

A Phylogenetic Analysis of the Bluegrass Genus *Poa* Based on cpDNA Restriction Site Data

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ABSTRACT. *Poa*, with about 575 species, is the largest genus of grasses, and has diversified throughout temperate, boreal, and arctic regions, and similar habitats through the tropics. This new phylogenetic study of *Poa* based on analysis of restriction site data from PCR amplified regions of chloroplast DNA (*trnT-trnE*, *trnF-trnV*, *trnV-rbcL*, *rbcL*-ORF106, *trnH-trnK*) expands previous sampling in the genus to where 1/5 to 1/6 of the species have been characterized for chloroplast DNA types. A broad phylogenetic structure detected in a previous study using restriction site mapping of *Poa* chloroplast DNA gained additional and robust support. Accounting for extended intra- and extragenic sampling, *Poa* remains monophyletic if *Austrofestuca* and *Parodiocloa* are included as sections within *P. subg. Poa*, and if *Poa subg. Andinae* is removed from the genus. Two new combinations are made: *Poa sect. Austrofestuca* and *Poa sect. Parodiocloa*. This new analysis supports the recognition of five major clades within *Poa*: 1) ArcSyl, *Poa subg. Arctopoa* sects. *Arctopoa* and *Aphydris*, and *P. subg. Poa sect. Sylvestres*; 2) BAPO, *P. subg. Poa* sects. (*Bolbophorum* + *Alpinae*) (*Parodiocloa* + *Ochlopoa*); 3) SPOSTA, *P. subg. Poa* sects. (*Secundae* (*Pandemos* (*Oriens* + *Stenopoa* + *Tichopoa* + *Abbreviatae*))); 4) PoM, *P. subg. Poa* sects. (*Poa* + *Macropoa*); 5) HAMBADD, *P. subg. Poa* sects. (*Homalopoa*, *Acutifoliae*, *Brizoides*, *Madropoa*, *Austrofestuca*, *Dasypoa*, *Dioicopoa*, and informal groups "Punapoa" and "Australopoa"). These clades diverge in the following arrangement from the outgroups: ArcSyl (BAPO (SPOSTA ((PoM) (HAMBADD))).

Poa L. is the largest genus of grasses. Independent assessments by Clayton and Renvoize (1986) and RJS indicate there are about 500 or 575 species, respectively (Table 1). The genus has diversified throughout temperate, boreal, and arctic regions, and islands of similar habitats through the tropics, at all latitudes habitable by vascular plants. *Poa* exhibits both high species diversity and a high degree of endemism in many regions. For example, there are 34 endemic species in Malesia (Veldkamp 1994), 36 species in Australia (Sharp and Simon 2002), and 34 in New Zealand (Edgar 1986), with only two or three native species shared between Australia and New Zealand, and none shared between these areas and the rest of the world. Extensive polyploidy, hybridization, and few useful morphological characters combine to make *Poa* a taxonomically challenging genus.

In contrast to other large grass genera (notably *Festuca* L. and *Panicum* L.), the monophyly of *Poa* has not been disproved, and no modern taxonomist nor data have seriously challenged its circumscription except by the removal of a few small, isolated groups of uncertain affinity. Modern revisions for several regions of the world have left *Poa* whole, or only removed one or a few species. In the opinion of RJS, there are few species that might be removed from the genus, but also a few small genera might be subsumed. Genera possibly belonging within *Poa*, or so little known as to require comparison, are *Aniselytron* Merr. (SE Asia; Korthof and Veldkamp 1984), *Austrofestuca* (Tzvelev) E. B. Alexeev (Australia; Alexeev 1976; Edgar 1986; Simon

1986; Jacobs 1990), *Dissanthelium* Trin. (mainly andean; Sorong 1998; Tovar 1993), *Dryopoa* Vickery (Australia; Vickery 1963), *Eremopoa* Rosh. (Mideast and central Asia; Bor 1960; Tzvelev 1976), *Neuropoa* Clayton (Australia; Clayton 1985), *Parodiocloa* C. E. Hubb. (Tierra del Fuego, Falkland and South Georgia Islands; Hubbard 1981; see comments in Edgar 1986), *Tzvelevia* E. B. Alexeev (Kerguelen Island; Alexeev 1985), and the *Colpodium* complex, comprising *Catabrosella* (Tzvelev) Tzvelev, *Colpodium* Trin., *Hyalopoa* (Tzvelev) Tzvelev, *Keniochloa* Meldris, and *Paracolpodium* (Tzvelev) Tzvelev (Mideast and central Asia, except for the african *Keniochloa*; Alexeev 1980; Alexeev and Tzvelev 1981; Hedberg and Hedberg 1994). Among these, only *Parodiocloa* is usually maintained in *Poa*, but its odd combination of characters has led some to exclude it. *Belardiocloa* Chiov., sometimes included in *Poa* (Clayton and Renvoize 1986) and sometimes not (Tzvelev 1976; Edmondson 1980, 1985), is now supported as a genus allied with, and possibly sister to, *Poa* in subtribe *Poinae* based on chloroplast DNA (cpDNA) analysis (Sorong et al. 1990; Sorong and Davis 2000). *Poidium* Nees, included in *Poa* by Clayton and Renvoize (1986) based on misunderstanding of the type element, has been confirmed as a genus in the *Briza* L. complex (Matthei 1975; Nicora and Rugolo de Agrasar 1981) within tribe *Aveneae* as it has *Aveneae* type cpDNA (Sorong et al. 1990; Sorong and Davis 2000).

The genus *Poa* has never been revised for more than one geographic region at a time, and in few cases has any one author been involved in revisions for more

than one region. *Poa* has been revised in Europe and Turkey (Edmondson 1978, 1980, 1985), the former USSR (Tzvelev 1976), Siberia (Olonova 1990), Russian Far East (Probatova 1985), Ethiopia and Eritrea (Phillips 1989, 1995), Iraq, Afghanistan, and Iran (Bor 1968, 1970), India, Pakistan, Nepal, Bhutan, Burma, and the Himalayas (Bor 1952a, 1952b, 1960; Melderis 1978; Rajbhandari 1991; Noltie 2002a, 2000b), Malesia (Veldkamp 1994), Australia (Vickery 1970; Simon 1993; Sharp and Simon 2002), New Zealand (Edgar 1986), and USA, Canada, and Latin America (Giussani 2000; Negritto and Anton 2000; Soreng et al. 2003a). A new treatment for China (Liou 2003) includes 231 validly published species, but this number is expected to decline substantially in the Flora of China, English edition (RJS with M. V. Olonova and Guanghua Zhu, in prep; the 575 world species estimate takes into account initial reductions to synonymy).

No worldwide classification of *Poa* currently exists, and there are few synthetic discussions of infrageneric variation within the genus as a whole (Edmondson 1975). All recent classifications are regionally based, and include those of Tzvelev (1976) for the former USSR, Edmondson (1978, 1980) for Europe, Soreng (1985, 1998) for North America, and Soreng et al. (2003a) for the New World. As understood here, *Poa* is divided into two small subgenera, *P.* subg. *Arctopoa* and *P.* subg. *Andinae*, and one large subgenus, *P.* subg. *Poa* (Table 1). *Poa* subg. *Arctopoa*, comprising five species, has also been recognized as a section in *Poa* (Tzvelev 1964) and as a separate genus (Probatova 1974, 1985). *Poa* subg. *Andinae* is a recently described subgenus (Nicora 1977, 1978) comprising a group of distinct *Poa* species from Patagonia, South America. *Poa* subg. *Poa*, with about 24 accepted sections identified and several recognizable infrasections, encompasses all of the other species in the genus.

Several other subgenera named within *Poa* are not recognized here. *Poa* sect. *Dioicopoa* had long been considered a subgenus by South American authors (Nicora 1977, 1978) and others, and was formally established in that rank by Edmondson (1978; see Soreng 1998), but clearly resolved within *P.* subg. *Poa* in cpDNA analyses (Soreng 1990; Gillespie and Boles 2001). *Poa* sect. *Ochlopoa* has been raised to a subgenus (Hylander 1953) and to a genus (Bohling and Scholz 2003), but no one has followed these treatments, and again cpDNA analysis put the section within a broadly defined *P.* subg. *Poa* (Soreng 1990; Gillespie and Boles 2001). Two other subgenera represent other genera: *Poa* subg. *Psilantha* (K. Koch) Boiss. belongs to *Eragrostis* Wolf. (subfam. Chloridoideae), and *P.* subg. *Pseudopoa* (K. Koch) Stapf is synonymous with the genus *Eremopoa*, a putatively close Asian relative of *Poa* (Tzvelev 1976; Clayton and Renvoize 1986).

The general phylogenetic structure of tribe Poeae

s.s. (i.e., excluding genera with Aveneae type cpDNA) was outlined based on cpDNA restriction sites (RS) and simultaneous analysis of these with morphological data by Soreng and Davis (2000). Two major lineages were detected. Subgroup 1 included subtribes Scolochloinae, Sesleriinae, Dactyliinae, Poinae, Alopecurinae, and Miliinae (*Avenula* (Dumort.) Dumort. and subtribes Airinae and Holcinae were also in this clade, but considered of possible hybrid origin). *Poa* is the largest genus in this clade. Subgroup 2 comprised subtribes Loliinae (*Festuca* and allies), Puccinelliinae, Cynosurinae, and Ammochloinae (= Parapholiinae), with *Festuca* the largest genus. Relationships within subgroup 2 have been further explored by Torrecilla and Catalán (2002) and Catalán et al. (2004) using ITS and cpDNA *trnL-trnF* sequence data. Their results did not agree in the placement of several subtribes; for example, subtribe Dactylidinae resolved within subgroup 2 and Puccinelliinae was allied with subtribe Poinae. No published study has yet focused on the subgroup that includes *Poa*.

DNA studies have been useful in delimiting *Poa* (Soreng and Davis 2000), interpreting its phylogenetic and biogeographic history (Soreng 1990; Gillespie and Boles 2001), identifying intergeneric hybrids (Darbyshire et al. 1992), detecting infrageneric hybridization and introgression, and characterizing infraspecific variation (Gillespie et al. 1997; Gillespie and Boles 2001). All previous phylogenetic analyses of the genus have been based on cpDNA restriction site (RS) analysis, and there have been none based on morphological data. Soreng (1990) identified five major clades and four subclades in *Poa* using RS analysis of whole cpDNA (mapped with various degrees of precision): (I *Arctopoa* + *Sylvestres*) ((II *Caespitosae* [= sect. *Alpinae*]) ((III *Ochlopoa*) ((IVa *Poa* + *Macropoa*) (IVb "Australopoa" (IVc1 *Homalopoa* + *Dasyopoa* + *Madropoa* + "Punapoa" (IVc2 *Dioicopoa*, the only clade of note resolved within the IVC polytomy))) ((VD *Secundae*) (VE *Pandemos* (*Stenopoa* + *Tichopoa* + *Abbreviatae* + *Oreinos*))))). Gillespie et al. (1997) and Gillespie and Boles (2001), using RS analysis of PCR products of cpDNA intergenic regions, detected essentially the same phylogenetic structure in *Poa*. In addition, focused sampling within species demonstrated the presence of significant infraspecific cpDNA variation in some species.

Chloroplast DNA RS analysis was chosen to construct an initial phylogenetic hypothesis of *Poa*. RS analysis, while less robust than sequence analysis, easily allows for the analysis of large numbers of individuals, which is particularly important in initial studies of taxonomically complex genera, such as *Poa*, and enables characterization of species and detection of multiple haplotypes. Given the high and variable ploidy levels of *Poa* and the potential problems associated with nuclear based phylogenies, such as multiple gene

TABLE 1. Classification of *Poa* with currently recognized subgenera and sections. For each section, the major cpDNA clade to which it belongs, approximate number of species, number of species sampled for cpDNA (including subspecific taxa in parentheses), and geographical region occupied are given. Species sampled include those in Soreng (1990) and two species, *P. badensis* and *P. infirma*, sampled by RJS, but previously unreported.

Subgenus	Section or major species group	cpDNA clade	# spp.	# spp. sampled	Geographical region
<i>Andinae</i>					
<i>Nicora</i>					
<i>Arcctopoa</i> (Griseb.) Probr.					
		–	8	2	Far South America (wetlands, sometimes saline) Central Asia and boreal North America
	<i>Aphladris</i> (Griseb.) Trin.	ArcSyl	4	1	Siberia, Mongolia, and Tibet (riparian, subalpine steppe)
	<i>Arcctopoa</i> (Griseb.) Tzvelev	ArcSyl	1	1	Boreal N Pacific and E Canada (seacoasts)
<i>Poa</i>					Worldwide
	<i>Abreviatæ</i> Tzvelev	SPOSTA	6	4 (5)	Beringia and W North American cordillera (arctic-alpine)
	<i>Acutifoliæ</i> Potztl	HAMBADD	2	1	South America (andean wet meadows)
	<i>Alpinae</i> (Nyman) Stapf	BAPO	7	3 ^a	Europe (montane), 1 circumboreal (low arctic-alpine)
	<i>Austrofestuca</i> (Tzvelev) Soreng & L. J. Gillespie (s.str.)	HAMBADD	2	1	Australia and New Zealand (coastal dunes)
	<i>Boilophorum</i> Asch. & Graebn.	BAPO	17	1	Mediterranean (grasslands and forest openings)
	<i>Brizoides</i> Potztl	HAMBADD	2	1	Japan and Australia (dunes and clay pan margins)
	<i>Disypoa</i> (Pilg.) Soreng	HAMBADD	3	3	Central and South America (andean, open ground)
	<i>Diotropoa</i> E. Desv.	HAMBADD	29	6	South America, 1 North America (steppe, prairie, alpine)
	<i>Honalopoa</i> Dumort.s.lat. (incl. <i>Diversipoa</i> Chrték & V. Jirásek)	HAMBADD	91	20	Worldwide, mainly 60°N to 40°S (cool temperate meadows, forest openings, and montane grasslands)
	<i>Leptophyllæ</i> J.R. Edm.	?	1	–	E Central Europe (mountain slopes)
	<i>Macropoa</i> F. Herm. ex Tzvelev	PoM	12	1	Asia (steppe)
	<i>Matropoa</i> Soreng	HAMBADD	11	6 (8)	W North America (coastal dunes, montane grasslands and meadows)
	<i>Monanotropoa</i> Parodi	?	1	–	South America (andean steppe)
	<i>Nanopoa</i> J.R. Edm.	?	1	–	S Europe (alpine, calciphile)
	<i>Nivicolæ</i> (Roshev.) Probr.	?	4	–	Far East Russia and Siberia (alpine meadows)
	<i>Ochlopoa</i> Asch. & Graebn.	BAPO	6	3 ^b	Mediterranean, Middle East, and Far East Asia (temperate, open ground to low alpine)
	<i>Oreinos</i> Asch. & Grabn.	SPOSTA	7	5	Circumboreal (wet subalpine to low arctic)
	<i>Pandemos</i> Asch. & Graebn.	SPOSTA	2	1	Mediterranean (meadows and forest openings)
	<i>Parodochloa</i> (C.E. Hubb.) Soreng & L. J. Gillespie	BAPO	1	1	Falkland, Magellanic and South Georgia Islands (coastal meadows and cliffs)
	<i>Paucifloræ</i> Pilg. ex Potztl (s.l.)	HAMBADD?	35	–	Borneo and New Guinea (mountain forest to alpine)
	<i>Plicatæ</i> Pilg. ex Potztl	HAMBADD?	1	–	Argentina (andean steppe)
	<i>Poa</i>	PoM	38	3 (9)	Circumarctic-boreal (mesic meadows to tundra)
	<i>Secundæ</i> Soreng	SPOSTA	9	8 (11)	North America, 1 Wrangell I., 2 Far South America (meadows, steppe, and open tundra)
	<i>Stenopoa</i> Dumort.	SPOSTA	59	6	Circumboreal, 1 South America (meadow, steppe, alpine and tundra)
	<i>Sylvestres</i> Soreng	ArcSyl	7	7	North America (temperate forests)
	<i>Tichopoa</i> Asch. & Graebn.	SPOSTA	2	1	Europe, possibly native in North America (mesic meadows)
	“ <i>Australopoa</i> ”	HAMBADD	35	5	Australia, few New Zealand (coastal to alpine grasslands and forest openings)

TABLE 1. Continued.

Subgenus	Section or major species group	cpDNA clade	# spp.	# spp. sampled	Geographical region
Poa?	"Jubatae"	?	1	1	SE Mediterranean (sandy coastal meadows)
?	New Zealand (uncharacterized)	HAMBADD?	33	—	New Zealand (coastal to alpine grasslands and forest openings)
?	"Punapoa"	HAMBADD	28	7	South America (andean steppe and puna)
?	Other	?	103	—	Africa, Arabia, India, Himalayas, and China
?	<i>Siphonocolletus</i> Hitchc.	?	3	—	Hawaii (cliffs)
?	"Darwinianae"	?	1	—	Magellanic Islands (wet rocks)
?	"Neuropoa"	?	1	—	Australia (dry interior, periodically inundated)
?	"Queenslandae"	?	1	—	NE Australia (rainforest margins)
TOTALS			575	98 (110)	

copies and pseudogenes, a chloroplast based phylogeny was preferred over a nuclear phylogeny as a first step. Recent DNA sequence studies by Torrecilla and Catalán (2002) and Catalán et al. (2004) on *Festuca* and allies have shown the nuclear and cpDNA phylogenies to be largely congruent, with conflict explained by past reticulation events.

Interspecific, intergeneric, and intertribal hybridization are a reality in the grasses. Although hybridization has long been postulated as a major source of variation in the grasses (Stebbins 1950), few wide crosses have been identified outside of experimental studies, and fewer yet (mostly in the wheat tribe, Triticeae) have been investigated in detail using sophisticated genetic analyses (Mason-Gamer 2001; Anderson 2002; Kishii 2002; Li 2002). Stabilized reticulation events of the distant past are difficult and time consuming to identify and characterize. To improve our understanding of this phenomenon in *Poa*, we believe that possible events should first be identified and characterized by deep sampling in the genus, including multiple populations of a species, and by comparison of cpDNA phylogenetic hypotheses with the traditional classifications based on morphology. From there, more detailed studies can focus on taxa that appear to be misplaced.

Here we present a new analysis of cpDNA lineages in *Poa*, following Gillespie's protocols, with extended world-wide and taxonomic diversity sampling. The goals of the study are to reassess the phylogenetic hypothesis of Soreng (1990), compare with previous classification systems (Tzvelev 1976; Edmondson 1980; Soreng 1998), identify contradictions in placements between cpDNA and traditional data, and evaluate the status of allied genera and isolated elements within *Poa*.

MATERIALS AND METHODS

Taxa Sampled. Seventy seven species (plus an additional ten infraspecific taxa) of *Poa* were chosen as a representative sectional, geographical, and morphological sample of worldwide diversity in the genus (Table 2). All three currently recognized subgenera of *Poa* were sampled, plus most sections and major species groups (Table 1). This included a species, *P. atropidiformis*, recently transferred to *Dissanthelium*, and another, *P. flabellata*, sometimes treated as the monotypic genus *Parodiochloa*. Species were included from all major geographic regions with the exception of Malesia and Africa. Material was unavailable for several small sections and species groups currently recognized in Europe and Russia, one section from the Hawaiian Islands, and two sections and three species groups from the southern hemisphere (Table 1). In addition, two genera, *Austrofestuca* and *Dryopoa*, considered as closely related to and possibly congeneric with *Poa* were sampled. The number of individuals sampled per species and subspecies of *Poa* ranged from one to 60 and one to 44, respectively.

Based on our previous cpDNA results (Gillespie and Boles 2001) *P. ammobila* is treated here as a distinct species rather than as a subspecies of *P. hartzii* (Soreng 1991). In addition, several collections treated as *P. pratensis* subsp. *pratensis* in our previous study were subsequently redetermined as *P. pratensis* subsp. *alpigena* (RJS, 2003). Collections of *P. pratensis* subsp. *agassizensis* (B. Boivin & D.

TABLE 2. Species of *Poa*, genera putatively related to *Poa* (*Austrofestuca*, *Dryopoa*), and outgroups (*Arctagrostis*, *Arctophila*, *Dupontia*, *Festuca*, *Lachnagrostis*, *Phippsia*, and *Puccinellia*) sampled for cpDNA analysis. Data are presented in the following sequence: Taxon, Section, ETU, Population location, Vouchers. Four vouchers indicated by “1” are from Soreng’s (1990) cpDNA study. Specimens of *P. pratensis* subsp. *pratensis* s.l. indicated by “2” and specimens of *P. pratensis* subsp. *alpigena* indicated by “3” were previously identified as *P. pratensis* subsp. *agnassizensis* and *P. pratensis* subsp. *pratensis*, respectively (Gillespie and Boles 2001). The collection of *Festuca rubra* (from Nicolson I., 69°53'N 129°02'W) lacks a herbarium voucher, but was identified based on leaf anatomy of silica gel dried leaf sample by L. Consaul (Canadian Museum of Nature). The two collections of *P. flabellata* are unvouchered collections made by Stony Wright in 2000 from the Falkland (Cape Dolphin, 51°14.165'S 58°57.882'W) and South Georgia Islands (Grytviken, 54°16.921'S 36°29.662'W).

- Arctagrostis latifolia* (R. Br.) Griseb., *Arctagrostis*, Canada, Nunavut, Gillespie et al. 6586, 6587 (CAN)
Arctophila fulva (Trin.) Rupr., *Arctophila*, Canada, Northwest Territories, Aiken 99-230 (CAN)
Austrofestuca pubinervis (Vickery) B. K. Simon, *Austrofestuca pubinervis*, Australia, Peterson et al. 14504 (US)
Dryopoa dives (F. Muell.) Vickery, *Dryopoa*, Australia, Soreng 5920 (US)
Dupontia fisheri R. Br., *Dupontia*, Canada, Nunavut, Gillespie et al. 6589, 6699 (CAN)
Festuca rubra L., *Festuca*, Canada, Northwest Territories
Lachnagrostis filiformis (G. Forst.) Trin., *Lachnagrostis*, Australia, Jacobs 8477 (NSW)
Phippsia algida (Sol.) R. Br., *Phippsia*, Canada, Nunavut, Gillespie 6253, 6668-1(CAN)
Poa abbreviata R. Br., sect. *Abbreviatae*, *abbreviata*, Canada, Nunavut, Gillespie 5724, 5731, 5810, 5814, 5816, 5818, 5957, 5959, 6028 (CAN); *Poa abbreviata* subsp. *pattersonii* (Vasey) Á. Löve, D. Löve & B. M. Kapoor, sect. *Abbreviatae*, *abbrev pattersonii*, USA, Alaska, Soreng 6292-1 (US); *Poa acinaciphylla* E. Desv., sect. *Acutifoliae*, *acinaciphylla*, Chile, Soreng 7169 (US); *Poa alpina* L., sect. *Alpinae*, *alpina*, Canada, Nunavut, Gillespie 5717, 5723, 6749-1 (CAN); Canada, Yukon, Soreng 5995-1 (US); Canada, Newfoundland, Djan-Chekar 00-126 (CAN); USA, Colorado, Gillespie 6299 (CAN); *Poa alsodes* A. Gray, sect. *Sylvestres*, *alsodes*, Canada, Quebec, Gillespie 6467 (CAN); *Poa cf. altaica* Trin., sect. *Stenopoa*, *altaica*, China, Tibet, Soreng 5530 (US); *Poa ammophila* A. E. Porsild, sect. *Secundae*, *ammophila*1, Canada, Northwest Territories, Gillespie 5851, 5869, 5870, 5882, 5883, 5890, 5892, 5908, 5910, 5911, 5912, 5915, 5916, 5921, 5933, 6397, 6398, 6403, 6405, 6448, 6451 (CAN); *ammophila*2, Canada, Northwest Territories, Gillespie 5909 (CAN); *Poa andina* Trin., subg. *Andinae*, *andina*, Chile, Soreng 7182 (US); *Poa androgyna* Hack., “Punapoa”, *androgyna*1, Chile, Peterson & Soreng 15707 (US); *androgyna*2, Chile, Peterson et al. 14637 (US); *Poa annua* L., sect. *Ochlopoa*, *annua*1, Canada, Ontario, Gillespie 6284 (CAN); Canada, British Columbia, Gillespie 6288 (CAN); *annua*2, Canada, British Columbia, Gillespie 6285 (CAN); *Poa arachnifera* Torrey, sect. *Dioicopoa*, *arachnifera*, USA, Oklahoma, Soreng 5801 (US); *Poa arctica* R. Br. subsp. *arctica*, sect. *Poa*, *arctica arctica*, Canada, Nunavut, Gillespie 5701, 5702, 5705, 5706, 5709, 5781, 5830, 5842, 6045, 6055, 6062, 6071, 6072, 6647 (CAN); Canada, Northwest Territories, Gillespie 5941, 6435 (CAN); Svalbard, Høigen 740-4 (O); *Poa arctica* subsp. *caespitans* Simmons ex. Nannf., sect. *Poa*, *arctica caespitans*, Canada, Nunavut, Gillespie 5704, 5722, 5843, 5964, 6041, 6044, 6068, 6069 (CAN); Svalbard, Høigen 078-5 (O); *Poa arctica* subsp. *lanata* (Scribn. & Merr.) Soreng, sect. *Poa*, *arctica lanata*, USA, Alaska, Soreng 6104-1, 6019-1, 6075-1 (US); *Poa arctica*, *viviparous* form, sect. *Poa*, *arctica viv*, USA, Alaska, Soreng 6037-1, 6055-2, 6106 (US); *Poa arida* Vasey, sect. *Secundae*, *arida*, USA, Oklahoma, Soreng 5802 (US); *Poa asperifolia* Bor., sect. *Stenopoa*?, *asperifolia*, China, Tibet, Soreng 5654 (US); *Poa atropidiformis* Hack., sect. *Homalopoa* s.l., *atropidiformis*, Chile, Soreng 7364 (US); *Poa autumnalis* Elliot, sect. *Sylvestres*, *autumnalis*, USA, Maryland, Soreng 4680 (US)
Poa bajaensis Soreng, sect. *Homalopoa*, *bajaensis*, Mexico, Peterson & Cayouette 15189 (US); *Poa bulbosa* L., sect. *Bolbophorum*, *bulbosa*1, USA, Nevada (introd. from Eur.), Soreng 5814 (US); *bulbosa*2, Spain, Catalán 13-2000 (UZ); *bulbosa*3, USA, Oregon (introd. from Eur.), Soreng 5952, 5958 (US)
Poa chaixii Vill., sect. *Homalopoa*, *chaixii*, Russia, St. Petersburg, Soreng 4677 (US); *Poa chambersii* Soreng, sect. *Homalopoa*, *chambersii*, USA, Oregon, Soreng 5858 (US); *Poa compressa* L., sect. *Tichopoa*, *compressa*, Canada, Quebec, Gillespie 6457 (CAN); USA, Colorado, Gillespie 6289 (CAN); *Poa curtifolia* Scribn., sect. *Secundae*, *curtifolia*, USA, Washington, Soreng 6347c1 (US); *Poa cusickii* subsp. *epilis* (Scribn.) W. A. Weber, sect. *Madropoa*, *cusickii epilis*, USA, Washington, Soreng 6350 (US); *Poa cusickii* Vasey subsp. *pallida* Soreng, sect. *Madropoa*, *cusickii pallida*1, USA, Nevada, Soreng 5829 (US); *cusickii pallida*2, USA, Nevada (“hansenii form”), Soreng 5830 (US); *Poa cuspidata* Nutt., sect. *Homalopoa*, *cuspidata*, USA, Maryland, Soreng 4679-3 (US)
Poa diaboli Soreng & Keil, sect. *Madropoa*, *diaboli*, USA, California, Frenzel & Haines s.n. (OBI); *Poa drummondiana* Nees, sect. *Brizoides*, *drummondiana*, Australia, Peterson et al. 14510 (US)
Poa eminens J. Presl, subg. *Arctopoa* sect. *Arctopoa*, *eminens*, Canada, Labrador, Gillespie 7010-3 (CAN); USA, Alaska, Soreng 6022 (US)
Poa fawcettiae Vickery, “Australopoa”, *fawcettiae*, Australia, Soreng 5919 (US); *Poa fendleriana* (Steud.) Vasey, sect. *Madropoa*, *fendleriana*1, USA, Colorado, Gillespie 6292, 6302 (CAN); *fendleriana*2, USA, Colorado, Gillespie 6308 (CAN); *Poa fernaldiana* Nannf., sect. *Oreinos*, *fernaldiana*, USA, New Hampshire, Gillespie 7015-3, 7017-2, 7019-5 (CAN); USA, New York, Gillespie 7013 (CAN); *Poa cf. fernaldiana* Nannf., sect. *Oreinos*, *fernald Baffin*, Canada, Nunavut, Gillespie 6731-1, 6731-5, 6731-8, 6734-1, 6738, 6775-1 (CAN); *Poa cf. fibrifera* Pilg., “Punapoa”, *fibrifera*, Chile, Peterson & Soreng 15615 (US); *Poa flabellata* (Lam.) Raspail, sect. *Paradiochloa*, *flabellata*, Falkland Islands, Wright 4NCD; South Georgia Islands, Wright 9NSG; *Poa flexuosa* Sm., sect. *Oreinos*, *flexuosa*, Norway, Brochmann 2000-3-1, 2000-3-3 (O), Brything 96-1-17 (O)
Poa glauca Vahl, sect. *Stenopoa*, *glauca*1, Canada, Nunavut, Gillespie 5700, 5715, 5802, 5804, 5805, 5823, 5831, 5834, 5963, 6005, 6006, 6007, 6755-1 (CAN); Canada, Northwest Territories, Gillespie 5873, 5897, 5913, 5931, 6353, 6452 (CAN); USA, Colorado, Gillespie 6303 (CAN); *glauca*2, Canada, Nunavut, Gillespie 5841 (CAN); Canada, Northwest Territories, Gillespie 5863, 5877 (CAN); *glauca*3, Canada, Northwest Territories, Gillespie & Consaul 6352 (CAN); *glauca*4, Chile, Soreng 7287 (US); *glauca*5, Canada, Quebec, Gillespie 6456 (CAN); *Poa glauca*, *viviparous* form, sect. *Stenopoa*, *glauca viv*, USA, Alaska, Soreng 6128-1 (US); *Poa glauca* × *hartzii*, *glauca* × *hartzii*1, Canada, Nunavut, Gillespie 6054 (CAN); *Poa grandis* Hand-Mazz., sect. *Homalopoa*, *grandis*, China, Soreng 5228 (US); *Poa gymnantha* Pilg., “Punapoa”, *gymnantha*, Chile, Peterson & Soreng 15656, 15730 (US)

TABLE 2. Continued.

- Poa hartzii* Gand. subsp. *hartzii*, sect. *Secundae*, *hartzii*1, Canada, Nunavut, Aiken 91-036 (CAN), Gillespie 5725, 5726, 5729, 5771, 5783, 5952, 6000, 6016, 6017, 6020, 6024, 6118, 6121, 6124 (CAN); Canada, Northwest Territories, Gillespie 6948-9, 6974-1, 6974-2, 6974-3, 6974-4 (CAN); Svalbard, Haïgen 719-3,730-4 (O), Nordal 95/5 (O); *hartzii*2, Canada, Nunavut, Gillespie 5738, 5740, 5807, 5824, 5833, 5835, 5849, 5945, 5960, 5988, 5990, 5997, 6130, 6146, 6319, 6323, 6333, 6351 (CAN); Canada, Northwest Territories, Gillespie 6397, 6398, 6948-7, 6951-6 (CAN); *Poa hartzii* subsp. *hartzii*, viviparous form, *hartzii*2 viv, Canada, Nunavut, Gillespie 6623-1, 6623-2, 6623-3, 6623-4, 6623-5, 6624-1 (CAN); Canada, Northwest Territories, Gillespie 6948-1, 6948-2, 6948-3, 6951-1, 6974-7, 6974-8, 6974-9 (CAN); USA, Alaska, Soreng 6242a-1 (US); *Poa hartzii* subsp. *alaskana* Soreng, sect. *Secundae*, *hartzii* alaskana, USA, Alaska, Soreng 6179-1, 6181-1 (US); *Poa holciformis* J. Presl, sect. *Diocopoa*, *holciformis*, Chile, Soreng 7166 (US); *Poa howellii* Vasey & Scribn., sect. *Homalopoa*, *howellii*, USA, Oregon, Soreng 5964 (US)
- Poa interior* Rydb., sect. *Stenopoa*, *interior*, USA, Alaska, Soreng 6136-1, 6333, 6346-1 (US)
- Poa kelloggii* Vasey, sect. *Sylvestres*, *kelloggii*, USA, California, Soreng 5962 (US); *Poa kurtzii* R. E. Fr., "Punapoa", *kurtzii*, Chile, Peterson & Soreng 15654 (US)
- Poa labillardieri* Steud., "Australopoa", *labillardieri*1, Australia, Soreng 5921 (US); *labillardieri*2, Australia, Jacobs 8483 (NSW); *Poa laetevirens* R. E. Fr., sect. *Dasypoa*, *laetevirens*, Chile, Peterson & Soreng 15641 (US); *Poa lanuginosa* Poir., sect. *Diocopoa*, *lanuginosa*, Chile, Soreng 7008 (US); *Poa leptocoma* Trin., sect. *Oreinos*, *leptocoma*, USA, Alaska, Soreng 6040-1, 6100 (US); *Poa* aff. *lilloi* Hack., "Punapoa", *lilloi*, Chile, Peterson & Soreng 15676 (US)
- Poa macrantha* Vasey, sect. *Madropoa*, *macrantha*, USA, Oregon, Soreng 5861 (US); *Poa macrocalyx* Trautv. & C. A. Mey., sect. *Poa*, *macrocalyx*, USA, Alaska, Soreng 6059-1, 6089-1, 6318-2 (US); *Poa marcida* Hitchc., sect. *Sylvestres*, *marcida*, USA, Alaska, Soreng 5974 (US); *Poa molinerii* Balb., sect. *Bolbophorum*, *molinerii*, Slovakia, Stoneberg Holt SH12 (BRNU)
- Poa napensis* Beetle, sect. *Secundae*, *napensis*, USA, California, Soreng 2926 (US); *Poa nemoralis* L., sect. *Stenopoa*, *nemoralis*1, USA, Maryland, Soreng 5856 (US); *nemoralis*2, USA, Oregon, Soreng 4682 (US); *nemoralis*3, USA, New York, Gillespie 6282 (CAN); *Poa nervosa* (Hook.) Vasey, sect. *Homalopoa*, *nervosa*, USA, Oregon, Soreng 5849 (US)
- Poa palustris* L., sect. *Stenopoa*, *palustris*, Canada, Ontario, Gillespie 6461 (CAN); *Poa paucispicula* Scribn. & Merr., sect. *Homalopoa* (previously *Oreinos*), *paucispicula*, USA, Alaska, Soreng 6033, 6101-1, 6169 (US); *Poa piperi* Hitchc., sect. *Madropoa*, *piperi*, USA, California, Soreng 5961 (US); *Poa porsildii* Gjaerev., sect. *Madropoa*, *porsildii*, USA, Alaska, Soreng 6147-1 (US); *Poa poiformis* (Labill.) Druce, "Australopoa", *poiformis*, Australia, Jacobs 8478 (NSW), Soreng 5911 (US); *Poa porphyroclados* Nees, "Australopoa", *porphyroclados*, Australia, Peterson et al. 14476 (US); *Poa pratensis* L. subsp. *pratensis* s.l., sect. *Poa*, *pratensis*, Canada, Quebec, Gillespie 6455, 6458 (CAN); Canada, British Columbia, Soreng 5986-2 (US); USA, Colorado, Gillespie 6291, 6309², 6310 (CAN); USA, New Hampshire, Gillespie 7018-4 (CAN); USA, New Mexico, Soreng 5803, 5805² (US); *Poa pratensis* subsp. *alpigena* (Lindm.) Hiitonen, sect. *Poa*, *pratensis*, Canada, Nunavut, Gillespie 5801, 5803, 5837, 6790-1 (CAN); Canada, Northwest Territories, Gillespie 5852³, 5858, 5866³, 5880, 5901³, 5927, 6358³ (CAN); Canada, British Columbia, Soreng 6340a-1 (US); USA, Alaska, Soreng 6023c, 6041-1 (US); USA, New Hampshire, Gillespie 7016-1, 7016-2 (CAN); Svalbard, Haïgen 715-4 (O); *Poa pratensis* subsp. *alpigena* var. *colpodea* (Th. Fr.) Soreng, sect. *Poa*, *pratensis*, Canada, Nunavut, Gillespie 5820, 5951, 6043 (CAN); Svalbard, Haïgen 746-2 (O); *Poa pratensis* subsp. *angustifolia* (L.) Lej., sect. *Poa*, *pratensis*, Canada, British Columbia (introduced from Europe), Soreng 5986-1 (US); *Poa pratensis* subsp. *irrigata* (Lindm.) H. Lindb., sect. *Poa*, *pratensis*, USA, Alaska, Soreng 6080a (US); *Poa pseudoabbreviata* Roshev., sect. *Abbreviatae*, *pseudoabbreviata*, USA, Soreng 6032-1 (US)
- Poa robusta* Steud., subg. *Andinae*, *robusta*, Chile, Soreng 7359 (US)
- Poa scaberula* Hook. f., sect. *Dasypoa*, *scaberula*, Chile, Peterson & Soreng 15575 (US); *Poa secunda* J. Presl. subsp. *secunda*, sect. *Secundae*, *secunda* *secunda*1, USA, Washington ("canbyi" form), Native Plants Inc. POCO4247; USA, Nevada, Soreng 5812 (US); USA, Oregon, Soreng 5951, 5859 (US); *secunda* *secunda*2, USA, Nevada, Soreng 5813 (US); *secunda* *secunda*3, Chile, Soreng 7293 (US); *Poa secunda* subsp. *juncifolia* (Scribn.) Soreng, sect. *Secundae*, *secunda* *juncifolia*, USA, Colorado, Soreng 5809 (US); USA ("ampla" form), Sharp Bros. Seed Co.; USA ("nevadensis" form), Davis et al. s.n. (BH); *Poa sieberiana* Spreng., "Australopoa", *sieberiana*, Australia, Jacobs 8482 (NSW); *Poa sikkimensis* (Stapf) Bor, sect. *Homalopoa*, *sikkimensis*, China, Soreng 5676 (US); *Poa stenantha* Trin., sect. *Secundae*, *stenantha*, USA, Alaska, Soreng 6068-1, 6099 (US); Chile, Soreng 7339 (US); *Poa stueckertii* (Hack.) Parodi, sect. *Diocopoa*, *stueckertii*, Chile, Soreng 7132 (US); *Poa supina* Schrad., sect. *Ochlopoa*, *supina*, USA, cultivated (from Europe), Soreng 5950-2 (US); *Poa sylvestris* A.Gray, sect. *Sylvestres*, *sylvestris*, USA, Maryland, Soreng 4678-3 (US)
- Poa tibetica* Stapf, subg. *Arctopoa* sect. *Aphydris*, *tibetica*, China, Tibet, Soreng 5481 (US); *Poa trivialis* L., sect. *Pandemos*, *trivialis*, USA, Maryland (introduced from Europe), Soreng 4681-1 (US)
- Poa cf. urssulensis* Trin., sect. *Stenopoa*, *urssulensis*, China, Tibet, Soreng 5634 (US)
- Poa wheeleri* Vasey, sect. *Homalopoa*, *wheeleri*1, USA, Nevada, Soreng 5825 (US); *wheeleri*2, USA, Washington, Soreng 5979 (US)
- Poa wolfii* Scribn., sect. *Sylvestres*, *wolfii*, USA, Missouri, Soreng 5800 (US)
- Poa* sp. 1, sect. *Homalopoa*?, China sp1, China, Gansu, Soreng 5461 (US)
- Puccinellia andersonii* Swallen, = *Pucc* *angustata*, Canada, Nunavut, Gillespie & Soreng 5790 (CAN); *Puccinellia angustata* (R. Br.) E. L. Rand. & Redfield, *Pucc* *angustata*, Canada, Nunavut, Gillespie 5732, 5733, 5784, 5786, 5836, 6159 (CAN); *Puccinellia arctica* (Hook.) Fernald & Weath., = *Pucc* *angustata*, Canada, Nunavut, Gillespie 5844 (CAN); *Puccinellia brugemannii* T. J. Sorensen, = *Pucc* *angustata*, Canada, Nunavut, Gillespie 5813 (CAN); *Puccinellia nuttalliana* (Schult.) Hitchc. (syn. *P. borealis* Swallen), = *Pucc* *angustata*, Canada, Nunavut, Gillespie & Consaul 6453 (CAN); *Puccinellia phryganodes* (Trin.) Scribn. & Merr., *Pucc* *phryganodes*, Canada, Nunavut, Gillespie 5850 (CAN); *Puccinellia poacea* T. J. Sorensen, = *Pucc* *angustata*, Canada, Nunavut, Gillespie 5744 (CAN); *Puccinellia vahliana* (Liebm.) Scribn. & Merr., *Pucc* *vahliana*, Canada, Nunavut, Gillespie 5808, 6682, 6794-1 (CAN)

Löve) R. L. Taylor & MacBryde in our previous study are treated here as *P. pratensis* subsp. *pratensis* s.l., since the former taxon is poorly understood and is not the focus of this study.

Six outgroup genera belonging to tribe Poeae s.s. were sampled (Table 2): *Arctagrostis* Griseb., *Arctophila* (Rupr.) Rupr. ex Anders-

son, *DuPontia* R. Br., *Festuca*, *Puccinellia* Parl., and *Phippsia* (Trin.) R. Br. One genus of tribe Aveneae was sampled: *Lachnagrostis* Trin.

DNA Extraction and PCR Amplification. Total DNA was extracted from silica-gel dried leaf tissue of individual plants following methods outlined in our previous studies (Gillespie et al. 1997;

Gillespie and Boles 2001). Extractions were also made using the DNeasy Plant Mini Kit (Qiagen, Mississauga, Ont.). For several Australian collections, DNA was extracted from leaf material preserved in absolute ethanol (*Jacobs 8482*) or preserved first in CTAB and then transferred to absolute ethanol (*Jacobs 8477, 8478, 8483*).

Five regions of the chloroplast genome located within the large single copy region were amplified via PCR: *trnT-trnF* (Taberlet et al. 1991), *rbcl-ORF106* (Arnold et al. 1991), *trnH-trnK* (Demesure et al. 1995), *trnF-trnV*, and *trnV-rbcL* (Dumoulin-Lapègue et al. 1997). The approximate length of each region in *Poa* is as follows: *trnT-trnF*, ~1800–1850 base pairs (bp); *trnF-trnV*, ~3100–3280 bp; *trnV-rbcL*, ~3900–4000 bp; *rbcl-ORF106*, ~2250–2550 bp; and *trnH-trnK*, ~1950–2000 bp. The five regions with their amplification reaction mixes and programs are described in previous studies (Gillespie et al. 1997; Gillespie and Boles 2001). Modifications made in this study include: 0.2 mM of each dNTP and an annealing temperature of 57°C for amplification of *trnT-trnF*; 1 μM of each primer, 0.2 mM of each dNTP, 20 μl “Q” solution (Qiagen), and 1 unit of Taq DNA polymerase for *rbcl-ORF106*. Length of the amplified products was estimated by comparison with known marker DNA ladders in 1.1% agarose gels stained with ethidium bromide (Sambrook et al. 1989).

The *rbcl-ORF106* region was difficult to amplify for many species using the primers described in Arnold et al. (1991), and was not successfully amplified for 27 species. Amplification problems were apparently due to the ORF106 primer, which appears to be part of variable spacer region, rather than a coding region as originally thought. A new “ORF106” primer was designed based on a new sequence of *Poa* generated using newly designed primers bounding the region containing the primer ORF106. This new primer has the following sequence: TTTTTCGACGAAGA-CCCGTCTGTGCAGC (ORF106bR). The region bounded by the original *rbcl* primer and the new ORF106 primer is about 50 bp shorter than the original region. Digests of this region could be easily interpreted in terms of restriction sites and were directly comparable to digests of the original region.

Restriction Site Analysis. Methods followed for performing restriction enzyme digests and the 25 enzymes used to screen for variable restriction fragment patterns are given in Gillespie et al. (1997) and Gillespie and Boles (2001). For this study, an additional eight species of *Poa* were screened to include sections not represented in the initial screening, and one additional outgroup, *Phippsia*, was screened.

Forty-four DNA region-enzyme combinations were determined to be useful, i.e., restriction fragment patterns were variable and interpretable within *Poa* and/or between *Poa* and outgroups. RS characters are as follows: *trnT-trnF* region with *Bst*OI enzyme (characters 1–2), *DdeI* (3–8), *DraI* (9–14), *EcoRI* (15–19), *NciI* (20), *RsaI* (21–22), *Sau3AI* (23–24), *XhoI* (25); *rbcl-ORF106* with *Bst*OI (26–27), *HaeIII* (28–30), *HhaI* (31–34), *MspI* (35–36), and *SinI* (37–39); *trnF-trnV* with *AluI* (40–47), *BglII* (48), *Bst*OI (49), *DdeI* (50–52), *EcoRI* (53–55), *HhaI* (56–60), *MspI* (61–69), *NciI* (70), *PstI* (71–72), *PvuII* (73), *RsaI* (74–78), *Sau96I* (79–80), *SinI* (81–82), *TaqI* (83–92), *XhoI* (93–94); *trnV-trnL* with *AluI* (95–97), *ApaI* (98–100), *BglII* (101), *DdeI* (102), *HaeIII* (103–106), *HincII* (107–108), *HinfI* (109–112), *PstI* (113), *SinI* (114–116); *trnH-trnK* with *AluI* (117–119), *DdeI* (120–121), *EcoRV* (122–123), *HaeIII* (124), *MspI* (125–127), *NciI* (128), and *PvuII* (129–130). Of these, one combination, *trnH-trnK* with *PvuII*, is new to this study.

All collections were analyzed for the 44 DNA region-enzyme pairs, with the exception of some collections belonging to extensively sampled taxa. These were analyzed for sites diagnostic for and variable within the major clade to which they belong. For example, some collections of *P. arctica* were processed only for sites informative for *P. sect. Poa*. Unusual results, such as unexpected placements or infrataxon variation, were checked by amplifying and digesting the DNA a second and often third time.

Restriction fragment patterns were interpreted in terms of RS presence (character state 1) versus absence (character state 0) (Dowling et al. 1990). For two regions, *trnF-trnV* and *rbcl-ORF106*, having considerable variation in length of PCR product, it was necessary to take length variation into account when interpreting

fragment pattern variation. Each taxon characterized by a single distinct RS profile was considered a separate evolutionary taxonomic unit (ETU). Where variation was detected within a taxon, collections were grouped based on RS profiles with each group representing a distinct haplotype considered as a separate ETU. Part way through this study we realized that the fragment patterns resulting from *MspI* and *NciI* digestion of the *trnF-trnV* region overlapped considerably, reflecting similar but not identical recognition sequences. Of the seven *NciI* sites included in our previous study (Gillespie and Boles 2001), six were identical to *MspI* sites and were thus excluded from the present study.

The final RS data matrix (TreeBASE study accession S1224, matrix accession M2124) comprised 120 ETUs and 130 RS characters, of which 22 are new to this study. For the purposes of the analysis six species of *Puccinellia* sharing an identical haplotype were considered as one ETU. The 120 ETUs represented only 81 different haplotypes, since some taxa shared the same haplotype. For example, all four subspecies and forms of *Poa arctica* examined shared the same haplotype. Data are for the most part complete, with missing data due primarily to unsuccessful amplification of a DNA region (2.5% missing data in total, 1.3% when the following two taxa are excluded). Considerable data are missing for two taxa, *Dryopoa dives* and *Poa* sp. 1, since amplifications were successful for only two of the five DNA regions, *trnT-trnF* and *trnH-trnK*, likely due to poor quality DNA. Three taxa (*P. annua*, *P. supina*, and *P. flabellata*) did not amplify for the *rbcl-ORF106* region with either the old or newly designed ORF106 primers.

The RS data matrix was analyzed by cladistic parsimony methods using the programs PAUP* version 4.0 beta 6 for Windows (Swofford 1998) and NONA (Goloboff 1999) used from within the interface WINCLADA (Nixon 2002). In PAUP* the heuristic search option was used with default settings, including a simple taxon addition sequence and tree bisection/reconnection (TBR) branch swapping. In NONA the heuristic search option was used with the multiple TBR+TBR search strategy, 20 replications and 20 starting trees held per replication. Characters were treated as normal reversible (Fitch parsimony, all character transformations equally likely) unless indicated otherwise. All outgroup taxa were included in the analyses, with *Lachnagrostis* used to root the cladograms a posteriori. Analyses were performed on the following data sets: 1) data matrix excluding the two taxa with extensive missing data, *Dryopoa* and *Poa* sp. 1, and two hypervariable characters, 26 and 29; 2) data matrix excluding *Dryopoa* and *Poa* sp. 1; and 3) complete data matrix. Data set 1 was also analyzed with characters treated as “Dollo” characters (parallel RS gains not allowed). Due to computational overload Maxtrees was set to 100,000 for analyses on data sets 2 and 3, and these analyses were repeated at least five times. PAUP* and NONA analyses gave identical trees and tree scores. Support for the cladistic relationships was assessed using bootstrap analysis (Felsenstein 1985) on data sets 1 and 2, with characters treated as normal reversible. Bootstrap analyses were performed in PAUP* with 10,000 replications and the fast stepwise addition search option. Bootstrap support values of 80% or more are considered strong support, those of 70–80% moderate support. WINCLADA was used to examine character state changes and consistency.

RESULTS

Cladistic analysis of data set 1 (i.e., excluding the two taxa with extensive missing data, *Dryopoa* and *Poa* sp.1, and two hypervariable characters, 26 and 29, discussed below) resulted in 2160 most parsimonious trees, 213 steps long with a consistency index excluding uninformative characters (CI) of 0.54 and a retention index (RI) of 0.93. The strict consensus tree showing bootstrap support (BS) values over 50% is illustrated in Fig. 1.

Analysis of data set 2 (i.e., excluding *Dryopoa* and

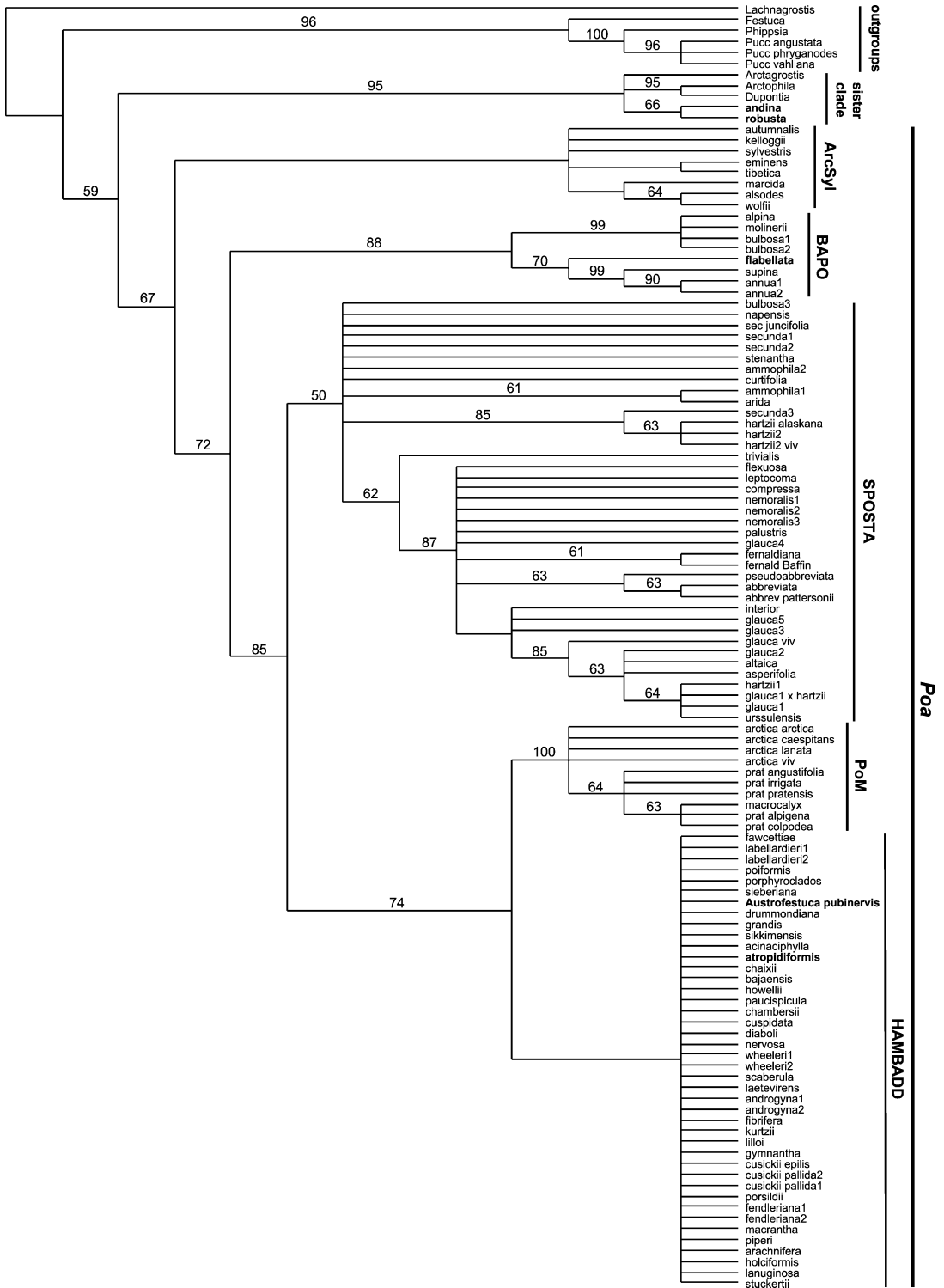


FIG. 1. Strict consensus tree of 2160 most parsimonious trees in analysis 1, Fitch parsimony analysis excluding highly variable characters 26 and 29 (Length = 213; CI = 0.54; RI = 0.93). Bootstrap values over 50% are given above branches. Abbreviations for terminal taxa are given in Table 2. The five major clades in *Poa* are labelled by acronyms defined in the text. *Poa* species not part of the *Poa* clade are indicated in bold. Species in the *Poa* clade belonging to other genera and those often included in other genera are indicated in bold.

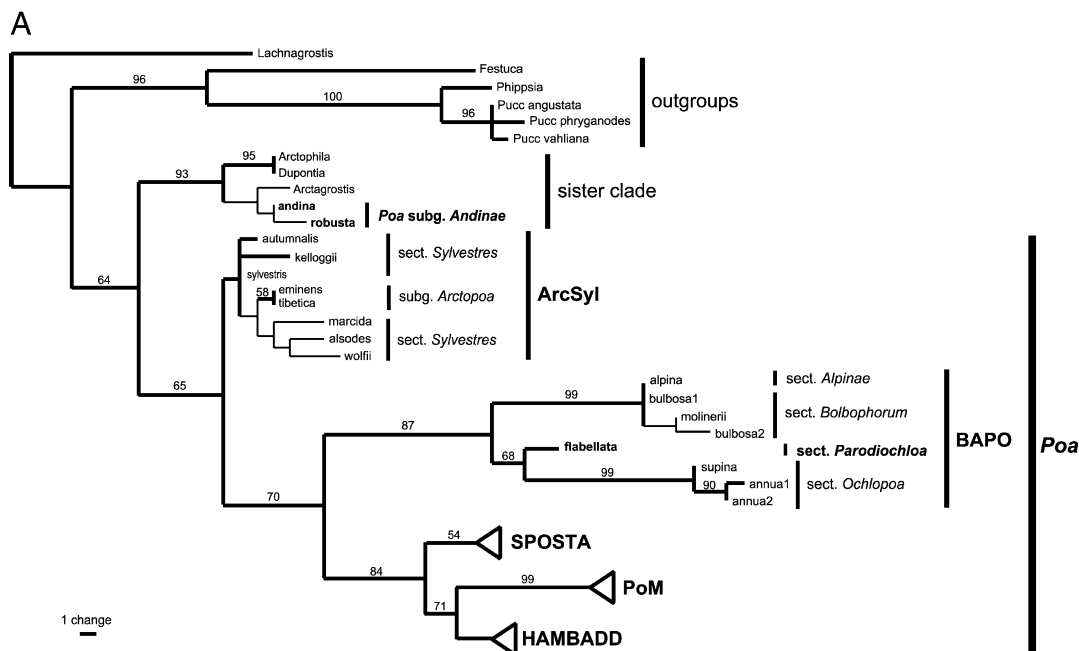


FIG. 2. One of 100,000 most parsimonious trees in analysis 2, Fitch parsimony analysis including highly variable characters 26 and 29 (Length = 230; CI = 0.51; RI = 0.92). The strict consensus tree is indicated by branches in bold and bootstrap values over 50% are given above branches. Abbreviations for terminal taxa are given in Table 2. The five major clades in *Poa*, labelled by acronyms defined in the text, and their component sections are given. *Poa* species not part of the *Poa* clade and species in the *Poa* clade belonging to other genera and those often included in other genera are indicated in bold. A. Basal clades of *Poa*, sister clade, and outgroups.

Poa sp.1) resulted in 100,000 most parsimonious trees, 230 steps long (CI, excluding uninformative characters = 0.51, RI = 0.92). One of the most parsimonious trees is illustrated in Fig. 2. Repeated analyses, all of which reached the Maxtree setting of 100,000, resulted in the same strict consensus tree (shown by bold lines in Fig. 2). The strict consensus tree was very similar to Fig. 1, and differed mostly in degree of resolution. The major difference was *P. sect. Secundae* as paraphyletic (Fig. 2B) rather than unresolved (Fig. 1). On the other hand, minor clades were generally less resolved in analysis 2. Clades present in the strict consensus tree in analysis 1 (Fig. 1), but not in analysis 2 (Fig. 2) were: (*P. andina* + *P. robusta*); (*P. marcida* (*P. alsodes* + *P. wolffii*)); and a clade comprising all *P. pratensis* subspecies plus *P. macrocalyx*. In addition, the *P. glauca* complex was less resolved, with *P. interior* and two *P. glauca* ETUs (*glauca3*, *glauca5*) not forming part of the main *P. glauca* clade.

Analysis of the complete data matrix (data set 3, 100,000 most parsimonious trees, 235 steps long, CI excluding uninformative characters = 0.50, RI = 0.92) resulted in a strict consensus tree identical to that of analysis 2 (Fig. 2), but including the two additional taxa, *Dryopoa* and *Poa* sp. 1. Repeated analyses, all of which reached the Maxtree setting of 100,000, resulted in the same strict consensus tree. *Dryopoa* resolved within the *Festuca*–*Phippsia*–*Puccinellia* outgroup clade

(only two of eight synapomorphies known for *Dryopoa*) and was positioned in a trichotomy with the *Festuca* branch and the *Phippsia*–*Puccinellia* clade. In the majority of trees, *Dryopoa* formed a clade with *Festuca*, sharing a single known synapomorphy, while in other trees *Dryopoa* diverged basal to the other three genera. The Chinese *Poa* sp. 1 formed a clade with *P. atropidiformis* within the HAMBADD clade of *Poa*, sharing two synapomorphies and differing by one character.

Treating characters as Dollo (i.e., parallel gains not allowed) in the analysis on data set 1 (i.e., excluding *Dryopoa*, *Poa* sp. 1, and characters 26 and 29) resulted in a similar strict consensus tree to Fig. 1, but somewhat more resolved (2304 trees, 260 steps, CI excluding uninformative characters = 0.44, RI = 0.98). The main difference from Figs. 1 and 2 was the sister relationship of ArcSyl and BAPO. Members of *P. sect. Secundae* resolved as a clade in this analysis versus a paraphyletic (Fig. 2B) or unresolved complex (Fig. 1) at the base of the SPOSTA clade. A third difference was *P. flabellata* diverging near the base of the clade comprising *P. sects. Alpinae* and *Bolbophorum*, rather than near the base of the *P. sect. Ochlopoa* clade (Fig. 2A).

All analyses resulted in strict consensus trees with the same basic primary structure, with *Poa* comprising the same five major clades (Figs. 1, 2: ArcSyl, BAPO,

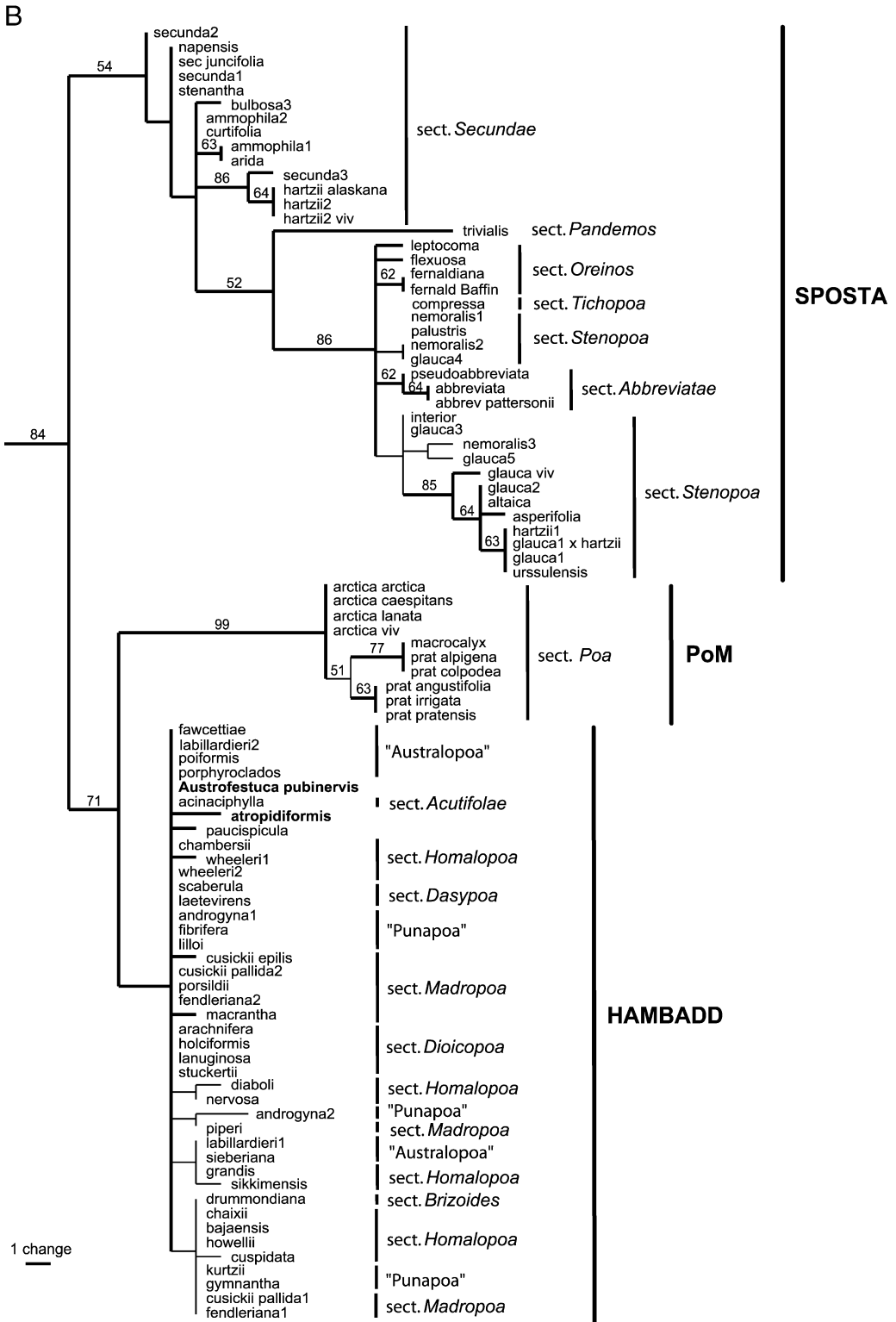


FIG. 2. (continued). B. Higher *Poa* clade.

SPOSTA, PoM, and HAMBADD). Differences among strict consensus trees were due to minor differences in branching order of taxa within a major clade, and rarely in branching order of major clades (only in the Dollo analysis). Differences among trees within an analysis were in minor rearrangements of taxa within major clades, even in analyses resulting in large numbers of trees. While some of the differences among trees can be explained by ambiguities due to missing data, others appear to be due to multiple origins of hypervariable characters.

Hypervariable Characters. To investigate levels of character homoplasy and consistency we examined the number of steps (length = L), CI, and RI (a measure of information content) of individual characters. In the analysis of data set 2 (i.e., including all characters, but excluded *Dryopoa* and *Poa* sp. 1), 109 of 130 characters were cladistically informative. Of these, about half (52 characters) were non-homoplasious (i.e., $L = 1$, 100% consistency, character state uniquely derived) and 14 had a single reversion or parallel gain ($L = 2$, 50% consistent). In contrast, nine characters showed a high level of homoplasy ($L \geq 5$, $CI \leq 20\%$). These nine sites are located mainly in the *trnT-trnF* (characters 5, 6, 10, 12) and *rbcL*-ORF106 (26, 29, 38) regions, with two in the *trnF-trnV* region (48, 56).

Three of these variable sites (5, 6, 48) had a low phylogenetic information content, potentially contributing more noise than structure to the cladogram. Characters 5 and 6 (*trnT-trnF*, *DdeI* enzyme) had five to six character state changes on individual trees. While loss of the RS in character 5 is one of six characters uniting *P. sect. Ochlopoa*, the same loss also occurred in several unrelated *Poa* species (*P. kelloggii*, *P. molinerii*, *P. atropidiformis*, and *P. sp.1*) and in *Lachnagrostis*. Both characters had low information content ($RI = 33$) and contributed little to cladogram structure, but did not result in any ambiguities in the phylogeny since losses occurred in unrelated taxa and were mostly autapomorphies. Likewise, a RS loss in character 48 (*trnF-trnV*, *Bgl* I; $RI = 42-57$) occurred in four unrelated lineages. Since it is a shared state only in some trees in one lineage (*P. andina* and *P. robusta*), this character resulted in only minor ambiguities.

Two characters with low consistency, but relatively high information content, were responsible for considerable phylogenetic noise. Character 26 (*rbcL*-ORF106, *Bst*O1) had a range of six to nine changes on individual trees ($RI = 72-82$). Character state changes, mostly RS gains, occurred in four of the five major *Poa* clades (none in the BAPO clade, but unknown for half of the ETUs) and its sister clade. Presence of the RS in *P. wolfii* (ArcSyl) and *P. robusta* (sister clade to *Poa*) and absence of the site in *P. pratensis* subsp. *alpigena* and *P. macrocalyx* (PoM) along with uncertainty of the ancestral state pulled these species to the base of their clades in

some trees, and was thus a main factor contributing to the lack of resolution in these clades. Nine ETUs in the HAMBADD clade often resolved as a clade (Fig. 2B) based on a shared RS gain, but sometimes formed an unresolved complex basal to all other HAMBADD members, depending on which state was considered ancestral.

Character 29 (*rbcL*-ORF106, *Hae*III) with six to eight character state changes and a high information content ($RI = 84-88$) was also responsible for lack of resolution in some clades and for the unexpected placement of several taxa. The character was variable in three of the five major *Poa* clades and its sister clade. Since absence of the RS was the most common state (and the only state in two *Poa* clades), this state was treated as ancestral in all clades. This resulted in the unexpected position of the *secunda2* ETU at the base of the SPOSTA clade (Fig. 2B) and lack of resolution in the ArcSyl and *Poa* sister clades in the strict consensus tree. Both characters 26 and 29 were determined to be part of a highly variable region located just downstream of the *rbcL* gene (Archambault and Gillespie 2003, unpubl. data). These hypervariable sites are useful in distinguishing among closely related species (e.g., *P. robusta* and *P. andina*), but in higher level studies result in ambiguities in cladogram structure, a very large number of most parsimonious trees, and sometimes unexpected and likely spurious placements and groupings of taxa. For this reason they were deleted from the main analysis.

Intraspecific Variation. Intraspecific variation in restriction sites was detected in 13 species of *Poa* (Table 2). Two haplotypes were detected in eight species: *P. annua*, *P. ammophila*, *P. androgyna*, *P. fendleriana*, *P. hartzii*, *P. labillardieri*, *P. pratensis*, and *P. wheeleri*. Four species, *P. bulbosa*, *P. cusickii*, *P. nemoralis*, *P. secunda*, had three haplotypes, while *P. glauca* had six haplotypes. Six hypervariable restriction sites (characters 10, 12, 26, 29, 38, 56) account for almost half of this intraspecific variation, including all the variation in *P. ammophila*, *P. androgyna*, *P. fendleriana*, *P. labillardieri*, and *P. pratensis*, and part of the variation in *P. cusickii*, *P. nemoralis*, *P. glauca*, and *P. secunda*. Additional intraspecific variation is accounted for by characters having zero information content, including two uniquely derived characters (68: *P. wheeleri*; 130: *P. glauca*, viviparous form) and two characters (89: *P. bulbosa*; 123: *P. nemoralis*.) with convergent apomorphic RS losses. While the majority of species with intraspecific variation have haplotypes that differ in one or few characters, two species, *P. hartzii* and *P. bulbosa*, have haplotypes that differ in numerous characters and are placed in different major clades (discussed under Hybridization and Reticulation).

Phylogeny. *Poa* is supported as a monophyletic clade (Fig. 1, BS = 67%; Fig. 2, BS = 65%), apart from

the inclusion or exclusion of several taxa. *Poa* subg. *Andinae* did not resolve in the *Poa* clade, but instead was included within the sister clade to *Poa*, together with the outgroups *Arctophila*, *Dupontia*, and *Arctagrostis* (Fig 1, BS = 95%; Fig. 2, BS = 93%). While relationships within this clade are unresolved overall, the two species examined, *P. andina* and *P. robusta*, were sister taxa in analysis 1 (BS = 66%), and in the majority rule consensus tree formed a clade with *Arctagrostis*. *Austrofestuca*, *P. atropidiformis* (most recently included within *Dissanthelium*), and *P. flabellata* (often treated as the monotypic genus *Parodiochloa*) fall well within *Poa*, while *Dryopoa* is placed in an outgroup clade comprising *Festuca*, *Phippsia*, and *Puccinellia*, and most frequently forming a clade with *Festuca*.

The major structure of the cpDNA phylogeny of *Poa* is supported with weak to strong bootstrap support (Figs. 1, 2). *Poa* can be subdivided into five major clades that are found in the strict consensus trees of all analyses performed. These clades, identified by acronyms based on their component sections, are described below. Note that description of cladogram structure refers to the strict consensus trees of all four analyses, unless indicated otherwise, and bootstrap values are given only for analyses 1 (first value) and 2 (second value).

ARC SYL (ARCTOPOA + SYLVESTRES). This is the basal clade within *Poa* (except in the Dollo analysis on data set 1 where a clade comprising ArcSyl and BAPO is basal-most), and comprises *P.* subg. *Arctopoa* and *P.* (subg. *Poa*) sect. *Sylvestres*. The clade itself has no bootstrap support (members share only one RS character), but its basal position within *Poa* and separation from all other *Poa* species has moderate support (BS = 72%, 70%; seven characters, four uniquely derived). Relationships within the clade are poorly resolved, with only four shared characters, none of which are uniquely derived (Fig. 2A). The two species of *P.* subg. *Arctopoa*, *P. eminens* and *P. tibetica*, shared an identical haplotype, distinguished from all other species of ArcSyl by a single character (25). In contrast, *P.* sect. *Sylvestres* did not resolve as a clade and species relationships were mostly unresolved, even though species differ by one to six characters. *Poa marcida*, *P. alsodes*, and *P. wolfii* resolved as a clade in the strict consensus trees of analysis 1 (Fig. 1, BS < 50%) and the Dollo analysis, but not in analyses 2 or 3.

BAPO ((BOLBOPHORUM + ALPINAE)(PARODIOCHLOA + OCHLOPOA)). Excluding ArcSyl this clade is sister to remaining *Poa* and comprises two sister groups, *P.* sects. *Bolbophorum* and *Alpinae* (BA subclade), and *Parodiochloa* and *P.* sect. *Ochlopoa* (PO subclade). The clade is strongly supported (BS = 88%, 87%) and its internal structure has mostly moderate to strong support (BS = 68–99%). The BA subclade is highly divergent, being characterized by nine synapomorphies, seven of which

are uniquely derived. *Poa* sect. *Ochlopoa* (*P. annua* and *P. supina*) is also a strongly supported, highly divergent clade (BS = 99%). *Poa flabellata* resolves as sister to *P.* sect. *Ochlopoa* (BS = 70%, 68%), except in the Dollo analysis where it is sister to the BA subclade.

SPOSTA (SECUNDAE (PANDEMOS (ORIENOS + STENOPOA + TICHOPOA + ABBREVIATAE))). All remaining species of *Poa* group into three main clades. The SPOSTA clade comprises *P.* sects. *Secundae*, *Pandemos*, *Oreinos*, *Stenopoa*, *Tichopoa*, and *Abbreviatae*. The clade is weakly supported (BS = 50%, 54%), united by three characters, two uniquely derived within *Poa*. The strict consensus trees show considerable structure within this clade with varying support (Figs. 1, 2B).

Species of *P.* sect. *Secundae* formed an unresolved complex at the base of the SPOSTA clade in analysis 1 (Fig. 1), a paraphyletic group in analyses 2 and 3 (Fig. 2B), and a clade in the Dollo analysis. In analyses 2 and 3, one of the *P. secunda* haplotypes (*secunda2*) resolved as the basal-most branch based on the hyper-variable character 29. The second branching event separates *P. napensis*, *P. stenantha*, and two *P. secunda* haplotypes from remaining species of SPOSTA, which are united by a single RS gain (character 74). Within *P.* sect. *Secundae* only two clades were present in all analyses (Figs. 1, 2B). One strongly supported clade (BS = 85%, 86%) groups the South American collection of *P. secunda* (*secunda3*) with the arctic species *P. hartzii*, the former curiously sharing two of the three uniquely derived synapomorphies of *P. hartzii*. The second clade comprises *P. ammophila* (the common haplotype) and *P. arida*, and is based on a shared RS loss in the highly variable character 56.

The remaining sections (*P.* sects. *Pandemos*, *Oreinos*, *Stenopoa*, *Tichopoa*, and *Abbreviatae*) form a weakly supported subclade POSTA (BS = 62%, 52%) united by three characters, two uniquely derived within *Poa* (characters 11, 117). *Poa trivialis* (*P.* sect. *Pandemos*) diverges at the base of this clade. The remaining sections form a strongly supported subclade OSTA (BS = 87%, 86%), united by four character state changes, including two uniquely derived RS gains (1, 22). Relationships within this clade are largely unresolved, with no separation of *P.* sects. *Stenopoa*, *Oreinos*, or *Tichopoa*. The only section that appears as monophyletic is *P.* sect. *Abbreviatae*, defined by one uniquely derived RS gain (2). *Poa compressa* (*P.* sect. *Tichopoa*) has a haplotype identical to *P. palustris* and one of the *P. nemoralis* haplotypes, both in *P.* sect. *Stenopoa*. Two of four taxa examined of *P.* sect. *Oreinos*, *P. fernaldiana* and a related taxon from SE Baffin Island, share an identical haplotype distinguished by one RS loss (93) unique within SPOSTA. All analyses reveal a strongly supported *P. glauca* complex clade (BS = 85%), comprising the majority of *P. glauca* collections sampled (three of six haplotypes, all North American) plus three Chinese-Cen-

tral Asian species (also included here is one of two *P. hartzii* subsp. *hartzii* haplotypes, discussed under Hybridization and Reticulation). The strict consensus tree in analysis 1 (Fig. 1), but not in other analyses, also shows a larger *P. glauca* complex clade (comprising the latter plus *P. interior* and two additional North American *P. glauca* haplotypes).

PoM (POA + MACROPOA). The clade grouping all taxa of *P. sect. Poa* is strongly supported (BS = 100%, 99%), with eight synapomorphies, including four uniquely derived within *Poa* (Figs. 1, 2B). Based on these results and those of Soreng's (1990) cpDNA analysis we define the PoM clade as comprising *P. sects. Poa* and *Macropoa*.

Three haplotypes were distinguished within *P. sect. Poa*, corresponding to the following taxa: *P. arctica*; *P. pratensis* subsp. *pratensis*, *angustifolia*, and *irrigata*; and *P. pratensis* subsp. *alpigena* (including var. *colpodea*) and *P. macrocalyx*. The latter haplotype is characterized by a large deletion in the *rbcL-ORF106* region. In the strict consensus trees in analysis 1 (Fig. 1) and the Dollo analysis a clade comprising all *P. pratensis* ETUs plus *P. macrocalyx* is supported by a unique RS loss (37). When character 26 is included (analyses 2 and 3), relationships among the three haplotypes are unresolved, since presence of the site groups *P. arctica* and the *P. pratensis* subsp. *pratensis* s.l. haplotype in some trees.

HAMBADD (HOMALOPOA + ACUTIFOLAE + MADROPOA + BRIZOIDES + AUSTRIFESTUCA + DIOICOPOA + DASYPOA). The final major clade comprises *P. sects. Homalopoa*, *Acutifolae*, *Madropoa*, *Brizoides*, *Austrifestuca*, *Dioicopoa*, *Dasyopoa*, and the "Australopoa" and "Punapoa" species groups. Although the clade was present in the strict consensus trees of all analyses, with all members sharing two RS losses (characters 15, 38; some taxa unknown for 15), it does not have bootstrap support.

Despite its size and taxon diversity, HAMBADD shows no internal structure in the strict consensus trees of analyses 1 and 2 (Figs. 1, 2B). A single clade is present in analysis 3 (Chinese *Poa* sp.1 and Chilean *P. atropidiformis* based on characters 4 and 5) and the Dollo analysis (*P. nervosa* and *P. diaboli*). Although 12 characters vary in HAMBADD in analysis 2, only four are shared by two or more taxa (Fig. 2B). Three characters are unique autapomorphies (characterizing ETUs *androgyna2*, *sikkimensis*, *wheeleri1*), while five (mostly RS losses) are autapomorphic within the PoM-HAMBADD clade. In analysis 2 cladograms show various groups based on one of the four shared characters (10, 12, 16, 26). Only characters 10 and 12 are homoplasious within HAMBADD. Character 12 (L = 5–6, RI = 83–86) groups two Chinese species of *P. sect. Homalopoa* with two species of "Australopoa." One of the two haplotypes of South American *P. androgyna* ("Pun-

apoa") also shares this character and is either included in this clade or with *P. piperi* of western USA (or sometimes both included in clade) based on a shared RS loss in character 10 (L = 4–5, RI = 92–94). Two species of western USA, *P. nervosa* and *P. diaboli*, share a RS loss (character 16, L = 3, RI = 85) and resolve as either a derived clade (Fig. 2B) or an unresolved complex basal to all other HAMBADD members depending on which state is considered ancestral. The hypervariable character 26 groups nine taxa belonging to *P. sects. Homalopoa*, *Madropoa*, *Brizoides*, and "Punapoa" in the majority of trees also depending on which state is ancestral (Fig. 2B).

DISCUSSION

Generic Boundary and Relationships of *Poa*. The phylogenetic analysis presented here indicates that *Poa* can be maintained as monophyletic if certain changes are made in its circumscription. However, the final makeup of the genus will remain unclear until all of the small, often isolated, putatively related taxa can be sampled. New evidence is presented here for five of these taxa, of which three should be included within *Poa*: *Austrifestuca*, *Parodiochloa*, and *Dissanthelium* (pro parte). Our results also suggest that *Poa* subg. *Andinae* should be excluded from the genus and that *Dryopoa* is not closely related to *Poa*.

TAXA INCLUDED WITHIN *POA*. *Austrifestuca* in the strict sense comprises two species of Australia and New Zealand (Simon 1986) [or one if *A. pubinervis* is included within *A. littoralis* (Labill.) Alexeev (Sharp and Simon 2002)]. Species were originally described in *Festuca* and treated as *F. subg. Austrifestuca* Tzvelev. The type species was subsequently recognized within *Poa* (St. Yves 1927; Zotov 1943), but this treatment was not generally followed. Alexeev (1976) elevated the subgenus to the rank of genus, a treatment accepted by Clayton and Renvoise (1986: 103) who considered it to be "an enigmatic genus" with a greater resemblance to *Poa* than *Festuca*. Most recently, *Austrifestuca* has been recognized in a broader sense by Clayton and Renvoise (1986) and Jacobs (1990) to include two monotypic Australian genera, *Hookerochloa* E. B. Alexeev and *Festucella* E. B. Alexeev, described by Alexeev (1985) for two species of *Festuca* (Vickery 1939). Based on our sampling (*A. pubinervis*, from Australia) *Austrifestuca* s.s. belongs in *Poa* in the derived HAMBADD clade, which is part of a strongly supported higher *Poa* clade (SPOSTA, PoM, and HAMBADD). This is consistent with the only other study, a preliminary DNA sequence study of *Festuca* by Lloyd et al. (2003), in which *A. littoralis* (from New Zealand) resolved as sister to a HAMBADD member above *P. pratensis* (pers. comm.). *Festucella eriopoda* (Vickery) E. B. Alexeev and *Hookerochloa hookeriana* (F. Muell. ex Hook. f.) E. B. Alexeev still need to be sampled to determine if all mem-

bers of *Austrofestuca* s.l. belong within *Poa*. These two species have some characters that preclude their immediate submersion into *Poa* (e.g., well developed awns) suggesting a possible affinity with *P.* subg. *Andinae*.

Austrofestuca s.l. has few diagnostic features to distinguish it from *Poa*, and shares some features with *Poa* s.s. and others with *Poa* subg. *Andinae*. Unlike *Poa* s.s., *A. littoralis* and *A. pubinervis* have a pointed lemma apex ("muticious" or "mucronate"), while *Festucella* and *Hookerchloa* have a distinct apical awn as in *Poa* subg. *Andinae*. All four species have a callus bearded with short straight hairs and villous hairs on the rachilla, and the distribution and form approach those found in some *Poa*, including *P.* subg. *Andinae* species. They have long spikelets (reaching 14–18 mm) and lemmas, additional glume nerves (five total, though the extra pair is short and sometimes obscure or absent), and lemmas sometimes with seven to 11 nerves. Aside from the awns, these states are all present, though variable, in *P. macrantha* and *P. douglasii* Nees of North America, the former a demonstrated HAMBADD member, and both coastal dune species like *A. littoralis* and *A. pubinervis*. *Austrofestuca* s.l. has typical *Poa* leaf cross-sectional anatomy (Alexeev 1985), with only two rows of bulliform cells, and shallow depressions between the lateral ridges, as well as sclerenchyma distributions common to other stout leaved *Poa*, but very unlike *Poa* subg. *Andinae*.

Parodiochloa is a monotypic genus (Hubbard 1981; Edgar 1986) of Tierra del Fuego, and the Falkland and South Georgia Islands. It is generally included in *Poa* subg. *Poa* as *P. flabellata* (Nicora 1978; Moore 1983; Clayton and Renvoize 1986). In our analysis both samples (from the Falklands and South Georgia) clearly align together in *Poa* within a strongly supported BAPO clade. The species is a large tussock grass, reaching 1 m in height, of open coastal peaty bogs and rocky habitats. Other unusual features are the usually shortly-awned lemmas, basally fused styles, ciliate lodicules, and the hispidulous to short villous rachilla. Some of these character states are shared with *Poa* subg. *Andinae*, *Austrofestuca*, *Festucella*, and *Hookerchloa*. The species lacks a dorsal woolly tuft of hairs (web) as in most *Poa*, a distinct beard (as in *Austrofestuca* s.l.), or a crown of hairs on the callus (some *Poa* subg. *Andinae*, *P.* sects. *Arctopoa* and *Secundae*). However, it has a leaf epidermis like *Poa* and *Austrofestuca* s.l., rather than like *P.* subg. *Andinae*. Although *Parodiochloa* resolved within BAPO, it appears to have no obvious derived morphological characters in common with other members of the clade.

Dissanthelium is a genus of 15–16 species distributed primarily in the Andes of Peru, Bolivia, and Chile (Tovar 1993). Soreng (1998) hypothesized that the genus is likely to be either a sister group to or an offshoot of

Poa based on similarities in leaf and caryopsis morphology. The Patagonian species, *P. atropidiformis*, was recently transferred to *Dissanthelium* based on similarity in spikelet morphology (Soreng 1998), while a variety of this species had originally been described as a species of *Dissanthelium*, *D. patagonicum* Parodi. In our analysis *P. atropidiformis* resolved in the derived HAMBADD clade and is strongly supported as a member of *Poa*. Based on these results the species has now been placed back into *Poa*, provisionally in a broadly defined *P.* sect. *Homalopoa* (Soreng et al. 2003a). The affinities of the remaining species of *Dissanthelium* still need to be examined to determine the status of this genus.

Arctopoa (Griseb.) Prob. is confirmed here as belonging within *Poa*. Species were mostly originally described in *Poa*, subsequently placed in a section of *Glyceria* R. Br. (Grisebach 1852), then reunited with *Poa* as a section (Tzvelev 1964), raised to a subgenus (Probatova 1971), and then recognized as a separate genus (Probatova 1974, 1985). Tzvelev (1976) maintained them in *Poa* as *P.* subg. *Arctopoa* with two sections, and this was followed by Olonova (1990) and Soreng (1991, 1998). *Poa eminens* is the sole species of *P.* sect. *Arctopoa* and occurs along boreal seashores and tidal marshes in the Russian Far East, Alaska, and eastern Canada. The four species of *P.* sect. *Aphydris* occur in weakly alkaline to saline wetlands in interior Far East Russia, Siberia, Mongolia, and Tibet. *Poa eminens* was demonstrated to belong within *Poa* by cpDNA RS analysis (Soreng 1990), a position confirmed here. New to this study is the placement of *P. tibetica* (*P.* sect. *Aphydris*) within *Poa* as sister to *P. eminens*, consistent with its traditional classification.

NEW COMBINATIONS IN *POA*. Based on our results confirming placement of two segregate genera within *Poa*, two new sectional combinations are made as follows:

***Poa* sect. *Austrofestuca* (Tzvelev) Soreng & L. J. Gillespie, stat. nov.** Basionym: *Festuca* subg. *Austrofestuca* Tzvelev, Bot. Zhurn. (Moscow and Leningrad) 56: 1257 (1971). TYPUS: *Festuca littoralis* Labill. [= *Poa billardierei* St.Yves, syn. *Poa triodioides* Zotov].

***Poa* sect. *Parodiochloa* (C. E. Hubbard) Soreng & L. J. Gillespie, stat. nov.** Basionym: *Parodiochloa* C. E. Hubbard, Bull. Brit. Mus. 8: 395 (1981). TYPUS: *Poa flabellata* (Lam.) Raspal.

TAXA EXCLUDED FROM *POA*. Our results suggest that the two examined species of *Poa* subg. *Andinae* (including the type species) should be excluded from the genus. The subgenus was recently described by Nicora (1977, 1978) for six species of *Poa* from Patagonia, South America. On morphological grounds, the subgenus should probably be expanded to include a few

additional species, *P. subenervis* Hack. of the same region (but *P. stepparia* Nicora excluded), and *P. cookii* (Hook. f.) Hook. f. and *P. ramosissima* Hook. f. from subantarctic islands. All species occur in cold wetlands, either coastal or brackish to fresh water interior ones. *Poa* subg. *Andinae* is distinct on morphological grounds, sometimes having well developed lemma awns (*P. andina*, awns to 3 mm long), fairly strongly ciliate ligules, a loose crown of callus hairs, and always with leaves with multiple, block-like and highly sclerified, longitudinal ridges adaxial to each vascular bundle, each ridge separated by narrow furrows with rows of bulliform cells. This combination of features is otherwise absent in *Poa*, but is similar to that found in *Bellardiachloa* (lemma awned, crown of callus hairs, and similar adaxial leaf blade epidermal features). Our preliminary data suggest that *P.* subg. *Andinae* is misplaced in *Poa* and should be considered a separate genus, belonging near *Arctagrostis*, *Arctophila*, and *Dupontia*. More extensive sampling of Poae genera is necessary for a more precise placement of the taxon.

Dryopoa is a monotypic genus of Australia, considered by its author to be allied with *Poa* (Vickery 1963). Its sole species was originally described in *Festuca* and then transferred to *Poa*, before being considered as a separate genus. More recently, *Dryopoa* has been allied with *Scolochloa* Link, and both genera considered as segregates of *Festuca* (Clayton and Renvoise 1986). Our analysis, based on incomplete data, supports placement near *Festuca*, rather than near *Poa*.

INFRATRIBAL RELATIONSHIPS. Analyses presented here resolve a Poinae clade, consistent with Soreng and Davis's (2000) analyses resolving a clade comprising subtribes Poinae, Alopecurinae, and Miliinae (the latter two not examined here). However, the two studies do not agree on structure within this clade and the closest ally of *Poa*. Soreng and Davis in both cpDNA and combined cpDNA and morphological analyses resolve *Poa* and *Bellardiachloa* as sister taxa [excluding *Puccinellia stricta* (Hook. f.) Blom] and the following structure: *Dupontia* ((*Bellardiachloa* + *Poa*) (*Arctagrostis* (*Milium* + *Beckmannia* + *Alopecurus* + *Phleum*))). Here *Poa* was sister to a strongly supported clade comprising all other Poinae genera sampled, *Arctagrostis*, *Dupontia*, *Arctophila*, and *P.* subg. *Andinae*.

Although infratribal relationships were not the focus of this study and few Poae genera were included, our results are consistent with Soreng and Davis's (2000) alignment of *Phippsia* and *Puccinellia* with the *Festuca* lineage, rather than with the study by Catalán et al. (2004), which supports its traditional alignment closer to *Poa* (Clayton and Renvoise 1986). Among the more than 20 species of *Puccinellia* evaluated for RS variation, all have proved to have a cpDNA type only remotely related to *Poa* and allied to *Phippsia*, *Scolochloa*, and *Catabrosa* Trin. (Soreng 1990; Choo et al. 1994; Gillespie

and Boles 2001). This group of allied genera is now treated as subtribe Puccinelliinae (Soreng et al. 2003b). *Puccinellia stricta*, reported by Soreng and Davis (2000) as sister to *Poa*, is now considered a probable sample switching error since new unpublished cpDNA sequence data of LG place the species within *Puccinellia*.

Phylogeny and Major Clades of *Poa*. The cpDNA phylogeny presented here, for the most part, is consistent with currently recognized classification systems of *Poa* (Tzvelev 1976; Edmondson 1980; Soreng 1998). The phylogeny closely matches the traditional species groups, infrageneric classification, and ideas on phylogenetic relationships based on morphological characters, and has allowed us to place some of the many species and species groups that have never previously been incorporated into an infrageneric classification. Despite extensive hybridization, polyploidy, and reticulation, and the suggestion of the genus as "a single huge polyploid complex" (Stebbins 1950, p. 405), there is considerable phylogenetic structure within the genus and clearly defined major clades based on cpDNA. There appears to be much deeper structure in *Poa* than is implied by its simple division into two subgenera.

Congruence among the cpDNA RS phylogenies presented here and in Soreng (1990) and Gillespie and Boles (2001) suggests that the proposed cpDNA phylogeny of *Poa* is highly stable. Soreng's analysis was based on a mostly independent set of restriction sites detected using digests of total cpDNA (only four enzymes were shared between the two studies, corresponding to a maximum overlap in sites of 7.7%), and included numerous species not sampled here (23 species in common, about 50% of the species were not resampled here). Gillespie and Boles's study, focused primarily on arctic species of *Poa*, was based on the same methods and DNA regions utilized here, but included fewer taxa (34 versus 92 in the present study). All three analyses support the division of *Poa* into five major clades (albeit with some differences in circumscription in Soreng's study) and the position of *ArcSyl* as the basal-most clade. Correspondence between the clades in Soreng's analysis and those defined here is as follows: Soreng's cpDNA group I = *ArcSyl*; groups II and III = BAPO; group IVA = PoM; IVB+C = HAMBADD; group V = SPOSTA. The five major clades of *Poa* are described in detail below, along with an overview of morphological characters supporting each clade and comparisons with recent classification systems.

ARCSYL. The *ArcSyl* clade, first described in Soreng (1990, group I), is confirmed as a monophyletic group, but without bootstrap support. The consistent union of *P.* subg. *Arctopoa* and *P.* sect. *Sylvestres* in molecular analyses is not supported by any known morphological or other traditional data. All analyses support its position as the basal-most clade in the genus,

except for those based on the Dollo criterion, which either resolve a clade comprising ArcSyl and BAPO (as detected here) or *P.* sect. *Alpinae* (Soreng 1990: group II) as basal to the rest of *Poa*.

The two sections of *P.* subg. *Arctopoa* resolve as sister taxa with weak or no bootstrap support, and differ in surprisingly few cpDNA characters from members of *P.* sect. *Sylvestres*. Species are united by ecological tolerance of salts and other minerals and similar wet habitat. All species are robust with long thick rhizomes and lemmas with soft hairs that are mostly confined to the basal portions of the veins. *Poa emineus* (monotypic *P.* sect. *Arctopoa*) has a crown of hairs rather than the typical *Poa* web on the callus, while *P.* sect. *Aphydris* lacks callus hairs. In addition to *P. tibetica* sampled here, there are three other known species of *P.* sect. *Aphydris*.

Poa sect. *Sylvestres* is a recently named section (Soreng 1998) based on a previously recognized species group of eastern North America (Marsh 1950) plus several species from western North America. All are species of rich, shady woodlands endemic to North America. So far no diagnostic characters, either morphological or molecular, have been identified that unites them. The section is placed in *P.* subg. *Poa* by the presence of a typical web on the callus of the lemma (except *P. autumnalis*, which is glabrous). The web is unique to *Poa* among grasses and based on the proposed phylogeny is likely to be an apomorphy of the genus, with lack of a web (e.g., *P.* subg. *Arctopoa*) due to loss rather than being a plesiomorphic state. All species expected to belong in the section (with the possible exception of *P. laxiflora* Buckley) have now been sampled and all resolve within ArcSyl. Within the section only one subclade was resolved comprising *P. alsodes*, *P. marcida*, and *P. wolfii* (*P. saltuensis* Fernald & Wiegand might also belong here as it united with *P. alsodes* in Soreng 1990), but no morphological characters have been identified to support this grouping.

BAPO. This clade is strongly supported here (and in Gillespie and Boles 2001), and comprises primarily two strongly supported main lineages, *P.* sects. *Bolbophorum* and *Alpinae*, and *P.* sect. *Ochlopoa*. In contrast, these lineages are paraphyletic in Soreng's (1990) analysis, with *P. alpina* (group II) diverging before *P. annua* (group III, *P.* sect. *Ochlopoa*) from the main *Poa* lineage. All three studies support the position of BAPO between ArcSyl and the rest of *Poa*, and the considerable genetic divergence of the two main lineages (indicated by long branch lengths). Although *P.* sects. *Alpinae* and *Bolbophorum* are usually closely allied or united in one section (Tzvelev 1976; Edmondson 1980), they have not previously been allied to *P.* sect. *Ochlopoa*. Nevertheless, the two lineages do share some morphological, ecological, and biogeographical features. They are mainly of open habitats, either subalpine, temperate steppe, or

Mediterranean grasslands. Most of the species are confined to a broadly defined European Mediterranean Region. One or a few representatives of each section extend eastward into Asia, while *P. alpina* is the only species indigenous to the New World, in arctic-alpine North America. Species are low growing and fairly tender leaved, with upper culm sheaths closed for about 1/4 of their length, or more in *P.* sect. *Ochlopoa* (1/3–2/3), and terete, usually smooth, panicle branches, and many tend to be calciphiles. *Poa* sect. *Bolbophorum* species have basally thickened sheaths as storage organs, and some have a web on the callus. *Poa* sect. *Alpinae* species lack callus hairs and are strictly intravaginally branching, with a tendency for the old dead sheaths to persist and envelope the newer shoots. *Poa* sect. *Ochlopoa* species are mostly annuals, of which *P. annua* and *P. infirma* have become widespread weeds, and several, including the perennial *P. supina*, can reproduce stoniferously by rooting at the decumbent stem nodes. Members of this section also lack callus hairs, generally have smooth epidermises (with few if any short hooked hairs, none on the palea keels though these are generally villous), and are gynomonocious, producing pistillate terminal flowers within spikelets.

The inclusion of *Parodiochloa* in the BAPO clade, and specifically as sister to the *P.* sect. *Ochlopoa* lineage seems odd, but is well supported in the cpDNA phylogeny. This large tussock grass of coastal habitats in southernmost South America seems to have no obvious derived morphological characters in common with other members of BAPO, and it is geographically isolated and as remote as possible from the other mainly western Eurasian members of the clade.

SPOSTA. This clade has been detected in all three cpDNA studies of *Poa* with the same general structure, although with limited character support in each case. *Poa* sect. *Secundae* elements assemble about the base as an unresolved complex (analysis 1), paraphyletic group (analyses 2 and 3; Gillespie & Boles, 2001), or clade (Dollo analysis; Soreng 1990, group VD). Species of *P.* sect. *Secundae* are generally of arid regions or somewhat saline wetlands, and are all primarily North American, with disjunct populations of *P. hartzii* in Svalbard and Wrangel Island in high arctic Eurasia, and *P. secunda* subsp. *secunda* and *P. stenantha* in southern South America. These species have sheaths closed 1/10–1/5 their length, moderately long anthers (1.5–3.5 mm), calluses with a crown of short hairs (0.2–2 mm long) or glabrous, and lemmas somewhat weakly keeled in some species. All nine species comprising the section (Soreng et al. 2003a), except for *P. unilateralis* Scribn., have now been sampled. Although Tzvelev (1976) placed *P. hartzii* in *P.* sect. *Abbreviatae*, Soreng (1991) placed it in *P.* sect. *Secundae*, a position confirmed here and in previous studies (Gillespie et al. 1997; Gillespie and Boles 2001).

The remaining taxa form a clade (POSTA = Soreng's group VE) in all three studies. *Poa* sect. *Pandemos* is the next lineage to diverge and, as in previous studies, has a long branch length and is well separated from *P.* sect. *Secundae* elements below and its OSTA sister group. The section is centered in Europe and is circumscribed to include only two species, *P. trivialis* and *P. fertiana* Bois. & Reut. Both species are short-lived, stoloniferous perennials, with densely scabrous panicle branches, sheaths closed 1/4–1/2, flat, acute tipped blades, long acute ligules, moderately short anthers (1.2–1.8 [–2.0] mm), lemmas sparsely hairy on the marginal veins and keel or only on the keel, and palea keels that are finely tuberculate but not beset with hooks.

The OSTA clade was strongly supported in the three studies, but with little internal structure. *Poa* sect. *Abbreviatae* was the only section in the clade that resolved as monophyletic. The section is circumscribed as having mostly intravaginal branching, sheaths closed only 1/6–1/4 their length, moderately scabrous panicle branches, and short anthers (0.2–1 [–1.8] mm long). Species are mainly calciphiles of alpine and arctic distribution. This small section has a centre of diversity in western North America and Far East Russia (Tzvelev 1976; Soreng et al. 2003a), with a single species (*P. abbreviata*) reaching Europe.

Poa sects. *Oreinos* and *Tichopoa* and some elements of *P.* sect. *Stenopoa* formed an unresolved complex at the base of OSTA with little genetic divergence. *Poa* sect. *Tichopoa*, native to Eurasia, is sometimes included as a subsection within *P.* sect. *Stenopoa* (Tzvelev 1976), and comprises two to three species depending on circumscription. Species share a rhizomatous habit and strongly compressed culms and nodes, but are otherwise indistinct from *P.* sect. *Stenopoa*. *Poa* sect. *Oreinos* is characterized by more or less smooth, terete or sulcate panicle branches and short anthers (0.2–1 [–1.3] mm long), combined with extravaginal branching, a caespitose or weakly stoloniferous habit, and sheaths closed mostly 1/3–1/2 of their length. They tend to be alpine or subalpine and prefer soggy habitats. Seven or ten species comprise the section, depending on whether members of the *P. laxa* Haenke complex (including *P. flexuosa* and *P. fernaldiana*) are treated as subspecies (Soreng 1985, 1990) or species (Tzvelev 1976; Edmondson 1980). Our samples of *P. flexuosa* from Norway, *P. fernaldiana* from eastern North America, and *P. leptocoma* s.s. all align in the OSTA polytomy, as does *P. paludigena* Fernald & Wiegand (Soreng 1990). The latter two species are unusual in this section in having quite scabrous branches (although *P. leptocoma* is variable in this regard). On the other hand, *P. paucispicula*, sometimes treated as a subspecies of *P. leptocoma* (Tzvelev 1976), resolved within HAMBADD (see discussion under that clade).

Poa sect. *Stenopoa* is a large, complex, mainly Eur-

asian section, with a few elements in North America and one disjunct in South America. The section did not resolve as a clade, but this is not surprising as it is presumably the group from which the other, more specialized OSTA sections are derived. Chromosome numbers are high and often variable, and hybridization and introgression occur frequently among species (Olonova 1998). Species are perennials without well developed rhizomes, with mainly extravaginal branching, sheaths closed 1/10–1/5 their length, panicle branches sharply angled (mostly densely scabrous along the angles), and anthers of moderate length ([1] 1.2–2 [–2.5] mm). The lemma hairs are generally short (< 1 mm) and the callus is glabrous or webbed. Probatova (1985) recognized two subsections in Far East Russia: *P.* subsects. *Breviligulatae* V. Jirásek (some culms nodes above the middle) and *Longiligulatae* V. Jirásek (culms nodes all below the middle). The clade in analysis 1 comprising *P. glauca* (major part), *P. interior*, and three Chinese-Central Asian species (*P. altaica*, *P. asperifolia*, and *P. urssulensis*) may correspond to *P.* sect. *Longiligulatae*. A subclade comprising the latter three species and two *P. glauca* haplotypes was detected in all analyses and was the only strongly supported clade in OSTA.

PoM. Analyses presented here and by Gillespie and Boles (2001) resolved a strongly supported *P.* sect. *Poa* clade. In Soreng's (1990) analysis, *P. iberica*, representing the closely related section *Macropoa*, is also located here (group IVA), differing from the two species of *P.* sect. *Poa* examined by a single autapomorphic character. All three studies support PoM and HAMBADD as sister clades, consistent with Edmondson's (1980) classification placing *P.* sects. *Poa* and *Macropoa* together and adjacent to *P.* sect. *Homalopoa* (the largest section in HAMBADD, and the only one in Eurasia). In contrast, Tzvelev's (1976) treatment of *P.* sect. *Poa* as a subsection in a broadly defined section together with *P.* sects. *Alpinae* and *Bolbophorum* (both members of BAPO) and the separation of this section and *P.* sect. *Macropoa* in his classification (*P.* sect. *Homalopoa* is positioned between) are not supported here.

Species of PoM are meadow, mesic steppe, or alpine-arctic plants native to the northern hemisphere. *Poa* sect. *Macropoa* is confined to temperate Eurasia, while *P.* sect. *Poa* is widespread in temperate and arctic areas and includes two species in Patagonia, *P. pratensis* subsp. *alpigena* and the endemic *P. yaganica* Speg. Plants of *P.* sect. *Poa* are rhizomatous and have sheaths closed (1/4–) 1/3–1/2 of their length and panicle branches terete and nearly smooth or moderately to less often densely scabrous. The anthers are moderate in length ([1.2–] 1.4–2.5 [–3] mm), the lemmas are pubescent with moderately long hairs on the nerves (1–2.5 mm), and there is a distinct web on the callus. *Poa* sect. *Macropoa*

species are similar, but have sheaths generally more closed (2/3–5/6) and glabrous lemmas and calluses.

Poa sect. *Poa* is species rich and fairly homogeneous, but is sometimes further subdivided into two groups: 1) *Poa* subsect. *Malacanthae* (Roshev.) Prob. (Probatova 1985), or *P.* sect. *Cenisia* Asch. & Graebn. (Edmondson 1978, 1980), encompasses *P. arctica* and relatives (including *P. lanata* Scribn. & Merr. and *P. macrocalyx*): plants with hairs between the lemma veins and between the palea keels, rather long hairs on the lemma veins, often hairs on the rachillas, and with generally two or three (up to five) panicle branches having few spikelets on them; 2) *Poa* subsect. *Poa* encompasses the *P. pratensis* complex: plants without hairs between the lemma veins or between the palea keels, generally shorter hairs on the lemma veins, lacking hairs on the rachillas, often with more panicle branches (three to five, sometimes two), and often relatively more numerous spikelets. Our cpDNA analyses also retrieved two groups in this section, but differed in the placement of *P. macrocalyx* within the *P. pratensis* complex. *Poa pratensis* subsp. *alpigena* and *P. macrocalyx* were found to share identical haplotypes, including a unique 170 bp deletion in the *rbcl-ORF106* region (Archambault and Gillespie 2003, unpubl. data). All *P. pratensis* elements and *P. macrocalyx* resolve as a clade when the highly variable character 26, which is located in this deletion, is excluded. Loss of the site in these taxa represents a unique synapomorphy and is not homologous with its absence in other *Poa* taxa.

HAMBADD. This is the largest of the major clades, both in terms of number of species (Table 1, 50 of 98 sampled for cpDNA) and number of sections or major species groups represented, but unfortunately little or no structure was detected within it. Here are placed members of groups from all over the world: *P.* sects. *Acutifoliae* (South America), *Austrofestuca* (Australia and New Zealand), *Brizoides* (Australia and Japan), *Dasyloa* (Central and South America), *Dioicopoa* (North and South America), *Homalopoa* (Eurasia, North, Central and South America), *Madropoa* (North America), informal groups “Australopoa” (Australia and New Zealand) and “Punapoa” (Central and South America), and *P. atropidiformis* (Patagonia). HAMBADD species range in habitat from moist rich temperate deciduous forests to arid subtropical cactus dominated deserts, from high puna and paramo to low arctic, and from wet saline meadows to dry steppe. In habit they range from ephemeral annuals to long lived perennials, from dwarfs no more than a few centimeters tall to 1.5 meters tall, and some have rhizomes, bulbs, or corms. In breeding system they range from primarily self fertilizing to obligate outcrossing. Most are hermaphroditic, but dicliny has developed to various degrees, including gynomonocism (*Homalopoa* s.l. and *Madropoa*), gynodioecism (*Madropoa*), and dioecism

(*Madropoa* and *Dioicopoa*) (Anton and Connor 1995; Soreng and Keil 2003).

With adaptations to so many niches, it is difficult to circumscribe the clade. The species mostly have upper culm sheaths that are closed 1/4 or more of their length, and the sheaths tend to be laterally compressed. Just about all other characters vary as much as possible within the constraints of the overall variation in *Poa*. For example, most of the species with callus hairs have a single dorsal web of woolly hairs, but in some there are three distinct webs (a dorsal tuft and two other tufts under the marginal veins in many *Dioicopoa*), sometimes the dorsal web is somewhat diffused across the callus but the hairs are still woolly (some *Madropoa*), and in some the callus hairs are sinuous or straight and more or less evenly distributed around the callus in one row (a crown) or multiple rows (a beard) (some *Dioicopoa*, some *Madropoa*, and *Austrofestuca*).

The highly unresolved HAMBADD clade was somewhat more resolved, though with little character support, in Soreng’s (1990) analysis, with “Australopoa” (IVB: *P. sieberiana*) basal to remaining species (group IVC) and three species of *P.* sect. *Dioicopoa* resolved as a clade (IVC2). In the present analysis a clade with two of five “Australopoa” species examined (including *P. sieberiana*) was also detected, but varied in membership. Species examined here of *P.* sect. *Dioicopoa* had identical RS profiles, but did not resolve as a clade. The group comprising nine species of *P.* sects. *Homalopoa*, *Madropoa*, *Brizoides*, and “Punapoa” is likely spurious since it includes at least three morphologically distinct taxa and is based on a highly variable character.

HAMBADD likely contains at least 1/3, perhaps as many as 2/3, of the species of the genus, yet we have discovered very little cpDNA variation and no stable phylogenetic structure within it. This suggests that the immediate ancestors of the clade spread widely across the world in fairly recent times and speciated rapidly. More sections and groups are expected to align in HAMBADD as they are tested. Among the unexpected placements was *P. paucispicula*, which has generally been placed in *P.* sect. *Oreinos* (SPOSTA clade). Three geographically separate samples gave the same result. The species has likely been misplaced and, based on a re-examination of morphology, is now thought to be a close relative of *P. reflexa* Vasey & Scribn. (*P.* sect. *Homalopoa*). *Poa* sect. *Brizoides* was of undetermined affinity within *Poa*, and we were surprised when it aligned here. Its two species, *P. drummondiana* and *P. tuberifera* Faurie ex Hack., are unusual in having thickened stem bases (not sheaths as in *P.* sects. *Bolbophorum* and some *Dioicopoa*) as storage organs, and occur in Australia and Japan, respectively.

Hybridization and Reticulation. The taxonomy of *Poa* has long been considered to be “complicated by the widespread occurrence of pomixy and introgress-

sion" (Bor 1952a, pp. 7, 8) and by high ploidy levels (Stebbins 1950). Hybridization is known and postulated to occur frequently in the genus (Tzvelev 1964, 1976), with many species and even higher taxa thought to have a hybrid origin (Soreng 1990). With a sound understanding of the morphologies of the taxa under study, comparisons of cpDNA phylogenies with the traditional classifications may reveal unusual placements that could have resulted from hybridization and introgression. Species may harbor two very different haplotypes that are obviously not related by descent, with one introduced by introgressive hybridization. Cases of stabilized introgressed populations or species have been well documented in which an introgressed haplotype dominates and may be the only one present (reviewed by Rieseberg and Soltis 1991; Rieseberg and Brunsfeld 1992).

Our studies have revealed two clear cases of inter-sectional hybridization and introgression of cpDNA. The first case, involving the arctic species *P. hartzii*, was first hypothesized by Gillespie et al. (1997), and confirmed in Gillespie and Boles (2001). Based on the presence of two very different haplotypes, one identical to the dominant *P. glauca* haplotype (*P. sect. Stenopoa*) and the other a unique haplotype within *P. sect. Secundae*, *P. hartzii* subsp. *hartzii* was hypothesized to have hybridized with the widespread arctic-alpine species *P. glauca*, resulting in *P. glauca* cpDNA transferred into some populations of the former species. In the present study, *P. hartzii* subsp. *alaskana* was found to have the same unique *Secundae* haplotype as the typical sub-species, providing additional evidence for this as the original haplotype of *P. hartzii*. Among the new sites examined for *P. hartzii* subsp. *hartzii*, the *P. glauca* haplotype was again found only in high arctic sites (Melville Island and Svalbard) and not in low arctic sites (Alaska), confirming that introgression is taking place only in the high arctic, but across a much wider geographical range than previously detected.

A second case of apparent chloroplast capture involves *P. bulbosa*. Soreng (1990) reported *Secundae* type cpDNA in *P. bulbosa* from California, but questioned whether the result was due to reticulation or natural relationship. In contrast, Gillespie and Boles (2001) reported *P. bulbosa* from Nevada as sister to *P. alpina*, a placement expected based on morphology and classification. The present study confirms the presence of two distinct haplotypes in *P. bulbosa*. Two new samples from Oregon were found to have *Secundae* type cpDNA close to *P. curtifolia* (a narrow endemic from Washington state), while a sample from Spain (where the species is native, and no members of *P. sect. Secundae* occur) aligns with *P. alpina* and *P. molinerii* (*P. sect. Bobophorum*). This is interpreted as a case of hybridization and introgression wherein the cpDNA of a remotely related group (*P. sect. Secundae*) is transferred across

species boundaries without the introduction of any outward signs of morphological intermediacy. This chloroplast capture has been detected only in some populations of *P. bulbosa* in western North America where this species is adventive and *P. sect. Secundae* species are widespread and common.

These examples raise the possibility that extensive hybridization within sections could have occurred yet would be more difficult to detect because the morphologies of more closely related species are often too similar. One possible example is *P. glauca* in which six haplotypes have been identified, some of which may have derived from hybridization and introgression with other species in *P. sect. Stenopoa*.

Biogeography. *Poa* is among the most widely distributed genera of flowering plants, occurring from high arctic regions to subantarctic islands. The five major clades have different ranges, but overlap considerably in distribution. One clade is centered in Eurasia (BAPO) and two in Eurasia-North America (SPOSTA and PoM), with all three reaching South America. ArcSyl is Asian-North American, while HAMBADD is worldwide. With all major clades present in temperate Asia and high species and sectional diversity in Europe and the Mediterranean region, our data provide further support for Soreng's (1990) hypothesis of Eurasia as the center of diversity and speciation. Each major clade appears to represent a major radiation and geographic expansion. We suggest that ArcSyl represents the earliest radiation, or possibly the remnants of two early radiations. BAPO represents the second major radiation, which spread geographically and then contracted in range. One early diverging lineage now survives as a single species, *P. (sect. Parodiochloa) flabellata*, in southern-most South America, a location remote from other members of the clade. HAMBADD hypothetically represents the most recent major expansion and radiation as the clade is highly derived within *Poa*, and although highly speciose and distributed worldwide, it has evidently had little time to develop cpDNA variation. Multiple expansions of HAMBADD species may have occurred during Pleistocene glacial periods, times dominated by cooler climates favorable to *Poa* (Hartley, 1961), and when larger land surface areas were present as sea levels dropped, and arctic, alpine, coastal meadow, and steppe habitats expanded. These range expansions were evidently followed by rapid speciation in the new regions (e.g., Australia).

Although adapted to a cold climate, *Poa* has managed to spread around the world quite well. Species typically have a tuft of hairs (web on the lemma callus) on their diaspores, which is evidently effective in dispersal by wind or animals. An analogous case is the cool climate genus *Epilobium* L., which also has a tuft of hairs on their diaspores (seeds in this case) and is widely distributed around the world (Raven 1976; Ra-

ven and Raven 1976). In contrast, *Festuca* lacks obvious special dispersal mechanisms and has not done so well in establishing and speciating in Malesia, Australia, and New Zealand, even though it is more speciose than *Poa* in the northern hemisphere and South America.

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