

# The generic position of *Austrofestuca littoralis* and the reinstatement of *Hookerchloa* and *Festucella* (Poaceae) based on evidence from nuclear (ITS) and chloroplast (*trnL-trnF*) DNA sequences

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## INTRODUCTION

The grass genus *Austrofestuca* was erected by Alexeev (1976) to accommodate *Festuca littoralis* Labill., this species having a number of morphological characters not found in other species of *Festuca*. Prior to this transfer, *A. littoralis* (Labill.) E.B.Alexeev had been variously placed within *Schedonorus*, *Triodia*, *Arundo*, *Poa*, and *Festuca*. Alexeev (1976) excluded *Austrofestuca* from *Poa* because the caryopsis of *A. littoralis* has a deep groove whereas in *Poa* it is flat or convex. However, *Austrofestuca littoralis* shares with *Poa* keeled glumes, keeled awnless lemmas, a short, oval hilum, 7 nerves in the lemma (found in a few species of *Poa* subgen. *Arctopoa*), and a pubescent callus (with some species of *Poa* and *Bellardiachloa*).

*Austrofestuca* now comprises four species. Simon (1986) made the new combination *A. pubinervis* (Vickery) B.K.Simon to accommodate Western Australian plants having a densely villous lemma and callus. However, Weiller et al. (1995 et seq.) regarded *A. pubinervis* as doubtfully distinct from *A. littoralis*, citing a dense villous lemma and callus on some eastern plants of *A. littoralis*. Subsequently, Jacobs (1990) transferred the monotypic genera *Festucella* and *Hookerchloa* to *Austrofestuca eriopoda* (Vickery) S.W.L.Jacobs and *A. hookeriana* (F.Muell.) S.W.L.Jacobs, respectively. Jacobs (1990) suggested that Alexeev (1985) had used non-qualitative leaf characters to differentiate *Festucella* and inconsistent floret characters to differentiate *Hookerchloa*. Nonetheless, the taxa differ in a wide range of quantitative and qualitative vegetative and reproductive characters (Table 1).

In this paper we discuss the generic position of three species of *Austrofestuca*: the type *A. littoralis*,

**Abstract** The segregation of the grass genus *Austrofestuca* from *Festuca* has been debated because in some respects *Austrofestuca* is morphologically similar to *Poa*. Analyses of DNA sequence information from nuclear (internal transcribed spacer) and chloroplast (*trnL-trnF*) genomes indicate that *Austrofestuca* is not monophyletic. *Austrofestuca littoralis* is closely related to *Poa*, while *A. eriopoda* and *A. hookeriana* are placed in a clade containing *Arctagrostis*, *Dupontia*, and *Arctophila*. Whilst *Austrofestuca littoralis* is nested within the *Poa* clade, our data do not exclude the possibility that *A. littoralis* is sister to *Poa*. A range of morphological characters supports the differentiation of *A. eriopoda* and *A. hookeriana* from *A. littoralis*. We reinstate the genera *Festucella* and *Hookerchloa* to accommodate *A. eriopoda* and *A. hookeriana*, respectively.

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a grass of coastal sand dunes in Australia and New Zealand, and the two other eastern Australian species in the genus, *A. hookeriana*, a grass of swampy habitats in cooler lowlands and subalpine to alpine areas of Victoria, New South Wales, and Tasmania, and *A. eriopoda*, a grass of sub-alpine and montane forests of New South Wales and Victoria (Harden 1993; Walsh & Entwisle 1994).

Apart from hairy lodicules, the morphology of *Austrofestuca* clearly identifies it as a member of the Poeae (Edgar & Connor 2000). We included in our analyses representatives of genera within the Poeae (selected from the phylogeny of Soreng & Davis 2000) where sequences were available on Genbank: *Alopecurus*, *Arctagrostis*, *Arctophila*, *Dactylis*, *Dupontia*, *Festuca*, *Lolium*, *Phleum*, *Poa*, *Puccinellia*, *Schedonorus*, *Sclerochloa*, and *Vulpia*. We present the results of phylogenetic analyses using sequences of the internal transcribed spacer (ITS) region of nuclear ribosomal DNA and the *trnL-trnF* intergenic spacer of chloroplast DNA.

## MATERIALS AND METHODS

A list of DNA sequences and their sources is shown in Table 2. Living specimens were obtained from field collections or grown from seed and maintained outdoors in pots. DNA was extracted from small

samples of young leaf-base material following the method of Carlson et al. (1991). RNA was removed by incubation with DNase-free RNase (F. Hoffman La Roche Ltd, Switzerland) for 15 min at 37°C.

Most polymerase chain reactions were done in 20 µl volumes, using AmpliTaq Gold PCR Master Mix (Applied Biosystems, California) following the manufacturer's instructions. Each reaction contained 8 pmol of each primer. Specimens from MEL were amplified in 50 µl volumes, using Promega PCR mastermix (Promega Corporation, Maddison, USA) and 30 pmol of each primer. To amplify the intergenic spacer between *trnL* (UAA) 3' exon and *trnF* (GAA) of the chloroplast DNA, we followed the protocol of Taberlet et al. (1991) using primers *e* and *f* and an annealing temperature of 53°C. The ITS regions were amplified using either the primers ITS-1 and ITS-4 from White et al. (1990) and the following amplification protocol: 95°C for 5 min, 35 cycles of 94°C for 45 s, 48°C for 45 s, 72°C for 2 min 10 s, followed by a final extension of 72°C for 10 min or (for MEL specimens) using the primers S3 (Käss & Wink 1997) and 26SE (Sun et al. 1994) and the following amplification protocol: 94°C for 4 min, 35 cycles of 94°C for 45 s, 48°C for 45 s, 72°C for 1 min, followed by a final extension step of 72°C for 7 min. PCR products were purified using spin column purification (QIAquick PCR Purification Kit, QIAGEN Pty Ltd, Australia). The approximate

**Table 1** Morphological variation between *Austrofestuca littoralis*, *A. eriopoda*, and *A. hookeriana*. From Jacobs & Hastings (1993), Walsh & Entwisle (1994), and Weiller et al. (1995 et seq.)

Character	<i>A. littoralis</i>	<i>A. eriopoda</i>	<i>A. hookeriana</i>
Leaf blade	folded	inrolled	flat or folded
Abaxial leaf surface	smooth	scabrous	scabrous
Leaf sclerenchyma	continuous abaxial layer	only associated with vascular bundles	only associated with vascular bundles
Inflorescence	contracted	open	open
Callus hairs	present or absent	present	present
Glumes	± equal	subequal to unequal	subequal to unequal
Glumes	shorter than or equal to spikelets	shorter than spikelets	shorter than spikelets
Glumes	long relative to adjacent lemmas	shorter than adjacent lemmas	shorter than adjacent lemmas
Glumes	smooth	smooth	scabrous
Lemmas	awnless	minutely awned	mucronate to awned
Abaxial palea surface	scabrous or hairy	glabrous to hairy	glabrous or scabrous
Lodicules	usually ciliate	sparsely ciliate or glabrous	sparsely ciliate or glabrous
Fruit length	2.6–3.8 mm	3.8–4.5 mm	2.6–3.4 mm
Habitat	coastal dunes	open montane to subalpine forest and grassland	swampy subalpine to alpine forest and grassland

**Table 2** Sources of DNA sequences used in the analyses. OTA numbers refer to voucher specimens in the University of Otago Herbarium, MEL numbers refer to voucher specimens in the National Herbarium of Victoria. AgResearch seed BL numbers refer to accessions from the Margot Forde Forage Germplasm Centre (New Zealand).

Taxa	Source	Reference	GenBank accession number	
			ITS	<i>trnL-trnF</i>
<b>Poeae</b>				
<i>Alopecurus vaginatus</i> (Willd.) Pall. ex Kunth	GenBank	Grebenstein et al. (1998)	AVA96920/1	
<i>Arctagrostis latifolia</i> (R.Br.) Griseb.	GenBank	Brysting et al. (unpubl.)	AY237843	AY237904
<i>Arctophila fulva</i> (Trin.) Andersson	GenBank	Brysting et al. (unpubl.)	AY237832	AY237901
<i>Austrofestuca littoralis</i> (Labill.) E.B.Alexeev	New Zealand, Wekakura (OTA 057892).	This paper	AY327791	AY327796
	New Zealand, Kaitorete Spit (OTA 058500).	This paper		AY528933
	Australia, Victoria, Port Fairy (MEL 2154455).	This paper	AY524824	AY528934
<i>A. eriopoda</i> (J.W.Vickery) S.W.L.Jacobs	Australia, New South Wales, Mount Foxlow (MEL 2125197).	This paper		AY559121
	Australia, New South Wales, Golburn (MEL 305017)	This paper	AY559122	
<i>A. hookeriana</i> (F.Muell.) S.W.L.Jacobs	Australia, New South Wales, Nungar Plain (MEL 2123239).	This paper	AY559123	AY559120
<i>Beckmannia eruciformis</i> (L.) Host	GenBank	Hemleben et al. (unpubl.)	BER389163/4	
<i>Catapodium rigidum</i> (L.) C.E.Hubb.	GenBank	Catalán et al. (2004)	AF532940	AF533034
<i>Cynosurus cristatus</i> L.	GenBank	Catalán et al. (2004)	AF532938	AF533032
<i>C. echinatus</i> L.	GenBank	Catalán et al. (2004)	AF532937	AF533031
<i>Dactylis glomerata</i> L.	New Zealand, Dunedin 057898).	This paper		AY327794
	GenBank	Hsiao et al. (1995)	L36512	
<i>D. hispanica</i> Roth	GenBank	Torrezilla & Catalán (2002)	AF393014	
	GenBank	Catalán et al. (2004)		AF533027
<i>Deschampsia alpina</i> (L.) Roem. & Schult	GenBank	Brysting et al. (unpubl.)	AY237845	
<i>D. flexuosa</i> (L.) Trin.	GenBank	Brysting et al. (unpubl.)	AY237846	AY237913
<i>D. sukatschewii</i> (Popl.) Kom.	GenBank	Brysting et al. (unpubl.)	AY237844	
<i>Dupontia fisheri</i> R.Br.	GenBank	Brysting et al. (unpubl.)	AY237882	AY237888
<i>Festuca brevipila</i> R.Tracey	GenBank	Tredway et al. (unpubl.)	AF147165	

(Continued over page)

**Table 2** (Continued)

Taxa	Source	Reference	GenBank accession number	
			ITS	<i>trnL-trnF</i>
<i>F. ovina</i> L.	Holland, AgResearch seed BL 1692 (OTA 057932). GenBank	This paper	AY327792	AY327798
<i>Holcus lanatus</i> L.	GenBank	Grebenstein et al. (1998)	HLA96916/7	
<i>Lolium perenne</i> L.	New Zealand, Dunedin (OTA 057897). GenBank	This paper		AY327799
<i>Monerma cylindrica</i> (Willd.) Coss. & Durieu	GenBank	Hsiao et al. (1995) Catalán et al. (2004)	L36517 AF532941	AF533035
<i>Parapholis incurva</i> (L.) C.E.Hubb.	GenBank	Catalán et al. (2004)	AF532942	AF533036
<i>Phleum phleoides</i> (L.) H.Karst	GenBank	Subbotin et al. (2004)	AF498396	
<i>Poa abbreviata</i> R.Br.	GenBank	Brysting et al. (unpubl.)	AY237835	AY237907
<i>Poa alpina</i> L.	France, AgResearch seed BP 318 (OTA 057895). GenBank	This paper	AY327793	
<i>P. alpina</i> var. <i>alpina</i>	GenBank	Brysting et al. (2000)	AY237837	Y18515
<i>P. alpina</i> var. <i>vivipara</i> L.	GenBank	Brysting et al. (2000)	AY237836	Y18516
<i>Poa arctica</i> R.Br.	GenBank	Brysting et al. (unpubl.)	AY237842	AY237909
<i>Poa glauca</i> Vahl	GenBank	Brysting et al. (unpubl.)	AY237839	AY237906
<i>Poa hartzii</i> ssp. <i>ammophila</i> (A.Pors.) R.J.Soreng	GenBank	Brysting et al. (unpubl.)	AY237840	AY237910
<i>P. flexuosa</i> Sm.	GenBank	Espelund et al. (2000)		AJ279204
	GenBank	Brysting et al. (unpubl.)	AY237838	
<i>P. jemtlandica</i> C.Richt.	GenBank	Brysting et al. (2000)		Y18513
<i>P. pratensis</i> L.	GenBank	Gaut et al. (2000)	AF171182	
	GenBank	Stoneberg-Holt et al. (unpubl.)		AY061957
<i>P. pratensis</i> ssp. <i>alpigena</i> (Blytt) Hiitonen	GenBank	Brysting et al. (unpubl.)	AY237833	AY237905
<i>P. pratensis</i> cv Midnight	GenBank	Gaut et al. (2000)	AF171182	
<i>P. pratensis</i> cv. Moravanka	GenBank			AY061953
<i>P. pratensis</i> cv. Slezanka	GenBank	Stoneberg Holt et al (unpubl.)		AY061955
<i>P. trivialis</i> L.	AgResearch seed BP. 1477 (OTA 057894) GenBank	This paper		AY327795
	GenBank	Charmet et al. (1997)	AJ240161	
<i>Puccinellia distans</i> l. (Jacq.) Parl.	GenBank	Catalán et al. (2004)	AF532934	AF533024
<i>Schedonorus phoenix</i> (Scop.) Holub	GenBank	Charmet et al. (1997)	AJ240153	
	GenBank	Torrecilla et al. (2003)		AY098995
<i>Sclerochloa dura</i> (L.) P.Beauv.	GenBank	Catalán et al. (2004)	AF532933	AF533023

**Table 2** (Continued)

Taxa	Source	Reference	GenBank accession number	
			ITS	<i>trnL-trnF</i>
<i>Sesleria argentea</i> (Savi) Savi	GenBank	Catalán et al. (2004)	AF532931	AF533030
<i>Sphenopus divaricatus</i>	GenBank	Catalán et al. (2004)	AF532939	AF533033
<i>Vulpia myuros</i> (L.) C.C.Gmel	New Zealand, Pisa Flat, Otago (OTA 057656). GenBank	This paper		AY327797
<i>Zingeria trichopoda</i> (Boiss.) P.Smirn.	GenBank	Charmet et al. (1997)	AJ240162	
	GenBank	Kotseruba et al. (2003)	AJ428835	
<b>Hordeae</b>				
<i>Agropyron mongolicum</i> Keng	GenBank	Hsiao et al. (1995)	L36481	
	GenBank	Mason-Gamer et al. (2002)		AF519117
<i>Hordeum murinum</i> L.	GenBank	Kim & Kwon (unpubl. data)	AY255047/ AY255071	
	GenBank	Nishikawa et al. (2002)		AB078470

concentration of each amplification product was determined by electrophoresis with a known amount of molecular marker (1 kb ladder, Invitrogen New Zealand Limited, Auckland). The purified PCR products were sequenced, using the original amplification primers, with Big Dye Terminator v. 3.0 or v. 3.1 cycle sequencing chemistry (Applied Biosystems) following the manufacturer's protocol. Electropherograms were edited and assembled using Autoassembler v. 1.3.0 (Applied Biosystems).

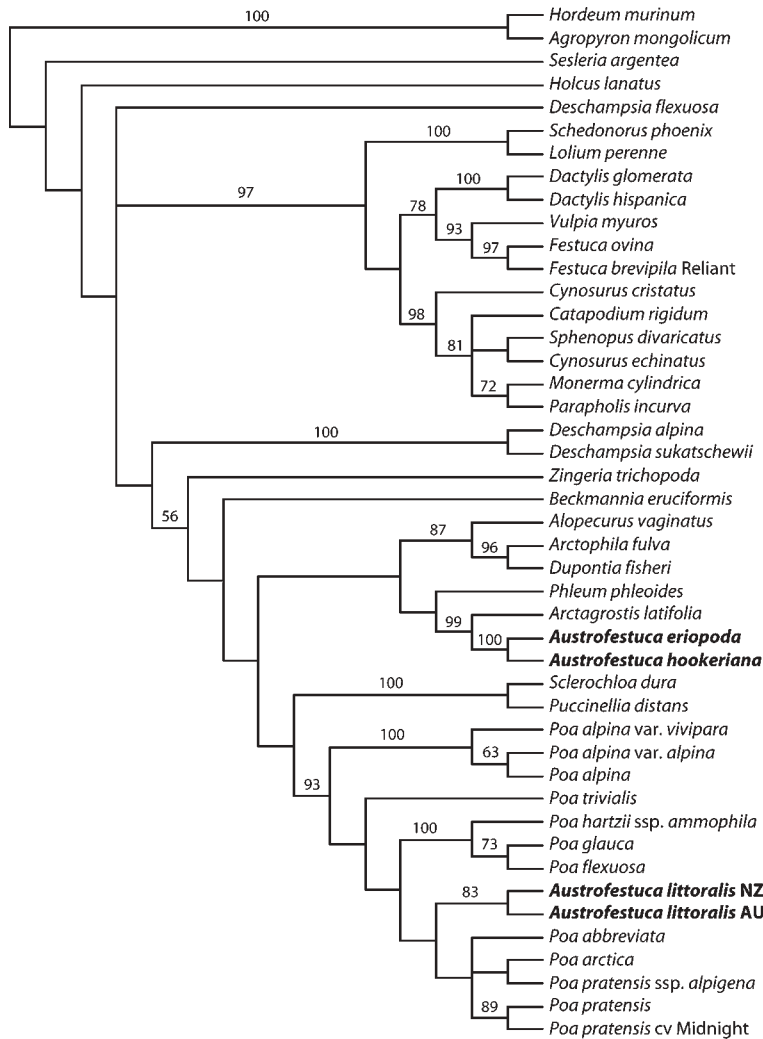
Sequences were aligned initially using ClustalX (Thompson et al. 1997) followed by manual adjustment using Se-Al (Rambaut 2002). We coded informative indels in the *trnL-trnF* spacer as binary characters for analysis. Gaps were treated as missing data. We analysed the ITS and *trnL-trnF* data sets separately by maximum parsimony using PAUP\* version 4.0b10 (Swofford 2002), with *Agropyron mongolicum* and *Hordeum murinum* (tribe Hordeae) as outgroups. For the *trnL-trnF* data set we did a branch-and-bound search, and for the ITS data set we did an exhaustive search. We assessed branch support by parsimony bootstrap analysis with 1000 replicate heuristic analyses using 5 random addition replicates in each bootstrap replicate and the tree bisection-reconnection branch swapping algorithm.

## RESULTS

Amplification produced an ITS fragment that was approximately 740 base pairs long in all species and a *trnL-trnF* fragment that was between 420 and 440 base pairs long. Trimming of sequences to exclude regions of poor quality (at either end of each sequence) resulted in sequences being used for alignment and analysis that were shorter than those amplified. The ITS sequence for the New Zealand collection of *A. littoralis* included only the ITS-1 region, due to poor quality of sequence in the ITS-2 region.

Alignment of ITS sequences gave a matrix with 787 characters. Fifteen base positions at the 3' end of the alignment were excluded from the analysis leaving 198 parsimony informative characters. Heuristic searching found 12 equally parsimonious trees of length 729 and consistency index = 0.429 excluding uninformative characters (Fig. 1).

The basal nodes in the tree are unsupported by bootstrap analysis. *Sesleria* and *Holcus* arise individually from the basal nodes of the tree. Next there is a trichotomy involving *Deschampsia flexuosa*, a clade of festucoid grasses, and a clade of two other species of *Deschampsia* and *Poa* allies. The festucoid clade is well supported by bootstrap



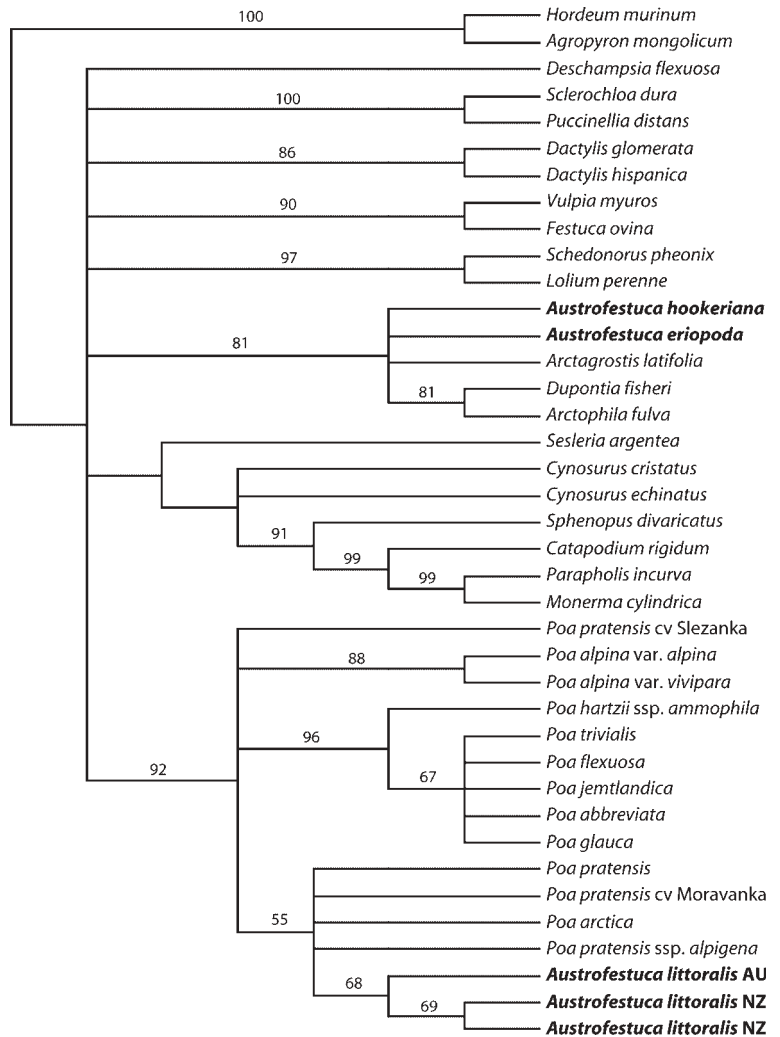
**Fig. 1** Strict consensus of 12 trees from the analysis of the ITS data set. Tree length = 729 steps excluding autapomorphic characters; consistency index = 0.429; retention index = 0.682. Bootstrap values (%) are from the analysis of 1000 bootstrap (heuristic random-order-entry) replicates.

analysis (97%) and is further divided into three subclades. The first of these is strongly supported (100%) and contains *Lolium* and *Schedonorus phoenix*. The second subclade contains *Dactylis*, *Vulpia*, and *Festuca* (78% support), and the third contains *Cynosurus*, *Catapodium*, *Sphenopus*, *Monerma*, and *Parapholis*. Relationships between these subclades are not supported by bootstrap analysis.

The *Deschampsia/Poa* allies clade contains many groups but many of the relationships between these groups lack bootstrap support. A well-supported (100%) clade containing two species of *Deschampsia* branches from the base of the *Deschampsia/Poa* allies clade. Next, *Zingeria trichopoda* and *Beckmannia eruciformis* are joined

individually to a clade of the remaining taxa. Within this clade, four main lineages are apparent. The first of these contains *Alopecurus*, *Arctophila*, and *Dupontia* (87%). Sister to this lineage is a clade of *Austrofestuca eriopoda*, *A. hookeriana*, and *Arctagrostis* (99%) with *Phleum* weakly joined at the base. The third lineage contains *Sclerochloa* and *Puccinellia* (100%). The remaining clade (93%) contains *Austrofestuca littoralis* and all the included species of *Poa*. Three collections of *Poa alpina* are sister to the other taxa within this clade. *Poa trivialis* is weakly joined to the remaining taxa. *Poa hartzii*, *P. glauca*, and *P. flexuosa* are a monophyletic (100%) sister group to another clade in which two collections of *Austrofestuca littoralis* (83%)

**Fig. 2** Strict consensus of 3930 trees from the analysis of the *trnL-trnF* data set. Tree length = 179 steps excluding autapomorphic characters; consistency index = 0.726; retention index = 0.858. Bootstrap values (%) are from the analysis of 1000 bootstrap (heuristic random-order-entry) replicates.



are sister to *P. abbreviata*, *P. arctica*, and *P. pratensis*.

Alignment of the *trnL-trnF* sequences resulted in a matrix with 1124 characters of which 108 were parsimony informative, including 20 binary characters. A maximum parsimony analysis of this data set produced 3930 equally parsimonious trees of length 179 and consistency index = 0.726 (Fig. 2).

As in the ITS analysis, *Austrofestuca* is not monophyletic on the *trnL-trnF* tree. The two New Zealand and one Australian collection of *A. littoralis* are monophyletic and are in an otherwise unresolved clade containing *P. arctica* and three collections of *Poa pratensis*. This clade is supported by only a 55% bootstrap value and is part of a larger “*Poa*”

clade (with 92% bootstrap support) containing another collection of *P. pratensis* (cv Slezanka), a monophyletic clade of two subspecies of *P. alpina* (88%), and a well-supported (96%) clade of *P. hartzii*, *P. trivialis*, *P. flexuosa*, *P. jemtlandica*, *P. abbreviata*, and *P. glauca*.

The other two species of *Austrofestuca* are not related to *Poa* at all. *A. hookeriana* and *A. eriopoda* are in a well-supported (81%) clade containing *Arctagrostis latifolia*, *Dupontia fisheri*, and *Arctophila fulva*. The relationships between these two *Austrofestuca* species and the other taxa in the clade are unresolved, but *D. fisheri* and *A. fulva* are sister taxa (81% bootstrap support). The remainder of the tree largely comprises small clades of closely

related taxa, with a basal polytomy. The relationship between the two clades containing species of *Austrofestuca* is not resolved, but there is very good support that the species belong to the clades that they are in. Other well-supported monophyletic groups from this analysis were clades containing (i) *Schedonorus* and *Lolium* (broad-leaved fescues), (ii) *Festuca* and *Vulpia* (narrow-leaved fescues), (iii) two species in the genus *Dactylis*, (iv) *Sclerochloa dura* and *Puccinellia flexuosa*, and (v) a clade containing the taxa (*Sphenopus divaricatus* (*Catapodium rigidum* (*Parapholis incurva* and *Monerma cylindrica*))).

## DISCUSSION

As it currently stands, the genus *Austrofestuca* is polyphyletic. The type species *A. littoralis* is related to members of *Poa* subsection *Poa*. *Austrofestuca eriopoda* and *A. hookeriana* are not at all related to *A. littoralis*: they are placed within the *Phleum* complex as described by Soreng & Davis (2000). We did not include *A. pubinervis* in our analyses, but it is likely that *A. pubinervis* will be closely aligned to *A. littoralis*. Both are species of coastal sand dunes, and Weiller et al. (1995 et seq.) noted that some specimens of eastern Australian *A. littoralis* have the same lemma and callus hair characters that are used to distinguish the Western Australian *A. pubinervis*.

The Australian and New Zealand collections of *A. littoralis* exhibited very little sequence variation and form a monophyletic group in the analyses of both data sets. Evidence of phylogenetic structure within this taxon appears to be an artefact of missing data. *Austrofestuca littoralis* was nested within the *Poa* clade, but higher order relationships within this clade are unresolved or at best poorly supported by bootstrap analysis. In the *trnL-trnF* tree (Fig. 2) the branch uniting *A. littoralis* with *P. pratensis* and *P. arctica* is only supported by a 55% bootstrap value; thus, the molecular data do not exclude the possibility that *A. littoralis* could be sister to *Poa*. Only a few species of *Poa* are represented in our analyses and wider taxon sampling within *Poa* and related taxa will be necessary to refine the closest relative of *A. littoralis*.

Comparison of morphological characters from *A. littoralis*, *Poa*, and *Festuca* corroborates the close relationship between *A. littoralis* and *Poa*. *Austrofestuca* was differentiated from *Festuca* on the basis of having keeled lemmas, glabrous ovaries,

pubescent lodicules, 5–11-nerved lower lemma, a shortly pubescent callus, and a short oval hilum (Alexeev 1976; Jacobs 1990). However, all of these characters can be found in *Poa* and some in *Festuca* (Edgar & Connor 2000). The single morphological character shared by *A. littoralis* and *Festuca*, but not by *Poa*, is a ventral groove on the caryopsis. The diagnostic importance of this character is negated by evidence from the ITS and *trnL-trnF* sequence information, with none of the three species of *Austrofestuca* showing any relationship to festucoid taxa.

On the basis of morphology, Clayton & Renvoize (1986) considered that *Austrofestuca* might be related to southern species of *Poa*. Chromosome numbers from New Zealand taxa are partially consistent with this hypothesis. *Austrofestuca littoralis* and the majority of New Zealand species of *Poa* are tetraploids with 28 chromosomes. Hair (1968) did note, however, some structural differences between the chromosomes of *A. littoralis* (as *Poa triodioides*) and those of tetraploid *Poa*. If further sampling shows that *A. littoralis* is best classified as a species of *Poa*, it would become the only species of *Poa* to be indigenous to both New Zealand and to Australia (although *P. cookii* on the subantarctic Macquarie Island, while politically Australian, is within the New Zealand Botanical Province). This wide distribution led Alexeev (1976) to consider that *A. littoralis* was a taxon of considerable age, which had evolved from ancestors similar to primitive species of *Festuca*. In the light of our molecular results, this hypothesis needs to be re-evaluated in the context of evolution and speciation in the genus *Poa*.

The strong phylogenetic evidence from two independently inherited genomes makes the retention of *A. eriopoda* and *A. hookeriana* within *Austrofestuca* untenable and the classification of Jacobs (1990) is rejected. *Austrofestuca eriopoda* is reinstated to *Festucella eriopoda* (Vickery) E. Alexeev and *A. hookeriana* to *Hookerchloa hookeriana* (F. Muell. ex Hook. f.) E. Alexeev. It is worth noting, however, that sequences from *F. eriopoda* and *H. hookeriana* were very similar to each other. Further study of morphological variation within and between these two species might provide grounds for combining them into a single genus. The relationships of these two species with other members of the *Phleum* complex also warrant further attention, in particular the close relationship to *Arctagrostis*, a monotypic genus of Arctic circumboreal areas.

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