

## Molecular Phylogeny of *Dissanthelium* (Poaceae: Pooideae) and its Taxonomic Implications

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**Abstract**—We investigated the phylogeny of the New World grass *Dissanthelium* to explore its monophyly, to examine relationships within the genus, and to investigate its relationship with *Poa*. Molecular phylogenetic analyses including a thorough sampling of *Dissanthelium* (seventeen of the 20 species) and DNA sequences from the nuclear ribosomal ITS and plastid *trnT-trnL-trnF* regions suggest that *Dissanthelium* is not monophyletic and is nested within *Poa*. However, ten species form a strongly supported clade (the *Dissanthelium* clade) in the ITS tree. We propose treating *Dissanthelium* and *Tovarochloa* as taxonomic synonyms of *Poa*. We erect two new sections in *Poa*: sect. *Dissanthelium*, comprising the *Dissanthelium* clade and *D. peruvianum*, and the monotypic sect. *Tovarochloa*. The necessary new combinations (*Poa aequalis*, *P. ampliaginata*, *P. calycina* var. *mathewsii*, *P. gigantea*, *P. macusaniensis*, *P. rahuii*, and *P. trollii*) and new names (*Poa* sections *Dissanthelium* and *Tovarochloa*, *P. apiculata*, *P. arcuata*, *P. boliviana*, *P. congesta*, *P. deminuta*, *P. linearifolia*, *P. parvifolia*, *P. serpaiana*, *P. swallenii*, and *P. thomasii*) are effected herein.

**Keywords**—Bayesian, *Dissanthelium*, ITS, maximum likelihood, *Poa*, *Tovarochloa*, *trnT-trnL-trnF*.

*Dissanthelium* Trin., a small, mainly Andean grass genus of dwarf species, is distinguished by two (rarely three) awnless florets mostly exceeded by equal glumes (Swallen and Tovar 1965) (Fig. 1A, B). Swallen and Tovar (1965) revised *Dissanthelium* and recognized 17 species, ten of which were newly described. Later, Tovar (1985) described three new species from Peru, bringing the total number to 20. The status of some species has changed over time; a few have been reduced to varieties, subspecies or synonymy (Nicora 1973; Soreng 1998; Soreng et al. 2003). Three species are annuals while the remainder are perennials. Most are gynomonocious (lower floret bisexual and upper floret pistillate; Fig. 1B), a few are bisexual, and one is possibly dioecious (N. Refulio-Rodriguez pers. obs.).

*Dissanthelium* is limited to the New World. Its distribution in South America is restricted to the Andes of Peru, Bolivia, Argentina, and Chile (Swallen and Tovar 1965; Renvoize 1998; Anton and Negritto 1997; Sulekic 1999) at elevations between 3,600 and 5,000 m with the exception of *D. patagonicum*, which occurs at low elevations in the Patagonian region of Argentina. Two species occur in North America, *Dissanthelium mathewsii*, which has a disjunct distribution, grows at high elevations on the volcanoes of central Mexico and also in the Andes of Peru and Bolivia. It is the only species in the genus with an amphi-Neotropical distribution. The other North American species, which grows at low elevations on islands, is *D. californicum*. It was presumed to be extinct until it was rediscovered in 2005 on Santa Catalina Island, California, U. S. A. (McCune and Knapp 2008). *Dissanthelium californicum* is also known from San Clemente Island, California, U. S. A. (rediscovered in 2010 (*Howe 1039*, RSA)) and an old collection from Guadalupe Island, Mexico. The placement of this species within *Dissanthelium* has been called into question. The species is an annual and is the only member of *Dissanthelium* that grows near sea level and in a Mediterranean-type climate. Hitchcock (1923, p. 224) wrote “this species does

not appear to be closely related to the other two [Andean species, the only ones recognized at the time], but it does not seem to be sufficiently different to constitute a distinct genus.” Further, Tovar, who contributed much to our knowledge of *Dissanthelium* (Swallen and Tovar 1965; Tovar 1985), believed that *D. californicum* may be misplaced in the genus (pers. comm. 2002).

The tribal placement of *Dissanthelium* within subfamily Pooideae based on spikelet morphology has been uncertain. Clayton and Renvoize (1986) included *Dissanthelium* in Aveneae by virtue of its long glumes. In contrast, Macfarlane (1987) and Watson and Dallwitz (1992) placed *Dissanthelium* in Poeae because of its awnless florets. Soreng et al. (2003), considering available morphological and molecular data, combined Aveneae and Poeae into the tribe Poeae (with 22 subtribes including Aveninae and Poinae), and placed *Dissanthelium* in the subtribe Poinae. Subsequently molecular studies by Gillespie et al. (2007, 2008, 2009) and Quintanar et al. (2007) confirmed the position of *Dissanthelium* in Poinae.

Molecular phylogenetic studies in *Poa* have sampled a few species of *Dissanthelium* and found that the genus is nested in *Poa* (Gillespie et al. 2007, 2008, 2009), specifically in subgen. *Poa* and supersection *Homalopoa* (Gillespie et al. 2008, 2009). *Poa* is the largest genus of grasses with more than 500 species. It is divided into five subgenera: *Ochlopoa*, *Poa* with supersections *Homalopoa* (HAMBADD) and *Poa* (POM), *Pseudopoa*, *Stenopoa*, and *Sylvestres* and approximately 22 sections and many subsections and informal species groups (Gillespie et al. 2007, 2008, 2009; Soreng et al. 2010).

In contrast to previous phylogenetic studies in *Poa* that have included at most three species of *Dissanthelium* (Gillespie et al. 2007, 2008, 2009), we investigate the phylogeny of *Dissanthelium* by sampling 17 of its species. Phylogenetic analyses were performed using DNA sequences from the

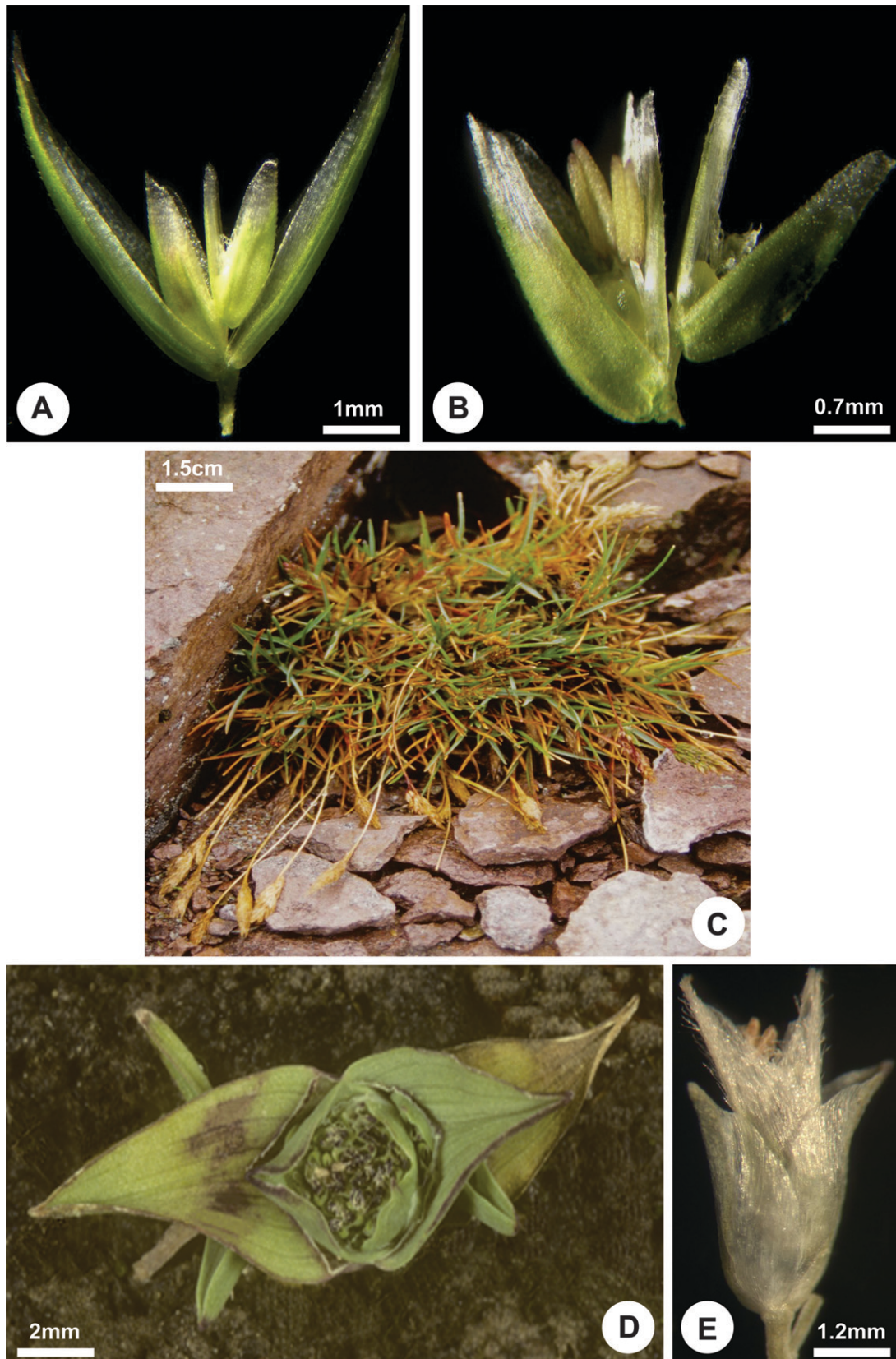


FIG. 1. *Dissanthelium breve* (A-C) and *Tovarochloa peruviana* (D-E). A, E. Spikelet. B. Florets, lower floret bisexual and upper floret pistillate. C, D. Plant. Photo D courtesy of J. T. Columbus.

nuclear ribosomal ITS and chloroplast *trnT-trnL-trnF* regions. We investigate the monophyly of *Dissanthelium* and examine interspecific relationships, including with special interest the position of *D. californicum* with respect to the Andean species. Based on our results we propose the transfer of *Dissanthelium* and *Tovarochloa* into *Poa*.

#### MATERIALS AND METHODS

**Taxon Sampling**—We sampled 17 of the 20 species of *Dissanthelium* recognized by Swallen and Tovar (1965) and Tovar (1985). Three species, *D. aequale* (Bolivia), *D. longiligulatum* (Bolivia), and *D. pygmaeum* (Peru), were not included in the analyses because searches for them in the field were unsuccessful. In addition, leaf material of these species could not be removed from herbarium specimens since they are known only from their types. The *Poa* sampling included representatives of all five subgenera as recognized by Gillespie et al. (2007, 2008, 2009). However, it was focused on the subgen. *Poa*, specifically on supersection *Homalopoa*, since previous molecular phylogenetic studies have shown that *Dissanthelium* is nested in supersection *Homalopoa* (Gillespie et al. 2008, 2009). In particular we included Andean species of *Poa* of supersection *Homalopoa* that are morphologically similar to *Dissanthelium*. The analyses included new DNA sequences of *Poa* as well as sequences that were previously deposited in GenBank by Gillespie et al. (2007, 2008, 2009). The Andean *Tovarochloa peruviana* was incorporated into this study because a possible relationship with *Dissanthelium* was suggested by Clayton and Renvoize (1986). The analyses included a total of 124 samples. The ingroup consisted of 107 samples; whenever possible more than one sample per species of *Dissanthelium* were included in the phylogenetic analyses to test species boundaries (Appendix 1). The outgroups consisted of 17 samples that include other genera of Poinae and subtribes related to Poinae, and one member of tribe Bromoeae. For the subtribes and sections of Poeae we follow the classification by Gillespie et al. (2008, 2009). Voucher information and GenBank accession numbers of the samples used in this study are provided in Appendix 1.

**DNA Isolation, Amplification, and Sequencing**—The nuclear ribosomal ITS region (ITS1 spacer + 5.8S exon + ITS2 spacer) and the chloroplast *trnT-trnL-trnF* region (*trnT-trnL* spacer, *trnL* 5' exon, *trnL* intron, *trnL* 3' exon, *trnL-trnF* spacer; hereafter referred to as *trnTLF*) were selected for use in this study because they have been widely used and informative in phylogenetic studies of grasses (e.g. Hamby and Zimmer 1988; Hsiao et al. 1999; Brysting et al. 2004; Torrecilla et al. 2004; Catalán et al. 2007), including *Poa* (Gillespie et al. 2007, 2008, 2009; Soreng et al. 2010).

Total DNA was isolated from leaf tissue dried in silica gel using a modification (Columbus et al. 1998) of the 2 × CTAB method of Doyle and Doyle (1987). To amplify the ITS region, the ITS4 and ITS5 primers designed by White et al. (1990) were employed (Table 1). Amplifications were carried out using 40 ng of DNA, 2 μL of each amplification primer with a concentration of 10 ng/μL, 5 μL of (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> 10 × PCR buffer, 3 μL of dNTPs, 0.25 μL of *Taq*, 5 μL of DMSO, and 28.75 μL of distilled water for a total volume of 50 μL. Amplifications were run in a Robocycler 96 (Stratagene, La Jolla, California), 39 cycles were run with a denaturing step at 94°C for 1 min, an annealing step at 48°C for 1 min,

an extension step at 72°C for 2 min, and a final extension at 72°C for 7 min. Amplification of *trnTLF* was performed using 25 ng of DNA, 1 μL of each amplification primer with a concentration of 10 ng/μL, 2.5 μL of (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> 10 × PCR buffer, 1.5 μL of MgCl<sub>2</sub>, 1.5 μL of dNTPs, 0.125 μL of *Taq*, 1.25 μL of DMSO and 13.625 μL of distilled water, for a total volume of 25 μL. Amplification of the *trnTLF* region was accomplished in two pieces. To amplify the *trnT-trnL* spacer, different primers were used because of amplification difficulties; most of the samples were amplified using A and D primers (Table 1). In other cases, primers B, and *trnTL* INT1F were used. Amplification of the *trnL* intron and the *trnL-trnF* spacer was more straightforward and only primers *trnL5'* Br and F were employed. Amplification reactions for the *trnT-trnL* spacer were run in a PTC-100™ thermal cycler (MJ Research, Inc., Waltham, Massachusetts) with an initial denaturing step of 4 min at 94°C, followed by 35 cycles with a denaturing step at 94°C for 1 min, an annealing step at 52°C for 1 min, an extension step at 72°C for 3 min, and a final extension at 72°C for 10 min. Amplification reactions for the *trnL* intron and *trnL-trnF* spacer regions were run in a Robocycler 96 (Stratagene), one cycle was run with a denaturing step at 94°C for 45 sec, an annealing step at 54°C for 45 sec, and an extension at 72°C for 2 min followed by 38 cycles with a denaturing step at 94°C for 45 sec, an annealing step at 52°C for 45 sec and an extension step at 72°C for 90 sec, and finished with a final extension at 72°C for 7 min. The PCR products were purified using the PEG precipitation protocol of Johnson and Soltis (1995). Sequencing reactions for the *trnTLF* region were performed using 6 ng of DNA, 1 μL of DMSO, 1 μL of primer (Table 1) with a concentration of 1.6 ng/μL, 4 μL of big dye buffer 5 ×, 1 μL of ABI Prism big dye terminator vers. 3.1 (Applied Biosystems, Foster City, California) and 12 μL of distilled water. The ITS sequencing reactions were similar except DMSO was not added. The sequencing reactions were run in a PTC-100™ Thermal Cycler (MJ Research, Inc.). DNA sequences were read using an ABI Prism 3100 automated sequencer (Applied Biosystems).

**Phylogenetic Analyses**—DNA single-stranded sequences were contiged using Sequencher 4.5 (Gene Codes Corporation, Ann Arbor, Michigan). The alignment of sequences was done manually based on the similarity criterion (Simmons 2004) and using Se-Al vers. 2.0a11 (Rambaut 1996). In the *trnTLF* data matrix 69 base pairs were removed before analyses from ambiguous sites. Aligned data matrices were deposited in TreeBASE (study number S11724).

Cladograms were rooted with *Bromus* based on the analysis of the subfamily Pooideae by Davis and Soreng (2007). Nucleotide substitution models were determined with the program jModelTest (Posada 2008) using the Akaike information criterion (AIC; Akaike 1974). The nucleotide substitution model SYM + G was obtained for ITS, and TVM + G for *trnTLF*.

Bayesian MCMC (Yang and Rannala 1997) and maximum likelihood (ML; Felsenstein 1973) analyses were conducted to infer phylogeny. Bayesian posterior probabilities (PP) were calculated with MrBayes vers. 3.1.2 (Ronquist and Huelsenbeck 2003). Analysis consisted of three separated runs for each locus, a random starting tree was employed; and one cold and three incrementally heated Markov chain Monte Carlo (MCMC) chains were run for 6,689,500 (ITS), and 2,426,500 (*trnTLF*) generations, respectively. Tree sampling was done every 500 generations. For *trnTLF* we opted to employ the GTR + G model instead of TVM + G because the latter is not implemented in MrBayes. Analyses were run until the value of the average standard deviation of split frequencies dropped

TABLE 1. Primers used in the amplification and sequencing of the ITS and *trnTLF* regions.

Primer name (sequence (5'-3'))	Amplification	Sequencing	Author/Source
ITS2 (GCTGCGTTCTTCATCGATGC)	✓	✓	White et al. (1990)
ITS3 (GCATCGATGAAGAACGCGAGC)	✓	✓	White et al. (1990)
ITS4 (TCCTCCGTTATTTGATATGC)	✓	✓	White et al. (1990)
ITS5 (GGAAGTAAAAGTCGTAACAAGG)	✓	✓	White et al. (1990)
A (CATTACAAATGCGATGCTCT)	✓	✓	Taberlet et al. (1991)
B (TCTACCGATTTCGCCATATC)	✓	✓	Taberlet et al. (1991)
<i>trnTL</i> INT1R (ATCCAAAAGTTTTCTCTCCCC)	✓	✓	This paper (designed by J. T. Columbus)
<i>trnTL</i> INT1F (GGGGAGAGAAAAACTTTTGGAT)	✓	✓	This paper (designed by J. T. Columbus)
<i>trnTL</i> INT3F (GTTAGCTTGATATGCTTAAC)	✓	✓	This paper (designed by J. T. Columbus)
<i>trnTL</i> INT4R (CGTCCGAGCCATATCAAATTG)	✓	✓	This paper (designed by J. T. Columbus)
<i>trnL5'</i> BR (GATATGGCGAAATCGGTAGA)	✓	✓	Columbus et al. (2007)
F (ATTGAACTGGTGACACGAG)	✓	✓	Taberlet et al. (1991)
<i>trnL</i> INT3F (GAGAGAGTCCCATTCTACATGTC)	✓	✓	Columbus et al. (2007)
D (GGGGATAGAGGACTTGAAC)	✓	✓	Taberlet et al. (1991)

below 0.01. The first 25% of samples were discarded as burn in (Huelsenbeck and Ronquist 2001). Stationarity was verified using the program Tracer version 1.4 (Rambaut and Drummond 2004). Maximum likelihood analysis was performed using RAxML version 7.0.4 (Stamatakis 2006; Stamatakis et al. 2008) at the CIPRES PORTAL 2 (<http://www.phylo.org/portal2/login/input.action>). The GTR + G model was used for each locus as recommended by the author (Stamatakis 2006) and 1,000 rapid bootstrap (BS; Felsenstein 1985) replicates were performed. Bayesian and RAxML trees were visualized and edited using Dendroscope version 2.4 (Huson et al. 2007).

## RESULTS

The ITS data matrix of 122 samples had an aligned length of 622 bp. Sequences of ITS were obtained for all accessions, except for *Poa interior*, and *P. occidentalis*. The 5' end was complete in all sequences; only 10 sequences were incomplete at the 3' end. Polymorphisms were almost completely absent in *Dissanthelium* samples. Only two polymorphic sites were observed in *D. trollii*. However, polymorphisms were common in samples of *Poa*, which potentially indicates cases of hybridization and introgression (Gillespie et al. 2010; Soreng 1990; Soreng et al. 2010). Polymorphisms may be rare in *Dissanthelium* because of inbreeding; outcrossing appears to be uncommon in the genus (Anton and Negritto 1997; N. Refulio-Rodriguez pers. obs.).

The *trnTLF* data matrix had 122 samples and an aligned length of 2,460 bp after removing 69 bp from ambiguous sites. Sequences of *trnTLF* were obtained for all accessions, except *Dissanthelium laxifolium*, and one sample of *D. expansum* (Peterson 16594). In a few cases both ends of the sequences were incomplete. Five samples were cloned to overcome *Taq* stutter problems caused by poly-N regions.

Analyses were performed for each marker separately because an incongruence length difference test (Farris et al. 1994) performed in PAUP\* 4.0b10 (Swofford 2002) with the data partitioned between ITS and the *trnTLF* found conflict between the partitions ( $p = 0.01$ ). Phylogenetic studies in *Poa* and Poinae have also shown conflicts between ITS and plastid gene trees. These conflicts led Gillespie et al. (2008, 2010) and Soreng et al. (2010) to avoid combining datasets.

The Bayesian trees were similar to those obtained from ML. The ITS tree is less resolved than the *trnTLF* tree (Figs. 2, 3), while in the ITS tree a polytomy includes the members of *Poa* subgen. *Poa* and subgen. *Stenopoa*. In the *trnTLF* tree the members of subgen. *Poa* and subgen. *Stenopoa* form clades. Similar differences in amount of resolution between the ITS and *trnTLF* trees were also found by Gillespie et al. (2008). Even though the ITS tree has less resolution than the *trnTLF* phylogeny a well-supported clade containing ten species of *Dissanthelium* is found within the subgen. *Poa*/*Stenopoa* clade (Fig. 2). In contrast in the *trnTLF* phylogeny there is a poorly supported clade containing *D. peruvianum*, the ten *Dissanthelium* species that form a strongly supported clade in the ITS phylogeny, and six (all Andean except for *P. mathewsii*) species of *Poa*. Also in the ITS tree, most of the species of *Dissanthelium* are resolved as monophyletic while in the *trnTLF* tree several species are in unresolved polytomies. Moreover, while in the ITS phylogeny *D. patagonicum* and *Poa atropidiformis* form a clade with low support, this clade was not recovered in the *trnTLF* tree. In both ITS and *trnTLF* trees (Figs. 2, 3) *Tovarochoa peruviana* is nested in *Poa*. In the *trnTLF* tree it is sister to the Andean *Aphanelytrum procumbens* with strong support (1.00 PP/92 BS). However, in the ITS tree they are

not sisters. Their positions are unresolved in the large clade containing species of *Poa* subgen. *Poa* and *Stenopoa*.

## DISCUSSION

The results of this study show all species of *Dissanthelium* sampled to be nested within *Poa* (Figs. 2, 3), a finding consistent with phylogenies of *Poa* in Gillespie et al. (2007, 2008, 2009) that included a few species of *Dissanthelium*. The molecular results found here and those of Gillespie et al. (2007, 2008, 2009) support prior hypotheses of a relationship between *Dissanthelium* and *Poa* based on morphological evidence. Nuttall (1848), when describing *D. californicum*, indicated that it is similar to *Poa*, and also has glumes that resemble those of *Danthonia* (Danthonioideae). Nicora (1973) studied the lemma morphology of *D. patagonicum* and noticed that it looks similar to that of *Poa atropidiformis*. She found that lemmas of *D. patagonicum* have five nerves (as in *Poa*) instead of the usual three in *Dissanthelium*. *Dissanthelium* typically is differentiated from *Poa* by its long glumes and lemma with three nerves (Tovar 1993). However, Anton and Negritto (1997) and Watson and Dallwitz (1992) reported lemmas with 3–5 nerves in *Dissanthelium*. Clayton and Renvoize (1986) noted *Dissanthelium* species with short glumes might be mistaken for a depauperate *Poa*. Anton and Negritto (1997) suggested a possible relationship between *Dissanthelium* and high Andean *Poa* species because they share similarities in sexual system (gynomonocy). Soreng (1998) indicated *Dissanthelium* may be a sister group of *Poa* or an offshoot of it, because both genera have similar adaxial leaf blade surfaces and caryopsis features; consequently, he believed that the long glumes of *Dissanthelium* show that this character is a homoplasious similarity between former subtribes Poeae and Aveneae. Our molecular results corroborate undeniably that the long glumes of *Dissanthelium* are an example of convergence. Thus, the placement of *Dissanthelium* in Aveneae based on its long glumes (Clayton and Renvoize 1986) was erroneous. In addition to the foregoing, studies of the lemma and leaf micromorphology, and leaf blade anatomy of *Dissanthelium* demonstrate that the genus is similar to the *Poa* (Refulio-Rodriguez 2007).

Relationships among *Poa* subgenera in the *trnTLF* tree (Fig. 3) are consistent with those found by Gillespie et al. (2009). The placement of several *Poa* species in the ITS tree (Fig. 2) is not consistent with the *trnTLF* tree (e.g. *P. abbreviata* and *P. trivialis*). These conflicts found in *Poa* could be due to hybridization, polyploidy, or long-branch attraction (Gillespie et al. 2008, 2010; Soreng et al. 2010).

In our *trnTLF* tree (Fig. 3), all species of *Dissanthelium* are nested within *Poa* subgen. *Poa* (1.00 PP/100 BS), specifically in the supersection *Homalopoa*. Supersection *Homalopoa* (Gillespie et al. 2007, 2008, 2009) includes ca. 340 species, seven sections (*Homalopoa*, *Acutifoliae*, *Madropoa*, *Brizoides*, *Anthochloa*, *Dasypoa*, and *Dioicopoa*; referred to as HAMBADD by Gillespie et al. (2007)), and various informal groups (e.g. "Punapoa"). In this study supersection *Homalopoa* was unresolved as monophyletic in the ITS tree. In previous studies the monophyly of this supersection was evidenced in the *trnTLF* and ITS+ETS trees and received low to good support (Gillespie et al. 2007, 2008, 2009). Although in our plastid tree supersection *Homalopoa* has good support (0.98 PP/79 BS) relationships among the sections are unresolved. In addition, our results indicate that not all of the sections and informal groups of supersection *Homalopoa* are monophyletic.

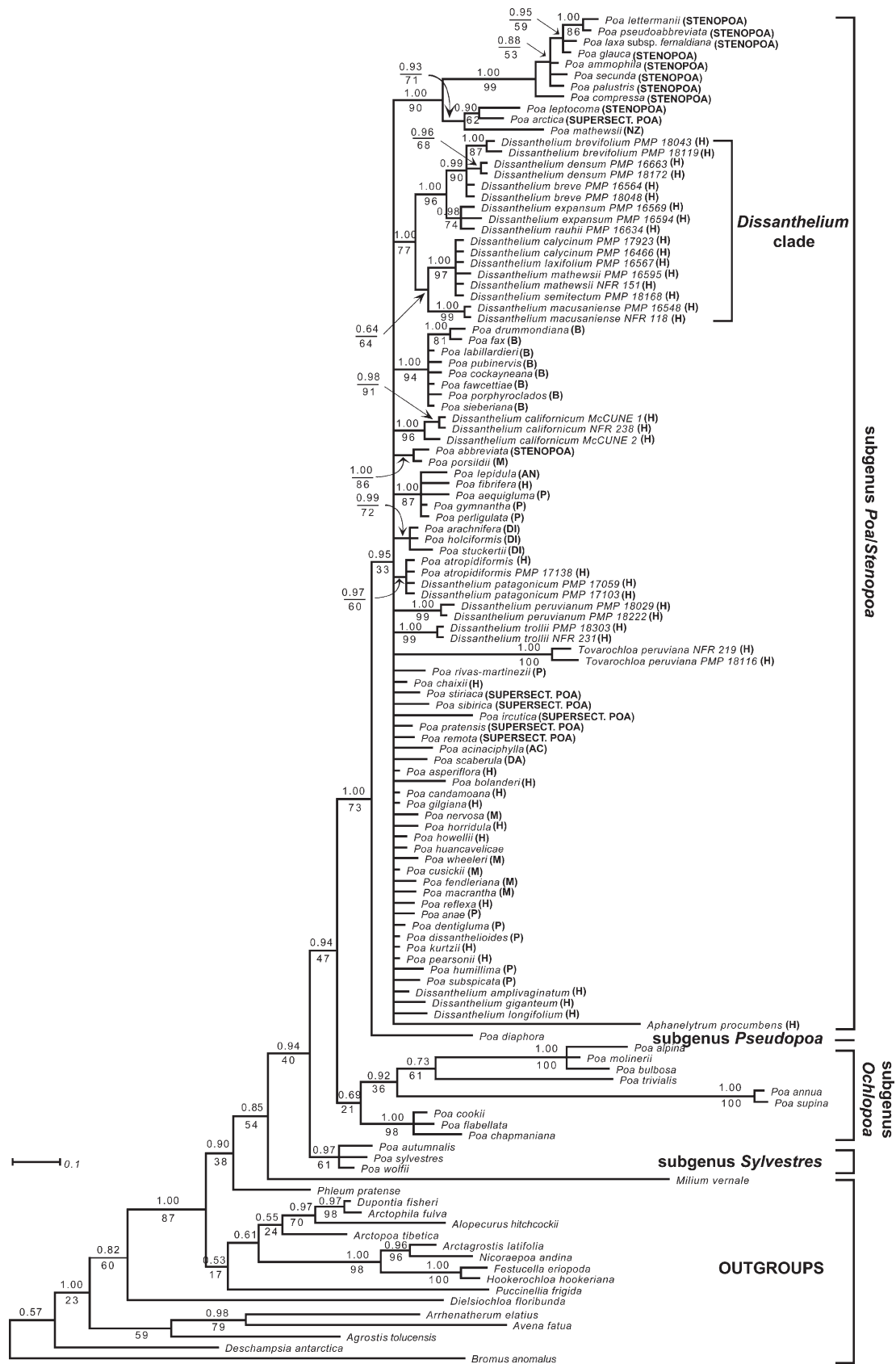


FIG. 2. Nuclear rDNA ITS majority-rule consensus phylogram of 10,036 trees generated from the Bayesian analysis. Numeric values above and below each branch are Bayesian posterior probabilities and ML bootstrap values, respectively. Abbreviations for sections and an informal group of the supersection *Homalopoa* (H = *Homalopoa*, AC = *Acutifoliae*, M = *Madropoa*, B = *Brizoides*, AN = *Anthochloa*, DA = *Dasypoa*, and DI = *Dioicopoa*, informal group "Punapoa" = P), and the subgenus *Stenopoa* (*Stenopoa* = subgenus *Stenopoa*). "NZ" indicates species of *Poa* from New Zealand a designated section.

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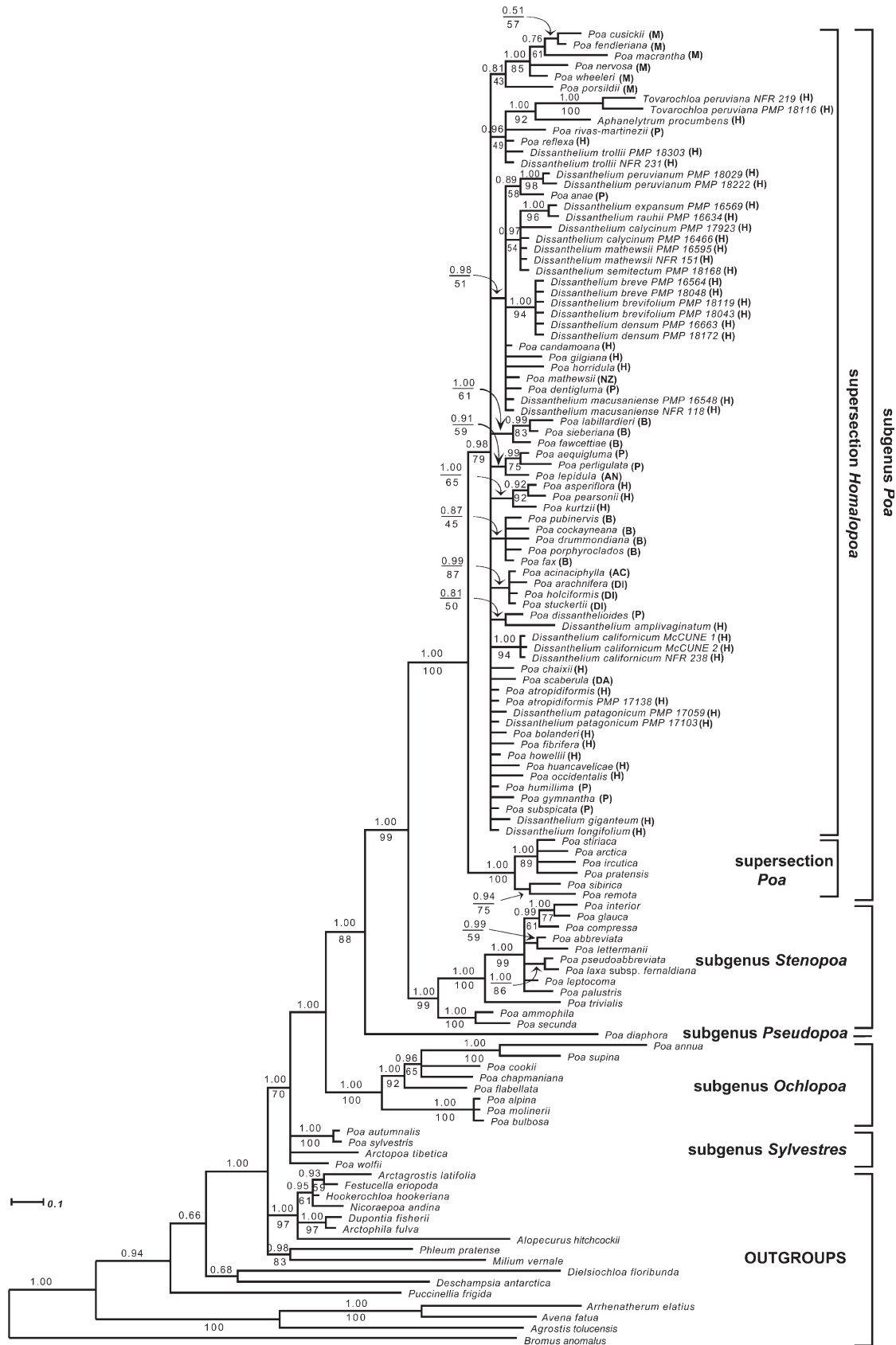


FIG. 3. Plastid *trnTLF* majority-rule consensus phylogram of 3,641 trees generated from the Bayesian analysis. Numeric values above and below each branch are Bayesian posterior probabilities and ML bootstrap values, respectively. Abbreviations for sections and an informal group of the supersection *Homalopoa* (H = *Homalopoa*, AC = *Acutifoliae*, M = *Madropoa*, B = *Brizoides*, AN = *Anthochloa*, DA = *Dasympoa*, and DI = *Dioicopoa*, informal group “*Punapoa*” = P). “NZ” indicates species of *Poa* from New Zealand without a designated section.

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Analyses by Gillespie et al. (2007) recovered some sections of supersection *Homalopoa* but with weak support. Although we include more South American representatives of supersection *Homalopoa* than in previous studies (Gillespie et al. 2007, 2008, 2009), resolution within this clade has not improved. The low DNA sequence variation and associated low support values found in the *Dissanthelium* clade and in *Poa* supersection *Homalopoa* may be due to rapid and recent diversification. Most species of *Dissanthelium* and *Poa* supersection *Homalopoa* included in our study are primarily distributed at high elevations in the Andes. It has been hypothesized that high elevation herbaceous plants may be of recent origin. Dated phylogenies suggest that some lineages of high elevation Andean plants diverged after the final uplift of the Andes, late Pliocene or early Pleistocene (ca. 2–4 millions of years ago Mya; Meudt and Simpson 2006; Hughes and Eastwood 2006).

*Dissanthelium* is not monophyletic in any of our analyses. While in our ITS phylogeny most of the species (10), including the type (*D. calycinum*), form a well-supported clade that we refer to as the *Dissanthelium* clade (Fig. 2), seven species (*D. amplivaginatatum*, *D. californicum*, *D. giganteum*, *D. longifolium*, *D. patagonicum*, *D. peruvianum*, and *D. trollii*) are found elsewhere within the subgen. *Poa/Stenopoa* clade. In our ITS phylogeny, the *Dissanthelium* clade (1.00 PP/77 BS) is composed of two subclades; in one subclade *D. macusaniense* is sister to a polytomy that includes *D. calycinum*, *D. laxifolium*, *D. mathewsii*, and *D. semitectum*; and in the second subclade *D. expansum*/*D. rauhii* are sister to a clade containing *D. breve*, *D. brevifolium*, and *D. densum*. All species in the *Dissanthelium* clade are found only in the Andes, except for *D. mathewsii*, which is also found on the volcanoes of central Mexico at high elevations.

Morphological characters used in the taxonomy of *Dissanthelium* include the aspect of the blades, size and shape of glumes and lemmas, ornamentation of lemmas, and size of the anthers, (Swallen and Tovar 1965; Tovar 1993). Some of these characters are phylogenetically informative in the *Dissanthelium* clade. For instance, in the subclade of the *Dissanthelium* clade formed by *D. expansum*, *D. rauhii*, *D. breve*, *D. densum*, and *D. brevifolium*, all species appear to have dull, as opposed to shiny blades. However, in this subclade the length of the glumes relative to the florets is variable (*D. breve*, *D. densum*, and *D. expansum* have glumes longer than the florets; and *D. brevifolium*, and *D. rauhii* have glumes as long as the florets) and therefore this character is not phylogenetically informative. In the polytomy that includes *D. calycinum*, *D. laxifolium*, *D. mathewsii*, and *D. semitectum*, all glumes are longer than the florets. These species are morphologically similar to one another and only the shape and size of the glumes and lemmas can be used to differentiate them. Because of this morphological similarity, Soreng (1998) treated *D. mathewsii* as a subspecies of *D. calycinum*. In the ITS tree, specimens of *D. mathewsii* from Peru (*Peterson 16595*) and from Mexico (*Refugio 151*) do not form an exclusive clade, but are in an unresolved polytomy with *D. calycinum*, *D. laxifolium*, and *D. semitectum* samples.

The seven species falling outside of the *Dissanthelium* clade and *Tovarochloa peruviana* are discussed below.

**DISSANTHELIUM AMPLIVAGINATUM**—In the *trnTLF* tree (Fig. 3), this species is sister to *Poa dissanthelioides*. However, this relationship has low support (0.81 PP/50 BS). In the ITS phylogeny its position in the subgen. *Poa/Stenopoa* clade is unresolved. *Dissanthelium amplivaginatatum* can be distinguished from the rest of the genus by its dense, oblong-ovoid panicle.

**DISSANTHELIUM CALIFORNICUM**—This annual species is the only member of the genus that grows in a Mediterranean-type climate, and, along with *D. patagonicum*, occurs near sea level. These two species are also distinct from the remaining species of *Dissanthelium* by having spikelets with up to three bisexual florets and hairy lemmas. Its distribution and morphology led Hitchcock (1923) and Tovar (pers. comm. 2002) to speculate that *D. californicum* may be misplaced in the genus. *Dissanthelium californicum* was presumed to be extinct (CNPS 2001) since it had not been seen for more than a hundred years. Fortunately it was rediscovered in 2005 on Santa Catalina Island, California (McCune and Knapp 2008), which allowed us to include it in this study and explore its affinity to the other members of *Dissanthelium*. In our ITS tree (Fig. 2) *D. californicum* is not part of the *Dissanthelium* clade and it is not sister to any of the seven *Dissanthelium* species that fall outside of this clade, nor to any species of *Poa*. Its placement in the subgen. *Poa/Stenopoa* clade is unresolved. In the *trnTLF* tree (Fig. 3) it is nested in supersection *Homalopoa* (Fig. 2), but its position is unresolved. Our results do not identify its closest relative. Future studies need to include more North American *Poa* species and more gene markers to improve the resolution within supersection *Homalopoa*.

**DISSANTHELIUM GIGANTEUM**—In the ITS and *trnTLF* analyses the position of this species is unresolved within the subgen. *Poa/Stenopoa* clade and supersection *Homalopoa* respectively. This species is the tallest (ca. 30–40 cm) growing in the high Andes. Morphologically, *D. giganteum* is distinct from the remaining species because its abaxial leaf blade epidermis is covered with hooks (Refugio-Rodriguez 2007).

**DISSANTHELIUM LONGIFOLIUM**—In all trees its position is unresolved as described for *D. giganteum*. *Dissanthelium longifolium* differs from others in the genus by having glumes that are slightly shorter than the florets, linear leaf blades that exceed the panicles, and a unique leaf blade anatomy (abaxial epidermis three cells thick; Refugio-Rodriguez 2007).

**DISSANTHELIUM PATAGONICUM**—Like *D. californicum*, this species grows at low elevations, and has spikelets with 2–3 bisexual florets and hairy lemmas. In the ITS tree, *D. patagonicum* forms a clade with *Poa atropidiformis* with moderate support (0.97 PP) in the Bayesian analysis, and with low support (60 BS) in the ML analysis. This relationship was not recovered in the *trnTLF* analysis. Morphologically, *D. patagonicum* is similar to *Poa atropidiformis* and only the presence of hairs on the lemma in *D. patagonicum* differentiates them. Because of this morphological similarity, Nicora (1973) transferred *D. patagonicum* into *Poa* as a variety of *P. atropidiformis* and Soreng (1998) transferred *P. atropidiformis* to *Dissanthelium*. *Poa atropidiformis*, like *D. patagonicum* grows in the Patagonian region of South America and they are sometimes sympatric.

**DISSANTHELIUM PERUVIANUM**—This annual species often occurs sympatrically in the Andes with another annual, *D. macusaniense*. In the *trnTLF* tree, *D. peruvianum* is sister to the Andean *Poa anae* but with low support (Fig. 3) and together they are part of a polytomy that includes six (all Andean except for *P. mathewsii*) species of *Poa* and ten species of *Dissanthelium* (the *Dissanthelium* clade in the ITS tree). Based on features of the spikelet, abaxial epidermis of the leaf blade, micromorphology of the lemma, and leaf blade anatomy (Refugio-Rodriguez 2007), *D. peruvianum* is similar to the species in the *Dissanthelium* clade. Consequently, as

presented below, we choose to include this species into *Poa* sect. *Dissanthelium*.

**DISSANTHELIUM TROLLII**—This is the only rhizomatous species in the genus. One specimen *Peterson 18303*, has long anthers, almost as long as the lemma, and a reduced gynoeceum. Another, *Refulio 231*, has staminodes and a well-developed gynoeceum, indicating that *D. trollii* may be dioecious. Although the spikelets are typical of the genus, the lemma epidermis is unique in that it is smooth (Refulio-Rodriguez 2007). In the *trnTLF* tree (Fig. 3) *D. trollii* is part of a poorly resolved clade formed by *Tovarochloa peruviana*/*Aphanelytrum procumbens*, *Poa rivas-martinezii*, and *Poa reflexa* with moderate support in Bayesian analysis (0.96 PP) and low support (49 BS) in ML. In the ITS tree its position is unresolved in the subgen. *Poa/Stenopoa* clade.

**TOVAROCHLOA PERUVIANA**—This rare, dwarf (Fig. 1D), annual species grows in shallow ephemeral pools in the Andes of Peru and Bolivia. It has one floret per spikelet (Fig. 1E). Clayton and Renvoize (1986) treated the monotypic *Tovarochloa* as a genus of uncertain affinity, but in their diagram of relationships of Aveneae it was placed next to *Dissanthelium*. The results from the Bayesian and ML analyses (Figs. 2, 3) show *T. peruviana* to be nested within *Poa*. Its position within *Poa* was also demonstrated by Gillespie et al. (2008). In our results the inclusion of this species in *Poa* supersection *Homalopoa* is supported in the *trnTLF* tree where it is sister to Andean *Aphanelytrum procumbens* with strong support (1.00 PP/92 BS). However, in the ITS tree *T. peruviana* and *A. procumbens* are not sisters and their positions in the subgen. *Poa/Stenopoa* clade are unresolved. In Gillespie et al. (2008) the sister relationship between *Tovarochloa* and *Aphanelytrum* has low support (58 BS) in the ITS maximum parsimony analysis and good support (87 BS) in the *trnTLF* analysis. The sister relationship between *T. peruviana* and *A. procumbens* might be a result of a long-branch attraction (Philippe et al. 2005; Kolaczowski and Thornton 2009). Morphologically, *Tovarochloa* differs from *Aphanelytrum procumbens*. In addition the abaxial

leaf blade epidermis and leaf blade anatomy of *Tovarochloa* is unique and distinct from all species of *Poa* and *Dissanthelium* included in this study (Refulio-Rodriguez 2007).

#### TAXONOMIC TREATMENT

Since the molecular phylogenies of this study and those of previous studies (Gillespie et al. 2007, 2008, 2009) support the inclusion of *Dissanthelium* and *Tovarochloa* in *Poa*, we make the necessary nomenclatural changes below. In addition we create two new sections in *Poa* (supersection *Homalopoa*). The first one, *Poa* sect. *Dissanthelium*, consists of species of the *Dissanthelium* clade and *D. peruvianum*. We recognize eight species and two varieties for *Poa* sect. *Dissanthelium* (*Poa arcuata*, *Poa calycina* var. *calycina*, and *Poa calycina* var. *mathewsii*, *Poa congesta*, *Poa macusaniensis*, *Poa parvifolia*, *Poa rauhii*, *Poa serpaiana*, and *Poa swallenii*). *Dissanthelium laxifolium* is synonymized with *Poa calycina* var. *calycina*, and *Dissanthelium semitectum* is synonymized with *Poa calycina* var. *mathewsii*. The second new section constitutes the monotypic *Poa* sect. *Tovarochloa*.

***Poa* sect. *Dissanthelium* (Trin.) N. F. Refulio-Rodriguez, comb. et stat. *Dissanthelium* Trin., *Linnaea* 10(3): 305. 1836. *Brizopyrum calycinum* J. Presl, *Reliq. Haenk.* 1(4–5): 281. 1830.—TYPE: PERU. *T. Haenke s. n.* (holotype: PR).'**

Annual or perennial, mostly dwarf, caespitose. Plants frequently gynomonoeious (lower floret bisexual and upper floret pistillate). Inflorescence a panicle, narrow (spike-like) to open. Spikelets usually with two florets. Rachilla disarticulating above glumes and between florets. Glumes two, equal or approximately so, oblong-lanceolate, lanceolate, ovate-lanceolate, arcuate, subacuminate, equaling or longer than the florets, 3-nerved. Lemma ovate or oblong, acute, subacute, obtuse, or toothed, usually scabrous, rarely glabrous or pubescent, 3(5)-nerved. Distribution North America (Mexico) and South America (Argentina, Chile, Bolivia, and Peru).

#### KEY TO THE SPECIES OF *POA* SECT. *DISSANTHELIUM* (ADAPTED FROM SWALLEN AND TOVAR 1965; TOVAR 1993)

1. Plants annual . . . . . 2
2. Lemma pubescent, apex dentate . . . . . 1. *Poa macusaniensis*
2. Lemma glabrous, apex entire . . . . . 2. *Poa serpaiana*
1. Plants perennial . . . . . 3
3. Abaxial leaf blade surface dull . . . . . 4
4. Glumes longer than the florets . . . . . 5
5. Glumes oblong-lanceolate or lanceolate, not arcuate . . . . . 6
6. Panicles loosely flowered, not spike-like . . . . . 3. *Poa swallenii*
6. Panicle dense, spike-like . . . . . 4. *Poa congesta*
5. Glumes narrow, subacuminate, arcuate . . . . . 5. *Poa arcuata*
4. Glumes as long as the florets . . . . . 7
7. Culms 2–4 cm long; panicles less than 1.5 cm long . . . . . 6. *Poa parvifolia*
7. Culms 6–9 cm long; panicles more than 3 cm long . . . . . 7. *Poa rauhii*
3. Abaxial leaf blade surface shiny . . . . . 8
8. Glumes 2.4–3 mm long; lower lemma 1.8–2.3 mm long, apex obtuse or subacute . . . . . 8. *Poa calycina* var. *calycina*
8. Glumes 3.5–4.2 mm long; lower lemma 2.4–2.8 mm long, apex acute . . . . . 9. *Poa calycina* var. *mathewsii*

1. ***Poa macusaniensis*** (E. H. L. Krause) N. F. Refulio-Rodriguez, comb. nov. *Graminastrum macusaniense* E. H. L. Krause, *Beih. Bot. Centralbl.* 32: 348. 1914. *Dissanthelium macusaniense* (E. H. L. Krause) R. C. Foster & L. B. Sm., *Phytologia* 12(5): 249. 1965.—TYPE: PERU. In pascuis prope Macusani, Jun. 1854, W. Lechler 1836 (holotype: P!; isotype: GOET, W).

2. ***Poa serpaiana*** N. F. Refulio-Rodriguez, nom. nov. *Phalaridium peruvianum* Nees & Meyen, *Gramineae* 29. 1841. *Dissanthelium peruvianum* (Nees & Meyen) Pilg., *Bot. Jahrb. Syst.* 37: 378. 1906. non *Poa peruviana* Jacq., *Collectanea* 1: 107. 1786 [1787].—TYPE: PERU. Ad lacum Titicacam, Apr., F. J. F. Meyen s. n. (isotype: B). The specific epithet honors Dr. Oscar Tovar Serpa,



without his devotion to grasses this study would not have been possible.

3. ***Poa swallenii*** N. F. Refulio-Rodriguez, nom. nov. *Dissanthelium expansum* Swallen & Tovar, *Phytologia* 11: 374. 1965. non *Poa expansa* J. F. Gmel., *Syst. Nat.* 181. 1791.—TYPE: PERU. Pinasnioc, Panticolla pass, about 3,600 m, Cook & Gilbert 1305 (holotype: US!). The specific epithet honors Dr. Jason R. Swallen who described the species for the first time.
4. ***Poa congesta*** N. F. Refulio-Rodriguez, nom. nov. *Dissanthelium densum* Swallen & Tovar, *Phytologia* 11: 374. 1965. non *Poa densa* Troitsky, *Izv. Glavn. Bot. Sada S.S.S.R.* 27: 619, f. 1. 1928.—TYPE: PERU. Huancavelica: Huancavelica Prov., Conaica Dist., entre Huaytanayoc y Manta, 4,500 m, 11 May 1956, O. Tovar 2547 (holotype: US!). The specific epithet refers to the crowded, spike-like panicle.
5. ***Poa arcuata*** N. F. Refulio-Rodriguez, nom. nov. *Dissanthelium breve* Swallen & Tovar, *Phytologia* 11: 371. 1965. non *Poa brevis* Hitchc., *Contr. U.S. Natl. Herb.* 24(8): 328. 1927.—TYPE: PERU. Huancavelica: Huancavelica Prov., Huaytanayoc-Tansiri, cerca a Manta, 4,400–4,500 m, 31 Mar. 1953, O. Tovar 1161 (holotype: US!). The specific epithet refers to the arcuate tips of the glumes.
6. ***Poa parvifolia*** N. F. Refulio-Rodriguez, nom. nov. *Dissanthelium brevifolium* Swallen & Tovar, *Phytologia* 11: 375. 1965. non *Poa brevifolia* DC., *Syn. Gall.* 131. 1806.—TYPE: PERU. Junin: Yauli, on loose “doby” slope, 13,600 ft, 25 May 1922, Macbride & Featherstone 933 (holotype: US!). The specific epithet refers to the small leaves.
7. ***Poa rauhii*** (Swallen & Tovar) N. F. Refulio-Rodriguez, comb. nov. *Dissanthelium rauhii* Swallen & Tovar, *Phytologia* 11: 376. 1965.—TYPE: PERU. Salcantay, 3,200 m, 29 May 1957, W. Rauh & G. Hirsch P-1418 (holotype: US!).
8. *POA CALYCINA* (J. Presl) Kunth, *Enum. Pl.* 1: 326. 1833. *Brizopyrum calycinum* J. Presl, *Reliq. Haenk.* 1(4–5): 281. 1830. *Dissanthelium calycinum* (J. Presl) Hitchc., *J. Wash. Acad. Sci.* 13(11): 224. 1923.—TYPE: PERU. T. Haenke s. n. (holotype: PR).
- Dissanthelium laxifolium* Swallen & Tovar, *Phytologia* 11: 370. 1965.—TYPE: PERU. Ancash: Bolognesi, 29 May 1956, E. Cerrate 2627 (holotype: US!).
9. ***Poa calycina* var. *mathewsii*** (Ball) N. F. Refulio-Rodriguez, comb. nov. *Deschampsia mathewsii* Ball, *J. Linn. Soc., Bot.* 22: 60. 1885. *Dissanthelium sclerochloides* Steud. ex E. Fourn., *Mexic. Pl.* 2: 112. 1886. *Dissanthelium mathewsii* (Ball) R. C. Foster & L. B. Sm., *Phytologia* 12(5): 249. 1965.—TYPE: PERU. Above Casapalca, 14,000–14,300 ft, 22 Apr. 1882, Ball s. n. (holotype: K; isotype: GH).
- Dissanthelium semitectum* Swallen & Tovar, *Phytologia* 11: 370. 1965.—TYPE: PERU. Junin, 12 Jun 1922, J. F. MacBride & W. Featherstone 1155 (holotype: US!).

Following are the nomenclatural changes for the species of *Dissanthelium* that were included in our molecular analysis but do not form part of the *Poa* sect. *Dissanthelium*:

***Poa amplivaginata*** (Tovar) N. F. Refulio-Rodriguez, comb. nov. *Dissanthelium amplivaginatum* Tovar, *Public. Mus. Hist. Nat., Ser. B, Bot.* 33: 7. 1985.—TYPE: PERU. Ancash:

Bolognesi, cumbre entre Pachacoto y la Unión, 4740 m, 19 Mar. 1983, O. Tovar et al. 9777 (holotype: USM!; isotype: MAF, MO, US!).

*Poa atropidiformis* var. *patagonica* (Parodi) Nicora, *Darwiniana* 18: 97. 1973. *Dissanthelium patagonicum* Parodi, *Physis* (Buenos Aires) 8: 80, f. 7. 1925.—TYPE: ARGENTINA. Santa Cruz: Rio Gallegos, 24 Dec. 1922, L. Dauber 180 (holotype: BA; isotype: SI, US!).

***Poa gigantea*** (Tovar) N. F. Refulio-Rodriguez, comb. nov. *Dissanthelium giganteum* Tovar, *Public. Mus. Hist. Nat., Ser. B, Bot.* 33: 7–8. 1985.—TYPE: PERU. Ancash: de Huaraz a La Unión, 4,590 m, 22 Mar. 1983, O. Tovar et al. 9831 (holotype: USM!; isotype: MAF, MO, US!).

***Poa linearifolia*** N. F. Refulio-Rodriguez, nom. nov. *Dissanthelium longifolium* Tovar, *Public. Mus. Hist. Nat. Lima, Ser. B, Bot.* 33:9–10. 1985. non *Poa longifolia* Trin., *Mém. Acad. Imp. Sci. Saint-Petersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat.* 4,2(1): 61. 1836. non *Poa longifolia* Hochst. ex A. Rich., *Tent. Fl. Abyss.* 2: 425. 1851.—TYPE: PERU. Huánuco: Dos de Mayo Prov., valle de Huallanca, césped de Puna con pajonal, 4,070 m, 23 Mar. 1983, O. Tovar et al. 9884 (holotype: USM!; isotype: MAF, MO, US!). The specific epithet refers to the very narrow leaf blades.

***Poa thomasii*** N. F. Refulio-Rodriguez, nom. nov. *Stenochloa californica* Nutt., *Proc. Acad. Nat. Sci. Philadelphia* 4: 25. 1848. *Dissanthelium californicum* (Nutt.) Benth., *Hooker's Icon. Pl.* 4: 56. 1881. non *Poa californica* Steud., *Syn. Pl. Glumac.* 1: 261. 1854.—TYPE: U. S. A. California: Santa Catalina Island, *Gambel s. n.* (holotype: GH!; isotype: US!). The specific epithet honors Thomas Nuttall who first described the species.

***Poa trollii*** (Pilg.) N. F. Refulio-Rodriguez, comb. nov. *Dissanthelium trollii* Pilg., *Notizbl. Bot. Gart. Berlin-Dahlem* 11: 778. 1933.—TYPE: BOLIVIA. La Union, *Troll 1966* (holotype: B).

Three species, *Dissanthelium aequale*, *D. longiligulatum*, and *D. pygmaeum*, were not included in our molecular analysis. However, the type specimens of all three were examined. Morphological similarities of the spikelet with the remaining species of *Dissanthelium* were found and based on these similarities we also transfer these species into *Poa*:

***Poa aequalis*** (Swallen & Tovar) N. F. Refulio-Rodriguez, comb. nov. *Dissanthelium aequale* Swallen & Tovar, *Phytologia* 11: 368. 1965.—TYPE: BOLIVIA. G. Mandon 1292A (holotype: US!).

***Poa boliviana*** N. F. Refulio-Rodriguez, nom. nov. *Dissanthelium longiligulatum* Swallen & Tovar, *Phytologia* 11: 369. 1965. non *Poa boliviensis* Hack. *Repert. Spec. Nov. Regni Veg.* 11: 25. 1912. non *Poa longiligula* Scribn. & T.A. Williams, *Circ. Div. Agrostol. U.S.D.A.* 9: 3. 1899.—TYPE: BOLIVIA. La Paz, 18,000–20,000 ft, 20 Jan. 1926, A. Guerrero s. n. (holotype: US!). The specific epithet refers to the endemic distribution of the species.

***Poa deminuta*** N. F. Refulio-Rodriguez, nom. nov. *Dissanthelium pygmaeum* Swallen & Tovar, *Phytologia* 11: 367. 1965. non *Poa pygmaea* Buchanan, *Indig. Grass. N. Zeal.*, t. 50A. 1880.—TYPE: PERU. Huancavelica: Huancavelica Prov., Coniaca Dist., Huaytanayoc-Tansiri, césped de Puna,

4,500 m, 11 May 1956, O. Tovar 2545 (holotype: US!). The specific epithet refers to the small size of plants of the species.

**Poa** sect. **Tovarochloa** (T. D. Macfarl. & But) N. F. Refulio-Rodríguez, comb. et stat. nov.—*Tovarochloa peruviana* T. D. Macfarl. & But, *Brittonia* 34(4): 478–481, f. 1. 1982 [= *Poa apiculata* N. F. Refulio-Rodríguez]

**Poa apiculata** N. F. Refulio-Rodríguez, nom. nov. *Tovarochloa peruviana* T. D. Macfarl. & But, *Brittonia* 34(4): 478–481, f. 1. 1982. non *Poa peruviana* Jacq., *Collectanea* 1: 107. 1786 [1787].—TYPE: PERU. Ausangate, 4,600 m, 11 May 1954, Rauh & Hirsch P1208 (holotype: US!; isotype: HEID). The specific epithet refers to the abrupt apical narrowing of the glumes and lemma.

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Subgenus *Poa*, Supersection *Homalopoa*, Section *Brizoides*, Subsect. *Australopoa*: *Poa cockayneana* Petrie—New Zealand; GQ324497, GQ324409; *Poa fawcettiae* Vickery—Australia; GQ324546, GQ324416; *Poa labillardierei* Steud.—Australia; EU792409, DQ354014; *Poa porphyroclados* Nees—Australia; GQ324537, GQ324448; *Poa sieberiana* Spreng.—Australia; GQ324550, GQ324458. Subgenus *Poa*, Supersection *Homalopoa*, Section *Brizoides*, Subsect. *Austrofestuca*: *Poa pubinervis* (Vickery) S. W. L. Jacobs—Australia; EU792408, DQ354048/DQ354049. Subgenus *Poa*, Supersection *Homalopoa*, Section *Brizoides*, Subsect. *Brizoides*: *Poa drummondiana* Nees—Australia; EU792411, DQ354013. Subgenus *Poa*, Supersection *Homalopoa*, Section *Brizoides*, Subsect. *Neuropoa*: *Poa fax* Willis & Court—Australia; EU792410, EU792460. Subgenus *Poa*, Supersection *Homalopoa*, Section *Dasypoa*: *Poa scaberula* Hook. f.—Chile; EU792412, EU792461. Subgenus *Poa*, Supersection *Homalopoa*, Section *Dioicopoa*: *Poa arachnifera* Torr.—U. S. A.; GQ324486, DQ354021; *Poa holciformis* J. Presl—Chile; GQ324512, DQ354054/DQ354055; *Poa stuckertii* (Hack.) Parodi—Chile; EU792414, DQ354022. Subgenus *Poa*, Supersection *Homalopoa*, Section *Homalopoa*, incertae sedis: *Aphanelytrum procumbens* (Hack.) Hack.—Peru; EU792419, EU792459; *Dissanthelium amplivaginatatum* Tovar—Peru; Peterson 17961 (RSA); **JF904820**, **JF904764**; *Dissanthelium breve* Swallen & Tovar—Peru; Peterson 16564 (RSA); **JF904821**, **JF904765**; Peterson 18048 (RSA); **JF904822**, **JF904766**; *Dissanthelium brevifolium* Swallen & Tovar—Peru; GQ324263, EU792468; Peterson 18119 (RSA); **JF904823**, **JF904767**; *Dissanthelium californicum* (Nutt.) Benth.—U. S. A.; McCune 1 (Wrigley Botanical Garden); **JF904824**, **JF904768**; McCune 2 (SBBG); **JF904825**, **JF904769**; *Refugio-Rodríguez* 238 (RSA); **JF904826**, **JF904770**; *Dissanthelium calycinum* (J. Presl) Hitchc.—Peru; EU792426, EU792466; EU792425, EU792467; *Dissanthelium densum* Swallen & Tovar—Peru; Peterson 16663 (RSA); **JF904827**, **JF904771**; Peterson 18172 (RSA); **JF904828**, **JF904772**; *Dissanthelium expansum* Swallen & Tovar—Peru; Peterson 16569 (RSA); **JF904829**, **JF904773**; Peterson 16594 (RSA); **JF904830**, —; *Dissanthelium giganteum* Tovar—Peru; Peterson 17960 (RSA); **JF904831**, **JF904774**; *Dissanthelium laxifolium* Swallen & Tovar—Peru; Peterson 16567 (RSA); **JF904832**, —; *Dissanthelium longifolium* Tovar—Peru; Peterson 17973 (RSA); **JF904833**, **JF904775**; *Dissanthelium macusaniense* (E. H. L. Krause) R. C. Foster & L. B. Sm.—Peru; Peterson 16548 (RSA); **JF904834**, **JF904776**; *Refugio-Rodríguez* 118 (RSA); **JF904835**, **JF904777**; *Dissanthelium mathewsii* (Ball) R. C. Foster & L. B. Sm.—Peru; Peterson 16595 (RSA); **JF904836**, **JF904778**; Mexico; *Refugio-Rodríguez* 151 (RSA); **JF904837**, **JF904779**; *Dissanthelium patagonicum* Parodi—Argentina; Peterson 17059 (RSA); **JF904838**, **JF904780**; Peterson 17103 (RSA); **JF904839**, **JF904781**; *Dissanthelium peruvianum* (Nees & Meyen) Pilg.—Peru; Peterson 18029 (RSA); **JF904840**, **JF904782**; EU792427, EU792465; *Dissanthelium rauhii* Swallen & Tovar—Peru; Peterson 16634 (RSA); **JF904841**, **JF904783**; *Dissanthelium semitectum* Swallen & Tovar—Peru; Peterson 18168 (RSA); **JF904842**, **JF904784**; *Dissanthelium trollii* Pilg.—Peru; Peterson 18303 (RSA); **JF904843**, **JF904785**; *Refugio-Rodríguez* 231 (RSA); **JF904844**, **JF904786**; *Tovarochloa peruviana* T. D. Macfarl. & But.—Peru; EU792429, EU792470; Bolivia; EU792428, EU792469. Subgenus *Poa*, Supersection *Homalopoa*, Section *Homalopoa*, s. s. and s. l.: *Poa asperiflora* Hack.—Peru; Peterson 18193 (RSA); **JF904813**, **JF904757**; *Poa atropidiformis* Hack.—Chile; GQ324489, DQ354020; Argentina; Peterson 17138 (RSA); **JF904819**, **JF904763**; *Poa blandieri* Vasey—U. S. A.; Ahart 11305 (RSA); **JF904814**, **JF904758**; *Poa candamoana* Pilg.—Peru; Peterson 18106 (RSA); **JF904815**, **JF904759**; *Poa chaixii* Vill.—Russia; EU792404, EU854590; *Poa chapmaniana* Scribn.—U. S. A.; Radford 44741 (RSA); **JF904816**, **JF904760**; *Poa fibrifera* Pilg.—Peru; Peterson 18210 (RSA); **JF904817**, **JF904761**; *Poa gilgiana* Pilg.—Peru; Peterson 18255 (RSA); **JF904818**, **JF904762**; *Poa horridula* Pilg.—Peru; Peterson 17888 (RSA); **JF904845**, **JF904787**; *Poa howellii* Vasey & Scribn.—U. S. A.; Soreng 5964 (US); **JF904846**, DQ354015; *Poa huancavelicae* Tovar—Peru; Peterson 17953 (RSA); **JF904847**, **JF904788**; *Poa kurtzii* R. E. Fr.—Chile; EU792413, DQ354018; *Poa occidentalis* Vasey—U. S. A.; Soreng 403 (US); —, **JF904789**; *Poa pearsonii* Reeder—Chile; Peterson 15676 (US); **JF904854**, DQ354017; *Poa reflexa* Vasey & Scribn.—U. S. A.; GQ324543, GQ324450; *Poa remota* Forselles—Czech Republic; GQ324544, GQ324451. Subgenus *Poa*, Supersection *Homalopoa*, Section *Madropoa*: *Poa cusickii* Vasey—U. S. A.; GQ324501, DQ354029; *Poa fendleriana* (Steud.) Vasey—U. S. A.; EU792403, DQ354027; *Poa macrantha* Vasey—U. S. A.; EU792407, DQ354028; *Poa nervosa* (Hook.) Vasey—U. S. A.; EU792405, DQ354025; *Poa porsildii* Gjaerev.—U. S. A.; GQ324538, DQ354024; *Poa wheeleri* Vasey—U. S. A.; EU792406, DQ354026. Subgenus *Poa*, Supersection *Homalopoa*, Group “Punapoa”: *Poa aequigluma* Tovar—Peru; Peterson 18117 (RSA); **JF904850**, **JF904791**; *Poa anae* Tovar—Peru; Peterson 18171 (RSA); **JF904851**, **JF904792**; *Poa dentigluma* Tovar—Peru; Peterson 17950 (RSA); **JF904852**, **JF904793**; *Poa dissanthelioides* Tovar—Peru; Peterson 18037 (RSA); **JF904853**, **JF904794**; *Poa humillima* Pilger—Peru; Peterson 18140 (RSA); **JF904855**, **JF904795**; *Poa gymnantha* Pilger—Peru; Peterson 17898 (RSA); **JF904856**, **JF904796**; *Poa perligulata* Pilger—Peru; Peterson 17914 (RSA); **JF904857**, **JF904797**; *Poa rivas-martinezii* Tovar—Peru; Peterson 17954 (RSA); **JF904860**, **JF904799**; *Poa subspicata*; Peterson 17972 (RSA); **JF904858**, **JF904798**. Subgenus *Poa*, Section *Leptophyllae*: *Poa stiriaca* Fritsch & Hayek—Austria; *Smarda* PS10 (BRNU); **JF904848**, AH015561. Subgenus *Poa*, Supersection *Poa*, Section *Ircuticae*: *Poa ircutica*

APPENDIX 1. Taxon; country; voucher collector and collection number (herbarium); GenBank accession numbers: ITS and *trnTLF*. GenBank accession numbers in bold indicate that sequences were obtained in this study. A dash (—) indicates that the sequence was not obtained. Voucher information is given only for samples sequenced in this study. For the subtribes and sections of Poeae we follow the classification by Gillespie et al. (2008, 2009).

Subgenus *Ochlopa*, Section *Arenariae*: *Poa alpina* L.—Canada; EU792390, DQ353986; *Poa bulbosa* L.—U. S. A.; GQ324492, GQ324404; *Poa molinerii* Balb.—Slovakia; EU792389, DQ354036/DQ354037. Subgenus *Ochlopa*, Section *Micrantherae*: *Poa annua* L.—Peru; Peterson 18256 (RSA); **JF904811**, **JF904756**; *Poa supina* Schrad.—U. S. A.; EU792387, DQ353984. Subgenus *Ochlopa*, Section *Parodiochloa*: *Poa cookii* (Hook. f.) Hook. f.—Kerguelen Island, sub-Antarctic; EU792382, EU792455; *Poa flabellata* (Lam.) Raspail—Falkland Islands; EU792380, DQ353982. Subgenus *Poa*, Section *Acutifoliae*: *Poa acinaciphylla* E. Desv.—Chile; Soreng 7169 (US); **JF904812**, DQ354023. Subgenus *Poa*, Supersection *Homalopoa*, Section *Anthochloa*: *Poa lepidula* (Nees & Meyen) Soreng & L. J. Gillespie—Peru; EU792422, EU792464. Subgenus *Poa*, Supersection *Homalopoa*, Section *Brizoides*, Subsect. *Australopoa*: *Poa cockayneana* Petrie—New Zealand; GQ324497, GQ324409; *Poa fawcettiae* Vickery—Australia; GQ324546, GQ324416; *Poa labillardierei* Steud.—Australia; EU792409, DQ354014; *Poa porphyroclados* Nees—Australia; GQ324537, GQ324448; *Poa sieberiana* Spreng.—Australia; GQ324550, GQ324458. Subgenus *Poa*, Supersection *Homalopoa*, Section *Brizoides*,

Roshev—Russia; EU792402, DQ354007. Subgenus *Poa*, Supersection *Poa*, Section *Macropoa*: *Poa sibirica* Roshev—Russia; GQ324547, GQ324455. Subgenus *Poa*, Supersection *Poa*, Section *Malacanthae*: *Poa arctica* R. Br.—Canada; GQ324487, DQ354009. Subgenus *Poa*, Supersection *Poa*, Section *Poa*, Subsection *Poa*: *Poa pratensis* L.—Peru; *Peterson 18107* (RSA); **JF904849**, **JF904790**. Subgenus *Poa*, (X clade), 'New Zealand E2': *Poa mathewsii* Petrie—New Zealand; GQ324525, GQ324435. Subgenus *Pseudopoa*, Section *Pseudopoa*: *Poa diaphora* Trin.—Turkey; EU792400, DQ353988. Subgenus *Stenopoa*, Section *Abbreviatae*: *Poa abbreviata* R. Br.—Canada; GQ324481, DQ353996; *Poa lettermanii* Vasey—U. S. A.; GQ324521, GQ324431; *Poa pseudoabbreviata* Roshev.—U. S. A.; EU792398, DQ353997. Subgenus *Stenopoa*, Section *Oreinos*: *Poa laxa* Haenke subsp. *fernaldiana* (Nannf.) Hyl.—U. S. A.; EU792399, DQ353995; *Poa leptocoma* Trin.—U. S. A.; *Soreng 6040-1* (US); **JF904859**, DQ353998. Subgenus *Stenopoa*, Section *Pandemos*: *Poa trivialis* L.—U. S. A.; GQ324555, GQ324462. Subgenus *Stenopoa*, Section *Secundae*: *Poa ammophila* A. E. Porsild—Canada; EU792392, DQ353992; *Poa interior* Rydb.—U. S. A.; —, DQ354002; *Poa secunda* J. Presl—U. S. A.; EU792393, DQ353991. Subgenus *Stenopoa*, Section *Stenopoa*: *Poa glauca* Vahl—Canada; EU792397, DQ354004; *Poa palustris* L.—U. S. A.; EU792396, DQ354000; *Poa compressa* L.—U. S. A.; EU792395, DQ354003. Subgenus *Sylvestres*, Section *Sylvestres*: *Poa autumnalis* Muhl. ex Elliott—U. S. A.; EU792379, DQ353979; *Poa sylvestris* A. Gray—U. S. A.; EU792375, DQ353980; *Poa wolfii* Scribn.—U. S. A.; EU792377, DQ354032/DQ354033.

**Outgroups**—Tribe Bromeae: *Bromus anomalus* Rupr. ex E. Fourn.—Mexico; *Refulio-Rodriguez 145* (RSA); **JF904806**, **JF904751**. Tribe Poeae, Subtribe Agrostidinae: *Agrostis tolucensis* Kunth—Mexico; *Refulio-Rodriguez 155* (RSA); **JF904802**, **JF904747**. Tribe Poeae, Subtribe Airinae: *Deschampsia antarctica* E. Desv.—Argentina; *Peterson 17079* (RSA); **JF904807**, **JF904752**. Tribe Poeae, Subtribe Alopecurinae: *Alopecurus hitchcockii* Parodi—Peru; *Peterson 18220* (RSA); **JF904810**, **JF904755**. Tribe Poeae, Subtribe Aveninae: *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl—Argentina; *Peterson 17319* (RSA); **JF904803**, **JF904748**; *Avena fatua* L.—U. S. A.; *Refulio-Rodriguez 140* (RSA); **JF904804**, **JF904749**. Tribe Poeae, Subtribe Loliiinae: *Dielsiochloa floribunda* (Pilg.) Pilg.—Peru; *Peterson 17963* (RSA); **JF904805**, **JF904750**. Tribe Poeae, Subtribe Miliinae: *Milium vernale* M. Bieb.—Spain; EU792340, DQ353963. Tribe Poeae, Subtribe Phleinae: *Phleum pratense* L.—U. S. A.; EU792341, DQ353964. Tribe Poeae, Subtribe Puccinelliinae: *Puccinellia frigida* (Phil.) I. M. Johnst.—Chile; *Peterson 15488* (RSA); **JF904808**, **JF904753**. Tribe Poeae, Subtribe Poinae: *Arctagrostis latifolia* (R. Br.) Griseb.—Canada; EU792351, DQ353969; *Arctophila fulva* (Trin.) Andersson—Canada; EU792347, DQ354058; *Arctopoa tibetica* (Munro ex Stapf) Prob.—China; EU792368, DQ353976; *Dupontia fisheri* R. Br.—Canada; EU792346, DQ353967; *Festucella eriopoda* (Vickery) E. B. Alexeev—Australia; EU792350, EU792433; *Hookerchloa hookeriana* (F. Muell. ex Hook. f.) E. B. Alexeev—Australia; EU792348, EU792435; *Nicoraepoa andina* (Trin.) Soreng & L. J. Gillespie—Chile; EU792354, DQ353971.