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PHYLOGENY OF *POA* (POACEAE) BASED ON *trnT*–*trnF* SEQUENCE DATA: MAJOR CLADES AND BASAL RELATIONSHIPS

LYNN J. GILLESPIE,^{1,4} ANNIE ARCHAMBAULT,^{1,2} AND ROBERT J. SORENG³

¹*Research Division, Canadian Museum of Nature, PO Box 3443, Station D, Ottawa, Ontario K1P 6P4, Canada;*

²*(aarchambault@mus-nature.ca);* ³*Department of Botany, US National Herbarium, National Museum of Natural History, Smithsonian Institution, PO Box 370012, Washington, D.C. 20013-7012, USA (sorengr@si.edu)*

⁴*Corresponding author (lgillespie@mus-nature.ca)*

ABSTRACT

Poa, the largest genus of grasses (Poaceae) with over 500 species, occurs throughout temperate and boreal regions in both hemispheres. A phylogenetic study of *Poa* based on *trnT*–*trnF* chloroplast DNA sequence data is presented focusing on basal relationships, major clades, generic boundaries, and placement of putatively closely related genera. Results support the monophyly of the main lineage of *Poa* if subgen. *Andinae* is excluded and *Anthochloa*, *Austrofestuca*, *Dissanthelium* (at least in part), and *Eremopoa* are included. The main *Poa* clade and subgen. *Andinae* resolve within a strongly supported Poinae–Alopecurinae–Miliinae clade (PAM). The subdivision of *Poa* into five major clades, proposed based on chloroplast restriction site data, is supported by sequence data. The basal-most clade (ArcSyl) comprises *Poa* subgen. *Arctopoa* and subgen. *Poa* sect. *Sylvestres*, two groups having disparate morphology, but similar cpDNA. The next-diverging clade (BAPO), comprising sects. *Bolbophorum*, *Alpinae*, *Parodiochloa*, and *Ochlopoa*, is strongly supported and characterized by highly divergent cpDNA. The majority of *Poa* species and sections form a strongly supported clade comprising major clades SPOSTA, PoM, and HAMBADD. Newly reported in this study is *Eremopoa* as a distinct lineage positioned between this higher *Poa* clade and BAPO. A revised infrageneric classification of *Poa* comprising five subgenera is proposed. Two new subgeneric divisions of *Poa* are proposed: subgen. **Stenopoa** for the SPOSTA clade and supersect. **Homalopoa** for the HAMBADD clade. The monotypic genus *Anthochloa* is reduced to *Poa* sect. **Anthochloa**, and its one species recognized as ***Poa lepidula***.

Key words: *Andinae*, *Anthochloa*, chloroplast DNA, *Dissanthelium*, *Eremopoa*, *Poa*, *Poinae*, *trnT*–*trnF*

INTRODUCTION

Poa is considered to be the largest genus of grasses (Poaceae), with over 500 species currently recognized (Gillespie and Soreng 2005). The genus is renowned to be taxonomically difficult, with hybridization, polyploidy, and apomixis common (Stebbins 1950; Clausen 1961; Tzvelev 1976; Hunziker and Stebbins 1987). Clayton and Renvoize (1986: 101) lament a “dearth of useful discriminatory characters” and comment that “*Poa* is an extremely uniform genus for which there is no satisfactory infrageneric classification.” Over 200 species have never been assigned to a section or otherwise placed within a subgeneric classification. The affinities of one-half of these species are unknown, while the remaining species are considered to belong to several informal species groups.

While there has yet to be a worldwide revision of *Poa* species or a worldwide infrageneric taxonomy, major advances have been made in classifications at a regional level over the past 30 years. The classifications of Tzvelev (1976) for the former USSR and Edmondson (1978) for Europe have proved to be informative, and have been extended to other regions, including western North America (Soreng 1985). The two most recent classifications of the genus, for North America (Soreng 1998) and the New World (Soreng et al. 2003a), while primarily building on the classifications of Tzvelev (1976) and Edmondson (1978, 1980), have also been influenced by recent phylogenetic analyses of chloro-

plast DNA restriction site (RS) data (Soreng 1990; Gillespie and Boles 2001; Gillespie and Soreng 2005).

As currently understood, *Poa* is divided into two small subgenera, *Arctopoa* and *Andinae*, and one large one, subgen. *Poa* (Soreng 1998; Soreng et al. 2003a). Subgenus *Arctopoa* comprises five species in two sections found in sea-shore and interior wetland habitats of northern, cool temperate regions. *Andinae* is a recently described subgenus (Nicora 1977) including six species of coastal and interior wetlands of Patagonia, South America. All remaining species are placed in subgen. *Poa*, worldwide in distribution and with about 23 accepted sections and several infrasectional taxa. Additional subgenera have been named, but these are not recognized in Soreng’s most recent classifications (Soreng 1998; Soreng et al. 2003a). Subgenus *Dioicopoa* (E. Desv.) J. R. Edm., widely recognized by South American botanists (Nicora 1977, 1978), was treated at the sectional level by Soreng (1998). *Poa* sect. *Ochlopoa* was raised to a subgenus by Hylander (1953) and even to a genus (Bohling and Scholz 2003), but no one has yet followed these treatments. Two other subgenera positioned in *Poa* when described actually represent other grass genera. Subgenus *Psilantha* K. Koch belongs to *Eragrostis* Wolf (Chloridoideae), and subgen. *Pseudopoa* is synonymous with the genus *Eremopoa*, a putatively close Asian relative of *Poa* (Tzvelev 1976; Clayton and Renvoize 1986).

Phylogenetic analyses of *Poa* have, until now, been based

only on cpDNA restriction site data (Soreng 1990; Gillespie et al. 1997; Gillespie and Boles 2001; Gillespie and Soreng 2005); no analysis has yet been published based on morphological or other molecular data. Results of these RS studies have been largely congruent, and the groups identified are in substantial agreement with recent classifications based on morphology. The most recent and broadest phylogenetic study is that of Gillespie and Soreng (2005) based on RS analysis of five PCR-amplified cpDNA regions. In that study, *Poa* was determined to be largely monophyletic and to comprise five major clades: ArcSyl (subgen. *Arctopoa* and subgen. *Poa* sect. *Sylvestres*), BAPO (subgen. *Poa* sects. *Bolbophorum*, *Alpinae*, *Parodiochloa*, and *Ochlopoa*), SPOSTA (subgen. *Poa* sects. *Secundae*, *Pandemos*, *Oreinos*, *Stenopoa*, and *Abbreviatae*), PoM (subgen. *Poa* sects. *Poa* and *Macropoa*), and HAMBADD (subgen. *Poa* sects. *Homalopoa*, *Acutifoliae*, *Madropoa*, *Brizoides*, *Austrofestuca*, *Dasyopoa*, *Dioicopoa*, plus informal groups “Punapoa” and “Australopoa”). These clades showed the following branching order: ArcSyl(BAPO(SPOSTA((PoM) (HAMBADD))). Two segregate genera, *Arctopoa* and *Parodiochloa*, sometimes included within *Poa*, and the genus *Austrofestuca* were confirmed as members of *Poa* (in the major clades ArcSyl, BAPO, and HAMBADD, respectively), as was *P. atropidiformis* (in HAMBADD), a species recently treated in *Dissanthelium*. On the other hand, *Poa* subgen. *Andinae* was determined to be misplaced in *Poa*, and was suggested to be a new genus allied with *Arctagrostis* in subtribe Poinae.

Soreng and Davis (2000) discuss the phylogeny of tribe Poeae based on a combined cpDNA RS and morphological analysis and present a revised classification of the tribe, subsequently updated in Soreng et al. (2003b). The main feature of this classification was the merging of the two poorly delimited tribes, Poeae and Aveneae, into an enlarged Poeae, and the recognition of two main chloroplast lineages, Poeae and Aveneae chloroplast types. Soreng and Davis (2000) identified two main groups within the Poeae chloroplast-type clade: subgroup 1, comprising subtribes Alopecurinae, Dactylidinae, Miliinae, Poinae, Scolochloinae, and Sesleriinae; and subgroup 2, comprising subtribes Cynosurinae, Loliinae (*Festuca* L. and allies), Parapholiinae, and Puccinelliinae. *Poa* resolved in a clade with *Bellardiochloa* and *Puccinellia stricta* (a species they hypothesized to be an intergeneric hybrid), within a clade comprising subtribes Poinae (*Arctagrostis*, *Dupontia*), Alopecurinae (*Alopecurus*, *Beckmannia*, *Phleum*), and Miliinae (*Milium*) in subgroup 1. The classification of genera of subtribe Poinae and related subtribes as accepted here (based on Soreng et al. 2003b with minor revisions) and compared to other recent classifications (Tzvellev 1976, 1989; Clayton and Renvoize 1986) are summarized in Table 1.

In the present study we explore the intra- and intergeneric relationships of *Poa* using cpDNA sequence data. We seek to test previously developed phylogenetic hypotheses of *Poa* based on cpDNA RS data (Gillespie and Soreng 2005) and the intergeneric relationships of *Poa* based on RS data alone and combined in analyses with morphological data (Soreng and Davis 2000). Restriction site analysis provided a useful initial tool for surveying genetic variation in *Poa* since it is relatively quick, inexpensive, and easily allows for processing large sample sizes and testing for known diagnostic

markers. Using this method, Gillespie and Boles (2001) detected no or only minor variation within *Poa* species in the cpDNA regions sampled. Although hybridization is thought to have occurred extensively in the genus (Clausen 1961) and indeed Gillespie and Boles (2001) detected two cases of cpDNA transfer, it did not appear to complicate phylogeny reconstruction and the resulting RS phylogenies corresponded well with recent classifications based on morphology. One disadvantage of RS data is problems associated with data interpretation and homoplasy (e.g., inability to distinguish between absence of a site due to substitution vs. deletion; Dowling et al. 1996). Sequence data have an advantage over RS data in being not or less subject to these potentially serious problems. Previous RS studies of *Poa* focused on sampling morphological diversity and taxonomic breadth. The present sequencing study has a broader focus, aiming to examine basal relationships within *Poa* and affinities of the genus, while also covering as much taxonomic breadth within *Poa* as feasible. The *trnT-trnF* region was chosen for sequencing based on our RS findings of sufficient phylogenetically informative variation within *Poa* for this region (Gillespie and Boles 2001; Gillespie and Soreng 2005) and on the availability of internal sequencing primers (Taberlet et al. 1991).

Our main goals in estimating the phylogeny of *Poa* and related genera based on cpDNA sequences were to (1) test the phylogenetic hypothesis of *Poa* based on cpDNA restriction site data, specifically the five major clades, (2) refine the generic boundary of *Poa*, (3) determine the status and position of small allied genera, and (4) explore the affinities of *Poa*.

MATERIALS AND METHODS

Taxa Sampled

Sixty-eight collections of *Poa* were sampled representing 59 species, all three currently recognized subgenera, 23 sections (including two recently described sections, *Austrofestuca* and *Parodiochloa*; Gillespie and Soreng 2005), and two informal species groups (Table 2). While fewer species were included compared with the latest RS study (Gillespie and Soreng 2005), the species sampled represent a greater taxonomic breadth and cover a broader geographical range. Three additional sections were included, sects. *Leptophyllae*, *Macropoa*, and *Nivicolae*, the first and last sampled for cpDNA for the first time. In addition, nine Eurasian and South American species were sampled for cpDNA for the first time. The sampling overlap between the two studies was 52 collections representing 48 species of *Poa*.

In an attempt to refine the boundary of *Poa* and determine affinities of the genus, we sampled 26 collections representing 21 allied and outgroup genera (Table 2). In addition to *Poa*, seven widely recognized genera were sampled in subtribe Poinae: *Anthochloa*, *Arctagrostis*, *Arctophila*, *Bellardiochloa*, *Dissanthelium*, *Dupontia*, and *Eremopoa* (Table 1, 2). Of these, cpDNA relationships of *Anthochloa*, *Dissanthelium*, and *Eremopoa* are determined for the first time. The closely allied subtribes Alopecurinae (*Alopecurus*, *Beckmannia*, and *Phleum*) and Miliinae (*Milium*) were sampled. Seven genera belonging to five additional subtribes within the Poeae chloroplast group of tribe Poeae were sampled: sub-

tribes Airinae (*Deschampsia* P. Beauv., recently transferred here by Soreng et al. 2003c, Dactylidinae (*Dactylis*), Lolinae (*Festuca*), Puccinelliinae (*Catabrosa*, *Phippsia*, and *Puccinellia*), and Sesleriinae (*Sesleria* Scop.). The following three more distant subtribes of the Aveneae chloroplast group of tribe Poeae were chosen as the outgroups: subtribes Aveninae (*Helictotrichon* Besser ex Schult. & Schult. f.), Phalaridinae (*Anthoxanthum* L. [syn. *Hierochloa* R. Br.], and Agrostidinae (*Agrostis* L.). Overlap with previous RS studies includes 11 collections of allied and outgroup genera (Soreng 1990; Soreng et al. 1990; Gillespie et al. 1997; Soreng and Davis 2000; Gillespie and Boles 2001; Gillespie and Soreng 2005).

DNA Extraction and Amplification of the cpDNA trnT-trnF Region

DNA was extracted from silica-gel-dried leaf material of all samples new to this study. The one exception was *Eremopoa songarica*, for which extractions were made from live leaf material. Total DNA was isolated from individual plants using DNeasy Plant Mini kits (QIAGEN Inc., Valencia, California, USA). Double-stranded DNA of the chloroplast region between *trnT* and *trnF* (TF) was amplified using primers “a” and “f” (Taberlet et al. 1991). This region includes the *trnL* intron and two nontranscribed spacer regions, *trnT-trnL* and *trnL-trnF*. Amplification of the TF region for difficult samples was done as separate regions using internal primers (“b”, “c”, “d” or “e”; Taberlet et al. 1991). *Taq* DNA polymerase (from various suppliers) was used in most of the reactions, but in some recalcitrant samples, DYNazyme ext DNA polymerase (MJ Research, Waltham, Massachusetts, USA) was used following the manufacturer’s instructions. Reactions using *Taq* polymerase were mostly performed in a 50 μ l volume with final concentration of 1 \times buffer, 1.75 mM MgCl₂ (total), 0.2 mM dNTP, 0.3 μ M of each primer, 1–4 units *Taq*, and 0.5 μ l DNA. Cycling conditions varied during the course of the study, but those most efficient were inspired from “long PCR” techniques and included an initial denaturation step of 5 min at 95°C, followed by 10 cycles of 94°C for 20 s, 55–58°C for 1 min, and 72°C for 5 min. Twenty cycles that followed were similar to the first set, with the difference that the elongation step (72°C) increased by 20 s per cycle. A final elongation step of 10 min completed the amplification reaction. Amplification products were purified using QIAquick PCR purification kits (QIAGEN) or Montage PCR columns (Millipore, Billerica, Massachusetts, USA). Nucleotide sequences of amplification products were determined using automated cycle sequencing (Applied Biosystems 3100-Avant). BigDye vers. 3.0 (Applied Biosystems, Inc., Foster City, California, USA) was used for sequencing reactions using one-fourth of the suggested Big Dye volume in a 10 μ l reaction. Internal primers (Taberlet et al. 1991) were used when required to ensure that both strands of the region were sequenced as completely as possible. Consensus sequences were assembled and edited using Sequencher vers. 4.0 and 4.1.4 (Gene Codes Corporation, Ann Arbor, Michigan, USA).

Sequence Alignment and Phylogenetic Analyses

Sequences were aligned using CLUSTALX multiple-sequence alignment program vers. 1.83 (Jeanmougin et al.

1998) and alignment was refined by eye using BioEdit vers. 5.0.9 (Hall 1999). Parsimony-informative gaps were treated as separate presence-absence characters (Simmons and Ochoterena 2000). Parsimony analyses were performed with PAUP* vers. 4.0b10 (Swofford 2002). Heuristic searches were conducted with the tree-bisection-reconnection (TBR), Collapse, and MulTrees options. Two search strategies were used: (1) MaxTrees set at 100,000 with the default option “Collapse branches if maximum length is zero” (MaxBrlen), and (2) 1000 random taxon addition replicates with the option “Collapse branches if minimum length is zero” (MinBrlen). Analyses were performed both with and without the gap characters. Stability of clades was estimated by bootstrap analysis (Felsenstein 1985) on the complete data matrix including gap characters using the second search strategy, full bootstrap option, 1000 replicates, and 10 heuristic searches per replicate. Clades with 80% or greater bootstrap support (BS) were considered strongly supported.

RESULTS

Chloroplast DNA trnT-trnF Sequences

The final aligned data matrix comprised 94 samples and 2349 nucleotide characters, with 20% (463) of the characters variable and 10% (238) parsimony informative. GenBank accession numbers of sequences are given in Table 2. We excluded one region of 53 base pairs (bp) in the *trnT-trnL* spacer (positions 103–155) that could not be unambiguously aligned due to numerous insertions-deletions (indels). In addition, 45 parsimony-informative indels were coded as binary characters and included in two of four analyses performed. Missing data represented <1% of the data set, with data missing primarily from the ends of sequences and also from regions adjacent to internal primers. Only three taxa were missing over 5% of the sequence (*Phippsia algida*, *Poa paucispicula* sample 2, and *P. sylvestres*; 7–12%).

Among the three noncoding regions making up the TF region, the proportion of variable and parsimony-informative nucleotide characters was higher in the longer *trnT-trnL* spacer than in the other two regions. Considering all sequences, 28% (260/938) of the sites were variable and 14% (134/938) parsimony informative in the *trnT-trnL* spacer; 21% (93/453) were variable and 12% (53/453) parsimony informative in the *trnL* intron; and 17% (114/657) were variable and 8% (53/657) parsimony informative in the *trnL-trnF* spacer. Considering just the ingroup *Poa* (i.e., the *Poa* clade in our analysis), 15% (140/907) of the sites were variable and 10% (89/907) parsimony informative in the *trnT-trnL* spacer; 10% (46/443) were variable and 5% (23/443) parsimony informative in the *trnL* intron; and 9% (58/646) were variable and 5% (32/646) parsimony informative in the *trnL-trnF* spacer.

Numerous indels were present in the aligned data matrix, including many that were parsimony informative. These did not cause problems with alignment, except for one small region excluded from the analysis (see above). Taxa with large unique deletions include *Poa howellii* (194 bp), *Agrostis mertensii* (170 bp), and *Deschampsia brevifolia* (70 bp). *Sesleria insularis*, on the other hand, is characterized by a unique 74 bp insertion. Among the larger parsimony-informative indels, the two species of *Helictotrichon* examined

Table 1. Placements of genera belonging to subtribe Poinae and the allied subtribes Alopecurinae, Miliinae, and Puccinellinae as proposed here and in Soreng et al. (2003b, 2003c), as compared with their placements in Clayton and Renvoize (1986) and Tzvelev (1976, 1989). Also included are all genera considered as allied with *Poa* by Clayton and Renvoize (1986). Since Clayton and Renvoize (1986) did not name subtribes or groups in tribe Poeae, the affinities of genera and the groups identified here are based on their Fig. 11 (p. 89), "Diagram of relationships in Poeae," and Fig. 12 (p. 117), "Diagram of relationships in Aveneae." These are balloon diagrams with many small genera appearing to arise from larger genera such as *Poa*. Thus, e.g., 16 Poeae–*Poa*–*Eremopoa* group" in this table indicates a genus in the *Eremopoa* cluster that diverges from the large *Poa* balloon. Tzvelev (1976) mostly includes only genera within the former USSR. Tzvelev (1989) was followed for genera occurring outside the former USSR. Subtribes are given in Tzvelev (1989). A = Aveneae-type cpDNA group; P = Poeae-type cpDNA group; * = cpDNA group confirmed (Soreng et al. 1990; Soreng and Davis 2000; Hunter et al. 2004; Gillespie and Soreng 2005; Davis and Soreng 2006; R. J. Soreng, J. I. Davis, and L. J. Gillespie unpubl. data).

Genus	Clayton and Renvoize (1986)	Tzvelev (1976, 1989)	Proposed here and Soreng et al. (2003b, c)
<i>Alopecurus</i> L.	Aveneae–Alopecurinae	Phleae–Alopecurinae	P*–Alopecurinae
<i>Aniselytrium</i> Merr.	Aveneae–Alopecurinae (as syn. of <i>Calamagrostis</i>) Adans.)	Poeae	P*–Poinae
<i>Anthochloa</i> Nees & Meyen	Meliceae	Poeae	P*–Poinae (as section of <i>Poa</i>)
<i>Aphanelytrium</i> Hack.	Poeae– <i>Poa</i> – <i>Aphanelytrium</i>	Poeae	P*–Poinae
<i>Arctagrostis</i> Griseb.	Poeae– <i>Poa</i> – <i>Arctagrostis</i>	Poeae–Cinninae	P*–Poinae
<i>Arctophila</i> (Rupr.) Anderss.	Poeae– <i>Poa</i> – <i>Colpodium</i> group	Poeae–Poinae	P*–Poinae
<i>Arctopoa</i> (Griseb.) Prob.	Poeae– <i>Poa</i> (as syn.)	Poeae–Poinae (1976; as subgenus of <i>Poa</i> ; 1989; as genus)	P*–Poinae (as subgenus of <i>Poa</i>)
<i>Austrofestuca</i> s.s. (Tzvelev) E. B. Alexeev	Poeae– <i>Poa</i> – <i>Austrofestuca</i>	Poeae	P*–Poinae (as section of <i>Poa</i>)
<i>Beckmannia</i> Host	Aveneae–Alopecurinae	Phleae–Alopecurinae	P*–Alopecurinae
<i>Bellardiachloa</i> Chiov.	Poeae– <i>Poa</i> (as syn.)	Poeae–Festucinae	P*–Poinae
<i>Calotheca</i> Desv.	Poeae– <i>Poa</i> – <i>Briza</i> (as syn.)	Poeae	A*–Brizinae s.l.
<i>Chascolytrium</i> Desv.	Poeae– <i>Poa</i> – <i>Briza</i> (as syn.)	Poeae	A*–Brizinae s.l.
<i>Catabrosa</i> P. Beauv.	Poeae– <i>Poa</i> – <i>Colpodium</i> group	Poeae–Poinae	P*–Puccinellinae
<i>Catabrossella</i> (Tzvelev) Tzvelev	Poeae– <i>Poa</i> – <i>Colpodium</i> (as syn.)	Poeae–Poinae	P–Puccinellinae
<i>Coleanthus</i> Seidel	Poeae– <i>Poa</i> – <i>Colpodium</i> group	Poeae–Coleanthinae	A–Agrostidinae?
<i>Colpodium</i> Trin.	Poeae– <i>Poa</i> – <i>Colpodium</i> group	Poeae–Poinae	P–Miliinae?
<i>Cornucopia</i> L.	Aveneae–Alopecurinae	Phleae	P–Alopecurinae
<i>Cutandia</i> Willk.	Poeae– <i>Poa</i> – <i>Desmazeria</i> group	Poeae–Festucinae	P*–Parapholinae
<i>Dactylis</i> L.	Poeae– <i>Poa</i> – <i>Dactylis</i>	Poeae–Dactylidinae	P*–Dactylimideae
<i>Dasyopoa</i> Pilg.	Poeae– <i>Poa</i> (as syn.)	Poeae	P*–Poinae (as section of <i>Poa</i>)
<i>Desmazeria</i> Dumort.	Poeae– <i>Poa</i> – <i>Desmazeria</i> group	Poeae	P*–Parapholinae
<i>Dissanthelium</i> Trin.	Aveneae–Aveninae	Poeae	P*–Poinae (with <i>Poa</i>)
<i>Dupononia</i> R. Br.	Poeae– <i>Poa</i> – <i>Colpodium</i> group	Poeae–Poinae	P*–Poinae
<i>Eremopoa</i> Rosh.	Poeae– <i>Poa</i> – <i>Eremopoa</i> group	Poeae–Poinae	P*–Poinae (as <i>Poa</i> subgen. <i>Pseudopoa</i>)
<i>Festucella</i> E. B. Alexeev	n/a	Poeae	P*–Poinae
<i>Gymmachne</i> Parodi	Poeae– <i>Poa</i> – <i>Briza</i> group (as syn. of <i>Rhombolium</i>)	Poeae	A*–Brizinae s.l.
<i>Hookerchloa</i> E. B. Alexeev	n/a	Poeae	P*–Poinae
<i>Hyalopoa</i> (Tzvelev) Tzvelev	Poeae– <i>Poa</i> – <i>Colpodium</i> (as syn.)	Poeae–Poinae	P–Poinae
<i>Libyella</i> Pamp.	Poeae– <i>Poa</i> – <i>Eremopoa</i> group	Poeae	P–Poinae
<i>Limmas</i> Trin.	Aveneae–Alopecurinae	Phleae–Alopecurinae	P–Alopecurinae
<i>Lindbergella</i> Bor	Poeae– <i>Poa</i> – <i>Eremopoa</i> group	Poeae–Poinae	P–Poinae
<i>Microbriza</i> Nicora & Rúgolo	Poeae– <i>Poa</i> – <i>Briza</i> group	Poeae	A*–Brizinae s.l. (as syn. of <i>Poidium</i>)
<i>Milium</i> L.	Stipeae—between <i>Oryzopsis</i> Michx. and <i>Trikeraita</i> Bor	Aveneae–Miliinae	P*–Miliinae

Table 1. Continued.

Genus	Clayton and Renvoize (1986)	Tzvelev (1976, 1989)	Proposed here and Soreng et al. (2003 <i>b, c</i>)
<i>Nephelochloa</i> Boiss.	Poeae– <i>Poa</i> – <i>Eremopoa</i> group	Poeae	P–Poinae?
<i>Neuropoa</i> W. D. Clayton	Poeae– <i>Poa</i> – <i>Eremopoa</i> group	Poeae	P–Poinae
<i>Paracolpodium</i> (Tzvelev)	Poeae– <i>Poa</i> – <i>Colpodium</i> (as syn.)	Poeae–Poinae	P–Puccinellinae
<i>Parafestuca</i> E. B. Alexeev	Poeae– <i>Poa</i> – <i>Parafestuca</i>	Poeae	A*–Aveninae (as syn. of <i>Koeleria</i> Pers.)
<i>Paradiorchloa</i> C. E. Hubb.	Poeae– <i>Poa</i> (as syn.)	Poeae	P*–Poinae (as section of <i>Poa</i>)
<i>Phippsia</i> (Trin.) R. Br.	Poeae– <i>Poa</i> – <i>Colpodium</i> group	Poeae–Poinae	P*–Puccinellinae
<i>Phleum</i> L.	Aveneae–Alopecurinae	Phleae–Phleinae	P*–Alopecurinae
<i>Poa</i> L.	Poeae– <i>Poa</i>	Poeae–Poinae	P*–Poinae
<i>Poidium</i> Nees	Poeae– <i>Poa</i> (as syn.)	Poeae	A*–Brizinae s.l.
<i>Puccinellia</i> Parl.	Poeae– <i>Puccinellia</i> group	Poeae–Poinae	P*–Puccinellinae
<i>Rhizocephalus</i> Boiss.	Aveneae–Alopecurinae	Phleae–Phleinae	P–Alopecurinae
<i>Rhombolytrum</i> E. Desv.	Poeae– <i>Poa</i> – <i>Briza</i> group	Poeae	A–Brizinae s.l.
<i>Sclerochloa</i> P. Beauv.	Poeae– <i>Poa</i> – <i>Desmazeria</i> group	Poeae–Poinae	P*–Puccinellinae
<i>Sphenopus</i> Trin.	Poeae– <i>Poa</i> – <i>Eremopoa</i> group	Poeae–Festucinae	P*–Parapholinae
<i>Tovarochloa</i> T. D. Macfarl. & But	Aveneae–Aveinae	Poeae	P*–Poinae
<i>Tzvelevia</i> E. B. Alexeev	n/a	Poeae	P–Poinae
<i>Zingieria</i> Smirnov	Aveneae–Alopecurinae	Aveneae–Agrostidinae	P–Miliinae?

share a 275 bp deletion and the two samples of *Eremopoa* share a 40 bp deletion. *Poa alpina*, *P. bulbosa*, and *P. molinerii* share both a deletion (64 bp) and an insertion (32 bp). Taxa sharing duplications include *P. acinaciphylla*, *P. archnifera*, and *P. stuckertii* (23 bp), *P. annua* and *P. supina* (20–22 bp), and all species in the POSTA subclade (12 bp).

Phylogenetic Analysis

Cladistic analysis of the complete data matrix including the gap characters resulted in trees 754 steps long with a consistency index (CI) of 0.68, excluding uninformative characters, a retention index (RI) of 0.92, and a rescaled consistency index (RC) of 0.72. Both search strategies resulted in identical tree statistics and strict consensus trees, and differed only in the number of most-parsimonious trees (upper limit of 100,000 trees was reached in the first analysis using MaxBrlen option; 120 trees in the second analysis using MinBrlen option) and in the degree of resolution of trees (more unresolved nodes in the second analysis). One of the most-parsimonious trees from the second analysis is illustrated in Fig. 1 and 2. The strict consensus tree (indicated by bold lines in Fig. 1 and 2) differs only in lacking the clade comprising *Poa marcida* and the *P. wolfii*–*P. alsodes* clade, the *P. holciformis*–*P. acinaciphylla* clade, and the *Arctagrostis*–*Poa* subgen. *Andinae* clade, and in the lack of resolution among *Festuca*, *Sesleria*, and the *Dactylis*–*Deschampsia* clade.

The analyses excluding gap characters resulted in 100,000 trees (MaxBrlen option) and 72 trees (MinBrlen option), each 679 steps long (CI = 0.69, excluding uninformative characters, RI = 0.92, RC = 0.74). The strict consensus tree was identical to that of the first analysis (Fig. 1, 2; bold lines), except for the following minor differences. In the major clade ArcSyl, *Poa marcida* is sister to the *P. wolfii*–*P. alsodes* clade (as in Fig. 2) and this clade forms a trichotomy with the *P. tibetica*–*P. eminens* clade and the *P. autumnalis*–*P. sylvestris* clade (i.e., the last two clades do not resolve together as one clade). Within the Poinae–Alopecurinae clade, the clade comprising *Alopecurus*, *Arctagrostis*, *Belardiachloa*, and *Poa* subgen. *Andinae* is not resolved. Relationships among basal members of the Poeae chloroplast group are somewhat more resolved, with *Festuca* diverging first as in Fig. 1.

Poa clade.—A main *Poa* clade (Fig. 1, 2) is strongly supported (BS = 84%). The clade resolved into five major internal clades (Fig. 2: ArcSyl, BAPO, SPOSTA, PoM, HAMBADD) plus one distinct lineage (*Eremopoa*). The clades BAPO, SPOSTA, and PoM have strong support (BS = 90–99%), while ArcSyl and HAMBADD have weak support (BS = 64%). Relationships among major clades are strongly supported (BS = 86–100%). Several allied genera were included within the *Poa* clade: *Anthochloa*, *Dissanthelium* (only *D. peruvianum* and *Poa atropidiformis*, recently included in this genus, were examined), and *Eremopoa*. Also included were the genera *Austrofestuca* s.s. and *Parodiachloa*, both recently reduced to sections of *Poa* (Gillespie and Soreng 2005).

Poinae–Alopecurinae–Miliinae (PAM) clade.—Sequence data showed strong support (BS = 99%) for a clade com-

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Table 2. Taxa of *Poa*, allied genera, and outgroups sampled. Origin, voucher information, and GenBank accession number(s) are given for each collection. Subgenus and section (if applicable) are given for *Poa* species. Voucher numbers, unless otherwise specified, refer to collections of L. J. Gillespie (deposited at CAN), R. J. Soreng (number prefixed with an "S" and specimen deposited at US unless otherwise indicated), and P. M. Peterson (number prefixed with a "P" and specimens deposited at US).

Taxon	Section	Specimen origin	Voucher	GenBank accession
<i>Poa</i> subgen. <i>Andinae</i> Nicora				
<i>P. andina</i> Trin.		Chile	S7182	DQ353971
<i>P. chonotica</i> Phil.		Chile	S7309	DQ353974
<i>P. pungionifolia</i> Speg.		Chile	S7336	DQ353973
<i>P. robusta</i> Steud.		Chile	S7358	DQ353975
<i>P. subenervis</i> Hack.		Chile	S7334	DQ353972
<i>Poa</i> subgen. <i>Arctopoa</i> (Griseb.) Prob.				
<i>P. eminens</i> J. Presl	<i>Arctopoa</i>	USA, Alaska	S6022	DQ353977
<i>P. tibetica</i> Stapf	<i>Aphydris</i>	China, Tibet	S5481	DQ353976
<i>Poa</i> subgen. <i>Poa</i>				
<i>P. abbreviata</i> R. Br.	<i>Abbreviatae</i>	Canada, Nunavut	5957	DQ353996
<i>P. acinaciphylla</i> E. Desv.	<i>Acutifoliae</i>	Chile	S7169	DQ354023
<i>P. alpina</i> L.	<i>Alpinae</i>	(1) Canada, Nunavut (2) USA, Colorado	6749-1 6299	DQ353986 DQ353985
<i>P. alsodes</i> A. Gray	<i>Sylvestres</i>	Canada, Quebec	6467	DQ353981
<i>P. ammophila</i> A. E. Porsild	<i>Secundae</i>	Canada, Northwest Territories	5851	DQ353992
<i>P. annua</i> L.	<i>Ochlopoa</i>	Canada, Ontario	6284	DQ353983
<i>P. arachnifera</i> Torrey	<i>Dioicopoa</i>	USA, Oklahoma	S5801	DQ354021
<i>P. arctica</i> R. Br. subsp. <i>arctica</i>	<i>Poa</i>	Canada, Nunavut	5701	DQ354009
<i>P. atropidiformis</i> Hack.	<i>Homalopoa</i> s.l. or <i>Dasydop?</i>	Chile	S7364	DQ354020
<i>P. autumnalis</i> Elliot	<i>Sylvestres</i>	USA, Maryland	S4680	DQ353979
<i>P. billardierei</i> St.-Yves (syn. <i>Austrofestuca littoralis</i> (Labill.) E. B. Alexeev)	<i>Austrofestuca</i>	Australia	P14510	DQ354048, DQ354049
<i>P. bulbosa</i> L.	<i>Bolbophorum</i>	(1) Spain (2) USA, Oregon	<i>Catalán 13-2000</i> (UZ) S5958	DQ354034, DQ354035 DQ354038, DQ354039
<i>P. compressa</i> L.	<i>Tichopoa</i>	Canada, Quebec	6457	DQ354003
<i>P. curtifolia</i> scribn.	<i>Secundae</i>	USA, Washington	S6347c-1	DQ353994
<i>P. cusickii</i> Vasey subsp. <i>pallida</i> Soreng	<i>Madropoa</i>	USA, Nevada	S5829	DQ354029
<i>P. drummondiana</i> Nees	<i>Brizoides</i>	Australia	P14504	DQ354013
<i>P. fendleriana</i> (Steud.) Vasey	<i>Madropoa</i>	USA, Colorado	6292	DQ354027
<i>P. fernaldiana</i> Nannf.	<i>Oreinos</i>	USA, New Hampshire	7015-3	DQ353995
<i>P. flabellata</i> (Lam.) Raspail	<i>Parodiochloa</i>	Falkland Islands	No voucher ^a	DQ353982
<i>P. glauca</i> Vahl	<i>Stenopoa</i>	Canada, Nunavut	5963	DQ354004
<i>P. hartzii</i> Gand. subsp. <i>hartzii</i>	<i>Secundae</i>	(1) Canada, Nunavut (2) Canada, Nunavut	5725 6623-5	DQ353990 DQ353993
<i>P. holciformis</i> J. Presl	<i>Dioicopoa</i>	Chile	S7166	DQ354054, DQ354055, DQ354056
<i>P. howellii</i> Vasey & Scribn.	<i>Homalopoa</i>	USA, Oregon	S5964	DQ354015
<i>P. interior</i> Rydb.	<i>Stenopoa</i>	USA, Alaska	S6136-1	DQ354002
<i>P. ircuitica</i> Roshev.	<i>Nivicolae</i>	Russia, Irkutsk	<i>Kasanovskiy 2002-7</i> (CAN)	DQ354007
<i>P. kurtzii</i> R. E. Fr.	"Punapoa"	Chile	P15654	DQ354018
<i>P. labillardieri</i> Steud.	"Australopoa"	Australia	S5921	DQ354014
<i>P. laetevirens</i> R. E. Fr.	<i>Dasyopoa</i>	Chile	P15641	DQ354019
<i>P. leptocoma</i> Trin.	<i>Oreinos</i>	(1) USA, Alaska (2) USA, Alaska	S6040-1 S6100	DQ353998 DQ353999
<i>P. aff. lilloi</i> Hack.	"Punapoa"	Chile	P15676	DQ354017
<i>P. macrantha</i> Vasey	<i>Madropoa</i>	USA, Oregon	S5861	DQ354028
<i>P. macrocalyx</i> Trautv. & C. A. Mey.	<i>Poa</i>	USA, Alaska	S6059-1	DQ354008
<i>P. marcida</i> Hitchc.	<i>Sylvestres</i>	USA, Alaska	S5974	DQ353978
<i>P. margilicola</i> Bernátová & Májovský	<i>Stenopoa</i>	Slovakia	No voucher ^b	DQ354001

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Table 2. Continued.

Taxon	Section	Specimen origin	Voucher	GenBank accession
<i>P. mariae</i> Reverd.	<i>Poa</i>	Russia, Khakasia	<i>Olonova 2002-7</i> (CAN)	DQ354005
<i>P. molinerii</i> Balb.	<i>Alpinae</i>	Slovakia	<i>Stoneberg SH13</i> (CAN)	DQ354036, DQ354037
<i>P. nervosa</i> (Hook.) Vasey	<i>Homalopoa</i>	USA, Oregon	<i>S5849</i>	DQ354025
<i>P. palustris</i> L.	<i>Stenopoa</i>	Canada, Ontario	<i>6461</i>	DQ354000
<i>P. paucispicula</i> Scribn. & Merr.	<i>Homalopoa</i>	(1) USA, Alaska	<i>S6033</i>	DQ354050, DQ354051
		(2) USA, Alaska	<i>S6169</i>	DQ354016
<i>P. prosildii</i> Gjaerev.	<i>Madropoa</i>	USA, Alaska	<i>S6147-1</i>	DQ354024
<i>P. pratensis</i> L. subsp. <i>alpigena</i> (Lindm.) Hii-tonen	<i>Poa</i>	Canada, Nunavut	<i>5801</i>	DQ354006
<i>P. pratensis</i> subsp. <i>angustifolia</i> (L.) Lej.	<i>Poa</i>	Spain	<i>Catalán s. n.</i> (8 Jun 2003, UZ16.2003)	DQ354012
<i>P. pratensis</i> subsp. <i>pratensis</i>	<i>Poa</i>	(1) USA, Colorado	<i>6291</i>	DQ354010
		(2) USA, Colorado	<i>6310</i>	DQ354011
<i>P. pseudoabbreviata</i> Roshev.	<i>Abbreviatae</i>	USA, Alaska	<i>S6032-1</i>	DQ353997
<i>P. riphaea</i> (Asch. & Graebn.) Fritsch	<i>Stenopoa</i> (previously <i>Oreinos</i>)	Czech Republic	No voucher ^c	DQ354040, DQ354041
<i>P. secunda</i> J. Presl. subsp. <i>juncifolia</i> (Scribn.) Soreng	<i>Secundae</i>	USA, Colorado	<i>S5809</i>	DQ353989
<i>P. secunda</i> subsp. <i>secunda</i>	<i>Secundae</i>	USA, Nevada	<i>S5812</i>	DQ353991
<i>P. sibirica</i> Roshev.	<i>Macropoa</i>	Russia, Khakasia	<i>Olonova 02-1</i> (CAN)	DQ354044, DQ354045
<i>P. stenantha</i> Trin.	<i>Secundae</i>	USA, Alaska	<i>S6068-1</i>	DQ354057
<i>P. stiriaca</i> Fritsch & Hayek	<i>Leptophyllae</i>	Austria	<i>Smarda PS10</i> (BRNU)	DQ354042, DQ354043
<i>P. stuckertii</i> (Hack.) Parodi	<i>Dioicopoa</i>	Chile	<i>S7132</i>	DQ354022
<i>P. supina</i> Schrad.	<i>Ochlopoa</i>	USA (cultivated)	<i>S5950-2</i>	DQ353984
<i>P. sylvestris</i> A. Gray	<i>Sylvestres</i>	USA, Maryland	<i>S4678-3</i>	DQ353980
<i>P. wheeleri</i> Vasey	<i>Homalopoa</i>	USA, Nevada	<i>S5825</i>	DQ354026
<i>P. wolfii</i> Scribn.	<i>Sylvestres</i>	USA, Missouri	<i>S5800</i>	DQ354032, DQ354033
Allied Genera and Outgroups				
<i>Agrostis mertensii</i> Trin.		USA, New Hampshire	<i>6802</i>	DQ353956
<i>Alopecurus borealis</i> Trin.		Canada, Nunavut	<i>6576</i>	DQ353966
<i>Anthochloa lepidula</i> Nees & Meyen		Chile	<i>P15604</i>	DQ354046, DQ354047
<i>Anthoxanthum monticolum</i> subsp. <i>alpinum</i> (Sw. ex Willd.) Soreng		Canada, Northwest Territories	<i>6859</i>	DQ353953
<i>Arctagrostis latifolia</i> (R. Br.) Briseb.		Canada, Nunavut	<i>6586</i>	DQ353969
<i>Arctophila fulva</i> (Trin.) Rupr.		Canada, Northwest Territories	<i>Aiken 99-230</i> (CAN)	DQ354058
<i>Beckmannia syzigachne</i> (Steud.) Fernald		USA, Wyoming	<i>S3513^d</i>	DQ353965
<i>Bellardiochloa variegata</i> (Lam.) Kerguelen		Yugoslavia	No voucher [USDA accession PI 253455] ^{de}	DQ353970
<i>Catabrosa aquatica</i> (L.) P. Beauv.		Chile	<i>S7150</i>	DQ353958
<i>Dactylis hispanica</i> Roth		Spain Territories	<i>S3682^d</i>	DQ353961
<i>Dissanthelium peruvianum</i> (Nees & Meyen) Pilg.		Chile	<i>P15744</i>	DQ354052, DQ354053
<i>Dupontia fisheri</i> R. Br.		(1) Canada, Nunavut	<i>6589</i>	DQ353967
		(2) Canada, Nunavut	<i>6699</i>	DQ353968
<i>Eremopoa songarica</i> (Schrenk) Roshev.		(1) Turkey	<i>S4165^f</i>	DQ353987
		(2) Turkey	<i>S4165^f</i>	DQ353988
<i>Festuca baffinensis</i> Polunin		Canada, Northwest Territories	<i>6920</i>	DQ353951, DQ353952
<i>Helictotrichon convolutum</i> (C. Presl) Henrard		Greece	<i>S3803</i>	DQ353954

Table 2. Continued.

Taxon	Section	Specimen origin	Voucher	GenBank accession
<i>H. sempervirens</i> (Vill.) Pilg.		USA, New York (cultivated)	S4622	DQ353955
<i>Milium vernale</i> M. Bieb.		Spain	S3748 ^d	DQ353963
<i>Phippsia algida</i> (Sol.) R. Br.		Canada, Nunavut	6253	DQ353949, DQ353950
<i>Phleum pratense</i> L.		USA, New York (cultivated)	No voucher ^{de}	DQ353964
<i>Puccinellia glaucescens</i> (Phil.) Parodi		Chile	S7152	DQ353960
<i>Pu. poacea</i> T. J. Sorenson		Canada, Nunavut	S744	DQ354030, DQ354031
<i>Pu. stricta</i> (Hook. f.) Blom		Australia	P14544	DQ353959
<i>Sesleria insularis</i> Sommier		Yugoslavia	S3889 (BH) (= USDA PI 253719) ^d	DQ353957

^a Sample collected by S. Wright in 2000 from Falkland Islands, Cape Dolphin, 51°14.165'S, 58°57.882'W (sample number: 4NCD).

^b Sample collected by D. Bernátová in 2001 from Slovakia, Veká Fatra Mts., highest part of the main ridge of the range, 48°56'20"N, 19°05'25"E, elev. 1509 m (sample number: DB1; no voucher collected because of rare status of species).

^c Sample collected by M. Koci in 5 Sep 2001 from type locality: Czech Republic, Moravia, Hrubý Jseník Park, Pradř Mt., Petrovy Kameny, 5.21 km WSW of the church in the village of Karlova Studánka, 50°04'08"N, 17°14'01"E, elev. 1430 m (sample number: MK1; no voucher specimen made because only known from type locality, which is well vouchered at BRNU).

^d DNA from cpDNA restriction site studies of Soreng (1990), Soreng et al. (1990), and Soreng and Davis (2000).

^e Distributed as *Poa araratica* Trautv., redetermined by Soreng.

^f Sequences obtained for two plants grown from seed from cited herbarium specimen differing in robustness and leaf width.

^g Contaminant in USDA PI 20228 seed accession.

prising Poeae subtribes Poinae, Alopecurinae, and Miliinae (Fig. 1). Within this clade, the following three clades were resolved: (1) the main *Poa* clade (above; Fig. 2), (2) a strongly supported clade (BS = 92%) including *Poa* subgen. *Andinae*, and the remaining genera examined of subtribe Poinae (*Arctagrostis*, *Arctophila*, *Bellardiachloa*, and *Dupontia*) plus two genera of subtribe Alopecurinae (*Alopecurus* and *Beckmannia*), and (3) a weakly supported clade (BS = 63%) comprising one genus of subtribe Alopecurinae (*Phleum*) and one of subtribe Miliinae (*Milium*). Relationships among these three clades were not resolved in the strict consensus trees, although the majority-rule consensus trees strongly favored (96% in the analysis including gaps, 93% in the analysis excluding gaps) a clade comprising the first two clades. All species examined of *Poa* subgen. *Andinae* were included within the second (Poinae–Alopecurinae) clade, but did not resolve as a clade in the strict consensus tree of either analysis. Relationships within this Poinae–Alopecurinae clade were not well resolved, with only two strongly supported internal clades present, an *Arctophila*–*Dupontia* clade (BS = 96%) and a clade comprising two species of *Poa* subgen. *Andinae*, *P. chonotica*, and *P. robusta* (BS = 96%).

Poeae chloroplast group clade.—All members of the Poeae chloroplast group of tribe Poeae formed a strongly supported clade (BS = 100%) separated from the outgroup genera examined belonging to the Aveneae chloroplast group of tribe Poeae (Fig. 1). While basal relationships in the clade were unresolved, two major internal clades were supported. Subtribe Puccinelliinae (*Catabrosa*, *Phippsia*, and *Puccinellia*) and the PAM clade formed a strongly supported clade (BS = 83%). *Dactylis* (subtribe Dactylidinae) and *Deschampsia*

(subtribe Airinae) also resolved as a strongly supported clade (BS = 92%).

DISCUSSION

Poa Phylogeny

Chloroplast DNA sequence data support the five major *Poa* clades (Fig. 2) initially proposed based on RS data (Gillespie and Soreng 2005). The proposed hypothesis of relationships among the clades is also supported by sequence analysis. All five clades and relationships among the clades have higher bootstrap support in the sequence analysis compared with the RS analysis (except for the PoM clade, which is strongly supported [BS = 99–100%] in both analyses). New to this study is the recognition of *Eremopoa* as a distinct lineage within *Poa* in addition to the five major clades (discussed below).

The sequence analysis, for the most part, confirms the phylogenetic structure previously detected within each major clade based on RS analysis (Gillespie and Soreng 2005), and provides additional resolution within some clades. Species sampled for cpDNA for the first time, belonging to sections previously sampled, were all resolved, as expected, in the appropriate major clade with, or at least near, other members of the same section. These include *P. molinerii* (sect. *Alpinae*) in BAPO, *P. margilicola* (sect. *Stenopoa*) and *P. riphaea* (sect. *Oreinos* or *Stenopoa*, discussed below) in SPOSTA, and *P. mariae* (sect. *Poa*) in PoM (Fig. 2). Apart from postulated cases of hybridization and introgression (Gillespie et al. 1997; Gillespie and Boles 2001; Gillespie and Soreng 2005), only one species, *P. paucispicula*, has so far not resolved as expected (discussed below). Structure

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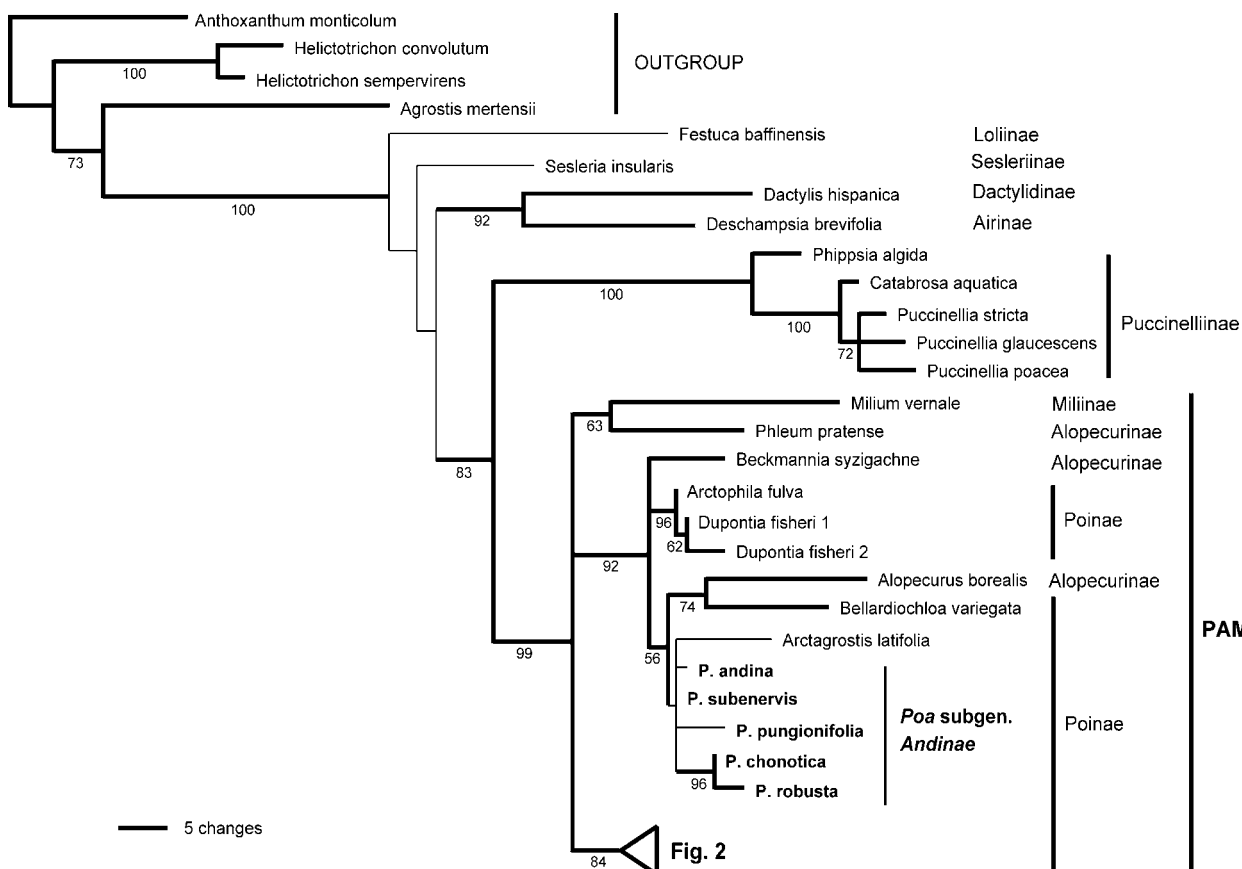


Fig. 1.—One of 80 most-parsimonious trees resulting from analysis of the complete data set including gap characters using the MinBrLen option (754 steps, CI = 0.67), showing relationships among genera and subtribes sampled of tribe Poeae, chloroplast group Poeae. The strict consensus tree is indicated by branches in bold. Bootstrap values above 50% are given below branches. The main *Poa* clade is indicated by a triangle and is shown in Fig. 2. *Poa* species not part of the main *Poa* clade are indicated in bold.

within each major clade and taxa included were discussed in detail in the most recent RS study (Gillespie and Soreng 2005), which examined a greater number of *Poa* species. The discussion below focuses on new findings and on differences between the two studies.

ArcSyl clade.—This basal-most clade in the main *Poa* clade shows little genetic divergence and is not well supported, though its separation from all other *Poa* species and from the two other PAM clades is strongly supported (Fig. 1, 2). These results confirm those previously found based on RS analysis (Gillespie and Soreng 2005). Both data sets resulted in a similar, poorly resolved internal basal structure. Subgenus *Poa* sect. *Sylvestres* does not resolve as a clade, while the two species examined of subgen. *Arctopoa* (*P. eminens* and *P. tibetica*) do resolve as a strongly supported clade. The sequence analysis including gap characters differs only in the probable spurious grouping of subgen. *Arctopoa* with two subgen. *Poa* sect. *Sylvestres* species (*P. autumnalis* and *P. sylvestris*) based on one shared unique indel (7 bp duplication). Other sect. *Sylvestres* species either lack the indel (*P. alsodes* and *P. marcida*) or have a different indel (7 bp insertion, *P. wolffii*), neither of which is a unique state shared with other species of *Poa* and allied genera.

BAPO clade.—The next clade to diverge, BAPO, shows a structure identical to that found in the RS analysis (Gillespie

and Soreng 2005) (Fig. 2). In both studies genetic divergence is high with both the clade and its internal structure strongly supported. The two main lineages correspond to well-defined sections, sect. *Ochlopoa* and the sister sects. *Alpinae* and *Bolbophorum*, though the two lineages had not previously been suggested as related. The position of the anomalous *P. flabellata* of southernmost South America (sometimes recognized as the monotypic genus *Parodiochloa*) is confirmed as a member of this clade, sister to sect. *Ochlopoa*.

SPOSTA clade.—The first of three higher *Poa* clades, SPOSTA, is strongly supported, with sect. *Secundae* sister to all other members (Fig. 2). The remaining sections, *Abbreviatae*, *Oreinos*, *Stenopoa*, and *Tichopoa*, form a strongly supported clade (POSTA) with little or no resolution of sections (sect. *Pandemos*, not examined here, was the basal-most branch in POSTA in RS studies [Soreng 1990; Gillespie and Boles 2001; Gillespie and Soreng 2005]). The main difference among studies was the status of sect. *Secundae*, which resolved as a weakly supported clade in this study, Soreng (1990), and the Dollo analysis in Gillespie and Soreng (2005), as an unresolved basal complex in the Dollo analysis in Gillespie and Boles (2001), and as a grade in all other analyses in Gillespie and Boles (2001) and Gillespie and Soreng (2005).

Poa riphaea, an alpine species known only from the type

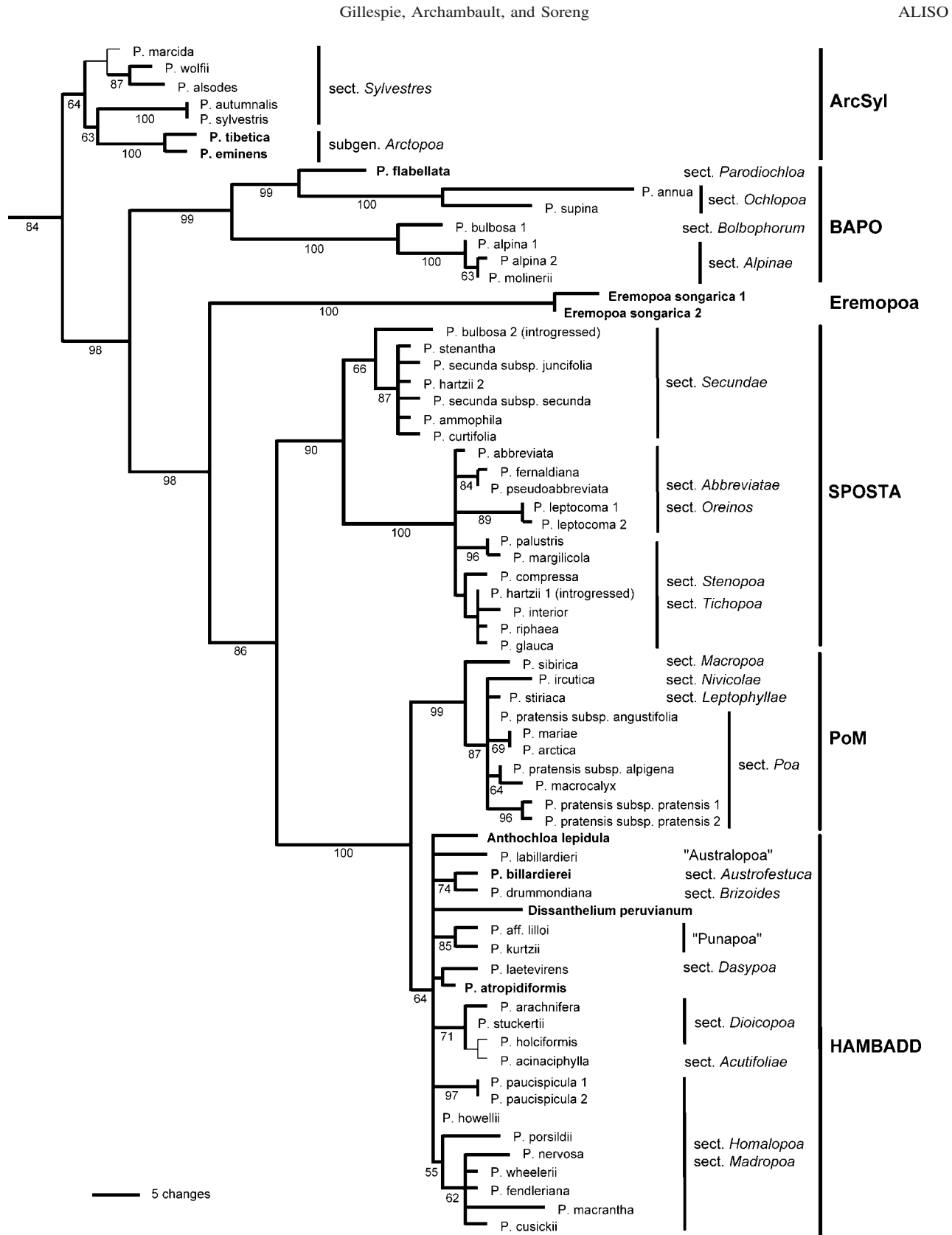


Fig. 2.—The main *Poa* clade of the tree as represented in Fig. 1 showing subgenera, sections, and major clades. The strict consensus tree is indicated by branches in bold. Bootstrap values above 50% are given below branches. Species previously belonging to other genera and those often included in other genera are shown in bold.

locality in the Czech Republic, has, until now, been considered to belong in sect. *Oreinos*. The species was originally published as a variety of *P. laxa* Haenke, a member of sect. *Oreinos*, and was treated as a synonym of that species by Edmondson (1980). However, it appears to be morphologically most similar to the widespread circumarctic-alpine species *P. glauca* (sect. *Stenopoa*), and may represent a southern alpine conspecific population or closely related species. Sequence data support a close affinity of *P. riphaea* with *P. glauca* and its transfer to sect. *Stenopoa*.

The two cases of intersectional hybridization and introgression first detected in RS studies (Gillespie et al. 1997; Gillespie and Boles 2001; Gillespie and Soreng 2005) and confirmed here involve species in the SPOSTA clade. *Poa hartzii* (sect. *Secundae*) has hybridized and introgressed with *P. glauca* (sect. *Stenopoa*), while *P. bulbosa* (BAPO clade) may have hybridized with a species, as yet unidentified, in sect. *Secundae* in North America. Both events appear to have resulted in a unidirectional chloroplast transfer from the second species to the first.

PoM clade.—Both sequence and RS data strongly support the PoM clade (Fig. 2). The small Eurasian sect. *Macropoa* (*P. sibirica* sampled here), previously sampled in the RS study of Soreng (1990), but not in Gillespie and Soreng (2005), is confirmed as a member of this clade and sister to the clade that includes sect. *Poa*. Two additional sections, *Leptophyllae* and *Nivicolae*, not previously examined for cpDNA, also resolved within PoM, both forming a polytomy with members of sect. *Poa*. Section *Nivicolae* includes four species (*P. ircutica* examined here) of alpine meadows in far eastern Russia and Siberia. Our results support Tzvelev's (1976) treatment of the section as closely related to sect. *Poa*. He treated it as one of four subsections in a broadly defined sect. *Poa* (comprising subsections. *Bulbosae* Jiras. [= sect. *Bolbophorum*], *Caespitosae* Jiras. [= sect. *Alpinae*], *Nivicolae* (Roshev.) Tzvelev, and *Poa*). More recently, Tzvelev (2000) considered the sect. *Nivicolae* species occurring in central Asia (*P. vereschaginii* Tzvelev) to belong to a more narrowly defined sect *Poa* (i.e., excluding subsections. *Bulbosae* and *Caespitosae*). The monotypic sect. *Leptophyllae* (*P. stiriaca*) of montane central Europe was described by Edmondson (1978) and placed by him between sects. *Homalopoa* and *Oreinos* (Edmondson 1980). Our results do not support this position, but instead support a close relationship with sect. *Poa* (Mečénovic 1939).

Relationships among species of sect. *Poa* are poorly resolved, with only two clades of two species each. The *P. arctica* complex (*P. arctica*, *P. mariae*) resolves as a weakly supported clade, but the subspecies of *P. pratensis* do not. The close relationship between *P. pratensis* subsp. *alpigena* (syn. *P. alpigena* Lindm.) and *P. macrocalyx* detected in RS analysis (Gillespie and Soreng 2005) is confirmed here. Although only weakly supported in this study (one unique shared nucleotide substitution), the two taxa were recently found to share a unique 170 bp deletion in the cpDNA *rbcl-psa1* spacer region (Archambault and Gillespie 2003). These findings do not support Probatova's (1985) placement of *P. macrocalyx* in sect. *Poa* subsect. *Malacanthae* (Roshev.) Prob. (= sect. *Cenisiae* Asch. & Graebn. of Edmondson

1980), which indicates an alliance with *P. arctica* and relatives rather than with the *P. pratensis* complex.

HAMBADD clade.—The HAMBADD clade is by far the largest, both in numbers of species and sections, and is the least resolved of the major clades (Fig. 2). Our previous RS study (Gillespie and Soreng 2005) showed no resolution of structure within this clade in the strict consensus trees, with only seemingly spurious subclades in some most-parsimonious trees. In the present sequence study, structure within the HAMBADD clade is partly resolved with internal clades mostly making sense morphologically and biogeographically. The RS study resolved the genus *Austrofestuca* within the HAMBADD clade, a position confirmed here. New to this study is the placement in this clade of two additional genera, *Anthochloa* and *Dissanthelium* (discussed below).

Five subclades (each comprising two or more species) are resolved based on sequence data, although most with weak support. Three clades comprise, respectively, two species of the South American "Punapoa" species group (clade strongly supported), two Australian species representing sects. *Austrofestuca* and *Brizoides*, and four species examined of the South American sects. *Acutifoliae* and *Dioicopoa*. Species examined of sects. *Homalopoa* and *Madropoa*, all from North America, resolve as a clade with the exception of *P. howellii*, which lacks the single shared nucleotide substitution due to a large deletion. The Patagonian species *P. atropidiformis* and the single species examined here of the South and Central American sect. *Dasyopoa* form the fifth clade (BS < 50%). The position of *P. atropidiformis* has been uncertain and these results provide weak evidence for an affinity with sect. *Dasyopoa*. Soreng (1998) had previously transferred the species to *Dissanthelium*, but more recently assigned it to *Poa* sect. *Homalopoa* s.l. (Soreng et al. 2003a) based on RS results unpublished at the time (Gillespie and Soreng 2005). There are only three *Poa* species whose relationships within HAMBADD are completely unresolved in the strict consensus tree: *P. howellii*, *P. labillardieri*, and *P. paucispicula*. *Poa labillardieri* represents another distinct lineage found in Australia, the "Australopoa" species group. Because of the lack of resolution within the HAMBADD clade in RS analysis (Gillespie and Soreng 2005), fewer species were examined in this study. However, given the above encouraging results of phylogenetic structure it would be well worth examining cpDNA sequences of additional species expected to place within HAMBADD.

Only one species of *Poa* did not place as predicted in RS (Gillespie and Soreng 2005) and sequence analyses. *Poa paucispicula* is classified in sect. *Oreinos* in most recent classifications (Tzvelev 1976; Probatova 1985), but it resolved as a member of the HAMBADD clade in both studies, based on three and two samples, respectively. The species does not appear closely allied with any other HAMBADD species examined in the sequence analysis, differing in seven or more characters from all species except *P. howellii* (which lacks many characters due to a large deletion). Although possibly representing another case of cpDNA introgression, this is thought to be a case of mistaken classification, and the species has been tentatively transferred to a broadly defined sect. *Homalopoa* (Soreng et al. 2003a).

Poa Subgen. *Andinae* Excluded from *Poa*

Both RS (Gillespie and Soreng 2005) and sequence analyses place *Poa* subgen. *Andinae* in a clade outside of, but allied to, the main *Poa* clade (Fig. 1). Restriction site analysis resolved the two species examined, *P. andina* and *P. robusta*, in a strongly supported clade with *Arctagrostis*, *Arctophila*, and *Dupontia* sister to the main *Poa* clade (Gillespie and Soreng 2005). Sequence data confirm this placement, and also place three additional species of the subgenus here.

Poa subgen. *Andinae* of coastal and interior cold wetlands of South America was recently described by Nicora (1977, 1978) for six species from Patagonia (*P. andina*, *P. chonotica*, *P. pungionifolia*, and *P. robusta* examined here). The group has recently been expanded based on morphological criteria to include several additional species (Soreng et al. 2003a; R. J. Soreng unpubl. data). One of these, *P. subnervis*, is confirmed here as a member of the subgenus.

In this study, which included many additional genera of subtribe Poinae and allied subtribes beyond those in the most recent RS study (Gillespie and Soreng 2005), subgen. *Andinae* resolved within the strongly supported Poinae–*Alopecurinae* clade, one of two clades allied to the *Poa* clade. Relationships within this clade were mostly poorly resolved. Subgenus *Andinae* did not resolve as a clade, and there was minimal genetic divergence among species and few shared characters. In the analysis including gap characters (Fig. 1) its species were part of a weakly supported internal clade, which included *Arctagrostis* and *Bellardiochloa* (both in subtribe Poinae), and, curiously, *Alopecurus* (subtribe *Alopecurinae*). While subgen. *Andinae* unquestionably does not belong within *Poa* and should be recognized as a new genus in subtribe Poinae (or accommodated in an existing Poinae genus) based on both morphology (see discussion in Gillespie and Soreng 2005) and cpDNA, its precise affinities remain unclear.

Allied Genera Included within *Poa*

Chloroplast DNA sequence data confirm the position of *Arctopoa*, *Austrofestuca*, and *Parodiochloa* in the genus *Poa* (Fig. 2), a result first obtained based on RS data (Gillespie and Soreng 2005). All three had previously been treated both within *Poa* and as distinct genera. Based on the RS results the genus *Austrofestuca* s.s. was reduced to *Poa* sect. *Austrofestuca* and *Parodiochloa* was reduced to *Poa* sect. *Parodiochloa*. A recent study by Hunter et al. (2004) based on ITS nuclear DNA and *trnL-trnF* cpDNA sequence data also confirms *Austrofestuca* s.s. as a member of the *Poa* clade. Although generally treated within *Poa*, *Arctopoa* was considered as a separate genus by Probatova (1974, 1985) and Tzvelev (1989). Based on a very distinct morphology and our cpDNA results (*P. eminens* and *P. tibetica* examined here), the five *Arctopoa* species are maintained as a distinct subgenus within *Poa* following Probatova (1971), Tzvelev (1976), Olonova (1990), Soreng (1991, 1998), and Soreng et al. (2003a).

New to this study are the placements of *Anthochloa*, *Eremopoa*, and a second species of *Dissanthelium* within *Poa*.

Anthochloa.—The genus *Anthochloa* was firmly embedded within *Poa* as a member of the HAMBADD clade in our

sequence analysis (Fig. 2). This monotypic genus of the high montane Andes in Peru, Bolivia, and northern Argentina and Chile is characterized by a dwarf perennial habit and unusual, conspicuous, broadly expanded, flabellate lemmas (Nicora and Rúgolo de Agrasar 1987). Clayton and Renvoize (1986) considered the genus to belong to the small tribe Meliceae, while Tzvelev (1989) included it in tribe Poeae (Table 1). Most recently Soreng et al. (2003b) allied the genus with *Poa* by treating it in subtribe Poinae of tribe Poeae. Morphologically and cladistically, the single species can easily be accommodated within *Poa*. Its unusual flabellate lemmas, apparently an adaptation to wind dispersal, can be considered as a character apomorphic in *Poa*, rather than diagnostic of a genus. We consider *Anthochloa lepidula* to be a derived species of *Poa* worthy of recognition at the sectional level. Two new combinations are proposed:

Poa sect. **Anthochloa** (Nees & Meyen) Soreng & L. J. Gillespie, comb. et stat. nov.

Basionym: *Anthochloa* Nees & Meyen, Reise um die Erde 2: 14 (1834).

Poa lepidula (Nees & Meyen) Soreng & L. J. Gillespie, comb. nov.

Basionym: *Anthochloa lepidula* Nees & Meyen, Reise um die Erde 2: 14 (1834).

Eremopoa.—The genus *Eremopoa* is included within *Poa* as a very distinct and strongly supported lineage diverging between the BAPO clade and the three higher *Poa* clades (SPOSTA, PoM, and HAMBADD; Fig. 2). *Eremopoa* appears to represent a sixth major group within *Poa*, in addition to the five major clades previously described. The genus comprises seven annual, rather similar species distributed from the eastern Mediterranean region to western China (Bor 1960; Tzvelev 1976; Edmondson 1980; Mill 1985). As with other annual taxa in *Poa*, such as *P. annua*, branch lengths on the phylogram (Fig. 2) are long indicating considerable genetic divergence relative to other *Poa* species. Although the species were originally treated as a subgenus or section under *Festuca* and subsequently under *Poa* (Hackel 1887; Stapf 1896), all modern authors have recognized them as a separate genus. Tzvelev (1976) considered *Eremopoa* as close to *Poa* in subtribe Poinae, a treatment followed by Soreng et al. (2003b). Likewise Clayton and Renvoize (1986: 105) treated it as a separate and recognizable genus allied to *Poa*, but also mentioned that it is “barely distinct from *Poa*.” In contrast, sequence data support recognition of *Eremopoa* as a subgenus and section within *Poa*. The following names are available: *Poa* subgen. *Pseudopoa* (K. Koch) Stapf sect. *Pseudopoa* (K. Koch) Hack.

Dissanthelium.—The two species examined here were positioned firmly within the higher *Poa* clade HAMBADD. The genus *Dissanthelium* comprises 15–16 species distributed primarily in high-elevation Andean puna habitats in Peru, Bolivia, and Chile, with two disjunct species, one in central Mexico and one on islands off the coasts of southern California, USA, and Baja California, Mexico. Clayton and Renvoize (1986: 126) treated the genus in tribe Aveneae subtribe Aveninae (Table 1), but considered it of uncertain affinity and also mentioned that some species “might be

mistaken as depauperate *Poa*.” In contrast, Tzvelev (1989) treated the genus in tribe Poeae, and Soreng et al. (2003b) classified it further in subtribe Poinae. *Poa atropidiformis*, a species recently transferred to *Dissanthelium* (Soreng 1998), but then placed back into *Poa* (Soreng et al. 2003b) based on our RS results (Gillespie and Soreng 2005), is here reconfirmed as a member of *Poa* (Fig. 2). New evidence presented here suggests that *D. peruvianum* also belongs within *Poa*. Although belonging to the same large and mostly poorly resolved major clade HAMBADD, the two species examined do not resolve as a clade in our analysis. The remaining species of *Dissanthelium* are currently being studied by N. F. Refulio (RSA) to determine if the genus should be subsumed in total within *Poa*.

Outline of Proposed Infrageneric Classification of Poa

A new infrageneric classification of *Poa* is proposed based on our current knowledge of the phylogenetic systematics of the genus. This preliminary classification will need to be modified and expanded as new data on the phylogeny of *Poa* and related genera become available. Seven small sections of uncertain affinity have not yet been examined for cpDNA and of the six informal species groups only two have so far been sampled. Over 100 species have never been assigned to a section or informal species group (Gillespie and Soreng 2005: Table 1).

We propose an expanded subgeneric classification system of five subgenera corresponding for the most part to the major clades within *Poa*. *Poa* subgen. *Arctopoa* is expanded to accommodate sect. *Sylvestres*. The *Eremopoa* lineage is recognized as a distinct subgenus, subgen. *Pseudopoa*. In order to be consistent with recognizing this subgenus it is reasonable to recognize subgen. *Ochlopoa* (Asch. & Graebn.) Hyl. as the oldest name available for grouping the four sections resolved in the BAPO clade. Since the SPOSTA clade is once again resolved and membership is fairly easily identified, it seems appropriate to place the sections in this clade in a separate subgenus also (subgen. *Stenopoa*, new combination given below). The numerous sections comprising the sister clades PoM and HAMBADD make up a now-reduced subgen. *Poa*, and each clade is recognized as a supersection. The monophyly of all subgenera is strongly supported, with the exception of subgen. *Arctopoa*. The names of two sections widely used and given in Table 2, sects. *Bolbophorum* and *Ochlopoa*, are changed here based on priority. The following new subgeneric and supersectional combinations are proposed:

POA subgen. **Stenopoa** (Dumort.) Soreng & L. J. Gillespie, comb. et stat. nov.

Basionym: *Poa* sect. *Stenopoa* Dumort., Observ. Gramin. Belg. 110, 112 (1823 [1824]).

POA supersect. **Homalopoa** (Dumort.) Soreng & L. J. Gillespie, comb. et stat. nov.

Basionym: *Poa* sect. *Homalopoa* Dumort., Observ. Gramin. Belg. 110 (1823 [1824]).

Taxonomic synopsis of POA L.:

Subgen. ARCTOPOA (Griseb.) Prob. (ArcSyl clade)

- Sect. APHYDRIS (Griseb.) Trin.
- Sect. ARCTOPOA (Griseb.) Tzvelev
- Sect. SYLVESTRES Soreng
- Subgen. OCHLOPOA (Asch. & Graebn.) Hyl. (BAPO clade)
 - Sect. ALPINA (Nyman) Stapf
 - Sect. ARENARIAE Stapf (syn. sect. *Bolbophorum* Asch. & Graebn.)
 - Sect. MICRANTHERAE Stapf (syn. sect. *Ochlopoa* Asch. & Graebn.)
 - Sect. PARODIOCHLOA (C. E. Hubb.) Soreng & L. J. Gillespie
- Subgen. POA
 - Supersect. **Homalopoa** (Dumort.) Soreng & L. J. Gillespie (HAMBADD clade)
 - Sect. ACUTIFOLIAE Potztl
 - Sect. **Anthochloa** (Nees & Meyen) Soreng & L. J. Gillespie
 - Sect. AUSTROFESTUCA (Tzvelev) Soreng & L. J. Gillespie
 - Sect. BRIZOIDES Potztl
 - Sect. DASYPOA (Pilg.) Soreng
 - Sect. DIOICOPOA E. Desv.
 - Sect. HOMALOPOA Dumort
 - Sect. MADROPOA Soreng
 - “Austalopoa” species group
 - “Punapoa” species group
 - Supersect. POA (PoM clade)
 - Sect. LEPTOPHYLLAE J. R. Edm.
 - Sect. MACROPOA F. Herm. ex Tzvelev
 - Sect. NIVICOLAE (Roshev.) Tzvelev
 - Sect. POA
- Subgen. PSEUDOPOA (K. Koch) Stapf (syn. *Eremopoa* Rosh.)
 - Sect. PSEUDOPOA (K. Koch) Hack.
- Subgen. **Stenopoa** (Dumort.) Soreng & L. J. Gillespie (SPOSTA clade)
 - Sect. ABBREVIATAE Tzvelev
 - Sect. OREINOS Asch. & Graebn.
 - Sect. PANDEMOS Asch. & Graebn.
 - Sect. SECUNDAE Soreng
 - Sect. STENOPOA Dumort.
 - Sect. TICHPOA Asch. & Graebn.

Sections of uncertain affinity:

- Sect. GLARIOSAE Stapf
- Sect. MONANDROPOA Parodi
- Sect. NANOPOA J. R. Edm.
- Sect. PAUCIFLORAE Pilg. ex Potztl
- Sect. PLICATAE Pilg. ex Potztl
- Sect. SIPHONOCOLEUS Hitchc.

Generic Relationships and Affinities of Poa

Sequence analysis strongly supports a clade comprising subtribes Poinae (including *Poa*), Alopecurinae, and Miliinae (Fig. 1, PAM clade). This clade was also supported in Davis and Soreng’s (2006) analysis of subfamily Pooideae based on sequence data and in Soreng and Davis’s (2000) analyses based on cpDNA RS characters alone and RS and morphological characters combined.

Sequence data presented here suggest that *Poa* is one of three main lineages within the PAM clade, but relationships among the lineages are unresolved (Fig. 1, 2). These lineages

are: the main *Poa* clade, a Poinae–Alopecurinae clade comprising all other members examined of subtribe Poinae (*Arctagrostis*, *Arctophila*, *Bellardiachloa*, *Dupontia*, and *Poa* subgen. *Andinae*) plus two genera of subtribe Alopecurinae (*Alopecurus* and *Beckmannia*), and an Alopecurinae (*Phleum*)–Miliinae (*Milium*) clade. The sequence-based phylogeny of Davis and Soreng (2006) is consistent with the phylogeny presented here, although it is less resolved and includes fewer Poinae taxa. The RS study of Gillespie and Soreng (2005) also resolved a main *Poa* lineage sister to a clade of all other Poinae examined including *Poa* subgen. *Andinae* (Alopecurinae and Miliinae were not examined). Soreng and Davis (2000) resolved a different phylogeny based on RS and morphological data—one that has not found support in subsequent studies. In their study *Poa* and *Bellardiachloa* were resolved as sister taxa (excluding *Puccinellia stricta*, discussed below), this clade sister to a clade comprising *Arctagrostis* plus members of subtribes Alopecurinae and Miliinae, and *Dupontia* basal to all of the above. Although the studies differ in the order of branching within the PAM clade, all resolve a paraphyletic subtribe Poinae, with genera of Alopecurinae and sometimes Miliinae nested within. In the combined RS and morphology analysis (Soreng and Davis 2000), Alopecurinae and Miliinae resolved as a clade within Poinae, while in the sequence analyses presented here and in Davis and Soreng (2006) only *Alopecurus* and *Beckmannia* are placed within Poinae, and the position of *Phleum* and *Milium* is unresolved with respect to Poinae. The placement of *Alopecurus* and *Beckmannia* within Poinae and outside the Alopecurinae–Miliinae clade is odd, and may perhaps reflect something unusual in the evolution of this cpDNA region, rather than indicating a close relationship.

Subtribe Puccinelliinae is resolved with strong support as sister to the PAM clade in our study and in Davis and Soreng (2006), but not in Soreng and Davis (2000). *Puccinellia*, the largest genus in the subtribe, is generally considered close to *Poa* (Tzvelev 1976; Tutin et al. 1980; Clayton and Renvoize 1986), although historically placed nearer to or within *Glyceria* R. Br. (Bentham and Hooker 1883; Hitchcock 1935). However, analyses based on RS and morphological data resolved *Puccinellia* in the major clade including *Festuca* and allies with one exception (Soreng and Davis 2000). The Australian species *Pu. stricta* resolved as sister to *Poa* and was postulated to be an intergeneric hybrid (Soreng and Davis 2000). The species was resampled here and found to belong firmly in *Puccinellia* (the previous sample is suspected to have been a contaminant in the USDA seed source). Sequence data provide support for *Puccinellia* and allies as a distinct, genetically divergent lineage (subtribe Puccinelliinae) that is more closely related to *Poa* than the RS data suggested, with the two genera allied as members of a Puccinelliinae–PAM clade (Fig. 1).

Further insight into the affinities of *Poa* and precise relationships of Poinae genera plus allied Alopecurinae and Millinae genera await completion of broader sequence analyses focused on tribe Poeae using multiple, independently inherited genes.

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