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A Multi-locus Plastid Phylogeny of the *Aulonemia* Clade (Poaceae: Bambusoideae: Bambuseae: Arthrostylidiinae) Reveals Three New Genera of Bamboo

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Abstract—Arthrostylidiinae (Poaceae: Bambusoideae), a subtribe of Neotropical woody bamboos with diverse morphology, comprises 200 species classified in 16 genera. Previous studies supported monophyly of the subtribe and recovered four major internal clades, however, some genera were found to be polyphyletic while others, like *Aulonemia* and *Colantheria*, were either undersampled or not included. *Aulonemia* and *Colantheria* are complex both in their taxonomy and morphology, and exhibit overlapping morphological characters. Prior morphological and molecular analyses suggested they share a close relationship, with *Colantheria* emerging as monophyletic and either nested within *Aulonemia* or sister to it, but these studies sampled relatively few species of each genus. The aims of this study were to increase taxon sampling to test the monophyly of *Aulonemia* and *Colantheria*, to investigate the relationships within the *Aulonemia* + *Colantheria* clade, and to revise their classification as appropriate towards a natural classification of the Arthrostylidiinae. We present a multi-locus plastid phylogeny of the Arthrostylidiinae with emphasis on *Aulonemia* and *Colantheria*. 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 67 taxa of Bambusoideae including all genera of Arthrostylidiinae. Phylogenetic trees were inferred using both Bayesian and maximum likelihood methods. *Aulonemia* was confirmed as polyphyletic and *Colantheria* was not supported as monophyletic. The phylogenetic position of *Myriocladus* within Arthrostylidiinae is resolved for the first time. All species of *Colantheria* were recovered within the clade containing most species of *Aulonemia*. Four species of *Aulonemia* (*A. radiata*, *A. effusa*, *A. setosa*, and *A. setigera*) grouped in other clades within the subtribe and these placements combined with morphological evidence support the establishment of three new genera: *Quixiume*, *Stelanemia* and *Vianaea*, to accommodate the four remarkable *Aulonemia* species. An updated key for the genera of the Arthrostylidiinae is provided, as well as taxonomic treatments for the three new genera, including the description of a new species in *Stelanemia*.

Keywords—Atlantic Forest, montane forests, *Myriocladus*, Neotropical bamboos.

The Neotropical woody bamboo (NWB) subtribe Arthrostylidiinae (Poaceae: Bambusoideae: Bambuseae) is currently composed of 200 species in 16 genera (Judziewicz et al. 1999; Ruiz-Sanchez et al. 2008, 2021; Clark et al. 2015; Vorontsova et al. 2016; Afonso et al. 2019; Andrade et al. 2020; Clark et al. 2020). The coastal Atlantic rainforest in Brazil is the main center of diversity of the subtribe, where several endemic genera and species occur (Judziewicz et al. 1999; Viana et al. 2009; Ruiz-Sanchez et al. 2021). Besides its taxonomic richness, Arthrostylidiinae is also the most morphologically diverse subtribe of the NWB (Clark et al. 2015). Together, Arthrostylidiinae, Guaduinae, and Chusqueinae comprise the three subtribes of the NWB clade (BPG 2012; Clark et al. 2015). The subtribe Guaduinae is strongly supported as the sister group of Arthrostylidiinae and each subtribe is strongly supported as monophyletic (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; Jesus-Costa et al. 2018).

Arthrostylidiinae is a natural group characterized by a set of morphological and anatomical features: the presence of (usually) a single primary branch bud at the mid-culm nodes, foliage leaves bearing fimbriae, intercostal sclerenchyma

fibers in the leaf blades, simple vasculature in the midrib and hypostomatic leaf blades with papillae usually developed only on the abaxial epidermis, and an abaxial green (waxless) marginal stripe (Soderstrom and Ellis 1987; Judziewicz et al. 1999; Ruiz-Sanchez et al. 2021). Amphistomatic foliage leaves have been recorded in some species of *Aulonemia* Goudot, *Colantheria* McClure & E.W.Sm., and *Merostachys* Spreng., in which the stomata are confined to just a narrow region on the adaxial surface over the abaxial green stripe (Santos-Gonçalves 2005; Viana et al. 2011). A green marginal stripe on the abaxial foliage leaf epidermis is a useful guide for recognizing members of Arthrostylidiinae; however, this feature is not present in all its species and also occurs in other subtribes of Bambuseae, and tribes of Bambusoideae (Judziewicz et al. 1999).

Phylogenetic relationships within Arthrostylidiinae were investigated by Tyrrell et al. (2012) and Jesus-Costa et al. (2018) based on plastid DNA sequence data. The former study included representatives of 11 of the then 13 recognized genera (the two unsampled genera were *Athrostachys* Benth. and *Myriocladus* Swallen). Jesus-Costa et al. (2018) built upon this work by adding additional representatives for previously sampled genera and the previously unsampled

Athrostachys. Both analyses recovered three to four moderately to strongly supported main lineages within Arthrostylidiinae. Tyrrell et al. (2012) named these clades based on the oldest sampled taxon in each while Jesus-Costa et al. (2018) numbered them such that Clade I corresponded to the *Arthrostylidium* clade, Clade II corresponded to the *Aulonemia* clade, and Clade III corresponded to the *Merostachys* clade (Tyrrell et al.'s Glaziophyton clade was not recovered by Jesus-Costa et al.). Despite robust molecular support, no morphological synapomorphies could be attributed to any of the clades.

These investigations, however, did reveal new alignments of morphological and anatomical characters in several genera, which led to novel taxa and new combinations: *Didymogonyx* (L.G.Clark & Londoño) C.D.Tyrrell, L.G.Clark & Londoño was elevated from a section of *Rhipidocladum* McClure to generic status (Tyrrell et al. 2012); the new genus *Cambajwa* P.L.Viana, L.G.Clark & Filg. was proposed to accommodate one species of *Aulonemia* resolved as sister to *Glaziophyton* Franch. (Viana et al. 2013); a species of *Atractantha* McClure was resolved as sister to the single species of *Athrostachys* and was subsequently transferred to the latter genus (Jesus-Costa et al. 2018); three species of *Arthrostylidium* were found to be members of subtribe Guaduinae and were placed in new genus *Tibisia* C.D.Tyrrell, Londoño & L.G.Clark (Tyrrell et al. 2018); and two specimens attributed to *Arthrostylidium* but recovered in Clade II as sister to *Aulonemia* and *Colantheia* were established in the new genus *Aulonemiella* L.G.Clark, Londoño, C.D.Tyrrell & Judz. (Clark et al. 2020).

Throughout all these studies, the relationship between *Colantheia* and *Aulonemia* has remained enigmatic. In Tyrrell et al. (2012), *Colantheia* was resolved as monophyletic, but nested within *Aulonemia*, which was, in turn, polyphyletic. This study, however, had only 5 (10%) and 3 (30%) representatives of *Aulonemia* and *Colantheia*, respectively. Using a subset of the same sequences, Jesus-Costa et al. (2018) similarly resolved a monophyletic *Colantheia* sister to *Aulonemia*. Nevertheless, both *Aulonemia* and *Colantheia* have many species and both genera have been poorly sampled phylogenetically; only the five *Aulonemia* species and three *Colantheia* species mentioned above have been included in phylogenetic analyses to date.

Aulonemia comprises 49 described species (Judziewicz et al. 1999; Clark et al. 2015; Vorontsova et al. 2016; Ruiz-Sanchez et al. 2021). The genus is distributed from Mexico to southern Brazil and most species occur in wet to moist, moderate to high elevation sites (Judziewicz et al. 1999). The Andean mountain chain 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 quartzite outcrops (Judziewicz et al. 1999; Judziewicz 2005; 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, long 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 complements 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 not always differentiated; fimbriate foliage leaves; and panicle synflorescences with two to five orders of branching bearing awned or mucous spikelets with two to seven glumes and few to many fertile florets, and one apical rudimentary floret represented by a sterile lemma (McClure 1973; Judziewicz et al. 1999; Viana et 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 with a more comprehensive phylogenetic hypothesis is required. Furthermore, defining the generic limits between *Aulonemia* and *Colantheia* has been a difficult task, since there is morphological overlap between these genera.

Colantheia includes ten species endemic to the Atlantic rainforest domain (Santos-Gonçalves et al. 2018; Jesus-Costa et al. 2019), almost all occurring in southern and southeastern Brazil with only one, *C. rhizantha* (Hack.) McClure, occurring, disjunct, in the province of Misiones in Argentina (Judziewicz et al. 1999; Santos-Gonçalves et al. 2018). As circumscribed by Santos-Gonçalves et al. (2018), *Colantheia* encompasses 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 weakly panicle synflorescences with limited branching; and relatively long and narrow spikelets with more or less elongated and exposed rachilla segments. *Colantheia 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-Gonç., Filg. & L.G.Clark, which also has lemmas with dark spots).

Colantheia 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 et al. 1982; Burman and Filgueiras 1993; Judziewicz et al. 1999, Santos-Gonçalves 2005). The morphological affinity between *Aulonemia* and *Colantheia* has been recognized for some time, and the similarity of the mid-culm branch complement and the occurrence of panicle synflorescences in some species of *Colantheia* reinforce this relationship (McClure 1973; Judziewicz et al. 1999; Santos-Gonçalves 2005; Santos-Gonçalves et al. 2018).

In view of the phylogenetic proximity and the overlap of morpho-anatomical features between both genera, we conducted a phylogenetic study of the Arthrostylidiinae based on analyses of multiple cpDNA regions and increased taxon sampling to achieve the following aims: 1) test the relationships within the *Aulonemia* + *Colantheia* clade; 2) test the monophyly of *Aulonemia* and *Colantheia*; and 3) revise the classification of the sampled species of *Aulonemia* and *Colantheia*, as appropriate, towards a natural classification.

MATERIALS AND METHODS

Taxon Sampling and Marker Selection—Sampling was optimized to include species of the genera *Aulonemia* and *Colantheia*. Overall, 67 species were sampled as follows: *Aulonemia* 22/49 (species sampled/species belonging to the genus), *Colantheia* 6/10, *Actinocladum* McClure ex Soderstr. 1/1, *Alvimia* Calderón ex Soderstr. & Londoño 2/3, *Arthrostylidium* 3/29, *Cambajuva* 1/1, *Athrostachys* 2/2, *Atractantha* 3/5, *Didymogonyx* 2/2, *Elytostachys* McClure 2/2, *Filgueirasia* 2/2, *Glaziophyton* 1/1, *Merostachys* 3/57, *Myriocladus* 1/13, *Rhipidocladum* McClure 3/21, *Chusquea* Kunth 2/202, *Apoclada* McClure 1/1, *Eremocaulon* 2/5, *Guadua* Kunth 2/33, *Olmea* 1/5 and *Otatea* (McClure & E.W.Sm.) C.E. Calderón & Soderstr. 1/13. All subtribes (Arthrostylidiinae, Guaduainae, 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 et al. 2007; Ruiz-Sanchez et al. 2008; Tyrrell et al. 2012). The complete list of taxa and voucher specimens is given in Appendix 1.

All specimens gathered for this study were collected legally with appropriate valid permits as required at the time of their gathering.

Seven plastid markers were selected: one partial gene (*ndhF*), 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 and Clark 2010; Tyrrell et al. 2012; Kelchner et al. 2013).

DNA Extraction, Amplification, Sequencing and Alignment—Genomic DNA was extracted from ca. 30–50 mg of leaf tissue dried in silica gel using a modified 2 × cetyl trimethylammonium bromide (CTAB) protocol (Doyle and Doyle 1987). The amplification primers, sequencing primers and thermal cycler protocols are described in Jesus-Costa et al. (2018). The polymerase chain reaction (PCR) was conducted in a final reaction volume of 40 µL containing 10–50 ng of template DNA, 1 × buffer, 2.5 mM of magnesium chloride (MgCl₂), 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). Plastid markers *ndhF*, *trnD-trnT*, *trnC-rpoB*, *rps16-trnQ*, and *rpl16* were sequenced using the internal forward and reverse primers identified in Jesus-Costa et al. (2018), and *trnT-trnL* and *rps16* were sequenced with their PCR primers.

Sequence reads were trimmed such that the leading and trailing bases with Phred quality scores at or below 13 were excluded prior to contig assembly. Polymorphic positions (coded as 'N') were examined using 4Peaks (Nucleobytes B. V., www.nucleobytes.com) and manually recoded to the nucleotide with greatest quality score for that position when the score difference was greater than 3, otherwise the position was assigned the most appropriate IUPAC ambiguity code. Contigs were aligned using a custom Python script (Tyrrell et al. 2024). Contig alignments were checked and adjusted with AliView v. 1.28 (Larsson 2014) and consensus assembly was performed using another custom Python script (Tyrrell et al. 2024).

Each marker was aligned with Muscle v. 3.8.31 (Edgar 2004) using default parameters. Alignments were examined and manually adjusted in AliView so that variable length single-nucleotide repeats were consistently aligned across taxa (this almost always required introducing a single base pair gap in all taxa except one with a longer repeat). Insertion/deletion gap sites were encoded (Simmons and Ochoterena 2000) as an exclusion character set in the nexus file assumptions block. All individual sequences obtained in this work are available in GenBank (Appendix 1) and alignment files are available in Tyrrell et al. (2024).

Phylogenetic Analyses—Maximum likelihood (ML) analyses were conducted using IQ-TREE v. 2.2.2 for Mac OS X 64-bit (Minh et al. 2020a) on a MacBook Pro. Initially, the data were partitioned into all seven loci, however, we employed the IQ-TREE automated ModelFinder procedure (Kalyanamoorthy et al. 2017) to select the optimal model partitioning scheme for the alignment. IQ-TREE's in-built phylogenetic terrace aware data structure was subsequently used to infer the final consensus tree (Chernomor et al. 2016). Branch support values (BS) for the consensus tree were calculated using 1000 iterations and the ultrafast bootstrap procedure (Hoang et al. 2018) resampling the optimized partitions, then sites within partitions (–sampling GENESITE; Gadagkar et al. 2005; Seo et al.

2005) and with the hill-climbing nearest neighbor interchange (–nni) search to reduce over-inflated values.

Gene trees were inferred using IQ-TREE following the parameters specified above, except that ModelFinder was not used to determine an optimized partitioning scheme. Gene (–gcf) and site (–scf 100) concordance factors (Minh et al. 2020b) were calculated for the branches of the ML consensus tree using IQ-TREE. A multispecies coalescent analysis was then carried out with ASTRAL-III (Zhang et al. 2018) using the gene trees and generating the default local posterior probability (PP) branch support values. Gene tree discordance was visualized using DiscoVista v. 1.0 (Sayari et al. 2018).

Approximately unbiased (AU) topology tests and RELL bootstrap proportions were calculated using IQ-TREE on trees constrained to conform to specified topologies. Tested topologies included enforcing a monophyletic group, regardless of other taxa: *Aulonemia* only; *Colantheia* only; *Aulonemia* and *Colantheia*, independently; a clade of *Aulonemia* + *Colantheia*; different configurations of the Arthrostylidiinae backbone topology; and the Multispecies Coalescent (MSC) tree (Table 1).

RESULTS

We produced 175 new plastid DNA sequences for 67 species of Bambuseae (Appendix 1). Not all cpDNA regions were amplified or sequenced for all taxa even after repeated attempts. The alignment of the combined sequence matrix contained 11,407 nucleotide characters, of which 698 were parsimony informative. The number of taxa and the aligned lengths of the sequences for each markers were, *ndhF* gene: 65 species (spp.), 2262 bp/106 parsimony-informative characters (PICs); *rps16*: 46 spp., 1211 bp/74 PICs; and *rpl16* introns: 53 spp., 1616 bp/69 PICs; and *rps16-trnQ*: 66 spp., 1403 bp/103 PICs; *trnC-rpoB*: 57 spp., 2030 bp/145 PICs; *trnD-trnT*: 60 spp., 1866 bp/119 PICs; and *trnT-trnL* intergenic spacers: 59 spp., 1019 bp/82 PICs. The data missing due to incomplete taxon sampling across regions represented approximately 44.99% of the total sequence matrix. Twenty taxa contained more than 50% gaps/ambiguity and four taxa (*Aulonemia cochabambensis* [90.35%], *Aulonemia robusta* [82.86%], *Elytostachys flavigera* [90.14%], and *Myriocladus virgatus* [73.20%]) failed a χ^2 test for composition at a 0.1 significance level.

The optimal partitioning scheme divided the loci into two partitions: one combining the *rps16-trnQ* + *trnD-trnT* + *ndhF* + *rps16* loci (partition 1) and the other combining the *trnC-rpoB* + *rpl16* + *trnT-trnL* loci (partition 2). For both partitions, the Kimura (1981) three parameter model using unequal, empirically derived, base frequencies with a relaxed gamma rate-heterogeneity with 3 (partition 1) or 4 (partition 2) categories ("FreeRate"; Yang 1995; Soubrier et al. 2012) achieved the best information criterion value. Base frequencies for partition 1 were calculated as: A = 0.335, C = 0.161, T = 0.170, and G = 0.334, and for partition 2 were: A = 0.331, C = 0.159, T = 0.148, and G = 0.362.

TABLE 1. Tests of alternative tree topologies using the approximately unbiased (AU) test and RELL bootstrap proportion. * = AU test result not significant at $\alpha = 0.05$.

Monophyletic Configuration	RELL Bootstrap Proportion	AU <i>p</i> value
<i>Aulonemia</i>	0	< 0.0001
<i>Colantheia</i>	0	< 0.0001
<i>Aulonemia</i> , <i>Colantheia</i>	0	< 0.0001
<i>Aulonemia</i> + <i>Colantheia</i>	0	< 0.0001
(<i>Aulonemia radiata</i> , (<i>Glaziophyton</i> + <i>Cambajuva</i>))	0.035	0.0914*
MSC Species Tree	0	0.0001

In the ML consensus tree (Fig. 1) and MSC species tree (Fig. S1), Chusqueinae, Guaduinae, and Arthrostylidiinae were each supported as monophyletic (100BS/0.99PP, 95BS/1.0PP, and 90BS/0.99PP, respectively) and Arthrostylidiinae was supported as sister (98BS/1.0PP) to the Guaduinae. Five

major clades were inferred within Arthrostylidiinae, but with variable resolution and support between the ML and MSC analyses, including: Clade I, consisting of all representatives from *Arthrostylidium*, *Didymogonyx*, *Elytostachys*, and *Rhipidocladum* (65BS and 0.64PP); Clade II, consisting of the majority

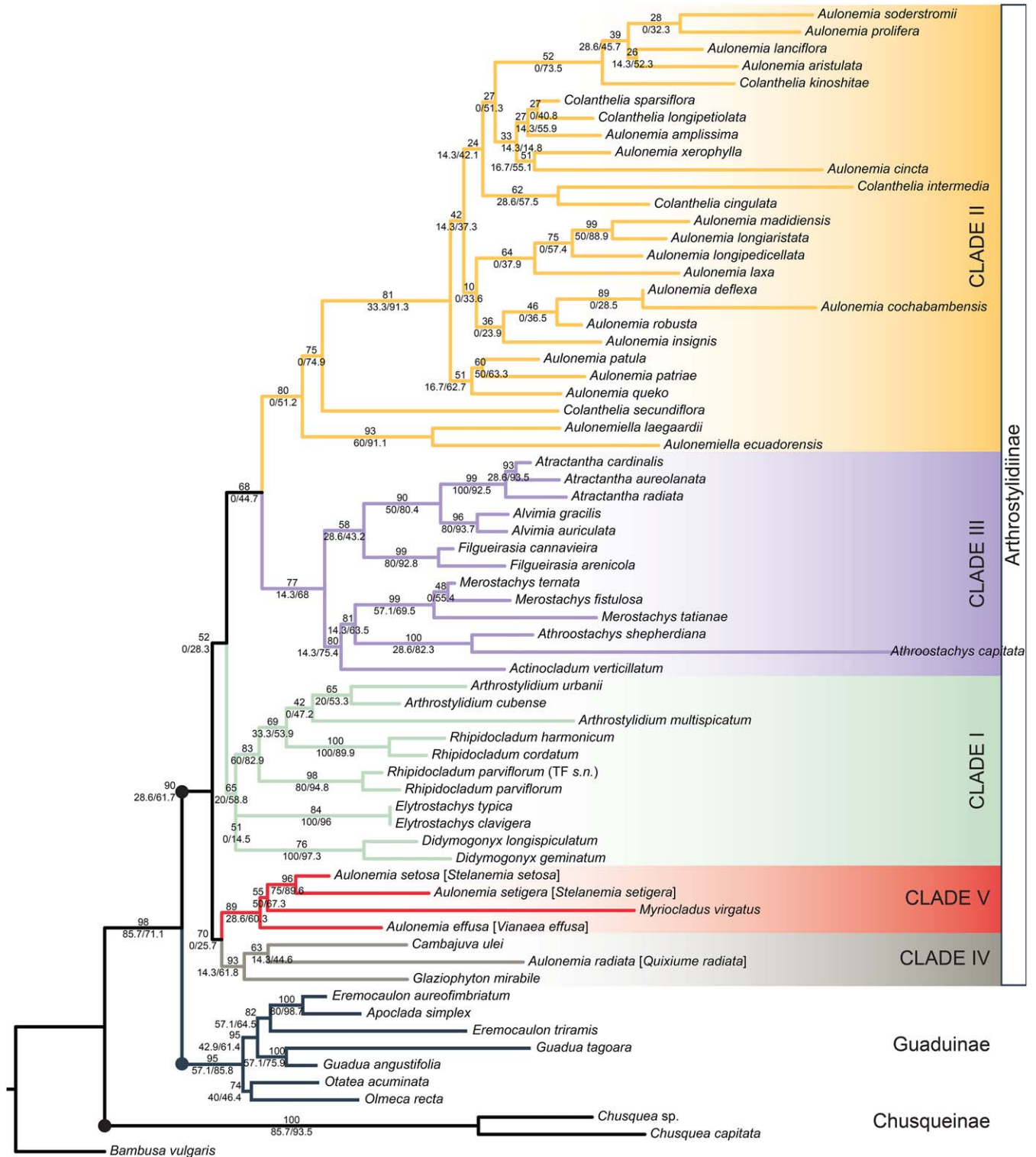


FIG. 1. Maximum likelihood (ML) tree of 67 individuals representing 66 taxa across 23 Neotropical woody bamboo genera (see Appendix 1 for specimen voucher details). Topology is inferred from plastid DNA sequences of *trnD-trnT*, *rps16-trnQ*, *trnC-rpoB*, *trnT-trnL* intergenic spacers, *rpl16* and *rps16* introns, and the *ndhF* gene. Bootstrap values displayed above branches, gene concordance and site concordance factors (separated by '/') are displayed below branches. Circles on the tree indicate subtribal clades and colored boxes highlight clade structure within Arthrostylidiinae. Clade names conform to those resolved in previous studies.

of the representatives from *Aulonemia* plus all representatives from *Colanthesia* and *Aulonemiella* (80BS/0.55PP [but 0.72PP if expanded to include the sister relationship with *Aulonemia radiata* (Rupr.) McClure & L.B.Sm. as seen in the MSC tree]); and Clade III, encompassing all representatives of *Actinocladum*, *Alvimia*, *Athroostachys*, *Atractantha*, *Filgueirasia*, and *Merostachys* (77BS/0.79PP); Clade IV, composed of *Cambajuva ulei* and *Glaziophyton mirabile* Franch., was recovered in the ML analysis with *Aulonemia radiata* nested within (93BS), but this clade was not recovered in the MSC tree. In both the ML and MSC trees, a new clade ("Clade V") containing three species of *Aulonemia* (*A. effusa*, *A. setigera* (Hack.) McClure, *A. setosa* (Londoño & L.G.Clark) P.L.Viana & Filg.) and *Myriocladus virgatus* Swallen was recovered (89BS/0.74PP). Relationships within Clade V have *Aulonemia setosa* and *A. setigera* forming a sister relationship (96BS/0.84PP), which was sister to *M. virgatus* (55BS/0.77PP), and that whole clade was resolved as sister to *A. effusa*.

Among the Arthrostylidiinae genera with multiple representative species, nine were supported as monophyletic: *Alvimia* (96BS/0.93PP), *Athroostachys* (100BS/0.88PP), *Atractantha* (99BS/1.0PP), *Aulonemiella* (93BS/0.87PP), *Didymogonyx* (76BS/0.95PP), *Elytrostachys* (84BS/0.67PP), *Filgueirasia* (99BS/0.98PP), and *Merostachys* (99BS/0.99PP). *Guadua* (Guaduinae), with two representatives, was also supported as monophyletic (100BS/0.75PP). Four genera, *Arthrostylidium*,

Aulonemia, *Colanthesia*, and *Rhipidocladum*, were not recovered as monophyletic.

Though *Aulonemia* and *Colanthesia* were each polyphyletic, all sampled taxa for each genus were resolved within the Arthrostylidiinae. The majority of the *Aulonemia* species and all the *Colanthesia* species were placed in Clade II. The clade containing the core *Aulonemia* species and all the *Colanthesia* species excluding *C. secundiflora*, is hereafter referred to as the *Aulonemia* + *Colanthesia* clade (81BS/1.0PP). The four species of *Aulonemia* not in the *Aulonemia* + *Colanthesia* clade grouped with representatives of Clades IV and V. Both analyses recover a non-monophyletic *Colanthesia*, but relationships within the *Aulonemia* + *Colanthesia* clade are poorly supported. *Colanthesia secundiflora* has moderate support for being either outside or sister to the *Aulonemia* + *Colanthesia* clade. The two species of *Aulonemiella* alternatively form a sister relationship with a clade containing *C. secundiflora* and the *Aulonemia* + *Colanthesia* clade in the ML tree (75BS), or form a clade with *C. secundiflora* (0.43PP), which is sister to the *Aulonemia* + *Colanthesia* clade (0.55PP) in the MSC analysis.

The relationships among the major clades were poorly supported in both trees. Examination of gene tree discordance diagrams (Figs. 2, S2) indicates considerable conflict in the backbone of the Arthrostylidiinae but also robust agreement for the existence of Clade V and the branching arrangements within that clade. Gene tree discord with the ML tree (Fig. 2)

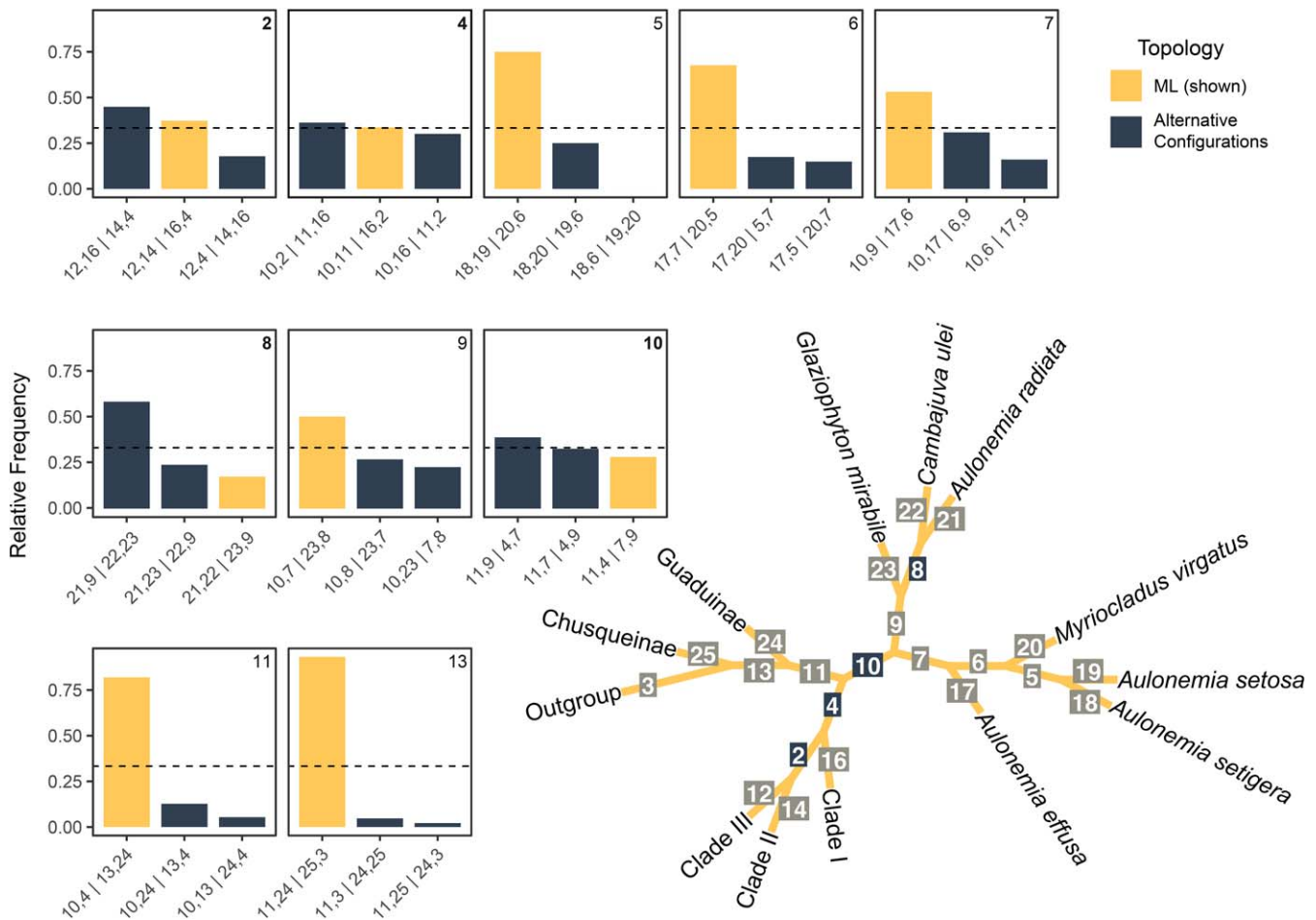


FIG. 2. Analysis of alternative maximum likelihood inferred phylogenetic topologies. Barplots represent frequency for each alternative branching configuration. Yellow bars are those recovered in Fig. 1 (this paper). Numbers on the tree correspond to the barplot for that branch. Bold and shaded numbers (2, 4, 8, 10) indicate branches with conflicting phylogenetic signal.

appears at the branch joining Clades I, II, and III to the rest of the tree (quartet 2), the branch joining those three clades with Clades IV + V and the rest of the tree (quartet 4), the Arthrostylidiinae backbone branch connecting all the major clades to Guaduinae and the outgroups (quartet 10), and the branch forming the relationship among *Glaziophyton*, *Cambajuva*, and *Aulonemia radiata* vs. the rest of the tree (quartet 8). On the MSC tree (Fig. S2), the branches joining *Cambajuva* to Clades I and III (quartet 14) and *Aulonemia radiata* to Clade II (quartet 13) are relatively equivocal with respect to the gene trees. Approximately unbiased (AU) topology tests rejected a monophyletic *Aulonemia*, monophyletic *Colanthesia*, or the monophyly of each genus together or apart. Topology tests also reject the MSC species tree topology in favor of the ML tree. Trees inferred with alternative topologies for quartets ML-2, MSC-13, and MSC-14 as described above were also rejected, however alternative topologies for ML-4, ML-10, and ML-8 were not rejected (Table 1).

DISCUSSION

In this study, we present the first comprehensively sampled phylogenetic analysis of *Aulonemia* and *Colanthesia* within the context of the NWBs. Our study expanded the sampling in both *Aulonemia* and *Colanthesia* with the inclusion of over half the currently recognized *Colanthesia* species, doubling that of previous studies (e.g. Tyrrell et al. 2012), and 40% of the *Aulonemia* species (triple that of Tyrrell et al. 2012). Unlike Tyrrell et al. (2012), we found a non-monophyletic *Colanthesia* intermixed with a non-monophyletic *Aulonemia*. The non-monophyly of *Aulonemia* and *Colanthesia* reflects, in part, the significant overlap of morphological features between these genera. In general, the main features used to distinguish them are: 1) presence of a girdle, often with a crest at its junction with the sheath in *Colanthesia* (vs. absence or only slight development of a girdle in *Aulonemia*), 2) relatively longer and narrower spikelets with the rachilla joints visible in *Colanthesia* (vs. shorter and wider spikelets with the florets strongly overlapping in *Aulonemia*), and 3) the presence of only a single divergent dominant branch per node in *Aulonemia* (vs. one divergent, dominant branch producing few to many smaller secondary branchlets per node in *Colanthesia*) (McClure 1973; Judziewicz et al. 1999; Viana 2010; Santos-Gonçalves et al. 2018; Clark et al. 2020). The imprecision in their circumscriptions is revealed by the fact that these characters are not consistently present or obvious in all species. For example, *C. kinoshitae* Santos-Gonç., Filg. & L.G.Clark and *C. secundiflora* have inconspicuous girdles, and *A. lanciflora* McClure & L.B.Sm. and *A. queko*, among others, can have more than one branch arising from the mid-culm nodes (McClure 1973; Judziewicz et al. 1999).

Many of the broad relationships found in other molecular studies are maintained here (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; Jesus-Costa et al. 2018). Our results continued to support the monophyly of and sister relationship between Arthrostylidiinae and Guaduinae, as well as the presence of the major clades within the Arthrostylidiinae. Unlike other studies (Guala 2003; Ruiz-Sanchez et al. 2008, 2011; Tyrrell et al. 2018), which demonstrated that some species belonging to Arthrostylidiinae genera had phylogenetic affinities with the

subtribe Guaduinae or vice versa, all newly sampled species here remained within Arthrostylidiinae.

Our results also parallel those of other studies which found some genera to be polyphyletic. In those works, the molecular discoveries were mirrored in morphological differences among characters that were considered polymorphic for genera, leading to taxonomic novelties (Ruiz-Sanchez et al. 2011; Tyrrell et al. 2012, 2018; Clark et al. 2020), a pattern similar to what we observed and will propose here. Culm leaf blade orientation in *Aulonemia* and *Colanthesia*, for example, must be reinterpreted given our results. Most species of *Aulonemia* and *Colanthesia* possess reflexed blades, except for *A. setigera*, *A. setosa*, and *C. secundiflora*, which express erect blades (*A. ulei* also had erect blades and previous work [Viana et al. 2013] demonstrated it should be transferred to a new genus). Our discovery of the distant relationship of *A. setigera* and *A. setosa* from the *Aulonemia* + *Colanthesia* clade and the potential sister relationship of *C. secundiflora* to this clade suggests reflexed blades may be a consistent character for the members of *Aulonemia* + *Colanthesia* clade and is a more important distinguishing character for higher-level relationships within Arthrostylidiinae than previously thought (however, see discussion under '*Aulonemia radiata*' below).

Gene Tree Discordance—The discordance in gene trees indicates possible incomplete lineage sorting as has been hypothesized for other bamboo groups (Guo et al. 2019), but it might also suggest hybridization events, paralogous genes, or some combination of these (Guo et al. 2021). The relationships among Clades I, II, III (BS 52%), IV, and V (BS 70%) remain equivocal, as does the resolution within Clade IV (*Glaziophyton* sister to *Cambajuva* + *A. radiata* vs. *A. radiata* sister to *Glaziophyton* + *Cambajuva*) when that clade is recovered. Our analyses demonstrate that these topologies are unresolvable with the available data and the addition of a wider suite of genomic markers will be needed to sort out these relationships. The results do, however, provide strong evidence for the separation of *A. effusa*, *A. radiata*, *A. setigera*, and *A. setosa* from *Aulonemia*.

Aulonemia radiata—From a morphological point of view, the phylogenetic positioning of *Aulonemia radiata* within Clade IV in the ML analysis was presupposed by the shared presence of tessellate leaf blades in *Aulonemia radiata* and the other two species of the clade (Table 2). Unlike *Glaziophyton mirabile* and *Cambajuva ulei*, which have erect, self-sustaining culms and erect leaf blades, *A. radiata* has clambering or semi-erect culms and reflexed to spreading leaf blades. These features also correlate with differences in habitat: *G. mirabile* and *C. ulei* are typically found in open montane environments (campos de altitude; Safford 1999) whereas *A. radiata* grows in montane cloud forests. All three species are, however, typically found in higher elevation sites of the Atlantic Rainforest domain. *Cambajuva ulei* is endemic to the Serra Geral of Southern Brazil (Viana et al. 2013), *G. mirabile* is endemic to a few rocky outcrops in the summits of the Serra dos Órgãos, Rio de Janeiro state (Fernandez et al. 2012), and *A. radiata* has a wider distribution in montane forests from southern to southeastern Brazil (Viana 2010). The MSC results supporting a sister relationship between *A. radiata* and Clade II and not resolving a Clade IV opens the possibility for an expanded circumscription of *Aulonemia*. To maintain *A. radiata* within *Aulonemia*, however, would require subsuming the well supported, morphologically and ecologically divergent genus *Aulonemiella*, along with all of *Colanthesia* into *Aulonemia*.

TABLE 2. Comparative morphology of *Cambajuva*, *Glaziophyton*, and *Quixiume* (Clade IV).

Character	<i>Cambajuva</i>	<i>Glaziophyton</i>	<i>Quixiume</i>
Culm habit	Erect	Erect	Initially erect, becoming clambering
Internode length (relative)	All subequal	Basal internode greatly elongated, apical ones successively much shorter	All subequal
Internode cross-partitioning	Absent	Present	Absent
Leaf differentiation	Dimorphic, culm leaves differentiated	Dimorphic, culm leaves differentiated	Culm leaves weakly differentiated
Foliage leaf sheath fimbriae	Erect, terete, 1–3.5 cm long, free	Erect, terete, less than 0.5 mm long, free	Erect, basally flattened, 3–12 cm long, free to entirely fused
Foliage leaf blade base	Efimbricate	Efimbricate	Efimbricate or fimbriate, if present fimbriae to 5 mm long
Synflorescence structure	Paniculate, first-order branches appressed to the main axis, subtending bracts absent	Open paniculate, subtending bracts present	Paniculate, first-order branches appressed to the main axis, subtending bracts absent
Synflorescence length (cm) × width (cm)	4.1–15 × 0.8–1.8	34–52 × 6–10	14–48 × 8–32
Spikelet length (cm)	1.2–2.2	0.8–1.2	2.5–5.2
Fertile floret number	2–4	(1–) 2 (–3)	4–10
Lemma indument (abaxial)	Puberulous	Glabrous	Sparsely pubescent to puberulous
Lemma apex	Awne	Mucronate	Awne
Habitat	High elevation grasslands	High elevation grasslands	Montane cloud forest, less commonly high elevation grasslands

Given the morphological differences and ML results that do not support a close relationship between *A. radiata* and its *Aulonemia* congeners, we consider the proposal to expand *Aulonemia* as unwarranted.

Myriocladus—Among the novel findings of our study, we provide the first molecular phylogenetic-based hypothesis for the placement of *Myriocladus* within the Arthrotyliidiinae. With this new addition, our results present the first comprehensive genus-level phylogenetic trees of the subtribe. Our finding that *Myriocladus* is resolved on a new branch (Clade V) of Arthrotyliidiinae (vs. being nested within a previously recovered clade) seems to correlate with some of the unusual morphology of this genus (Tables 2, 3). *Myriocladus virgatus* shares some morphological similarities with *Glaziophyton* (an unusually long basal internode followed by several shorter internodes and erect culm leaf blades; McClure 1973; Judziewicz 1998; Judziewicz et al. 1999) and *Aulonemia effusa* (erect, typically unbranched culms, leathery leaves with reduced pseudopetioles, open paniculate synflorescences, and spikelets with awned bracts; Judziewicz 1998; Viana 2010). These three species also all grow in similar open, rocky habitats often at elevations above 1000 m. Though we found *Glaziophyton* and *M. virgatus* to occupy separate clades, the relationship was poorly resolved. Thus, we cannot exclude the possibility that these taxa or clades may prove to be more closely related when additional representatives of the 13 species of *Myriocladus* are added to the analysis.

Aulonemia effusa, **A. setigera**, **A. setosa**—The morphological similarities between *M. virgatus* and *A. effusa* are reinforced by our finding of a close relationship among these species (Table 3). In contrast, *A. setigera* and *A. setosa* share several morphological characteristics, but differ from the other two species of Clade V. Both *A. setigera* and *A. setosa* have differentiated culm leaves (vs. leaves not dimorphic in *A. effusa* and *M. virgatus*), young internodes with dense, velvety 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*, and laterally compressed spikelets in *A. effusa* and elliptical to oval spikelets in *M. virgatus*) (Judziewicz 1998; Viana 2010). *Myriocladus* is restricted to the tepuis of the Guyana Plateau of northern Brazil, Venezuela, and the Guianas (Judziewicz 1998; Viana 2010) and is not sympatric with the other three species, which are endemic to the Atlantic Rainforest region of Brazil. The most widespread of these, *A. setosa*, can be found in the states of Espírito Santo, Rio de Janeiro, São Paulo, and Minas Gerais. The remaining species are more restricted, with *A. effusa* occurring in the campos rupestres of the Espinhaço Range of eastern Brazil (in the states of Minas Gerais and Bahia), and *A. setigera* found in the states of Rio de Janeiro and Bahia.

TAXONOMIC TREATMENT

With respect to the circumscriptions of *Aulonemia* and *Colantheia*, we are not yet recommending taxonomic changes. We recovered the type species of *Aulonemia* (*A. queko*), *Colantheia* (*C. cingulata*), and the synonymized former genus *Matudacalamus* Maekawa (*A. laxa*) all within Clade II, however, the relationships within this clade were largely unresolved, apart from *Colantheia secundiflora*. For the four species of *Aulonemia* unambiguously placed in other major clades of Arthrotyliidiinae, we propose the following taxonomic changes: 1) establish a new genus to accommodate *A. radiata*, 2) establish a new genus to accommodate *A. setigera* and *A. setosa*, and describe a new species within it, and 3) establish a new genus to accommodate *A. effusa*. Although *A. radiata* shares the presence of tessellate leaf blades with the other members of Clade IV (a putative synapomorphy for the group), it does not fit within the circumscriptions of either *Glaziophyton* or *Cambajuva*, thus warranting a new genus. *Aulonemia setigera* and *A. setosa* form a well-supported monophyletic group related to *Myriocladus*, but their morphology differs markedly from *Myriocladus*. Thus, these two species

TABLE 3. Comparative morphology of *Myriocladus*, *Stelanemia* and *Vianaea* (Clade V).

Character	<i>Myriocladus</i>	<i>Stelanemia</i>	<i>Vianaea</i>
Culm habit	Erect	Initially erect to decumbent, becoming clambering to scandent or leaning and climbing	Erect
Culm size (m × cm)	0.3–6(8) × 0.3–2	2–13 × 0.2–2	0.4–2.5 × 0.3–1.2
Internode length (relative)	Basal internode usually greatly elongated, apical ones successively much shorter	All subequal	All subequal
Leaf differentiation	Monomorphic, culm leaves not differentiated	Dimorphic, culm leaves differentiated	Monomorphic to weakly dimorphic, culm leaves at most poorly differentiated
Foliage leaf blade texture	Coriaceous	Chartaceous	Coriaceous
Foliage leaf blade base	Symmetrical to slightly asymmetrical, subcordate, truncate or rounded	Asymmetrical, rounded to attenuate	Symmetrical, subcordate
Synflorescence shape	Ovoid to narrowly pyramidal	Spiciform to oblong	Oblong to pyramidal
Synflorescence width (cm)	1.5–25	0.3–4.5	15–28
Spikelet length (cm)	0.28–1.3	1.5–4.8	1.6–3.1
Number of glumes	2–3	2–7	2–3
Number of fertile florets	1–12	2–8	4–5
Distribution and Habitat	Pantepui region (Venezuela, Guiana, Brazil), on sandstone tepui summits and slopes in open, swampy or gallery forest vegetation	Atlantic Forest, Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo states, Brazil	Rocky grasslands and outcrops (campo rupestre) of Minas Gerais and Bahia states, Brazil.

also warrant establishment of a new genus. The molecular data clearly indicate that *A. effusa* is more closely related to *Myriocladus virgatus*, *A. setigera*, and *A. setosa* than it is to the type clade of *Aulonemia*. The species is morphologically distinct from *A. setigera* and *A. setosa* but somewhat suggestive of *Myriocladus* in gross morphology, yet distinct in its

synflorescence structure and geographic distribution. The molecular data place this species as sister to a clade containing *M. virgatus*, *A. setigera*, and *A. setosa*. We have elected to establish a monotypic genus for this species. These generic level changes will provide a more natural classification of the subtribe, both morphologically and evolutionarily.

KEY TO THE GENERA OF ARTHROSTYLIDIINAE

1. Culms regularly cross-partitioned like a rush, normally leafless; Serra dos Órgãos, Rio de Janeiro state, Brazil *Glaziophyton*
1. Culms not cross-partitioned, normally leafy; widespread or variously localized across the Neotropical region 2
 2. Mid-culm nodes with branches or secondary buds borne on two sides of a flattened, triangular plate (a fan-shaped or apiculate array) derived from a single bud per node 3
 3. Culm leaves with the blade erect 4
 4. Internodes all more or less equally elongated along the length of the culm; bud triangular in outline *Rhipidocladum*
 4. One elongated internode alternating with one very short internode along the length of the culm; bud cordate in outline *Didymogonys*
 3. Culm leaves with the blade spreading to usually reflexed 5
 5. Foliage leaf blades dimorphic, those of the terminal node much larger than those of the lateral branches; culm and foliage leaf sheaths usually with distinctively ruffled margins at the apex (derived from fused fimbriae) *Actinocladum*
 5. Foliage leaf blades all about the same size; culm and foliage leaf sheaths with chartaceous margins that may or may not bear usually unfused fimbriae at the apex *Merostachys*
 2. Mid-culm nodes with one dominant branch and two or more smaller lateral branches (or buds) or a single branch per node derived from a single bud per node or bearing 1–8 buds or branches in a row 6
 6. Culms with the basalmost internode greatly elongated with successive internodes of variable lengths (some very short) or elongated internodes alternating with 1–4 very short internodes along the length of the culm 7
 7. Culms with the elongated internodes alternating with 1–4 very short internodes along the length of the culm; Andes *Aulonemia* [in part (*A. herzogiana*, *A. hirtula*, *A. queko*)]
 7. Culms with the basalmost internode greatly elongated with successive internodes of variable lengths (some very short); Guiana Highlands 8
 8. Culms 1.5–3.5 cm in diameter, up to 15 m long, initially erect then leaning on woody vegetation; foliage leaf blades linear-lanceolate, attenuate at the base; Cerro Marahuaka, Venezuela *Arthrostyliidium schomburgkii* (Benn.) Munro
 8. Culms usually less than 1.5 cm in diameter, not more than 6 m tall, erect; foliage leaf blades lanceolate or usually broader, often with rounded or cordate bases; widespread on tepui summits in the Guiana Highlands *Myriocladus* (in part)
 6. Internodes all more or less equally elongated along the length of the culm 9
 9. Culm leaves poorly or not differentiated from the foliage leaves, blades more or less fully developed 10
 10. Culms solid *Aulonemia* [in part (*A. goyazensis*, *A. prolifera*, *A. soderstromii*)]
 10. Culms hollow to pith-filled, but the lumen always distinguishable 11
 11. Foliage leaf sheaths bearing erect, basally flattened fimbriae 3–12 cm long, the blades tessellate, often with fimbriae to 5 mm long on the basal portion *Quixiume*
 11. Foliage leaf sheaths bearing erect to spreading, terete to basally flattened fimbriae 0.15–4 (6.5) cm long, the blades not tessellate, efimbriate 12
 12. Foliage leaf blades chartaceous or membranaceous; culms erect, leaning or scandent *Aulonemia* (most species)
 12. Foliage leaf blades leathery to coriaceous; culms erect, occasionally leaning 13

13. Foliage leaf blades erect to spreading, base subcordate; restricted to rocky outcrops (campos rupestres) in the states of Bahia and Minas Gerais. *Vianaea*
13. Foliage leaf blades reflexed, base rounded; tepuis of the Guiana Shield or cerrado in the state of Goiás and the Federal District, in Brazil. *Aulonemia* [in part (*A. deflexa*, *A. xerophylla*)]
9. Culm leaves usually well differentiated from foliage leaves, or differentiated but with blades reduced to a small mucro or absent 14
14. Culm leaves with blades erect 15
15. Culms 0.45–1.75 m tall, erect; 1–8 subequal buds or branches in a line per mid-culm node; Brazilian cerrado *Filgueirasia*
15. Culms 1–20(–25) m tall, clambering or scandent or hanging or erect; one bud per node developing into (1–)3–5(–many) branches per mid-culm node, subequal or the central branch dominant but not in a linear array; widespread but almost entirely absent from the Brazilian cerrado 16
16. Culms erect; foliage leaf blades erect, tessellate; high elevation grasslands in Santa Catarina and Rio Grande do Sul states, Brazil *Cambajuvá*
16. Culms clambering or scandent to hanging; foliage leaf blades lax or reflexed, not tessellate; widespread and associated with forest vegetation 17
17. Culms 1–2.5 mm in diameter, 1–6 m long; Atlantic forests of São Paulo state, Brazil *Colantheia secundiflora* Santos-Gonç., Filg. & L.G.Clark
17. Culms (1–)3–25(–35) mm in diameter, 3–15(–25) m long; widespread 18
18. Culm leaf sheaths with a small to well-developed corky crest or flange at the juncture with the girdle 19
19. Culm leaves loosely clasping the culm, tapering to a rounded to acute apex, the blade apparently absent, represented by a mucro 1–2 mm long; state of Bahia *Atractantha radiata* McClure
19. Culm leaves appressed to the culm, sheath and blade developed, subequal or one somewhat longer than the other; Brazil (Pará), Suriname, Guiana and Venezuela *Arthrotylidium* [in part (*A. scandens* McClure, *A. cachimboense* Lopes-Neto & P.L.Viana)]
18. Culm leaf sheaths lacking any crest or flange at the juncture with the girdle, but sometimes a ring of hairs present. 20
20. Internodes solid, sometimes developing a narrow lumen in old culms. 21
21. Culm leaf sheaths with a dark, thickened girdle; foliage leaf blades apically acuminate, the sheaths bearing spreading, straight to curly fimbriae 0.1–0.66 cm long *Alvimia* [in part (*A. auriculata* Soderstr. & Londoño, *A. gracilis* Soderstr. & Londoño)]
21. Culm leaf sheaths with a brown to stramineous girdle similar in thickness to the sheaths; foliage leaf blades apically setose, the sheaths bearing erect, slightly wavy fimbriae 0.3–6 cm long *Stelanemia*
20. Internodes hollow, thick-walled 22
22. Nodal line annular, corky; culm leaves papery; bud/branches borne on a weakly developed promontory; endemic to igapó in affluents of the Rio Negro in southwestern Amazonas, Venezuela and northwestern Amazonas, Brazil *Atractantha amazonica* Judz. & L.G.Clark
22. Nodal line flattened in side view, not corky; culm leaves papery to woody; bud/branches borne on a usually well-developed promontory; widespread including the West Indies . 23
23. Culm leaf sheaths with a dark, thickened girdle; endemic to the coastal forests of Bahia, Brazil *Alvimia lancifolia* Soderstr. & Londoño
23. Culm leaf sheaths with the girdle, if developed, the same color and thickness as the sheaths; widespread including the West Indies but not in Bahia, Brazil *Arthrotylidium* [in part (*A. fimbrinodum*, *A. grandifolium*, *A. simpliciusculum*)]
14. Culm leaves with blades reflexed 24
24. Fimbriae on culm and foliage leaf sheaths 1–10 cm long, straight, free, more or less terete, erect on culm leaves, erect to spreading on foliage leaves; Central America and northern Andes but absent from the West Indies *Elytostachys*
24. Fimbriae on culm and foliage leaf sheaths absent or 0.2–12 cm long (if greater than 4 cm long then flattened and often partially or completely connate), wavy or curly at least at the apex, sometimes straight, erect to spreading on both culm and foliage leaves; South America or the West Indies 25
25. Foliage leaf blades abaxially strongly tessellate, the inner ligules 3–12 cm long or confluent with fimbriae. . 26
26. Synflorescences a contracted to open panicle, synflorescence branches appressed to the main axis, 25–45 cm long; southeastern Brazil. *Quixiume*
26. Synflorescences an open panicle, synflorescence branches ascending at a 45 degree angle from the main axis, up to 25 cm long; Andes of Peru *Aulonemia parviflora* (J. Presl) McClure
25. Foliage leaf blades abaxially without evident cross-veins (not tessellate), the inner ligules less than 1 cm long and not confluent with fimbriae. 27
27. Culm leaves lacking any corky flange or crest at the juncture of the sheath and girdle; West Indies or the Andes. 28
28. Culm internodes hollow, terete; West Indies *Arthrotylidium* (in part)
28. Culms internodes solid, often somewhat flattened in the plane lateral to the bud or branch complement; Andes of Colombia and Ecuador *Aulonemiella*
27. Culm leaves with a corky flange or crest present at the juncture of the sheath and girdle; Atlantic forest of southeastern Brazil and Misiones, Argentina. 29
29. Branch complement of usually 3 subequal branches; foliage leaf blades with the midrib excentric. . *Athroostachys*
29. Branch complement of usually 1 dominant plus 2 to many smaller secondary branches; foliage leaf blades with the midrib more or less centric 30
30. Juncture of culm leaf sheath and girdle bearing a prominent flange; culms 0.5–2 cm in diameter, 10–20 m long; restricted to Espírito Santo and Bahia, Brazil *Atractantha* (most species)
30. Juncture of culm leaf sheath and girdle bearing a narrow crest; culms 0.1–0.6 cm in diameter, 1–6 m long; Argentina (Misiones) and Brazil (Rio Grande do Sul to Espírito Santo) *Colantheia* (in part)

Quixiume C.D.Tyrrell, L.G.Clark, P.L.Viana & Santos-Gonç., gen. nov. TYPE: *Aulonemia radiata* (Rupr.) McClure & L.B.Sm. ≡ *Quixiume radiata* (Rupr.) C.D.Tyrrell, L.G.Clark, P.L.Viana & Santos-Gonç.

Diagnosis—*Quixiume* differs from all other genera of the Arthrotylidiinae in having the combination of usually weakly differentiated culm leaves, culms with a distinguishable lumen, the internodes subequally elongated along its length, one dominant branch at mid-culm nodes, bearing foliage leaf sheaths with erect, basally flattened fimbriae and tessellate leaf blades, these often with 1–5 mm long fimbriae near the base, and synflorescences with first-order branches appressed to the main axis.

Rhizomes short necked pachymorph. **Culms** erect, forming dense clumps, or becoming clambering over other vegetation; internodes hollow, thin walled, terete, glabrous, papillose (striate in dried material); nodes with a uniformly horizontal line, supranodal ridge conspicuous. **Culm leaves** weakly undifferentiated or only gradually differentiated from foliage leaves. **Branch complement** consisting of one branch, which occasionally has smaller diameter branches at its basal nodes. **Foliage leaves** with fimbriae flattened at the base, erect, straight to undulate, scaberulous, free to entirely fused, forming a membranaceous structure confluent with the inner ligule; blade spreading to deflexed, glabrous, chartaceous, tessellate. **Synflorescences** a contracted to open panicle, first-order branches appressed to the main axis. **Spikelets** terete to slightly compressed laterally, consisting of 2–3 glumes, 0–1 sterile lemmas, 4–10 fertile florets, and a rudimentary terminal floret. **Glumes** and **Lemmas** awned. **Lodicules** 3, **Anthers** 3.

Etymology—*Quixiume* is a transliteration of an indigenous name associated with woody bamboos in southern and western Brazil. This orthography has been affiliated with *Chusquea capituliflora* (Munro 1868), however, it is a clear cognate of the homologous *Crissiuma* or *Criciuma*, which refers to various species of scrambling bamboo in *Aulonemia* or *Chusquea*. *Criciuma* Soderstr. & Londoño (Soderstrom and Londoño 1987) was synonymized with *Eremocaulon* and is not available.

Notes—Although this new monotypic genus shares tessellate foliage leaf blades with the other two monotypic genera in Clade IV, *Glaziophyton* and *Cambajuvua*, it has a unique combination of other diagnostic features and does not fit well within the circumscription of either previously described genus (Table 2). See the treatment of *Quixiume radiata* below for additional details.

Quixiume radiata (Rupr.) C.D.Tyrrell, L.G.Clark, P.L.Viana & Santos-Gonç., comb. nov. ≡ *Arundinaria radiata* Rupr., Actis Acad. Caes. Petrop. Ser. VI, Tom. V. 2de part., Bambuseae: 25, t. 15, f. 9. 1839. ≡ *Aulonemia radiata* (Rupr.) McClure & L.B.Sm., Fl. Il. Catarin. 1(Gram-Supl.): 56. 1967. TYPE: BRAZIL. Gram erectum ramosum in sylvis umbrosis, s.d. [Jan 25 sin annum], *L. Riedel s.n.* (holotype: LE [photo!]; isotype: US barcode 00139488 [fragment!]).

Aulonemia glaziovii (Hack.) McClure, Smithsonian Contr. Bot. 9: 56. 1973. ≡ *Arundinaria glaziovii* Hack., Oesterr. Bot. Z. 53(2): 72. 1903. TYPE: BRAZIL, Minas Gerais, haut, del Itacolomy, 28 Jul 1890, A.F.M. *Glaziou 18614* (holotype: W, photo!, isotypes: US-2808856!, US-1163027!, P-524498!, P-625416, photo!, P-625417, photo!, P-625418, photo!).

Aulonemia ramosissima (Hack.) McClure, Smithsonian Contr. Bot. 9: 58. 1973. ≡ *Arundinaria ramosissima* Hack., Oesterr. Bot. Z. 53(2): 74. 1903. ≡ *Arundinaria glaziovii* var. *macroblephara* E.G.Camus, Bambusées 41, Atlas t. 34, f. 8, 1913. ≡ *Arundinaria macroblephara* Glaz. ex Camus, Bambusées: 41. 1913. TYPE: BRAZIL, Rio de Janeiro, Alto-Macahé, 4 Jun. 1892, A.F.M. *Glaziou 20149* (holotype: W No. 1916–0009960, photo!, isotypes: P!, US-1647812!, US-80199!).

Aulonemia fimbriatifolia L.G.Clark, Rev. Bras. Bot. 27(1): 31, f. 1A–B. 2004. TYPE: BRAZIL, São Paulo, Alto da Serra, mata de Estação Biológica, 6 Dec. 1936, F.C. *Hoehne* & A. *Gerht s.n.* (holotype: SP-36504!, isotypes: SPF!, IBGE!, US-1764156!, US-1764157!, US-2926655!).

Culms 1.5–6.5 m long, 0.5–1 cm diameter; internodes 15–35 cm long, all subequally elongated, hollow, thin walled, terete, glabrous, papillose (striate in dried material), castaneous or green to purplish, mottled; nodes with a uniformly horizontal line; buds 6.5–18 mm long, 6–11 mm wide, triangular, oval-lanceolate to widely oval, glabrous, prophylls ciliate. **Foliage leaves** with sheaths slightly keeled, 4.2–16.5 cm long, glabrous or sometimes pubescent toward the apex, glabrous, greenish to pale brown, not mottled or mottled toward the apex, fimbriae 3–12 cm long, pale to purplish, deciduous or persistent; pseudopetioles 2–3 mm long, adaxially hipidulous to pubescent, abaxially glabrous; outer ligules ca. 0.5 mm long, membranous to membranous-ciliate, inner ligules not visible, confluent with the fimbriae; blades lanceolate to linear-lanceolate, 12.5–31 cm long, 1.2–6 cm wide, spreading to deflexed, adaxially glabrous, green, abaxially glabrous, glaucous with a conspicuous marginal green stripe, transverse veins conspicuous, evidently tessellate, base asymmetrical, rounded to attenuate, apex long acuminate, margins antrorsely scabrous, often with fimbriae up to 5 mm long near the base. **Synflorescences** oblong, 14–48 cm long, 8–32 cm wide; peduncles glabrous; pedicels 4–75 mm long, 0.1–0.2 mm diameter, glabrous. **Spikelets** 2.5–5.2 cm long, 0.2–0.6 cm wide, linear. **Glumes**: first glume 1.7–3.2 mm long, 1–3-veined, glabrous to scaberulous, pale, usually acute, seldom obtuse, mucronate to awned, awns 1.5–3 mm long; second glume 3.3–5.3 mm long, 3–5-veined, glabrous to scaberulous, pale, usually acute, awned, awns 1.5–3 mm long; third glume, when present, 5–7.5 mm long, 3–7-veined, glabrous to scaberulous, mottled, awned, awns 2–2.3 mm long; rachilla internode 3.3–5.4 mm long, glabrous. **Lemmas** 6–9.5 mm long, 7–9(–11)-nerved, puberulous, glabrescent, sometimes purplish or plumbeous, acute, awned, awns (1.6–) 2.4–6.3 mm long. **Paleas** 5.6–7.3 mm long, sometimes larger than the lemma, 2-nerved, glabrous, scaberulous on the keels toward the apex, pale, apex acute to navicular. **Lodicules** triangular to ovate-lanceolate, ciliate. **Anthers** 4–5.8 mm long, yellowish. **Ovaries** 0.8–1.1 mm long, linear to ellipsoid, pilose at apex. **Caryopses** unknown. Figures 3, 4.

Distribution and Habitat—Known from the states of Santa Catarina, Paraná, São Paulo, Rio de Janeiro and Minas Gerais (Fig. 5), in high mountain formations of Serra do Mar, Serra da Mantiqueira, and Cadeia do Espinhaço.

This species has been recorded in Dense Ombrophilous Forest, Mixed Ombrophilous Forest, and Campos de Altitude, between 900 and 2000 m elevation. The southernmost populations, in Santa Catarina and Paraná, were collected between 800 and 1000 m elevation, while lower latitude

(more northerly) populations were mostly found above 1500 m.

Etymology—In the original description, the author does not explain the origin of the specific epithet, but it presumably refers to the branching pattern of the synflorescence.

Phenology—The collections examined in this work suggest a reproductive cycle of approximately 12 yr. However, there is an abundance of collections from individuals with sporadic flowering, possibly indicating this species does not always conform to a gregarious semelparous life history.

Informal Conservation Assessment—If an IUCN assessment were performed, we hypothesize that this species would be categorized as Not Threatened, as it occurs across a broad area of southeastern and southern Brazil.

Notes—*Quixiume radiata* shares some characteristics with *Cambajuvu ulei* (tessellate leaf blades, paniculate synflorescences with branches appressed to the main axis and awned spikelets), and *S. setigera* and *S. setosa* in Clade V (synflorescences with branches appressed to the main axis and elongated spikelets) but can be distinguished from all of these based on the suite of characters described above.

The considerable number of synonyms for this species are probably the result of immature type material for many of the names and polymorphic characters. The variable morphology is seemingly correlated with differences in habitat (from open, high altitude grasslands to montane evergreen forests) and age. Some vegetative and floral characters, however, are consistent and informative, especially the glabrous, tessellate leaf blades, erect fimbriae that are basally flattened, the oblong paniculate synflorescence with second-order branches appressed to the main axis, and the spikelets with aristate and pubescent to puberulous lemmas. The fimbriae on the base of the blades found in *Q. radiata*, although unique for this species, are frequently absent.

The type material (*Riedel s.n.*) consists of fragments of flowering branches with immature synflorescences, still partially enclosed in the leaf sheath. The spikelets are highly immature, and that ambiguity may also account for the several synonyms of this species. The characters we consider relevant for determination can be observed in Riedel's collection. The characters used by Hackel (1903) when describing *A. ramosissima* and *A. glaziovii* are polymorphic, yet the type specimens of both species have the diagnostic characters outlined in our refined delineation.

Clark (2004), based on specimens and in situ observations, identified several morphological characteristics absent from any of the type material, namely leaf blades tending to be larger (exceeding 30 cm in length) and with unusual fimbriae at their base. These characteristics led the author to propose *A. fimbriatifolia* for the individuals with them. Fieldwork and additional herbarium specimen analysis also revealed plasticity in the characters Clark (2004) considered diagnostic among *A. radiata*, *A. glaziovii*, *A. ramosissima*, and *A. fimbriatifolia* (leaf blade dimensions, presence of leaf blade fimbriae, number of fertile florets, and presence of indumentum or spots on the lemmas).

Camus's (1913) treatment had previously introduced confusion among these species. Despite considering *A. radiata*, *A. ramosissima*, and *A. glaziovii* as distinct species, Camus proposed a variety for *A. glaziovii*, *A. glaziovii* var. *macroblephara* Camus, based on type material already designated for *A. ramosissima* (he additionally mis-referenced this taxon, in the same treatment, as simply *A. macroblephara*).

Additional Specimens Examined—Brazil. —MINAS GERAIS: Aiuruoca, Parque Estadual do Papagaio, 22°04' S 44°40' W [-22.066667°, -44.666667°] 1900 m, 12 Mar 2008, veg, *Viana, P.L. 3282 et al.* (BHCB); Alagoa, Parque Estadual do Papagaio, Ao longo do Rio do Charco, 22°07' 53" S 44°43' 13" W [-22.131389°, -44.720278°] 1634 m, 13 May 2008, veg, *Viana, P.L. 3524 et al.* (BHCB, UWSP); 22°12' 53" S 44°44' 14" W [-22.214722°, -44.737222°] 1697 m, 10 Nov 2007, veg, *Viana, P.L. 3282 et al.* (BHCB); Alto Caparaó, Parque Nacional do Caparaó, 20°25' S 41°49' 50" W [-20.416667°, -41.830556°] 22 Dec 2006, veg, *Viana, P.L. 2546 et al.* (BHCB, UWSP); Serra do Caparaó, 1700 m, 9 Feb 1890, fl, *Schwacke, J. 6784 (R)*; 8 Feb 1890, fl, *Schwacke, J. s.n.* (R 16035, US); Carrancas, Serra do Perdizes, 21°35' 12" S 44°35' 49" W [-21.586667°, -44.596944°] 1560 m, 2 Dec 2007, veg, *Viana, P.L. 3320 et al.* (BHCB, UWSP); Catas Altas, RPPN Caraça, Pico Inficionado, 20°06' 51" S 43°27' 06" W [-20.114167°, -43.451667°] 1950 m, 2 Aug 2008, veg, *Viana, P.L. 3750 & Oliveira, C.T.* (BHCB); 20°06' 51" S 43°27' 06" W [-20.114167°, -43.451667°] 1950 m, 2 Aug 2008, veg, *Viana, P.L. 3750 & Oliveira, C.T.* (BHCB); 20°08' S 43°26' W [-20.133333°, -43.433333°] 2010 m, 23 Apr 2005, veg, *Viana, P.L. 2185 et al.* (BHCB); Felício dos Santos, APA Felício, 18°13' S 43°15' W [-18.216667°, -43.25°] 1300 m, 10 Jun 2006, veg, *Viana, P.L. 2500 et al.* (BHCB, K, NY, RB); Itamonte, Parque Estadual da Serra do Papagaio, Trilha para a cachoeira do Charco, 19 Aug 2009, veg, *Giacomin, L.L. 1010 et al.* (BHCB); Lima Duarte, Parque Estadual do Ibitipoca, 21°42' S 43°52' W [-21.7°, -43.866667°] 1200 m, 2 Feb 1991, veg, *Clark, L.G. 778 & Morel, M.* (BHCB, ISC, MO, RB, SP, US); 29 Jun 2006, veg, *Ferreira, F.M. 1050 et al.* (BHCB, CEPEC, RB, SPF); Ouro Preto, Parque Estadual do Itacolomi, Pico do Itacolomi, 6 Jun 2009, veg, *Mota, N.F.O. 1476 (BHCB)*; Rio Preto, Serra Negra, 21°52' 31" S 43°53' 29" W [-21.875278°, -43.891389°] 1341 m, 11 Apr 2007, veg, *Viana, P.L. 2842 et al.* (BHCB); São Gonçalo do Rio Preto, Parque Estadual do Rio Preto, 18°12' S 43°19' W [-18.2°, -43.316667°] 28 Mar 2008, veg, *Viana, P.L. 3488 et al.* (BHCB, UWSP); 450 m, 15 Aug 2004, veg, *Viana, P.L. 850 & Mota, N.F.O.* (BHCB); —PARANÁ: Campina Grande do Sul, Pico do Paraná, 1600 m, 24 Jul 1988, fl, *Bornschein, M.R. 50 (MBM)*; Campina Grande do Sul, Pico do Paraná, Serra Ibitiraquire, 25°18' S 49°03' W [-25.3°, -49.05°] 1500 m, 30 Nov 1996, fl, *Cordeiro, J. 1379 & Ribas, O.S. (MBM, SPF)*; 1000 m, 14 Jul 1996, fl, *Ribas, O.S. 1448 & Schwerdt, F. (MBM, SPF)*; 1650 m, 8 Sep 2003, fl, *Scheer, M. 456 & Mocoehinski, A.Y. (MBM, UPCB)*; 1500 m, 5 Oct 1997, fl, *Silva, J.M. 2045 et al. (MBM)*; Guaratuba, Serra do Araçatuba, 1437 m, 23 Feb 2002, fl, *Ribas, O.S. 4403 et al. (ISC, MBM)*; Quatro Barras, Morro Sete, 24 Sep 1977, fl, *Cervi, A.C. 6350 (MBM, UPCB)*; 25°20' S 48°52' W [-25.333333°, -48.866667°] 850 m, 9 Mar 1994, veg, *Clark, L.G. 1195 et al. (MBM, ISC, MO, SP, US)*; 25°21' S 48°53' W [-25.35°, -48.883333°] 1200 m, 11 Mar 1992, veg, *Cordeiro, J. 815 & Barbosa, E. (BHCB, CESJ, ESA, HUEFS, INPA, MBM, RB, SP, SPF)*; Serra da Graciosa, 25°15' S 48°50' W [-25.25°, -48.833333°] 1150 m, 18 Mar 1991, veg, *Clark, L.G. 936 et al. (ISC, MBM, MO, US)*; 25°19' 12" S 48°54' 45" W [-25.32°, -48.9125°] 860 m, 24 Feb 2008, veg, *Viana, P.L. 3473 et al. (BHCB, UWSP)*; —RIO DE JANEIRO: Macae, Pico do Frade de Macae, 7 Feb 1985, fl, *Martinelli, G. 10646 et al. (F, RB, US)*; Parque Nacional do Itatiaia, 5 Nov 1977, veg, *Toledo, J.C. s.n. (HRCB1034)*; —SANTA CATARINA: Campo Alegre, Serra do Iqueringim, 26°03' S 49°03' W [-26.05°, -49.05°] 870 m, 16 Mar 1991, veg, *Clark, L.G. 926 & Oliveira, W. (ISC, MBM, MO, US)*; 16 Mar 1991, fl, *Clark, L.G. 927 & Oliveira, W. (ISC, MBM, NY, RB, SP, US)*; Garuva, Monte Crista, 26°02' 18" S 48°53' 22" W [-26.038333°, -48.889444°] 900 m, 2 Sep 1960, fl, *Reitz, R. 9821 & Klein, R.M. (HBR, MBM, US)*; Rancho Queimado, 11 Aug 1960, fl, *Reitz, R. 9706 & Klein, R.M. (HBR, MBM, NY, RB, US)*; São Francisco do Sul, Morro do Campo Alegre, 3 Sep 1960, fl, *Reitz, R. 9739 & Klein, R.M. (US)*; —SÃO PAULO: Barreiro, Serra da Bocaina, 1600 m, s.d., veg, *Segadas-Vianna, F. 2965 (R)*; Biritiba Mirim, Estação Ecológica Boracéia, 23°36' S 45°58' W [-23.6°, -45.966667°] 770 m, 24 Feb 1991, veg, *Clark, L.G. 824 & Morel, M. (ISC, MBM, MO, RB, US)*; 24 Oct 2007, veg, *Viana, P.L. 3170 et al. (BHCB, UWSP)*; 23°39' 54" S 45°54' 24" W [-23.665°, -45.906667°] 950 m, 24 Oct 2007, veg, *Viana, P.L. 3172 et al. (BHCB, UWSP)*; 23°39' 54" S 45°54' 24" W [-23.665°, -45.906667°] 950 m, 24 Oct 2007, veg, *Viana, P.L. 3174 et al. (BHCB, UWSP)*; Paranaipacaba, Estação Biológica, 29 Jun 1948, fl, *Kuhlmann, M. 3137 (US)*; 18 Mar 1948, fl, *Kuhlmann, M. 3138 (MO, US)*; 29 May 1969, fl, *Mattos, J. 15444 (US)*; Paranaipacaba, Estação Biológica, Alto da Serra, Estação Biológica, 29 Jun 1948, fl, *Joly, A.B. s.n. (SPF-84535)*; São José do Barreiro, Serra da Bocaina, Morro da Boa Vista, 22°43' 51" S 44°38' 19" W [-22.730833°, -44.638611°] 1536 m, 24 Mar 2009, veg, *Shirasuna, R.T. 2249 (BHCB, SP, UWSP)*; São José do Barreiro, Serra da Bocaina, Morro da Boa Vista, arredores do Parque Nacional da Serra da Bocaina, 22°42' 21" S 44°38' 16" W [-22.705833°, -44.637778°] 15 Oct 2007, veg, *Versieux, L.M. 448 & Calvente, A.M. (BHCB, SP)*; Serra da Bocaina, 22°45' S 44°47' W [-22.75°, -44.783333°] 1440 m, 4 Mar 1992, veg, *Clark, L.G. 1060 & Windisch, P. (MBM, MO, US, ISC)*;

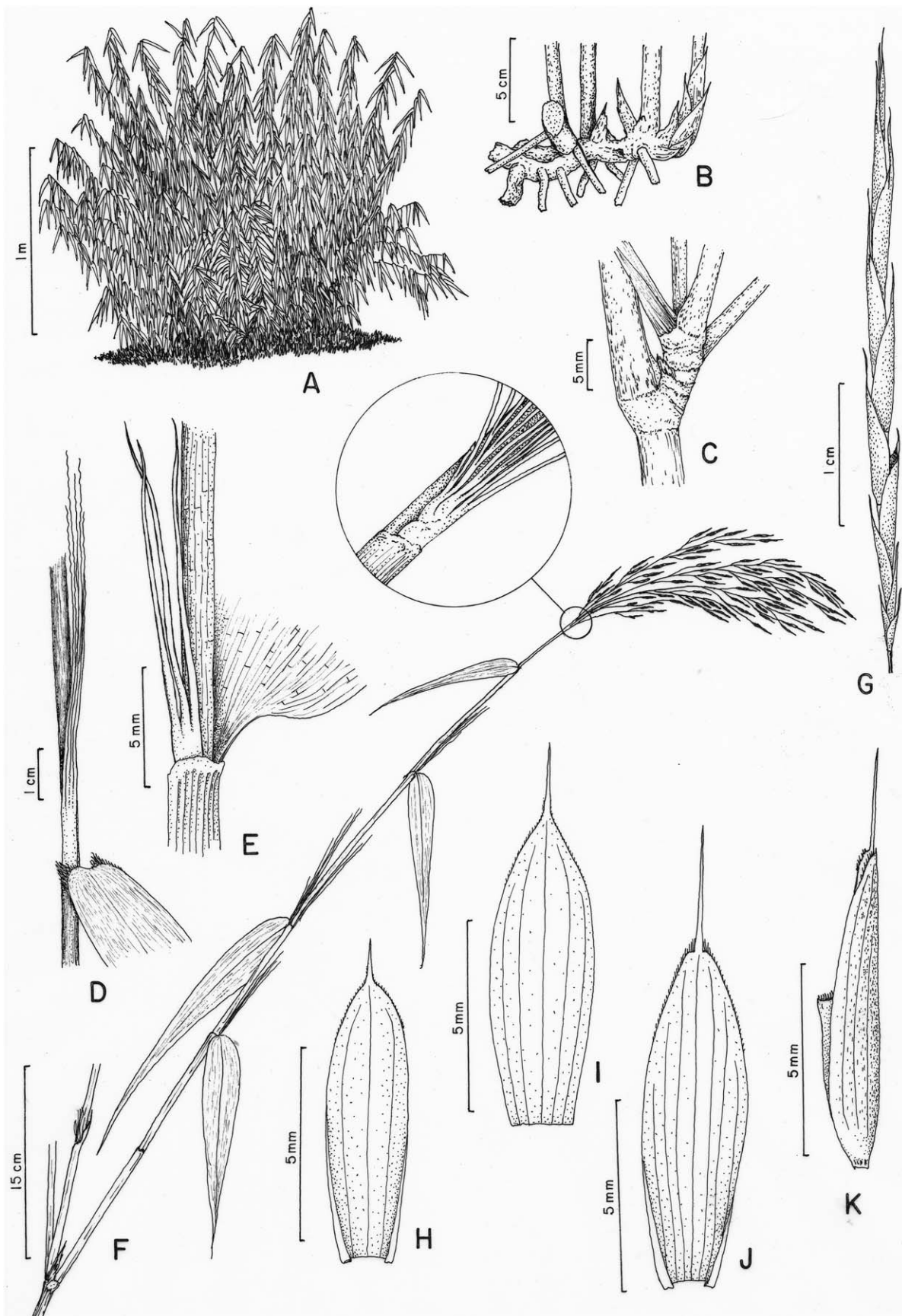


FIG. 3. *Quixiume radiata*. A. Habit in high altitude open areas. B. Rhizomes. C. Mid-culm branch complement. D. Detail of fimbriae at the base of a foliage leaf blade. E. Foliage leaf, junction of the sheath and blade showing fimbriae. F. Flowering branch, with detail of the synflorescence branching pattern. G. Spikelet. H-J. Adaxial views of: H. Glume I; I. Glume II; J. Glume III. K. Fertile floret with rachilla internode, in lateral view. (A-C Viana 2547; D-K. Garcia 2015).



FIG. 4. *Quixiume radiata*. A. Culms and rhizomes. B. Mid-culm region. C. Habit. D. Culm leaves. E. Mid-culm branch complement. F. Vegetative branch. G. Branch complements near culm apex. H. Foliage leaf, junction of the sheath and blade showing fimbriae. I. Close-up of fimbriae at the base of a foliage leaf blade with back light highlighting the leaf blade tessellate venation. (A–C. *Viana* 3172; D. *Viana* 3320; E–F. *Viana* 2842; G–I. *Viana* 3282).

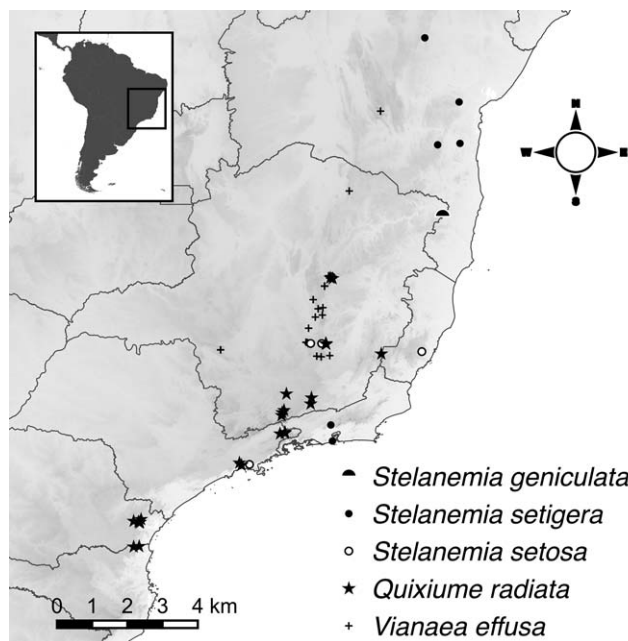


FIG. 5. Distribution of new bamboo taxa in Brazil. Half circles = *Stelanemia geniculata*; Filled circles = *Stelanemia setigera*; open circles = *Stelanemia setosa*; stars = *Quixiume radiata*; plus symbols = *Vianaea effusa*.

Parque Estadual da Serra do Mar, Núcleo Crucutu, trilha do rio Ingazeiro, 16 Jun 2000, fl, Garcia, R.J.F. 2015 et al. (BHCB, SP.).

Vianaea C.D.Tyrrell, L.G.Clark, Santos-Gonç. & Afonso, gen. nov. TYPE: *Aulonemia effusa* (Hack.) McClure ≡ *Vianaea effusa* (Hack.) C.D.Tyrrell, L.G.Clark, Santos-Gonç. & Afonso.

Diagnosis—*Vianaea* differs from all other genera of the Arthrostylidiinae in having the combination of poorly or undifferentiated culm leaves, erect culms with a distinguishable lumen (hollow or medullous), the internodes subequally elongated along its length, one dominant branch at mid-culm nodes, bearing foliage leaf sheaths with fimbriae and erect to spreading, coriaceous, basally subcordate leaf blades, synflorescences an open panicle, with first-order branches divergent to the main axis, and awned spikelets.

Rhizomes short necked pachymorph. **Culms** erect, forming dense clumps; internodes medullous or hollow, thick-walled, terete, glabrous, young internodes usually covered with whitish wax, smooth; nodes with uniformly horizontal line, supranodal ridge inconspicuous. **Culm leaves** undifferentiated from foliage leaves. **Branch complement** consisting of one divergent branch. **Foliage leaves** with fimbriae terete, erect to effuse, straight to slightly wavy, smooth, free or fused at the base forming discrete auricles; blades erect to spreading, glabrous, leathery, not tessellate. **Synflorescences** an open panicle, first-order divergent to the main axis. **Spikelets** slightly compressed laterally, consisting of 2–3 glumes, 1 sterile lemma, 4–5 fertile florets, and a rudimentary terminal floret. **Glumes** mucronate to awned. **Lemmas** awned, rarely mucronate. **Lodicules** 3, **anthers** 3.

Etymology—*Vianaea* honors our colleague and Brazilian botanist Pedro Lage Viana, world authority on Brazilian *Aulonemia*, who lived his early life in Minas Gerais, the state from where the type species is primarily known.

Vianaea effusa (Hack.) C.D.Tyrrell, L.G.Clark, Santos-Gonç. & Afonso, comb. nov. ≡ *Arundinaria effusa* Hack., Oesterr.

Bot. Z. 53(2): 71. 1903. ≡ *Arthrostylidium effusum* (Hack.) McClure, Fieldiana, Bot. 28(1): 31. 1951. ≡ *Aulonemia effusa* (Hack.) McClure, Smithsonian Contr. Bot. 9: 56. 1973. LECTOTYPE (designated here): BRAZIL. Serra de Ouro Branco prope São Julião, 22 Dec 1885, A.F.M. Glaziou 15623 (lectotype: P No. P02642603!; isolectotypes: C, K, US No. 1021437 [fragment!], W No. 1916–0010103!).

Culms 0.4–2.5 m long, 0.3–1.2 cm diameter; internodes 0.6–22.6 cm long, all subequally elongated, medullous or fistulous, thick-walled, terete, glabrous, young usually covered with whitish wax, smooth, uniformly light brown; nodes with a uniformly horizontal line; buds 0.5–2.6 mm long, 0.5–0.8 mm wide, obovate to elliptical, glabrous, prophylls ciliate at apex. **Foliage leaves** with sheaths rounded, 4.7–8.3 cm long, glabrous to puberulent between the veins, generally with evident deposition of wax in young leaves, ciliate in the apical portion, light brown; fimbriae 0.2–1.4 cm long, stramineous, deciduous; pseudopetioles 1.0–2.3 mm long, adaxially glabrous, densely waxy, abaxially glabrous; outer ligules 0.1–0.2 mm long, membranous to membranous-ciliate, inner ligules 0.8–2.7 mm, membranous-ciliate; blades oval-lanceolate, 3.5–19.5 cm long, 1.0–3.9 cm wide, adaxially glabrous, glaucous, abaxially glabrous, glaucous with an inconspicuous marginal green stripe, transverse veins inconspicuous, base symmetrical to slightly asymmetrical, subcordate, apex acuminate, pungent, margins antorsely and retrorsely scabrous. **Synflorescences** oblong to pyramidal, 23–42 cm long, 15–28 cm wide; peduncles glabrous; pedicels 4.5–32.5 mm long, 0.1–0.2 mm wide, scaberulous. **Spikelets** 1.6–3.1 cm long, 0.1–0.4 cm wide, linear to linear-lanceolate. **Glumes**: first glume 1.4–3.4 mm long, 1(–3)-veined, glabrous, ciliate towards apex or not, stramineous, acute to acuminate, mucronate to awned, awn 0.2–2.0 mm long; second glume 3.7–6.0 mm long, 3–6-veined, glabrous, stramineous, acute, ciliate or not, mucronate to awned, awn 0.3–0.9 mm long; third glume, when present, 4.7–7.1 mm long, 5–9-veined, glabrous, rough, stramineous, vinaceous to atro-purplish, awned, awn 0.4–0.9 mm long, rachilla internode 2.5–5 mm long, glabrous. **Lemmas** 6.1–10.7 mm long, 7–11-nerved, glabrous, rough, vinaceous to dark purplish sometimes with discolored spots, acute, awned, rarely mucronate, awn 0.5–3.7 mm long. **Paleas** 6.0–8.2 mm long, 4–6-nerved, glabrous, rough, scaberulous on keels near apex, not mottled, generally vinaceous, apex acute, sometimes emarginate. **Lodicules** obovate to elliptical, ciliate. **Anthers** 4.5–6 mm long, yellow. **Ovaries** 1.0–1.5 mm long, ellipsoid, glabrous to pilose at apex. **Caryopses** unknown. Figures 6, 7.

Distribution and Habitat—Known from the states of Minas Gerais and Bahia (Fig. 5) from 900–1550 m elevation. *Vianaea effusa* is a common component of the rocky field landscapes of the Espinhaço Range in Minas Gerais but is more rare in the Bahian portion of this range. It also occurs on the quartzite formations of the Quadrilátero Ferrífero, in Minas Gerais, extending through the mountains of the São João Del Rey and Serra da Canastra regions.

Etymology—The epithet (from Latin, effusus, -a, -um) refers to the effuse, lax aspect of the synflorescences.

Phenology—Examination of flowering herbarium specimens reveals two potential interpretations of the reproductive cycle. There are documented occurrences of gregarious flowering between 1968 and 1970, in Serra do Cipó (Irwin 20303, 20393, Eiten 11043, Duarte 12598), between 1982 and 1984, in the Diamantina Plateau (Burman 698, Filgueiras 1118,

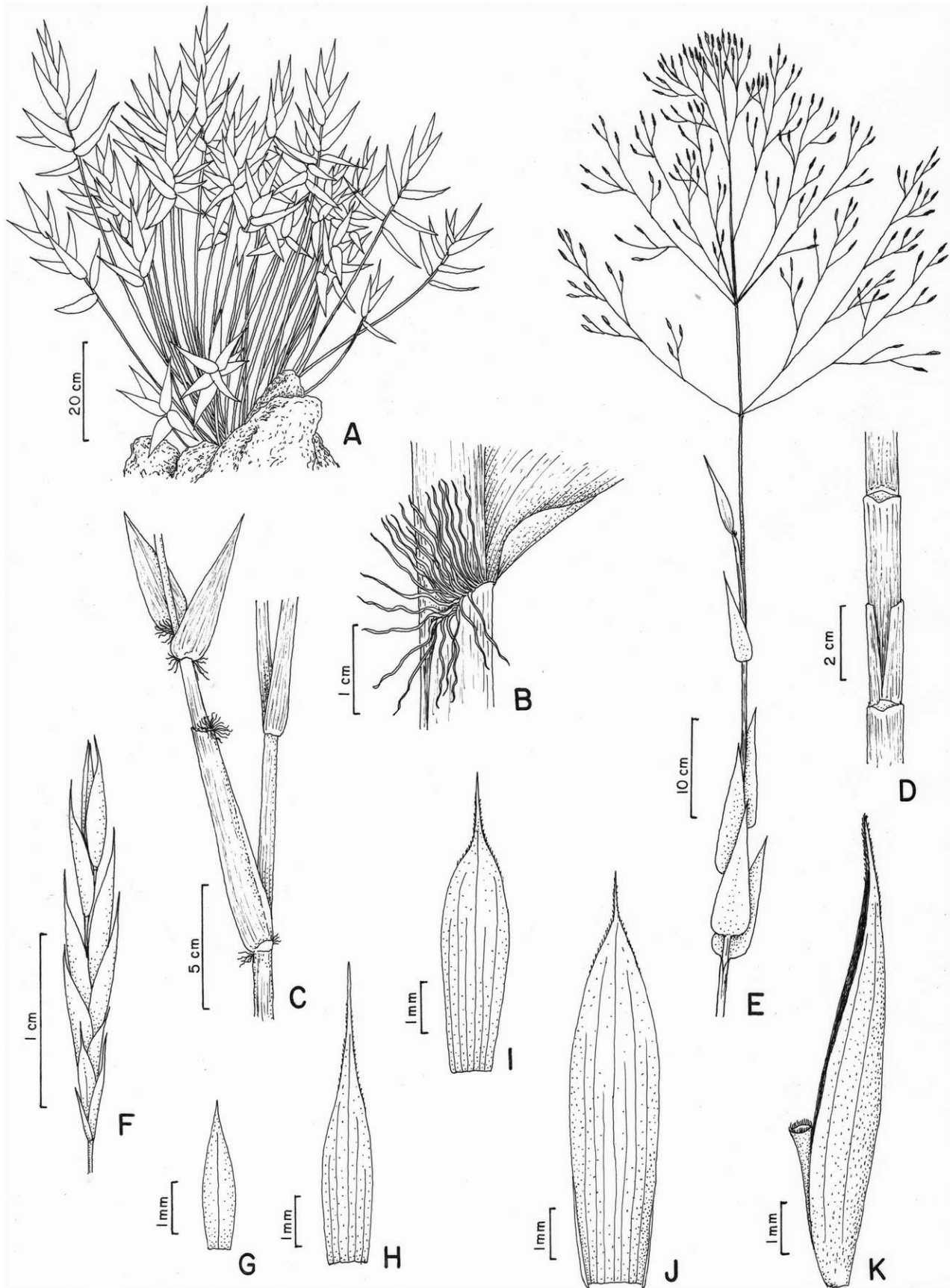


FIG. 6. *Vianaea effusa*. A. Habit. B. Foliage leaf, junction of the sheath and blade showing fimbriae. C. Branch complement at mid-culm node. D. Mid-culm nodes with persistent leaf sheaths. E. Flowering branch. F. Spikelet. G-J. Adaxial views of: G. Glume I; H. Glume II; I. Glume III. J. Sterile lemma. K. Fertile floret with rachilla internode, in lateral view. (A-C. *Viana* 2787; D-K. *Viana* 3764).



FIG. 7. *Vianaena effusa*. A–B. Habit. C. Culm, basal portion. D. Culm, middle portion. E. Culm apex with detail of foliage leaf fimbriae. F. Culm apex with detail of foliage leaf blades. G. Flowering individual. H–I. Spikelets. (A–F. *Viana* 2787; G–I. *Viana* 1565).

Longhi- Wagner CFSC-2955, Menezes CFSC-3297) and between 1991 and 1994, again in the Serra do Cipó. Considering only the collections from Serra do Cipó, which has been exhaustively studied (Madeira et al. 2008), the interval would be 21 to 26 yr. Considering collections from the Diamantina region together with those from Serra do Cipó, however, would reduce the interval to an estimated 13 to 16 yr.

Informal Conservation Assessment—Vulnerable: VU A1cd+B1ab(iii)

Despite its wide distribution in Minas Gerais and Bahia, including within protected areas, we hypothesize that *V. effusa* would be categorized as Vulnerable according to IUCN criteria, if a formal assessment were performed. In Minas Gerais, the synflorescences are avidly collected for sale as decorative jewelry and dried floral arrangements (along with other grasses, Eriocaulaceae, Cyperaceae and Xyridaceae). Considering the long reproductive cycles of woody bamboos, this harvest may be unsustainable, impairing recruitment and reducing genetic diversity of the species (Giulietti et al. 1996).

Notes—Hackel (1903) cited four specimens collected by Glaziou in his description of *Arundinaria effusa* (Glaziou 15623, 16627, 17449, 17915), all of them collected between 1884 and 1888. Among the syntypes, Glaziou 15623 at the National Museum of Natural History, France (P) fits the morphological description in the protologue and has more detailed information about the locality. This was our reason for selecting it as the lectotype. The specimens of Glaziou 17449 (C, P, US, W) have smaller leaf blades (3–8 cm) than mentioned in the protologue (10–15 cm), and Glaziou 17915 (C, K, P, W) and 16627 (C, W, US) have immature panicles, not yet effuse, with their branches ascending and still adpressed to the main axis of the synflorescence. The condition of these collections was not referenced in the protologue.

Inconsistencies concerning the geographical locality indicated in the four syntypes were detected, but easily unraveled. The specific localities on the specimen labels are well known locations in Minas Gerais state, however, the labels indicate the state of Rio de Janeiro. In both the Glaziou 15623 and 17915 collections, the localities are “haut de la d’Ouro Branco” and “Serra de Ouro Branco prope São Julião” respectively. This almost certainly refers to the Ouro Branco mountain, in Ouro Branco municipality, where a profuse population of this species occurs (Longhi-Wagner and Welker 2012). The syntypes Glaziou 16627 and 17449 were collected from “São João Del Rey, Serra do Lenheiro” and “Serra de Lenheiro”, which is a well-known mountain (Lenheiro mountain) in São João Del Rey municipality, where *A. effusa* was recently documented (Marino 220, BHCB). The revision of the Brazilian species of *Aulonemia* (Viana 2010) did not cite *A. effusa* for Rio de Janeiro state.

Vianaea effusa forms beautiful clumps up to two meters tall, with grayish foliage, usually associated with rocky outcrops. It is adapted to open, rocky environments, where fire is a common disturbance. Several specimens examined show charred stems providing evidence that the plant had survived past fires. This is also common in species of *Myriocladus* (Judziewicz 1998).

The close phylogenetic relationship of *V. effusa* with *Myriocladus* is also mirrored in their habitat preference, as *Myriocladus* also occurs on quartzite formations of the Guiana Plateau. The biogeographical connection between the Espinhaço Range and the Guiana Plateau has long been noted in the

literature (Steyermark 1982; Giulietti and Pirani 1988; Berry and Riina 2005) and exemplified by the distributional pattern of other grasses such as *Apochloa* Zuloaga & Morrone (Sede et al. 2008), *Chusquea* (Clark 1989, 1992), and *Dichanthelium* (Hitche. & Chase) Gould (Zuloaga et al. 1993).

Species observed in sympatry with *V. effusa*, and typical of outcrop habitat, include: *Vellozia* Vand. spp. (Velloziaceae), *Apochloa* Zuloaga & Morrone spp., *Paepalanthus* Mart. spp., and others. Among the bamboos, *Chusquea nutans* L.G.Clark occurs in marshes and gallery forests in the Espinhaço Range, and *Actinocladum verticillatum* and *Filgueirasia cannavieira* (Silveira) Guala are typical species of the nearby cerrado regions (Viana 2010).

Additional Specimens Examined—Brazil. —BAHIA: Abaíra, Bicota, alto da serra, no caminho para o Vira Saia, 13°19'42" S 41°51'09" W [-13.328333°, -41.8525°] 12 Dec 2009, veg, Cardoso, D. 2824 et al. (HUEFS); Abaíra, Bicota, alto da serra, no caminho para o Vira Saia, Chapada Diamantina, Garimpo do Bicota, 13°20' S 41°51' W [°, °] 1400–1750 m, 24 Mar 1992, veg, Stannard, B. CFSC-52823 & Silva, T. (F, ISC, NY, RB, SP, SPF, UB); —MINAS GERAIS: Brumadinho, Parque Estadual do Rola Moça, 20°04'36" S 44°01'36" W [-20.076667°, -44.026667°] 1360 m, 25 Jul 2009, fl, Carmo, F.F. 4806 (BHCB); Brumadinho, Parque Estadual do Rola Moça, Serra da Calçada, 20°07' S 43°58' W [-20.116667°, -43.966667°] 1300 m, 29 Jan 1991, veg, Clark, L.G. 770 et al. (BHCB, ISC, MBM, MO, RB, SP, US); 13 Jun 2004, fl, Viana, P.L. 3764 & França, G. (BHCB, UWSP); 13 Jun 2004, fl, Viana, P.L. 3764 & França, G. (BHCB); 20°05' S 43°59' W [-20.083333°, -43.983333°] 29 May 2001, veg, Viana, P.L. 58 (BHCB); Conceição do Mato Dentro, Serra do Cipó, 21 Mar 1978, fl, Burman, A.G. 217 (BHCB, SP); 3 Nov 1934, veg, Sampaio, A. 6903 (R); Conceição do Mato Dentro, Serra do Cipó, Parque Natural Municipal Ribeirão do Campo, 19°04' S 43°32' W [-19.066667°, -43.533333°] 1200 m, 20 Dec 2002, veg, Viana, P.L. 383 et al. (BHCB); Congonhas do Norte, Serra da Mangabeira, 18°50' S 43°49' W [-18.833333°, -43.816667°] 26 Apr 1982, fl, Furlan, A. CFSC-8450 et al. (BHCB, SPF, UB); Conselheiro Mata, Jun 1934, fl, Brade, A.C. 13401 (RB); Couto de Magalhães de Minas, Chapada do Couto, 17 Jul 1984, fl, Furlan, A. CFSC-4686 et al. (ISC, SPF); Datas, 1400 m, 5 Apr 1983, fl, Martinelli, G. 9152 & Lauenberger, B.E. (BHCB, NY, RB); Diamantina, 15 Apr 1973, veg, Anderson, W.R. 8977 (MO, NY, UB); Diamantina, Serra de Santo Antônio, 10 Feb 1982, fl, Burman, A.G. 698 & Sendulsky, T. (BHCB, SP); 29 Mar 1983, fl, Burman, A.G. 862 (BHCB, SP); 20 Jan 1984, fl, Filgueiras, T.S. 1116 & Burman, A.G. (IBGE, SP); 20 Jan 1984, Filgueiras, T.S. 1118 & Burman, A.G. (IBGE, SP); Diamantina, 1 Feb 1947, veg, Eglar, W. B-4701130320 (RB); Diamantina, 22 Feb 1983, fl, Simonis, E. CFSC-4002 (SPF); 8 Apr 1982, fl, Longhi-Wagner, H.M. CFSC- 2955 et al. (BHCB, SPF); Diamantina, estrada para Milho Verde, 1283 m, 10 Apr 1982, fl, Menezes, N.L. CFSC-3297 et al. (BHCB, SPF); 49 miles from Diamantina, 1158 m [3800 feet], 22 Dec 1959, fl, Maguire, B. 44755 et al. (US); Itabirito, Serra de Itabirito, 13 Nov 2006, veg, Messias, M.C.T.B. 1187 (OUPR); Jaboticatubas, Serra do Cipó, 19°17' S 43°33' W [-19.283333°, -43.55°] 1250 m, 11 Mar 1969, fl, Eiten, G. 11043 & Eiten, L.T. (MO, SP, UB, US); 13 Feb 1973, fl, Hatschbach, G. 31530 & Ahumada, Z. (MBM); Jaboticatubas, Serra do Cipó, Usina Pacifico Mascarenhas, 19 Apr 1939, fl, Mello Barreto 8696 (BHCB, US); Jaboticatubas, Serra do Cipó, Usina Pacifico Mascarenhas, Chapeu do Sol, 1000 m, 29 Apr 1952, Smith, L.B. 7030 et al. (US); 19°40' S 43°57' W [-19.666667°, -43.95°] 1000 m, 29 Apr 1952, fl, Smith, L.B. 7030 (R, ISC); Lagoa Santa, Gruta da Lapinh, s.d., veg, Carmello, S.M. 66–910 (BOTU); Nova Lima, Morro do Chapéu, 24 Feb 1983, veg, Andrade, P.M. 1318 & Grandi, T.S.M. (BHCB, CEN); 24 Feb 1983, Grandi, T.S.M. 1318 (BHCB); Ouro Branco, haut de las d’Ouro Branco, Jun 1884, fl, Glaziou, A.F.M. 15623 (C, K, P, US); Serra de Ouro Branco, 20°28'59" S 43°42'45" W [-20.483056°, -43.7125°] 1550 m, 23 Dec 2007, veg, Viana, P.L. 2787 et al. (BHCB); Serra de Ouro Branco, caminho para a Serra de Ouro Branco, Dec 1891, fl, Damazio, L. s.n. (RB); Rio Pardo de Minas, Serra Nova, 15°39'38" S 42°45'54" W [-15.660556°, -42.765°] 1000 m, 13 Mar 2007, veg, Salino, A. 11726 et al. (BHCB); Santana do Riacho, Serra do Cipó, 23 Feb 1970, fl, Duarte, A.P. 12598 (BHCB, CESJ, HUEFS, MBM); 5 Mar 1958, veg, Heringer, E.P. 22109 & Castellanos (R); 1250 m, 16 Feb 1968, fl, Irwin, H.S. 20303 & Maxwell, H.S. (NY, SP, UB, US); 1300 m, 17 Feb 1968, fl, Irwin, H.S. 20393 & Maxwell, H.S. (F, MO, NY, RB, SP, UB); 13 Jan 1951, veg, Pires, J.M. 2729 & Black, G.A. (US); 29 Jul 1977, fl, Sendulsky, T. s.n. (BHCB, SP); Santana do Riacho, Serra do Cipó, Chapeu do Sol, 900 m, 28 Mar 1925, veg, Chase, A. 9151 (US); 1000–1100 m, 28 Mar 1925, fl, Chase, A. 9214 (US); Santana do Riacho, Serra do Cipó, Chapeu do Sol, Estrada da Conceição do Cerro, 28 Jun 1972, veg, Occhioni, P. 5197 (HUEFS); 20°30' S 43°35' W [-20.5°, -43.583333°] 15 May 1990, veg, Arbo,

M.M. 4183 et al. (MBM, RB, SP, SPF, US); 28 Jul 1991, fl, *Giulietti, A.M. CFSC-12629 et al.* (SPF); Santana do Riacho, Serra do Cipó, Chapeu do Sol, Estrada da Conceição do Cerro, MG010, prox. Km101, 24 Sep 2002, veg, *Kinoshita, L.S. C-064 et al.* (UEC); 26 Apr 1978, fl, *Martinelli, G. 4323* (RB, US); 27 Mar 1991, fl, *Pirani, J.R. CFSC-12194 et al.* (SPF, ISC); 31 May 1991, fl, *Pirani, J.R. CFSC-13249 et al.* (SP); Santana do Riacho, Serra do Cipó, Chapeu do Sol, Estrada da Conceição do Cerro, MG010, prox. Km101, Lapinha, 19°06'01" S 43°40'23" W [-19.100278°, -43.673056°] 1483 m, 22 Apr 2006, veg, *Pirani, J.R. 5505 et al.* (SPF); Santana do Riacho, Serra do Cipó, Chapeu do Sol, Estrada da Conceição do Cerro, MG010, prox. Km101, Lapinha, Fazenda Mojolos, 19°20'35" S 43°45'15" W [-19.343056°, -43.754167°] s.d., veg, *Yamamoto, K. CFSC-169 et al.* (UEC); 20°30' S 43°35' W [-20.5°, -43.583333°] 17 Feb 1993, fl, *Zuloaga, F.O. 4562 & Morrone, O.* (IBGE, MO); São Golçalo do Rio Preto, Parque Estadual do Rio Preto, 18°12' S 43°19' W [-18.2°, -43.316667°] 28 Mar 2008, fl, *Viana, P.L. 3490 et al.* (BHCB); 18°08' S 43°22' W [-18.133333°, -43.366667°] 8 Apr 2000, veg, *Lombardi, J.A. 3827 & Lara, A.C.M.* (BHCB, ISC); 18°12' S 43°20' W [-18.2°, -43.333333°] 1400 m, 30 Oct 2003, veg, *Viana, P.L. 1071 et al.* (BHCB); 18°12' 19" S 43°20' 06" W [-18.205278°, -43.335°] 1345 m, 4 Feb 2004, fl, *Viana, P.L. 1565 et al.* (BHCB); 20°28' S 43°20' W [-20.466667°, -43.334°] 1550 m, 23 Dec 2007, veg, *Viana, P.L. 2787 et al.* (BHCB); São João Del Rey, Serra do Lenheiro, 13 Oct 1886, *Glaziou, A.F.M. 16627* (C, P, US Nos. 1127451!, 1127456!, 2808861! & 1021439 [fragment!]; W No. 1916-0009095!); haut de la Serra de Lenheiro, 24 Apr 1888, *Glaziou, A.F.M. 17449* (C, P, US Nos. 1021438 [fragment!]; W Nos. 1916-0009096!, 1916-0009120!); May 1896, fl, *Silveira, A. 1094* (R); São Roque de Minas, Parque Nacional da Serra da Canastra, Trilha para Casca D'anta, 20 Mar 1998, fl, *Arce, V. 2 et al.* (ISC); 20°18' S 46°31' W [-20.3°, -46.516667°] 13 Jan 1996, fl, *Romero, R. 3301 et al.* (BHCB, HUFU); 20°18' S 46°31' W [-20.3°, -46.516667°] 21 Feb 1997, fl, *Romero, R. 3904 et al.* (BHCB, HUFU); Serro, Milho Verde, 18°26'30" S 43°29'10" W [-18.441667°, -43.486111°] 1250 m, 3 Dec 1991, fl, *Hensold, N. 333* (SPF); 18°26' S 43°29' W [-18.433333°, -43.483333°] 13 Jun 2006, veg, *Viana, P.L. 2142 et al.* (CESI); Tiradentes, Serra de São José, 1090 m, 27 Jan 2007, veg, *Marino, F. 220* (BHCB); s.l., s.d., fl, *Krieger, L. 20173* (CESI); s.l., s.d., fl, [Collector unknown] (BHCB 293); s.l., 5 May 1991, fl, *Azevedo, M.L.M. 949 & Filgueiras, T.S.* (IBGE, MO, SP); s.l., 11 Mar 1943, fl, *Black, G.A. 3262B* (US); Localidade duvidosa Rio de Janeiro, s.d., *Glaziou, A.F.M. 17915* (US-1021440 [fragment!]; W No. 1916-0009121!).

Stelanemia C.D.Tyrrell, L.G.Clark, P.L.Viana & Santos-Gonç., gen. nov. TYPE: *Aulonemia setigera* (Hack.) McClure ≡ *Stelanemia setigera* (Hack.) C.D.Tyrrell, L.G.Clark, P.L.Viana & Santos-Gonç.

Diagnosis—*Stelanemia* differs from all other genera of the Arthrostylidiinae in having the combination of clambering or scandent culms, with subequally elongated internodes, well differentiated culm and foliage leaves, culm leaves with erect

blades, foliage leaves with reflexed, non-tessellate foliage leaf blades that are apically setose or caudate, synflorescences with first-order branches adpressed to the main rachis, and awned spikelets.

Rhizomes short necked pachymorph. **Culms** initially erect to decumbent, becoming clambering over other vegetation; internodes solid or with a narrow lumen in old culms, terete, with white velvety deciduous trichomes below the nodal line in young culms, smooth or papillose; nodes with uniformly horizontal line, supranodal ridge conspicuous or inconspicuous. **Culm leaves** clearly distinct from foliage leaves, fimbriae flattened or cylindrical, erect, wavy, or curly, free or fused, blades erect. **Branch complement** consisting of one divergent branch, with smaller branchlets at their basal nodes. **Foliage leaves** with fimbriae flattened or cylindrical, erect, wavy, scarberulous, free or fused at the base; blades erect to spreading, glabrous to sparsely pilose on both sides, chartaceous, not tessellate. **Synflorescences** a contracted to open panicle, first-order branches appressed to the main rachis. **Spikelets** terete, consisting of 2–7 glumes, 0–1 sterile lemmas, 2–8 fertile florets, and a rudimentary terminal floret. **Glumes and lemmas** awned. **Lodicules** 3, **anthers** 3.

Distribution and Habitat—*Stelanemia* is known from the states of Bahia, Espírito Santo, Minas Gerais, São Paulo, and Rio de Janeiro in Brazil, where it inhabits moist broadleaf ("Dense Ombrophilous") or Seasonal Semideciduous forests in the Atlantic Forest or transition zone between the Atlantic Forest, Cerrado, and Caatinga ecoregions. Species of the genus are found between 500 and 1300 m elevation.

Etymology—*Stelanemia* is a compound of the Greek stela (column/pillar) and nemos (forested pasture/glade). The *nemos* portion is a tribute to *Aulonemia*, the genus from which the two core species were transferred, and indicative of the type of habitat where the species are found. Stela refers to the columnar or pillar-like nature of bamboo culms.

Notes—A long apical projection of the culm leaf blades is peculiar for the subtribe but is present in all three species herein assigned to *Stelanemia* (setose in *S. setigera* and *S. setosa*, and caudate in *S. geniculata*).

KEY TO THE SPECIES OF STELANEMIA

1. Culms hollow, a distinct lumen always visible, even if small. *S. setosa*
1. Culms solid or, rarely, with discrete internal air channels. 2
 2. Mid-culm internodes 0.8–1.7 cm in diameter; leaf blades 18–41 cm long, 3.6–7.2 cm wide, apex setose; fimbriae (0.8)1.5–6.1 cm, terete. *S. setigera*
 2. Mid-culm internodes 0.2–0.4 cm in diameter; leaf blades 2.5–14 cm long, 0.5–1.2 cm wide, apex acuminate, fimbriae 0.3–1.4 cm, flattened. *S. geniculata*

Stelanemia geniculata P.L.Viana & Filg., sp. nov. TYPE: BRAZIL, Minas Gerais, Santa Maria do Salto, Fazenda Duas Barras, 16°24'26" S, 40°02'32" W, 822 m, 5 Jun. 2009, veg, *Viana, P.L. 4303 et al.* (holotype: BHCB, isotypes: IBGE, HUEFS, ISC, MBM, MO, NY, RB, SP, UWSP).

Diagnosis—This species is most similar to *Stelanemia setigera* (≡ *Aulonemia setigera*) and *Stelanemia setosa* (≡ *Aulonemia setosa*) but differs by having solid culms (vs. hollow or with a very small lumen in *S. setigera*), not wider than 4 mm (vs. 5 + mm); culm leaves with blades up to 1.1 cm long (vs. longer than 3.5 cm), acuminate to caudate at the apex, but never setose (vs. always setose); branch complement consisting of one branch, with several smaller geniculate branchlets at their basal nodes (vs. smaller branchlets straight); and foliage leaf blades 2.5–14 cm long (vs. 6.5–41), 0.5–1.2 cm wide (vs.

0.9–7.2), lanceolate to linear lanceolate (vs. lanceolate), acuminate at the apex (vs. setose).

Culms 2.0–5 m long, 0.2–0.4 cm diameter; internodes 10.2–22.5 cm long, solid, glabrous or with an ephemeral band of white velvety trichomes just below the nodes, smooth, light brown, mottled or uniform; nodes with a uniformly horizontal line, supranodal ridge conspicuous, intranodal area 0.4–0.6 cm long, 0.4–0.6 cm wide, glabrous; buds 4.4–5.5 mm long, 2.8–3.6 mm wide, obovate, glabrous. **Culm leaves** persistent; sheaths 3.2–4.8 cm long, 1.3–1.9 cm wide, adaxially pubescent, glabrescent, abaxially pubescent, glabrescent, greenish, becoming stramineous with age, margins glabrous on one side, pubescent on the other, fimbriae 0.2–0.9 cm long, flattened, erect, wavy to curly, free or fused at base forming auricles, inner ligules ca. 0.4 mm long; blades 2.3–4.5 cm long,

0.6–1.1 cm wide, oval lanceolate, abaxially glabrous, adaxially pubescent, apex long acuminate to caudate. **Branch complement** consisting of one branch, with several smaller geniculate branches at their basal nodes, forming a fasciculate complex of branches. **Foliage leaves** with sheaths rounded to slightly keeled toward the apex, 1.8–4.2 cm long, glabrous to pubescent abaxially, ciliate on one margin, green, mottled; fimbriae tardily deciduous, 0.3–1.4 cm long; erect, wavy, flattened, free or fused at base, stramineous; pseudopetioles 1.1–2.5 mm long, adaxially puberulous, abaxially glabrous; outer ligules ca. 0.5 mm long, membranous-ciliolate, inner ligules ca. 0.3 mm long, membranous or membranous-ciliolate; blades 2.5–14 cm long, 0.5–1.2 cm wide, lanceolate to linear lanceolate, erect, adaxially glabrous, except for one scaberulous margin, green, abaxially glabrous to sparsely pilose, glaucous with a conspicuous marginal green stripe covering almost half of blade width, apex acuminate, margins antrorsely scabrous. **Synflorescences** unknown. Figure 8.

Distribution and Habitat—This species occurs in the extreme northeast of the state of Minas Gerais, close to the border with Bahia (Fig. 5). The type locality consists of an area of moist broadleaf forest (known as a Dense Ombrophilous Forest), between 600 and 900 m, in the Alto Cariri State Park. It is an extensive area with humid forests associated with a large granite mountain complex, located in the transition zone between the Atlantic Forest area and Caatinga ecoregion.

Etymology—The epithet refers to the typical branching pattern of this species where the branchlets are strongly bent (geniculate) at the basal nodes.

Phenology—This species is only known from a vegetative collection.

Informal Conservation Assessment—If an IUCN assessment were performed, we hypothesize that this species would be categorized as Critically Endangered: CR B1ab(iii)-c(iv), because only one small population is known to exist, even after intensive search by the authors for other populations of this species in the region.

Notes—*Stelanemia geniculata* is known only from the type collection. Its morphological and foliar anatomical features clearly place this species within subtribe Arthrotyliidiinae. The species shares the following features with the other two species of *Stelanemia*: foliage leaf blades with glaucous leaf coloration making the dark green, abaxial, marginal stripe very distinct; solid culms (although *S. setosa* can also have a small lumen); presence of white velvety trichomes below the nodal line on young culms; and culm leaves morphologically differentiated from the foliage leaves, with erect, oval to lanceolate blades, and a long acuminate to caudate apex.

Stelanemia setigera (Hack.) C.D.Tyrrell, L.G.Clark, P.L.Viana & Santos-Gonç., comb. nov. \equiv *Arundinaria setigera* Hack., Oesterr. Bot. Z. 53(2): 73. 1903. \equiv *Aulonemia setigera* (Hack.) McClure, Smithsonian Contr. Bot. 9: 58. 1973. LECTOTYPE (designated here): BRAZIL. Rio de Janeiro: Dec 1888, *Glaziou 17916* (lectotype: W No. 1916-0009963; isolectotypes: P!, US Nos. 2809005 [fragment!] & 734829!).

Arthrotylidium aristatum Glaz. ex Camus, *Bambusées* 67, t. 40, f. A. 1913. TYPE: BRAZIL, Rio de Janeiro, pres de Petropolis, *Glaziou s.n.* (Holotype: P!).

Culms 2.2–8 m long, 0.8–1.5 cm diameter; internodes 15–32 cm long, solid or sometimes with a narrow lumen on

old culms, occasionally slightly flattened above nodes, glabrous or with an ephemeral band of white velvety trichomes just below the nodes, papillose, brown, mottled or uniform; nodes with a uniformly horizontal line, supranodal ridge conspicuous or inconspicuous, intranodal area 0.5–1.8 cm long, 0.8–1.7 cm wide, glabrous to slightly wooly; buds 8.5–23 mm long, 8–13 mm wide, triangular, oval-lanceolate to broadly oval, prophylls ciliate. **Culm leaves** deciduous; sheaths 8.5–17.5 cm long, 3.3–5.7 cm wide, adaxially glabrous, glossy dark brown, abaxially wooly, becoming glabrous with age, stramineous, margins glabrous, fimbriae 0.1–0.5 cm long, cylindrical, erect to effuse, strongly undulating to curled, fused at base forming auricles, inner ligules 0.2–0.8 mm long; blades 9.8–16.5 cm long, 3.0–4.8 cm wide, triangular to oval-lanceolate, adaxially glabrous to sparsely pilose, abaxially glabrous to wooly, apex setose. **Branch complement** consisting of one divergent branch, with smaller branchlets at their basal nodes, these not geniculate. **Foliage leaves** with sheaths keeled towards apex or along entire length, 6.6–16.2 cm long, glabrous to velutinous, green, mottled light brown to slightly vinaceous, fimbriae 0.8–6.1 cm long, cylindrical, erect, wavy, scaberulous, free or rarely fused at base forming auricles, persistent or tardily deciduous; pseudopetioles 5.5–13.4 mm long, adaxially pubescent, verrucular, abaxially glabrous to sparsely pilose, verrucular; outer ligules 0.7–1.2 mm long, membranous, inner ligules ca. 0.5 mm, membranous-ciliolate; blades 18–41 cm long, 3.6–7.2 cm wide, lanceolate, erect to spreading, adaxially glabrous to sparsely pilose, green, abaxially glabrous to sparsely pilose, glaucous, with a conspicuous marginal green stripe, apex setose, margins antrorsely scabrous. **Synflorescences** oblong, 22–43 cm long, 1.2–4.5 cm wide; peduncle glabrous; pedicels 1.2–8.8 mm long, 0.2–0.5 mm wide. **Spikelets** 3.4–4.8 cm long, linear, with 3–8 fertile florets. **Glumes**: first glume ca. 3 mm long, 3-veined, glabrous, acute, awn 3.0–3.5 mm long; second glume 4.4–5.2 mm long, 7-veined, glabrous, acute, ciliate, awn ca. 5 mm long; third glume ca. 5 mm long, 7–9-veined, glabrous, papillose, stramineous, awn ca. 5 mm long; fourth glume ca. 5.5 mm long, 7–9-veined, glabrous papillose, ciliolate, awn ca. 2.3 mm long; fifth glume ca. 7 mm long, 7–9-veined, glabrous, papillose, ciliolate, awn ca. 2.3 mm long; sixth glume ca. 7.7 mm long, 9–10-veined, glabrous, papillose, apex ciliate, awn ca. 4 mm long; seventh glume ca. 7.7 mm long, 9–10-veined, glabrous, papillose, apex ciliate, awn 4–4.8 mm long; rachilla internode ca. 5.7 mm long, glabrous, rough towards the apex. **Lemmas** 9–10 mm long, 9–13-nerved, glabrous, papillose, light brown, spotted, apex acute to obtuse, rounded, awn 4.0–5.8 mm long. **Paleas** 8.5–9.5 mm, sometimes longer than lemma, 4–5-nerved, glabrous, scaberulous on keels near apex, not mottled, apex navicular to rounded. **Anthers** 5.0–5.5 mm long, cream. **Ovaries** 1.8–2 mm long. **Caryopses** unknown. Figures 9, 10.

Distribution and Habitat—This species is known from the states of Bahia and Rio de Janeiro (Fig. 5) but restricted to the Atlantic Forest. The species has been documented in Dense Ombrophilous Forest between 500 and 980 m elevation. The existing specimens are from forests on hilltops in the coastal city of Rio de Janeiro (Pico da Tijuca, Morro Queimado), forest areas in Petrópolis, RJ, and, disjunctly, forests in mountainous areas in the state of Bahia.

Etymology—The epithet refers to the characteristic setose apex of the leaf blades of this species.



FIG. 8. *Stelanemia geniculata*. A. Habit. B–C. Vegetative branch with foliage leaf blades: B. Adaxial side. C. Abaxial side. D–E. Mid-culm branch complements. F. Branch complements near culm apex. G. Foliage leaf, junction of the sheath and blade showing fimbriae. H–J. Culm leaves. (*Viana 4303*).

Phenology—All flowering collections are from Rio de Janeiro and have an interval between 40 and 43 yr. There are two collections dated in 1888 (*Glaziou 17916* and *17451*), two in the period 1931–1932 (*Brade 11119* and *11285*) and one in 1972 (*Soderstrom 1845*).

Informal Conservation Assessment—If an IUCN assessment were performed, we hypothesize that this species would be categorized as Not Threatened due to its wide range of occurrence, occurring from Bahia to Rio de Janeiro.

Notes—The species is characterized by its vigorous appearance, with solid culms up to 1.5 cm in diameter and exceptionally large leaf blades ($18\text{--}41 \times 3.6\text{--}7.2$ cm). It forms dense clusters with arched culms.

Hackel (1903) cites two *Glaziou* collections in the original description (*Glaziou 17916* and *470*) but points out that *Glaziou 470* is in poor condition. We verified this during examination and found the collection to consist of senescent branches with few spikelets and sparse associated leaves. *Glaziou 17916*, however, corresponds well with the original description and

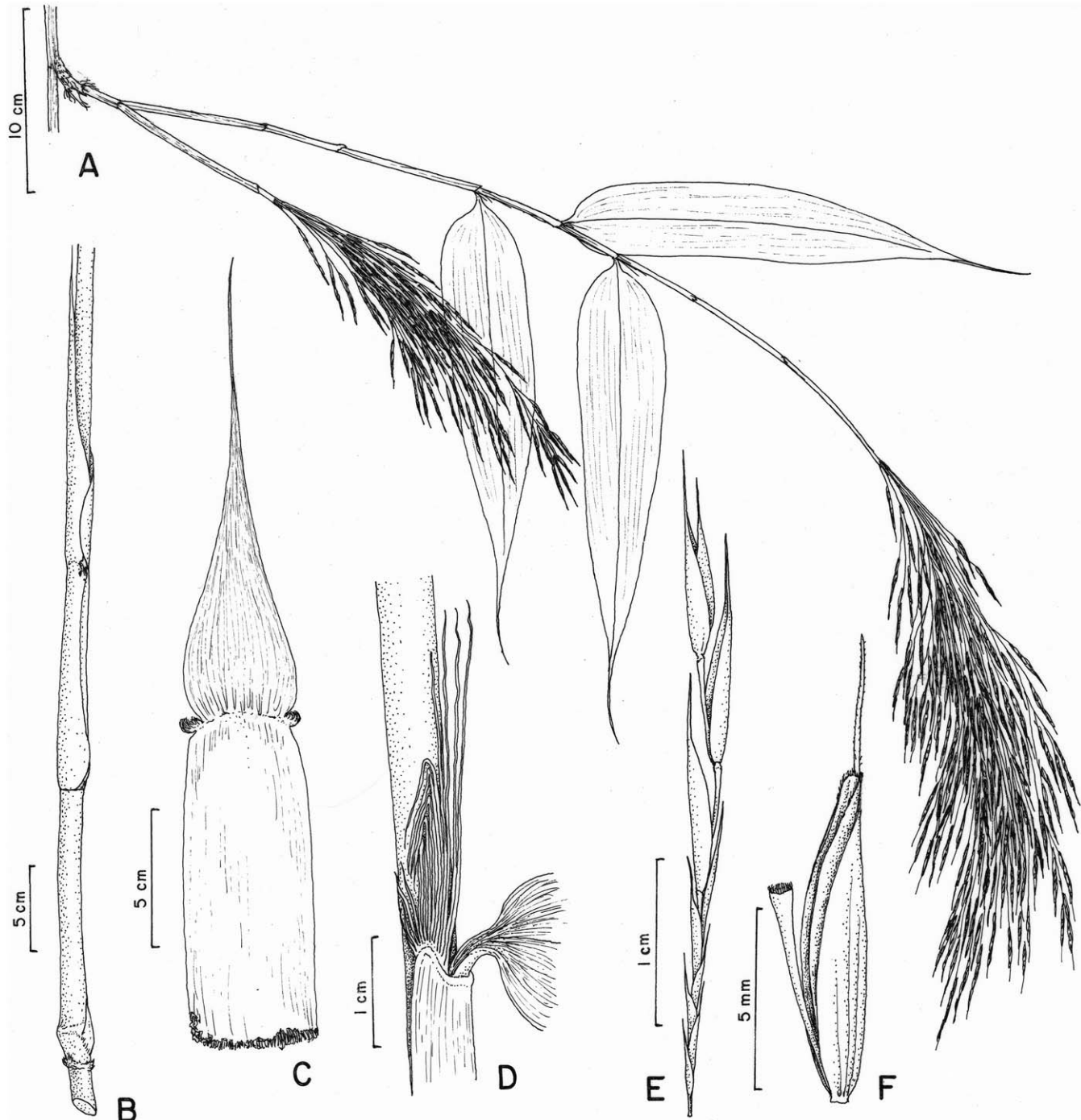


FIG. 9. *Stelanema setigera*. A. Flowering branch. B. Culm leaves at mid-culm nodes. C. Culm leaf, abaxial view. D. Foliage leaf, junction of the sheath and blade showing fimbriae. E. Spikelets. F. Fertile floret with rachilla internode, in lateral view. (A, E–F. *Glaziou 17916*; B–D. *Viana 3610*).



FIG. 10. *Stelanemia setigera*. A–B. Habit. C. Mid-culm branch complement. D. Culm leaf. E. Vegetative branch. F. Foliage leaf, junction of the sheath and blade showing fimbriae and sheath apical extension. G. Habitat, in Tijuca National Park, Rio de Janeiro. (A–C. Viana 3610).

the specimen at W is in excellent condition and was therefore chosen as a lectotype.

Additional Specimens Examined—Brazil. —BAHIA: Amargosa, Serra do Timbó, Fazendo do Sr. Arlindo, 13°03'45" S 39°33'45" W [-13.0625°, -39.5625°] ca. 800 m, 16 Nov 2007, veg, *Ferreira, F.M. 1789 et al.* (CEPEC, HUEFS); Barro Preto, Serra da Pedra Lascada, 14°16'13" S 39°32'10" W [-14.270278°, -39.536111°] 980 m, 13 Mar 2007, veg, *Oliveira, R.P. 1226 et al.* (HUEFS, CEPEC); Boa Nova, Fazenda Farofa (Dr. Mauro), estrada entre Boa Nova e Dário Meira, 14°18'45" S 40°11'15" W [-14.3125°, -40.1875°] 24 Oct 2007, veg, *Ferreira, F.M. 1667 et al.* (CEPEC, HUEFS); Miguel Calmon, Piemonte da Diamantina, 11°11'15" S 40°33'45" W [-11.1875°, -40.5625°] 2 Aug 2006, veg, *Santos, J.S. 181 et al.* (ALCB); —RIO DE JANEIRO: Rio de Janeiro, Parque Nacional da Tijuca, Morro Queimado, 22°57'45" S 43°15'22" W [-22.9625°, -43.256111°] 710 m, 14 Jul 2008, veg, *Viana, P.L. 3610 et al.* (BHCB, RB); 525 m, 24 Feb 1972, fl, *Soderstrom, T.R. 1845 et al.* (INPA, RB, US); Rio de Janeiro (Distrito Federal) Tijuca, Pico da Tijuca, 15 Feb 1925, veg, *Chase, A. 8496* (US); Rio de Janeiro (Distrito Federal) Tijuca, Pico da Tijuca, Corcovado, 12 Sep 1872, veg, *Glaziou, A.F.M. 5720* (US); s.d., fl, *Glaziou, A.F.M. 470* (P, US, W Nos. 1904-0011013!, 1904-0011018!, 1904-0013227!, 1916-0009964!); Petropolis, 3 May 1888, fl, *Glaziou, A.F.M. 17451* (P, NY, US); Petropolis, ReBio Tinguá, Estrada do Imperador, Km 8, 22°29'33" S 43°18'05" W [-22.4925°, -43.301389°] 500 m, 14 Mar 2007, veg, *Lima, H.C. 6562 et al.* (BHCB, RB); Province de Rio de Janeiro, 27 May 1986, fl, *Glaziou, A.F.M. s.n.* (P).

Stelanemia setosa (Londoño & L.G.Clark) C.D.Tyrrell, L.G.Clark, P.L.Viana & Santos-Gonç., comb. nov. \equiv *Eremocaulon setosum* Londoño & L.G.Clark, Syst. Bot. 27(4): 719–721. 2002. \equiv *Aulonemia setosa* (Londoño & L.G.Clark) P.L.Viana & Filg., Brittonia 63(1): 104–107. 2011. TYPE: BRAZIL. São Paulo: Mun. Salesópolis, Estação Biológica Boraceia/Reserva Hidrológica do Rio Claro-SABESP, trail to Campos da Boraceia, 850 m, 22°36'S, 45°54'W, 25 Feb 1991, L.G. Clark & M. Morel 829 (holotype: SP No. 252416!; isotypes: COL No. 565390, ISC!, MBM No. 194534!, MO Nos. 5664522!, 5664523!, NY, RB, SJRP, US Nos. 3436758!, 3436759!); EPITYPE (designated by Viana et al. in Brittonia 63(1): 104. 2011): BRAZIL. Minas Gerais: Mun. Felício dos Santos, APA Felício, 18°10' S, 43°17' W, 1000–1400 m, 8 Oct 2004, P.L.Viana 2229 (BHCB; isoeotypes: IBGE, ISC!, RB No. 581799, US, UWSP).

Culms 2–13 m long, 0.5–2.0 cm diameter; internodes 12.5–35(–40) cm long, hollow, thick-walled, terete, occasionally slightly flattened above nodes, glabrous or with an ephemeral band of white velvety trichomes just below the nodes, usually persistent close to the nodal region, papillose, brown, mottled or uniform; nodes with a uniformly horizontal line, supranodal ridge conspicuous, intranodal area 0.6–1.6 cm long 0.9–2.3 cm wide, glabrous; buds 11–18 mm long, 8–11 mm wide, largely elliptical to oval-lanceolate, glabrous, prophylls ciliate at apex. **Culm leaves** persistent or deciduous; sheaths 8–18.5 cm long, 2.8–6.1 cm wide, adaxially glabrous, shiny copper-brown, abaxially wooly, becoming glabrous with age, stramineous, margins glabrous to ciliate, fimbriae 0.1–0.3 cm long, cylindrical, erect to effuse, strongly undulating to curled, fused at base forming auricles, inner ligules ca. 0.4 mm long; blades 3.5–4.5 cm long, 0.6–1 cm wide, triangular to oval-lanceolate, adaxially pubescent, abaxially sparsely pilose to pubescent, apex setose, or sometimes acuminate. **Branch complement** consisting of one divergent branch, occasionally with smaller branchlets at its basal nodes, these not geniculate. **Foliage leaves** with sheaths keeled, 7.1–13.3 cm long, glabrous or with sparse adpressed whitish trichomes, green, mottled light brown to slightly vinaceous, fimbriae 0.3–1.7 cm long, cylindrical, erect,

slightly wavy, free, stramineous, deciduous; pseudopetioles 1.4–3.4 mm long, adaxially glabrous to sparsely pubescent, abaxially glabrous to sparsely pubescent; outer ligules ca. 0.5 mm long, membranous-ciliate, inner ligules 1.5–5 mm, membranous; blades 6.2–22.5 cm long, 0.9–3.5 cm wide, lanceolate, erect to spreading, adaxially glabrous to sparsely pilose, green, abaxially pilose, glaucous, with a conspicuous marginal green stripe, base rounded, apex setose, rarely just acuminate, margins antrorsely scabrous. **Synflorescences** a spike-like panicle, 22–72 cm long, 0.3–1.6 cm wide; peduncle glabrous; pedicels 0.9–4.6 mm long, 0.3–0.4 mm diameter. **Spikelets** 1.5–2.6(3.2) cm long, linear, with 2–5 fertile florets. **Glumes**: first glume 2.3–4 mm long, 1–3-veined, glabrous, ciliate towards apex, acute to obtuse, awn 2.0–3.2 mm long; second glume 4.7–5.1 mm long, 5–6-veined, glabrous, acute, ciliate, awn ca. 3.5 mm long; third glume, when present, ca. 6 mm long, 7–8-veined, glabrous, papillose, usually spotted, awn 3.3–3.8 mm long; fourth through seventh glumes, when present, ca. 6.1 mm long, 7–8-veined, glabrous, papillose, usually spotted, apex ciliate, awn 3.3–3.8 mm long; rachilla internode ca. 5.8 mm long, glabrous, rough towards the apex. **Lemmas** ca. 8 mm long, ca. 11-nerved, glabrous, papillose, light brown, spotted, acute, awns 3.5–7.8 mm long. **Paleas** ca. 9 mm, usually larger than lemma, 8-nerved, glabrous, sometimes papillose, scaberulous on keels near apex, not mottled, apex rounded to apiculate. **Anthers** 4.2–5.5 mm long, vinaceous to greenish. **Ovaries** 1.3–1.7 mm long. **Caryopses** ca. 4.8 mm long, oblong, light brown. Figure 11.

Distribution and Habitat—This species is known from the states of Minas Gerais, Espírito Santo, São Paulo, and Rio de Janeiro, in Seasonal Semideciduous Forest and Dense Ombrophilous Forest, occurring exclusively within the Atlantic Forest. It has been generally recorded at elevations between 800 and 1300 m, with only one collection from Santos, São Paulo, described as 100 m above sea level (Viana et al. 2011).

Etymology—The epithet *setosa* refers to the characteristic setose apex of the leaf blades of this species.

Phenology—Based on the specimens examined, four populations of *S. setosa* have been documented with gregarious flowering. There are two 1985 collections: one in Rio de Janeiro (*Martinelli 10635*) and one in Espírito Santo (*Zuloaga 2399*). There is a flowering collection from the state of São Paulo (*Souza 3463*) in 2000 and between 2004 and 2006, a densely flowering population was documented in Minas Gerais (*Viana 1358, 2229, 3762*). These data suggest a flowering cycle between 15 and 21 yr.

Informal Conservation Assessment—If an IUCN assessment were performed, we hypothesize that this species would be categorized as Not Threatened.

Notes—This species is closely related to *S. setigera*, but can be easily distinguished from the latter by the (1) fistulose (vs. solid or, rarely, with a lumen smaller than 1 mm in diameter) culms, (2) smaller leaves which rarely exceed 20 cm in length (vs. 18–41 cm) and synflorescences spikelike, reaching a maximum width of 1.6 cm (vs. oblong, having first-order branches and spreading more than 2 cm wide).

Additional Specimens Examined—Brazil. —ESPÍRITO SANTO: Domingos Martins, selva en cerro del Dr. Kautsky, 20°21' S 40°39' W [-20.35°, -40.65°] 600 m, 11 May 1985, fl, *Zuloaga, F.O. 2399 et al.* (BHCB, RB, WIS); MINAS GERAIS: Barão de Cocais, RPPN Caraça, Próximo à RPPN Cachoeira do Capivari, 20°06'49" S 43°34'08" W [-20.113611°, -43.568889°] 1462 m, 28 May 2008, veg, *Viana, P.L. 3760 & Leite, F.S.F.* (BHCB, UWSP); Felício dos Santos, APA Felício, Arredores do Parque Estadual do Rio Preto, 1200 m, 8 Aug 2004, fl, *Viana, P.L. 1858 & Mota, N.F.O.* (BHCB); Felício dos

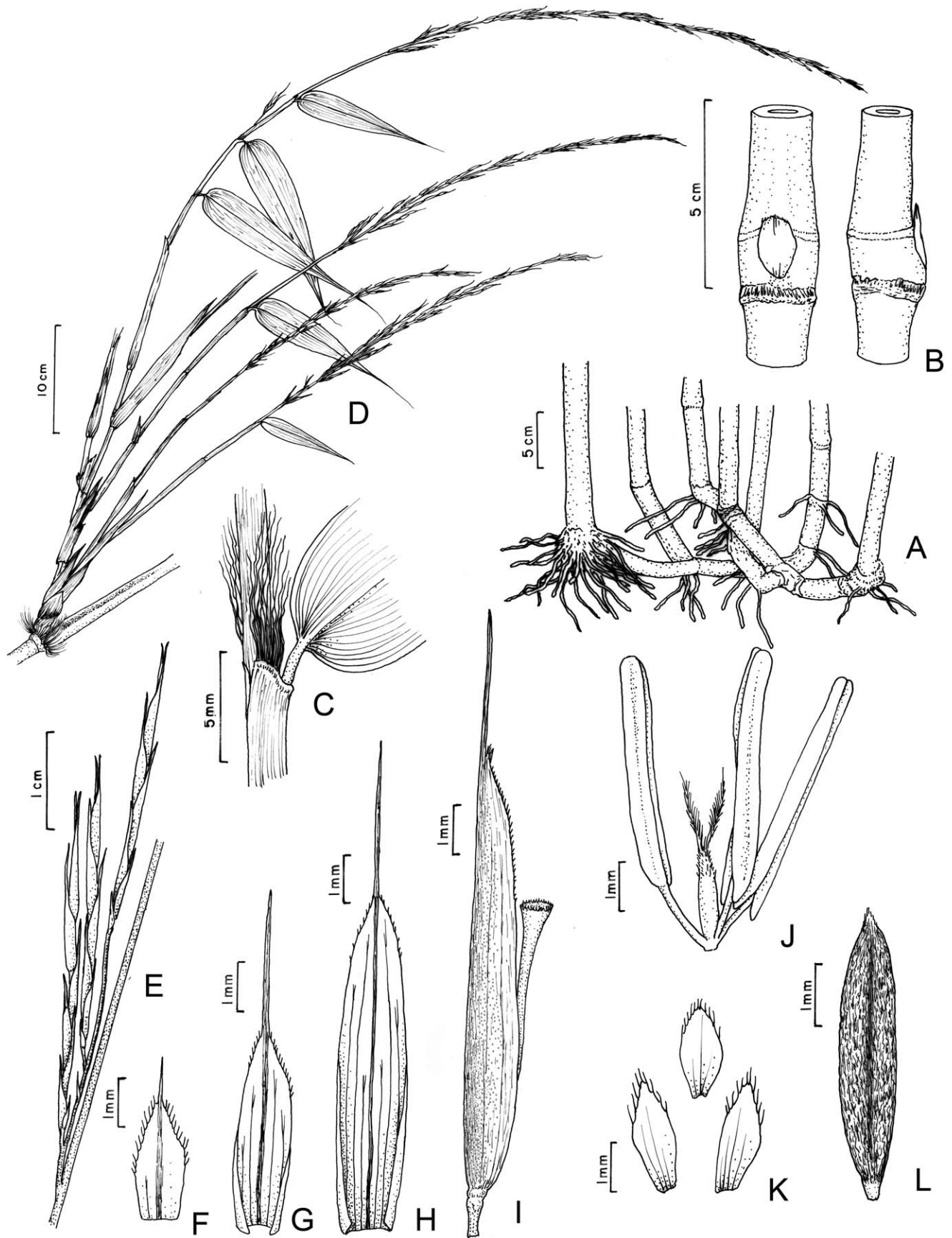


FIG. 11. *Stelanismia setosa*. A. Rhizomes. B. Mid-culm node with branch bud. C. Foliage leaf, junction of the sheath and blade showing fimbriae. D. Flowering branch. E. Branches of synflorescence. F. Glume I. G. Glume II. H. Glume III. I. Fertile floret with rachilla internode, in lateral view. J. Gynoecium and androecium. K. Lodicules. L. Caryopsis. (Viana 2229).

Santos, APA Felício, Arredores do Parque Estadual do Rio Preto, Mata do Isidoro, 1300 m, 11 Jun 2006, fl, Viana, P.L. 3762 et al. (BHCB, UWSP); 18°10' S 43°17' W [-18.166667°, -43.283333°] 1000 m, 8 Oct 2004, fl, Viana, P.L. 2229 et al. (BHCB, UWSP); Nova Lima, próximo ao córrego do Boia-deiro, 20°06'44" S 43°53'26" W [-20.112222°, -43.890556°] 23 Aug 2008, veg, Viana, P.L. 3461 et al. (BHCB); Rio Acima, 10 May 2009, veg, Viana, P.L. 4306 (BHCB); —RIO DE JANEIRO: Macaé, Pico do Frade de Macaé, 7 Feb 1985, fl, Martinelli, G. 10635 et al. (BHCB, F, RB, US); —SÃO PAULO: Caraguatuba, Parque Estadual da Serra do Mar, 23°38'44" S 45°40'21" W [-23.645556°, -45.6725°] 1100 m, 25 Apr 2000, fl, Souza, J.P. 3463 et al. (CEN); Santos, 100 m, 7 May 2007, veg, Garcia, R.J.F. 3038 et al. (BHCB, PMSP).

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AUTHOR CONTRIBUTIONS

APSG, CJC, LGC, and PLV designed the study. APSG, CJC, EALA, LGC, LOO, and PLV conducted field and laboratory work. CDT performed bioinformatics and analyses. CDT and PLV created figures. CDT, CJC, LGC, and PLV wrote the manuscript. All authors contributed to the article and approved the submitted version.

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APPENDIX 1. Taxon, origin, specimen voucher, and GenBank accession numbers for DNA regions used in this study [*ndhF*, *rpl16*, *rps16*, *trnC-rpoB*, *trnD-trnT*, *rps16-trnQ*, *trnT-trnL*]. A dash (—) indicates data were not available or were not able to be sequenced, and an asterisk (*) indicates a sequence was newly produced here.

ARTHROSTYLIIDIINAE 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 multispicatum* Pilg., Puerto Rico, LG Clark & G Reiners 1508 (ISC), [JQ408532, JQ408574, —, —, JQ408630, JQ408453, JQ408592]. *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 Vinicius-Silva 15 (VIC), [MG458235, MG458241, MG458252, MG458262, MG458268, MG458274, MG458281]. *Athroostachys shepherdiana* (Santos-Gonçalves, Filg. & L.G. Clark) C. 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), [MH033658*, MH033661*, MH033687*, MH033719*, MH033743*, MH033764*, MH033793*]. *Aulonemia aristulata* (Döll) McClure, Brazil, CJ Costa et al. 61 (VIC), [MW711023*, MH033662*, MH033688*, MH033720*, MH033744*, MH033765*, MH033794*]. *Aulonemia cincta* P.L.Viana & Filg., Brazil, P Viana s.n. (BHCB), [MW711007*, MH033663*, MH033689*, MH033721*, —, MH033766*, MH033795*]. *Aulonemia cochabambensis* Judz. & L.G.Clark, Bolivia, B Ståhl 5660 (ISC), [—, —, —, —, —, MH033767*, —]. *Aulonemia deflexa* (N.E.Br.) McClure, Brazil, P Viana 3443 (MG), [MW711011*, MH033664*, MH033690*, MH033722*, MH033745*, MH033768*, MH033796*]. *Aulonemia hirtula* (Pilg.) McClure, Ecuador, LG Clark & P Asimbaya 1412 (ISC), [JQ408540, —, MH033692*, JQ408498, JQ408638, —, —]. *Aulonemia insignis* Judz. & L.D.Gibbons, Bolivia, A Fuentes & WV Muller 14008 (UWSP), [MW711012*, MH033666*, MH033693*, MH033725*, MH033747*, MH033770*, MH033798*]. *Aulonemia lanciflora* McClure & L.B.Sm., Brazil, CJ Costa 98 (VIC), [MW711016*, MH033667*, MH033694*, MH033725*, MH033748*, MH033771*, MH033799*]. *Aulonemia laxa* (F.Maek.) McClure, Mexico, T Mejia-Saulés 2090 (XAL), [MW711021*, MH033668*, MH033695*, MH033726*, MH033749*, MH033772*, MH033800*]. *Aulonemia longiaristata* L.G.Clark & Londoño, Ecuador, LG Clark 1434 (ISC), [MW711014*, MH033669*, MH033696*, MH033727*, —, MH033774*, MH033802*]. *Aulonemia longipedicellata* Renvoize, Bolivia, A Fuentes et al. 10766 (UWSP), [MW711009*, MH033670*, MH033697*, MH033728*, MH033750*, MH033773*, MH033801*]. *Aulonemia madidiensis* Judz., D.C.Ziegler & Zueger, Bolivia, A Araujo-Murakami et al. 1741 (UWSP), [MW711013*, MH033671*, MH033698*, MH033729*, MH033751*, MH033775*, MH033803*]. *Aulonemia patriae* R.W.Pohl, Costa Rica, C Tyrrell et al. 44 (ISC), [JQ408541, —, —, JQ408499, JQ408639, JQ408458, —]. *Aulonemia patula* (Hack.) McClure, Ecuador, LG Clark et al. 1075 (ISC), [JQ408542, JQ408578, —, JQ408500, JQ408640, JQ408459, JQ408599]. *Aulonemia patula*, Ecuador, LG Clark & PA 1400 (ISC), [—, —, MH033699*, —, —, —]. *Aulonemia prolifera* P.L.Viana & Filg., Brazil, CJ Costa 106 (VIC), [MW711025*, MH033672*, MH033700*, MH033730*, MH033752*, MH033776*, MH033804*]. *Aulonemia queko* Goudot, Ecuador, LG Clark & P Asimbaya 1445 (ISC), [JQ408543, JQ408579, MH033701*, JQ408501, JQ408641, JQ408460, JQ408600]. *Aulonemia robusta* L.G.Clark & Londoño, Colombia, X Londoño & E Ruiz-Sanchez 994 (UWSP), [—, —, MH033703*, —, —, MH033778*, —]. *Aulonemia soderstromii* P.L.Viana, Filg. & Judz., Brazil, CJ Costa 109 (VIC), [MW711017*, MH033676*, MH033706*, MH033734*, MH033756*, MH033781*, MH033808*]. *Aulonemia xerophylla* P.L.Viana & Filg., Brazil, CJ Costa et al. 94 (VIC), [MW711026*, MH033677*, MH033707*, MH033735*, MH033757*, MH033782*, MH033809*]. *Aulonemiella laegaardii* L.G.Clark, Londoño & Judz., Ecuador, LG Clark et al. 1101 (QCA), [JQ408530, JQ408573, —, JQ408490, JQ408629, JQ408451, JQ408591]. *Aulonemiella ecuadorensis* (Judz. & L.G.Clark) L.G.Clark, Londoño & Judz., Colombia, X Londoño 900 (COL), [JQ408528, —, —, JQ408489, JQ408627, JQ408449, JQ408593]. *Cambajua ulei* (Hack.) P.L.Viana, L.G.Clark & Filg., Brazil, LG Clark & X

Londoño 1048 (ISC), [JQ408544, —, —, JQ408502, JQ408642, JQ408461, JQ408601]. *Cambajua ulei*, Brazil, PL Viana s.n. (BHCB), [—, MH033678*, MH033708*, —, —, —]. *Colanthea cingulata* (McClure & L.B.Sm.) McClure, Brazil, T Filgueiras s.n. (ISC), [JQ408545, —, —, —, JQ408643, —, JQ408602]. *Colanthea cingulata*, Brazil, CJ Costa et al. 125 (VIC), [—, MH033679*, MH033709*, MH033736*, —, MH033783*, —]. *Colanthea intermedia* (McClure & L.B.Sm.) McClure, Brazil, AP Santos-Gonçalves 553 (VIC), [—, —, —, —, JQ408645, —, JQ408604]. *Colanthea intermedia*, Brazil, CJ Costa et al. 107 (VIC), [MW711010*, MH033680*, MH033710*, MH033737*, —, MH033784*, —]. *Colanthea kinoshitae* Santos-Gonç., Filg. & L.G. Clark, Brazil, CJ Costa et al. 129 (VIC), [MW711015*, MH033681*, MH033711*, MH033738*, MH033758*, MH033785*, MH033810*]. *Colanthea longipetiolata* C.Jesus-Costa & A.P.Santos-Gonçalves, Brazil, CJ Costa et al. 72 (VIC), [MW711008*, MH033683*, MH033714*, MH033740*, MH033759*, MH033788*, MH033812*]. *Colanthea secundiflora* Santos-Gonç., Filg. & L.G.Clark, Brazil, AP Santos-Gonçalves 353 (VIC), [MW711022*, —, MH033712*, —, —, MH033786*, —]. *Colanthea sparsiflora* Santos-Gonç., Filg. & L.G.Clark, Brazil, AP Santos-Gonçalves 496 (VIC), [MW711024*, MH033684*, MH033715*, —, —, MH033789*, MH033813*]. *Didymogonyx geminatum* (McClure) McClure, Venezuela, F Ely 2 (ISC), [JQ408562, —, —, —, JQ408660, JQ408477, JQ408614]. *Didymogonyx longispiculatum* Londoño & L.G.Clark, Colombia, X Londoño & E Ruiz-Sanchez 995 (ISC), [JQ408558, —, —, JQ408513, JQ408656, JQ408473, —]. *Elytostachys clavigera* McClure, Costa Rica, R Pohl 13572 (ISC), [JQ408547, —, —, —, —, —]. *Elytostachys 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, MH033716*, JQ408506, JQ408649, JQ408466, JQ408606]. *Glaziophyton mirabile* Franch., Brazil, T Sarahyna et al. 1066 (ISC), [JQ408552, U54748, KC020582.1, JQ408507, JQ408650, JQ408467, JQ408607]. *Merostachys fistulosa* Döll, Brazil, R Vinicius-Silva 50 (VIC), [MG458237, MG458245, MG458256, MG458264, MG458270, MG458277, MG458283]. *Merostachys riedeliana* Rupr. ex Döll, R Vinicius-Silva 20 (VIC), [MW711027*, —, —, —, —, —]. *Merostachys tatanica* Santos-Gonçalves, Carvalho-Okano & Filg., Brazil, R Vinicius-Silva 18 (VIC), [MG458238, MG458246, MG458257, MG458265, MG458271, MG458278, MG458284]. *Merostachys ternata* Nees, Brazil, LG Clark & W Oliveira 1023 (ISC), [JQ408555, —, —, JQ408510, JQ408653, JQ408471, JQ408610]. *Merostachys ternata*, R Vinicius-Silva 30 (VIC), [—, MG458247, MG458258, —, —, —, —]. *Myriocladum virgatum* Swallen, Brazil, E Afonso 140 (MG), [MW711019*, —, —, —, MH033760*, MH033790*, MH033814*]. *Quixiame radiata* (Rupr.) C.D.Tyrrell, L.G.Clark, P.L.Viana, Santos-Gonç., Brazil, CJ Costa 69 (VIC), [MH033660*, MH033673*, MH033702*, MH033731*, MH033753*, MH033777*, MH033805*]. *Rhipidocladum parviflorum* (Trin.) McClure, Brazil, T Filgueiras s.n. (ISC), [JQ408567, —, —, JQ408521, JQ408665, JQ408481, JQ408617]. *Rhipidocladum parviflorum*, CJ Costa 92 (VIC), [—, MG458248, MG458259, —, —, —, —]. *Rhipidocladum aff. parviflorum*, Brazil, T Filgueiras s.n. (ISC), [JQ408557, —, —, JQ408512, JQ408655, JQ408472, JQ408621]. *Rhipidocladum harmonium* (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]. *Stelanemia setigera* (Hack.) C.D.Tyrrell, L.G.Clark, P.L.Viana, Santos-Gonç., Brazil, CJ Costa 126 (VIC), [MW711018*, MH033674*, MH033704*, MH033732*, MH033754*, MH033779*, MH033806*]. *Stelanemia setosa* (Londoño & L.G.Clark) C.D.Tyrrell, L.G.Clark, P.L.Viana, Santos-Gonç., Brazil, CJ Costa 85 (VIC), [MW711020*, MH033675*, MH033705*, MH033733*, MH033755*, MH033780*, MH033807*]. *Vianaea effusa* (Hack.) C.D.Tyrrell, L.G.Clark, Santos-Gonç., Afonso, Brazil, CJ Costa 88 (VIC), [MH033659*, MH033665*, MH033691*, MH033723*, MH033746*, MH033769*, MH033797*]. **CHUSQUEINAE** Soderstr. & R.P.Ellis—*Chusquea capituliflora* Trin., Brazil, AP Santos-Gonçalves 620 (VIC), [MG458239, MG458249, MG458260, MG458266, MG458272, MG458279, MG458285]. *Chusquea* sp., 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. & R.P.Ellis

Londoño, Brazil, *A Carvalho* 4393 (CEPEC), [JQ408549, EF589616, —, JQ408504, JQ408647, JQ408464, —]. *Eremocaulon triramis* Jesus-Costa & Londoño, Brazil, *CJ Costa et al.* 108 (VIC), [—, MH033685*, MH033717*, MH033741*, MH033761*, MH033791*, MH033815*]. *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), [MW711006*, MH033686*, MH033718*, MH033742*, MH033762*, MH033792*, MH033816*]. *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, FJ751706, FJ643982, FJ643796, FJ644133].

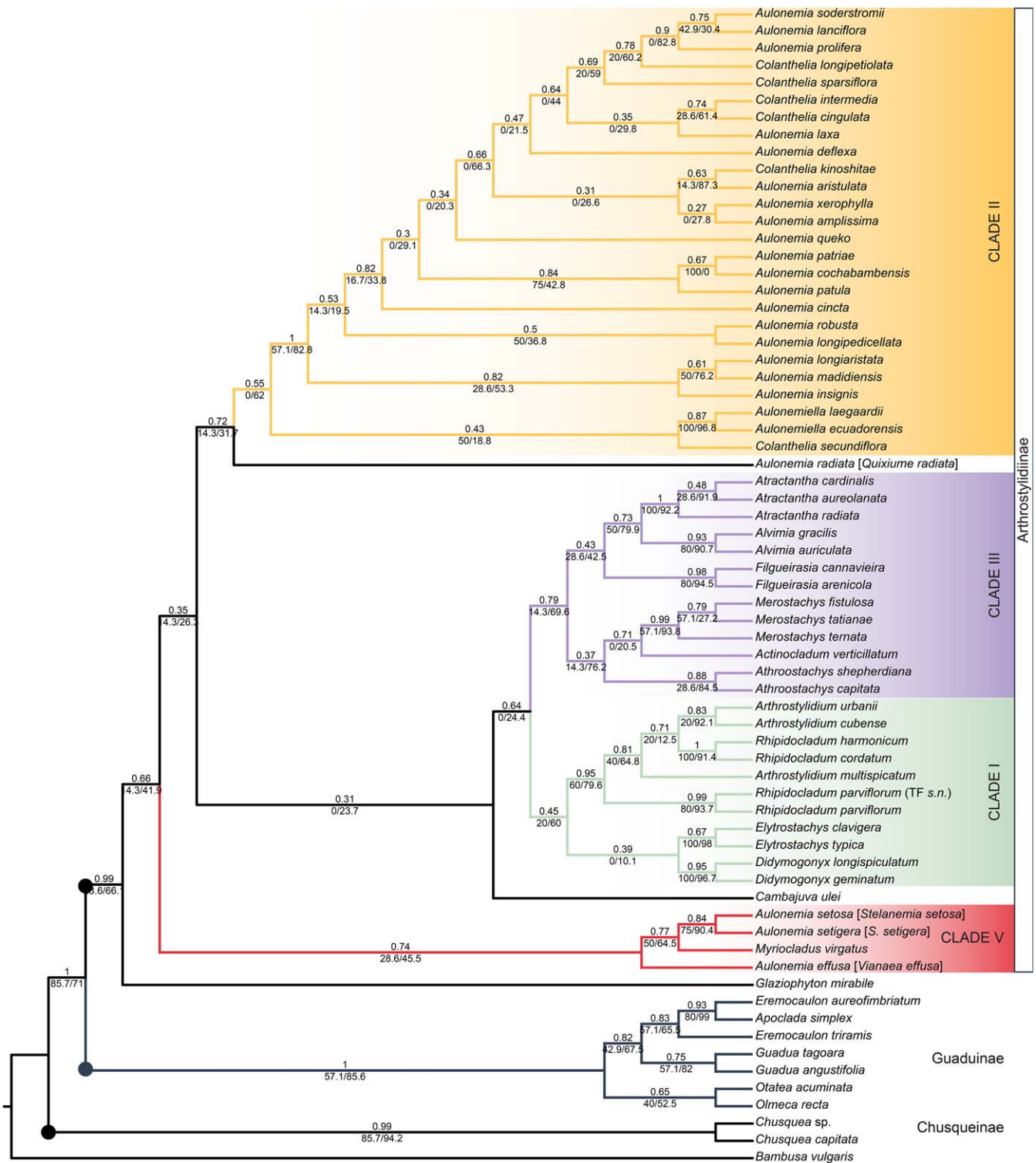


FIG. S1. Multispecies Coalescent (MSC) species tree of 67 individuals representing 66 taxa across 23 Neotropical woody bamboo genera (see Appendix 1 for specimen voucher details). Topology is inferred from plastid DNA sequences of *trnD-trnT*, *rps16-trnQ*, *trnC-rpoB*, *trnT-trnL* intergenic spacers, *rpl16* and *rps16* introns, and the *ndhF* gene. Local posterior probabilities for each node are displayed above the branches, gene concordance and site concordance factors (separated by '/') are displayed below branches. Circles on the tree indicate subtribal clades and colored boxes highlight clade structure within Arthrostylidiinae. Clade names conform to those resolved in previous studies.

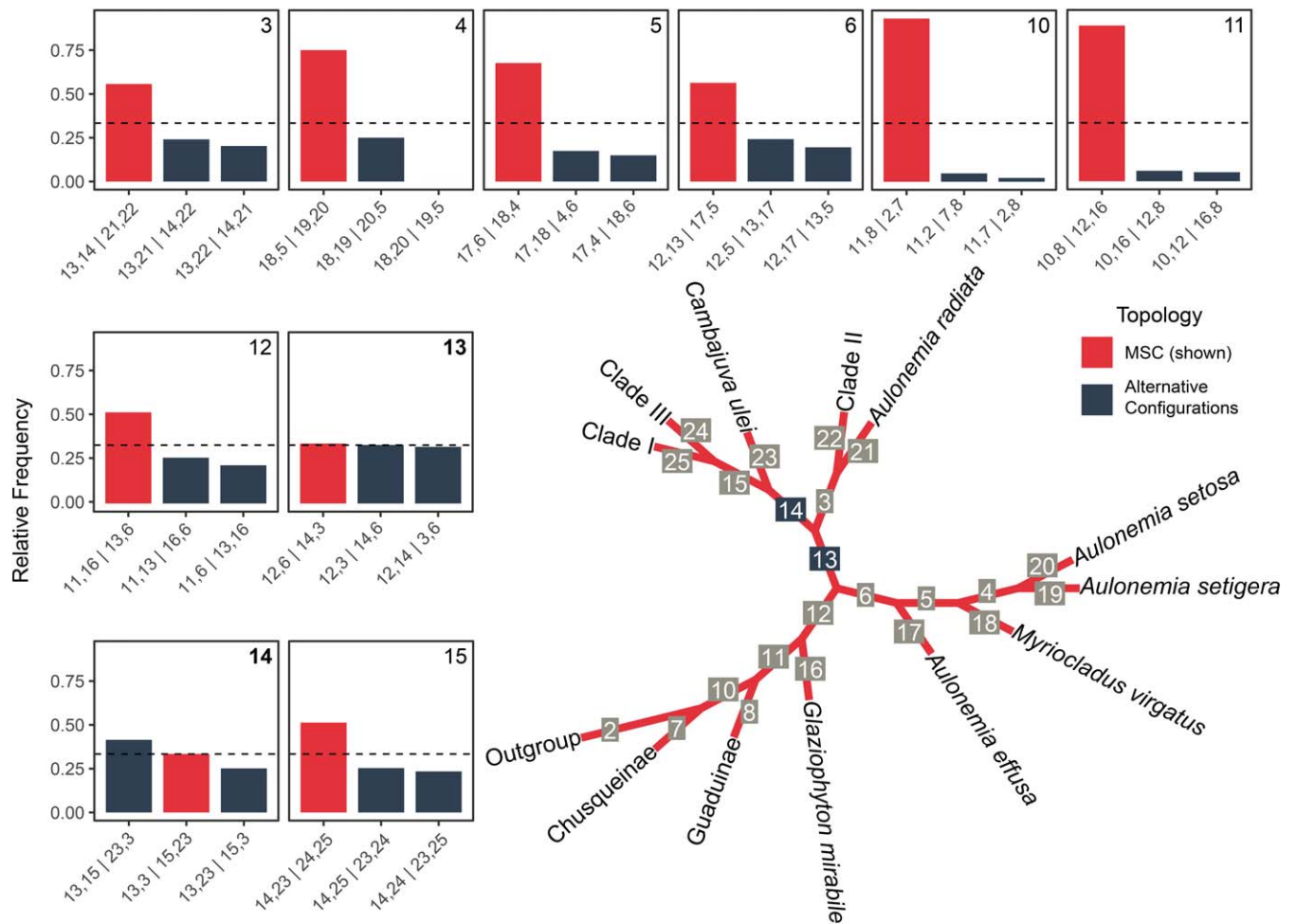


FIG. S2. Analysis of alternative multispecies coalescent inferred phylogenetic topologies. Barplots represent frequency for each alternative branching configuration. Red bars are those recovered in Supplemental Fig. S1 (this paper). Numbers on the tree correspond to the barplot for that branch. Bold and shaded numbers (13, 14) indicate branches with conflicting or ambiguous signal.