Phylogenetic relationships of Australian *Poa* (Poaceae: Poinae), including molecular evidence for two new genera, *Saxipoa* and *Sylvipoa*

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Abstract. Phylogenetic relationships among Australian species of *Poa* and other subtribe Poinae genera were studied on the basis of plastid *trn*T–*trn*L–*trn*F and nuclear ribosomal ITS and ETS DNA sequence data. Molecular evidence is provided for two new monotypic endemic Australian genera, *Sylvipoa* and *Saxipoa*, on the basis of two species formerly included in *Poa*, *P. queenslandica* and *P. saxicola*, respectively. Both new genera resolved in a clade with three subtribe Poinae genera, the Australian genus *Hookerochloa*, the South American genus *Nicoraepoa*, and the arctic genus *Arctagrostis*. *Sylvipoa* and *Nicoraepoa* are sister taxa. *Saxipoa* resolved as sister to these plus *Arctagrostis*, but also shares DNA sequence characters with *Hookerochloa*, suggesting a possible hybrid origin. All other Australian *Poa* species studied resolved in a subclade within the *P.* subgenus *Poa* supersection *Homalopoa* clade, supporting their classification together in an expanded *P. section Brizoides*. Five New Zealand and one New Guinea species also resolved in this subclade, supporting their membership in this section. We postulate a minimum of two dispersal events into Australia, one for *Poa*.

Introduction

The grass genus *Poa*, with some 500 species worldwide, is species-rich in the Australia–New Zealand–Malesian region (Australasia). In recent treatments, *Poa* included 43 endemic species from Australia (Walsh *et al.* 2009), 32 from New Zealand, with one coastal species native to both Australia and New Zealand (Edgar and Connor 2000), and 35 in the Malesian flora, with the majority endemic to New Guinea (Veldkamp 1994). The relationships of the majority of these species are poorly known and, up to now, very few have been placed in infrageneric classifications of the genus (Tzvelev 1976; Edmondson 1980; Soreng 1998, 2007; Soreng *et al.* 2003; Gillespie and Soreng 2005; Zhu *et al.* 2006; Gillespie *et al.* 2007, 2008; Soreng and Gillespie 2007). Soreng *et al.* (2009) provided a review of the taxonomic history of the Australian *Poa* species.

Poa is a member of subtribe Poinae (including Cinninae), which comprises 21 currently recognised genera (*Agrostopoa*, *Aniselytron*, *Apera*, *Arctagrostis*, *Arctophila*, *Arctopoa*, *Bellardiochloa*, *Cinna*, *Cyathopus*, *Dupontia*, *Gaudiniopsis*, *Hookerochloa*, *Libyella*, *Limnodea*, *Lindbergella*, *Nephelochloa*, *Nicoraepoa*, *Saxipoa*, *Sylvipoa*, *Ventenata*) (Soreng *et al.* 2000; Gillespie *et al.* 2008, in press; Davidse *et al.* 2009), plus two genera likely to belong in Poinae on the basis

of a recent molecular study (Parvotrisetum, Simplicia) (Döring 2009). An additional 13 Poinae genera were previously recognised, and are now mostly synonymised under Poa (Gillespie and Soreng 2005; Gillespie et al. 2007, 2008, in press; Soreng et al. 2007); included here are Aphanelytrum, Dissanthelium and Tovarochloa, which belong within Poa, but have yet to be transferred (Refulio-Rodriguez 2007; Gillespie et al. 2008). All the Poinae genera grow in temperate to cold climatic zones. In Australia, this subtribe includes three endemic genera, Hookerochloa, Saxipoa and Sylvipoa, in addition to the widespread genus Poa. The previously recognised Australian genera Austrofestuca (shared with New Zealand) and Neuropoa have recently been merged into Poa (Gillespie and Soreng 2005; Gillespie et al. 2008), and Festucella has been merged into Hookerochloa (Jacobs et al. 2008). All other Poinae genera from the southern hemisphere (Anthochloa, Aphanelvtrum, Dasypoa, Dissanthelium, Parodiochloa, and Tovarochloa from South America, and Tzvelevia from Heard and Kerguelen islands in the southern Indian Ocean) are phylogenetically nested within Poa (Gillespie and Soreng 2005; Gillespie et al. 2007, 2008), with the exception of the recently described South American genus Nicoraepoa (Soreng and Gillespie 2007; Gillespie et al.

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2008), and the New Zealand endemic genus *Simplicia* (Döring 2009).

Relationships within the genus Poa have been examined in molecular phylogenetic studies, initially with plastid restrictionsite data (Soreng 1990: Gillespie and Boles 2001: Gillespie and Soreng 2005), and subsequently with plastid trnT-trnL-trnF (TLF) sequence data (Gillespie et al. 2007), plus nuclear rDNA (nrDNA) internal transcribed spacer (ITS) sequence data (Gillespie et al. 2008; Soreng et al. in press), and most recently with nrDNA external transcribed spacer (ETS) data (Gillespie et al. in press). All previously sampled Australian Poa (nine species, including the following Austrofestuca s.s. and *Neuropoa* species: *Austrofestuca littoralis* = *P*. *billardierei*, Austrofestuca pubinervis, P. drummondiana, P. fawcettiae, P. fax, P. labillardierei, P. poiformis, P. porphyroclados and P. sieberiana; Soreng 1990; Hunter et al. 2004; Gillespie and Soreng 2005; Patterson et al. 2005; Gillespie et al. 2007, 2008) were determined to belong in the same major Poa clade, P. subgenus Poa supersection Homalopoa (Dumort.) Soreng & L.J.Gillespie (HAMBADD clade sensu Gillespie and Soreng 2005; Gillespie et al. 2007, 2008). Nosov and Rodionov (2008) published an ITS study of Poa that included 17 sequences of New Zealand Poa species (provided by Richard Gardner, Jeanette Keeling, Peter de Lange, Shane Wright and Ewen Cameron - see Acknowledgements).

Two new monotypic genera, Saxipoa and Sylvipoa, are published in a companion paper in this issue (Soreng et al. 2009), to accommodate two morphologically divergent and unusual Australian species formerly placed in Poa, namely, P. saxicola and P. queenslandica. The two genera differ considerably in habit and habitat; Saxipoa is a short plant with narrow panicles of rocky alpine or subalpine habitats, whereas Sylvipoa is a tall plant with large open panicles of temperate rainforest margins and openings. In the same paper, a new infrageneric classification is proposed for the remaining Australian Poa species. Poa section Brizoides Pilg. ex Potztal (in P. subgenus Poa supersection Homalopoa) was expanded to encompass all the Australian species, and six New Zealand and one New Guinean species. Four subsections were established to accommodate most of these species: Australopoa Soreng, L.J.Gillespie & S.W.L.Jacobs; Austrofestuca (Tzvelev) Soreng, L.J.Gillespie & S.W.L.Jacobs; Brizoides (Pilg. ex Potztal) Soreng, L.J.Gillespie & S.W.L.Jacobs; and Neuropoa (Clayton) Soreng, L.J.Gillespie & S.W.L.Jacobs.

Here, we provide molecular evidence for the recognition of *Saxipoa* and *Sylvipoa* and for their phylogenetic relationships within subtribe Poinae. We place the remaining Australian *Poa* species in a phylogenetic context, and provide molecular support for the new infrageneric classification. Biogeographic connections among Australasian Poinae are discussed.

Materials and methods

Taxon sampling

The sampling of taxa used here builds on our earlier molecular phylogenetic studies of *Poa* and subtribe Poinae (Gillespie and Boles 2001; Gillespie and Soreng 2005; Gillespie *et al.* 2007, 2008, in press; Soreng *et al.* in press). For *Poa*, we sampled 122 individuals representing 100 species (Appendix 1), including

26 of the 41 species of Australian Poa (including species formerly included in Austrofestuca and Neuropoa), 20 species from New Zealand and one from New Guinea. The analysis also included a broad taxonomically and geographically representative sample of 53 additional Poa species, including three of Dissanthelium (combinations pending in Poa). Our sampling within Poa includes elements of every major lineage within the genus resolved in our previous molecular phylogenetic studies (Gillespie and Boles 2001; Gillespie and Soreng 2005; Gillespie et al. 2007, 2008, in press); we sampled most extensively in the major clade (subgenus Poa) in which the Australian species resolved. Outside of Poa in subtribe Poinae (including Cinninae), we sampled 11 genera and 17 species, including the Australian genus Hookerochloa (including Festucella), and the two new monotypic endemic genera, Saxipoa and Sylvipoa. Taxa of putative hybrid origins (e.g. Arctopoa, Nicoraepoa pugionifolia, P. abbreviata and P. annua; see Gillespie et al. in press; Soreng et al. in press) and two South American genera (Aphanelvtrum, Tovarochloa) that resolve on long branches within Poa (Gillespie et al. 2008) were not included in the analyses because they do not contribute to the understanding of the Australian lineages.

The following taxa representative of the four other subtribes of the large clade comprising Poinae and related subtribes (PPAM clade, Gillespie et al. 2008) were also included: Alopecurinae (2 genera: Alopecurus, Beckmannia; 3 species), Miliinae (1)genus: Milium; 2 species), Phleinae (1 genus: Phleum; species) and Puccinelliinae (2 genera: Catabrosa, 1 Puccinellia; 3 species) (Appendix 1). The classification of tribe Poeae s.l. followed here is that of Soreng et al. (2000 [version 27 Oct. 2008]), with modifications for these four subtribes based on Gillespie et al. (2008, in press; Döring 2009). Five outgroup genera were included as representatives of the other two major tribe Poeae s.l. clades (see Gillespie et al. 2008), namely, Anthoxanthum (subtribe Phalaridinae s.l.), Agrostis (Agrostidinae), Deschampsia (Airinae s.l.), Festuca (Loliinae), and Helictotrichon s.s. (Aveninae). New sequence data for the Australian genus Dryopoa (subtribe uncertain) were also included.

DNA sequences and data matrix

The majority of sequences were generated at the Canadian Museum of Nature, with 68 plastid, 80 ITS and 144 ETS sequences newly generated for the present study (Appendix 1) (~20% of these new sequences were also used in two studies submitted just before the present study, namely, Gillespie et al. in press, Soreng et al. in press). Two plastid and 13 ITS sequences were downloaded from GenBank; all other sequence data were first published in our previous studies based on plastid and ITS sequence data (Gillespie et al. 2007, 2008). Our methods of DNA extraction, amplification and direct sequencing of TLF and ITS are outlined in Gillespie et al. (2008). A region of ~460-500 base pairs (bp) at the 3' end of the nrDNA external transcribed spacer (ETS) was amplified and sequenced by using the same reaction conditions as for ITS and primers 18S-R (Starr et al. 2004) and RETS4-F, a primer newly designed in our laboratory (5'-TGGCTACGCGAGCGCATGAG-3'). Although designed specifically for use in *Poa*, the RETS4-F primer also successfully amplified all other genera in subtribe Poinae and many other tribe Poeae taxa.

Sequence assembly and editing, automated alignment and manual alignment editing were performed with Sequencher vers. 4.7 (Gene Codes Corp., Ann Arbor, MI, USA), ClustalX ver. 1.83 (Jeanmougin *et al.* 1998) and BioEdit ver. 5.0.9 (Hall 1999), respectively, as outlined in Gillespie *et al.* (2008). Obvious and unambiguous nucleotide variants within a sequence (i.e. double peaks of approximately equal strength on electropherogram traces, or at least unambiguous double peaks in an otherwise clean sequence) were coded as polymorphisms by using standard IUB ambiguity codes.

TLF, ITS, and ETS sequence alignments were merged into a single nexus format data matrix (data matrix available from the authors on request). The majority of samples had complete or near complete sequence data for all three regions. For 22 samples, sequence data for only one or two of the three data partitions were available as follows: three samples with only ITS and ETS data (Bellardiochloa polychroa, Milium effusum, Poa hybrida), two with TLF and ITS data (Anthoxanthum monticola, Drvopoa dives), 13 with only ITS data (all GenBank samples from New Zealand) and four (Milium effusum, Poa hybrida, P. meionectes G7348, P. sieberiana AY589145) with only TLF data (Appendix 1). Sixteen of these samples were downloaded from GenBank; the other six samples did not successfully amplify or sequence. For each terminal taxon in the combined data matrix, TLF, ITS and ETS sequences were from the same collection and individual, except for Milium effusum and Poa hybrida (Appendix 1).

Phylogenetic analyses

The decision to combine the plastid and the two nuclear ribosomal data partitions was based on examination and comparison of the separate preliminary maximum parsimony analyses of the three data partitions, and taking into account the results of incongruence length difference (ILD) tests (Farris et al. 1994) performed previously on a comparable Poinae dataset (Gillespie et al. in press). In the current dataset, the positions of Australian species did not conflict among the three data partitions when each partition was analysed separately. Although the ILD tests performed previously on similar datasets indicated that both ITS+ETS and TLF+ ITS+ETS partitions were incongruent, this incongruence was primarily due to the conflicting positions of several species groups within Poa. These data partitions were not significantly incompatible for other Poinae genera, apart from several putative hybrid genera and species that were excluded from analyses here. Therefore, given our focus on the Australian taxa, combining data partitions is justified for the purposes of the present paper. Conflict in the Poa clade will be explored and described in a future paper.

Following exploratory parsimony analyses of TLF, ITS, ETS, ITS + ETS and TLF + ITS + ETS data partitions, the following three final parsimony analyses were run: TLF (plastid), ITS + ETS (nrDNA), and TLF + ITS + ETS (combined) analyses (Table 1). The number of terminals was 144 in the TLF analysis, 158 in the ITS + ETS analysis and 137 in the TLF + ITS + ETS analysis. Missing data represented <1% of each of the three data partitions. In the TLF partition, apart from missing bases in

conserved primer regions and at the ends of some sequences, three samples were incomplete, missing either the trnT-trnL spacer or the *trnL-trn*F spacer (Appendix 1); two of these were excluded from the TLF analysis because the missing data appeared to result in a clade collapse; however, they were included in the combined analysis (P. cita, P. clelandii). Terminal taxa were complete for all data partitions in the ITS+ETS and TLF+ITS+ETS analyses, with the exception of 13 samples in the nrDNA analysis that included only ITS data (sequences downloaded from GenBank), and two samples (Anthoxanthum monticola, Dryopoa dives) included in both analyses that were missing the ETS data partition. We excluded from the TLF + ITS + ETS analysis 15 species of P. subgenus Poa that resolved in the 'X clade' in the ITS + ETS tree (see Results) because the positions they resolve in are incongruent between the TLF and ITS + ETS trees.

Maximum parsimony (MP) and bootstrap analyses were performed in PAUP* 4.0b10 (Swofford 2002) as outlined in Gillespie *et al.* (2008). Insertion–deletion (indel) characters were not included in these analyses. Two heuristic search strategies were used, including (1) maximum tree setting of 90 000, no replication and (2) 100 random addition replicates, 900 trees saved per replicate (both search strategies gave the same results). Bootstrap analyses were performed with 1000 replicates, with 10 random addition sequences per replicate, TBR swapping, and the 'MULTREES' setting turned off because of long search times (DeBry and Olmstead 2000). Following the suggestion of Starr *et al.* (2004), bootstrap support (BS) for clades is characterised as very poor (<55%), poor (55–64%), moderate (65–74%), good (75–84%), very good (85–94%) or strong (95–100%).

Results

Sequence characteristics

Summary characteristics of the TLF, ITS and ETS data partitions, both separate and combined, are given in Table 1. The combined TLF+ITS+ETS aligned data matrix comprised 3930 characters, of which 722 positions (explained below) were deleted for a total of 3208 characters in the final analysed

Table 1. Summary statistics for maximum parsimony analyses of separate TLF, ITS and ETS datasets, and combined datasets

Total bases, total number of aligned bases; Char, no. of characters included in each analysis; PI char, no. of parsimony-informative characters; %PI char, percentage parsimony-informative characters; L, length of most parsimonious trees; CI, consistency index; CIexcPU, CI excluding parsimonyuninformative characters; and RI, retention index

Parameter	TLF (Fig. 1)	ITS	ETS	ITS+ETS (Fig. 2)	TLF + ITS + ETS (Fig. 3)
No. of terminals	144	158	142	158	137
Total bases	2053	654	680	1334	3930
Char	1972	654	582	1236	3208
PI char	196	189	223	413	626
%PI char	9.9	28.9	38.3	33.4	19.5
L	666	815	921	1776	2414
CI	0.751	0.481	0.555	0.510	0.569
CIexcPU	0.634	0.408	0.470	0.430	0.470
RI	0.923	0.817	0.855	0.832	0.850

data matrix. The TLF data partition was by far the longest, but with the lowest percentage of parsimony-informative characters, whereas the ETS partition was the shortest, but contained the most parsimony-informative characters. Detailed characteristics of TLF and ITS sequences were described in Gillespie *et al.* (2007, 2008). In the aligned TLF data matrix, an 81-bp region of ambiguous alignment in the *trn*T–*trn*L spacer was deleted before analysis; no positions were deleted from the ITS data matrix. In the ITS data, there was no evidence for the presence of pseudogenes in the 5.8S coding region; the 5.8S gene was highly conserved in all ITS sequences except for one 9-bp region (percentage parsimony-informative characters was 9% in the 5.8S region v. 36% in ITS1 and 35% in ITS2, and indels were absent from all 5.8S sequences).

The aligned ETS data matrix comprised a total of 680 characters, of which 98 base positions were excluded from the analysis for a total of 582 analysed characters. One 12-bp region of ambiguous alignment was excluded. Also excluded were 86 positions corresponding to four insertions; all of these insertions lacked variable nucleotide characters, two were unique to a single sample, including a 64-bp insertion in *P. infirma*, and two were shared by two samples. For individual samples, the length of the ETS region that was sequenced and included in the data matrix ranged from ~500 bp (numerous species) to 567 bp (*P. infirma*).

In the TLF data matrix, four indels were shared among Australasian taxa, and two were shared by samples within a species. Saxipoa and Hookerochloa (both species) shared a 20-bp insertion. All three samples of Saxipoa shared a 20-bp duplication (adjacent to and repeating the latter 20-bp insertion) and a 10-bp duplication. Poa affinis and P. poiformis (S5911) shared a unique 20-bp insertion. An 8-bp insertion was shared by the following 15 Australian samples: P. amplexicaulis, P. billardierei, P. clelandii, P. drummondiana, P. fax, P. ensiformis, P. fawcettiae (MEL2323765), P. fordeana (G7326), P. homomalla, P. meionectes (G7348), P. porphyroclados, P. orba, P. orthoclada, P. pubinervis and P. sallacustris; and the following three New Zealand samples: P. cita, P. cockavneana and P. sieberiana (AY589145). Poa fax, P. fordeana (G7326), P. lowanensis and P. poiformis (G7381) shared a 4-bp deletion. Only one informative indel was present among Australasian taxa in the ETS data matrix, namely, a 2-bp duplication shared by P. orba and P. sallacustris. There were no indels among Australasian taxa in the ITS data matrix. Although indels were not coded and included in the analysis, those that support multi-species clades are indicated on the phylograms (Figs 1–3).

Within-individual (i.e. intra-accession) variation was detected in some nrDNA sequences by using the direct sequencing approach, suggesting the presence of two (or possibly more) variant or paralagous sequences within a sample. Single nucleotide variants ('polymorphisms') were detected in about 7% of the ITS sequences (in the ITS1 and ITS2 regions, none found in the 5.8S region) and 16% of the ETS sequences for the samples sequenced in our lab (i.e. excluding those downloaded from GenBank, Appendix 1). Insertion-deletion (indel) variants were detected in about 4% of the ITS sequences and 10% of the ETS sequences; these variants were detected within a single sequencing reaction and resulted in a difficult to read chromatogram trace downstream from indel sites. To interpret this indel variation, sequences from multiple reverse- and forward-sequencing reactions, plus those from internal primers in the case of ITS, were used to form a consensus sequence. Base variants were coded with standard IUB ambiguity codes. For indel variants, the dominant variant was coded, or where peaks were equal in size, the longest variant; in examples cited below the variant coded is given first. Only variants in Australian species are described here; none were found in New Zealand species sequenced for the present study, only minor nucleotide variation was found in the New Guinean species sampled, and variants in other species are described in Gillespie et al. (2008, in press). Taxa from outside the Australasian region included in the present study did not have infra-sample indel variants or extensive nucleotide variants, except for Catabrosa and Aniselytron (in the latter case, only the ITS variant that was not incongruent with the TLF and ETS data was included here).

ITS sequences of all three samples of *Saxipoa saxicola* shared three insertion/deletion (indel) variants and seven base variants. Table 2 lists these 10 variants and gives the Poinae taxa that shared each variant. *Sylvipoa queenslandica* had one ITS indel variant (ITS2, Position 590: –/CGTA), the insertion being a duplication unique to this sample.

One position in the aligned ETS matrix (Characters 342, 343) was highly variable among and within Australian Poa samples. Both samples of P. helmsii and one sample of P. phillipsiana (G7346) had an indel variant at this position, with the variant being G/AC, G/AC and AC/C, respectively. These three samples shared one variant (AC) not found in any other sample or taxon analysed. The P. helmsii samples shared their other variant (G) with P. orba and P. sallacustris (and samples given below polymorphic for this site), whereas the second variant of P. phillipsiana (C) was common to all other Australian Poa. Several other Australian species and samples exhibited C/G nucleotide variation at this site, e.g. P. costiniana (G7356-1), P. ensiformis, P. phillipsiana (G7369) and P. poiformis (G7381), whereas P. porphyroclados showed C/A base variation at this site. Two other positions in the ETS data matrix (Characters 286 and 551) were also highly variable among Australian Poa species and samples, and also exhibited some within individual nucelotide variation.

Poa homomalla (for which we obtained sequence data after completion of analyses) has TLF sequences identical to *P. sallacustris* and *P. orba*, and ITS and ETS identical (apart

Fig. 1. Phylogram of subtribes Poinae, Alopecurinae, Miliinae and Puccinelliinae (PPAM clade), resulting from maximum parsimony analysis of the plastid TLF sequence data (length = 663 steps; CI excluding uninformative characters = 0.63). The strict consensus tree is indicated by bold lines on one of the 90 000 most parsimonious trees. Bootstrap values of \geq 50% are given on the branches. Informative indels are indicated to the left of the tree. Species represented by more than one sample are followed by abbreviated collection information (or GenBank accession number when downloaded from GenBank). Australian species are indicated in bold; New Zealand species of *Poa* are indicated by 'NZ', followed by a letter corresponding to one of the species groups (A–C and E) outlined by Edgar (1986); 'X' refers to species that are members of the X clade in the nrDNA analysis; members of subtribe Alopecurinae are indicated by 'A'. One sample containing only *trn*T–*trn*L and *trn*L intron data is noted as 'TLL'. Major clades and subclades are indicated on the right; species assemblages that resolve as clades in the nrDNA analysis; and combined analyses are noted by dashed lines.





from minor base polymorphisms) to *P. clelandii*, *P. costiniana*, *P. fawcettiae* (S5919), *P. keysseri*, *P. phillipsiana* and *P. poiformis* (S5911).

Parsimony analyses

Results given here focus on the Australasian species of *Poa* and subtribe Poinae. Positions and relationships of other *Poa*, Poinae and PPAM clade species are mostly described in previous papers (Gillespie *et al.* 2007, 2008, in press; Soreng *et al.* in press).

Plastid analysis

Maximum parsimony analysis of the TLF data matrix resulted in 90 000 trees (the maximum saved), 666 steps long (Table 1). Figure 1 illustrates one of the most parsimonious trees, with the strict consensus tree indicated by bold lines.

The PPAM clade is moderately supported (BS = 69%), with subtribe Puccinelliinae strongly supported (BS = 96%) as sister to all other members (subtribes Alopecurinae, Miliinae, Phleinae, and Poinae). The sister clade is divided into two main clades with moderate to good support, namely, Poa (BS = 74%) and a clade comprising all sampled Poinae genera except Poa and including Alopecurus and Beckmannia (subtribe Alopecurinae) (Clade 1: BS = 85%). Two additional lineages, Milium and Phleum, resolve together in a clade in the bootstrap tree (BS = 66%), but not in the strict consensus tree. Five genera for which multiple species were included resolved as monophyletic; these include Alopecurus (BS=89%), Catabrosa (BS=86%), Dupontia (BS=80%), Milium (BS=97%) and Poa (including Dissanthelium for which combinations in *Poa* are pending; BS = 74%). The two samples of Arctagrostis latifolia also resolved as monophyletic (BS = 99%). Cinna, Hookerochloa, Nicoraepoa and Saxipoa did not resolve as monophyletic; relationships among their species and samples were not or poorly resolved, and there was little sequence divergence among the latter three genera. The three samples of Saxipoa shared two unique insertions (a 10-bp duplication and a 20-bp duplication) providing some TLF evidence for the monophyly of the genus.

The two new Australian genera, *Saxipoa* and *Sylvipoa*, resolved within Clade 1. Relationships within the part of Clade 1 that included these genera (Fig. 1: HSAQN group) were not or poorly resolved. Both genera had sequences most similar to, and in one case (*Saxipoa saxicola* MEL2323764) identical to, samples of *Hookerochloa* and *Nicoraepoa* (except for two duplications in *Saxipoa*, and one insertion shared with *Hookerochloa*). All other Australian taxa of Poinae were included within *Poa*, in a very well supported supersection *Homalopoa* clade (BS = 91%) within *P*. subgenus *Poa* (BS = 100%). Included in the supersection *Homalopoa* clade were all sampled Australian species of *Poa*, including species sometimes previously treated under *Austrofestuca* (*P. billardierei*, *P. pubinervis*) and *Neuropoa* (*P. fax*), and all New Zealand *Poa* (except Edgar's (1986) Group A1 species, *P. cookii*, from the Sub-Antarctic

Islands). Relationships within this large clade were poorly resolved as a result of very low levels of sequence divergence. Six Australian *Poa* samples (*P. cheelii*, *P. helmsii* (2 collections), *P. hookeri*, *P. meionectes* (one of two collections: *G7316*) and *P. sieberiana* (one of three collections: *J8482*)) form a subclade, with poor bootstrap support (BS = 63%) based on a single shared character. Two Australian samples, *P. affinis* and *P. poiformis* (one of two collections: *S5911*), formed a subclade (BS = 63%), which was further supported by a unique 20-bp insertion. A group of 13 Australian samples resolved as a clade in some of the most parsimonious trees, and was further supported by a shared 8-bp insertion (Fig. 1); two New Zealand samples, *P. cockayneana* and *P. sieberiana* (AY589145, cultivated sample native to Australia), also shared this insertion, but did not resolve in this clade.

Nuclear ribosomal analysis

Maximum parsimony analysis of the combined ITS and ETS data matrix resulted in 90 000 trees (the maximum saved), 815 steps long (Table 1; Fig. 2).

In this nrDNA analysis, a clade of all PPAM members (BS=93%) resolved into the following three main clades: Puccinelliinae (BS=100%), Poa (BS=87%) and Clade 1 (BS=84%) comprising all Poinae taxa, except Poa, and including Alopecurus and Beckmannia (Alopecurinae). Relationships among these three clades and the two separate lineages, Phleum and Milium, were poorly resolved. All genera for which multiple species were included resolved as monophyletic; these (BS = 99%).include Alopecurus Bellardiochloa (BS = 86%), Catabrosa (BS = 100%), Cinna (BS = 89%), Hookerochloa (BS = 93%), Milium (BS = 100%), Nicoraepoa (BS = 94%) and Poa (including Dissanthelium for which combinations in *Poa* are pending; BS = 87%). All genera in which multiple samples of the same species were included also resolved as monophyletic: Arctagrostis (BS = 99%), Dupontia (BS = 85%) and Saxipoa (91%).

Both *Saxipoa* and *Sylvipoa* resolved in Clade 1, in a very strongly supported subclade with *Arctagrostis*, *Hookerochloa* and *Nicoraepoa* (HSAQN clade; BS = 100%). *Sylvipoa* resolved as sister to *Nicoraepoa* (BS = 68%), in a strongly supported clade with *Arctagrostis* (AQN; BS = 96%). *Saxipoa* resolved as sister to this clade, with moderate support (BS = 73%).

All Australian *Poa* species sampled, including those sometimes previously placed in *Austrofestuca* and *Neuropoa* (Fig. 2: subsections *Austrofestuca* and *Neuropoa*), resolved together in a subclade (section *Brizoides*; BS = 67%) within a large clade comprising the majority of *Poa* subgenus *Poa* species (BS = 91%), but not including those belonging to the X clade (Fig. 2, see below). Also included in the section *Brizoides* subclade were five New Zealand *Poa* species (all sampled species of Edgar's (1986) Group C) and one from New Guinea. Phylogenetic structure within section *Brizoides* was

Fig. 2. Phylogram of subtribes Poinae, Alopecurinae, Miliinae and Puccinelliinae (PPAM clade), resulting from maximum parsimony analysis of the nuclear ribosomal ITS and ETS sequences (length = 1776 steps; CI excluding uninformative characters = 0.43); the strict consensus tree is indicated by bold lines; labelling conventions and abbreviations follow those for Fig. 1. Samples with only ITS data (i.e. missing ETS data) are indicated by 'ITS'. Major clades and subclades are indicated on the right; taxa not corresponding to clades in this analysis, but that do resolve as clades in the plastid (Fig. 1) and combined analyses (Fig. 2), are noted by dashed lines.



Table 2.	Intra-accession indel and base variants in ITS	S sequences of Saxipoa saxicola

Variants were identical in sequences of all three accessions sampled (except for one minor difference in one variant in the ITS2 region). Position in the aligned ITS data matrix, and other Poinae taxa sharing each variant are given. Genera belonging to the same subclade as *Saxipoa saxicola* are given first: A = *Arctagrostis*; H = *Hookerochloa*; N = *Nicoraepoa*; Q = *Sylvipoa queenslandica*; followed by other Poinae genera. For indel variants, the first variant given was the one coded; base variants were coded with base ambiguity codes

Position	ITS region	Variants	Variant 1	Variant 2
70	ITS1	C/T	C: HAQN, most Poinae	T: N, many Poa
88	ITS1	G/A	G: HAQN, most Poinae	A: some Poa (subg. Stenopoa; P. diaphora)
130	ITS1	-/C	C: HAN, most Poinae (T: N, Poa flabellata; G: Q)	-: unique to Saxicola
216	ITS1	C/T	C: HAQN, most Poinae	T: Poa subg. Ochlopoa, Cinna arundinacea
234	ITS1	C/T	C: HAQN, most Poinae	T: most Poa, Cinna latifolia
446, 449	ITS2	AC/-, ACC/-A	AC, ACC: H, most Poinae	-: AQN
465-467	ITS2	CAG/AT	CAG: H, most Poinae	AT: AN (CT: Q)
483	ITS2	T/G	T: H, Cinna	G: AQN, most Poinae
495	ITS2	A/C	A: H, Cinna	C: AQN, most Poinae
584	ITS2	T/A	T: H, most Poinae	A: AQN

^AAC/- in accessions *G7353-1* and *G7353-4*; ACC/- in MEL2323764.

poorly resolved, with only two small clades supported, namely, subsection Austrofestuca (both species and all three collections sampled; BS = 65%) and the two collections sampled of P. fordeana (BS = 97%). Two of the New Zealand species (P. cita and P. cockayneana) formed a clade in the bootstrap analysis (BS = 70%), but not in the MP strict consensus tree. One ETS indel provides additional support for a clade comprising P. orba and P. sallacustris, which resolved in some of the most parsimonious trees (Fig. 2). The majority of species in the primarily Australian section Brizoides clade showed little sequence divergence, and collections of the same species often did not resolve together. Much of the sequence variation can be accounted for by several hypervariable characters in the ETS data matrix (Positions 286, 342, 343 and 551, described above under Sequence characteristics), which vary within species, both between and within samples, as well as between species.

Although the majority of *P*. subgenus *Poa* species formed a large clade in the ITS+ETS analysis, 15 species that resolved within the *P*. subgenus *Poa* clade in the TLF analysis (Fig. 1) resolved outside of this clade. These species resolved as a subclade (Fig. 2: X clade) of the sister clade to this large clade that includes most subgenus *Poa* species. The X clade includes 13 species from New Zealand (Groups A2, B, D–F; Edgar 1986) and two species of *P*. subgenus *Poa* supersection *Poa* section *Malacanthae* (Roshev.) Olon. (*P. smirnowii* from Asia and the circumarctic species *P. arctica*). Sister to the X clade is a clade of three diploid species belonging to three European sections of *Poa* that are not considered members of *P*. subgenus *Poa* (Figs 1–3: N clade).

Combined plastid and nuclear ribosomal analysis

Maximum parsimony analysis of the combined TLF, ITS and ETS data matrix resulted in 90 000 trees (the maximum saved), 2414 steps long (Table 1, Fig. 3).

The PPAM clade and three major internal clades, Puccinelliinae, *Poa* and Clade 1, resolved with strong support (BS = 98–100%). Both *Phleum* and *Milium* resolved with *Poa* in a moderately supported clade (BS = 65%); this clade and Clade 1 resolved together as the sister clade to subtribe Puccinelliinae, with good support (BS = 82%). All genera for which multiple species or samples were included resolved as monophyletic, including *Alopecurus* (BS = 100%), *Arctagrostis* (BS = 100%), *Catabrosa* (BS = 100%), *Cinna* (BS = 77%), *Dupontia* (BS = 95%), *Hookerochloa* (BS = 92%), *Milium* (BS = 100%), *Nicoraepoa* (BS = 94%), *Poa* (including *Dissanthelium*; BS = 100%) and *Saxipoa* (BS = 91%).

Both *Saxipoa* and *Sylvipoa* resolved in Clade 1, within a subclade with *Arctagrostis*, *Hookerochloa*, and *Nicoraepoa* (Fig. 3: HSAQN clade; BS = 100%). *Sylvipoa* resolved as sister to *Nicoraepoa* (BS = 71%), and these in a very well supported clade with *Arctagrostis* (BS = 93%). *Saxipoa* resolved as sister to this clade, with moderate support (BS = 65%).

Australian Poa species (including those sometimes previously placed in Austrofestuca and Neuropoa) resolved in the supersection Homalopoa clade (BS = 76%) within a very strongly supported Poa subgenus Poa clade (BS = 100%). All Australian species resolved in a subclade (BS = 87%), section Brizoides, together with two New Zealand species (P. cita and P. cockayneana, of Edgar's (1986) Group C) and one New Guinean species (P. keysseri). Relationships within this clade were mostly poorly resolved, with only the following five multi-species clades being supported: subsection Austrofestuca (2 species; BS = 94%); subsection Austrofestuca, P. amplexicaulis, P. fawcettiae (MEL2323765) and P. orthoclada (BS = 63%); P. cita and P. cockavneana (BS = 94%); P. affinis and P. poiformis (S5911) (BS=63%); and P. orba and P. sallacustris (BS = 66%, clade not present in the strict consensus tree). Shared indels provided additional support for

Fig. 3. Phylogram of subtribes Poinae, Alopecurinae, Miliinae and Puccinelliinae (PPAM clade), resulting from maximum parsimony analysis of combined plastid TLF and nuclear ribosomal ITS and ETS sequences (length 2414 steps; CI excluding uninformative characters = 0.47); the strict consensus tree is indicated by bold lines; labelling conventions and abbreviations follow those for Fig. 1. Species that belong to the X Clade in the nrDNA analysis (Fig. 2) are excluded here. Two samples missing the ETS data partition are indicated by 'TI'; three samples with partial TLF data, but including ITS and ETS data, are indicated as follows: trnT-trnL and trnL intron = 'TLIE'; trnL intron and trnL-trnF spacer = 'LFIE'. The inset on left shows the *Poa* supersection *Homalopoa* clade, with horizontal branches lengthened to show the branching pattern more clearly.

the last two clades (Fig. 1). The following three species, with two samples each, also resolved as clades: *P. fordeana* (BS = 71%), *P. helmsii* (BS = 55%) and *P. keysseri* (BS = 63%). A large clade of 14 Australian and two New Zealand samples that was present in the majority of most parsimonious trees, but not in the strict consensus tree, was further supported by a shared insertion (not present in *P. fordeana G7321*) (Fig. 3). As noted in the Materials and methods, X clade species were excluded from this combined analysis because of incompatibility between TLF and ITS + ETS datasets.

Discussion

In the present paper, we focus on the relationships of Australasian *Poa* and of two Australian genera newly segregated from *Poa*, namely, *Saxipoa* and *Sylvipoa*. More detailed discussions of relationships among genera within subtribe Poinae and taxa of intergeneric hybrid origin are provided in Gillespie *et al.* (2008, in press). Gillespie and Boles (2001), Gillespie and Soreng (2005), Gillespie *et al.* (2007, 2008, in press) and Soreng *et al.* (in press) discussed phylogenetic structure within the genus *Poa*.

Saxipoa and Sylvipoa - two new Australian genera

Saxipoa and Sylvipoa are two newly described monotypic genera endemic to Australia, based on species formerly placed in the genus Poa, P. saxicola and P. queenslandica, respectively (Soreng et al. 2009). All analyses, plastid, nrDNA and combined, resolved Saxipoa and Sylvipoa within a well to strongly supported clade, comprising subtribe Poinae (all genera except Poa) and Alopecurinae s.s. (i.e. minus Phleinae) (Figs 1-3): Clade 1. Within Clade 1, a strongly supported subclade of Arctagrostis, Hookerochloa, Nicoraepoa, Saxipoa and Sylvipoa (HSAQN clade) was resolved in the nrDNA and combined plastid and nrDNA analyses (this part of Clade 1 was unresolved in the plastid analysis). Gillespie et al. (2008, in press) reported a similar phylogenetic structure in Clade 1 (as 'Poinae (-Poa)'), without the inclusion of samples from the two new genera described here, and found a subclade of Arctagrostis, Hookerochloa and Nicoraepoa (HAN of the HSAQN subclade). Within the HSAQN clade, all genera resolved as monophyletic (or were not resolved in the plastid analysis). Hookerochloa (including Festucella; Jacobs et al. 2008) was sister to the other four genera. A clade of Arctagrostis, Nicoraepoa and Sylvipoa had very good to strong support (Figs 2, 3: AQN clade).

Neither Clade 1 nor the HSAQN subclade has any obvious morphological synapomorphies. Geographically, HSAQN includes all the southern hemisphere genera in Clade 1 (apart from wide-ranging species of *Alopecurus* and one species of *Cinna*). However, within HSAQN, *Arctagrostis* is strictly arctic and has single-flowered spikelets, whereas the other genera are restricted to the southern hemisphere in Australia, New Zealand and South America, and have multiple-flowered spikelets. *Arctagrostis*, with its single-flowered spikelets and broad, flat, morphologically unspecialised leaf blades, has more morphological features in common with the principally northern hemisphere genera sometimes placed in subtribe Cinninae, i.e. *Cinna* (Eurasia and North America, except *C. poiformis* which extends from Mexico to Bolivia), *Limnodea* (North America), *Aniselytron* and *Cyathopus* (South-east Asia). The latter four genera grow in warm to cool temperate habitats. Because Cinninae genera are all intermingled with Poinae genera, we included them in the subtribe Poinae (Gillespie *et al.* in press). The new genus *Agrostopoa* (endemic to Colombia) has recently been included in Poinae on the basis of morphology (Davidse *et al.* 2009), adding yet another genus with single-flowered spikelets to the subtribe.

Morphologically, Sylvipoa is readily differentiated from other genera of the HSAQN clade and from Poa. We entered into the present study anticipating that it may not belong in Poa and might be a new genus, possibly related to the monotypic Australian genus Dryopoa (both are broad-leaved forest grasses with similar blades, open sheaths and large open panicles) (Vickery 1963). Sylvipoa is evidently not related to Drvopoa, a genus with much larger spikelets that resolves outside of the PPAM clade (Figs 1-3). Sylvipoa resolved as sister to the southern South American genus Nicoraepoa in the nrDNA and combined analyses, but was on a moderately long branch (17 bp differences) in the combined analysis, was and highly differentiated from the latter genus in morphology (Soreng et al. 2009; Nicoraepoa morphology was described in detail in Soreng and Gillespie 2007), and the two genera share no apparent morphological synapomorphies.

Saxipoa is distinguishable from Poa by a combination of characters, including densely plumose stigmas without secondary branching, ciliate glume and lemma margins, and sheaths open to near the base (Soreng et al. 2009). These features make Saxipoa quite recognisable, but they do not, by themselves or in combination, make the genus stand out sharply from Poa. In this case, the DNA data provided the critical evidence that this taxon did not belong within Poa. Saxipoa is most similar to the Australian genus Hookerochloa, sharing several morphological characters, including densely pubescent rachillas and sheath margins fused only at base (discussed in Soreng et al. 2009). Saxipoa resolved as the sister to the AQN subclade with moderate support, but also shares some DNA sequence characteristics with Hookerochloa, including a 20-bp insertion in TLF sequences. All three samples of Saxipoa were found to have the same 10 within-individual base and within-indel variants in ITS sequences, of which five in the ITS2 region have one variant shared with Hookerochloa and the other with Arctagrostis, Nicoraepoa and Sylvipoa (AQN clade) (Table 2). These variants suggested the presence of at least two paralagous ITS copies in Saxipoa. The high number and pattern of within-individual variants ('polymorphisms'), low bootstrap support for its position as sister to the AON clade, and some sequence similarity with Hookerochloa suggested that Saxipoa may be an old hybrid between Hookerochloa and the AQN lineage. The different affinities suggested by the variants in the ITS1 region (Table 2: one variant shared with Arctagrostis, Hookerochloa, Nicoraepoa, Sylvipoa, and most other Poinae, the second variant shared mostly with species of Poa) v. the ITS2 region may also suggest incomplete homogenisation, chimeric sequences and a possible genetic contribution from Poa.

Dryopoa - not a member of the PPAM clade

Dryopoa is a monotypic genus endemic to Australia that was considered by its author to be allied to *Poa* (Vickery 1963). The taxonomic position of *Dryopoa* remains uncertain; its single species, a tall grass of forest understorey with large panicles, was originally described in *Festuca*, then transferred to *Poa*, before being treated as a separate monotypic genus. More recently, Clayton and Renvoize (1986) suggested that *Dryopoa* is very similar to *Scolochloa*, and considered both genera to be segregates of *Festuca*. On the basis of plastid and ITS data (ETS data missing), all three analyses placed *Dryopoa* outside of the PPAM clade, with moderate (plastid) to strong support (combined plastid and nrDNA). This confirms previous results based on plastid restriction-site data that showed that the genus was not close to *Poa* (Gillespie and Soreng 2005).

The X Clade

Before discussing relationships of Australian and New Zealand Poa we need to introduce an anomalous clade, here called the X clade, that was detected in our nrDNA analysis (Fig. 2). Positions of X clade taxa were incongruent between the nrDNA analysis and the plastid analysis (Figs 1, 2). For this reason, and because we do not yet understand the nature of the clade in which they resolve in the nrDNA trees, this set of taxa was excluded from the combined analysis. A similar clade was also resolved by Nosov and Rodionov (2008, fig. 1 as NZ1) for a smaller set of New Zealand Poa species and P. arctica on the basis of ITS data alone. Although more than a dozen extra-New Zealand species have been resolved in the X clade in our exploratory analyses of nrDNA sequence data (L. J. Gillespie and R. J. Soreng, unpubl. data), here we included only two exemplars from the P. arctica complex (P. subgen. Poa supersection Poa section Malacanthae) to show that species with this nrDNA type do not exclusively grow in New Zealand. The X clade is strongly supported in both separate ITS and ETS analyses, and in the combined nrDNA analysis, and resolves as sister to the N clade (Fig. 2). The X clade has not been detected in plastid analyses; in the plastid tree presented here (Fig. 1), the taxa that resolve in the X clade in the nrDNA analysis (Fig. 2) are scattered within the strongly supported P. subgenus Poa clade. When the X clade elements are included in a combined plastid and nrDNA analysis, the X clade is still resolved and is sister to a clade of all other P. subgenus Poa species (tree not shown). Although X clade taxa collectively are morphologically and geographically heterogeneous, in plastid analyses (here and e.g. Gillespie and Soreng 2005; Gillespie et al. 2007) most of these taxa (including all taxa studied here) resolve in P. subgenus Poa, in each supersection clade. As shown in Fig. 1, the P. arctica complex resolved within supersection Poa, and the New Zealand species were scattered within supersection Homalopoa. A few X clade taxa, however, have plastid DNA undifferentiated from those in the main clade of P. subgenus Stenopoa (L. J. Gillespie and R. J. Soreng, unpubl. data). So far, the X clade taxa all come from around the Pacific Ocean basin and the Himalayas, and none is from Europe (except the circumboreal P. arctica). In the present study, no X clade elements were detected among sampled Australian Poa. All sampled New Zealand species of Edgar's

Groups A2, B, D, E and F (but not those of A1 or C) resolved in the strongly supported X clade in the nrDNA analysis.

We hypothesise that the X clade involves paralogous nrDNA copies, perhaps derived from homologous chromosomes from allopolyploid genomes (no members are diploids), or some distorted evolution of the nuclear ribosomal region (possibly duplication of the nrDNA region onto another chromosome within a single genome). Further work requires a thorough investigation of the nature of the X clade via cloning of the DNA region, and selective staining of chromosome spreads. The important result here is that the New Zealand *Poa*, except for those of Edgar's Groups A1 and C, resolved in the X clade.

Australian Poa – a recently diversified clade

Our molecular results support the inclusion of all sampled species of Australian Poa, one species of New Guinea (P. keysseri), the five sampled species of Edgar's Group C from New Zealand (Edgar 1986; Edgar and Connor 2000), and no other taxa, in a single lineage within P. subgenus Poa supersection Homalopoa. These species resolved together in a clade in the nrDNA and combined analyses, with moderate to very good support, respectively, despite the relatively low levels of sequence divergence of most species in this subgenus. Although the plastid analysis did not resolve this Australasian lineage and levels of sequence divergence were even lower, the same species did resolve together in two subclades in the majority of trees. We placed all of these species in the newly expanded and circumscribed Poa section Brizoides (Soreng et al. 2009). Membership in this section of all other Australian Poa species not tested for DNA was extrapolated on the basis of their shared morphology.

The Poa section Brizoides clade is part of a worldwide supersection Homalopoa clade that includes about two-thirds of the species in the genus. Phylogenetic structure within this large supersection clade is not well resolved, likely owing to the paucity of DNA characters, and also to homoplasy resulting in part from several highly variable DNA characters. Supersection Homalopoa contains ~300 species, presently organised in seven sections (Homalopoa, Acutifoliae, Madropoa, Brizoides, Anthochloa, Dasypoa and Dioicopoa; sometimes abbreviated HAMBADD; Gillespie et al. 2007). Supersection as Homalopoa also includes miscellaneous unnamed groups of species, and three genera not yet synonymised under Poa (Aphanelvtrum, Dissanthelium and Tovarochloa) (Gillespie and Soreng 2005; Gillespie et al. 2007, 2008). As can be said of most of supersection Homalopoa, its position on the cladogram combined with limited DNA and morphological divergence suggests that section Brizoides is recent in origin. DNA variation within supersection Homalopoa was insufficient to resolve what group might be sister to this Australasian section.

Soreng *et al.* (2009) placed most *Poa* section *Brizoides* species within the following four subsections: *Australopoa* (with 35 spp. in Australia, six in New Zealand, and possibly one in New Guinea), *Austrofestuca* (2 spp.), *Brizoides* (1 sp.) and *Neuropoa* (1 sp.). Within section *Brizoides*, species relationships were poorly resolved and there was not sufficient DNA variation to resolve any smaller sets of taxa with good support, except for subsection *Austrofestuca*, which was strongly

supported as a clade in our nrDNA and combined analyses. Most Australian Poa can be placed in these four subsections on the basis of shared morphological characteristics. The majority of species appear to represent variations of the widespread P. labillardierei-P. sieberiana complex, and we place all of these in subsection Australopoa (Appendix 1). Soreng et al. (2009) left the following four morphologically diverse Australian species insertae sedis within section Brizoides: P. fordeana, P. homomalla, P. orba and P. sallacustris.

A unique 8-bp insertion in the plastid data matrix provided an additional synapomorphy for a clade present in the majority of the most parsimonious trees in the combined analysis (a similar but smaller clade was present in the plastid tree). The insertion was present in subsections Austrofestuca, Brizoides, Neuropoa, the four Australian 'insertae sedis' species, six samples of the Australian subsection Australopoa, and the two sampled species of subsection Australopoa from New Zealand (Fig. 3). The insertion was absent from most subsection Australopoa samples (21) and from P. keysseri of New Guinea. Only one of two to four samples of section Australopoa species, P. fawcettiae, P. meionectes, and P. sieberiana, had the insertion: these individuals may have gained the insertion by plastid capture. The presence of the insertion in only one of two samples of P. fordeana ('insertae sedis') is also likely to be the result of plastid capture; the two samples had identical nrDNA sequences and resolved as a strongly supported clade in the nrDNA tree, but resolved in separated positions in the plastid tree. In the combined analysis, these two samples formed a moderately supported subclade within the clade supported by the 8-bp insertion, which suggests that the insertion was lost in P. fordeana G7321 through a gain of a plastid type from a subsection Australopoa species outside this clade (in the plastid analysis this sample resolved among section Australopoa members lacking the insertion in the majority of most parsimonious trees).

Species with the insertion mostly have rhizomes, stolons or at least well developed extravaginal branching systems, or have corms (P. drummondiana) or an annual habit (P. fax), and their sheaths are mostly closed between 30 and 90% of their length (except for several subsection Australopoa species). Species without the insertion (all of which belong to subsection Australopoa, excluding P. fordeana G7321) are mostly tufted, without rhizomes or stolons, and with sheaths closed mostly less than 35% of their length. Thus, there appears to be a correlation between the presence of the 8 bp plastid insertion and the presence of a loose habit with rhizomes or stolons and more closed sheaths, and other diverse life history traits, including annual life cycle or the presence of corms, as reflected in our subsectional taxonomy.

Among members of this clade supported by the 8-bp insertion, P. fordeana shares a combination of morphological features with P. fax and no other Australian Poa; these include flat flaccid leaf blades (also present in P. drummondiana), short branched inflorescences with crowded and elongated spikelets and lemmas with particularly dense silky appressed pubescence along the veins and sometimes between them. Both species grow in seasonal wetlands, with P. fax growing in subsaline soils. The two species also share a 4-bp deletion (along with

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perennial habit and thinner lemmas, and perhaps provides a link between the subsections Neuropoa and Australopoa. Apart from belonging to this clade, no other molecular support was found for Walsh's (1991) postulated link between P. fordeana and P. sallacustris. Both P. sallacustris and P. orba resemble P. fordeana in having a strongly rhizomatous habit and lacking truncate ciliate ligules. The first two species often resolved together in the nrDNA and combined trees (with moderate support in the latter) and shared a unique 2-bp insertion in the ETS sequence. Soreng et al. (2009) initially speculated that P. orba might be hybridogenic in origin, involving P. pratensis, but our new DNA data suggest the species is more likely simply a part of the diverse section Brizoides clade.

Although Soreng et al. (2009) indicated that P. homomalla ('insertae sedis') shares characteristics with P. supersection Poa section Macropoa F.Herm. ex Tzvelev. on the basis of its more closed and strongly keeled sheaths, long rhizomes, acute and smooth ligule apices, and glabrous lemmas, both plastid and nrDNA sequence data indicate that it belongs to the section Brizoides clade. Presence of the 8-bp TLF insertion, along with shared morphological characters (rhizomes, quite closed sheaths and aerial branching of the culm), suggests that P. homomalla belongs among those species that have the insertion. Certainly, the DNA data support accommodating all of the above morphologically diverse species in section Brizoides, but some additional or different groupings might be employed in the future.

Of the eight Australian and one New Guinean species, for which multiple samples were included, only three, namely, P. fordeana, P. helmsii and P. kevsseri, resolved as clades, with poor to moderate support, in the combined analysis. Among the remaining species, samples of P. costiniana and P. poiformis showed little sequence divergence and resolved near each other, whereas samples of P. phillipsiana and P. fawcettiae were more divergent and separated on the tree. An 8-bp insertion was present in the TLF sequence of one of the samples of P. fordeana and P. fawcettiae, but not in the other (Fig. 1). Among samples of the morphologically variable and very common, widespread taxon P. sieberiana, two resolved near each other and showed little sequence divergence, whereas a third showed more divergence (all lacked the 8-bp TLF insertion, Fig. 1). A fourth sample with only TLF data, taken from a cultivated plant in New Zealand (AY589145), resolved outside of the section Brizoides species assemblage in the plastid analysis (and had the 8-bp insertion, Fig. 1), suggesting that it may be a misidentification (identity of this GenBank sample could not be confirmed) or that it has undergone introgression and possibly plastid capture. In the plastid analysis, two samples of P. meionectes also had divergent TLF sequences, each belonging to a different clade. Poa is renowned to be a taxonomically challenging genus (e.g. Bor 1952; Clayton and Renvoize 1986), and the Australian species are no exception (Vickery 1970). The identification of all vouchers was reconfirmed (one sample, S5921, initially called P. labillardierei, was redetermined as P. helmsii), so misidentification of samples is unlikely, although remains a possibility, given the difficulty of assigning specimens to species. More likely

explanations for samples of a species not resolving together include hybridisation and introgression (and possible plastid transfer), lineage sorting, and/or extensive homoplasy resulting from several hypervariable positions. More detailed studies, including those involving cloning of multiple samples per species, will be necessary to sort out relationships among Australian *Poa* species.

New Guinea Poa – an Australian connection

Poa keysseri of New Guinea is not substantially morphologically differentiated from the species of subsection *Australopoa*, because it has, like most species of the subsection, short-truncate to obtuse ciliate-rimmed ligules, sheaths closed ~12% of their length, blades folded, narrow and somewhat firm, panicles loose, with branches scabrous all over, and blunt lemma apices. This species resolved within the section *Brizoides* clade, with nrDNA sequences being identical to seven subsection *Australopoa* samples and plastid sequences with one to three autapomorphic characters.

Malesian Poa were revised by Veldkamp (1994) to include 38 endemic and three introduced species, 34 of these are endemic to New Guinea, one is endemic to each of Sabah and Celebes. About one-third of the endemic species are similar to P. keysseri in morphology, in having strongly 5-nerved lemmas (characteristic of subgenus Poa), whereas the remaining two-thirds of the endemics have intermediate nerves that are indistinct (characteristic of subgenus Stenopoa) or obsolete (otherwise unknown in Poa). Among the New Guinean species with strongly 5-nerved lemmas, only P. keysseri has truncate ciliate-rimmed ligules, characteristic of most species of subsections Australopoa and Austrofestuca. At this point, we can reasonably include P. keysseri in section Brizoides, and perhaps within subsection Australopoa; however, unlike other subsection Australopoa elements, it has a combination of a callus web and glabrous lemmas. The placement of any other Malesian Poa (Veldkamp 1994) in this section requires further study.

New Zealand Poa – at least three lineages

Edgar (1986) and Edgar and Connor (2000) outlined the following 10 groups and subgroups within New Zealand Poa: A1, A2, B, C1, C2, D, E1, E2, F1 and F2. Among these groups, we have detected three major DNA lineages corresponding to (1) A1, (2) C and (3) A2, B, D, E1, E2, F1 and F2. (1) Poa cookii s.l. (Edgar included P. hamiltonii here) and P. ramosissima (for which only ITS data are available) belong to Edgar's Group A1. These species resolved as members of the Sub-Antarctic Island Parodiochloa-Tzvelevia clade in analyses here and in Gillespie et al. (2008), and were placed in P. subgenus Ochlopoa section Parodiochloa on the basis of this DNA data, and their unusual leaf anatomy (Soreng and Gillespie 2007). Hair (1968) and Edgar (1986) anticipated their close relationship with P. flabellata. (2) P. cockayneana, P. cita, P. chathamica, P. anceps and P. litorosa (ITS data only for the last three species) of New Zealand resolved in the section Brizoides clade in the nrDNA and combined analyses. These species belong to Subgroups C1 and C2 (Edgar 1986; Edgar and Connor 2000), and we place them in P. section Brizoides subsection Australopoa (Soreng et al. 2009). This position is entirely consistent with Edgar's placement of Australian species introduced into New Zealand (*P. labillardierei* and *P. sieberiana*) within her Group C1. (3) We have examined representatives of all other of Edgar's New Zealand groups by using ITS data, and representatives of A2, B and E2 for ETS, ITS and plastid data. All the sampled taxa of this set have X clade-type nrDNA (Fig. 2). Those examined for plastid DNA resolved outside of the section *Brizoides* assemblage, but within subgenus *Poa* supersection *Homalopoa*, and did not resolve into any New Zealand monophyletic subsets. Although Edgar (1986) and Edgar and Connor (2000) accepted the genus *Austrofestuca s.s.* in New Zealand, we now place it in *P. section Brizoides* subsection *Austrofestuca*.

Biogeography

Our phylogenetic hypothesis suggests a recent origin and diversification of the Australasian Poa section Brizoides clade and an older origin for the subtribe Poinae HSAQN clade, which includes the Australian genera Hookerochloa (also in New Zealand), Saxipoa and Sylvipoa. Because there are no Poa or Poinae fossils other than those from the late Pleistocene and Holocene, dating of these events would be highly speculative. Eurasia is postulated to be the centre of origin for Poa on the basis of species diversity and geographical distribution of basal lineages (Soreng 1990), and similarly the majority of Poinae genera are Eurasian or primarily so. The origin of the temperate tribe Poeae has been estimated at ~21 million years ago (time of divergence between the Triticeae and Poeae s.l. lineages) (Inda et al. 2008), well after the separation of Australia and South America from Antarctica estimated at ~37 million years ago (McLoughlin 2001). Thus, distributions of subtribe Poinae taxa in Australasia result from long-distance dispersal, and not vicariance.

At least two dispersal events into Australia are postulated for subtribe Poinae, one for Poa and one for the three other Australian Poinae genera, namely, Hookerochloa, Saxipoa and Sylvipoa. Our phylogenetic hypothesis suggests several scenarios for the latter three genera, and from one to three dispersal events. The HSAQN clade may have diversified in Australia (following dispersal to Australia of the clade ancestor), with dispersals outward to South America (Nicoraepoa) and the northern hemisphere (Arctagrostis). Or there may have been two dispersal events into Australia (Hookerochloa and Sylvipoa), with Saxipoa evolving from one of these lineages or originating from a hybridisation event between these two lineages. Alternatively, Hookerochloa, Saxipoa and Sylvipoa may each represent a separate dispersal event into Australia; however, given that three of five HSAQN clade genera are endemic to Australia, this seems the least likely hypothesis.

In *Poa*, there is evidence of only one DNA lineage in Australia, that which diversified into what we call *P*. section *Brizoides*. This same lineage also occurs in New Guinea and New Zealand, but is not known outside of Australasia. In New Guinea, we have evidence of at least two lineages, with one including species in section *Brizoides* (represented by *P. keysseri*) and the other including species with ITS and plastid genomes matching subgenus *Stenopoa* (L. J. Gillespie and R. J. Soreng, unpubl. data; *P. papuana* Stapf). In New Zealand, we have evidence of at

least the following three lineages: one with representatives of two subsections of section Brizoides, subsections Australopoa (Edgar's (1986) Groups C1 and C2) and Austrofestuca; a second lineage (A1) that has colonised the Sub-Antarctic Islands (P. subgen, Ochlopoa section Parodiochloa): and a third lineage with X clade-type nrDNA (A2, B, D-F). The third lineage may have heterogeneous origins in New Zealand, but further study of extra-New Zealand taxa with X clade nrDNA is needed to evaluate this possibility. Because species of subsections Austrofestuca (confined to coastal sand dunes) and Brizoides are native to both Australia and New Zealand, origin of the subsections could have taken place in either geographic region, and dispersal could have been in either direction. Given that section Brizoides is most diverse and speciose in Australia, the more likely scenario is that both lineages evolved in Australia and secondarily established in New Zealand. Thus, Poa lineages have probably colonised New Zealand at least four times.

In New Zealand, the X clade nrDNA genome is associated with plastids of *P*. subgenus *Poa* supersection *Homalopoa* in the species tested (A2, B and E), although those species do not resolve among species of section *Brizoides* (plastid data not available for species of New Zealand Groups D and F). The combination of supersection *Homalopoa* plastids and X clade nrDNA genomes is also present in South-east Asian species (e.g. in *P. acroleuca* Steud. and relatives; L. J. Gillespie and R. J. Soreng, unpubl. data). If this combination of genomes has originated only once, then this may provide a geographic connection between these South-east Asian *Poa* species and New Zealand *Poa* of the X clade.

Soreng (1990) suggested that the Australia and New Zealand 'Australopoa' group (now subsection *Australopoa*) might be derived from a South American ancestor. At this point, we cannot confirm or reject this hypothesis. Although we have included a series of representative *Poa* species from around the world, including multiple lineages from Eurasia and South America, we have not resolved a supported sister-group relationship for the *Brizoides* lineage. Asian *Poa* connections are certainly possible (Veldkamp 1994), and are hinted at in some most parsimonious nrDNA trees by the inclusion of Eurasian taxa (*P. chaixii, P. ircutica* and *P. polycolea*) in a polytomy with the *Brizoides* clade. In summary, it seems likely that an ancestor of *P.* section *Brizoides* entered Australia, and diversified *in situ* with two subsequent long-distance dispersals to New Zealand.

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Appendix		

voucher information and GenBank accession numbers GenBank numbers in bold indicate new sequences submitted for the present paper; all other sequences are from Gillespie *et al.* (2007, 2008, in press), except for those downloaded from GenBank, which are indicated by 'GB', followed by the literature reference where first published or by the authors who submitted the sequence(s) and, where known, by the voucher information. Incomplete TLF sequences are indicated under 'TLF GenBank' as TLL = *trn*T-*trn*L spacer and *trn*L intron, or LLF = *trn*L intron and *trn*L-*trn*F spacer. Herbarium acronyms follow Thiers (continuously updated). Under 'Country of origin':

		ACT=Au	stralian Capital Territory	r; NSW=New South Wale	ss; WA = Western Australia	•		
Taxon	Chromosome number	<i>Poa</i> subgenus- supersection	Poa section- subsection (and NZ group)	Country of origin	Voucher	TLF GenBank	ITS GenBank	ETS GenBank
Tribe Poeae – PPAM clade Subtribe Alopecurinae								
Alopecurus borealis Trin.	56			Canada, Nunavut	Gillespie <i>et al.</i> 6576 (CAN)	DQ353966	EU792345	GQ324237
A. gerardii Vill.	14			Greece	Soreng et al. 7494 (US)	EU792432	EU792344	GQ324238
Beckmannia syzigachne (Steud.) Femald	14, 28			USA, Wyoming	Soreng 3513 (US)	DQ353965	EU792342	GQ324255
Subtribe Miliinae								
Milium effusum L.	14, 28			Finland	GB: Quintanar <i>et al.</i> 2007	DQ631501, DQ631435	I	I
M. effusum	14, 28			Canada, Quebec	Gillespie 7422 (CAN)	I	GQ324477	GQ324273
M. vernale M.Bicb. Subtribe Dhleinge	14, 28			Greece	Soreng 3748 (US) ^B	DQ353963	EU792340	GQ324274
Phleum pratense L.	14, 28, 42, 56, 63, 70, 84			USA, cultivated	No voucher	DQ353964	EU792341	GQ324284
Subtribe Poinae								
Aniselytron treutleri				China, Yunnan	Soreng et al. 5229 (US)	GQ324395	GQ324469	GQ324240
(Kuntze) Sojak								
Apera interrupta (L.)	14			Argentina	Peterson et al. 19173	EU792439	EU792364	GQ324242
P.Beauv.								
Arctagrostis latifolia (R.Br.) Griseb.	56			Canada, Nunavut	Archambault 157 (CAN)	EU792434	EU792353	GQ324244
A. latifolia	56			Canada, Nunavut	Gillespie et al. 6586	DQ353969	EU792351	GQ324245
	ç				(CAN)	D.02 64060		
Arctopnua Jutva (Trin.) Rupr.	47			Canada, Northwest Territories	AIKEN 99-230 (UAN)	8c04ccDU	EU /9234 /	GQ324240
Bellardiochloa polychroa				Turkey	Soreng & Guney 4191	I	EU792363	GQ324256
(Trautv.) Roshev.					(SU)			
<i>B. variegata</i> (Lam.) Kerguelen	14			Greece	Soreng <i>et al.</i> 7519-1 (US)	EU792438	EU792361	GQ324257
Cinna arundinacea L.	28			USA, West Virginia	Soreng & Olonova 7462 (US)	EU792436	EU792343	GQ324260
C. latifolia (Trevir.	28			USA, California	Peterson et al. 19769	GQ324396	GQ324473	GQ324261
ex Göpp)				ſ	(SU)			
Dissanthe lium		Poa supersect.		Peru ^E	Peterson & Refulio	EU792468	EU792424	GQ324263
<i>brevifolium</i> Swallen & Tovar		Homalopoa			18043 (US)			

						maannintt		
GQ324290	GQ324486	DQ354021	Soreng 5801 (US)	USA, Oklahoma	Dioicopoa	P. supersect. Homalopoa	32, 56, 63, 84	ra Torrey
			unpubl. (AK-282943)		Australopoa 'C2'	Homalopoa		<i>lyphylla</i> dgar
I	AY686666	I	GB: Gardner et al.	New Zealand ^E	Brizoides subsect.	P. supersect.	28	j.Forst.
			(MEL 2223/00)		Austratopoa	Homatopoa		ller & Ish
GQ324289	GQ324484	GU324400	Walsh s.n.	Australia, Victoria	Brizoides subsect.	P. supersect.		aulis
GQ324288	EU792374	DQ353981	Gillespie 6467 (CAN)	Canada, Quebec	Sylvestres	Sylvestres		A.Gray
GQ324287	GQ324483	DQ353985	Gillespie 6299 (CAN)	USA, Colorado	Alpinae	Ochlopoa	21–48, 56	(
,	,	,	7311-2 (US)		Australopoa	Homalopoa		
G0324285	GO324482	GO324399	Lange 6060 (AK-286743) Gillespie & Jacobs	Australia. ^E NSW	Brizoides subsect.	P. supersect.		Br
			unpubl.					n
I	AY686667	I	GB: Gardner et al.	New Zealand ^E	'New Zealand B'	P. (X clade)	28	niana arifolia
GQ324282	GQ324479	EU792442	Soreng 7155 (US)	Chile				vis subsp.
			(SU)					<i>iniana</i> (Nicora, & L.J.Gillespie
GQ324281	EU792358	EU792443	Peterson et al. 19186	Argentina				ubenervis rvis subsp.
			(SN)					& L.J.Gillespie
GQ324283	EU792359	DQ353972	(US) Soreng & Soreng 7334	Chile				& L.J.Gillespie rvis (Hack.)
GQ324279	EU792357	DQ353975	Soreng & Soreng 7358	Chile				a (Steud.)
•			(SU)					& L.J.Gillespie
GO324276	EU792355	DO353974	Soreng & Soreng 7309	Chile				lespie <i>ica</i> (Phil.)
GQ324275	EU792354	DQ353971	Soreng & Soreng 7182 (US)	Chile				<i>oa andina</i> Soreng &
GQ324272	EU792348	EU792435	Jacobs 9127 (NSW)	Australia, ^E NSW				<i>iana</i> (F.Muell. k.f.) E.B.
GQ324271	EU792350	GQ324397	Jacobs 9129 (NSW)	Australia, ^E NSW				auuus la
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GQ324270	EU792349	EU792433	Jacobs 9128 (NSW)	Australia, ^E NSW				hloa eriopoda
GQ324267	GQ324475	DQ353968	Gillespie et al. 6699	Canada, Nunavut			44, 88	
GQ324266	EU792346	DQ353967	Gillespie <i>et al.</i> 6589 (CAN)	Canada, Nunavut			44, 88	fisheri R.Br.
GQ324265	EU792415	DQ354052, DQ354053	Peterson & Soreng 15744 (US)	Chile		P. supersect. Homalopoa		<i>mum</i> (Nees & Pilg.
GQ324264	EU792426	EU792466	Peterson & Refulio 16466 (US)	Peru		P. supersect. Homalopoa		uum (J.Presl)

			Appe	ndix 1. (continued)				
Taxon	Chromosome number	Poa subgenus- supersection	Poa section- subsection (and NZ group)	Country of origin	Voucher	TLF GenBank	ITS GenBank	ETS GenBank
P. arctica R.Br. subsp. arctica	36, 38, 42, 56, 60–65, 68, 70–78, 80–86, 106	P. supersect. Poa	Malacanthae	Canada, Nunavut	Gillespie & Aiken 5701 (CAN)	DQ354009	GQ324487	GQ324291
P. astonii Petrie	28	Poa (X clade)	'New Zealand B'	New Zealand ^E	Lloyd s.n. (OTA 058919)	GQ324401	GQ324488	GQ324292
P. atropidiformis Hack. var. atropidiformis		P. supersect. Homalopoa	Homalopoa s.l., Dissanthelium s.l.	Chile	Soreng & Soreng 7364 (US)	DQ354020	GQ324489	GQ324293
P. autumalis Elliott P. badensis Haenke ex Willd.	28 14, 18–21, 28	Sylvestres Ochlopoa	Sylvestres Bolbophorum	USA, Maryland Bulgaria	Soreng 4680 (US) Hajkova <i>et al.</i> 2004-12 (BRNU, US)	DQ353979 GQ324402	EU792379 GQ324490	GQ324294 GQ324295
P. billardierei StYves	28	P. supersect. Homalopoa	Brizoides subsect. Austrofestuca	Australia, NSW	Gillespie <i>et al.</i> 7382 (CAN)	GQ324403	GQ324491	GQ324296
P. billardierei (as Austrofestuca littoralis (Labill.) Alexeev)	28	P. supersect. Homalopoa	Brizoides subsect. Austrofestuca	New Zealand ^E	GB: Hunter et al. 2004	I	AY524824	I
P. breviglumis Hook. f.	28	Poa (X clade)	'New Zealand E2'	New Zealand ^E	GB: Gardner <i>et al.</i> unpubl. (AK-281888)	I	AY 68 665 6	I
P. buchananii Zotov	28	Poa (X clade)	'New Zealand F2'	New Zealand ^E	GB: Gardner <i>et al.</i> unpubl. (AK-281045)	Ι	AY 68 6654	I
P. bulbosa L.	14, 21–49, 56	Ochlopoa	Bolbophorum	Spain	Catalan 13-2000 (UZ)	DQ354034, DO354035	EU792388	GQ324297
P. bulbosa subsp. vivipara (Koeler) Arcang.	21-49, 56	Ochlopoa	Bolbophorum	USA, Nevada (introduced from Europe)	Soreng 5814 (US)	GQ324404	GQ324492	GQ324298
P. chaixii Vill.	14	P. supersect. Homalopoa	Homalopoa s.s.	Russia	Soreng 4677 (US)	EU854590	EU792404	GQ324299
P. chaixii	14	P. supersect. Homalopoa	Homalopoa s.s.	Germany	Soreng 7524 (US)	GQ324405	GQ324493	GQ324300
P. chathamica Petrie	112	P. supersect. Homalopoa	Brizoides subsect. Australopoa 'C2'	New Zealand ^E	GB: Gardner <i>et al.</i> unpubl. (CHR-562183)	I	AY686665	I
P. cheelii Vickery		P. supersect. Homalopoa	Brizoides subsect. Australopoa	Australia, ^E NSW	Gillespie & Jacobs 7332-1 (CAN)	GQ324406	GQ324494	GQ324301
P. cita Edgar	84	P. supersect. Homalopoa	Brizoides subsect. Australopoa 'Cl'	New Zealand ^E	Lloyd s.n. (OTA 058916)	3 Q324407 (TLL)	GQ324495	GQ324302
P. clelandii Vickery		P. supersect. Homalopoa	Brizoides subsect. Australopoa	Australia, ^E Victoria	Walsh s.n. (MEL2323767)	GQ324408(LLF)	GQ324496	GQ324303
P. cockayneana Petrie	112	P. supersect. Homalopoa	Brizoides subsect. Australopoa 'Cl'	New Zealand ^E	Lloyd s.n. (OTA 058921)	GQ324409	GQ324497	GQ324304

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P. colensoi Hook.f.	28	P. (X clade)	'New Zealand B'	New Zealand ^E	Lloyd s.n.	GQ324410	GQ324498	GQ324305
P_cookii (Hook f)		Ochlanoa	Parodiochloa 'Al'	Crozet Islands (sub-	(OTA 058923) Hennion Gen 1 (P)	FI 1792454	F11792383	GO324306
Hook.f.		notomoo		Antarctic)				
P. cookii		Ochlopoa	Parodiochloa 'Al'	Kerguelen Islands (suh-Antarctic)	Hennion Gen8 (P)	EU792455	EU792382	GQ324307
P. costiniana Vickery		P. supersect.	Brizoides subsect.	Australia, ^E NSW	Gillespie et al. 7356-1	GQ324411	GQ324499	GQ324308
D accetuiana		Homalopoa	Australopoa	A ctuolia E MCW	(CAN) Gillogaio at al 7267	033447	00314500	00311300
г. сознинана		r. supersect. Homalopoa	brizoutes subsect. Australopoa	Ausualia, NSW	(CAN) (CAN)	71++7000	000047000	60647670
P. cusickii Vasey subsp.	56	P. supersect.	Madropoa	USA, Nevada	Soreng 5829 (US)	DQ354029	GQ324501	GQ324310
cusickii P. dianhora Trin.	14, 28, 42	Homalopoa Pseudonoa	Pseudonoa	Turkev	Soreng & Günev 4165	DO353987.	E11792400	GO324311
					(US)	DQ353988		
P. dipsacea Petrie	28	Poa (X clade)	New Zealand D^{γ}	New Zealand	GB: Gardner <i>et al.</i> unpubl.	I	AY 686670	I
P dolosa Boiss & Heldr	14	(N clade)	'Oreinos'	Buloaria	(AK-285251) Stonehero SH18 (UIS)	GO324413	GO324503	G0324313
P. drummondiana Nees	-	P. supersect.	Brizoides subsect.	Australia, ^E WA	Peterson et al. 14504	DQ354013	EU792411	GQ324314
		Homalopoa	Brizoides	Ę	(NS)			
P. ensiformis Vickery		P. supersect.	Brizoides subsect.	Australia, ^E NSW	Gillespie <i>et al. 7379</i> (CAN)	GQ324415	GQ324504	GQ324315
P. fawcettiae Vickery		P. supersect.	Brizoides subsect.	Australia, ^E NSW	Soreng & Peterson	GQ324416	GQ324506	GQ324317
		Homalopoa	Australopoa	<u>.</u>	5919 (US)			
P. Jawcettiae		P. supersect. Homalonoa	<i>Brizoides</i> subsect. Australonoa	Australia, [–] Victoria	Walsh s.n. (MFL 2323765)	GQ324417	cUc4324DD	GQ324310
P. fax Willis & Court		P. supersect.	Brizoides subsect.	Australia, ^E NSW	Jacobs 9339 (NSW)	EU792460	EU792410	GQ324318
D fondloniona (Stand)	26 58 60 64	Homalopoa	Neuropoa	TISA Colombo	Gillesning 6202 (CAND	DO354077	EI 1707403	CO37/310
Vasey	+0, 00-00, 01+	1. supersect. Homalopoa	nodoinnia	USA, CUIUIAUO	(NTRO) 2620 AIdeanin	170+CCDC	C0476107	
<i>P. flabellata</i> (Lam.) Rasnail	28	Ochlopoa	Parodiochloa	Falkland Islands	Wright 4NCD (seed voucher US)	DQ353982	EU792380	GQ324320
P. flabellata	28	Ochlopoa	Parodiochloa	South Georgia Islands	Wright 9NSG (seed	EU792453	EU792381	GQ324321
P. fordeana F.Muell.		P. supersect.	Brizoides	Australia, ^E NSW	voucher US) Gillespie <i>et al.</i> 7321-1	GO324419	GO324507	G0324322
, , ,		Homalopoa		F	(CAN)			
P. fordeana		P. supersect. Homalopoa	Brizoides	Australia, [~] NSW	Gillespie & Jacobs 7326-2 (CAN)	GQ324420	GQ324508	GQ324323
P. glauca Vahl	32, 42, 50, 56–58, 64, 65, 70, 75, 78	Stenopoa	Stenopoa	Canada, Nunavut	Gillespie 5804 (CAN)	GQ324421	AY237839	GQ324324
P. gymnantha Pilg.	70	P. supersect. Homalopoa	'punapoa'	Chile	Peterson & Soreng 15656 (US)	EU792462	EU792417	GQ324325
P. helmsii Vickery		P. supersect. Homalopoa	Brizoides subsect. Australonoa	Australia, ^E ACT	Gillespie <i>et al.</i> 7339 (CAN)	GQ324422	GQ324509	GQ324326
P. helmsii Vickery	28, 56, 84	P. supersect. Homalopoa	Brizoides subsect. Australopoa	Australia, ^E NSW	Soreng & Peterson 5921 (US)	DQ354014 (as P. labillardierei)	EU792409 (as P. labillardierei)	GQ324327

(Continued next page)

Taxon	Chromosome number	Poa subgenus- supersection	Poa section- subsection	Country of origin	Voucher	TLF GenBank	ITS GenBank	ETS GenBank
			(dnors art nim)	1				Î
P. hesperia Edgar	28	Poa (X clade)	'New Zealand B'	New Zealand ^E	Lloyd s.n. (OTA 058922)	GQ324423	GQ324510	GQ324328
P. hiemata Vickery		P. supersect. Homalopoa	Brizoides subsect. Australopoa	Australia, ^E NSW	Gillespie <i>et al. 7</i> 354 (CAN)	GQ324424	GQ324511	GQ324329
P. holciformis J. Presl		P. supersect. Homalopoa	Dioicopoa	Chile	Soreng & Soreng 7166 (US)	DQ354054, DQ354055, D0354056	GQ324512	GQ324330
P. homomalla Nees		P. supersect. Homalopoa	Brizoides	Australia, ^E WA	Macfarlane 4536 (PERTH)	GQ324425	GQ324513	GQ324331
P. hookeri Vickery		P. supersect. Homaloroa	Brizoides subsect. Australonoa	Australia, ^E NSW	Gillespie <i>et al. 7</i> 370 (CAN)	GQ324426	GQ324514	GQ324332
P. hybrida Gaudin	14	P. supersect. Homalopoa	Homalopoa s.s.	Turkey	Soreng 4263 (US)	I	GQ324515	GQ324333
P. hybrida Gaudin	14	P. supersect. Homalopoa	Homalopoa s.s.	Greece	GB: Patterson <i>et al.</i> 2005 (USDA PI 249765)	AY589130	I	I
P. imbecilla Sol. ex Spreng.	28	Poa (X clade)	'New Zealand E2'	New Zealand ^E	GB: Gardner <i>et al.</i> unpubl. (AK-286463)	I	AY686658	I
P. infirma Kunth P. ircutica Roshev.	14 28	Ochlopoa P. supersect. Poa	<i>Micrantherae</i> <i>Poa</i> subsect. <i>Nivicolae</i>	Spain Russia, Irkutsk	Catalan 3-2000 (UZ) Kasanovskiy 2002-7 (CAN)	GQ324427 DQ354007	GQ324516 EU792402	GQ324334 GQ324335
P. kerguelensis (Hook. f.) Steud		Ochlopoa	Tzvelevia	Kerguelen Islands ^E (sub-Antarctic)	Hennion Gen5 (P)	EU792457	EU792385	GQ324336
P. kerguelensis (Hook. f.) Steud		Ochlopoa	Tzvelevia	Kerguelen Islands ^E (sub-Antarctic)	Hennion Gen6 (P)	EU792456	EU792384	GQ324337
P. keysseri Pilg.	28	P. supersect. Homalopoa	Brizoides	New Guinea	Stančík 4925 (US)	GQ324428	GQ324517	GQ324338
P. keysseri	28	P. supersect. Homalopoa	Brizoides	New Guinea	Stančík 4935 (US)	GQ324429	GQ324518	GQ324339
P. kirkii Buchanan	28	Poa (X clade)	'New Zealand E1'	New Zealand ^E	GB: Gardner <i>et al.</i> unpubl. [de Lange 5651 (AK-282065)]	I	AY 686657	I
P. kurtzii R.E.Fr.		P. supersect. Homalopoa	Homalopoa s.l.	Chile	Peterson & Soreng 15654 (US)	DQ354018	EU792413	GQ324340
P. laxa subsp. flexuosa (Sm.) Hyl.	42, 43, 81	Stenopoa	Oreinos	Norway	Brochmann 2000-3-1 (O)	GQ324418	GQ324520	GQ324342
P. labillardierei Steud.	28, 58, 84	P. supersect. Homalopoa	Brizoides subsect. Australopoa	Australia, ^E NSW	Gillespie <i>et al.</i> 7318 (CAN)	GQ324430	GQ324519	GQ324341
P. lepidula (Nees & Meyen) Soreng & L.J.Gillespie		P. supersect. Homalopoa	Anthochloa	Chile	Peterson <i>et al.</i> 18138 (US)	EU792464	EU792422	GQ324344
P. lepidula		P. supersect. Homalopoa	Anthochloa	Chile	Peterson & Soreng 15604 (US)	EU792471	EU792416	GQ324343

P. lettermanii Vasey	14	Stenopoa	Abbreviatae	USA, Colorado	Soreng & Soreng	GQ324431	GQ324521	GQ324345
P. ligulata Boiss. P. litorosa Cheeseman	14 266	Ochlopoa P. supersect. Homalopoa	Bolbophorum Brizoides subsect. Australopoa 'C1'	Spain New Zealand ^E	JACA 166095 JACA 166095 GB: Gardner <i>et al.</i> unpubl. [de Lange 5595 (AK-281151)]	GQ324432 (TLL) _	GQ324522 AY 686662	GQ324346 _
P. lowanensis G.N. Walsh		P. supersect. Homalopoa	Brizoides subsect. Australonoa	Australia, ^E Victoria	Walsh s.n. (MEL2323766)	GQ324433	GQ324523	GQ324347
P. macrantha Vasey	28	P. supersect. Homalopoa	Madropoa	USA, Oregon	Soreng 5861 (US)	DQ354028	EU792407	GQ324348
P. macrocalyx Trautv. & C.A.Mey.	42–100	P. supersect. Poa	Malacanthae	USA, Alaska	Soreng & Soreng 6318-1 (US)	GQ324434	GQ324524	GQ324349
P. mathewsii Petrie	28	Poa (X clade)	'New Zealand E2'	New Zealand ^E	Lloyd s.n. (OTA 058920)	GQ324435	GQ324525	GQ324350
P. media (L.) Cav.	14	Ochlopoa (N Clade)	Bolbophorum	Bulgaria	Hajkova <i>et al</i> . 2004-11 (US)	GQ324436	GQ324526	GQ324351
P. media	14	Ochlopoa (N Clade)	Bolbophorum	Bulgaria	Stoneberg SH17 (US)	GQ324437	GQ324527	GQ324352
F. melonecies J. Vickery		F. supersect. Homalopoa	<i>Brizoiaes</i> subsect. Australopoa	Australia, NSW	Utilespie & Jacobs 7316-1 (CAN)	GU324438	00324328	505435J
P. meionectes		P. supersect.	Brizoides subsect.	Australia, ^E NSW	Gillespie et al. 7348	GQ324439	I	Ι
P. molinerii Balb.	14, 28	потаюроа Ochlopoa	Austratopoa Alpinae	Slovakia	(CAIN) Stoneberg SH13	DQ354036,	EU792389	GQ324354
		č	ċ	-	(CAN)	DQ354037		
P. nemoralis L.	28, 33, 35, 42, 48, 56	Stenopoa	Stenopoa	Bulgaria	Hajkova <i>et al.</i> 2004-18 (BRNU)	GQ324440	GQ324529	GU324355
P. nervosa (Hook.)	28	P. supersect.	Madropoa	USA, Oregon	Soreng 5849 (US)	DQ354025	EU792405	GQ324356
Vasey	00	Homalopoa	"C A buoloo Zold"	Morry Zoolon dE	CD. Condana at al		U27707/X V	
1 . no vue-zenunane Hack.	07			New regiand	unpubl. [Lange 5654 (AK-282179)]	I	600000 TV	I
P. orba G.N. Walsh		P. supersect.	Brizoides	Australia, ^E Victoria	Walsh s.n.	GQ324441	GQ324530	GQ324357
P. orthoclada		P. supersect.	Brizoides subsect.	Australia, ^E Victoria	(Malsh s.n.	GQ324442	GQ324531	GQ324358
G.N. Walsh <i>P nhillinsiana</i> I Vickery		Homalopoa P sumersect	Australopoa Brizoides subsect	Australia ^E NSW	(MEL2323761) Gillesnie <i>et al</i> 7346	CO374443	CO374537	CO374350
(Homalopoa	Australopoa	in our formanes	(CAN)			
P. phillipsiana		P. supersect.	Brizoides subsect.	Australia, ^E NSW	Gillespie <i>et al.</i> 7369	GQ324444	GQ324533	GQ324360
P. poiformis (Labill.)	56-68	<i>Homatopoa P</i> . supersect.	Australopoa Brizoides subsect.	Australia, ^E NSW	(CAN) Gillespie <i>et al.</i> 7381	GQ324445	GQ324534	GQ324361
Druce P. poiformis		Homalopoa P. supersect.	Australopoa Brizoides subsect.	Australia, ^E NSW	(CAN) Soreng & Peterson	GQ324446	GQ324535	GQ324362
P. polycolea Stapf		Homalopoa P. supersect.	Australopoa Poa subsect.	China, Yunnan	5911 (US) Wen <i>et al.</i> Tibet-1316	GQ324447	GQ324536	GQ324363
P. porphyroclados Nees		Homalopoa P. supersect.	Nivicolae Brizoides subsect.	Australia. ^E WA	(US) Peterson <i>et al.</i> 14476	GO324448	G0324537	GO324364
		Homalopoa	Australopoa		(SU)	,	,	,
P. porsildii Gjaerev.		P. supersect. Homalopoa	Madropoa	USA, Alaska	Soreng & Soreng 6147-1 (US)	DQ354024	GQ324538	GQ324365

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Taxon	Chromosome number	Poa subgenus- supersection	Poa section- subsection (and NZ group)	Country of origin	Voucher	TLF GenBank	ITS GenBank	ETS GenBank
P. pratensis L. subsp. pratensis	25-124	P. supersect. Poa	Poa subsect. Poa	USA, Colorado	Gillespie 6291 (CAN)	DQ354010	GQ324542	GQ324369
<i>P. pratensis</i> subsp. <i>alpigena</i> (Lindm.) Hiltonen	28–127	P. supersect. Poa	Poa subsect. Poa	Canada, Nunavut	Gillespie 5801 (CAN)	DQ354006	GQ324539	GQ324366
P. pratensis subsp. angustifolia (L.) Lei.	28, 46–66, 70–72	P. supersect. Poa	Poa subsect. Poa	Spain	Catalán s.n. (UZ)	DQ354012	GQ324540	GQ324366
P. pratensis subsp. irrigata (Lindm.) H. Lindb.	38–117	P. supersect. Poa	Poa subsect. Poa	USA, Alaska	Soreng & Soreng 6044 (US)	GQ324449	GQ324541	GQ324368
P. pseudoabbreviata Roshev.	14	Stenopoa	Abbreviatae	USA, Alaska	Soreng & Soreng 6032-1 (US)	DQ353997	EU792398	GQ324370
P. pubinervis (Vickery) SWL.Jacobs, L.J.Gillespie & Sorene	51	P. supersect. Homalopoa	Brizoides subsect. Austrofestuca	Australia, ^E WA	Peterson <i>et al.</i> 14510 (US)	DQ354048, DQ354049	EU792408	GQ324371
P. ramosissima Hook.f.	28	Ochlopoa	Parodiochloa (New Zealand 'A1')	New Zealand ^E	GB: Gardner <i>et al.</i> unpubl. [Wright (AK-282001)]	I	AY 686655	I
P. remota Forselles	14	P. supersect. Homalopoa	Homalopoa s.s.	Kyrgyz Republic	Soreng et al. 7540 (US)	GQ324452	GQ324545	GQ324372
P. sallacustris G.N. Walsh		P. supersect. Homalopoa	Brizoides	Australia, ^E Victoria	Walsh s.n. (MEL2323760)	GQ324453	GQ324546	GQ324373
P. saltuensis Fernald & Wiegand	28	Sylvestres	Sylvestres	Canada, Ontario	Gillespie 7043 (CAN)	EU792451	EU792378	GQ324374
P. scaberula Hook.f.		P. supersect. Homalopoa	Dasypoa	Chile	Peterson & Soreng 15575 (US)	GQ324454	EU792412	GQ324375
P. sibirica Roshev. subsp. sibirica	14	P. supersect. Poa	Macropoa	Russia, Khakasia	Olonova 2002-1 (CAN)	DQ354044, DO354045	EU792401	GQ324376
P. sieberiana Spreng.		P. supersect.	Brizoides subsect.	Australia, ^E NSW	Gillespie <i>et al.</i> 7319	GQ324456	GQ324548	GQ324377
P. sieberiana		<i>Homalopoa</i> <i>P.</i> supersect.	Australopoa Brizoides subsect.	Australia, ^E NSW	(CAN) Gillespie <i>et al. 7374</i> (CAN)	GQ324457	GQ324549	GQ324378
P. sieberiana		потаюроа P. supersect. Homalopoa	Austratopoa Brizoides subsect. Australopoa	Australia, ^E NSW	Jacobs 8482 (NSW)	GQ324458	GQ324550	GQ324379
P. sieberiana		P. supersect. Homalopoa	Brizoides subsect. Australopoa	New Zealand (cult.)	GB: Patterson <i>et al.</i> 2005 (USDA PI 263863)	AY589145	I	I
P. smirnowii subsp. mariae (Reverd.) Tzvelev	[42, 70 for subsp. <i>smirnowii</i>]	P. supersect. Poa	Malacanthae	Russia, Khakasia	Olonova 2002-07 (CAN)	DQ354005	GQ324551	GQ324380
<i>P. spania</i> Edgar & Molloy		Poa (X clade)	'New Zealand F1'	New Zealand ^E	GB: Gardner <i>et al.</i> unpubl. (AK-282077)	I	AY 686668	I

Appendix 1. (continued)

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⁽Continued next page)

			App	endix 1. (continued)				
Taxon	Chromosome number	Poa subgenus- supersection	Poa section- subsection (and NZ group)	Country of origin	Voucher	TLF GenBank	ITS GenBank	ETS GenBank
Subtribe Phalaridinae Anthoxanthum monticole (Bigelow) Veldkamp subsp. alpinum (Sw. e. Willd.) Soreng	z 56 x			Canada, Northwest Territories	Gillespie & Consaul 6859 (CAN)	DQ353953	EU792323	I
^A Chromosome numbers are gi taken from secondary taxono	iven to indicate pla mic literature that	oidy level. Literature ci t we believe provide rel	itations for the original colliable distillations of the l	ounts are mostly reported i primary literature (Tzvelev	n the Index to Plant Chromo / 1976; Moore 1982; Veldk	ssome Numbers (Gol amp 1994; Barkworth	dblatt and Johnson 1979- 1 et al. 2007). Additional	-), but are also references for

http://www.publish.csiro.au/journals/asb

2 5 λ 5 Exert from secondary taxonomic inclaure that we betwee providence chromosome numbers of Poa are given in Soreng *et al.* (in press). ^BCorrected from Soreng 3770, R.J. Soreng, September 2006. ^CContaminant in USDA PI 202208 seed accession. ^ERefers to species endemic to the country indicated.