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A phylogeny and classification of the Muhlenbergiinae (Poaceae: Chloridoideae: Cynodonteae) based on plastid and nuclear DNA sequences[1]

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- *Premise of the study*: To understand the origins of C_4 grasslands, we must have a better interpretation of plant traits via phylogenetic reconstruction. Muhlenbergiinae, the largest subtribe of C_4 grasses in Mexico and the southwestern United States (with 176 species), is taxonomically poorly understood.
- *Methods*: We conducted a phylogenetic analysis of 47 genera and 174 species using six plastid regions (*ndhA* intron, *ndhF, rps16-trnK, rps16* intron, *rps3*, and *rpl32-trnL*) and the nuclear ITS 1 and 2 (ribosomal internal transcribed spacer) regions to infer evolutionary relationships and revise the classification.
- *Key results*: In our analyses, *Muhlenbergia* (ca. 153 species) is paraphyletic, with nine genera (*Aegopogon*, *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Lycurus*, *Muhlenbergia*, *Pereilema*, *Redfieldia*, *Schaffnerella*, and *Schedonnardus*) found nested within. We recognized the following five well-supported monophyletic lineages within *Muhlenbergia*: subg. *Muhlenbergia*, with species that have phosphoenolpyruvate carboxykinase-like leaf anatomy and long, scaly rhizomes; subg. *Trichochloa* with long-lived species that are relatively tall (up to 3 m); subg. *Clomena* with 3-nerved upper glumes; sect. *Pseudosporobolus* species with narrow panicles and plumbeous spikelets; and sect. *Bealia* species with lemmas with hairy margins and midveins.
- *Conclusions:* We propose expanding the circumscription of *Muhlenbergia* to include the other nine genera in this subtribe and make the following new combinations: ***Muhlenbergia*** **subg.** ***Bealia***, ***M. diandra***, ***M. geminiflora***, ***M. paniculata***, ***M. phleoides***, ***M*. subg. *Pseudosporobolus*** (also lectotipified), ***M. solisii***, ***M. tricholepis***. We also propose several new names: ***M. ammophila***, ***M. columbi***, ***M. plumosa***. Our phylograms suggest that *Muhlenbergia* originated in North America because the sister (*Sohnsia filifolia* and Scleropogoninae) is composed of predominantly North American species.

Key words: biogeography; Chloridoideae; classification; ITS; *Muhlenbergia*; Muhlenbergiinae; phylogeny; plastid DNA sequences; Poaceae.

Grassland ecosystems are one of the most easily recognized biomes in the world, covering about 40% of the earth's surface (World Resources, 2000; Gibson, 2009), and they are also threatened and highly endangered. Humans evolved with grasslands, and we depend on grasses and grasslands for our sustenance directly as crops (rice, corn, and wheat) and indirectly as forage for herbivores. However, only a small fraction of grassland ecosystems remains intact today, and we need to study the biodiversity of this important biome from an evolutionary perspective before it is destroyed.

The Muhlenbergiinae Pilg. is a diverse assemblage of C_4 grasses containing 176 species that dominate grasslands in the western hemisphere. Species such as *Muhlenbergia montana* (Nutt.) Hitchc. (mountain muhly) and *M. rigida* (Kunth) Kunth (purple muhly) are the most common grass species of high-plateau grasslands in north central Mexico, the southwestern United States, and, to a lesser extent, along the Andean Cordillera of South America. Yet evolutionary relationships and a modern classification of the Muhlenbergiinae based on the study of molecular characters have not been completed. To understand the origins and rise of C_4 grasslands, a better interpretation of plant traits via phylogenetic reconstruction is essential (Edwards et al., 2010).

The placement of *Muhlenbergia* Schreb. within the grasses has been the subject of many papers since the genus was included in the subfamily Festucoideae, tribe Agrostideae by Hitchcock (1935) [see Table 1 for a summary of taxonomic treatments in the Muhlenbergiinae]. The subtribe Muhlenbergiinae was first circumscribed by Pilger (1956) where he recognized a single genus, *Muhlenbergia* with the following eight sections: *Acroxis* (Trin.) Bush, *Bealia* (Scribn.) Pilg., *Cinnastrum* (E. Fourn.) Pilg., *Clomena* (P. Beauv.) Pilg., *Muhlenbergia*, *Podosemum* (Desv.) Pilg., *Pseudosporobolus* Parodi, and *Stenocladium* (Trin.) Bush. In this same treatment, Pilger recognized the genus *Epicampes* J. Presl (included in subtribe Sporobolinae Ohwi by Pilger), a name now placed in synonymy within *Muhlenbergia*. Subsequent authors have agreed that Pilger's infrageneric treatment of *Muhlenbergia* was not phylogenetically informative (Soderstrom, 1967; Pohl, 1969; Morden, 1985; Peterson and Annable, 1991). With the accumulation of

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Table 1. Primary taxonomic treatments found in the Muhlenbergiinae and the number of species in each taxon.

Author	Taxa treated	No. of species
Hitchcock, 1935	*Muhlenbergia*, USA and Mexico	110
Pilger, 1956	Muhlenbergiinae with 8 sections	—
Soderstrom, 1967	*Muhlenbergia* subg. *Podosemum* (=*Trichochloa*) sect. *Epicampes*	26
Pohl, 1969	*Muhlenbergia* subg. *Muhlenbergia*	12
Türpe 1973	*Aegopogon*	3
J. Reeder, 1976	*Redfieldia*	1
C. Reeder, 1985	*Lycurus*	3
Peterson, 1989b	*Bealia*	1
Peterson and Annable, 1990	*Blepharoneuron*	2
Peterson and Annable, 1991	"annual" species of *Muhlenbergia*	29
Peterson and Annable, 1992	*Chaboissaea*	4
Morden and Hatch, 1996	*Muhlenbergia repens* complex	6
Herrera Arrieta, 1998	*Muhlenbergia montana* complex	15
Peterson, 2000	Muhlenbergiinae with 6 genera	165
Columbus et al., 2002	*Schaffnerella*	1

other types of data, i.e., leaf and embryo anatomy, *Muhlenbergia* became firmly placed in the Chloridoideae, although it has been aligned in a variety of tribes/subtribes, including Eragrostideae and Sporobolinae (Reeder, 1957; Stebbins and Crampton, 1961; Clayton and Renvoize, 1986; Peterson et al., 1995, 1997).

Species within the Muhlenbergiinae are morphologically highly variable and can be characterized as having membranous ligules (rarely a line of hairs); paniculate inflorescences that are rebranched or composed only of primary branches; spikelets that are usually solitary but sometimes in pairs or triads, with cleistogenes (self-pollinated flowers that do not open at maturity) occasionally present in the leaf sheaths; one floret (rarely more) per spikelet that is perfect, staminate, or sterile; glumes that are awned or unawned; lemmas 3-nerved, awned or unawned; and a base chromosome number of $x = 8–10$ (Peterson et al., 1995, 1997, 2007a, b; Peterson, 2000). Two subtypes of C_4 photosynthesis based on nicotinamide adenine dinucleotide cofactor malic enzyme (NAD-ME) and phosphoenolpyruvate carboxykinase (PCK) have been found in the Muhlenbergiinae with a few verified by biochemical assay (Gutierrez et al., 1974; Brown, 1977; Hattersley and Watson, 1992).

On the basis of anatomy, morphology, and cytology, Soderstrom (1967) distinguished two subgenera within *Muhlenbergia* and divided *M.* subg. *Podosemum* (Desv.) Soderstr. (=*M.* subg. *Trichochloa* A. Gray, an older name) into two sections, sect. *Podosemum* (Desv.) Pilg. and sect. *Epicampes* (J. Presl) Soderstr. Two years later, Pohl (1969) completed a revision of 12 closely related species that he believed represented the entire *M.* subg. *Muhlenbergia* in North America. Based on anatomy, morphology, cytology, and flavonoid chemistry, 29 annual species of *Muhlenbergia* have been investigated and placed in tentative natural groups (Peterson and Rieseberg, 1987; Peterson, 1988a, b, 1989a; Peterson et al., 1989; Peterson and Annable, 1991). Morden and Hatch (1987, 1996) investigated the anatomical and morphological variation of six species they referred to as the *M. repens* complex. A biosystematics study investigating the *M. montana* complex (consisting of 15 species) has been completed (Herrera and Grant, 1993, 1994; Herrera Arrieta, 1998). Molecular genetic data of intersimple sequence repeats (ISSRs) were investigated for *M. capillaris* (Lam.) Trin., *M. expansa* (Poir.) Trin., and *M. sericea* (Michx.) P. M. Peterson (Gustafson and Peterson, 2007).

The Muhlenbergiinae currently consists of 10 genera: *Aegopogon* (four spp. in North and South America; Türpe, 1973; Levin and Moran, 1989), *Bealia* (one sp., *B. mexicana* Scribn. in northern Mexico; Peterson, 1989b; Peterson et al., 1993), *Blepharoneuron* [two spp. in North America, *B. shepherdii* (Vasey) P. M. Peterson & Annable and *B. tricholepis* (Torr.) Nash, the latter an important range grass in the southwestern USA and northern Mexico; Peterson and Annable, 1990, 2003], *Chaboissaea* [four spp., three in central Mexico and *C. atacamensis* (Parodi) P. M. Peterson & Annable in Argentina and Bolivia; Peterson and Annable, 1992; Peterson and Herrera Arrieta, 1995; Sykes et al., 1997], *Lycurus* [three spp., including the amphitropical disjunct *L. setosus* (Nutt.) C. Reeder; Peterson and Morrone, 1998], *Muhlenbergia* [147 spp. centered in northern Mexico and the southwestern USA, containing the important range grass *M. montana* and the amphitropical disjuncts *M. arenicola* Buckley and *M. torreyi* (Kunth) Hitchc. ex Bush; Peterson and Ortíz Diaz, 1998; Peterson, 2003; Herrera Arrieta and Peterson, 2007; Peterson et al., 2007b; but also with seven species located in southeast Asia; Wu and Peterson, 2006]; *Pereilema* (four spp. in North, Central, and South America), *Redfieldia* [one sp., *R. flexuosa* (Thurb. ex A. Gray) Vasey in the southwestern USA, of probable hybrid origin; Reeder, 1976; Duvall et al., 1994], *Schaffnerella* [one sp., *S. gracilis* (Benth.) Nash in San Luis Potosí, Mexico; Columbus et al., 2002], and *Schedonnardus* [one sp., *S. paniculatus* (Nutt.) Trel., an amphitropical disjunct with spicate primary inflorescence branches]. Ninety-six percent of the species within the Muhlenbergiinae are native to the western hemisphere, and more than 80% of these are native to North America (Peterson et al., 2007a). Amphitropical disjuncts within the Muhlenbergiinae thus far tested have been shown to have North American origins (Peterson and Herrera Arrieta, 1995; Sykes et al., 1997; Peterson and Morrone, 1998; Peterson and Ortíz Diaz, 1998; Peterson et al., 2007a). Within *Muhlenbergia*, there are 127 species indigenous to North America (86%); 125 of these occur in Mexico (center of species diversity) and, of these, 56 are endemic (Peterson et al., 2007a).

In preliminary molecular analyses, *Muhlenbergia* has appeared paraphyletic, with all nine remaining genera of Muhlenbergiinae nested within (Duvall et al., 1994; Hilu and Alice, 2001; Columbus et al., 2007, 2010; Peterson et al., 2010). Plastid restriction site markers supported the inclusion of *Bealia* Scribn., *Blepharoneuron* Nash, *Chaboissaea* E. Fourn., *Lycurus*, *Pereilema* J. Presl, and *Redfieldia* Vasey in the same subtribe as *Muhlenbergia* (Duvall et al., 1994). Columbus et al. (1998) found that *Aegopogon* Humb. & Bonpl. ex Willd. and *Schaffnerella* Nash, traditionally placed near *Bouteloua* Lag., actually were closely aligned with the large genus *Muhlenbergia*. What is quite unusual about these two genera is that they do not at first appear morphologically similar to *Muhlenbergia*. *Aegopogon* has spikelets in triads with the central sessile floret perfect and the two lateral pedicelled florets staminate or sterile. *Muhlenbergia* has only solitary spikelets. Hilu and Alice (2001) in their phylogeny of the Chloridoideae based on *matK* sequences included *Schedonnardus* Steud. in a well-supported clade with *Aegopogon* and *Muhlenbergia*. On the basis of anatomical characters, *Muhlenbergia* appears to be divisible into three major groups corresponding to two subgenera, *Muhlenbergia* subg. *Muhlenbergia* and *M.* subg. *Trichochloa,* the latter subgenus with two sections, *Muhlenbergia* sect. *Epicampes* and *M.* sect. *Podosemum* (Peterson 2000; Peterson and Herrera Arrieta, 2001). Analyzing ITS and *trnL-trnF* sequences of 52 species of

Muhlenbergia, Columbus et al. (2010) also found support for two clades containing species of *Muhlenbergia* subg. *Muhlenbergia* and *M.* subg. *Trichochloa*. In a large molecular study of the entire Chloridoideae, Peterson et al. (2010) found strong support for the five clades within 33 sampled species of Muhlenbergiinae: *Muhlenbergia* subg. *Muhlenbergia*, *M.* subg. *Trichochloa*, *M.* sect. *Bealia*, *M.* subg. *Clomena*, and an unnamed clade that includes three species of *Chaboissaea*, two species of *Lycurus*, *Redfieldia*, *Schaffnerella*, *Schedonnardus*, *M. arenacea* (Buckley) Hitchc., *M. richardsonis* (Trin.) Rydb., and *M. uniflora* (Muhl.) Fernald.

Using an analysis of plastid and nuclear DNA sequences, we provide a clear phylogeny for 124 of the 176 (70%) species that occur in the Muhlenbergiinae. We estimate the phylogeny of the Muhlenbergiinae based on the analysis of seven molecular markers (nuclear ITS and plastid *ndhA* intron, *ndhF, rps16-trnK, rps16* intron, *rps3*, and *rpl32-trnL* DNA sequences). Previously, Columbus et al. (2010) considered 52 species of *Muhlenbergia* (plus 14 additional species from the other nine Muhlenbergiinae genera) for two molecular markers (nuclear ITS and plastid *trnL-F* DNA sequences). We include an expanded survey of the Muhlenbergiinae by sampling an additional 105 species for seven markers (687 new sequences), which is a significant advance over Peterson et al. (2010) and Columbus et al. (2010). Our study includes 109 species of *Muhlenbergia,* 15 additional species from the other nine Muhlenbergiinae genera and sequences for six plastid and ITS markers. We compare the ITS and plastid based phylogenies with the classifications in Columbus et al. (2010) and Peterson et al. (2001, 2007a, 2010). In addition, we seek morphological and anatomical characters supporting relationships in the molecular phylogenies and propose changes to the classification.

MATERIALS AND METHODS

Taxon sampling—Representatives of 37 genera were chosen as outgroups from the Chloridoideae clade in Peterson et al. (2010): *Aeluropus*, *Allolepis*, *Astrebla*, *Austrochloris*, *Blepharidachne*, *Bouteloua*, *Chloris*, *Crypsis*, *Cynodon*, *Dasyochloa*, *Distichlis*, *Eleusine*, *Erioneuron*, *Gouinia*, *Gymnopogon*, *Hilaria*, *Jouvea*, *Lepturus*, *Microchloa*, *Monanthochloe*, *Monelytrum*, *Mosdenia*, *Munroa*, *Orinus*, *Perotis*, *Pogonarthria*, *Scleropogon*, *Sohnsia*, *Sporobolus*, *Swallenia*, *Tragus*, *Trichoneura*, *Tridens*, *Trioidia*, *Vaseyochloa*, *Willkommia*, and *Zoysia* (for a complete list of species see Appendix 1).

Voucher information and GenBank numbers for 178 accessions representing 162 species are given in Appendix 1. Fifteen of the accessions included a second sample from a different location for the same species. All vouchers are deposited in the Smithsonian Institution, United States National Herbarium (US). The majority of samples (89%) used in this study were collected by P. M. Peterson from 1984 to 2008. In addition, where feasible, we sampled older herbarium specimens to maximize the number of outgroup genera in the Chloridoideae.

Molecular methods—All procedures where performed in the Laboratory of Analytical Biology (LAB) at the Smithsonian Institution. DNA was isolated using the BioSprint 96 DNA Plant Kit (Qiagen, Valencia, California, USA) following the protocol of the manufacturer. PCR amplifications were performed in MJ Research or PE 9700 thermal cyclers. Genomic DNA was combined with 1× reaction buffer (200 mM Tris-HCl, 500 mM NH_4) [Bioline Biolase Taunton, Madison, Wisconsin, USA] without Mg^{2+}, 2 mM $MgCl_2$, 200 mM dNTPs, 1.5 μL of *Taq* polymerase (Bioline Biolase Taunton), 40 pmol/μL each of forward and reverse primers.

We targeted seven regions for sequencing: three from the plastid large single copy (LSC) region: *rps3* (coding), *rps16* intron, and 3′*rps16*-5′*trnK* (spacer); three from the small single copy (SSC) region: *ndhF* (coding), *ndhA* intron, and *rpl32-trnL* (spacer); and nrDNA ITS. Intergenic spacers *rpl32-trnL* (SSC) and *rps16-trnK* (LSC) are two of the top ranked, most variable noncoding regions for phylogenetic studies in the angiosperms (Shaw et al., 2007). We chose the widely used *ndhF* gene (SSC) to recover phylogenetic relationships because it proved useful in other groups of grasses (Giussani et al., 2001; Soreng et al., 2007; Romaschenko et al., 2010). The sequences, melting temperature, quality, and references for the primers used are given in Peterson et al. (2010).

The amplification parameters for all plastid and the nuclear ribosome ITS regions follow Peterson et al. (2010). All PCR products were cleaned with ExoSAP-IT (USB, Cleveland, Ohio, USA). DNA sequencing was performed with BigDye Terminator Cycle Sequencing v.3.1 (PE Applied Biosystems, Foster City, California, USA) according to the following parameters: 80°C, 5 min; 25 or 30 cycles of 95°C for 10 s, 50°C for 5 s and 60°C for 4 min. Sequenced products were analyzed on an ABI PRISM 3730 DNA Analyzer 7900HT. The regions *rpl32-trnL*, *rps3*, *rps16* intron, 3′*rps16*-5′*trnK*, *ndhF* (coding region), and ITS were sequenced in one direction. Relatively short regions (500–750 bp) covered by our primers were easily interpreted allowing us to accumulate sequences from different parts of the genome for phylogenetic inference (Shaw et al., 2005, 2007). The *ndhA* intron (933 bp) was sequenced in both directions and the program Sequencher 4.8 (Gene Code Corp., Ann Arbor, Michigan, USA, 1991–2007) was employed to produce the contig sequence for the entire region.

Phylogenetic analyses—Sequence alignment was done manually using the program BioEdit v.7.0.5.3 (Hall, 1999). Several ambiguously aligned regions were excluded from analyses. The length of sequences and amount of excluded data for each region is presented in Table 2. We used the maximum parsimony analysis implemented in PAUP* to calculate the tree length (TL), consistency index (CI), homoplasy index (HI), retention index (RI), and rescaled consistency index (RC) for separate and combined regions (Table 2). No data were excluded from *rps3, rps16* intron, and *ndhA* intron. All gaps were treated as missing data. We used maximum likelihood and Bayesian analysis to infer phylogeny. The maximum likelihood (ML) analysis was conducted with the program GARLI 0.951 (Zwickl, 2006). Bayesian and maximum likelihood analyses yielded trees

TABLE 2. Summary data for six plastid regions and nrDNA ITS used in this study.

Characteristic	*ndhF*	*rpl32-trnL*	*rps16-trnK*	*rps3*	*rps16* intron	*ndhA* intron	Plastid	ITS	Combined plastid+ITS
Aligned sequence length	796	1389	1222	590	1368	1424	6789	814	7603
Average sequence length	734	695	723	579	745	933	4409	669	5078
No. of taxa	163	175	174	174	165	161	177	172	179
No. of excluded characters	2	364	213	0	0	0	579	89	743
Proportion of excluded characters (%)	0.3	26.2	17.4	0.0	0.0	0.0	8.5	10.9	9.8
No. of PIC	169	258	221	85	159	256	1148	312	1460
PIC/SL	0.230	0.371	0.306	0.147	0.213	0.274	0.260	0.466	0.288
Tree length	569	761	575	254	400	708	3369	2373	5859
Consistency index	0.4271	0.5361	0.5513	0.4764	0.5800	0.5508	0.508	0.284	0.407
Homoplasy index	0.5729	0.4639	0.4487	0.5236	0.4200	0.4492	0.492	0.716	0.593
Retention index	0.8344	0.8450	0.8428	0.8679	0.8768	0.8674	0.844	0.689	0.784
Rescaled consistency index	0.3564	0.4530	0.4646	0.4135	0.5086	0.4778	0.429	0.196	0.319
Akaike information criterion	GTR+G	TVM+G	TVMef+G	TVM+G	K81uf+G	K81uf	GTR+G	GTR+G	GTR+G

Notes: PIC, parsimony informative characters; SL = sequence length with visually similar topology, i.e., the trees are visually the same, but some branch lengths could differ minutely. A test run of Bayesian analysis for the combined data sets under the single GTR+G model yielded the same topology and posterior probability (PP) values as the Bayesian analysis for a partitioned data set performed under models suggested by MODELTEST for separate regions.

The Akaike information criterion (AIC) scores are indicated in Table 2 (Kimura, 1981; Tavaré, 1986; Posada and Crandall, 1998). Very little conflict was observed among maximum likelihood trees in the individual plastid analyses. The incongruence length difference (ILD) test (Farris et al., 1994) was implemented in the program WinClada ver. 1.00.08 (Nixon, 2002) to test for incongruence between the ITS and plastid data sets. Default parameters for 1000 replicates were executed.

Bootstrap analyses (Felsenstein, 1985) were performed for the ML analysis using GARLI with the default parameters for 1000 replicates, with the program PAUP* ver. 4.0b10 (Swofford, 2000) used to compute the bootstrap consensus tree. Bootstrap (BS) values of 90–100% were interpreted as strong support, 70–89% as moderate, and 50–69% as weak.

Bayesian posterior probabilities were estimated using the program MRBAYES ver. 3.01 (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2005) with DNA substitution models selected using the program MrModeltest ver. 1.1b (Nylander, 2002). The plastid data set and combined plastid+ITS data set for Bayesian analysis were then partitioned into two subsets that were processed implementing different parameters suggested by MrModeltest concerning the model for among site rate variation, number of substitution types, substitution rates, and gamma shape parameter. All other parameters were left at default settings. Each Bayesian analysis was initiated with random starting trees and was initially run for 2 million generations, sampling once per 100 generations. The analysis was continued until the value of standard deviation of split sequences dropped below 0.01 as the convergence diagnostic value (Huelsenbeck and Ronquist, 2001). The fraction of the sampled values discarded as burn in was set at 0.25.

RESULTS

Phylogenetic analyses—A total of 687 sequences representing 105 species are newly reported in GenBank (Appendix 1). Lengths sequenced for individual regions are noted in Table 2. Plastid *rpl32-trnL* had the highest rate of amplification and successful sequencing with 99% of taxa recovered across the entire data set. Recovery in other plastid regions ranged from 91–98%, and the effectiveness of sequencing the ITS region was 97% (Table 2). An average of 4.5% of data was missing across the entire data set. As expected, ITS provided the most information per aligned nucleotide (Table 2; the ratio of the number of parsimony informative characters (PIC) per sequence length (SL) was 0.466, compared with 0.147–0.371 for plastid regions).

Analysis of ITS sequences—There are five major clades within a monophyletic Muhlenbergiinae (moderate support), labeled in Fig. 1 as *Muhlenbergia* sect. *Bealia* (strong support), *M*. subg. *Trichochloa* (strong support), *M*. subg. *Clomena* (moderate support), *M*. sect. *Pseudosporobolus* (weak support), and *M*. subg. *Muhlenbergia* (moderate support). *Muhlenbergia* sect. *Bealia* and subg. *Trichochloa* share a common ancestor (strong support), and *M*. subg. *Clomena* and sect. *Pseudosporobolus* form a clade (moderate support) that is sister to *M*. subg. *Muhlenbergia* (strong support). *Muhlenbergia ramulosa* is sister to the rest of the Muhlenbergiinae.

Muhlenbergia sect. *Bealia* consists of 20 taxa and contains strongly supported clades of *M. caxamarcensis* and *M. filiformis*; two accessions of *Blepharoneuron shepherdii*; *M. argentea*, *M. eludens*, and *M. flavida*; *M. arenicola* and *M. torreyi*, which are sister to eight annual species; and *M. minutissima* and *M. sinuosa*. There are 42 taxa included within *M*. subg. *Trichochloa* clade (six of these have two samples per species) and these show very little sequence divergence because all branches are very short. A single clade exhibits strong support for two accessions of *M. lucida*. *Muhlenbergia* subg. *Clomena* contains 11 taxa (two of these have two samples per species) divided into two well-supported clades: *M. durangensis*-*M. flaviseta* sister to the remaining species. *Muhlenbergia* sect. *Pseudosporobolus* consists of 22 taxa (three of these have two samples per species) and contains strongly supported clades comprising *M. implicata* and *M. jaime-hintoni*; two different accessions of *M. uniflora*; *M. fastigiata* sister to two accessions of *M. richardsonis*; two different accessions of *Lycurus setosus*; and *Chaboissaea subbiflora*, *C. atacamensis*, and *C. ligulata*. There are 38 taxa within *M*. subg. *Muhlenbergia* (two of these have two samples per species) with seven well-supported clades: *M. spiciformis* and *M. tenuifolia*; *M. appressa, M. brandegei*, and *M. microsperma*; *Pereilema beyrichianum* and *P. crinitum*; *M. ciliata*, *M. pectinata*, and *M. tenella*; *Aegopogon cenchroides* and *A. tenellus*; *M. andina*, *M. curtifolia*, and *M. thurberi*; and *M. sobolifera* and *M. tenuiflora*.

Analysis of plastid sequences—As in the ITS tree, five major clades appear to be within a monophyletic Muhlenbergiinae (strongly supported), and these are labeled in Fig. 2 as *Muhlenbergia* sect. *Bealia* (weakly supported), *M*. subg. *Trichochloa* (moderately supported), *M*. subg. *Clomena* (moderately supported), *M*. sect. *Pseudosporobolus* (weakly supported), and *M*. subg. *Muhlenbergia* (strongly supported). Species composition in each of these five clades is identical with the ITS-derived phylogram, except for the five additional taxa included in the data set. As in the ITS-derived phylogram, *Muhlenbergia* sect. *Bealia* and subg. *Trichochloa* share a common ancestor (strongly supported), and *M*. subg. *Clomena* and sect. *Pseudosporobolus* form a clade (moderately supported) that is sister to *M*. subg. *Muhlenbergia* (moderately supported. *Muhlenbergia ramulosa* is sister to *M*. sect. *Bealia* and *M*. subg. *Trichochloa* (strongly supported).

There is considerably higher backbone support among clades within *Muhlenbergia* sect. *Bealia*, and there is one additional taxon not included in the ITS data set, *M. vaginata*, that forms a clade with *M. filiformis* (strongly supported); sister to this is *M. caxamarcenis* (strongly supported). Other strongly supported clades in *M*. sect. *Bealia* include *M. arizonica*-*M. argentea*-*M. eludens*-*M. flavida*, two species of *Blepharoneuron* with two accessions of *B. shepherdii*, and two clades that are sister: ((*M. minutissima, M. texana*)(*M. sinuosa* (*M. brevis, M. depauperata*))) and ((*M. arenicola*, *M. torreyi*)(*M. fragilis* (*M. annua, M. majalcensis*))).

Muhlenbergia subg. *Trichochloa* contains more internal support as compared to the ITS-derived phylogeny with strong support for separate clades containing *M. elongata*, *M. emersleyi*, and *M. lucida*; and *M. involuta*, *M. reverchonii*, and *M. sericea.* The two accessions each of *M. dubia*, *M. lucida*, *M. pubescens*, and *M. rigida* do not form sister groups. In the *M*. subg. *Clomena* clade, *Muhlenbergia filiculmis*, *M. jonesii*, two accessions of *M. montana* and *M. virescens*, *M. quadridentata* and *M. straminea* form a well-supported clade; sister to this are *M. crispiseta*-*M. peruviana* pair (strongly supported). As in the ITS-derived phylogeny, *M. durangensis*-*M. flavida* pair (strongly supported) is sister to the remaining species in *M*. subg. *Clomena*.

Backbone support for *M*. sect. *Pseudosporobolus* is much higher in the plastid-derived phylogram, and the topology is somewhat different than in the ITS tree. Strongly supported clades include two accessions of *Lycurus setosus*, *M. palmirensis*-*M. villiflora* var. *villosa*, *Chaboissaea subbiflora* sister

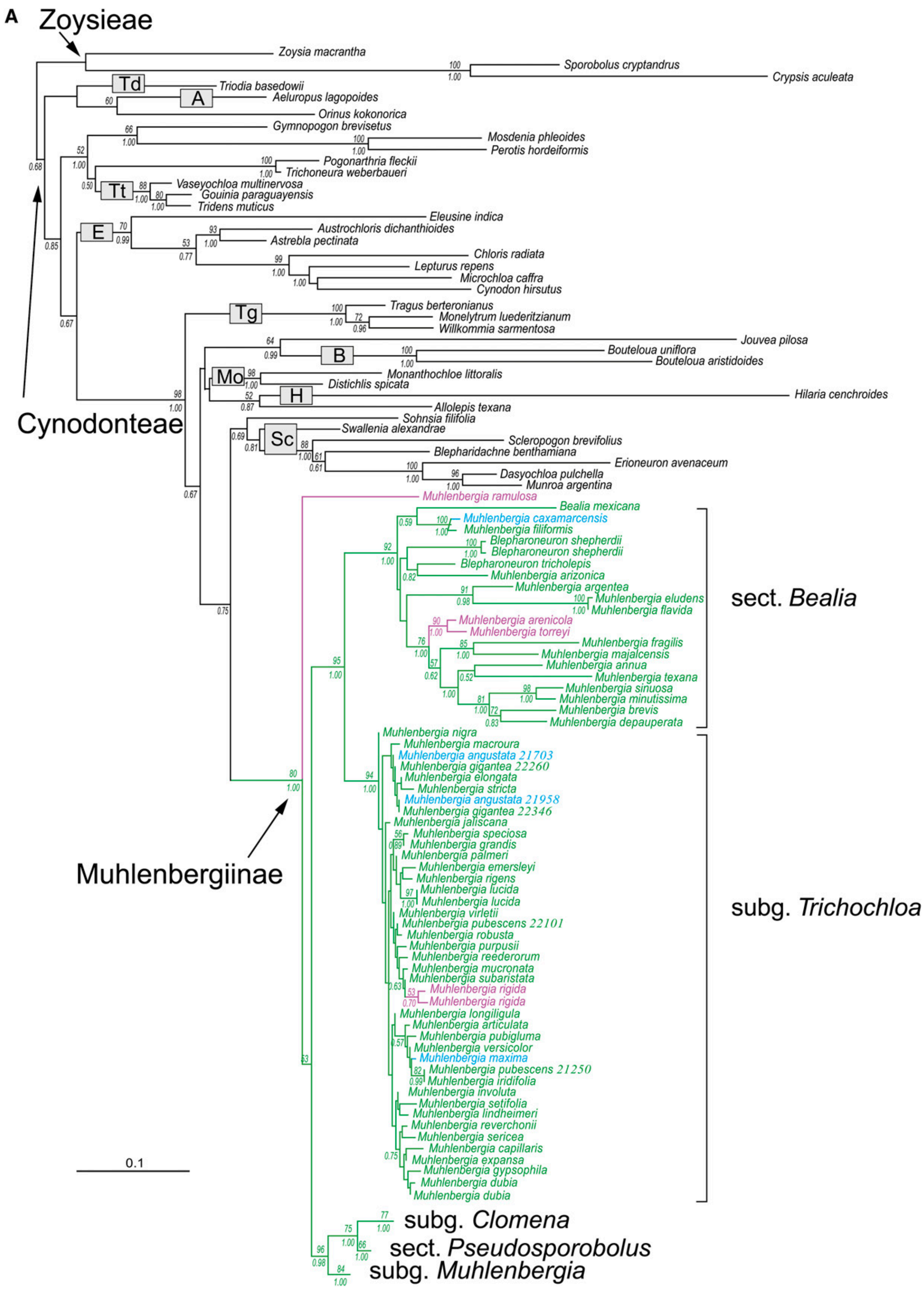
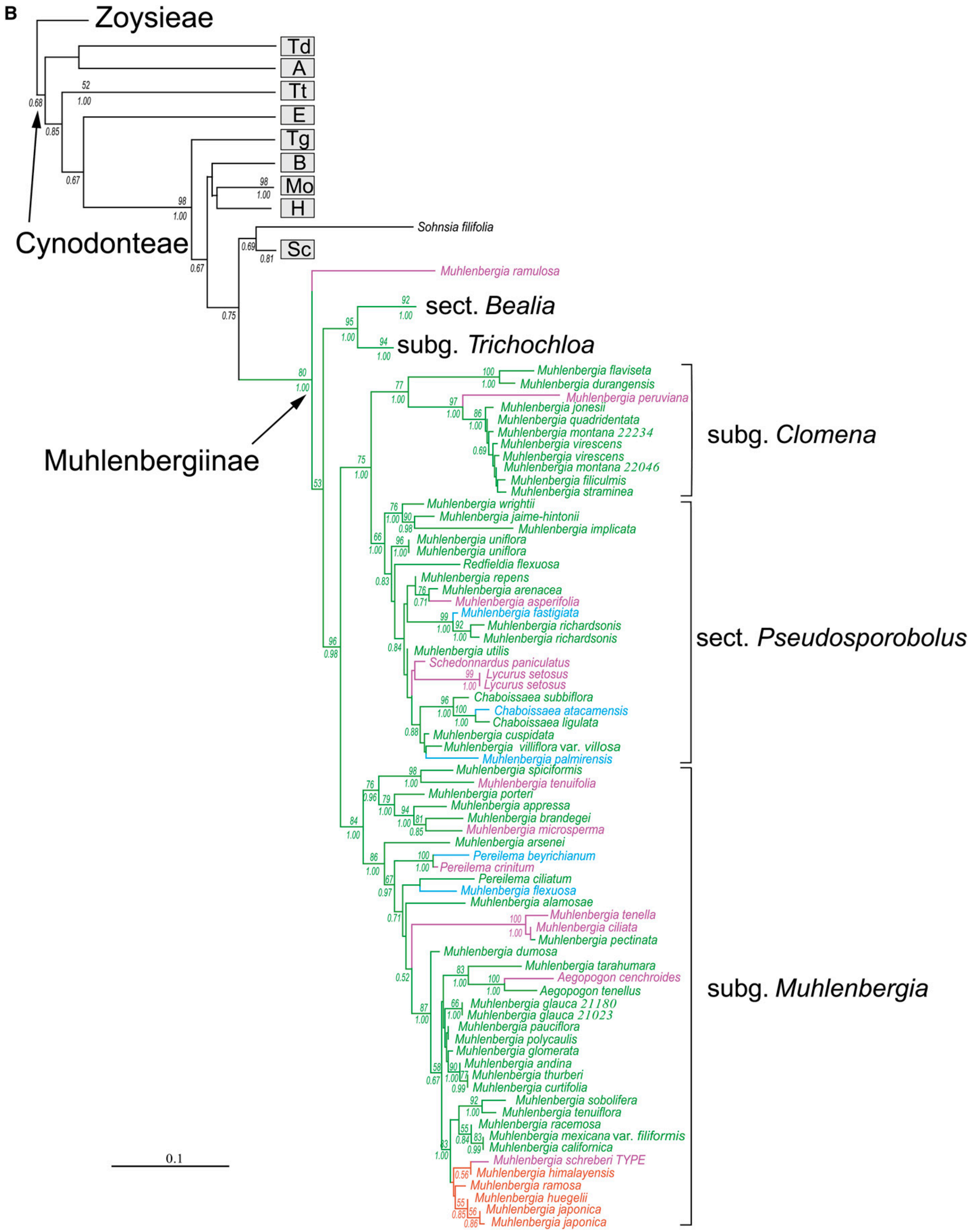


Fig. 1. Phylogram of best maximum likelihood tree from analysis of nuclear ITS data. Numbers above branches represent bootstrap values; numbers below branches are posterior probability values. (A) Detail of upper portion and (B) lower portion of phylogram. Abbreviations for subtribes: A = Aeluropodinae, B = Boutelouinae, E = Eleusininae, H = Hilariinae, Mo = Monanthochloinae, Sc = Scleropogoninae, Td = Triodinae, Tg = Traginae, Tt = Tridentinae. Taxon color indicates native distribution: green = North America, blue = South America, purple = North and South America, red = southeast Asia.


B
Zoysieae
Td
A
Tt
E
Tg
B
Mo
H
Cynodonteae
Sohnsia filifolia
Sc
Muhlenbergia ramulosa
sect. Bealia
subg. Trichochloa
Muhlenbergiinae
Muhlenbergia flaviseta
Muhlenbergia durangensis
Muhlenbergia peruviana
Muhlenbergia jonesii
Muhlenbergia quadridentata
Muhlenbergia montana 22234
Muhlenbergia virescens
Muhlenbergia virescens
Muhlenbergia montana 22046
Muhlenbergia filiculmis
Muhlenbergia straminea
subg. Clomena
Muhlenbergia wrightii
Muhlenbergia jaime-hintonii
Muhlenbergia implicata
Muhlenbergia uniflora
Muhlenbergia uniflora
Redfieldia flexuosa
Muhlenbergia repens
Muhlenbergia arenacea
Muhlenbergia asperifolia
Muhlenbergia fastigiata
Muhlenbergia richardsonis
Muhlenbergia richardsonis
Muhlenbergia utilis
Schedonnardus paniculatus
Lycurus setosus
Lycurus setosus
Chaboissaea subbiflora
Chaboissaea atacamensis
Chaboissaea ligulata
Muhlenbergia cuspidata
Muhlenbergia villiflora var. villosa
Muhlenbergia palmirensis
sect. Pseudosporobolus
Muhlenbergia spiciformis
Muhlenbergia tenuifolia
Muhlenbergia porteri
Muhlenbergia appressa
Muhlenbergia brandegei
Muhlenbergia microsperma
Muhlenbergia arsenei
Pereilema beyrichianum
Pereilema crinitum
Pereilema ciliatum
Muhlenbergia flexuosa
Muhlenbergia alamosae
Muhlenbergia tenella
Muhlenbergia ciliata
Muhlenbergia pectinata
Muhlenbergia dumosa
Muhlenbergia tarahumara
Aegopogon cenchroides
Aegopogon tenellus
Muhlenbergia glauca 21180
Muhlenbergia glauca 21023
Muhlenbergia pauciflora
Muhlenbergia polycaulis
Muhlenbergia glomerata
Muhlenbergia andina
Muhlenbergia thurberi
Muhlenbergia curtifolia
Muhlenbergia sobolifera
Muhlenbergia tenuiflora
Muhlenbergia racemosa
Muhlenbergia mexicana var. filiformis
Muhlenbergia californica
Muhlenbergia schreberi TYPE
Muhlenbergia himalayensis
Muhlenbergia ramosa
Muhlenbergia huegelii
Muhlenbergia japonica
Muhlenbergia japonica
subg. Muhlenbergia
0.1

to *C. atacamensis*-*C. ligulata*, *Redfieldia flexuosa* sister to two accessions of *M. uniflora*, *M. fastigiata* sister to *M. repens*-*M. utilis* with these three sister to two accessions of *M. richardsonis*. One other large clade with strong support includes *Schedonnardus paniculatus* as sister to a clade of (in phylogenetic order) three species of *Chaboissaea*, *M. cuspidata*, *M. palmirensis*-*M. villiflora* var. *villosa*, *M. wrightii*, *Schaffnerella gracilis*, and two accessions of *Lycurus setosus*. *Muhlenbergia jaime-hintoni* is sister to *Redfieldia flexuosa*-*M. uniflora* (Fig. 2B) rather than to *M. implicata* in the ITS tree (Fig. 1B).

The topology of the plastid-derived phylogram for *M*. subg. *Muhlenbergia* is similar to that portrayed by the ITS-derived phylogram, although many branches have higher support values and the topology of a few clades is different. A derived, moderately supported clade with all species occurring in southeast Asia includes *M. ramosa* sister (strongly supported) to two accessions of *M. japonica* (moderately supported) and *M. himalayensis*-*M. huegelii* (strongly supported). Other strongly supported clades include*M. racemosa*-*M. tenuiflora* (in the ITS tree, *M. tenuiflora* forms a strongly supported clade with *M. sobolifera*), *M. andina* sister to *M. curtifolia*-*M. thurberi*, *M. pauciflora* and *M. glauca* 21023 (there are two different accessions for this species, see Appendix 1) -*M. polycaulis*, *Pereilema beyrichianum*-*P. crinitum*, *M. breviseta*-*M. dumosa*, *M. alamosae* sister to *M. tarahumara* that is sister to *Aegopogon cenchroides*-*A. tenellus*, *M. arsenei* (in the ITS tree, *M. arsenei* is sister to *Pereilema crinitum*-*P. beyrichianum*) sister to *M. tenella* -*M. ciliata*-*M. pectinata*, *M. spiciformis*-*M. tenuifolia* sister to *M. porteri* that is sister to *M. appressa*-*M. brandegei*-*M. microsperma*. *Muhlenbergia mexicana* var. *filiformis* is a moderately supported sister to clade (*M. sobolifera* (*M. californica* (*M. racemosa*, *M. tenuiflora*))), whereas in the ITS tree it is sister to *M. californica* in a larger clade, ((*M. sobolifera*, *M. tenuiflora*)(*M. racemosa* (*M. californica*, *M. mexicana* var. *filiformis*))).

Analysis of combined plastid and ITS sequences—The ILD test ($P = 0.1667$; 99% confidence level) failed to reject the null hypothesis of congruence between the ITS and plastid data sets; therefore, we combined them. As in the ITS and combined plastid trees, five major clades seem to be within a monophyletic Muhlenbergiinae (strongly supported), and these are labeled in Fig. 3 as *Muhlenbergia* sect. *Bealia* (strongly supported), *M*. subg. *Trichochloa* (strongly supported), *M*. subg. *Clomena* (moderately supported), *M*. sect. *Pseudosporobolus* (moderately supported), and *M*. subg. *Muhlenbergia* (strongly supported). Species composition in each of these five clades is again identical with the ITS and plastid-derived phylograms. As in the other analyses, *Muhlenbergia* sect. *Bealia* and subg. *Trichochloa* share a common ancestor (strongly supported), and *M*. subg. *Clomena* and sect. *Pseudosporobolus* form a clade (strongly supported) that is sister to *M*. subg. *Muhlenbergia* (strongly supported). *Muhlenbergia ramulosa* is sister to *M*. sect. *Bealia* and *M*. subg. *Trichochloa* as in the ITS-derived phylogram.

The overall topology of the combined phylogram is remarkably similar to that of the plastid-derived tree, even in the terminal branches. There are only some minor differences with the plastid phylogeny, most notably in *M*. sect. *Pseudosporobolus* where *M. fastigiata* is sister (strongly supported) to two accessions of *M. richardsonis* and in *M*. subg. *Muhlenbergia* where *M. sobolifera*-*M. tenuiflora* form a clade (strongly supported) that is sister (strongly supported) to *M. racemosa*, *M. californica*, and *M. mexicana* var. *filiformis*. However, these relationships were depicted in the ITS-derived phylogram. Therefore, in the following sections we will refer to the combined plastid ITS-derived phylogram when discussing evolutionary scenarios. In the discussion section, we make all necessary combinations and new names within *Muhlenbergia.*

Analysis of outgroups—Determination of the sister to the Muhlenbergiinae allows us to test the monophyly of the subtribe and to polarize morphological and anatomical characters. The ITS and plastid trees differed in relative branch length, support values that occur on these branches, and topology among the 38 taxa used as outgroups. In the ITS phylogram (Fig. 1) the sister to the Muhlenbergiinae was a clade (PP = 0.75) containing *Sohnsis filifolia* as sister to the Scleropogoninae. In the plastid and combined ITS/plastid tree (Figs. 2, 3), *Sohnsia filifolia* was sister to the Muhlenbergiinae, and the Scleropogoninae was the sister group to both of these. Relative positions of *Swallenia*, *Tragus*, and *Jouvea* differ among the ITS, plastid, and combined ITS/plastid phylograms. Relationships among these three taxa in the tribe Cynodonteae have been thoroughly investigated by Peterson et al. (2010) using a much broader sample.

DISCUSSION

Monophyly of the Muhlenbergiinae is moderately to strongly supported by our data in all trees and *Muhlenbergia*, as traditionally treated by agrostologists, is depicted as paraphyletic with *Aegopogon*, *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Lycurus*, *Pereilema*, *Redfieldia*, *Schaffnerella*, and *Schedonnardus* embedded within this clade (Duvall et al., 1994; Hilu and Alice, 2001; Columbus et al., 2007, 2010; Peterson et al., 2010). Because the monophyly of *Muhlenbergia* s.s. or s.l. is not supported by phylogenetic analysis of ITS, *matK*, *ndhA* intron, *ndhF, rps16-trnK, rps16* intron, *rps3*, and *rpl32-trnL, trnL-trnF* sequences, and RFLP studies (Duvall et al., 1994; Hilu and Alice, 2001; Columbus et al., 2007, 2010; Peterson et al., 2010), we are incorporating all nine genera within *Muhlenbergia*. Within the *Muhlenbergia* clade (=Muhlenbergiinae) there are five large, well-supported clades: *Muhlenbergia* sect. *Bealia*, *M.* subg. *Trichochloa*, *M.* subg. *Clomena*, *M.* sect. *Pseudosporobolus*, and *M*. subg. *Muhlenbergia*.

The *M*. subg. *Muhlenbergia* clade includes only species that exhibit PCK-like leaf anatomical characteristics, where the chlorenchyma is composed of tabular cells that are indistinctly radiate and continuous between bundles [PCK type, defined as centrifugal/evenly distributed photosynthetic carbon reduction (PCRD) cell chloroplasts (with grana), the major veins (which, at maturity have a protoxylem lacuna and large metaxylem elements) are surrounded by two bundle sheaths, an inner mestome sheath of elongate nonchlorenchymatous cells and an outer chlorenchymatous sheath of shorter PCRD cells (designated XyMS+structural type; Hattersley and Watson, 1976, 1992; Dengler et al., 1986) with suberized lamella, fan- to shield-shaped bulliform cells without formation of a complete column of colorless cells from the adaxial to the abaxial surface, and species that have four or more secondary and/or tertiary vascular bundles between consecutive primary vascular bundles (Peterson and Herrera Arrieta, 2001). Morphologically, members of the *M*. subg. *Muhlenbergia* clade have broad, flat leaf blades, most have well-developed, scaly, and creeping rhizomes, and panicles that are usually narrow at maturity

(*M. porteri* is an exception with open, 6–15 cm wide panicles) (Peterson, 2003). Our study supports a previous hypothesis of Peterson and Herrera Arrieta (2001) that within *Muhlenbergia* the evolution of the PCK subtype of photosynthesis was a single evolutionary event. Early in the evolution of *Muhlenbergia*, the PCK-like condition appears to have arisen once, because all species that have been chemically assayed as PCK occur in this clade (Gutierrez et al., 1974; Brown, 1977). Ecologically, *Muhlenbergia* PCK-like species are able to flourish in shaded sites and forest margins with low-light intensities and moist-humid microhabitats that are not normally occupied by their NAD-ME relatives.

In our ITS phylogram within the *M.* subg. *Muhlenbergia* clade, species of *Pereilema* do not appear monophyletic because they form a poorly supported grade (BS = 67, PP = 0.97), and *P. ciliatum* is paired with *M. flexuosa* (unsupported). In our plastid and combined phylogram, all species of *Pereilema* form a weak to moderately supported clade. Because it would require quite a few parallel evolutionary events to select for the morphological features expressed in this genus, our plastid markers may be a better estimate of phylogeny in this lineage. All four species of *Pereilema* have two unique characters: sterile, bristle-like spikelets that subtend the fertile spikelets and prominent blade auricles that are usually ciliate (Peterson, 2000).

Embedded with *M.* subg. *Muhlenbergia* is a strongly supported clade containing *Aegopogon cenchroides* and *A. tenellus*. The four species of *Aegopogon* have a false spike with each branch usually bearing three spikelets with one larger spikelet perfect and the other two smaller and often staminate or rudimentary (two spikelets in *A. bryophilus* Döll with one spikelet often not developed) (Peterson, 2000). The recently described species *M. tarahumara* (Peterson and Columbus, 2009) was found in our study to be sister to *Aegopogon* in all trees. *Muhlenbergia tarahumara* differs from other species of *Aegopogon* by having panicle branches with only two terminal, perfect spikelets (Peterson and Columbus, 2009). Anatomically, *M. tarahumara* also differs from other species in *M.* subg. *Muhlenbergia* by having noncontiguous chlorenchyma separated by columns of colorless cells between adjacent vascular bundles. Other species in this clade (*M. pauciflora* and *M. polycaulis*) exhibit this leaf anatomical characteristic, at least near the middle of the blades. However, near the leaf margins, the tertiary vascular bundles of these latter two species have chlorenchyma tissue that is continuous between each adjacent vascular bundle. All other characteristics, i.e., presence of two bundle sheaths, uneven outline of the outer sheath, round shape of chloroplasts in the outer sheath, and centrifugal/peripheral position of the chloroplasts in each cell, are predictive of PCK for *M. pauciflora*, *M. polycaulis*, and *M. tarahumara*. Because the habitat where *M. tarahumara* is found is rather xeric (slopes, ridge tops, rock outcrops), the columns of colorless cells between adjacent vascular bundles, like most NAD-ME species, facilitate involution of the leaf blades, an adaption to periods of drought. PCK-like leaf anatomy appears to have arisen once in the evolution of the Muhlenbergiinae, and this morphology is linked to species that occupy slightly more mesic habitats (Peterson and Herrera Arrieta, 2001). The anatomical structure found in *M. tarahumara,* and to some extent in *M. pauciflora* and *M. polycaulis,* might be in direct response to the environment where reversion to NAD-ME-like leaf structure is likely an adaptive feature.

The Chinese species *M. himalayensis*, *M. hueglii*, *M. japonica*, and *M. ramosa* form a clade within *M.* subg. *Muhlenbergia* with moderate bootstrap support in the plastid and combined plastid/ITS phylograms, suggesting a single colonization event, most likely from North American origins. Only seven native species of *Muhlenbergia* occur in southeast Asia, and all seven are reported in the flora of China (Wu and Peterson, 2006). The Asian species of *Muhlenbergia* are predominately rhizomatous (only *M. duthieana* Hack. is loosely caespitose without rhizomes) and occur in similar habitats to most species in *M.* subg. *Muhlenbergia*, such as mountain slopes, forests, and along moist roadsides. *Muhlenbergia californica*, *M. mexicana* var. *filiformis*, *M. racemosa*, *M. schreberi*, *M. sobolifera*, and *M. tenuiflora* are sister to these Chinese species, and together they are sister to the remaining species within *M.* subg. *Muhlenbergia*, suggesting that colonization from North America to southeastern Asia occurred relatively recently in the evolution of this subgenus (Figs. 1–3).

Three sections of *Muhlenbergia* recognized by Pilger (1956): sect. *Acroxis* (*M. dumosa*, *M. mexicana*, *M. polycaulis*, and *M. racemosa*), sect. *Muhlenbergia* (*M. schreberi*), and sect. *Stenocladium* (*M. bushii* R. W. Pohl, *M. hueglii*, *M. japonica*, *M. ramosa*, *M. sobolifera*, and *M. tenuiflora*) included species in our subg. *Muhlenbergia* clade. In our phylograms, there are no clades that correspond with Pilger's sections; therefore, we agree with earlier authors that his treatment was not phylogenetically informative (Soderstrom, 1967; Pohl, 1969; Morden, 1985; Peterson and Annable, 1991).

Although the clade of species representing the *M.* subg. *Trichochloa* is strongly supported in our analyses (Figs. 1, 3), there is little resolution among members, likely reflecting very low levels of divergence within our plastid and nrDNA ITS sequences. The low level of divergence may be a consequence of rapid speciation events. It is possible that some species delimitations of subg. *Trichochloa* are not tenable because of recent diversification although it may also be the case that suitable molecular markers have yet to be applied. Within *Muhlenbergia*, this group is by far the most difficult to determine because there are very few morphological differences among the taxa and discrete (nonplastic) characteristics are few. Anatomically, most species in this clade have sclerosed phloem, a crown of inflated cells located adaxially to the primary vascular bundles, unequal secondary and tertiary vascular bundles, and primary vascular bundles that are either rectangular or obovate/elliptic in shape (Peterson and Herrera Arrieta, 2001). Species in *M.* subg. *Trichochloa* are erect, relatively tall (0.8–3 m), robust and stout, caespitose perennials that have unnerved or 1-nerved glumes (Soderstrom, 1967; Peterson, 2000). Pilger (1956) recognized *M.* sect. *Cinnastrum* with narrowly contracted, spicate panicles (*M. angustata, M. macroura*, and *M. rigens*) and *M.* sect. *Podosemum* with open panicles, lemmas long aristate, new shoots inside the sheaths (intravaginal), and ligule extended (*M. articulata*, *M. capillaris*, *M. distichophylla*, *M. longiglumis*, *M. rigida*, and *M. stricta*). Pilger's two sections do not include the same species as *M.* subg. *Trichochloa* sects. *Epicampes* and *Podosemum* as described in Peterson and Herrera Arrieta (2001), but the species treated by Soderstrom (1967) in his subg. *Podosemum* (=*M.* subg. *Trichochloa*) are the same.

The clade of *M.* subg. *Clomena* (=*M. montana* complex sensu Herrera Arrieta, 1998) is moderately supported in our analysis, and morphologically, this complex includes species that have 3-nerved upper glumes that are often 3-toothed and densely caespitose individuals with lower leaf sheaths that become flat and somewhat papery at maturity (Reeder and Reeder, 1995; Herrera Arrieta, 1998). *Muhlenbergia argentea*, a species with 1-nerved upper glumes, slightly compressed-keeled sheaths,

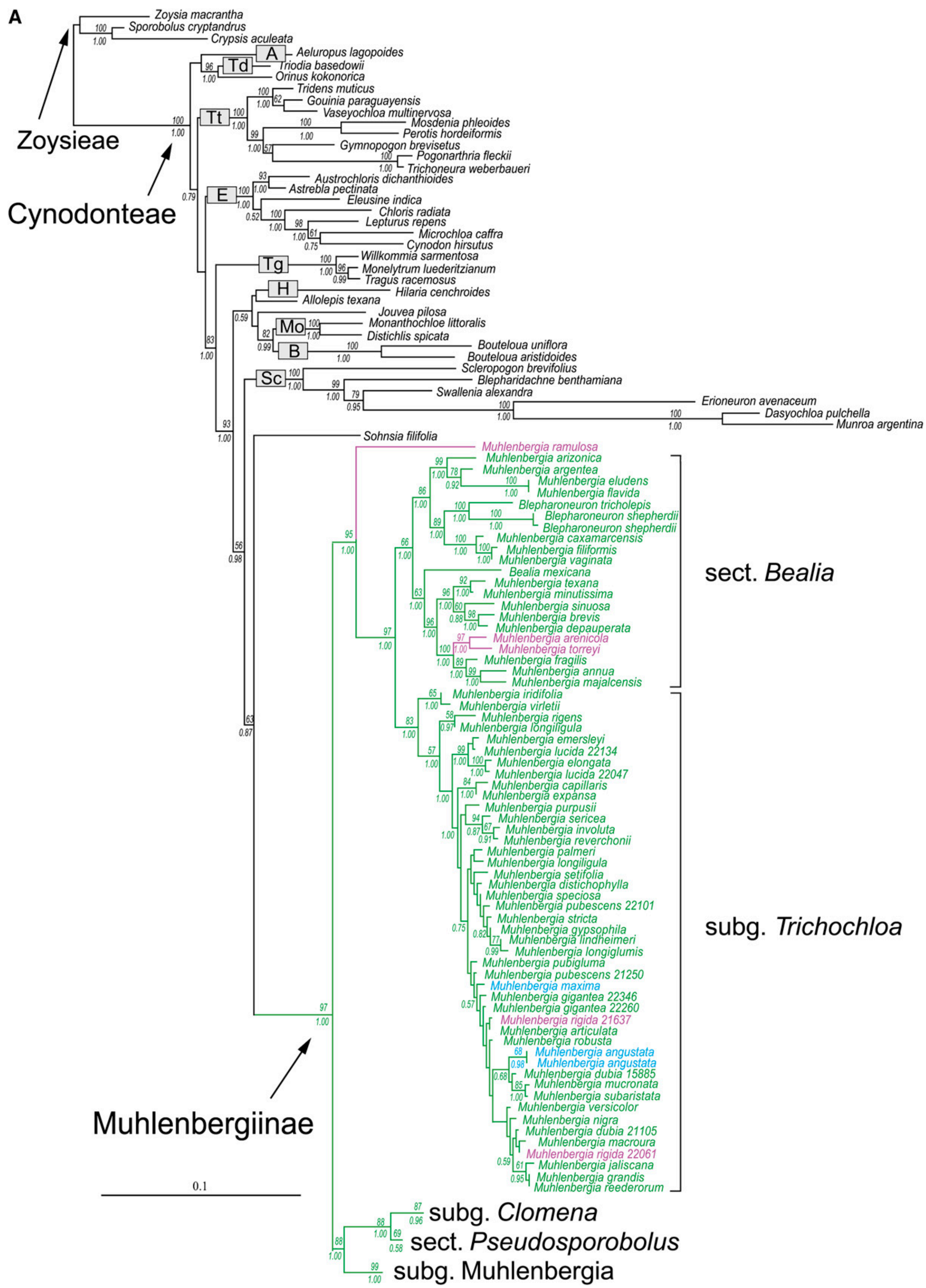
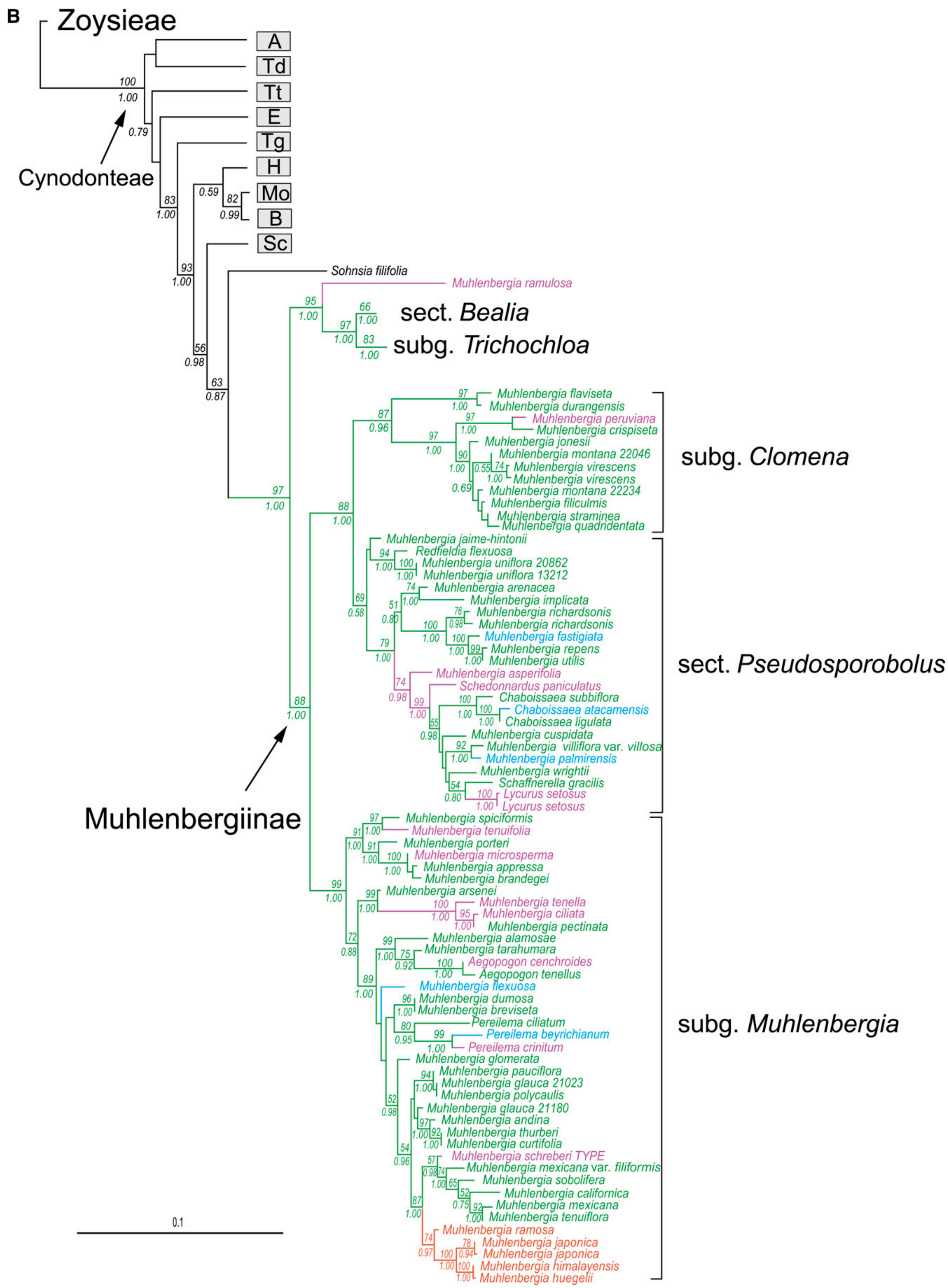


Fig. 2. Phylogram of best maximum likelihood tree from analysis of plastid data. Numbers above branches represent bootstrap values; numbers below branches are posterior probability values. (A) Detail of upper portion and (B) lower portion of phylogram. Abbreviations for subtribes: A = Aeluropodinae, B = Boutelouinae, E = Eleusininae, H = Hilariinae, Mo = Monanthochloinae, Sc = Scleropogoninae, Td = Triodinae, Tg = Traginae, Tt = Tridentinae. Taxon color indicates native distribution: green = North America, blue = South America, purple = North and South America, red = southeast Asia.


B
Zoysieae
A
Td
Tt
E
Tg
H
Mo
B
Sc
Cynodonteae
Sohnsia filifolia
Muhlenbergia ramulosa
sect. Bealia
subg. Trichochloa
Muhlenbergia flaviseta
Muhlenbergia durangensis
Muhlenbergia peruviana
Muhlenbergia crispiseta
Muhlenbergia jonesii
Muhlenbergia montana 22046
Muhlenbergia virescens
Muhlenbergia virescens
Muhlenbergia montana 22234
Muhlenbergia filiculmis
Muhlenbergia straminea
Muhlenbergia quadridentata
subg. Clomena
Muhlenbergia jaime-hintonii
Redfieldia flexuosa
Muhlenbergia uniflora 20862
Muhlenbergia uniflora 13212
Muhlenbergia arenacea
Muhlenbergia implicata
Muhlenbergia richardsonis
Muhlenbergia richardsonis
Muhlenbergia fastigiata
Muhlenbergia repens
Muhlenbergia utilis
Muhlenbergia asperifolia
Schedonnardus paniculatus
Chaboissaea subbiflora
Chaboissaea atacamensis
Chaboissaea ligulata
Muhlenbergia cuspidata
Muhlenbergia villiflora var. villosa
Muhlenbergia palmirensis
Muhlenbergia wrightii
Schaffnerella gracilis
Lycurus setosus
Lycurus setosus
sect. Pseudosporobolus
Muhlenbergiinae
Muhlenbergia spiciformis
Muhlenbergia tenuifolia
Muhlenbergia porteri
Muhlenbergia microsperma
Muhlenbergia appressa
Muhlenbergia brandegei
Muhlenbergia arsenei
Muhlenbergia tenella
Muhlenbergia ciliata
Muhlenbergia pectinata
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Muhlenbergia tarahumara
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Muhlenbergia dumosa
Muhlenbergia breviseta
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Pereilema beyrichianum
Pereilema crinitum
Muhlenbergia glomerata
Muhlenbergia pauciflora
Muhlenbergia glauca 21023
Muhlenbergia polycaulis
Muhlenbergia glauca 21180
Muhlenbergia andina
Muhlenbergia thurberi
Muhlenbergia curtifolia
Muhlenbergia schreberi TYPE
Muhlenbergia mexicana var. filiformis
Muhlenbergia sobolifera
Muhlenbergia californica
Muhlenbergia mexicana
Muhlenbergia tenuiflora
Muhlenbergia ramosa
Muhlenbergia japonica
Muhlenbergia japonica
Muhlenbergia himalayensis
Muhlenbergia huegelii
subg. Muhlenbergia
0.1

and flattened caryopses (Reeder and Reeder, 1995) was included by Herrera Arrieta (1998) in her study of the *M. montana* complex; however, this taxon occurs in our clade of *M.* subg. *Bealia*. We provide evidence for the exclusion of *M. argentea* and the addition of two annual species, *M. crispiseta* and *M. peruviana* (Peterson and Annable, 1991) to be included in *M.* subg. *Clomena*. Within our clade of *M.* subg. *Clomena*, there are three strongly supported subclades, one that includes the two annual species, a second that includes *M. durangensis* and *M. flaviseta*, and a third that includes those species with morphologies very similar to *M. montana*. Some individuals of *M. montana* and *M. virescens* have sclerosed phloem. This characteristic apparently has arisen four times within *Muhlenbergia* because it also is found in subg. *Trichochloa*, in *M. arenicola* and *M. torreyi* (subg. *Bealia*), and in *M. jaime-hintoni* (sect. *Pseudosporobolus*) (Peterson and Herrera Arrieta, 2001).

The moderately supported clade of *M.* sect. *Pseudosporobolus* (Fig. 3) includes a diverse assemblage of species, such as *Schedonnardus paniculatus*, that has panicles with long primary branches that do not rebranch, hence containing nearly sessile spikelets; *Redfieldia flexuosa* with 2–6-flowered spikelets, a line of hairs for a ligule, and open and diffuse panicles with capillary branches very similar to *M. asperifolia*, also occasionally with 2- or 3-flowered spikelets; *Schaffnerella gracilis*, a little known endemic of San Luis Potosí, Mexico (Columbus et al., 2002) that has panicles composed of short primary branches, each bearing a triad of 1-flowered spikelets, 7–9-nerved lemmas that have 3–5 awns, all enclosed in a spathiform sheath; *Lycurus setosus* with spikelets that are grouped in pairs, one sessile and one pedicellate; and *Chaboissaea* with one or two (occasionally three) florets per spikelet, the lower floret perfect and the upper florets staminate or sterile (Reeder, 1985; Sánchez and Rúgolo de Agrasar, 1986; Peterson and Annable, 1992; Peterson 2000; Peterson et al., 2007b). Embedded in *M.* sect. *Pseudosporobolus* is a strongly supported clade (Fig. 3) consisting of *M. fastigiata*, *M. repens*, *M. richardsonis*, and *M. utilis*, all earlier treated as the *M. repens* complex (Morden, 1985; Morden and Hatch, 1987, 1996). These four species are characterized by having short culms seldom exceeding 40 cm in height; a rhizomatous perennial habit, short involute leaf blades; short, narrow, contracted panicles; plumbeous spikelets; and unawned or mucronate lemmas (Morden, 1985; Morden and Hatch, 1987, 1996). *Muhlenbergia villiflora* var. *villosa* was included in Morden's *M. repens* complex, but in our analyses, it is sister to the Ecuadorian endemic *M. palmirensis* (Fig. 3, moderately supported; Fig. 2, strongly supported). Most species in *M.* sect. *Pseudosporobolus* have well-developed abaxial and adaxial sclerenchyma in their primary vascular bundles, narrow panicles, usually plumbeous spikelets, and unawned to mucronate lemmas (Peterson and Herrera Arrieta, 2001). Exceptions to these general trends include the short-awned *Lycurus setosus* and long-awned *M. implicata,* and the broad and open-panicled *M. asperifolia, M. implicata*, and *Redfieldia flexuosa*. The characteristic of having 2–3(–6)-flowered spikelets is also quite common in *M.* sect. *Pseudosporobolus* because it is found in *Chaboissaea atacamensis*, *C. ligulata*, *C. subbiflora*, *M. arenacea*, *M. asperifolia*, *M. cuspidata*, *M. fastigiata*, *M. richardsonis*, *M. uniflora*, and *Redfieldia flexuosa*.

The strongly supported clade of *M.* sect. *Bealia* contains few unique morphological characteristics shared among its members. However, all species in this clade have lemmas with hairy margins and midveins and caespitose or tufted culms, characters that are shared by many species in the *M.* subg. *Trichochloa* and subg. *Clomena*. Of the 20 species in *M.* sect *Bealia*, 14 are annual, with only *Blepharoneuron tricholepis, M. arenicola*, *M. argentea*, *M. arizonica*, *M. caxamarcensis*, and *M. torreyi* being perennial. *Blepharoneuron* was originally erected by Nash (1898) to emphasize the densely pilose margins and midvein of the lemma found in *B. tricholepis*. *Blepharoneuron shepherdii* also has densely pilose margins and midvein of the lemma and a base chromosome number of $x = 8$, prompting Peterson and Annable (1990) to place *Muhlenbergia shepherdii* (Vasey) Swallen in *Blepharoneuron*. The overall morphology of *B. shepherdii* with species in the *M. fragilis*-*M. annua*-*M. majalcensis* clade (Fig. 3, moderately supported) and the *M. minutissima*-*M. sinuosa* pair (Fig. 3, moderately supported) is striking because all are slender annuals with unawned lemmas, with capillary, flexuous pedicels that are often nodding (Peterson and Annable, 1990, 1991). Sister to the *Blepharoneuron* pair is a strongly supported clade comprising *M. caxamarcensis, M. filiformis*, and *M. vaginata* (Fig. 3). With the inclusion of *M. ligularis* (Columbus et al., 2010), these latter four taxa form a tight assemblage of short-lived perennial to annual, mat-forming species with short culms not exceeding 35 cm in height, narrow to loosely contracted panicles, and unawned, mucronate or short-awned lemmas (Laegaard and Sánchez Vega, 1990; Peterson and Annable, 1991). Morphologically, these four species closely resemble the *M. repens* complex (*M.* sect. *Pseudosporobolus*) as previously discussed, but differ primarily by lacking well-developed rhizomes, a characteristic common in *M.* subg. *Muhlenbergia* and *M. arenacea*, *M. asperifolia*, *M. jaime-hintonii*, *M. palmirensis*, *M. villiflora* var. *villosa*, and *Redfieldia flexuosa*, all members of *M.* sect. *Pseudosporobolus*.

In our study, *M. ramulosa* does not align within any subgenus or section but is sister to all Muhlenbergiinae in the ITS phylogram (not well supported in Fig. 1) or sister to *M.* sect. *Bealia* and *M.* subg. *Trichochloa* in the plastid and combined phylograms (strongly supported in Figs. 2 and 3). Earlier molecular studies of the Muhlenbergiinae (ITS and *trnL-F*) are also unable to confirm the affinity of *M. ramulosa* (Columbus et al., 2010), clearly a distinctive taxon, phylogenetically, wherever it belongs. Morphologically, *M. ramulosa* is very similar to many of the small delicate annuals that reside in *M.* sect. *Bealia*. At this time, we are not prepared to erect a subgeneric ranking to accommodate only *M. ramulosa*.

Cleistogamous spikelets appear to have evolved twice within the Muhlenbergiinae, once in the *M.* subg. *Muhlenbergia* where *M. appressa*, *M. brandegei*, and *M. microsperma* (all annuals) form a strongly supported clade (Fig. 3) and in *M.* sect. *Pseudosporobolus* known only from a few collections of *M. cuspidata* (Morden and Hatch, 1984). The formation of cleistogamous spikelets could actually be more common among the Muhlenbergiinae, but is undocumented to date.

Sclerosed phloem appears to have evolved a minimum of four times within the Muhlenbergiinae because it is found in *M. arenicola*-*M. torreyi* clade in sect. *Bealia*, the subg. *Trichochloa* clade, the subg. *Clomena* clade, and in *M. jaime-hintonii* (sect. *Pseudosporobolus*). In a cladogram derived entirely on the analysis of 16 anatomical characters within *Muhlenbergia*, Peterson and Herrera-Arrieta (2001) indicated that sclerosed phloem originated twice.

Biogeography—All three phylograms suggest that the Muhlenbergiinae originated in North America; for example, the sister group (Scleropogoninae in Fig. 1; or *Sohnsia filifolia* and Scleropogoninae in Figs. 2 and 3) are predominantly North

American species. The phylogenetic arrangement of the various tribes, subtribes, and genera in our analysis is similar to that found in Peterson et al. (2010) in which the Zoysieae is sister to the Cynodonteae, and within the Cynodonteae nested clades of the Aeluropodinae and Triodiinae are first, followed by the Orcuttiinae (not included), Tridentinae, Eleusininae, Tripogoninae (not included), Pappophorinae (not included), Traginae, an almost entirely New World clade with the *Allolepis*-*Jouvea*-Hilariinae sister to the Monanthochloinae-Scleropogoninae, *Sohnsia filifolia*, *Lepturidium insulare* Hitchc. & Ekman (not included), and the remaining Muhlenbergiinae. Within the Muhlenbergiinae, multiple independent radiations to South America have occurred one or more times in each of the three subgenera and two sections (blue and purple taxa in Figs. 1–3), and 15 species occur in both North and South America. The study of amphitropical disjunctions within the Muhlenbergiinae has indicated a North American origin and recent introduction into South America for at least three species (Peterson and Herrera Arrieta, 1995; Sykes et al., 1997; Peterson and Morrone, 1998; Peterson and Ortíz Diaz, 1998; Peterson et al., 2007a). Other plant groups with similar desert, amphitropical disjunct distributions have all been postulated to be of recent origin, i.e., late Pliocene to Pleistocene (Raven, 1963; Wen and Ickert-Bond, 2009).

Within *M*. subg. *Muhlenbergia*, there is evidence for a single colonization event in southeastern Asia (red taxa in Figs. 1–3). Intercontinental disjunctions between eastern North America and eastern Asia have been investigated in insects (von Dohlen et al., 2002) and plants (Wen, 1999, 2001; Wen et al., 2002). This floristic disjunction has resulted from fragmentation and range restriction of a widespread mesophytic forest during the past that attained its intercontinental distribution via the Bering and North Atlantic land bridges (e.g., Manchester, 1999; reviewed in Wen, 1999, 2001). Because the Asian *Muhlenbergia* clade is deeply nested, it seems likely that these species attained their current distribution recently, at least post Pleistocene. Estimates of introduction dates will be the topic of a forthcoming biogeographic study with the use of additional markers and a more complete sample of the species in the subtribe.

Taxonomy—Because our molecular analysis renders *Muhlenbergia* paraphyletic, we propose incorporating *Aegopogon*, *Bealia*, *Blepharoneuron*, *Chaboissaea*, *Lycurus*, *Pereilema*, *Redfieldia*, *Schaffnerella*, and *Schedonnardus* within *Muhlenbergia*. *Muhlenbergia* is the oldest name. Expansion of the circumscription to include these nine genera within *Muhlenbergia* requires the least amount of nomenclatural changes and still allows us to recognize a strongly supported monophyletic and morphologically cohesive unit. A complete classification for the Chloridoideae of the New World can be found in Soreng et al. (2009), and an attempt to place most genera within the subfamily into the four recognized tribes is found in Peterson et al. (2010). Below, we list all species in these nine genera and provide their name in *Muhlenbergia*. Our analysis also supports the recognition of five major clades within *Muhlenbergia*, and for consistency in rank, we propose two new subgeneric combinations below.

Muhlenbergia alopecuroides (Griseb.) P. M. Peterson & Columbus, Madroño 55(2): 159. 2008. Basionym: *Lycurus alopecuroides* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 255–256. 1874. Heterotypic synonym: *Pleopogon setosum* Nutt., Proc. Acad. Nat. Sci. Philadelphia 4: 25. 1848. *Lycurus setosus* (Nutt.) C. Reeder, Phytologia 57: 287. 1985. non *Muhlenbergia setosa* (Kunth) Trin.

Muhlenbergia ammophila P. M. Peterson, nom. nov. Replaced name: *Graphephorum flexuosum* Thurb. ex A. Gray, Proc. Acad. Nat. Sci. Philadelphia 1863: 78. 1864. *Redfieldia flexuosa* (Thurb. ex A. Gray) Vasey, Bull. Torrey Bot. Club 14: 133. 1887. non *Muhlenbergia flexuosa* Hitchc. Notes: The species is usually found growing on sand hills and dunes; therefore, it seems appropriate to emphasize its habitat requirement by using the epithet "ammophila" or sand loving.

Muhlenbergia atacamensis Parodi, Revista Argent. Agron. 15: 248. 1948. *Chaboissaea atacamensis* (Parodi) P. M. Peterson & Annable, Madroño 39(1): 19. 1992.

Muhlenbergia subg. ***Bealia*** (Scribn.) P. M. Peterson, comb. stat. nov. Basionym: *Bealia* Scribn., The True Grasses 104, f. 45a. 1890. *Muhlenbergia* sect. *Bealia* (Scribn.) Pilg., Die Natülichen Planzenfamilien, Zweite Auflage 14d: 71. 1956.

Muhlenbergia beyrichianum Kunth, Enum. Pl. 1: 200. 1833. *Pereilema beyrichianum* (Kunth) Hitchc., Contr. U. S. Natl. Herb. 24(8): 385. 1927.

Muhlenbergia biloba Hitchc., Contr. U. S. Natl. Herb. 17(3): 294. 1913. Replaced name: *Bealia mexicana* Scribn., The True Grasses 103, f. 45a. 1890. non *Muhlenbergia mexicana* (L.) Trin., Gram. Unifl. Sesquifl. 189, 190, 297, t. 5, f. 8. 1824.

Muhlenbergia bryophilus (Döll) P. M. Peterson, Caldasia 31(2): 279. 2009. Basionym: *Aegopogon bryophilus* Döll, Fl. Bras. 2(3): 239. 1880.

Muhlenbergia cenchroides (Humb. & Bonpl. ex Willd.) P. M. Peterson, Caldasia 31(2): 280. 2009. Basionym: *Aegopogon cenchroides* Humb. & Bonpl. ex Willd., Sp. Pl. 4(2): 899. 1806.

Muhlenbergia columbi P. M. Peterson, nom. nov. Replaced name: *Schaffnera gracilis* Benth., Hooker's Icon. Pl. 14: 59. T. 1378. 1882. later near hom., non *Schaffneria* Moore (1857). non *Muhlenbergia gracilis* (Kunth) Trin. *Schaffnerella gracilis* (Benth.) Nash, N. Amer. Fl. 17(2): 141. 1912. Notes: The specific epithet commemorates J. Travis Columbus who led a trip to San Luis Potosí, Mexico and was the first to collect this enigmatic species again more than 120 yr after the original collections by J. G. Schaffner between 1876 and 1880 (Columbus et al., 2002).

Muhlenbergia decumbens Swallen, Bol. Soc. Bot. Mexico 23: 30–32. F. 4. 1959. *Chaboissaea decumbens* (Swallen) Reeder & C. Reeder, Phytologia 65(2): 156. 1988.

Muhlenbergia diandra (R. W. Pohl) P. M. Peterson, comb. nov. Basionym: *Pereilema diandrum* R. W. Pohl, Novon 2(2): 102. 1992.

Muhlenbergia geminiflora (Kunth) P. M. Peterson, comb. nov. Basionym: *Aegopogon geminiflorus* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 133, t. 43. 1816. Heterotypic synonyms: *Lamarkia tenella* DC., Cat. Pl. Hort. Monsp. 120. 1813. *Aegopogon tenellus* (DC.) Trin., Gram. Unifl. Sesquifl. 164. 1824. non *Muhlenbergia tenella* (Kunth) Trin.

Muhlenbergia ligulata (E. Fourn.) Scribn. & Merr., Bull. Div. Agrostol. USDA 24. 19. 1901. Basionym: *Chaboissaea ligulata* E. Fourn., Mexic. Pl. 2: 112t. 1. 1886.

Muhlenbergia paniculata (Nutt.) P. M. Peterson, comb. nov. Basionym: *Lepturus paniculatus* Nutt., Gen. N. Amer. Pl. 1: 81. 1818. *Schedonnardus paniculatus* (Nutt.) Trel., Annual Rep. Geol. Surv. Arkansas 1888(4): 236. 1891.

Muhlenbergia pereilema P. M. Peterson, Caldasia 31(2): 293. 2009. Replaced name: *Pereilema crinitum* J. Presl, Reliq. Haenk. 1(4–5): 233, t. 37, f. a–f. 1830. non *Muhlenbergia crinita* (L. f.) Trin.

Muhlenbergia phalaroides (Kunth) P. M. Peterson, Caldasia 31(2): 294. 2009. Basionym: *Lycurus phalaroides* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 142. 1816.

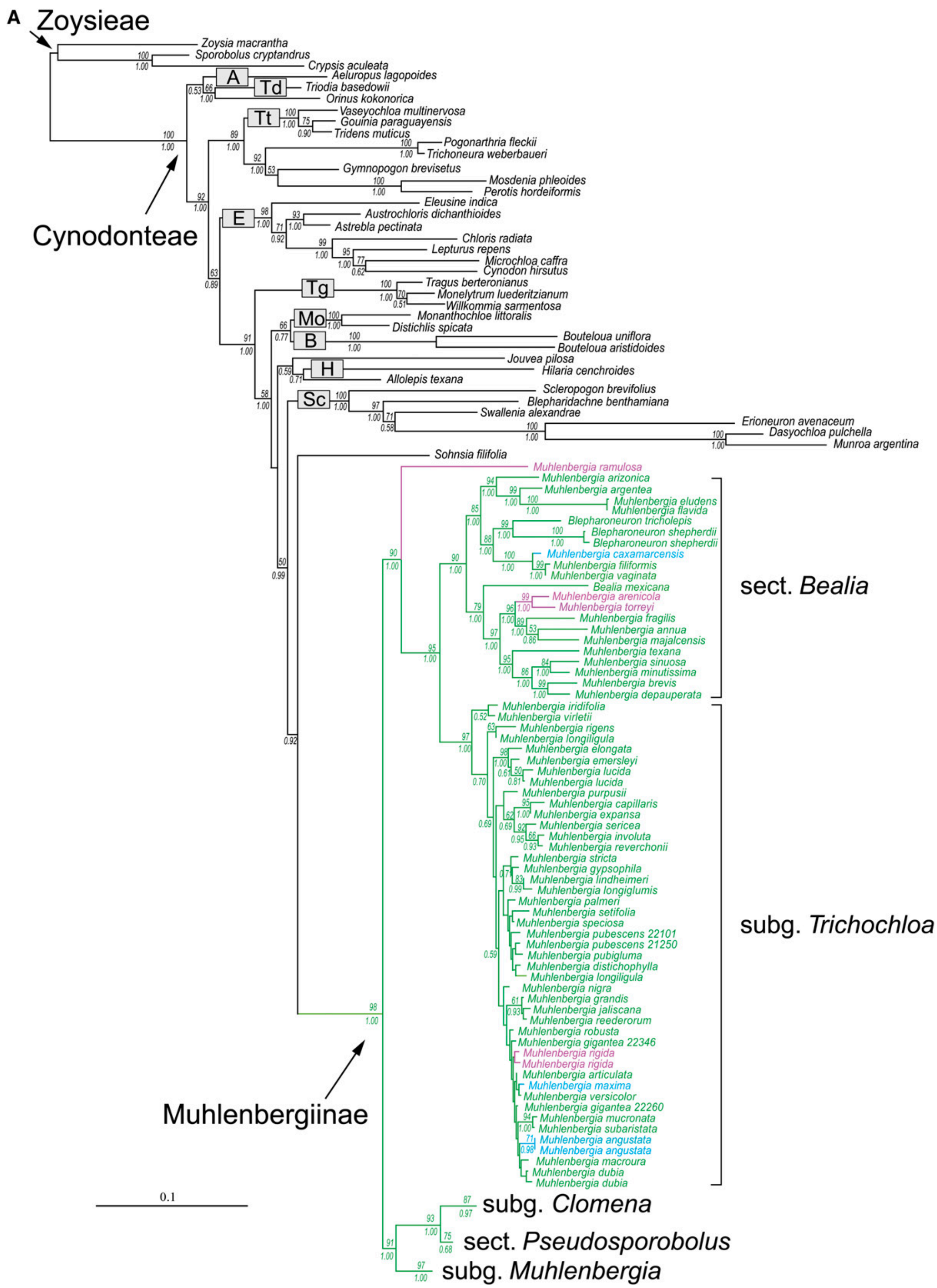
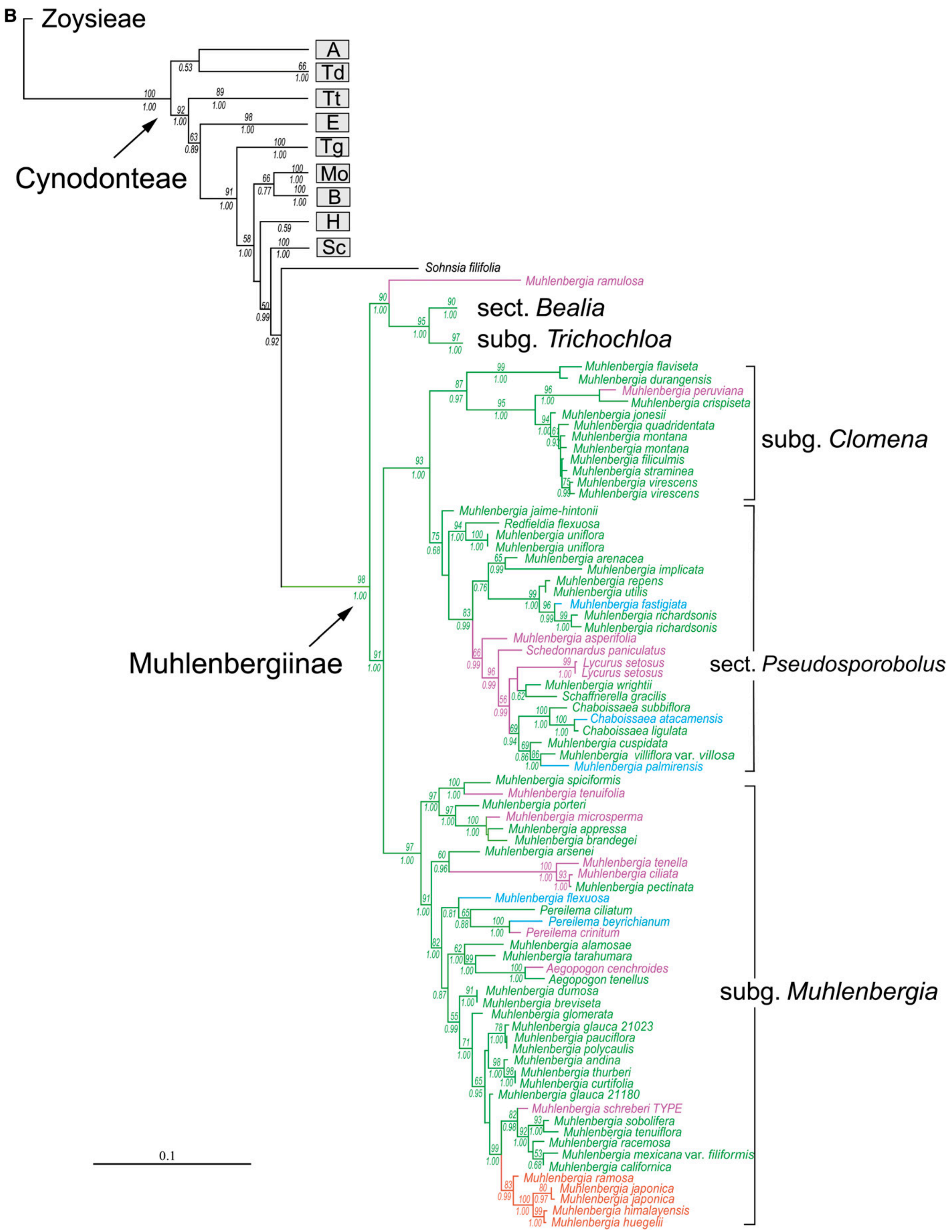


Fig. 3. Phylogram of best maximum likelihood tree from analysis of combined plastid and ITS data. Numbers above branches represent bootstrap values; numbers below branches are posterior probability values. (A) Detail of upper portion and (B) lower portion of phylogram. Abbreviations for subtribes: A = Aeluropodinae, B = Boutelouinae, E = Eleusininae, H = Hilariinae, Mo = Monanthochloinae, Sc = Scleropogoninae, Td = Triodiinae, Tg = Traginae, Tt = Tridentinae. Taxon color indicates native distribution: green = North America, blue = South America, purple = North and South America, red = southeast Asia.


B
Zoysieae
A
Td
Tt
E
Tg
Mo
B
H
Sc
Cynodonteae
Sohnsia filifolia
Muhlenbergia ramulosa
sect. Bealia
subg. Trichochloa
Muhlenbergia flaviseta
Muhlenbergia durangensis
Muhlenbergia peruviana
Muhlenbergia crispiseta
Muhlenbergia jonesii
Muhlenbergia quadridentata
Muhlenbergia montana
Muhlenbergia montana
Muhlenbergia filiculmis
Muhlenbergia straminea
Muhlenbergia virescens
Muhlenbergia virescens
subg. Clomena
Muhlenbergia jaime-hintonii
Redfieldia flexuosa
Muhlenbergia uniflora
Muhlenbergia uniflora
Muhlenbergia arenacea
Muhlenbergia implicata
Muhlenbergia repens
Muhlenbergia utilis
Muhlenbergia fastigiata
Muhlenbergia richardsonis
Muhlenbergia richardsonis
Muhlenbergia asperifolia
Schedonnardus paniculatus
Lycurus setosus
Lycurus setosus
Muhlenbergia wrightii
Schaffnerella gracilis
Chaboissaea subbiflora
Chaboissaea atacamensis
Chaboissaea ligulata
Muhlenbergia cuspidata
Muhlenbergia villiflora var. villosa
Muhlenbergia palmirensis
sect. Pseudosporobolus
Muhlenbergiinae
Muhlenbergia spiciformis
Muhlenbergia tenuifolia
Muhlenbergia porteri
Muhlenbergia microsperma
Muhlenbergia appressa
Muhlenbergia brandegei
Muhlenbergia arsenei
Muhlenbergia tenella
Muhlenbergia ciliata
Muhlenbergia pectinata
Muhlenbergia flexuosa
Pereilema ciliatum
Pereilema beyrichianum
Pereilema crinitum
Muhlenbergia alamosae
Muhlenbergia tarahumara
Aegopogon cenchroides
Aegopogon tenellus
Muhlenbergia dumosa
Muhlenbergia breviseta
Muhlenbergia glomerata
Muhlenbergia glauca 21023
Muhlenbergia pauciflora
Muhlenbergia polycaulis
Muhlenbergia andina
Muhlenbergia thurberi
Muhlenbergia curtifolia
Muhlenbergia glauca 21180
Muhlenbergia schreberi TYPE
Muhlenbergia sobolifera
Muhlenbergia tenuiflora
Muhlenbergia racemosa
Muhlenbergia mexicana var. filiformis
Muhlenbergia californica
Muhlenbergia ramosa
Muhlenbergia japonica
Muhlenbergia japonica
Muhlenbergia himalayensis
Muhlenbergia huegelii
subg. Muhlenbergia
0.1

Muhlenbergia phleoides (Kunth) P. M. Peterson, comb. nov. Basionym: *Lycurus phleoides* Kunth, Nov. Gen. Sp. (quarto ed.) 1: 142, t. 45. 1816.

Muhlenbergia plumosa P. M. Peterson, nom. nov. Replaced name: *Pereilema ciliatum* E. Fourn, Mexic. Pl. 2: 93. 1886 non *Muhlenbergia ciliata* (Kunth) Trin. Notes: The new name emphasizes the small feathery hairs on the surface of the fascicled spikelets and the sterile bristles that surround the fertile spikelets.

Muhlenbergia subg. ***Pseudosporobolus*** (Parodi) P. M. Peterson, comb. stat. nov. Basionym: *Muhlenbergia* unranked *Pseudosporobolus* Parodi, Physis. Revista de la Sociedad Argentina de Ciencias Naturales 9: 207. 1928. *M.* sect. *Pseudosporobolus* (Parodi) Pilg., Die Natülichen Planzenfamilien, Zweite Auflage 14d: 71. 1956. Lectotype: *Muhlenbergia fastigiata* (J. Presl) Henrard, designated here. Parodi (1928) and Pilger (1956) did not explicitly indicate the type species for this taxon.

Muhlenbergia shepherdii (Vasey) Swallen, Contr. U. S. Natl. Herb. 29(4): 204. 1947. Basionym: *Sporobolus shepherdii* Vasey, Bull. Torrey Bot. Club 14: 8. 1887. *Blepharoneuron shepherdii* (Vasey) P. M. Peterson & Annable, Syst. Bot. 15: 519. 1990.

Muhlenbergia solisii (G. A. Levin) P. M. Peterson, comb. nov. Basionym: *Aegopogon solisii* G. A. Levin, Mem. San Diego Soc. Nat. Hist. 16: 61. 1989.

Muhlenbergia subbiflora Hitchc., N. Amer. Fl. 17(6): 437. 1935. *Chaboissaea subbiflora* (Hitchc.) Reeder & C. Reeder, Phytologia 65(2): 156. 1988.

Muhlenbergia tricholepis (Torr.) P. M. Peterson, comb.nov. Basionym: *Vilfa tricholepis* Torr., Pacif. Railr. Rep. 4(5): 155. 1857. *Blepharoneuron tricholepis* (Torr.) Nash, Bull. Torrey Bot. Club 25(2): 88. 1898.

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APPENDIX 1. Specimens sampled, vouchers (all housed at the United States National Herbarium, US), country, and GenBank accessions for DNA sequences. Sequences generated by this study are in boldfaced type; all other sequences are from Peterson et al. (2010).

Taxon	Voucher	Country	*ndhF*	*rpl32-trnL*	*rps16-trnK*	*rps3*	ITS	*rps16* intron	*ndhA* intron
Aegopogon cenchroides Humb. & Bonpl. ex Willd.	*Peterson 22045 & Saarela*	Mexico	GU359613	GU360011	GU360578	GU360143	GU359259	GU360274	GU359403
Aegopogon tenellus (DC.) Trin.	*Peterson 22044 & Saarela*	Mexico	GU359592	GU360012	GU360577	GU360128	GU359260	GU360278	GU359392
Aeluropus lagopoides (L.) Trin. ex Thwaites	*Weinert s.n. & Mosawi*	Iraq	GU359591	GU360013	GU360576	GU360085	GU359261	GU360284	GU359391
Allolepis texana (Vasey) Soderstr. & H. F. Decker	*Hitchcock 7541*	Mexico	GU359577	GU360015	GU360573	GU360088	GU359264	GU360318	GU359388
Astrebla pectinata (Lindl.) F. Muell. ex Benth.	*Chalmers 5*	Australia	GU359585	GU359861	GU360567	GU360095	GU359286	GU360311	GU359421
Austrochloris dichanthioides (Everist) Lazarides	*Anson s.n.*	Australia	GU359584	GU359860	GU360566	GU360113	GU359272	GU360310	GU359420
Bealia mexicana Scribn.	*Peterson 7946, Annable & Herrera*	Mexico	—	GU359859	GU360550	GU360098	GU359258	GU360309	—
Blepharidachne benthamiana (Hack.) Hitchc.	*Melix 570 & Cherobini*	Argentina	GU359582	GU359857	GU360579	GU360100	GU359275	—	—
Blepharoneuron shepherdii (Vasey) P. M. Peterson & Annable	*Peterson 20013& Sanchez Alvarado*	Mexico	—	**HM143139**	**HM143625**	**HM143242**	**HM143038**	**HM143529**	**HM143346**
Blepharoneuron shepherdii (Vasey) P. M. Peterson & Annable	*Peterson 22452 & Saarela*	Mexico	GU359580	GU359854	GU360560	GU360102	GU359277	GU360320	GU359419
Blepharoneuron tricholepis (Torr.) Nash	*Peterson 22099 & Saarela*	Mexico	GU359576	GU359853	GU360559	GU360103	GU359278	GU360305	GU359418
Bouteloua aristidoides (Kunth) Griseb.	*Peterson 21994 & Saarela*	Mexico	GU359570	GU359852	GU360558	GU360104	GU359279	GU360304	GU359417
Bouteloua uniflora Vasey	*Peterson 21423, Saarela & Stančik*	Mexico	GU359567	GU359848	GU360606	GU360133	GU359232	GU360296	GU359383
Chaboissaea atacamensis (Parodi) P. M. Peterson & Annable	*Peterson 19626, Soreng, Salariato, & Panizza,*	Argentina	GU359729	GU359879	GU360595	GU360115	GU359344	GU360489	GU359382
Chaboissaea ligulata E. Fourn.	*Peterson 22416 & Saarela*	Mexico	GU359718	GU359863	GU360551	GU360069	GU359273	GU360440	GU359381
Chaboissaea subbiflora (Hitchc.) Reeder & C. Reeder	*Peterson 21158, Saarela, Rosen & Reid*	Mexico	GU359707	GU359877	GU360518	GU360036	GU359318	GU360439	GU359428
Chloris radiata (L.) Sw.	*Peterson 22278 & Saarela*	Mexico	GU359724	GU359872	GU360513	GU360048	GU359321	GU360434	GU359366
Crypsis aculeata (L.) Aiton	*Soreng 5469 & Peterson*	China	GU359573	GU359841	GU360599	GU360140	GU359238	GU360402	GU359362
Cynodon hirsutus Stent	*Smook 6616*	South Africa	GU359751	GU359876	GU360594	GU360135	GU359229	GU360452	GU359358
Dasyochloa pulchella (Kunth) Willd. ex Rydb.	*Peterson 21992 & Saarela*	Mexico	GU359689	GU359864	GU360505	GU360039	GU359330	GU360482	GU359369
Distichlis spicata (L.) Greene	*Peterson 19309, Soreng, Salariato & Panizza*	Argentina	GU359695	GU359801	GU360499	GU360032	GU359346	GU360475	GU359478
Eleusine indica (L.) Gaetrn.	*Peterson 21362, Saarela & Flores Villegas*	Mexico	GU359698	GU359797	GU360496	GU360031	GU359338	GU360472	GU359473
Erioneuron avenaceum (Kunth) Tateoka	*Peterson 19329, Soreng, Salariato & Panizza*	Argentina	GU359773	GU359822	GU360525	GU360063	GU359310	GU360403	GU359441
Gouinia paraguayensis (Kuntze) Parodi	*Peterson 11526 & Annable*	Argentina	GU359732	GU359817	GU360504	GU360058	GU359314	GU360384	GU359437
Gymnopogon grandiflorus Roseng., B. R. Arill. & Izag.	*Peterson 16642 & Refulio-Rodriguez*	Peru	GU359733	GU359816	GU360581	GU360057	GU359200	GU360383	GU359436
Hilaria cenchroides Kunth	*Peterson 22339 & Saarela*	Mexico	GU359736	GU359813	GU360697	GU360055	GU359143	GU360380	GU359424
Jouvea pilosa (J. Presl) Scribn.	*Peterson 11017 & Annable*	Mexico	GU359737	GU359812	GU360696	GU360173	GU359144	GU360379	GU359433
Lepturus repens R. Br.	*Whistler 9853*	Diego Garcia Island	GU359730	GU359893	GU360691	GU360228	GU359150	GU360428	GU359427
Lycurus setosus (Nutt.) C. Reeder	*Peterson 20960, Saarela, Lara Contreras & Reyna Alvarez*	Mexico	GU359744	GU359976	GU360688	GU360224	GU359152	GU360426	GU359425
Lycurus setosus (Nutt.) C. Reeder	*Peterson 22008*	Mexico	GU359745	GU359975	GU360687	GU360223	GU359153	GU360425	GU359451
Microchloa caffra Nees	*Smook 10441*	South Africa	GU359746	GU359972	GU360670	GU360206	GU359155	GU360424	GU359453

APPENDIX 1. Continued

Taxon	Voucher	Country	*ndhF*	*rpl32-trnL*	*rps16-trnK*	*rps3*	ITS	*rps16* intron	*ndhA* intron
Monanthochloe littoralis Engelm.	*Moran 10570*	Mexico	GU359748	GU359970	GU360699	GU360235	GU359157	GU360422	GU359460
Monelytrum luederitzianum Hack.	*Smook 10031*	South Africa	GU359749	GU359969	GU360682	GU360218	GU359158	GU360421	GU359459
Mosdenia phleoides (Hack.) Stent	*Schweickerdt 1542*	South Africa	GU359750	GU359967	GU360681	GU360216	GU359159	GU360420	GU359458
Muhlenbergia alamosae Vasey	*Peterson 22104 & Saarela*	Mexico	**HM143436**	**HM143140**	**HM143626**	**HM143243**	**HM143039**	**HM143530**	**HM143347**
Muhlenbergia andina (Nutt.) Hitchc.	*Peterson 10432, Annable & Weinpahl*	USA	**HM143437**	**HM143141**	—	**HM143244**	**HM143040**	**HM143531**	**HM143348**
Muhlenbergia angustata (J. Presl) Kunth	*Peterson 21703, Soreng, LaTorre & Rojas Fox*	Peru	**HM143438**	**HM143142**	**HM143627**	**HM143245**	**HM143041**	**HM143532**	**HM143349**
Muhlenbergia angustata (J. Presl) Kunth	*Peterson 21958, Soreng & Montoya Quino*	Peru	**HM143439**	**HM143143**	**HM143628**	**HM143246**	**HM143042**	**HM143533**	**HM143350**
Muhlenbergia annua (Vasey) Swallen	*Peterson 22022& Saarela*	Mexico	**HM143440**	**HM143144**	**HM143629**	**HM143247**	**HM143043**	**HM143534**	**HM143351**
Muhlenbergia appressa C. O. Goodd.	*Peterson 4183 & Annable*	USA	GU359618	GU359962	GU360676	GU360211	GU359164	GU360415	GU359443
Muhlenbergia arenacea (Buckley) Hitchc.	*Peterson 10624 & Annable*	Mexico	GU359619	GU359961	GU360675	GU360210	GU359165	GU360414	GU359452
Muhlenbergia arenicola Buckley	*Peterson 19947 & Lara-Contreras*	Mexico	GU359620	GU359960	GU360674	GU360209	GU359166	GU360413	GU359462
Muhlenbergia argentea Vasey	*Peterson 22095 & Saarela*	Mexico	**HM143441**	**HM143145**	**HM143630**	**HM143248**	**HM143044**	**HM143535**	**HM143352**
Muhlenbergia arizonica Scribn.	*Peterson 22173 & Saarela*	Mexico	**HM143442**	**HM143146**	**HM143631**	**HM143249**	**HM143045**	**HM143536**	**HM143353**
Muhlenbergia arsenei Hitchc.	*Peterson 15208 & Cayouette*	Mexico	**HM143443**	**HM143147**	**HM143632**	**HM143250**	**HM143046**	**HM143537**	**HM143354**
Muhlenbergia articulata Scribn.	*Peterson 13386 & Knowles*	Mexico	—	**HM143148**	**HM143633**	**HM143251**	**HM143047**	**HM143538**	**HM143355**
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi	*Peterson 15452, Soreng, Finot & Judziewicz*	Chile	**HM143444**	**HM143149**	**HM143634**	**HM143252**	**HM143048**	**HM143539**	**HM143356**
Muhlenbergia brandegeei C. Reeder	*Peterson 4760 & Annable*	Mexico	GU359621	GU359959	GU360711	GU360208	GU359167	GU360412	GU359450
Muhlenbergia brevis C. O. Goodd.	*Peterson 22023 & Saarela*	Mexico	**HM143445**	**HM143150**	**HM143635**	**HM143253**	**HM143049**	**HM143540**	**HM143357**
Muhlenbergia breviseta Griseb. ex E. Fourn.	*McVaugh 22930*	Mexico	—	—	**HM143636**	—	—	—	—
Muhlenbergia californica Vasey	*Peterson 5013 & Barron*	USA	**HM143446**	**HM143151**	**HM143637**	**HM143254**	**HM143050**	**HM143541**	**HM143358**
Muhlenbergia capillaris (Lam.) Trin.	*Peterson 14236, Weakley & LeBlond*	USA	**HM143447**	**HM143152**	**HM143638**	**HM143255**	**HM143051**	**HM143542**	**HM143359**
Muhlenbergia caxamarcensis Lægaard & Sánchez Vega	*Peterson 21965, Soreng & Montoya Quino*	Peru	**HM143448**	**HM143153**	**HM143639**	**HM143256**	**HM143052**	**HM143543**	**HM143360**
Muhlenbergia ciliata (Kunth) Trin.	*Peterson 22193 & Saarela*	Mexico	**HM143449**	**HM143154**	**HM143640**	**HM143257**	**HM143053**	**HM143544**	**HM143361**
Muhlenbergia crispiseta Hitchc.	*Peterson 10768, Annable & Valdes Reyna*	Mexico	—	—	—	**HM143258**	—	—	—
Muhlenbergia curtifolia Scribn.	*Peterson 5631 & Annable*	USA	**HM143450**	**HM143155**	**HM143641**	**HM143259**	**HM143054**	**HM143545**	**HM143362**
Muhlenbergia cuspidata (Torr. ex Hook.) Rydb.	*Hill 35331*	USA	—	**HM143156**	—	**HM143260**	**HM143055**	**HM143546**	—
Muhlenbergia depauperata Scribn.	*Peterson 21293, Saarela & Flores Villegas*	Mexico	**HM143451**	**HM143157**	**HM143642**	**HM143261**	**HM143056**	**HM143547**	**HM143363**
Muhlenbergia distichophylla (J. Presl) Kunth	*Peterson 15913 & Valdes Reyna*	Mexico	**HM143452**	**HM143158**	**HM143643**	**HM143262**	—	**HM143548**	**HM143364**
Muhlenbergia dubia E. Fourn.	*Peterson 15885 & Valdes Reyna*	Mexico	**HM143454**	**HM143159**	**HM143645**	**HM143264**	**HM143058**	**HM143549**	**HM143366**
Muhlenbergia dubia E. Fourn.	*Peterson 21105 & Saarela*	Mexico	**HM143453**	**HM143160**	**HM143644**	**HM143263**	**HM143057**	**HM143550**	**HM143365**
Muhlenbergia dumosa Scribn. ex Vasey	*Peterson 13438, Knowles, Dietrich & Braxton*	Mexico	**HM143455**	**HM143161**	**HM143646**	**HM143265**	**HM143059**	**HM143551**	**HM143367**
Muhlenbergia durangensis Y. Herrera	*Peterson 13644, Knowles, Dietrich, Braxton & Gonzalez Elizondo*	Mexico	**HM143456**	**HM143162**	**HM143647**	**HM143266**	**HM143060**	**HM143552**	**HM143368**
Muhlenbergia elongata Scribn. ex Beal	*Peterson 22164 & Saarela*	Mexico	**HM143457**	**HM143163**	**HM143648**	**HM143267**	**HM143061**	**HM143553**	**HM143369**
Muhlenbergia eludens C. Reeder	*Peterson 22188 & Saarela*	Mexico	**HM143458**	**HM143164**	**HM143649**	**HM143268**	**HM143062**	**HM143554**	**HM143370**
Muhlenbergia emersleyi Vasey	*Peterson 22096 & Saarela*	Mexico	GU359622	GU359958	GU360672	GU360207	GU359168	GU360411	GU359449

APPENDIX 1. Continued

Taxon	Voucher	Country	*ndhF*	*rpl32-trnL*	*rps16-trnK*	*rps3*	ITS	*rps16* intron	*ndhA* intron
Muhlenbergia expansa (Poir.) Trin.	*Peterson 14234, Weakley & LeBlond*	USA	**HM143459**	**HM143165**	**HM143650**	**HM143269**	**HM143063**	**HM143555**	**HM143371**
Muhlenbergia fastigiata (J. Presl) Henrard	*Peterson 21512, Soreng, LaTorre & Rojas Fox*	Peru	**HM143460**	**HM143166**	**HM143651**	**HM143270**	**HM143064**	**HM143556**	**HM143372**
Muhlenbergia filiculmis Vasey	*Peterson 11954 & Annable*	USA	**HM143461**	**HM143167**	**HM143652**	**HM143271**	**HM143065**	**HM143557**	**HM143373**
Muhlenbergia filiformis (Thurb. ex S. Watson) Rydb.	*Peterson 10433, Annable & Weinpahl*	USA	—	**HM143168**	**HM143653**	**HM143272**	**HM143066**	**HM143558**	**HM143374**
Muhlenbergia flavida Vasey	*Peterson 22237 & Saarela*	Mexico	**HM143462**	**HM143169**	**HM143654**	**HM143273**	**HM143067**	**HM143559**	**HM143375**
Muhlenbergia flaviseta Scribn.	*Peterson 22409 & Saarela*	Mexico	GU359623	GU359957	GU360685	GU360250	GU359127	GU360410	GU359448
Muhlenbergia flexuosa Hitchc.	*Peterson 20373, Soreng & Romaschenko*	Peru	**HM143463**	**HM143170**	**HM143655**	**HM143274**	**HM143068**	**HM143560**	**HM143376**
Muhlenbergia fragilis Swallen	*Peterson 22194 & Saarela*	Mexico	**HM143464**	**HM143171**	**HM143656**	**HM143275**	**HM143069**	**HM143561**	**HM143377**
Muhlenbergia gigantea (E. Fourn.) Hitchc.	*Peterson 22260 & Saarela*	Mexico	GU359663	GU359966	GU360680	GU360215	GU359160	GU360419	GU359457
Muhlenbergia gigantea (E. Fourn.) Hitchc.	*Peterson 22346 & Saarela*	Mexico	**HM143465**	**HM143172**	**HM143657**	**HM143276**	**HM143070**	**HM143562**	**HM143378**
Muhlenbergia glauca (Nees) B. D. Jacks.	*Peterson 21023, Saarela, Lara Contreras & Reyna Alvarez*	Mexico	**HM143467**	**HM143173**	**HM143658**	**HM143278**	**HM143072**	**HM143563**	**HM143379**
Muhlenbergia glauca (Nees) B. D. Jacks.	*Peterson 21180, Saarela, Gonzalez Elizondo, Rosen & Reid*	Mexico	**HM143466**	**HM143174**	**HM143659**	**HM143277**	**HM143071**	**HM143564**	**HM143380**
Muhlenbergia glomerata (Willd.) Trin.	*Peterson 20924, Saarela & Howard*	USA	GU359638	GU359954	GU360716	GU360253	GU359114	GU360407	GU359445
Muhlenbergia grandis Vasey	*Peterson 13413, Knowles, Dietrich & Braxton*	Mexico	**HM143468**	**HM143175**	**HM143660**	**HM143279**	**HM143073**	**HM143565**	**HM143381**
Muhlenbergia gypsophila Reeder & C. Reeder	*Peterson 15840 & Valdes Reyna*	Mexico	**HM143469**	**HM143176**	**HM143661**	**HM143280**	**HM143074**	—	**HM143382**
Muhlenbergia himalayensis Hack. ex Hook. f.	*Soreng 5666, Peterson & Sun Hang*	China	**HM143470**	**HM143177**	**HM143661** **HM143662**	**HM143281**	**HM143075**	**HM143566**	**HM143383**
Muhlenbergia huegelii Trin.	*Soreng 5344, Peterson & Sun Hang*	China	**HM143471**	**HM143178**	**HM143663**	**HM143282**	**HM143076**	**HM143567**	**HM143384**
Muhlenbergia implicata (Kunth) Trin.	*Peterson 22266, Saarela*	Mexico	**HM143472**	**HM143179**	**HM143664**	**HM143283**	**HM143077**	**HM143568**	**HM143385**
Muhlenbergia iridifolia Soderstr.	*Peterson 6133 & Annable*	Mexico	**HM143473**	**HM143180**	—	**HM143284**	**HM143078**	—	—
Muhlenbergia jaime-hintonii P. M. Peterson & Valdés-Reyna	*Peterson 15841& Valdes Reyna*	Mexico	**HM143474**	**HM143181**	**HM143665**	**HM143285**	**HM143079**	**HM143569**	**HM143386**
Muhlenbergia jaliscana Swallen	*Peterson 6149 & Annable*	Mexico	**HM143475**	**HM143182**	**HM143666**	**HM143286**	**HM143080**	**HM143570**	**HM143387**
Muhlenbergia japonica Steud.	*Soreng 5240, Peterson & Sun Hang*	China	**HM143477**	**HM143183**	**HM143667**	**HM143287**	**HM143081**	**HM143571**	**HM143388**
Muhlenbergia japonica Steud.	*Soreng 5301, Peterson & Sun Hang*	China	**HM143476**	**HM143184**	**HM143668**	**HM143288**	**HM143082**	**HM143572**	**HM143389**
Muhlenbergia jonesii (Vasey) Hitchc.	*Peterson 4861 & Annable*	USA	**HM143478**	**HM143185**	**HM143669**	**HM143289**	**HM143083**	—	**HM143390**
Muhlenbergia lindheimeri Hitchc.	*Peterson 6280 & Annable*	USA	**HM143479**	**HM143186**	**HM143670**	**HM143290**	**HM143084**	**HM143573**	**HM143391**
Muhlenbergia longiglumis Vasey	*Peterson 13666, Knowles, Dietrich, Braxton & Gonzalez Elizondo*	Mexico	—	—	**HM143671**	**HM143291**	—	—	—
Muhlenbergia longiligula Hitchc.	*Peterson 15224 & Cayouette*	USA	**HM143480**	**HM143187**	**HM143672**	**HM143292**	**HM143085**	**HM143574**	–
Muhlenbergia lucida Swallen	*Peterson 22047 & Saarela*	Mexico	**HM143482**	**HM143189**	**HM143673**	**HM143293**	**HM143087**	**HM143576**	**HM143393**
Muhlenbergia lucida Swallen	*Peterson 22134 & Saarela*	Mexico	**HM143481**	**HM143188**	**HM143674**	**HM143294**	**HM143086**	**HM143575**	**HM143392**
Muhlenbergia macroura (Kunth) Hitchc.	*Peterson 22062 & Saarela*	Mexico	GU359624	GU359956	GU360683	GU360265	GU359125	GU360409	GU359447
Muhlenbergia majalcensis P. M. Peterson	*Peterson 4519 & Annable*	Mexico	**HM143483**	**HM143190**	**HM143675**	**HM143295**	**HM143088**	**HM143577**	**HM143394**
Muhlenbergia maxima Lægaard & Sánchez Vega	*Peterson 21884, Soreng & Sanchez Vega*	Peru	**HM143484**	**HM143191**	**HM143676**	**HM143296**	**HM143089**	**HM143578**	—

Appendix 1. Continued

Taxon	Voucher	Country	*ndhF*	*rpl32-trnL*	*rps16-trnK*	*rps3*	ITS	*rps16* intron	*ndhA* intron
Muhlenbergia mexicana var. *filiformis* (Torr.) Scribn.	*Peterson 20861 & Saarela*	USA	**HM143485**	**HM143192**	**HM143678**	**HM143298**	**HM143091**	**HM143579**	**HM143395**
Muhlenbergia mexicana (L.) Trin.	*Peterson 5562 & Annable*	USA	**HM143486**	**HM143193**	**HM143677**	**HM143297**	**HM143090**	**HM143580**	**HM143396**
Muhlenbergia microsperma (DC.) Kunth	*Peterson 21855 & Soreng*	Peru	**HM143487**	**HM143194**	**HM143679**	**HM143299**	**HM143092**	**HM143581**	**HM143397**
Muhlenbergia minutissima (Steud.) Swallen	*Peterson 22012 & Saarela*	Mexico	—	**HM143195**	**HM143680**	**HM143300**	**HM143093**	—	—
Muhlenbergia montana (Nutt.) Hitchc.	*Peterson 22046 & Saarela*	Mexico	**HM143488**	**HM143196**	**HM143681**	**HM143301**	**HM143094**	**HM143582**	**HM143398**
Muhlenbergia montana (Nutt.) Hitchc.	*Peterson 22234 & Saarela*	Mexico	GU359705	GU359964	GU360678	GU360213	GU359162	GU360417	GU359455
Muhlenbergia mucronata (Kunth) Trin.	*Peterson 22038 & Saarela*	Mexico	**HM143489**	**HM143197**	**HM143682**	**HM143302**	**HM143095**	**HM143583**	**HM143399**
Muhlenbergia nigra Hitchc.	*Peterson 16097 & Rosales*	Mexico	**HM143490**	**HM143198**	**HM143683**	**HM143303**	**HM143096**	**HM143584**	**HM143400**
Muhlenbergia palmeri Vasey	*Peterson 5478 & Annable*	USA	**HM143491**	**HM143199**	**HM143684**	**HM143304**	**HM143097**	**HM143585**	**HM143401**
Muhlenbergia palmirensis Grignon & Lægaard	*Peterson 9317 & Judziewicz*	Ecuador	—	**HM143200**	**HM143685**	**HM143305**	**HM143098**	**HM143586**	**HM143402**
Muhlenbergia pauciflora Buckley	*Peterson 22048 & Saarela*	Mexico	**HM143492**	**HM143201**	**HM143686**	—	**HM143099**	**HM143587**	**HM143403**
Muhlenbergia pectinata C. O. Goodd.	*Peterson 22108 & Saarela*	Mexico	**HM143493**	**HM143202**	**HM143687**	**HM143306**	**HM143100**	**HM143588**	**HM143404**
Muhlenbergia peruviana (P. Beauv.) Steud.	*Peterson 22440 & Saarela*	Mexico	GU359625	GU359955	GU360713	GU360221	GU359154	GU360408	GU359446
Muhlenbergia polycaulis Scribn.	*Peterson 22092 & Saarela*	Mexico	**HM143494**	**HM143203**	**HM143688**	**HM143307**	**HM143101**	**HM143589**	—
Muhlenbergia porteri Scribn. ex Beal	*Peterson 19846 & Lara Contreras*	Mexico	**HM143495**	**HM143204**	**HM143689**	**HM143308**	**HM143102**	**HM143590**	**HM143405**
Muhlenbergia pubescens (Kunth) Hitchc.	*Peterson 21250 & Saarela*	Mexico	**HM143496**	**HM143205**	**HM143691**	**HM143310**	**HM143103**	**HM143592**	**HM143406**
Muhlenbergia pubescens (Kunth) Hitchc.	*Peterson 22101 & Saarela*	Mexico	**HM143497**	**HM143206**	**HM143690**	**HM143309**	**HM143104**	**HM143591**	**HM143407**
Muhlenbergia pubigluma Swallen	*Peterson 15838 & Valdes Reyna*	Mexico	**HM143498**	**HM143207**	**HM143692**	**HM143311**	**HM143105**	**HM143593**	**HM143408**
Muhlenbergia purpusii Mez	*Peterson 6227 & Annable*	Mexico	**HM143499**	**HM143208**	**HM143693**	**HM143312**	**HM143106**	**HM143594**	**HM143409**
Muhlenbergia quadridentata (Kunth) Trin.	*Peterson 16103 & Rosales*	Mexico	**HM143500**	**HM143209**	**HM143694**	**HM143313**	**HM143107**	—	**HM143410**
Muhlenbergia ramosa (Hack. ex Matsum.) Makino	*Soreng 5302, Peterson & Sun Hang*	China	**HM143501**	**HM143210**	**HM143695**	**HM143314**	**HM143108**	**HM143595**	**HM143411**
Muhlenbergia ramulosa (Kunth) Swallen	*Peterson 22447 & Saarela*	Mexico	GU359627	GU359953	GU360717	GU360254	GU359115	GU360406	GU359444
Muhlenbergia reederorum Soderstr.	*Peterson 21262 & Saarela*	Mexico	**HM143502**	**HM143211**	**HM143696**	**HM143315**	**HM143109**	—	**HM143412**
Muhlenbergia repens (J. Presl) Hitchc.	*Peterson 7900 & Annable*	USA	**HM143503**	**HM143212**	**HM143697**	**HM143316**	**HM143110**	**HM143596**	**HM143413**
Muhlenbergia reverchonii Vasey & Scribn.	*Peterson 6285 & Annable*	USA	**HM143504**	**HM143213**	**HM143698**	**HM143317**	**HM143111**	**HM143597**	**HM143414**
Muhlenbergia richardsonis (Trin.) Rydb.	*Peterson 19817, Saarela & Sears*	USA	GU359617	GU359978	GU360677	GU360212	GU359163	GU360431	GU359454
Muhlenbergia richardsonis (Trin.) Rydb.	*Peterson 7832 & Annable*	USA	**HM143505**	**HM143214**	**HM143699**	**HM143318**	**HM143112**	**HM143598**	**HM143415**
Muhlenbergia rigens (Benth.) Hitchc.	*Peterson 22129 & Saarela*	Mexico	GU359629	GU359951	GU360729	GU360256	GU359117	GU360357	GU359481
Muhlenbergia rigida (Kunth) Kunth	*Peterson 21637, Soreng, LaTorre & Rojas Fox*	Peru	GU359616	GU359952	GU360718	GU360255	GU359116	GU360405	GU359380
Muhlenbergia rigida (Kunth) Kunth	*Peterson 22061 & Saarela*	Mexico	**HM143506**	**HM143215**	**HM143700**	**HM143319**	**HM143113**	**HM143599**	**HM143416**
Muhlenbergia robusta (E. Fourn.) Hitchc.	*Peterson 15928 & Valdes Reyna*	Mexico	**HM143507**	**HM143216**	**HM143701**	**HM143320**	**HM143114**	**HM143600**	—
Muhlenbergia schreberi J. F. Gmel.	*Peterson 19443, Soreng, Salariato & Panizza*	Argentina	GU359765	GU359950	GU360679	GU360214	GU359161	GU360404	GU359456
Muhlenbergia sericea (Michx.) P. M. Peterson	*Peterson 14843, Blackburn & Peterson*	USA	**HM143508**	**HM143217**	**HM143702**	**HM143321**	**HM143115**	**HM143601**	**HM143417**

Appendix 1. Continued

Taxon	Voucher	Country	*ndhF*	*rpl32-trnL*	*rps16-trnK*	*rps3*	ITS	*rps16* intron	*ndhA* intron
Muhlenbergia setifolia Vasey	*Peterson 20942, Saarela, Lara Contreras & Reyna Alvarez*	Mexico	**HM143509**	**HM143218**	**HM143703**	**HM143322**	**HM143116**	**HM143602**	**HM143418**
Muhlenbergia sinuosa Swallen	*Peterson 7976, Annable & Herrera*	Mexico	—	**HM143219**	**HM143704**	**HM143323**	**HM143117**	**HM143603**	**HM143419**
Muhlenbergia sobolifera (Muhl. ex Willd.) Trin.	*Peterson 20834 & Saarela*	USA	**HM143510**	**HM143220**	—	**HM143324**	**HM143118**	**HM143604**	**HM143420**
Muhlenbergia speciosa Vasey	*Peterson 13616, Dietrich, Braxton, & Gonzalez Elizondo*	Mexico	**HM143511**	**HM143221**	**HM143705**	**HM143325**	**HM143119**	**HM143605**	**HM143421**
Muhlenbergia spiciformis Trin.	*Peterson 22362 & Saarela*	Mexico	**HM143512**	**HM143222**	**HM143706**	**HM143326**	**HM143120**	**HM143606**	**HM143422**
Muhlenbergia straminea Hitchc.	*Peterson 15238 & Cayouette*	USA	**HM143513**	**HM143223**	**HM143707**	**HM143327**	**HM143121**	**HM143607**	—
Muhlenbergia stricta (J. Presl) Kunth	*Peterson 13709*	Mexico	**HM143514**	**HM143224**	**HM143708**	**HM143328**	**HM143122**	**HM143608**	**HM143423**
Muhlenbergia subaristata Swallen	*Peterson 21243 & Saarela*	Mexico	**HM143515**	**HM143225**	**HM143709**	**HM143329**	**HM143123**	**HM143609**	**HM143424**
Muhlenbergia tarahumara P. M. Peterson & Columbus	*Peterson 22053 & Saarela*	Mexico	**HM143516**	**HM143226**	**HM143710**	**HM143330**	**HM143124**	**HM143610**	**HM143425**
Muhlenbergia tenella (Kunth) Trin.	*Peterson 22141 & Saarela*	Mexico	**HM143517**	**HM143227**	**HM143711**	**HM143331**	**HM143125**	**HM143611**	—
Muhlenbergia tenuiflora (Willd.) Britton, Sterns & Poggenb.	*Peterson 15778 & Saarela*	USA	**HM143518**	**HM143228**	**HM143712**	**HM143332**	**HM143126**	**HM143612**	**HM143426**
Muhlenbergia tenuifolia (Kunth) Kunth	*Peterson 22344 & Saarela*	Mexico	**HM143519**	**HM143229**	**HM143713**	**HM143333**	**HM143127**	**HM143613**	**HM143427**
Muhlenbergia texana Buckley	*Peterson 22016 & Saarela*	Mexico	—	**HM143230**	**HM143714**	**HM143334**	**HM143128**	**HM143614**	—
Muhlenbergia thurberi (Scribn.) Rydb.	*Peterson 5619 & Annable*	USA	**HM143520**	**HM143231**	**HM143715**	**HM143335**	**HM143129**	**HM143615**	**HM143428**
Muhlenbergia torreyi (Kunth) Hitchc. ex Bush	*Peterson 19429, Soreng, Salariato & Panizza*	Argentina	GU359630	GU359992	GU360720	GU360266	GU359118	GU360267	—
Muhlenbergia uniflora (Muhl.) Fernald	*Peterson 13212, Annable, Pizzolato, Gordon, Frett, Frick, Morrone & Griner*	USA	**HM143521**	**HM143232**	**HM143716**	**HM143337**	**HM143130**	**HM143616**	**HM143429**
Muhlenbergia uniflora (Muhl.) Fernald	*Peterson 20862 & Saarela*	USA	GU359631	GU359994	GU360715	GU360258	GU359119	GU360275	GU359463
Muhlenbergia utilis (Torr.) Hitchc.	*Peterson 5735 & Annable*	USA	**HM143522**	**HM143233**	**HM143717**	**HM143338**	**HM143131**	**HM143617**	**HM143430**
Muhlenbergia vaginata Swallen	*Peterson 22417 & Saarela*	Mexico	—	**HM143234**	**HM143718**	—	—	**HM143618**	—
Muhlenbergia versicolor Swallen	*Peterson 9913 & Annable*	Mexico	—	**HM143235**	**HM143719**	**HM143339**	**HM143132**	**HM143619**	—
Muhlenbergia villiflora var. *villosa* (Swallen) Morden	*Peterson 15811 & Valdes Reyna*	Mexico	**HM143523**	**HM143236**	**HM143720**	**HM143340**	**HM143133**	**HM143620**	**HM143431**
Muhlenbergia virescens (Kunth) Trin.	*Peterson 21259 & Saarela*	Mexico	**HM143524**	**HM143237**	**HM143721**	**HM143341**	**HM143135**	**HM143622**	**HM143433**
Muhlenbergia virescens (Kunth) Trin.	*Peterson 22412 & Saarela*	Mexico	**HM143525**	**HM143238**	**HM143722**	**HM143342**	**HM143134**	**HM143621**	**HM143432**
Muhlenbergia virletii (E. Fourn.) Soderstr.	*Peterson 9724 & Campos Villanueva*	Mexico	**HM143526**	**HM143239**	—	**HM143343**	**HM143136**	—	—
Muhlenbergia wrightii Vasey ex J. M. Coult.	*Peterson 20964, Saarela, Lara Contreras & Reyna Alvarez*	Mexico	**HM143527**	**HM143240**	**HM143723**	**HM143344**	**HM143137**	**HM143623**	**HM143434**
Muhlenbergia x involuta Swallen	*Peterson 6284 & Annable*	USA	**HM143528**	**HM143241**	**HM143724**	**HM143345**	**HM143138**	**HM143624**	**HM143435**
Munroa argentina Griseb.	*Peterson 15505, Soreng & Judziewicz*	Chile	GU359633	GU360006	GU360723	GU360260	GU359121	—	GU359385
Orinus kokonorica (K. S. Hao) Keng ex X. L. Yang	*Soreng 5447, Peterson & Sun Hang*	China	GU359628	GU359999	GU360728	GU360259	GU359140	GU360270	GU359399
Pereilema beyrichianum (Kunth) Hitchc.	*Peterson 20366, Soreng & Romaschenko*	Peru	GU359597	GU359995	GU360712	GU360247	GU359129	GU360280	GU359493
Pereilema ciliatum E. Fourn.	*Peterson 20106, Hall, Alvarez Marvan & Alvarez Jimenez*	Mexico	GU359598	GU359979	GU360719	GU360246	GU359130	GU360281	GU359516
Pereilema crinitum J. Presl	*Peterson 22191 & Saarela*	Mexico	GU359599	GU359993	GU360710	GU360245	GU359131	GU360282	GU359519
Perotis hordeiformis Nees	*Soreng 5717, Peterson & Sun Hang*	China	GU359600	GU359991	GU360708	GU360243	GU359132	GU360283	GU359520

Appendix 1. Continued

Taxon	Voucher	Country	*ndhF*	*rpl32-trnL*	*rps16-trnK*	*rps3*	ITS	*rps16* intron	*ndhA* intron
Redfieldia flexuosa (Thurb. ex A. Gray) Vasey	*Peterson 7845* & *Annable*	USA	GU359604	GU359985	GU360702	GU360191	GU359138	GU360289	GU359525
Schaffnerella gracilis (Benth.) Nash	*Schaffner 134*	Mexico	—	GU359981	—	—	—	—	—
Schedonnardus paniculatus (Nutt.) Trel.	*Peterson 12070* & *Annable*	USA	GU359609	GU359936	GU360673	GU360170	GU359201	GU360375	GU359529
Scleropogon brevifolius Phil.	*Peterson 19280, Soreng, Salariado* & *Panizza*	Argentina	GU359611	GU359919	GU360635	GU360167	GU359203	–	GU359530
Sohnsia filifolia (E. Fourn.) Airy Shaw	*Peterson 11129* & *Annable*	Mexico	GU359612	GU359918	GU360634	GU360166	GU359204	GU360350	GU359531
Sporobolus cryptandrus (Torr.) A. Gray	*Peterson 22003* & *Saarela*	Mexico	GU359674	GU359914	GU360631	GU360162	GU359208	GU360354	GU359524
Swallenia alexandrae (Swallen) Soderstr. & H. F. Decker	*Carter 2784*	USA	GU359669	GU359920	GU360639	GU360154	GU359217	GU360364	GU359512
Tragus berteronianus Schult.	*FLSP 457*	Peru	GU359675	GU359898	GU360616	GU360148	GU359224	GU360370	GU359503
Trichoneura eleusinoides (Rendle) Ekman	*Seydel 448*	South Africa	GU359601	GU359988	GU360705	GU360240	GU359135	GU360277	GU359522
Trichoneura weberbaueri Pilg.	*Peterson 15686* & *Soreng*	Chile	GU359681	GU359948	GU360668	GU360194	GU359172	GU360361	GU359565
Tridens muticus (Torr.) Nash	*Peterson 21997*& *Saarela*	Mexico	GU359682	GU359947	GU360667	GU360195	GU359173	GU360321	GU359557
Triodia basedowii Pritz.	*Peterson 14437, Soreng* & *Rosenberg*	Australia	GU359683	GU359946	GU360666	GU360205	GU359174	GU360322	GU359550
Vaseyochloa multinervosa (Vasey) Hitchc.	*Swallen 10041*	USA	GU359656	GU359925	GU360646	GU360177	GU359193	GU360342	GU359544
Willkommia sarmentosa Hack.	*Schweickerdt 2181*	South Africa	GU359657	GU359924	GU360645	GU360252	GU359194	GU360343	GU359545
Zoysia macrantha Desv.	*Soreng 5913* & *Peterson*	Australia	GU359660	GU360017	GU360641	GU360020	GU359142	GU360346	GU359558