American Journal of Botany 94(9): 1554–1569. 2007.

PHYLOGENY OF THE TRIBE AVENEAE (POOIDEAE, POACEAE) INFERRED FROM PLASTID *TRNT-F* AND NUCLEAR ITS SEQUENCES[1]

ALEJANDRO QUINTANAR,[2,4] SANTIAGO CASTROVIEJO,[2] AND PILAR CATALÁN[3]

[2]Real Jardín Botánico de Madrid, CSIC, Madrid, Spain; and
[3]Escuela Politécnica Superior de Huesca, Universidad de Zaragoza, Zaragoza, Spain

New insights into evolutionary trends in the economically important oat tribe (Aveneae) are presented. Plastid *trnT-F* and nuclear ribosomal ITS sequences were used to reconstruct the phylogeny of the Aveneae–Poeae–Seslerieae complex (Pooideae, Poaceae) through Bayesian- and maximum parsimony-based analyses, separately and in combination. The plastid data identified a strongly supported core Aveneae lineage that separated from other former Aveneae and Poeae groups. Koeleriinae, Aveninae, and Agrostidinae emerged as the main groups of this core Aveneae, which also included other minor subgroups with uncertain relationships and a few former Poeae members. Several former Aveneae representatives were also placed in independent sublineages in Poeae. Seslerieae resolved as close allies of Poeae or Aveneae in the plastid and nuclear topologies, respectively. Because of the intermingling of some Aveneae and Seslerieae lineages in Poeae and vice versa, we propose to expand Poeae to include all the aforementioned lineages. This best reflects our current understanding of the phylogeny of these important temperate grasses and sheds light on their evolutionary history.

Key words: Aveneae; grass systematics and evolution; molecular phylogenetics; plastid and nuclear DNA sequence data; Poeae; Pooideae; Seslerieae.

The oat tribe, Aveneae Dumort. (including Agrostideae Dumort.), is the second largest tribe in subfamily Pooideae Benth. and is one of the main groups of the grass family [Poaceae (R. Br.) Barnhart]. It includes the economically important oats, one of the most ancient food supplies for humankind, and many of the most abundant grasses of temperate ecosystems. It comprises about 57 genera and 1050 species (Clayton and Renvoize, 1986) that inhabit temperate-to-arctic regions throughout the world (Stebbins, 1956; Stebbins and Crampton, 1961; Clayton, 1975, 1981; MacFarlane and Watson, 1980, 1982; Clayton and Renvoize, 1986; MacFarlane, 1987; Watson and Dallwitz, 1992). Traditionally, the Aveneae have been characterized by morphologic traits related to their archtypical spikelet form of long glumes (relative to spikelet length) and a tendency toward a reduced number of flowers per spikelet, commonly 1, 2, or 2–3 per spikelet. Other, apparently derived, features of Aveneae include a soft endosperm with lipid energy reservoirs, which presumably has adaptive value. Most of these features have been interpreted as resulting from evolutionary trends that have yielded highly specialized taxa (Clayton and Renvoize, 1986; Röser, 1997).

Another remarkable feature of the tribe is the inclusion of a large radiation of annual genera, mostly in the pan-Mediterranean region, adapted to arid conditions and disturbance. These annual species usually colonize ephemeral, often-disturbed habitats, whereas most of the perennial taxa grow in temperate grassland formations in natural, less-disturbed areas (Clayton and Renvoize, 1986; Röser, 1997).

Aveneae classification and its taxonomical borders with its sister tribe Poeae R. Br. have varied historically depending on an author's interpretations of the tribe's morphologic heterogeneity; consequently, the adscription of many of its genera has been problematical (Table 1). In modern classifications, Aveneae have been separated from Poeae (and partly from Seslerieae Koch) based on the floral traits cited (Tzvelev, 1976; MacFarlane and Watson, 1982; Clayton and Renvoize, 1986; Watson and Dallwitz, 1992). Tzvelev (1989), however, did not recognize Aveneae but transferred their members to the large tribe Poeae, although Phleeae Dumort. (including Phalarideae Kunth) was separated from Poeae. An increasing number of phylogenetic studies in recent decades have helped to clarify evolutionary relationships within the subfamily Pooideae (Soreng et al., 1990; Davis and Soreng, 1993; Nadot et al., 1994; Hsiao et al., 1995; Catalán et al., 1997; GPWG, 2001). However, the details of the phylogeny of Aveneae have remained largely unexplored. Most phylogenetic surveys related to the avenoids have focused on particular genera, like *Helictotrichon* (Grebenstein et al., 1998), *Avena* (Rodionov et al., 2005), *Arrhenatherum* (S. Nisa et al., unpublished data), and *Deschampsia* (Chiapella, 2007).

The first phylogenetic study with a large sampling of Aveneae taxa was by Soreng and Davis (2000), who also explored the relationships of its sister tribe Poeae. Their combined analysis of plastid restriction site data and structural data resulted in a consensus topology where the sister divergence of the main Aveneae and Poeae lineages was blurred by several admixtures of misplaced genera of the opposite tribe. Genera traditionally classified in Poeae, such as *Briza*, *Chascolytrum* Desv., *Poidium* Nees, and *Torreyochloa* G. L. Church, were resolved as closely related to different Aveneae lineages. Conversely, other genera formerly recognized as Aveneae, like *Avenula*, *Alopecurus*, *Holcus*, and *Phleum*, were nested within different clades of Poeae. Finally, Soreng and Davis placed Aveneae within Poeae and recog-

[1] Manuscript received 26 June 2006; revision accepted 11 July 2007.

The authors thank J. Müller, R. Soreng, and C. Stace for valuable comments and revision of an earlier version of the manuscript; L. A. Inda, E. Pérez, M. Pimentel, and J. G. Segarra for their support and assistance in the laboratory; and J. Müller, P. M. Peterson, M. Pimentel, M. Sequeira, R. J. Soreng, and the curators of the JACA, MA, and US herbaria for providing fresh samples and herbarium materials for the analyses. This work was subsidized by the Ministerio de Ciencia y Tecnología of Spain (projects REN2003-02818/GLO and REN2002-04634-C05-05).

[4] Author for correspondence (e-mail: quintanar@rjb.csic.es)

nized a series of subtribes of Aveneae that were later expanded (Soreng et al., 2003). Past intertribal hybridization events were advocated as a plausible explanation for the present existence of certain Avenae taxa with Poeae plastid genomes and vice versa, while most other cases were attributed to traditional misclassifications (Soreng and Davis, 2000). The systematic and evolutionary placement of the tribe Seslerieae with respect to Aveneae and Poeae has also been debated (Table 1). Seslerieae includes several genera characterized by their strongly condensed inflorescences, often subtended by glume-like bracts. The few molecular studies on single representatives of *Sesleria* (Soreng and Davis, 2000; Catalán et al., 2004; Gillespie et al., 2006) indicated that this genus was close to either Aveneae or Poeae, but the relationships were not satisfactorily resolved. Duthieinae Potzal, which was subsumed by Clayton and Renvoize (1986) under Aveneae but is characterized by primitive traits such as havingthree lodicules and three stigmas, was considered distantly related to Pooideae but rather close to Arundinoideae Burmeist. (Watson and Dallwitz, 1992) or Stipeae Dumort. (Soreng et al., 2003).

There is a current and increasing interest in the boundaries of Aveneae and the evolutionary relationships among Aveneae lineages and the closely allied Poeae and Seslerieae. Consequently, we initiated an extended phylogenetic survey of these groups using nuclear and plastid data. In the present study, we include 42 genera of Aveneae (56% of its generic diversity sensu Watson and Dallwitz, 1992) and three genera of Seslerieae. Of the main Poeae lineages, 20 genera are included (32% of the total). Our phylogenetic reconstructions are based on analyses of DNA sequences from both the plastid *trnT-F* region and the nuclear ribosomal ITS region (ITS1–5.8S-ITS2). Use of nuclear and organellar phylogenies is recognized as a reasonably sound approach for understanding the history of groups that have presumably experienced reticulate evolution (Soltis and Kuzoff, 1995). The value of sequences of the plastid *trnT-F* region (*trnT-L* spacer and the useful *trnL* intron–*trnL* 3′ exon–*trnL-F* spacer) for resolving phylogenetic relationships was shown in the separation of the main lineages of the large subtribes Loliinae Dumort. (Torrecilla et al., 2004; Catalán et al., 2004) and Poinae Dumort. (Brysting et al., 2004; Hunter et al., 2004) of Poeae. The ITS region has also been shown to be informative for phylogenetic inference in several Aveneae (*Helictotrichon*, Grebenstein et al., 1998; *Avena*, Rodionov et al., 2005; *Deschampsia*, Chiapella, 2007) and in the subtribe Loliinae of Poeae (Charmet et al., 1997; Gaut et al., 2000; Torrecilla and Catalán, 2002; Torrecilla et al., 2004; Catalán et al., 2004), mostly because of its biparental inheritance, the coupled effect of concerted evolution (Baldwin et al., 1995), and a moderate rate of mutation (Torrecilla and Catalán, 2002) in temperate-climate grasses. By separate and combined analysis of data from these two independent genomic sources, we aim to reconstruct a phylogeny that can be used as a baseline to interpret the evolutionary trends of the highly relevant but inadequately explored oat tribe.

MATERIALS AND METHODS

Plant material—Sampling was designed to be representative of the taxonomic/phenotypic diversity in the Aveneae tribe and included 105 species and subspecies of 42 genera from the main lineages thought to belong to this tribe (Watson and Dallwitz, 1992). Generic representatives of all subtribes of Aveneae recognized by Tzvelev (1976) and by Clayton and Renvoize (1986) (except Duthieinae) were sampled and incorporated into the analysis. Our sampling includes representatives from subtribes Airinae Fr., Agrostidinae Fr., Alopecurinae Dumort., Anthoxanthinae A. Gray, Aveninae J. Presl, Beckmanniinae Nevski, Gaudiniinae Holub, Holcinae Dumort., Koeleriinae Asch. & Graebn., Miliinae Dumort., Phalaridinae Fr., Phleinae Dumort., and Ventenatinae Holub (Appendix). The poorly studied subtribe Koeleriinae was more exhaustively sampled in our study with a wide representation of the *Koeleria* and *Trisetum* taxa, as well as representatives of their supposedly allied genera *Avellinia, Dielsiochloa*, *Graphephorum, Rostraria, Sphenopholis*, and *Ventenata*. Sampling of the sister tribe Poeae (32 taxa, 20 genera) included representatives of the main lineages of this group, i.e., the subtribes Loliinae and its close allies Parapholiinae Caro, Cynosurinae Fr., and Dactylidinae Stapf, and Poinae and its close ally Puccinelliinae Soreng & J. I. Davis, for which new sequences were provided (Appendix), plus other lineages with an unexpectedly close relation to Aveneae (*Briza*) or an uncertain attribution and relationships (*Anthochloa*, *Catabrosa*, *Cinna*, *Scolochloa*, etc.) (Table 1). Representatives of Seslerieae (Tzvelev, 1976) (Table 1) also were included in our survey (three genera, four taxa; Appendix). Our systematic scheme follows the tribal and subtribal circumscriptions proposed by Tzvelev (1976) and Watson and Dallwitz (1992), and the generic ordering of Tutin et al. (1980).

DNA isolation, amplification, and sequencing—Leaf tissue from either fresh silica-gel-dried materials or herbarium vouchers was ground to powder in liquid nitrogen. Total DNA was isolated from each sample following the procedures of the DNeasy Plant Mini Kit (Qiagen (Qiagen group, F. Hoffmann—Spain Izasa S.A.)). The plastid *trnT-F* was amplified and sequenced separately for the *trnT-L* and *trnL-F* subregions using external primer pairs *a*-forward/*b*-reverse and *c*-forward/*f*-reverse, respectively, as described by Taberlet et al. (1991). The primer pair combination *fern*-forward/*f*-reverse (Torrecilla et al., 2003) also was used for *trnL-F* amplification. Fifty-microliter PCR reactions were prepared with 5 μL 10× buffer, 5 μL $MgCl_2$ (3 mM), 2 μL dNTPs (10 mM), 1 μL forward primer (50 μM), 1 μL reverse primer (50 μM), 34.5 μL ddH_2O, 0.5 μL Taq (1.5 u), and 1 μL DNA. Amplifications were performed as follows: one denaturing cycle of 60 s at 94°C; 30 cycles including a 15-s denaturing at 94°C, a 30-s annealing at 45°C, and a 60-s extension at 72°C; followed by a termination step of 7 min at 72°C. The ITS region (ITS1–5.8S-ITS2) was amplified and sequenced using the external primer pair combinations KRC-forward/ITS4-reverse and ITS1-forward/ITS4-reverse (Torrecilla and Catalán, 2002). Fifty-microliter PCR reactions were prepared in a reaction mix that consisted of 5 μL 10× buffer, 2 μL $MgCl_2$ (3 mM), 2.5 μL dNTPs (0.5 mM), 1.25 μL forward primer (50 μM), 1.25 μL reverse primer (50 μM), 36.7 μL ddH_2O, 0.3 μL *Taq* polymerase (1.5 u), and 1 μL DNA. Amplifications were carried out under the following conditions: one denaturing cycle of 3 min at 94°C; 35 cycles of a 1-min denaturing at 94°C, a 1-min annealing at 50°C, and a 1-min extension at 72°C; followed by a termination step of 7 min at 72°C. All PCR products were purified with the QIAquick PCR Purification Kit (Qiagen). When more than one PCR band was recovered, the suitable amplified band was separated on 1% agarose gels, excised, and purified using the QIAquick Gel Extraction Kit (Qiagen). Clean PCR products were sequenced with the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems). Five-microliter sequencing reactions were prepared with 1.5 μL 5× sequencing buffer, 1 μL sequencing mix, 1 μL primer, 1.5 μL ddH2O, and 5 μL purified DNA. PCR was performed with one denaturing cycle of 1 min at 95°C; 99 cycles of 10-s denaturing at 95°C, a 5-s annealing at 50°C, and a 4-s extension at 60°C; then a termination step of 4 min at 60°C.

Sequence alignments and phylogenetic analyses—The *trnT-F*, *trnL-F*, and ITS sequences were aligned separately using the program ClustalX, version1.83 (Thompson et al., 1997). Manual alignment was further performed on each data matrix with the aid of the program Se-Al v. 2.0a11 (Rambaud, 1996). The boundaries of the plastid *trnL-F* region and the nuclear ITS region were determined according to those established by Catalán et al. (2004) for the subtribe Loliinae, and the boundaries of the plastid *trnT-F* region were determined according to those established by Mason-Gamer et al. (2002) for the tribe Triticeae Dumort. The concatenated *trnT-F* and *trnL-F* data sets were united into a single *trnT-F* plastid data matrix of taxa common to the two separate data matrices. A total of 75 new ITS sequences (GenBank accession numbers DQ336815–336834 and DQ539562–539616), 97 new *trnT-L* (DQ336855–336880, DQ367404–367407, and DQ631481–631547), and 73 new *trnL-F* sequences (DQ336835–336854 and DQ631428–631480) were generated for this study. Another 67 ITS and 26 *trnL-F* sequences were

TABLE 1. Placement of the Aveneae and Seslerieae representatives included in our study in selected classification systems.

Ascherson and Graebner (1898–1902)	Maire et al. (1953)	Prat (1960)	Tzvelev (1976)	Tutin et al. (1980)	Clayton and Renvoize (1986)	Watson and Dallwitz (1992)	Soreng et al. (2003)
Aveneae	**Aveneae**	**Aveneae**	**Aveneae**	**Aveneae**	**Aveneae**	**Aveneae**	**Poeae**
	Airinae		**Airinae**		**Aveninae**		**Airinae**
Aira	*Aira*	*Aira*	*Aira*	*Aira*	*Aira*	*Aira*	*Aira*
Corynephorus		*Corynephorus*	*Corynephorus*	*Corynephorus*	*Corynephorus*	*Corynephorus*	*Corynephorus*
Deschampsia		*Deschampsia*	*Deschampsia*	*Deschampsia*	*Deschampsia*	*Deschampsia*	
			Holcinae				**Holcinae**
Holcus		*Holcus*	*Holcus*	*Holcus*	*Holcus*	*Holcus*	*Holcus*
Airopsis	*Airopsis*	*Airopsis*		*Airopsis*	*Airopsis*	*Airopsis*	
Periballia	*Periballia*	*Periballia*		*Periballia*	*Periballia*	*Periballia*	
Antinoria	*Antinoria*				*Antinoria*	*Antinoria*	
	Aveninae		**Aveninae**				**Aveninae**
Arrhenatherum	*Arrhenatherum*	*Arrhenatherum*	*Arrhenatherum*	*Arrhenatherum*	*Arrhenatherum*	*Arrhenatherum*	*Arrhenatherum*
Avena	*Avena*	*Avena*	*Avena*	*Avena*	*Avena*	*Avena*	*Avena*
Avenula/ Helictotrichon	*Avenula/ Helictotrichon*	*Avenula/ Helictotrichon*	*Avenula/ Helictotrichon*	*Avenula/ Helictotrichon*	*Avenula/ Helictotrichon*	*Avenula/ Helictotrichon*	*Helictotrichon*
	Pseudarrhena-therum			*Pseudarrhena-therum*	*Pseudarrhena-therum*	*Pseudarrhena-therum*	
	Corynephorus						
	Deschampsia						
	Holcus		**Gaudiniinae**				
Gaudinia	*Gaudinia*	*Gaudinia*	*Gaudinia*	*Gaudinia*	*Gaudinia*	*Gaudinia*	*Gaudinia*
	Avellinia		**Koeleriinae**	*Avellinia*	*Avellinia*	*Avellinia*	
	Koeleria	*Koeleria*	*Koeleria*	*Koeleria*	*Koeleria*	*Koeleria*	*Koeleria*
	Rostraria	*Rostraria*	*Rostraria*	*Rostraria*	*Rostraria*	*Rostraria*	*Rostraria*
Trisetum	*Trisetum*	*Trisetum*	*Trisetum*	*Trisetum*	*Trisetum*	*Trisetum*	*Trisetum*
					Dielsiochloa	*Dielsiochloa*	*Dielsiochloa*
					Graphephorum	*Graphephorum*	*Graphephorum*
			Ventenatinae		*Sphenopholis*	*Sphenopholis*	*Sphenopholis*
Ventenata	*Ventenata*	*Ventenata*	*Ventenata*	*Ventenata*	*Ventenata*	*Ventenata*	*Cinna*
					Dissanthelium		
Agrostideae	**Agrostideae**	**Agrostideae**					
Agrostidinae	**Agrostidinae**		**Agrostidinae**		**Alopecurinae**		**Agrostidinae**
Agrostis	*Agrostis*	*Agrostis*	*Agrostis*	*Agrostis*	*Agrostis*	*Agrostis*	*Agrostis*
	Ammophila	*Ammophila*	*Ammophila*	*Ammophila*	*Ammophila*	*Ammophila*	*Ammophila*
Apera	*Apera*	*Apera*	*Apera*		*Apera*	*Apera*	*Apera*
Calamagrostis		*Calamagrostis*	*Calamagrostis*	*Calamagrostis*	*Calamagrostis*	*Calamagrostis*	*Calamagrostis*
Gastridium	*Gastridium*	*Gastridium*	*Gastridium*	*Gastridium*	*Gastridium*	*Gastridium*	*Gastridium*
Lagurus	*Lagurus*	*Lagurus*	*Lagurus*	*Lagurus*	*Lagurus*	*Lagurus*	
Polypogon	*Polypogon*	*Polypogon*	*Polypogon*	*Polypogon*	*Polypogon*	*Polypogon*	*Polypogon*
			Zingeria		*Zingeria*	*Zingeria*	
	Triplachne	*Triplachne*		*Triplachne*	*Triplachne*	*Triplachne*	
Chaetopogon	*Chaetopogon*	*Chaetopogon*		*Chaetopogon*	*Chaetopogon*	*Chaetopogon*	
Cinna		*Cinna*			*Cinna*	*Cinna*	
					Deyeuxia	*Deyeuxia*	*Deyeuxia*
						Ammochloa	
Miborinae	**Miborinae**						
Mibora	*Mibora*	*Mibora*	*Mibora*		*Mibora*	*Mibora*	*Deschampsia*
			Phleeae				*Ventenata*
Phleinae	**Phleinae**		**Alopecurinae**				**Alopecurinae**
Alopecurus	*Alopecurus*	*Alopecurus*	*Alopecurus*	*Alopecurus*	*Alopecurus*	*Alopecurus*	*Alopecurus*
			Phleinae				
Phleum	*Phleum*	*Phleum*	*Phleum*	*Phleum*	*Phleum*	*Phleum*	*Phleum*
Chlorideae		**Isolated**	**Beckmanniinae**				
Beckmannia		*Beckmannia*	*Beckmannia*		*Beckmannia*	*Beckmannia*	*Beckmannia*
Phalarideae (sub Panicoideae)	**Phalarideae**	**Phalarideae**	**Phalarideae**				
			Anthoxanthinae		**Phalaridinae**		**Phalaridinae**
Anthoxanthum	*Anthoxanthum*	*Anthoxanthum*	*Anthoxanthum*	*Anthoxanthum*	*Anthoxanthum*	*Anthoxanthum*	*Anthoxanthum*
Hierochloe		*Hierochloe*	*Hierochloe*	*Hierochloe*	*Hierochloe*	*Hierochloe*	*Hierochloe*
			Phalaridinae				
Phalaris	*Phalaris*	*Phalaris*	*Phalaris*	*Phalaris*	*Phalaris*	*Phalaris*	*Phalaris*
Stipeae	**Stipeae**	**Stipeae**	**Miliinae**	**Milieae**	**Stipeae**		**Miliinae**
Milium	*Milium*	*Milium*	*Milium*	*Milium*	*Milium*	*Milium*	*Milium*
				Zingeria			*Mibora*
Poeae	**Poeae**	**Poeae**	**Poeae**	**Poeae**	**Poeae**	**Poeae**	
Festucinae	**Festucinae**		**Brizinae**				**Brizinae**
Briza	*Briza*	*Briza*	*Briza*	*Briza*	*Briza*	*Briza*	*Briza*
			Poinae				
Catabrosa	*Catabrosa*	*Catabrosa*	*Catabrosa*	*Catabrosa*	*Catabrosa*		

TABLE 1. Continued.

Ascherson and Graebner (1898–1902)	Maire et al. (1953)	Prat (1960)	Tzvelev (1976)	Tutin et al. (1980)	Clayton and Renvoize (1986)	Watson and Dallwitz (1992)	Soreng et al. (2003)
		Colpodium	*Colpodium*		*Colpodium*	*Colpodium*	
Koeleriinae		*Dissanthelium*		*Apera*	*Gymnachne*	*Gymnachne*	*Gymnachne*
Avellinia		*Avellinia*		*Beckmannia*	*Hellerochloa*	*Hellerochloa*	
Koeleria				*Mibora*	*Parafestuca*	*Parafestuca*	
			Cinninae			*Dissanthelium*	
			Cinna	*Cinna*			
			Scolochloeae	**Scolochloeae**			**Scolochloinae**
		Scolochloa	*Scolochloa*	*Scolochloa*	*Scolochloa*	*Scolochloa*	*Scolochloa*
					Meliceae	**Meliceae**	
		Anthochloa			*Anthochloa*	*Anthochloa*	*Anthochloa*
							Puccinellinae
						Catabrosa	*Catabrosa*
Pappophoreae			**Seslerieae**	**Seslerieae**		**Seslerieae**	
	Sesleriinae		**Sesleriinae**				**Sesleriinae**
Oreochloa	*Oreochloa*	*Oreochloa*	*Oreochloa*	*Oreochloa*	*Oreochloa*	*Oreochloa*	
Sesleria	*Sesleria*	*Sesleria*	*Sesleria*	*Sesleria*	*Sesleria*	*Sesleria*	*Sesleria*
			Ammochloinae				
	Ammochloa	*Ammochloa*	*Ammochloa*	*Ammochloa*	*Ammochloa*		
			Echinariinae				
Echinaria	*Echinaria*	*Echinaria*	*Echinaria*	*Echinaria*	*Echinaria*		

retrieved from GenBank and included in the analyses. Of these, 10 partially complete ITS sequences (ITS1 and ITS2 spacers) were used in our phylogenetic survey, and the absent characters (5.8S gene) were coded as missing data (Appendix). Gaps that were potentially informative were coded as binary presence/absence characters and added to the respective sequence data set for parsimony cladistic analysis.

Bayesian and cladistic analyses were made on both individual and combined plastid *trnT-F* and nuclear ITS data sets using the programs MrBayes v. 3.0 (Huelsenbeck and Ronquist, 2002) and PAUP* v. 4.0 beta 10 (Swofford, 2002), respectively. Bayesian inference searches were performed independently for each data set (*trnT-F* matrix, ITS matrix, and combined *trnT-F* + ITS matrix) with MrBayes, using the optimal nucleotide substitution model previously selected for each case. This model was developed by calculating likelihood ratios for 56 substitution models using the program Model Test v. 3.06 (Posada and Crandall, 1998). The three data sets generated the same optimal general time-reversible model with a proportion of invariable sites (GTR+G+I) and four gamma rate categories, which was imposed on the subsequent analyses. The analysis of each separate data set was performed through 1 000 000 generations by the Markov chain Monte Carlo (MCMC), with three hot chains (hot temperature 0.2) and one cold chain, sampling every 100 generations and allowing the program to estimate the likelihood parameters required. The log-likelihood scores of sample points were plotted against generation time to estimate the number of generations needed to converge to a stable equilibrium value (Huelsenbeck and Ronquist, 2002; Leaché and Reeder, 2002). Sampled points from the generation previous to stationary were discarded using the burn-in option of MrBayes. New Bayesian searches of 5 000 000 MCMC generations were conducted for each data set using the topologies sampled from them to construct the respective 50% majority-rule consensus topologies and calculate the posterior probability support (PPS) of their lineages.

Parsimony-based analyses were conducted through two heuristic searches, each aimed at recovering all possible equally shortest cladograms. An initial search was completed with the following parameters: closest addition of taxa, tree-bisection-reconstruction (TBR) branch swapping, and the Mulpars option (multiple parsimony cladograms saved). The second search, which tried to find other putatively shorter or equally parsimonious islands, consisted of 10 000 replicates of random-order-entry-starting cladograms with random addition of taxa, tree-bisection-reconnection (TBR) branch swapping, and saving no more than 10 cladograms of length equal to or less than 10 per replicate. All equally parsimonious reconstructions obtained from the two searches were used to compute the final strict consensus cladograms. *Brachypodium distachyon* (L.) P. Beauv. (Brachypodieae Harz) and *Secale cereale* L. (Triticeae) were used as outgroups; *B. distachyon* was used to root the cladograms. Branch support for the optimal topologies found under these parsimony strategies was estimated through 10 000 bootstrap replicates (Felsenstein, 1985) using the strategy of DeBry and Olmstead (2000), which consisted of random addition of taxa and TBR branch swapping, but saving fewer cladograms per replicate to reduce computation time.

Conflicts between the topologies obtained from Bayesian and parsimony searches were analyzed visually. Incongruences between plastid and nuclear cladistic topologies were analyzed statistically using the nonparametric Wilcoxon signed rank test (Templeton, 1983; Mason-Gamer and Kellogg, 1996). For this purpose, separate *trnT-F* and ITS matrices of 92 common taxa were constructed from each data set, and a combined *trnT-F*/ITS matrix was also created. The *trnT-F*/ITS combination of data sets were compared by counting the number of steps required by each data set on its own optimal topology (MP strict consensus) and on pairwise combinations with three constraint topologies (the MP strict consensus and the 70% majority rule bootstrap consensus obtained from the rival data set and the MP strict consensus obtained from the combined data matrix). The number of steps required in each case was calculated with PAUP* v. 4.0 beta 10, as indicated in Mason-Gamer and Kellogg (1996). Significance values of the Wilcoxon signed rank tests were obtained from the Vassatstats online application (http://faculty.vassar.edu/lowry/wilcoxon.html), which provide two-tailed significance values.

RESULTS

The trnT-F data set—The sequenced plastid *trnT-F* region comprised 2455 aligned nucleotide positions, 1195 of them corresponding to the *trnT-L* subregion and 1260 to the *trnL-F* subregion. A total of 1065 positions were variable (43.3%, 496 in *trnL-F* and 569 in *trnT-L*), and 586 were potentially parsimony informative (23.8%, 252 in *trnL-F* and 334 in *trnT-L*). Informative gaps were frequent across the entire sequenced *trnT-F* region, and a 30-nucleotide gap (positions 355–384) was shared by the members of the Koeleriinae core: *Avellinia*, *Gaudinia*, *Koeleria*, *Rostraria*, *Trisetum*, and *Parafestuca*. By contrast, the *trnL-F* subregion had seven informative indels. A large, 285-nucleotide gap (positions 219–503) was synapomorphic for the members of Koeleriinae (*Avellinia*, *Gaudinia*, *Graphephorum*, *Koeleria*, *Rostraria*, *Parafestuca*, *Sphenopholis*, and *Trisetum*) and Aveninae (*Arrhenatherum*, *Avena*, and *Helictotrichon* subgenus *Helictotrichon*) lineages. Within Koeleriinae, *Gaudinia fragilis*, *Trisetum loeflingianum*, and *T. ovatum*, here named the *Trisetum ovatum* group, showed a

common nine-nucleotide indel (positions 1000–1008), whereas *Rostraria pumila, R. salzmannii, R. cristata, R. obtusiflora*, *Trisetum gracile*, and *T. flavescens*, here named the *Trisetum flavescens* group, shared a large, 108-nucleotide gap (positions 897–1004). Another large gap of 188 nucleotides (positions 316–503) was synapomorphic for all representatives of Agrostidinae (*Agrostis*, *Ammophila*, *Calamagrostis*, *Chaetopogon*, *Gastridium*, *Polypogon*, and *Triplachne*), as well as *Briza*, *Airopsis*, and *Gymnachne*. This group also shared an additional common five-nucleotide gap (positions 40–54). *Holcus* and *Deschampsia* s.s. (*D. cespitosa*, *D. setacea*) each had genus-specific gaps five nucleotides long (positions 235–239 and 164–168, respectively).

The Bayesian topologies reached a stable likelihood value after the burn-in of 1000 phylograms. The 50% majority rule consensus phylogram is shown in Fig. 1. Phylogenetic relationships are relatively well resolved at the deepest branches of the *trnT-F* topology. In the parsimony-based analyses, the first heuristic search yielded 839 900 cladograms that were 2353 steps long (L) and had a consistency index (CI) (excluding uninformative characters) of 0.59 and retention index (RI) of 0.76. The second search did not find any further island of equally parsimonious cladograms. The strict consensus of all these most parsimonious cladograms (not shown) was compared with the Bayesian-based phylogram. Bayesian and parsimony-based topologies were largely congruent and had similar levels of support for the main lineages (Fig. 1). The supertribal Aveneae-Poeae-Seslerieae complex was resolved as monophyletic and highly supported (100% posterior probability support [PPS]; 100% bootstrap support [BS]) when *Secale cereale* and *Brachypodium distachyon* were used as outgroups. Within this complex, there was an early divergence between a highly supported "core Aveneae" lineage (100% PPS; 100% BS) and a Poeae s.l. lineage (100% PPS; 95% BS), the latter including the main Poeae subgroups plus many former Aveneae groups (Fig. 1). Core Aveneae comprised five highly supported subgroups: (1) Koeleriinae + Aveninae + *Lagurus* (100% PPS; 100% BS), (2) Anthoxanthiinae (100% PPS; 100% BS), (3) Agrostidinae (100% PPS; 100% BS), (4) *Airopsis* + *Briza* (100% PPS; 83% BS), and (5) *Phalaris*. In the Bayesian phylogram, *Phalaris* was sister to a group formed by the other lineages, which further split into the sister subgroups (1)/(2) and (3)/(4), while Anthoxanthinae showed the sister relationship of *Anthoxanthum* and *Hierochloe*; however, none of those relationships, except that of the sister lineages Agrostidinae/*Airopsis* + *Briza* (99% PPS; 80% BS), were well supported (Fig. 1), and they collapsed into a polytomy in the parsimony-based topology (not shown).

The Koeleriinae + Aveninae + *Lagurus* group had an initial polytomy of *Lagurus*, *Avena*, and a series of remaining taxa that diverged into successive weakly supported paraphyletic Aveninae lineages (*Helictotrichon* s.s. and *Arrhenatherum*) and a highly supported subgroup of Koeleriinae taxa (100% PPS; 82% BS) (Fig. 1). In the parsimony-based cladogram, the three Aveninae genera with two species sampled were resolved as monophyletic and sister to Koeleriinae but with low support (not shown). Within the Koeleriinae lineage, the American *Graphephorum* and *Sphenopholis* joined in a relatively well-supported sublineage (100% PPS; 72% BS), sister to an Eurasian sublineage (parsimony-based cladogram) or collapsed with it (Bayesian phylogram). This group in turn diverged into a highly supported *Koeleria* s.l. lineage (100% PPS; 90% BS) and a less supported *Trisetum* s.l. lineage (96% PPS). *Gaudinia*, *Parafestuca*, and some representatives of annual *Trisetum* fell in the *Koeleria* s.l. subgroup, which included all the *Koeleria* studied, whereas *Avellinia* and *Rostraria* were embedded in the *Trisetum* s.l. subgroup that encompassed the remaining samples of *Trisetum*. Little resolution was observed in Koeleriinae, except for the strong relationships recovered for the *Trisetum ovatum* group (*Gaudinia fragilis, T. loeflingianum*, *T. ovatum*; 100% PPS, 96% BS), the *Trisetum flavescens* group (*Rostraria* spp., *T. flavescens*, *T. gracile*; 100% PPS, 100% BS), and the *Koeleria splendens/T. hispidum* lineage (100% PPS; 86% BS). Agrostidinae had three early divergent unresolved or poorly supported lineages (*Gymnachne*, *Ammophila*, *Calamagrostis*) and a highly supported lineage (100% BS) in which *Triplachne/Gastridium* (100% PPS; 97% BS) were sister to the *Agrostis* group (100% PPS) (that included the sister *Polypogon* and *Chaetopogon*, 100% PPS, 97% BS). *Briza* joined with *Airopsis* in a highly supported group (100% PPS; 83% BS).

Poeae s.l. diverged in two weakly supported lineages: Poinae plus several former Aveneae + Puccinelliinae (78% PPS) and a large, polytomic, and poorly supported group that included Loliinae and its close allies, Seslerieae, and the rest of the former Aveneae (89% PPS), such as Airinae, *Deschampsia* s.s., *Holcus*, and *Avenula* s.s. The first lineage diverged into two groups: (1) a poorly supported group (55% PPS) with sister relationships between *Avenula pubescens* and *Milium*, and between *Poa* and the closely related *Anthochloa* and *Dissanthelium* (100% PPS); (2) a group (100% PPS) comprising *Cinna*, *Ventenata*, and *Alopecurus*. Puccinelliinae were formed by the sister taxa *Puccinellia* and *Catabrosa* (100% PPS; 100% BS). The highly supported Airinae (100% PPS; 100% BS) comprised *Aira,* sister to a strong subgroup composed of *Corynephorus*, *Deschampsia maderensis*, *D. flexuosa*, and *Periballia* (100% PPS; 89% BS). The second lineage encompassed many former Aveneae and Poeae: *Deschampsia* s.s., *Holcus*, Seslerieae + *Mibora* (98% PPS), Parapholiinae/Cynosurinae (92% PPS), Dactylidinae + *Ammochloa* (89% PPS; 59% BS), and Loliinae + *Avenula* (53% PPS). There was a close and strongly supported relationship of the avenoid *Dielsiochloa* to *Hellerochloa* and to representatives of *Festuca* sect. *Aulaxyper* Dumort. (*F. rubra* group) (100% PPS; 97% BS). Weakly supported sister relationship of *Ammochloa* to Dactylidinae (89% PPS) and the inclusion of *Mibora* in Seslerieae (*Sesleria*, *Oreochloa*, and *Echinaria*), joined with *Oreochloa* (100% PPS; 88% BS)were also evident.

ITS data set—The sequenced nuclear ITS region included 665 aligned nucleotide positions, of which 400 were variable (60.1%, 162 in ITS1 and 204 in ITS2) and 303 were potentially parsimony informative (45.5%, 130 in ITS1 and 154 in ITS2). An eight-nucleotide gap in the ITS1 region (positions 55–62) was considered synapomorphic for Koeleriinae (*Gaudinia*, *Koeleria*, *Graphephorum*, *Parafestuca*, *Rostraria*, *Sphenopholis*, and *Trisetum*).

The Bayesian topologies reached a stable likelihood value after the burn-in of 1110 phylograms. The 50% majority rule consensus phylogram is shown in Fig. 2. The first heuristic search of our parsimony-based analyses yielded 510 800 cladograms of $L = 2289$, eight steps longer than the 25 equally shortest cladograms found by the second search ($L = 2281$, CI $= 0.32$, and RI $= 0.66$). The strict consensus of all these most parsimonious cladograms (not shown) was compared with the Bayesian-based topology. Bayesian and parsimony-based

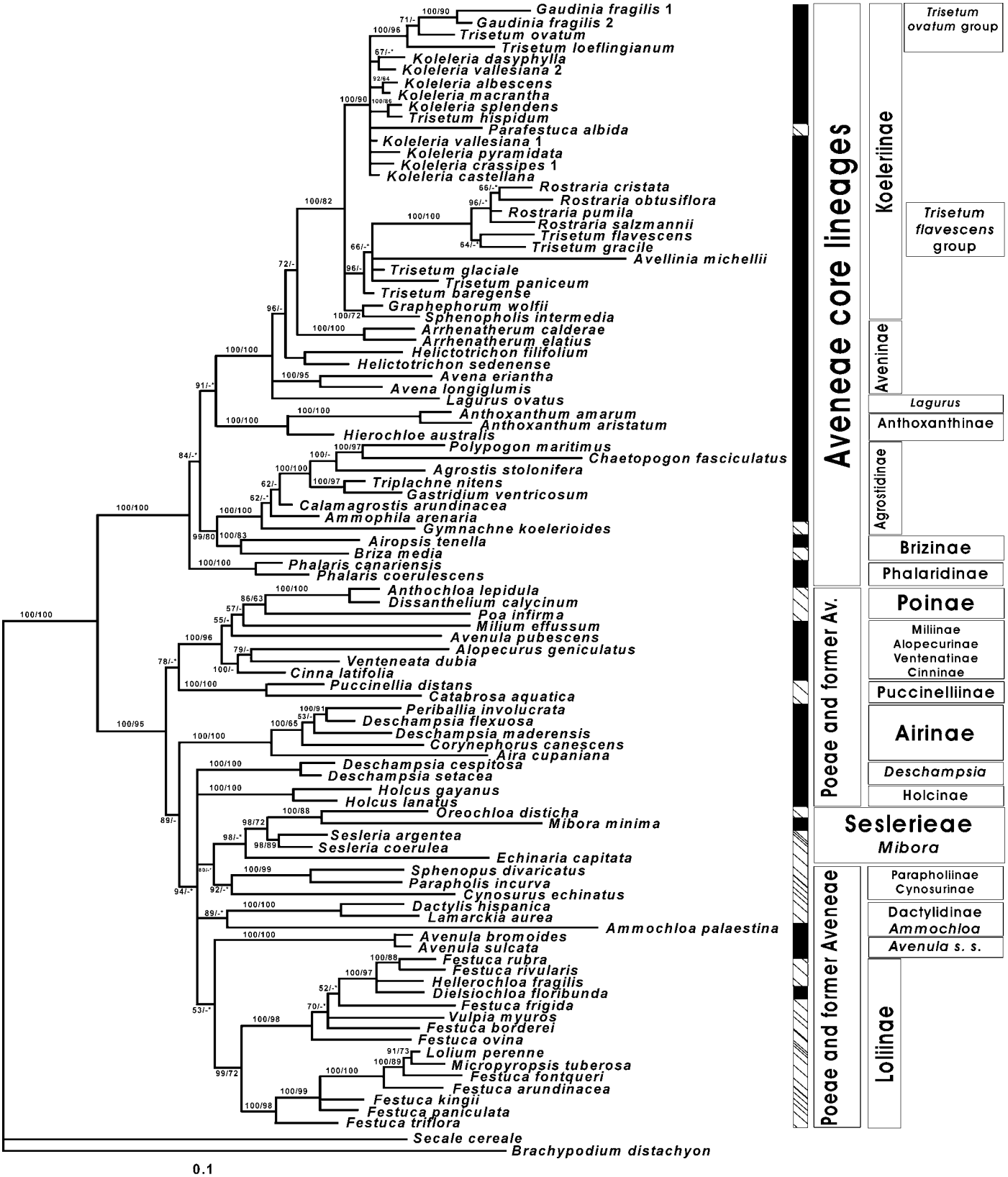

Fig. 1. The *trnT-F* search. The 50% majority rule consensus phylogram obtained by Bayesian inference. The scale represents 0.1 substitutions per site. Values above branches indicate posterior probability support (PPS)/bootstrap support (BS) values of the groups. A dash means BS $< 50\%$. The groups that collapsed in the parsimony-based cladogram are marked with asterisks at their nodes. On the right, the black bar indicates those taxa formerly classified as Aveneae.

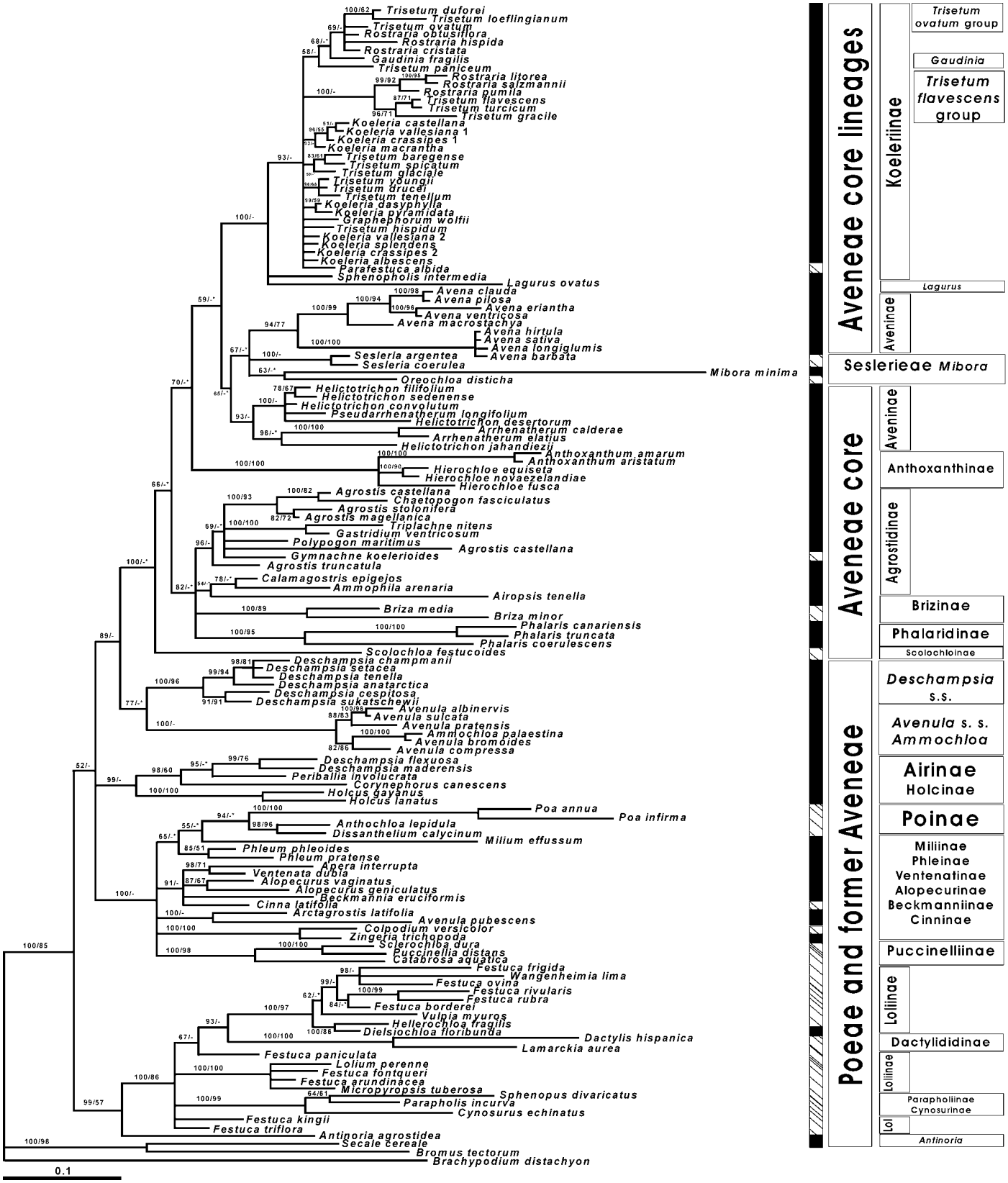

Fig. 2. ITS search. The 50% majority rule consensus phylogram obtained by Bayesian inference. The scale represents 0.1 substitutions per site. Values above branches indicate posterior probability support (PPS)/bootstrap support (BS) values of the groups. A dash means BS $< 50\%$. The groups that collapsed in the parsimony-based cladogram are marked with asterisks at their nodes. On the right, the black bar indicates those taxa formerly classified as Aveneae.

topologies were largely congruent (Fig. 2), although the relationships, especially at deep nodes, generally resolved better in the Bayesian topology. Despite the overall weakness of the internal nodes of the ITS topology, the main lineages recovered from the ITS data were largely congruent with those recovered from the *trnT-F* data (Fig. 1). In the ITS topology, the supertribe Aveneae–Poeae–Seslerieae also was monophyletic and well supported (100% PPS; 85% BS) when *Brachypodium*, *Secale*, and *Bromus* were used as outgroups.

An early divergence separated Loliinae and allies (including *Dielsiochloa* and *Antinoria*) (99% PPS; 67% BS) from all remaining Aveneae–Poeae–Seslerieae taxa, which formed a poorly supported group (52% PPS). Surprisingly, the avenoid *Antinoria* was sister to a well-supported Loliinae + allies (100% BS; 86% BS) in which Parapholiinae/Cynosurinae (100% PPS; 99% BS) and Dactylidinae (100% PPS; 100% BS) lineages intermingled with *Festuca*. *Dielsiochloa* also was shown to be close to *Festuca* sect. *Aulaxyper* (*F. rubra* group), joining in a highly supported subgroup with *Hellerochloa* (100% PPS; 86% BS).

The large group of the remaining taxa collapsed into three groups poorly supported by parsimony-based analyses. One of these included the core Aveneae + Seslerieae + *Scolochloa* (100% PPS) and the *Deschampsia* s.s. + *Avenula* s.s. + *Ammochloa* (77% PPS) lineages, a second one the Airinae + *Holcus* lineages (99% PPS), and the third one the Poinae + allied lineages (100% PPS) (Fig. 2). Weak divergences and polytomies were found at the deep nodes of the core Aveneae + Seslerieae+ *Scolochloa* group. Koeleriinae (including *Lagurus*) (100% PPS) and Aveninae (including Seslerieae) (65% PPS) formed two groups, but the second was weakly supported. Within the largely unresolved Koeleriinae, the *Trisetum flavescens* group again was recovered (100% PPS), with *Rostraria* subsp. (99% PPS, but excluding *Rostraria cristata*, *R. hispida*, and *R. obtusiflora*) clearly separated from perennial *Trisetum* (96% PPS). Within the *Trisetum ovatum* group, only *T. duforei* and *T. loeflingianum* (100% PPS) had any relationship. *Koeleria pyramidata* and *K. dasyphylla* were linked (99% PPS). Aveninae resolved into two separate lineages: a relatively well-supported *Avena* group (94% PPS; 77% BS) with sectional resolution as reported by Rodionov et al. (2005), that formed a polytomy with the Seslerieae representatives plus *Mibora*. In turn, *Arrhenatherum*, *Helictotrichon*, and *Pseudarrhenatherum* formed a group (93% PPS) in which *Helictotrichon* was paraphyletic to a well-supported subgroup (100% PPS) that also included *Pseudarrhenatherum*. Within the better-sampled and strongly supported Anthoxanthinae (100% PPS; 100% BS), a polytomy is formed by *Hierochloe* and *Anthoxanthum* lineages in the Bayesian phylogram (Fig. 2). Agrostidinae formed a moderately supported lineage (96% PPS), except for *Calamagrostis* and *Ammophila*, which joined with *Airopsis* (54% PPS), and *Agrostis* was paraphyletic and most of its sampled species formed a group in which *Chaetopogon* was embedded (100% PPS; 93% BS). A strong relationship between *Triplachne* and *Gastridium* was again recovered by these data (100% PPS; 100% BS). *Phalaris* and *Briza*, collapsing at the base of the group, and *Scolochloa*, as sister to the whole group, completed this weak and large lineage. The Airinae lineage included *Deschampsia flexuosa, D. maderensis, Periballia*, and *Corynephorus* (98% PPS; 60% BS). Poinae + Puccinellinae (100% PPS) had a large basal polytomy of five lineages: (1) *Poa* + *Anthochloa/Dissanthelium* (94% PPS), which were weakly grouped with *Milium* and *Phleum* (65% PPS); (2) *Apera* + *Ventenata* + *Alopecurus* + *Beckmannia* + *Cinna* (91% PPS); (3) *Arctagrostis* + *Avenula pubescens* (100% PPS); (4) *Colpodium* + *Zingeria* (100% PPS; 100% BS); and (5) Puccinellinae (*Sclerochloa*, *Puccinellia*, and *Catabrosa*; 100% PPS; 98% BS).

Combined ITS/trnT-F data set—Most of the conflicts affected relationships that were only weakly supported by one set of data (Figs. 1 and 2). The main incongruences occurred in the distinct placements of the Seslerieae + *Mibora* group in the *trnT-F* and ITS topologies. *Sesleria*, *Oreochloa*, *Ammochloa*, and *Mibora* aligned within a highly supported Poeae s.l. lineage in the plastid topology (Fig. 1) but within the poor to moderately supported Aveneae + Seslerieae + *Deschampsia* + *Avenula* s.s. lineage in nuclear topology (Fig. 2). The Wilcoxon signed rank tests showed significant incongruence between the plastid and the nuclear topologies. The *trnT-F* data strongly rejected the ITS strict consensus ($P < 0.001$) and the 70% ITS MR bootstrap consensus ($P < 0.001$); similarly, the ITS data strongly rejected the *trnT-F* strict consensus ($P < 0.001$) and the 70% *trnT-F* MR bootstrap consensus ($P < 0.001$). However, because of the scarce support recovered for many of the relationships by the ITS data, their rejection by the *trnT-F* data may not reflect strong conflict between them. The combined topology, which is similar to the plastid one, was not rejected by the plastid *trn*L-F-region data subset ($P > 0.26$) but was weakly rejected by the plastid *trnT-L*-region data subset ($0.036 < P < 0.073$) and by the ITS data set ($0.030 < P < 0.060$), thus indicating some discordances within the plastid data set. While this test is useful for global comparisons, it is also recognized to be problematic; topologies are likely to be rejected topologies because of the presence of spurious nodes in the rival constraint (Mason-Gamer and Kellogg, 1996). In addition, the overall high congruence between the plastid and nuclear Aveneae and Poeae lineages moved us to combine the two matrices and to perform further phylogenetic analyses. The combined *trnT-F*/ITS data set was made of 92 co-sequenced accessions (Appendix). In the combined topologies, it was clear that the large, highly structured, plastid DNA data set overwhelmed the much smaller and less informative ITS data set. Because of the scant information provided by the combined topology, we did not show it here, referring to it only when justified.

DISCUSSION

Aveneae core lineage—Although it had been suggested that Aveneae were more advanced than Poeae (Clayton and Renvoize, 1986), our analyses confirmed the insights of Soreng and Davis (2000), which indicated that Aveneae and Poeae were intermingled. Despite this admixture, our combined and plastid analyses recovered two main groups composed of mainly Aveneae and mainly Poeae taxa, respectively (nuclear analyses did not render these two quite definited groups but this should be carefully considered due to the scarce support obtained for this topology at its deepest nodes). The group primarily with Aveneae is named hereafter the core Aveneae lineage, because it included representatives of the most typical infratribal Aveneae taxa (Table 1), Koeleriinae, Aveninae, and Agrostidinae, as well as minor groups obscurely related to the previous groups, such as

Lagurus, Anthoxanthinae, *Airopsis*, *Phalaris*, and *Scolochloa* (Figs. 1 and 2). Additionally, it included a few Poeae representatives such as *Briza*, *Parafestuca*, and *Gymnachne* (Figs. 1 and 2), although some Poeae representatives potentially related to this core Aveneae, such as *Chascolytrum*, *Poidium*, and *Torreyochloa*, were not studied here (cf. Soreng and Davis, 2000).

Koeleriinae and Lagurus—Trisetum has been considered the ancestral lineage of Koeleriinae because of its less reduced lemma (Clayton and Renvoize, 1986; Mosulishvili, 2000). The lemma of *Trisetum* is three-awned with a main, often geniculate, dorsal awn inserted from low down to near the top, and two more or less developed, additional awnlets arising from the lateral veins at the apex. The closely related perennial *Koeleria* has muticous, mucronate, or apically or subapically awned lemma.

Koeleriinae also includes ephemeral species adapted to dry, open places from the Mediterranean to the western Himalayas. They are placed either in *Trisetaria* Forssk., a name lately fallen into disuse and applied to the annual species of *Trisetum*, or in *Rostraria*, a small genus with straight, or sometimes slightly curved, subapical awned lemmas. Additionally, the annual Mediterranean genus *Avellinia* was placed in *Trisetaria* (Clayton and Renvoize, 1986) or in *Rostraria* (Romero Zarco, 1996) because of similarities in its lemma. The American *Sphenopholis*, separated from *Trisetum* by Scribner (1906) because of its ovate glumes and florets disarticulating below the glumes, and *Graphephorum*, with a lemma with an entire apex and a reduced dorsal awn (subapical mucro) (Finot et al., 2004, 2005a, b), were also considered to be related to *Trisetum* (Clayton and Renvoize, 1986).

Koeleriinae were recovered in all our analyses, although they were more strongly supported by the plastid data (cf. Figs. 1 and 2). Neither *Koeleria* nor *Trisetum* formed monophyletic groups, but all *Koeleria* representatives were grouped into a well-supported lineage, which also included several species of *Trisetum*. Relationships within *Koeleria* spp. were not resolved satisfactorily by the present analyses, and *K. vallesiana* and *K. crassipes* appeared to be polyphyletic. *Parafestuca*, a monotypic endemic genus from Madeira traditionally included in the Poeae (Alexeev, 1985; Clayton and Renvoize, 1986; Watson and Dallwitz, 1992), was placed within this group (Figs. 1 and 2). *Parafestuca* was included in *Koeleria*, not only because of its placement here, but also because its morphology is typical of the genus *Koeleria* (Soreng et al., 2003; Quintanar et al., 2006). This mostly perennial lineage also included the *Trisetum ovatum* group, that comprised the annual *T. loeflingianum*, *T. ovatum*, and the small genus *Gaudinia*, with either strongly contracted panicles (*Trisetum* representatives) or racemes of spikelets (*Gaudinia*). However, the circumscription of this group was less clear in the ITS topology, which recovered only a strong relationship for *T. loeflingianum* and *T. duforei* (Fig. 2). Another *Trisetum* species, the perennial *T. hispidum*, was unexpectedly linked with *Koeleria splendens* in a relatively well-supported group (Figs. 1 and 2).

The remaining *Trisetum* taxa were included in a weakly supported group that also included all the *Rostraria* taxa studied and *Avellinia* (Fig. 1). The relationships of *R. pumila* and *R. salzmannii* (plus *R. litorea*, Fig. 2) with the perennial *T. flavescens* and *T. gracile* (plus *T. turcicum* in Fig. 2) were corroborated by all the data sets, whereas the relationships of *R. cristata* and *R. obtusiflora* with this last group were supported only by plastid data (Fig. 1). This *Trisetum flavescens* group, enlarged with *Rostraria*, corresponds with *Trisetum* sect. *Trisetum*. This section was typified by *T. flavescens* and characterized by more or less open, oval-to-pyramidal panicles (Finot et al., 2004, 2005b). The close relationship found between *Trisetum* and *Rostraria* agrees with earlier reports that highlighted the strong resemblances between the lemma of both genera (Hubbard, 1937; Holub, 1974; Jonsell, 1978). *Rostraria cristata*, *R. obtusiflora*, *R. hispida*, and *T. paniceum* were resolved by ITS data as relatives of the *T. ovatum* group, but with little support (Fig. 2). Another *Trisetum* group, formed by *T. baregense*, *T. glaciale*, and *T. paniceum*, was recovered only by the combined data set (not shown) but not by separate plastid and nuclear data. *Trisetum glaciale* was resolved as a sister to the *T. baregense–T. spicatum* group in a moderately supported lineage (Fig. 2). This group corresponds with *Trisetum* sect. *Trisetaera* Asch. & Graebn., typified by *T. spicatum* and characterized by dense, spiciform, and narrow panicles (Finot et al., 2004, 2005b). *Avellinia*, only studied for plastid data, remained in an unresolved placement within this last group (Fig. 1). This genus might be an independent annual derivation from a different perennial *Trisetum* line.

Graphephorum and *Sphenopholis* were placed within Koeleriinae by all analyses (Figs. 1 and 2) and resolved as sister lineages by the plastid and combined topologies (Fig. 1). These results confirm the close relationships found between *Sphenopholis* and *Trisetum* by Soreng and Davis (2000) and the morphologic affinities between *Graphephorum* and *Trisetum* reported by Finot et al. (2005a). However, a larger sampling of American *Koeleria* and *Trisetum* taxa is needed before their systematics can be further assessed. Finally, this Koeleriinae lineage can be distinguished by a set of morphologic features, such as 2–5 florets per spikelet, a relatively small spikelet, a keeled lemma (as opposed to more or less rounded lemmas, as in *Avellinia, Gaudinia*, and some *Trisetum* species), a poorly developed awn, glabrous ovary (hairy in *Gaudinia* and in some *Trisetum* species, with an apical appendage in *Graphephorum*), short hilum, and liquid endosperm.

The Mediterranean genus *Lagurus* was part of a polytomy that included either the Koeleriinae and Aveninae lineages by plastid data (Fig. 1) or only Koeleriinae representatives by nuclear data (Fig. 2). *Lagurus* has historically been included in Agrostidinae (Table 1) based on its one-flowered spikelets, but other general features of this monotypic genus, such as a glabrous ovary, short hilum, and liquid endosperm, connect it to Koeleriinae.

Aveninae—Genera of this subtribe have been characterized traditionally by their long glumes, laterally compressed spikelets with 1–2 (7) female fertile florets, and more or less developed dorsal awns. *Helictotrichon* s.s. (excluding *Avenula*, discussed later), traditionally considered as perennial oats, separates from the mostly annual *Avena* based on its scabrid and more strongly keeled glumes and on its linear-lanceolate lodicules (Baum, 1968); however, the taxonomic boundaries between *Helictotrichon* and other perennial Aveninae, such as the European and Mediterranean *Arrhenatherum* with an either hermaphroditic or female upper floret, and the Western European *Pseudarrhenatherum*, with one incomplete floret proximal to the hermaphroditic one, were never clear on the basis of morphology.

Aveninae, including *Avena*, *Arrhenatherum*, *Pseudarrhena-*

therum, and *Helictotrichon*, were paraphyletic to Koeleriinae in the plastid Bayesian phylogram (Fig. 1) but were united in a weakly supported group sister to Koeleriinae in the parsimony-based topologies and nuclear phylogram (Fig. 2), suggesting a potential origin of Koeleriinae from within Aveninae. *Helictotrichon*, including most of the sampled taxa of this genus (subgenus *Helictotrichon*), and *Pseudarrhenatherum* were grouped, agreeing with the limited morphologic differentiation found between them (Clayton and Renvoize, 1986). *Helictotrichon* subgenus *Tricholemma* Röser (*H. jahandiezii*), on the other hand, was sister to *Arrhenatherum* (Fig. 2). This Aveninae lineage can be characterized by a set of morphologic features such as large spikelets, 1–7 florets per spikelet, hairy ovary, long-linear hilum, grooved embryo, and mostly solid endosperm.

Agrostidinae, Anthoxanthinae, and allies—Agrostidinae, the third main subtribe of Aveneae, have been characterized mainly by their small, one-flowered spikelets. They were resolved as one of the main lineages of the core Aveneae (Figs. 1 and 2). The large genus *Agrostis* was resolved as para/polyphyletic in the ITS analysis, with *Chaetopogon* nested in a strongly supported *Agrostis* s.s. subgroup sister to *A. truncatula* (Fig. 2). *A. truncatula* differs from other *Agrostis* in the microstructure of the lemma and in its open and diffuse panicle and was placed in subgenus *Zingrostis* by Romero García et al. (1988). The strong sister relationship recovered for the pan-Mediterranean genera *Triplachne* and *Gastridium* in all analyses corroborate previous ideas about their morphologic affinities (Clayton and Renvoize, 1986). *Calamagrostis* and *Ammophila* were placed in Agrostidinae (Fig. 1), but their position was unresolved using nuclear data (Fig. 2). All these genera have been included in Aveneae, except *Gymnachne*. This South American genus has many florets (3–6) per spikelet and one stamen per floret and has been placed in Poeae (Table 1) or in Poeae subtribe Brizinae (Soreng et al., 2003). This Agrostidinae lineage has a set of morphologic features, such as small spikelets, a single floret per spikelet (except *Gymnachne*), glabrous ovary, short hilum (long-linear in *Ammophila*), and mostly solid endosperm (liquid in some *Agrostis* and *Polypogon* species), that in conjunction separate Agrostidinae from both Koeleriinae and Aveninae.

Eurasian *Briza* traditionally have been classified as Poeae in all morphology-based systems (Table 1) but were included within Aveneae in molecular surveys (Soreng et al., 1990; Hsiao et al., 1995; Soreng and Davis, 2000; see also Figs. 1 and 2). The small subapical awns in *Briza* and other closely related Poeae, such as *Chascolytrum* and *Poidium*, were considered to be a morphologic evidence of their affinities to Aveneae (Soreng and Davis, 2000). The small genus *Airopsis*, which was classified historically as Airinae (Maire et al., 1953; Albers and Butzin, 1977) based on its putative similarity with *Aira*, was placed with other representatives of the subtribe in the vicinity of Agrostidinae and *Briza*. The broadly ovate, ventricose glumes of monotypic *Airopsis* resemble those of *Briza*, and this may reflect its true affinities. The plastid data showed a sister relationship of *Briza* plus *Airopsis* to Agrostidinae, but this relationship was not supported by nuclear data (Figs. 1 and 2).

Anthoxanthum, *Hierochloe*, and *Phalaris*, traditional members of Anthoxanthinae (Table 1), have one distal female-fertile floret per spikelet with proximal sterile—*Anthoxanthum*, *Phalaris*—or male/neuter—*Hierochloe*—florets. *Anthoxanthum* and *Hierochloe* also share aromatic coumarin-scented shoots, glabrous ovary, short hilum, small embryo, and hard endosperm, whereas *Phalaris* differs because of its non-aromatic shoots, small or large embryo, and a long-linear hilum. The first two genera joined in a strongly supported group sister to Koeleriinae + Aveninae lineages (Figs. 1 and 2), and nuclear data additionally showed a paraphyletic perennial *Hierochloe* including a perennial-to-annual monophyletic *Anthoxanthum* in the parsimony-based topology (not shown). Anthoxanthinae included just these two genera; despite the relationship between *Anthoxanthum* and *Phalaris* found by Soreng and Davis (2000), our data clearly separated them from *Phalaris* (Figs. 1 and 2). Phalaridiinae is restricted to *Phalaris*, a genus of still uncertain relationships with respect to the groups mentioned earlier, although the plastid topology suggests that *Phalaris* is sister to all other core Aveneae (Fig. 1).

On the other hand, *Scolochloa*, a wet-meadow grass from the northern hemisphere that was classified in its own tribe Scolochloeae Tzvelev or as a subtribe of Poeae (Table 1), was sister to all core Aveneae lineages in the ITS phylogram (Fig. 2, not sampled in the plastid analyses). Its hairy ovary, long-linear hilum, and hard endosperm may be plesiomorphic in core Aveneae (cf. Baum, 1968).

Former Aveneae lineages related to the traditional Poeae subtribes—Loliinae and its allied subtribes Parapholiinae, Cynosurinae, and Dactylidinae, and Poinae and its allied subtribe Puccinelliinae had poorly supported relationships to many former Aveneae groups, and/or incorporated other genera also classified as Aveneae (see *Dielsiochloa* and Loliinae) (Figs. 1 and 2). Seslerieae were close to Aveninae (ITS, Fig. 2) or sister to Parapholiinae/Cynosurinae (*trnT-F*, Fig. 1), or to the whole large Poeae + former Aveneae group in the combined topologies.

Closest relatives of Poinae—A morphologically diverse assemblage of Aveneae, such as *Avenula pubescens*, *Alopecurus*, *Apera*, *Beckmannia*, *Cinna*, and *Ventenata*, formed a well-supported group with *Poa* and relatives, although relationships within this large group were unclear (Figs. 1 and 2). *Avenula pubescens* represents an independent split from *Helictotrichon* (*Helictotrichon* subgenus *Pubavenastrum* (Vierh.) Holub), and it was not related to either the core Aveneae-allied *Helictotrichon* s.s. or the Loliinae-allied *Avenula* s.s. (discussed later). This species is morpho-anatomically quite different from other *Avenula* (Romero Zarco, 1984; Röser, 1989, 1997), although its external appearance is that of a "typical" Aveninae. Grebenstein et al. (1998) and Soreng and Davis (2000; plastid data alone) also recovered an isolated placement for this plant, close to *Alopecurus* (Grebenstein et al., 1998; BS 75%). Here, *A. pubescens* joined with *Arctagrostis* as part of a polytomy in a poorly supported ITS-based group (Fig. 2). This latter genus, which has sometimes been placed in Aveneae (Table 1), was shown to be a close ally of *Poa* subg. *Andinae* in the more detailed study of Poinae of Gillespie et al. (2006).

In the same assemblage we found *Alopecurus* and *Phleum*, two genera distributed throughout the temperate northern hemisphere and South America and traditionally placed in Aveneae (Table 1) (Figs. 1 and 2), confirming previous findings by Soreng and Davis (2000) and Gillespie et al. (2006). *Beckmannia*, characterized by its long glumes and one- or two-flowered spikelets and usually treated as Aveneae

(Table 1), has also been considered to be related to Poeae (Avdulov, 1931; Reeder, 1953) and was placed close to *Alopecurus* in the ITS topology of Rodionov et al. (2005; BS 66%). The European-Mediterranean *Apera*, commonly included in Agrostidinae (Table 1) because of its single-flowered spikelet, was also placed in Poeae (Tutin et al., 1980). The temperate Eurasian and American *Cinna* (Aveneae or Aveninae, see Table 1), was resolved as a close relative of *Sphenopholis* and *Trisetum* by Soreng and Davis (2000). Its alignment with Poinae and relatives is consistent with its recognition as subtribe Cinninae Caruel of Poeae. The unexpected placement recovered for the small xerophytic annual genus *Ventenata* contradicts traditional classifications in which it was included in *Avena* (Reichenbach, 1830; Koch, 1854; Ledebour, 1853), Aveneae, or the *Trisetum* group (Clayton and Renvoize, 1986) (Table 1). The nongaping paleas and slightly grooved caryopsis (Eig, 1929) separate *Ventenata* from Koeleriinae, and the phylogenetic relationships recovered here could support its classification in a separate subtribe, Ventenatinae.

Two small Eurasian genera, *Colpodium* and *Zingeria*, formed a strongly supported lineage in this assemblage (Fig. 2). Despite previous attributions of *Zingeria* to Agrostidinae or Aveneae (Table 1), this group was also reported by Rodionov et al. (2005; BS 100%) in a sister placement to *Alopecurus* and *Beckmannia* (BS 52%). Both genera have a single-flowered spikelet, more or less awnless lemma, glabrous ovary, short hilum, and a reduced base chromosome number, from 2 to 4. The paleoartic genus *Milium,* with dorsiventrally compressed, one-flowered spikelets and awnless lemma, has been placed in either Aveneae, Stipeae Dumort., or its own tribe, Milieae Link (Table 1). The position of *Milium* in our topologies confirms the results of Soreng and Davis (2000) and Gillespie et al. (2006), definitively places it in this heterogeneous group (Figs. 1 and 2), and is consistent with its treatment as a separate subtribe. Finally, despite the placement of *Anthochloa* in Aveneae (Stebbins and Crampton, 1961) or Meliceae (Clayton and Renvoize, 1986), this monotypic genus, characterized by a broadly expanded, flabellate lemma, and the pooid *Dissanthelium* (Aveneae in Clayton and Renvoize, 1986), were found to be sister to *Poa*, although with rather poor support (Figs. 1 and 2). This confirms their previous placement in Poeae (Soreng et al., 2003) and findings by Gillespie et al. (2006) that places these and other minor genera such as *Austrofestuca* and *Eremopoa* with *Poa*.

Puccinelliinae were weakly supported as sister to Poinae and relatives by the plastid data alone (Fig. 1) and included *Puccinellia*, *Catabrosa*, and *Sclerochloa*. The close relationship of the holarctic *Puccinellia* and the pan-Mediterranean *Sclerochloa* in the nuclear topologies confirms earlier findings by Choo et al. (1994) and Catalán et al. (2004). The linking of the helophytic to mesophytic *Catabrosa*, included in Meliceae (Watson and Dallwitz, 1992), to this group also supports previous findings (Soreng et al., 1990; Choo et al., 1994; Gillespie et al., 2006). All these genera have (1) 2–10 florets per spikelet, noncarinate lemma, glabrous ovary, short hilum, and hard endosperm.

Closest relatives of Loliinae—Airinae, which traditionally included the large, worldwide *Deschampsia*, *Aira*, and several other small genera, are characterized by 2 (3) florets per spikelet and usually straight or somewhat bent awns originating from near the base to below the lemma apex. *Deschampsia* was traditionally divided into two sections that were later segregated into two independent genera, *Deschampsia* and *Avenella*, based on differences in lodicule shape, root histology, and spikelet architecture (Frey, 1999). The recent phylogenetic study of Chiapella (2007), based on combined nuclear and plastid data, has shown independent origins for these two genera, a scenario also corroborated by our data (Figs. 1 and 2). Airinae, excluding *Deschampsia* s.s., showed the successive early divergences of *Aira* and *Corynephorus* and included *Avenella*, represented here by the European *Deschampsia flexuosa* and the Madeiran endemic *D. maderensis* (Fig. 1). Plastid data suggest that *Avenella* is paraphyletic, the Mediterranean annual *Periballia* being derived from within it (Fig. 1). Despite the suggested affinities of *Holcus* and *Deschampsia* (Clayton and Renvoize, 1986), our study did not confirm a close relationship of *Holcus* to either *Deschampsia* s.s. or Airinae, it being weakly resolved as sister group to this last lineage only in nuclear analyses (Fig. 2). The morphologic distinctness of *Holcus*, which is characterized by its modified spikelets with a lower, awnless hermaphroditic floret, an upper, straight-to-hooked, awned male floret, and variable base chromosome number ($n = 4, 7$), supports its placement in the monogeneric subtribe Holcinae. The placements of *Deschampsia* s.s., Airinae, and *Holcus*, being part of a polytomy with Loliinae and relatives (*Deschampsia* and *Holcus*) or sister to them (Airinae) (Fig. 1), is not supported by the nuclear data, that placed them sister to core Aveneae (*Deschampsia* plus *Avenula*) or in polytomy with all of them and Poinae and its relatives (Airinae and *Holcus*) (Fig. 2).

The separation of *Helictotrichon* s.s. (see Aveninae) from *Avenula* (*Helictotrichon* subgenera *Pratavenastrum* (Vierh.) Holub) has been controversial because of their general similarity to Aveninae, although other morpho-anatomic characters distinguish them (Kerguélen, 1975; Tutin et al., 1980; Gervais, 1983). Our plastid analyses resolved *Avenula* s.s. as sister lineage to Loliinae (Fig. 1), and including *Ammochloa*, a small annual Mediterranean genus usually treated as Poeae or Seslerieae (Table 1) and, more rarely, as sister to Aveneae (MacFarlane, 1987). Nuclear data placed *Avenula* sister to *Deschampsia* s.s. (Fig. 2), agreeing with Grebenstein et al. (1998; 40% BS). This placement for *Avenula* separate from the Aveneae core lineages agrees with the earlier findings of Grebenstein et al. (1998) and Soreng and Davis (2000) and corroborates the polyphyly of *Helictotrichon* s.l. The plastid data placed *Ammochloa* as sister to Dactylidinae but with poor support (Fig. 1). The main morphologic features of *Ammochloa*, a condensed inflorescence, glabrous ovary, short hilum and hard endosperm, are not those of *Avenula* but are shared by the closest relatives of Loliinae (Parapholiinae, Cynosurinae, and Dactylidinae). However, the high mutation rate of the *trnT-F* region of *Ammochloa*, reflected by its long branch (Fig. 1), may have disturbed the reconstruction of the plastid phylogeny.

Festuca sect. *Aulaxyper* (*F. rubra* group) showed a strongly supported sister relationship to a lineage formed by *Dielsiochloa* and the festucoid *Hellerochloa*, two restricted Central and South American genera (Figs. 1 and 2). *Dielsiochloa*, a small endemic genus restricted to Bolivia and Peru, traditionally has been included in Aveneae (Table 1). Despite its long-linear hilum and hard endosperm, it has been considered to be related to *Trisetum* because its lemmas have straight dorsal awns (Clayton and Renvoize, 1986). Finally, *Antinoria*, a small Mediterranean genus with short hilum, glabrous ovary, and

characteristic of damp places, was considered as part of Airinae by some authors (Albers and Butzin, 1977). Our results placed it as a sister group to Loliinae, Parapholiinae, Cynosurinae, and Dactylidinae (Fig. 2).

Misplaced lineages: Seslerieae and Mibora—The strongest conflicts observed between plastid and nuclear topologies affected the placements of the representatives of Seslerieae and *Mibora*. *Sesleria*, *Oreochloa*, and *Echinaria*, three European and Mediterranean genera characterized by their strongly condensed inflorescences and traditionally classified in Seslerieae (Table 1), along with *Mibora*, formed a moderately supported group in both analyses (Figs. 1 and 2). Seslerieae and Mibora linked with core Aveneae or with Poeae in the nuclear and plastid topologies, respectively. This could indicate a hybrid origin of the representatives of this lineage.

Morphology does not confirm the unexpectedly strong relationship recovered between *Mibora* and *Oreochloa* using plastid data (Fig. 1). The western Mediterranean–Atlantic genus *Mibora*, characterized by its dwarf habit and single-flowered spikelets, traditionally has been placed in either Agrostidinae (sometimes in its own subtribe Miborinae Asch. & Graebn.) or Alopecurinae (Table 1). Soreng and Davis (2000) found *Mibora* resolved in Agrostidinae in their cladistic analysis of structural data, but plastid data alone placed it in Poeae; Soreng et al. (2003) tentatively placed it in Miliinae. The high mutation rate of this annual lineage, reflected by its long branches (Figs. 1 and 2), could have disturbed the parsimony and Bayesian reconstructions. Further analyses of larger samples of the Seslerieae group representatives are required to clarify their relationships.

Evolutionary history of Aveneae, Poeae, and Seslerieae—The presence of many groups, formerly placed in Aveneae, that our analyses place in the neighborhood of Loliinae or Poinae could be due to past hybridizations. Seslerieae, which have pooid plastid and avenoid nuclear genomes, may have resulted from past intertribal reticulation events that resulted in a new, morphologically distinct lineage. In fact, extensive past reticulation has been repeatedly invoked to explain the failure to reconcile topologies recovered from nuclear and plastid data in Pooideae (Davis and Soreng, 1993; Mason-Gamer and Kellogg, 1996) and to explain the presence of pooid taxa with an avenoid genome and vice versa (Soreng and Davis, 2000).

Although our nuclear ITS data do not strongly contradict our plastid data, some former Aveneae, such as *Deschampsia* s.s. and *Avenula* s.s., were placed sister to core Avenae by the nuclear data (Fig. 2), despite the more distant relationship provided by combined and plastid data (Fig. 1). This could suggest potential topologic disturbances caused by the putative paralogy of ITS ribotypes and homoplasy, a phenomenon that often blurs ITS phylogenetic reconstructions, especially in polyploid-rich groups (Álvarez and Wendel, 2003; Stace, 2005) such as some Aveneae. This scenario also could indicate that the morphologic traits of many former Aveneae lineages could be plesiomorphic or largely homoplasious. It also might reflect the consequences of lineage sorting if the ancestral Aveneae, Poeae, and Seslerieae diversified faster than the fixation of gene copies in these lineages. However, reticulation and lineage sorting scenarios are not easily differentiated a priori (Kellogg et al., 1996), and both could have operated together (Catalán et al., 2004). Further analysis of other nuclear single-copy genes and organellar genes might help to detect the origin of each group and the nature of potential horizontal gene transfer events, thus unraveling the evolutionary history of the supertribal complex.

Large, species-rich lineages, such as Koeleriinae, Agrostidinae, Loliinae, Poinae, etc., with a strong internal structure were generally distinguished from other small, less-diversified, satellite lineages, such as Airinae, *Alopecurus*, Anthoxanthinae, *Antinoria, Avenula*, *Briza*, *Deschampsia*, *Holcus*, *Milium*, *Phalaris*, *Phleum*, and *Scolochloa*. Most of them are usually sister groups to these large lineages groups in our topologies (Figs. 1 and 2). The relatively high frequency of annual radiations of species adapted to xeric environments in the large groups contrasts with the predominant mesophytic-to-helophytic perennial elements of the satellite groups. Soreng and Davis (2000) speculated on the potential ancestry of the helophytic *Amphibromus*, *Torreyochloa*, and *Scolochloa*, also first divergent elements in their topologies, thus indicating a temperate wetland origin for Aveneae and Poeae. Our results seem to support that hypothesis, but some of those satellite groups do not retain some of the characters considered ancestral of the complex, i.e., long-linear hilum, hairy ovary, multiflowered spikelets, multinerved glumes, and elaborate awns (cf. Baum, 1968). This reinforces the idea of a widely extended morphologic homoplasy within the complex.

Taxonomic recommendations—Systematically, the neat separation of the Aveneae core lineages (Aveninae, Agrostidinae, Koeleriinae, Anthoxanthinae, and allies) from Poeae and the remaining former Aveneae groups in the plastid topology could support tribal status for the groups that form that core. Certainly, acceptance of this tribal rank would be consistent with most traditional classificatory proposals in Pooideae (Table 1). However, many former Aveneae lineages mentioned should be excluded from it, and the reconstituted Aveneae would lack its distinctive morphologic features. An alternative treatment could be the division of the complex into three subtribes: (1) the Aveneae core groups, (2) Poinae and its closest Aveneae relatives, and (3) Loliinae and its closest Aveneae relatives. However, these groups have overall weak support, especially by nuclear data, and they also lack distinctive features. In accordance with the proposals of Soreng and Davis (2000) and other authors (Tzvelev, 1989, pro parte; GPWG, 2001; Soreng et al., 2003), we propose to accept an enlarged Poeae that would include the former Aveneae, Poeae, and Seslerieae lineages. This tribe can be split into different subtribes, such as Aveninae, Koeleriinae, Agrostidinae, Loliinae, Poinae, and others, as we probe its phylogenetic structure more deeply. This way we can avoid taxonomic conflicts between the phylogeny of these lineages and the maintenance of older ranks that lack the morphologic attributes that define them.

LITERATURE CITED

ALBERS, F., AND F. BUTZIN. 1977. Taxonomie und Nomenklatur der Subtriben Aristaveninae und Airinae (Gramineae–Aveneae). *Willdenowia* 8: 81–84.

ALEXEEV, E. B. 1985. Novye rody slakov. *Byulleten' Moskovskogo Obshchestva Ispytatelej Prirody. Otdel biologicheskii* 90: 102–109.

ÁLVAREZ, I., AND J. F. WENDEL. 2003. Ribosomal ITS sequences and plant phylogenetic inference. *Molecular Phylogenetics and Evolution* 29: 417–434.

ASCHERSON, P. F. A., AND K. O. P. P. GRAEBNER. 1898–1902. Synopsis der

Mitteleuropaischen Flora, vol. Glumiflorae 1. Graminae. Wilhelm Engelmann, Leipzig, Germany. 795 pp.

AVDULOV, N. P. 1931. Karyo-systematiche untersuchung der familie Gramineen. *Trudy po prikladnoi botanike, genetike i selektsii*. Supplement 44.

BALDWIN, B. G., M. J. SANDERSON, J. M. PORTER, M. F. WOJCIECHOWSKI, C. S. CAMPBELL, AND M. J. DONOGHUE. 1995. The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Annals of the Missouri Botanical Garden* 82: 247–277.

BAUM, B. R. 1968. Delimitation of the genus *Avena* (Gramineae). *Canadian Journal of Botany* 46: 121–132.

BLATTNER, F. R. 2004. Phylogenetic analysis of *Hordeum* (Poaeae) as inferred by nuclear rDNA ITS sequences. *Molecular Phylogenetics and Evolution* 33: 289–299.

BRYSTING, A. K., M. F. FAY, I. J. LEITCH, AND S. G. AIREN. 2004. One or more species in the arctic grass genus *Dupontia*?—a contribution to the Panarctic Flora project. *Taxon* 53: 365–382.

CATALÁN, P., E. A. KELLOGG, AND R. G. OLMSTEAD. 1997. Phylogeny of Poaceae subfamily Pooideae based on chloroplast *ndh*F gene sequences. *Molecular Phylogenetics and Evolution* 8: 150–166.

CATALÁN, P., P. TORRECILLA, J. A. LÓPEZ RODRÍGUEZ, AND R. OLMSTEAD. 2004. Phylogeny of the festucoid grasses of subtribe Loliinae and allies (Poeae, Pooideae) inferred from ITS and *trn*L-F sequences. *Molecular Phylogenetics and Evolution* 31: 517–541.

CHARMET, G., C. RAVEL, AND F. BALFOURIER. 1997. Phylogenetic analysis in the *Festuca-Lolium* complex using molecular markers and ITS rDNA. *Theoretical and Applied Genetics* 94: 1038–1046.

CHIAPELLA, J. 2007. A molecular phylogenetic study of *Deschampsia* (Poaceae: Aveneae) inferred from nuclear ITS and plastid *trn*L sequence data: support for the recognition of *Avenella* and *Vahlodea*. *Taxon* 56: 55–64.

CHOO, M. K., R. J. SORENG, AND J. I. DAVIS. 1994. Phylogenetic relationships among *Puccinellia* and allied genera of Poaceae as inferred from chloroplast DNA restriction site variation. *American Journal of Botany* 81: 119–126.

CLAYTON, W. D. 1975. Chorology of the genera of Gramineae. *Kew Bulletin* 30: 111–132.

CLAYTON, W. D. 1981. Evolution and distribution of grasses. *Annals of the Missouri Botanical Garden* 68: 5–14.

CLAYTON, W. D., AND S. A. RENVOIZE. 1986. Genera graminum, grasses of the world. Her Majesty's Stationery Office, London, UK. 389 pp.

DAVIS, J. I., AND R. J. SORENG. 1993. Phylogenetic structure in the grass family (Poaceae) as inferred from chloroplast DNA restriction site variation. *American Journal of Botany* 70: 1444–1454.

DEBRY, R. W., AND R. G. OLMSTEAD. 2000. A simulation study of reduced tree-search effort in bootstrap resampling analysis. *Systematic Biology* 49: 171–179.

EIG, A. 1929. Zwei neue Gramineengattungen von der *Ventenata*-Gattung gesondert. *Repertorium specierum novarum regni vegetabilis* 26: 65–79.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

FINOT, V. L., P. M. PETERSON, R. J. SORENG, AND F. O. ZULOAGA. 2004. A revision of *Trisetum*, *Peyritschia*, and *Sphenopholis* (Poaceae: Pooideae: Aveninae) in Mexico and Central America. *Annals of the Missouri Botanical Garden* 91: 1–30.

FINOT, V. L., P. M. PETERSON, R. J. SORENG, AND F. O. ZULOAGA. 2005a. A revision of *Trisetum* and *Graphephorum* (Poaceae: Pooideae: Aveninae) in North America North of México. *Sida* 21(3): 1419–1453.

FINOT, V. L., P. M. PETERSON, F. O. ZULOAGA, R. J. SORENG, AND O. MATTHEI. 2005b. A revision of *Trisetum* (Poaceae: Pooideae: Aveninae) in South America. *Annals of the Missouri Botanical Garden* 92: 533–568.

FREY, L. 1999. *Avenella*: a genus of the Aveneae (Poaceae) worthy of recognition. *Fragmenta floristica et geobotanica. Supplement*. 7: 27–32.

GAUT, B. S., L. P. TREDWAY, C. KUBIK, R. L. GAUT, AND W. MEYER. 2000. Phylogenetic relationships and genetic diversity among members of the *Festuca–Lolium* complex (Poaceae) based on ITS sequence data. *Plant Systematics and Evolution* 224: 33–53.

GERVAIS, C. 1983. Wide hybridization attempts in the tribe Aveneae Nees. *Botanica Helvetica. Bulletin de la Société Botanique Suisse*. 93: 195–212.

GILLESPIE, L. J., A. ARCHAMBAULT, AND R. J. SORENG. 2006. Phylogeny of *Poa* (Poaceae) based on *trn*T—*trn*F sequence data: major clades and basal relationships. *Aliso* 23: 420–434.

GPWG (GRASS PHYLOGENY WORKING GROUP). 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). *Annals of the Missouri Botanical Garden* 88: 373–457.

GREBENSTEIN, B., M. RÖSER, M. SAUER, AND V. HEMBELEN. 1998. Molecular phylogenetic relationships in Aveneae (Poaceae) species and other grasses as inferred from ITS1 and ITS2 rDNA sequences. *Plant Systematics and Evolution* 213: 233–250.

HOLUB, J. 1974. New names in Phanerogamae 3. *Folia geobotanica et phytotaxonomica* 9: 261–275.

HSIAO, C., N. J. CHATTERTON, AND K. H. ASAY. 1995. Molecular phylogeny of the Pooideae (Poaceae) based on nuclear rDNA (ITS) sequences. *Theoretical and Applied Genetics* 90: 389–398.

HUBBARD, C. E. 1937. *Trisetum*. *In* A. W. Hill [ed.], Flora of tropical Africa. L. Reeve, Kent, UK. 192 pp.

HUELSENBECK, J. P., AND F. RONQUIST. 2002. MrBayes. Bayesian inference of phylogeny. v. 3.0. *Bioinformatics* 17: 754–755.

HUNTER, A. M., D. A. ORLOVICH, K. M. LLOYD, W. G. LEE, AND D. J. MURPHY. 2004. The generic position of *Austrofestuca* littoralis and the reinstatement of *Hookerochloa* and *Festucella* (Poaceae) based on evidence from nuclear (ITS) and chloroplast (*trn*L-*trn*F) DNA sequences. *New Zealand Journal of Botany* 42: 253–262.

JONSELL, B. 1978. Nomenclatural and taxonomic notes on *Trisetum* Pers. and *Lophochloa* Reichenb. (Gramineae). *Botanical Journal of the Linnean Society* 76: 320–322.

KELLOGG, E. A., R. APPELS, AND R. J. MASON-GAMER. 1996. When gene trees tell different stories, incongruent gene trees for diploid genera of the Triticeae (Gramineae). *Systematic Botany* 21: 321–347.

KERGUÉLEN, M. 1975. Les Gramineae (Poaceae) de la flore francaise. Essai de mise au point taxonomique et nomenclatural. *Lejeunia* 75: 1–343.

KOCH, W. D. J. 1854. Synopsis florae germanicae et helveticae, vol. 2. Friederici Wilmans, Francofurti, Germany. 964 pp.

KOTSERUBA, V., D. GERNAND, A. MEISTER, AND A. HOUBEN. 2003. Uniparental loss of ribosomal DNA in the allotetraploid grass *Zingeria trichopoda* (2n=8). *Genome* 46: 156–163.

LEACHÉ, A. D., AND T. N. REEDER. 2002. Molecular systematics of the eastern fence lizard (*Sceloporus undulatus*): a comparison of parsimony likelihood, and Bayesian approaches. *Systematic Biology* 51: 44–68.

LEDEBOUR, K. F. VON. 1853. Flora rossica, vol. 4. Stuttgart, Germany. 741 pp.

MACFARLANE, T. D. 1987. Poaceae subfamily Pooideae. *In* R. Sorderstrom, K. W. Hilu, C. S. Campbell, and M. E. Barkworth [eds.], Grass systematics and evolution. Smithsonian Institution, Washington, D.C., USA. 473 pp.

MACFARLANE, T. D., AND L. WATSON. 1980. The circumscription of Poaceae subfamily Pooideae, with notes on some controversial genera. *Taxon* 29: 645–666.

MACFARLANE, T. D., AND L. WATSON. 1982. The classification of Poaceae subfamily Pooideae. *Taxon* 31: 178–203.

MAIRE, R., M. GUINOCHET, AND L. FAUREL. 1953. Flore de l'Afrique du Nord, vol. 2. P. Lechevalier, Paris, France. 374 pp.

MASON-GAMER, R. J., AND E. A. KELLOGG. 1996. Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Systematic Biology* 45: 524–545.

MASON-GAMER, R. J., N. L. ORME, AND C. M. ANDERSON. 2002. Phylogenetic analysis of North American *Elymus* and the monogenomic Triticeae (Poaceae) using three chloroplast DNA data sets. *Genome* 45: 991–1002.

MOSULISHVILI, M. 2000. Directions of evolution of subtribe Koeleriinae (Gramineae). *Bulletin of the Georgia Academy of Science* 161(3): 496–498.

NADOT, S., R. BAJON, AND B. LEJEUNE. 1994. The chloroplast gene *rps4* as a tool for the study of Poaceae phylogeny. *Plant Systematics and Evolution* 191: 27–38.

POSADA, D., AND K. A. CRANDALL. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

PRAT, H. 1960. Vers une classification naturelle des graminées. *Bulletin de la Société Botanique de France* 107: 32–79.

QUINTANAR, A., P. CATALÁN, AND S. CASTROVIEJO. 2006. Adscription of *Parafestuca albida* (Lowe) E.B. Alexeev to *Koeleria* Pers. *Taxon* 55: 664–670.

RAMBAUD, A. 1996. Sequence lignment editor (Se-Al), version 1.0 alpha 1. [Computer program] Oxford University, Oxford, UK.

REEDER, J. R. 1953. Affinities of the grass genus *Beckmannia* Host. *Bulletin of the Torrey Botanical Club* 80: 187–196.

REICHENBACH, H. G. L. 1830. Flora germanica excursoria, vol. 1. Leipzig, Germany. 434 pp.

RODIONOV, A. V., N. B. TYUPAL, E. C. KIM, E. M. MACHS, AND I. G. LOKUSTOV. 2005. Genome composition of the autotetraploid oat species *Avena macrostachya* determined by comparative analysis of the ITS1 and ITS2 sequences: on the oat karyotype evolution on early events of oats species divergence. *Russian Journal of Genetics* 41(1): 1–11.

ROMERO GARCÍA, A. T., G. BLANCA LÓPEZ, AND C. MORALES TORRES. 1988. Revisión del género *Agrostis* L. (Poaceae) en la Península Ibérica. *Ruizia* 7: 1–160.

ROMERO ZARCO, C. 1984. Revisión taxonómica del género *Avenula* (Dumort.) Dumort. (Gramineae) en la Península Ibérica e Islas Baleares. *Lagascalia* 13: 39–146.

ROMERO ZARCO, C. 1996. Contribución al conocimiento de las gramíneas del N de Marruecos. *Lagascalia* 18: 310–321.

RÖSER, M. 1989. Karyologische, systematische und chorologische Untersuchungen an der Gattung *Helictotrichon* Besser ex Schultes & Schultes im westlichen Mittelmeergebiet. *Dissertationes Botanicae* 145: 1–250.

RÖSER, M. 1997. Patterns of diversification in the Mediterranean oat grasses (Poaceae: Aveneae). *Lagascalia* 19: 101–120.

SCRIBNER, F. L. 1906. The genus *Sphenopholis*. *Rhodora* 8: 137–146.

SOLTIS, D. E., AND R. K. KUZOFF. 1995. Discordance between nuclear and chloroplast phylogenies in the *Heuchera* group (Saxifragaceae). *Evolution* 49: 727–742.

SORENG, R. J., AND J. I. DAVIS. 2000. Phylogenetic structure in Poaceae subfamily Pooideae as inferred from molecular and morphological characters: misclassification versus reticulation. *In* S. W. L. Jacobs and J. Everett [eds.], Grasses: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia. 416 pp.

SORENG, R. J., J. I. DAVIS, AND J. J. DOYLE. 1990. A phylogenetic analysis of chloroplast DNA restriction site variation in Poaceae subfam. Pooideae. *Plant Systematics and Evolution* 172: 83–97.

SORENG, R. J., P. M. PETERSON, G. DAVIDSE, E. J. JUDZIEWICZ, F. O. ZULOAGA, T. S. FILGUEIRAS, AND O. MORRONE. 2003. Catalogue of New World grasses (Poaceae). IV. Subfamily Pooideae. *Contributions from the United States National Herbarium* 48: 1–725.

STACE, C. A. 2005. Plant taxonomy and biosystematics—does DNA provide all the answers? *Taxon* 54: 999–1007.

STEBBINS, G. L. 1956. Cytogenetics and evolution of the grass family. *American Journal of Botany* 43: 890–905.

STEBBINS, G. L., AND B. CRAMPTON. 1961. A suggested revision of the grass genera of temperate North America. *Recent Advances in Botany* 1: 133–145.

SUBBOTIN, S. A., E. L. KRALL, I. T. RILEY, V. N. CHIZHOV, A. STAELENS, M. DE LOOSE, AND M. MOENS. 2004. Evolution of the gall-forming plant parasitic nematodes (Tylenchida: Anguinidae) and their relationships with hosts as inferred from internal transcribed spacer sequences of nuclear ribosomal DNA. *Molecular Phylogenetics and Evolution* 30: 226–235.

SWOFFORD, D. L. 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0 beta 10. [Computer program]. Sinauer, Sunderland, Massachusetts, USA.

TABERLET, P., L. GIELLY, G. PATOU, AND J. BOUVET. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.

TEMPLETON, A. R. 1983. Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and the apes. *Evolution* 37: 221–244.

THOMPSON, J. D., T. J. GIBSON, F. PLEWNIAK, F. JEANMOUGIN, AND D. G. HIGGINS. 1997. The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24: 4876–4882.

TORRECILLA, P., AND P. CATALÁN. 2002. Phylogeny of broad-leaved and fine-leaved *Festuca* lineages (Poaceae) based on nuclear ITS sequences. *Systematic Botany* 27: 241–251.

TORRECILLA, P., J. A. LÓPEZ RODRÍGUEZ, AND P. CATALÁN. 2004. Phylogenetic relationships of *Vulpia* and related genera (Poeae, Poaceae) based on analysis of ITS and *trn*L-F sequences. *Annals of the Missouri Botanical Garden* 91: 124–158.

TORRECILLA, P., J. A. LÓPEZ RODRÍGUEZ, D. STANCIK, AND P. CATALÁN. 2003. Systematics of *Festuca* sects. *Eskia* Willk., *Pseudatropis* Kriv., *Amphigenes* (Janka) Tzvel., *Pseudoscariosa* Kriv., and *Scariosae* Hack. based on analysis of morphological characters and DNA sequences. *Plant Systematics and Evolution* 239: 113–139.

TUTIN, T. G., V. H. HEYWOOD, N. A. BURGES, D. M. MOORE, D. H. VALENTINE, S. M. WALTERS, AND D. A. WEBB [EDS.], 1980. Flora Europaea, vol. 5, Poaceae. Cambridge University Press, Cambridge, UK. 452 pp.

TZVELEV, N. N. 1976. Zlaki SSSR. Nauka Publishers, Leningrad, Russia. [English translation: 1983. Grasses of the Soviet Union. Amerid Publishing, New Delhi, India. 1196 pp.]

TZVELEV, N. N. 1989. The system of grasses and their evolution. *Botanical Review* 55: 141–204.

WATSON, L., AND M. J. DALLWITZ. 1992. The grass genera of the world. CAB International Wallingford, Oxon, UK. 1081 pp.

APPENDIX. Voucher information and GenBank accession numbers for taxa used in this study. A dash indicates that the region was not sampled. Voucher specimens belong to the following collections: AQ = Alejandro Quintanar collection; ARAN = Herbario de la Sociedad de Ciencias Aranzadi; CA = Carlos Aedo collection; CN = Carmen Navarro collection; ES = Elvira Sauquillo collection; JACA = Herbario del Instituto Pirenaico de Ecología de Jaca; MA = Herbario del Real Jardín Botánico de Madrid; MERC = Herbario de la Universidad de Mérida (Venezuela); MP = Manuel Pimentel collection; MS = Miguel Sequeira collection; PC = Pilar Catalán collection; RS = Robert Soreng collection; SC = Santiago Castroviejo collection; UZ = Herbario de la Universidad de Zaragoza.

Taxon—GenBank accessions: ITS, *trnL-F*, *trnT-L*; *Voucher specimen* or data source.

Agrostis castellana Boiss. & Reut.—DQ539591, —, —; Spain: Guadalajara (1997), *MA 648799*. ***A. magellanica*** Lam.—AY705883, —, —; Gardner et al. (unpublished). ***A. stolonifera*** L.—DQ336815, DQ336835, DQ336860; Spain: Huesca: Ordesa (1996), *JACA 380196*. ***A. truncatula*** Parl. subsp. ***commista*** Castrov. & Charpin—DQ539592, —, —; Spain: A Coruña, Montes do Pindo (1994), *MA 581339*. ***Aira cupaniana*** Guss.—DQ631442, DQ631508; Spain: Jaén, La Carolina (1988), *JACA 348895*. ***Airopsis tenella*** (Cav.) Coss. & Durand—DQ539582, DQ631445, DQ631511; Portugal: Mogadouro (1997), *JACA 62597*. ***Alopecurus geniculatus*** L.—DQ539571, DQ631433, DQ631499; Spain: Guadalajara, El Cubillo de Uceda (1997), *MA 642779*. ***A. vaginatus*** (Willd.) Pall. ex Kunth—Z96920 & Z96921, —, —; Grebenstein et al. (1998); Caucasus, Ossethi. ***Ammochloa palaestina*** Boiss.—DQ539587, DQ631451, DQ631517; Spain:

Almería, Tabernas (1986), *MA 478222*. ***Ammophila arenaria*** (L.) Link—DQ539590, DQ631456, DQ631522; Spain: A Coruña, Carballo (2004), *MP s/n*. ***Anthochloa lepidula*** Nees & Meyen—DQ539566, DQ631430, DQ631496; Bolivia: Dpto. La Paz, Cumbre near La Paz (2002), *MA 721313*. ***Anthoxanthum amarum*** Brot.—DQ539584, DQ631448, DQ631514; Spain: Asturias, La Coba (1994), *MA 539163*. ***A. aristatum*** Boiss.—DQ539585, DQ631449, DQ631515; Spain: Pontevedra, Cabo Silleiro, *ES s/n*. ***Antinoria agrostidea*** (DC.) Parl.—DQ539562, —, —; Spain: Zamora, Tábara (1996), *MA 651156*. ***Apera interrupta*** (L.) P. Beauv.—DQ539570, —, —; Spain: Huesca (1988), *JACA 167088*. ***Arrhenatherum elatius*** (L.) P. Beauv. ex J. & C. Presl subsp. ***bulbosum*** (Willd.) Schübl. & Martens—DQ336821, DQ336841, DQ336866; Spain: Zaragoza (1999), *JACA 128099*. ***A. calderae*** A. Hansen—DQ539596, DQ631462, DQ631528; Spain: Canarias, Tenerife (2003), *SC 17370*. ***Avellinia michelii*** (Savi) Parl.—, DQ631465, DQ631531; Spain: Huesca, Monzón (1991), *JACA 304591*. ***Avena barbata*** Pott ex Link—AY093613, —, —; Moore and Field (2005). ***A. clauda*** Durieu—AY522432, —, —; Rodionov et al. (2005), Azerbaijan. ***A. eriantha*** Durieu—DQ336822, DQ336842, DQ336867; Spain: Madrid, Chinchón (2001); *UZ JARL 032001*. ***A. hirtula*** Lag.—AY522435, —, —; Rodionov et al. (2005), Israel. ***A. longiglumis*** Durieu—DQ539597, DQ631463, DQ631529; France: Nice (1986), *JACA 428986*. ***A. macrostachya*** Balansa ex Coss. & Durieu—AY522433, —, —; Rodionov et al. (2005), Algeria. ***A. pilosa*** Scop.—AY530162, —, —; Rodionov et al. (2005), Azerbaijan. ***A. sativa*** L.—AY520821, —, —; Rodionov et al. (2005), Germany. ***A. ventricosa*** Balansa ex Coss.—AY522437, —, —; Rodionov et al. (2005), Cyprus. ***Avenula albinervis*** (Boiss.) M. Laínz—AJ389123 & AJ389124, —, —; Hemleben et al. (unpublished). ***A. bromoides*** (Gouan) H. Scholz— —, DQ631459, DQ631525; Spain: Huesca, Valfarta (1995), *JACA 75295*. ***A. bromoides***—Z96844 & Z96845, —, —; Grebenstein et al. (1998); France, Maury. ***A. compressa*** (Heuff.) W. Sauer & H. Chmelitschek—Z96848 & Z96849, —, —; Grebenstein et al. (1998); Turkey, Vil. Bolu. ***A. sulcata*** (Gay ex Boissier) Dumort.—DQ539595, DQ631461, DQ631527; Spain: Ciudad Real, Fuencaliente (1996), *MA 597123*. ***A. pratensis*** (L.) Dumort.—Z96860 & Z96859, —, —; Grebenstein et al. (1998); Caucasus, Pikritis Khevsureti. ***A. pubescens*** (Huds.) Dumort.— —, DQ631460, DQ631526; Spain: Huesca, Cerler (1997), *JACA 177197*. ***A. pubescens***—Z96876 & Z96877, —, —; Grebenstein et al. (1998); Caucasus, Ossethi.

Beckmannia eruciformis (L.) Host—AJ389163, —, —; Hemleben et al. (unpublished). ***Brachypodium distachyon*** (L.) Beauv.—AF303399, AF478500, DQ336855; Slovenia: Ljubljana, Torrecilla & Catalán (2002). ***Briza media*** L.—DQ539583, DQ631446, DQ631512; Spain: Huesca: Panticosa (2000) *PC s/n*. ***B. minor*** L.—L36510, —, —; Hsiao et al. (1995). *Bromus tectorum* L.—AJ608154, —, —; Blattner (2004).

Calamagrostis arundinacea (L.) Roth— —, DQ631455, DQ631521; Spain: Navarra, Orbaitzeta (2001), *ARAN 64564*. ***C. epigejos*** (L.) Roth—AJ306449, —, —; Jakob & Blattner (unpublished). ***Chaetopogon fasciculatus*** (Link) Hayek—DQ539593, DQ631457, DQ631523; Spain: Cáceres, Torrejón el Rubio (1983), *MA 252874*. ***Catabrosa aquatica*** (L.) P. Beauv.—DQ539565, DQ631429, DQ631495; Spain: Huesca, Sallent, Portalet (2004), *UZ, PC s/n*. ***Cinna latifolia*** (Trevir. ex Göpp.) Griseb.—DQ539569, DQ631432, DQ631498; Finland: South Häme (1982), *MA 363675*. ***Colpodium versicolor*** (Steven) Schmalh.—AY497472, —, —; Russia: Teberda, Rodionov et al. (2005). ***Corynephorus canescens*** (L.) P. Beauv.—DQ539578, DQ631440, DQ631506; Spain: Soria, Miño de Medinaceli (2004), *AQ 1079*. ***Cynosurus echinatus*** L.—AF532937, AF533031, DQ631482; Spain: Soria, Monte Valonsadero, Catalán et al. (2004).

Dactylis glomerata L.—AF393013, AF533028, DQ631481; Spain: Zaragoza, Moncayo, Torrecilla & Catalán (2002). ***Deschampsia antartica*** E. Desv.—AF521900, —, —; Corach et al. (unpublished). ***D. cespitosa*** (L.) P. Beauv.—DQ539579, DQ631441, DQ631507; Andorra, Pont de Capigol (2002), *MA 700212*. ***D. chapmanii*** Petrie—AY752476, —, —; Gardner et al. (unpublished). ***D. flexuosa*** (L.) Trin.—DQ539577, DQ631439, DQ631505; Andorra, Puerto de Envalira (2002), *MA 689503*. ***D. maderensis*** (Hackel & Bornm.) Buschm.—DQ539616, DQ631480, DQ631547; Portugal: Madeira: ca. Pico Arieiro (2004), *MS 4507*. ***D. setacea*** (Huds.) Hack.—DQ539615, DQ631479, DQ631546; Spain: Lugo, Vilalba (2000), *MA 653850*. ***D. tenella*** Petrie—AY752475, —, —; Gardner et al. (unpublished). ***Deyeuxia lacustris*** Edgar & Connor—AY705887, —, —; Gardner et al. (unpublished). ***Dielsiochloa floribunda*** (Pilg.) Pilg.—DQ539563, DQ631428, DQ631494; Bolivia: Dpto. La Paz, Cumbre near La Paz (2002), *MA 721312*. ***Dissanthelium calycinum*** (J. Presl) Hitchc.—DQ539567, DQ631431, DQ631497; Bolivia: Dpto. La Paz, Cumbre near La Paz (2002), *MA 721311*.

Echinaria capitata (L.) Desf.— —, DQ631453, DQ631519; Spain: Murcia, Moratalla (1997), *MA 591692*.

Festuca arundinacea (P. Beauv.) Schreber—AF519976, AY098995, DQ367405; Spain: Lugo, Láncara, Catalán et al. (2004). ***F. frigida*** (Hack.) K. Richt.—AF478481, AF478521, DQ631485; Spain: Granada, Veleta, Catalán et al. (2004). ***F. borderei*** (Hack.) K. Richt.—AF303403, AF478510, DQ631484; Spain: Huesca, Vallibierna, Torrecilla & Catalán (2002). ***F. fontqueri*** St.-Yves—AF303404, AF533044, DQ631486; Morocco: Rif Mountains, Torrecilla & Catalán (2002). ***F. kingii*** (S. Watson) Cassidy—AF303410, AY099004, DQ631487; USA: Colorado, Boulder Co, Flat Irons, Catalán et al. (2004). ***F. ovina*** L.—AF532959, AF533063, DQ367406; Germany: Thüringen, Saale-Holzland-Kreis, Catalán et al. (2004). ***F. paniculata*** (L.) Schinz. & Thell. subsp. ***paniculata***—AF303407, AF533046, DQ336858; France: Mont Aigoual, Torrecilla & Catalán (2002). ***F. rivularis*** Boiss.—AF478475, AF478512, DQ631488; Spain: Huesca, Cotiella, Torrecilla & Catalán (2002). ***F. rubra*** L.—AY118088, AY118099, DQ336857; Switzerland: Valais, Desses des Ferret, Catalán et al. (2004). ***F. triflora*** Desf.—AF538362, AF533052, DQ631483; Spain: Granada, Grazalema, Catalán et al. (2004).

Gastridium ventricosum (Gouan) Schinz & Thell.—DQ336817, DQ336837, DQ336862; Spain: Baleares, Mallorca, Puigpunyent (1998), *MA 618134*. ***Gaudinia fragilis*** (L.) P. Beauv. (1)—DQ539600, DQ631467, DQ631533; Spain: Ourense, O Barco de Valdeorras (1989), *MA 517046*. ***G. fragilis*** (2)— —, DQ631478, DQ631545; Spain: Ciudad Real, Fuencaliente (1996), *MA 597178*. ***Graphephorum wolfii*** (Vasey) Vasey ex Coult.—DQ336823, DQ336843, DQ336868; USA: California, Sierra Nevada (2004), *RS 7416*. ***Gymnachne koelerioides*** (Trin.) Parodi—DQ539594, DQ631458, DQ631524; Chile (2001), *RS 7035*.

Helictotrichon convolutum (C. Presl) Henrard—Z96820 & Z96821, —, —; Grebenstein et al. (1998); Dalmatia. ***H. desertorum*** (Less.) Pilg.—AJ389095 & AJ389096, —, —; Hemleben et al. (unpublished). ***H. filifolium*** (Lag.) Henrard—DQ336819, DQ336839, DQ336864; Spain: Almería (1997), *MA 591453*. ***H. jahandiezii*** (Litard. ex Jahand. & Maire) Potztal—Z96840 & Z96841, —, —; Grebenstein et al. (1998); Morocco, Moyen Atlas. ***H. sedenense*** (Clar. ex Lam & DC.) Holub—DQ336820, DQ336840, DQ336865; Spain: Huesca (1997), *JACA 177297*. ***Hellerochloa fragilis*** (Luces) Rauschert—AF532960, AF533059, DQ631492; Venezuela: Mérida, Páramo de Piedras Blancas, *MERC, PC s/n*. ***Hierochloe australis*** (Schrad.) Roem. & Schult.— —, DQ631447, DQ631513; Finland: South Häme (1991), *MA 696177*. ***H. equiseta*** Zotov—AY705901, —, —; Gardner et al. (unpublished). ***H. fusca*** Zotov—AY705902, —, —; Gardner et al. (unpublished). ***H. novae-zelandiae*** Gand.—AY705900, —, —; Gardner et al. (unpublished). ***Holcus gayanus*** Boiss.—DQ539574, DQ631436, DQ631502; Spain: Asturias, Puente del Infierno (1998), *MA 655816*. ***H. lanatus*** L.—DQ539575, DQ631437, DQ631503; Italy: Abruzzo, Sorgente del Tirino (2002), *MA 699215*.

Koeleria albescens DC.—DQ336824, DQ336844, DQ336870; Spain: A Coruña (2003), *MA 706574*. ***K. crassipes*** Lange (1)—DQ539603, DQ631469, DQ631535; Spain: Madrid (2003), *MA 706575*. ***K. crassipes*** (2)—DQ539602, —, —; Spain: Madrid (2003), *MA 706580*. ***K. dasyphylla*** Willk.—DQ336825, DQ336845, DQ336871; Spain: Cádiz (1993), *MA 526298*. ***K. macrantha*** (Ledeb.) Schult.—DQ336826, DQ336846, DQ336872; Spain: Huesca (2001), *JACA 264664*. ***K. pyramidata*** (Lam.) P. Beauv.—DQ336827, DQ336847, DQ336873; Spain: Lleida (1999), *JACA 147297*. ***K. splendens*** C.

Presl—DQ336828, DQ336848, DQ336874; Italy (2000), *MA 645409*. ***K. vallesiana*** (Honck.) Gaudin subsp. ***vallesiana*** (1)—DQ336829, DQ336849, DQ336875; Spain: Madrid (2003), *MA 706578*. ***K. vallesiana*** subsp. ***vallesiana*** (2)—DQ539604, DQ631470, DQ631536; Spain: Palencia (1995), *MA 560050*. ***K. vallesiana*** subsp. ***castellana*** (Boiss. & Reut.) Domin—DQ539601, DQ631468, DQ631534; Spain: Madrid, Aranjuez (2004), *AQ 997*.

Lagurus ovatus L.—DQ539598, DQ631464, DQ631530; Spain: Almería, Cuevas del Almanzora (1998), *MA 613465*. ***Lamarckia aurea*** (L.) Moench—AF532935, AF533029, DQ631490; Spain: Zaragoza, Puente Almozara (2000), Catalán et al. (2004). ***Lolium perenne*** L.—AF303401, AF478504, DQ367404; England (cv.), Torrecilla & Catalán (2002).

Mibora minima (L.) Desv.—DQ539589, DQ631454, DQ631520; Spain: Madrid, Boadilla del Monte (2004), *AQ 977*. ***Milium effusum*** L.—DQ539573, DQ631435, DQ631501; Finland: Lapponia sompiensis, Sodankylä (1996), *JACA 199998*.

Oreochloa disticha (Wulfen) Link—DQ539588, DQ631452, DQ631518; Spain: Palencia, Cervera de Pisuerga (1997), *MA 590914*.

Parafestuca albida (Lowe) E.B. Alexeev—AF532930, AF533022, DQ336869; Portugal: Madeira, Pico do Arieiro (2001), *MA 721307*. ***Parapholis incurva*** (L.) C.E. Hubb.—AF532942, AF533036, DQ631491; Spain: Zaragoza, Vedado de Peñaflor, Catalán et al. (2004). ***Periballia involucrata*** (Cav.) Janka—DQ539576, DQ631438, DQ631504; Spain: Ciudad Real, Solana del Pino (1996), *MA 597226*. ***Phalaris canariensis*** L.—DQ539580, DQ631443, DQ631509; Spain: Huesca, Cuarte (cultivated), *AQ 1429*. ***P. coerulescens*** Desf.—DQ539581, DQ631444, DQ631510; Spain: Cáceres, Malpartida de Plasencia (2001), *MP s/n*. ***P. truncata*** Guss. ex Bertol.—L36522, —, —; Hsiao et al. (1995). ***Phleum phleoides*** (L.) H. Karst.—AF498396, —, —; Subbotin et al. (2004). ***P. pratense*** L. subsp. ***bertolonii*** (DC.) Bornm.—DQ539568, —, —; Spain: Ciudad Real, Fuencaliente (1996), *MA 597217*. ***Poa annua*** L.—AF521901, —, —; Corach et al. (unpublished). ***P. infirma*** Kunth—AF393012, AF488773, DQ367407; Spain: Zaragoza, La Jota, Torrecilla & Catalán (2002). ***Polypogon maritimus*** Willd.—DQ336818, DQ336838, DQ336863; Spain: Ciudad Real, Valverde (1999), *MA 648807*. ***Pseudarrhenatherum longifolium*** (Thore) Rouy—AJ389161 & AJ389162, —, —; Hemleben et al. (unpublished). ***Puccinellia distans*** (L.) Parl.—AF532934, AF533024, DQ336859; Spain: Navarra, Lazagurría, Catalán et al. (2004).

Rostraria cristata (L.) Tzvelev—DQ336833, DQ336853, DQ336879; Spain: Tarragona (1999), *JACA 630099*. ***R. hispida*** (Savi) Dogan—DQ539610, —, —; Spain: Sevilla (1977), *MA 278005*. ***R. litorea*** (All.) Holub—DQ539611, —, —; France: Corse (1981), *MA 392462*. ***R. obtusiflora*** (Boiss.) Holub—DQ539612, DQ631475, DQ631541; Israel (1989), *MA 498402*. ***R. pumila*** (Desf.) Tzvelev—DQ336834, DQ336854, DQ336880; Spain: Almería (1998), *MA 613459*. ***R. salzmannii*** (Boiss. & Reut.) Holub—DQ539613, DQ631476, DQ631542; Tunisia (1999), *MA 693894*.

Secale cereale L.—AF303400, AF478501, DQ336856; USA: Torrecilla & Catalán (2002). ***Sesleria argentea*** (Savi) Savi—AF532931, AF533030, DQ631544; Spain: Navarra, Araxes, Catalán et al. (2004). ***S. coerulea*** (L.) Scop.—DQ539586, DQ631450, DQ6315106; Spain: Huesca, Puértolas (2001), *JACA 266634*. ***Sclerochloa. dura*** (L.) P. Beauv.—AF532933, AF533023, —; Spain: Segovia, Sepúlveda, Catalán et al. (2004). ***Scolochloa festucacea*** (Willd.) Link—DQ539564, —, —; Finland: Joutsa (1992), *MA 692842*. ***Sphenopholis intermedia*** (Rydb.) Rydb.—DQ539599, DQ631466, DQ631532; USA: Kentucky, Dobertson Co. (1995), *MA 721314*. ***Sphenopus divaricatus*** (Gouan) Reichenb.—AF532939, AF533033, DQ631493; Spain: Zaragoza, Vedado de Peñaflor, Catalán et al. (2004).

Triplachne nitens (Guss.) Link—DQ336816, DQ336836, DQ336861; Spain: Almería, Playa de Carboneras (1982), *MA 292711*. ***Trisetum baregense*** Laffitte & Miégeville—DQ539605, DQ631471, DQ631537; Spain: Huesca (1998), *JACA 120998*. ***T. drucei*** Edgar—AY752485, —, —; Gardner et al. (unpublished). ***T. dufourei*** Boiss.—DQ539606, —, —; Spain: Cádiz (1993), *JACA 284999*. ***T. flavescens*** (L.) P. Beauv.—DQ336830, DQ336850, DQ336877; Bulgaria (2004), *CA 10141*. ***T. glaciale*** Boiss.—DQ539614, DQ631477, DQ631543; Spain: Granada, Pico Veleta (1986), *MA 398253*. ***T. gracile*** (Moris) Boiss.—DQ539607, DQ631472, DQ631538; Italy: Sardegna (2003), *SC 17158*. ***T. hispidum*** Lange—DQ336831, DQ336851, DQ336376; Spain: León, Valverde de la Sierra (1994), *MA 542627*. ***T. loeflingianum*** (L.) P. Beauv.—DQ539608, DQ631473, DQ631539; Spain: Huesca (1996), *JACA 307296*. ***T. ovatum*** Pers.—DQ336832, DQ336852, DQ336878; Spain: Toledo, Hinojosa de San Vicente (1995), *MA 556705*. ***T. paniceum*** (Lam.) Porsild—DQ539609, DQ631474, DQ631540; Spain: Jaén, Andújar (2003), *MA 652453*. ***T. spicatum*** (L.) K. Richt.—AY752486,—,—; Gardner et al. (unpublished). ***T. tenellum*** (Petrie) A.W. Hill—AY752487, —, —; Gardner et al. (unpublished). ***T. turcicum*** Chrtek—Z96902 & Z96903, —, —; Grebenstein et al. (1998); Caucasus, Dzhavachethi. ***T. youngii*** Hook. f.—AY752488, —, —; Gardner et al. (unpublished).

Ventenata dubia (Leers) Cosson—DQ539572, DQ631434, DQ631500; Bulgaria (2004), *CN 5025*. ***Vulpia myuros*** (L.) C.C. Gmel.—AY118092, AY118103, DQ631489; USA: Washington, Seattle, Lake Forest Park, Catalán et al. (2004).

Wangenheimia lima (L.) Trin.—AF478498, AF478536, —; Spain: Zaragoza, Vedado de Peñaflor, Catalán et al. (2004).

Zingeria trichopoda (Boiss.) P. A. Smirn.—AJ428835, —, —; Kotseruba et al. (2003).