A phylogenetic analysis of *Poaceae* tribe *Poeae sensu lato* based on morphological characters and sequence data from three plastid-encoded genes: evidence for reticulation, and a new classification for the tribe

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Summary. Phylogenetic analysis of variation in 18 morphological characters and structural and nucleotide sequence variation in three plastid-encoded genes provides a well-supported hypothesis of relationships within *Poaceae* supertribe *Poodae*. This supertribe includes tribes *Poeae*, *Aveneae* and *Hainardieae*, and other small tribes. Of the circa 135 genera that are assigned to this group, 57 were sampled, representing all major groups and most of the minor groups that have been recognised as tribes or subtribes. Historical and modern classifications of *Poodae* are reviewed and examined with respect to relationships detected by the phylogenetic analyses. Two major plastid DNA lineages are detected, corresponding in general to groups traditionally recognised as *Aveneae* and *Poeae*, but about one fifth of the genera are placed in positions that conflict with traditional classifications. When comparing trees obtained from the morphological character set with those obtained from simultaneous analysis of the morphological and molecular character sets, the character distributions on the trees reveal substantial differences between homoplasy levels for several morphological characters. These results suggest the possibility of wide hybrid origins for some groups, especially the subtribe *Airinae*. A revised classification is provided for *Poodae*, with all previously recognised tribes subsumed within a broadly circumscribed *Poeae sensu lato*, in which accepted genera are accommodated in 21 subtribes. *Aveneae* and smaller groups that have been recognised previously as tribes, including *Hainardieae*, *Phalarideae*, *Phleeae* and *Seslerieae*, are reduced to subtribes. Monophyly of many of the subtribes has at least some molecular support, but other subtribes need further study, particularly involving nuclear genes, to better determine their relationships and to investigate possible hybrid origins.

Key words. *Aveneae*, *Poaceae*, *Poeae*, *Pooideae*, DNA, grasses, phylogenetics.

Introduction and historical treatment

The grass family, *Poaceae* (R. Br.) Barnh., includes some 800 genera and 11,000 – 13,000 species. A phylogenetic classification of the family was recently proposed, with 12 subfamilies and 42 tribes recognised (GPWG 2001). *Pooideae* Benth. is the largest of these subfamilies, encompassing one third of all grass species in 14 tribes. Members of *Pooideae* are cool-season grasses, predominating over, to completely replacing, other subfamilies of grasses in cool-temperate and Mediterranean to arctic climates. They sharply decrease in relative abundance and numbers in warm-temperate climates that have moist summers, and are nearly absent from regions with tropical climates. Of the c. 3560 species in the *Pooideae*, about 2260 belong to supertribe *Poodae* L. Liu, which includes the widely recognised tribes *Poeae* R. Br., *Aveneae*, and *Hainardieae*, and the less frequently recognised tribes *Agrostideae*, *Cynosureae*, *Milieae*, *Phalarideae*, *Phleeae*, *Scolochloeae* and *Seslerieae*. The monumental contribution of Clayton & Renvoize (1986), perhaps the most frequently cited world-wide classification of *Poaceae* of the past 20 years, employed the first three of these tribal names (*Poeae*, *Hainardieae* and *Aveneae*, with four subtribes recognised in *Aveneae*) to cover all taxa in *Poodae* except *Milieae*, which they placed in *Stipeae*. By our estimates, *Poodae* includes c. 135 of the c. 200 genera of subfamily *Pooideae* (Appendix I).

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Here, we briefly review historical circumscriptions of *Poodae*, we present and analyse new plastid DNA and morphological data that bear on current circumscriptions and relationships within this group, we discuss character distributions relating to the segregation from *Poeae* of *Hainardieae* and *Aveneae* as applied by Clayton & Renvoize (1986), and we present a modified classification of the supertribe (Appendix I). Although phylogenetic analyses of plastid DNA have detected two major lineages within *Poodae* that correspond in large part to traditional circumscriptions of *Aveneae* and *Poeae*, one fifth of the genera of these tribes are intermixed in ways that are contrary to Clayton & Renvoize's classification, and that are specifically incongruent with relationships previously inferred on the basis of morphological features (Soreng *et al.* 1990, Davis & Soreng 1993, Soreng & Davis 1998, 2000, Davis & Soreng 2007). In light of these findings, the classification that we propose for *Poodae* places all genera in one tribe, *Poeae sensu lato*, which is subdivided into 21 subtribes.

The history of 'natural' classifications within *Poaceae* effectively begins with Robert Brown's (1814) division of the grasses into the specialised tribe *Paniceae* and a larger and more heterogeneous tribe *Poeae*. While the *Paniceae* have turned out to be a fairly natural group (now expanded to subfamily *Panicoideae*), the taxa in Brown's *Poeae* have been subdivided and rearranged extensively during the ensuing period of nearly 200 years in response to an increasingly detailed understanding of the diversity and phylogeny of this large and complex assemblage.

Kunth (1815) arranged the genera that Brown (1814) had assigned to *Poeae* within smaller and more homogeneous groups. Although most of these groups were assigned the out-of-sequence rank of 'section', and thus are nomenclaturally invalid (International Code of Botanical Nomenclature [ICBN] Art. 33.7 [in Greuter *et al.* 2000]), Kunth's groupings were useful for identification, and they proved to be influential. He proposed a system of ten 'sections'. In addition to many genera that are excluded from the modern *Pooideae*, he included most of Clayton & Renvoize's (1986) *Aveneae* and *Poeae* in two 'sections': 1) 'Agrostidea' (including most of Clayton & Renvoize's subtribes *Alopecurinae* and *Phalaridinae* [authorities for names of accepted subtribes of *Poeae sensu lato* are provided in Appendix II]); and 2) 'Bromae', with three subsets, 'Avenacea' (including most of Clayton & Renvoize's subtribe *Aveninae*), 'Arundinacea', and 'Bromae vera' (including most taxa included by Clayton & Renvoize in tribes *Poeae* and *Bromeae*).

In the decade that followed, most of Kunth's (1815) suprageneric names were validly published and ranked by other authors, and Brown's (1814) genera of *Poeae* were reclassified into families (often as 'ordo'), subfamilies (often as 'subordo'), tribes and subtribes (Berchtold & Presl 1820, Gray 1821, Dumortier 1824, 1829, Trinius 1824, Spenner 1825, Link 1827, Reichenbach 1828, Kunth 1829, Nees von Esenbeck 1829; for additional review and commentary on suprageneric nomenclature of *Poaceae*, see Clayton 1981; for listings of verified validly published suprageneric taxa, see Reveal 2003 onward). During this period, *Poeae* took on a much more restricted meaning than that of Brown, but were still quite heterogeneous. Dumortier (1824), in "Observations sur les Graminées de la Flore Belgique", recognised 17 tribes in *Poaceae*, with genera of *Poodae* falling into two 'series': 1) *Triticeae*, *Cynosureae*, *Poeae*, *Festuceae*, *Bromeae*, *Aveneae*, *Arundineae*; and 2) *Agrostideae*, *Phleeae*, *Oryzeae*, *Stipeae*, *Paniceae*, *Cynodonteae*, 'Lepiureae' (*Leptureae*), *Saccharineae*, *Andropogoneae*, and *Maydeae* (spellings, including terminations, here and below are corrected from the original following ICBN rules unless they are set in quotations, and only validly published names are in italics).

The stabilisation of nomenclatural rules (initiated in the early 1800s [Candolle 1813] and first formalised by the Paris Congress of 1867 [Candolle 1867]; for a review of the history of nomenclature and the ICBN see Nicolson 1991), and the establishment of accepted practices for the application of suprageneric ranks, has also affected the classifications we have inherited. As the hierarchy of ranks was formalised, the rank of order was restricted to groupings of families, and the ranks of family and tribe were applied to successively smaller groups, eventually reaching the diversity implied by those ranks today. Treating the grasses as a set of families (e.g. Berchtold & Presl 1820) lost favour, and few subsequent authors have chosen to separate the bamboos and earlier-diverging small lineages as families (Herter 1940; Nakai 1943). Also, ICBN Art. 19.5 established that names of suprageneric taxa must be based on generic stem names, so names such as *Frumenteae* Krause and *Maydeae* Adans. were deemed illegitimate. With discoveries of new taxa, and more detailed investigations of the family, earlier classifications were refined over the following three decades (Endlicher 1830, Presl 1830, 1846, Reichenbach 1830, Kunth 1833, Beilschmied 1833, Fries 1835, Nees von Esenbeck 1834, Bluff, Nees von Esenbeck & Schauer 1836, Nees von Esenbeck 1836, 1841, Burmeister 1837, Koch 1837, Grisebach 1846, 1853, Parlatore 1845, Cosson & Germaine de St.-Pierre 1845, Steudel 1853 – 1854, Grenier & Godron 1855).

Bentham (1861) first established the currently correct name, *Pooideae*, for the subfamily that includes tribe *Poeae*, displacing Link's (1827) earlier subfamily

name, *Festucoideae*. ICBN Articles 18 and 19 require that the type genus of a family be the stem for higher ranks that include that genus, up to and including the rank of family (thus *Poa* L., subtribe *Poinae*, tribe *Poeae*, supertribe *Poodae*, subfamily *Pooideae*, and family *Poaceae*). Article 16 specifies that this may continue beyond the rank of family, as in order Poales Small, superorder Poanae Takht. ex Reveal & Doweld, etc. Bentham employed subfamilies *Pooideae* and *Panicoideae* to group grass tribes into two major sets comparable to Brown's (1814) two original tribes. He expanded his 1861 classification in 1878, in a landmark paper in 1881, and in '*Genera Plantarum*' (Bentham & Hooker 1883). In these treatments, Bentham applied names for tribe *Festuceae* subtribes *Festucinae*, *Eragrostidinae* and *Melicinae* in roughly the same sense as the combined subfamilies *Echinarioideae*, *Festucoideae*, *Glycerioideae* and *Cynosuroideae* of Link (1827) or tribes *Bromeae*, *Cynosureae*, *Festuceae* and *Poeae* of Dumortier (1824).

How much the maturing Austrian agrostologist Edward Hackel, in his classifications of 1883 and 1887, owed to Bentham, or vice versa, would be interesting to know. Although Bentham's and Hackel's two monumental world-wide classifications of grasses differ in minor ways, Hackel's descriptions are substantially more detailed, as they include information concerning microcharacters and starch types. Otherwise, the two classifications are based primarily on inflorescence and spikelet architecture. Bentham's tribe *Festuceae* included the following subtribes: *Pappophoreae*, *Triodieae*, *Arundineae*, *Seslerieae*, *Eragrostideae*, *Meliceae*, *Centotheceae* and 'Eufestuceae'. Hackel recognised a ninth subtribe, *Brachypodiinae* (which he should have called subtribe *Brominae*), including *Boissiera* Hochst. & Steud., *Brachypodium* P. Beauv., *Bromus* L. and *Megalachne* Steud., based on the presence of simple, roundish starch grains and the development of the 'outermost nucellus' (the aleurone layer) into a strong, thick-walled layer.

The heterogeneity of Bentham's and Hackel's conceptions of tribe *Festuceae* is apparent in that the included subtribes are now referred to four subfamilies: *Arundinoideae*, *Centothecoideae* (or *Panicoideae* tribe *Centotheceae*), *Chloridoideae* and *Pooideae*. Even *Poeae* in the narrowest sense, subtribe 'Eufestuceae' *sensu* Hackel, includes genera now generally assigned to diverse subfamilies and tribes: *Uniola* L. (polyphyletic: *Chloridoideae* and *Panicoideae* tribe *Centotheceae*), *Distichlis* Raf. and *Aeluropus* Trin. (*Chloridoideae*), *Lasiochloa* Kunth (= *Tribolium* Desv.) and *Schismus* P. Beauv. *Danthonioideae*), *Brylkinia* F. Schmidt (*Brylkinieae*), *Pleuropogon* R. Br. and *Glyceria* R. Br. (*Meliceae*), *Graphephorum* Desv. (*Aveneae* plastid DNA lineage subtribe *Aveninae*), *Briza* L. (*Aveneae* plastid DNA lineage subtribe *Brizinae*), *Desmazeria* Dumort., *Wangenheimia* Moench, *Dactylis* L., *Cynosurus* L., *Lamarckia* Moench, *Sclerochloa* P. Beauv., *Nephelochloa* Boiss., *Poa* L., *Colpodium* Trin., *Dupontia* R. Br., *Scolochloa* Link, *Atropis* (Trin.) Griseb. (= *Puccinellia* Parl.), *Festuca* L., *Catapodium* Link and *Scleropoa* Griseb. (Soreng & Davis 1998, 2000, GPWG 2001, Davis & Soreng 2007, etc.).

The classifications of subfamily *Pooideae* and its tribes and subtribes by Bentham and Hackel served as the basis of most floristic and monographic accounts over the next half to three quarters of a century, including the influential works of A. S. Hitchcock (1935, 1951). Tribe *Poeae*, usually called *Festuceae*, was quite heterogeneous, and included most grasses with simple panicles, spikelets disarticulating above the glumes, glumes shorter than the adjacent lemmas, an indeterminate number of florets (though greater than one), lemmas either unawned or with terminal or nearly terminal awns of any number, and compound starch grains.

As we are discussing *Poeae* in relation to *Aveneae sensu* Clayton & Renvoize (1986), the historical classification and modern circumscription of the latter tribe also should be brought into context. Bentham and Hackel recognised three consecutive tribes within subfamily *Pooideae*: *Aveneae*, *Phalarideae* and *Agrostideae* (the latter with three subtribes, *Stipinae*, *Phleinae* and *Agrostidinae*). Clayton & Renvoize (1986) united these three tribes as tribe *Aveneae* subtribes *Aveninae*, *Phalaridinae*, and *Alopecurinae* (syn. *Agrostideae* in their system), and aside from various genera excluded from their subfamily *Pooideae*, they removed the genera of *Stipeae* and added subtribe *Duthieinae* to *Aveneae*. We will not consider elements of the *Duthieinae* further here, as they are now considered to be closely related to tribe *Stipeae* (Soreng *et al.*, 2003, 2005 onwards, Davis & Soreng 2007). Taxa within *Aveneae* in the sense of Clayton & Renvoize can be described as similar to those of *Poeae*, but with spikelets having exactly one, exactly two, or an indeterminate number of florets greater than one, glumes as long as or longer than the adjacent lemmas, lemmas commonly awned, with the awn attached dorsally and often geniculate, the lemma apex sometimes bifid, and the endosperm frequently soft or liquid.

The generic elements of one other small group, recognised as tribe *Hainardieae* by Greuter & Rechinger (1967) and by Clayton & Renvoize (1986), were historically scattered, or included in tribe *Hordeeae* (= *Triticeae*) subtribes *Leptureae* and *Loliinae* in Bentham's and Hackel's systems. Of the genera of *Hainardieae sensu* Clayton & Renvoize tested for plastid DNA type, all are placed within *Poeae sensu stricto*, and in three separate lineages within that group. *Scribneria* Hack. is probably related to *Deschampsia* P. Beauv. *sensu stricto* (see Soreng & Davis

2000, Davis & Soreng 2007). *Narduroides* Rouy is related to the fine-leaved *Festuca* clade (Torrecilla & Catalán 2002, Torrecilla *et al.* 2004, Catalán *et al.* 2004). *Hainardia* Greuter and *Parapholis* C. E. Hubb. are related to *Catapodium* (as suggested by Clayton & Renvoize 1986: 110), *Cutandia* Willk., *Desmazeria* and *Sphenopus* Trin. (Soreng & Davis 2000). Hence, the latter have been united into a more broadly delimited *Poeae* subtribe *Parapholiinae* (Soreng & Davis 2000; Soreng *et al.* 2003, 2005 onwards) based on a plastid DNA lineage showing progressive reduction of the inflorescences and spikelets, and a shift to disarticulation below the glumes.

Two additional anomalous genera displaced from *Poeae* and *Aveneae* in Clayton & Renvoize's (1986) system, dating back to separations in Bentham's and Hackel's and earlier systems, should be returned to supertribe *Poodae*. *Anthochloa* Nees & Meyen (*Meliceae* in the Clayton & Renvoize system) is derived from within *Poa* (Gillespie *et al.* 2007), and *Milium* L. (*Stipeae* in the Clayton & Renvoize system) belongs in *Poeae*, near *Poa* (Soreng & Davis 2000).

As discussed amply elsewhere (Roshevits 1946, Stebbins 1956, Tateoka 1957, Stebbins & Crampton 1961, Gould 1968, Tzvelev 1976, 1989, Clayton & Renvoize 1986, GPWG 2001), and on the basis of studies published from the 1930s onward on chromosomes, anatomy, embryos, lodicules and correlated physiological and ecological characteristics, the broadly circumscribed subfamily *Pooideae* of Bentham and of Hackel was determined to be polyphyletic. It was evident that Bentham's and Hackel's *Pooideae* comprised several distinct and independently derived lineages now apportioned among subfamilies *Chloridoideae*, *Bambusoideae*, *Arundinoideae*, *Danthonioideae*, *Ehrhartoideae* and *Pooideae*. The mid-twentieth century syntheses of newer and older data produced classifications of subfamily *Pooideae* that excluded extraneous genera from the *Pooideae*, and particularly from *Poeae*, *Aveneae* and *Hainardieae*, by the presence of various combinations of the following set of characteristics: culm internodes solid, ligule margins ciliate, leaf epidermis with bicellular microhairs, stomata with triangular or tall, dome-shaped subsidiary cells, panicoid-type or saddle-shaped silica bodies, leaf cross-section with more than one vascular bundle in the midrib, fusoid or arm cells in the mesophyll, Kranz anatomy (C_4 physiology), lodicules that are strongly veined and have truncate, fleshy apices, small chromosomes of base numbers other than $x = 7$, large embryos and embryo formulas other than F+FF.

Apart from the placement of *Hainardieae*, the circumscriptions of *Poeae* and *Aveneae* by Clayton & Renvoize (1986) and Macfarlane & Watson (1980, 1982; followed by Watson & Dallwitz 1992) are much alike. If a few genera are excluded (*Ampelodesmos* Link [Soreng & Davis 2000], *Megalachne* and *Podophorus* Phil. [Soreng *et al.* 2003, 2005 onwards, as these genera have 2 – 3 stigmas and lemma awns entered by more than the dorsal vein], and genera placed in subtribe *Duthieinae* by Clayton & Renvoize or placed provisionally in '*Aveneae*' or '*Arundinoideae*' by Watson & Dallwitz), what remains is a series of genera that are fairly easily assigned to *Poeae* or *Aveneae* on the basis of length of glumes relative to the lemmas, position and shape of awns, and number of florets per spikelet, as recognised by Clayton & Renvoize and Watson & Dallwitz.

Classifications are iteratively improved, with various systems passed along through time with additions and changes made by successive generations of taxonomists. They provide a framework for apportioning taxa among progressively smaller and more homogeneous sets of taxa that ideally are more closely related to each other than to any other sets. An advantage or disadvantage of classifications over phylogenies (depending upon one's point of view) is that classifications are more flexible, because they do not specify exact relationships among the members of a set (although this is sometimes implied through linear organisation of the terminal taxa), except to the extent that subsets are grouped into more inclusive sets. Historically, classifications were mostly inspired by the need for simplified organisation and based upon educated guesswork as to the relationships among taxa. With the advent of phylogenetic analysis, it has become possible to assess relationships by objective and repeatable methods, and thereby to test hypotheses of relationships implied by existing classifications. The application of DNA restriction site and sequence data, as analysed by formal phylogenetic methods, has had an enormous impact on our ability to test these hypotheses and to highlight anomalous relationships. Investigations in recent years into relationships among the subfamilies of grasses (e.g. GPWG 2001) and within and among tribes of *Poodae* have improved our understanding of these taxa (e.g. Catalán *et al.* 1997, Grebenstein *et al.* 1998, Röser *et al.* 2001, Torrecilla & Catalán 2002, Torrecilla *et al.* 2003, 2004, Soreng & Davis 2000, Brysting *et al.* 2004, Catalán *et al.* 2004, Hunter *et al.* 2004, Davis & Soreng 2007, Gillespie *et al.* 2007).

In this paper, we present data from nucleotide sequences of three plastid-encoded genes and 18 anatomical and morphological characters, in order to examine relationships and character distributions within *Poodae*, and employ these results in a re-examination of the taxonomy of this group. An impetus for these studies has been the observation that a number of genera usually placed in *Poeae* (*Briza*, *Calotheca* Desv., *Chascolytrum* Desv., *Parafestuca* E. B.

Alexeev [syn. *Koeleria* Pers.], *Poidium* Nees [syn. *Microbriza* Nicora & Rúgolo], *Rhombolytrum* Link and *Torreyochloa* G. L. Church) either have *Aveneae*-type plastid DNA (i.e. they are placed by cladistic analysis of plastid DNA characters among genera traditionally included in *Aveneae*) or have morphological affinities to genera that have been placed in this group by plastid DNA data. The apparent discrepancy between groupings based on morphology and those based on plastid DNA also occurs in the reverse direction, as groups of genera with traditional *Aveneae* morphology have *Poeae*-type plastid DNA. These include *Aira* L., *Alopecurus* L. *Aniselytron* Merr., *Apera* Adans., *Avenella* Koch ex Steud., *Avenula* (Dumort.) Dumort., *Beckmannia* Host, *Deschampsia*, *Dielsiochloa* Pilg., *Dissanthelium* Trin., *Holcus* L., *Mibora* Adans., *Molineriella* Rouy, *Phleum* L., *Vahlodea* Fries, *Zingera* P. A. Smirn. and presumably several others that are morphologically similar to these, but as yet untested for DNA types: *Cornucopiae* L., *Corynephorus* P. Beauv., *Limnas* Trin., *Periballia* Trin., *Rhizocephalus* Boiss. and *Tovarochloa* T. D. Macfarl. & Butt (Soreng & Davis 2000, Soreng *et al.* 2005 onward, Davis & Soreng 2007).

Although some authors had expressed doubts that the traditional separation of *Poeae* and *Aveneae* was natural, the phylogenetically mixed nature of these tribes was initially exposed when Soreng *et al.* (1990) published the first plastid DNA evidence showing that several genera of each tribe had plastid DNA types of the other. Tzvelev (1987, 1989) was the first modern taxonomist to combine *Aveneae* and *Poeae*, and corroborating DNA evidence has led some subsequent authors to follow suit (Soreng & Davis 2000, GPWG 2001, Soreng *et al.* 2005 onward, Davis & Soreng 2007). Modern classifications of *Poodae* from the 1970s onward, by Tzvelev (1976, 1987, 1989), Tutin *et al.* (1980), Clayton & Renvoize (1986), Macfarlane & Watson (1982) and Watson & Dallwitz (1992), are similar in terms of the genera that are included, but vary substantially with regard to the tribes and subtribes that are recognised, and in their indications of the relationships suggested among these groupings (Table 1). These authors also differed in terms of the relationships suggested by their classifications between this set of taxa and the related tribes *Bromeae* and *Triticeae*. Clayton and Renvoize (1986) and Tutin *et al.* (1980) placed *Bromeae* and *Triticeae* between *Poeae* and *Aveneae*, whereas the other authors recognized *Bromeae* and *Triticeae* as an independent group. Molecular data have consistently placed *Bromeae* and *Triticeae* in a clade that is the sister group to *Poodae* (e.g. Soreng & Davis 2000, GPWG 2001, Davis & Soreng 2007). This set of three tribes has been resolved as a monophyletic group, with *Brachypodieae* as their sister group (e.g. GPWG 2001, Davis & Soreng 2007). We refer to this set of tribes, including *Brachypodieae*, as the core *Pooideae*. Among its elements, we exclude *Brachypodieae*, *Bromeae* and *Triticeae* from our working classification of *Poodae* (Fig. 1), but include representatives of these groups as outgroups in the present analysis.

Tzvelev (1976) provided a detailed tribal and subtribal classification for the USSR, in which genera

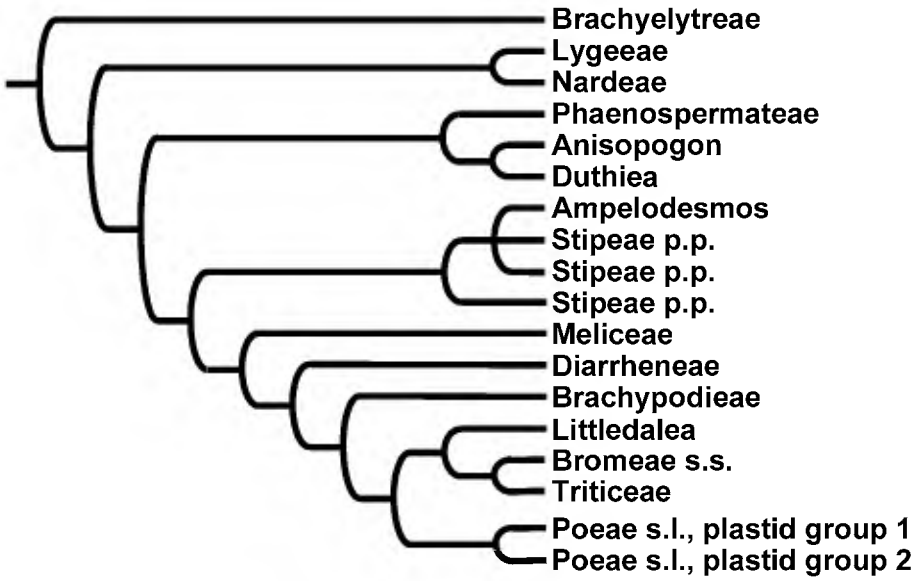

Fig. 1. Summary of phylogenetic relationships within *Poaceae* subfamily *Pooideae*, as resolved by four-gene analysis of Davis & Soreng (2007).

Table 1. Comparison of accepted tribes and subtribes within supertribe *Poodae* among systems proposed by Tzvelev (1976, 1987, 1989), Clayton & Renvoize (1986), Watson & Dallwitz (1992), and the present treatment. The tribes and subtribes are listed on the left as arranged by Tzvelev (1976), and additional taxa not mentioned there are listed below as 'Other tribes' and 'Other subtribes'. *Ampelodesmeae/Ampelodesminae* and *Duthieinae* are the only two taxa in the table excluded from supertribe *Poodae* in the present classification. PA– = tribe *Poeae*, plastid DNA group 1 (*Aveneae* type); PP– = tribe *Poeae*, plastid DNA group 2 (*Poeae* type); p.p. = pro parte. '+' indicates acceptance of a taxon, a leading '–' generally indicates that the tribe or subtribe was placed in synonymy or at least that its typical elements were included in a different suprageneric taxon. An asterisk indicates that plastid DNA data concerning the placement of a subtribe is not available.

Tribes	Subtribes	Tzvelev (1976)	Clayton & Renvoize	Tzvelev (1986)	Watson & Dallwitz (1987,1989)	Present treatment (1992)
Aveneae		+	+	–, in *Poeae*	+	–, in *Poeae*
	Aveninae	+	+, in *Aveneae*	–, in *Poeae*	–, in *Aveneae*	+, in PA-
	Gaudiniinae	+	–, in *Aveneae-Aveninae*	–, in *Poeae*	–, in *Aveneae*	–, in PA-*Aveninae*
	*Ventenatinae**	+	–, in *Aveneae-Aveninae*	–, in *Poeae*	–, in *Aveneae*	Needs further study, PP. p.p.
	Koeleriinae	+	–, in *Aveneae-Aveninae*	–, in *Poeae*	–, in *Aveneae*	–, in PA-*Aveninae*
	Airinae	+	–, in *Aveneae-Aveninae*	–, in *Poeae*	–, in *Aveneae*	+, in PP-
	Holcinae	+	–, in *Aveneae-Aveninae*	–, in *Poeae*	–, in *Aveneae*	–, in PP-*Airinae*
	Miliinae	+	–, in *Stipeae*	–, in *Poeae*	–, in *Aveneae*	+, in PP-
	Agrostidinae	+	–, in *Aveneae-Alopecurinae*	–, in *Poeae*	–, in *Aveneae*	+, in PA-
Phalarideae		+	–, in *Aveneae-Phalaridinae*	–, in *Phleeae*	–, in *Aveneae*	–, in PA-*Phalaridinae*
	Phalaridinae	+	+, in *Aveneae*	–, in *Phleeae*	–, in *Aveneae*	+, in PA-
	Anthoxanthinae	+	–, in *Aveneae-Phalaridinae*	–, in *Phleeae*	–, in *Aveneae*	–, in PA-*Phalaridinae*
Phleeae		+	–, in *Aveneae-Alopecurinae*	+	–, in *Aveneae*	–, in PP-*Alopecurinae*
	Beckmanniinae	+	–, in *Aveneae-Alopecurinae*	–, in *Phleeae*	–, in *Aveneae*	–, in PP-*Alopecurinae*
	Phleinae	+	–, in *Aveneae-Alopecurinae*	–, in *Phleeae*	–, in *Aveneae*	–, in PP-*Alopecurinae*
	Alopecurinae	+	+, in *Aveneae*	–, in *Phleeae*	–, in *Aveneae*	+, in PP-near *Poinae*
Scolochloeae		+	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	–, in PP-*Scolochloinae*
	Scolochloinae	+	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	+, in PP–
Poeae		+	–, in *Poeae*	+	+	+
	Festucinae	+	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	–, in PP-*Loliinae*

Table 1. (contd.)

Tribes	Subtribes	Tzvelev (1976)	Clayton & Renvoize	Tzvelev (1986)	Watson & Dallwitz (1987,1989)	Present treatment (1992)
Poeae (contd.)						
	Loliinae	As *Festucinae*	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	+, in PP-
	Psilurinae	+	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	–, in PP-*Loliinae*
	Poinae	+	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	+, in PP-
	Dactylidinae	+	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	+, in PP-
	Brizinae	+	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	+, in PA-
	Cinninae	+	–, in *Aveneae-Alopecurinae*	–, in *Poeae*	–, in *Aveneae*	Need further study
	*Coleanthinae**	+	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	Need further study
Hainardieae		+, as *Monermeae*	+	–, in *Poeae*	–, in *Poeae*	–, in PP-
	Parapholiinae	No	–, in *Hainardieae*	–, in *Poeae*	–, in *Poeae*	+, in PP- p.p. and extended
Seslerieae		+	–, in *Poeae*	–, in *Phleeae*	+	–, in PP-
	Sesleriinae	+	–, in *Poeae*	–, in *Phleeae*	–, in *Seslerieae*	+, in PP-
	Echinariinae	+	–, in *Poeae*	–, in *Phleeae*	–, in *Seslerieae*	+, in PP-
	*Ammochloinae**	+	–, in *Poeae*	–, in *Phleeae*	–, in *Aveneae*	+, in PP-
Other tribes	**Other subtribes**					
	Scribneriinae	N/A	–, in *Hainardieae*	–, in *Poeae*	–, in *Aveneae*	+, in PP-
	Torreyochloinae	–, in *Poeae-Poinae*	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	+, in PA-
	Puccinelliinae	–, in *Poeae-Poinae*	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	+, in PP-
	Miborinae	–, in *Aveneae-Agrostidinae*	–, in *Aveneae-Alopecurinae*	–, in *Phleeae*	–, in *Aveneae*	+, in PP-
	SA '*Briza*' *s.l.*	N/A	–, in *Poeae*	–, in *Poeae*	–, in *Poeae*	+, in PA-
	Duthieinae s. Clayton & Renvoize	–, p.p. *Aveneae-Aveninae*	+, in *Aveneae*	–, in *Poeae* and *Arundinoideae*	–, in *Aveneae* or *Arundinoideae*, undecided	+, near *Stipeae*/ *Phaenospermateae*
Ampelodesmeae		N/A	–, in *Poeae*	+	–, in *Arundinoideae*	–, in *Stipeae*
	Ampelodesminae	N/A	–, in *Poeae*	–, in *Ampelodesmeae*	–, in *Arundinoideae*	+, in *Stipeae*

of *Poodae* were apportioned among seven tribes, five of which he divided into 24 subtribes (Table 1). Later, Tzvelev (1987, 1989) placed most of these genera in *Poeae* (including those previously assigned by himself and other authors to *Agrostideae*, *Aveneae*, *Cinneae*, *Cynosureae*, *Festuceae*, *Milieae*, *Monermeae* [*Hainardieae* as applied], *Hubbardieae* [included in *Panicoideae* by Clayton & Renvoize] and *Scolochloeae*), but he maintained tribe *Phleeae* (including *Phalarideae* and *Seslerieae*). This trend towards the consolidation of tribes has continued, and in the three most recent world synopses of grass genera (Clayton & Renvoize 1986, Tzvelev 1989, Watson & Dallwitz 1992), only *Poeae*, *Aveneae*, and two smaller tribes, *Hainardieae* and *Phleeae*, in various combinations, have been recognised (Table 1). In our classification, supertribe *Poodae* consists of c. 135 genera within a single tribe *Poeae sensu lato* (Appendix II), which encompasses some 24 historically named tribes, of which only *Poeae* (in various senses), *Aveneae*, *Hainardieae*, *Phleeae*, *Scolochloeae* and *Seslerieae* have been accepted in modern floras.

We are interested in determining whether reasons for the contradictory placements of taxa in plastid DNA phylogenies and the *Poeae*, *Aveneae* and *Hainardieae* of Clayton & Renvoize (1986) will be apparent in nuclear DNA phylogenies, but appropriate data have been slow to appear. Whatever might be indicated by data from the nuclear genome, the contradictory placements by plastid DNA and Clayton & Renvoize's classification, the latter of which is based on structural characters, would remain. A large proportion of the apparently contradictory placements of genera are confined to three subtribes: genera of *Brizinae* (placed in *Poeae* by Clayton & Renvoize) have *Aveneae*-type plastid DNA, and genera of *Airinae* and *Alopecurinae p.p. typica* (placed in *Aveneae* by Clayton & Renvoize) have *Poeae*-type plastid DNA. It may be that some of these lineages continued to diversify following hybridization among lineages, with plastid DNA derived from one ancestral line and nuclear DNA largely from another, but other seemingly contradictory placements may be caused by misinterpretation of the homologies of morphological characteristics (Soreng & Davis 2000), or by the retention of plesiomorphic morphological characters within early-diverging members of a group that acquired its signature morphological profile later.

Methods

Taxon sample

On the basis of previous classifications (Clayton & Renvoize 1986, Tzvelev 1989, Watson & Dallwitz 1992) and molecular studies focused on *Pooideae* or *Poeae* (Soreng & Davis 2000, Catalán *et al.* 2004, Davis & Soreng 2007), the taxon sample was selected to cover as many postulated groups as possible within *Poodae*. The overall sample included 74 species from 64 genera of *Pooideae* (Appendix I), of which 66 species and 57 genera belong to *Poodae*. Eight species from the four tribes believed to be most closely related to this group (Davis & Soreng 2007) also were included. These four groups are *Bromeae*, *Triticeae* (collectively believed to constitute all or most of the sister group of *Poodae*), *Brachypodieae* and *Diarrheneae*, with *Diarrhena* P. Beauv. (the outgroup taxon believed to be least closely related to *Poodae*) used to root the trees. Of the six tribes to which recent floras assign genera of *Poodae*, the sample includes representatives of all except the monotypic *Scolochloeae*, which was sampled by Soreng & Davis 2000, and there placed within the *Poeae* plastid group. One or more representatives of each of the major groups diagrammed by Clayton & Renvoize (1986; in their Figures 11 and 12) were included, as were one or more representatives of most of the minor groups that are depicted as diverging from the major groups in those diagrams.

Several genera sometimes included in *Poodae sensu* Watson & Dallwitz (1992) were excluded from the analysis on the basis of the results of previous analyses (Soreng & Davis 1998, 2000, Davis & Soreng 2007) that placed them outside the core *Pooideae* (*Ampelodesmos*, *Danthoniastrum* (Holub) Holub, *Duthiea* Hack., *Metcalfia* Conert, and *Sinochasea* Keng). Also excluded (though placed in *Aveneae* by Clayton & Renvoize 1986) is *Euthryptochloa* Cope, as its one recognised species is conspecific with *Phaenosperma globosa* Benth. (Clayton *et al.* 2002 onward). *Megalachne*, *Podophorus*, *Pseudodanthonia* Bor & C. E. Hubb. and *Stephanachne* Keng were excluded on the basis of the presence of characteristics found elsewhere only outside of the core *Pooideae* (three lodicules, three styles, or lateral veins of the lemma merging with the central awn), and/or because of apparent close relationships to genera already excluded on the basis of DNA studies (Soreng *et al.* 2003, 2005 onwards).

Morphological methods

Twenty-five structural characters were scored, of which 18 are morphological or anatomical and seven are plastid DNA insertion/deletion (indel) and inversion characters. Each character is numbered and named, with its states described, in Appendix III, and the character-state matrix is presented in Table 2. This set of morphological characters represents a subset of those used by Soreng & Davis (1998, 2000), slightly modified by the GPWG (2001), and slightly modified again here as indicated in Appendix III. This character set was selected on the basis of the presence of cladistically informative

Table 2. Structural character data (cf. Appendix III). Characters 1 – 18 are morphological and anatomical features. Characters 19 – 25 are structural features (inversions and indels) of the three plastid-encoded genes. Codes: – = character inapplicable for taxon; ? = character state unobserved for taxon; polymorphisms and state ambiguities: A = [01]; B = [02]; C = [03]; D = [023]; E = [123]; F = [13]; G = [23]; H = [24].

Taxon	Character number																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Diarrhena obovata	0	1	1	0	4	A	0	0	1	A	1	1	0	0	1	1	1	0	0	0	0	0	0	1	0
Brachypodium pinnatum	0	0	1	0	4	1	0	0	1	0	1	0	1	0	1	1	0	0	1	0	0	0	0	1	0
Bromus inermis	1	1	1	0	4	A	D	0	1	0	0	1	1	0	1	1	0	0	1	?	0	0	0	1	0
Bromus suksdorfii	1	1	1	0	4	1	D	0	1	1	0	1	1	0	1	1	0	0	1	?	0	0	0	1	0
Elymus trachycaulus	0	0	1	0	4	A	0	0	1	0	1	0	1	0	1	1	0	0	1	0	0	0	0	1	0
Hordeum vulgare	0	0	0	0	1	1	0	0	1	A	1	0	1	0	1	1	0	0	0	0	0	0	0	1	0
Littledalea tibetica	0	1	1	0	4	0	–	–	1	1	A	0	1	0	A	1	0	?	1	0	0	0	0	1	0
Triticum aestivum	0	0	A	0	4	A	C	0	1	0	1	0	1	0	1	1	0	0	1	0	0	0	0	1	0
Agrostis tenerrima	0	1	1	0	1	A	2	1	1	0	0	0	0	0	A	0	1	1	1	0	0	0	0	1	0
Aira caryophyllea	0	1	1	0	2	A	2	1	1	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1
Aira cupaniana	0	1	1	0	2	A	2	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	1
Alopecurus magellanicus	0	1	0	0	1	1	2	1	0	–	–	0	0	1	0	0	1	1	1	0	0	0	0	1	0
Alopecurus textilis	0	1	0	0	1	1	2	1	0	–	–	0	0	1	0	0	1	1	1	0	0	0	0	1	0
Amphibromus scabrivalvis	0	1	1	0	4	1	2	1	1	0	0	0	1	0	1	1	1	1	1	0	0	0	0	1	0
Aniselytron truetleri	0	1	1	0	1	A	0	A	1	A	0	0	0	0	0	0	1	?	1	0	0	0	0	1	0
Anthoxanthum odoratum	0	A	1	1	1	A	2	1	0	–	–	0	0	0	0	0	1	1	1	0	0	0	0	1	0
Arctagrostis latifolia	0	1	1	0	1	A	0	0	1	A	0	0	A	0	0	0	?	1	1	0	0	0	0	1	0
Avena sativa	0	1	1	0	4	A	2	A	1	0	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0
Avenella flexuosa	0	1	1	0	2	A	2	A	1	A	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0
Avenula hookeri	0	1	1	0	4	1	2	1	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	1	0
Beckmannia syzigachne	0	1	0	0	1	A	0	0	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0
Bellardiochloa variegata	0	1	1	0	4	1	C	0	1	1	1	0	0	0	0	0	?	1	1	0	0	0	0	1	0
Briza minor	0	1	1	0	4	0	–	–	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0
Calamagrostis arudinacea	0	1	1	0	1	1	2	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0
Calamagrostis canadensis	0	1	1	0	1	1	2	A	1	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0
Calotheca brizoides	0	1	1	0	4	1	C	0	1	1	0	0	0	0	1	0	?	1	1	0	0	0	0	1	0
Catabrosa aquatica	1	1	1	0	4	0	–	–	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0
Chascolytrum subaristatum	0	1	1	0	4	A	0	0	1	0	0	0	0	0	1	0	?	1	1	0	0	0	0	1	0
Cutandia memphitica	0	1	A	0	4	A	G	0	1	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0
Cynosurus cristatus	0	1	1	0	4	1	0	0	1	1	0	0	0	0	A	A	1	A	1	0	0	0	0	0	0
Dactylis glomerata	1	1	1	0	4	1	B	0	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0
Deschampsia cespitosa	A	1	1	0	H	1	2	A	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0
Desmazeria sicula	0	A	1	0	4	0	–	–	1	A	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
Dichelachne micrantha	0	1	1	0	1	1	D	A	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0
Dielsiochloa floribunda	0	1	1	0	4	1	2	0	1	1	0	0	A	0	1	1	1	?	1	0	0	0	0	1	0
Dupontia fisheri	1	1	1	0	4	A	0	0	1	A	0	0	0	0	A	0	?	?	1	0	0	0	0	1	0
Echinopogon caespitosus	0	1	1	0	1	1	G	0	1	0	1	0	A	0	1	1	1	?	1	0	0	0	0	1	0
Festuca rubra	0	1	1	0	4	1	0	0	1	1	A	0	0	0	1	1	1	0	1	0	0	0	0	1	0
Festuca subverticillata	0	1	1	0	4	0	–	–	1	A	0	0	1	0	1	1	A	?	1	0	0	0	0	1	0
Festucella eriopoda	0	1	1	0	4	1	C	0	1	A	A	0	0	0	1	0	?	?	1	0	0	0	0	1	0
Gastridium ventricosum	0	1	1	0	1	1	2	0	1	0	0	0	0	0	0	0	?	1	1	0	0	0	0	1	0
Gaudinia fragilis	0	0	1	0	4	1	2	1	1	1	A	0	1	0	1	0	1	1	1	1	0	0	0	1	0
Gaudinia hispanica	0	0	1	0	4	0	–	–	1	1	0	0	1	0	1	0	1	1	1	1	0	1	0	1	0
Graphephorum wolfii	0	1	1	0	4	A	B	0	1	0	0	0	0	0	0	0	?	1	1	1	0	0	0	1	0

Table 2. (contd.)

Taxon	Character number																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Gymnachne koelerioides	0	1	1	0	4	A	C	0	1	0	0	0	0	0	1	0	1	?	1	0	0	0	0	1	0
Helictotrichon convolutum	0	1	1	0	4	1	2	A	1	0	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0
Helictotrichon mortonianum	0	1	1	0	4	1	2	A	1	0	0	0	1	0	1	1	1	1	1	1	0	0	0	1	0
Holcus lanatus	0	1	0	1	1	A	2	1	1	A	0	0	0	0	A	0	1	1	1	0	0	0	0	1	0
Hookerochloa hookeriana	0	1	1	0	4	1	0	0	1	1	A	0	0	0	1	0	?	?	1	0	0	0	0	1	0
Koeleria loweana	0	1	1	0	4	A	0	0	1	A	0	0	0	0	0	0	?	1	1	1	0	0	0	1	0
Leucopoa kingii	0	1	1	0	4	0	–	–	1	0	0	0	1	0	1	1	1	?	1	0	0	0	0	1	0
Lolium perenne	0	0	1	0	4	A	C	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	1	1	0
Lolium rigidum	0	0	1	0	4	A	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	1	1	0
Mibora minima	0	0	1	0	1	0	–	–	A	–	0	0	0	1	0	0	?	1	1	0	0	0	0	1	0
Milium vernale	0	1	1	0	1	0	–	–	1	A	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0
Molineriella laevis	0	1	1	0	2	A	2	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0
Parapholis incurva	0	0	0	0	1	0	–	–	1	0	0	0	0	0	A	0	1	1	1	0	0	0	0	0	0
Phleum pratense	A	1	1	0	1	A	0	0	1	A	0	0	0	A	0	0	1	1	1	0	0	0	0	1	0
Poa alpina	1	1	1	0	4	0	–	–	1	1	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0
Poa andina	0	1	1	0	4	1	0	0	1	A	0	0	0	0	1	0	?	?	1	0	0	0	0	1	0
Poa billardierei	0	1	1	0	4	0	–	–	1	1	1	0	0	0	1	0	?	?	1	0	0	0	0	1	0
Podagrostis thurberiana	0	1	1	0	1	0	–	–	1	0	0	0	0	0	0	0	?	1	1	0	0	0	0	1	0
Polypogon monspeliensis	0	1	0	0	1	1	D	A	1	0	0	0	0	0	A	0	1	1	1	0	0	0	0	1	0
Puccinellia distans	0	1	1	0	4	0	–	–	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0
Rostraria pubescens	0	1	1	0	4	A	B	0	1	0	0	0	0	0	0	0	?	1	1	1	0	0	0	1	0
Schedonorus arundinaceus	0	1	1	0	4	A	0	0	1	1	0	0	0	0	1	1	1	0	1	0	0	0	1	1	0
Sclerochloa dura	A	A	A	0	4	0	–	–	1	1	0	0	0	0	A	0	1	A	1	0	0	0	0	1	0
Sesleria caerulea	1	1	1	0	4	A	0	0	1	1	A	0	1	1	0	0	1	0	1	0	0	0	0	1	0
Sphenopus divaricatus	A	1	1	0	4	0	–	–	1	0	0	0	0	0	1	0	?	1	1	0	1	0	0	0	0
Torreyochloa pauciflora	0	1	1	0	4	0	–	–	1	1	0	0	1	0	1	0	1	?	1	0	0	0	0	1	0
Triplachne nitens	0	1	1	0	1	1	2	1	0	–	–	0	0	0	1	0	?	?	1	0	0	0	0	1	0
Trisetum canescens	0	1	A	0	4	1	B	A	1	0	1	0	1	0	0	0	1	1	1	1	0	0	0	1	0
Vahlodea atropurpurea	0	1	1	0	2	1	2	1	1	0	0	0	0	0	1	1	1	?	1	0	0	0	0	1	0
Vulpia macrstachys	0	A	1	0	4	1	0	0	1	0	0	0	A	0	1	1	1	1	1	0	0	0	0	1	0

variation within the ingroup, particularly where the states were relevant to the discrimination among taxa recognised in modern classifications. All morphological characters initially were scored as reported in Watson & Dallwitz (1992) for each genus. The character states for each species were reassessed on the basis of our understanding of the limits of each genus (Soreng *et al.* 2003, 2005 onwards). For example, *Briza sensu lato* is divided as recognised by Matthei (1975), *Deschampsia* and *Helictotrichon* Bess. are each divided into three genera, etc., and *Trisetum canescens* Buckley is treated as a species of *Trisetum* Pers. rather than of *Helictotrichon*. We also employ concepts that are narrower than those expressed by Watson & Dallwitz for *Agrostis* L., *Festuca* and *Poa*, removing *Podagrostis* Scribner & Merr., *Leucopoa* Griseb. and *Schedonorus* P. Beauv., and *Bellardiochloa* Chiov. from these three genera, respectively. Investigating smaller and relatively invariable morphological units is preferable to the scoring of larger, heterogeneous groups (Nixon & Davis 1991), but most of these interpretations of genera, which are narrower than those recognised by Watson & Dallwitz or Clayton & Renvoize, also have some support from molecular analyses. When a genus was polymorphic for a character, or when a more subtle division of states than presented by Watson & Dallwitz was deemed

appropriate, specimens were examined at US, and species descriptions were consulted in relevant floras and other reference sources (Hitchcock 1935, Hitchcock *et al.* 1969, Tzvelev 1976, 1987, Cronquist *et al.* 1977, Tutin *et al.* 1980, Clayton & Renvoize 1986, Nicora & Rúgolo de Agrasar 1987, Gleason & Cronquist 1991, Clayton *et al.* 2002 onwards). Thus, all states can be regarded as having been scored for the particular species named in Appendix I unless otherwise noted (e.g. for starch types, where only one or a few species per genus have been surveyed).

DNA methods

Nucleotide sequence variation in three plastid-encoded genes, *atpB*, *matK*, and *ndhF*, was determined by the authors from total genomic DNA isolations, following standard PCR and automated cycle sequencing protocols, for all representatives of *Poodae* in the analysis, and for most of the outgroups, with the remainder obtained from GenBank (Appendix I). The use of external amplification primers allowed determination of sequences extending to both ends of *matK* and to the 3′ ends of *atpB* and *ndhF*, as follows. The primer set used for *matK* includes some that correspond to flanking regions within *trnK* at both ends of *matK*, following Hilu *et al.* (1999). Amplification and sequencing of *atpB* was conducted with primers specific to regions within this gene and within the neighbouring gene *atpE*, which is situated beyond the 3′ terminus of *atpB* (cf. Hoot *et al.* 1995; Appendix IV). *ndhF* is situated predominantly or wholly within the small single copy (SSC) region, near the boundary between the SSC and the inverted repeat (IR) region, with its 3′ terminus extending into the IR region in some grass species. *ndhH* is situated near the other end of the SSC region, with its 5′ terminus extending into the IR region in some grass species (Ogihara *et al.* 2002, Davis & Soreng 2007). For taxa in which a portion of either of these genes extends into the IR region, a duplicate copy of that portion resides in both IR regions, and *ndhH* has this property in nearly all species of *Pooideae* that have been examined (Davis & Soreng 2007). Thus, primers specific to regions near the 5′ terminus of *ndhH* bind to the duplicate copy of this region that lies in the IR region, beyond the 3′ terminus of *ndhF* in these species, and can be used in the amplification and sequencing of *ndhF*. Similarly, *rps15* lies entirely within the IR region, near the IR/SSC boundary, and primers specific to this gene also can be used in the sequencing of *ndhF*, as they were in the present study.

Data analysis

Nucleotide sequences of the three genes and scores for the morphological and molecular structural characters were combined into one matrix, which was deposited in TreeBASE (study accession *S1651*). The data were subjected to cladistic analysis with all characters weighted equally and treated as non-additive (i.e. the states unordered), and with *Diarrhena* specified as the outgroup for the purpose of rooting. The molecular structural characters consisted of two inversions (in *ndhF*) and five indels (three in *ndhF* and one in each of the other two genes). The two *ndhF* inversions, three and six nucleotides in length, have been identified previously (Davis & Soreng 2007). There are 11 nucleotides between them (cf. Appendix III, characters 19 and 20), and although the alignment of the inversions themselves was regarded as unambiguous, the presence of additional indels renders alignment of other portions of this region ambiguous. Therefore, the nucleotides of the inversions were included in the analysis, but the rest of a length-variable region that includes them (30 nucleotides in *Triticum aestivum* L.) was excluded. The nucleotides of the inversions were included by adding a copy of these nine nucleotides in the matrix, using the observed nucleotide sequences for taxa interpreted as lacking the inversions, and the reverse complements of the observed sequences for taxa interpreted as having the inversions. The seven DNA structural characters, including the two inversions, were also included as separate presence/absence characters (Appendix III). Locations of these structural features (Appendix III) and primers (Appendix IV) are specified according to sequences in the complete plastid genome of *Triticum aestivum* (GenBank accession *NC 002762*).

Parsimony searches and a jackknife analysis (see below) were conducted following the removal of cladistically uninformative characters from the data set. Parsimony analyses were conducted with the multi-thread version of NONA vers. 1.6 (i.e., 'PARANONA' compiled 26 Feb 1998; Goloboff 1993), using the default polytomy settings. These settings allow polytomies to occur (*poly=*) and resolve a clade, rather than a polytomy, only when support for the resolution is unambiguous (*amb –*). Support for a group is regarded as unambiguous when the length of the branch subtending the group is greater than zero under all possible character optimisations. Tree searches began with 1000 search initiations, each involving Wagner Tree construction with a random taxon entry sequence, followed by branch-breaking swapping (BB) (i.e., tree-bisection-reconnection swapping [TBR], cf. Davis *et al.* 2005) with up to 20 shortest trees retained. This uses the command *mult**, preceded by *rs 0* and *hold/20*. Trees accumulated during these searches were then subjected to additional BB swapping with up to 100,000 trees retained and swapped, using the commands *hold 100000* and *max**. Analyses were conducted of the entire data matrix (the 'combined analysis') and of

various subsets. Subsets subjected to separate analysis included the entire set of molecular characters (nucleotides plus DNA structural characters, the 'molecular analysis'); each of the three genes separately (with each including the corresponding DNA structural characters); and the morphological and anatomical structural characters (i.e. characters 1 – 18 in Table 2, the 'morphological analysis'). The number of steps in each morphological character was assessed in all trees obtained by the combined and morphological analyses using the *change** command in NONA.

Support for clades resolved by the combined analysis was assessed by jackknife analysis (Farris *et al.* 1996), using WinClada vers. 1.00.08 (Nixon 2002) running NONA as a daughter process for tree searches, and employing the same character and polytomy settings used in the basic analyses of relationships. There were 1000 jackknife replicates, each consisting of four search initiations, with up to 20 trees retained during BB swapping after each search initiation (*hold/20; mult*4*), followed by additional BB swapping of shortest trees with up to 100 trees retained (*hold 100; max**). WinClada also was used to examine character transformations on the resulting trees, to determine tree lengths and related indices, and to generate figures.

Results

The *atpB* portion of the matrix consists of one informative indel and 1524 aligned nucleotides, of which 140 (9.3%) are informative. The *matK* portion of the matrix consists of one informative indel and 1554 aligned nucleotides, of which 290 (18.7%) are informative. The *ndhF* portion of the matrix consists of two informative inversions, three informative indels, and 2223 aligned nucleotides. The removal of 51 of these sites from the region in which the two inversions occur, and the reintroduction of nine sites, representing the nucleotides of the inverted regions, with the sequences of taxa inferred to have the inversions replaced with their reverse complements, leaves a total of 2181 *ndhF* nucleotides, of which 324 (14.9%) are cladistically informative. The total informative portion of the molecular matrix thus comprises seven structural characters and 754 nucleotide sites. Among these sites c. 19% are from *atpB*, 38% from *matK*, and 43% from *ndhF*. Further analysis of patterns of variation within these three genes will be discussed in another contribution (in prep.).

The *atpB* analysis yielded more than 100,000 trees of length 351, consistency index (CI) 0.50 and retention index (RI) 0.79; the *matK* analysis yielded 720 trees of length 739, CI 0.54 and RI 0.83; and the *ndhF* analysis yielded 288 trees of length 949, CI 0.47 and RI 0.82. The three-gene molecular analysis yielded ten most-parsimonious trees of length 2054, CI 0.50 and RI 0.82. This tree length exceeds the sum of lengths of trees obtained from the three separate molecular analyses by 15 steps (0.7%). The consensus of the 10 trees from the molecular analysis is presented in Fig. 2, with jackknife support indicated for all resolved groups, and with annotations indicating which groups are resolved by each of the single-gene analyses.

Of the 1332 cells in the morphology matrix (Table 2, chars. 1 – 18), 32 (2.4%) are scored as unobserved, 43 (3.2%) as inapplicable, and 104 (7.8%) as polymorphic or state ambiguous, with the remaining 1153 (87%) scored as a single state. All of the cells scored as unobserved are in characters 17 and 18, starch type and lipid presence/absence. Most of the inapplicable characters involve characteristics of awns and lodicules in taxa that lack these structures. Analysis of the 18-character morphology matrix yielded the maximum of 100,000 trees of length 65, CI 0.29 and RI 0.78. The consensus of these trees has little resolution, and they are not discussed further.

Analysis of the combined matrix of 779 informative characters (761 molecular characters and 18 morphological characters) yields eight most-parsimonious trees of length 2187, CI 0.48 and RI 0.80. This tree length exceeds the sum of lengths of trees obtained from the separate morphological and three-gene molecular analyses by 68 steps, or 3.2%. The number of steps in the molecular matrix, when mapped on each of these trees, is 2055, one more than the number of steps in these characters on trees obtained by analysis of the molecular matrix. The other 67 extra steps are in the morphological character set, which has 132 steps on each of the eight trees, more than twice as many as the 65 steps in these characters on trees obtained from the morphological matrix. One of these eight trees is presented in Fig. 3, with 142 transformations indicated for the 25 structural characters (132 steps for 18 morphological characters and 10 steps for seven molecular characters) under delayed transformation optimisation.

Discussion

Molecular versus morphological data

The molecular character set supports a well-resolved set of relationships (Fig. 2), while the morphological data set does not (cladograms not illustrated). The addition of the morphological data to the molecular data does not alter the large-scale structure obtained with the molecular characters alone (cf. Figs. 2 & 3), although certain local relationships are affected. Another indication of the degree to which the

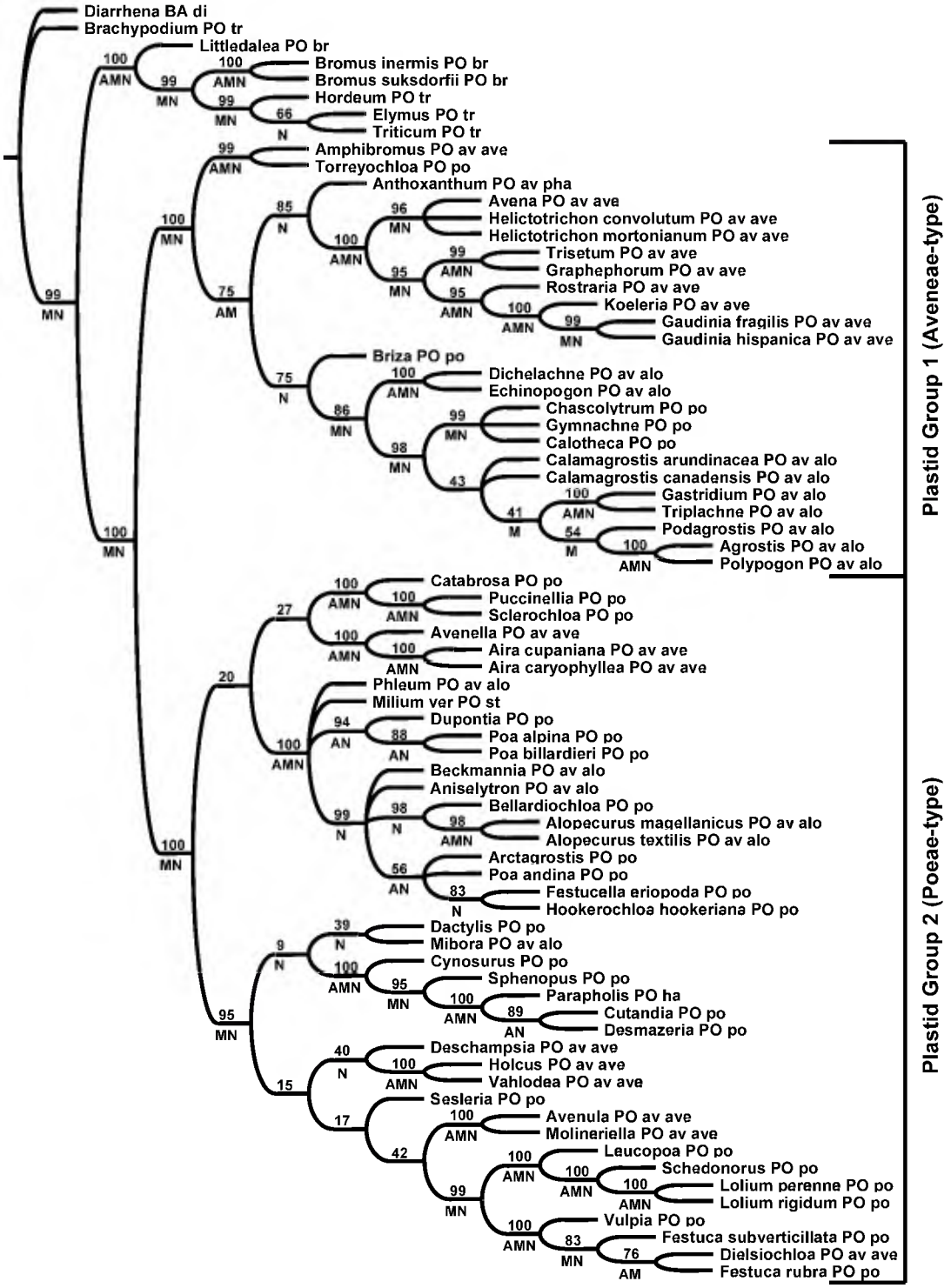

Fig. 2. Consensus of ten most-parsimonious trees depicting phylogenetic relationships among 66 representatives of *Poaceae* tribe *Poeae sensu lato* and eight outgroup taxa (cf. Appendix I). Resolved by combined analysis structural variation (cf. Appendix III, characters 19 – 25) and DNA nucleotide sequence variation in three plastid-encoded genes, *atpB*, *matK*, and *ndhF*. Numbers above nodes are jackknife percentages; letters below nodes (A, M, and N) identify clades that are resolved by single-gene analyses (*atpB*, *matK* and *ndhF*, respectively). Taxonomic assignments by Clayton & Renvoize (1986; in some cases inferred for recently described taxa) are indicated by two-letter codes in upper case for subfamilies (BA, *Bambusoideae*; PO, *Pooideae*), two-letter codes in lower case for tribes (av, *Aveneae*; br, *Bromeae*; di, *Diarrheneae*; ha, *Hainardieae*; po, *Poeae*; st, *Stipeae*; tr, *Triticeae*), and three-letter codes in lower case for subtribes of *Aveneae* (alo, *Alopecurinae*; ave, *Avenina*e; pha, *Phalaridinae*). Designations of two major clades of plastid genomes are indicated on the right.

molecular data set dominates the results of the combined analysis is apparent in the fact that the number of steps in the molecular character set on trees from the combined analysis (2055) exceeds the number of steps in the same character set on molecular trees (2054) by one (0.05%), whereas the number of steps in the morphological character set on trees from the combined analysis (132) exceeds the number of steps in these characters on morphology trees (65) by 67 (103%).

Among the three genes, *matK* and *ndhF* each contribute c. 40% of the available characters, and each independently supports a majority of the groups that are resolved in the combined molecular analysis (Fig. 2). In particular, *matK* and *ndhF* both place all representatives of the *Bromeae* and *Triticeae* in a monophyletic group that is sister of a monophyletic *Poodae*, and both support the division of *Poodae* into two major subclades, one corresponding largely to the traditional *Aveneae* (Plastid Group 1), and the other to the traditional *Poeae* (Plastid Group 2). Of these groupings, only the placement of *Bromeae* with *Triticeae* is supported independently by *atpB*, which contributes less than half as many informative characters to the molecular matrix as either *matK* or *ndhF*. Although *atpB* contributes less than the other two genes to the determination of overall relationships, each of the three genes independently supports many of the constituent groupings within the major clades, and several groups that are not supported by any of the genes individually are resolved by the combined molecular matrix.

As already noted, the addition of the morphological data to the molecular data does not result in major changes in the groups that are resolved relative to those resolved by the molecular data alone (cf. Figs. 2 and 3). Also, analysis of the morphology matrix resolves very little, and on the basis of these results, it might be concluded that the morphological matrix has little phylogenetically informative variation. Indeed, an analysis by Kellogg & Watson (1993) using morphological data from Watson & Dallwitz (1992) also yielded little phylogenetic structure. Those authors suggested that the lack of resolution that they observed could be attributed to high levels of homoplasy and rampant reticulation, and we draw similar conclusions. However, it is notable that the present morphological matrix has more than twice as many steps on trees from the combined analysis as on the trees favoured by morphology alone. Although little is resolved by morphology alone, it is evident that there are some relationships (i.e. some of those in the combined tree) that are strongly contradicted by the morphological data, or to put the point differently, relationships favoured by the molecular data are in strong conflict with those favoured by the morphological data.

Support for two major clades within the core *Pooideae*

Like the present analysis, previous phylogenetic analyses of molecular data that used taxon samples including multiple members of diverse tribes of *Poaceae* subfamily *Pooideae* (Soreng *et al.* 1990, Soreng & Davis 2000, GPWG 2001, Davis & Soreng 2007) have consistently detected two major clades within the core *Pooideae*. One corresponds to supertribe *Triticodae* T. D. Macfarl. & L. Watson (tribes *Bromeae* and *Triticeae*, with *Littledalea* Hemsl. sometimes placed as sister to this pair of tribes), the other to supertribe *Poodae*. The latter group comprises c. 135 genera, including most of the genera placed in tribes *Aveneae* and *Poeae* by Clayton & Renvoize (1986) and by Watson & Dallwitz (1992), plus those separated from these two tribes and variously placed in the small tribes *Hainardieae* (Clayton & Renvoize) or *Phleeae* (Tzvelev 1989). Tribe *Brachypodieae* is the most likely sister group of the clade that comprises *Triticodae* and *Poodae* (Davis & Soreng 2007; see Fig. 1 of present paper) and, as noted earlier, we refer to these three groups collectively as the core *Pooideae*. Clayton & Renvoize (1986: Fig. 5) interpreted *Aveneae* as sister to a group that included six tribes. Within the latter group, a lineage consisting of *Meliceae* and *Brylkinieae* was regarded as the sister of a group that consisted of *Poeae*, *Hainardieae*, *Bromeae* and *Triticeae*, with the latter two treated as sisters, and the first two of these four lying near the point of divergence of the *Bromeae/Triticeae* group. However, DNA data have consistently placed taxa of *Aveneae* and *Poeae* together, and have excluded *Meliceae* from the minimal grouping that includes the taxa of *Aveneae*, *Poeae*, *Triticeae* and *Bromeae*. Not surprisingly, *Brylkinieae* has been placed as the sister group of *Meliceae*, and hence outside the core *Pooideae* (unpublished data). The sister group of the core *Pooideae* had been unresolved or weakly supported in previous treatments (e.g. Soreng & Davis 2000), but *Diarrheneae* is placed in this position (Fig. 1), with 100% jackknife support, by the multigene study with the most extensive sampling of *Pooideae* tribes and outgroups to date (Davis & Soreng 2007). As stated above, several additional genera also have been excluded from the core *Pooideae* on the basis of DNA analyses, and they will receive no further discussion here.

The combined analysis identifies two of the 18 morphological/anatomical characters as unambiguous synapomorphies of supertribe *Poodae* (i.e. synapomorphies of this group in all eight most-parsimonious trees under all possible character-optimisation schemes). These are presence of a nonlinear hilum (character 16, state 0) and presence of lipid in the endosperm (character 18, state 1). Additional potential synapomorphies of this group, present in all most-parsimonious trees, under some

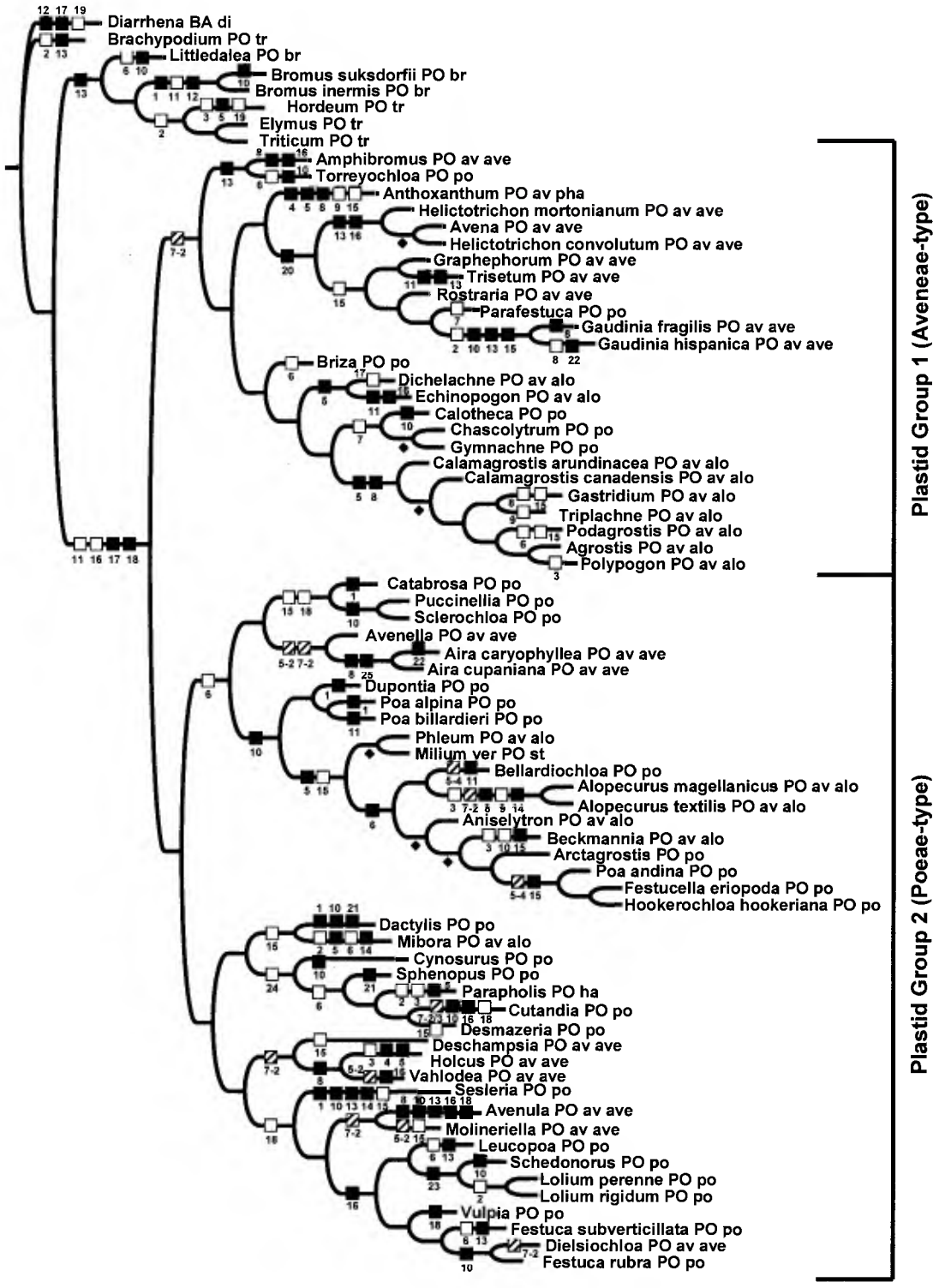

Fig. 3. One of eight most-parsimonious trees depicting phylogenetic relationships among 66 representatives of *Poaceae* tribe *Poeae sensu lato* and eight outgroup taxa (cf. Appendix I). Resolved by combined analysis of molecular and morphological data. Branches not present in the consensus tree are marked with solid diamonds. Taxon and clade labels are as in Fig. 2. Transformations in 25 structural characters (Table 2, Appendix III) under a delayed transformation optimisation regime are depicted as numbered boxes on internodes. The number associated with each box (or the first of two numbers in cases in which two numbers linked by a hyphen are present) is the character number in Appendix III. Open boxes signify transformation to state 0, solid boxes to state 1. Boxes with diagonal lines signify transformation to a state other than 0 or 1, with the state(s) indicated by the number(s) following the hyphen.

but not all optimisations, are dorsal awn attachment (character 7, state 2), absence of cilia on lodicules (character 11, state 0), absence of ovary pubescence (character 13, state 0) and presence of compound starch grains (character 17, state 1). Of these character transformations, the four that are present under delayed transformation optimisation on the tree depicted in Fig. 3 are indicated there.

Structural characteristics of the ancestral node of *Poodae* (i.e. the inferred character states for the last common ancestor of the group, including states either originating at that node or retained from an earlier point of origin) include sheath margins free; inflorescence paniculate; presence of two or more female-fertile florets per spikelet; absence of proximal female-sterile florets; spikelet disarticulation above the glumes; lemmas awned, the awn position either terminal or dorsal, the awn nongeniculate; lodicules present, unlobed, and glabrous; ovary lacking an appendage, and either glabrous or pubescent; styles free; fruit with a sulcus, the hilum nonlinear; and endosperm with compound starch grains and lipid. This description specifies a mosaic of characteristics generally considered typical of *Poeae* and *Aveneae* under recent circumscriptions. Although it excludes specialised features of some distinctive groups within *Poodae* as ancestral states for the overall group (e.g. spicate inflorescences, solitary florets, presence of proximal female-sterile florets, and geniculate awns), the ambiguity concerning awn position on the lemma demonstrates the difficulty in assigning the last common ancestor of all taxa of *Poodae* to either of the two major tribes recognised by Clayton & Renvoize (1986). It should be recognised, however, that the reconstructed character set for the base of this clade is influenced by the relationships resolved within the group. Thus, the intermixture of elements of *Poeae* and *Aveneae* within this clade, as detected by the molecular and combined analyses (see below), contributes to the ambiguity that is observed with respect to the ancestral features of *Poodae*.

Support for two groups of intermixed morphologies within *Poodae*

Of the tribes and subtribes of Poodae recognised by Tzvelev (1976) but not included in the present analysis, Soreng & Davis (2000) previously confirmed that three (*Scolochloeae*, *Echinariinae* and *Psilurinae*) belong in Poeae *sensu* Clayton & Renvoize, leaving only *Coleanthinae*, *Ammochloinae* and *Ventenatinae* (which together include a total of four genera) unsampled in one or another of our plastid DNA studies. Two major clades, both of them strongly supported, have been resolved repeatedly within *Poodae* by plastid DNA analyses, and both groups have 100% jackknife support in the present molecular analysis (Fig. 2). Plastid Group 1 ('*Aveneae*-type') generally corresponds in membership to the *Aveneae* of Clayton & Renvoize (1986), and Plastid Group 2 ('*Poeae*-type') generally corresponds to the *Poeae* of Clayton & Renvoize, including all examined genera of the *Hainardieae* of Clayton & Renvoize and *Phleeae* of Tzvelev (1989). However, as already noted, a substantial number of the genera placed in these clades by plastid DNA data, as well as by the combined analysis, are in positions that conflict with traditional morphology-based classifications.

Among the genera traditionally placed in *Poeae*, but falling in Plastid Group 1, are *Torreyochloa* (generally considered closely related to or included within *Puccinellia*), *Briza*, *Calotheca* and *Chascolytrum*, and additionally *Poidium* in Soreng & Davis (2000). The latter four of these genera, and others, are sometimes placed in subtribe *Brizinae* (Soreng *et al.* 2003, 2005 onward) or in *Briza sensu lato* (e.g. Clayton & Renvoize 1986). Conversely, several genera traditionally placed in *Aveneae* by Clayton & Renvoize and other authors fall in Plastid Group 2: *Aira*, *Avenella*, *Avenula*, *Deschampsia*, *Molineriella* and *Vahlodea* (sometimes placed in subtribes *Airinae*); *Holcus* (sometimes placed in subtribe *Holcinae*); *Alopecurus*, *Beckmannia* and *Phleum* (sometimes placed in tribe *Phleeae* or *Aveneae* subtribe *Alopecurinae*, which was included in subtribe *Agrostidinae* by Clayton & Renvoize); *Milium* (sometimes placed in tribe *Stipeae* or *Aveneae* subtribe *Miliinae*); and *Aniselytron* (sometimes placed in *Calamagrostis*, as by Clayton & Renvoize). If we add to this list of conflicting placements those genera not yet tested with plastid DNA but closely allied on the basis of morphological similarities to taxa that have been tested (and previously placed together in subtribes or other small groups of genera in various systems), and provisionally accept the groupings supported by plastid DNA analyses as indicative of actual phylogenetic relationships of the taxa, >20% of the genera of *Poodae* have been misplaced in recent classifications in terms of their tribal assignments (Appendix II).

Although two unambiguous structural synapomorphies are detected for *Poodae* by the combined analysis, none is detected for either of the two major clades within this group on any of the eight most-parsimonious trees. One transformation is indicated in Fig. 3 for Plastid Group 1 (a transformation in awn position from terminal to dorsal), but both of these states occur in both groups, and this particular transformation occurs on this branch only under delayed transformation optimisation. No structural synapomorphy for Plastid Group 2 is detected under any optimisation scheme. In recognition of this situation, while acknowledging the pressing need for further research into the reasons behind these results, we include all genera of the supertribe *Poodae* in one large tribe, *Poeae*.

Several subclades have been detected within the two major plastid DNA groups. Some of these subclades include sets of genera that have homogeneous morphologies, whereas others include genera that are connected by reasonable character transitions. As a means for highlighting the current state of understanding of these groups, we have reorganised the genera, and recognise these subclades as subtribes, as did Tzvelev (1976) and various other agrostologists, but with various modifications (Appendix II). Relationships among some of the subclades that are recognisable as subtribes are well supported in the molecular tree (Fig. 2). Other subtribes provisionally recognised on morphological grounds are not resolved as monophyletic by the current data matrix, but jackknife support for alternative relationships is weak (*Agrostidinae*, *Brizinae*, *Alopecurinae* and *Poinae* in the senses applied here). Subtribe *Airinae* breaks into three parts, *Aira* + *Avenella* (group AA), *Avenula* + *Molineriella* (group AM), and *Deschampsia* + *Holcus* + *Vahlodea* (group DHV), with group AA strongly supported as remote from groups AM and DHV. A summary of our provisional subtribes follows, with superscripted jackknife support (in the molecular tree) for each recognised plastid DNA lineage, an X for groups not resolved as monophyletic or with jackknife support <50%, or a Z for groups represented by only one exemplar, and thus not tested for monophyly: ^{100}Group 1 – ^{99}*Torreyochloinae* ^{75}(^{85}(^{Z}*Phalaridinae* ^{100}*Aveninae*) ^{75}(intermixed ^{X}*Brizinae* and ^{X}*Agrostidinae*)); ^{100}Group 2 – ^{X}(^{X}(^{100}*Puccinelliinae* ^{100}*Airinae p.p.* group AA) ^{100}(intermixed ^{X}*Alopecurinae* ^{X}*Poinae* ^{Z}*Miliinae*)) ^{95}(^{X}(^{X}(^{Z}*Dactylidinae* ^{Z}*Miborinae*) ^{100}(^{Z}*Cynosurinae* ^{95}*Parapholiinae*)) ^{X}(^{X}*Airinae p.p.* group DHV ^{X}(^{Z}*Sesleriinae* ^{X}(^{100}*Airinae p.p.* group AM) ^{100}*Loliinae*))).

Among the structural characters of the three genes, some are consistent with the relationships resolved by the combined and molecular analyses, and others are not. The three-nucleotide inversion in *ndhF* (character 19, Appendix III) is present as state 0 in *Diarrhena* and *Hordeum*, and as state 1 in all other taxa in the sample (Table 2). Because the only two taxa with state 0 are nonadjacent, this character has an RI of 0 in the present sample, but the observed distribution is consistent with an earlier interpretation (Davis & Soreng 2007) that is based on a broader sampling of *Pooideae*: state 0 is plesiomorphic for the *Pooideae*, state 1 is a synapomorphy for the Core *Pooideae*, and there is a reversion to state 0 in *Hordeum* (Fig. 3). The six-nucleotide inversion in *ndhF* (character 20) is present as state 1 in all nine taxa sampled from subtribe *Aveninae* (Table 2, Appendix II), and as state 0 in all other taxa in the sample, including *Anthoxanthum*, the sole representative of *Phalaridinae*, which is placed as the sister of *Aveninae* (Fig. 3). Thus, the six-nucleotide inversion character has a CI and RI of 1, with state 1 interpreted as an unambiguous synapomorphy of *Aveninae*. Among the indels, characters 21 and 22 each occur as insertions in *ndhF* that are present in two taxa and, in both cases, the two taxa with the insertion are not sisters, and the RI is 0. In character 23, a six-nucleotide insertion in *ndhF* is present in three taxa (*Schedonorus* and both species of *Lolium*) that are resolved as a monophyletic group within the *Loliinae*. In character 24, a six-nucleotide deletion in *matK* is observed in *Cynosurus* (the sole representative of *Cynosurinae*) and all four representatives of *Parapholiinae*. These five taxa are resolved as a clade, with the deletion therefore interpreted as a synapomorphy of this grouping of two subtribes. Finally, in character 25, a 27-nucleotide insertion in *atpB* is present in both species of *Aira*, but not in the third representative of *Airinae* (*Avenella*); thus, it is interpreted as a synapomorphy of the monophyletic genus *Aira*, within *Airinae*, pending further sampling.

Morphological characters represent 2.3% of the combined data set, and the inclusion of these characters in the combined analysis had only a minor effect on the inferred phylogenetic structure, as compared to the results obtained by the molecular analysis. The main difference in the trees was the partial stabilisation of structure in the clade that includes *Poinae*, *Alopecurinae* and *Miliinae* (the PAM group; see Gillespie *et al.* 2007). As noted above, this group has 100% jackknife support in the molecular tree. Relationships are unresolved among *Phleum*, *Milium* and two subclades (of three and nine taxa, with representatives of two and eight genera, respectively) in the molecular consensus tree. In the combined analysis the two-genus clade (consisting of *Dupontia* and *Poa*) was resolved as sister to a group consisting of *Milium*, *Phleum* and the eight genus clade as follows: ((*Dupontia Poa*) (*Milium Phleum* (*Aniselytron Beckmannia* (*Alopecurus Bellardiochloa*) (*Arctagrostis* Griseb. (*Poa* subg. *Andinae* E. G. Nicora (*Festucella* E. B. Alexeev *Hookerochloa* E. B. Alexeev)))))). For more information on this clade see Brysting *et al.* 2004, Hunter *et al.* 2004, Gillespie & Soreng 2005, and Gillespie *et al.* 2007.

The morphological features used to characterise tribe *Hainardieae* by Clayton & Renvoize (1986) were presence of a bilateral raceme (unilateral in *Narduroides*) with the spikelets broadside to the rhachis and sunken into it, the glumes side by side, the ovary glabrous and unappendaged, and strictly one-flowered or with two or more fertile florets. Presence of a straight awn from a sinus was noted to occur in *Scribneria*. Of the genera assigned to this group, disarticulation is strictly above the glumes only in *Scribneria* and *Narduroides*, two genera that

appear to be only distantly related to *Hainardia* and *Parapholis* in molecular analyses (Soreng & Davis 2000, Torrecilla & Catalán 2002). Clayton & Renvoize (1986: 110) described *Hainardieae* as, "A small group of genera in which the rhachis internode is progressively integrated with the spikelet. They are best recognised by the collateral glumes, but are otherwise fairly close to annual members of *Poeae* with a short hilum such as *Catapodium*. They have specialised in adaptations to saline soils." As noted by Soreng & Davis (2000), *Hainardia* and *Parapholis* of this tribe are placed in a small clade in molecular and combined molecular and morphological analyses with genera of a small cluster illustrated in Clayton & Renvoize's Fig. 11 that includes *Catapodium*, *Cutandia*, and *Desmazeria* (with *Sphenopus* in close proximity). This suggests that the reduced panicles of the latter four genera, and the tendency towards disarticulation of panicle branches and spikelets, as exhibited in *Cutandia*, are transitional to the racemes and spikelet disarticulation below the glumes seen in the core *Hainardieae*. All of these genera (again, except *Scribneria* and *Narduroides*) tolerate saline conditions. On the basis of these patterns, we suggest that presence of a raceme was given too much weight in the circumscription and ranking of *Hainardieae* by Clayton & Renvoize, but also note that there is evidence of a monophyletic group of eight genera, if somewhat differently framed, and that recognition of a subtribe *Parapholiinae* is warranted (Appendix II).

In evaluating patterns of homoplasy, it is useful to examine the number and pattern of occurrence of character transformations in individual characters on trees from the combined analysis. The following example covers the 25 structural characters (morphological and molecular) on the randomly selected most-parsimonious tree that is depicted in Fig. 3. Each character number, in bold, is followed by two unparenthesised numbers. The first is the number of autapomorphic transformations within *Poeae sensu lato* from the inferred plesiomorphic state for this group under delayed transformation optimisation. The second is the number of synapomorphic transformations from the plesiomorphic state (i.e. the number of groups of two or more terminals marked by such transformations). The latter number is followed in parentheses by the number of taxa within each group, including those that exhibit further transformations in the character. A superscript 'r' indicates each additional transformation within a group (either a reversal to the plesiomorphic state or a transformation to another state), and a number after an ^{r} indicates the number of taxa in the clade with that state, if more than one: 1: 5,0; 2: 2,2(2,2); 3: 4,1(2); 4: 2,0; 5: 6,4(2,3,7,11^{rr3}); 6: 7,2(4,20^{r9}); 7: 1,5(2,2,3,3,25^{rr3}); 8: 4,4(2,2,2,6^{r}); 9: 2,1(2); 10: 8,4(2,2,2,14^{r}); 11: 4,0; 12: 0,0; 13: 5,3(2,2,3); 14: 2,1(2); 15: 7,4(2,3,6^{r2},11^{rr3}); 16: 5,2(3,8); 17: 1,0; 18: 1,2(3,11^{rr}); 19: 0,0; 20: 0,1(9); .21: 2,0; 22: 2,0; 23: 0,1(3); 24: 0,1(5); 25: 0,1(2). Thus, in character 18, lipid presence arises once within *Poeae sensu lato* as an autapomorphy, and twice as a synapomorphy, uniting a group of three taxa in one case, and a group of 11 in the other, with two reversals within the latter group, each of them autapomorphic.

Characters 5 – 8, 10, 15 – 16, 18 and 20 all mark clades that include at least six taxa, whereas characters 1 – 4, 9, 11 – 14, 17, 19 and 21 – 25 do not. It should be noted that the distinction between large and small groups reflects many factors, including the pattern of taxon sampling of this study, and that a transformation that appears as an autapomorphy in the present analysis actually might unite a genus that includes hundreds of species, with just one of them sampled for this analysis. However, in light of the present focus on groups of genera, with a broad sampling of genera across this polymorphic tribe, and minimal sampling within genera, the patterns that are detected represent a step towards an understanding of large-scale variation patterns in structural characters in this group. In character 7, dorsal awn attachment is determined to have originated six times within *Poeae sensu lato*. In one instance, it unites a group of 25 taxa, and although it is lost twice within this group, and originates elsewhere five other times, this character is synapomorphic for a major clade that corresponds to Plastid Group 1.

Although the morphological characters as a group exhibit more than twice as many steps on the combined trees as on the morphological trees, individual characters vary widely in this respect. The number of steps in each of the morphological characters is constant among the eight trees derived from the combined analysis, but varies for all but two of the 18 morphological characters among the 100,000 trees derived from the morphological analysis (Appendix III). When the number of steps in a character varies among trees from the morphological analysis, the difference in number of steps between the two analyses also must be a range. Among the various ways that the incongruence indicated by these differences can be quantified, a direct approach is simply to count the minimum number of extra steps implied for each character in trees from the combined analysis, relative to the number implied by the morphological analysis. Thus, with 2 – 5 steps in character 1 in the morphological analysis, and six steps in the combined analysis (Appendix III), the minimum number of additional steps implied by the combined analysis for this character is 1. Among the 18 morphological characters, the minimum number

of additional steps in the combined analysis is 0 – 3 for eleven characters (characters 1 – 4, 9, 11 – 12, 14 and 16 – 18), 4 for two characters (6 and 13), and 6 – 8 for five characters (5, 7 – 8, 10 and 15). Within the latter two sets, character 5 describes the number of female-fertile florets per spikelet, characters 6 – 8 describe awn presence/absence and the position of attachment and shape of the awn, and characters 10, 13 and 15 describe presence/absence of lateral lobes of lodicules, ovary pubescence, and fruit sulcus, respectively.

The large numbers of steps in some of these characters (as opposed to the additional steps implied by the combined analysis) can be attributed in part to lack of precision in their scoring. For example, a broad sulcus on a dorsally compressed fruit is distinct, but on a laterally compressed or nearly cylindrical fruit it becomes more difficult to distinguish a distinct from an indistinct sulcus. Scoring might be improved by incorporating a calculation of sulcus depth and breadth relative to fruit depth and breadth. Similarly, lodicules that are long and slender, and that lack lobes, as found in many members of Plastid Group 1, are easily scored as unlobed. However, lobes can vary from large and lateral to small and nearly terminal, so lobe presence includes a range of morphologies. Despite these difficulties, we found that among the trees produced by the morphological data alone, these characters frequently supported clades or demarcated the origins of grades of genera similar to those outlined in the diagrams of Clayton & Renvoize (1986; their Figures 11 and 12).

Another potential source of homoplasy in the morphological characters is the conventional explanation, i.e. parallelisms and reversals to ancestral states in the evolutionary history of the taxa. For example, if awn position has shifted multiple times, between dorsal and apical positions on the lemmas, and in a variety of lineages, this character provides poor evidence of phylogenetic relationship, and the traditional distinction between *Poeae* and *Aveneae* (and other small tribes), based in part on this feature, is artificial. This explanation certainly applies to many or most of the homoplasious transformations observed in the combined analysis, and the data at hand do not force us to seek alternative explanations. However, alternative explanations cannot be ruled out.

When the minimum number of steps in a morphological character in the combined trees exceeds the corresponding number in the morphological analysis by several steps, it is reasonable to consider alternative explanations. This pattern is observed for lodicule lobing, in which there are 6 – 9 steps in trees obtained from the morphological analysis and 15 in the combined analysis. Lodicule lobing is infrequent in Plastid Group 1, and in genera of *Airinae*, whereas lobes are quite common in taxa of Group 2 other than *Airinae*. Similarly, the presence of a geniculate awn has been one of the best indicators of membership in the *Aveneae* (*sensu* Clayton & Renvoize 1986 and Watson & Dallwitz 1992). It is common in Group 1, and in *Airinae* and *Alopecurinae sensu stricto* of Group 2, and absent in taxa of Group 2 other than *Airinae*, *Alopecurinae sensu stricto* and a few other taxa assigned to *Aveneae* by Clayton & Renvoize. The anomalous nature of *Airinae* suggests that hybridization may have occurred, and argues for continued investigation of this possibility. Similarly, characters 7 and 8 describe the position and form of awns, both of which are significant characters in the traditional distinction between *Poeae* and *Aveneae*, and the combined trees imply a minimum of six and eight extra steps in these characters, respectively. Dorsal awns are nearly universal in Plastid Group 1, but they arise about five times within Group 2, where they occur in *Airinae*, *Holcinae*, *Alopecurinae* and other groups; the pattern is similar for geniculate awns. Continued investigation of phylogenetic relationships among these lineages, using genes from the nuclear genome, might help to clarify reasons for this incongruence.

A new classification of *Poeae*

The need for biologically informative and predictive classifications leads taxonomists to re-evaluate classifications periodically, particularly when substantially newer data and phylogenetic analyses become available. It has been more than a decade since the last world-wide classifications of grasses were completed (Clayton & Renvoize 1986; Tzvelev 1989; Watson & Dallwitz 1992), and little molecular phylogenetic information was available at the time that they were produced. The lineage under study here, supertribe *Poodae*, was divided by the authors of these three treatments into 1) *Aveneae*, *Poeae* and *Hainardieae*, 2) *Phleeae* and *Poeae*, and 3) *Aveneae* and *Poeae*, respectively, with *Aveneae* and *Poeae* quite large, and *Hainardieae* and *Phleeae* relatively small tribes. We conclude, as discussed above, from accumulated DNA phylogenetic data, that none of these groups as previously circumscribed is monophyletic. For now it seems preferable to include the genera of these four tribes in one large tribe, *Poeae*, with two major plastid lineages that correspond imperfectly to *Aveneae* and *Poeae*. The latter group includes most of the elements of *Hainardieae* and *Phleeae*. Within this single broadly circumscribed tribe *Poeae*, there is evidence to support the recognition of a series of smaller lineages and groups that can be treated provisionally as subtribes (Table 1, Appendix II).

Regarding the two major plastid DNA lineages, there are several potential explanations (none of

them mutually exclusive with the others) for the conflicting distribution of morphological phenotypes in the plastid DNA phylogenetic trees with respect to the conventional delimitations of tribes *Aveneae* and *Poeae* as outlined by Clayton & Renvoize (1986) or Watson & Dallwitz (1992). First, reticulation is possibly, if not probably, an explanation for some of the unexpected placements of taxa (particularly for *Airinae*), and lineage sorting of ancestral character polymorphisms may explain other observed anomalies. In either of these cases, the characters that exhibit the conflicting patterns would be homologous in terms of their genetic basis, and the observed incongruence would be attributed to descent processes that resulted in the nonhierarchic distributions of these characters. Second, the key characteristics historically used to separate these two tribes may be more evolutionarily plastic than generally assumed (see discussion of CI and RI of morphological characters). These considerations lead us to conclude that it is unlikely that there are two major evolutionary lineages with independent phylogenetic histories that correspond to the traditionally defined *Aveneae* and *Poeae*. The histories of the taxa in *Poodae* are likely to be entangled to such a degree that it is inappropriate to maintain the tribal distinctions. This leaves us with a large and heterogeneous tribe *Poeae* that has somewhat less precise though perhaps more accurate predictive power than previous multitribal systems. Within this enlarged tribe *Poeae* there seems to be strong correspondence, within smaller sets of genera, between morphological phenotypes and the plastid DNA relationships that have been detected. Many of these smaller series and isolated genera have been named as tribes or subtribes under older classifications, and it seems useful to apply those names to these sets. Further understanding of relationships within and among these groups will require more intensive sampling within and among genera, with more variable loci, along the lines taken by Choo *et al.* (1994) for *Puccinelliinae*, Grebenstein *et al.* (1998) and Röser *et al.* (2001) for *Helictotrichon*, Torrecilla & Catalán (2002), Torrecilla *et al.* (2003, 2004) and Catalán *et al.* (2004) for *Festuca* and the *Loliinae* lineage, Mason-Gamer *et al.* (1998) and Mason-Gamer (2001) for *Triticeae*, and Soreng (1990), Gillespie & Soreng (2005) and Gillespie *et al.* (2007) for *Poa* and *Poinae*.

To go beyond the accumulated evidence from plastid DNA phylogenies and produce a world-wide classification one must extrapolate from relationships of genera in DNA trees, morphology of the tested genera and the probable affinities of unsampled genera, as inferred from morphology alone. In this exercise, we reconsider the utility and reliability of the smaller groupings named in previous classifications, and retain those groupings that appear to have a reasonably high probability of representing natural lineages. Some of the subtribes we have chosen to recognise provisionally are, in fact, not monophyletic in plastid DNA trees. This is tolerated in cases in which support for alternative relationships in the DNA data is weak. In such cases, our assessment of overall morphological relationships is allowed to prevail, but as always, provisionally. This procedure allows for the fact that the plastid phylogeny is based upon one nonrecombining segment of genetic material. It is possible that with deeper sampling of taxa, and with the incorporation of evidence from independently inherited genes, relationships supported by morphological phenotypes may correspond more closely to those supported by the summary plastid DNA phylogenies, because the collective phenotypes are a proxy for more genes than the plastid DNA. Should this result not be realised, our classification will be adjusted appropriately. Additionally, further study will likely provide more evidence for past or ongoing episodes of hybridization and lineage sorting within and perhaps among elements of these subtribes.

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Appendix I.

Taxa, accessions sampled for DNA sequence variation, and GenBank accession numbers for sequences of three plastid-encoded genes. All sequences were obtained by the authors from the listed accessions, except for seven that were obtained from GenBank (for which GenBank accession numbers are listed in parentheses). Herbarium acronyms are as in Holmgren *et al.* (1990).

Taxon name	Accession information	*atpB*	*matK*	*ndhF*
Outgroups				
Diarrhena obovata (Gleason)	*J. I. Davis* 756 (BH) Brandenberg	DQ780979	DQ786905	DQ786833
Brachypodium pinnatum (L.) P. Beauv.	*J. I. Davis* 760 (BH); grown from USDA Plant Intr. Sta. 440170	DQ780965	DQ786891	AY622312
Bromus inermis Leyss.	*J. I. Davis* 762 (BH); grown from USDA Plant Intr. Sta. 314071	DQ780967	(AF164398)	DQ786821
Bromus suksdorfii Vasey	*R. J. Soreng* 7412 (US)	DQ780968	DQ786894	DQ786822
Elymus trachycaulus (Link) Gould ex Shinners	*R. J. Soreng* 4291b (BH)	DQ780984	DQ786910	DQ786838
Hordeum vulgare L.	No accession; all three sequences obtained from GenBank	(X00408)	(AB078138)	(U22003)
Littledalea tibetica Hemsl.	*R. J. Soreng* 5487; 5490; 5494 (US)	DQ780998	DQ786924	DQ786852
Triticum aestivum L.	No accession; all three sequences obtained from GenBank	(NC 002762)	(NC 002762)	(NC 002762)
Poeae s.l.				
Agrostis tenerrima Trin.	*R. J. Soreng 3734* (BH)	DQ780951	DQ786877	DQ786805
Aira caryophyllea L.	*R. J. Soreng 5953b* (US)	DQ780952	DQ786878	DQ786806
Aira cupaniana Guss.	*R. J. Soreng* s.n. (BH); grown from RBG, Kew, seed bank 27827 (K)	DQ780953	DQ786879	DQ786807
Alopecurus magellanicus Lam.	*R. J. Soreng* 3514 (BH)	DQ780954	DQ786880	DQ786808
Alopecurus textilis Boiss.	*R. J. Soreng* s.n. (BH); grown from USDA Plant Intr. Sta. 229431	DQ780955	DQ786881	DQ786809

Taxon name	Accession information	*atpB*	*matK*	*ndhF*
Amphibromus scabrivalvis (Trin.) Swallen	*R. J. Soreng* 7013 (US)	DQ780956	DQ786882	DQ786810
Aniselytron treutleri (Kuntze) Soják	*R. J. Soreng* 5229 (US)	DQ780957	DQ786883	DQ786811
Anthoxanthum odoratum L.	*R. J. Soreng* 4292 (BH)	DQ780958	DQ786884	DQ786812
Arctagrostis latifolia (R. Br.) Griseb.	*R. J. Soreng* 6016 (US)	DQ780959	DQ786885	DQ786813
Avena sativa L. 'ASTRO'	*J. I. Davis* 759 (BH)	DQ780960	DQ786886	DQ786814
Avenella flexuosa (L.) Drejer.	*R. J. Soreng* 7305b (US)	DQ780961	DQ786887	DQ786815
Avenula hookeri (Scribn.) Holub	*R. J. Soreng 6305* (US)	DQ780962	DQ786888	DQ786816
Beckmannia syzigachne (Steud.) Fernald	*R. J. Soreng 3513* (BH)	DQ780963	DQ786889	DQ786817
Bellardiochloa variegata (Lam.) Kerguélen	Grown from USDA Plant Intr. Sta. 253455; no voucher	DQ780964	DQ786890	DQ786818
Briza minor L.	*J. I. Davis* 761 (BH); grown from USDA Plant Intr. Sta. 378653	DQ780966	DQ786892	DQ786820
Calamagrostis arundinacea (L.) Roth	*R. J. Soreng* 7411 (US)	DQ780969	DQ786895	DQ786823
Calamagrostis canadensis Michx.	*R. J. Soreng* 7414 (US)	DQ780970	DQ786896	DQ786824
Calotheca brizoides (Lam.) Desv.	*R. J. Soreng* 7014 (US)	DQ780971	DQ786897	DQ786825
Catabrosa aquatica (L.) P. Beauv.	*R. J. Soreng* 3861 (BH)	DQ780972	DQ786898	DQ786826
Chascolytrum subaristatum (Lam.) Desv.	*R. J. Soreng* 7020 (US)	DQ780973	DQ786899	DQ786827
Cutandia memphitica (Spreng.) K. Richt.	*L. Boulos & T. Cope* 17676 (E)	DQ780974	DQ786900	DQ786828
Cynosurus cristatus L.	Grown from RBG, Kew, seed bank 39006 (K)	DQ780975	DQ786901	DQ786829
Dactylis glomerata L. subsp. *hackelii* (Asch. & Graebn.) Cif. & Giacom.	*R. J. Soreng* 3692 (BH)	DQ780976	DQ786902	DQ786830
Deschampsia cespitosa (L.) P. Beauv. subsp. *cespitosa*	*R. J. Soreng* 7417 (US)	DQ780977	DQ786903	DQ786831
Desmazeria sicula (Jacq.) Dumort.	*R. J. Soreng* s.n. (BH); grown from RBG, Kew, seed bank 17332 (K)	DQ780978	DQ786904	DQ786832
Dichelachne micrantha (Cav.) Domin	*R. J. Soreng 5901* (US)	DQ780980	DQ786906	DQ786834
Dielsiochloa floribunda (Pilg.) Pilg.	*P. M. Peterson et al.* 14566 (US)	DQ780981	DQ786907	DQ786835
Dupontia fisheri R. Br. (DAO)	*J. Cayouette & Y. Dalpé* C6779-4	DQ780982	DQ786908	DQ786836
Echinopogon caespitosus C.E. Hubb.	*R. J. Soreng* 5900 (US)	DQ780983	DQ786909	DQ786837
Festuca rubra L.	*R. J. Soreng* 7424 (US)	DQ780985	DQ786911	DQ786839
Festuca subverticillata (Pers.) E. B. Alexeev	*J. I. Davis* 754 (BH)	DQ780986	DQ786912	DQ786840

Taxon name	Accession information	*atpB*	*matK*	*ndhF*
Festucella eriopoda (Vickery) E. B. Alexeev	*S. Jacobs* 9128 (NSW)	DQ780987	DQ786913	DQ786841
Gastridium ventricosum (Gouan) Schinz & Thell.	Grown from RBG, Kew, seed bank 5430 (K)	DQ780988	DQ786914	DQ786842
Gaudinia fragilis (L.) P. Beauv.	*J. I. Davis* 764 (BH); grown from USDA Plant Intr. Sta. 442496	DQ780989	DQ786915	DQ786843
Gaudinia hispanica Stace & Tutin	*R. J. Soreng 3654* (BH, US)	DQ780990	DQ786916	DQ786844
Graphephorum wolfii (Vasey) Vasey ex Coult.	*R. J. Soreng* 7416 (US)	DQ780991	DQ786917	DQ786845
Gymnachne koelerioides (Trin.) Parodi	*R. J. Soreng* 7035 (US)	DQ780992	DQ786918	DQ786846
Helictotrichon convolutum (C. Presl) Henrard	*R. J. Soreng* 3803 (BH)	DQ780993	DQ786919	DQ786847
Helictotrichon mortonianum (Scribn.) Henrard	*R. J. Soreng* 7427 (US)	DQ780994	DQ786920	DQ786848
Holcus annuus Salzm. ex C. A. Mey.	*R. J. Soreng* 3642 (BH)	DQ780995	DQ786921	DQ786849
Hookerochloa hookeriana (F. Muell. ex Hook. f.) E. B. Alexeev	*S. Jacobs* 9127 (NSW)	DQ780996	DQ786922	DQ786850
Koeleria loweana Quintanar, Catalán & Castrov. (formerly *Parafestuca albida* (Lowe) E. B. Alexeev)	*M. Sequeira* 4033A (herbarium of the University of Zaragoza)	DQ781004	DQ786930	DQ786858
Leucopoa kingii (S. Watson) W. A. Weber	*R. J. Soreng* 3515 (BH)	DQ780997	DQ786923	DQ786851
Lolium perenne L.	*J. I. Davis* 765 (BH); grown from USDA Plant Intr. Sta. 418710	DQ780999	DQ786925	DQ786853
Lolium rigidum Gaudin	*R. J. Soreng* 3696 (BH)	DQ781000	DQ786926	DQ786854
Mibora minima (L.) Desv.	*J. A. Devesa* 3885 (BH)	DQ781001	DQ786927	DQ786855
Milium vernale M. Bieb.	*R. J. Soreng* 3748 (BH)	DQ781002	DQ786928	DQ786856
Molineriella laevis (Brot.) Rouy	*R. J. Soreng* 3613 (BH)	DQ781003	DQ786929	DQ786857
Parapholis incurva (L.) C. E. Hubb.	Grown from RBG, Kew, seed bank 24867 (K)	DQ781005	DQ786931	DQ786859
Phleum pratense L.	*R. J. Soreng* 4293 (BH)	DQ781006	DQ786932	DQ786860
Poa alpina L.	*R. J. Soreng* 6115-1 (US)	DQ781007	DQ786933	DQ786861
Poa andina Trin.	*R. J. Soreng* 7212 (US)	DQ781008	DQ786934	DQ786862
Poa billardierei St.-Yves	*P. M. Peterson et al. 14510* (US)	DQ781009	DQ786935	DQ786863
Podagrostis thurberiana (Hitchc.) Hultén	*R. J. Soreng 7419* (US)	DQ781010	DQ786936	DQ786864
Polypogon monspeliensis (L.) Desf.	*J. Rumely* s.n.; no voucher	DQ781011	DQ786937	DQ786865
Puccinellia distans (Jacq.) Parl.	*J. I. Davis* 755 (BH)	DQ781012	DQ786938	DQ786866
Rostraria pubescens (Desf.) Tzvelev	*R. J. Soreng* 3793 (BH)	DQ781013	DQ786939	DQ786867

Taxon name	Accession information	*atpB*	*matK*	*ndhF*
Schedonorus arundinaceus	*R. J. Soreng* 7437 (US) (Schreb.) Dumort.	DQ781014	DQ786940	DQ786868
Sclerochloa dura (L.) P. Beauv.	*R. J. Soreng* 3862 (BH)	DQ781015	DQ786941	DQ786869
Sesleria caerulea (L.) Ard.	*J. I. Davis* 768 (BH)	DQ781016	DQ786942	DQ786870
Sphenopus divaricatus	*R. J. Soreng* 3700 (BH) (Gouan) Rchb.	DQ781017	DQ786943	DQ786871
Torreyochloa pauciflora	*J. I. Davis* 533 (BH) (J. Presl) G. L. Church	DQ781018	DQ786944	DQ786872
Triplachne nitens (Guss.) Link	*R. J. Soreng* 3701 (BH)	DQ781019	DQ786945	DQ786873
Trisetum canescens Buckley	*R. J. Soreng* 3383a (BH)	DQ781020	DQ786946	DQ786874
Vahlodea atropurpurea (Wahlenb.) Fr. ex Hartm.	*R. J. Soreng* 6316 (US)	DQ781021	DQ786947	DQ786875
Vulpia microstachys (Nutt.) Munro	*R. J. Soreng* 7406 (US)	DQ781022	DQ786948	DQ786876

Appendix II.

A proposed subtribal classification of the genera of Poaceae subfamily Pooideae supertribe Poodae tribe Poeae, representing a revision of the tribal and subtribal classification of tribes Poeae, Aveneae, and Hainardieae as delimited by Clayton & Renvoize (1986; = C&R). The proposed assignments are based on analyses of plastid DNA variation and morphology, with taxa not sampled for plastid DNA assigned according to morphology (* = plastid DNA examined in this or another study).

Taxa with *Aveneae*-type plastid DNA or postulated to belong to this group on the basis of morphology.

subtribe Torreyochloinae *Soreng & J. I. Davis*[2,3]: **Amphibromus* Nees[4,5], **Torreyochloa* G. L.Church[3].

subtribe *Aveninae J. Presl*[6]: **Arrhenatherum* P. Beauv., *Avellinia* Parl.[6], **Avena* L., **Gaudinia* P. Beauv., *Gaudiniopsis* (Boiss.) Eig, **Graphephorum* Desv., **Helictotrichon* Besser ex Schult. & Schult. f. *s.s.*, **Koeleria* Pers., **Lagurus* L.[7], *Leptophyllochloa* C. E. Calderón ex Nicora[8], *Peyritschia* E. Fourn., **Rostraria* Trin., **Sphenopholis* Scribn., **Trisetaria* Forssk., **Trisetum* Pers[9].

subtribe Cininae *Caruel*[7]: **Cinna* L.[7] *Limnodea* Dewey[7]

subtribe Phalaridinae *Fr.*[10]: **Anthoxanthum* L., **Phalaris* L.

subtribe Brizinae *Tzvelev*[3]: *Airopsis* Desv.[5], **Briza* L.[3], **Calotheca* Desv.[11], **Chascolytrum* Desv.[11], **Erianthecium* Parodi[3], **Gymnachne* Parodi[12], **Poidium* Nees[13], *Relchela* Steud.[5], *Rhombolytrum* Link.[3]

subtribe Agrostidinae *Fr.*[7]: **Agrostis* L.[7], **Ammophila* Host[7], *Ancistragrostis* S. T. Blake[7], *Bromidium* Nees & Meyen[14], **Calamagrostis* Adans.[7], **Chaetopogon* Jaubert[7], *Cyathopus* Stapf[7], **Gastridium* P. Beauv.[7], *Hypseochloa* C. E. Hubb.[7], **Lachnagrostis* Trin.[14], **Podagrostis* (Griseb.) Scribn. & Merr.[14], **Polypogon* Desf.[7], **Triplachne* Link[7], **Dichelachne* Endl.[7], **Echinopogon* P. Beauv.[7], *Pentapogon* R. Br.[7], *Simplicia* Kirk[7].

Taxa with *Poeae*-type plastid DNA or postulated to belong to this group on the basis of morphology.

subtribe Coleanthinae *Rouy*[3]: *Coleanthus* Seidl[3].

subtribe Miborinae *Asch. & Graebn.*[7]: **Mibora* Adans[7].

subtribe Scolochloinae (*Tzvelev*) *Tzvelev*[3]: **Scolochloa* Link.

subtribe Airinae *Fr.*[5]: **Aira* L.[5], **Avenella* Parl.[15], **Avenula* (Dumort.) Dumort.[4], **Corynephorus* P. Beauv.[5], **Deschampsia* P. Beauv.[5] *s.s.*, **Holcus* L.[5], **Molineriella* Rouy[16], *Periballia* Trin.[5], **Vahlodea* Fr.[15]

subtribe Ammochloinae *Tzvelev*[3]: *Ammochloa* Boiss.

subtribe Cynosurinae *Fr.*[3]: **Cynosurus* L.

subtribe Dactylidinae *Stapf*[8]: **Dactylis* L., **Lamarckia* Moench.

subtribe Loliinae *Dumort.*[3]: **Castellia* Tineo, **Ctenopsis* De Not.[17] **Dielsiochloa* Pilg.[5], **Drymochloa* Holub.[18], **Dryopoa* Vickery, **Festuca* L., **Leucopoa* Griseb.[18], **Loliolum* V. I. Krecz. & Bobrov, **Lolium* L., **Micropyropsis* Romero Zarco & Cabezudo, **Micropyrum* (Gaudin) Link, **Narduroides* Rouy[19], *Pseudobromus* K. Schum.[18], **Psilurus* Trin.[19], **Schedonorus* P. Beauv.[18], **Vulpia* C. C. Gmel., **Vulpiella* (Batt. & Trab.) Burollet, *Wangenheimia* Moench.

subtribe Parapholiinae *Caro*[19]: *Agropyropsis* (Trab.) A. Camus[19], **Catapodium* Link[3], **Cutandia* Willk.[3], **Desmazeria* Dumort.[3], **Hainardia* Greuter[19], **Parapholis* C. E. Hubb.[19], *Pholiurus* Host ex Trin.[19], **Scleropoa* Griseb.[3], **Sphenopus* Trin.[3].

subtribe Scribneriinae *Soreng & J. I. Davis*[2]: **Scribneria* Hack[19].

subtribe Sesleriinae *Parl*[3]: **Echinaria* Desf., *Oreochloa* Link, **Sesleria* Scop., *Sesleriella* Deyl.[20]

subtribe *incertae sedis*: *Antinoria* Parl.[5]

subtribe Puccinelliinae *Soreng & J. I. Davis*[2]: **Catabrosa* P. Beauv.[3], *Catabrosella* (Tzvelev) Tzvelev[21], *Oreopoa* H. Scholz[2], **Paracolpodium* (Tzvelev) Tzvelev[21], **Phippsia* (Trin.) R. Br.[3], *Pseudosclerochloa* Tzvelev[27], **Puccinellia* Parl.[3], **Sclerochloa* P. Beauv[3].

subtribe Alopecurinae *Dumort.*[5]: **Alopecurus* L.[5], **Beckmannia* Host[5], *Cornucopiae* L.[5], *Limnas* Trin.[5], **Phleum* L.[5], *Pseudophleum* Do?an[22], *Rhizocephalus* Boiss[5].

subtribe Miliinae *Dumort.*[23]: **Colpodium* Trin.[3], **Milium* L.[23], **Zingera* P.A.Smirn[5].

subtribe Poinae *Dumort.*[3]: * *Aniselytron* Merr.[24], **Anthochloa* Nees & Meyen[25, 28], **Apera* Adans.[7], **Aphanelytrum* Hack., **Arctagrostis* Griseb., **Arctophila* (Rupr.) Rupr. ex Andersson, **Arctopoa* (Griseb.) Prob., **Austrofestuca* (Tzvelev) E. B. Alexeev[28], **Bellardiochloa* Chiov.[13], **Dissanthelium* Trin.[5, 28], **Dupontia* R. Br., **Festucella* E. B. Alexeev[2,26], **Hookerochloa* E. B. Alexeev[2,26], *Hyalopoa* (Tzvelev) Tzvelev[21], *Libyella* Pamp., *Lindbergella* Bor, *Nephelochloa* Boiss., *Neuropoa* Clayton, **Poa* L., **Tovarochloa* T. D. Macfarl. & But[5, 28], *Tzvelevia* E. B. Alexeev[2], *Ventenata* Koeler[5].

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[1] The following footnotes (except 2 and 28, the latter of which refers to taxa proposed for inclusion within *Poa*), describe the placement of taxa by Clayton & Renvoize (1986), where they differ substantially from that in the present treatment. [2]Taxon published nearly simultaneously with or after Clayton & Renvoize. [3]Placed in tribe *Poeae* (Clayton & Renvoize did not recognise any subtribes in tribe *Poeae*). [4]Placed in *Helictotrichon*. [5]Placed in *Aveneae* subtribe *Aveninae*. [6]Placed in *Trisetaria*. [7]Placed in *Aveneae* subtribe *Alopecurinae*. [8]Placed in *Koeleria*. [9]The species used here was placed in *Helictotrichon*. [10]Placed in *Aveneae* subtribe *Phalaridinae*. [11]Placed in *Briza*. [12]Placed in *Rhombolytrum*. [13]Placed in *Poa*. [14]Placed in *Agrostis*. [15]Placed in *Deschampsia*. [16]Placed in *Periballia*. [17]Placed in *Vulpia*. [18]Placed in *Festuca*. [19]Placed in tribe *Hainardieae*. [20]Placed in *Sesleria*. [21]Placed in *Colpodium*. [22]Placed in *Phleum*. [23]Placed in *Stipeae*. [24]Placed in *Calamagrostis*. [25]Placed in tribe *Meliceae*. [26]Placed in *Austrofestuca*. [27]Placed in *Puccinellia*. [28]Belongs within *Poa*.

Appendix III.

Character and state definitions for eighteen morphological and anatomical features (characters 1 – 18) and seven plastid DNA structural features (characters 19 – 25) as scored for representative taxa of *Poaceae* tribe *Poeae sensu lato* and outgroups (tribes *Brachypodieae, Bromeae, Diarrheneae*, and *Triticeae*; cf. Appendix I). Multiple states [in brackets] signify polymorphism or subset ambiguity (i.e., cases in which the observed feature is potentially assignable to two or more recognised states). Data sources: ASH = Hitchcock (1935), FE = Tutin *et al.* (1980), G&C = Gleason & Cronquist (1991), pers. obs. = Soreng or Davis (based on US, K, or BH specimens), TZ = Tzvelev (1976, 1983), W&D = Watson & Dallwitz (1992), WGF = Clayton *et al.* (2002). The three numbers immediately following each character number are the number of steps (LC), consistency index (CI), and retention index (RI), respectively, on most-parsimonious trees obtained by the combined analysis. For morphological and anatomical characters, the fourth number or range (LM) is the number or range in number of steps on most-parsimonious trees obtained by the morphological analysis. Additional steps implied by polymorphism within terminals are not included in the calculation of these numbers.

1: (LC 6; CI 16; RI 16; LM 2 – 5) Sheath margins of culm leaves free versus fused: 0 = free or fused basally; 1 = fused at least 1/4 of length (previously scored for any shoots, here only for culms). *Festuca rubra* = 0 (has fused sterile shoot sheaths, but open culm sheaths). *Elymus* = 0 (has partially fused sterile shoot sheaths, but open culm sheaths). *Helictotrichon* = 0 (as differentiated from *Avenula*). *Poa alpina* = 1 (*Poa* is variable [01]). *Puccinellia distans* = 0 (some other *Puccinellia* are [01]).

2: (LC 6; CI 16; RI 44; LM 3 – 4) Branching of inflorescence (exclusive of pedicels): 0 = absent (i.e.; spike or raceme or individual spikelets); 1 = present (i.e. panicle). *Brachypodium pinnatum* = 0 (W&D give as "rarely paniculate", but this is absent, or too rare to be of consequence, at least in our species, as it is not mentioned in FE or WGF).

3: (LC 6; CI 16; RI 16; LM 4 – 5) Disarticulation above glumes: 0 = absent; 1 = present (any disarticulation sufficient even if not above both glumes).

4: (LC 2; CI 50; RI 0; LM 1 – 2) Proximal female-sterile florets in female-fertile spikelets: 0 = absent; 1 = present.

5: (LC 13; CI 15; RI 54; LM 6 – 7) Number of female-fertile florets in female-fertile spikelets: 1 = one; 2 = two; 4 = two or more and variable.

6: (LC 11; CI 9; RI 37; LM 3 – 7) Central awn on lemma: 0 = absent; 1 = present. *Diarrhena obovata* = [01] (The species is sometimes called 'mucronate' W&D, or sharply pointed ASH. The mucronate apex is entered by lateral veins (teste G&C, and pers. obs.), and is called a cusp by G&C. However, TZ called the tribe awnless). *Trisetum canescens* = 1 (with removal of *Graphephorum*, *Trisetum* is rarely unawned). *Graphephorum wolfii* = [01] (usually without an awn, infrequently with a short awn to 1 mm). *Anthoxanthum odoratum* = [01] (the developed sterile lemma is awned, the fertile lemma unawned). *Chascolytrum subaristatum* = [01] (this species sometimes produces a slightly subapical mucro).

7: (LC 9; CI 11; RI 65; LM 2 – 3) Central awn attachment: 0 = terminal or subterminal (these two conditions are treated as a single state, with subterminal applying to cases in which magnification is required to determine that an awn is not strictly terminal); 2 = dorsal; 3 = from a minute notch; among the sampled taxa this state occurs only as a subset ambiguity, and does not correspond to the well-developed sinus that occurs, e.g., in *Danthonia* DC.). Inapplicable if state of character 6 is 0.

8: (LC 9; CI 11; RI 33; LM 1) Central awn shape: 0 = straight or sinuous; 1 = geniculate or bigeniculate. Inapplicable if state of character 6 is 0.

9: (LC 3; CI 33; RI 33; LM 1 – 2) Lodicules in female fertile florets: 0 = absent; 1 = present.

10: (LC 15; CI 6; RI 26; LM 6 – 9) Lodicule lateral lobing if membranous: 0 = absent; 1 = present. Inapplicable if state of character 9 is 0, or if lodicules are present but extremely minute.

11: (LC 6; CI 16; RI 37; LM 3 – 5) Lodicule cilia: 0 = absent (i.e.; glabrous); 1 = present. Inapplicable if state of character 9 is 0.

12: (LC 2; CI 50; RI 50; LM 1 – 2) Ovary appendage: 0 = absent; 1 = present.

13: (LC 10; CI 10; RI 50; LM 3 – 6) Ovary pubescence: 0 = absent (i.e.; glabrous); 1 = present.

14: (LC 3; CI 33; RI 33; LM 3) Styles fused for some portion of the length: 0 = absent (i.e.; free to base); 1 = present.

15: (LC 14; CI 7; RI 38; LM 3 – 6) Fruit sulcus: 0 = absent or barely developed; 1 = present and shallow or deep.

16: (LC 8; CI 12; RI 69; LM 3 – 5) Hilum shape: 0 = nonlinear (or less than $^1/_3$ the grain); 1 = linear short ($^1/_3$ or more of the grain) or linear long.

17: (LC 3; CI 33; RI 71; LM 3 – 4) Starch compound grains: 0 = absent (i.e.; simple grains only); 1 = present. Usually scored for the genus. *Festuca subverticillata* = [01] (W&D state for *Festuca* "containing compound starch grains (mostly?), containing only simple starch grains (e.g. *F. paradoxa*)." As *F. paradoxa* is closely related to our species, which we do not know to have been examined, the character is scored as polymorphic in the genus.

18: (LC 6; CI 16; RI 66; LM 3 – 4) Endosperm lipid: 0 = absent; 1 = present. This is often reported in the literature for the species we sampled, but if not, and if it is not reported by W&D as variable for a given genus it is scored here as for the genus. For some species, soft or liquid endosperm was taken as diagnostic for lipid. For a few species, translucent-appearing caryopses were taken as diagnostic, because lipids have a 'clearing' effect (i.e., *Helictotrichon s.s.*, *Podagrostis* and *Vahlodea*), whereas caryopses of species in genera reportedly lacking lipid are opaque and appear dry.

19: (LC 2; CI 50; RI 0) 3 bp inversion in *ndhF* at sites corresponding to nucleotides 1918 – 1920 in *Triticum aestivum* reference sequence: 0 = absent (sequence is GTA or modification); 1 = present (sequence is TAC or modification).

20: (LC 1; CI 100; RI 100) 6bp inversion in *ndhF* at sites corresponding to nucleotides 1932 – 1937 in *Triticum aestivum* reference sequence: 0 = absent (sequence is GAAAAA or modification); 1 = present (sequence is TTTTTC or modification.

21: (LC 2; CI 50; RI 0) 6 bp indel in *ndhF* region just after nucleotide 1487 in *Triticum aestivum* reference sequence: 0 = nucleotides absent; 1 = nucleotides present.

22: (LC 2; CI 50; RI 0) 6 bp indel in *ndhF* region just after nucleotide 1494 in *Triticum aestivum* reference sequence: 0 = nucleotides absent; 1 = nucleotides present.

23: (LC 1; CI 100; RI 100) 6 bp indel in *ndhF* region just after nucleotide 1947 in *Triticum aestivum* reference sequence: 0 = nucleotides absent; 1 = nucleotides present.

24: (LC 1; CI 100; RI 100) 6 bp indel in *matK* region just after nucleotide 364 in *Triticum aestivum* reference sequence: 0 = nucleotides absent; 1 = nucleotides present.

25: (LC 1; CI 100; RI 100) 27bp indel in *atpB* region just after nucleotide 177 in *Triticum aestivum* reference sequence: 0 = nucleotides absent; 1 = nucleotides present.

Appendix IV.

Primers used to amplify and sequence three plastid-encoded genes. Primers specific to sites within each gene, as well as those specific to sites within neighbouring genes and gene fragments (see text), were utilised as follows: *atpB* (*atpE*); *matK* (*trnK*); *ndhF* (*ndhH*, *rps15*). Each primer name consists of 1) the name of the gene to which it is specific, 2) the numerical position of the corresponding nucleotide that is closest to the 5′ end of the gene in the plastid genome sequence of *Triticum aestivum* (GenBank accession number *NC_002762*), regardless of the direction in which the primer reads, and 3) a letter (F = forward; R = reverse) designating the direction in which the priming function proceeds, relative to the direction in which the gene is transcribed. Primers were developed by the authors, except as indicated.

	Primer sequence
atpB	
atpB 1F (modified from Hoot *et al.* 1995)	5′ – tat gag aac caa tcc tac tac ttc t – 3′
atpB 358F	5′ – aat ttg ggt cct gta gat aSt agt gc – 3′
atpB 819F	5′ – taa tat ctt tcg ttt tgt tca agc ag – 3′
atpB 354R	5′ – taS tat cta cag gac cca aat tgt ca – 3′
atpB 429R	5′ – cWg ttt caa aga tgg ata att tcg ta – 3′
atpB 470R	5′ – cac gYc gat aag gag cta aaa gat – 3′
atpB 906R	5′ – tgc aaa gaa ccc att tct gta cta – 3′
atpB 979R	5′ – caa atc gtc Ygc agg tac ata aac – 3′
atpB 1254R	5′ – ttt ttc Ktg ctc ttg cta cag tta aa – 3′
atpB 1318R	5′ – tac ttt ccY gga gaa ccR gta aaa ac – 3′
atpB 1494R (modified from Hoot *et al.* 1995)	5′ – tca gta cat aaa gat tta att tca t – 3′
atpE 118R	5′ – gga ccc ata tct acW gct gtg tta at – 3′
atpE 196R	5′ – tca tta tta act att ctS gca aaa cc – 3′
matK	
trnK 43F	5′ – Rct atg atc ttt tac aca ttt gga tga a – 3′
matK 24F	5′ – att gYa cta tgt atc aYc att Yga taa a – 3′
matK 73F	5′ – ctR Wtt caa gta gaa ata caa atg gaa a – 3′
matK 315F	5′ – ggt taa tYa tcc taa cca aga tcg – 3′
matK 628F	5′ – cat tta ttg cga ttt ctt ctc aac ta – 3′
matK 922F	5′ – ctt atR cat tat gtt cga tat caa gg – 3′
matK 1066F	5′ – aac caa tta RMa aac tct tgc ttc – 3′
matK 463R	5′ – gag cgt aaa ttc tga aaY ttK ggt at – 3′
matK 791R	5′ – aKa tgM taa tgg taa gca aga aga tt – 3′
matK 1228R	5′ – cca gta caa aat tga gct ttt gat aa – 3′
matK 1588R	5′ – acc agg tcR ttg atW cSt ata ata tc – 3′
matK 1574R	5′ – ata cgg aKa ata tcc aaa tac caa ata c – 3′
trnK 2499R	5′ – gga tgg agt aga taa tta ttc ctt gtt a – 3′
ndhF	
ndhF 1F (Olmstead & Sweere 1994)	5′ – atg gaa caK aca tat Saa tat gc – 3′
ndhF 45F	5′ – act tcc agt tat tat gtc aat ggg Rtt t – 3′
ndhF 274F (modified from Olmstead & Sweere 1994)	5′ – ctt act tct att atg tta ata cta at – 3′
ndhF 309F	5′ – Wgg aaY Yat ggt tct tat tta tag tga c – 3′
ndhF 532F	5′ – gcK ttt Dta act aat cgt gta ggg ga – 3′
ndhF 818F	5′ – gaa ttt ttc ttV tag ctc gag ttY ttc – 3′
ndhF 933F	5′ – tca Rag aga tat taa aag aag Ytt agc c – 3′
ndhF 978F	5′ – att ggg tta tat gat gtt agc tct agg t – 3′
ndhF 1194F	5′ – ttt att ggg tac act ttc tct ttg tg – 3′
ndhF 1318F (modified from Olmstead & Sweere 1994)	5′ – gga tta act gcV ttt tat atg ttt cg – 3′
ndhF 1421F	5′ – att caa tat cSt tat ggg gaa aaa g – 3′
ndhF 1811F	5′ – tac agt tgg tca tat aat cgY ggt t – 3′