CRISTIELLE DE JESUS COSTA

ESTUDOS FILOGENÉTICOS MOLECULARES E TAXONÔMICOS NA SUBTRIBO ARTHROSTYLIDIINAE (POACEAE: BAMBUSOIDEAE: BAMBUSEAE)

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*.

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APROVADA: 22 de março de 2018.

Jéferson Nunes Fregonezi

Livia Echternacht Andrade

Pedro Lage Viana

Lynn Gail Clark
(Coorientadora)

Ana Paula Santos Gonçalves
(Orientadora)

A minha amada mãe, Cida, meu maior exemplo de
vida e minha grande incentivadora, dedico.

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NOTA BENE

Nesta tese são apresentados vários nomes novos [*Colanthelia kinoshitae* Santos-Gonç., Filg. & L.G. Clark, *C. secundiflora* Santos-Gonç., Filg. & L.G. Clark, *C. sparsiflora* Santos-Gonç., Filg. & L.G. Clark, *C. longipetiolata* Jesus-Costa & Santos-Gonçalves e *Athroostachys shepherdiana* (Santos-Gonç., Filg. & L.G. Clark) Jesus-Costa & Santos-Gonçalves)]. A autora enfatiza que esta tese não é considerada local efetivo de publicação de tais nomes, pois os mesmos serão devidamente validados em artigos científicos publicados em periódicos específicos, após a eventual aprovação desta tese. Com esta nota, a autora quer evitar a possível aplicação de *nomen nudum* (McNeill et al. 2012) para os novos nomes aqui apresentados.

SUMÁRIO

RESUMO

COSTA, Cristielle de Jesus, D.Sc., Universidade Federal de Viçosa, março de 2018. **Estudos filogenéticos moleculares e taxonômicos na subtribo Arthrostylidiinae (Poaceae: Bambusoideae: Bambuseae).** Orientadora: Ana Paula Santos Gonçalves. Coorientadores: Luiz Orlando de Oliveira e Lynn Gail Clark.

Arthrostylidiinae (Poaceae: Bambusoideae), com 191 espécies e 15 gêneros, é a maior subtribo do clado dos bambus lignificados neotropicais (NWB). Suas espécies estão distribuídas predominantemente na costa Atlântica do Brasil, a qual é considerada o principal centro de diversidade da subtribo. Além da diversidade taxonômica, Arthrostylidiinae é também uma das subtribos morfologicamente mais complexas e diversa do clado NWB. Estudos filogenéticos prévios sustentam o monofiletismo de Arthrostylidiinae e registram quatro clados principais; no entanto, as relações filogenéticas internas ainda são pouco compreendidas, e existem vários gêneros polifiléticos que carecem de trabalhos filogenéticos com amostragem adequada. Esta tese compreende estudos filogenéticos moleculares e taxonômicos em quatro gêneros (*Athroostachys*, *Atractantha*, *Aulonemia* e *Colanthelia*) de Arthrostylidiinae. *Athroostachys*, aqui amostrado pela primeira vez em estudos filogenéticos, é um gênero monoespecífico de bambu escandente, caracterizado por apresentar complemento de ramo com três ramos subiguais e fimbrias proeminentes nas folhas do colmo e dos ramos. *Atractantha* é um pequeno gênero de bambus escandentes reconhecido frequentemente pela presença de canais periféricos de ar no colmo e pelas espiguetas pungentes arranjadas em sinflorescências capitadas ou escorpióides; a filogenia prévia para a subtribo sustentou o monofiletismo do gênero; porém, este foi insuficientemente amostrado. *Aulonemia* e *Colanthelia*, por sua vez, são gêneros complexos quanto à taxonomia e morfologia de suas espécies, as quais exibem significante sobreposição de caracteres morfológicos diagnósticos a nível de gênero. O estudo filogenético prévio para a subtribo sugere relacionamento próximo entre ambos os gêneros, com *Colanthelia* emergindo como monofilético dentro de *Aulonemia*. O capítulo I testa o monofiletismo de *Colanthelia* e investiga o relacionamento filogenético no clado *Aulonemia* + *Colanthelia*, por meio de sequências de sete marcadores moleculares plastidiais (um gene: *ndhF* e seis regiões não codificadoras: *rpl16*, *rps16*, *trnD-trnT, trnT-trnL, rps16-trnQ* e *trnC-rpoB*) de 73 espécies de Bambuseae. Análises Bayesianas e de Máxima Verossimilhança foram utilizadas como métodos de reconstrução filogenética. Os resultados obtidos confirmaram *Aulonemia* como polifilético;

entretanto, *Colanthelia* emerge polifilético no interior do clado *Aulonemia* + *Colanthelia.* Todas as espécies de *Colanthelia* e a maioria das *Aulonemia* amostradas se agruparam no clado *Aulonemia* + *Colanthelia*. Quatro espécies de *Aulonemia* agruparam-se em outros clados de Arthrostylidiinae, e evidências morfológicas sustentam o estabelecimento de novos táxons para acomodar estas espécies atípicas, que claramente não se enquadram na atual circunscrição de *Aulonemia*. O capítulo II apresenta a descrição de uma espécie nova de *Colanthelia* ocorrente no Parque Nacional do Caparaó. São fornecidas descrição morfológica, ilustração, chave de identificação que inclui todas as espécies do gênero e comparação morfológica com a espécie morfologicamente mais próxima, bem como comentários sobre hábitat, distribuição e conservação. O capítulo III testa o monofiletismo de *Atractantha* a partir da ampliação de sua amostragem, e investiga o posicionamento filogenético de *Athroostachys.* Para este estudo, foram utilizadas as mesmas regiões plastidiais investigadas no capítulo I para 44 espécies amostradas de Bambuseae. Neste cenário, *Atractantha* emergiu polifilético. *Atractantha shepherdiana* é altamente sustentada como grupo irmão de *Athroostachys capitata*, e este clado é altamente sustentado como grupo irmão de *Merostachys.* Com base na filogenia molecular e em evidências morfológicas, propõe-se a transferência de *A. shepherdiana* para *Athroostachys*. A nova combinação, *Athroostachys shepherdiana* é proposta e uma redescrição de *Athroostachys* é fornecida, além de uma chave de identificação e ilustração comparativa entre ambas as espécies.

ABSTRACT

COSTA, Cristielle de Jesus, D.Sc., Universidade Federal de Viçosa, March, 2018. **Molecular phylogenetic and taxonomic studies in the Arthrostylidiinae (Poaceae: Bambusoideae: Bambuseae).** Adviser: Ana Paula Santos Gonçalves. Co-advisers: Luiz Orlando de Oliveira and Lynn Gail Clark.

Arthrostylidiinae (Poaceae: Bambusoideae), with 191 species and 15 genera, is the most diverse subtribe of the neotropical woody bamboo (NWB) clade. Its species are distributed predominantly in the coastal Atlantic rainforest of Brazil, which is considered the main diversity center of the subtribe. Besides its taxonomic diversity, Arthrostylidiinae is also one of the morphologically more complex subtribes of the NWB clade. Previous phylogenetic studies support the monophyly of Arthrostylidiinae and recover four main clades; however, internal phylogenetic relationships are still poorly understood, and there are several polyphyletic genera that need phylogenetic study with adequate sampling. This thesis comprises molecular phylogenetic and taxonomic studies in four genera (*Athroostachys*, *Atractantha*, *Aulonemia*, and *Colanthelia*) of Arthrostylidiinae. *Athroostachys*, here sampled for the first time in phylogenetic studies, is a monospecific genus of scandent bamboo, characterized by the presence of a branch complement with three subequal branches and prominent fimbriae on the culm leaves and foliage leaves. *Atractantha* is a small genus of scandent bamboos recognized frequently by the presence of peripheral air canals in the internodes and pungent florets arrayed in capitate or scorpioid synflorescences; the previous phylogeny of the subtribe supported the monophyly of the genus, but it was insufficiently sampled. *Aulonemia* and *Colanthelia*, on the other hand, are complex taxonomically and morphologically, and the two genera exhibit significant overlapping of diagnostic characters. The previous phylogenetic study of the subtribe suggests a close relationship between the two genera, with *Colanthelia* emerging as monophyletic within *Aulonemia*. In chapter I, the monophyly of *Colanthelia* is tested and phylogenetic relationships in the *Aulonemia* + *Colanthelia* clade are investigated through analysis of sequences of seven plastid markers (coding: *ndhF*; non-coding: *trnC-rpoB, rps16-trnQ, trnT-trnL, rps16, trnD-trnT,* and *rpl16*) of 73 species of Bambuseae. Bayesian inference and maximum likelihood were used as the methods of phylogenetic reconstruction. The results obtained confirmed *Aulonemia* as polyphyletic, but *Colanthelia* emerged as polyphyletic within the *Aulonemia* + *Colanthelia* clade. Four species of *Aulonemia* grouped in other clades of Arthrostylidiinae, and morphological evidence supports the establishment of new taxonomic categories to accommodate these anomalous species that do not fit within the current circumscription of *Aulonemia*. Chapter II presents the description of a new species of *Colanthelia* occurring in the National Park of Caparaó. A morphological description, an illustration, an identification key that includes all species of the genus and a morphological comparison with the most similar species are provided, as well as commentary about habitat, distribution and conservation. In chapter III, the monophyly of *Atractantha* is tested based on an increased sampling, and the phylogenetic position of *Athroostachys* is also investigated. For this study, the same plastid markers as in manuscript I were used to analyze 44 species of Bambuseae. In this scenario, *Atractantha* emerged as polyphyletic. *Atractantha shepherdiana* is strongly supported as sister to *Athroostachys capitata*, and this clade is strongly supported as sister to *Merostachys.* Based on the molecular phylogeny and morphological evidence, the transfer of *A. shepherdiana* to *Athroostachys* is proposed. The new combination, *Athroostachys shepherdiana*, and a new description of *Athroostachys* are provided, in addition to a key and a comparative illustration of both species.

INTRODUÇÃO GERAL

Bambusoideae Luerss. constitui uma das 12 subfamílias de Poaceae (Soreng et al. 2015, 2017) e conta com aproximadamente 1.670 espécies, reunidas em 125 gêneros (Clark et al. 2015; Vorontsova et al. 2016; Soreng et al. 2017). Amplamente distribuída, Bambusoideae representa a única subfamília dentre as gramíneas a diversificar-se em ambientes florestais, sendo componente típico de florestas tropicais das Américas e Ásia (Judziewicz et al. 1999).

Os bambus são caracterizados morfoanatomicamente por apresentarem folhas relativamente largas, pseudopecioladas e mesofilo com células fusóides e células invaginantes bem desenvolvidas (Soderstrom & Ellis 1987; Judziewicz et al. 1999; Clark et al. 2015).

Evidências morfológicas e moleculares sustentam o monofiletismo da subfamília (GPWG 2001; Kelchner et al. 2013) e indicam que a diversificação tenha ocorrido em três grandes linhagens, classificadas tradicionalmente em tribos: bambus lenhosos tropicais (Bambuseae, 966 espécies), lenhosos temperados (Arundinarieae, 581 espécies) e bambus herbáceos (Olyreae, 123 espécies) (Sungkaew et al. 2009; Kelchner et al. 2013; Clark et al. 2015; Soreng et al. 2017). Bambuseae, por sua vez, é formada por duas linhagens, o clado dos bambus lenhosos paleotropicais (PWB) composto por oito subtribos e o clado dos bambus lenhosos neotropicais (NWB) representado por Arthrostylidiinae, Guaduinae e Chusqueinae (Soreng et al. 2017). Os bambus lenhosos neotropicais apresentam expressiva diversidade no Brasil, especialmente nas Florestas Amazônica e Atlântica (Judziewicz et al. 1999; Filgueiras & Santos-Gonçalves 2004; Kelchner et al. 2013; Soreng et al. 2017).

Arthrostylidiinae com 15 gêneros e 191 espécies é a subtribo morfologicamente mais diversa do clado dos bambus lenhosos neotropicais (Clark et al. 2015; Parma et al. 2016; Vinícius-Silva et al. 2016; Vorontsova et al. 2016), e apresenta a costa Atlântica do Brasil como principal centro de diversidade e endemismo (Judziewicz et al. 1999). Suas espécies são reconhecidas por um conjunto de características morfológicas e anatômicas: rizomas simpodiais, gemas únicas nos nós do mediocolmo (exceto em *Filgueirasia* Guala), folhas dos ramos normalmente fimbriadas, estria marginal discolor na face abaxial da lâmina foliar, lâminas foliares com feixes de esclerênquima intercostal, sistema vascular simples na nervura central e margens foliares com diferenças anatômicas estruturais acentuadas (Soderstrom & Ellis 1987; Judziewicz et al. 1999). As lâminas foliares são geralmente hipoestomáticas; no entanto, a condição anfiestomática foi registrada para todas as espécies de *Colanthelia* McClure & E.W. Sm., *Aulonemia* Goudot e *Merostachys* Spreng., até agora investigadas, nas quais os estômatos adaxiais estão restritos à uma faixa estreita sobre a estria marginal discolor abaxial (Santos-Gonçalves 2005; Gomes 2009).

É notável nas últimas três décadas o crescente esforço dos sistematas filogeneticistas para compreender a diversidade morfológica e a história evolutiva dos bambus, bem como o empenho em estabelecer classificações baseadas em princípios filogenéticos (Kellogg & Watson 1993; Clark et al. 1995; Kelchner & Clark 1997; Zhang & Clark 2000; Ruiz-Sanchez et al. 2008; Triplett & Clark 2010; Fisher et al. 2009, 2014; Sungkaew et al. 2009; Ruiz-Sanchez 2011; Tyrrell et al. 2012; Kelchner et al. 2013, Attigala et al. 2016; Jesus-Costa et al. no prelo). Embora existam evidências, tanto morfológicas quanto moleculares, que embasam o reconhecimento do monofiletismo de Arthrostylidiinae, suas relações filogenéticas internas ainda são pouco compreendidas.

O estudo de Tyrrell et al. (2012) constitui, até o momento, o único trabalho com enfoque filogenético para a subtribo; o relacionamento filogenético dentro de Arthrostylidiinae foi investigado por meio de seis regiões de DNA plastidial e foram amostrados 11 dos 13 gêneros até então reconhecidos para a subtribo. Em termos de rearranjos taxonômicos, dois novos gêneros foram descritos: *Didymogonyx* (L.G. Clark & Londoño) C.D. Tyrrell, L.G. Clark & Londoño e *Cambajuva* P.L. Viana, L.G. Clark & Filg., sendo o último descrito com base na filogenia supracitada, associada a análises morfoanatômicas (Viana et al. 2013). Alguns gêneros foram resolvidos como monofiléticos; no entanto, alguns nós internos permaneceram pouco resolvidos devido a amostragem insuficiente de determinados gêneros, dentre eles *Aulonemia* Goudot, *Colanthelia* e *Atractantha* McClure. *Colanthelia* emergiu como monofilético dentro de *Aulonemia* que foi polifilético; porém ambos os gêneros foram pobremente amostrados. Apenas seis espécies de *Aulonemia* e três espécies de *Colanthelia* foram foram incluídas nas análises (Tyrrell et al. 2012). *Atractantha* também foi resolvido como monofilético, mas não foi amostrado em sua totalidade.

Aulonemia reúne atualmente 48 espécies, sendo o segundo gênero mais especioso de Arthrostylidiinae (Clark et al. 2015; Vorontsova et al. 2016). Suas espécies distribuem-se desde o México até o sul do Brasil e são encontradas preferencialmente em formações de altitudes elevadas, tais como florestas altimontanas, campos de altitude, campos rupestres e páramos andinos (Judziewicz et al. 1999; Viana 2010). A composição específica de *Aulonemia* é marcada por expressiva heterogeneidade morfológica; inclui plantas com hábito ereto a escandente, colmos fistulosos ou sólidos; complemento de ramo com um único ramo divergente, que em algumas espécies pode ser acompanhado por numerosos ramos menores laterais; promontório conspícuo ou inconspícuo; folhas dimórficas ou não, com fímbrias na região ligular e lâminas deflexas a reflexas; sinflorescências em panículas (3–5 ordens de ramificação), espiguetas aristadas ou múticas, com duas a sete glumas, dois a dez antécios férteis e um antécio apical rudimentar (Judziewicz et al. 1999; Viana 2010).

De acordo com a nova circunscrição proposta por Santos-Gonçalves et al. (no prelo) e adotada por Jesus-Costa et al. (em preparação), *Colanthelia* é composto por dez espécies endêmicas da Floresta Atlântica, sendo nove endêmicas do Brasil e uma ocorrente no sul do Brasil e também norte da Argentina (Santos-Gonçalves et al. no prelo; Jesus-Costa et al. em preparação). A caracterização morfológica de *Colanthelia* é bastante sobreposta à de *Aulonemia*, sendo a presença do "girdle", complemento de ramo com um ramo divergente dominante (de diâmetro aproximado do colmo principal) e poucos a numerosos ramos secundários menores, sinflorescência racemosa ou paniculada com ramificação limitada [1–2 (–3) ordens de ramificação] e espiguetas relativamente longas e estreitas, as principais características utilizadas para o reconhecimento de *Colanthelia*.

A afinidade morfológica entre *Aulonemia* e *Colanthelia* tem sido reconhecida há algum tempo (McClure 1973; Judziewicz & al. 1999; Santos-Gonçalves 2005; Santos-Gonçalves et al. no prelo); *Colanthelia* inclusive foi estabelecido por McClure (1973) com base na transferência de três espécies de *Aulonemia*. Diante da sobreposição de caracteres diagnósticos para ambos os gêneros e do caráter polifilético de *Aulonemia*, estudos filogenéticos consistentes para estes táxons fazem-se necessários.

Atractantha é facilmente distinguido dos demais gêneros de Arthrostylidiinae por apresentar canais periféricos de ar nos colmos de algumas espécies e espiguetas pungentes frequentemente arranjadas em inflorescências capituliformes ou escorpióides (Judziewicz 1992). Atualmente conta com seis espécies, cinco ocorrentes na Floresta Atlântica na Bahia e norte do Espírito Santo, e uma endêmica das Florestas de Igapó no Amazonas e no sudeste da Venezuela (Judziewicz 1992; Santos-Gonçalves et al. 2011). Nas análises de Tyrrell et al. (2012) *Atractantha* emergiu como monofilético; no entanto, apenas três espécies foram amostradas, e *A. shepherdiana* Santos-Gonç., Filg. & L.G. Clark, espécie mais recentemente descrita (Santos-Gonçalves et al. 2011) e conhecida apenas em estádio vegetativo, não foi analisada na referida filogenia da subtribo.

Considerando-se a necessidade de estudos filogenéticos com ampla amostragem em *Aulonemia*, *Colanthelia* e *Atractantha*, o objetivo deste trabalho foi gerar hipóteses filogenéticas para os gêneros de Arthrostylidiinae supracitados. A tese aqui apresentada foi organizada em três capítulos, conforme listado abaixo, os quais foram redigidos na forma de manuscritos científicos, como disposto nas normas de redação de teses e dissertações da Universidade Federal de Viçosa.

Capítulo I: Molecular phylogenetics of *Aulonemia* and *Colanthelia* (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae) based on multi-locus plastid sequences. Encontra-se formatado de acordo com as normas do periódico **Taxon**.

Capítulo II: *Colanthelia longipetiolata* (Poaceae: Bambusoideae), a new species of woody bamboo from the Brazilian Atlantic Forest. Encontra-se formatado de acordo com as normas do periódico **Systematic Botany**.

Capítulo III: Molecular phylogeny of *Atractantha*, and the phylogenetic position and circumscription of *Athroostachys* (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae). Aceito para publicação no periódico **Systematic Botany**.

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Capítulo I: Molecular phylogenetics of *Aulonemia* and *Colanthelia* (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae) based on multi-locus plastid sequences

Normas: Taxon

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Abstract Arthrostylidiinae (Poaceae: Bambusoideae) is a complex subtribe of neotropical woody bamboos that currently comprises 191 species classified in 15 genera. Previous studies support its monophyly and recover four major clades; however, some genera are polyphyletic and some taxa remain undersampled. *Aulonemia* and *Colanthelia* are complex in both their taxonomy and morphology, and they exhibit significant overlapping of morphological characters. A prior molecular phylogeny of the subtribe suggested a close relationship, with *Colanthelia* emerging as monophyletic and nested within *Aulonemia*, but relatively few species were sampled. Phylogenetic relationships in *Aulonemia* and *Colanthelia* remain unresolved and more in-depth sampling is necessary. The aims of this study were to test the monophyly of *Colanthelia,* to investigate phylogenetic relationships within the *Aulonemia* + *Colanthelia* clade, and to revise their classification as appropriate towards a natural classification of the Arthrostylidiinae. We present a multi-locus plastid phylogeny with emphasis on *Aulonemia* and *Colanthelia*. We used sequences of seven plastid markers (one coding: *ndhF*; six non-coding: *trnC-rpoB, rps16-trnQ, trnT-trnL, rps16, trnD-trnT* and *rpl16*) from 73 species of Bambuseae; all genera of Arthrostylidiinae were sampled; approximately 70% of the species *Colanthelia* and 50% of the species *Aulonemia* were sampled. Both Bayesian inference and maximum likelihood analyses were performed. *Aulonemia* was confirmed as polyphyletic, but *Colanthelia* was not maintained as monophyletic. All species of *Colanthelia* fell within the Aulonemia clade, along with most species of *Aulonemia*. Four species of *Aulonemia* (*A. radiata*, *A. effusa*, *A. setosa*, and *A. setigera*) grouped in other major clades within the subtribe and morphological evidence supports the establishment of new genera or taxonomic transfers to accommodate these anomalous species that clearly do not fit in the current circumscription of *Aulonemia*. The results also support submerging *Colanthelia* into *Aulonemia*.

Keywords Atlantic forest; plastid phylogeny; montane forests; *Myriocladus*; Neotropical bamboos.

Resumo Arthrostylidiinae (Poaceae: Bambusoideae) é uma subtribo complexa de bambus lignificados neotropicais que atualmente compreende 191 espécies classificadas em 15 gêneros. Estudos prévios sustentam sua monofilia e registram quatro grandes clados; no entanto, alguns gêneros são polifiléticos e alguns táxons permanecem não amostrados. *Aulonemia* e *Colanthelia* são complexos em suas taxonomia e morfologia, e exibem significante sobreposição de caracteres morfológicos. A filogenia molecular da subtribo sugere relação próxima entre ambos os gêneros, com *Colanthelia* emergindo como monofilético dentro de *Aulonemia*, mas relativamente poucas espécies foram amostradas. O relacionamento filogenético em *Aulonemia* e *Colanthelia* permanece não resolvido e uma amostragem mais ampla é necessária. Os objetivos deste estudo são testar a monofilia de *Colanthelia*, investigar o relacionamento filogenético dentro do clado *Aulonemia* + *Colanthelia* e revisar sua classificação, conforme apropriado, em direção à classificação natural de Arthrostylidiinae. Apresentamos uma filogenia plastidial multilocus com ênfase em *Aulonemia* e *Colanthelia*. Utilizamos sequências de sete marcadores plastidiais (um codante: *ndhF* e seis não codantes: *trnC-rpoB, rps16-trnQ, trnT-trnL, rps16, trnD-trnT* e *rpl16*) para 73 espécies de Bambuseae; todos os gêneros de Arthrostylidiinae foram amostrados; aproximadamente 70% das espécies de *Colanthelia* e 50% das espécies *Aulonemia* foram amostradas. Ambas análises de Inferência bayesiana e máxima verossimilhança foram realizadas. *Aulonemia* foi confirmado como polifilético, mas *Colanthelia* não se manteve como monofilético. Todas as espécies de *Colanthelia* caíram dentro do clado Aulonemia, juntamente com a maioria das espécies de *Aulonemia.* Quatro espécies de *Aulonemia* (*A. radiata*, *A. effusa*, *A. setosa* e *A. setigera*) agruparam-se em outros clados maiores dentro da subtribo e evidências morfológicas sustentam o estabelecimento de novos gêneros ou transferências taxonômicas para acomodar estas espécies atípicas, que claramente não se enquadram na atual circunscrição de *Aulonemia*. Os resultados também sustentam a emergência de *Colanthelia* dentro de *Aulonemia*.

Palavras-chave Bambus neotropicais; filogenia plastidial; floresta Atlântica; florestas Montanas; *Myriocladus*.

INTRODUCTION

The neotropical woody bamboo (NWB) subtribe Arthrostylidiinae (Poaceae: Bambusoideae: Bambuseae) is currently composed of 15 genera and 191 species (Judziewicz & al., 1999; Clark & al., 2015; Vorontsova & al., 2016). The coastal Atlantic rainforest in Brazil, where several endemic genera and species occur, is the main center of diversity of the subtribe (Judziewicz & al., 1999; Viana & al., 2009). Besides its taxonomic richness, Arthrostylidiinae is also the most morphologically diverse subtribe of the NWB (Clark & al., 2015). Together, Arthrostylidiinae, Guaduinae and Chusqueinae comprise the three subtribes of the NWB clade (BPG, 2012).

Arthrostylidiinae is a natural group characterized by a set of morphological and anatomical features: usually a single primary branch bud at the mid-culm nodes, foliage leaves bearing fimbriae, intercostal sclerenchyma fibers in the foliage leaf blades, simple vasculature in the midrib and hypostomatic leaf blades with papillae usually developed only on the abaxial epidermis (Soderstrom & Ellis, 1987; Judziewicz & al., 1999). Amphistomatic foliage leaves have been recorded in some species in two genera (i.e., *Colanthelia* McClure & E.W. Sm., *Merostachys* Spreng. and *Aulonemia* Goudot), in which the stomates are confined to just a narrow region on the adaxial surface over the abaxial green stripe (Santos-Gonçalves, 2005). A green marginal stripe on the abaxial foliage leaf epidermis is useful in identifying of Arthrostylidiinae; however, this feature is not present in some of its species and also can occur in other subtribes of Bambuseae and even in the Arundinarieae and Olyreae, the other two tribes of Bambusoideae (Judziewicz & al., 1999).

The subtribe Guaduinae is strongly supported as the sister group of Arthrostylidiinae and each subtribe is strongly supported as monophyletic (Zhang & Clark, 2000; Ruiz-Sanchez & al., 2008; Fisher & al., 2009; Sungkaew & al., 2009; Ruiz-Sanchez, 2011; Tyrrell & al., 2012; Kelchner & al., 2013; Jesus-Costa & al., in press). The phylogenetic relationship between these subtribes has been investigated based mainly on plastid sequence data and anatomical features and, as a consequence, some changes in the classification of reciprocally misplaced taxa have been made. Guala & al. (2000) in a phylogeny based on *ndhF* gene sequence data found that two species previously described in Guaduinae were allied with the Arthrostylidiinae clade; supported by molecular and morphological data these species were described as a new genus (*Filgueirasia* Guala) of subtribe Arthrostylidiinae (Guala, 2003). Ruiz-Sanchez & al. (2008), in contrast, using morphological and molecular evidence found two species of *Aulonemia* Goudot (Arthrostylidiinae) nested within the Guaduinae, which were subsequently transferred to *Olmeca* Soderstr. (Ruiz-Sanchez & al., 2011). Viana & al. (2011) transferred a species described in *Eremocaulon* Londoño & Clark (Guaduinae) to *Aulonemia* (Arthrostylidiinae) based on floral and anatomical characters.

Phylogenetic relationships within Arthrostylidiinae were investigated by Tyrrell & al. (2012), based on plastid DNA sequence data. In that analysis 11 of the then 13 recognized genera were sampled (the two unsampled genera were *Athroostachys* Benth. and *Myriocladus* Swallen). Arthrostylidiinae was divided into four moderately to strongly supported main lineages (the Glaziophyton, Arthrostylidium, Aulonemia, and Merostachys clades), however no morphological synapomorphy was attributed to any of them. *Didymogonyx* (L.G. Clark & Londoño) C.D. Tyrrell, L.G. Clark & Londoño was elevated to generic status in Tyrrell & al. (2012). Subsequently, the new genus *Cambajuva* P.L. Viana, L.G. Clark & Filg. was proposed by Viana & al. (2013) to accommodate one species of *Aulonemia* resolved as sister to *Glaziophyton* Franch. based on the molecular analysis of Tyrrell & al. (2012) and on morphoanatomical characters. *Colanthelia* was resolved as monophyletic, but nested within *Aulonemia*, which in turn was polyphyletic. Nevertheless, both *Aulonemia* and *Colanthelia* were poorly sampled; only six *Aulonemia* species and three *Colanthelia* species were included in that phylogeny (Tyrrell & al., 2012).

Aulonemia comprises 48 species (Vorontsova & al., 2016). The genus is distributed from Mexico to southern Brazil and the majority of the species occur in wet to moist, moderate to high elevation sites (Judziewicz & al., 1999). The central and northern Andes and the Atlantic rainforest in Brazil are the main centers of diversity of the genus, but some species are endemic to the tepuis of the Guayana highlands. *Aulonemia xerophylla* P.L. Viana & Filg. is restricted to gallery forests of the Cerrado domain in central Brazil, and *A. effusa* (Hack.) McClure is found in open campo rupestre vegetation on quartzitic outcrops (Judziewicz, 2005; Judziewicz & al., 1999; Viana, 2010).

Besides being one of the most species-rich genera of the Arthrostylidiinae, *Aulonemia* is also one of most morphologically heterogeneous of the NWB. The genus includes plants with erect to climbing culms, hollow or solid internodes, elongated and subequal internodes or long alternating with one to four short internodes [the character state present in the type species, *A. queko* Goudot, and two additional species, *A. herzogiana* (Henrard) McClure and *A. hirtula* (Pilg.) McClure]; branch complement with a divergent-dominant branch that, in some species, bears few to numerous smaller secondary branchlets produced at the basal nodes; a poorly to well developed promontory; culm leaves and foliage leaves differentiated or not; fimbriate foliage leaves; and paniculate synflorescences with two to five orders of branching bearing awned or muticous spikelets with two to seven glumes and few to many, overlapping fertile anthoecia, and one apical rudimentary anthoecium represented by a sterile lemma (McClure 1973; Judziewicz & al., 1999; Viana & al., 2011). As a result of the non-monophyly of the genus and its morphological heterogeneity, mainly related to vegetative features, the limits of the current circumscription of *Aulonemia* have been questioned, and its revision in light of a more comprehensive phylogenetic estimation is required. Furthermore, defining the generic limits between *Aulonemia* and *Colanthelia* has been a difficult task, since there is morphological overlap between these genera.

Colanthelia includes ten species endemic to the Atlantic rainforest domain (Santos-Gonçalves & al., in press; Jesus-Costa & al., in prep.), almost all occurring in southern and southeastern in Brazil with only one, *C. rhizantha* (Hack.) McClure, also occurring disjunctly in the province of Misiones in Argentina (Judziewicz & al., 1999; Santos-Gonçalves & al., in press). As circumscribed by Santos-Gonçalves & al. (in press) *Colanthelia* includes plants erect to climbing with hollow, thick-walled culms; internodes elongated and of similar length; a promontory below the bud at each node; a branch complement with the primary branch clearly dominant over the multiple secondary branches borne from its basal nodes; culm leaves differentiated from the foliage leaves and with a relatively well developed girdle and a crest or skirt at the juncture of the sheath and girdle; racemose or paniculate synflorescences with limited branching of up to 2 (–3) orders; and relatively long and narrow spikelets with more or less elongated and exposed rachilla segments. *Colanthelia secundiflora* Santos-Gonç., Filg. & L.G. Clark differs from the remaining species of the genus because of its erect culm leaf blades, secund spikelets and lemmas with dark spots, while the other species possess reflexed culm leaf blades, non-secund spikelets and lemmas uniform in color (except *C. sparsiflora* Santos-Gonc., Filg. & L.G. Clark, which also has lemmas with dark spots).

Colanthelia was first described by McClure & E. W. Sm. in McClure (1973), and included seven species transferred from *Aulonemia*, *Arundinaria* Michx. and

Arthrostylidium Rupr. (McClure, 1973; Smith & al., 1981, 1982; Burman & Filgueiras, 1993; Judziewicz & al., 1999, Santos-Gonçalves, 2005). The morphological affinity between *Aulonemia* and *Colanthelia* has been recognized for some time, and the similarity of the mid-culm branch complements and the occurrence of paniculate synflorescences in some species of *Colanthelia* reinforce this relationship (McClure, 1973; Judziewicz & al., 1999; Santos-Gonçalves, 2005; Santos-Gonçalves & al., in press). Tyrrell & al.'s (2012) phylogeny provided strong support for a relationship between these genera, with a monophyletic *Colanthelia* nested within *Aulonemia*.

In view of the phylogenetic proximity and the overlap of morphoanatomical features between both genera, a phylogenetic study of the Arthrostylidiinae subtribe based on the analyses of multiple plastid DNA regions was conducted to achieve the following aims: 1) to investigate relationships within the *Aulonemia* + *Colanthelia* clade; 2) to test the monophyly of *Colanthelia*; and 3) to revise the classification of the sampled species of *Aulonemia* and *Colanthelia* as appropriate towards a natural classification of the Arthrostylidiinae.

MATERIALS AND METHODS

Taxon sampling and marker selection. — Sampling was optimized to include species of the genera *Aulonemia* and *Colanthelia*. Overall, 73 species were sampled as follows: *Aulonemia* 23/48 (species sampled/species belonging to the genus), *Colanthelia* 7/10, *Actinocladum* McClure ex Soderstr. 1/1, *Alvimia* Calderón ex Soderstr. & Londoño 2/3, *Arthrostylidium* 8/31, *Cambajuva* 1/1, *Athroostachys* 2/2, *Atractantha* McClure 3/5, *Didymogonyx* 2/2, *Elytrostachys* McClure 2/2, *Filgueirasia* 2/2, *Glaziophyton* 1/1, *Merostachys* 3/52, *Myriocladus* 1/12, *Rhipidocladum* McClure 5/19, *Chusquea* Kunth 2/178, *Apoclada* McClure 1/1, *Eremocaulon* 2/4, *Guadua* Kunth 2/32, *Olmeca* 1/5 and *Otatea* (McClure & E.W. Sm.) C.E. Calderón & Soderstr. 1/8. All subtribes (Arthrostylidiinae, Guaduinae and Chusqueinae) and genera of the NWB were sampled. *Bambusa vulgaris* Schrad. ex J.C. Wendl. (Paleotropical woody clade) was designated to root the phylogenetic trees (Clark & al., 2007; Ruiz-Sanchez & al., 2008; Tyrrell & al., 2012). The complete list of taxa and voucher specimens is given in Appendix 1.

Seven plastid markers were selected: one gene (*ndhF* 3' half), four intergenic spacers (*trnD-trnT*, *trnC-rpoB*, *trnT-trnL* and *rps16-trnQ*) and two introns (*rpl16* and *rps16*). The choice of these molecular markers was based on previous studies, which demonstrated that they provide a good phylogenetic signal in the subfamily (Triplett & Clark, 2010; Tyrrell & al., 2012; Kelchner & al., 2013).

DNA extraction, amplification, sequencing and alignment. — Genomic DNA was extracted from ca 30-50 mg of leaves dried in silica gel using a modified 2x cetyl trimethylammonium bromide (CTAB) protocol (Doyle & Doyle, 1987). The amplification primers, sequencing primers and thermal cycler protocols are described in Table 1. The polymerase chain reaction (PCR) was made in a final reaction volume of 40 µL containing 10-50 ng of template DNA, 1x buffer, 2.5 mM of magnesium chloride ($MgCl_2$), 0.2 mM deoxyribonucleotide triphosphates (dNTPs), 0.2 µM each primer and 1 unit *Taq* DNA polymerase (Invitrogen Corp., San Diego, EUA). The amplifications were carried on a T100 thermal cycler (Bio-Rad Laboratories, Inc., Hercules, CA, USA). PCR products were purified using exonuclease I and Shrimp Alkaline Phosphatase (Affymetrix USB, Santa Clara, California, USA). The purified PCR products were sequenced with the BigDye terminator v3.1 sequencing kit on a 3730xl automated sequencer (Applied Biosystems Inc., Foster City, California, USA) by the company Macrogen Inc. (Seoul, Korea). Each plastid marker was sequenced using forward and reverse primers.

Sequences reads were edited, assembled and aligned manually using Sequencher 4.8 (GeneCodes, Ann Arbor, MI). Polymorphic positions were coded following the International Union of Pure and Applied Chemistry (IUPAC) nucleotide ambiguity codes. Gaps were binary coded by applying the approach of Simmons & Ochoterena (2000) implemented in SeqState 1.4.1 (Müller, 2005) and appended to the DNA sequence matrix. All individual sequences obtained in this work are available in GenBank (Appendix 1).

Phylogenetic analyses. — Maximum likelihood (ML) analyses were conducted on RAxML (Randomized Axelerated Maximum Likelihood) using RAxML-HPC BlackBox via the CIPRES Science Gateway under the GTR + G model of sequence evolution (as recommended by the RAxML manual). Node support values were estimated using the rapid bootstrap algorithm implemented in RAxML employing 1,000 replicates (Stamatakis & al., 2008). We consider 90–100% BS as strongly, 80–89% BS as moderate and 70–79% as poor supported for the topology.

Bayesian inference (BI) analyses were performed using MrBayes 3.2.6 (Ronquist & al., 2012) through the CIPRES Science Gateway Portal (Miller & al., 2010). The best evolutionary models were determined in MrModeltest 2.2 (Nylander, 2004), according to the Akaike Information Criterion (AIC) (Posada & Buckley, 2004).The GTR+I+G was suggested for six of the regions (*ndhF*, *rpl16*, *rps16*, *trnD-trnT*, *trnC-rpoB*, and *rps16-trnQ*), while GTR+G was suggested for the *trnT-trnL* spacer. The Markov Chain Monte Carlo search was implemented with four independent runs of 50 million generations with trees sampled every 5,000 generations. The first 25% of the trees were discarded as burn-in and the remainder was used to generate a majority rule consensus tree with posterior probabilities (PPs) for each node. Average standard deviation of split frequencies at the end of each run was below 0.01. In Tracer 1.5 (Drummond & al., 2012), the effective sample size (ESS) presented values well above 200 for all statistics, that ensured that the selected settings were sufficient to the sampling (Zhang & al., 2010). Posterior probabilities ≥ 0.95 were considered strongly supported, those 0.90 to 0.94 as moderately supported.

To detect possible incongruence of the separate datasets, we applied the procedures described by Wiens (1998). We compared the trees of the individual markers to identify the presence of supported clades (≥ 70%) that were incongruent among data partitions. Because the trees generated from the individual datasets did not show any conflicting supported clades, combined analyses were performed for the plastid dataset.

RESULTS

Data Matrix. — We produced 181 new sequences for species of Bambuseae in the present study, and the rest came from GenBank (for GenBank accessions for all sequences, see Appendix 1). Not all cpDNA regions were amplified or sequenced for some samples, even after repeated attempts; however, to obtain a more complete phylogeny, the samples with incomplete data were included in the analyses. Statistics for analyses and general information for cpDNA regions are summarized in Table 2. The alignment of the combined dataset contained 7,884 nucleotide characters plus 41 indel characters, and the missing data (from incomplete taxa) represented approximately 14% of the total analyzed sequences. For the *trnT-trnL* spacer, characters 616-636 were excluded from the aligned matrix due to the excess variability of the region immediately after a sequence of mononucleotides that made this region unreliable.

Phylogeny. — The trees resulting from the individual plastid region analyses were much less resolved and supported than the phylogenetic trees based on the combined dataset and comparisons among those trees revealed no significant incongruence. Likewise, because the trees of the ML analyses were much less resolved and supported than the BI trees, the results and discussion are based on the BI tree obtained from combining all seven markers (Fig. 1). In both BI and ML analyses of each individual marker, only the *ndhF* gene and the *trnC-rpoB* spacer supported the monophyly of each subtribe.

Chusqueinae, Guaduinae and Arthrostylidiinae were each strongly supported as monophyletic [1.00/100 (PP/BS), 1.00/100 and 1.00/100, respectively]. Arthrostylidiinae was highly supported as sister (1.00/100) to the Guaduinae. Within the Arthrostylidiinae, five moderately to strongly supported lineages were recovered: the Glaziophyton clade (I: 1.00/93), the Arthrostylidium clade (II: 1.00/80), the Aulonemia clade (III: 1.00/79), the Merostachys clade (IV: 1.00/93), and the Myriocladus clade (V: 0.98/-). The Glaziophyton clade (Fig. 1, I) was sister to the remainder of the subtribe and it was composed of *Cambajuva ulei* sister (1.00/93) to *Glaziophyton mirabile* Franch. + *Aulonemia radiata* (Rupr.) McClure & L.B. Sm. (0.71/-). The Aulonemia clade (Fig. 1, III) was strongly supported in the BI analysis, as sister (0.98/-) to the Merostachys clade (Fig. 1, IV). The Merostachys clade was composed of representatives of the genera *Actinocladum, Athroostachys, Merostachys, Alvimia, Atractantha,* and *Filgueirasia*, each of them strongly supported as monophyletic in both phylogenetic analyses. Most *Arthrostylidium* species grouped in the Arthrostylidium clade, except for two species that nested in Aulonemia clade; *Arthrostylidium* and *Rhipidocladum* were clearly not monophyletic, while *Elytrostachys* and *Didymogonyx* were each strongly supported (both with support values of 1.00/100) as monophyletic. Because the aim of this study is to investigate the phylogeny of the genera *Aulonemia* and *Colanthelia*, clades II and IV will be not described in detail.

Aulonemia and *Colanthelia* were each polyphyletic, although all of the sampled species of each were resolved within the Arthrostylidiinae. The Aulonemia clade was composed almost exclusively of only *Aulonemia* and *Colanthelia* species, except for two species of *Arthrostylidium* (*Ar.* sp. *LC 1101* + *Ar.* sp. *XL 900*) that form the sister group (1.00/79) to all remaining taxa. Four species of *Aulonemia* grouped with representatives of other clades (I and V). *Aulonemia radiata* nested within the Glaziophyton clade (clade I), as sister to *Glaziophyton mirabile*, but without significant support (0.71/-) for this position. Three species of *Aulonemia* (*A. effusa*, *A. setosa* and *A. setigera*) fell within the Myriocladus clade (clade V), along with *M. virgatus* Swallen (type species), with strong support in the BI analysis (0.98/-); and *A. setosa* and *A. setigera* composed a highly supported clade (1.00/99), which was resolved as sister to *A. effusa*, but this relationship was not significantly supported (0.54/-).

The ML and BI analyses recovered all of the remaining species of *Aulonemia* and all sampled *Colanthelia* species in a poorly supported clade, here designed as the *Aulonemia* + *Colanthelia* clade (0.66/71), with *C. secundiflora* sister (1.00/100) to the remaining *Colanthelia* and *Aulonemia* species. Overall, the relationships within the *Aulonemia* + *Colanthelia* clade were reasonably well resolved and supported in the BI tree (Fig. 1). The *Aulonemia* + *Colanthelia* clade (minus *C. secundiflora*) was divided into two clades (A and B), although these did not have significant support values. However, the chloroplast phylogeny suggested strong geographic partitioning of the sampled *Aulonemia* species, because all Andean plus the one sampled Central American and one sampled Guianan Shield *Aulonemia* species formed one clade (A: 0.73/-), with the Mexican *A. laxa* (F. Maek.) McClure very poorly supported as sister to the Brazilian *Aulonemia* species in the other clade (B: 0.56/-). Relationships within the *Aulonemia* + *Colanthelia* clade were better resolved in the BI analysis, in which the following clades were strongly supported: *Colanthelia* sp. *APS 151* + *C. kinoshitae* Santos-Gonç., Filg. & L.G. Clark (0.99/-), *A. lanciflora* McClure & L.B. Sm. + *A. prolifera* P.L. Viana & Filg. (1.00/-), *C. cingulata* (McClure & L.B. Sm.) McClure + *C. intermedia* (McClure & L.B. Sm.) McClure (1.00/-), and *A. longiaristata* L.G. Clark & Londoño + *A. madidiensis* Judz., D.C. Ziegler & Zueger (1.00/83).

Indels. — Simple indel coding resulted in the addition of 41 indel characters (listed in Table 3) to the combined plastid matrix. In the concatenated matrix, we found many indels that supported the monophyly of some genera (indel **g**: *Filgueirasia*, **s**: *Atractantha*, **d'**: *Athroostachys*, **e'**: *Alvimia*, **g'**: *Guadua*, and **l'**: *Didymogonyx*) or clades (**u**: *Aulonemia* + *Colanthelia*, **j**: *A. setosa* + *A. setigera*, and **z**: *Athroostachys* + *Merostachys*). The subtribe Chusqueinae shared eight exclusive indels (**p**, **c'**, **m**, **q**, **r**, **t**, **v**, and **j'**). The largest indel was a deletion of 237 bp (595-831) in the *rps16-trnQ* intergenic spacer shared by *G. mirabile* and *Ca. ulei* (Hack.) P.L. Viana, L.G. Clark & Filg. The BI tree with indels mapped onto the topology is presented in Fig. 2.

DISCUSSION

Our study concentrated on investigating the relationship between *Aulonemia* and *Colanthelia* and testing the monophyly of *Colanthelia*; thus, the results here presented allow us to improve phylogenetic understanding of the Aulonemia clade. Unlike some studies (Ruiz-Sanchez & al., 2008, 2011), which demonstrated that some species described in *Aulonemia* exhibited phylogenetic affinity with the subtribe Guaduinae, all *Aulonemia* species sampled in our phylogeny remained within the Arthrostylidiinae. As found in other molecular phylogenetic analyses of the NWB (Zhang & Clark, 2000; Ruiz-Sanchez & al., 2008; Fisher & al., 2009; Sungkaew & al., 2009; Ruiz-Sanchez, 2011; Tyrrell & al., 2012; Kelchner & al., 2013; Jesus-Costa & al., in press), Arthrostylidiinae and Guaduinae are strongly supported as monophyletic subtribes and as sister to each other. This relationship has long been suggested by some authors (Soderstrom & Ellis, 1987; Ruiz-Sanchez & al., 2008) and molecular data has confirmed the phylogenetic proximity between these subtribes. The occurrence of refractive papillae on the leaf epidermises has been proposed as a possible synapomorphy (Tyrrell & al., 2012), although there is no detailed morphological investigation in this regard.

The previous molecular phylogeny of Tyrrell & al. (2012) focused on broader questions such as the monophyly of and the relationships among the genera of the Arthrostylidiinae and included only six of the recognized species of *Aulonemia* and three species of *Colanthelia*. That phylogeny suggested a close relationship between these two genera, with *Colanthelia* emerging as monophyletic with moderate support (0.91 PP and 97 BS in maximum parsimony) and nested within *Aulonemia*. Our study expanded considerately the sampling of both, with the inclusion of approximately 70% of the currently recognized species in *Colanthelia* and 50% of the *Aulonemia* species. The type species *A. queko* and *C. cingulata* were included in the analyses, as well as *A. laxa* (the type species of *Matudacalamus* Maekawa, which was synonymized with *Aulonemia* by McClure in 1973). Our results agree in part with those of Tyrrell & al. (2012), in that *Aulonemia* is confirmed as polyphyletic, but the improvement in sampling showed that *Colanthelia* is not monophyletic.

The non-monophyly of *Aulonemia* and *Colanthelia* reflects in part the imprecise delimitation of these genera, which exhibit a significant overlap of morphological features. Among the many characters shared by both genera are the hollow and thick-walled internodes with a small lumen (but thin-walled with a large lumen in some species of *Aulonemia*), a conspicuous or inconspicuous promontory; one divergent, dominant branch per node producing few to many smaller secondary branchlets from its basal nodes (present in all *Colanthelia* species and some *Aulonemia* species); culm leaves usually with reflexed blades (erect blades in *A. setosa*, *A. setigera* and *C. secundiflora*) and the girdle conspicuous or inconspicuous; fimbriate foliage leaves; and paniculate synflorescences (present in all *Aulonemia* species and some *Colanthelia* species) (McClure, 1973; Judziewicz & al., 1999; Viana, 2010; Santos-Gonçalves & al., in press). Differentiating these genera is a rather difficult task, since the main features used in their recognition are not always present in all species. The two genera have been distinguished by the presence of a girdle, often with a crest at its junction with the sheath, and relatively longer and narrower spikelets with the rachilla joints visible in *Colanthelia* (vs. the girdle absent or only slightly developed, and shorter and wider spikelets with the florets strongly overlapping in *Aulonemia*), and the usual presence of only one branch per node in *Aulonemia* species (vs. one divergent, dominant branch per node producing few to many smaller secondary branchlets in all *Colanthelia* species) (McClure, 1973; Judziewicz & al., 1999; Viana, 2010; Santos-Gonçalves & al., in press). However, there are *Colanthelia* species in which the girdle is inconspicuous and some *Aulonemia* species with a branch complement consisting of one dominant branch and few to several secondary branchlets per node (as observed in all *Colanthelia* species).

Aulonemia + Colanthelia clade. — According to our study, *Colanthelia* is polyphyletic, contrary to Tyrrell & al. (2012). All species of *Colanthelia* sampled fell within the Aulonemia clade (clade III, Fig. 1), together with most species of *Aulonemia*, in the *Aulonemia* + *Colanthelia* clade. The **u** indel, consisting of a small deletion of 5 bp in the *rpl16* intron, provided additional support for the *Aulonemia* + *Colanthelia* clade. *Colanthelia secundiflora* is sister to the remaining species of this clade; interestingly, it is the only one with erect culm leaf blades and spikelets secund in racemose synflorescences, while the rest of the species in the *Aulonemia* + *Colanthelia* clade have deflexed to reflexed culm leaf blades and racemose or paniculate synflorescences with the spikelets not secund.

Tyrrell & al. (2012) showed that most of the morphological characters used to distinguish genera inside the Arthrostylidiinae are not synapomorphic, but may be plesiomorphic or the result of convergent evolution. According to the sampling used in our phylogeny, the paniculate synflorescence can be considered a plesiomorphic character state, observed in the Myriocladus clade, *Didymogonyx*, the *Alvimia* + *Atractantha* clade, the *Aulonemia* + *Colanthelia* clade (with a reversal to a racemose synflorescence in *Colanthelia secundiflora*, *Colanthelia sparsiflora* and *Colanthelia* sp. nov. *CJC 72*) and the Glaziophyton clade (with a reversal to a racemose synflorescence in *Cambajuva ulei*). The occurrence of secund spikelets is not so common in Arthrostylidiinae, as the spikelets of most species of subtribe arise bilaterally along the synflorescence axis or in some other arrangement (Judziewicz & al., 1999). This condition of spikelets arrayed unilaterally is found only in *Arthrostylidium merostachyoides* R.W. Pohl, in some *Rhipidocladum* species [of the species sampled in this study, only *R. parviflorum* (Parodi) McClure and *R. maxonii* (Hitchc.) McClure have secund synflorescences] and in most *Merostachys* species.

Colanthelia intermedia and *C. cingulata* form a highly supported monophyletic group in the BI analysis, even in individual analyses from individual markers. Among all *Colanthelia* species, this clade has the largest geographic distribution, occurring in the Atlantic forest in the states of Rio Grande do Sul, Santa Catarina, and Rio de Janeiro, although the two species do not share any exclusive morphological feature (McClure, 1973; Santos-Gonçalves & al., in press). Likewise, *Colanthelia kinoshitae* and *C.* sp. *APS 151* compose a strongly supported clade. *Colanthelia* sp. *APS 151* is most morphologically similar to *C. distans*, and both species occur in Minas Gerais state and have the foliage leaf blades glabrous on both surfaces. However, *C. distans* is cited as probably extinct by Santos-Gonçalves & al. (in press) and, for this reason, could not be included in this study.

Aulonemia hirtula and *A. queko* (the type species) group in the same polytomy, and both (along with *A. herzogiana*, not sampled here) exhibit one very long internode alternating with one to four short internodes along the length of the culm, while the remaining species of *Aulonemia* all have subequal internode lengths. Unequal culm internode lengths are found in only five genera of Arthrostylidiinae: *Arthrostylidium* (1 species), *Aulonemia* (three species), *Didymogonyx* (all species), *Glaziophyton* and *Myriocladus* (all but two species). However, the patterns vary, and Tyrrell & al. (2012) mapped at least three states for this character (except in *Myriocladus*, which they did not sample) and inferred that each different pattern arose independently. The three *Aulonemia* species mentioned above also have thick-walled internodes and culm leaves differentiated from the foliage leaves.

Among the species of *Aulonemia* that occur in Brazil, *A. amplissima* (Nees) McClure is the one that most resembles the remaining sampled Andean and Central American species, typically of middle to high altitude formations [*A. cochabambenis* Judz. & L.G. Clark, *A. patriae* R.W. Pohl, *A. patula* (Pilg.) McClure, *A. deflexa* (N.E. Br.) McClure, *A. robusta* L.G. Clark & Londoño, *A. insignis* Judz. & L.D. Gibbons, *A. longiaristata*, *A. madidiensis*, and *A. longipedicellata* Renvoize], in sharing culms with thin walls, no differentiation between culm leaves and foliage leaves, foliage leaf blades subcordate to ovate-lanceolate, and synflorescences open paniculate (Viana, 2010). However, as indicated in the results (Fig. 2), *A. amplissima* fell within the Brazilian clade (clade B) of the *Aulonemia* + *Colanthelia* clade, reflecting a strong geographic signal. Fisher & al. (2014) in a phylogenetic study of *Chusquea*, another Neotropical woody bamboo genus, found similar results to those showed here. Species of *Chusquea* are found mostly in montane forests and high-elevation grasslands in Mexico, Central America, the Andes, and southeastern Brazil, a distribution similar to but wider than that of *Aulonemia*, both in extent and in elevational range (Clark, 1997; Judziewicz & al., 1999). As in this analysis, Fisher & al.'s (2014) multi-locus plastid phylogeny did not agree with the taxonomic groupings within *Chusquea*, but rather suggested strong geographic partitioning of relationships within the Euchusquea clade.

As discussed above, in the *Aulonemia* + *Colanthelia* clade, two main lineages were recovered, clades A and B, but these do not correspond to any taxonomic grouping; however, it was observed that the plastid phylogeny shows a strong geographic structuring in the relationships of the *Aulonemia* species, as seen in *Chusquea* by Fisher & al. (2014). Clade B, although effectively not supported (0.56/-), contains a moderately to strongly supported (0.96/-) group of only species restricted to Brazil (*A. cincta, A. xerophylla, A. amplissima, A. aristulata, A. soderstromii, A. prolifera,* and *A. lanciflora*), and one species endemic to Mexico (the northernmost limit of the genus), *A. laxa*, which for now is considered sister to the Brazilian taxa with no support. Clade A also effectively has no support (0.73/-), but consists of *A. cochabambensis, A. hirtula, A. patriae, A. patula, A. queko, A. robusta, A. deflexa, A. insignis, A. longiaristata, A. madidiensis,* and *A. longipedicellata*, all but one species restricted to the Andes or the Guianan Shield (*A. deflexa*), with *A. patriae* endemic to Costa Rica (Vorontsova & al., 2016). Recent and rapid radiation within clade A or B of the *Aulonemia* + *Colanthelia* clade may explain the incongruence between the plastid phylogeny and morphology, as postulated for the Euchusquea clade by Fisher & al.

(2014), but other explanations are possible (e.g., incomplete lineage sorting, hybridization) and remain to be tested.

Most species of *Aulonemia* and all species of *Colanthelia* grouped in *Aulonemia* + *Colanthelia* clade. However, four atypical species of *Aulonemia* unambiguously grouped with other major clades within the subtribe. *Aulonemia radiata* fell in the Glaziophyton clade, and *A. effusa, A. setosa* and *A. setigera* grouped in the Myriocladus clade.

Glaziophyton clade. —From a morphological point of view, the phylogenetic positioning of *Aulonemia radiata* within the Glaziophyton clade (clade I, Fig. 1) was expected, since *A. radiata*, together with the species of the Glaziophyton clade, shares the presence of tessellate leaf blades, which is a possible morphological synapomorphy for this lineage (Viana, 2010; Tyrrell & al., 2012). Unlike the other two species of the Glaziophyton clade, *Glaziophyton mirabile* and *Cambajuva ulei,* which have erect, self-sustaining culms and erect leaf blades, *A. radiata* has clambering or erect culms and reflexed to patent leaf blades. These features, however, seem to be correlated with the habitat where these taxa occur, as *G. mirabile* and *Ca. ulei* are typically found in open montane environments called *campos de altitude* (Safford, 1999), whereas *A. radiata* grows in montane cloud forests. All three species of the Glaziophyton clade are typically found in higher elevation sites of the Atlantic Rainforest domain: *Ca. ulei* is endemic to the Serra Geral of Southern Brazil (Viana & al., 2013); *G. mirabile* is endemic to a few rocky outcrops in the summits of the Serra dos Órgãos, Rio de Janeiro state (Fernandez & al. 2012); and *A. radiata* has a wider distribution in montane forests from southern to southeastern Brazil (Viana 2010). In the phylogenetic treatment of gaps, indel **i** (a deletion of 237 bp in *rps16-trnQ*), was shared by *G. mirabile* and *Ca. ulei* but not by *A. radiata,* contrary to the position of *A. radiata* as sister to *G. mirabile*.

In this phylogeny presented, in general, the use of indels as characters in phylogenetic analyses increased the resolution of the trees and provide support for some taxa. Indels are especially frequent in introns and intergenic spacer regions of cpDNA and the importance of these character have be recognized in the phylogenetic analysis of diffent taxonomic groups (Graham & al., 2000).

Myriocladus clade. — *Aulonemia setosa* and *A. setigera* form a strongly supported clade within the Myriocladus clade (clade V), which also includes *Aulonemia effusa* and *Myriocladus virgatus*. Both species share differentiated culm leaves (vs. leaves not dimorphic in *A. effusa* and *M. virgatus*), young internodes velvety with dense trichomes, foliage leaf blades with a setose apex, synflorescences with the branches appressed to the main axis and terete spikelets (vs. internodes glabrous and covered with whitish wax, foliage leaf blades with an acuminate apex, and synflorescences with branches divergent in both *A. effusa* and *M. virgatus*, with laterally compressed spikelets in *A. effusa* and elliptical to oval spikelets in *M. virgatus*) (Judziewicz 1998; Viana, 2010). Besides the mentioned morphological characteristics, *A. setosa* and *A. setigera* share an insertion of 5 bp (indel **j**) in the *rps16-trnQ* intergenic spacer. The circumscription of *Aulonemia* according to McClure (1973) and Judziewicz & al. (1999) includes plants with culm leaf blades reflexed, except in *A. ulei*, now *Cambajuva ulei* (Viana & al., 2013) and *A. setosa* and *A. setigera*, in which the culm leaf blades are erect. Similarly to *Ca. ulei*, *A. setosa* and *A. setigera* did not group in the Aulonemia clade (III) and are morphologically anomalous within *Aulonemia*.

Aulonemia effusa exhibits some morphological features that suggest an affinity with species of *Myriocladus*, such as the erect, typically unbranched culms, leathery leaves with reduced pseudopetioles, the open paniculate synflorescences, and the spikelets with awned bracts (Judziewicz, 1998; Viana, 2010). Besides the morphological similarity, *A. effusa* also grows in similar habitats (open sandstones formations, at altitudes above 1000 meters) with the species of *Myriocladus*, although *A. effusa* occurs in the campos rupestres of the Espinhaço Range in the states of Minas Gerais and Bahia, and *Myriocladus* is endemic to the tepuys of the Guyana Plateau in northern Brazil, Venezuela and the Guianas (Judziewicz, 1998; Viana, 2010). This relationship is confirmed in this study, which suggests that *M. virgatus* is sister to the *A. effusa* + (*A. setosa* + *A. setigera*) clade; however, despite the morphological similarity of *A. effusa* and *M. virgatus*, in the molecular phylogeny their relationship is only moderately supported. *Myriocladus* and *Glaziophyton* share some similarities, such as the unusual long basal internode followed by several shorter internodes and erect leaf blades (McClure, 1973; Judziewicz, 1998; Judziewicz & al., 1999); however, an increased sampling in *Myriocladus* is necessary to elucidate this relationship, and also the relationships of *A. effusa* within clade V.

We therefore recommend the following taxonomic changes to establish monophyletic groups in the Arthrostylidiinae: 1) transfer all *Colanthelia* species to *Aulonemia*, because the current circumscription of *Colanthelia* does not represent a natural grouping; 2) establish a new genus to accommodate *A. radiata*, which although resolved as part of the well-supported Glaziophyton clade and sharing the presence of tessellate leaf blades as a putative synapomorphy of this clade, does not fit within either *Glaziophyton* or *Cambajuva*; 3) establish a new genus to accommodate *A. setosa* and *A. setigera,* which are well supported as a monophyletic group outside of *Aulonemia* based on both molecular and morphological data; and 4) transfer *Aulonemia effusa* to *Myriocladus,* as the molecular data clearly indicate that it does not belong within *Aulonemia*, and its phylogenetic position as well as morphological characters suggest its repositioning in *Myriocladus.* With respect to the expanded circumscription of *Aulonemia,* because none of the recovered clades within the *Aulonemia* + *Colanthelia* clade seem to correspond to the morphological groups, it is not possible to establish an infrageneric classification for the genus at this time.

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Table 1. Description of amplification primers, sequencing primers, PCR protocols and size of seven chloroplast regions used in this study.

Region	Primer sequence (5’→ 3’)	PCR protocol	Region size (bp)	Reference
ndhF 3’	972F: GTCTCAATTGGGTTATATGATG 2110R: CCCCCTAYATATTTGATACCTTCTCC Seq: 1318F: GGATTAACTGCGTTTTATATGTTTCG 1603R: GCATAGTATTTCTTCCCGTTTCATGAGG	94ºC, 1 m; 30× (94ºC, 1 m 30 s; touchdown 53-43ºC, 2 m; 72ºC, 3 m); 72ºC, 10 m	1140	Triplett & Clark, 2010
rps16	rps16F: AAACGATGTGGTARAAAGCAAC rps16R: AACATCWATTGCAASGATTCGATA	94ºC, 2 m; 35× (94ºC, 45 s; touchdown 58-48ºC, 30 s; 72ºC, 1 m); 72ºC, 5 m	860	Shaw & al., 2005
trnD-trnT	trnD-for: ACCAATTGAACTACAATCCC trnT-rev: CCCTTTTAACTCAGTGGTA Seq: trnY-rev: CTCTTTGCTTTGGATCTAG trnE-for: GCCTCCTTGAAAGAGAGATG	94ºC, 2 m; 35× (94ºC, 45 s; touchdown 58-48.5ºC, 1 m; 72ºC, 1 m 15 s); 72ºC, 5 m	1100	Triplett & Clark, 2010

rps16-trnQ	1F: GCACGTTGCTTTCTACCACA 1574R: ATCCTTCCGTCCCAGATTTT Seq: 334F: CGAGATGGTCAATCCTGAAATG 628R: CTTTTGGTATTCKAGTCGAAG	94ºC, 2 m; 35× (95ºC, 1 m; 50ºC, 30 s; +15ºC, 0.3ºC/s; 65ºC, 5 m); 65ºC, 5 m	1120	Triplett & Clark, 2010
trnT-trnL	trnT-L F: CATTACAAATGCGATGCTCT trnT-L R: TCTACCGATTTCGCCATATC	95ºC, 2 m; 35× (95ºC, 1 m; 48ºC, 10 s; +17ºC, 0.3ºC/s; 65ºC, 5 m); 65ºC, 5 m	830	Triplett & Clark, 2010
trnC-rpoB	trnC: TGGGGATAAAGGATTTGCAG rpoB: ATTGTGGACATTCCCTCRTT Seq: jt400-for: CAGGTCCGAACAGCATTA jt700-rev: CGTAGTAGTAGAATTGCTAG	94ºC, 2 m; 35× (96ºC, 1 m; touchdown 56-46ºC, 2 m; 72ºC, 3 m); 72ºC, 5 m	1185	Triplett & Clark, 2010
rpl16	F71: GCTATGCTTAGTGTGTGACTCGTTG R1661: CGTACCCATATTTTTCCACCACGAC Seq: SAK8: CCATCCCACCCAATGAAG R1516: CCCTTCATTCTTCCTCTATGTTG	95ºC, 2 m; 35× (95ºC, 1 m; 50ºC, 10 s; +15ºC, 0.3ºC/s; 65ºC, 4 m); 65ºC, 5 m	1100	F71 and R1661: Jordan & al., 1996; R1516: Kelchner & Clark, 1997; SAK8: Tyrrell & al., 2012

Table 2. Statistics for analyses and general information for cpDNA regions for Bambuseae.

Characteristic	*ndhF*	*trnC-rpoB*	*rpL16*	*rps16*	*rps16-trnQ*	*trnD-trnT*	*trnT-trnL*	Combined
Number of taxa	70	62	54	50	69	65	59	73
Aligned length (bp)	1,173	1,374	1145	854	1215	1305	818	7884
Variable characters	90	86	74	36	99	78	58	521
Informative characters	86	76	61	29	86	85	35	459
(%)	(7.33%)	(5.53%)	(5.33%)	(3.4%)	(7.08%)	(6.51%)	(4.28%)	(5.8%)

Table 3. Phylogenetically informative indels in the concatenated plastid sequence matrix in Bambusoideae species analyzed.

Matrix character no.	Position	Marker	Size (bp)	Type	Letter	Taxa
7886	29-32	*rps16-trnQ*	4	Insertion	a	*Ar. pubescens*, *R. parviflorum*, *R.* sp. *TF s.n.*
7887	107-111	*rps16-trnQ*	5	Deletion	b	*Ot. acuminata*
7888	160-163	*rps16-trnQ*	4	Insertion	c	*Ar. pubescens, Ar. cubense, Ar. multispicatum, Ar. urbanii, R. parviflorum, R. harmonicum, R. cordatum, R. sp. TF s.n., Ar. venezuelae*
7889	458-466	*rps16-trnQ*	9	Insertion	d	*Ap. simplex*, *E. aureofimbriatum*
7890	509-515	*rps16-trnQ*	7	Deletion	e	*Ar.* sp. *LC 1101*, *Ar.* sp. *XL 900*, *E.* sp. *CJC 108*, *R. harmonicum*, *Rh. cordatum*
7891	541-562	*rps16-trnQ*	22	Insertion	f	*F. arenicola*
7892	563-576	*rps16-trnQ*	14	Insertion	g	*F. arenicola, F. cannavieira*
7893	577-581	*rps16-trnQ*	5	Insertion	h	*F. arenicola, F. cannavieira, A. setosa, A. setigera*
7894	595-831	*rps16-trnQ*	237	Deletion	i	*Gl. mirabile*, *Ca. ulei*
7895	841-845	*rps16-trnQ*	5	Insertion	j	*A. setosa*, *A. setigera*
7896	917-922	*rps16-trnQ*	6	Insertion	k	*C.* sp. *CJC 72*, *C. sparsiflora*, *C. kinoshitae*, *C.* sp. *APS 151*, *A. xerophylla*, *A. soderstromii*, *A. prolifera*, *A. lanciflora*, *A. aristulata*, *A. amplissima*

7897	974-978	*rps16-trnQ*	5	Insertion	l	*Ca. ulei*
7898	1019-1056	*rps16-trnQ*	38	Deletion	m	*Ch. capituliflora*, *Ch.* sp. *SG 652*
7899	1140-1145	*rps16-trnQ*	6	Insertion	n	All except *B. vulgaris, A. cochabambense*, *Ch. capitulifora*, *Ch.* sp. *SG 652*
7900	1149-1162	*rps16-trnQ*	14	Insertion	o	*E.* sp. *CJC 108*
7901	1834-1839	*ndhF*	6	Insertion	p	*Ch. capituliflora*, *Ch.* sp. *SG 652*
7902	2509-2514	*rpl16*	6	Deletion	q	*Ch. capituliflora*, *Ch.* sp. *SG 652*
7903	2680-2685	*rpl16*	6	Deletion	r	*Ch. capituliflora*, *Ch.* sp. *SG 652*
7904	2737-2741	*rpl16*	5	Insertion	s	*At. aureolanata*, *At. cardinalis*, *At. radiata*
7905	2747-2769	*rpl16*	23	Deletion	t	*Ch. capituliflora*, *Ch.* sp. *SG 652*
7906	2845-2849	*rpl16*	5	Deletion	u	*C.* sp. *APS 151*, *A. cincta*, *A. aristulata*, *A. amplissima*, *A. lanciflora*, *A. prolifera*, *A. xerophylla*, *A. soderstromii*, *C. kinoshitae*, *C. intermedia*, *C. cingulata*, *C. sparsiflora*, *C.* sp. *CJC 72*
7907	3071-3081	*rpl16*	11	Deletion	v	*Ch. capituliflora*, *Ch.* sp. *SG 652*
7908	3335-3339	*rpl16*	5	Insertion	w	All except *B. vulgaris*, *A. patula*, *A. effusa*
7909	3445-3461	*rpl16*	17	Insertion	x	*A. effusa*, *C. kinoshitae*
7910	3723-3745	*rps16*	23	Insertion	y	*E.* sp. *CJC 108*, *Ap. simplex*

7911	3803-3807	*rps16*	5	Deletion	z	*Athr. capitata*, *Athr. shepherdiana*, *M. fistulosa*, *M. tatianae*, *M. ternata*
7912	3874-3891	*rps16*	18	Deletion	a'	*R. parviflorum*, *Ar. merostachyoides*
7913	4437-4442	*trnC-rpoB*	6	Insertion	b'	*A. cincta*, *Ca. ulei*
7914	4886-4890	*trnC-rpoB*	5	Insertion	c'	*Ch. capituliflora*, *Ch.* sp. *SG 652*
7915	5003-5006	*trnC-rpoB*	4	Insertion	d'	*Athr. capitata*, *Athr. shepherdiana*
7916	5066-5183	*trnC-rpoB*	118	Deletion	e'	*Al. auriculata*, *Al. gracilis*
7917	5593-5605	*trnC-rpoB*	13	Insertion	f'	*R.* sp. *TF s.n.*, *R. parviflorum*
7918	5666-5670	*trnC-rpoB*	5	Insertion	g'	*G. tagoara*, *G. angustifolia*
7919	5808-5812	*trnD-trnT*	5	Insertion	h'	All except *B. vulgaris, Ap. simplex*, *Ch.* sp. *SG 652*, *E. aureofimbriatum*, *E.* sp. *CJC 108*, *G. tagoara*, *G. angustifolia*, *Ot. acuminata*, *Ol. recta*
7920	5865-5870	*trnD-trnT*	6	Deletion	i'	*G. tagoara*, *G. angustifolia*, *Ap. simplex*
7921	6085-6123	*trnD-trnT*	39	Deletion	j'	*Ch. capituliflora*, *Ch.* sp. *SG 652*
7922	6101-6105	*trnD-trnT*	5	Insertion	k'	*My. virgatus*, *Ar.* sp. *XL 900*, *Athr. capitata*, *A. aristulata*
7923	6424-6430	*trnD-trnT*	7	Insertion	l'	*D. geminatum*, *D.* aff. *longispiculatum*
7924	6503-6508	*trnD-trnT*	6	Insertion	m'	All except *B. vulgaris, Ap.*

						simplex, *Ch.* sp. *SG 652*, *Ch. capituliflora*, *E. aureofimbriatum*, *E.* sp. *CJC 108*, *G. tagoara*, *G. angustifolia*, *Ol. recta*, *Ot. acuminata*
7925	6676-6679	*trnD-trnT*	4	Insertion	n'	*E. aureofimbriatum*, *Ap. simplex*
7926	7082-7086	*trnT-trnL*	5	Insertion	o'	*Ar. urbanii*, *Ar.* sp. *XL 900*

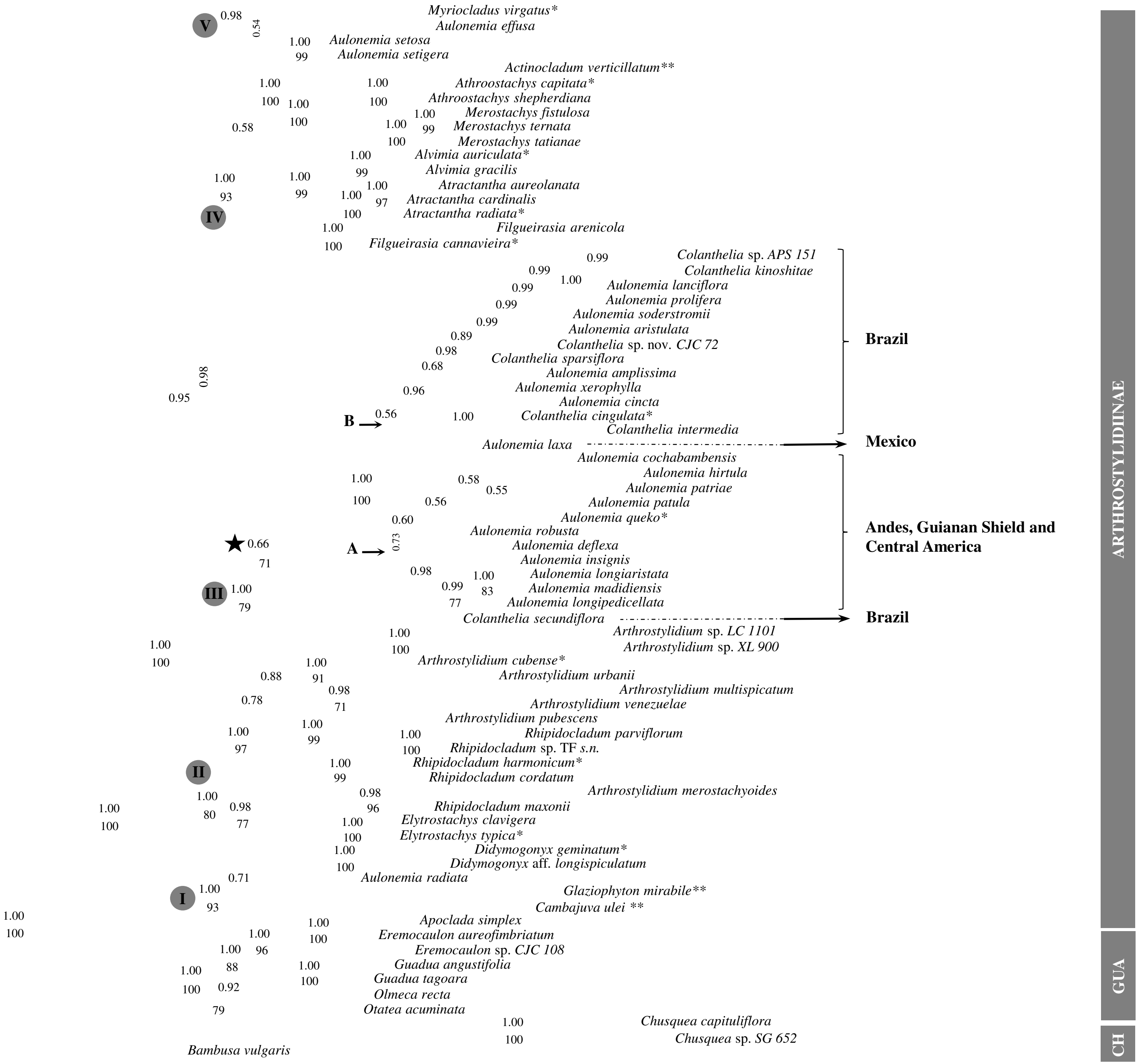
V
0.98
0.54
Myriocladus virgatus*
Aulonemia effusa
1.00
99
Aulonemia setosa
Aulonemia setigera
Actinocladum verticillatum**
1.00
100
1.00
100
Athroostachys capitata*
Athroostachys shepherdiana
1.00
100
1.00
99
Merostachys fistulosa
0.58
1.00
100
Merostachys ternata
Merostachys tatianae
1.00
99
Alvimia auriculata*
Alvimia gracilis
1.00
93
1.00
99
1.00
97
Atractantha aureolanata
1.00
100
Atractantha cardinalis
Atractantha radiata*
IV
1.00
100
Filgueirasia arenicola
Filgueirasia cannavieira*
0.99
Colanthelia sp. APS 151
0.99
1.00
Colanthelia kinoshitae
0.99
Aulonemia lanciflora
0.99
Aulonemia prolifera
0.99
Aulonemia soderstromii
0.89
Aulonemia aristulata
0.98
Colanthelia sp. nov. CJC 72
0.68
Colanthelia sparsiflora
0.98
0.95
Aulonemia amplissima
0.96
Aulonemia xerophylla
Aulonemia cincta
B
0.56
1.00
Colanthelia cingulata*
Colanthelia intermedia
Aulonemia laxa
Brazil
Mexico
Aulonemia cochabambensis
1.00
100
0.58
0.55
Aulonemia hirtula
Aulonemia patriae
0.56
Aulonemia patula
0.60
Aulonemia queko*
Aulonemia robusta
★ 0.66
71
A
0.73
Aulonemia deflexa
Aulonemia insignis
0.98
1.00
83
Aulonemia longiaristata
0.99
77
Aulonemia madidiensis
III
1.00
79
Aulonemia longipedicellata
Colanthelia secundiflora
Andes, Guianan Shield and Central America
Brazil
1.00
100
Arthrostylidium sp. LC 1101
1.00
100
Arthrostylidium sp. XL 900
1.00
91
Arthrostylidium cubense*
0.88
Arthrostylidium urbanii
0.98
71
Arthrostylidium multispicatum
0.78
Arthrostylidium venezuelae
Arthrostylidium pubescens
1.00
99
1.00
97
1.00
100
Rhipidocladum parviflorum
Rhipidocladum sp. TF s.n.
II
1.00
99
Rhipidocladum harmonicum*
Rhipidocladum cordatum
Arthrostylidium merostachyoides
0.98
96
1.00
100
1.00
80
0.98
77
Rhipidocladum maxonii
1.00
100
Elytrostachys clavigera
Elytrostachys typica*
1.00
100
Didymogonyx geminatum*
Didymogonyx aff. longispiculatum
Aulonemia radiata
0.71
I
1.00
93
Glaziophyton mirabile**
Cambajuva ulei **
1.00
100
1.00
100
Apoclada simplex
1.00
96
Eremocaulon aureofimbriatum
1.00
88
Eremocaulon sp. CJC 108
1.00
100
1.00
100
Guadua angustifolia
0.92
79
Guadua tagoara
Olmeca recta
Otatea acuminata
1.00
100
Chusquea capituliflora
Chusquea sp. SG 652
Bambusa vulgaris
ARTHROSTYLIDIINAE
GUA
CH

Fig. 1. Bayesian topology tree based on combined cpDNA dataset of *trnD-trnT*, *rps16-trnQ*, *trnC-rpoB*, *trnT-trnL* intergenic spacers, *rpl16* and *rps16* introns, and the *ndhF* gene. Numbers above branches are BI posterior probabilities (PP); numbers below branches are bootstrap support (BS) values from the Maximum likelihood analysis. The clades resolved are indicated with following symbols: I = Glaziophyton clade, II = Arthrostylidium clade, III = Aulonemia clade, IV = Merostachys clade, V = Myriocladus clade, GUA = Guaduinae, CH = Chusqueinae, = *Aulonemia* + *Colanthelia* clade, * = type species, ** = monotypic genus. The blue branches represent species of *Aulonemia* and the red branches represent species of *Colanthelia.*

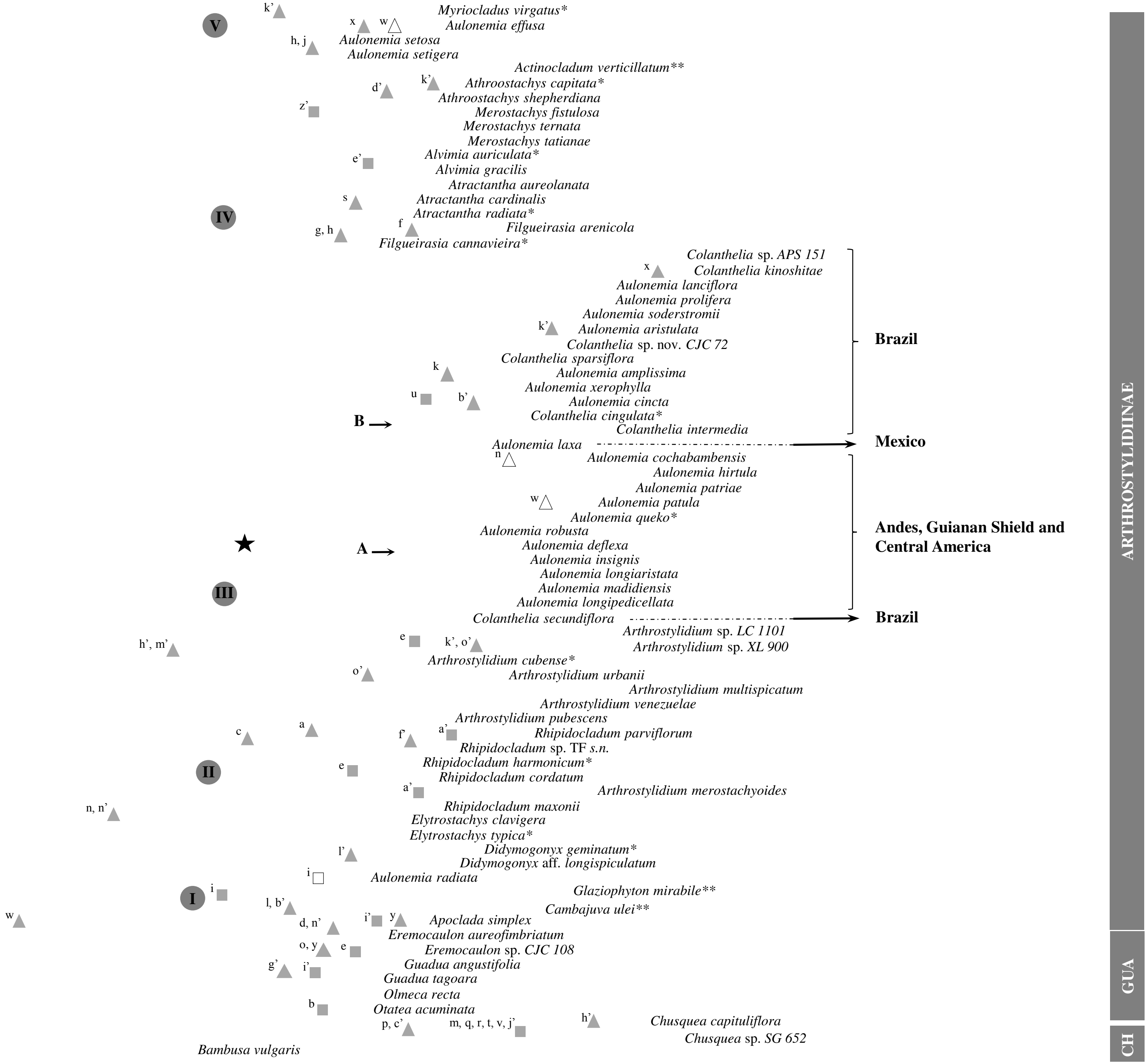
V
k'
x
w
Myriocladus virgatus*
Aulonemia effusa
h, j
Aulonemia setosa
Aulonemia setigera
Actinocladum verticillatum**
d'
k'
Athroostachys capitata*
Athroostachys shepherdiana
z'
Merostachys fistulosa
Merostachys ternata
Merostachys tatianae
e'
Alvimia auriculata*
Alvimia gracilis
Atractantha aureolanata
s
Atractantha cardinalis
IV
Atractantha radiata*
f
g, h
Filgueirasia arenicola
Filgueirasia cannavieira*
Colanthelia sp. APS 151
x
Colanthelia kinoshitae
Aulonemia lanciflora
Aulonemia prolifera
Aulonemia soderstromii
k'
Aulonemia aristulata
Colanthelia sp. nov. CJC 72
Brazil
Colanthelia sparsiflora
k
Aulonemia amplissima
u
b'
Aulonemia xerophylla
Aulonemia cincta
Colanthelia cingulata*
B
Colanthelia intermedia
Aulonemia laxa
Mexico
n
Aulonemia cochabambensis
Aulonemia hirtula
Aulonemia patriae
w
Aulonemia patula
Aulonemia queko*
Andes, Guianan Shield and Central America
Aulonemia robusta
★
A
Aulonemia deflexa
Aulonemia insignis
Aulonemia longiaristata
III
Aulonemia madidiensis
Aulonemia longipedicellata
Colanthelia secundiflora
Brazil
Arthrostylidium sp. LC 1101
e
h', m'
k', o'
Arthrostylidium sp. XL 900
Arthrostylidium cubense*
o'
Arthrostylidium urbanii
Arthrostylidium multispicatum
Arthrostylidium venezuelae
Arthrostylidium pubescens
c
a
f'
a'
Rhipidocladum parviflorum
Rhipidocladum sp. TF s.n.
Rhipidocladum harmonicum*
II
e
Rhipidocladum cordatum
a'
Arthrostylidium merostachyoides
n, n'
Rhipidocladum maxonii
Elytrostachys clavigera
Elytrostachys typica*
l'
Didymogonyx geminatum*
Didymogonyx aff. longispiculatum
i
Aulonemia radiata
i
I
Glaziophyton mirabile**
l, b'
Cambajuva ulei**
w
d, n'
i'
y
Apoclada simplex
Eremocaulon aureofimbriatum
o, y
e
Eremocaulon sp. CJC 108
g'
i'
Guadua angustifolia
Guadua tagoara
Olmeca recta
b
Otatea acuminata
h'
Chusquea capituliflora
p, c'
m, q, r, t, v, j'
Chusquea sp. SG 652
Bambusa vulgaris
ARTHROSTYLIDIINAE
GUA
CH

Fig. 2. Bayesian topology tree based on combined cpDNA dataset of *trnD-trnT*, *rps16-trnQ*, *trnC-rpoB*, *trnT-trnL* intergenic spacers, *rpl16* and *rps16* introns, and the *ndhF* gene. Numbers above branches are BI posterior probabilities (PP); numbers below branches are bootstrap support (BS) values from the Maximum likelihood analysis. The clades resolved are indicated with following symbols: I = Glaziophyton clade, II = Arthrostylidium clade, III = Aulonemia clade, IV = Merostachys clade, V = Myriocladus clade, GUA = Guaduinae, CH = Chusqueinae, = *Aulonemia* + *Colanthelia* clade, * = type species, ** = monotypic genus. Insertions (solid triangle) and deletions (solid square) are denoted by lower-case letters and are identified in Table 3. The blue branches represent species of *Aulonemia* and the red branches represent species of *Colanthelia.*

Appendix 1. List of taxa sampled in this study. Taxa, origin, voucher, and GenBank accession numbers [*ndhF, rpl16, rps16, trnC-rpoB, trnD-trnT, rps16-trnQ, trnT-trnL*]. Dash (—) indicates missing data. GB refers to the sequences generated in this study, which are in submition process in GenBank.

ARTHROSTYLIDIINAE Soderstr. & R.P.Ellis— ***Actinocladum verticillatum*** (Nees) McClure ex Soderstr., Brazil, *T Filgueiras s.n.* (ISC), [JQ408524, JQ408570, —, JQ408485, JQ408623, JQ408445, JQ408586]. ***Actinocladum verticillatum,*** Brazil, *CJ Costa 89* (VIC), [—, —, MG458251, —, —, —, —]. ***Alvimia auriculata*** Soderstr. & Londoño, Brazil, *AP Santos-Gonçalves 598* (VIC), [JQ408525, —, —, JQ408486, JQ408624, JQ408446, JQ408587]. ***Alvimia gracilis*** Soderstr. & Londoño, Brazil, *A Carvalho et al. 4389* (CEPEC), [JQ408526, JQ408571, —, JQ408487, JQ408625, JQ408447, JQ408588]. ***Arthrostylidium cubense*** Rupr., Cuba, *X Londoño 957* (ISC), [JQ408529, JQ408572, —, —, JQ408628, JQ408450, JQ408590]. ***Arthrostylidium merostachyoides*** R.W. Pohl, Costa Rica, *C Tyrrell et al. 36* (ISC), [JQ408531, —, —, JQ408491, —, JQ408452, —]. ***Arthrostylidium multispicatum*** Pilg., Puerto Rico, *LG Clark & G Reiners 1508* (ISC), [JQ408532, JQ408574, —, —, JQ408630, JQ408453, JQ408592]. ***Arthrostylidium pubescens*** Rupr., Costa Rica, *C Tyrrell et al. 42* (ISC), [JQ408533, JQ408575, —, —, JQ408631, JQ408454, —]. ***Arthrostylidium*** **sp.**, Ecuador, *LG Clark et al. 1101* (QCA), [JQ408530, JQ408573, —, JQ408490, JQ408629, JQ408451, JQ408591]. ***Arthrostylidium*** **sp.**, Colombia, *X Londoño 900* (COL), [JQ408528, —, —, JQ408489, JQ408627, JQ408449, JQ408593]. ***Arthrostylidium urbanii*** Pilg., Cuba, *X Londoño 851* (ISC), [JQ408534, JQ408576, —, JQ408492, JQ408632, JQ408455, JQ408594]. ***Arthrostylidium venezuelae*** (Steud.) McClure, Costa Rica, *C Tyrrell et al. 43* (ISC), [JQ408535, —, —, JQ408493, JQ408633, —, —]. ***Athroostachys capitata*** (Hook.) Benth., Brazil, *R Vinícius-Silva 15* (VIC), [MG458235, MG458241, MG458252, MG458262, MG458268, MG458274, MG458281]. ***Athroostachys shepherdiana*** (Santos-Gonçalves, Filg. & L.G. Clark) Jesus-Costa & Santos-Gonçalves, Brazil, *CJ Costa et al. 114* (VIC), [MG458236, MG458242, MG458255, MG458263, MG458269, MG458276, MG458282]. ***Atractantha aureolanata*** Judz., Brazil, *AP Santos-Gonçalves 596* (VIC), [JQ408536, —, —, JQ408494, JQ408634, —, JQ408595]. ***Atractantha aureolanata***, Brazil, *AP Santos-Gonçalves 658* (VIC), [—, MG458243, MG458253, —, —, MG458275, —]. ***Atractantha cardinalis*** Judz., Brazil, *AP Santos-Gonçalves 591* (VIC), [JQ408537, —, —, JQ408495, JQ408635, JQ408456, JQ408596]. ***Atractantha cardinalis***, Brazil, *AP*

Santos-Gonçalves 657 (VIC), [—, MG458244, MG458254, —, —, —, —]. ***Atractantha radiata*** McClure, Brazil, *A Carvalho 4362* (CEPEC), [JQ408538, JQ408577, KC020568.1, JQ408496, JQ408636, JQ408457, JQ408597]. ***Aulonemia amplissima*** (Nees) McClure, Brazil, *CJ Costa et al. 78* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia aristulata*** (Döll) McClure, Brazil, *CJ Costa et al. 61* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia cincta*** P.L. Viana & Filg., Brazil, *P Viana s.n.* (BHCB), [GB, GB, GB, GB, —, GB, GB]. ***Aulonemia cochabambensis*** Judz. & L.G. Clark, Bolivia, *B Ståhl 5660* (ISC), [—, —, —, —, —, GB, —]. ***Aulonemia deflexa*** (N.E.Br.) McClure, Brazil, *P Viana 3443* (MG), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia effusa*** (Hack.) McClure, Brazil, *CJ Costa 88* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia hirtula*** (Pilg.) McClure, Ecuador, *LG Clark & P Asimbaya 1412* (ISC), [JQ408540, —, GB, JQ408498, JQ408638, —, —]. ***Aulonemia insignis*** Judz. & L.D. Gibbons, Bolivia, *A Fuentes & WV Muller 14008* (UWSP), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia lanciflora*** McClure & L.B. Sm., Brazil, *CJ Costa 98* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia laxa*** (F. Maek.) McClure, Mexico, *T Mejía-Saulés 2090* (XAL), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia longiaristata*** L.G. Clark & Londoño, Ecuador, *LG Clark 1434* (ISC), [GB, GB, GB, GB, —, GB, GB]. ***Aulonemia longipedicellata*** Renvoize, Bolivia, *A Fuentes et al. 10766* (UWSP), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia madidiensis*** Judz., D.C.Ziegler & Zueger, Bolivia, *A Araujo-Murakami et al. 1741* (UWSP), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia patriae*** R.W.Pohl, Costa Rica, *C Tyrrell et al. 44* (ISC), [JQ408541, —, —, JQ408499, JQ408639, JQ408458, —]. ***Aulonemia patula*** (Pilg.) McClure, Ecuador, *LG Clark et al. 1075* (ISC), [JQ408542, JQ408578, —, JQ408500, JQ408640, JQ408459, JQ408599]. ***Aulonemia patula*** (Pilg.) McClure, Ecuador, *LG Clark & PA 1400* (ISC), [—, —,GB, —, —, —, —]. ***Aulonemia prolifera*** P.L. Viana & Filg., Brazil, *CJ Costa 106* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia queko*** Goudot, Ecuador, *LG Clark & P Asimbaya 1445* (ISC), [JQ408543, JQ408579,GB, JQ408501, JQ408641, JQ408460, JQ408600]. ***Aulonemia radiata*** (Rupr.) McClure & L.B. Sm., Brazil, *CJ Costa 69* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia robusta*** L.G. Clark & Londoño, Colombia, *X Londoño & E Ruiz-Sanchez 994* (UWSP), [—, —, GB, —, —, GB, —]. ***Aulonemia setigera*** (Hack.) McClure, Brazil, *CJ Costa 126* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia setosa*** (Londoño & L.G.Clark) P.L. Viana & Filg., Brazil, *CJ Costa 85* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia soderstromii*** P.L. Viana, Filg. & Judz., Brazil, *CJ Costa 109* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Aulonemia xerophylla*** P.L. Viana & Filg., Brazil, *CJ Costa et al. 94* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Cambajuva ulei*** (Hack.) P.L. Viana, L.G. Clark & Filg., Brazil, *LG Clark & X Londoño 1048* (ISC), [JQ408544, —, —, JQ408502, JQ408642, JQ408461, JQ408601]. ***Cambajuva ulei***, Brazil, *PL Viana s.n.* (BHCB), [—, GB, GB, —, —, —, —]. ***Colanthelia cingulata*** (McClure & L.B. Sm.) McClure, Brazil, *T Filgueiras s.n.* (ISC), [JQ408545, —, —, —, JQ408643, —, JQ408602]. ***Colanthelia cingulata*** (McClure & L.B. Sm.) McClure, Brazil, *CJ Costa et al. 125* (VIC), [—, GB, GB, GB, —, GB, —]. ***Colanthelia intermedia*** (McClure & L.B. Sm.) McClure, Brazil, *AP Santos-Gonçalves 553* (VIC), [—, —, —, —, JQ408645, —, JQ408604]. ***Colanthelia intermedia*** (McClure & L.B. Sm.) McClure, Brazil, *CJ Costa et al. 107* (VIC), [GB, GB, GB, GB, —, GB, —]. ***Colanthelia kinoshitae*** Santos-Gonç., Filg. & L.G. Clark, Brazil, *CJ Costa et al. 129* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Colanthelia secundiflora*** Santos-Gonc., Filg. & L.G. Clark, Brazil, *AP Santos-Gonçalves 353* (VIC), [GB, —, GB, —, —, GB, —]. ***Colanthelia* sp.**, Brazil, *AP Silva 151* (VIC), [GB, GB, GB, GB, —, GB, GB]. ***Colanthelia longipetiolata*** C. Jesus-Costa & A.P. Santos-Gonçalves, Brazil, *CJ Costa et al. 72* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Colanthelia sparsiflora*** Santos-Gonç., Filg. & L.G. Clark, Brazil, *AP Santos-Gonçalves 496* (VIC), [GB, GB, GB, —, —, GB, GB]. ***Didymogonyx geminatum*** (McClure) McClure, Venezuela, *F Ely 2* (ISC), [JQ408562, —, —, —, JQ408660, JQ408477, JQ408614]. ***Didymogonyx aff. longispiculatum*** Londoño & L.G. Clark, Colombia, *X Londoño & E Ruiz-Sanchez 995* (ISC), [JQ408558, —, —, JQ408513, JQ408656, JQ408473, —]. ***Elytrostachys clavigera*** McClure, Costa Rica, *R Pohl 13572* (ISC), [JQ408547, —, —, —, —, —, —]. ***Elytrostachys typica*** McClure, Colombia, *X Londoño 985* (COL), [JQ408548, —, —, —, JQ408646, JQ408463, —]. ***Filgueirasia arenicola*** (McClure) Guala, Brazil, *T Filgueiras s.n.* (ISC), [JQ408550, —, —, JQ408505, JQ408648, JQ408465, JQ408605]. ***Filgueirasia cannavieira*** (Silveira) Guala, Brazil, *T Filgueiras s.n.* (ISC), [JQ408551, JQ408580, GB, JQ408506, JQ408649, JQ408466, JQ408606]. ***Glaziophyton mirabile*** Franch., Brazil, *L Sarahyna et al. 1066* (ISC), [JQ408552, U54748, KC020582.1, JQ408507, JQ408650, JQ408467, JQ408607]. ***Merostachys fistulosa*** Döll, Brazil, *R Vinícius-Silva 50* (VIC), [MG458237, MG458245, MG458256, MG458264, MG458270, MG458277, MG458283]. ***Merostachys tatianae*** Santos-Gonçalves, Carvalho-Okano & Filg., Brazil, *R Vinícius-Silva 18* (VIC), [MG458238, MG458246, MG458257, MG458265, MG458271, MG458278, MG458284]. ***Merostachys ternata*** Nees, Brazil, *LG Clark & W Oliveira 1023/ R Vinícius-Silva 30* (ISC/VIC), [JQ408555, MG458247, MG458258, JQ408510, JQ408653, JQ408471, JQ408610]. ***Myriocladus virgatus*** Swallen, Brazil, *E Afonso 140*

(MG), [GB, —, —, —, GB, GB, GB]. ***Rhipidocladum maxonii*** (Hitchc.) McClure, Costa Rica, *C Tyrrell et al. 46* (ISC), [JQ408564, —, —, JQ408518, JQ408662, —, —]. ***Rhipidocladum parviflorum*** (Trin.) McClure, Brazil, *T Filgueiras s.n.* (ISC), [JQ408567, —, —, JQ408521, JQ408665, JQ408481, JQ408617]. ***Rhipidocladum parviflorum*** (Trin.) McClure, Brazil, *CJ Costa 92* (VIC), [—, MG458248, MG458259, —, —, —, —]. ***Rhipidocladum harmonicum*** (Parodi) McClure, Ecuador, *LG Clark et al. 1128* (QCA), [JQ408563, JQ408582, —, JQ408517, JQ408661, JQ408478, JQ408615]. ***Rhipidocladum cordatum*** C.D. Tyrrell & L.G. Clark, Ecuador, *LG Clark 1464* (QCA), [JQ408561, JQ408581, —, JQ408516, JQ408659, JQ408476, JQ408622]. ***Rhipidocladum* sp.**, Brazil, *T Filgueiras s.n.* (ISC), [JQ408557, —, —, JQ408512, JQ408655, JQ408472, JQ408621]. **CHUSQUEINAE Soderstr. & R.P.Ellis—** ***Chusquea* sp.** Trin., Brazil, *AP Santos-Gonçalves 620* (VIC), [MG458239, MG458249, MG458260, MG458266, MG458272, MG458279, MG458285]. ***Chusquea* aff. *capitata***, Brazil, *AP Santos-Gonçalves 652* (VIC), [MG458240, MG458250, MG458261, MG458267, MG458273, MG458280, MG458286]. **GUADUINAE Soderstr. & R.P.Ellis—** ***Apoclada simplex*** McClure & L.B.Sm., Brazil, *LG Clark & W Oliveira 1027* (ISC), [JQ408527, —, KC020566.1, JQ408488, JQ408626, JQ408448, JQ408589]. ***Eremocaulon aureofimbriatum*** Soderstr. & Londoño, Brazil, *A Carvalho 4393* (CEPEC), [JQ408549, EF589616, —, JQ408504, JQ408647, JQ408464,—]. ***Eremocaulon* sp.**, Brazil, *CJ Costa et al. 108* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Guadua angustifolia*** Kunth., Colombia, *X Londoño & LG Clark 931* (ISC), [FJ643714, FJ751664, KC020583.1, FJ643910, FJ644003, FJ643817, FJ644154]. ***Guadua tagoara*** (Nees), Brazil, *AP Silva 171* (VIC), [GB, GB, GB, GB, GB, GB, GB]. ***Olmeca recta*** Soderstr., Mexico, *LG Clark 1313* (ISC), [JQ408556, —, —, JQ408511, JQ408654, JQ408468, JQ408611]. ***Otatea acuminata*** (Munro) C.E.Calderón & Soderstr., Mexico, *LG Clark 1312* (ISC), [AF182350, U54749, KC020589.1, FJ751705, FJ751732, FJ751678, JQ408612]. **BAMBUSINAE J.Presl in C.Presl—*Bambusa vulgaris*** Schrad., Cultivated, *JG Sanchez-Ken 666* (ISC), [FJ643709, AY912192, KC020569.1, FJ751706, FJ643982, FJ643796, FJ644133].

Capítulo II: *Colanthelia longipetiolata* (Poaceae: Bambusoideae), a New Species of Woody Bamboo from the Brazilian Atlantic Forest

Normas: Systematic Botany

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Abstract*—*Colanthelia is a woody bamboo genus belonging to the Arthrostylidiinae and currently includes nine species. It can be recognized by a suite of morphological characters including hollow and thick-walled culms, branch complement with a promontory in the base and a dominant divergent branch bearing few to many secondary small branchlets from its base, racemose or weakly paniculate synflorescences, and relatively long and narrow spikelets with visible rachilla internodes. During recent fieldwork in Minas Gerais state, a new species, ***Colanthelia longipetiolata***, from the Brazilian Atlantic forest was collected, which is here described and illustrated. So far as we know, the species is endemic to the Caparaó National Park, in Minas Gerais state. Comments on its habitat, distribution and conservation status are provided; a morphological comparison between *C. longipetiolata* and *C. sparsiflora* is presented, as well as a revised identification key to all species of the genus.

Keywords—Arthrostylidiinae, endemic species, PARNA Caparaó, Woody bamboos.

Resumo—*Colanthelia* é um gênero de bambus lenhosos pertencente à subtribo Arthrostylidiinae e inclui, atualmente, nove espécies. O gênero pode ser reconhecido por um conjunto de caracteres morfológicos tais como: colmos fistulosos e com parede espessada, complementos de ramo com um promontório na base e um ramo divergente dominante acompanhado por poucos a muitos ramos secundários menores a partir da base, sinflorescência racemosa ou paniculada com ramificação limitada, e espiguetas relativamente longas e estreitas com entrenós da ráquila visíveis. Em expedições recentes no estado de Minas Gerais, Brasil, uma nova espécie, ***Colanthelia longipetiolata,*** ocorrente na Floresta Atlântica brasileira foi coletada, a qual é aqui descrita e ilustrada. Até onde se sabe, a espécie é aparentemente endêmica do Parque Nacional do Caparaó, Minas Gerais. Foram elaborados comentários sobre habitat, distribuição e status de conservação; uma comparação morfológica entre *C. longipetiolata* e *C. sparsiflora* é apresentada assim como uma chave de identificação revisada para todas as espécies do gênero.

Palavras-chave—Arthrostylidiinae, bambus lenhosos, espécie endêmica, PARNA Caparaó.

The subfamily Bambusoideae (Poaceae) exhibits extensive diversity in the Neotropics, principally in the Brazilian Atlantic forest, which is considered an important hotspot of diversity and endemism of bamboos (Clark 1990; Judziewicz et al. 1999). Despite the continued loss of forest areas, many new species of woody bamboos have recently been described for this biome (Viana & Filgueiras 2014; Parma et al. 2016; Vinícius-Silva et al. 2016; Santos-Gonçalves et al. 2017).

Colanthelia McClure & E.W. Sm. is classified within the subtribe Arthrostylidiinae (Bambuseae) and currently includes nine species (Judziewicz et al. 1999; Santos-Gonçalves 2005; Santos-Gonçalves et al. in press.). It can be distinguished by the following combination of morphological characters: erect to climbing, hollow, thick-walled culms; promontory well developed at the base of branch complement; branch complements with a dominant divergent branch bearing few to many secondary branches from its basal nodes; culm leaves with a crest or skirt at the juncture of the sheath and the girdle frequently present; racemose or weakly paniculate synflorescences [1–2 (–3) orders of branching]; spikelets with exposed rachilla segments, 2 glumes, 2–16 fertile anthoecia, and an apically reduced anthoecium (McClure 1973; Santos-Gonçalves et al. in press.).

The species of *Colanthelia* are distributed in southern to southeastern Brazil and only one, *C. rhizantha* (Hack.) McClure, also occurs in Argentina (Judziewicz et al. 1999; Santos-Gonçalves et al. in press.). All species occur in forest habitats, growing at elevations of 0 to about 1,600 meters (Lizarazu 2013; Santos-Gonçalves 2005; Santos-Gonçalves et al. in press.). *Colanthelia* is one of the 11 genera of bamboos endemic to the Atlantic Forest biome (Stehmann et al. 2009; Ferreira et al. 2013; Viana et al. 2013).

During recent fieldwork in Caparaó National Park, Minas Gerais state, Brazil, a distinctive species of *Colanthelia* was collected, which is described here as a new species, *Colanthelia longipetiolata*. A detailed morphological description and an illustration of this new species are provided, along with comments on its habitat, distribution, conservation and affinities with morphologically similar species. Additionally, an identification key to the all species of the genus is included.

MATERIAL AND METHODS

The new species here presented is described from botanical material collected in Caparaó National Park in Minas Gerais state; no earlier herbarium collections of the new taxon are known. Herbarium acronyms follow Thiers (2017). The morphological description and terminology follow Judziewicz et al. (1999). The length of the blades and synflorescences were made from the base to the apex, excluding the pseudopetiole and peduncle, respectively; spikelet length was taken from the base of glume I to the apex, excluding the pedicel. A revised identification key based on the one produced by Santos-Gonçalves et al. (in press.) is also presented.

TAXONOMIC TREATMENT

Colanthelia longipetiolata C. Jesus-Costa & Santos-Gonçalves, *sp. nov.*—TYPE: BRAZIL. Minas Gerais: Alto Caparaó, Parque Nacional do Caparaó, 26 February 2016 (fl.), *C. Jesus-Costa, R. Vinícius-Silva, & M. C. F. Dias 95* (holotype: VIC!; isotypes: ISC!, MO!, SP!).

This species is similar to *Colanthelia sparsiflora* Santos-Gonç., Filg. & L.G. Clark in having internodes, girdles and foliage leaf sheaths glabrous and in the racemose synflorescences with widely spaced spikelets. However, it differs from *C. sparsiflora* by absence of auricles on the culm and foliage leaves (vs. present), the conspicuous promontory (vs. inconspicuous), culm leaf blades adaxially pubescent (vs. glabrous), glumes well developed, 9–16 mm long (vs. scale-like and 1–2 mm long), and lemmas with 6–11 nerves (vs. 5–7).

Rhizomes pachymorph, short-necked. Culms initially erect or decumbent, becoming clambering, 4–6 m long. Internodes 14.5–44 cm long, 3–8 mm in diam., hollow, cylindrical, glabrous, striate, yellowish-green, sometimes purplish and pubescent when young, walls 0.6–4 mm thick, ratio of wall thickness: culm diam. 0.44–0.8, walls moderately thick to very thick, lumen 0.3–2.6 mm in diam.; girdle conspicuous to inconspicuous, glabrous or pubescent when young; nodal line horizontal, glabrous; nodal region 1.7–6.5 mm long, 2–8.14 mm in diam., glabrous; supranodal ridge conspicuous, smooth; bud one per node, ovate-lanceolate to lanceolate, 2.7–5.8 mm long, 2.4–4.9 mm wide, glabrous; prophylls pubescent and ciliate along the apex; promontory conspicuous. Culm leaf sheaths 12–16.2 × 2–3.6 cm, persistent, glabrous or pubescent when young, margin glabrous, greenish to brown; auricles absent; girdle inconspicuous, glabrous or pubescent when young; fimbriae 0.3–14 mm long, erect, cylindrical, pubescent; outer ligule absent to inconspicuous; inner ligule 0.2–1 mm long, membranous, apex ciliate; pseudopetioles absent to conspicuous, 1–2 mm long, adaxially pubescent; blades 3.5–6 × 1–2.1 cm, triangular to ovate-lanceolate, erect to reflexed, deciduous, pubescent adaxially, glabrous abaxially, apex acute to acuminate. Branch complement with 1–3 (–4) branches, branches 12–88 cm long, not rebranching at the lower nodes, lower nodes sometimes geniculate. Foliage leaves 3–25 per branch; sheaths 3–7.1 cm × 2–6 mm, glabrous abaxially, margins glabrous to slightly ciliolate, yellowish-green to pale brown; auricles absent; fimbriae 0.2–1 cm long, erect, greenish to purplish when young, then becoming brown, cylindrical, pubescent; outer ligule ca. 0.3 mm long, membranous, apex ciliate; inner ligule 0.2–0.6 mm long; pseudopetioles 0.8–5.8 × 1–1.7 mm, dark brown and pubescent adaxially, yellow-green to brown and glabrous abaxially; blades 8.5–19 × 1.5–2.5 cm, ovate–lanceolate to lanceolate, patent, chartaceous, with 3–10 scabrous marginal ribs with minute antrorse strigose trichomes on the adaxial surface, glabrous elsewhere, glabrous abaxially, base asymmetrical, rounded, apex acuminate, margins antrorsely scabrous. Synflorescences racemose, terminal and lateral, 3.8–19.5 × 0.5–1.2 cm, spikelets 1–6; spikelets widely spaced and not secund; rachis sulcate, glabrous; pedicels 1–11 × 0.7–0.9 mm, sulcate, glabrous to pubescent. Spikelets 1.2–5.8 × 0.2–0.4 cm, laterally compressed; fertile anthoecia 3-7; glumes unequal; lower glume 9–11 × 1.3–2 mm, 3–5-nerved, glabrous abaxially, pubescent adaxially, brown, apex acute to acuminate; upper glume 12.2–16 × 4.3–5 mm, 9–11-nerved, brown and glabrous abaxially, brown with dark spots and pubescent adaxially, apex mucronate; rachilla internodes 6–8.5 mm long, glabrous; lemma 11–18 × 3–4.5 mm, glabrous abaxially, pubescent adaxially from the middle portion towards the apex, 6–11-nerved; brown with dark spots, apex acute, awnless; palea 9–12 mm × 2–2.8 mm, 2-nerved, nerves ciliate, puberulous between the keels, brown. Lodicules 2.3–3.4 × 0.7–1 mm, lanceolate, puberulent, with long hairs at the tip. Anthers 1.4–2.8 mm, yellowish. Ovary 1–2 × 0.4 mm, glabrous, light-cream to brown; style glabrous, 0.4–0.8 mm; stigmas slightly plumose, light-cream. Caryopsis not seen.

Distribution and Habitat*—Colanthelia longipetiolata* is only known from a single population in the Caparaó National Park, Alto Caparaó, Minas Gerais state, Brazil. It was collected along one margin of a river at an elevation of 1641 m, along the border of vegetation known as semideciduous seasonal Alluvial Forest (Veloso et al. 1991).

***Etymology*—**The specific epithet refers to the length of the foliage leaf pseudopetioles of this species, which are the longest in the genus.

Conservation Status*—Colanthelia longipetiolata* might be considered critically endangered (CR) according to the criteria B2a + D adopted by the IUCN (IUCN 2017), if all IUCN guidelines were followed. The single population known is not abundant and is restricted to a very small area, which is no larger than 1 km^2.

Paratypes**—**BRAZIL. Minas Gerais: Alto Caparaó, Parque Nacional Alto Caparaó, Cachoeira Bonita, 17 August 2015 (veg.), *C. Jesus-Costa et al. 72* (VIC); idem, 08 April 2016 (veg.), *C. Jesus-Costa et al. 101* (VIC); idem, 08 April 2016 (veg.), *C. Jesus-Costa et al. 102* (VIC); idem, 08 April 2016 (veg.), *C. Jesus-Costa et al. 103* (VIC).

Comments**—***Colanthelia longipetiolata* is morphologically close to *C. sparsiflora*. Both species possess glabrous and striate internodes, glabrous girdles, culm leaves with the outer ligule inconspicuous, foliage leaves with sheaths and margins glabrous, pseudopetioles dark-brown adaxially, and racemose synflorescences with widely spaced spikelets. However, these species can be distinguished easily by the erect fimbriae and lack of auricles on the culm and foliage leaves of *C. longipetiolata* (vs. auricles present and fimbriae spreading in *C. sparsiflora*), as well as the well-developed glumes 9–16 mm long in *C. longipetiolata* (vs. scale-like and 1–2 mm long in *C. sparsiflora*) and lemmas with 6–11 nerves (vs. 5–7 in *C. sparsiflora*). A summary of diagnostic features for these two species is presented in Table 1.

TABLE 1. Morphological comparison of *C. longipetiolata* and *C. sparsiflora*.

Characters	***C. longipetiolata***	***C. sparsiflora***
Promontory	conspicuous	inconspicuous
Culm leaf sheath margin indument	glabrous	ciliate
Auricles on the culm and foliage leaves	absent	present
Adaxial indument of the culm leaf blade	pubescent	glabrous
Position of the foliage leaf fimbriae	erect	spreading
Foliage leaf pseudopetiole length (mm)	0.8–5.8	2–3
Synflorescence length (cm)	3.8–19.5	7–13
Spikelet length (cm)	1.2–5.8	1.4–2.3
Glume length (mm)	lower glume 9–11, upper glume 12.2–16	reduced to scales (ca. 1–2)
Lemma number of nerves	6–11	5–7
Ovary	glabrous	pubescent

KEY TO THE SPECIES OF *COLANTHELIA*

1. Foliage leaf sheaths bearing auricles at the apex … 2

1. Foliage leaf sheaths without auricles at the apex … 5

2. Lower and upper glumes reduced, lower and upper glumes 1–2 mm long … *C. sparsiflora*

2. Lower and upper glumes well developed, lower glume 2.5–5 mm long and upper glume 3.2–6 mm long … 3

3. Lower glume 5–7-nerved; culm leaf sheaths without fimbriae and auricles at the apex ... *C. burchellii*

3. Lower glume 1–3-nerved; culm leaf sheaths bearing both fimbriae and auricles at the apex ... 4

4. Lemmas 5.5–8.2 mm long; synflorescences with 2–5 branches; rachis glabrous to glabrate; spikelets with L:W = 5–12; culm leaf sheaths glabrous to glabrate on the abaxial surface ... *C. kinoshitae*

4. Lemmas 8–11 mm long; synflorescences with 7–11 branches; rachis puberulous to puberulent; spikelets with L:W = 16.5–34; culm leaf sheaths densely pubescent on the abaxial surface ... *C. cingulata*

5. Lower and upper glumes reduced to scales, both ca. 0.2 mm long; spikelets with a thick internode below the first floret ... *C. distans*

5. Lower and upper glumes well developed, lower glume 2–11 mm long and upper glume 3.2–16 mm long; spikelets with a slender, flat internode below the first floret ... 6

6. Culm leaf blades erect; spikelets secund (unilateral); lemmas with dark spots ... *C. secundiflora*

6. Culm leaf blades erect to reflexed; spikelets two-ranked; lemmas uniform in color or with dark spots … 7

7. Lemma and palea very unequal in length (lemma sometimes approximately twice the size of the palea) … 8

7. Lemma and palea equal to subequal in length ... 9

8. Blades of foliage leaves glabrous on both surfaces; spikelets 7.9–12 cm long; lemma glabrous and without dark spots … *C. macrostachya*

8. Blades of foliage leaves with 3–10 scabrous marginal ribs with minute antrorse strigose trichomes on the adaxial surface; spikelets 1.2–5.8 cm long; lemma pubescent adaxially and with dark spots … *C. longipetiolata*

9. Spikelets 5–16-flowered; mature spikelets dark–colored; culm leaf girdle glabrous ... *C. intermedia*

9. Spikelets 3–7-flowered; mature spikelets light brown to brown; culm leaf girdle pubescent ... *C. rhizantha*

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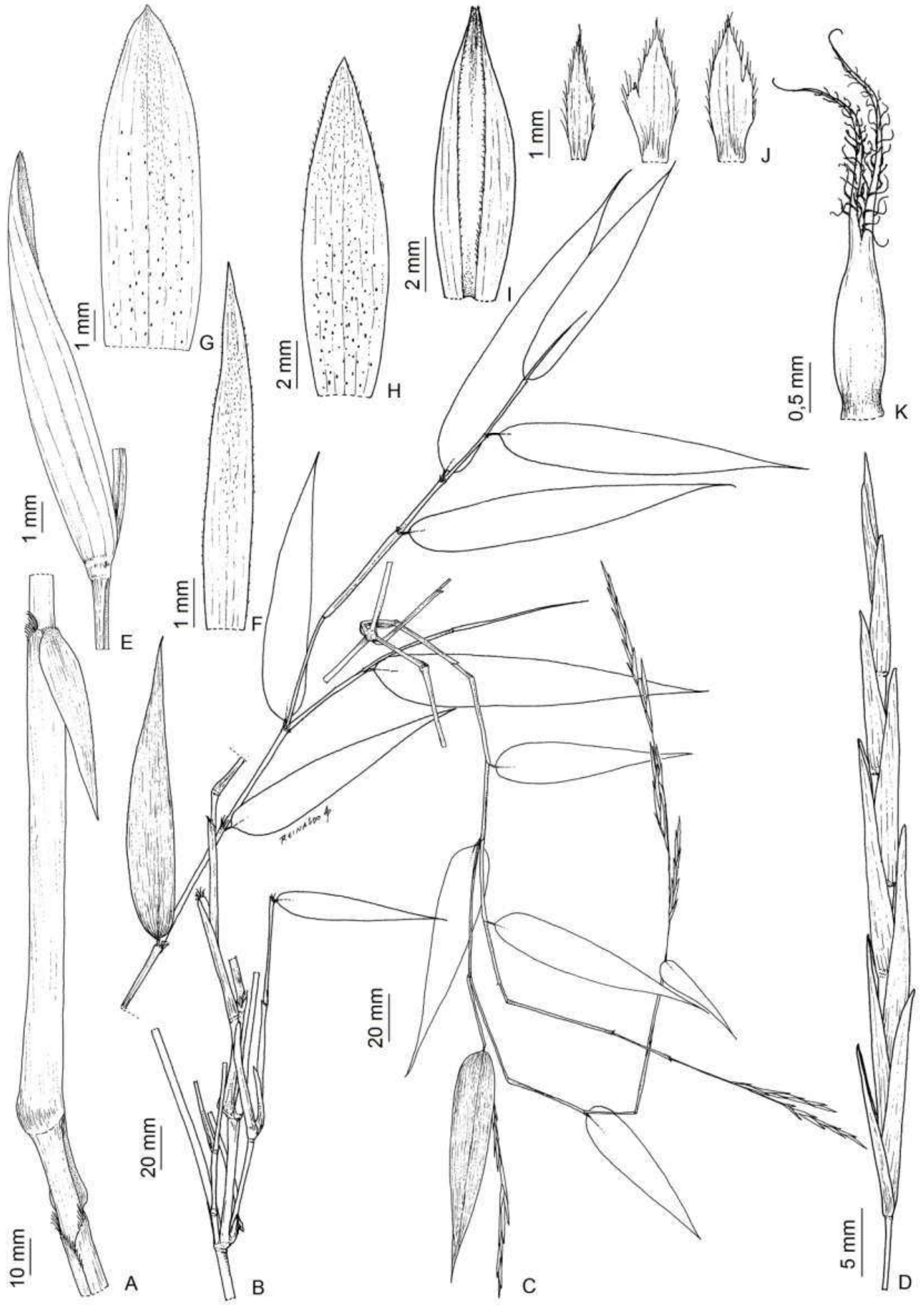

FIG. 1. *Colanthelia longipetiolata* C. Jesus-Costa & A.P. Santos-Gonçalves. A. Culm leaf. B. Vegetative branch. C. Flowering branch. D. Spikelet. E. Anthoecium and rachilla internode in lateral view. F. Lower glume, adaxial view. G. Upper glume, adaxial view. H. Lemma, adaxial view. I. Palea. J. Lodicules. K. Gynoecium. *C. Jesus-Costa, R. Vinícius-Silva, & M. C. F. Dias 95* (VIC). Illustrated by Reinaldo Pinto.

Capítulo III: Molecular Phylogeny of *Atractantha*, and the Phylogenetic Position and Circumscription of *Athroostachys* (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae)

Aceito: Systematic Botany

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Abstract—*Atractantha* and *Athroostachys* are Neotropical woody bamboo genera (Poaceae: Bambusoideae: Arthrostylidiinae) that occur mainly in the Brazilian Atlantic forest from Bahia to Rio de Janeiro, with a single *Atractantha* species in southern Venezuela and in northwestern Amazonas state in Brazil. Previous phylogenetic studies resolved *Atractantha* as monophyletic, however, only three of its six species have been sampled. The aims of this study were to test the monophyly of *Atractantha* based on a broader sampling of the genus, and to investigate the phylogenetic position of the monotypic *Athroostachys*, previously unsampled in any molecular phylogeny. Seven plastid regions (*ndhF*, *rps16*, *rpl16*, *trnC-rpoB*, *trnD-trnT*, *rps16-trnQ*, and *trnT-trnL*), both coding and non-coding, were analyzed for 38 species of Arthrostylidiinae and eight species of other subtribes of Bambuseae. Bayesian inference and maximum likelihood analyses were performed for individual regions and the combined plastid dataset. *Atractantha*, in its current circumscription, is polyphyletic. *Atractantha shepherdiana* is strongly supported as sister to *Athroostachys capitata*, and this clade is strongly supported as sister to *Merostachys*. Besides the molecular evidence, morphological data support the transfer of *A. shepherdiana* to *Athroostachys*. The new combination ***Athroostachys shepherdiana*** and a new description of *Athroostachys* are here proposed. A key to the two species of *Athroostachys* herein recognized and an illustration of the main distinguishing vegetative features of both species are provided.

Keywords—*Athroostachys capitata*, *Atractantha shepherdiana*, cpDNA, Neotropical woody bamboos.

Resumo—*Atractantha* e *Athroostachys* são gêneros neotropicais de bambus lignificados (Poaceae: Bambusoideae: Arthrostylidiinae) que ocorrem principalmente na Floresta Atlântica no Brasil, desde a Bahia até o Rio de Janeiro, com uma única espécie de *Atractantha* disjunta no sul da Venezuela e no noroeste do estado do Amazonas no Brasil. Estudos filogenéticos demonstraram que *Atractantha* é monofilético, no entanto sua amostragem tem sido incompleta. Os objetivos desse estudo foram testar a monofilia de *Atractantha* a partir da ampliação de sua amostragem e investigar o posicionamento filogenético de *Athroostachys.* Apresentamos a primeira filogenia com amostragem de *Athroostachys.* Foram sequenciadas sete regiões plastidiais (*ndhF*, *rps16*, *rpl16*, *trnC-rpoB*, *trnD-trnT*, *rps16-trnQ* e *trnT-trnL*) para 38 espécies de Arthrostylidiinae e oito espécies de outras subtribos de Bambuseae. Foram realizadas análises Bayesianas e de máxima verossimilhança para os dados individuais e combinados. *Atractantha*, com a atual circunscrição, é polifilético. *Atractantha shepherdiana* é altamente sustentada como grupo irmão de *Athroostachys capitata*, e este clado é altamente sustentado como grupo irmão de *Merostachys*. Além das evidências moleculares, dados morfológicos sustentam a transferência de *A. shepherdiana* para o gênero *Athroostachys*. A nova combinação ***Athroostachys shepherdiana*** e uma nova descrição de *Athroostachys* são aqui propostos. Uma chave de identificação das duas espécies de *Athroostachys* aqui reconhecidas e uma ilustração das principais características vegetativas distintivas entre ambas espécies são fornecidas.

Palavras-chave*—Athroostachys capitata*, *Atractantha shepherdiana*, cpDNA, bambus lenhosos neotropicais.

Atractantha McClure is a Neotropical woody bamboo genus belonging to the subtribe Arthrostylidiinae (McClure 1973; Judziewicz 1992; Judziewicz et al. 1999; Clark et al. 2015). The genus was described by McClure in 1973 and, as currently recognized, includes six species: *Atractantha amazonica* Judz. & L.G. Clark, *A. aureolanata* Judz., *A. cardinalis* Judz., *A. falcata* McClure, *A. radiata* McClure and *A. shepherdiana* Santos-Gonçalves, Filg. & L.G. Clark (Judziewicz 1992; Judziewicz et al. 1999; Santos-Gonçalves et al. 2011; Vorontsova et al. 2016). Five of these species occur in the Atlantic Forest biome of coastal Brazil, from sea level to 650 meters in elevation, in the states of Bahia and northern Espírito Santo. Habitats within the Atlantic Forest include humid forests and the sandy coastal forests locally known as restinga, where these species climb into the tree canopy and hang down often nearly to the ground. One species, *A. amazonica*, occurs in both southern Venezuela and the state of Amazonas in Brazil, along riverbanks in igapó forest (Judziewicz 1992).

Atractantha includes plants with the following combination of characters: rhizomes pachymorph and short-necked; culms slender and hollow (*A. amazonica* and *A. shepherdiana*) to solid (*A. falcata*) and with peripheral air canals in some species (frequently present in *A. aureolanata*, *A. cardinalis* and *A. radiata*); a promontory present at the base of the branch complement; mid-culm nodes with 2–5 main branches which re-branch to form many smaller branchlets; culm leaf sheaths with a dark, thickened, flangelike girdle, and, in some, one side of the basal margin of the sheath strongly to slightly auricled (*A. cardinalis*, *A. radiata*); culm leaf blades deciduous, variable in size (in *A. radiata* absent or represented only by a mucro, in other species linear to lanceolate and reflexed); fimbriae present on the apices of both culm and foliage leaf sheaths; and florets pungent and needlelike, often arrayed in fan-shaped, capitate or scorpioid clusters (Judziewicz 1992; Judziewicz et al. 1999; Santos-Gonçalves et al. 2011).

Based on these morphological features, *Atractantha* was presumed to be closely related to *Alvimia* C.E. Calderón ex Soderstr. & Londoño, *Arthrostylidium* Rupr. and *Elytrostachys* McClure (Judziewicz 1992; Judziewicz et al. 1999). *Atractantha* and *Arthrostylidium* have similar vegetative branching patterns in which the branch complement at mid-culm nodes exhibits one to several main branches that re-branch to form many smaller secondary and tertiary branchlets (Judziewicz 1992). Similarities between *Atractantha* and *Elytrostachys* are indicated by the presence of reflexed culm leaf blades and pedicellate florets with a setose prolongation of the rachilla internode, which bears a rudimentary floret (Judziewicz 1992). *Atractantha* (with the exception of *Atractantha amazonica*) and *Alvimia* have the same geographic range and share some features, such as the scandent habitat, branching morphology, and the presence of pseudospikelets (Soderstrom and Londoño 1988; Judziewicz et al. 1999; Tyrrell et al. 2012), but *Alvimia* differs in its erect culm leaf blades and fleshy fruits.

The most detailed prior molecular phylogenetic study of the arthrostylidioid bamboos based on chloroplast DNA (cpDNA) sequence data strongly supported *Atractantha* as a monophyletic genus (Tyrrell et al. 2012). However, only three species (*A. aureolanata*, *A. cardinalis* and *A. radiata*) were sampled in that study. *Atractantha* was strongly supported as sister to *Alvimia*, and that clade was resolved as sister to *Filgueirasia* Guala with a posterior probability of 0.97. In contrast, no phylogenetic affinity with *Arthrostylidium* or *Elytrostachys* was supported.

Athroostachys Benth. is a poorly known monospecific genus classified in the Arthrostylidiinae based on certain anatomical and morphological features (e.g., the occurrence of intercostal sclerenchyma and an abaxial green marginal stripe on the foliage leaf blades) (Judziewicz et al. 1999). *Athroostachys capitata* (Hook.) Benth. occurs in the Brazilian Atlantic forest from Bahia to Rio de Janeiro growing at elevations of 30 to 110 meters (Judziewicz et al. 1999). The available morphological evidence suggests that *Athroostachys* is related either to *Merostachys*, based on similarities in the fimbriae and the spikelets, or to the *Alvimia* + *Atractantha* clade, based on the presence of three to five main branches per node and bracteate synflorescences (McClure 1973; Tyrrell et al. 2012). Nevertheless, until now

Athroostachys has never been included in any phylogenetic study, morphological or molecular (Soderstrom and Ellis 1987; Judziewicz et al. 1999). Therefore, the main goals of the present study, based on an analysis of multiple cpDNA regions, are to: 1) re-evaluate the monophyly of *Atractantha* using a broader sampling of the genus; and 2) test the phylogenetic position of *Athroostachys* within the Neotropical woody bamboos.

MATERIALS AND METHODS

Taxon Sampling and Marker Selection—A total of 46 species was included in the analysis (Appendix 1). We sampled four species of *Atractantha*: *A. aureolanata*, *A. cardinalis*, *A. radiata*, and *A. shepherdiana.* Overall, 14 of the 15 currently recognized genera of the Arthrostylidiinae were sampled, with only *Myriocladus* Swallen lacking, and all genera of Guaduinae and Chusqueinae were also sampled. Trees were rooted with *Bambusa vulgaris* Schrad. ex J.C. Wendl. (Paleotropical woody bamboo clade, Bambuseae) (Clark et al. 2007; Ruiz-Sanchez et al. 2008; Tyrrell et al. 2012).

Based on previous studies in the Bambusoideae (Triplett and Clark 2010; Tyrrell et al. 2012; Kelchner et al. 2013), seven plastid DNA regions were selected: one gene (*ndhF* 3’ half), four intergenic spacers (*trnD-trnT, trnT-trnL, rps16-trnQ,* and *trnC-rpoB*) and two introns (*rpl16* and *rps16*).

DNA Extraction, Amplification, Sequencing and Alignment—Total genomic DNA was extracted from 30–50 mg of leaves dried in silica gel using a modified 2× cetyl trimethylammonium bromide (CTAB) protocol (Doyle and Doyle 1987). Seven chloroplast DNA regions [one gene (*ndhF* 3’ half), four intergenic spacers (*trnD-trnT*, *trnC-rpoB*, *trnT-trnL* and *rps16-trnQ*) and two introns (*rpl16* and *rps16*)] were chosen based on previous studies in the subfamily (Triplett and Clark 2010; Tyrrell et al. 2012; Kelchner et al. 2013). The amplification primers, sequencing primers and thermal cycler protocols are described in Table 1. The polymerase chain reaction (PCR) was made in a final reaction volume of 40 µL containing 10–50 ng of template DNA, 1x buffer, 2.5 mM of magnesium chloride ($MgCl_2$), 0.2 mM deoxyribonucleotide triphosphates (dNTPs), 0.2 µM each primer and 1 unit *Taq* DNA polymerase (Invitrogen Corp., San Diego, California). The amplifications were carried out on a T100 thermal cycler (Bio-Rad Laboratories, Inc., Hercules, California). The PCR products were purified using exonuclease I and shrimp alkaline phosphatase (Affymetrix USB, Santa Clara, California). The purified PCR products were sequenced with the BigDye terminator v3.1 sequencing kit on a 3730xl automated sequencer (Applied Biosystems Inc., Foster City, California) by the company Macrogen Inc. (Seoul, Korea). Each plastid marker was sequenced using forward and reverse primers.

Sequence eletropherograms were edited, assembled and aligned manually using Sequencher 4.1 (GeneCodes, Ann Arbor, Michigan). Polymorphic positions were coded following the International Union of Pure and Applied Chemistry (IUPAC) nucleotide ambiguity codes. Gaps were binary coded by applying the approach of Simmons and Ochoterena (2000) implemented in SeqState 1.4.1 (Müller 2005) and appended to the DNA sequence matrix. All individual sequences obtained in this work are available in GenBank (Table 1).

***Phylogenetic Analyses*—** Maximum likelihood (ML) and Bayesian analysis (BI) were used to reconstruct the trees, in both analysis the concatenated dataset was partitioned by individual plastid markers. ML analyses were conducted on RAxML and node support values were estimated using the rapid bootstrap algorithm employing 1000 replicates (Stamatakis et al. 2008). We consider 90–100% BS as strong, 80–89% BS as moderate and ≤ 79% as poor support for the topology.

Bayesian inference was performed using MrBayes 3.2.6 (Ronquist et al. 2012) through the CIPRES Science Gateway Portal (Miller et al. 2010). The fittest evolutionary models were selected by the Akaike information criterion (AIC) (Posada and Buckley 2004) using MrModeltest 2.2 (Nylander 2004). Markov Chain Monte Carlo (MCMC) was conducted using the same models used for the ML analyses and consisted of four independent runs of 50,000,000 generations each with a tree sampled every 5,000 generations. The first 250 trees were discarded as burn-in and the remainder were used to generate a majority rule consensus tree with posterior probabilities (PPs) for each node. Average standard deviation of split frequencies at the end of each run was below 0.01. In Tracer 1.5 (Drummond et al. 2012), the effective sample size (ESS) presented values well above 400 for all statistics, which ensured that the selected settings were sufficient to the sampling (Zhang et al. 2010). Posterior probabilities ≥ 0.95 were considered strongly supported, those of 0.90 to 0.94 as moderately supported.

Analyses (ML and BI) were independently conducted on the concatenated dataset partition and on each individual markers to check the congruence between loci. To detect possible incongruence of the separate datasets, we applied the procedures described by Wiens (1998). We compared the trees of the individual markers to identify the presence of supported clades (≥ 70%) that were incongruent among data partitions. Because the trees generated from the individual datasets did not show any conflicting supported clades, the combined analyses were performed for the plastid dataset.

RESULTS

Statistics for analyses and general information for cpDNA regions are summarized in Table 2. For the *trnT-trnL* spacer, positions 616-636 were excluded in the aligned matrix, due to the excess variability of the region immediately following a sequence of mononucleotides that made this region unreliable. The trees derived from the cpDNA individual markers did not produce conflicting topologies; however, the clades were neither well resolved nor well supported. Therefore, the results and discussion are based on the BI topology of the combined plastid dataset (Fig 1). The topologies of the BI majority-rule tree and the ML tree showed no conflicts, but differed somewhat in levels of resolution.

For BI, the evolutionary model selected for the *trnD-trnT* and *rps16-trnQ* spacers, the *rpl16* intron, and the *ndhF* gene was GTR + I + G; for the *rps16* intron, GTR + I; and for the *trnC-rpoB* and *trnT-trnL* spacers, GTR + G.

The three subtribes of Neotropical woody bamboos, Chusqueinae (clade A), Guaduinae (clade B) and Arthrostylidiinae (clade C), were each highly supported as monophyletic (1.00/100 PP/BS, 1.00/100 and 1.00/100). The Chusqueinae was sister (1.00/100) to the strongly supported Arthrostylidiinae + Guaduinae clade (1.00/100).

As seen in Fig. 1, Arthrostylidiinae was divided into five main lineages: *Glaziophyton* Franch.; *Cambajuva* P.L. Viana, L.G. Clark & Filg.; the Arthrostylidium clade (clade I: 0.98/39); the Aulonemia clade (clade II: 1.00/55); and the Merostachys clade (clade III: 1.00/87). *Glaziophyton* was supported as sister to the rest of the subtribe, but the position of *Cambajuva ulei* (Hack.) P.L. Viana, L.G. Clark & Filg. was weakly supported, appearing as sister (0.60/-) to the Arthrostylidium + [Aulonemia + Merostachys] clade. In this scenario, the following genera were strongly supported as monophyletic: *Merostachys* Spreng. (1.00/100), *Alvimia* (1.00/99), *Filgueirasia* (1.00/100), *Aulonemia* Goudot (1.00/56), *Colanthelia* McClure & E.W. Sm. (1.00/99), *Didymogonyx* (L.G. Clark & Londoño) C.D. Tyrrell, L.G. Clark & Londoño (1.00/100), and *Elytrostachys* (1.00/100). Although monophyletic in the BI analysis, *Aulonemia* was weakly supported in the ML analysis.

There is a core group of three species of *Atractantha* (*A. aureolanata*, *A. cardinalis* and *A. radiata*) that was highly supported as monophyletic (1.00/100) and was sister to *Alvimia* (1.00/100). The core *Atractantha* + *Alvimia* clade was moderately supported as sister (1.00/61) to *Filgueirasia.* However, *Atractantha*, as currently circumscribed, was not supported as monophyletic because *A. shepherdiana* was highly supported as sister (1.00/100) to *Athroostachys capitata*; this clade was in turn strongly supported as sister (1.00/98) to *Merostachys*.

DISCUSSION

According to our results, Arthrostylidiinae and Guaduinae are monophyletic subtribes and strongly supported as sister to each other, with Chusqueinae strongly supported as sister to the Arthrostylidiinae + Guaduinae clade, corroborating many phylogenetic hypotheses previously reported in the literature (Zhang and Clark 2000; Ruiz-Sanchez et al. 2008; Fisher et al. 2009; Sungkaew et al. 2009; Ruiz-Sanchez 2011; Tyrrell et al. 2012; Kelchner et al. 2013). *Athroostachys* had never been included in any phylogenetic studies; therefore our results, for the first time, confirm the classification of this genus in the subtribe Arthrostylidiinae.

Within Arthrostylidiinae, *Glaziophyton* is poorly supported as sister to the remainder of the subtribe. In Tyrrell et al. (2012) *Glaziophyton mirabile* Franch. together with *Cambajuva ulei* formed the Glaziophyton clade; however, in this study, *C. ulei* does not group with *Glaziophyton*, but rather appears as sister to the Arthrostylidium + [Aulonemia + Merostachys] clade with poor support. We recovered the three other clades (Arthrostylidium, Aulonemia, Merostachys) within Arthrostylidiinae reported by Tyrrell et al. (2012), with the Aulonemia clade sister to the

Merostachys clade. However, despite the consistency in these topologies, no morphological synapomorphies have been attributed to these clades.

Tyrrell et al. (2012) investigated the relationships among 11 of the then 13 recognized genera of the Arthrostylidiinae using six chloroplast DNA regions; neither *Athroostachys* nor *Myriocladus* was sampled in that study and *Cambajuva* was described subsequently based in part on these results (Viana et al. 2013). Although Tyrrell et al. (2012) resolved *Atractantha* as monophyletic, the monophyly of *Atractantha* was not maintained when sampling in the genus and the number of chloroplast DNA regions studied were increased. Our results showed that, as currently circumscribed, *Atractantha* is polyphyletic, but a core group of three species (*A. aureolanata*, *A. cardinalis* and the type species *A. radiata*) is highly supported as monophyletic in all phylogenetic analyses. The core *Atractantha* species, along with the unsampled *A. falcata*, share their geographic distribution (all are endemics to the Bahian coastal forest), the presence of solid culms often with peripheral air canals and pseudospikelets (Judziewicz 1992; Judziewicz et al. 1999). Within this core there is a well-supported subgroup composed of *A. aureolanata* and *A. cardinalis;* this subgroup shares the presence of a dark, swollen sub-basal callus abaxially at the juncture of the culm leaf sheath and girdle (Judziewicz 1992). To attain a more complete phylogenetic understanding of *Atractantha* and to comprehend the evolution of some morphological characters, mainly the reproductive structures, additional phylogenetic analyses must be conducted including *A. falcata* and especially *A. amazonica* (the only species of the genus with true spikelets and with a disjunct geographic distribution). However, based on morphology (the presence of pseudospikelets and their shape, as well as synflorescence structure) and their sympatric distribution, we predict with confidence that core *Atractantha* would include a fourth species, *A. falcata*, if DNA sequences for it were available.

Atractantha shepherdiana was described in *Atractantha*, but it is known only in the vegetative stage (Santos-Gonçalves et al. 2011). Although the vegetative morphology of *A. shepherdiana* is consistent with both *Atractantha* and *Athroostachys*, the latter had not been sampled in a molecular analysis at the time, and the preliminary data for *A. shepherdiana* placed it with *Atractantha*. However, based on the cpDNA sequence data analyses presented here, *A. shepherdiana* is strongly supported as sister to *Athroostachys capitata* and this clade is strongly supported as sister to *Merostachys*. Therefore, the present classification of *Atractantha shepherdiana* in *Atractantha* is untenable. In addition to the molecular evidence, morphological data support the transfer of *Atractantha shepherdiana* to *Athroostachys*. *Atractantha shepherdiana* is similar to *Athroostachys capitata* in the following morphological features (Fig. 2): internodes hollow with a small lumen, branch complement with 1–3 main branches, presence of a well-developed promontory at the mid-culm nodes, young internodes with the upper and lower portions covered with tomentose-velvety ochre trichomes, girdle culm leaves and nodal line of foliage leaves conspicuously conspicuously covered by hirtellous-hispid dark-brown trichomes, the overlapping margin of both culm and foliage leaf sheaths densely ciliate, and culm leaf blades reflexed. *Atractantha shepherdiana* can be distinguished from *Athroostachys capitata* mainly because of the occurrence of spreading fimbriate auricles on the culm and foliage leaf sheaths in *Athroostachys capitata* (versus auricles absent and fimbriae erect in *Atractantha shepherdiana*).

Actinocladum and *Merostachys*, strongly supported as sister in Tyrrell et al. (2012), share the apsidate (fan-shaped) arrangement of subequal branches at the mid-culm nodes and nucoid caryopses. Our analysis unambiguously places *Athroostachys capitata* + *Atractantha shepherdiana* as sister to *Merostachys*, with *Actinocladum* sister to that clade, thus requiring new hypotheses about the evolution of these morphological characters. The nucoid caryopsis was proposed as a synapomorphy for *Actinocladum* + *Merostachys*; however, the fruit type for *Athroostachys capitata* and *Atractantha shepherdiana* is unknown. Because the nucoid fruit type is unknown elsewhere within the Arthrostylidiinae, or for that matter within the Neotropical woody bamboo clade, we predict that *Athroostachys* will ultimately prove to possess nucoid caryopses. Fan-branching, on the other hand, is labile within the Arthrostylidiinae; Tyrrell et al. (2012) recovered one origin at the base of the Arthrostylidium clade, with some reversals, and another origin in the *Actinocladum* + *Merostachys* clade. The most parsimonious assumption, based on the current analysis, is that the *Athroostachys capitata* + *Atractantha shepherdiana* clade represents another independent origin of three subequal branches from a single bud (as seen in *Atractantha*). The presence of a well-developed promontory, also labile in the Arthrostylidiinae, likely represents another independent origin in the *Athroostachys capitata* + *Atractantha shepherdiana* clade.

McClure (1973) had noted the apparent superficial similarity of *Athroostachys* and *Merostachys*, based on the prominent fimbriae (as oral setae), and *Athroostachys capitata* was even described originally as a species of *Merostachys* based on similarities of the spikelets. The sister relationship of these two genera is here confirmed by plastid DNA sequence data.

Taxonomic Implications**—**The transfer of *Atractantha shepherdiana* to *Athroostachys* requires a new combination, as follows. We also provide an emended generic description of *Athroostachys* to accommodate the variation represented by *A. shepherdiana*.

Athroostachys Benth., Gen. Pl. 3: 1208 (1883)

Type species: *Athroostachys capitata* (Hook.) Benth.

Rhizomes pachymorph, short-necked. Culms initially erect, becoming scandent to clambering on the neighboring vegetation. Mid-culm internodes subequal, hollow, thick-walled, with a small lumen, cylindrical, young internodes with the upper and lower portions covered with tomentose-velvety ochre trichomes. Nodal line horizontal, supranodal line inconspicuous, with a single bud per node borne on a conspicuous promontory. Culm leaves with a dark, thickened girdle covered by hirtellous-hispid light to dark-brown trichomes; sheaths with the overlapping margin ciliate, auricles absent or present, prominent fimbriae erect or spreading; external ligule absent; internal ligule present; pseudopetiolate blades erect to reflexed. Branch complement with three subequal main branches. Foliage leaf with a thickened girdle covered by hirtellous-hispid light to dark-brown trichomes; sheaths with the overlapping margin ciliate, auricles absent or present, fimbriae present, erect or spreading; internal and external ligules present; blades lanceolate-oblong, a green marginal stripe conspicuous on the abaxial surface, not tessellate, margins antrorsely scabrous. Synflorescence capitate with true pedicellate spikelets. Spikelets laterally compressed, consisting of 2 glumes, a single fertile anthoecium and an apical rudimentary anthoecium on the rachilla extension. Glumes sub-equal; lower and upper glumes ovate, apex acute, 7-nerved, awned; lemma ovate, 7-nerved, pubescent, apex acuminate, awnless; palea, 2-nerved, keels ciliate; lodicules 3, lanceolate, ciliate; anthers 3; stigmas 2. Fruit not seen.

Geographic distribution and habitat**—** *Athroostachys* is endemic to Atlantic forest of Brazil and its species grow at elevations of 30 to 110 meters. *Athroostachys shepherdiana* (Santos-Gonçalves, Filg. & L.G. Clark) C. Jesus-Costa & Santos-Gonçalves is found in sandy coastal plains in Atlantic forest know as Restinga, in the states of Bahia and Espírito Santo, while *Athroostachys capitata* occurs Atlantic forest latu sensu in Rio de Janeiro, Minas Gerais, and Bahia (Judziewicz et al. 1999; Santos-Gonçalves et al. 2011).

Athroostachys shepherdiana (Santos-Gonçalves, Filg. & L.G. Clark) C. Jesus-Costa & Santos-Gonçalves, comb. nov. Basionym: *Atractantha shepherdiana* Santos-Gonc., Filg. & L. G. Clark. Syst. Bot. 36(2): 310-313. 2011. TYPE: BRASIL. Espírito Santo: Linhares, Reserva Natural da Vale do Rio Doce, Estrada Jacarandá, próximo ao Aceiro da Aracruz, 19°23'27.96"S, 40°4'19.92"W, ca. 60 meters, 14 Oct 2002, *A. P. Santos-Gonçalves & K. Matsumoto 510* (holotype UEC!; isotypes IBGE!, ISC!, K!, MBM!, MO!, RB!, SP!, UFMG!, US!).

KEY TO THE SPECIES OF *ATHROOSTACHYS*

1. Culm and foliage leaf sheaths bearing fimbriate and spreading auricles at the summit; foliage leaf sheaths with light brown trichomes along the overlapping margin; Rio de Janeiro, Minas Gerais, and Bahia *Athroostachys capitata*

1. Culm and foliage leaf sheaths lacking auricles, bearing erect fimbriae at the summit; foliage leaf sheaths with dark brown trichomes along the overlapping margin; Espírito Santo and Bahia *Athroostachys shepherdiana*

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AUTHOR CONTRIBUTIONS

This work combined data obtained from both the M.S. and Ph.D. studies of C. Jesus-Costa and was developed under the supervision of Dr. Santos-Gonçalves and Dr. Clark. The fieldwork; DNA extraction, amplification, sequencing and alignment of sequences; and phylogenetic analyses were done by C. Jesus-Costa. Manuscript preparation, editing and review were done by C. Jesus-Costa, L. G. Clark and A. P. Santos-Gonçalves.

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TABLE 1. Description of amplification and sequencing primers, PCR protocols and length of seven chloroplast markers.

Region	Primer sequence (5’→ 3’)	PCR protocol	Region length (bp)	Reference
ndhF 3’	972F: GTCTCAATTGGGTTATATGATG 2110R: CCCCCTAYATATTTGATACCTTCTCC Seq: 1318F: GGATTAACTGCGTTTTATATGTTTCG 1603R: GCATAGTATTTCTTCCCGTTTCATGAGG	94ºC, 1 m; 30× (94ºC, 1 m 30 s; touchdown 53–43ºC, 2 m; 72ºC, 3 m); 72ºC, 10 m	1140	Triplett and Clark 2010
rps16	rps16F: AAACGATGTGGTARAAAGCAAC rps16R: AACATCWATTGCAASGATTCGATA	94ºC, 2 m; 35× (94ºC, 45 s; touchdown 58–48ºC, 30 s; 72ºC, 1 m); 72ºC, 5 m	860	Shaw et al. 2005
trnD-trnT	trnD-for: ACCAATTGAACTACAATCCC trnT-rev: CCCTTTTAACTCAGTGGTA Seq: trnY-rev: CTCTTTGCTTTGGATCTAG trnE-for: GCCTCCTTGAAAGAGAGATG	94ºC, 2 m; 35× (94ºC, 45 s; touchdown 58–48.5ºC, 1 m; 72ºC, 1 m 15 s); 72ºC, 5 m	1100	Triplett and Clark 2010

rps16-trnQ	1F: GCACGTTGCTTTCTACCACA 1574R: ATCCTTCCGTCCCAGATTTT Seq: 334F: CGAGATGGTCAATCCTGAAATG 628R: CTTTTGGTATTCKAGTCGAAG	94ºC, 2 m; 35× (95ºC, 1 m; 50ºC, 30 s; +15ºC, 0.3ºC/s; 65ºC, 5 m); 65ºC, 5 m	1120	Triplett and Clark 2010
trnT-trnL	trnT-L F: CATTACAAATGCGATGCTCT trnT-L R: TCTACCGATTTCGCCATATC	95ºC, 2 m; 35× (95ºC, 1 m; 48ºC, 10 s; +17ºC, 0.3ºC/s; 65ºC, 5 m); 65ºC, 5 m	830	Triplett and Clark 2010
trnC-rpoB	trnC: TGGGGATAAAGGATTTGCAG rpoB: ATTGTGGACATTCCCTCRTT Seq: jt400-for: CAGGTCCGAACAGCATTA jt700-rev: CGTAGTAGTAGAATTGCTAG	94ºC, 2 m; 35× (96ºC, 1 m; touchdown 56–46ºC, 2 m; 72ºC, 3 m); 72ºC, 5 m	1185	Triplett and Clark 2010
rpl16	F71: GCTATGCTTAGTGTGTGACTCGTTG R1661: CGTACCCATATTTTTCCACCACGAC Seq: SAK8: CCATCCCACCCAATGAAG R1516: CCCTTCATTCTTCCTCTATGTTG	95ºC, 2 m; 35× (95ºC, 1 m; 50ºC, 10 s; +15ºC, 0.3ºC/s; 65ºC, 4 m); 65ºC, 5 m	1100	F71 and R1661: Jordan et al. 1996; R1516: Kelchner and Clark 1997; SAK8: Tyrrell et al. 2012

TABLE 2. Statistics for analyses and general information for cpDNA regions for Bambuseae.

Characteristic	*ndhF*	*trnC-rpoB*	*rpL16*	*rps16*	*rps16-trnQ*	*trnD-trnT*	*trnT-trnL*	Combined
Number of taxa	43	32	28	17	39	42	35	44
Aligned length (bp)	1167	1330	1113	849	1188	1273	813	7733
Variable characters	78	88	63	24	96	65	51	440
Informative characters (%)	78 (6.68%)	50 (3.75%)	51 (4.58%)	19 (2.24%)	70 (5.89%)	52 (4.08%)	24 (2.95%)	341 (4.41%)

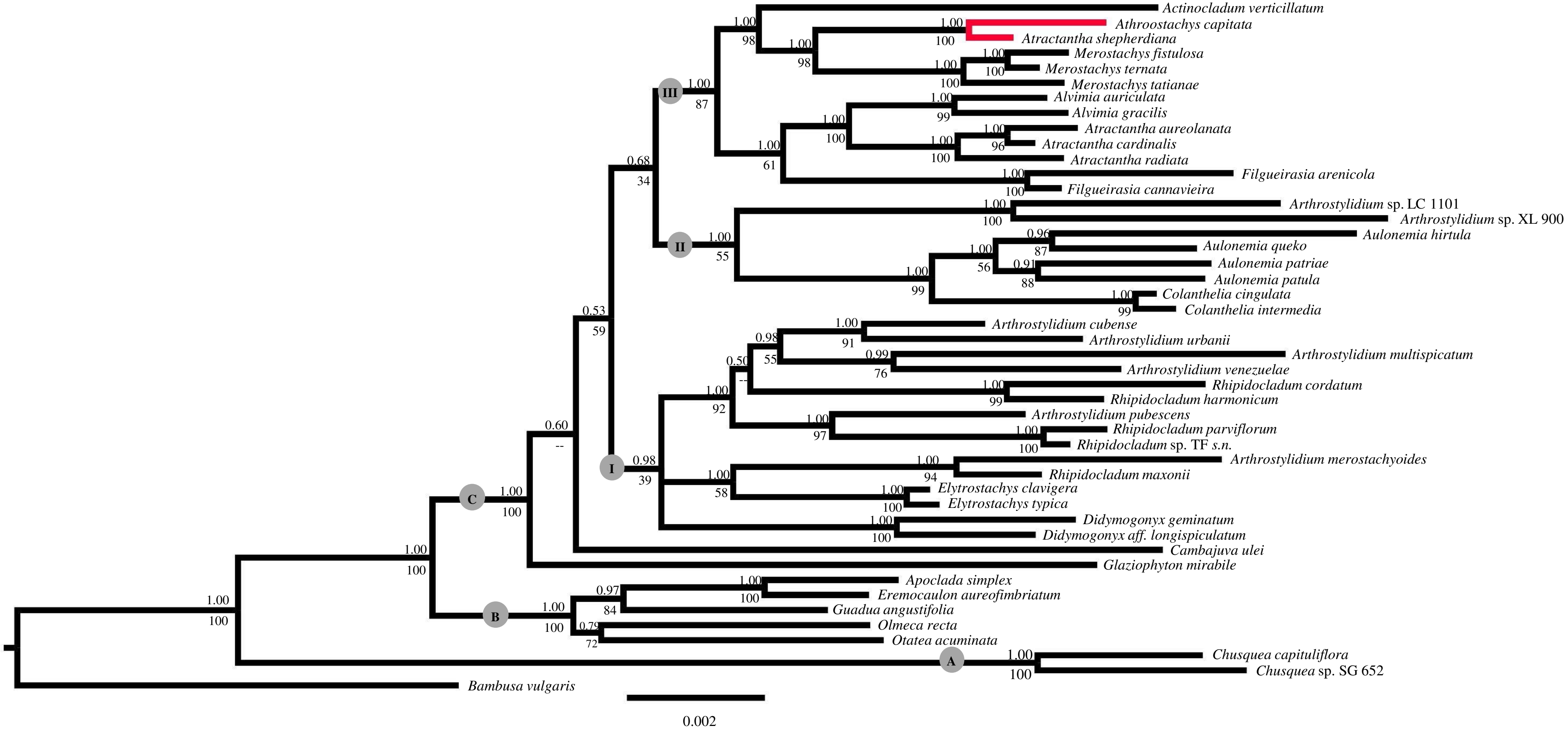
Actinocladum verticillatum
1.00
98
Athroostachys capitata
1.00
100
Atractantha shepherdiana
1.00
98
Merostachys fistulosa
1.00
100
Merostachys ternata
1.00
100
Merostachys tatianae
III
1.00
87
Alvimia auriculata
1.00
99
Alvimia gracilis
Atractantha aureolanata
1.00
96
Atractantha cardinalis
1.00
100
Atractantha radiata
1.00
100
1.00
61
0.68
34
Filgueirasia arenicola
1.00
100
Filgueirasia cannavieira
Arthrostylidium sp. LC 1101
1.00
100
Arthrostylidium sp. XL 900
Aulonemia hirtula
0.96
87
Aulonemia queko
1.00
56
Aulonemia patriae
0.91
88
Aulonemia patula
II
1.00
55
1.00
99
Colanthelia cingulata
1.00
99
Colanthelia intermedia
0.53
59
Arthrostylidium cubense
1.00
91
Arthrostylidium urbanii
0.98
55
Arthrostylidium multispicatum
0.99
76
Arthrostylidium venezuelae
0.50
--
Rhipidocladum cordatum
1.00
99
Rhipidocladum harmonicum
1.00
92
Arthrostylidium pubescens
1.00
97
Rhipidocladum parviflorum
1.00
100
Rhipidocladum sp. TF s.n.
0.60
--
I
0.98
39
Arthrostylidium merostachyoides
1.00
94
Rhipidocladum maxonii
1.00
58
Elytrostachys clavigera
1.00
100
Elytrostachys typica
C
1.00
100
Didymogonyx geminatum
1.00
100
Didymogonyx aff. longispiculatum
1.00
100
Cambajuva ulei
Glaziophyton mirabile
Apoclada simplex
1.00
100
Eremocaulon aureofimbriatum
0.97
84
Guadua angustifolia
1.00
100
B
1.00
100
Olmeca recta
0.79
72
Otatea acuminata
A
Chusquea capituliflora
1.00
100
Chusquea sp. SG 652
Bambusa vulgaris
0.002

FIG. 1. Phylogram based on the majority-rule consensus tree from the BI analysis of the combined cpDNA dataset of *trnD-trnT*, *rps16-trnQ*, *trnC-rpoB*, *trnT-trnL* intergenic spacers, *rpl16* and *rps16* introns, and *ndhF* gene. Numbers above branches are BI posterior probabilities (PP); numbers below branches are bootstrap support (BS) values from the ML analysis.

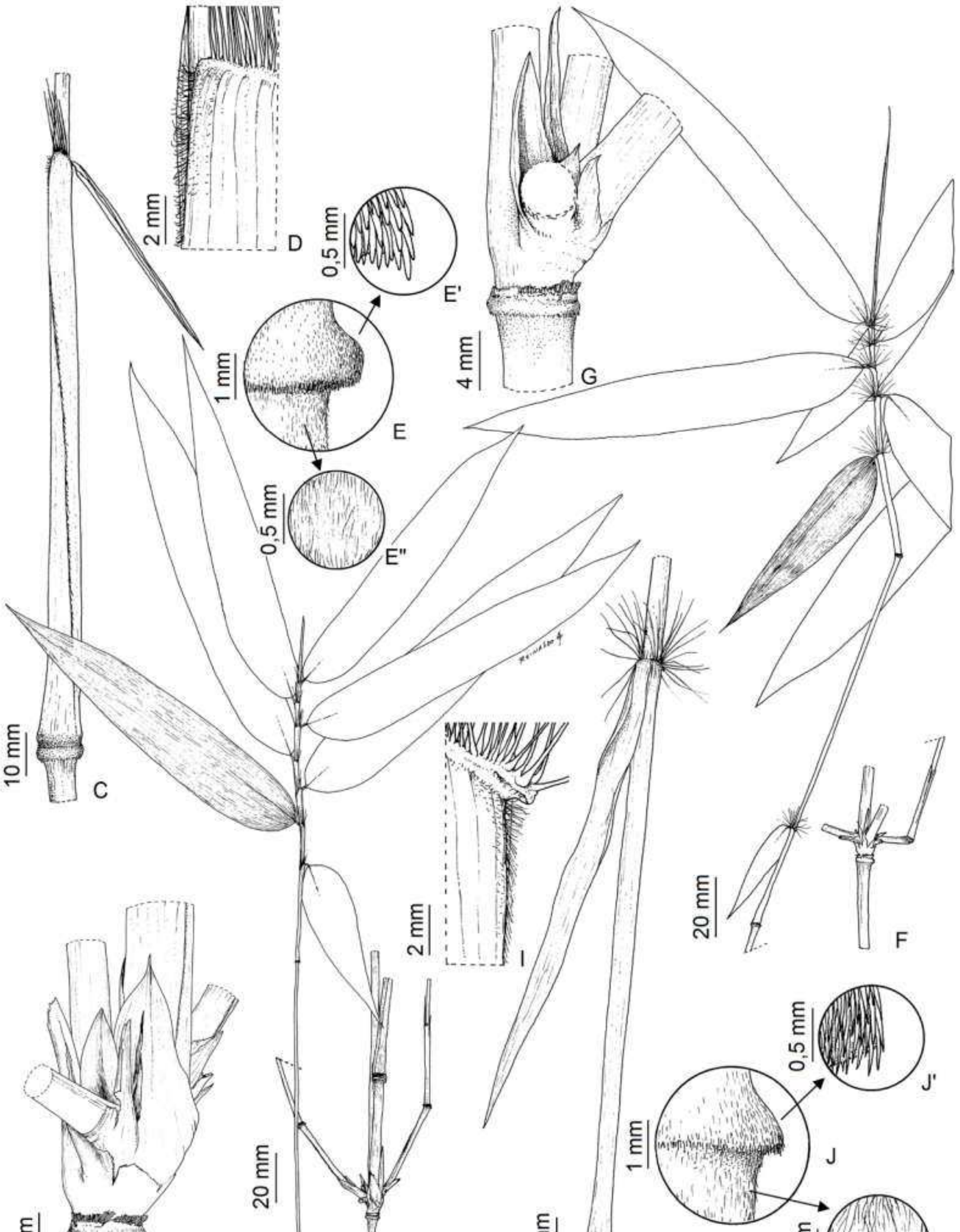

FIG. 2. Morphological comparison between *Atractantha shepherdiana* and *Athroostachys capitata.* A–E. *Atractantha shepherdiana*. A. Branch complement with foliage leaves. B. Mid-culm node and branch complement showing the promontory and three main branches. C. Culm leaf. D. Apex of the culm leaf sheath, showing erect fimbriae and the ciliate overlapping margin of the leaf sheath. E. Nodal line. E'. Detail of the hirtellous-hispid trichomes of the girdle. E". Detail of the tomentose-velvety trichomes of the upper portion of a young internode. F–J. *Athroostachys capitata*. F.

Branch complement with foliage leaves. G. Mid-culm node and branch complement showing the promontory and three main branches. H. Culm leaf. I. Apex of the leaf culm sheath, showing spreading fimbriate auricles and the ciliate overlapping margin of the leaf sheath. J. Nodal line. J'. Detail of the hirtellous-hispid trichomes of the girdle. J". Detail of the tomentose-velvety trichomes of the upper portion of a young internode. (Illustration by Reinaldo Pinto).

APPENDIX 1. Taxa, vouchers used in this study and associated locality, collector, collection number, herbarium information, and GenBank accession numbers [*ndhF* 3'*, rpl16, rps16, trnC-rpoB, trnD-trnT, rps16-trnQ, trnT-trnL*]. A dash (—) indicates the molecular region was not sequenced. An asterisk (*) before the GenBank accession number indicates a sequence generated for this study.

Arthrostylidiinae— *Actinocladum verticillatum* (Nees) McClure ex Soderstr., Brazil, *T Filgueiras s.n.* (ISC), [JQ408524, JQ408570,—, JQ408485, JQ408623, JQ408445, JQ408586]. ***Actinocladum verticillatum***, Brazil, *CJ Costa 89* (VIC), [—,—, *MG458251,—,—,—,—]. ***Alvimia auriculata*** Soderstr. & Londoño, Brazil, *AP Santos-Gonçalves 598* (VIC), [JQ408525,—,—, JQ408486, JQ408624, JQ408446, JQ408587]. ***Alvimia gracilis*** Soderstr. & Londoño, Brazil, *A Carvalho et al. 4389* (CEPEC), [JQ408526, JQ408571,—, JQ408487, JQ408625, JQ408447, JQ408588]. ***Arthrostylidium cubense*** Rupr., Cuba, *X Londoño 957* (ISC), [JQ408529, JQ408572,—,—, JQ408628, JQ408450, JQ408590]. ***Arthrostylidium merostachyoides*** R.W. Pohl, Costa Rica, *C Tyrrell et al. 36* (ISC), [JQ408531,—,—, JQ408491,—, JQ408452,—]. ***Arthrostylidium multispicatum*** Pilg., Puerto Rico, *LG Clark & G Reiners 1508* (ISC), [JQ408532, JQ408574,—,—, JQ408630, JQ408453, JQ408592]. ***Arthrostylidium pubescens*** Rupr., Costa Rica, *C Tyrrell et al. 42* (ISC), [JQ408533, JQ408575,—,—, JQ408631, JQ408454,—]. ***Arthrostylidium* sp.**, Ecuador, *LG Clark et al. 1101* (QCA), [JQ408530, JQ408573,—, JQ408490, JQ408629, JQ408451, JQ408591]. ***Arthrostylidium* sp.**, Colombia, *X Londoño 900* (COL), [JQ408528,—,—, JQ408489, JQ408627, JQ408449, JQ408593]. ***Arthrostylidium urbanii*** Pilg., Cuba, *X Londoño 851* (ISC), [JQ408534, JQ408576,—, JQ408492, JQ408632, JQ408455, JQ408594]. ***Arthrostylidium venezuelae*** (Steud.) McClure, Costa Rica, *C Tyrrell et al. 43* (ISC), [JQ408535,—,—, JQ408493, JQ408633,—,—]. ***Athroostachys capitata*** (Hook.) Benth., Brazil, *R Vinícius-Silva 15* (VIC), [*MG458235, *MG458241, *MG458252, *MG458262, *MG458268, *MG458274, *MG458281]. ***Atractantha aureolanata***

Judz., Brazil, *AP Santos-Gonçalves 596* (VIC), [JQ408536,—,—, JQ408494, JQ408634,—, JQ408595]. ***Atractantha aureolanata***, Brazil, *AP Santos-Gonçalves 658* (VIC), [—, *MG458243, *MG458253,—,—, *MG458275,—]. ***Atractantha cardinalis*** Judz., Brazil, *AP Santos-Gonçalves 591* (VIC), [JQ408537,—,—, JQ408495, JQ408635, JQ408456, JQ408596]. ***Atractantha cardinalis***, Brazil, *AP Santos-Gonçalves 657* (VIC), [—, *MG458244, *MG458254,—,—,—,—]. ***Atractantha radiata*** McClure, Brazil, *A Carvalho 4362* (CEPEC), [JQ408538, JQ408577, KC020568.1, JQ408496, JQ408636, JQ408457, JQ408597]. ***Atractantha shepherdiana*** Santos-Gonçalves, Filg. & L.G. Clark, Brazil, *CJ Costa et al. 114* (VIC), [*MG458236,*MG458242, *MG458255, *MG458263, *MG458269, *MG458276, *MG458282]. ***Aulonemia hirtula*** (Pilg.) McClure, Ecuador, *LG Clark & P Asimbaya 1412* (QCA), [JQ408540,—,—, JQ408498, JQ408638,—,—]. ***Aulonemia patriae*** R.W.Pohl, Costa Rica, *C Tyrrell et al. 44* (ISC), [JQ408541,—,—, JQ408499, JQ408639, JQ408458,—]. ***Aulonemia patula*** (Pilg.) McClure, Ecuador, *LG Clark et al. 1075* (QCA), [JQ408542, JQ408578,—, JQ408500, JQ408640, JQ408459, JQ408599]. ***Aulonemia queko*** Goudot, Ecuador, *LG Clark & P Asimbaya 1445* (QCA), [JQ408543, JQ408579,—, JQ408501, JQ408641, JQ408460, JQ408600]. ***Cambajuva ulei*** (Hack.) P.L. Viana, L.G. Clark & Filg., Brazil, *LG Clark & X Londoño 1048* (ISC), [JQ408544,—,—, JQ408502, JQ408642, JQ408461, JQ408601]. ***Colanthelia cingulata*** (McClure & L.B.Sm.) McClure, Brazil, *T Filgueiras s.n.* (ISC), [JQ408545,—,—,—, JQ408643,—, JQ408602]. ***Colanthelia intermedia*** (McClure & L.B.Sm.) McClure, Brazil, *AP Santos-Gonçalves 553* (VIC), [—,—,—,—, JQ408645, JQ408462, JQ408604]. ***Didymogonyx geminatum*** (McClure) McClure, Venezuela, *F Ely 2* (ISC), [JQ408562,—,—,—, JQ408660, JQ408477, JQ408614]. ***Didymogonyx* aff. *longispiculatum*** Londoño & L.G. Clark, Colombia, *X Londoño & E Ruiz-Sanchez 995* (ISC), [JQ408558,—,—, JQ408513, JQ408656, JQ408473,—]. ***Elytrostachys clavigera*** McClure, Costa Rica, *R Pohl 13572* (ISC), [JQ408547,—,—,—,—,—,—]. ***Elytrostachys typica*** McClure, Colombia, *X Londoño 985* (COL), [JQ408548,—,—,—, JQ408646, JQ408463,—]. ***Filguerasia arenicola*** (McClure) Guala, Brazil, *T Filgueiras s.n.* (ISC), [JQ408550,—,—, JQ408505, JQ408648, JQ408465, JQ408605]. ***Filguerasia cannavieira*** (Silveira) Guala, Brazil, *T Filgueiras s.n.* (ISC), [JQ408551, JQ408580,—, JQ408506, JQ408649, JQ408466, JQ408606]. ***Glaziophyton mirabile*** Franch., Brazil, *L Sarahyba et al. 1066* (ISC), [JQ408552, U54748, KC020582.1, JQ408507, JQ408650, JQ408467, JQ408607]. ***Merostachys fistulosa*** Döll, Brazil, *R Vinícius-Silva 50* (VIC), [*MG458237, *MG458245, *MG458256, *MG458264, *MG458270, *MG458277, *MG458283]. ***Merostachys tatianae*** Santos-Gonçalves, Carvalho-Okano & Filg., Brazil, *R Vinícius-Silva 18* (VIC), [*MG458238, *MG458246, *MG458257, *MG458265, *MG458271, *MG458278, *MG458284]. ***Merostachys ternata*** Nees, Brazil, *LG Clark & W Oliveira 1023/ R Vinícius-Silva 30* (ISC/VIC), [JQ408555, *MG458247, *MG458258, JQ408510, JQ408653, JQ408471, JQ408610]. ***Rhipidocladum maxonii*** (Hitchc.) McClure, Costa Rica, *C Tyrrell et al. 46* (ISC), [JQ408564,—,—, JQ408518, JQ408662,—,—]. ***Rhipidocladum parviflorum*** (Trin.) McClure, Brazil, *T Filgueiras s.n.* (ISC), [JQ408567,—,—, JQ408521, JQ408665, JQ408481, JQ408617]. ***Rhipidocladum parviflorum***, Brazil, *CJ Costa 92* (VIC), [—, *MG458248, *MG458259,—,—,—,—]. ***Rhipidocladum harmonicum*** (Parodi) McClure, Ecuador, *LG Clark et al. 1128* (QCA), [JQ408563, JQ408582,—, JQ408517, JQ408661, JQ408478, JQ408615]. ***Rhipidocladum cordatum*** C.D. Tyrrell & L.G. Clark, Ecuador, *LG Clark 1464* (QCA), [JQ408561, JQ408581,—, JQ408516, JQ408659, JQ408476, JQ408622]. ***Rhipidocladum* sp.**, Brazil, *T Filgueiras s.n.* (ISC), [JQ408557,—,—, JQ408512, JQ408655, JQ408472, JQ408621]. **Chusqueinae—*Chusquea* sp.** Trin., Brazil, *AP Santos-Gonçalves 620* (VIC), [*MG458239, *MG458249, *MG458260, *MG458266, *MG458272, *MG458279, *MG458285]. ***Chusquea* aff. *capitata*** Ness, Brazil, *AP Santos-Gonçalves 652* (VIC), [*MG458240, *MG458250, *MG458261, *MG458267, *MG458273, *MG458280, *MG458286]. **Guaduinae— *Apoclada simplex*** McClure & L.B.Sm., Brazil, *LG Clark & W Oliveira 1027* (ISC), [JQ408527,—, KC020566.1, JQ408488, JQ408626, JQ408448, JQ408589]. ***Eremocaulon aureofimbriatum*** Soderstr. & Londoño, Brazil, *A Carvalho 4393* (CEPEC), [JQ408549, EF589616,—, JQ408504, JQ408647, JQ408464,—]. ***Guadua angustifolia*** Kunth., Colombia, *X Londoño & LG Clark 931* (ISC), [FJ643714, FJ751664, KC020583.1, FJ643910, FJ644003, FJ643817, FJ644154]. ***Olmeca recta*** Soderstr., Mexico, *LG Clark 1313* (ISC), [JQ408556,—,—, JQ408511, JQ408654, JQ408468, JQ408611]. ***Otatea acuminata*** (Munro) C.E.Calderón & Soderstr., Mexico, *LG Clark 1312* (ISC), [AF182350, U54749, KC020589.1, FJ751705, FJ751732, FJ751678, JQ408612]. **Bambusinae—*Bambusa vulgaris*** Schrad., Cultivated, *J Sanchez-Ken 666* (ISC), [FJ643709, AY912192, KC020569.1, FJ751706, FJ643982, FJ643796, FJ644133].

CONCLUSÕES GERAIS

Os estudos filogenéticos moleculares e taxonômicos em Arthrostylidiinae resultantes desta tese revelaram novidades sobre o relacionamento filogenético interno da subtribo e ampliaram a base de sequências moleculares de bambus lignificados neotropicais, especialmente de espécies brasileiras.

Neste estudo, por meio de uma maior amostragem taxonômica e molecular, *Atractantha* emergiu como polifilético; este resultado difere do que se obteve anteriormente no único estudo filogenético, disponível na literatura até o momento, com ênfase em na subtribo. *A. shepherdiana* foi fortemente sustentada como grupo irmão de *Athroostachys capitata.* Adicionalmente à filogenia molecular, evidências morfológicas sustentam a transferência de *A. shepherdiana* para *Athroostachys*. Este é o primeiro estudo que testou o posicionamento filogenético de *Athroostachys*, e os resultados aqui obtidos corroboram dados da literatura ao posicionar o gênero como grupo irmão de *Merostachys*.

Trabalhos de campo permitiram a descoberta de uma espécie nova de *Colanthelia*, a qual é aqui apresentada: *C. longipetiolata* Jesus-Costa & Santos-Gonçalves.

O estudo filogenético aqui conduzido, com amostragem concentrada em *Colanthelia* e *Aulonemia*, confirmou *Aulonemia* como polifilético; no entanto, *Colanthelia* emergiu não monofilético. Todas as espécies de *Colanthelia* e a maioria das espécies de *Aulonemia* amostradas agruparam-se no clado *Aulonemia* + *Colanthelia*; entretanto, quatro espécies atípicas de *Aulonemia* mostraram maior afinidade filogenética com outros clados de Arthrostylidiinae, e evidências morfológicas sustentam o estabelecimento futuro de novos táxons para acomodar estas espécies que não se enquadram na atual circunscrição de *Aulonemia*. A filogenia resultante revela o universo morfológico heterogêneo de ambos os gêneros e ressalta a necessidade de rearranjos taxonômicos nestes grupos.

Arthrostylidiinae é extremamente complexa e diversa quanto aos caracteres morfológicos utilizados para distinguir os seus gêneros; assim, ressaltamos a importância de estudos morfológicos futuros que contribuirão para compreensão da evolução de caracteres dentro desta subtribo.