and *Athroostachys* (Jesus-Costa *et al.*, 2018). Tyrrell *et al.* (2012) did not include *Athroostachys*, recovering *Actinocladum* and *Merostachys* as sister genera. They noted the shared features and the need for more detailed morphological and molecular studies in this clade. Jesus-Costa *et al.* (2018) sampled *Athroostachys* for the first time in a phylogenetic molecular analysis and recovered it as sister to *Merostachys* with *Actinocladum* sister to that clade. These findings suggest new interpretations about the evolution of some characters, mainly those shared by *Actinocladum* and *Merostachys* (Jesus-Costa *et al.*, 2018), because these two genera are morphologically more similar to each other than *Athroostachys* is to either.

Merostachys currently does not have infrageneric categories and, to date, taxonomic studies in the genus have been insufficient to support such a classification. However, recent intensive and detailed morphological work in herbaria provided the basis for the recognition of informal morphological groups (Table 1 and Table 2), although these remain to be tested. We started the morphological work (Vinícius-Silva *et al.*, 2016; Parma *et al.*, 2016; Vinícius-Silva *et al.*, 2018), which was integrated with the results from some other prior studies (Sendulsky, 1995; Sendulsky, 1997; Sendulsky, 2001; Lizarazu, Rúgolo-de-Agrasar & Vega, 2011), in an effort to document and sample all the major morphological variation present within the genus in order to ensure appropriate sampling for a molecular phylogenetic analysis.

In view of the foregoing, we undertook a molecular phylogenetic analysis of *Merostachys* based on a broader sampling and employing multiple plastid DNA regions with the following goals: (1) to test the monophyly of *Merostachys*; (2) to re-evaluate the placement of *Merostachys* with regard to *Actinocladum* and *Athroostachys*; and (3) to estimate species relationships within *Merostachys*, testing previously established informal morphological groupings.

MATERIAL AND METHODS

TAXON SAMPLING

In total we selected 64 species to be analyzed, among which 29 had their sequences generated for this study; sequences of the other 35 species were downloaded from GenBank (https://www.ncbi.nlm.nih.gov/genbank/) (Appendix 1). Leaf material was obtained in the field and dried and stored in silica gel (Chase & Hills, 1991). Our sampling concentrated on *Merostachys*, which was here represented by 31 species. Among them, *Merostachys* sp.1 and *Merostachys* sp.2 refer to two new species which are being described and prepared for publication (Vinícius-Silva *et al.*, in preparation). We also included species from all other Arthrostylidiinae genera with only *Myriocladus* Swallen lacking. All genera of the subtribes Guaduinae and Chusqueinae were also sampled. *Melocanna baccifera* (Roxb.) Kurz and *Bambusa bambos* (L.) Voss (of the Paleotropical woody bamboo clade, Bambuseae) also were included in our analyses and the latter species was chosen to root the phylogenetic trees.

DNA EXTRACTION, AMPLIFICATION, SEQUENCING AND ALIGNMENT

Total genomic DNA was extracted following Doyle & Doyle (1990) and Arbelaéz-Cortés *et al.* (2007) at the Unit of Plant Growth of the Universidade Federal de Viçosa, Minas Gerais state, Brazil. We selected seven markers – one gene (*ndhF 3'* half), four intergenic spacers (*rps16-trnQ*, *trnC-rpoB*, *trnD-trnT* and *trnT-trnL*) and two introns (*rpl16* and *rps16*) based on previous studies with bamboos (Triplett & Clark, 2010;

Tyrrell *et al.*, 2012; Kelchner & BPG, 2013; Jesus-Costa *et al.*, 2018). The amplification primers, sequencing primers and thermal cycler protocols are described in Table 3.

The extracted DNA was amplified by polymerase chain reaction (PCR) on both Techne TC-412 and Techne TC-512 Thermal Cyclers (Wendel Laboratory, Iowa State University, Iowa, USA). PCR reactions were performed using the GoTaq® Green Master Mix, 2x (PROMEGA, Madison, WI, USA) following the protocol with an adjustment for a final volume of 25 µL. Amplification products were cleaned with Polyethylene Glycol precipitation following Paithankar & Prasad (1991) or using the QIAquick® PCR Purification Kit (QIAGEN, GmbH, Hilden, Germany).

Sequencing was performed by an automated 3730×l DNA Analyzer (Applied Biosystems) at the DNA Facility of the Iowa State University Office of Biotechnology. Sequence electropherograms were checked visually, edited, base-called, assembled and aligned manually using Sequencer 4.1 (GeneCodes, Ann Arbor, Michigan). Gaps introduced in the alignment were treated as binary (presence/absence characters) by applying the approach of Simmons & Ochoterena (2000) implemented in SeqState 1.4.1 (Müller, 2005). All individual sequences obtained in this study are deposited in GenBank (Appendix 1).

PHYLOGENETIC ANALYSES

All data were analyzed using Maximum Parsimony (MP), which was performed using PAUP, version 3.1 (Swofford, 1991); Maximum likelihood (ML) using RAxML, version 8.2.10 (Stamatakis, 2014); and Bayesian Inference (BI) carried out in MrBayes, version 3.2 (Ronquist *et al.*, 2012). All analyses were conducted through the CIPRES Science Gateway Portal (Miller, Pfeiffer & Schwartz, 2010) with concatenated data partitions and on each individual marker. Bootstrap support (BS) for the MP and ML analyses was considered strong (90–100%), moderate (80–89%) or poor (≤ 79%). In the same way we classified the Posterior Probability (PP) values for BI as strong ≥ 0.95, moderate 0.90–0.94 and poor ≤ 0.89.

MP was conducted with tree bisection-reconnection (TBR) branch swapping and the initial trees were generated by 10000 random stepwise addition replicates. The strict consensus trees were obtained and support for each node was assessed by bootstrap analysis with 2000 replicates through the heuristic search method. All characters were treated as unweighted and unordered. The ML analyses were carried out using RAxML version 8.2.10 and node support was obtained using the rapid bootstrap algorithm with 1000 replicates (Stamatakis, 2014). The search for the best-scoring ML tree was performed with the general time-reversible model of DNA sequence evolution with gamma-distributed rate heterogeneity (GTRGAMMA model). BI was performed according to the best fit evolutionary model which was selected by the Akaike information criterion (AIC) (Posada & Buckley, 2004) using MrModeltest 2.2 (Nylander, 2004). The Markov chain Monte-Carlo algorithm was executed with four runs with 50 million generations each and sampling every 5000 generations. The first 25% of the trees were discarded as burnin and the remaining trees were used to construct the majority rule consensus tree and then the PP for each node was calculated.

To check the congruence between loci, we applied the procedures following Wiens (1998), conducting the analyses independently on the concatenated dataset partition and on each individual marker. The trees from each marker were compared to identify the presence of supported clades (≥70%) that were incongruent among data partitions. The trees generated from each individual marker did not present any conflict and thus we conducted the combined analysis on the concatenated dataset.

RESULTS

The combined and aligned data resulted in a matrix with 7913 base pairs and 148 indel characters. Among these data, only 4.9% were parsimony informative (Table 4). Table 4 also shows the alignment length and percentage of parsimony informative and variable characters for each individual marker. Some regions of certain species either were not able to be sequenced or were not available in GenBank and thus were considered as missing data (Appendix 1), which represents approximately 13% of the alignment matrix. We performed three different phylogenetic analyses with similar results in the general topology and relationships among groups/clades. However, our results and discussion are based on the BI tree of the combined plastid markers, since this tree presented the best resolved topology (Fig. 1).

We inferred indels in the alignments of all seven markers included in our analyses; most of them were found in the *trnD-trnT* partition (34 coded indels), followed by *rps16-trnQ* (32); *rpl16* (26); *trnC-rpoB* (21); *trnT-trnL* (21); *rps16* (10) and *ndhF* (4). The largest deletion, 245 bp long, was detected in *Rhipidocladum harmonicum* (Parodi) McClure in *trnT-trnL* and the largest insertion, 58 bp, was found in *Chusquea bambusoides* Hack. in *trnD-trnT*. Twenty-two indels were useful to support clades in our phylogenetic analyses (Table 5) and they were mapped on the molecular topology (Fig. 2).

The monophyly of each Neotropical woody bamboo subtribe was highly supported: Chusqueinae (A) – (100 MLBS/100 MPBS/1.00 PP, hereafter in this order); Guaduinae

(B) – (100/100/1.00) and Arthrostylidiinae (C) – (100/100/1.00). Chusqueinae was strongly supported as sister (100/100/1.00) to the Arthrostylidiinae + Guaduinae clade (100/100/1.00). Within the Arthrostylidiinae four main lineages were recovered (Fig. 1): the Glaziophyton clade (I) – (…/97/1.00); the Arthrostylidium clade (II) – (100/99/1.00); the Aulonemia clade (III) – (100/99/1.00); and the Merostachys clade (IV) – (94/85/1.00). The Glaziophyton clade (*Glaziophyton* Franch. + *Cambajuva* P.L.Viana, L.G.Clark & Filg.) was weakly supported as sister to the rest of the subtribe (…/…/0.85).

Within the Arthrostylidium clade (II), the monophyly of *Arthrostylidium* Rupr. was well supported (100/100/1.00), but *Rhipidocladum* was resolved as paraphyletic, with poor support (70/70/0.77) for the position of *R. pittieri* (Hack.) McClure sister to *Arthrostylidium* and strong support for *R. harmonicum* as sister to that clade. Within the Aulonemia clade (III), *Colanthelia* McClure & E.W.Sm. was strongly supported as monophyletic (99/94/1.00), however the BI and ML analyses suggested the non-monophyly of *Aulonemia* Goudot based on the position of *A. queko* Goudot sister to *Colanthelia*, but with poor support (51/…/0.54). On the other hand, the MP analysis (not shown) weakly supported the monophyly of *Aulonemia* (56% BS). *Didymogonyx* was poorly supported (66/64/0.93) as sister to the Aulonemia clade, and this clade was part of a poorly supported trichotomy including *Elytrostachys typica* McClure and the Merostachys clade (IV).

The Merostachys clade (IV) is composed of two subclades (IVa and IVb). Clade IVa (71/61/0.99) is composed of three monophyletic and well-supported genera: *Atractantha* McClure (100/100/1.00); *Alvimia* C.E.Calderón ex Soderstr. & Londoño (100/100/1.00), which are sister to each other and *Filgueirasia* Guala (100/100/1.00), supported as sister to *Atractantha* + *Alvimia*. Clade IVb (100/98/1.00) is composed of *Merostachys*, *Athroostachys* and *Actinocladum*. *Athroostachys* was moderately to strongly supported as sister to *Merostachys* (87/84/0.99) and *Actinocladum* was well supported as sister to *Athroostachys* + *Merostachys*.

Within *Merostachys*, two reasonably well supported main clades (1 and 2) were resolved. Clade 1 (97/89/1.00) encompasses four species with a topology strongly supporting *M. calderoniana* Send. as sister (100/100/1.00) to *M. leptophylla* Send. + *M. procerrima* Send. (66/62/0.98) and *M. rondoniensis* Send. as sister to that clade. Clade 2 (99/88/1.00) encompasses the remaining sampled *Merostachys* species, with the majority of them in a polytomy (clade 3) supported only in the BI analysis (0.93). *Merostachys espessa* Viníc.-Silva, L.G.Clark & Santos-Gonç. was weakly supported (47/…/0.94) as sister to the polytomy, with *M. annulifera* Send. sister to *M. espessa* + clade 3.

Within clade 3, some minor groupings were resolved, of which some received moderate support: *M.* aff. *multiramea* Hack. + *M. speciosa* Spreng. (61/57/0.95); *Merostachys* sp.1 + (*M. ximenae* D.F.Parma, Viníc-Silva & Santos-Gonç. + *M. argyronema* Lindm.) (82/72/0.86); *M. filgueirasii* Send. + *M. mexicana* Ruiz-Sanchez & L.G.Clark (82/85/0.94); *M. ternata* Nees + (*M. tatianae* Santos-Gonç., Carv.-Okano & Filg. + *M. fistulosa* Döll) (…/…/0.89) and *M. riedeliana* Rupr. ex Döll + *M. scandens* Send. (…/…/0.95). The last two grouping were not supported in the ML or MP analyses, but had, respectively, moderate and strong support in BI.

DISCUSSION

According to the results presented here, the three Neotropical woody subtribes (Arthrostylidiinae, Guaduinae and Chusqueinae) are monophyletic, and Chusqueinae is highly supported as sister to the Arthrostylidiinae + Guaduinae clade. Not surprisingly, these results are completely consistent with prior studies (Ruiz-Sanchez, Sosa & Mejía-Saules, 2008; Sungkaew *et al.*, 2009; Ruiz-Sanchez, 2011; Tyrrell *et al.*, 2012; Kelchner & BPG, 2013; Jesus-Costa *et al.*, 2018).

Within the Arthrostylidiinae, the majority of clades observed in our results are congruent with the findings of Tyrrell *et al.* (2012) and Jesus-Costa *et al.* (2018). However, some of these clades are worth highlighting. The Glaziophyton clade is moderately supported as sister to remainder of the subtribe, which was also reported by Tyrrell *et al.* (2012). The clade is composed of *Glaziophyton mirabile* Franch. and *Cambajuva ulei* (Hack.) P.L.Viana, L.G.Clark & Filg. and these two species, besides occurring in montane grassland (Viana, Filgueiras & Clark, 2013), share the presence of strongly tessellate foliage leaf blades (Tyrrell *et al.*, 2012; Viana *et al.*, 2013) and paniculate synflorescences (Viana *et al.*, 2013). In contrast, the analysis of Jesus-Costa *et al.* (2018) showed *G. mirabile* as sister to the rest of the subtribe, although with poor support.

Inside the Aulonemia clade, our analyses showed *Aulonemia* as paraphyletic to *Colanthelia*. These results are different from those found by Tyrrell *et al.* (2012) and Jesus-Costa *et al.* (2018), which resolved these genera as monophyletic albeit with limited sampling. On the other hand, our findings appear to be congruent with Jesus-Costa *et al.* (in preparation), which focuses on a better understanding of the relationship between these two genera based on increased sampling in both.

In contrast to Tyrrell *et al.* (2012) and Jesus-Costa *et al.* (2018), in which *Didymogonyx* was resolved within the Arthrostylidium clade, *Didymogonyx geminatum* (McClure) C.D.Tyrrell, L.G.Clark & Londoño was resolved as sister to the Aulonemia clade in our analyses. This topology is congruent with Tyrrell *et al.* (2018), even though they did not sample *Colanthelia*, in that they recovered a sister relationship between *Didymogonyx* and *Aulonemia*. Despite the sister relationship of *D. geminatum* with *Aulonemia* and *Colanthelia* recovered here and in Tyrrell *et al.* (2018), *Didymogonyx* is most similar to *Rhipidocladum* based on morphological characters (Tyrrell *et al.*, 2012).

The Arthrostylidium clade includes *Arthrostylidium* and *Rhipidocladum* which were recovered, respectively, as monophyletic and paraphyletic. Previous analyses carried out by Tyrrell *et al.* (2012) and Jesus-Costa *et al.* (2018) with an increased sampling indicated the polyphyly of both genera. These two studies resolved *Didymogonyx* (see discussion above) and *Elytrostachys* as members of the Arthrostylidium clade, with *Elytrostachys* moderately to strongly supported as sister to *Arthrostylidium merostachyoides* R.W.Pohl + *Rhipidocladum maxonii* (Hitchc.) McClure, species not included here. In our analyses *Elytrostachys* did not group with any other genus in any major clade and its position in the trichotomy with the Merostachys clade + [the Aulonemia clade + *Didymogonyx*] was extremely poorly supported. The incongruence in the positions of both *Didymogonyx* and *Elytrostachys* may be due to differences in sampling density, especially in the Arthrostylidium clade, because the more comprehensive analysis of Jesus-Costa *et al.* (in preparation) provides moderate to strong support for the position of these two genera in the Arthrostylidium clade.

The Merostachys clade (IV), also supported by Tyrrell *et al.* (2012) and Jesus-Costa *et al.* (2018) encompasses clade IVa (*Alvimia* + *Atractantha* and *Filgueirasia*) and clade IVb (*Merostachys* + *Athroostachys* and *Actinocladum*) (Figs. 1, 2). *Alvimia* and *Atractantha* are sister genera and distributed in the same geographic range in the Brazilian Atlantic Forest in Bahia state (except for *Atractantha amazonica* Judz. & L.G.Clark) (Judziewicz *et al.*, 1999). Besides that, they share the presence of pseudospikelets and the scrambling habit (Soderstrom & Londoño, 1988). *Filgueirasia*, despite being supported as sister to *Alvimia* + *Atractantha*, is recorded only from the Cerrado domain and it exhibits a distinctive morphology, mainly due to the presence of true spikelets, erect culms and branches, and multiple buds (Guala, 2003; Judziewicz *et al.*, 1999).

The main focus of this study was to provide a molecular phylogeny of *Merostachys* with a broader sampling than in previous studies in order to extend knowledge of the evolutionary history of this genus. The first insights about *Merostachys* in a phylogenetic context were reported in studies by Tyrrell *et al.* (2012) and Jesus-Costa *et al.* (2018), both of which strongly supported its monophyly, although based on different sets of species. Our analyses, with expanded sampling, also strongly supported *Merostachys* as a monophyletic genus, and furthermore resolved two well supported clades within it. The morphological groups were mostly not congruent with these two clades, but the comparison allowed us to formulate hypotheses for further testing. Our insights and comments about the relationships among the species of *Merostachys* and among *Merostachys* and its most closely related genera are discussed below.

PHYLOGENETIC RELATIONSHIPS AMONG *MEROSTACHYS*, *ATHROOSTACHYS* AND *ACTINOCLADUM* (CLADE IVb)

The first phylogenetic analysis to include *Athroostachys* was performed by Jesus-Costa *et al.* (2018) and they resolved it as sister to *Merostachys* with strong support, with *Actinocladum* sister to *Athroostachys* + *Merostachys*. We recovered the same topology in our phylogenetic estimation, but with more moderate support for the sister relationship of *Athroostachys* and *Merostachys*. To date, *Athroostachys* encompasses two species (Jesus-Costa *et al.*, 2018), but its type species, *A. capitata* (Hook.) Benth., was previously originally described in *Merostachys* (Hooker, 1840) and only later transferred to its current genus (Hooker & Bentham, 1883).

McClure (1973) described *Athroostachys* as close to *Merostachys* based on its fimbriae and spikelet morphology, reflecting the initial placement of *A. capitata* within *Merostachys*. The same author, nevertheless, emphasized that these features are not enough to infer an evolutionary relationship between them. Indeed, fimbriae are very general in Arthrostylidiinae and it is possible to observe considerable variation in their shape and size among species in the subtribe. Thus, this character is not sufficiently consistent to support a relationship between *Merostachys* and *Athroostachys*. The presence of reflexed and deciduous culm leaf blades also is shared by both genera and by *Actinocladum*, however this feature characterizes other genera in Arthrostylidiinae (Judziewicz *et al.*, 1999; Tyrrell *et al.*, 2012).

The similarities between the reproductive characteristics of *Athroostachys* and *Merostachys* were not detailed by McClure (1973), nevertheless, a short-pedicellate spikelet is the most obvious feature shared by both (Judziewicz *et al.*, 1999). In addition, the presence of a single floret per spikelet and the dimensions of the glumes are similar between *Athroostachys* and most of the species in *Merostachys*. Another probable important feature is the fruit of *Athroostachys*, which unfortunately still is unknown. Both *Merostachys* and *Actinocladum* have a nucoid caryopsis, which is otherwise unknown in the subtribe. For this reason, Jesus-Costa *et al.* (2018) speculated that *Athroostachys* also likely possesses this fruit type.

Despite these similarities, *Athroostachys* exhibits some morphological features that distinguish it from both *Merostachys* and *Actinocladum*: (1) culm leaves with a dark, thickened girdle covered by hirtellous-hispid, light to dark-brown trichomes; (2) a branch complement with three subequal branches arising from a single bud borne on a conspicuous promontory; (3) a capitate synflorescence; and (4) spikelets with the pedicel subtended by a bract (McClure, 1973; Jesus-Costa *et al.*, 2018). These characters appear to be consistent and thus, along with the molecular data, corroborate the generic status of *Athroostachys*.

Actinocladum currently is monotypic, including only *A. verticillatum* (Soderstrom, 1981; Judziewicz *et al.*, 1999); however, other material (including *Pianissola & Clark 179*, which we here sampled) from Bahia state appears to be a new species, although a detailed morphological analysis is necessary to confirm this hypothesis. In addition to the nucoid caryopsis (see above), *Actinocladum* and *Merostachys* share the fan-branching (apsidate) pattern, in which a more or less triangular plate bearing subequal branches on the upper two sides arises from a single bud (Tyrrell *et al.*, 2012). However, as demonstrated by Tyrrell *et al.* (2012), apsidate branching also occurs in other genera of the subtribe (e.g., *Didymogonyx*, *Rhipidocladum*).

Other features also are shared by *Actinocladum* and some species of *Merostachys*. The fimbriae on both culm and foliage leaves in *Actinocladum* are fused basally, and this is also observed in *M. speciosa* and *M. fimbriolaminata* Vinic.-Silva, Cupert.-Eisenl. & Santos-Gonç.; however, in this latter species the fimbriae are almost completely fused (Vinícius-Silva *et al.*, 2016). The internodes in *Actinocladum* are often filled by a pith, which also can be seen in *M. medullosa* and sometimes in *M. espessa*, yet in *Actinocladum* the pith has a spongy consistency, while in *Merostachys* it is tougher. The base of the synflorescence in *Actinocladum* has a minute bract, which also is seen in *M. claussenii* var. *mollior* Döll, but in *Actinocladum* the structure is inconspicuous and in *Merostachys* species it is better-developed (0.7-2.2 cm long) (Vinícius-Silva *et al.*, 2018). Lastly, *Actinocladum* has spikelets with many florets (4-10); although the majority of *Merostachys* species have only one floret per spikelet, *M. pluriflora* Munro ex Camus has 2-3 florets and *M. polyantha* McClure has 4-6 florets.

Actinocladum and *Athroostachys* share few morphological traits, the main similarity being the rudimentary floret on the rachilla extension. In these two genera, this floret is relatively well developed (9.5-15 mm long) and it is possible to distinguish the lemma from the palea, which usually is very small. In contrast, *Merostachys* exhibits a smaller, inconspicuous rudimentary floret (a true rudiment) 0.3-0.5 mm long, and it is difficult to distinguish between its lemma and palea. On the other hand, when we compare *Actinocladum* to the *Merostachys* + *Athroostachys* clade, it is distinguished by the following features: (1) erect habit (*versus* scandent or initially erect and becoming scandent or arching toward the apex); (2) two kinds of foliage leaves: the blades of the upper nodes are larger and broader than those from mid-culm complements (*versus* only one kind of foliage leaf); and (3) long-pedicellate spikelets (*versus* sessile or short-pedicellate) (Soderstrom, 1981; Judziewicz *et al.*, 1999).

Another important feature in this context is related to the habitat of these plants. *Actinocladum* is typical of the Brazilian Savannas (Cerrado) (Soderstrom, 1981; Judziewicz *et al.*, 1999) and is also recorded from a similar area in northeastern Bolivia (Killeen, 1990). The genus is tolerant to drought and fire and has dormant and protected buds at the culm base, which are stimulated to develop after fires (Judziewicz *et al.*, 1999). Meanwhile, *Merostachys* and *Athroostachys* are found in forests, growing in the understory or along the borders (Judziewicz *et al.*, 1999). As the two genera grow in areas with a lower incidence of fires than the Cerrado region, we did not detect the presence of morphological adaptations related to fire tolerance from our fieldwork and we also did not find anything about this in the literature. Probably, in mature individuals of these genera, the rhizomes are not destroyed and can resprout after fire as suggested by Akinlabi *et al.* (2017) for woody bamboos in general.

The sister relationship between *Actinocladum* and *Merostachys* initially inferred by Tyrrell *et al.* (2012) caused us to consider synonymizing these genera based on their morphological similarities, especially the apparently unique occurrence of nucoid caryopses in this clade. However, after Jesus-Costa *et al.* (2018) documented the placement of *Athroostachys* in this clade as sister to *Merostachys*, which was corroborated in this study, a re-evaluation of the morphology and status of these three genera became necessary.

Characters of *Athroostachys* such as the presence of a conspicuous promontory and the branch complement with three subequal branches are labile and likely represent one independent origin in this genus (Jesus-Costa *et al.*, 2018), given that these traits also can be observed in *Atractantha* (Tyrrell *et al.*, 2012). Similarly, fan-branching was mentioned by Tyrrell *et al.* (2012) as having independent origins in Arthrostylidiinae, one of them in the *Merostachys* + *Actinocladum* clade. The topology from our analysis suggests either an independent origin of fan-branching in *Actinocladum* and another in *Merostachys*, or one origin in the common ancestor of the clade and a loss in *Athroostachys*.

Lastly, the morphological characteristics here discussed, along with habitat, when considered together with our molecular results support the recognition of both *Actinocladum* and *Athroostachys* as distinct genera, despite any similarities with *Merostachys*.

LINEAGES WITHIN *MEROSTACHYS*

Our results show two well supported lineages in *Merostachys* (clade 1 and clade 2). Clade 1 is composed of four species, which share the presence of spikelets sparsely arranged on the rachis and shiny florets (or at least, a shiny palea) (Fig. 1; Table 2). *Merostachys calderoniana*, *M. procerrima* and *M. leptophylla* form a strongly supported clade, with *M. rondoniensis* sister to it. The three first species are from the Brazilian Atlantic Forest Domain (Sendulsky, 1997) and have shiny florets and a waxy coating on both culm leaf sheaths and internodes. Two other species, *M. magnispicula* Send. and *M. sparsiflora* Rupr. (not sampled), also are recorded for the same phytogeographic domain and they share these same characteristics, so we hypothesize that they probably will also fall within clade 1.

Merostachys rondoniensis, on the other hand, has a floret with only the palea shiny; its culm leaf sheaths and internodes lack a waxy coating and it is restricted to the Amazon Forest domain (Fig. 2) (Sendulsky, 1997). Three other non-sampled species, *M. retrorsa* McClure, *M. maguireorum* McClure and *M. pauciflora* Swallen, resemble *M. rondoniensis* in the dimensions of their spikelets and the arrangement of the spikelets in the synflorescence. These species, with the exception of *M. maguireorum*, also are characterized by having florets with shiny paleas (Table 2). *Merostachys retrorsa* and *M. maguireorum* are from Amazonian Venezuela, whereas *M. pauciflora* is recorded from tropical rain forests in Belize and Nicaragua (Pohl & Davidse, 1994). Thus, we predict these species would also fall within clade 1 if we had obtained sequence data for them.

Clade 2 includes the majority of the *Merostachys* species sampled (Fig. 1). Within it we observe clade 3, which is a polytomy with poor resolution and unclear relationships among the species. Reproductive structures are not known for all of the species in clade

2, however, for those for which these structures are described, the florets are dull (Table 2). We predict that the species of this clade that at present are known only vegetatively will likely share the presence of dull florets. If these hypotheses are confirmed from more efforts in the field and if in a broader sampling these two main groups are maintained, these two clades may provide the basis for infrageneric categories in *Merostachys*.

The polytomic clade 3 encompasses five smaller groupings with moderate to high support. These groups are not supported by any obvious morphological synapomorphies and most of them are composed of morphologically different species. One of these groups, *M. ternata* + (*M. tatianae* + *M. fistulosa*), also was reported by Jesus-Costa *et al.* (2018) and Jesus-Costa *et al.* (in preparation). Among the five groupings within clade 3, this is the only one that exhibits morphological similarity among the species (Tables 1 and 2). These three species share thick branches, large foliage leaf blades and robust spikelets, although these character states can be seen, not necessarily covarying, in other species of the genus (Vinícius-Silva *et al.*, 2018).

Another grouping within clade 3 includes *M. filgueirasii* and *M. mexicana,* but despite moderate support for their sister relationship from our molecular data, they are not particularly similar in their morphology. On the other hand, they are the only species of clade 3 not recorded from the Brazilian Atlantic Forest (Fig. 2). *Merostachys filgueirasii* is found in gallery forest within the Cerrado domain (Sendulsky, 1995) and *M. mexicana* inhabits montane cloud forests in Mexico (Ruiz-Sanchez *et al.*, 2018). Because *M. rondoniensis* (from the Amazon Forest) was fairly strongly supported as sister to a group of species from the Brazilian Atlantic Forest in clade 1, and did not associate with these other two extra-Atlantic Forest species, we can ask if there is any phylogenetic relationship associated with the geographic distribution of the species within clades 1 and

2. Sampling from other geographic regions, mainly the Amazon, Central America and the Andes, is necessary to test this hypothesis and elucidate the biogeography of *Merostachys*.

MORPHOLOGY OF *MEROSTACHYS* IN A MOLECULAR PHYLOGENETIC CONTEXT

Based on morphological characters, some groups of similar *Merostachys* species have been defined. In previous studies carried out by T. Sendulsky, she referred to the *M. multiramea* complex (Sendulsky, 1995) and the "Group Speciosa" (Sendulsky, 2001). The *M. multiramea* complex encompasses 10 species which previously had all been identified as *M. multiramea* (Sendulsky, 1995). The species can be distinguished by their reproductive structures, but they are very similar according to their vegetative characters, which generated some of the prior misidentifications. The "Group Speciosa" is composed of four species, which are very similar in their reproductive structures (Sendulsky, 2001), but easily separated by vegetative characters. In our molecular analysis we included four species from the *M. multiramea* complex (*M.* aff. *multiramea*, *M. filgueirasii*, *M. scandens* and *M. skvortzovii* Send.) and the four species forming "Group Speciosa" (*M. brevigluma* Send., *M. kunthii* Rupr., *M. neesii* Rupr. and *M. speciosa*). Despite possible relationships among these species based on morphology, these informal groups were not supported in our molecular analysis (Fig. 1).

Since beginning our studies in *Merostachys* a major goal has been to obtain a consistent morphological basis to allow us to contribute to the resolution of taxonomic issues and give us support to advance in other studies such as molecular analyses. As a result of these efforts, we were able to recognize morphological groups in *Merostachys* from vegetative or reproductive characters (Tables 1 and 2). It is worth emphasizing that the number of species included in groups defined by reproductive characters (Table 2) is lower because the flowers of some species in the genus are unknown.

The vegetative features used to define the groups were the presence or absence of an infranodal band of trichomes in the culm, diameter of the branches, presence or absence of fimbriae and presence or absence of a thick nodal region (Table 1), while the groups recognized from the reproductive characters were related to spikelet length, surface of the floret (shiny or dull), number of florets per spikelet and arrangement of the spikelets on the synflorescence (Table 2). These characters have been very useful in *Merostachys* for the preparation of identification keys in taxonomic studies (Parma *et al.*, 2016; Vinícius-Silva *et al.*, 2016; Vinícius-Silva *et al.*, 2018; Vinícius-Silva *et al.*, in preparation).

Through the morphological datasets we created, it was possible to gain insights about the possible affinities among the species of *Merostachys* as well as to predict groupings in our phylogenetic analysis. However, most of the morphological groupings were not supported in our molecular phylogenetic analysis. On the other hand, as a majority of the *Merostachys* species was supported in a polytomy (clade 3), implying a lack of resolution and suggesting that these species are phylogenetically close, we cannot discard the possibility that some relationships between the molecular data and these morphological groups will be congruent in future analyses.

Whether the florets are shiny or dull was the only character that did show an interesting correlation. As mentioned previously, clade 1 is characterized by species either with shiny florets or at least a shiny palea (*M. rondoniensis*), while most of the species included in clade 2 have dull florets (at least, the species for which reproductive structures are known). Our knowledge still is too incomplete to justify the recognition of infrageneric categories within *Merostachys*, but these results are promising and provide the basis for future research.

Finally, still with regard to reproductive features, it is important to emphasize that among the species not included in our analyses, *M. maguireorum* is one of the most important to be sampled in future research. It exhibits dull florets but the characteristics of its synflorescence (*e.g.* the arrangement of spikelets and dimensions of spikelet bracts) are very similar to *M. rondoniensis*. The inclusion of *M. maguireorum* will allow us to test the consistency of these reproductive characteristics in a phylogenetic context.

MEROSTACHYS EVOLUTION

The lack of resolution within the polytomic clade 3 in our phylogenetic tree may have more than one explanation. First, the conserved nature of these plastid regions means that they may not be sufficiently informative for this group. One option for future work is to obtain sequences from the complete plastid genome of these species. The complete plastome, for example, has provided interesting results for temperate woody bamboos, with better resolution (Wysocki *et al.*, 2015; Attigala *et al.*, 2016; Ma *et al.*, 2017) when compared with analyses based on only selected chloroplast or nuclear markers (Triplett & Clark, 2010; Yang *et al.*, 2010; Yang *et al.*, 2013; Attigala *et al.*, 2014). It will also be critical in future studies to include nuclear markers, since these have biparental inheritance and, depending on the marker, may be more informative, giving us more insights into the evolutionary history of *Merostachys*.

Another possible reason for this polytomy is the long generation time exhibited by these plants, ca. 30–50 years (Janzen, 1976; Guilherme & Ressel, 2001; Liebsh & Reginato, 2009; Guerreiro, 2014). Long generation times, as seen in the woody bamboos, can cause slow evolutionary rates (Gaut *et al.*, 1997; Andreasen & Baldwin, 2001; Smith & Donoghue, 2008; Ma *et al.*, 2017). In species characterized by this reproductive pattern, the genome is copied with low frequency leading to fewer mutations per unit of time (Bromham, 2009), which could explain the molecular similarity among these species.

Yet another explanation for the low resolution visualized in this clade is the probable recent radiation of its species. A recent origin usually is associated with short branches in the topology of a phylogenetic tree (as seen in our results), which produce a poor phylogenetic signal (Philippe *et al.*, 2011). A short divergence time does not allow species to accumulate synapomorphies or to coalesce their gene histories (Wiens *et al.*, 2008); that is, evolutionary time was not sufficient for the accumulation of the mutations necessary to allow the resolution of relationships within this clade in a molecular analysis.

A lineage undergoing recent radiation presents a challenge for phylogenetic analysis because the “true” relationships among the species cannot be resolved due to processes such as hybridization and incomplete lineage sorting, which are reflected in incongruence between different molecular datasets and between molecular and morphological data (Rieseberg & Soltis, 1991; Rieseberg, Whitton & Linder, 1996; Jacobb & Blattner, 2006; Maddison & Knowles, 2006; Willyard, Cronn & Liston, 2009; Drábková & Vlček, 2010; Blanco-Pastor, Vargas & Pfeil, 2012; Xu *et al.*, 2012; Zhou *et al.*, 2017). Regarding the woody bamboos, a rapid radiation has been reported in the temperate bamboos (Triplett & Clark, 2010; Attigala *et al.*, 2014; Zhang *et al.*, 2016) and also in *Chusquea* Kunth, a Neotropical bamboo genus (Fisher, Clark & Kelchner, 2014).

Hybridization is not a phenomenon expected to be important in the evolutionary history of woody bamboos, mainly because of their long reproductive cycles with infrequent flowering events and asynchronous flowering between species (Janzen, 1974;

Clark, Davidse & Ellis, 1989; Fisher *et al.*, 2014). Nevertheless, hybridization, both ancient and recent, has been documented in woody bamboos or discussed as a possible explanation for incongruence in molecular analyses (Triplett & Clark, 2010; Triplett, Oltrogge & Clark, 2010; Triplett *et al.*, 2014; Goh *et al.*, 2011; Yang *et al.*, 2013; Fisher *et al.*, 2014).

Most species of clade 3 are from the Brazilian Atlantic Forest, but not all of them share the same geographic distribution (sympatry) along this coastal domain. And despite some species presenting similar flowering cycles, the majority of individuals analyzed in herbaria or collected in the field from among the sampled species did not show an intermediate morphology between any other pairs of taxa. A specific case involves *M. kunthii* and *M. brevigluma*, which were cited, previously, by Sendulsky (2001) as possible hybrids between *M. neesii* and *M. speciosa*. Forming the "Group Speciosa", these four species are very close morphologically mainly in their reproductive structures (Sendulsky, 2001); it is only *M. brevigluma* that exhibits some features intermediate between *M. neesii* and *M. speciosa* (*e.g.* the scant and sometimes deciduous fimbriae).

Nevertheless, despite the possible sympatry of the putative parental species (*M. neesii* and *M. speciosa*), the possible hybrids (*M. kunthii* and *M. brevigluma*) are recorded from different locations, which decreases the likelihood that these two species originated through hybridization. Besides that, our molecular data do not show a close relationship of the putative hybrids with either of the putative parental species; a sister relationship with at least the maternal species would be expected if *M. kunthii* or *M. brevigluma* were of hybrid origin from either putative parent. On the contrary, *M. speciosa* grouped with *M.* aff. *multiramea*, which has a really distinct morphology and *Merostachys brevigluma*, *M. kunthii* and *M. neesii* were part of the large polytomy comprising clade 3. On the other hand, as this clade exhibits a lack of resolution, we cannot reject the possibility *M. kunthii* or *M. brevigluma* would be sister to *M. neesii* in a future analysis.

Another process that might be influencing our plastid phylogenetic estimates in *Merostachys* is incomplete lineage sorting. This phenomenon is characterized by the persistence of ancestral polymorphisms during speciation events (Maddison, 1997; Wendel & Doyle, 1998). That is, if the ancestor of clade 3 were polymorphic for haplotypes, the short divergence time among the species during speciation did not allow the coalescence of these alleles into a single haplotype in the new lineages (Maddison & Knowles, 2006), which could explain the low resolution and lack of correlation with morphological data. It would be interesting, in future analyses, to sample nuclear markers to help detect possible incongruence between topologies from both datasets (plastid and nuclear regions), which is very common in incomplete lineage sorting events (Drábková & Vlček, 2010).

It can be very difficult to distinguish the effects of hybridization vs. incomplete lineage sorting in a phylogenetic analysis of a young species group (Wendel & Doyle, 1998). However, as the species encompassed in clade 3 do not exhibit, simultaneously, (1) sympatry; (2) flowering in the same period; and (3) intermediate morphology, we hypothesize that incomplete lineage sorting is most likely process to be influencing evolution within this species group in *Merostachys*.

ACKNOWLEDGEMENTS

We acknowledge support from the following funding agencies: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) in the International Doctoral Program in Sandwich (PDSE, nº 88881.135178/2016-01 to R. Vinícius-Silva), Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG, grant APQ-03255-16 to A.P. Santos-Gonçalves), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, grants 563545/2010-0-REFLORA to A.P. Santos-Gonçalves and 401526/2014-3-PVE to R.P. Oliveira), Bamboos of the Americas (BOTA) and the Ned Jaquith Foundation (grants to R. Vinícius-Silva to support the fieldwork). We are grateful to Dr. Adriano Nunes-Nesi and Dr. Wagner L. Araújo for allowing us access to the Plant Growth Unit (Universidade Federal de Viçosa) and Dr. Jonathan Wendel for allowing us access to the Wendel Lab (Iowa State University). We thank Corrinne E. Grover, Guanjing Hu, Anna Tuchin and Marcelo G.M.V. Vaz for assistance with the lab work. We also thank Christian Silva, Cristielle de Jesus-Costa, Lakshmi Attigala and Wallace M.B São-Mateus for help with the phylogenetic analyses; Mayco S. Werllen-Sousa and Nelson Túlio L. Pena for help in the editions of the figures and Robert Soreng for support during a visit to the US National Herbarium, Washington D.C., USA.

AUTHOR CONTRIBUTIONS

This work is derived from the Ph.D. thesis of RVS, which was developed under the supervision of APSG, LGC and JNF. The concept for the study and funding acquisition were provided by RVS, APSG and LGC. The fieldwork, morphological analyses and the generation of molecular data from DNA extraction, amplification, sequencing and alignment sequences were conducted by RVS. Most of the lab work (amplification and sequencing) carried out by RVS was strongly supported and supervised by LGC. Main manuscript preparation was done by RVS and it was reviewed and edited by APSG, LGC and JNF.

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Table 1. Morphological groups in *Merostachys* based on vegetative characters. *Merostachys bradei* Pilg. and *M. sellovii* Munro were not included in any morphological group. The material analyzed from *M. bradei* is composed only of a synflorescence fragment and two foliage leaf blades. Specimens of *M. sellovii* were not found in any herbaria visited by us and in the protologue the herbarium where the type material was deposited is not given. *Merostachys ciliata* and *M. brevispica* were not included in the group related to the infranodal band of trichomes in the culm because the specimens we were able to analyze did not have internodes and were composed only of floriferous branches. * = Species included in our phylogenetic analyses. ** = Species included in our sampling (*M. multiramea*), however the lack of reproductive structures did not allow us to confirm the identification of the material designated as *M.* aff. *multiramea*.

Infranodal band of trichomes in the culm		Branch diameter	
Absent	**Present**	**0.5–2 mm wide**	**2.5–7 mm wide**
M. annulifera Send.*;	*M. abadiana* Send.; *M. argentea* Send.;	*M. abadiana*; *M. argentea;*	*M. espessa**;
M. argyronema Lindm.*;	*M. burmanii* Send.*; *M. caucaiana*	*M. argyronema**; *M. annulifera**;	*M. fimbriata*;
M. bifurcata Send.;	Send.; *M. claussenii* Munro; *M. exserta*	*M. bifurcata*; *M. brevigluma**;	*M. fimbriolaminata**;
M. brevigluma Send.*;	Munro ex Camus; *M. filgueirasii*	*M. brevispica* Munro;	*M. fistulosa**;
M. calderoniana Send.*;	Send.*; *M. fimbriata* Send.;	*M. burmanii**;	*M. latifolia*;
M. espessa Viníc.-Silva,	*M. fimbriolaminata* Viníc.-Silva,	*M. calderoniana**; *M. caucaiana*;	*M. magnispicula*;
L.G.Clark & Santos-Gonç.*;	Cuper.-Eisenl. & Santos-Gonç.*;	*M. ciliata* McClure & L.B.Sm.;	*M. pluriflora**;
M. fistulosa Döll*; *M. kunthii*	*M. fischeriana* Rupr. ex Döll*;	*M. claussenii*; *M. exserta*;	*M. polyantha*;
Rupr.*; *M. leptophylla* Send.*;	*M. glauca* McClure & L.B.Sm.;	*M. filgueirasii**; *M. fischeriana**;	*M. procerrima**;
M. magnispicula Send.;	*M. kleinii* Send.; *M. lanata* Send.*;	*M. glauca*; *M. kleinii*; *M. kunthii**;	*M. ramosissima*;
M. maguireorum McClure;	*M. latifolia* R.W.Pohl;	*M. lanata**; *M. leptophylla**;	*M. retrorsa*;

M. medullosa Send.* ; _M. neesii_ Rupr.*; _M. procerrima_ Send.*; _M. ramosa_ Pianiss., Viníc.-Silva & L.G.Clark*; _M. sparsiflora_ Rupr.; _M. speciosa_ Spreng.*; _M. tatianae_ Santos-Gonç., Carv.-Okano & Filg.*; _M. vestita_ McClure & L.B.Sm.; and _Merostachys_ sp.1*	_M. magellanica_ Send.; _M. mexicana_ Ruiz-Sanchez & L.G.Clark*; _M. multiramea_ Hack.**; _M. pauciflora_ Swallen; _M. petiolata_ Döll*; _M. pilifera_ Send.; _M. polyantha_ McClure; _M. pluriflora_ Munro ex Camus*; _M. ramosissima_ Send.; _M. retrorsa_ McClure; _M. riedeliana_ Rupr. ex Dölll*; _M. rondoniensis_ Send.*; _M. scandens_ Send.*; _M. skvortzovii_ Send.*; _M. ternata_ Nees*; _M. ximenae_ D.F.Parma., Viníc.-Silva & Santos-Gonç.*; _M. yungasensis_ Lizarazu; and _Merostachys_ sp.2*	_M. magellanica_; _M. maguireorum_; _M. medullosa_*; _M. mexicana_*; _M. multiramea_**; _M. neesii_*; _M. pauciflora_; _M. petiolata_*; _M. pilifera_; _M. ramosa_*; _M. rondoniensis_*; _M. scandens_*; _M. skvortzovii_*; _M. sparsiflora_; _M. vestita_; and _Merostachys_ sp.1*	_M. riedeliana_*; _M. speciosa_*; _M. tatianae_*; _M. ternata_*; _M. ximenae_*; _M. yungasensis_; and _Merostachys_ sp.2*

Fimbriae		Nodal region thick and ring-like	
Absent	Present	Absent	Present
M. fistulosa*; M. kunthii*; and M. neesii*	M. abadiana; M. argentea; M. argyronema*; M. annulifera*; M. bifurcata; M. brevigluma*; M. brevispica; M. burmanii*; M. calderoniana*; M. caucaiana; M. ciliata; M. claussenii; M. exserta; M. espessa*; M. filgueirasii*; M. fimbriata; M. fimbriolaminata*; M. fischeriana*; M. glauca; M. kleinii; M. lanata*; M. latifolia; M. leptophylla*; M. magellanica; M. magnispicula; M. maguireorum; M. medullosa*; M. mexicana*; M. multiramea**;	M. abadiana; M. argentea; M. argyronema*; M. bifurcata; M. brevigluma*; M. brevispica; M. burmanii*; M. calderoniana*; M. caucaiana; M. ciliata; M. claussenii; M. exserta; M. espessa*; M. filgueirasii*; M. fimbriata; M. fischeriana*; M. fistulosa*; M. glauca; M. kleinii; M. kunthii*; M. lanata*; M. latifolia; M. leptophylla*; M. magellanica; M. magnispicula; M. maguireorum; M. medullosa*; M. mexicana*; M. multiramea**;	M. annulifera* M. fimbriolaminata*; and M. ximenae*

	M. pauciflora; _M. petiolata_*; _M. pilifera_; _M. pluriflora_*; _M. polyantha_; _M. procerrima_*; _M. ramosa_*; _M. retrorsa_; _M. riedeliana_*; _M. rondoniensis_*; _M. scandens_*; _M. skvortzovii_*; _M. sparsiflora_; _M. speciosa_*; _M. tatianae_*; _M. ternata_*; _M. vestita_; _M. ximenae_*; _M. yungasensis_; _Merostachys_ sp.1*; and _Merostachys_ sp.2*	_M. neesii_*; _M. pauciflora_; _M. petiolata_*; _M. pilifera_; _M. pluriflora_*; _M. polyantha_; _M. procerrima_*; _M. ramosa_*; _M. retrorsa_; _M. riedeliana_*; _M. rondoniensis_*; _M. scandens_*; _M. skvortzovii_*; _M. sparsiflora_; _M. speciosa_*; _M. tatianae_*; _M. ternata_*; _M. vestita_; _M. yungasensis_; _Merostachys_ sp.1*; and _Merostachys_ sp.2*

Table 2. Morphological groups in _Merostachys_ based on reproductive characters. The number of species in these groups is lower than those based on vegetative characters because reproductive structures are not known for some species. * = Species included in our phylogenetic analyses. ** = Species included in our sampling (_M. multiramea_), however the lack of reproductive structures did not allow us to confirm the identification of the material designated as _M._ aff. _multiramea_. [1] = Species with only shiny paleas (not florets). [2] = Species characterized as having only 1 floret per spikelet, but sporadically 1-2 florets per spikelet can be observed.

Spikelet length		**Number of florets per spikelets**		
5-10 mm long	**More than 10 mm long**	**1 floret**	**1–2 florets**	**2–6 florets**
_M. burmanii_*;	_M. abadiana_; _M. annulifera_*;	_M. abadiana_; _M. annulifera_*;	_M. kleinii_ and	_M. bradei_;
M. caucaiana;	_M. argyronema_*; _M. bifurcata_;	_M. argyronema_*; _M. bifurcata_;	_M. multiramea_**	_M. pluriflora_*;
M. exserta;	_M. bradei_; _M. brevigluma_*;	_M. brevigluma_*[1]; _M. brevispica_;		and
_M. fischeriana_*;	_M. brevispica_;	_M. burmanii_*; _M. calderoniana_*;		_M. polyantha_
M. glauca;	_M. calderoniana_*; _M. ciliata_;	_M. caucaiana_[1]; _M. ciliata_;		
_M. lanata_*;	_M. claussenii_; _M. filgueirasii_*;	_M. claussenii_; _M. exserta_[1];		
_M. leptophylla_*;	_M. fistulosa_*; _M. kleinii_;	_M. filgueirasii_*; _M. fischeriana_*;		
_M. petiolata_*; and	_M. kunthii_*; _M. latifolia_;	_M. fistulosa_*; _M. glauca_;		
Merostachys sp.1*	_M. magellanica_;	_M. kunthii_*; _M. lanata_*; _M. latifolia_;		
	M. magnispicula;	_M. leptophylla_*; _M. magellanica_;		
	M. maguireorum;	_M. magnispicula_; _M. maguireorum_;		
		_M. medullosa_*; _M. mexicana_*;		

_M. medullosa_*; _M. mexicana_*; _M. multiramea_**; _M. neesii_*; _M. pauciflora_; _M. pilifera_; _M. pluriflora_*; _M. polyantha_; _M. procerrima_*; _M. ramosissima_; _M. retrorsa_; _M. riedeliana_*; _M. rondoniensis_*; _M. scandens_*; _M. skvortzovii_*; _M. sparsiflora_; _M. speciosa_*; _M. tatianae_*; _M. ternata_*; _M. ximenae_*; and _M. yungasensis_	_M. neesii_*; _M. pauciflora_; _M. petiolata_*; _M. pilifera_; _M. procerrima_*; _M. ramosissima_; _M. retrorsa_; _M. riedeliana_*[1]; _M. rondoniensis_*; _M. scandens_*; _M. skvortzovii_*; _M. sparsiflora_; _M. speciosa_*; _M. tatianae_*; _M. ternata_*; _M. ximenae_*; _M. yungasensis_; and _Merostachys_ sp.1*

Floret		**Arrangement of spikelets**	
Shiny	**Dull**	**Solitary**	**Grouped in pairs, triads, sometimes solitary**
_M. calderoniana_*; _M. leptophylla_*; _M. magnispicula_; _M. pauciflora_; _M. procerrima_*; _M. retrorsa_; _M. rondoniensis_*[1]; and _M. sparsiflora_	_M. abadiana_; _M. annulifera_*; _M. argyronema_*; _M. bifurcata_; _M. bradei_; _M. brevigluma_*; _M. brevispica_; _M. burmanii_*; _M. caucaiana_; _M. ciliata_; _M. claussenii_; _M. exserta_; _M. filgueirasii_*; _M. fischeriana_*; _M. fistulosa_*; _M. glauca_; _M. kleinii_; _M. kunthii_*; _M. lanata_*; _M. latifolia_; _M. magellanica_; _M. maguireorum_; _M. medullosa_*; _M. mexicana_*; _M. multiramea_**; _M. neesii_*;	_M. abadiana_; _M. annulifera_*; _M. argyronema_*; _M. bifurcata_; _M. bradei_; _M. brevigluma_*[2]; _M. brevispica_; _M. calderoniana_*; _M. caucaiana_[2]; _M. ciliata_; _M. claussenii_; _M. exserta_[2]; _M. filgueirasii_*; _M. fischeriana_*; _M. fistulosa_*; _M. glauca_; _M. kleinii_; _M. kunthii_*; _M. lanata_*; _M. leptophylla_*; _M. magellanica_; _M. magnispicula_; _M. maguireorum_; _M. medullosa_*; _M. mexicana_*; _M. multiramea_**;	_M. burmanii_*; _M. latifolia_; _M. ramosissima_; _M. tatianae_*; _M. ternata_*; _M. ximenae_*; and _Merostachys_ sp.1*

_M. petiolata_*; _M. pilifera_; _M. pluriflora_*; _M. polyantha_; _M. ramosissima_; _M. riedeliana_*; _M. scandens_*; _M. skvortzovii_*; _M. speciosa_*; _M. tatianae_*; _M. ternata_*; _M. ximenae_*; _M. yungasensis_; and _Merostachys_ sp.1*	_M. neesii_*; _M. pauciflora_; _M. petiolata_*; _M. pilifera_; _M. pluriflora_*; _M. polyantha_; _M. procerrima_*; _M. retrorsa_; _M. riedeliana_*[2]; _M. rondoniensis_*; _M. scandens_*; _M. skvortzovii_*; _M. sparsiflora_; _M. speciosa_*; and _M. yungasensis_

Table 3. Plastid DNA primers used for amplification and sequencing, length of amplified regions and PCR parameters.

Region	Primers sequences (5'-3')	Region Length (bp)	PCR Parameters	Reference
ndhF	972F: GTC TCA ATT GGG TTA TAT GAT G 2110R: CCC CCT AYA TAT TTG ATA CCT TCT CC SEQ.: 1318F: GGA TTA ACT GCG TTT TAT ATG TTT CG 1603R: GCA TAG TAT TTC CCG TTT CAT GAG G	1140	94ºC, 1m; 30x (94ºC, 1m 30s; touchdown 53–43ºC, 2m; 72ºC, 3m); 72ºC 10m	Olmstead & Sweere (1994)
rps16-trnQ	1F: GCA CGT TGC TTT CTA CCA CA 1574R: ATC CTT CCG TCC CAG ATT TT SEQ.: 334F: CGA GAT GGT CAA TCC TGA AAT G 628R: CTT TTG GTA TTC KAG TCG AAG	1120	95ºC, 2m; 35x (95ºC, 1m; 50ºC, 10s; +15ºC, 0.3ºC/s; 65ºC, 5m); 65ºC, 5m	Triplett & Clark (2010)

trnC-rpoB	trnC: TGG GGA TAA AGG ATT TGC AG rpoB: ATT GTG GAC ATT CCC TCR TT SEQ: jt400-for: CAG GTC CGA ACA GCA TTA jt700-rev: CGT AGT AGT AGA ATT GCT AG	1185	94ºC, 2m; 35x (96ºC, 1m; touchdown 56–46ºC, 2m; 72ºC, 3m); 72ºC, 5m	Triplett & Clark (2010)
trnD-trnT	trnD-for: ACC AAT TGA ACT ACA ATC CC trnT-rev: CCC TTT TAA CTC AGT GGT A SEQ: trnY-rev: CTC TTT GCT TTG GAT CTA G trnE-for: GCC TCC TTG AAA GAG AGA TG	1100	94ºC, 2m; 35x (94ºC, 45s; touchdown 58–48.5ºC, 1m; 72ºC, 1m15s); 72ºC, 5m	Triplett & Clark (2010)
trnT-trnL	trnT-L F: CAT TAC AAA TGC GAT GCT CT trnT-L R: TCT ACC GAT TTC GCC ATA TC	830	95ºC, 2m; 35x (95ºC, 1m; 48ºC, 10s; +17ºC, 0.3ºC/s; 65ºC, 5m); 65ºC, 5m	Triplett & Clark (2010)

rpl16	F71: GCT ATG CTT AGT GTG TGA CTC GTT G R1661: CGT ACC CAT ATT TTT CCA CCA CGA C SEQ: SAK8: CCA TCC CAC CCA ATG AAG R1516: CCC TTC ATT CTT CCT CTA TGT TG	1100	95ºC, 2m; 35x (95ºC, 1m; 50ºC, 10s; +15ºC, 0.3ºC/s; 65ºC, 4m); 65ºC, 5m	F71 and R1661: Jordan *et al.* (1996); R1516: Kelchner & Clark (1997); SAK8: Tyrrell *et al.* (2012)
rps16	rps16F: AAA CGA TGT GGT ARA AAG CAA C rps16R: AAC ATC WAT TGC AAS GAT TCG ATA	860	94ºC, 2m; 35x (94ºC, 45s; touchdown 58–48ºC, 30s; 72ºC, 1m); 72ºC, 5m.	Shaw *et al.* (2005)

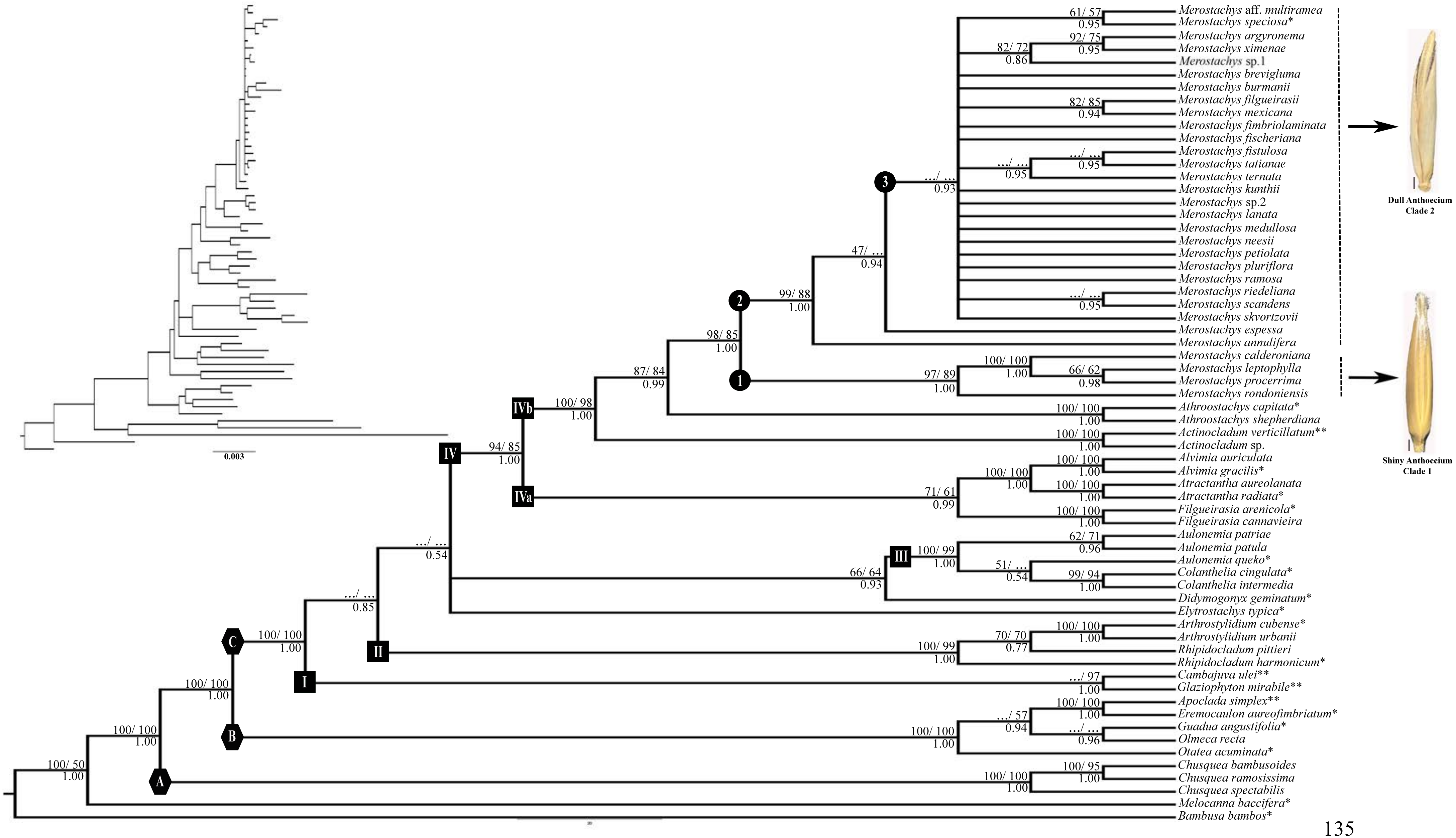
Table 4. Statistics for analyses and general information for plastid markers used in this study.

Characteristics	***ndhF***	***rps16-trnQ***	***trnC-rpoB***	***trnD-trnT***	***trnT-trnL***	***rpl16***	***rps16***	**Combined**
Number of taxa	59	58	55	64	60	53	43	64
Aligned length (bp)	1171	1197	1308	1361	855	1147	900	7913
Variable characters	65	116	117	101	74	70	33	574
Informative characters (%)	69 (5.8%)	67 (5.6%)	43 (3.2%)	71 (5.2%)	60 (7.0%)	55 (4.7%)	22 (2.4%)	389 (4.9%)

Table 5. Phylogenetically informative indels in the concatenated plastid sequence matrix of the species analyzed.

Position	Marker	Size (bp)	Type	Symbol	Clade
1339–1342	*rps16-trnQ*	4	Insertion	a	Arthrostylidium clade
1633–1641	*rps16-trnQ*	9	Insertion	b	*Apoclada simplex* + *Eremocaulon aureofimbriatum*
1765–1783	*rps16-trnQ*	19	Insertion	c	*Filgueirasia arenicola* + *Filgueirasia cannavieira*
1793–1841	*rps16-trnQ*	49	Deletion	d	Glaziophyton clade
1951–2019	*rps16-trnQ*	69	Deletion	e	Glaziophyton clade
2876–2895	*trnC-rpoB*	20	Insertion	f	Guaduinae subtribe
2896–2900	*trnC-rpoB*	5	Insertion	g	*Atractantha aureolanata* + *Atractantha radiata*
2944–2947	*trnC-rpoB*	4	Insertion	h	*Athroostachys capitata* + *Athroostachys shepherdiana*
3007–3117	*trnC-rpoB*	111	Deletion	i	*Alvimia auriculata* + *Alvimia gracilis*
3864–3869	*trnD-trnT*	6	Insertion	j	*A. simplex* + *E. aureofimbriatum*
3925–3945	*trnD-trnT*	21	Insertion	k	*Guadua angustifolia* + *Olmeca recta*
4126–4129	*trnD-trnT*	4	Insertion	l	*A. simplex* + *E. aureofimbriatum*
4312–4317	*trnD-trnT*	6	Insertion	m	Arthrostylidiinae subtribe
4699–4704	*trnD-trnT*	6	Deletion	n	*Chusquea bambusoides* + *Chusquea ramosissima*

4719–4732	*trnD-trnT*	14	Deletion	o	*C. bambusoides* + *C. ramosissima*
5004–5007	*trnD-trnT*	4	Insertion	p	Arthrostylidiinae subtribe
5592–5609	*trnT-trnL*	18	Insertion	q	*Merostachys calderoniana* + (*M. leptophylla* + *M. procerrima*)
5685–5690	*trnT-trnL*	6	Insertion	r	*A. simplex* + *E. aureofimbriatum* + (*G. angustifolia* + *O. recta*)
6224–6228	*rpl16*	5	Insertion	s	*A. aureolanata* + *A. radiata*
6247–6260	*rpl16*	14	Deletion	t	*C. bambusoides* + *C. ramosissima*
6560–6570	*rpl16*	11	Deletion	u	*C. bambusoides* + *C. ramosissima*
7818–7821	*rps16*	4	Deletion	v	Arthrostylidiinae + Guaduinae clade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61/ 57
0.95
92/ 75
0.95
82/ 72
0.86
82/ 85
0.94
.../ ...
0.95
.../ ...
0.95
.../ ...
0.93
47/ ...
0.94
.../ ...
0.95
99/ 88
1.00
98/ 85
1.00
87/ 84
0.99
100/ 100
1.00
66/ 62
0.98
97/ 89
1.00
100/ 98
1.00
100/ 100
1.00
100/ 100
1.00
94/ 85
1.00
100/ 100
1.00
100/ 100
1.00
100/ 100
1.00
71/ 61
0.99
100/ 100
1.00
62/ 71
0.96
100/ 99
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51/ ...
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99/ 94
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66/ 64
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100/ 100
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.../ 57
0.94
.../ ...
0.96
100/ 100
1.00
100/ 95
1.00
100/ 100
1.00
100/ 50
1.00
1
2
3
IV
IVa
IVb
III
II
I
A
B
C
Merostachys aff. *multiramea*
*Merostachys speciosa**
Merostachys argyronema
Merostachys ximenae
Merostachys sp.1
Merostachys brevigluma
Merostachys burmanii
Merostachys filgueirasii
Merostachys mexicana
Merostachys fimbriolaminata
Merostachys fischeriana
Merostachys fistulosa
Merostachys tatianae
Merostachys ternata
Merostachys kunthii
Merostachys sp.2
Merostachys lanata
Merostachys medullosa
Merostachys neesii
Merostachys petiolata
Merostachys pluriflora
Merostachys ramosa
Merostachys riedeliana
Merostachys scandens
Merostachys skvortzovii
Merostachys espessa
Merostachys annulifera
Merostachys calderoniana
Merostachys leptophylla
Merostachys procerrima
Merostachys rondoniensis
*Athroostachys capitata**
Athroostachys shepherdiana
*Actinocladum verticillatum***
Actinocladum sp.
Alvimia auriculata
*Alvimia gracilis**
Atractantha aureolanata
*Atractantha radiata**
*Filgueirasia arenicola**
Filgueirasia cannavieira
Aulonemia patriae
Aulonemia patula
*Aulonemia queko**
*Colanthelia cingulata**
Colanthelia intermedia
*Didymogonyx geminatum**
*Elytrostachys typica**
*Arthrostylidium cubense**
Arthrostylidium urbanii
Rhipidocladum pittieri
*Rhipidocladum harmonicum**
*Cambajuva ulei***
*Glaziophyton mirabile***
*Apoclada simplex***
*Eremocaulon aureofimbriatum**
*Guadua angustifolia**
Olmeca recta
*Otatea acuminata**
Chusquea bambusoides
Chusquea ramosissima
Chusquea spectabilis
*Melocanna baccifera**
*Bambusa bambos**
Dull Anthoecium
Clade 2
Shiny Anthoecium
Clade 1

Figure 1. Phylogram (left) and cladogram (right) based on the majority-rule consensus tree from the BI analysis of the combined plastid dataset. Support values are listed as maximum likelihood bootstrap/ maximum parsimony bootstrap above the branches and Bayesian posterior probability below the branches. The dull floret is from *M. riedeliana* (*Santos-Gonçalves et al. 286*) and the shiny floret is from *M. calderoniana* (*Fiaschi et al. 2651*). * = type species, ** = monotypic genus. Scale-bar on florets is 1 mm. Labeled nodes are referenced in the text and their respective geometric shapes on the phylogenetic tree refer to Neotropical subtribes (hexagons); clades within subtribe Arthrostylidiinae (squares); and clades within *Merostachys* (circles).

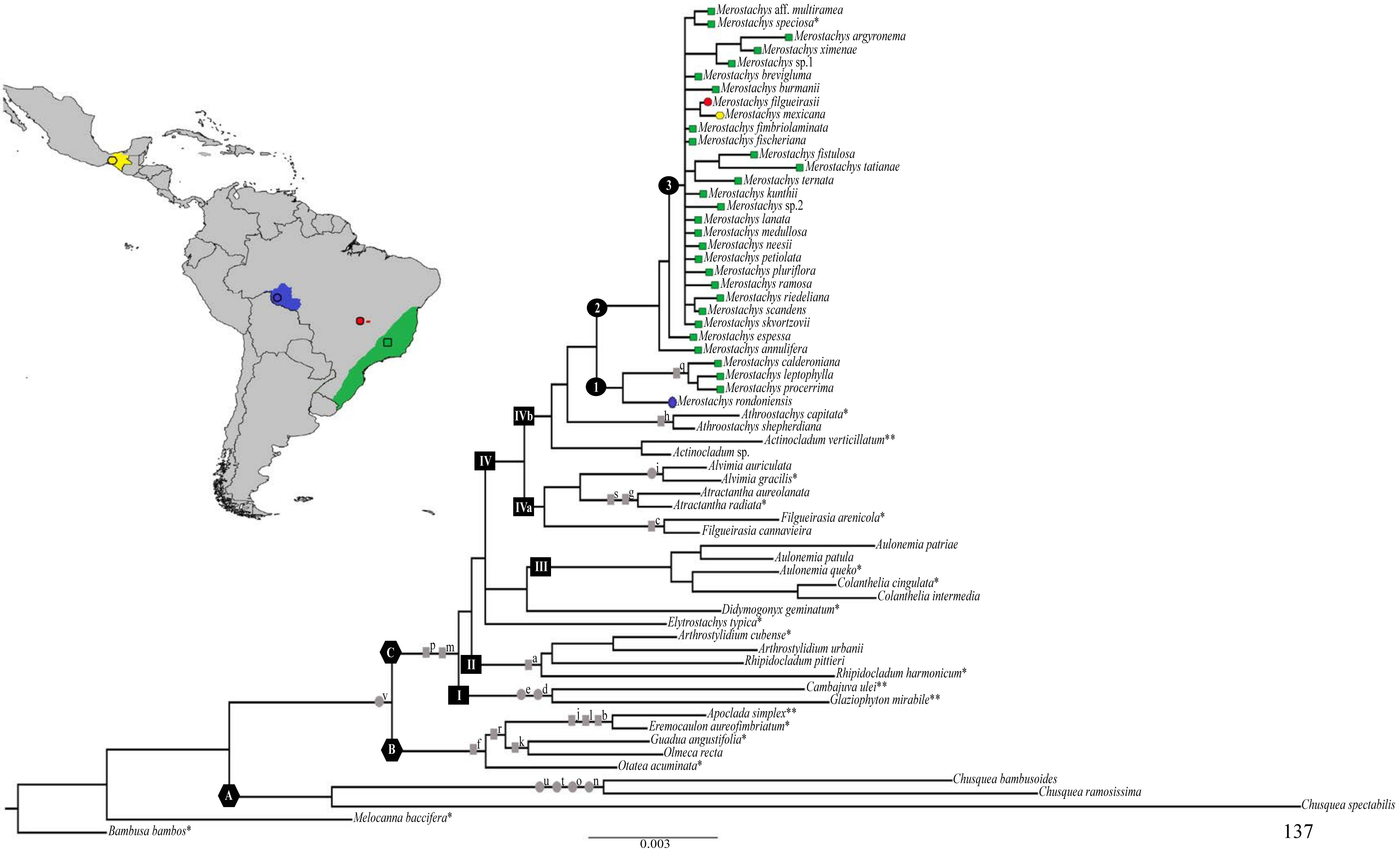
Merostachys aff. multiramea
Merostachys speciosa*
Merostachys argyronema
Merostachys ximenae
Merostachys sp.1
Merostachys brevigluma
Merostachys burmanii
Merostachys filgueirasii
Merostachys mexicana
Merostachys fimbriolaminata
Merostachys fischeriana
Merostachys fistulosa
Merostachys tatianae
Merostachys ternata
3
Merostachys kunthii
Merostachys sp.2
Merostachys lanata
Merostachys medullosa
Merostachys neesii
Merostachys petiolata
Merostachys pluriflora
Merostachys ramosa
2
Merostachys riedeliana
Merostachys scandens
Merostachys skvortzovii
Merostachys espessa
Merostachys annulifera
q
Merostachys calderoniana
Merostachys leptophylla
1
Merostachys procerrima
Merostachys rondoniensis
IVb
h
Athroostachys capitata*
Athroostachys shepherdiana
Actinocladum verticillatum**
Actinocladum sp.
IV
i
Alvimia auriculata
Alvimia gracilis*
s
g
Atractantha aureolanata
Atractantha radiata*
IVa
c
Filgueirasia arenicola*
Filgueirasia cannavieira
Aulonemia patriae
Aulonemia patula
III
Aulonemia queko*
Colanthelia cingulata*
Colanthelia intermedia
Didymogonyx geminatum*
Elytrostachys typica*
Arthrostylidium cubense*
C
p
m
Arthrostylidium urbanii
II
a
Rhipidocladum pittieri
Rhipidocladum harmonicum*
v
I
e
d
Cambajuva ulei**
Glaziophyton mirabile**
j
l
b
Apoclada simplex**
Eremocaulon aureofimbriatum*
r
B
f
k
Guadua angustifolia*
Olmeca recta
Otatea acuminata*
u
t
o
n
Chusquea bambusoides
A
Chusquea ramosissima
Chusquea spectabilis
Melocanna baccifera*
Bambusa bambos*
0.003

Figure 2. Bayesian topology tree based on combined plastid dataset. Insertions (solid square) and deletions (solid circles) are indicated by lower-case letters which are identified in Table 5. Color shapes at the end of branches from *Merostachys* species correspond to geographical distribution areas as indicated on the map. * = type species, ** = monotypic genus. Labeled nodes are referenced in the text and their respective geometric shapes on the phylogenetic tree refer to Neotropical subtribes (hexagons); clades within subtribe Arthrostylidiinae (squares); and clades within *Merostachys* (circles).

APPENDIX 1. Taxa, origin, voucher, herbarium information, and GenBank accession numbers for the seven plastid DNA regions used to infer phylogeny [*ndhF*, *rps16-trnQ*, *trnC-rpoB*, *trnD-trnT*, *trnT-trnL*, *rpl16*, *rps16*]. AC – André Carvalho; ASG – Ana Paula Santos-Gonçalves; AT – Atchara Teerawatananon; BI – Bogor, Indonesia; CJC – Cristielle Jesus-Costa; CT – Christopher Tyrrell; DP – Daniele Parma; EP – Evandro Pianissola; ERS – Eduardo Ruiz-Sanchez; EA – Edley Silva; FE – Francisca Ely; GN – Giovanni Neves; JC – Juan Carrión; JIS – José Ilton da Silva; KMW – Khoon-Meng Wong; LC – Lynn Clark; LS – Luiz Sarahyba; MC – Mônica Cupertino; MF – Marcelo Fragomeni; PA – Patrício Asimbaya; RS – Rodney Schmidt; RVS – Ronaldo Vinícius-Silva; SB – Sérgio Bordignon; SS – Sarawood Sungkaew; TF – Tarciso Filgueiras; UMB – University of Malaya Bambusetum; WO – Walter de Oliveira; WZ – Wei-Ping Zhang; XL – Ximena Londoño. A dash (—) indicates the molecular region was not sequenced. Asterisks (*) refer to accession number of sequences generated in this study but still not submitted to GenBank.

Arthrostylidiinae—*Actinocladum verticillatum* (Nees) McClure ex Soderstr., Brazil, *TF s.n.* (ISC), [JQ408524, JQ408445, JQ408485, JQ408623, JQ408586, JQ408570, —]. ***Actinocladum verticillatum***, Brazil, *CJC 89* (VIC), [—, —, —, —, —, —, MG458251]. ***Actinocladum* sp.**, Brazil, *EP & LC 179* (HUEFS), [*, *, *, *, *, *, *]. ***Alvimia auriculata*** Soderstr. & Londoño, Brazil, *ASG 598* (VIC), [JQ408525, JQ408446, JQ408486, JQ408624, JQ408587, —, —]. ***Alvimia gracilis*** Soderstr. & Londoño, Brazil, *AC et al. 4389* (CEPEC), [JQ408526, JQ408447, JQ408487, —, —, JQ408571, —]. ***Alvimia gracilis***, Brazil, *ASG 604* (ISC), [—, —, —, JQ408625, JQ408588, —, —]. ***Arthrostylidium cubense*** Rupr., Cuba, *XL 957* (ISC), [JQ408529, JQ408450, —, JQ408628, JQ408590, JQ408572, —]. ***Arthrostylidium urbanii*** Pilg., Cuba, *XL 851* (ISC), [JQ408534, JQ408455, JQ408492, JQ408632, JQ408594, JQ408576, —]. ***Athroostachys capitata*** (Hook.) Benth., Brazil, *RVS & MC 15* (VIC), [MG458235, MG458274, MG458262, MG458268, MG458281, MG458241, MG458252]. ***Athroostachys shepherdiana*** (Santos-Gonç., Filg. & L.G. Clark) C. Jesus-Costa & Santos-Gonç., Brazil, *CJC et al. 114* (VIC), [MG458236, MG458276, MG458263, MG458269, MG458282, MG458242, MG458255]. ***Atractantha aureolanata*** Judz., Brazil, *ASG 596* (VIC), [JQ408536, —, JQ408494, JQ408634, JQ408595, —, —]. ***Atractantha aureolanata***, Brazil, *ASG 658* (VIC), [—, MG458275, —, —, —, MG458243, MG458253]. ***Atractantha radiata*** McClure, Brazil, *ASG 599* (ISC), [JQ408538, —, JQ408496, —, JQ408597, JQ408577, —]. ***Atractantha radiata***, Brazil, *AC 4362* (CEPEC), [—, JQ408457, —, JQ408636, —, —, KC020568]. ***Aulonemia patriae*** R.W.Pohl, Costa Rica, *CT et al. 44* (ISC), [JQ408541, JQ408458, JQ408499, JQ408639, —, —, —]. ***Aulonemia patula*** (Pilg.) McClure, Ecuador, *LC et al. 1075* (ISC), [JQ408542, JQ408459, JQ408500, JQ408640, JQ408599, JQ408578, —]. ***Aulonemia queko*** Goudot, Ecuador, *LC & PA 1445* (ISC), [JQ408543, JQ408460, JQ408501, JQ408641, JQ408600, JQ408579, —]. ***Cambajuva ulei*** P.L.Viana, L.G.Clark & Filg., Brazil, *LC & XL 1048* (ISC), [JQ408544, JQ408461, JQ408502, JQ408642, JQ408601, —, —]. ***Colanthelia cingulata*** (McClure & L.B.Sm.) McClure, Brazil, *TF s.n.* (ISC), [JQ408545, —, —, —, JQ408602, —, —]. ***Colanthelia cingulata***, Brazil, *ASG 538* (ISC), [—, —, —, JQ408643, —, —, —]. ***Colanthelia intermedia*** (McClure & L.B.Sm.) McClure, Brazil, *ASG 553* (ISC), [—, JQ408462, —

, JQ408645, JQ408604, —, —]. ***Didymogonyx geminatum*** (McClure) C.D.Tyrrell, L.G.Clark & Londoño, Venezuela, *FE 2* (ISC), [JQ408562, JQ408477, —, JQ408660, JQ408614, —, —]. ***Elytrostachys typica*** McClure, Colombia, *XL 985* (ISC), [JQ408548, JQ408463, —, JQ408646, —, —, —]. ***Filgueirasia arenicola*** (McClure) Guala, Brazil, *TF s.n.* (ISC), [JQ408550, JQ408465, JQ408505, JQ408648, JQ408605, —, —]. ***Filgueirasia cannavieira*** (Silveira) Guala, Brazil, *TS s.n.* (ISC), [JQ408551, JQ408466, JQ408506, JQ408649, JQ408606, JQ408580, —]. ***Glaziophyton mirabile*** Franch., Brazil, *LS et al. 1066* (ISC), [JQ408552, JQ408467, JQ408507, JQ408650, JQ408607, AF133471, KC020582]. ***Merostachys* aff. *multiramea*** Hack., Brazil, *RS & SB s.n.* (VIC), [*, *, *, *, *, *, *]. ***Merostachys annulifera*** Send., Brazil, *JC et al. 1775* (VIC), [*, *, *, *, *, *, *]. ***Merostachys argyronema*** Lindm., Brazil, *RVS & GN 129* (VIC), [*, —, —, *, *, *, *]. ***Merostachys brevigluma*** Send., Brazil, *RVS et al. 107* (VIC), [*, *, *, *, *, *, *]. ***Merostachys burmanii*** Send., Brazil, *RVS et al. 85* (VIC), [*, *, *, *, *, *, *]. ***Merostachys calderoniana*** Send., Brazil, *RVS et al. 94* (VIC), [*, *, *, *, *, *, *]. ***Merostachys espessa*** Vinic.-Silva, L.G.Clark & Santos-Gonç., Brazil, *RVS et al. 32* (VIC), [*, *, *, *, *, *, *]. ***Merostachys filgueirasii*** Send., Brazil, *RVS et al. 64* (VIC), [*, *, *, *, *, *, *]. ***Merostachys fimbriolaminata*** Vinic.-Silva, Cupert.-Eisenl. & Santos-Gonç., Brazil, *RVS & JIS 24* (VIC), [*, *, *, *, *, *, *]. ***Merostachys fischeriana*** Rupr. ex Döll, Brazil, *RVS & ES 12* (VIC), [*, *, *, *, *, *, *]. ***Merostachys fistulosa*** Döll, Brazil, *RVS et al. 50* (VIC), [MG458237, MG458277, MG458264, MG458270, MG458277, MG458245, MG458256]. ***Merostachys kunthii*** Rupr., Brazil, *RVS et al. 103* (VIC), [*, *, *, *, *, *, *]. ***Merostachys lanata*** Send., Brazil, *RVS & CJC 113* (VIC), [*, *, *, *, *, *, *]. ***Merostachys leptophylla*** Send., Brazil, *RVS*

& MC 21 (VIC), [*, *, *, *, *, *, *]. ***Merostachys medullosa*** Send., Brazil, *RVS & CJC 112* (VIC), [*, *, *, *, *, *, *]. ***Merostachys mexicana*** Ruiz-Sanchez & L.G.Clark, Mexico, *ERS et al. 542* (IBUG), [*, *, *, *, *, *, *]. ***Merostachys neesii*** Rupr., Brazil, *RVS s.n.* (VIC), [—, —, —, *, *, —, —]. ***Merostachys petiolata*** Döll, Brazil, *RVS et al. 106* (VIC), [*, *, *, *, *, *, *]. ***Merostachys pluriflora*** Munro ex Camus, Brazil, *RVS & GN 127* (VIC), [*, *, *, *, *, *, *]. ***Merostachys procerrima*** Send., Brazil, *RVS & CJC 116* (VIC), [*, *, *, *, *, *, *]. ***Merostachys ramosa*** Pianiss., Vinic.-Silva & L.G.Clark, Brazil, *RVS & DP s.n.* (VIC), [*, *, *, *, *, *, *]. ***Merostachys riedeliana*** Rupr. ex Döll, Brazil, *RVS & MC 20* (VIC), [*, *, *, *, *, *, *]. ***Merostachys rondoniensis*** Send., Brazil, *MF 1759* (CEN), [—, —, —, *, *, *, —]. ***Merostachys scandens*** Send., Brazil, *RVS & GN 125* (VIC), [*, *, *, *, *, *, *]. ***Merostachys skvortzovii*** Send., Brazil, *RVS & GN 128* (VIC), [*, *, *, *, *, *, *]. ***Merostachys speciosa*** Spreng., Brazil, *RS & SB s.n.* (VIC), [*, *, *, *, *, *, *]. ***Merostachys* sp.1**, Brazil, *RVS et al. 23* (VIC), [*, *, *, *, *, *, *]. ***Merostachys* sp.2**, Brazil, *RVS et al. 91* (VIC), [*, *, *, *, *, *, *]. ***Merostachys tatianae*** Santos-Gonç., Carv.-Okano & Filg., Brazil, *RVS & MC 18* (VIC), [MG458238, MG458278, MG458265, MG458271, MG458284, MG458246, MG458257]. ***Merostachys ternata*** Nees, Brazil, *LC & WO 1023* (ISC), [JQ408555, JQ408471, JQ408510, JQ408653, JQ408610, —, —]. ***Merostachys ternata***, Brazil, *RVS et al. 30* (VIC), [—, —, —, —, —, MG458247, MG458258]. ***Merostachys ximenae*** Parma, Vinic.-Silva & Santos-Gonç., Brazil, *RVS & DP 57* (VIC), [*, —, *, *, —, *, *]. ***Rhipidocladum harmonicum*** (Parodi) McClure, Ecuador, *LC et al. 1128* (ISC), [JQ408563, JQ408478, JQ408517, JQ408661, JQ408615, JQ408582, —]. ***Rhipidocladum pittieri*** (Hack.) McClure, Cultivated, *LC &*

WZ 1349 (ISC), [JQ408568, JQ408482, JQ408522, JQ408666, JQ408618, JQ408584, KC020596]. **Chusqueinae—*Chusquea bambusoides*** Hack., Brazil, *LC et al. 1029* (ISC), [FJ751649, FJ751688, FJ751715, FJ751742, KC020548, AY912194, KC020575]. ***Chusquea ramosissima*** Lindm., Brazil, *AC et al. 4358* (ISC), [KF945309, —, —, KF945208, KF945368, U54751, —]. ***Chusquea spectabilis*** L.G.Clark, Colombia, *XL & LC 919* (ISC), [—, FJ751698, FJ751725, FJ751752, KC020550, —, KC020578]. **Guaduinae—*Apoclada simplex*** McClure & L.B.Sm., Brazil, *LC & WO 1027* (ISC), [JQ408527, JQ408448, JQ408488, JQ408626, JQ408589, KC020511, KC020566]. ***Eremocaulon aureofimbriatum*** Soderstr. & Londoño, Brazil, *AC et al. 4393* (ISC), [JQ408549, JQ408464, JQ408504, JQ408647, —, —, —]. ***Eremocaulon aureofimbriatum***, Brazil, *ASG 590* (UEC), [—, —, —, —, —, EF589616, —]. ***Guadua angustifolia*** Kunth, Colombia, *XL & LC 931* (ISC), [FJ751641, FJ751680, FJ643910, FJ644003, FJ644154, FJ751664, KC020583]. ***Olmeca recta*** Soderstr., Mexico, *LC 1313* (ISC), [JQ408556, JQ408468, JQ408511, JQ408654, JQ408611, —, —]. ***Olmeca recta***, Mexico, *ERS 132* (XAL), [—, —, —, —, —, EF589622, —]. ***Otatea acuminata*** (Munro) C.E.Calderón & Soderstr., Mexico, *LC et al. 1312* (ISC), [—, FJ751678, FJ751705, FJ751732, JQ408612, U54749, KC020589]. ***Otatea acuminata***, Cultivated, *LC & WZ 1348* (ISC), [AF182350, —, —, —, —, —, —]. **Bambusinae—*Bambusa bambos*** (L.) Voss, Cultivated, *BI1* (BZ), [KF365018, —, —, —, —, —, —]. ***Bambusa bambos***, Cultivated, *KMW s.n.* (KLU), [—, JN033887, JN033914, JN033942, —, —, —]. ***Bambusa bambos***, China, *F1012110* (KUN),[—, —, —, —, KF797196, —, —]. ***Bambusa bambos***, Thailand, *SS & AT 030704-16* (KUFF), [—, —, —, —, —, —, EU434179]. **Melocanninae—*Melocanna baccifera*** (Roxb.) Kurz., Cultivated, *XL &*

LC 930 (ISC), [AF182348, —, —, KC020537, KC020555, KC020518, KC020585].

Melocanna baccifera, Malaysia, *UMB acc. 75* (KLU), [—, FJ416347, GU390934, —, —, —, —].

CONCLUSÕES GERAIS

Os estudos taxonômicos conduzidos durante a realização dessa pesquisa nos permitiram conhecer melhor o gênero *Merostachys* em relação à sua morfologia. As análises morfológicas aqui realizadas foram importantes para solucionar certas questões taxonômicas presentes no gênero e avançar em outras, as quais ainda necessitam de mais esforços para que possam ser esclarecidas. Além disso, os dados morfológicos levantados neste trabalho fornceram uma base para os estudos moleculares e podem embasar investigações futuras.

Merostachys speciosa, espécie tipo do gênero, foi redescrita. Além disso, uma relectotipificação foi proposta, afim de eleger, claramente, um lectótipo para a espécie, uma vez que na primeira lectotipificação, o espécime eleito como tal não foi designado de maneira adequada.

Três novas espécies de *Merostachys* foram descritas: *M. lagevianae*; *M. judziewiczii* e *M. soderstromii*. Sendo assim, o número de espécies para o gênero aumenta para 57. Adicionalmente, *M. bifurcata* e *M. procerrima* tiveram suas descrições emendadas a partir do registro, pela primeira vez, de suas respectivas estruturas reprodutivas.

Problemas taxonômicos envolvendo a circunscrição de *M. medullosa*., *M. magnispicula* e *M. procerrima* foram solucionados e essas espécies foram redelimitadas. *Merostachys magnispicula* e *M. procerrima* foram consideradas como espécies distintas a partir de dados morfológicos e ecológicos. Uma vez que o gênero ainda apresenta espécies de delimitaçao duvidosa, a ecologia pode ser uma alternativa interessante na resolução de outras questões taxonômicas.

Os estudos filogenéticos foram conduzidos com 31 espécies de *Merostachys*, (28 a mais em relação ao amostrado em estudos anteriores) com a geração de 183 novas sequências de DNA plastidial. A partir dessa ampla amostragem, *Merostachys* teve seu monofiletismo confirmado e a análise dos dados moleculares e morfológicos nos pertimiram tratá-lo juntamente com *Actinocladum* e *Athroostachys*, como gêneros distintos.

A não congruência entre a maioria dos grupos morfológicos e os clados sustentados na filogenia molecular não nos permite reconhecer subgêneros em *Merostachys*. No entanto, a correlação encontrada entre a superfície do flósculo (reluzente vs. opaco) e os dados moleculares é um passo importante neste contexto e pode nos ajudar a direcionar futuros estudos, principalmente em relação à amostragem de espécies chave para as próximas análises.

A politomia obsevarda em um dos clados em *Merostachys* nos sugere uma série de possíveis explicações para tal situação. Porém, a partir dos dados coletados durante a execução dessa pesquisa e, consequentemente, do conhecimento até aqui agregado acerca da morfologia, acreditamos que o sorteio incompleto de linhagens seja o mais provável evento a influenciar a evolução desse grupo de espécies.

Os resultados obtidos até o presente momento são extremamente importantes ao conhecimento do gênero *Merostachys*, no entanto são necessários ainda mais esforços para que outras questões possam ser solucionadas. Trabalhos de campo e estudos morfológicos são ainda necessários, principalmente em função de que algumas espécies possuem uma delimitação duvidosa e a coleta das mesmas, principalmente em estádio reprodutivo, é essencial. Além disso, esses trabalhos podem colaborar para o reconhecimento e descrição de novos táxons.

Análises filogenéticas futuras também são necessários a partir de uma abordagem ainda mais ampla. Nesse contexto é interessante a inclusão de espécies provenientes das demais regiões onde *Merostachys* ocorre. Uma amostragem desse cunho possibilitará o acesso à filogeografia do gênero, além de verificar se há uma relação entre a distribuição geográfica e os dados moleculares e, também, averiguar se os clados encontrados nesse estudo se mantêm com a inclusão de outras espécies. Por fim, nessas novas análises, o sequenciamento do plastoma ou mesmo a utilização marcadores nucleares e/ou a inclusão de múltiplos acessos para cada espécies podem fornecer uma melhor resolução na topologia e ajudar a esclarecer melhor as relações de afinidades entre os táxons amostrados.