# Phylogenetic relationships in subtribe Poinae (Poaceae, Poeae) based on nuclear ITS and plastid *trn*T–*trn*L–*trn*F sequences[1]

**Lynn J. Gillespie, Robert J. Soreng, Roger D. Bull, Surrey W.L. Jacobs, and Nancy F. Refulio-Rodriguez**

**Abstract:** The worldwide temperate subtribe Poinae comprises the largest grass genus, *Poa* (500+ species), and multiple additional small genera. We explore generic boundaries and relationships among genera of Poinae using nuclear ribosomal internal transcribed spacer data (ITS) and plastid *trn*T–*trn*L–*trn*F (TLF) sequence data. ITS and TLF analyses are mostly congruent with regards to circumscription of genera, and with respect to relationships among Poinae genera, but tree structure is generally better supported among genera in the ITS strict consensus tree. ITS and TLF both support two main Poinae lineages: (*i*) *Poa* and (*ii*) a clade comprising all other sampled Poinae. Nine small genera were nested within the large *Poa* clade, including *Aphanelytrum*, *Dissanthelium*, and *Tovarochloa*, supporting inclusion of these as sections within *Poa*. In the second clade, three subclades support close relationships among *Nicoraepoa*, *Hookerochloa*, and *Arctagrostis*; *Arctophila* and *Dupontia*; and *Apera*, *Bellardiochloa*, and *Ventenata*. Genera of the related subtribes Alopecurinae, Cinninae, and Miliinae were mixed among or in part external to Poinae in different ways in ITS and TLF analyses, and only subtribe Puccinelliinae was strongly supported and monophyletic. ITS analyses supported placement of *Catabrosella*, *Hyalopoa*, and *Paracolpodium* in Puccinelliinae (no TLF data available). The position of *Poa* subgenus *Arctopoa* is incongruent between the two analyses: TLF data support inclusion within *Poa* and ITS data place it outside of *Poa*. Similarly, TLF data resolves the genus *Aniselytron* outside of *Poa*, whereas ITS data place it within *Poa*. Based on these results and a consideration of morphology, we recognize *Arctopoa* and *Aniselytron* as genera, probably of ancient hybrid origins. Nothogenus ×***Duarctopoa*** is coined for *Arctopoa* × *Dupontia*, with a single nothospecies ×***Duarctopoa labradorica***. A new combination is provided for *Poa* subg. *Sylvestres*.

*Key words:* DNA, hybridization, phylogeny, *Poa*, Poaceae, Poeae.

**Résumé :** La sous-tribu des régions tempérées mondiales des Poinae comporte les *Poa*, le plus grand genre d'herbes avec plus de 500 espèces, ainsi que de multiples petits genres additionnels. Les auteurs ont exploré les limites génériques et les relations au sein des Poinae, en utilisant les données de l'espaceur interne transcrit de l'ADN ribosomique nucléique (ITS) et les données de séquences plastidiques *trn*T–*trn*L–*trn*F (TFL). Les analyses ITS et TFL concordent généralement quant à la circonscription des genres et aux relations entre les genres de Poinae, mais le dendrogramme des genres est généralement mieux supporté dans l'arbre ITS à strict consensus. Les ITF et les TFL supportent tous les deux, deux lignées principales de Poinae: (*i*) *Poa* et (*ii*) un clade comportant tous les autres échantillons de Poinae. Neuf petits genres se retrouvent au sein du grand clade *Poa*, incluant *Aphanelytrum*, *Dissanthelium* et *Tovarochloa*, supportant leur regroupement dans une section les *Poa*. Dans le second clade, trois sous clades supportent d'étroites relations entre *Nicoraepoa*, *Hookerochloa* et *Arctagrostis*; *Arctophila* et *Dupontia*; et *Apera*, *Bellardiochloa* et *Ventenata*. Les genres des sous tribus apparentées Alopecurinae, Cinninae et Miliinae se retrouvent en partie mêlés avec ou en marge des Poinae de différentes manières selon les analyses ITS et TFL; et seulement la sous tribu Puccinelliinae trouve un solide support monophylétique. Les analyses ITS supportent la localisation des *Catabrosella*, *Hyalopoa* et *Paracolpodium* dans les Pucinelliinae (aucun TFL disponible). Il n'y a pas de concordance entre les deux analyses pour la position des *Poa* subg. *Arctopoa*. De même, les données TFL situent le genre *Anisetylon* à l'extérieur des *Poa*, alors que les données ITS le placent dans les *Poa*. Sur la base de ces résultats et des observations morphologiques, les auteurs reconnaissent les *Arctopoa* et les *Aniselytron* comme genres, probablement d'origine hybride ancienne. On crée le nothogenre ×***Duarctopoa***, contenant une seule nothoespèce ×***Duractopoa labradorica***. On crée une nouvelle combinaison pour les *Poa* subg. *Sylvestres*.

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**L.J. Gillespie[2] and R.D. Bull.** Research Division, Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, ON K1P 6P4, Canada.
**R.J. Soreng.** Department of Biology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA.
**S.W. Jacobs.** National Herbarium, Royal Botanic Gardens, Sydney, NSW, 2000, Australia.
**N.F. Refulio-Rodriguez.** Rancho Santa Ana Botanic Garden, Claremont, CA 91711-3157, USA.

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[2] Corresponding author (e-mail: lgillespie@mus-nature.ca).

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*Mots-clés :* ADN, hybridation, phylogénie, *Poa*, Poaceae, Poeae.

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## Introduction

The large subtribe Poinae and related smaller subtribes Alopecurinae, Cinninae, Miliinae, and Puccinelliinae are widely distributed, cool temperate grasses belonging to tribe Poeae. Together these subtribes include, as currently recognized, between 33 and 43 genera and about 830 species; Poinae has between 14 and 22 genera and about 550 species (Soreng et al. 2003*b*, 2007) (Table 1). Their taxonomic histories are complex; their circumscription and taxon membership have changed considerably since they were first described (Tables 1 and 2) and are still unsettled.

Within the grasses, a clade of supertribe Poodae (tribe Poeae s. l.) plus supertribe Triticodae (tribes Bromeae and Triticeae) is sister to tribe Brachypodieae, and these together constitute the core members of the grass subfamily Pooideae (Davis and Soreng 2007). The tribe Poeae s. l. was recently reclassified (Soreng and Davis 2000; Barker et al. 2001; Soreng et al. 2003*a*, 2003*b*, 2007) to include both Poeae s. str. (sensu Tzvelev 1976; Macfarlane and Watson 1982; Clayton and Renvoize 1986) and Aveneae, plus other smaller tribes that are generally recognized as allied to or included in Poeae or Aveneae. Soreng et al. (2007), following the lead of Tzvelev (1976), accepted 22 subtribes for about 140 genera within tribe Poeae s. l.

For the 22 genera of subtribe Poinae listed in Soreng et al. (2007), at least preliminary DNA evidence was available to support membership within Poinae for all but five of these genera (Table 1). The largest genus is *Poa*, with more than 500 species; those genera outside *Poa* have 1–6 species.

Subtribe Poinae sensu Soreng et al. (2007) is characterized by open or contracted panicles, generally moderate-sized spikelets that are laterally compressed and disarticulate above the glumes and, when multiple-flowered, between the florets, with generally well-developed glumes that sometimes exceed the adjacent lemmas, and no sterile florets below the fertile ones. The lemmas are keeled, generally laterally compressed, and awnless or with short terminal awns. Lemma calluses are frequently pubescent. The ovary is usually glabrous and the caryopsis has a short hilum. Poinae genera are cool temperate and boreal to Mediterranean and arctic, of aquatic to subxeric habitats, with cool growing seasons. Typical of tribe Poeae, their base chromosome number is $x = 7$ and the chromosomes are medium-large to large, and caryopses contain compound starch grains and embryos of the F + FF type. Typical of subfamily Pooideae, they have $C_3$ photosynthesis with non-Kranz anatomy, and they lack microhairs (Barker et al. 2001).

The history of the application of subtribe Poinae is reviewed here in Tables 1 and 2; that of tribe Poeae was reviewed by Soreng et al. (2007). Subtribe Poinae was established by Dumortier (1829) to include genera with panicles of indeterminately multiple-flowered spikelets with glumes shorter than the adjacent lemmas, and lemmas without awns (Table 2). It was used as synonymous with subtribe Festucinae J. Presl (1830) by Bentham (1881) and Hackel (1887), but few of the original genera remain (Table 2). Few modern authors, however, have used the rank of subtribe in tribe Poeae s. str., preferring to recognize the constituent genera as allied or similar elements within a broadly circumscribed tribe Poeae, as did Clayton and Renvoize (1986), and Watson and Dallwitz (1992). Tzvelev (1976), however, treated the genera placed in Poeae s. l. (i.e., as in Soreng et al. 2007) within 7 tribes and 23 subtribes (2 tribes without a subtribe), and divided the genera of Poeae s. str. into 7 subtribes. Covering the Soviet Union, Tzvelev included 12 genera in subtribe Poinae, 7 of which are now placed in the closely related subtribe Puccinelliinae, and *Torreyochloa*, which is now considered remote from Poinae (Table 1). He excluded a few genera later placed in Poinae by Soreng et al. (2007). Soreng et al. (2003*a*) considered genera occurring in the New World and expanded tribe Poeae s. l. to include tribes Aveneae, Phalarideae, Phleeae, Hainardieae, Scolochloeae, and Seslerieae, dividing it into 18 subtribes, and further refined subtribe Poinae (Table 1).

Much DNA data concerning generic complexes and the infratribal phylogenetic structure of Poeae s. l. has emerged recently (Soreng and Davis 2000; Torrecilla and Catalán 2002; Torrecilla et al. 2003, 2004; Catalán et al. 2004; Gillespie and Soreng 2005; Rodionov et al. 2005; Davis and Soreng 2007; Döring et al. 2007; Gillespie et al. 2007; Quintanar et al. 2007; Soreng et al. 2007). Soreng et al. (2007) evaluated the morphology of the tribe in conjunction with sequence data for five plastid genes, and provided a new subtribal classification for Poeae for the World (Table 1). However, the devil is in the details and exact relationships of genera and good data on the putative monophyly of genera in subtribe Poinae and surrounding subtribes still require deeper and more focused sampling, particularly in the larger and variable genera, like *Poa*, and sequence data are still needed for various smaller genera that were previously unstudied using DNA. Aspects of the Soreng et al. (2007) classification of the tribe Poeae s. l. that are pertinent to the present paper are reviewed below, as it is critical to understand why subtribes Alopecurinae and Miliinae are placed near subtribe Poinae rather than among or within the tribes or subtribes with which they are traditionally allied.

The previous separation of Poeae s. l. into two major tribes, Aveneae and Poeae, was based on morphology (mainly relative glume to lemma length; awn presence/absence, position and shape; and floret number) (Macfarlane and Watson 1982; Clayton and Renvoize 1986; Watson and Dallwitz 1992). The separation of Aveneae and Poeae has been strongly supported by plastid DNA analyses (Soreng and Davis 2000; Davis and Soreng 2007; Döring et al. 2007; Quintanar et al. 2007; Soreng et al. 2007). Although two main plastid clades are strongly supported and highly divergent, one with "Poeae-type" plastids, and one with "Aveneae-type" plastids (Soreng and Davis 2000), the membership of the two clades inferred from plastid data differs from that in the two morphologically circumscribed tribes for about 20% of the genera (Soreng and Davis 2000; Davis and Soreng 2007; Döring et al. 2007; Gillespie et al. 2007; Quintanar et al. 2007; Soreng et al. 2007). Many genera have been reclassified based on the plastid data, and the set of genera placed in Poinae and closely related subtribes has changed substantially over time (Tables 1 and 2) (Soreng and Davis 2000; Soreng et al. 2003*a*, 2003*b*, 2007). In addition, two genera, *Anthochloa* and *Milium*, not classified in Poeae or Aveneae, but in Meliceae and Stipeae, by Clayton and Renvoize (1986), were found to have Poeae-type plastids, and both have been shown to be closely allied to, or to belong within, Poinae (Soreng and Davis 2000; Gillespie et al. 2007). *Anthochloa* is now recognized as a section within *Poa* (Gillespie et al. 2007).

For genera with Poeae-type plastids, recent DNA sequence-based studies (Davis and Soreng 2007; Döring et al. 2007; Gillespie et al. 2007; Quintanar et al. 2007; Soreng et al. 2007) support the concept of two major lineages as suggested by Clayton and Renvoize (1986): one with *Poa* and allied genera including *Puccinellia*, and one including *Festuca* and allied genera. However, genera of subtribes Miliinae and Alopecurinae s. str., and several other genera, previously placed in other tribes, had to be added to the *Poa* lineage (Soreng and Davis 2000), and more than 10 genera had to be removed (Table 1). Some genera formerly thought to be related to *Poa* (Clayton and Renvoize 1986) have proved to have plastid types phylogenetically well removed from the *Poa* lineage. *Briza* and other *Briza*-like genera, and *Parafestuca* (=*Koeleria*) and *Torreyochloa* have Aveneae-type plastids (Soreng and Davis 2000; Soreng et al. 2007) and are placed in other subtribes. *Sphenopus*, *Catapodium*, *Desmazeria*, and *Cutandia* have all been placed in Parapholiinae, and *Dactylis* has been placed in Dactylidinae, both subtribes near to *Festuca* and its subtribe Loliinae (Soreng and Davis 2000; Soreng et al. 2007). Plastid DNA evidence from the single species of the Australian genus *Dryopoa* Vickery (Vickery 1963) place it near to *Festuca* (Gillespie and Soreng 2005); and Soreng et al. (2007) suggested it did not belong near Poinae but to Loliinae (as per placement by Clayton and Renvoize 1986).

Gillespie et al. (2007) in testing the monophyly of *Poa* found support for subtribe Puccinelliinae as the sister group to a clade of Poinae, Alopecurinae, and Miliinae (PAM). Genera of Alopecurinae were intermixed with genera of Poinae; while relationships of Poinae genera to the one Miliinae genus examined were unresolved. PAM resolved into three main clades: (*i*) *Milium* and *Phleum*, (*ii*) *Poa*, and (*iii*) all other genera of Alopecurinae and Poinae examined. Most previous studies not focused on *Poa* have only included one or a few exemplars of this mega-genus, with few exemplars of other Poinae, Alopecurinae, and Miliinae genera. Plastid data have supported the monophyly of *Poa* (Gillespie and Soreng 2005; Gillespie et al. 2007), with a few modifications. The few cases of incongruence between the plastid data and the morphology-based classification led to a reexamination of the morphology and a revised classification incorporating the placements suggested by the plastid data. For example, *Bellardiochloa*, which was included in *Poa* by Clayton and Renvoize (1986), has repeatedly been resolved as independent from *Poa* in plastid analyses (Soreng et al. 1990; Soreng and Davis 2000; Gillespie and Soreng 2005; Döring et al. 2007; Gillespie et al. 2007; Soreng et al. 2007), reinforcing the separation of *Bellardiochloa* on morphological grounds (Tzvelev 1976; Edmondson 1980; Mill 1985; Soreng and Gillespie 2007; Soreng et al. 2007). Plastid evidence also suggested that *Poa* subgenus *Andinae* was not a member of *Poa*, but instead was allied to other Poinae genera (Gillespie and Soreng 2005; Gillespie et al. 2007). Soreng and Gillespie (2007) described a new genus, *Nicoraepoa*, for this group of six Andean species, based on evidence from morphology, plastid DNA, and preliminary nrDNA results. Conversely, *Austrofestuca* and *Eremopoa*, once included in *Poa*, but long excluded (Bor 1960; Alexeev 1976; Tzvelev 1976, 1989; Clayton and Renvoize 1986; Edgar 1986; Simon 1986; Jacobs 1990), were reunited with *Poa*, based on plastid DNA, and are now treated as sections within *Poa* (Gillespie and Soreng 2005; Gillespie et al. 2007). Hunter et al. (2004) studied the relationship of the Australian genera *Hookerochloa* and *Festucella* to *Austrofestuca* s. str. using ITS and *trn*L–*trn*F sequences. They determined that the former genera were closely related, but could not be included in a broadly defined *Austrofestuca* (Simon 1986; Jacobs 1990), as the type species of that genus was embedded within *Poa* (see Table 3). *Parodiochloa* is generally treated within *Poa* (e.g., Nicora 1978; Clayton and Renvoize 1986), but some authors excluded it (Hubbard 1981; see comments in Edgar 1986). Plastid data confirmed it belongs within *Poa*, and it is now treated as a section of *Poa* (Gillespie and Soreng 2005; Gillespie et al. 2007; Soreng and Gillespie 2007).

Several additional molecular studies have included informative samples of Puccinelliinae and PAM genera, aside from the broader scale studies already mentioned. A recent study of *trn*T–*trn*L–*trn*F (TLF) and ITS data in tribe Poeae s. l. (Quintanar et al. 2007) also placed *Alopecurus*, *Anthochloa*, *Cinna*, *Dissanthelium*, *Milium*, *Poa*, *Ventenata*, and the isolated *Avenula* species, *Avenula pubescens*, in a group closely matching what we call the PAM plastid clade, but also including genera of the small subtribes Cinninae and Ventenatinae, all as the sister clade to Puccinelliinae. Döring et al. (2007) used the *mat*K plastid gene to show that *Gaudiniopsis*, *Cyathopus*, and *Hyalopoa* also belong in this taxonomic vicinity. *Anthochloa* and one species of *Dissanthelium* were nested within *Poa* subgenus *Poa* in Gillespie et al. (2007) (see Tables 1 and 3). New data on *Tovarochloa* and much additional data on *Dissanthelium* also place these genera within *Poa* (Refulio-Rodriguez 2007; with nomenclatural emendations pending). Byrsting et al. (2004) investigated the origin of *Dupontia* and concluded that it was close to *Arctophila*, but they could not implicate any other genus as a possible parent in the putative hybrid origin of *Dupontia*.

Phylogenetic relationships within *Poa* based on plastid TLF data were evaluated by Gillespie and Soreng (2005) and Gillespie et al. (2007). Six major internested clades or lineages formed the basis of five subgenera and two supersections in their revised infrageneric classification. Table 3 provides details of names of accepted subgenera and sections in *Poa*, and clade acronyms standing for sets of sections included in each subgenus: *Poa* subg. *Poa*, by far the largest, was divided into two supersections. However, there has been little ITS data published for *Poa*.

A few exclusively nuclear studies on Poeae s. l. exist that cover some Poinae elements. Grebenstein et al. (1998) examined ITS1 and ITS2 (the two internal transcribed spacer regions of the nuclear rDNA genes) for the genus *Helictotrichon* s. l. and other *Avena* allies. Due to limited outgroup selection, however, they did not realize that *Helictotrichon* s. str. (subtribe Aveninae) was phylogenetically remote from two of its subgenera (now treated as *Avenula* s. str. and *Avenula* (s. l.) *pubescens*), and more particularly that *A. pubescens* might somehow be related to Poinae elements (Quintanar et al. 2007). Another genus complex long presumed to be allied to Poinae includes *Catabrosella*, *Colpodium*, and *Paracolpodium* (Tzvelev 1976; Alexeev 1980; Alexeev and Tzvelev 1981; Clayton and Renvoize 1986; Hedberg and Hedberg 1994): ITS data placed these (and *Zingeria*, formerly placed in Agrostidinae) in the proximity of a very limited sample of PAM and Puccinelliinae genera (Rodionov et al. 2005), a result reconfirmed with broader taxonomic sampling by Quintanar et al. (2007).

Quintanar et al. (2007) published the most extensive ITS analysis of Poeae and Aveneae to date, with 62 genera and 105 species. They resolved representatives of 16 genera and *A. pubescens* in a clade of Puccinelliinae and PAM genera (see Fig. 2 of Quintanar et al. (2007)). This is essentially the same assemblage as detected in their parallel investigation of TLF (reviewed above). They provided the first resolution of *Apera*, *Ventenata*, *Cinna* and *Avenula pubescens* among PAM genera. The placement of *A. pubescens* has been at odds with its inclusion in *Helictotrichon* s. l. or *Avenula* s. str. (Grebenstein et al. 1998; Soreng and Davis 2000), but this is the first analysis resolving it near to *Poa*. Soreng and Davis (2000) discuss it as a likely intergeneric hybrid in origin (see also karyotype analyses by Winterfeld 2006, and Winterfeld and Röser 2007).

Poinae genera examined for neither plastid nor nuclear DNA, or in other cases mentioned but not yet formally published in a comprehensive phylogenetic analysis, include *Libyella*, *Lindbergella*, *Nephelochloa*, *Neuropoa*, *Oreopoa*, *Tovarochloa*, and *Tzvelevia*.

Here we present our first nuclear ITS and additional plastid DNA sequence data for Poinae and related subtribes, and explore phylogenetic relationships in this group. Our specific objectives are as follows:

1. Examine the monophyly of subtribe Poinae and its relationship to other subtribes of Poeae.
2. Evaluate placements by new molecular data, either TLF, ITS or both, for several PAM and Puccinelliinae genera (*Aniselytron*, *Aphanelytrum*, *Bellardiochloa*, *Eremopoa*, *Hyalopoa*, *Nicoraepoa*, *Neuropoa*, *Tovarochloa*, *Tzvelevia*).
3. Compare nuclear and plastid phylogenies, highlight areas of well-supported congruent and incongruent placements of taxa.
4. Evaluate ITS data support for the phylogeny of *Poa* and the revised classification based on plastid DNA evidence presented in Gillespie et al. (2007).

## Methods

### Taxa sampled

Our sampling was designed to be representative of the taxonomic diversity in subtribe Poinae, while adequately sampling diversity in the related subtribes Alopecurinae, Miliinae, and Puccinelliinae. For tribal and subtribal taxonomy we follow Soreng et al. (2007).

Representatives of 21 genera accepted or generally segregated from *Poa* and 67 species of Poinae (sensu Soreng et al. 2007) were sampled (Tables 1 and 4); this includes all currently (and many previously) recognized Poinae genera with the exception of four rarely collected monotypic genera from the eastern Mediterranean region for which material was not available (*Lindbergella*, *Libyella*, *Nephelochloa*, and *Oreopoa*). Sampling in the largest genus *Poa* (40 species sampled) included species belonging to all major sections and previously identified plastid DNA clades (Table 4) (Gillespie et al. 2007), with a focus on broad phylogenetic relationships. Seven species from 3 of 7 genera of Alopecurinae (Soreng et al. 2007), 5 species from the 3 genera of Miliinae (sensu Soreng et al. 2007), and 10 species from 6 of 9 nonhybrid genera previously proposed for inclusion in Puccinelliinae (sensu Soreng et al. 2003*a*; modified by Soreng et al. 2007) were sampled. The species sampled and their GenBank accession numbers are provided in Table 4.

To provide a phylogenetic context, we included 32 species from 15 additional Poeae genera belonging to subtribes Airinae, Dactylidinae, Loliinae, Sesleriinae, Agrostidinae, Aveninae, and Phalaridinae (the latter three subtribes, traditionally considered within tribe Aveneae, are called "core Aveneae" (Quintanar et al. 2007), as they combine "Aveneae-type" plastids and morphology). *Brachypodium* (subfamily Pooideae, tribe Brachypodieae) and *Bromus* (subfamily Pooideae, tribe Bromeae; in ITS analysis only) were included as outgroup taxa, as suggested by the analysis of subfamily Pooideae by Davis and Soreng (2007).

Our ITS data matrix comprises 170 sequences (168 accessions), of which 105 are presented for the first time here, with 64 derived from published studies, and one an unpublished sequence from GenBank. The TLF data matrix of 133 sequences (132 accessions) includes 42 new sequences, 69 presented previously in Gillespie et al. (2007), and 22 sequences from other publications.

### DNA extraction, amplification, and sequencing

We extracted DNA primarily from silica-gel dried material using a silica-based column approach (Alexander et al. 2007), similar to commercially available DNA extraction kits. The plastid DNA region between *trn*T and *trn*F (TLF), including the spacer region *trn*T–*trn*L (TL), the *trn*L gene and its intron (L intron), and the spacer region *trn*L–*trn*F (LF), was amplified in two sections using primer pairs "a3" (J. Travis Columbus (Rancho Santa Ana Botanic Garden), personal communication) and "d" (Taberlet et al. 1991), and "c" and "f" (Taberlet et al. 1991). The nuclear ribosomal internal transcribed spacer region (ITS1–5.8S-ITS2) was amplified using primers "KRC" (Torrecilla and Catalán 2002) and "AB102" (Douzery et al. 1999). Both TLF and ITS amplifications were performed in a 15 μL volume with

**Table 1.** Genera of subtribe Poinae, their classification according to Clayton and Renvoize (1986) and Tzvelev (1976, 1989), their current made in the present paper.

| Genus (in italic) or Subtribe (in bold) | No. spp. | Distribution | Clayton and Renvoize (1986) |
|---|---|---|---|
| **Poinae** | | | **Poeae** |
| *Aniselytron* Merr. | 2 | Southeast Asia | Aveneae–Alopecurinae (as synonym of *Calamagrostis* Adans.) |
| *Anthochloa* Nees & Meyen | 1 | Andes | Meliceae |
| *Apera* Adans. | 5 | Eurasia | Aveneae–Alopecurinae |
| *Aphanelytrum* Hack. | 2 | Andes | Poeae–*Poa*–*Aphanelytrum* |
| *Arctagrostis* Griseb. | 1 | Arctic | Poeae–*Poa*–*Arctagrostis* |
| *Arctophila* (Rupr.) Anderss. | 1 | Arctic, boreal | Poeae–*Poa*–*Colpodium* group |
| *Arctopoa* (Griseb.) Prob. | 5 | East Asia and boreal coasts of North America | Poeae–*Poa* (as syn.) |
| *Austrofestuca* s. str. (Tzvelev) E.B. Alexeev | 2 | Australia and New Zealand | Poeae–*Poa*–*Austrofestuca* |
| *Bellardiochloa* Chiov. | 4 | Eurasia | Poeae–*Poa* (as syn.) |
| *Dasypoa* Pilg. | 1 | Andes | Poeae–*Poa* (as syn.) |
| *Dissanthelium* Trin. | 15 | Andes, to Mexican and Californian Pacific islands | Aveneae–Aveninae |
| *Dupontia* R. Br. | 1 | Arctic | Poeae–*Poa*–*Colpodium* group |
| *Eremopoa* Roshev. | 6 | Asia | Poeae–*Poa*–*Eremopoa* group |
| *Festucella* E.B. Alexeev | 1 | Australia | n/a |
| *Gaudiniopsis* (Boiss.) Eig | 5 | Eurasia | Aveneae–Aveninae |
| *Hookerochloa* E.B. Alexeev | 2 | Australia | *n/a* |
| *Libyella* Pamp. | 1 | North Africa | Poeae–*Poa*–*Eremopoa* group |
| *Lindbergella* Bor | 1 | Cyprus | Poeae–*Poa*–*Eremopoa* group |
| *Nephelochloa* Boiss. | 1 | Turkey | Poeae–*Poa*–*Eremopoa* group |
| *Neuropoa* W.D. Clayton | 1 | Australia | Poeae–*Poa*–*Eremopoa* group |
| *Parodiochloa* C.E. Hubb. | 5 | Sub-Antarctic Islands, Indian Ocean, New Zealand, southern Atlantic islands and Tierra del Fuego | Poeae–*Poa* (as syn.) |
| *Poa* L. | 500+ | Widespread | Poeae–*Poa* |
| *Tovarochloa* T.D. Macfarl. & But | 1 | Andes | Aveneae–Aveninae |
| *Tzvelevia* E.B. Alexeev | 1 | Indian Ocean sub-Antarctic Islands | n/a |
| *Ventenata* Koeler | 3 | Eurasia | Aveneae–Aveninae |
| **Cinninae** | | | **Aveneae–Alopecurinae** |
| *Cinna* L. | 3 | Boreal and mountain islands south to Peru | Aveneae–Alopecurinae |
| *Limnodea* Dewey | 1 | S.C., North America | Aveneae–Alopecurinae |
| *Cyathopus* Stapf | 1 | Sikkim to Yunnan | Aveneae–Alopecurinae |
| **Alopecurinae** | | | **Aveneae–Alopecurinae** |
| *Alopecurus* L. | 50 | Widespread | Aveneae–Alopecurinae |
| *Beckmannia* Host | 2 | Boreal | Aveneae–Alopecurinae |
| *Cornucopiae* L. | 2 | Mediterranean | Aveneae–Alopecurinae |
| *Limnas* Trin. | 2 | NE Asia | Aveneae–Alopecurinae |
| *Phleum* L. | 20 | Widespread, mainly Eurasia | Aveneae–Alopecurinae |
| *Pseudophleum* Dogan | 1 | Turkey | Aveneae–Alopecurinae |
| *Rhizocephalus* Boiss. | 1 | Mediterranean | Aveneae–Alopecurinae |
| **Miliinae** | | | **Stipeae** |
| *Colpodium* Trin. | 5 | Asia, African highlands | Poeae–*Poa*–*Colpodium* group |
| *Mibora* Adans. | 1 | Mediterranean | Aveneae–Alopecurinae |
| *Milium* L. | 7 | Boreal | Stipeae–between *Oryzopsis* Michx. and *Trikeraia* Bor. |
| *Zingeria* P.A. Smirn. | 5 | Mediterranean | Aveneae–Alopecurinae |
| **Puccinelliinae** | | | **Poeae–Puccinellia group** |
| *Catabrosa* P. Beauv. | 4 | Widespread | Poeae–*Poa*–*Colpodium* group |

status and classification according to Soreng et al. (2003a, 2003b; New World grasses only) and Soreng et al. (2007), and modifications

| Tzvelev (1976; or if not then in1989[a]) | Soreng et al. (2003*a*, 2003*b*) | Soreng et al. (2007) | Modifications made here |
|---|---|---|---|
| **Poeae–Poinae** | **P*–Poinae** | **P*–Poinae** | No change |
| Poeae[a] | n/a | P*–Poinae | Intergeneric hybrid |
| Poeae[a] | P*–Poinae | P*–Poinae, *Poa* sect. *Anthochloa* | No change |
| Aveneae–Agrostidinae | A–Agrostidinae | P–Poinae | P*–Poinae(–*Poa*) |
| Poeae[a] | P*–Poinae | P*–Poinae | Combinations pending within *Poa* |
| Poeae–Cinninae | P*–Poinae | P*–Poinae | No change |
| Poeae–Poinae | P*–Poinae | P*–Poinae | No change |
| Poeae–Poinae (as subgenus of *Poa*, 1976; as a genus, 1989) | P*–Poinae *Poa* subg. *Arctopoa* | P*–Poinae, *Arctopoa* | Intergeneric hybrid |
| Poeae[a] | n/a | P*–Poinae, *Poa* sect. *Austrofestuca* | No change |
| Poeae–Festucinae | n/a | P*–Poinae, *Bellardiochloa* | No change |
| Poeae[a] | P*–Poinae, *Poa* sect. *Dasypoa* | P*–Poinae, *Poa* sect. *Dasypoa* | No change |
| Poeae[a] | P*–Poinae | P*–Poinae within *Poa* | Combinations pending within *Poa* |
| Poeae–Poinae | P*–Poinae | P*–Poinae | No change |
| Poeae–Poinae | P*–Poinae *Poa* subg. *Pseudopoa* | P*–Poinae, *Poa* subg. *Pseudopoa* | Some combs. pending within *Poa* |
| Poeae[a] | n/a | P*–Poinae | = *Hookerochloa* |
| Aveneae–Ventenatinae | n/a | Aveneae–Aveninae | P*–Poinae(–*Poa*) |
| Poeae[a] | n/a | P*–Poinae | *Hookerochloa* expanded |
| Poeae[a] | n/a | P–Poinae | No change |
| Poeae–Poinae[a] | n/a | P–Poinae | No change |
| Poeae[a] | n/a | P–Poinae | No change |
| Poeae[a] | n/a | P*–Poinae | P*–*Poa* sect. *comb. pending* |
| Poeae[a] | P*–Poinae *Poa* sect. *Parodiochloa* | P*–Poinae, *Poa* sect. *Parodiochloa* | No change |
| Poeae–Poinae | P*–Poinae | P*–Poinae | No change |
| Poeae[a] | P*–Poinae | P***–Poinae | Combinations pending within *Poa* |
| Poeae[a] | n/a | P–Poinae | P*–Poinae ?*Poa* sect. *Parodiochloa* |
| Aveneae–Ventenatinae | A–Agrostidinae | P–Poinae | P*–Poinae(–*Poa*) |
| **Poeae–Cinninae** | **A[†]–Cinninae** | **A[†]–Cinninae** | **P*–Poinae(–*Poa*) (Cinninae)** |
| Poeae–Cinninae | A[†]–Cinninae | A[†]–Cinninae | P*–Poinae(–*Poa*) (Cinninae) |
| Poeae[a] | A–Cinninae | A–Cinninae | P– Poinae(–*Poa*) (Cinninae) |
| Poeae[a] | n/a | A–Agrostidinae | P*–Poinae(–*Poa*) (Cinninae) |
| **Phleeae–Alopecurinae** | **P*–Alopecurinae** | **P*–Alopecurinae** | **P*–PAM Alopecurinae** |
| Phleeae–Alopecurinae | P*–Alopecurinae | P*–Alopecurinae | No change |
| Phleeae–Beckmanniinae | P*–Alopecurinae | P*–Alopecurinae | No change |
| Phleeae | n/a | P–Alopecurinae | No change |
| Phleeae–Alopecurinae | n/a | P–Alopecurinae | No change |
| Phleeae–Phleinae | P*–Alopecurinae | P*–Alopecurinae | No change |
| Phleeae–Phleinae[a] | n/a | P–Alopecurinae | No change |
| Phleeae–Phleinae | n/a | P–Alopecurinae | No change |
| **Poeae–Miliinae** | **P*–Miliinae** | **P*–Miliinae** | **P*–PAM Miliinae** |
| Poeae–Poinae | P–Puccinelliinae | $\text{P}^{\text{ITS}}$–Miliinae | No change |
| Aveneae–Agrostidinae | P*–Miliinae | P*–Miborinae | P*[c]– Sesleriinae |
| Aveneae–Miliinae | P*–Miliinae | P*–Miliinae | No change |
| Aveneae–Agrostidinae | n/a | $\text{P}^{\text{ITS}}$–Miliinae | No change, but P*–Puccinelliinae? |
| **Poeae–Poinae** | **P*–Puccinelliinae** | **P*–Puccinelliinae** | No change |
| Poeae–Poinae | P*–Puccinelliinae | P*–Puccinelliinae | No change |

**Table 1** (*concluded*).

| Genus (in italic) or Subtribe (in bold) | No. spp. | Distribution | Clayton and Renvoize (1986) |
|---|---|---|---|
| *Catabrosella* (Tzvelev) Tzvelev | 6 | Asia | Poeae–*Poa–Colpodium* (as syn.) |
| *Hyalopoa* (Tzvelev) Tzvelev | 4 | Asia | Poeae–*Poa–Colpodium* (as syn.) |
| *Oreopoa* H. Scholz & Parolly | 1 | Turkey | n/a |
| *Paracolpodium* (Tzvelev) Tzvelev | 3 | Asia | Poeae–*Poa–Colpodium* (as syn.) |
| *Phippsia* (Trin.) R. Br. | 2 | Arctic | Poeae–*Poa–Colpodium* group |
| *Pseudosclerochloa* Tzvelev | 2 | Eurasia | Poeae–Puccinellia group |
| *Puccinellia* Parl. | 150 | Widespread | Poeae–*Puccinellia* group |
| *Sclerochloa* P. Beauv. | 3 | Eurasia | Poeae–*Poa–Desmazeria* group |
| Miscellaneous genera sometimes placed near *Poa* | | | |
| *Briza* L. | 6 | Eurasia, Africa | Poeae–*Poa–Briza* group |
| *Calotheca* Desv. | 1 | South America | Poeae–*Poa–Briza* (as syn.) |
| *Chascolytrum* Desv. | 6 | South America | Poeae–*Poa–Briza* (as syn.) |
| *Coleanthus* Seidel | 1 | Eurasia | Poeae–*Poa–Colpodium* group |
| *Cutandia* Willk. | 3 | Mediterranean | Poeae–*Poa–Desmazeria* group |
| *Dactylis* L. | 1 | Eurasia | Poeae–*Poa–Dactylis* |
| *Desmazeria* Dumort. | 3 | Mediterranean | Poeae–*Poa–Desmazeria* group |
| *Gymnachne* Parodi | 1 | South America | Poeae–*Poa–Briza* group (as syn. of *Rhombolytrum*) |
| *Microbriza* Nicora & Rúgolo | 1 | South America | Poeae–*Poa–Briza* group |
| *Poidium* Nees | 10 | South America | Poeae–*Poa* (as syn.) |
| *Relchela* Steud. | 1 | South America | Aveneae–Aveninae |
| *Rhombolytrum* E. Desv. | 2 | South America | Poeae–*Poa–Briza* group |
| *Sphenopus* Trin. | 2 | Mediterranean | Poeae–*Poa–Eremopoa* group |
| *Torreyochloa* G.L. Church | 2 | North America, eastAsia | Poeae–Puccinellia group |

**Note:** A–, postulated Aveneae alliance; P–, postulated Poeae s. str. alliance; A or P with an asterisk (*), plastid type confirmed. $^{ITS}$, relationship confirmed

[a]Tzvelev 1989, covering grass genera of the World not treated in 1976, included tribes Agrostidinae, Aveneae, Cinninae, Cynosureae, Festuceae, separation of Phleeae (including Seslerieae and *Mibora*) and Phalarideae. Tzvelev (1976) treating USSR genera recognized tribes Aveneae, Monermeae

[†]Plastid DNA result now considered erroneous (see text).

[c]ITS placement conflicts with placement of subtribe Sesleriinae based on plastid DNA.

final concentration of 1× buffer, 1.5 mmol/L $MgCl_2$, 0.2 mmol/L dNTP, 0.25 µmol/L of each primer, 0.3 units *Taq*, and 1.5 µL of 1:10 dilutions of extracted DNA. Undiluted DNA was used for difficult samples. The following cycling conditions were used: 1 min at 95 °C, followed by 30 cycles of 95 °C for 45 s, 58 °C for 45 s, and 72 °C for 90 s (ITS) or 2 min (TLF). A final elongation step of 72 °C for 5 min completed the amplification reactions. Amplification products were purified using the enzymes Exonuclease I and shrimp alkaline phosphatase. BigDye version 3.1 (Applied Biosystems, Inc., Foster City, Calif.) was used for sequencing reactions using 0.5 µL of Big Dye in a 10 µL reaction. To ensure complete coverage of the regions, an internal primer “b” (Taberlet et al. 1991) was used for sequencing the “a3–d” section of TLF and an internal primer “its3” (White et al. 1991) was used for ITS sequencing. The primer “AB102” was replaced by “its4” (White et al. 1991) for sequencing as this was found to give better results. Sequencing reaction products were purified via ethanol – EDTA – sodium acetate precipitation. Nucleotide sequences of both strands of the amplification products were determined using automated cycle-sequencing on an Applied Biosystems 3100-Avant automated sequencer. Where sequences were messy due to apparent polymorphism or unexpected results were obtained, samples were reamplified and resequenced, and when possible additional collections were processed and analyzed.

### Sequence alignment and phylogenetic analysis

Consensus sequences for each sample were assembled and edited using Sequencher version 4.7 (Gene Codes Corp., Ann Arbor, Mich.). For samples having two or more sequence variants, obvious nucleotide variants (double peaks on electropherogram trace of approximately equal strength) were coded using IUB ambiguity codes. In the case of length variants, the dominant variant was coded and submitted to GenBank, or where both variants were observed in about equal intensities on the trace files, then the longest was coded. The 170 ITS sequences and 135 TLF sequences were aligned using ClustalX version 1.83 (Jeanmougin et al. 1998) and the resulting alignment was refined by eye using BioEdit version 5.0.9 (Hall 1999). Aligned lengths of the TLF and ITS sequence datasets were 2804 bases and 636 bases, respectively. Unambiguous parsimony informative insertions and deletions (indels) were coded as separate presence/absence characters using the simple indel coding method of Simmons and Ochoterena (2000), with overlapping indels coded as in Graham et al. (2000). Inter- or intra-sample length variations in mononucleotide repeats were generally not considered informative and were not coded as indels unless they could be unambiguously interpreted. Parsimony analyses were performed on each dataset separately with PAUP* 4.0b10 (Swofford 2002). Heuristic searches were conducted with tree bisection–reconnection (TBR), Collapse, and MulTrees options, and a maximum of

| Tzvelev (1976; or if not then in1989[a]) | Soreng et al. (2003*a*, 2003*b*) | Soreng et al. (2007) | Modifications made here |
|---|---|---|---|
| Poeae–Poinae | P–Puccinelliinae | $\mathrm{P}^{\mathrm{ITS}}$–Puccinelliinae | No change |
| Poeae–Poinae | n/a | P–Poinae | $\mathrm{P}^{\mathrm{ITS}}$–Puccinelliinae, P*–Poinae |
| n/a | n/a | P–Puccinelliinae | No change |
| Poeae–Poinae | P–Puccinelliinae | $\mathrm{P}^{\mathrm{ITS}}$–Puccinelliinae | No change |
| Poeae–Poinae | P*–Puccinelliinae | P*–Puccinelliinae | No change |
| Poeae–Poinae (in *Puccinellia*) | n/a | P–Puccinelliinae | No change |
| Poeae–Poinae | P*–Puccinelliinae | P*–Puccinelliinae | No change |
| Poeae–Poinae | P*–Puccinelliinae | P*–Puccinelliinae | No change |
| | | | |
| Poeae–Brizinae | A*–Brizinae s. l. | A*–Brizinae | No change |
| Poeae[a] | A*–Brizinae s. l. | A*–Brizinae s. l. | No change |
| Poeae[a] | A*–Brizinae s. l. | A*–Brizinae s. l. | No change |
| Poeae–Coleanthinae | A–Agrostidinae? | A–Agrostidinae? | No change |
| Poeae–Festucinae | P*–Parapholiinae | P*–Parapholiinae | No change |
| Poeae–Dactylidinae | P*–Dactylinideae | P*–Dactylinideae | No change |
| Poeae[a] | P*–Parapholiinae | P*–Parapholiinae | No change |
| Poeae[a] | A–Brizinae s. l. | A*–Brizinae s. l. | No change |
| | | | |
| Poeae[a] | A*–Brizinae s. l. (as syn. of *Poidium*) | A*–Brizinae s. l. (as syn. of *Poidium*) | No change |
| Poeae[a] | A*–Brizinae s. l. | A*–Brizinae s. l. | No change |
| n/a | A–Brizinae s. l. | A*–Brizinae s. l. | No change |
| Poeae[a] | A–Brizinae s. l. | A–Brizinae s. l. | No change |
| Poeae–Festucinae | P*–Parapholiinae | P*–Parapholiinae | No change |
| Poeae–Poinae | A*–Torreyochloinae | A*–Torreyochloinae | No change |

by nrDNA ITS where plastid DNA has not been studied.

Milieae, Monermeae, Hubbardieae, and Scolochloeae within Poeae, with 17 subtribes (without aligning the genera in them), but continuing the (Hainardieae), Phalarideae, Phleeae, Poeae, Scolochloeae, and Seslerieae, with a series of subtribes.

100 000 trees were saved. Analyses were performed both with and without the indel characters, and with and without one taxon which appeared to cause extensive clade collapse (*Avenula pubescens*). Nucleotide variant sites were treated as uncertain rather than "polymorphic" for the purposes of the analysis. The strength of clade support was estimated using bootstrap analysis (Felsenstein 1985) on each data matrix. A search strategy of 100 000 random taxon addition replicates and the "fast bootstrap" option (i.e., no branch swapping) was used owing to the long run times. Bootstrap support values over 50% are given. We consider clades with 80% or greater bootstrap support (BS) to be relatively strongly supported, those with between 50 and 79% to be moderately supported (Felsenstein and Kishino 1993; Hillis and Bull 1993).

## Results

### *trn*T–*trn*L–*trn*F analysis

#### *TLF sequences*

The plastid TLF dataset comprises 2804 aligned nucleotide positions and 87 indel characters. After excluding 11 large indel regions (see below) the total number of nucleotide characters analyzed was 2222. Of these characters, 368 bp were parsimony informative (PI) and 219 bp represent variable but parsimony uninformative characters. Missing data represented <1% of the dataset, with data missing primarily from the ends and in the vicinity of primer sites in the conserved *trn*L gene regions. For several species (*Sclerochloa dura* (L.) P. Beauv., *Aniselytron treutleri* (Kunze) Soják, *Festuca eskia* Ramond ex DC.) and collections only L intron and *trn*L–*trn*F sequences (LLF) were available (Table 4). The 87 indels considered to be potentially phylogenetically informative among all taxa (69 among Alopecurinae, Miliinae, Poinae, and Puccinelliinae) comprised 59 insertions and 28 deletions, and were distributed as follows: TL, 37; L intron, 27; LF, 23. Indels did not cause problems in alignment except for one large region with many indels, which was excluded from the analysis (also excluded in Gillespie et al. 2007). Ten regions (14–101 bp long) with few mostly large insertions and no informative nucleotide substitutions were also excluded from the dataset and analysis. Unambiguous informative indels in these 11 regions were coded as separate indel characters.

#### *TLF phylogenetic analysis*

Parsimony analysis of the data matrix including indel characters but excluding *A. pubescens* resulted in the maximum 100 000 trees, which are 1183 steps long with a consistency index (CI) of 0.705 and 0.633, with and without parsimony uninformative characters, respectively. A phylogram illustrating one of the most parsimonious trees with

**Table 2.** Early concepts of subtribe Poinae, a historical review of genera classified in subtribes of Poaceae that included the genus *Poa*.

| Subtribe | Genera |
|---|---|
| Poinae Dumort. | (Dumortier 1829): *Airopsis*, *Briza*, *Centotheca*, *Eragrostis*, *Glyceria*, *Melica*, *Molinia* (as *Enodium*), ***Poa***, *Triodia*, *Triplasis* (as *Uralepis*), *Uniola* |
| Festucinae J. Presl. | (As applied by Bentham 1881, and Hackel 1887): *Pleuropogon*, *Brylkinia*, *Uniola*, *Distichlis*, *Briza*, *Desmazeria*, *Wangenheimia*, *Aeluropus*, *Lasiochloa* (=*Tribolium*), *Dactylis*, *Cynosurus*, *Lamarckia*, *Sclerochloa*, *Schismus*, ***Nephelochloa***, ***Poa***, *Colpodium*, ***Dupontia***, *Scolochloa*, *Graphephorum*, *Glyceria*, *Atropis* (=*Puccinellia*), *Festuca*, *Catapodium*, and *Scleropoa* |

**Note:** Genera listed in bold were still included in subtribe Poinae by Soreng et al. (2007). Genera not in bold in the previous classifications have been placed by various authors in other subfamilies, tribes, or subtribes (see Table 1 for modern concepts of Poinae).

**Table 3.** Infrageneric classification of *Poa* L. and clade acronyms as applied by Gillespie and Soreng (2005) and Gillespie et al. (2007) based on phylogenetic studies of plastid DNA data.

| | *Poa* subgenus (supersection) | Clade | *Poa* sections |
|---|---|---|---|
| 1 | *Arctopoa* (Griseb.) Prob. | **ArcSyl** | *Arctopoa* (Griseb.) Tzvelev, *Sylvestres* Soreng |
| 2 | *Ochlopoa* (Asch. & Graebn.) Hyl. | **BAPO** | *Arenariae* Stapf (syn.: sect. *Bolbophorum* Asch. & Graebn.), *Alpinae* (Nyman) Stapf, *Parodiochloa* (C. E. Hubb.) Soreng & L.J. Gillespie, *Micrantherae* Stapf (syn.: sect. *Ochlopoa* Asch. & Graebn.) |
| 3 | *Pseudopoa* (K. Koch.) Stapf. | *Pseudopoa* lineage (syn. *Eremopoa*) | *Pseudopoa* (K. Koch.) Hack. |
| 4 | *Stenopoa* (Dumort.) Soreng & L.J. Gillespie | **SPOSTA** | *Secundae* Soreng, *Pandemos* Asch. & Graebn., *Oreinos* Asch. & Graebn., *Stenopoa* Dumort., *Tichopoa* Asch. & Graebn., *Abbreviatae* Tzvelev |
| 5 | *Poa* (*Poa*) | **PoM** | *Leptophyllae* J.R. Edm., *Macropoa* F. Herm. ex Tzvelev, *Nivicolae* (Roshev.) Tzvelev, *Poa* |
| | (*Homalopoa* (Dumort.) Soreng & L.J. Gillespie) | **HAMBADD** | *Acutifoliae* Potztal, *Anthochloa* (Nees & Meyen) Soreng & L.J. Gillespie, *Austrofestuca* (Tzvelev) Soreng & L.J. Gillespie, *Brizoides* Potztal, *Dasypoa* (Pilg.) Soreng, *Dioicopoa* E. Desv., *Homalopoa* Dumort., *Madropoa* Soreng; and several informal species groups |

**Note:** Clade acronyms (in bold) were used as shorthand to identify major sets of sections of *Poa*. Subgenera classification follows Gillespie et al. (2007). The subgenera were postulated to have diverged from their most recent common ancestor in the following order 1(2(3(4 & 5))).

the strict consensus tree shown in bold lines is given in Fig. 1.

Two major Poeae clades were resolved in the TLF analysis: (*i*) subtribes Aveninae, Agrostidinae, Phalaridinae (core Aveneae) (bootstrap support (BS) = 100); (*ii*) subtribes Loliinae, Dactylidinae, Sesleriinae, Airinae, Alopecurinae, Miliinae, Poinae, and Puccinelliinae (BS = 93). Clade 2 was subdivided into three clades: (*i*) subtribes Loliinae, Dactylidinae, Sesleriinae, Airinae (BS = 54); (*ii*) subtribe Puccinelliinae (BS = 100); (*iii*) subtribes Poinae, Alopecurinae, Miliinae, plus *Cinna* and *Ventenata* (PAM) (BS = 89). The latter two formed a clade (PPAM), but with less than 50% bootstrap support.

The large PAM clade, the focus of this study, comprising subtribes Poinae, Alopecurinae, and Miliinae (no data yet for *Zingeria* and *Colpodium*), resolved into four clades or lineages: (*i*) *Phleum* (only one species sampled); (*ii*) *Milium* (BS = 86); (*iii*) *Poa*, *Arctopoa*, *Aphanelytrum*, *Dissanthelium*, *Neuropoa* (*Poa fax* Willis & Court), and *Tovarochloa* (*Poa* clade) (BS = 73); (*iv*) all remaining genera of subtribes Alopecurinae and Poinae [called here the Poinae(–*Poa*) clade (i.e., Poinae minus *Poa*)] (BS = 68). Relationships among these four lineages were not well supported. Relationships among genera in the Poinae(–*Poa*) clade were mostly poorly resolved, and only the following clades were supported: *Arctophila*, *Dupontia* (BS = 95); *Apera*, *Bellardiochloa* (BS = 99); and these two plus *Ventenata* (BS = 65).

Lineages (see Table 3 for explanation of clade acronyms) within the *Poa* clade in order of divergence are as follows: (*i*) ArcSyl (BS = 59); (*ii*) BAPO (BS = 97); (*iii*) *Pseudopoa*, only one species examined; (*iv*) SPOSTA (BS = 98); and (*v*) PoM + HAMBADD (BS = 100). Of the two sister clades comprising the latter lineage, PoM is well supported (BS = 97), while the large HAMBADD clade including *Poa fax* (*Neuropoa*) and the genera *Aphanelytrum, Dissanthelium*, and *Tovarochloa* is moderately supported (BS = 52). Relationships among these five *Poa* clades were strongly supported (BS = 85–100).

The analysis excluding indel characters and *A. pubescens* (1053 steps, CI = 0.705 and 0.624, with and without uninformative characters, respectively) resulted in a strict consensus tree (not shown) very similar to the tree in Fig. 1, differing mostly in being somewhat less resolved (only relationships in *Poa* sect. *Sylvestres* were more resolved, but these were not well supported). The analysis including *A. pubescens* and indel characters (1220 steps, CI = 0.698 and 0.624, with and without uninformative characters, respectively) also resulted in a very similar strict consensus tree, and differed only in being slightly less resolved. *Avenula pubescens* formed a polytomy with *Milium*, *Phleum*, the *Poa* clade, and Poinae(–*Poa*).

## ITS analysis

### *ITS sequences*

The nuclear ribosomal ITS dataset comprised 636 aligned nucleotides, of which 301 were potentially parsimony informative and 74 were variable but parsimony uninformative. Missing data represented <1% of the dataset, or <0.5% with *A. pubescens* excluded. Only ITS1 was present for one sample each of *Poa billardierei* Steud. and *A. pubescens*, and only ITS2 for two *A. pubescens* samples (Table 4). Thirty-seven potentially parsimony informative indels (1–4 bp long) were coded, including 12 deletions and 7 insertions in ITS1, and 11 deletions and 7 insertions in ITS2.

### *ITS sequence variants*

Some ITS sequences exhibited a low degree of intra sample variants ("polymorphism" but likely representing different loci) due to either single nucleotide variations or variable length mononucleotide repeats. For example, both *Poa flabellata* (Lam.) Raspail collections sampled have the same variant site (A/G) in ITS2 (seen as a double peak in the trace file, with each peak of approximately equal strength). The majority of these single-base variant sites are unique to a collection or species.

Less common was length variation in a mononucleotide repeat, which causes a shift in the sequence read of one variant with respect to the other variant and a garbled electropherogram trace downstream of the mutation. Provided that only one such mutation is present in a sequence, the consensus of the forward and reverse sequences allowed for a complete read, as was the case for all but one sample in this study. Species and collections with length variation in a mononucleotide repeat include *Poa alpina* L. (*Gillespie et al. 6749-1*), *Poa bulbosa* L. (*Catalán 13-2000*), and *Deschampsia brevifolia* R. Br.

One collection exhibited variant ITS copies that suggest recent hybridization. *Arctopoa tibetica* (Stapf) Prob. (*Olonova 2003-07*) had an unusual variable region in ITS1 comprising a single nucleotide variable site combined with a 1 bp indel that was not associated with a mononucleotide repeat (CAAAC/CCAAAG at sites 153–158); the first variant was identical to a second sample of *A. tibetica* examined (*Soreng 5481*), the second was common to most other species sampled, including the two other species of *Arctopoa*. This sequence also had two variable sites in ITS2 (A/G, A/G) that again showed the same affinities. Repeated amplification and sequencing produced the same results. The sequence used in the analyses and submitted to GenBank included the first variant.

Variant sites in *Nicoraepoa pugionifolia* (Speg.) Soreng & L.J. Gillespie also suggest possible hybridization. The single collection examined was found to have length variation at two sites (AAAACAGA/AAAAAGA at sites 15–22, 5 or 6 Cs at sites 213–218, both variants of approximate equal intensity on the electropherogram trace) resulting in a messy region of 194 bases in ITS1 in the consensus sequence as seen in Sequencher version 4.7. By carefully reading the two otherwise identical overlapping sequence traces (shifted by one base pair with respect to each other), it was possible to infer an unambiguous sequence. Affinities of the two variants at the first site include most genera versus those unique to *N. pugionifolia*; at the second site, most *Nicoraepoa* versus *Poa*.

Only minor variation in ITS was observed in this study, and no cases of divergent sequences belonging to the same collection were observed using our direct sequencing approach. No evidence for the presence of paralogues was detected, except for one possible case; sequences were of approximately equal length and the 5.8S rDNA sequence was highly conserved except for a short sequence in a loop region known to be variable. Initial attempts at sequencing two samples of *Aniselytron* produced sequences that did not readily align except for the 5.8S region. A GenBank BLAST search on one of these sequences (*Ma 140*) showed that it was closest to *Phleum*, but with only ca. 80% similarity. These sequences appear likely to be divergent paralogues. Sequencing of a third sample yielded an easily alignable sequence.

### *ITS phylogenetic analysis*

Parsimony analysis of the data matrix including indel characters, but excluding *A. pubescens* resulted in the maximum 100 000 trees, which are 1408 steps long (CI = 0.396 and 0.322, with and without parsimony uninformative characters, respectively; RI = 0.814). A phylogram illustrating one of the most parsimonious trees and elements seen in the strict consensus tree (indicated in bold lines) is given in Fig. 2.

Three major Poeae clades were resolved: (*i*) subtribes Loliinae and Dactylidinae (Loliinae s.l. clade; BS = 92); (*ii*) subtribes Aveninae, Agrostidinae, Phalaridinae, and Sesleriinae (core Aveneae + Sesleriinae clade; BS = 62) (elements of subtribe Airinae also resolved as sister groups to this lineage with BS < 50); and (*iii*) subtribes Puccinelliinae, Poinae, Alopecurinae, and Miliinae, plus *Cinna* and *Ventenata* (PPAM clade, BS < 50) (Fig. 2A). Relationships among these three clades and many deep relationships in the clades were poorly supported.

Within the PPAM clade, a major focus of this study, the following clades were resolved (Fig. 2A): (*i*) *Colpodium* and *Zingeria* (BS = 100); (*ii*) *Milium* (BS = 94); (*iii*) *Poa* clade including *Aniselytron*, *Aphanelytrum*, *Dissanthelium*, *Neuropoa* (*P. fax*), and *Tovarochloa* (but excluding species previously treated in *Poa* subg. *Arctopoa*) (BS = 54); (*iv*) *Phleum* (BS = 84); (*v*) *Arctagrostis*, *Festucella*, *Hookerochloa*, and *Nicoraepoa* (BS = 93); (*vi*) *Arctopoa* and *Cinna* (BS = 68); (*vii*) *Apera* and *Bellardiochloa* (BS = 99), and these two plus *Ventenata* (BS = 65); (*viii*) *Arctophila* and *Dupontia* (BS = 88), and these two plus *Alopecurus* (BS = 65); (*ix*) subtribe Puccinelliinae including *Hyalopoa* (BS = 81). Relationships among these clades were not were not supported by bootstrap analysis.

Clades within the *Poa* clade in order of divergence (relative to Fig. 2B) are: (*i*) sect. *Sylvestres* and the genus *Aniselytron* (BS = 55); (*ii*) sects. *Alpinae* and *Arenariae* (BS = 100), sect. *Micrantherae* (BS = 100); (*iii*) sects. *Parodiochloa* and *Tzvelevia*, and *N. pugionifolia* (BS = 99); (*iv*)

**Table 4.** Collections examined for ITS and TLF, with voucher information, country of origin (for our samples and from other studies (with subgenus and section given only for *Arctopoa* and *Poa*).

| Taxon | Tribe–subtribe | Subgenus | Section |
|---|---|---|---|
| *Agrostis capillaris* L. | Aveneae–Agrostidinae | | |
| *Agrostis mertensii* Trin. | Aveneae–Agrostidinae | | |
| *Agrostis stolonifera* L. | Aveneae–Agrostidinae | | |
| *Agrostis stolonifera* | Aveneae–Agrostidinae | | |
| *Alopecurus borealis* Trin. | Poeae–Alopecurinae | | |
| *Alopecurus gerardii* Vill. | Poeae–Alopecurinae | | |
| *Alopecurus vaginatus* (Willd.) Pall. ex Kunth | Poeae–Alopecurinae | | |
| *Aniselytron treutleri* (Kunze) Soják | Poeae–Poinae(–*Poa*) | | |
| *Aniselytron treutleri* | Poeae–Poinae(–*Poa*) | | |
| *Aniselytron treutleri* | Poeae–Poinae(–*Poa*) | | |
| *Anthoxanthum monticola* (Bigelow) Veldkamp subsp. *alpinum* (Sw. ex Willd.) Soreng | Aveneae–Phalaridinae | | |
| *Apera interrupta* (L.) P. Beauv. | Poeae–Poinae(–*Poa*) | | |
| *Aphanelytrum peruvianum* Sánchez Vega, P.M. Peterson, Soreng & Laegaard | Poeae–Poinae–*Poa* | | |
| *Aphanelytrum procumbens* Hack | Poeae–Poinae–*Poa* | | |
| *Aphanelytrum procumbens* | Poeae–Poinae–*Poa* | | |
| *Aphanelytrum procumbens* | Poeae–Poinae–*Poa* | | |
| *Arctagrostis latifolia* (R. Br.) Griseb. | Poeae–Poinae(–*Poa*) | | |
| *Arctagrostis latifolia* | Poeae–Poinae(–*Poa*) | | |
| *Arctagrostis latifolia* | Poeae–Poinae(–*Poa*) | | |
| *Arctagrostis latifolia* | Poeae–Poinae(–*Poa*) | | |
| *Arctophila fulva* (Trin.) Rupr. | Poeae–Poinae(–*Poa*) | | |
| *Arctophila fulva* | Poeae–Poinae(–*Poa*) | | |
| *Arctophila fulva* | Poeae–Poinae(–*Poa*) | | |
| *Arctopoa eminens* (J. Presl) Prob. (formerly *Poa eminens* J. Presl) | Poeae–Poinae | | *Arctopoa* |
| *Arctopoa eminens* | Poeae–Poinae | | *Arctopoa* |
| *Arctopoa eminens* | Poeae–Poinae | | *Arctopoa* |
| *Arctopoa subfastigiata* (Trin.) Prob. (formerly *Poa subfastigiata* Trin.) | Poeae–Poinae | | *Aphydris* |
| *Arctopoa subfastigiata* | Poeae–Poinae | | *Aphydris* |
| *Arctopoa tibetica* (Stapf) Prob. (formerly *Poa tibetica* Stapf) | Poeae–Poinae | | *Aphydris* |
| *Arctopoa tibetica* | Poeae–Poinae | | *Aphydris* |
| *Arctopoa tibetica* | Poeae–Poinae | | *Aphydris* |
| *Avenula aetolica* (Rech. f.) Holub. | Poeae–Airinae | | |
| *Avenula bromoides* (Gouan) H. Scholz | Poeae–Airinae | | |
| *Avenula hookeri* (Scribn.) Holub | Poeae–Airinae | | |
| *Avenula pubescens* (Huds.) Dumort. | Poeae–Airinae | | |
| *Avenula pubescens* | Poeae–Airinae | | |
| *Avenula pubescens* | Poeae–Airinae | | |
| *Avenula pubescens* | Poeae–Airinae | | |
| *Avenula sulcata* (J. Gay ex Boiss.) Dumort. | Poeae–Airinae | | |
| *Beckmannia eruciformis* (L.) Host | Poeae–Alopecurinae | | |
| *Beckmannia syzigachne* (Steud.) Fernald | Poeae–Alopecurinae | | |
| *Bellardiochloa polychroa* (Trautv.) Roshev. | Poeae–Poinae(–*Poa*) | | |
| *Bellardiochloa variegata* (Lam.) Kerguélen | Poeae–Poinae(–*Poa*) | | |
| *Bellardiochloa variegata* | Poeae–Poinae(–*Poa*) | | |
| *Brachypodium distachyon* (L.) P. Beauv. | Brachypodieae | | |
| *Brachypodium phoenicoides* (L.) P. Beauv. ex Roem. & Schult. | Brachypodieae | | |
| *Brachypodium sylvaticum* (Huds.) P. Beauv. | Brachypodieae | | |
| *Bromus tectorum* L. | Bromeae | | |
| *Catabrosa aquatica* (L.) P. Beauv. | Poeae–Puccinelliinae | | |
| *Catabrosa aquatica* | Poeae–Puccinelliinae | | |
| *Catabrosa werdermannii* (Pilg.) Nicora & Rúgolo | Poeae–Puccinelliinae | | |
| *Catabrosella variegata* (Boiss.) Tzvelev | Poeae–Puccinelliinae | | |

where known), or general distribution (other studies, indicated in parentheses), GenBank accession number, and classification

| Country of origin | Voucher | TLF GenBank No. | ITS GenBank No. |
|---|---|---|---|
| Russia | | — | [AF498395] |
| USA, New Hampshire | Gillespie 6802 CAN | DQ353956 | — |
| Spain | 1. | [DQ336860, DQ336835] | [DQ336815] |
| Russia | 2. | — | [EF541167] |
| Canada, Nunavut | Gillespie et al. 6576 CAN | DQ353966 | **EU792345** |
| Greece | Soreng et al. 7494 US | **EU792432** | **EU792344** |
| Caucasus | | — | [Z96920, Z96921] |
| China | 1. Ma 140 KUN | **EU792440** LLF | **EU854592**<br>(paralogue?) |
| China | 2. Soreng 5229 US | **EU792441** LLF | — |
| China | 3. Soreng 5264 US | — | **EU792373** |
| Canada, NWT[a] | Gillespie & Consaul 6859 CAN | DQ353953 | **EU792323** |
| Argentina | Peterson et al. 19173 US | **EU792439** | **EU792364** |
| Peru | Sanchez Vega et al. 11718 US | — | **EU792421** |
| Peru | 1. Peterson et al. 20582 US | **EU792459** | **EU792419** |
| Peru | 2. Peterson & Refulio 16571 US | — | **EU792423** |
| Peru | 3. Peterson & Refulio 16581 US | **EU792458** LLF | **EU792420** |
| Canada, Nunavut | 1. Gillespie et al. 6586 CAN | DQ353969 | **EU792351** |
| Canada, Nunavut | 2. Archambault 157 CAN | **EU792434** | **EU792353** |
| Canada, Nunavut | 3. Archambault 145 CAN | — | **EU792352** |
| (Panarctic) | 4. | — | [AY237843] |
| Canada, NWT[a] | 1. Aiken 99–230 CAN | DQ354058 | **EU792347** |
| (Panarctic) | 2. | — | [AY237831] |
| (Panarctic) | 3. | — | [AY237832] |
| USA, Alaska | 1. Soreng 6022 US | DQ353977 | **EU792366** |
| Canada, Labrador | 2. Gillespie 7010–3 CAN | **EU792447** | **EU792367** |
| Canada, Labrador | 3. Gillespie 7010–2 CAN | **EU792446** | — |
| Mongolia | 1. W6 18199 W94049 (GRIN ID#) | **EU792448** | **EU792372** |
| Mongolia | 2. W6 18244 W94096 (GRIN ID#) | **EU792449** | **EU792371** |
| Russia | 1. Olonova 2003–07 CAN | **EU792444** | **EU792369** |
| China, Tibet | 2. Soreng et al. 5481 US | DQ353976 | **EU792368** |
| Kyrgyz Republic | 3. Soreng et al. 7626 US | **EU792445** | **EU792370** |
| Greece | Soreng et al. 7514 US | **EU792437** | **EU792329** |
| (W Europe) | | [DQ631525, DQ631459] | [Z96844, Z96845] |
| Russia | | — | [AY870327] |
| Eurasia | | [DQ631526/DQ631460] | [Z96870, Z96871] |
| Russia | | — | [AY870326] ITS1 |
| (Eurasia) | | — | [Z96873] ITS2 |
| (Eurasia) | | — | [Z96875] ITS2 |
| Spain | | [DQ631527, DQ631461] | [DQ539595) |
| (Eurasia) | | — | [AJ389163] |
| USA, Wyoming | Soreng 3513 US | DQ353965 | **EU792342** |
| Turkey | Soreng & Güney 4191 US | — | **EU792363** |
| Greece | 1.Soreng et al. 7519–1 US | **EU792438** | **EU792361** |
| Yugoslavia | 2. USDA PIS 253455 | DQ353970 | **EU792362** |
| Slovenia | | [DQ336855, AF478500] | — |
| (Europe) | | — | [AF019781] |
| (Eurasia) | | — | [AJ608155] |
| (Eurasia, pan-temperate weed) | | — | [AJ608154] |
| Chile | 1. Soreng & Soreng 7150 US | DQ353958 | **EU792334** |
| Russia | 2. | — | [EF577510] |
| Argentina | Peterson et al. 19371 US | **EU792431** | **EU792333** |
| Turkey | 1. Soreng & Davis 4044 US | — | **EU792332** |

**Table 4** (*continued*).

| Taxon | Tribe–subtribe | Subgenus | Section |
|---|---|---|---|
| *Catabrosella variegata* | Poeae–Puccinelliinae | | |
| *Cinna arundinacea* L. | Aveneae–Aveninae | | |
| *Cinna latifola* (Trevir. ex Göpp.) Griseb. | Aveneae–Aveninae | | |
| *Colpodium versicolor* (Steven) Schmalh. | Poeae–Miliinae | | |
| *Colpodium versicolor* | Poeae–Miliinae | | |
| *Colpodium versicolor* | Poeae–Miliinae | | |
| *Dactylis glomerata* L. | Poeae–Dactylidinae | | |
| *Dactylis glomerata* | Poeae–Dactylidinae | | |
| *Dactylis glomerata* subsp. *hispanica* (Roth) Nyman | Poeae–Dactylidinae | | |
| *Deschampsia antarctica* E. Desv. | Poeae–Airinae | | |
| *Deschampsia antarctica* | Poeae–Airinae | | |
| *Deschampsia brevifolia* R. Br. | Poeae–Airinae | | |
| *Dichelachne lautumia* Edgar & Connor | Aveneae–Agrostidinae | | |
| *Dissanthelium brevifolium* Swallen & Tovar | Poeae–Poinae–*Poa* | | |
| *Dissanthelium calycinum* (J. Presl) Hitchc. | Poeae–Poinae–*Poa* | | |
| *Dissanthelium calycinum* | Poeae–Poinae–*Poa* | | |
| *Dissanthelium calycinum* | Poeae–Poinae–*Poa* | | |
| *Dissanthelium peruvianum* (Nees & Meyen) Pilg. | Poeae–Poinae–*Poa* | | |
| *Dissanthelium peruvianum* | Poeae–Poinae–*Poa* | | |
| *Dryopoa dives* (F. Muell.) Vickery | Poeae–Loliinae | | |
| *Dupontia fisheri* R. Br. | Poeae–Poinae(–*Poa*) | | |
| *Dupontia fisheri* | Poeae–Poinae(–*Poa*) | | |
| *Dupontia fisheri* | Poeae–Poinae(–*Poa*) | | |
| *Dupontia fisheri* | Poeae–Poinae(–*Poa*) | | |
| *Dupontia fisheri* | Poeae–Poinae(–*Poa*) | | |
| *Festuca baffinensis* Polunin | Poeae–Loliinae | | |
| *Festuca californica* Vasey | Poeae–Loliinae | | |
| *Festuca eskia* Ramond ex DC. | Poeae–Loliinae | | |
| *Festuca hystrix* Boiss. | Poeae–Loliinae | | |
| *Festuca lasto* Boiss. | Poeae–Loliinae | | |
| *Festuca ovina* L. | Poeae–Loliinae | | |
| *Festuca paniculata* (L.) Schinz & Thell. | Poeae–Loliinae | | |
| *Festuca rubra* L. | Poeae–Loliinae | | |
| *Festuca spectabilis* Jan | Poeae–Loliinae | | |
| *Festuca triflora* J.F. Gmel. | Poeae–Loliinae | | |
| *Festucella eriopoda* (Vickery) E.B. Alexeev | Poeae–Poinae(–*Poa*) | | |
| *Festucella eriopoda* | Poeae–Poinae(–*Poa*) | | |
| *Festucella eriopoda* | Poeae–Poinae(–*Poa*) | | |
| *Helictotrichon convolutum* (C. Presl) Henrard | Aveneae–Aveninae | | |
| *Helictotrichon sempervirens* (Vill.) Pilg. | Aveneae–Aveninae | | |
| *Hellerochloa fragilis* (Luces) Rauschert (*Helleria fragilis*) | Poeae–Loliinae | | |
| *Hookerochloa hookeriana* (F. Muell. ex Hook.f.) E.B. Alexeev | Poeae–Poinae(–*Poa*) | | |
| *Hookerochloa hookeriana* | Poeae–Poinae(–*Poa*) | | |
| *Hyalopoa pontica* (Bal.) Tzvelev | Poeae–Puccinelliinae | | |
| *Lolium perenne* L. | Poeae–Loliinae | | |
| *Milium effusum* L. | Poeae–Miliinae | | |
| *Milium vernale* M. Bieb. | Poeae–Miliinae | | |
| *Nicoraepoa andina* (Trin.) Soreng & L.J. Gillespie | Poeae–Poinae(–*Poa*) | | |
| *Nicoraepoa chonotica* (Phil.) Soreng & L.J. Gillespie | Poeae–Poinae(–*Poa*) | | |
| *Nicoraepoa pugionifolia* (Speg.) Soreng & L.J. Gillespie | Poeae–Poinae(–*Poa*) | | |
| *Nicoraepoa robusta* (Steud.) Soreng & L.J. Gillespie | Poeae–Poinae(–*Poa*) | | |
| *Nicoraepoa robusta* | Poeae–Poinae(–*Poa*) | | |
| *Nicoraepoa subenervis* (Hack.) Soreng & L.J. Gillespie subsp. *subenervis* | Poeae–Poinae(–*Poa*) | | |
| *Nicoraepoa subenervis* subsp. *spegazziniana* (Nicora) Soreng & L.J. Gillespie | Poeae–Poinae(–*Poa*) | | |
| *Nicoraepoa subenervis* subsp. *spegazziniana* | Poeae–Poinae(–*Poa*) | | |
| *Paracolpodium altaicum* (Trin.) Tzvelev | Poeae–Puccinelliinae | | |

| Country of origin | Voucher | TLF GenBank No. | ITS GenBank No. |
|---|---|---|---|
| Russia | 2. | — | [AY862811] |
| USA, West Virginia | Soreng & Olonova 7462 US | **EU792436** | **EU792343** |
| Finland | | [DQ631498, DQ631432] | [DQ539569] |
| (Eurasia) | 1. | — | [AJ867445] |
| (Eurasia) | 2. | — | [AJ867446] |
| (Eurasia) | 3. | — | [AY497472] |
| (Eurasia & cult.) | 1. | — | [AF393013] |
| (Eurasia & cult.) | 2. | — | [L36512] |
| Spain | Soreng 3682 US | DQ353961 | — |
| Argentina | Peterson et al. 17079 US | **EU792463** | — |
| (Argentina, Chile) | | — | [AF521900] |
| Canada, NWT[a] | Gillespie & Consaul 6810b CAN | DQ353962 | **EU792328** |
| New Zealand | | — | [AY705893] |
| Peru | Peterson & Refulio 18043 US | **EU792468** | **EU792424** |
| Peru | 1. Peterson & Refulio 16466 US | **EU792466** | **EU792426** |
| Peru | 2. Peterson et al. 17923 US | **EU792467** | **EU792425** |
| Peru | 3. | [DQ631497, DQ631431] | [DQ539567] |
| Chile | 1. Peterson & Soreng 15744 US | DQ354052, DQ354053 | **EU792415** |
| Peru | 2. Peterson & Refulio 18222 US | EU792465 | **EU792427** |
| Australia | Jacobs 9239 NSW | EU792430 | — |
| Canada, Nunavut | 1. Gillespie et al. 6589 CAN | DQ353967 | **EU792346** |
| Canada, Nunavut | 2. Gillespie et al. 6699 CAN | DQ353968 | — |
| (panarctic) | 3. | — | [AY237858] |
| (panarctic) | 4. (C12008) | — | [AY237885] |
| (panarctic) | 5. (C56954) | — | [AY237869] |
| Canada, NWT[a] | Gillespie & Consaul 6920 CAN | DQ353951, DQ353952 | — |
| (USA) | | — | [AF532956] |
| (SW Europe) | | [AF478508] LLF | — |
| (Spain) | | — | [AF478480] |
| (Spain) | | — | [AF303418] |
| (Eurasia & cult.) | | [DQ367406, AF533063] | [AY327792] |
| (Europe) | | [DQ336858, AF533050] | [AF303407] |
| (panboreal & cult.) | | [DQ336857, AY118099] | — |
| (Europe) | | — | [AF519977] |
| (Europe) | | — | [AF538362] |
| Australia | 1. Jacobs 9128 NSW | **EU792433** | **EU792349** |
| Australia | 2. Jacobs 9129 NSW | — | **EU792350** |
| (Australia) | 3. | — | [AY559122] |
| Greece | Soreng 3803 US | DQ353954 | **EU792324** |
| USA, cult. | Soreng 4622 US | DQ353955 | **EU792325** |
| (Colombia) | | — | [AF532960] |
| Australia | 1. Jacobs 9127 NSW | **EU792435** | **EU792348** |
| Australia | 2. | — | [AY559123] |
| Turkey | Soreng 4188 US | — | **EU792365** |
| (Europe) | | [DQ367404, AF478504] | [AF303401] |
| Finland | | [DQ631501, DQ631435] | [DQ539573] |
| Greece | Soreng 3748 US (corrected from 3370) | DQ353963 | **EU792340** |
| Chile | Soreng & Soreng 7182 US | DQ353971 | **EU792354** |
| Chile | Soreng & Soreng 7309 US | DQ353974 | **EU792355** |
| Chile | Soreng & Soreng 7336 US | DQ353973 | **EU792360** |
| Chile | 1. Soreng & Soreng 7358 US | DQ353975 | **EU792357** |
| Chile | 2. Soreng & Soreng 7359 US | — | **EU792356** |
| Chile | Soreng & Soreng 7334 US | DQ353972 | **EU792359** |
| Argentina | 1. Peterson et al. 19186 US | **EU792443** | **EU792358** |
| Chile | 2. Soreng 7155 US | **EU792442** | — |
| Russia | | — | [EF432735] |

**Table 4** (*continued*).

| Taxon | Tribe–subtribe | Subgenus | Section |
|---|---|---|---|
| *Phalaris arundinacea* L. | Aveneae–Phalaridinae | | |
| *Phippsia algida* (Sol.) R. Br. | Poeae–Puccinelliinae | | |
| *Phippsia algida* | Poeae–Puccinelliinae | | |
| *Phleum phleoides* (L.) Karsten | Poeae–Alopecurinae | | |
| *Phleum pratense* L. | Poeae–Alopecurinae | | |
| *Poa alpina* L. | Poeae–Poinae–*Poa* | *Ochlopoa* | *Alpinae* |
| *Poa alpina* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Alpinae* |
| *Poa alpina* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Alpinae* |
| *Poa alpina* var. *alpina* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Alpinae* |
| *Poa alpina* var. *vivipara* L. | Poeae–Poinae–*Poa* | *Ochlopoa* | *Alpinae* |
| *Poa alsodes* A. Gray | Poeae–Poinae–*Poa* | *Sylvestres* (named here) | *Sylvestres* |
| *Poa ammophila* A.E. Porsild | Poeae–Poinae–*Poa* | *Stenopoa* | *Secundae* |
| *Poa annua* L. | Poeae–Poinae–*Poa* | *Ochlopoa* | *Micrantherae* |
| *Poa annua* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Micrantherae* |
| *Poa annua* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Micrantherae* |
| *Poa autumnalis* Elliott | Poeae–Poinae–*Poa* | *Sylvestres* | *Sylvestres* |
| *Poa billardierei* St.-Yves (as *Austrofestuca littoralis* (Labill.) Alexeev) | Poeae–Poinae–*Poa* | *Poa* | *Austrofestuca* |
| *Poa billardierei* (as *Austrofestuca littoralis*) | Poeae–Poinae–*Poa* | *Poa* | *Austrofestuca* |
| *Poa bulbosa* L. | Poeae–Poinae–*Poa* | *Ochlopoa* | *Arenariae* |
| *Poa bulbosa* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Arenariae* |
| *Poa bulbosa* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Arenariae* |
| *Poa chaixii* Vill. | Poeae–Poinae–*Poa* | *Stenopoa* | *Homalopoa* |
| *Poa compressa* L. | Poeae–Poinae–*Poa* | *Stenopoa* | *Tichopoa* |
| *Poa compressa* | Poeae–Poinae–*Poa* | *Stenopoa* | *Tichopoa* |
| *Poa cookii* (Hook. f.) Hook. f. | Poeae–Poinae–*Poa* | *Ochlopoa* | *Parodiochloa* |
| *Poa cookii* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Parodiochloa* |
| *Poa curtifolia* Scribn. | Poeae–Poinae–*Poa* | *Stenopoa* | *Secundae* |
| *Poa diaphora* Trin. (*Eremopoa songarica* (Shrenk) Roshev.) | Poeae–Poinae–*Poa* | *Pseudopoa* | *Pseudopoa* |
| *Poa drummondiana* Nees | Poeae–Poinae–*Poa* | *Poa* | *Brizoides* |
| *Poa fax* Willis & Court (*Neuropoa fax* (Willis & Court) Clayton) | Poeae–Poinae–*Poa* | *Poa* | *?* |
| *Poa fendleriana* (Steud.) Vasey | Poeae–Poinae–*Poa* | *Poa* | *Madropoa* |
| *Poa flabellata* (Lam.) Raspail | Poeae–Poinae–*Poa* | *Ochlopoa* | *Parodiochloa* |
| *Poa flabellata* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Parodiochloa* |
| *Poa glauca* Vahl. | Poeae–Poinae–*Poa* | *Stenopoa* | *Stenopoa* |
| *Poa glauca* | Poeae–Poinae–*Poa* | *Stenopoa* | *Stenopoa* |
| *Poa gymnantha* Pilg. | Poeae–Poinae–*Poa* | *Poa* | "Punapoa" |
| *Poa ircutica* Roshev | Poeae–Poinae–*Poa* | *Poa* | *Poa* |
| *Poa kelloggii* Vasey | Poeae–Poinae–*Poa* | *Sylvestres* | *Sylvestres* |
| *Poa kerguelensis* (Hook. f.) Steud. (*Tzvelevia kerguelensis* (Hook. f.) E.B. Alexeev) | Poeae–Poinae–*Poa* | *Poa* | *Parodiochloa?* |
| *Poa kerguelensis* | Poeae–Poinae–*Poa* | *Poa* | *Parodiochloa?* |
| *Poa kurtzii* R.E. Fr. | Poeae–Poinae–*Poa* | *Poa* | "Punapoa" |
| *Poa labillardierei* Steud. | Poeae–Poinae–*Poa* | *Poa* | "Australopoa" |
| *Poa laxa* Haenke subsp. *fernaldiana* (Nannf.) Hyl. | Poeae–Poinae–*Poa* | *Stenopoa* | *Oreinos* |
| *Poa lepidula* (Nees & Meyen) Soreng & L.J. Gillespie | Poeae–Poinae–*Poa* | *Poa* | *Anthochloa* |
| *Poa lepidula* | Poeae–Poinae–*Poa* | *Poa* | *Anthochloa* |
| *Poa macrantha* Vasey | Poeae–Poinae–*Poa* | *Poa* | *Madropoa* |
| *Poa marcida* Hitchc. | Poeae–Poinae–*Poa* | *Sylvestres* | *Sylvestres* |
| *Poa molinerii* Balb. | Poeae–Poinae–*Poa* | *Ochlopoa* | *Alpinae* |
| *Poa nervosa* (Hook.) Vasey | Poeae–Poinae–*Poa* | *Poa* | *Homalopoa* |
| *Poa palustris* L. | Poeae–Poinae–*Poa* | *Stenopoa* | *Stenopoa* |
| *Poa palustris* | Poeae–Poinae–*Poa* | *Stenopoa* | *Stenopoa* |

| Country of origin | Voucher | TLF GenBank No. | ITS GenBank No. |
|---|---|---|---|
| (Panboreal & cult.) | | [AY589138] | — |
| Canada, Nunavut | 1. Gillespie 6253 CAN | DQ353949, DQ353950 | **EU792331** |
| Canada, Nunavut | 2. Gillespie & Consaul 6913–1 CAN | — | **EU792330** |
| (Europe) | | — | [AF498396] |
| USA, cult. | No voucher[b] | DQ353964 | **EU792341** |
| Canada, Nunavut | 1. Gillespie et al. 6749–1 CAN | DQ353986 | **EU792390** |
| USA, Colorado | 2. Gillespie 6299 CAN | DQ353985 | — |
| (panboreal) | 3. | [AY589122] | — |
| (panboreal) | 4. (Brysting 96–1-4 O) | — | [AY237837] |
| (Europe) | (Brysting 96–1-9 O) | — | [AY237836] |
| Canada, Quebec | Gillespie 6467 CAN | DQ353981 | **EU792374** |
| Canada, NWT[a] | Gillespie 5851 CAN | DQ353992 | **EU792392** |
| China | 1. Soreng 7456 US | **EU792452** | — |
| Canada, Ontario | 2. Gillespie 6284 CAN | DQ353983 | **EU792386** |
| (pan- temperate) | 3. | — | [AF521901] |
| USA, Maryland | Soreng 4680 US | DQ353979 | **EU792379** |
| New Zealand | 1. | — | [AY327791] ITS1 |
| New Zealand | 2. | — | [AY524824] |
| Spain | 1. Catalán 13–2000 UZ | DQ354034, DQ354035 | **EU792388** |
| USA, Nevada | 2. Soreng 5958 US | **EU792472** | **EU792391** |
| (Eurasia) | 3. | [AY589127] | — |
| Russia | Soreng 4677 US | **EU854590** | **EU792404** |
| Canada, Quebec | Gillespie 6457 CAN | DQ354003 | **EU792395** |
| | | AY589128 | — |
| Crozet Island (sub-Antarctic Islands) | 1. Hennion Gen1 CAN | **EU792454** | **EU792383** |
| Kerguelen Is. (sub-Antarctic Islands) | 2. Hennion Gen8 CAN | **EU792455** | **EU792382** |
| USA, Washington | Soreng et al. 6347c-1 US | DQ353994 | **EU792394** |
| Turkey | 1, 2. Soreng & Güney 4165 US[c] | DQ353987, DQ353988 | **EU792400** |
| Australia | Peterson et al. 14504 US | DQ354013 | **EU792411** |
| Australia | Jacobs 9339 NSW | **EU792460** | **EU792410** |
| USA, Colorado | Gillespie 6292 CAN | DQ354027 | **EU792403** |
| Falkland Islands | 1. Wright 4NCD[d] | DQ353982 | **EU792380** |
| South Georgia Islands | 2. Wright 9NSG[d] | EU792453 | **EU792381** |
| Canada, Nunavut | 1. Gillespie & Chatenoud 5963 CAN | DQ354004 | **EU792397** |
| Canada, Nunavut | 2. Gillespie 5804 CAN | — | [AY237839] |
| Chile | Peterson & Soreng 15656 US | **EU792462** | **EU792417** |
| Russia, Irkutsk | Kasanovskiy 2002–7 CAN | DQ354007 | **EU792402** |
| USA, California | Soreng 5962 US | **EU792450** | **EU792376** |
| Kerguelen Is. (sub-Antarctic Islands) | 1. Hennion Gen5 CAN | **EU792457** | **EU792385** |
| Kerguelen Is. (sub-Antarctic Islands) | 2. Hennion Gen6 CAN | **EU792456** | **EU792384** |
| Chile | Peterson & Soreng 15654 US | DQ354018 | **EU792413** |
| Australia | Soreng & Peterson 5921 US | DQ354014 | **EU792409** |
| USA, New Hampshire | Gillespie 7015–3 CAN | DQ353995 | **EU792399** |
| Chile | 1. Peterson & Soreng 15604 US | **EU792471** | **EU792416** |
| Chile | 2. Peterson et al. 18138 US | **EU792464** | **EU792422** |
| USA, Oregon | Soreng 5861 US | DQ354028 | **EU792407** |
| USA, Oregon | Soreng & Soreng 5974 US | DQ353978 | — |
| Slovakia | Stoneberg SH13 CAN | DQ354036, DQ354037 | **EU792389** |
| USA, Oregon | Soreng 5849 US | DQ354025 | **EU792405** |
| Canada, Ontario | 1. Gillespie 6461 CAN | DQ354000 | **EU792396** |
| (panboreal) | 2. | [AY589137] | — |

**Table 4** (*concluded*).

| Taxon | Tribe–subtribe | Subgenus | Section |
|---|---|---|---|
| *Poa pratensis* L. ‘midnight’ | Poeae–Poinae–*Poa* | *Poa* | *Poa* |
| *Poa pratensis* subsp. *pratensis* | Poeae–Poinae–*Poa* | *Poa* | *Poa* |
| *Poa pratensis* subsp. *alpigena* (Lindm.) Hiitonen | Poeae–Poinae–*Poa* | *Poa* | *Poa* |
| *Poa pratensis* subsp. *alpigena* | Poeae–Poinae–*Poa* | *Poa* | *Poa* |
| *Poa pseudoabbreviata* Roshev. | Poeae–Poinae–*Poa* | *Stenopoa* | *Abbreviatae* |
| *Poa pubinervis* (Vickery) S.W.L. Jacobs, L.J. Gillespie & Soreng (as *Austrofestuca littoralis* or *P. billardierei* in previous papers) | Poeae–Poinae–*Poa* | *Poa* | *Austrofestuca* |
| *Poa ramosissima* Hook. f. | Poeae–Poinae–*Poa* | *Ochlopoa* | *Parodiochloa* |
| *Poa saltuensis* Fernald & Wiegand | Poeae–Poinae–*Poa* | *Sylvestres* | *Sylvestres* |
| *Poa scaberula* Hook.f. | Poeae–Poinae–*Poa* | *Poa* | *Dasypoa* |
| *Poa secunda* J. Presl. subsp. *secunda* | Poeae–Poinae–*Poa* | *Stenopoa* | *Secundae* |
| *Poa sibirica* Roshev. | Poeae–Poinae–*Poa* | *Poa* | *Macropoa* |
| *Poa stuckertii* (Hack.) Parodi | Poeae–Poinae–*Poa* | *Poa* | *Dioicopoa* |
| *Poa supina* Schrad. | Poeae–Poinae–*Poa* | *Ochlopoa* | *Micrantherae* |
| *Poa supina* | Poeae–Poinae–*Poa* | *Ochlopoa* | *Micrantherae* |
| *Poa sylvestris* A. Gray | Poeae–Poinae–*Poa* | *Sylvestres* | *Sylvestres* |
| *Poa wheeleri* Vasey | Poeae–Poinae–*Poa* | *Poa* | *Homalopoa* |
| *Poa wolfii* Scribn. | Poeae–Poinae–*Poa* | *Sylvestres* | *Sylvestres* |
| *Puccinellia distans* (Jacq.) Parl. | Poeae–Puccinelliinae | | |
| *Puccinellia glaucescens* (Phil.) Parodi | Poeae–Puccinelliinae | | |
| *Puccinellia poacea* T.J. Sørensen | Poeae–Puccinelliinae | | |
| *Puccinellia stricta* (Hook. f.) Blom | Poeae–Puccinelliinae | | |
| *Puccinellia vahliana* (Leibm.) Scribn. | Poeae–Puccinelliinae | | |
| *Puccinellia vahliana* | Poeae–Puccinelliinae | | |
| *Schedonorus arundinaceus* (Schreb.) Dumort. (*Festuca arundinacea*) | Poeae–Loliinae | | |
| *Sclerochloa dura* (L.) P. Beauv. | Poeae–Puccinelliinae | | |
| *Sesleria caerulea* (L.) Ard. | Poeae–Sesleriinae | | |
| *Sesleria insularis* Sommier | Poeae–Sesleriinae | | |
| *Sesleria tenerrima* (Fritsch.) Hayek | Poeae–Sesleriinae | | |
| *Tovarochloa peruviana* T.D. Macfarl. & But | Poeae–Poinae–*Poa* | | |
| *Tovarochloa peruviana* | Poeae–Poinae–*Poa* | | |
| *Ventenata dubia* (Leers) Coss. | Poeae–Poinae(–*Poa*) | | |
| *Vulpia bromoides* (L.) S.F. Gray | Poeae–Loliinae | | |
| *Zingeria biebersteiniana* (Claus) P. Smirnov | Poeae–Miliinae | | |
| *Zingeria biebersteiniana* | Poeae–Miliinae | | |
| *Zingeria trichopoda* (Boiss.) P.A. Smirn. | Poeae–Miliinae | | |

**Note:** Sequences new to this paper indicated in bold, other TLF samples from Gillespie et al. (2007); samples from GenBank indicated in square brackets. cate ITS1/ITS2. TF and ITS partial sequences indicated by LLF and ITS1/ITS2, respectively.

[a] Northwest Territories

[b] Contaminant in USDA 20228 seed accession.

[c] Two plants grown from seed from same herbarium specimen.

[d] Not vouchered, see Gillespie et al. (2007) for collection information.

subg. *Pseudopoa* (only one species sampled); (*v*) subg. *Stenopoa* (SPOSTA) (BS = 100); and (*vi*) subg. *Poa* (PoM + HAMBADD) including the genera *Aphanelytrum*, *Dissanthelium*, *Neuropoa*, and *Tovarochloa* (BS < 50). Groups resolved within subg. *Poa* include the following: South American *Tovarochloa* and *Aphanelytrum* (BS = 58); an Australian clade including type species formerly treated as *Austrofestuca* and *Neuropoa* (BS = 69); and South American *Poa gymnantha* Pilg. and *Poa lepidula* (Nees & Meyen) Soreng & L.J. Gillespie (formerly *Anthochloa*) (BS = 66).

Parsimony analysis of the data matrix excluding indel characters and *A. pubescens* resulted in the maximum 100 000 trees (1348 steps long, CI = 0.388 and 0.312, with and without uninformative characters, respectively; RI = 0.803). The strict consensus tree was almost identical to Fig. 2 and differed only in less resolution in four minor clades. Analysis of the data matrix including *A. pubescens* and indel characters resulted in 100 000 trees (1445 steps long, CI = 0.390 and 0.316, with and without uninformative characters, respectively; RI = 0.811). The strict consensus tree was similar to Fig. 2, but basal relationships were much less resolved, with *A. pubescens* part of a large polytomy of PPAM, core Aveneae, and Airinae members.

## Discussion

The tribe Poeae has undergone numerous changes in circumscription and infratribal classification in recent years (Soreng et al. 2007). The Poeae s. l. tribe and subtribe clas-

| Country of origin | Voucher | TLF GenBank No. | ITS GenBank No. |
|---|---|---|---|
| (panboreal & cult.) | | — | [AF171183] |
| USA, Colorado | Gillespie 6291 CAN | DQ354010 | — |
| Canada, Nunavut | Gillespie 5801 CAN | DQ354006 | — |
| (panarctic) | (Brysting 00–8-26 O) | — | [AY237833] |
| USA, Alaska | Soreng & Soreng 6032–1 US | DQ353997 | **EU792398** |
| Australia | Peterson et al. 14510 US | DQ354048, DQ354049 | **EU792408** |
| New Zealand | | — | [AY686655] |
| Canada, Ontario | Gillespie 7043 CAN | **EU792451** | **EU792378** |
| Chile | Peterson & Soreng 15575 US | **EU792461** | **EU792412** |
| USA, Nevada | Soreng 5812 US | DQ353991 | **EU792393** |
| Russia, Siberia | Olonova 2002–1 CAN | DQ354044, DQ354045 | **EU792401** |
| Chile | Soreng & Soreng 7132 US | DQ354022 | **EU792414** |
| USA, cult. | 1. Soreng & Cayouette 5950–2 US | DQ353984 | **EU792387** |
| (Europe) | 2. | [AY589127] | — |
| USA, Maryland | Soreng 4678–3 US | DQ353980 | **EU792375** |
| USA, Nevada | Soreng 5825 US | DQ354026 | **EU792406** |
| USA, Missouri | Soreng 5800 US | DQ354032, DQ354033 | **EU792377** |
| Spain | | [DQ336859] | — |
| Chile | 1. Soreng & Soreng 7152 US | DQ353960 | **EU792338** |
| Canada, Nunavut | Gillespie & Aiken 5744 CAN | DQ354030, DQ354031 | **EU792337** |
| Australia | Peterson et al. 14544 US | DQ353959 | **EU792339** |
| Canada, Nunavut | 1. Gillespie 5808 CAN | **EU854591** | **EU792336** |
| Canada, Nunavut | 2. Gillespie et al. 6682 CAN | — | **EU792335** |
| Spain | | [DQ367405, AF533045] | [AF532951] |
| (Europe) | | [AF533023] LLF | [AF532933] |
| Russia | | — | [EF565132] |
| Yugoslavia | Soreng 3889 BH | DQ353957 | **EU792326** |
| Greece | Soreng 7501–1 US | — | **EU792327** |
| Peru | 1. Peterson & Refulio 18116 US | **EU792470** | **EU792429** |
| Bolivia | 2. Refulio et al. 219 RSA | **EU792469** | **EU792428** |
| Bulgaria | | [DQ631500, DQ631434] | [DQ539572] |
| (Europe) | | — | [AF478485] |
| (Asia Minor) | 1. | — | [AJ428836] |
| (E Europe, SW Asia) | 2. | — | [DQ910765] |
| (SW Asia) | | — | [AJ428835] |

For TLF two GenBank numbers indicate sequence in two parts (typically *trn*T-*trn*L/*trn*L intron and *trn*L-*trn*F (LLF)); for ITS two numbers indi-

sification employed by Soreng et al. 2007) will be used as the basis for discussion unless otherwise stated. Tribe Poeae has about 140 genera and some 2260 species in 22 subtribes. The generic makeup of most of the subtribes, however, is mostly based on morphological cues along with molecular data for one to several exemplars. Few subtribes have been rigorously tested against molecular data: Loliinae (Catalán et al. 2004; Torrecilla et al. 2004); Aveninae (including Koeleriinae; Grebenstein et al. 1998; Quintanar et al. 2007); and Parapholiinae (Soreng and Davis 2000; Torrecilla et al. 2004). And even these studies were substantially incomplete for genera and infrageneric diversity.

Here we aimed to resolve the membership, structure, and relationships of the large and diverse subtribe Poinae. However, Poinae exemplars studied did not resolve as a clade, but were found to be intermixed with representatives sampled of subtribes Alopecurinae, Cinninae, Miliinae, and Puccinelliinae (Figs. 1 and 2A; this clade here called PPAM). We will discuss the relationships of each of the larger groups and subtribes in turn, beginning with the arrangement of subtribes in Poeae, and then proceeding through PPAM, Puccinelliinae, Miliinae, Alopecurinae, Cinninae, to Poinae and its large genus *Poa*, and evidence for hybridization at several levels. We provide two nomenclatural changes.

## Major clades in Poeae s. l.

Genera of all 22 Poeae subtribes tested in various studies

**Fig. 1.** Phylogram and summary of the strict consensus tree resulting from parsimony analysis of the complete TLF data matrix including indel characters but excluding *Avenula pubescens* (1183 steps long; CI excluding uninformative characters = 0.633). The strict consensus tree is indicated in bold lines on one of the 100 000 most parsimonious trees. Bootstrap values above 50% are given above branches; branches lacking a value have less than 50% support. Members of subtribe Alopecurinae are indicated by "•", and Cinniinae by "←". An outgroup taxon (*Brachypodium*) used to root the tree is not shown. Unexpected or incongruent placements are highlighted in bold, including genera placing within the *Poa* clade and "*Poa*" species outside *Poa*.

aligned in two well supported plastid clades, those that include taxa with Aveneae-type plastids (core Aveneae) and those that include taxa with Poeae-type plastids (Poeae s. str.) (here, and Soreng et al. 1990; Soreng and Davis 2000; Catalán et al. 2004; Davis and Soreng 2007; Döring et al. 2007; Quintanar et al. 2007; Soreng et al. 2007). However, the confirmed members of these plastid clades only correspond to these two tribes as traditionally conceived based on morphological data about 80% of the time. With nuclear ribosomal ITS sequence data (here, and Quintanar et al. 2007) core Aveneae subtribes are nested among elements of Poeae s. str., and the traditional tribes and genera assigned to them are even further intertwined (Fig. 2A). ITS data reinforce the decision to adopt Poeae s. l. to include all other named tribes in supertribe Poodae (Soreng and Davis 2000; Barker et al. 2001; Quintanar et al. 2007; Soreng et al. 2007).

TLF (Fig. 1) and ITS (Fig. 2A) analyses were consistent in resolving three main clades within Poeae s. l.: (*i*) core Aveneae; (*ii*) Loliinae s. l. (incl. Dactylidinae); and (*iii*) Puccinelliinae, Poinae, Alopecurinae, and Miliinae (PPAM clade). These results were consistent with those of Quintanar et al. (2007) in their study focusing on elements formerly separated in tribe Aveneae. However, in both studies TLF and ITS trees differ in the support for these three clades, relationships among the clades, and in the position of two subtribes, Sesleriinae and Airinae. The TLF analyses provide good support for all three clades, while ITS analyses show only a well supported Loliinae s. l. clade. The core Aveneae clade has only moderate support in our ITS analyses, but had high posterior probability but no bootstrap support in Quintanar et al. (2007). Regarding relationships among the three clades, both ITS studies show a Loliinae s. l. clade as sister to a core Aveneae + PPAM clade, although with no bootstrap support in our study or that of Quintanar et al. (2007). This contrasts to the strongly supported plastid sister clades, the Loliinae s. l. + PPAM clade (Poeae-type plastids) and the core Aveneae clade (Aveneae-type plastids), found in these two and other studies (Döring et al. 2007; Quintanar et al. 2007; Soreng et al. 2007). In ITS trees in both studies members of Sesleriinae and Airinae elements align with the core Aveneae clade, while in the above TLF and other plastid based trees they are strongly supported as having Poeae-type plastids.

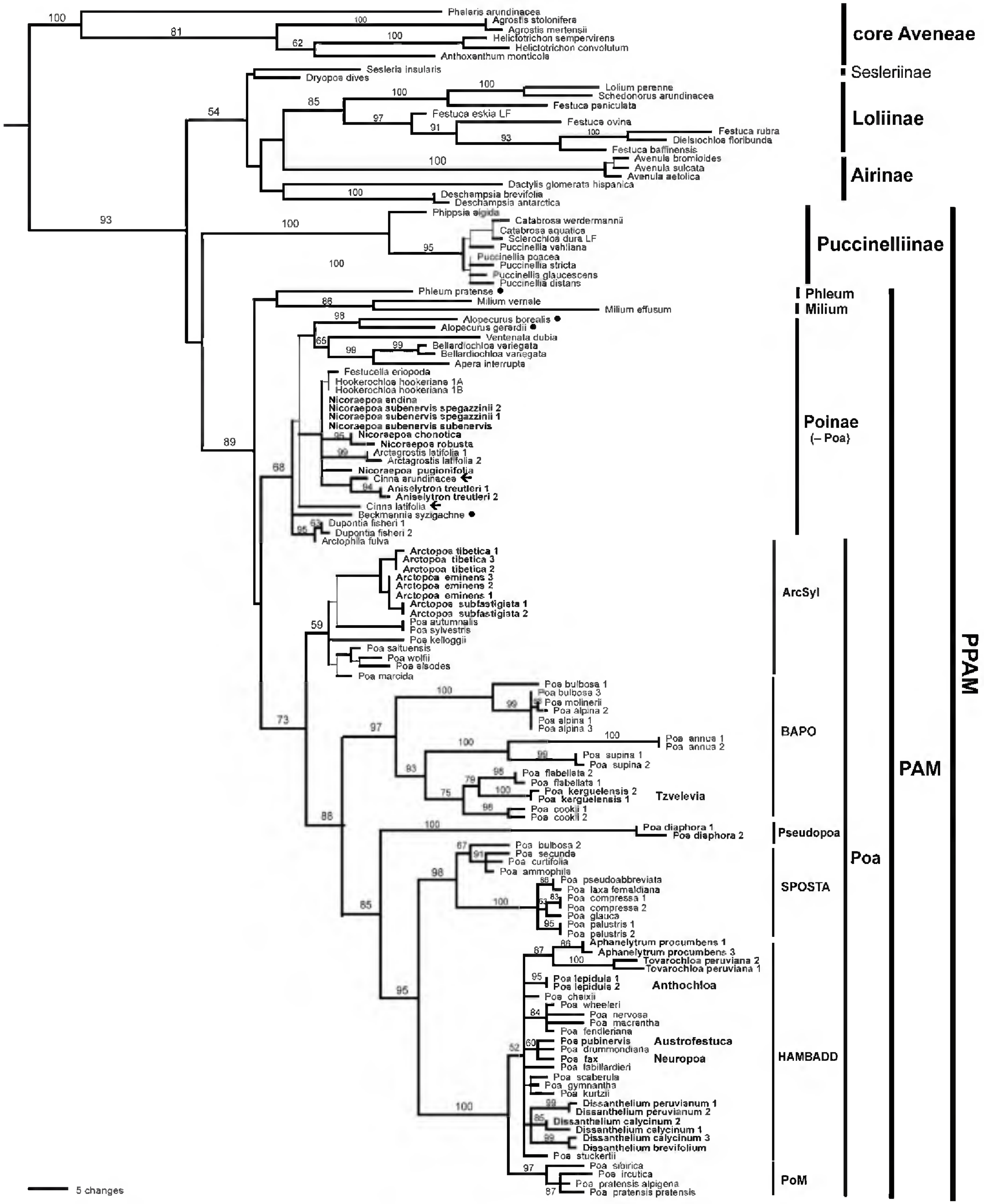
Regarding Poeae s. l. ITS trees, a few points contrast sharply with present and previous plastid DNA results. Three subtribes (Cinninae, Miborinae, and Sesleriinae) with placements in these three major ITS clades are strikingly incongruent with the plastid groupings outlined by the Soreng et al. (2007) classification. The placements in ITS trees of *Cinninae* (in the PPAM clade versus among genera with Aveneae-type plastid DNA) and Sesleriinae (within Aveninae versus among genera with Poeae-type plastid DNA) are of particular interest. Based on our new ITS and TLF data and that of Quintanar et al. (2007) *Cinna* apparently belongs among Poinae elements (see the subsection on subtribe Cinninae, below).

In subtribe Sesleriinae, we included three species of *Sesleria* for ITS and Quintanar et al. (2007) sampled two species of *Sesleria* and one of *Oreochloa*. In both ITS analyses Sesleriinae was nested among genera of Aveninae, particularly close to *Avena*, *Helictotrichon* s. str. and allies. In contrast, in the present plastid DNA analysis and those of Soreng et al. (2007) and Quintanar et al. (2007), Sesleriinae are resolved in a Poeae-type plastid lineage on a branch with subtribe Loliinae. Such consistently radically different results between plastid and nrDNA data strongly point to hybridization being involved in the origin of Sesleriinae (see the section on Reticulate evolution, below). It is worth noting that *Mibora*, the sole genus in subtribe Miborinae was nested among Sesleriinae in the ITS and TLF analyses of Quintanar et al. (2007). *Mibora* was on the Loliinae branch in the plastid analysis of Soreng et al. (2007) though not with Sesleriinae, but was sister to *Sesleria* in the previous plastid analysis by Davis and Soreng (2007). In each case *Mibora* was on a long branch. We suggest that *Mibora* represents a line of morphological reduction and shortened longevity tandem to *Oreochloa* (with which it shares a reduced habit, inflorescence, etc.), and recommend that subtribe Miborinae be subsumed within Sesleriinae (Table 1).

### PPAM clade: relationships of subtribes Puccinelliinae, Poinae, Alopecurinae, and Miliinae

The PPAM clade, including subtribes Alopecurinae, Miliinae, Poinae, and Puccinelliinae plus *Cinna* and *Ventenata*, was present in both TLF and ITS strict consensus trees, consistent with previous TLF and ITS analyses of tribe Poeae s. l. (Quintanar et al. 2007). *Cinna*, commonly placed in Cinninae, and *Ventenata*, sometimes placed in Ventenatinae, both sometimes placed in Aveneae s. l., will be discussed by genus or subtribe name in sections below. Quintanar et al. also showed *Avenula* (subg. *Pubavenastrum*) *pubescens*, *Cinna*, and *Ventenata* mixed among other PPAM genera (more below). Here we find that the addition of *A. pubescens* collapses all major PPAM internal structure in the ITS strict consensus tree (tree briefly described in results). It has been argued elsewhere that this unusual species is an intergeneric hybrid (Soreng and Davis 2000). Thus we left it out of our primary analyses.

Support for the PPAM clade is mostly weak; in our study PPAM has < 50% bootstrap support in either TLF or ITS trees. The PPAM clade had full support in the ITS analyses of Quintanar et. al. (2007), but PPAM internal structure collapsed into a polytomy of five subsets, one being Puccinelliinae. Puccinelliinae and PAM are commonly sister groups in plastid trees (but see Soreng and Davis 2000, where Puccinelliinae were in a clade with Loliinae), with the Puccinelliinae by itself (e.g., here; Davis and Soreng 2007;



Quintanar et al. 2007) or in one study with Airinae elements (Soreng et al. 2007). As PPAM appears in our strict consensus trees and the Puccinelliinae clade is nested within Poinae in our ITS trees, and these two subtribes are historically treated as closely allied, we feel justified in speaking of PPAM as a clade of note.

**Fig. 2.** Phylogram and strict consensus tree resulting from parsimony analysis of the complete ITS data matrix including indel characters but excluding *Avenula pubescens* (1408 steps long; CI excluding uninformative characters = 0.322). The strict consensus tree is indicated in bold lines on one of the 100 000 most parsimonious trees. Bootstrap values above 50% are given above branches; branches lacking a value have less than 50% support. Major clades are indicated on the right. Outgroups (*Brachypodium* and *Bromus*) used to root the tree are not shown. A. Complete tree, with position of *Poa* clade indicated. Members of subtribe Alopecurinae are indicated by "•", and Cinniinae by "←". Species previously within *Poa* and other unexpected or incongruent placements are highlighted in bold. B. *Poa* clade. Genera, or species previously included in other genera, are indicated in bold.

The major structure of the PPAM clade in the TLF and ITS trees differs primarily in the relationships of the subtribes, specifically regarding whether Puccinelliinae or Miliinae (note: *Zingeria* and *Colpodium* not yet examined for plastid DNA), respectively, is sister to the remaining taxa. Whereas Puccinellinae and PAM have strong support as sister clades here and in other plastid DNA studies (Soreng and Davis 2000; Davis and Soreng 2007; Döring et al. 2007; Gillespie et al. 2007; Quintanar et al. 2007; Soreng et al. 2007), there is no support for the order of branching of the subtribes in ITS.

Both ITS and TLF analyses resolve a Puccinelliinae clade, a *Poa* clade, and a clade we will discuss as "Poinae(–*Poa*)". *Poa* is separated from all other Poinae genera (except those that resolve within it), and is moderately well supported. Alopecurinae genera are intermixed in Poinae (Figs. 1 and 2A); so, neither Poinae nor Alopecurinae appear to be monophyletic, but Puccinelliinae are well supported as a clade. Miliinae and *Phleum* form additional lineages, which are separate in ITS, but resolve as a clade in TLF analyses. Including *A. pubescens* in the ITS analysis caused PPAM to collapse, and the species was a part of a large polytomy of PPAM subclades, core Aveneae, and Airinae members. *Avenula pubescens* has little impact on our plastid analysis, and is included in PAM.

## Puccinelliinae subtribe is supported as monophyletic

Subtribe Puccinelliinae resolved as a strongly supported clade in both nrDNA and plastid studies, past and present. Its position, although different in ITS versus plastid analyses, and its generic constitution are consistent with previous analyses, which included fewer genera but sometimes more species (Choo et al. 1994; Gillespie and Soreng 2005; Rodionov et al. 2005; Davis and Soreng 2007; Döring et al. 2007; Gillespie et al. 2007; Quintanar et al. 2007; Soreng et al. 2007). *Phippsia* is strongly to moderately supported as the sister group to the remainder in both sets of analyses presented here. The TLF tree shows limited resolution in Puccinelliinae beyond that. However, ITS data are available for four additional genera usually placed in or near *Poa* and *Puccinellia*. Our ITS tree (Fig. 2A) supports a further division of Puccinelliinae into a subclade of *Puccinellia* and *Sclerochloa*, and a subclade with *Catabrosa* as sister to *Hyalopoa*, *Paracolpodium* and *Catabrosella*. The latter three genera are commonly placed in the genus *Colpodium* s.l. (sensu Clayton and Renvoize 1986), but sometimes segregated as genera (Tzvelev 1976). Our ITS result supports refining the original concept of the Puccinelliinae (Soreng et al. 2003*a*) to include *Hyalopoa* (tentatively placed in Poinae by Soreng et al. 2007), and exclude *Colpodium* s. str. (Soreng et al. 2007). The separation of *Colpodium* s.str. from the segregate genera is well supported. Although the *Colpodium* plus *Zingeria* clade is five branches removed from Puccinelliinae (Fig. 2A), there is no bootstrap support to prove these clades are not sister groups to one another. *Zingeria* was resolved in a well supported polytomy with Puccinelliinae genera in the plastid analysis by Döring et al. (2007)

Morphological characters linking *Hyalopoa* with Puccinelliinae versus Poinae are few. However, it shares totally smooth panicle branches and spikelet bracts with *Catabrosa*, *Catabrosella*, *Paracolpodium*, and *Phippsia* (Tzvelev 1976). We recommend that it should be placed in Puccinelliinae. However, further study is needed because Döring et al. (2007) resolved a second species of *Hyalopoa* with *Poa pratensis* L.

## Miliinae subtribe detected

In the most recent circumscription, Miliinae included only *Milium*, *Colpodium*, and *Zingeria* (Soreng et al. 2007). This grouping is based on the shared presence of wide open panicles, single-flowered spikelets with glumes that equal the floret, and lemmas that are weakly dorso-ventrally compressed and rounded across the back. Chromosome numbers were thought to have proceeded along a common path to reduction as *Milium* have $x = 4$, 5, 7, and 9, *Zingeria* have $x = 2$, 4 and 6, and *Colpodium* have $x = 2$ (Tzvelev and Zhukova 1974; Rodionov et al. 2005). In our main ITS analysis a Miliinae clade comprising these three genera was resolved, but with <50% bootstrap support. *Colpodium* and *Zingeria* form a well supported clade sister to *Milium*. In the ITS analysis including *A. pubescens*, the *Colpodium*–*Zingeria* clade was in a polytomy of several PPAM lineages, as also shown by Quintanar et al. (2007). At this point it remains plausible that the subtribe Miliinae sensu Soreng et al. (2007) is monophyletic, but far from certain. Plastid data for *Colpodium* and *Zingeria* are needed to test this relationship. The plastid analysis of Döring et al. (2007) supported *Zingeria* in a polytomy with Puccinelliinae genera, and *Milium* among Poinae and Alopecurinae elements. In the ITS analysis of Quintanar et al. (2007), the *Colpodium* plus *Zingeria* clade was not resolved with *Milium*.

## Subtribe Alopecurinae s. str. is not resolved

Alopecurinae s. str. (i.e., minus Agrostidinae and Cinninae; Soreng et al. 2007) includes seven genera (*Alopecurus*, *Beckmannia*, *Cornucopiae*, *Limnas*, *Phleum*, *Pseudophleum*, and *Rhizocephalus*). This group has characteristics that were used to assign this set of genera to tribe Aveneae s.l. (glumes equaling or exceeding the floret, dorsal awns), and place them within subtribe Alopecurinae s.l. (presence of single flowered spikelets) by Clayton and Renvoize (1986). In Clayton and Renvoize's broad conception of this subtribe, elements of Agrostidinae s. str. formed the major lineage,

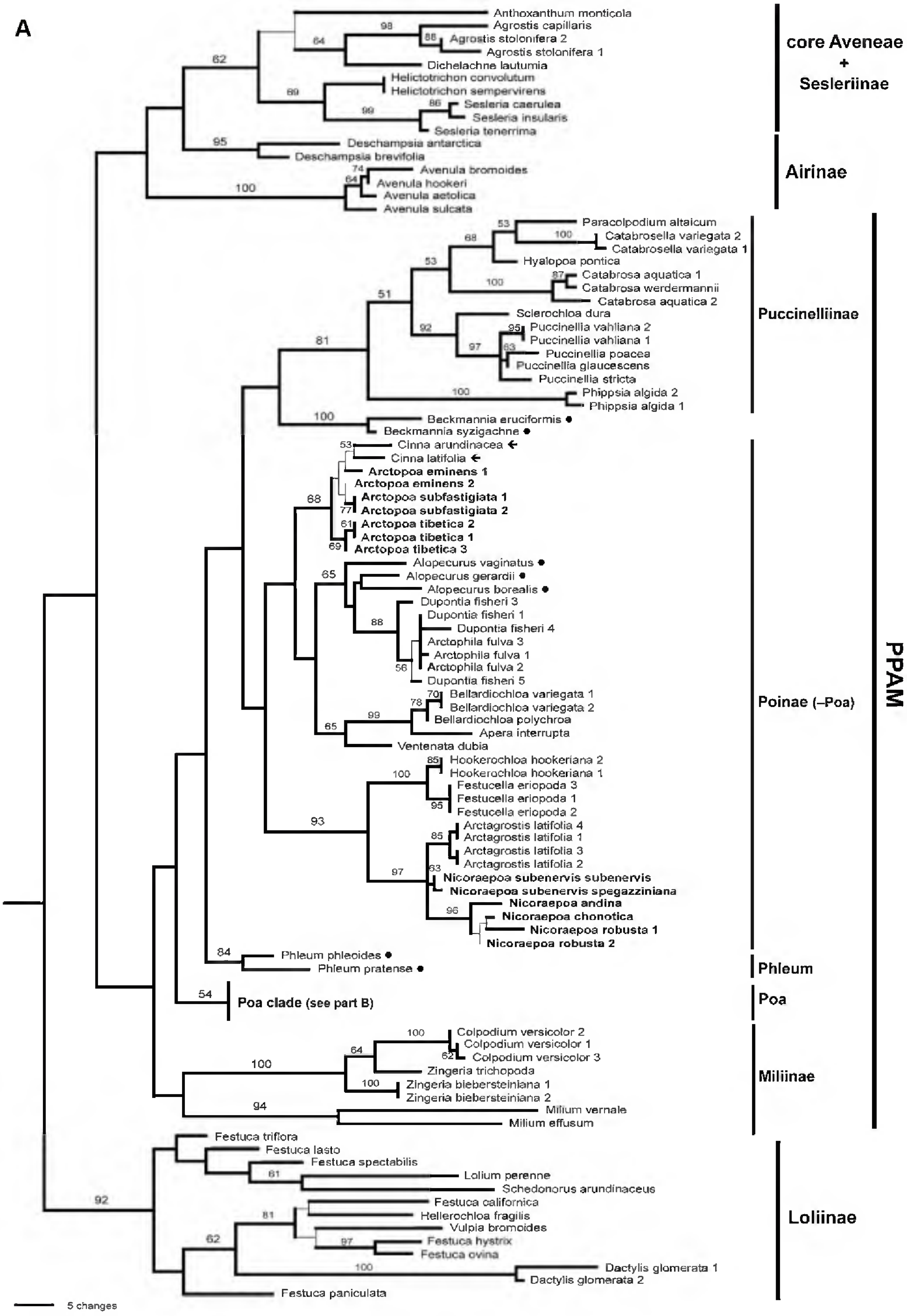
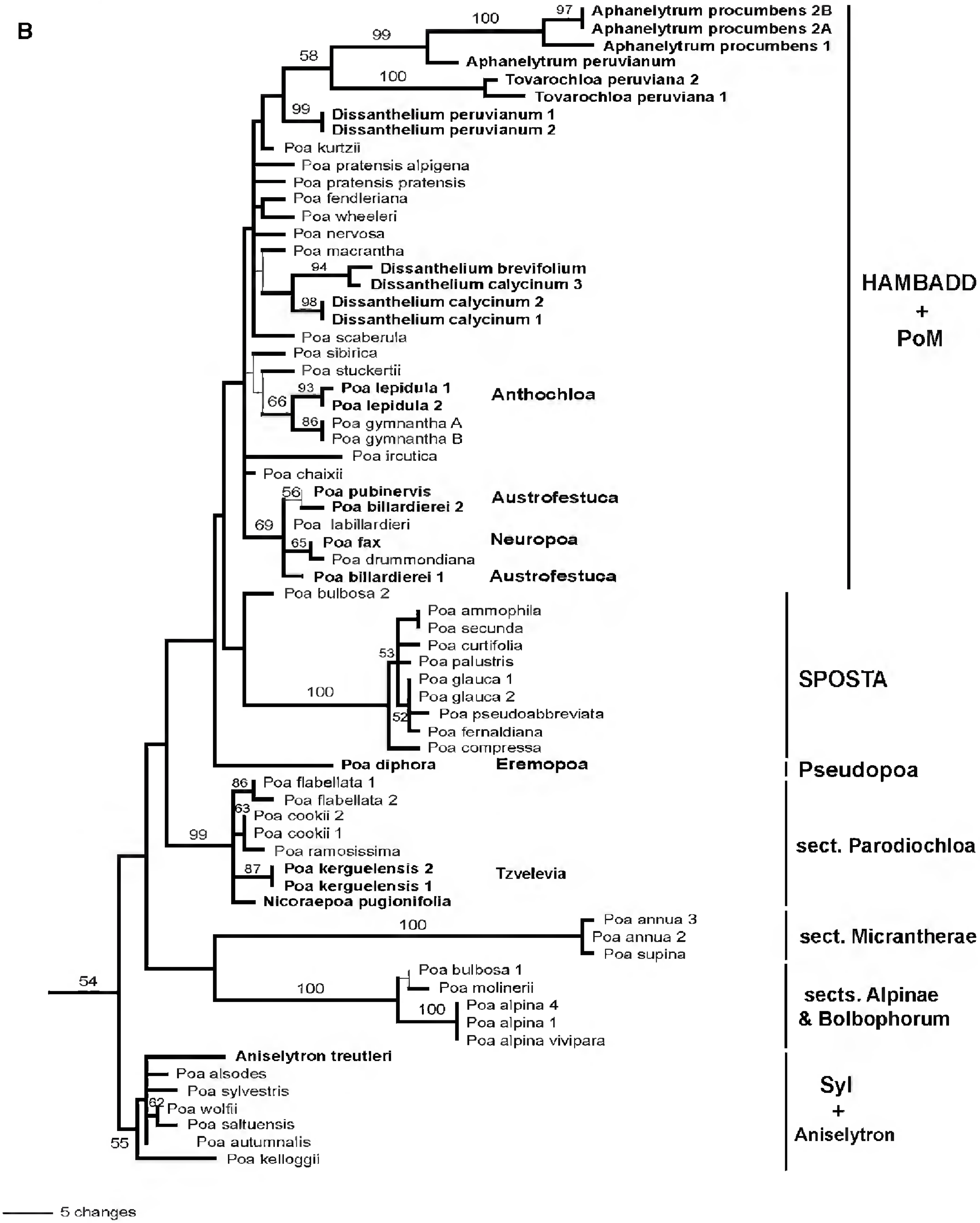

A
Anthoxanthum monticola
98
Agrostis capillaris
88
Agrostis stolonifera 2
64
Agrostis stolonifera 1
62
Dichelachne lautumia
Helictotrichon convolutum
Helictotrichon sempervirens
89
86
Sesleria caerulea
99
Sesleria insularis
Sesleria tenerrima
95
Deschampsia antarctica
Deschampsia brevifolia
74
Avenula bromoides
64
Avenula hookeri
100
Avenula aetolica
Avenula sulcata
53
Paracolpodium altaicum
100
Catabrosella variegata 2
68
Catabrosella variegata 1
Hyalopoa pontica
53
87
Catabrosa aquatica 1
100
Catabrosa werdermannii
Catabrosa aquatica 2
51
Sclerochloa dura
95
Puccinellia vahliana 2
92
Puccinellia vahliana 1
81
97
63
Puccinellia poacea
Puccinellia glaucescens
Puccinellia stricta
100
Phippsia algida 2
Phippsia algida 1
100
Beckmannia eruciformis ●
Beckmannia syzigachne ●
53
Cinna arundinacea ←
Cinna latifolia ←
Arctopoa eminens 1
Arctopoa eminens 2
68
Arctopoa subfastigiata 1
77
Arctopoa subfastigiata 2
61
Arctopoa tibetica 2
Arctopoa tibetica 1
69
Arctopoa tibetica 3
Alopecurus vaginatus ●
65
Alopecurus gerardii ●
Alopecurus borealis ●
Dupontia fisheri 3
Dupontia fisheri 1
88
Dupontia fisheri 4
Arctophila fulva 3
Arctophila fulva 1
56
Arctophila fulva 2
Dupontia fisheri 5
70
Bellardiochloa variegata 1
78
Bellardiochloa variegata 2
99
Bellardiochloa polychroa
65
Apera interrupta
Ventenata dubia
85
Hookerochloa hookeriana 2
100
Hookerochloa hookeriana 1
Festucella eriopoda 3
Festucella eriopoda 1
95
Festucella eriopoda 2
93
Arctagrostis latifolia 4
85
Arctagrostis latifolia 1
Arctagrostis latifolia 3
Arctagrostis latifolia 2
97
63
Nicoraepoa subenervis subenervis
Nicoraepoa subenervis spegazziniana
Nicoraepoa andina
96
Nicoraepoa chonotica
Nicoraepoa robusta 1
Nicoraepoa robusta 2
84
Phleum phleoides ●
Phleum pratense ●
54
Poa clade (see part B)
100
Colpodium versicolor 2
64
Colpodium versicolor 1
62
Colpodium versicolor 3
100
Zingeria trichopoda
100
Zingeria biebersteiniana 1
Zingeria biebersteiniana 2
94
Milium vernale
Milium effusum
Festuca triflora
Festuca lasto
Festuca spectabilis
61
Lolium perenne
Schedonorus arundinaceus
92
Festuca californica
81
Hellerochloa fragilis
Vulpia bromoides
62
97
Festuca hystrix
Festuca ovina
100
Dactylis glomerata 1
Dactylis glomerata 2
Festuca paniculata
5 changes
core Aveneae
+
Sesleriinae
Airinae
Puccinelliinae
Poinae (–Poa)
PPAM
Phleum
Poa
Miliinae
Loliinae

**Fig. 2.** (*concluded*).



and those of Alopecurinae s. str. were arrayed as a minor group. Tzvelev (1976), emphasizing both similarities and differences among the genera, considered *Alopecurus*, *Beckmannia*, and *Phleum* to belong to three separate subtribes in tribe Phleeae, which he placed near Aveneae. Tzvelev's Phleeae were united based on the shared combination of dense spicate panicles (transitional in *Beckmannia*), spikelets single-flowered (or in *Beckmannia* sometimes two-flowered, the upper one staminate) and disarticulating below the glumes, glumes usually equal to the floret and uniform in size and shape and equilaterally inserted, caryopses laterally compressed with an apical rostellum, styles fused at their base, and primary stigmatic branches short. More recently Alopecurinae s. str. were treated as a single subtribe, but placed near subtribe Poinae (Soreng et al. 2003*a*, 2007). It is difficult enough to imagine how such a complex set of character state transitions evolved from states generally considered pleisiomorphic in PAM (Soreng et al. 2007) or PPAM, or Poeae s. l. It seems improbable that such complex transitions developed independently at least three times in PPAM.

DNA evidence to unite these genera in Alopecurinae s. str. is lacking in our TLF and ITS analyses. Only three Alopecurinae genera have been sampled in molecular analyses: *Alopecurus*, *Beckmannia*, and *Phleum*. These genera always resolve among elements of Poinae in DNA studies (Soreng and Davis 2000; Davis and Soreng 2007; Döring et al. 2007; Gillespie et al. 2007; Quintanar et al. 2007; Soreng et al. 2007), however, they are always separated from one another by one or more Poinae genera. DNA bootstrap evidence to reject monophyly of the subtribe is limited. In our ITS analysis *Alopecurus* is in a moderately well-supported clade with two Poinae genera, but the positions of *Phleum* and *Beckmannia* are resolved without bootstrap support. In the plastid analysis of Soreng et al. (2007), there was strong bootstrap support for separating *Phleum*, *Alopecurus*, and *Beckmannia* from each other among elements of Poinae. A Bayesian analysis of ITS data (Quintanar et al. 2007) also rejected the union of *Phleum* and *Alopecurus*.

The hypothesis that the genera of Alopecurinae s. str. evolved independently needs further testing. In the meantime we propose to continue to retain Alopecurinae in the present sense (Soreng et al. 2007), pending additional sampling and stronger data contradicting this morphologically well-defined group.

### Subtribe Cinninae is placed among members of subtribe Poinae

Cinninae in the narrowest sense applied includes *Cinna* and *Limnodea* (Soreng et al. (2007). More recently, based on morphological considerations and plastid data from Döring et al. (2007), *Cyathopus* was placed in Cinninae (Soreng et al. 2003*b*) (2008 update). The placement of *Cinna* and its relationships are controversial. Tzvelev (1976) tentatively placed *Cinna* and *Arctagrostis* in Cinninae within a narrowly defined Poeae s. str. In Flora Europaea (Tutin et al. 1980) *Arctagrostis* and *Cinna* are placed among genera of Poeae s. str., although the two are not sequentially aligned, and *Cinna* is placed adjacent to *Apera*. Clayton and Renvoize (1986) arrayed *Cinna*, *Cyathopus,* and *Limnodea* together in Aveneae subtribe Alopecurinae s. l., but placed *Arctagrostis* as an ally of *Poa* in Poeae s. str. Watson and Dallwitz (1992) also placed *Cinna*, *Cyathopus,* and *Limnodea* in Aveneae s. l., and *Arctagrostis* in Poeae s. str. These four genera, plus *Aniselytron* and *Apera*, have laterally compressed single-flowered spikelets and glumes shorter than the first floret, which allies them with Poinae rather than Miliinae or Agrostidinae. *Cinna*, *Cyathopus,* and *Limnodea* have spikelets that disarticulate below the glumes, an apomorphic state in PPAM (Soreng et al. 2007). *Cinna*, *Aniselytron*, *Apera*, *Arctagrostis* and *Cyathopus* have paleas that are chlorophyllous, nearly as long as their lemmas, and distinctly keeled, and thus are unlike most other genera placed in Agrostidinae. The panicles in all six genera are loosely contracted to open (*Arctagrostis* can be spicate, but the panicles are not nearly so reduced as in Alopecurinae s. str.). Genera of Agrostidinae s. str. commonly exhibit the advanced states of paleas that are usually reduced and (or) hyaline, colorless, and faintly keeled (Clayton and Renvoize 1986; R.J. Soreng, personal observation). *Aniselytron* was included in *Calamagrostis* within Aveneae by Clayton and Renvoize (1986), but they noted it was odd (*Calamagrostis* belongs in the core Aveneae clade in both TLF and ITS analyses; Quintanar et al. 2007). *Cinna* was resolved in Aveneae near the genera *Trisetum* and *Sphenopholis* by Soreng and Davis (2000), but that DNA result is now considered a laboratory error. Soreng et al. (2007) recognized subtribe Cinninae in Poeae s. l., among other subtribes with Aveneae-type plastid DNA, but with the caveat that further study was needed owing to indications that the previous result was spurious. Our TLF and ITS trees are in agreement with those of Quintanar et al. (2007), showing that *Cinna* belongs in PPAM.

Because species of *Cinna*, *Aniselytron*, and *Arctagrostis* all appear in a clade of the TLF tree with no or few branches separating them and with no bootstrap support negating their union, it might seem reasonable to classify these genera together on morphological grounds. However, retaining Cinninae in this sense as a subtribe is strongly contradicted by our ITS analyses. In our ITS tree, *Arctagrostis* resolves with *Nicoraepoa* in a strongly supported clade, *Cinna* is with *Arctopoa*, and *Aniselytron* is within *Poa* with *Poa* sect. *Sylvestres* (where *Arctopoa* is resolved in our TLF analyses). Clearly the different relationships detected here are anything but straight-forward. For now we tentatively consider all Cinninae elements to be members of subtribe Poinae s. l.

### Poinae (including Cinninae)

Excluding Miliinae and Puccinelliinae discussed above as being distinct from Poinae in TLF and (or) ITS trees, and Alopecurinae which is morphologically well delineated, we are left with PPAM subtribes Cinninae and Poinae. These remaining PPAM elements form a large and diverse Poinae subtribe with 17 to 26 genera.

ITS and TLF trees were consistent in including all Poinae genera, except for *Poa* (and two partial exceptions discussed below) within a clade called here the Poinae(–*Poa*) clade. Relationships among these Poinae genera were similar in ITS and TLF trees, and bootstrap support for differences is absent or weak in most cases In both analyses *Arctophila* and *Dupontia*, and *Apera* and *Bellardiochloa* pairings are well supported, and *Ventenata* is moderately well supported as the sister group to *Apera* and *Bellardiochloa*. A clade with *Hookerochloa* and *Festucella* as sister to *Arctagrostis* and *Nicoraepoa* is strongly supported in the ITS analysis; a clade including the latter four genera plus *Cinna* and *Aniselytron* is also detected in the TLF strict consensus tree, but with no bootstrap support.

Both ITS and TLF analyses suggest that the genus *Poa* comprises a clade separate from all other Poinae genera. However, the composition of this *Poa* clade differs between nuclear and plastid trees regarding the placement of the two Poinae genera *Arctopoa* and *Aniselytron*. *Arctopoa* (previously *Poa* subg. *Arctopoa*) is placed within *Poa* with species of *Poa* sect. *Sylvestres* in TLF trees (Fig. 1), but with *Cinna* well within the Poinae(*–Poa*) clade in ITS trees (Fig. 2A); for *Aniselytron* the exact reverse was true. These significantly different placements provide evidence of reticulate evolution (see section on Reticulate evolution, below).

Other plastid studies included fewer Poinae genera and showed relationships among elements of Poinae to be less resolved, but those analyses are reasonably consistent with the present results (Davis and Soreng 2007; Döring et al. 2007; Gillespie et al. 2007; Quintanar et al. 2007). In the Rodionov et al. (2005) ITS analysis a clade of *Alopecurus*, *Arctagrostis*, *Arctophila*, *Arctopoa* (as *Poa schischkinii*), *Dupontia*, and *Phleum* was detected, but the Quintanar et al. (2007) analysis included too few strictly Poinae elements to evaluate groupings.

The systematics and origin of the putative hybrid genus *Dupontia* was studied in depth by Byrsting et al. (2004). As found in that study, both our ITS and plastid DNA analyses indicate a close affinity of *Dupontia* with *Arctophila*, but neither study provided evidence for a second lineage being involved in the origin of *Dupontia* (see section on Reticulate evolution; hybridization with *Arctopoa*, below).

### *Ventenata*: the significance of awn position and presence on lemmas

It seems strange that *Ventenata*, which is traditionally placed in tribe Aveneae subtribe Aveninae (Clayton and Renvoize 1986; Watson and Dallwitz 1992) or sometimes in its own subtribe Ventenatinae (Tzvelev 1976) (Table 1), should be positioned within the PPAM clade. *Ventenata* species have spikelets with a terminal awn on the lemma of the proximal floret, and a dorsal awn on the lemmas of the distal 1–3 florets, and the distal lemmas are deeply divided at the apex. This shows that both dorsal and terminal awns develop regularly within spikelets of individuals, with developmental control shifting from one floret to the next along the axis of the maturing spikelet. The transformation from terminal to dorsal awns, like other traits (Kellogg 1990, 2000), is probably simply genetically controlled via sequential timing of developmental signals, i.e., heterochrony. In some other Poeae genera, an awn is suppressed on the distal floret but developed on the proximal floret (e.g., *Arrhenatherum*), or vice-versa (e.g., *Holcus*; where there are two developed florets, one with and one without an awn, above two additional repressed proximal florets). Thus, we should not expect that the presence or absence of a terminal versus dorsal awn, or even presence versus absence of awns within a taxon, is necessarily highly phylogenetically informative. Presence of a dorsal awn is the primary characteristic used for assigning genera to the traditional tribe Aveneae (Tzvelev 1976; Clayton and Renvoize 1986; Watson and Dallwitz 1992). However, Soreng et al. (2007) showed that the presence of dorsal awns is a characteristic that has probably arisen and been lost multiple times in Poeae s.l., and could even have been the ancestral state in the tribe.

In both TLF and ITS trees *Ventenata* resolved in the Poeae(*–Poa*) clade as sister group to *Apera* plus *Bellardiochloa* with moderate bootstrap support. Quintanar et al. (2007) showed similar well supported placements for the genus in their TLF and ITS trees in a clade equivalent to our PPAM clade, but their study did not include *Bellardiochloa*, and included *Apera* only for ITS. Soreng et al. (2007) classified *Ventenata* in Poinae and *Gaudiniopsis* (which was either classified with (Tzvelev 1976) or within *Ventenata* (Clayton and Renvoize 1986)) in Aveninae, based on differences in lodicule and inflorescence morphologies and preliminary DNA data for *Ventenata* (A. Quintanar, personal communication; Quintanar et al. 2007). Simultaneously to Soreng et al. (2007), Döring et al. (2007) presented new plastid data for *Gaudiniopsis* that resolve it as sister to *Apera* plus *Bellardiochloa,* with strong bootstrap support. So we conclude that *Gaudiniopsis* and *Ventenata* should be placed with *Apera* and *Bellardiochloa*, as a Mediterranean clade of Poinae genera with awns. This group could be called subtribe Ventenatinae, but we feel this is an unnecessary subdivision given the weak support for, and complicated structure of, surrounding PPAM clades.

### Molecular support for the new Andean Poinae genus *Nicoraepoa*

*Nicoraepoa* comprises six species (Soreng and Gillespie 2007), five formerly placed in *Poa* subg. *Andinae* and one, *Nicoraepoa subenervis* (Hack.) Soreng & L.J. Gillespie, in *Poa* subg. *Poa* (Nicora 1978). *Nicoraepoa* is endemic to South America, inhabiting coastal and interior Patagonian wetlands. Our new ITS and TLF phylogenies confirm previous plastid results placing these species outside of *Poa* (Soreng and Davis 2000; Gillespie and Soreng 2005; Gillespie et al. 2007). All species of the new genus, except *Nicoraepoa erinacea* (Speg.) Soreng & L.J. Gillespie, have now been sampled. In our ITS trees, four *Nicoraepoa* species (but not *N. pugionifolia*) align in a strongly supported Poinae(*–Poa*) clade with the panarctic genus *Arctagrostis* and Australian genera *Hookerochloa* and *Festucella* in our ITS tree (Fig. 2A). All five tested *Nicoraepoa* species align in a similar (but expanded and internally poorly resolved) polytomy in our TLF analysis, and this clade is two moderately supported branches away from *Poa*. (Fig. 1) Our results strongly support the exclusion of *Nicoraepoa* from *Poa* and its treatment as a separate genus. The gross morphological and anatomical features of *Nicoraepoa*, *Hookerochloa*, *Festucella*, *Arctagrostis*, and *Poa* are reviewed by Soreng and Gillespie (2007) and Jacobs et al. (2008).

Needless to say, however, phylogenetic histories are often more complicated than anticipated. In our ITS analyses (Fig. 2B) *N. pugionifolia* (unknown ploidy level) resolves within *Poa* with *Poa* sect. *Parodiochloa* species (a second sample of *N. pugionifolia* from a different location has an identical ITS sequence; unpublished). The only species of the latter section of *Poa* that occurs in South America is *P. flabellata* ($2n = 28$). Morphologically, *N. pugionifolia* and *N. erinacea* have firm, narrow, convolute leaves like *P. flabellata*, whereas the other four *Nicoraepoa* species have broad and mostly flat leaves. There are several conceivable scenarios here to explain the *N. pugionifolia* ITS type, but all include hybridization at some level (see section on Reticulate evolution, below). However, we will need more samples, including the rare *N. erinacea*, and possibly single copy gene studies, to sort this tangled history out.

### Molecular evidence for separating *Hookerochloa* s.l. from *Austrofestuca*

The Australian monotypic genera *Hookerochloa* and *Festucella* described by Alexeev (1985) were synonymized under the Australian – New Zealand genus *Austrofestuca* (Jacobs 1990). Recent ITS and *trn*L–*trn*F evidence suggested they were misplaced in *Austrofestuca* and should be recognized as distinct genera (Hunter et al. 2004). ITS and TLF data presented here, and the plastid study of Soreng et al. (2007) strongly support their suggestion that the first two genera are closely related to each other and distantly related to *Austrofestuca*. *Hookerochloa* and *Festucella* appear to be closely related to *Nicoraepoa* and *Arctagrostis* in our analyses and that of Soreng et al. (2007). *Austrofestuca* s. str., on the other hand, is strongly supported as a member of *Poa* subg. *Poa* supersect. *Homalopoa* (Gillespie and Soreng 2005; Gillespie et al. 2007; see also the following section). Taxonomic considerations and a detailed discussion of morphology are the focus of a separate paper (Jacobs et al. 2008) where *Festucella* is submerged into *Hookerochloa*.

### *Poa* clade: molecular circumscription and major groups

*Poa* appears as a moderately supported clade in TLF (Fig. 1) and ITS (Fig. 2B) trees. Intergeneric reticulation is apparent in three cases, where taxa are resolved with support within *Poa* in TLF, but outside *Poa* in ITS trees (Fig. 2A), or vice versa (see section on Reticulate evolution, below).

Within *Poa* we provide new or additional data to subsume several genera; see Table 3 for subgeneric classification of *Poa* and clade acronyms published by Gillespie et al. (2007). New TLF and ITS data for two monotypic southern hemisphere genera, *Neuropoa* (Clayton 1985) and *Tzvelevia* (Alexeev 1985), resolve these genera within *Poa* (Figs. 1 and 2B). Placements of these genera in *Poa* clades are consistent and strongly supported by TLF and ITS analyses, and their species already had names in *Poa* before the new genera were described. *Neuropoa* aligns in *Poa* subg. *Poa* along with *Poa* sect. *Austrofestuca* and other Australian *Poa* including *P. drummondiana* (type of *Poa* sect. *Brizoides*), with moderate bootstrap support in both TLF and ITS trees. Our results also reconfirm placement of *Austrofestuca* s. str. within *Poa*, based on previous ITS and plastid DNA analyses (Hunter et al. 2004; Gillespie and Soreng 2005; Gillespie et al. 2007; Soreng et al. 2007). Three Andean genera (*Anthochloa*, *Dissanthelium*, *Tovarochloa*) resolved within *Poa* subg. *Poa*, confirming previous results (Gillespie and Soreng 2005; Gillespie et al. 2007; Refulio-Rodriguez 2007). New TLF and ITS data for a fourth Andean genus *Aphanelytrum*, now with two species (Sánchez Vega et al. 2007), also place that genus in *Poa* subg. *Poa*. The new species, *Aphanelytrum peruvianum* Sánchez Vega, P.M. Peterson, Soreng & Laegaard, resolves in an intermediate position between the highly derived *Aphanelytrum procumbens* Hack (29 bp changes) and other South American members of the subgenus. *Aphanelytrum* is a well supported sister to *Tovarochloa* in both TLF and ITS trees. Refulio-Rodriguez (2007) suggested that *Dissanthelium* may not be monophyletic, based on DNA data. Our analyses are inconclusive on this point, but do place the three *Dissanthelium* species tested (including the type species of the genus) within *Poa* subg. *Poa* as was detected by Refulio-Rodriguez (2007) using samples of nearly all *Dissanthelium* species and more species of *Poa*. In our TLF tree, *Dissanthelium* is resolved as monophyletic but with <50% bootstrap support; our ITS analysis placed one species apart from the others, but again without support. The placements of *Eremopoa* (=*Poa* subg. *Pseudopoa*) and *Parodiochloa* in *Poa*, based on plastid DNA data and their recent recognition as sections within *Poa* (Gillespie and Soreng 2005; Gillespie et al. 2007), is now confirmed by ITS data.

Regarding relationships within *Poa*, our ITS tree shows substantial congruence with trees generated from plastid DNA restriction site (Soreng 1990; Gillespie and Soreng 2005) and TLF sequence data presented here and by Gillespie et al. (2007). However, the TLF and ITS trees also exhibit a few differences. The order of divergence of the TLF major clades given in Table 3 is strongly supported (Fig. 1): ArcSyl, BAPO, *Pseudopoa* (syn. *Eremopoa*), SPOSTA, HAMBADD, and PoM. Our ITS clades are very similar in composition (except for putative hybrids) with the order of divergence as follows: Syl, *Alpinae*–*Arenariae*–*Micrantherae*, *Parodiochloa*, *Pseudopoa*, SPOSTA, and intermixed PoM and HAMBADD elements (Fig. 2B), but the differences are not well supported. A detailed discussion of major clades, infrageneric relationships and reticulation in *Poa*, will be the focus of a separate paper.[3] Only the major differences and those of interest in understanding the phylogeny of Poinae and related subtribes will be discussed here.

Our ITS data agrees with TLF evidence that the clade containing *Poa* sect. *Sylvestres* is the sister group to the rest of *Poa*, with moderate bootstrap support in both cases. TLF data had suggested that *Poa* subg. *Arctopoa* also belongs in the clade with *Sylvestres*, and Gillespie and Soreng (2005) called this clade ArcSyl. The ITS data, in complete contrast, places *Arctopoa* in a clade with *Cinna* species; a bootstrap supported position well outside of *Poa*. The implications of these incongruent positions of *Arctopoa*, and the reverse situation for *Aniselytron*, are discussed below (see section on Reticulate evolution, below). In the ITS analysis, *Aniselytron* “jumps” from near *Cinna* in the Poinae(–*Poa*) clade in the TLF tree to the *Poa* clade in the ITS tree where it resolves in a polytomy of *Poa* sect. *Sylvestres* elements. This curious position swapping is further discussed below as evidence of reticulation (see section on Reticulate evolution, below).

The genera *Anthochloa*, *Aphanelytrum*, *Austrofestuca*,

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[3] L. Gillespie and R. Soreng. Manuscript in preparation.

*Dissanthelium*, *Neuropoa*, and *Tovarochloa* align within the large and well supported TLF clade called HAMBADD (Fig. 1), along with many sections of *Poa* (*Homalopoa, Brizoides, Dasypoa, Dioicopoa, Macropoa*, and informal groups Australopoa, Punapoa). In the ITS analysis (Fig. 2B) these genera all align within the clade with intermixed HAMBADD and PoM elements.

Most of the elements of the revised subgeneric classification system based on morphology and plastid DNA data presented in Gillespie et al. (2007) are supported by the ITS results. However, ITS results excluding *Arctopoa* from *Poa* suggest a new subgenus is needed for *Poa* sect. *Sylvestres*.

***Poa* subg. *Sylvestres*** (V.L. Marsh ex Soreng) Soreng & L.J. Gillespie, comb. et stat. nov. Basionym: *Poa* sect. *Sylvestres* V.L. Marsh ex Soreng, Novon 8(2): 188. 1998.

### Molecular support for the close relationship of *Tzvelevia* and *Poa* sect. *Parodiochloa* and the expansion of the latter to include sub-Antarctic island species of *Poa*

The genus *Tzvelevia* was recently included in *Poa* as sect. *Tzvelevia*, and *Poa* sect. *Parodiochloa* was emended to include several sub-Antarctic island species of *Poa* on the basis of morphological and leaf anatomical data (Soreng and Gillespie 2007). Here we present new plastid and ITS results that for the most part support these conclusions, and additionally demonstrate a close relationship between these two sections.

*Parodiochloa* originally included the single species *P. flabellata*, a large tussock grass endemic to Tierra del Fuego, and the Falkland, South Georgia, and Gough islands, all adjacent to South America, and introduced elsewhere (Nicora 1978; Hubbard 1981; Clayton and Renvoize 1986; Soreng and Gillespie 2007). Edgar (1986) was the first to suggest an affinity between this species and two sub-Antarctic island species of *Poa*, *Poa cookii* (Hook. f.) Hook. f. (of islands in the southern Indian Ocean) and *Poa ramosissima* Hook. f. (of islands south of New Zealand). Soreng and Gillespie (2007), on the basis of morphology and preliminary ITS data uniting *P. ramosissima* and *P. flabellata,* expanded *Poa* sect. *Parodiochloa* to include these two species plus *Poa hamiltonii* T. Kirk, *Poa foliosa* Hook. f., and *Poa tennantiana* Petrie (all from islands south of New Zealand). Only *P. flabellata* had previously been assigned to a section of *Poa*. Of the species examined here, *P. ramosissima* (no plastid data available) plus *P. cookii* resolve with *P. flabellata* in a strongly supported polytomy (with *Tzvelevia*), thus supporting their inclusion in *Poa* sect. *Parodiochloa*; the latter two species are united in a clade, again with *Tzvelevia,* in the TLF tree. Further molecular data is needed to resolve the affinities of these interesting sub-Antarctic island species.

*Tzvelevia* is a monotypic genus described for *Poa kerguelensis* (Hook. f.) Steud. of the Kerguelen and Heard islands in the southern Indian Ocean, and is differentiated from *Poa* principally on the basis of a long narrow hilum (Alexeev 1985). Soreng and Gillespie (2007) determined the hilum to be within the range of that in other *Poa* and returned the species to *Poa* as sect. *Tzvelevia*, but its relationships within *Poa* were not evident from its streamlined morphology. Subsequently, we obtained samples of *Tzvelevia* for DNA analysis and both ITS and TLF trees firmly support the close relationship of sections *Tzvelevia* and *Parodiochloa*. The TLF analysis moderately supports *P. flabellata* plus *P. kerguelensis* as sister to *P. cookii*, suggesting that *P. kerguelensis* may best be included within sect. *Parodiochloa*.

### Reticulate evolution

Inconsistencies in the resolution of species or genera between our plastid and ITS analyses, supported by strong or moderately strong bootstrap results, point to hybridization and reticulate evolution between *Poa* and other Poinae genera, and among subtribes of Poeae. Taxa with such highly incongruent positions between our TLF and ITS trees are summarized below:

1. *Aniselytron* resolves near *Cinna arundinacea* L. in TLF, but with *Poa* sect. *Sylvestres* species in ITS.
2. *Arctopoa* is resolved within *Poa* with *Poa* sect. *Sylvestres* in TLF, but outside *Poa* with *Cinna* species in ITS.
3. *Nicoraepoa pugionifolia* is resolved with other *Nicoraepoa* in TLF, but with *Poa* sects. *Parodiochloa* and *Tzvelevia* in ITS.
4. *Sesleria* species have a Poeae-type plastid as confirmed in several studies using different plastid markers, but align with or within subtribe Aveninae in ITS trees.

All these cases are examples of probable wide hybridization in Poeae s.l. Soreng and Davis (2000) discussed evidence for reticulation in Poeae and Pooideae based on plastid DNA trees, cytological evidence, and morphology. Kellogg and Watson (1993) predicted that much of the morphological variability in Pooideae complexes such as Poeae s.l. was the result of reticulation, as postulated by Stebbins (1950). It is probable that further detailed molecular phylogenetic analyses in Poeae using both plastid and nuclear DNA markers will reveal many additional examples of reticulation. Below we discuss the evidence for resurrecting *Arctopoa* as a genus as it impacts on a nothogenus name ×*Dupoa*, and provides insight into speciation beyond a primary hybridization event.

### *Arctopoa*, or *Poa* subg. *Arctopoa*: an ancient intergeneric hybrid?

*Arctopoa* is commonly treated as a subgenus in *Poa* (Tzvelev 1976; Liu et al. 2006; Soreng 2007), although Tzvelev (1989) and Probatova (1974, 1985) accept it as a genus. *Arctopoa* comprises *Arctopoa eminens* (J. Presl), a boreal-subarctic seashore species distributed from the Russian Far East to eastern Canada, and two principal allies, *A. tibetica* of Central Asian mountains from the Altai Mountains to the Tibetan plateau, and *Arctopoa subfastigiata* (Trin.) Prob. of subsaline riparian drainages in the eastern Asian Mongolian steppes (Liu et al. 2006). The first species and the latter two species are distributed taxonomically in the two sections of the genus. Two more localized species are *Arctopoa trautvetteri* (Tzvelev) Prob. and *Arctopoa schischkinii* (Tzvelev) Prob. (Tzvelev 1976; Liu et al. 2006). In our TLF tree the three major *Arctopoa* species are resolved as a clade within the *Poa* clade that includes *Poa* sect. *Sylvestres*, and this small ArcSyl clade is the sister group to all other species of *Poa*. In contrast, in our ITS analyses these three *Arctopoa* species resolve outside of

*Poa* nested among other Poinae genera. Rodionov et al. (2005) included *A. schischkinii* (as *Poa schischkinii*) in their ITS analysis, and that species was resolved in a similar Poinae assemblage outside *Poa*. These results are consistent with a hypothesis of *Poa* subg. *Arctopoa* being a stabilized ancient hybrid lineage between a non-*Poa* member of subtribe Poinae, presumably now extinct, and a species of *Poa* that is either extinct or unsampled, but which evidently had a plastid type sharing DNA sequence synapomorphies with *Poa* sect. *Sylvestres*. *Arctopoa* are easily distinguished from *Poa* by their long, stout rhizomes and ciliate lemma margins (Liu et al. 2006), and are morphologically and ecologically distant from *Poa* sect. *Sylvestres*.

*Arctopoa eminens* and *Dupontia fisheri* R. Br. are known to hybridize. The intergeneric hybrid genus ×*Dupoa* (=*Dupontia* × *Poa*) includes a well documented sterile clonal hybrid between *Poa* (subg. *Arctopoa*) *eminens* and *D. fisheri* that occurs in northern Quebec–Labrador (Cayouette and Darbyshire 1993). Although *Dupontia* itself is suspected to be of hybrid origin, neither Cayouette and Darbyshire (1993) nor Byrsting et al. (2004) found any evidence for *Dupontia* having captured a plastid or nuclear genome marker from *Arctopoa* or *Poa*. Thus a new nothogenus is needed for *Arctopoa* hybrids with *Dupontia*.

Nothogenus novo ×***Duarctopoa*** Soreng & Gillespie, *Arctopoa* × *Dupontia*. Type: × ***Duarctopoa labradorica*** (Steud.) Soreng & Gillespie comb. nov. (*Arctopoa eminens* × *Dupontia fisheri*). Basionym: *Poa labradorica* Steud. Syn. Pl. Glum. 1: 252 (1854).

## Conclusions

The subtribe Poinae is resolved as nonmonophyletic in plastid and ITS trees, as it always includes elements of Alopecurinae and Cinninae intercalated among its genera. Subtribes Miliinae and Puccinelliinae also do not clearly resolve as independently derived from the most recent common ancestor of the above subtribes. We review modern classifications of this collective set of subtribes, called PPAM, and propose taxonomic rearrangements of these based on current evidence (Table 1). A clade including all tested PPAM and a few other elements (which are subsumed) is detected both by our plastid and nrDNA strict consensus trees. A clade containing these subtribes has been strongly supported in other studies, but in our analyses only the PAM portion (Poinae (including Cinninae), Alopecurinae, Miliinae) is strongly supported, and then only in our plastid analysis. Puccinelliinae are strongly supported in each analysis, but the other subtribes are either unresolved or, in one case, unsupported. The genus *Poa* is monophyletic, if we except evidence of reticulation in three cases, and we subsume several small genera. Our ITS and TLF trees are largely congruent in arrangements of sections of *Poa*, and the minor differences between them are not supported. Analyses of new data from Refulio-Rodriguez's dissertation (2007) on the Andean genera *Dissanthelium* and *Tovarochloa,* and our new sequences for *Aphanelytrum*, *Anthochloa*, *Austrofestuca*, *Eremopoa*, *Parodiochloa*, *Neuropoa*, and *Tzvelevia,* provide a sound basis for including these genera within *Poa*, and for excluding *Arctopoa*, *Bellardiochloa*, and *Nicoraepoa* (Table 1). Refulio-Rodriguez will provide nomenclatural changes for *Dissanthelium* and *Tovarochloa* in a separate paper.

The detected phylogenetic history of Poinae intermixed with Alopecurinae and Cinninae remains perplexing, especially for the separately resolved elements of the morphologically well defined Alopecurinae. Perhaps we are only scratching the surface regarding the influence of reticulation in the diversification of these groups. Or perhaps their evolution is better recorded in other stretches of DNA. Evidently it will take data from additional DNA regions, and probably more sophisticated genetic analyses, to successfully unravel this history. For now, we are satisfied that we have made a substantial contribution in this direction.

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