

## Phylogenetics of the Grass ‘Aveneae-Type Plastid DNA Clade’ (Poaceae: Pooideae, Poeae) Based on Plastid and Nuclear Ribosomal DNA Sequence Data

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**Abstract**—We conducted phylogenetic analyses of plastid *trnL-F* and nuclear ribosomal ITS DNA sequence data to infer phylogenetic relationships among and within the five subtribes (Agrostidinae, Aveninae, Brizinae, Phalaridinae and Torreyochloinae) of the Aveneae-type plastid DNA clade of Poaceae tribe Poeae. We sampled widely across the clade by analyzing new and previously published DNA sequence data. Species of *Calamagrostis* from Mexico, Central America, and South America are part of the *Trisetum* lineage in subtribe Aveninae. Several genera of Agrostidinae do not appear to be monophyletic in their current circumscriptions, and most aspects of their relationships are not clear. Subtribe Brizinae is not monophyletic, as European species of *Briza* s.l. are a distinct lineage that is not closely related to South American species; the latter group is allied closely with subtribe Agrostidinae, but their interrelationships remain largely equivocal. Subtribe Phalaridinae probably is not monophyletic, as *Anthoxanthum* / *Hierochloe* and *Phalaris* are not inferred to be sister taxa.

**Keywords**—*Calamagrostis*, grasses, ITS, Poaceae, Poeae, phylogeny, plastid DNA, taxonomy, *Trisetum*.

The cool-season grass lineage, Pooideae Benth., is the largest of the 13-14 subfamilies (Grass Phylogeny Working Group 2001; Sánchez-Ken et al. 2007) in the diverse and cosmopolitan grass family (Poaceae Barn.). It includes wheat (*Triticum* L.), barley (*Hordeum* L.), and oats (*Avena* L.), which are the world's most important temperate cereal crops. Multiple phylogenetic analyses have identified the major evolutionary lineages within Pooideae (e.g., Davis and Soreng 2007; Döring et al. 2007; Soreng et al. 2007; Bouchenak-Khelladi et al. 2008; Schneider et al. 2009); most of these are currently recognized as tribes and subtribes (Soreng et al. 2007). Pooideae tribe Poeae R. Br. s.l. – the single tribe of supertribe Poodae L. Liu – is the most species-rich of the major lineages, with some 2260 species distributed in cool-temperate, Mediterranean and arctic climates (Soreng et al. 2007). Over the last two centuries taxa now included in tribe Poeae s.l. have been variously arranged in multiple smaller tribes and subtribes (reviewed by Soreng et al. 2007; see also Quintanar et al. 2007; Gillespie et al. 2008). Of these the Aveneae Dumort. (the oat tribe) and the Poeae s.s. have been recognized most widely, distinguished on the basis of several morphological characters (e.g., Clayton and Renvoize 1986), most of which are quite homoplasious (Soreng et al. 2007).

Multiple molecular phylogenetic studies have demonstrated that Aveneae and Poeae s.s. are not monophyletic in any of their traditional circumscriptions (e.g., Soreng and Davis 2000; Davis and Soreng 2007; Döring et al. 2007; Quintanar et al. 2007; Soreng et al. 2007; Schneider et al. 2009). These findings have resulted in a generally broad acceptance of an expanded circumscription of Poeae – similar to that proposed by Tzvelev (1989) – that includes all taxa previously included in Poeae s.s. and Aveneae (Soreng et al. 2003, 2007; Quintanar et al. 2007). Within Poeae s.l. two major clades have been identified repeatedly in analyses of plastid DNA. These lineages have been recognized informally as 'taxa with Aveneae-type plastid DNA' and 'taxa with Poeae-type plastid DNA' (Soreng and Davis 2000), names that reflect the morphology-based classifications of the most core taxa in each clade. The most recent classification of Poeae – developed on the basis of available phylogenetic evidence – recognized 16 subtribes in the Poeae-type plastid DNA clade and six subtribes in the Aveneae-type plastid DNA clade [subtribe Cinninae Caruel was placed in the Aveneae-type plastid DNA clade but subsequent work has indicated that it is part of the Poeae-type plastid DNA clade (Quintanar et al. 2007; Soreng et al. 2007; Gillespie et al. 2008). Evolutionary patterns have been addressed across several subtribes in the Poeae-type plastid DNA clade, including Airinae Fr. (Chiappella 2007), Loliinae Dumort. (Torrecilla and Catalán 2002; Catalán et al. 2004; Hunter et al. 2004; Torrecilla et al. 2004; Inda et al. 2008) and Poinae Dumort. (Gillespie and Soreng 2005; Gillespie et al. 2007, 2008). The Aveneae-type plastid DNA clade, however, has received considerably less detailed phylogenetic study.

The five subtribes in the Aveneae-type plastid DNA clade sens. Soreng et al. (2007) – Agrostidinae Fr., Aveninae J. Presl, Brizinae Tzvelev, Phalaridinae Fr.,

Torreyochloinae Soreng & J. I. Davis – are each comprised of two to several genera. Focused phylogenetic studies have been undertaken for Brizinae (Essi et al. 2008) and for multiple genera of Aveninae, including *Arrhenatherum* P. Beauv. (Nisa et al., unpubl.), *Avena* (Rodionov et al. 2005; Nikoloudakis and Katsiotis 2008) and *Helictotrichon* Besser ex Schult. & Schult. f. (Greibenstein et al. 1998). The few studies that have sampled widely across the Aveneae-type plastid DNA lineages are mostly those that were more broadly assessing relationships among elements of the traditionally circumscribed Aveneae and Poeae (e.g., Davis and Soreng 2007; Soreng et al. 2007; Döring et al. 2007; Quintanar et al. 2007). The most densely sampled of these examined nuclear ribosomal ITS and plastid *trnT-F* data from over 100 Poeae s.l. species (Quintanar et al. 2007). Analyses of these data inferred several major clades that generally correspond to the subtribal circumscriptions sens. Soreng et al. (2007), but most aspects of relationship among the subtribes/major lineages were not inferred with strong support. A major finding was that the multiple sampled species of *Trisetum* Pers., *Koeleria* Pers., *Rostraria* Trin., *Gaudinia* J. Gay, *Graphophorum* Desv., and *Parafestuca* E.B. Alexeev (= *Koeleria loweana* Quintanar, Catalán & Castrov.; Quintanar et al. 2006) – all included in subtribe Aveninae by Soreng et al. (2007) – were considerably intermixed in both plastid and nuclear trees, raising questions about generic circumscriptions among these taxa.

Subtribe Agrostidinae Fr. – the most species-rich lineage in the Aveneae-type plastid DNA clade – includes ca. 16 genera and some 550 species (Clayton and Renvoize 1986) distributed globally in temperate regions and tropical mountains, yet it remains one of the least studied of the major lineages of Poeae, at least from a phylogenetic perspective. The subtribe is characterized morphologically by its single-flowered spikelets. The lineage includes the diverse, ecologically important and taxonomically difficult genera *Agrostis* L. (ca. 220 spp.) and *Calamagrostis* Adans. s.l. (ca. 270 spp.), plus multiple genera that are smaller, often-monotypic and in some cases variously recognized: *Ammophila* Host (2 spp.), *Ancistragrostis* S. T. Blake (2 spp.), *Bromidium* Nees & Meyen, *Chaetopogon* Janchen (1 sp.), *Gastridium* P. Beauv. (2 spp.), *Hypseochloa* C. E. Hubb. (2 spp.), *Lachnagrostis* Trin. (ca. 20 spp.), *Podagrostis* (Griseb.) Scribn. & Merr. (ca. 6 spp.), *Polygogon* Desf. (18 spp.), *Triplachne* Link (1 sp.), *Dichelachne* Endl. (5 spp.), *Echinopogon* P. Beauv. (7 spp.), and *Pentapogon* R. Br. (1 sp.) (Soreng et al. 2007). The taxonomy of many of the larger genera in particular is complicated by apomixis and polyploidy (e.g., Greene 1984) and many species are morphologically similar.

The principal taxonomic problems in subtribe Agrostidinae are centered on generic concepts, a problem shared by other large grass genera such as *Bromus* (Saarela et al. 2007) and *Muhlenbergia* (Columbus et al. 2010) in which numerous small segregate genera are (or have been) recognized on the basis of one or a few unique morphological features. The reed-grass genus, *Calamagrostis*, is typically characterized as having single-flowered spikelets, one- or three-veined glumes as long as or exceeding the floret in length (rarely slightly shorter), non-keeled

lemmas that are membranous or cartilaginous (infrequently hyaline), usually with a single dorsally attached awn (rarely awnless), and a callus with a crown of hairs (Clayton and Renvoize 1986; Watson and Dallwitz 1992). *Calamagrostis* is widely recognized in North America, Central America and Europe (e.g., Hitchcock 1951; Conert 1989; Pohl and Davidse 1994; Peterson et al. 2004; Marr et al. 2007; Peterson and Saarela, in press). In parts of the Old World, however, many authors have recognized the segregate genus *Deyeuxia* Clarion ex P. Beauv. (e.g., Bor 1960; Lu 1987; Veldkamp 1996; Simon 1993; Lu and Phillips 2006; Lu et al. 2006), distinguished from *Calamagrostis* s.s. on the basis of differences in glume length, callus vestiture, rachilla presence/absence and rachilla vestiture (see key in Phillips and Chen 2003); other Old World authors have taken a more conservative taxonomic approach and recognized a more broadly circumscribed *Calamagrostis* that includes *Deyeuxia* (e.g., Tzvelev 1976; Koyama 1987). South American species of this generic complex, which comprise a substantial proportion of its diversity in the New World, are also generally recognized in *Deyeuxia* (Rúgolo de Agrasar 1978, 2006; Rúgolo de Agrasar and Villavicencio 1998). Two south Asian species previously considered as part of this group have been variously recognized in a third genus, *Aniselytron* Merr., but morphological and molecular evidence have revealed that *Aniselytron* is a member of Poeae subtribe Poinae (in the Poeae-type plastid DNA clade) and not closely related to *Calamagrostis* s.l. (Ma et al. 2005; Soreng et al. 2007; Gillespie et al. 2008). Generic circumscription of *Agrostis* is also problematic. The boundaries of *Agrostis* relative to the *Calamagrostis* / *Deyeuxia* complex are not clear because of the existence of morphologically intermediate taxa in eastern Asia (Phillips and Chen 2003). The genera *Podagrostis* and *Polypogon* have been variously included in *Agrostis* or recognized as distinct, and some Australian and New Zealand species of subtribe Agrostidinae have been recognized in each of *Agrostis*, *Deyeuxia* and/or the small Australasian genus *Lachnagrostis* Trin. (e.g., Edgar and Forde 1991; Edgar 1995; Jacobs 2001).

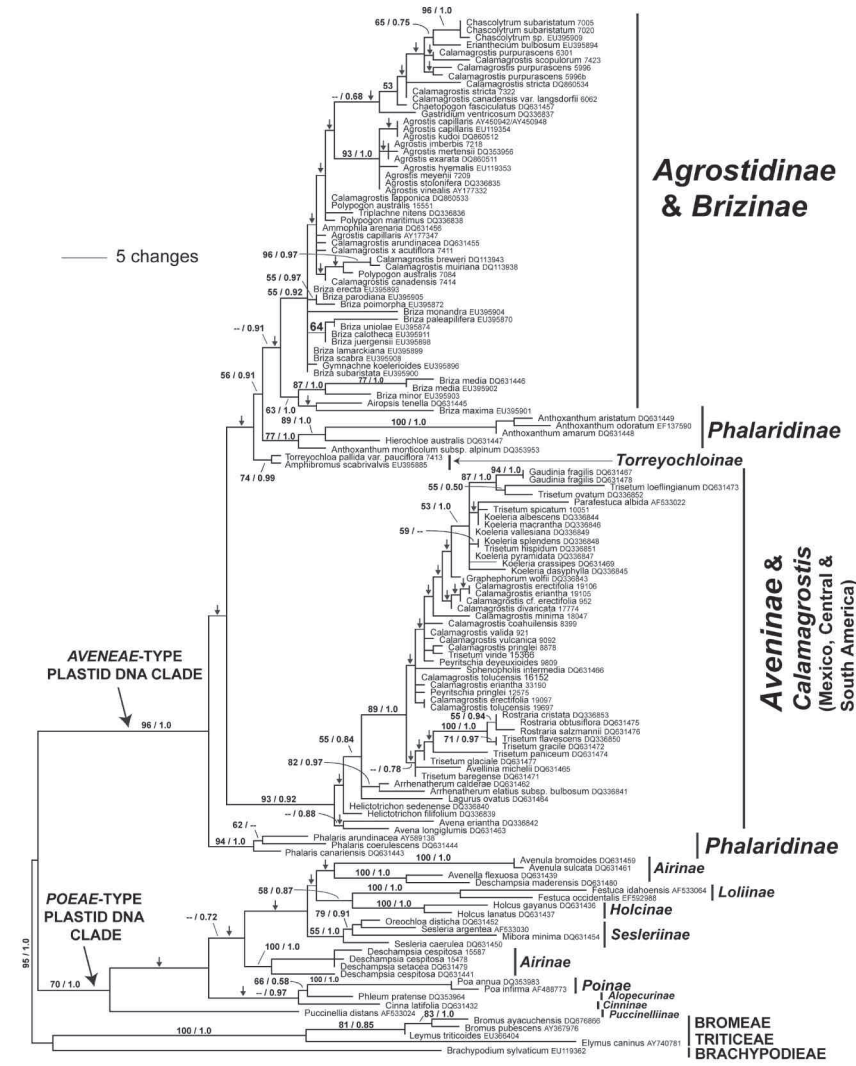
Molecular data clearly have potential to provide insight into this seemingly intractable taxonomic conglomerate, but they have only been examined cursorily in subtribe Agrostidinae. The objectives of this study are to characterize phylogenetic relationships among major lineages in the Aveneae-type plastid DNA clade, with a focus on taxa of subtribe Agrostidinae. Here we present our preliminary results from the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA and the plastid *trnL*(UAA)-*trnF*(GAA) region. These two regions are among the mostly widely utilized in lower-level phylogenetic and evolutionary studies across land plants, and previous work in Poaceae is no exception. Many of the existing ITS and *trnL-F* data for Poaceae, however, have not previously been combined and analyzed. In this study we build on and take full advantage of previous sequencing efforts by analyzing our new nuclear ribosomal and plastid data with much of the existing data for taxa of the Aveneae-type plastid DNA clade in subtribe Poeae. Our analyses represent

a dense and broad level of taxon sampling that has not been realized previously for the Aveneae-type plastid DNA clade.

### *Materials and Methods*

**Taxon and Genome Sampling**—Most of the specimens newly sampled in this study were collected in the field by the authors (Appendix 1). We extracted DNA from silica-gel dried leaf material and herbarium specimens using a slightly modified version of the protocol outlined by Alexander et al. (2007). The region we refer to as ITS, which includes the two internal transcribed spacer regions (ITS1 and ITS2) and the 5.8S nuclear ribosomal DNA locus, was amplified and sequenced using primers ITS1 and ITS4 (White et al. 1990). The *trnL-F* region, which for most of the sampled taxa includes the 5'-end of the *trnL*(UAA) exon, the *trnL*(UAA) intron, the *trnL*(UAA)-*trnF*(GAA) intergenic spacer and the 3'-end of the *trnF*(GAA) gene, was amplified and sequenced with primers developed by Taberlet et al. (1991). Intron and exon boundaries for the *trnL-F* region were determined by comparison with the complete plastid genome of *Agrostis stolonifera* L. (Saski et al. 2007). PCR amplification reactions consisted of 7.83  $\mu$ L of DNA grade H<sub>2</sub>O, 1.5  $\mu$ L of 10X Sigma Buffer, 2.5 mM of MgCl<sub>2</sub>, 0.2 mM dNTPs, 0.25  $\mu$ M of each primer, 0.04 U/ $\mu$ L JUMP *Taq*, and 1.5  $\mu$ L of DNA template. The thermal profile was: 1 cycle of 3 min at 94°C; 30 cycles of 45 sec at 95°C, 45 sec at 45°C, and 90 sec at 72°C; and 1 cycle of 3 min at 72°C. Sequencing products were generated using a BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Foster City, California, U.S.A.) with 1  $\mu$ L (ca. 50 ng) of template DNA and the following thermal profile: 25 cycles of 10 sec at 96°C, 5 sec at 45°C, and 4 min at 60°C. Sequencing reactions were analyzed using an Applied Biosystems Prism 3100 automated DNA sequencer. We performed base-calling and contig assembly using Sequencher 4.7 (Genes Code Corporation, Ann Arbor, Michigan).

**Data Assembly and Phylogenetic Analyses**—We combined our new data with previously published data obtained from GenBank (Appendix 1). We focused our sampling on the Aveneae-type plastid DNA clade, but included taxa from across tribe Poeae to provide a broad taxonomic context for our analyses. We produced preliminary alignments with ClustalX v2.0.10 (Larkin et al. 2007) and modified the alignments manually using Se-Al v2.0 (Rambault 2002). To ensure accuracy after our alignments were complete we cross-checked all previously published sequence data back to their GenBank flat files. We analyzed the plastid and nuclear ribosomal data sets separately and did not attempt to combine them because sampling in each is not parallel. Maximum parsimony searches were conducted using PAUP\* version 4.0b10 (Swofford 2002) with all characters and character-state changes equally weighted, tree bisection-reconnection (TBR) branch swapping, 100 random addition replicates saving 100 trees per replicate, and otherwise default settings. We performed Bayesian analyses with MrBayes 3.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003).



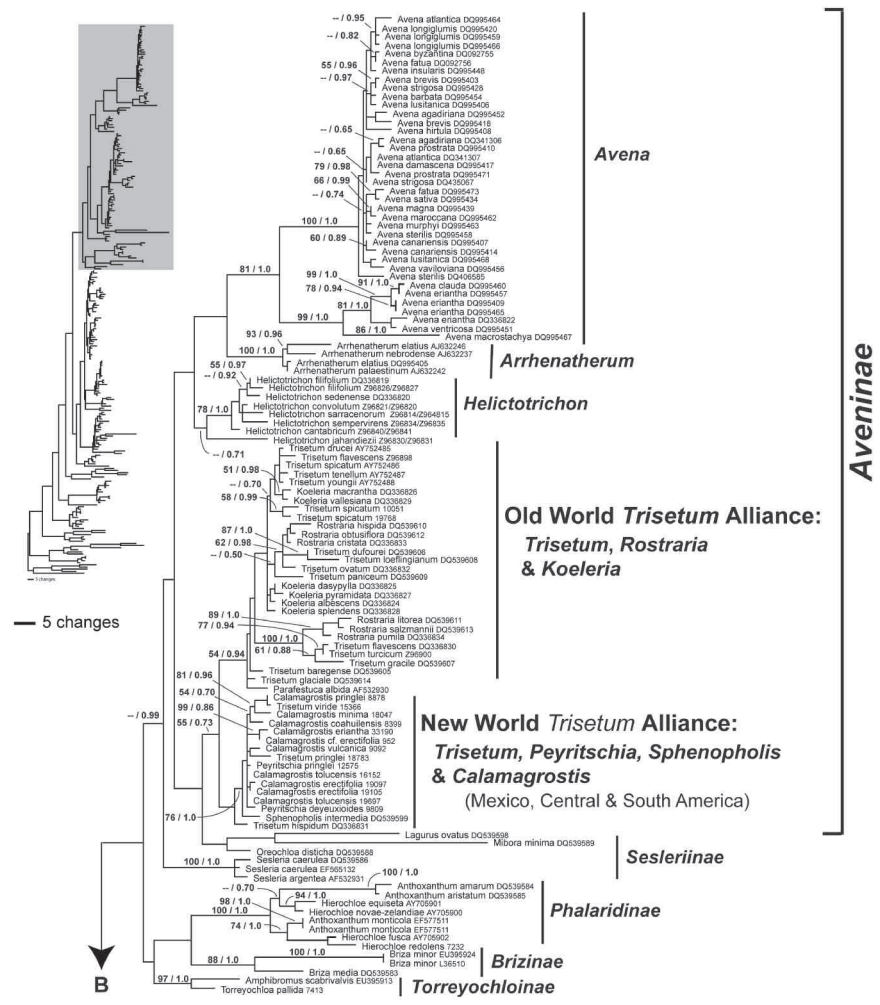
**Fig. 1.** Phylogram of one of 10,000 most-parsimonious tree from analyses of *trnL-F* plastid DNA sequence data for Poaceae tribe Poeae (tree length = 723, CI = 0.708, RI = 0.871). Numbers along branches are bootstrap support values from parsimony analyses and posterior probabilities from Bayesian analyses, respectively. Small arrows (↓) indicate branches that collapse in the strict consensus tree from parsimony analyses. Numbers adjacent to taxon names are GenBank accession numbers for previously published sequence data and collection numbers or herbarium accession numbers for new sequence data (see Appendix 1 for details). Subtribes are indicated following the classification proposed by Soreng et al. (2007).

To determine the optimal model for each of the datasets, we used the hierarchical likelihood ratio test (hLRT) and the Akaike information criterion (AIC), as implemented in ModelTest version 3.7 (Posada and Crandall 1998). The optimal models chosen were GTR +  $\Gamma$  + I (hLRT) and SYM +  $\Gamma$  + I (AIC) for the ITS data set and TVM +  $\Gamma$  (hLRT) and GTR +  $\Gamma$  + I (AIC) for the plastid data set. For both Bayesian analyses we used the GTR +  $\Gamma$  + I model, which in both cases was the more-complex of the models chosen. We ran one million (plastid) and 2.5 million (nrDNA) generations in the Bayesian analyses, which were sufficient for the standard deviation of split frequencies (a convergence diagnostic) to stabilize below 0.05 in each analysis. We sampled the chains every 100 generations and determined posterior probabilities by calculating majority rule consensus trees in PAUP\*, excluding the first 25% of the sampled trees as burn-in. Species from the tribes Brachypodieae, Bromeeae, and Triticeae (see Appendix 1) were used to root the trees in all analyses, based on the results of other studies (e.g., Davis and Soreng 2007). We use the terms ‘weak’, ‘moderate’, and ‘strongly-’ or ‘well-supported’ in reference to clades that received bootstrap support values of <70, 70-90, and 91-100, respectively; and posterior probabilities <80, 80-94, and 95-100, respectively.

## Results

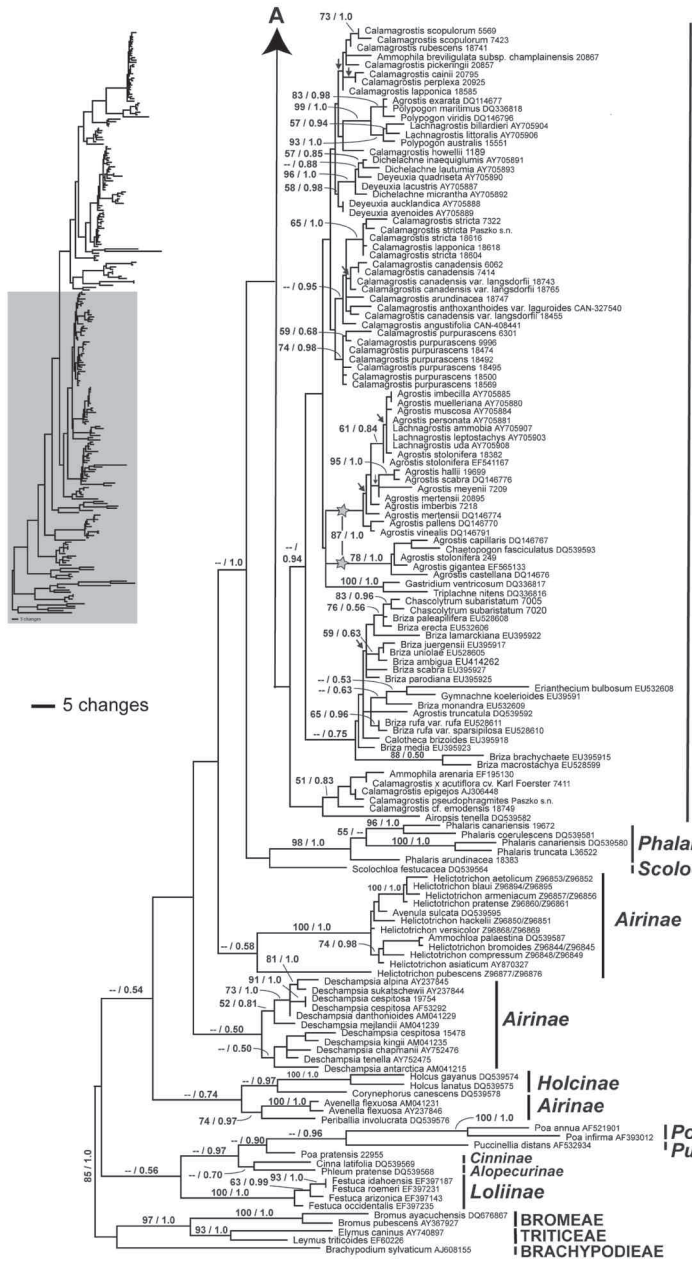
**Analyses of Plastid Sequences**—Bootstrap support values for many branches across the plastid tree are weak (i.e., < 70%); only a few clades receive moderate to strong support (Fig. 1). Analyses of plastid data support the Aveneae-type plastid DNA clade [bootstrap proportion (BP) = 96%; posterior probability (pp.) = 1.0] and Poeae-type plastid DNA clade (BP = 70%; pp. = 1.0) with moderate to strong support. Within the Aveneae-type plastid DNA clade, plastid analyses identify several major lineages. One large clade (BP = 93%; pp. = 0.92) includes multiple genera that are members of subtribe Aveninae (i.e., *Arrhenatherum*, *Avena*, *Gaudinia*, *Grappheporum*, *Helictotrichon*, *Koeleria*, *Lagurus*, *Peyritschia*, *Rostraria*, *Sphenopholis* and *Trisetum*), all sampled species of *Calamagrostis* from Mexico and Central America, and the one sampled species of *Calamagrostis* from South America (*C. minima*). Most relationships among species in this large clade are unresolved and poorly supported.

The subtribes Agrostidinae and Brizinae are not inferred to be monophyletic. Species of Agrostidinae sampled from multiple genera, excluding those *Calamagrostis* species that are part of the Aveninae lineage, are intermixed in a large, weakly to moderately supported lineage with New World species of Brizinae (BP = 55%; pp. = 0.92). All individuals of *Agrostis* except one accession of *A. capillaris* are a clade (BP = 93%; pp. = 1.0). The European species of Brizinae and *Airopsis tenella* are united in a separate clade (BP = 63%; pp. = 1.0); in Bayesian analyses this lineage is allied with the larger Agrostidinae / New World-Brizinae clade, with moderate support (pp. = 0.91).



**Fig. 2.** Phylogram of one of 10,000 most-parsimonious trees from maximum parsimony analyses of nuclear ribosomal ITS data for Poaceae tribe Poeae (tree length = 2117, CI = 0.346, RI = 0.796). Numbers along branches are bootstrap support values from parsimony analyses and posterior probabilities from Bayesian analyses, respectively. Arrows ( $\downarrow$ ) indicate branches that collapse in the strict consensus tree from parsimony analyses. Numbers adjacent to taxon names refer to GenBank accession numbers for previously published sequence data and collection numbers or herbarium accession numbers for new sequence data (see Appendix 1 for details). The two lineages identified by stars are a clade in Bayesian and some most-parsimonious trees. Subtribes are indicated following the classification proposed by Soreng et al. (2007). A. Aveninae, Sesleriinae, Phalaridinae, Brizinae (in part), Torreyochloinae. B. Agrostidinae, Brizinae (in part), Phalaridinae, Scolochloinae, and Poeae-type plastid DNA subtribes.





**Agrostidinae & Brizinae**

**Phalaridinae  
Scolochloinae**

**Airinae**

**Airinae**

**Holcinae  
Airinae**

**Poaceae  
Puccinelliinae**

**Cinninae  
Alopecurinae  
Lolinae**

**BROMEAE  
TRITICEAE  
BRACHYPODIEAE**

The monophyly of the subtribe Phalaridinae is not recovered in plastid data analyses: species of *Anthoxanthum* / *Hierochloe* are a clade (BP = 77%; pp. = 1.0) and species of *Phalaris* are a clade (BP = 94%; pp. = 1.0), but these two lineages are not sister taxa. Plastid analyses identify the *Anthoxanthum* / *Hierochloe* clade to be part of a larger clade that includes Agrostidinae and Brizinae, with weak to moderate support (BP = 56%, pp. = 0.91). The placement of the *Phalaris* lineage in the Aveneae-type plastid DNA clade is equivocal. Subtribe Torreyochloinae is monophyletic (BP = 74%; pp. = 0.99), but its relationships with other lineages in the clade are not clear.

**Analyses of Nuclear Ribosomal DNA Sequence Data**—The deepest branches in the ITS trees are not supported in the bootstrap analysis, and no clades are recovered that correspond to the Aveneae-type and Poeae-type plastid DNA clades identified in the analyses of plastid data (Fig. 2). Bayesian analyses identify with strong support (pp. = 0.99; Fig. 2-3) a large clade that includes all elements of the Aveneae-type plastid DNA clade inferred in the plastid data analyses plus subtribe Sesleriinae Parl. (*Mibora*, *Oreochloa*, *Sesleria*). In Bayesian analyses, an *Avena*-Sesleriinae-*Helictotrichon*-*Arrhenatherum* clade is moderately supported (pp. = 0.82; Fig. 3), and taxa of Sesleriinae are moderately supported as sister taxa of *Avena* (pp. = 0.86; Fig. 3). These latter topologies do not receive bootstrap support in parsimony analyses (Fig. 2). A clade that includes *Trisetum* and its allies, species of *Calamagrostis* from Mexico, Central America, and South America, and *Lagurus* is supported strongly (pp. = 1.0; Fig. 3).

Analyses of the nuclear ribosomal DNA data identify several clades that correspond to genera or generic complexes, but in most cases their interrelationships receive little support, particularly in parsimony analyses. Genera inferred to be monophyletic with the current taxon sampling include: *Avena* (BP = 81%; pp. = 1.0), *Arrhenatherum* (BP = 100%; pp. = 1.0), *Sesleria* (BP = 100%; pp. = 1.0), *Anthoxanthum* / *Hierochloe* (BP = 100; pp. = 1.0), *Phalaris* (BP = 98%; pp. = 1.0). A large but weakly supported lineage (BP = 55%; pp. = 0.73) comprises two major clades: one that includes (mostly) European species of *Trisetum* and its allies (BP = 54%; p = 0.94), and one that includes species of *Calamagrostis* from Mexico, Central and South America, and North American species of *Trisetum* (excluding *T. spicatum*), *Peyritschia* and *Sphenopholis* (BP = 76%; pp. = 1.0). Taxa of Agrostidinae are not a clade in parsimony or Bayesian analyses, but several smaller lineages are identified that include species of *Agrostis* (excluding the sampled accession of *A. exarata*), *Lachnagrostis* and *Chaetopogon* (BP = 87%; pp. = 1.0); species of *Polypogon*, *Lachnagrostis* and the sampled accession of *A. exarata* (BP = 99%; pp. = 1.0); and New Zealand species of *Deyeuxia* and *Dichelachne* (BP = 58%; pp. = 0.98). New World species of Brizinae are weakly united in a clade in Bayesian analyses (pp. = 0.75), and both parsimony and Bayesian analyses resolve a clade that includes *Briza minor* and one accession of *B. media* (BP = 88%; pp. = 1.0); these two clades are not sister taxa.

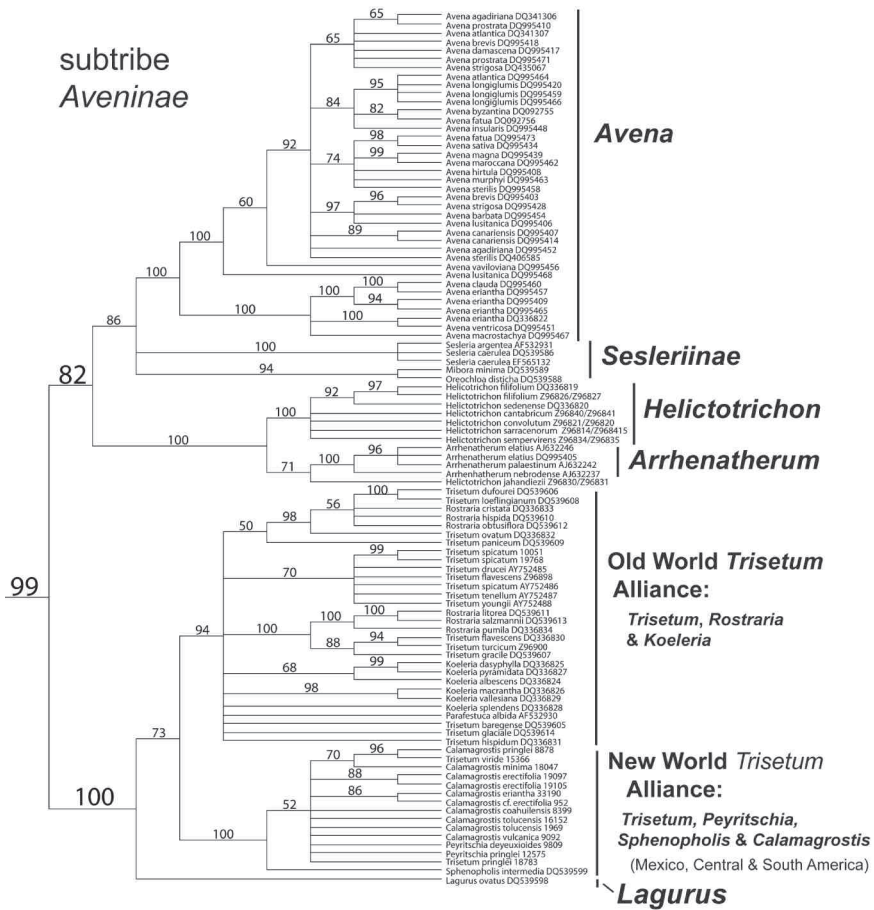
## Discussion

The results of our plastid DNA analyses are fully congruent with previous work in distinguishing the Aveneae-type plastid DNA clade and the Poeae-type plastid DNA clade. In our nuclear ribosomal analyses, however, we find no support for the Aveneae-type plastid DNA clade in parsimony analyses, whereas in Bayesian analyses we identify a clade that includes taxa that are part of the Aveneae-type plastid DNA clade in analyses of plastid data, plus subtribe Sesleriinae, consistent with the findings of Quintanar et al. (2007). Our analyses confirm the substantially different placements of taxa of Sesleriinae in nuclear ribosomal and plastid tree that independent alignments and analyses of the same data found previously (Quintanar et al. 2007; Gillespie et al. 2008).

The deepest branches – those that subtend subtribes and/or indicate their phylogenetic relationships – in the Aveneae-type plastid DNA clade in our plastid and nuclear ribosomal trees are not fully resolved or strongly supported. Among the subtribal circumscriptions sens. Soreng et al. (2007), we find only Torreyochloinae to be consistently recovered and supported as monophyletic; the monophyly of Aveninae is supported only in our analyses of plastid data. Support levels for most deep branches in our trees are low, as found in previous studies; our phylogenetic inferences are therefore not incongruent with those based on data from three plastid genes (*atpB*, *matK*, *ndhF*) plus morphology (Soreng et al. 2007), those based on data from *matK* (Döring et al. 2007) or those based on a smaller taxon sampling for a similar data complement (Quintanar et al. 2007). Despite these multiple attempts to reconstruct the deep evolutionary history of the major lineages in the Aveneae-type plastid DNA clade, deep relationships in the clade remain largely equivocal.

**Subtribe Aveninae: Trisetum and Allies**—Our plastid data for the most part identify a lineage that corresponds to subtribe Aveninae sensu Soreng et al. (2007). The plastid data identify a clade that includes *Avena*, *Helictotrichon* s.s., *Arrhenatherum*, and a morphologically heterogeneous group of genera recognized by multiple workers that includes: *Trisetum*, *Gaudinia*, *Graphephorum*, *Koeleria*, *Lagurus*, *Peyritschia*, *Rostraria*, *Trisetaria* and *Sphenopholis* (hereafter collectively referred to as *Trisetum* and allies). Parsimony analyses of the nuclear ribosomal data provide no support for this large clade, whereas Bayesian analyses provide strong support for a lineage that includes these genera/lineages plus Sesleriinae (see above). The lack of support in parsimony analyses is likely due to sampling error (i.e., insufficient parsimony-informative variation detected along these deeper branches of the phylogenetic tree) and/or homoplasy.

*Trisetum* and allies have been included in subtribe Aveninae (e.g., Clayton and Renvoize 1986; Soreng et al. 2007) or in a separate subtribe, Koeleriinae Asch. & Graebn. (e.g., Tzvelev 1976; Quintanar et al. 2007). Quintanar et al. (2007) recovered this lineage as monophyletic, as we do in our analyses here. A major and unexpected finding of our study, however, is that the species of *Calama-*



**Fig. 3.** Majority rule consensus tree from Bayesian analyses of nuclear ribosomal ITS DNA sequence data. Only the subtribe *Aveninae* subtree from the analysis is shown. Numbers above branches are posterior probabilities. The three posterior probability values with large-sized fonts identify lineages that receive strong posterior probabilities but which are not identified in parsimony analyses (see Fig. 2).

*grostis* that we sampled from Mexico, Central America, and South America, are also part of this *Aveninae* clade. These species of *Calamagrostis* are not closely related to the sampled species of *Calamagrostis* from Canada, the United States, and Europe – they are not even part of the *Agrostidinae* lineage. In plastid trees they are generally intermixed with species of *Trisetum* and its allies. The nuclear ribosomal data support a similar topology, and provide even further insight into the putative evolutionary history of these grasses. The nuclear ribosomal data identify two major lineages, each of which largely corresponds to a distinct geographical region. One lineage includes all sampled taxa of *Trisetum* and al-

lies (except *T. spicatum*) from North America and all sampled Mexican-Central-South American species of *Calamagrostis*; the other includes all sampled taxa of *Trisetum* and allies from the Old World, including the globally distributed *T. spicatum*. In its current circumscription, *Calamagrostis* differs primarily from *Trisetum* and allies in having one-flowered spikelets (vs. two or more in *Trisetum* and allies), though it has been observed that some Mexican *Calamagrostis* species occasionally have two florets per spikelet (Chimal Hernández 1987; McVaugh 1983). Affinities between the Mexican-Central-South American *Calamagrostis* species and *Trisetum* and allies have not been hypothesized previously. The morphological characteristics of these misplaced species of *Calamagrostis* need to be reconsidered in light of their newly realized evolutionary affinities, and nomenclatural adjustments will be required to classify the taxa in a way that reflects their evolutionary history. This necessitates consideration of the systematics of *Trisetum* and allies, which we review here.

*Trisetum* is a worldwide, temperately-distributed genus of about 70 species that are generally characterized by having: first glumes one- to three-nerved, second glumes three- to five-nerved, lemma apices with two to four short awns with the central awn inserted above the middle of the lemma, paleas that are not tightly enclosed by the lemma, and an androecium with three stamens (Finot et al. 2004). The generic circumscription of *Trisetum* has varied over time. In the Old World, Eurasian annual species have been variously recognized in *Trisetum* or in smaller genera such as *Lophochloa*, *Rostraria* and/or *Trisetaria*. Recent phylogenetic work found species of *Trisetum*, *Trisetaria*, *Lophochloa* and *Rostraria* these and other genera (*Koeleria*, *Gaudinia*) to be generally intermixed in analyses of nuclear ribosomal and plastid DNA sequence data (Quintanar et al. 2007). These evolutionary inferences from molecular data are consistent with recent morphological work that found species of *Rostraria* and *Koeleria* to be similar to *Trisetum* in lemma epidermal characteristics (Finot et al. 2006). Micromorphological data have not been produced for any New World species of *Calamagrostis*, but such data potentially could be useful in identifying characters that ally the Mexican–Central–South American species with *Trisetum* or that otherwise distinguish the distantly related lineages of *Calamagrostis* that we have identified.

In the New World, allies of *Trisetum* include the relatively small genera *Graphophorum*, *Peyritschia* and *Sphenopholis*, each of which differs from *Trisetum* in several minor morphological characteristics, and which at one time have all been recognized in a more broadly defined *Trisetum*. Two species from Mexico that are now included in *Peyritschia* (*P. pringlei*) and *Trisetum* (*T. mexicanum* (Swallen) S.D. Koch) were previously recognized in the genus *Deschampsia* (subtribe Airinae, Poeae-type plastid DNA clade) but transferred to their current genera after careful consideration of several morphological characteristics (Koch 1979). Of these two species we have sampled *P. pringlei*, and our analyses confirm that the taxon was misplaced in *Deschampsia*. *Trisetum* is the largest and most wide-

ranging of the four genera in the New World, occurring throughout North, Central, and South America (Finot et al. 2004, 2005a, 2005b). *Grappheporum*, with two species endemic to North America, differs from *Trisetum* in having an entire lemma apex, the dorsal awn reduced to a subapical mucro, and paleas that are tightly enclosed by the margins of the lemma (Finot et al. 2005b). *Peyritschia* ranges from Mexico to Ecuador and differs from *Trisetum* in having one-nerved glumes, bilobed lemmas that are awned near the base or from the middle of the back, or awns reduced to a subapical mucro, paleas that are tightly enclosed by the margins of the lemma, and an androecium of two stamens (Torres and Koch 1987; Finot et al. 2006). *Peyritschia* also differs from *Trisetum* in multiple lemma epidermal characteristics; on this basis several species were recently transferred from *Trisetum* to *Peyritschia* (Finot et al. 2005c, 2006) and seven species are now recognized in the genus (Finot et al. 2006). *Sphenopholis*, with six species endemic to North and Central America (Finot et al. 2004; Daniel 2007), differs from *Trisetum* in having spikelets that disarticulate below the glumes and upper glumes that are oblanceolate to obovate (Finot et al. 2004). Despite the well-characterized morphological differences among these genera, there are no obvious distinctions among them in our molecular analyses, though we have not yet sampled this group in detail. Nevertheless, we are able to demonstrate clearly that the sampled Mexican-Central-South American *Calamagrostis* species are misclassified in their current genus. Increased species-level sampling of *Trisetum* and its allies, which now must be recognized to include some *Calamagrostis* taxa, will be required to draw conclusions regarding appropriate generic limits for these taxa. Future work should aim to sample heavily from the New and Old Worlds, and particularly from regions such as New Zealand (Edgar 1998) and China (Wu and Phillips 2006) that harbour species of *Trisetum* that have not yet been sampled in any molecular analyses. Such work will also need to consider the many South American species of *Calamagrostis* / *Deyeuxia*. The single South American species that we have considered here (*C. minima*) is indeed misplaced in *Calamagrostis*, and it thus seems likely that the same pattern might hold for all or some of the other South American species.

**Subtribes Brizinae and Agrostidinae**—Most of the sequence data analyzed here for taxa in subtribe Brizinae was generated and published by Essi et al. (2008). They identified two clades: one of South American (New World) species, and one of European species. They did not include any other taxa from the Aveneae-type plastid DNA clade as part of the ingroup in their analyses and consequently, they generally inferred the two major lineages of Brizinae to be reciprocally monophyletic sister taxa. Our denser taxon sampling here for the Aveneae-type plastid DNA clade indicates that the evolutionary history of these two putative lineages of Brizinae is not so clear. In our plastid trees we find the New World taxa of Brizinae – which have been variously recognized in a single variable genus (*Briza* s.l.) or multiple smaller genera (*Calotheca*, *Chascolytrum*, *Gymmachne* Parodi, *Poidium* Nees, *Rhombolytrum* Link, *Microbriza* Parodi ex Nicora

& Rúgolo; Matthei 1975) – to be part of a larger clade that also includes taxa of Agrostidinae. The plastid trees identify the three Eurasian species of *Briza* (*B. maxima*, *B. minor*, *B. media*) plus the European/ North African *Airopsis tenella* (not sampled by Essi et al. 2008) as a distinct lineage, similar to the plastid trees in Quintanar et al. (2007). In our Bayesian analyses this Old World-*Briza*-*Airopsis* lineage is moderately supported as the sister group of the Agrostidinae-New World-Brizinae clade. Congruent with our plastid-based findings here, the analyses of *matK* by Döring et al. (2007) identified their one-sampled species of Old World *Briza* (*B. media*) to be distinct from a strongly supported lineage that included taxa of Agrostidinae and of New World Brizinae (i.e., *Chascolytrum* spp.). Our analyses of nuclear ribosomal data also distinguish these Old World and New World lineages of Brizinae (*Airopsis tenella* is not part of this lineage according to nuclear ribosomal data), with the exception that one of the two accessions of *B. media* sampled for ITS is allied with the South America taxa of Brizinae. This divergent sequence (relative to the sequences of the two accessions of *B. media* sampled for plastid data and the other accession of *B. media* sampled for the ITS regions) was also placed among New World taxa in the analyses of Essi et al. (2008). They discussed hybridization as a possible source of the incongruence between the plastid and nuclear regions for this accession, but it is also possible that one of the two ITS sequences analyzed here is erroneous. Additional accessions of *B. media* should be studied to clarify this situation.

Identification of a clade here that includes all sampled taxa of Agrostidinae (excluding those *Calamagrostis* species that are allied with *Trisetum* and part of the Aveninae lineage) and the New World species of Brizinae is similar to the results of other recent studies (Döring et al. 2007; Soreng et al. 2007). Our plastid trees in particular do not distinguish the sampled taxa of Agrostidinae and New World taxa of Brizinae as separate lineages, despite their current recognition in distinct subtribes. Resolution of these groups is somewhat increased in our analyses of the nuclear ribosomal DNA regions, which find weak Bayesian support for a clade that includes the New World taxa of Brizinae. These latter data indicate that this Brizinae lineage is probably distinct, but the current evidence seems insufficient to warrant recognition of both Agrostidinae and Brizinae as subtribes in their current circumscriptions, given that the monophyly of each receives no support here.

Among taxa of Agrostidinae we find substantial intermixing of species from different genera. In the analyses of plastid data, all of the sampled species of *Agrostis* except one accession of *A. capillaris* form a monophyletic group, whereas in analyses of the nuclear ribosomal data, all but one sampled species of *Agrostis*, three species of *Lachnagrostis*, and the monotypic *Chaetopogon* are a clade. The one sampled accession of *Agrostis exarata* examined here is inferred to be part of a clade that includes species of *Polypogon* and *Lachnagrostis*, consistent with previous suggestions that *A. exarata* might be more closely allied with *Polypogon* because of the presence of awned glumes in some individuals

and intraspecific taxa (Beetle 1945). To confirm this result molecular data from additional accessions of this taxon should be studied. Our analyses of nuclear ribosomal data also infer a weakly supported clade that includes taxa of *Deyeuxia* and *Dichelachne* from New Zealand, suggesting that these species share a common origin. Relationships among most sampled species of *Calamagrostis* are not clear, but we do find weak support from Bayesian analyses of the ITS data for a putative Eurasian lineage that includes such taxa as *C. emodensis*, *C. epigejos*, and *C. pseudophragmites*. The two sampled *Calamagrostis* taxa from eastern Russian (*C. angustifolia*; *C. anthoxanthoides*) are not part of this Eurasian lineage; they are closely related to such North American species as *C. canadensis* and *C. purpurascens*, at least in Bayesian analyses. One Eurasian species, *C. arundinacea* – the type species for the genus *Calamagrostis* – is allied with these latter North American and Russian taxa in the ITS analyses. This result should be confirmed in future work with additional accessions of the taxon. The limited molecular variation observed within *Calamagrostis* is consistent with that observed in an early restriction site study of the genus (Teeri et al. 1984). Overall, most aspects of relationship among taxa of Agrostidinae are not clear and it is premature to draw conclusions regarding generic limits among these taxa. Given the low amount of plastid and nuclear ribosomal molecular variation observed here, it is evident that much more data will likely be needed to gain insight into the evolutionary history of these grasses. It will be critical to achieve dense taxon sampling that includes all of the smaller, variously recognized genera, plus elements of the diversity of the larger genera from throughout their global ranges.

**Phalaridinae**—The subtribe Phalaridinae is currently circumscribed to include the *Anthoxanthum-Hierochloe* generic complex (sometimes treated as a single genus, *Anthoxanthum* [Soreng et al. 2003]) and *Phalaris* (Soreng et al. 2007). Our plastid and nuclear ribosomal DNA analyses do not support this subtribal circumscription, as other studies have also found. We find *Anthoxanthum* / *Hierochloe* and *Phalaris* to be distinct lineages, but we do not find any evidence that they are sister taxa. The trees inferred by Döring et al. (2007) and Quintanar et al. (2007), who did not consider these two lineages to be con-subtribal, are fully consistent with our observations here (Soreng et al. [2007] did not sample *Phalaris* thus comparisons with that study cannot be made). Nevertheless, these various studies do not provide strong evidence that *Anthoxanthum* / *Hierochloe* and *Phalaris* are not sister taxa. It thus remains unclear whether it is appropriate to include *Anthoxanthum* and *Phalaris* in the single subtribe Phalaridinae. Should further evidence unequivocally indicate that *Anthoxanthum* and *Phalaris* are not sister taxa, it might become prudent to recognize each in its own subtribe; in such a case, the name Anthoxanthinae A. Gray is available at the appropriate rank.

The evolutionary affinities of *Anthoxanthum* / *Hierochloe* and *Phalaris* relative to the remainder of the Aveneae-type plastid DNA clade are not yet clear. Their



placements are equivocal in nuclear ribosomal analyses here and elsewhere (Quintanar et al. 2007), but there is a minor difference between our plastid results and those reported previously. In our plastid data analyses we weakly infer *Anthoxanthum* / *Hierochloe* to be part of a larger lineage that also includes Agrostidinae and Brizinae, whereas previous analyses found *Anthoxanthum* to be part of a larger clade – with consistently low support – that also includes the Aveninae lineage (Döring et al. 2007; Quintanar et al. 2007; Soreng et al. 2007).

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## Appendix 1

Taxa and collections sampled, and GenBank accession numbers for new and previously published nuclear ribosomal ITS (indicated by \*) and plastid *trnL-F* (indicated by †) sequence data. Studies from which previously published data were obtained are indicated by superscript numbers that refer to the literature citations listed below.

\* \* \*

### New Sequence Data

Tribe Poeae, 'Aveneae-type plastid DNA clade'

SUBTRIBE AGROSTIDINAE FR.

*Agrostis imberbis* Phil. – Chile: Araucanía, R.J. Soreng & N.L. Soreng 7218 (US), \*FJ377618, †GQ266674. *Agrostis mertensii* Trin. – U.S.A.: New Hampshire, P.M.

Peterson & J.M. Saarela 20895 (CAN, US), \*FJ377620. *Agrostis meyenii* Trin. – Chile: Araucanía, R.J. Soreng & N.L. Soreng 7209 (US), \*FJ377619, †FJ394555. *Agrostis stolonifera* L. – Canada: Alberta, P.M. Peterson, J.M. Saarela & S. Smith 18382 (CAN-59104I, US), \*FJ377622; U.S.A.: Oregon, J.M. Saarela & A. Roe 249 (CAN-590286), \*FJ377621

*Ammophila breviligulata* Fernald subsp. *champlainensis* (F. Seym.) P.J. Walker, C.A. Paris & Barrington ex Barkworth – U.S.A.: New York, P.M. Peterson & J.M. Saarela 20867 (CAN, US), \*FJ377623.

*Calamagrostis angustifolia* Kom. – Russia: E Siberia, Yakutia, S. Tumanova s.n. (CAN-40844I), \*FJ377625. *Calamagrostis anthoxanthoides* (Munro ex Hook. f.) Regel, Uzbekistan: Surxondaryo Province, W Gissar Range, I. Vassilczenko & L. Vassiljeva s.n. (CAN-327540), \*FJ377626. *Calamagrostis arundinacea* (L.) Roth – Canada: British Columbia, cultivated at University of British Columbia Botanical Garden, Vancouver, P.M. Peterson & J.M. Saarela 18747 (CAN, US), \*GQ266675. *Calamagrostis cainii* Hitchc. – U.S.A.: Tennessee, P.M. Peterson & J.M. Saarela 20795 (CAN, US), \*FJ377627. *Calamagrostis canadensis* (Michx.) P. Beauv. – U.S.A.: Alaska, R.J. Soreng & N.L. Soreng 6062 (US), \*FJ377628, †FJ394566; U.S.A.: California, R.J. Soreng & N.L. Soreng 7414 (US), \*FJ377632, †FJ394558. *Calamagrostis canadensis* var. *langsдорffii* (Link) Inman – Canada: British Columbia, P.M. Peterson, J.M. Saarela & S. Smith 18455 (CAN-590827, US), \*FJ377629; Canada: British Columbia, P.M. Peterson, J.M. Saarela & S. Smith 18743 (CAN-590764, US), \*FJ377630; U.S.A.: Washington, P.M. Peterson, J.M. Saarela & S. Smith 18765 (CAN-590820, US), \*FJ377631. *Calamagrostis coahuilensis* P.M. Peterson, Soreng & Valdés-Reyna – México: Coahuila, P.M. Peterson, J. Valdés-Reyna & J.A. Villarreal 8399 (US), \*FJ377633, †FJ394556. *Calamagrostis divaricata* P.M. Peterson & Soreng – México: Durango, P.M. Peterson, M.S. González Elizondo & G. Teña González 17774 (US), †FJ394559. *Calamagrostis* cf. *emodensis* Griseb. – Canada: British Columbia, cultivated at University of British Columbia Botanical Garden, Vancouver, P.M. Peterson & J.M. Saarela 18749 (CAN-590955, US), \*FJ377634. *Calamagrostis erectifolia* Hitchc. – México: Jalisco, P.M. Peterson & F. Sánchez Alvarado 19105 (US-03496197), \*FJ377635, †FJ394562; México: Jalisco, P.M. Peterson & F. Sánchez Alvarado 19106 (US), †FJ394561; México: Jalisco, P.M. Peterson & F. Sánchez Alvarado 19097 (US-03496203), \*FJ377636, †FJ394560. *Calamagrostis* cf. *erectifolia* Hitchc. – México: Distrito Federal, F. Iltis & R. Koeppen 952 (MEXU, US), \*FJ377624, †FJ394564. *Calamagrostis eriantha* (Kunth) Steud. – México: Veracruz, Nee et al. 33190 (US), \*FJ377653, †FJ394563. *Calamagrostis holmii* Lange – U.S.A.: Alaska, R.J. Soreng & N.L. Soreng 6204 (US), \*FJ377637. *Calamagrostis howellii* Vasey – U.S.A.: Washington, R. Spellenberg, M. Spellenberg & D. Sutherland 1189 (CAN-302143), \*FJ377638. *Calamagrostis lapponica* (Wahlenb.) Hartm. – Canada: Northwest Territories, P.M. Peterson, J.M. Saarela & S. Smith 18585 (CAN, US), \*FJ377639; Canada: Northwest Territories, P.M. Peterson, J.M. Saarela & S. Smith

18618 (CAN, US), \*FJ377640. *Calamagrostis minima* (Pilg.) Tovar – Peru: Junin, P.M. Peterson & N. Refulio 18047 (US-03491408), \*FJ377641, †FJ394565. *Calamagrostis perplexa* Scribn. – U.S.A.: New York, P.M. Peterson, J.M. Saarela & T.G. Howard 20925 (CAN, US), \*FJ377642. *Calamagrostis pickeringii* A. Gray – U.S.A.: New York, P.M. Peterson & J.M. Saarela 20857 (CAN, US), \*FJ377643. *Calamagrostis pringlei* Scribn. ex Beal – México: Chihuahua, R. Spellenberg, R. Soreng, R. Corral & T. Lebgue 8878 (NMC), \*FJ377645, †FJ394567. *Calamagrostis pseudophragmites* (Haller f.) Koeler – Poland: Malopolska, B. Paszko s.n. (KRAM-559893), \*FJ377646. *Calamagrostis purpurascens* R. Br. – Canada: Yukon, P.M. Peterson, J.M. Saarela & S. Smith 18474 (CAN-590829, US), \*FJ377647; Canada: Yukon, R.J. Soreng & N.L. Soreng 6301 (US), \*FJ377651, †FJ394570; Canada: Yukon, R.J. Soreng 5996 (US), †FJ394568; Canada: Yukon, R.J. Soreng 5996b (US), †FJ394569; Canada: Northwest Territories, P.M. Peterson, J.M. Saarela & S. Smith 18569 (CAN-590803, US), \*FJ377648; Canada: Alberta, P.M. Peterson, J.M. Saarela & S. Smith 18415 (CAN-590798, US), \*FJ377650; U.S.A.: Alaska, P.M. Peterson, J.M. Saarela & S. Smith 18500 (CAN-590813, US), \*FJ377649. *Calamagrostis rubescens* Buckley – Canada: British Columbia, P.M. Peterson, J.M. Saarela & S. Smith 18741 (CAN-59075, US), \*FJ377652. *Calamagrostis scopulorum* M.E. Jones – U.S.A.: Colorado, R.J. Soreng & N.L. Soreng 7423 (US), \*FJ377654, †FJ394571; U.S.A.: Utah, Franklin 5569 (CAN-531332), \*FJ377655. *Calamagrostis stricta* (Timm) Koeler – Canada: Yukon, P.M. Peterson, J.M. Saarela & S.J. Smith 18604 (CAN-590928, US), \*FJ377659; Canada: Yukon, P.M. Peterson, J.M. Saarela & S.J. Smith 18492 (CAN-590784, US), \*FJ377657; Canada: Yukon, P.M. Peterson, J.M. Saarela & S.J. Smith 18616 (CAN-590932, US), \*FJ377656; Sweden: Norrbotten Co., B. Paszko s.n. (KRAM-559883), \*FJ377658; Chile: Magallanes, R.J. Soreng & N.L. Soreng 7322 (US), \*FJ377644, †FJ394572. *Calamagrostis tolucensis* (Kunth) Trin. ex Steud. – México: México, P.M. Peterson & Y. Herrera-Arrieta 16152 (US-00844232), \*FJ377660, †FJ394573; México: Oaxaca, Gereau et al. 19697 (US), \*FJ377661, †FJ394574. *Calamagrostis valida* Sohns, México: Jalisco, J. Villa C. 921 (US), †FJ394575. *Calamagrostis vulcanica* Swallen – Guatemala: San Marcos, N. Gallardo, M. Vasquez & R. Luacarca 9092 (MEXU), \*FJ377662, †FJ394576. *Calamagrostis* × *acutiflora* (Schrad.) DC. ‘Karl Foerster’ – U.S.A.: Maryland, cultivated, R. J. Soreng 7411 (US), \*FJ377663, †FJ394557.

*Polypogon australis* Brongn. – Chile: Antofagasta, P.M. Peterson, R.J. Soreng & E.J. Judziewicz 15551 (US-3445677), \*FJ377671, †FJ394582; Chile: Valparaiso, R.J. Soreng & N.L. Soreng 7084 (US), †FJ394583.

SUBTRIBE AVENINAE J. PRESL.

*Peyritschia deyeuxioides* (Kunth) Finot – México: Oaxaca, P.M. Peterson & A. Campos-Villanueva 9809 (US), \*FJ377668, †FJ394580. *Peyritschia pringlei* (Scribn.) S.D. Koch – México: Chihuahua, P.M. Peterson & C.R. Annable 12575 (US), \*FJ377679, †FJ394581.



*Trisetum spicatum* (L.) K. Richt. – U.S.A.: California, P.M. Peterson, J.M. Saarela & C.J. Sears 19768 (CAN, US), \*FJ377674; México: Coahuila, P.M. Peterson, C.R. Annable & J. Valdés-Reyna 1005I (US-3436717), \*FJ377675, †FJ394585. *Trisetum viride* (Kunth) Kunth – México: Coahuila, P.M. Peterson & J. Valdés-Reyna 18783 (US-03496166), \*FJ377676; México: Coahuila, P.M. Peterson & J. Cayouette 15366 (US), \*FJ377678, †FJ394586.

SUBTRIBE BRIZINAE TZVELEV

*Chascolytrum subaristatum* (Lam.) Desv. – Chile: Bio-Bio, R.J. Soreng & N.L. Soreng 7005 (US), \*FJ377665, †FJ394577; Chile: Bio-Bio, R.J. Soreng & N.L. Soreng 7020 (US), \*FJ377664, †FJ394578.

SUBTRIBE PHALARIDINAE FR.

*Hierochloe redolens* (Vahl) Roem. & Schult. – Chile: Los Lagos, R.J. Soreng & N.L. Soreng 7232 (US), \*FJ377667.

*Phalaris arundinacea* L. – Canada: Alberta, P.M. Peterson, J.M. Saarela & S. Smith 18383 (CAN, US), \*FJ377669. *Phalaris canariensis* L. – U.S.A.: California, P.M. Peterson, J.M. Saarela & C.J. Sears 19672 (CAN, US), \*FJ377670.

Tribe Poeae, ‘Poeae-type plastid DNA clade’

SUBTRIBE AIRINAE FR.

*Deschampsia cespitosa* (L.) P. Beauv. – Chile: Atacoma, P.M. Peterson & E. Judziewicz 15478 (US-3446822), \*FJ377666, †FJ394579; Chile: Antofagasta, P.M. Peterson & R.J. Soreng 15587 (US), †FJ394554.

SUBTRIBE POINAE DUMORT.

*Poa pratensis* L. – U.S.A.: Utah, S. Goodrich 22955 (CAN) – \*FJ377677.

SUBTRIBE TORREYCHLOINAE SORENG

*Torreyochloa pallida* (Torr.) G.L. Church var. *pauciflora* (J. Presl) J.I. Davis – U.S.A.: California, R.J. Soreng & N.L. Soreng 7413 (US), \*FJ377672, †FJ394584.

## Previously Published Sequence Data

Tribe Poeae, ‘Aveneae-type plastid DNA clade’

SUBTRIBE AGROSTIDINAE FR.

*Agrostis capillaris* L., \*DQ146767<sup>16</sup>, †AY450948<sup>25</sup>, †AY450942<sup>25</sup>, †AY177347<sup>26</sup>, †EU1193542<sup>8</sup>. *Agrostis castellana* Boiss & Reut, \*DQ146768<sup>16</sup>. *Agrostis exarata* Trin., \*DQ146770<sup>16</sup>, \*DQ860511<sup>24</sup>. *Agrostis gigantea* Roth, \*EF565133<sup>18</sup>. *Agrostis hyemalis* (Walter) Britton, Sterns & Poggenb., \*EU119353<sup>28</sup>. *Agrostis imbecilla* Zotov, \*AY705885<sup>7</sup>. *Agrostis kudoii* Honda, \*DQ860512<sup>24</sup>. *Agrostis muelleriana*

Vickery, \*AY705880<sup>7</sup>. *Agrostis muscosa* Kirk, \*AY705884<sup>7</sup>. *Agrostis mertensii* Trin., \*DQI46774<sup>16</sup>, \*DQ353956<sup>28</sup>. *Agrostis pallens* Trin., \*DQI46775<sup>16</sup>. *Agrostis personata* Edgar, \*AY705881<sup>7</sup>. *Agrostis scabra* Willd., \*DQI46776<sup>16</sup>. *Agrostis stolonifera* L., \*EF541167<sup>8</sup>, †DQ336835<sup>15</sup>. *Agrostis vinealis* Schreb., \*DQI46791<sup>16</sup>, \*AY177332<sup>27</sup>.

*Ammochloa palaestina* Boiss., \*DQ539587<sup>15</sup>.

*Ammophila arenaria* (L.) Link, \*EF195130<sup>1</sup>, †DQ631456<sup>15</sup>.

*Calamagrostis arundinacea* (L.) Roth, †DQ631455<sup>15</sup>. *Calamagrostis breweri* Thurb. ex Bol., \*DQ113943<sup>31</sup>. *Calamagrostis epigejos* (L.) Roth, \*AJ306448<sup>10</sup>. *Calamagrostis lapponica* (Wahlenb.) Hartm., †DQ860533<sup>24</sup>. *Calamagrostis muiriana* B. L. Wilson & S. Gray, \*DQ113938<sup>31</sup>. *Calamagrostis stricta* (Timm) Koeler, †DQ860534<sup>24</sup>.

*Chaetopogon fasciculatus* (Link) Hayek, †DQ631457<sup>15</sup>.

*Deyeuxia aucklandica* (Hook. f.) Zotov, \*AY705888<sup>7</sup>. *Deyeuxia avenoides* (Hook. f.) Buchanan, \*AY705889<sup>7</sup>. *Deyeuxia lacustris* Edgar & Connor, \*AY705887<sup>7</sup>. *Deyeuxia quadriseta* (Labill.) Benth., \*AY705890<sup>7</sup>.

*Dichelachne inaequiglumis* (Hack. ex Cheesem.) Edgar & Connor, \*AY705891<sup>7</sup>. *Dichelachne lautumia* Edgar & Connor, \*AY705893<sup>7</sup>. *Dichelachne micrantha* (Cav.) Domin, \*AY705892<sup>7</sup>.

*Gastridium ventricosum* (Gouan) Schinz & Thell., \*DQ336817<sup>15</sup>, †DQ336837<sup>15</sup>.

*Lachnagrostis ammobia* Edgar, \*AY705907<sup>7</sup>. *Lachnagrostis billardieri* (R. Br.) Trin., \*AY705904<sup>7</sup>. *Lachnagrostis littoralis* (Hack.) Edgar subsp. *salaria* Edgar, \*AY705906<sup>7</sup>. *Lachnagrostis leptostachys* (Hook. f.) Zotov, \*AY705903<sup>7</sup>. *Lachnagrostis uda* Edgar, \*AY705908<sup>7</sup>.

*Polypogon maritimus* Willd., †DQ336838<sup>15</sup>. *Polypogon viridis* (Gouan) Breistr., \*DQI46796<sup>16</sup>.

*Triplachne nitens* (Guss.) Link, \*DQ336816<sup>15</sup>, †DQ336836<sup>15</sup>.

#### SUBTRIBE AVENINAE J. PRESL

*Arrhenatherum calderae* A. Hansen \*DQ631462<sup>15</sup>. *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl, †DQ995405<sup>13</sup>. *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl subsp. *sardoum* (E. Schmid) Gamisans, \*AJ632246<sup>14</sup>. *Arrhenatherum nebrodense* Brullo, Miniss. & Spamp., \*AJ632237<sup>14</sup>. *Arrhenatherum palaestinum* Boiss., \*AJ632242<sup>14</sup>.

*Avena agadiriana* B.R. Baum & Fedak, \*DQ995452<sup>13</sup>, DQ341306<sup>21</sup>. *Avena atlantica* B.R. Baum & Fedak, \*DQ995464<sup>13</sup>, \*DQ341307<sup>17</sup>. *Avena barbata* Pott ex Link, \*DQ995454<sup>13</sup>. *Avena brevis* Roth, \*DQ995418<sup>13</sup>, \*DQ995403<sup>13</sup>. *Avena byzantina* K. Koch, \*DQ092755<sup>21</sup>. *Avena canariensis* B.R. Baum, Rajhathy & D.R. Sampson, DQ995414<sup>13</sup>, DQ995407<sup>13</sup>. *Avena clauda* Durieu, \*DQ995460<sup>13</sup>. *Avena damascena* Rajhathy & B.R. Baum, \*DQ995417<sup>13</sup>. *Avena eriantha* Durieu, \*DQ995465<sup>13</sup>, \*DQ995457<sup>13</sup>, \*DQ995409<sup>13</sup>, \*DQ336822<sup>15</sup>, †DQ336842<sup>15</sup>. *Avena fatua* L., \*DQ995473<sup>13</sup>, \*DQ092756<sup>21</sup>. *Avena hirtula* Lag., \*DQ995408<sup>13</sup>. *Avena insularis* Ladiz., \*DQ995448<sup>13</sup>. *Avena longiglumis* Durieu, \*DQ995459<sup>13</sup>, \*DQ995420<sup>13</sup>, \*DQ995466<sup>13</sup>, †DQ631463<sup>15</sup>. *Avena lusitanica* (Tab. Morais) B.R. Baum, \*DQ995406<sup>13</sup>, \*DQ995468<sup>13</sup>. *Avena macrostachya* Balansa & Durieu, \*DQ995467<sup>13</sup>. *Avena magna* H.C. Murphy & Terrell, \*DQ995439<sup>13</sup>. *Avena marocana* Gand., \*DQ995462<sup>13</sup>. *Avena murphyi* Ladiz., \*DQ995463<sup>13</sup>. *Avena prostrata* Ladiz., \*DQ995471<sup>13</sup>, \*DQ995410<sup>13</sup>. *Avena sativa* L., \*DQ995434<sup>13</sup>. *Avena sterilis* L., \*DQ995458<sup>13</sup>. *Avena strigosa* Schreb., \*DQ995428<sup>13</sup>, \*DQ435067<sup>18</sup>. *Avena sterilis* subsp. *ludoviciana* (Durieu) J.M. Gillett & Magne, \*DQ406585<sup>21</sup>.

*Avenula bromoides* (Gouan) H. Scholz., †DQ631459<sup>15</sup>. *Avenula sulcata* (J. Gay ex Boiss.) Dumort., \*DQ539595<sup>15</sup>, †DQ631461<sup>15</sup>.

*Gaudinia fragilis* (L.) P. Beauv., †DQ631467<sup>15</sup>, †DQ631478<sup>15</sup>.

*Grappheporum wolfii* (Vasey) Vasey ex Coult., †DQ336843<sup>15</sup>.

*Helictotrichon aetolicum* (Rech. f.) Holub, \*Z96853<sup>8</sup>, \*Z96852<sup>8</sup>. *Helictotrichon armeniacum* (Schischk.) Grossh., \*Z96857<sup>8</sup>, \*Z96856<sup>8</sup>. *Helictotrichon blauii* (Asch. & Janka) C.E. Hubb. subsp. *blauii*, \*Z96864<sup>8</sup>, \*Z96865<sup>8</sup>. *Helictotrichon bromoides* (Gouan) C.E. Hubb. subsp. *bromoides*, \*Z96844<sup>8</sup>, \*Z96845<sup>8</sup>. *Helictotrichon cantabricum* (Lag.) Gervais, \*Z96830<sup>8</sup>, \*Z96831<sup>8</sup>. *Helictotrichon compressum* (Heuff.) Henrard, \*Z96848<sup>8</sup>, \*Z96849<sup>8</sup>. *Helictotrichon convolutum* (C. Presl) Henrard, \*Z96821<sup>8</sup>, \*Z96820<sup>8</sup>. *Helictotrichon filifolium* (Lag.) Henrard subsp. *filifolium*, \*Z96826<sup>8</sup>, \*Z96827<sup>8</sup>, \*DQ336819<sup>15</sup>, †DQ336839<sup>15</sup>. *Helictotrichon hackelii* (Henriq.) Henrard, \*Z96850<sup>8</sup>, \*Z96851<sup>8</sup>. *Helictotrichon jahandiezii* (Litard. ex Jahand. & Maire) Potztal, \*Z96840<sup>8</sup>, \*Z96841<sup>8</sup>. *Helictotrichon pratense* (L.) Pilg., \*Z96860<sup>8</sup>, \*Z96861<sup>8</sup>. *Helictotrichon pubescens* (Huds.) Pilg., \*Z96877<sup>8</sup>, \*Z96876<sup>8</sup>. *Helictotrichon sarracenorum* (Gand.) Holub, \*Z96814<sup>8</sup>, \*Z96815<sup>8</sup>. *Helictotrichon sedenense* (Clar. ex Lam. & DC.) Holub, \*DQ336820<sup>15</sup>, †DQ336840<sup>15</sup>. *Helictotrichon sempervirens* (Vill) Pilg., \*Z96834<sup>8</sup>, \*Z96835<sup>8</sup>. *Helictotrichon versicolor* (Vill.) Pilg., \*Z96868<sup>8</sup>, \*Z96869<sup>8</sup>.

*Koeleria albescens* DC., †DQ336844<sup>15</sup>, \*DQ336824<sup>15</sup>. *Koeleria crassipes* Lange, †DQ631469<sup>15</sup>. *Koeleria dasyphylla* Willk., \*DQ336825<sup>15</sup>, †DQ336845<sup>15</sup>. *Koeleria macrantha* (Ledeb.) Schult., \*DQ336826<sup>15</sup>, †DQ336846<sup>15</sup>. *Koeleria pyramidata* (Lam.)

P. Beauv., \*DQ336827<sup>15</sup>, †DQ336847<sup>15</sup>. *Koeleria splendens* C. Presl, \*DQ336828<sup>15</sup>, †DQ336848<sup>15</sup>. *Koeleria vallesiana* (Honck.) Gaudin, \*DQ336829<sup>15</sup>, †DQ336849<sup>15</sup>.

*Lagurus ovatus* L., \*DQ539598<sup>5</sup>, †DQ631464<sup>15</sup>.

*Parafestuca albida* (Lowe) E.B. Alexeev, \*AF532930<sup>4</sup>, †AF533022<sup>4</sup>.

*Rostraria cristata* (L.) Tzvelev \*DQ336833<sup>15</sup>, †DQ336853<sup>15</sup>. *Rostraria hispida* (Savi) Dogan, \*DQ539610<sup>15</sup>. *Rostraria litorea* (All.) Holub, \*DQ539611<sup>15</sup>. *Rostraria obtusiflora* (Boiss.) Holub, \*DQ539612<sup>15</sup>, †DQ631475<sup>15</sup>. *Rostraria pumila* (Desf.) Tzvelev \*DQ336834<sup>15</sup>, †DQ336854<sup>15</sup>. *Rostraria salzmännii* (Boiss. & Reut.) Holub, \*DQ539613<sup>15</sup>, †DQ631476<sup>15</sup>.

*Sphenopholis intermedia* (Rydb.) Rydb., \*DQ539599<sup>15</sup>, †DQ631466<sup>15</sup>.

*Trisetum baregense* Laffitte & Miégeville, †DQ631471<sup>15</sup>, \*DQ539605<sup>15</sup>. *Trisetum drucei* Edgar, \*AY752485<sup>17</sup>. *Trisetum dufourei* Boiss., \*DQ539606<sup>15</sup>. *Trisetum flavescens* (L.) P. Beauv., \*Z96898<sup>8</sup>, \*DQ336830<sup>15</sup>, †DQ336850<sup>15</sup>. *Trisetum glaciale* Boiss., \*DQ539614<sup>15</sup>, †DQ631477<sup>15</sup>. *Trisetum gracile* (Moris) Boiss., \*DQ539607<sup>15</sup>, †DQ631472<sup>15</sup>. *Trisetum hispidum* Lange, \*DQ336831<sup>15</sup>, †DQ336851<sup>15</sup>. *Trisetum loeflingiana* (L.) P. Beauv., \*DQ539608<sup>15</sup>, †DQ631473<sup>15</sup>. *Trisetum ovatum* Pers., \*DQ336832<sup>15</sup>, †DQ336852<sup>15</sup>. *Trisetum paniceum* (Lam.) Porsild, \*DQ539609<sup>15</sup>, †DQ631474<sup>15</sup>. *Trisetum spicatum* (L.) K. Richt., \*AY752486<sup>7</sup>. *Trisetum tenellum* (Petrie) A.W. Hill, \*AY752487<sup>7</sup>. *Trisetum youngii* Hook. f., \*AY752488<sup>7</sup>. *Trisetum turcicum* Chrtek, \*Z96900<sup>8</sup>, \*Z96901<sup>8</sup>.

#### SUBTRIBE BRIZINAE TZVELEV

*Briza ambigua* Hack., \*EU414262<sup>6</sup>. *Briza brachychaete* Ekman, \*EU395915<sup>6</sup>. *Briza calotheca* (Trin.) Hack., †EU395911<sup>6</sup>. *Briza erecta* Lam., \*EU532606<sup>6</sup>, †EU395893<sup>6</sup>. *Briza juergensii* Hack., \*EU395917<sup>6</sup>, †EU395898<sup>6</sup>. *Briza lamarckiana* Nees, \*EU395922<sup>6</sup>, †EU395899<sup>6</sup>. *Briza macrostachya* (J. Presl) Steud., \*EU528599<sup>6</sup>. *Briza maxima* L., †EU395901<sup>6</sup>. *Briza media* L., \*EU395923<sup>6</sup>, \*DQ539583<sup>15</sup>, †DQ631446<sup>15</sup>, †EU395902<sup>6</sup>. *Briza minor* L., \*L36510<sup>9</sup>, †EU395903<sup>6</sup>. *Briza monandra* (Hack.) Pilg., \*EU532609<sup>6</sup>, †EU395904<sup>6</sup>. *Briza paleapilifera* Parodi, \*EU528608<sup>6</sup>. *Briza parodiana* Roseng., B.R. Arrill. & Izag, \*EU395925<sup>6</sup>, †EU395905<sup>6</sup>. *Briza poimorpha* (J. Presl) Henrard, \*EU395872<sup>6</sup>. *Briza rufa* (J. Presl) Steud. var. *rufa*, \*EU528611<sup>6</sup>. *Briza rufa* var. *sparsipilosa* Roseng., Arrill. & Izag, \*EU528610<sup>6</sup>. *Briza scabra* (Nees ex Steud.) Ekman, \*EU395927<sup>6</sup>, †EU395908<sup>6</sup>. *Briza subaristata* Lam., †EU395900<sup>6</sup>. *Briza uniolae* (Nees) Steud., \*EU528605<sup>6</sup>, †EU395874<sup>6</sup>.

*Calotheca brizoides* (Lam.) Desv., \*EU395918<sup>6</sup>.

*Chascolytrum* sp., †EU395909<sup>6</sup>.

*Erianthecium bulbosum* Parodi, \*EU532608<sup>6</sup>, †EU395894<sup>6</sup>.

*Gymnachne koelerioides* (Trin.) Parodi, \*EU395919<sup>6</sup>, †EU395896<sup>6</sup>.

SUBTRIBE PHALARIDINAE FR.

*Anthoxanthum amarum* Brot., \*DQ539584<sup>15</sup>, †DQ631448<sup>15</sup>. *Anthoxanthum monticulum* (Bigelow) Veldkamp, \*EF577511<sup>18</sup>. *Anthoxanthum monticulum* subsp. *alpinum* (Sw. ex Willd.) Soreng, †DQ353953<sup>28</sup>. *Anthoxanthum odoratum* L., \*EF137590<sup>30</sup>.

*Hierochloe australis* (Schrad.) Roem. & Schult., †DQ631447<sup>15</sup>. *Hierochloe equisetata* Zotov, \*AY705901<sup>7</sup>. *Hierochloe fusca* Zotov, \*AY705902<sup>7</sup>. *Hierochloe novaezelandiae* Gand., \*AY705900<sup>7</sup>.

*Phalaris canariensis* L., \*DQ539580<sup>15</sup>, †DQ631443<sup>15</sup>. *Phalaris coerulea* Desf., \*DQ539581<sup>15</sup>, †DQ631444<sup>15</sup>. *Phalaris truncata* Guss. Ex Bertol., \*L36522<sup>9</sup>.

SUBTRIBE TORREYCHLOINAE SORENG

*Amphibromus scabrivalvis* (Trin.) Swallen, \*EU395913<sup>6</sup>, †EU395885<sup>6</sup>.

Tribe Poeae, Poeae-type plastid DNA clade

SUBTRIBE AIRINAE FR.

*Avenella flexuosa* (L.) Drejer [as *Deschampsia flexuosa* (L.) Trin.], \*AY237846<sup>3</sup>, \*AM041231<sup>5</sup>, †DQ631439<sup>15</sup>.

*Deschampsia alpina* (L.) Roem. & Schult., \*AY237845<sup>3</sup>. *Deschampsia antarctica* E. Desv., \*AM041215<sup>5</sup>. *Deschampsia cespitosa* (L.) P. Beauv., \*AF532929<sup>4</sup>, †DQ631441<sup>15</sup>. *Deschampsia chapmanii* Petrie, AY752476<sup>7</sup>. *Deschampsia danthonioides* (Trin.) Munro, \*AM041229<sup>5</sup>. *Deschampsia flexuosa* (L.) Trin. *Deschampsia kingii* (Hook. f.) E. Desv., \*AM041235<sup>5</sup>. *Deschampsia maderensis* (Hackel & Bornm.) Buschm., †DQ631480<sup>15</sup>. *Deschampsia mejlandii* C.E. Hubb., AM041239<sup>5</sup>. *Deschampsia setacea* (Huds.) Hack., †DQ631479<sup>15</sup>. *Deschampsia sukatschewii* (Popl.) Roshev. subsp. *borealis* (Trautv.) Tzvelev, \*AY237844<sup>3</sup>. *Deschampsia tenella* Petrie, \*AY752475<sup>7</sup>.

*Periballia involuocrata* Janka, \*DQ539576<sup>15</sup>.

SUBTRIBE ALOPECURINAE DUMORT.

*Phleum pratense* L., \*DQ539568<sup>15</sup>; †DQ353964<sup>28</sup>.

SUBTRIBE CINNINAE CARUEL

*Cinna latifolia* (Trevir ex Göpp.) Griseb., \*DQ539569<sup>15</sup>, †DQ631432<sup>15</sup>.

SUBTRIBE LOLIINAE DUMORT.

*Festuca arizonica* Vasey, \*EF397143<sup>11</sup>. *Festuca idahoensis* Elmer, \*EF397187<sup>11</sup>, †AF533064<sup>4</sup>. *Festuca roemerii* (Pavlick) E.B. Alexeev, \*EF397231<sup>11</sup>. *Festuca occidentalis* Hook., \*EF397235<sup>11</sup>, †EF592988<sup>32</sup>.

SUBTRIBE MILIINAE DUMORT.

*Mibora minima* (L.) Desv., \*DQ539589<sup>15</sup>, †DQ631454<sup>15</sup>.

SUBTRIBE POINAE DUMORT.

*Poa annua* L., \*AF521901<sup>23</sup>, †DQ353983<sup>28</sup>. *Poa infirma* Kunth, \*AF393012<sup>22</sup>, †AF488773<sup>22</sup>.

SUBTRIBE PUCCINELLIINAE SORENG & J.I. DAVIS

*Puccinellia distans* (Jacq.) Parl., \*AF532934<sup>4</sup>, †AF533024<sup>15</sup>.

SUBTRIBE HOLCINAE DUMORT.

*Holcus lanatus* L., \*DQ539575<sup>15</sup>, †DQ631437<sup>15</sup>. *Holcus gayanus* Boiss., \*DQ539574<sup>15</sup>, †DQ631436<sup>15</sup>.

SUBTRIBE SCOLOCHLOINAE (TZVELEV) SORENG

*Scolochloa festucacea* (Willd.) Link, \*DQ539564<sup>15</sup>.

SUBTRIBE SESLERIINAE PARL.

*Oreochloa disticha* (Wulfen) Link, \*DQ539588<sup>15</sup>, †DQ631452<sup>15</sup>.

*Sesleria argentea* (Savi) Savi, \*AF532931<sup>4</sup>, †AF533030<sup>4</sup>. *Sesleria caerulea* (L.) Scop., \*DQ539586<sup>15</sup>, †DQ631450<sup>4</sup>.

Tribe Brachypodieae Harz.

*Brachypodium sylvaticum* (Huds.) P. Beauv., \*AJ608155<sup>2</sup>, †EU119362<sup>29</sup>.

Tribe Bromeae dumort.

*Bromus ayacuchensis* Saarela & P.M. Peterson, \*DQ676867<sup>19</sup>, †DQ676866<sup>19</sup>. *Bromus pubescens* Muhl. ex Willd., \*AY367927<sup>20</sup>, †AY367976<sup>20</sup>.

Tribe Triticeae Dumort.

*Elymus caninus* (L.) L., \*AY740897<sup>12</sup>, †AY740781<sup>33</sup>.

*Leymus triticoides* (Buckl.) Pilg., \*EF602026<sup>12</sup>, †EU366404<sup>34</sup>.

<sup>1</sup>E.M. Batelaan et al. (unpublished data); <sup>2</sup>Blattner (2004); <sup>3</sup>Brysting et al. (2004); <sup>4</sup>Catalán et al. (2004); <sup>5</sup>Chiapella (2007); <sup>6</sup>Essi et al. (2008); <sup>7</sup>R.C. Gardner et al.